Behav Ecol Sociobiol (2005) 59: 250–257
DOI 10.1007/s00265-005-0031-x

ORIGINAL ARTICLE

Anne Gro Vea Salvanes · Victoria A. Braithwaite

Exposure to variable spatial information in the early rearing environment generates asymmetries in social interactions in cod (*Gadus morhua*)

Received: 9 December 2004 / Revised: 9 May 2005 / Accepted: 6 June 2005 / Published online: 10 August 2005

Abstract Many re-introduction programs used for conservation of populations and species threatened with extinction advocate the use of enriched rearing environments to train animals how to behave appropriately in the wild. Curiously, most of the current fish re-stocking programs have paid little attention to lessons previously learned in bird and mammal re-introductions. Many rehabilitation programs that use releases of hatchery fish observe higher mortality in released fish compared to wild, with most mortality arising shortly after release. One explanation for this mortality is based purely on selection processes; many hatchery fish normally selected out of the population thrive in the predator free, food-rich hatcheries. Alternatively, mortalities may be high because hatchery nursery environments fail to shape fish behaviour appropriately. Here, we empirically address the effect of enrichment in the early rearing environment in coastal cod (*Gadus morhua*). We find asymmetries in aggressive behaviour when fish reared in plain or enriched environments are allowed to interact. Furthermore, cod reared in standard, impoverished, hatchery environments spend less time in shelter, are more active, and show weaker anti-predator responses than fish reared with access to heterogeneous spatial cues. These results suggest that the constant, plain environments of fish farms may generate behavioural deficits that could reasonably be expected to be associated with lower survival in fish released into the wild.

Key words Cod · Nursery habitat · Spatial environment · Asymmetry in aggression · Anti-predator response

Communicated by J. Krause

A. G. V. Salvanes (✉)
Department of Biology, University of Bergen,
P.O. Box 7800, N-5020 Bergen, Norway
e-mail: Anne.Salvanes@bio.uib.no
Tel.: +47-55584487
Fax: +47-55584450

V. A. Braithwaite
Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh,
EH9 3JT, UK

Introduction

There is growing evidence that what an animal experiences in its early life can have considerable effects on its behaviour as an adult. For example, the conditions experienced by juvenile homing pigeons influence the types of cue these birds use to encode spatial information. Birds reared in environments that have plenty of free flowing air typically learn a map based on olfactory information, others provided with the opportunity to view rich visual landscapes show a preference for maps based on visual cues (Wiltschko et al. 1987; Braithwaite and Guilford 1995). Similarly, there are sensitive phases during which the future phenotypic preferences for a sexual partner are shaped. Here, the animal forms preferences that are similar to, but slightly different from, the parental phenotype (e.g. ten Cate and Vos 1999).

The consequences of early life experience have more recently caught the attention of bird and mammal conservation biologists that have re-introduced captive-reared individuals (e.g. Nicoll et al. 2003; Britt et al. 2004). Such work has illustrated how increasing environmental complexity in the captive environment, sometimes referred to as environmental enrichment, can increase both behavioural and neuronal plasticity, improve cognitive performance, and that together these ultimately improve the survival chances of the re-introduced species (Hunter et al. 2002; Kempermann et al. 2002; Bredy et al. 2003; Rabin 2003).

In contrast, the related field of re-stocking in fish, that attempts to counter the effects of over-fishing and environmental degradation, has typically relied on releasing large numbers of juveniles that have been reared in featureless hatchery environments. Despite the widespread use of this practice, there is considerable evidence that it does not work because of the high mortality experienced by the released individuals (Godin 1978; Nordeide et al. 1994; Phillipart 1995; Olla et al. 1994; 1998; Hilborn 1998; Brown and Laland 2001).

There are two main explanations underlying the mortality of released fish. First, owing to the relaxed selection processes occurring in the hatchery environment (for example, the safe, food rich environment allows more fish to survive than would do naturally, Weber and Fausch 2003) a proportion of the hatchery fish will be unsuited to life in the wild, and these fish are quickly removed from the population after release. Alternatively, fish reared in hatcheries have only experienced impoverished environments, and they may be unable to develop appropriate behavioural repertoires to enable them to survive in the variable and complex natural environment. To distinguish between these two explanations is important because they have very different implications for the policies directed towards re-stocking. Whether or not to concentrate on imposing stricter selection in the hatchery, and/or to improve hatchery environments to increase the quality of fish produced for release in terms of improving their behavioural flexibility.

However, there is also a third variable that should be considered in relation to re-introduction work; the genetic background of the population to be released. In natural populations it is known that behaviour like other life history traits varies as a function of both genotype and the environment (Immelmann 1975; Carrol and Cornelli 1999; Salvanes et al. 2004). Populations adapt to local selection pressures, and phenotypic traits can be expressed differently in different areas (e.g. Odling-Smee and Braithwaite 2003). Thus re-introduction work should also take into account the genetic background of the individuals, for the geographical area in which the animals are to be released (Machordom et al. 1999; Svåsand et al. 2000; Aprahamian et al. 2003).

A related area that has received considerable attention is the aggressive behaviour of hatchery fish; hatchery fish can be more aggressive than wild fish, and there are concerns that they out-compete wild fish when they are released (Berejikian et al. 1996; Einum and Fleming 1997; Fleming and Einum 1997; Metcalfe et al. 2003). A number of studies have investigated what might underlie the aggressive behaviour of hatchery reared fish. On the whole, however, these studies have not separated genetic background, environment, density, life stage and other contributing effects (see review in Weber and Fausch 2003). Some work has looked at genetic and environmental effects in pair-wise contests between fish from different backgrounds (Swain et al. 1990; Berejikian et al. 1996, 2000, 2001; Einum and Fleming 1997; Rhodes and Quinn 1998; Metcalfe et al. 2003). These studies have shown that domesticated strains can dominate, however experience with a complex environment can also make individuals more likely to win aggressive interactions.

Overall, there seems to be little consensus about the effects of enrichment on aggression and territoriality. In rainbow trout, territory size is smaller in fish from enriched environments (Imre et al. 2002), and in zebra fish, increased habitat complexity reduces aggression and the ability to monopolize resources (Basquill and Grant 1998). Moreover, in brown trout, growth rate in aggressive fish is lower in more complex habitats (Höjesjö et al. 2004), and swimming activity and feeding rate are lower in enriched compared to non-enriched environments (Sundbaum and Nasund 1998). Furthermore, Pacific salmon (steelhead) fry reared in enriched environments showed higher frequencies of threat displays, and were socially dominant over fry reared in conventional tanks (Berejikian et al. 2000, 2001). Finally, truly wild Atlantic salmon are found to dominate wild-origin or domesticated individuals reared in conventional hatcheries (Metcalfe et al. 2003). The effect of habitat complexity could thus depend on species and the context; whether contestants that meet come from similar or different nursery environments.

One way to disentangle environmental influences from genetic background is to use offspring from wild fish reared in captivity, and to divide larvae from one spawning stock equally between different types of controlled rearing environment. In this way, the effects of genetic differences are minimized, and exposure to different rearing environment will be controlled. Later examination of behaviour when individuals reared in different environments interact in "common-garden" experiments then identifies the environmental influence on behaviour. "Common-garden" experiments have successfully been used to identify genetic differences in growth between fish populations. For example, offspring from wild parents from different geographical areas reared in common environments show different growth rates (Conover and Schultz 1995; Foster and Endler 1999) and different feeding behaviours (Salvanes et al. 2004).

Here, we use these types of method to disentangle the effects of rearing environment from genotype for coastal cod, a species which has been over-fished for a long time, and that has been used in re-stocking attempts (Svåsand et al. 2000). Effects of enrichment of hatchery habitats on the behaviour of cod have also been studied by Braithwaite and Salvanes (2005). Here, the nursery environment was manipulated with respect to spatial cues and food distribution. This demonstrated that hatchery fish need to experience both variability in how and when food is available, and spatial variability to promote flexible behaviour. The work reported here, focuses specifically on the influence of the underwater spatial environment alone during the nursery period and its effects on later social interactions. This is done by disentangling the effect of spatial cues in the rearing environment, whilst controlling for genotypic effects, by rearing fish from the same spawning stock in two types of nursery habitat that differed in one factor; spatial cues. Fish grew up in either enriched or conventional hatchery tanks for 28 weeks and were tested afterwards in interactions in common experimental tanks ("common-garden"). They were tested for i) differences in response to aggressive interactions, and whether these changed over time; ii) potential bias in attacks; iii) response to simulated predator attacks.

Methods

Origin of the fish

To control for the genetic background, we used offspring from brood stock of wild-caught individuals, spawned on the same day. These were divided randomly between two types of rearing environments that differed only with respect to spatial cues. We used wild parents to minimize any domestication effects, so that the natural genetic variation of the fish used did not deviate greatly from wild cod. There will, nevertheless, always be individual variation in a group of fish, even among full-siblings, so to control for this we used individuals as fixed effects in the statistical analyses. In this way, we were able to separate each individual's constant genetic characteristic from the effect of nursery background (see Statistical Analysis below).

Larvae were initially housed for 8 weeks in 7,000 l tanks before a sub sample of 200 fish were divided equally between two types of rearing tanks (95×95×60 cm) and maintained on a diet of fish pellets for 28 weeks. Tanks were supplied with aerated; flowing seawater (c.10±1 °C) at a depth of 40cm, and the room was maintained on a 12:12 L:D photoperiod with daylight fluorescent tubes positioned 1.5 above the center of each rearing tank.

For both rearing environments we created food variability by varying the position of the feeder and the time at which fish were fed. Food could be presented in four possible 2-h intervals across the day (between 08:00–16:00 h). A pseudorandom feeding schedule that created large variation in food encounter was used. Although this could not be regarded as strictly random from a statistical point of view, it introduced the impression of being "variable" for the fish that could not have any a priori expectation of when and where they got food. Fish could receive food in one meal in the first 2 h, or this could be spread across two, three or four feeding intervals. All fish had access to the same amount of food per day.

Fish were raised in two types of nursery environment; one with spatial cues to create a heterogeneous environment (HET-fish), and one recreating the regular, homogeneous hatchery environment (HOM-fish). Pebbles and rocks (cobble) and a weighted, plastic model of kelp provided the spatial environment, and the position of these was randomly changed once a week. To control for handling effects, HOM-fish were also disturbed for the same length of time. The tanks were situated side-by side in a climate-controlled room and experienced the same levels of disturbance. Disturbance occurred while flushing tanks for debris every third day, while loading feed on the feeders, and when cleaning tanks. Tanks were cleaned every 8-weeks and this involved removing the fish using a black hand net (25×30 cm). We ensured that fish from both backgrounds had similar experiences of being captured by this net.

Owing to space constraints, we were limited to using one rearing tank per treatment (HET, HOM), thus we cannot rule out tank effects. We have therefore assumed that any non-specific effect of tank is less likely to explain the differences observed than the effects of the treatments themselves. We believe that this assumption is justified because the original 200 larvae were randomly distributed between the treatments to ensure that fish of differing competitive ability and/or learning potential would be equally represented in each tank. In addition, considerable care was taken to ensure that the only factors that differed between rearing tanks were the treatments themselves (e.g. both tanks were situated side-by-side to minimize differences in environmental disturbance; the tanks received identical lighting, temperature, noise and vibration). Furthermore, we have previously found effects of enrichment in two independent experiments using the same types of tank and materials as those used here (Braithwaite and Salvanes, in press).

The experiment

36 individual HET-fish (weight 44.3±1.2 g) and 36 HOM-fish (weight 52.6±1.7 g) were anaesthetized using a solution of Metacaine (MS222) and colour tagged externally. After recovery, the cod were randomly divided among 12 test tanks (95×95×60 cm), with three individuals from each background in each tank, and all individuals with different coloured tags. Release of fish to their respective test tanks took approximately 5 min from the first to the last fish. The fish were then acclimated overnight before the first observations were made. Observations of behaviours were performed on experimental days 1–4, and 7 and 8. Observers were blind to fish nursery background. The observation tanks were plain when observing aggressive interactions, but were supplied with plastic kelp about 3 h later when examining stress responses. To avoid bias in the observations, the order in which the fish in the tanks were observed was rotated randomly between days.

Observation of aggressive interactions

The number of initiated aggressive interactions between two individuals were noted and then pooled into one 'attack' variable; i) initiator shows a curved body display with pelvic fins erect on each side; ii) move towards another fish's body part; iii) move snout into the body of another fish and iv) nip another fish's body. A second variable, 'flee' consisted of responses shown if a fish moved backwards to escape an attack, or if it swam toward the side and escaped.

All 12 experimental tanks were observed for 20 min each day, and numbers of aggressive interactions were noted for each experimental tank. On days 1–4, the number of interactions an individual was involved in and whether it fled or not were noted. On experimental days 7 and 8 the observations were refined, noting for each event "who did what to whom" and who fled. This information was used to determine whether attacks were made towards fish from the same or different nursery backgrounds. These observations were made without kelp or cobble present in the test tanks.

Observation of stress response

Approximately 3 h after observing the aggressive interactions, plastic kelp was placed in the rear left corner of each tank. The swimming activity of each individual was recorded five times separated by 2-min intervals (for example, was a cod motionless on the bottom, swimming on the bottom, swimming in the water column, or using the water inlet tube or the kelp for shelter). These data were used to form the background pre-stressor measures.

A 30 sec chase with a net (6×6 cm green hand-net) was used to create a mildly stressful experience. This was used to try and mimic a chase by a predator. Recovery from the stressor was monitored over 10 min by repeating the type of observations as described above for individual fish. The same type of treatment was conducted on experimental days 1–4, and 7 and 8.

Data analysis

Aggressive interactions

Response to aggressors was measured as the number of flees from received attacks (depending on nursery background), number of initiated attacks, and experimental day. These were analyzed using Components of Variance Analysis (CVA) which takes into account repeated measures (Winer et al. 1991; Diggle et al. 1994). We also used CVA to examine the proportion of attacks made to fish from the same or different nursery backgrounds during each of the 20-min observations on experimental days 7 and 8. The response variable was standardized to account for the fact that for each individual in a tank, there were three individuals belonging to the alternative nursery background, and two belonging to the same nursery rearing treatment. Proportional data were arcsine transformed. We ran analyses both including and excluding weight as a covariate, but as it was insignificant ($p>0.6$), we omitted ‘weight’ from the models.

Stress response

The probabilities of staying in shelter or being active in general (background) and while recovering from a simulated predator attack (mild stressor) were examined by defining a binary response variable as being 1 if two or more individuals hid in shelter or were active, and as 0 if not. We used logistic regression separately on shelter use and activity (because *GLM’s* cannot analyze binary repeated measures data) with each individual specified with a fixed effect (Hamilton 1992). We ran analyses including and excluding weight as a covariate, but as it was insignificant ($p>0.9$), we omitted ‘weight’ from the models.

We tested for differences between fish with different background in size (weight) and Fulton’s condition factor using paired *t*-test assuming equal variance.

Results

Comparisons of aggressive behaviour

Individuals from homogeneous nursery tanks (HOM-fish) fled more often than those from heterogeneous tanks (HET-fish) when they received aggressive attacks from other fish (CVA; $F_{1,316} = 5.6$, $p=0.021$, Fig. 1a). The fleeing was not dependent on the overall level of aggression ($F_{18,316} = 1.31$, $p=0.214$). Although there was no overall difference in absolute levels of aggression ($F_{1,316}=1.14$, $p=0.242$), there was a difference in the type of fish that the cod directed their attacks towards (Fig. 1b). HET-fish initiated significantly more attacks towards fish from the HOM-nursery background (CVA, $F_{1,28}=5.10$, $p=0.028$). This did not depend on absolute level of aggression, ($F_{15,28}=0.79$, $p=0.68$), or on day ($F_{1,28}=0.01$, $p=0.92$). The bias in HET-fish attacking HOM-fish (64.2% of initiated attacks) occurred despite HOM-fish being ca. 10% larger than HET-fish (paired *t*-test, $t=3.46$, $p<0.001$). HOM-fish were larger (49±1 g) than HET-fish (42±1 g), but there were no overall differences in condition factor ($t=0.36$; $p=0.72$). Although HOM-fish were larger than HET-fish, size did not contribute significantly to the model when weight was specified as a covariate in the CVA ($p>0.69$).

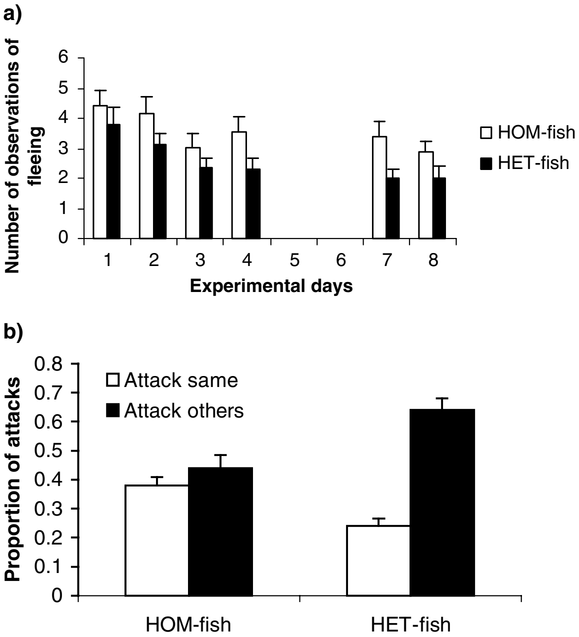

Fig. 1 (**a**) Change over experimental days for cod from heterogeneous (HET-fish) and homogeneous (HOM-fish) nursery backgrounds in the number of times (±SE) an individual flees if it is attacked by another fish. (**b**) Proportion of attacks (±SE) initiated towards cod of the same or other nursery background on experimental days 7 and 8. The nursery backgrounds were either heterogeneous (cobble and kelp) or homogeneous (plain tank). Interactions were recorded in “common-garden” experiments using plain tank

HOM-fish initiated more attacks towards fish from the same nursery background than HET-fish did ($F_{1,28}=4.61$, $p=0.036$), and neither the absolute level of aggression ($F_{15,28}=0.75$, $p=0.72$), nor the day ($F_{1,28}=0.02$, $p=0.89$), or size ($F_{1,28}=0.02$, $p=0.61$) were significant.

Responses to a mild stressor

Overall, cod from heterogeneous nursery backgrounds had lower basic activity (logistic regression, $Z=-4.00$, $p<0.001$, Fig. 2a) and used shelter for longer periods

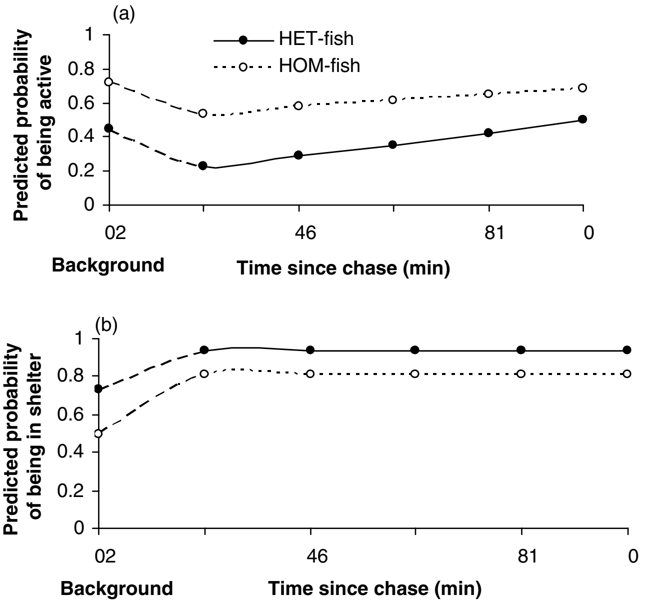

Fig. 2 The probability that (**a**) two or more fish are active and (**b**) two or more fish use shelter before (background) and during the first 10 min after applying a simulated predator attack on cod from heterogeneous and homogeneous nursery tanks when they were tested in "common-garden" experiments. Plastic kelp was placed as a potential shelter in a corner of each tank. Equations of the logistic regressions are as follows: probability of being in shelter (background) $= 1/(1+e^{-(0.989B)})$; probability of being in shelter after a mild stressor $= 1/(1+e^{-(0.306B+1.455)})$; probability of being active (background) $= 1/(1+e^{-(-0.156B+0.94)})$; probability of being active after a mild stressor $= 1/(1+e^{-(-1.499B+0.078B+0.071TB)})$; where B=0 for HOM-fish and B=1 for HET-fish, and T refers to time since the simulated predator attack. Only significant parameters are included in the equations

($Z=2.71$, $p=0.007$, Fig. 2b) than fish from homogeneous nurseries. This effect did not change over the 8 days of the experiment ($p>0.10$) and size had no effect on activity ($p=0.93$), or on use of shelter ($p=0.33$).

Both HET- and HOM-fish responded similarly to being chased by the net, but HET-fish were less active after the chase (logistic regression, $Z=-4.00$, $p<0.001$, Fig. 2a). Both reduced activity immediately after the chase compared to background levels, but activity increased again during the first 10 min after the stressor had been applied ($Z=2.36$, $p=0.018$, Fig. 2a). HET-fish was faster in recovering compared to the HOM-fish (Fig. 2a), but the estimated parameter for the interaction between nursery background and time since simulated attack was not significant ($Z=1.66$, $p=0.097$). Size had no effect on activity after stress ($p=0.93$). Cod from both treatments used more shelter after the simulated predator attack (Fig. 2b), and again, HET-fish were observed to use the shelter more than HOM-fish ($Z=4.27$, $p<0.001$). Although both groups were seen to be recovering, neither group returned to the basic level of activity within the 10-min observation period (Fig. 2a), and size had no effect ($p=0.32$). There was a weak reduction in shelter use during the investigated time period after exposure, but the effect of time since simulated attack was not significant ($Z=-1.74$, $p=0.083$).

Discussion

This study reveals two key observations. First, the behaviour of wild-origin juvenile coastal cod exposed to spatial cues in the nursery environment over 28 weeks is different to that observed in cod from the same genetic background, but reared in a plain nursery environment. Differences were observed in aggressive behaviour, in the relative use of shelter, and whether fish were pelagic or more associated to spatial structures on the bottom, and was not influenced by size differences. Second, the response to a simulated predator attack is partly influenced by exposure to spatial cues in the environment and partly innate.

Our results are in line with those reported by Berejikian et al. (2000, 2001) who studied steelhead juveniles and Metcalfe et al. (2003) studying Atlantic salmon. Berejikian and co-authors showed that fry reared in an enriched hatchery environment achieved a higher social dominance rank than size-matched fry reared in conventional hatchery environments. Metcalfe and co-workers (2003) found that domesticated juvenile Atlantic salmon could dominate wild-origin fish if they had both been raised in a common hatchery environment, but that wild-origin fish dominated hatchery fish if they received a 2 day period to settle before the interactions (prior-residence effects), and furthermore, truly wild fish could dominate hatchery-reared fish regardless of whether they were from a wild line or a domesticated line. Effects of enrichment on aggression are also found in several freshwater species (Nijman and Heuts 2000). In contrast, Rhodes and Quinn (1998) found that hatchery reared, Coho salmon dominated size-matched wild salmon from the same genetic background, even when the wild fish were prior residents. Prior experience with enrichment therefore appears to influence dominance behaviour in marine, freshwater and anadromous fish, but whether enrichment promotes or reduces aggression depends on the species and whether individuals that compete have experienced the same or different environmental backgrounds. Here, our results show that cod after 28 weeks in a nursery containing spatial cues produce asymmetric aggression directed to cod that have had no experience with spatial cues. Previous work using cod reared with and without the same type of enrichment for shorter times, demonstrated in two independent studies that enrichment generates fish with more flexible behavioural capacities (Braithwaite and Salvanes 2005). For example, experience with spatial cues alone or in combination with variable feeding regime produced cod that were faster at reacting to novel prey and quicker at switching to feed on natural, wild prey. These fish were also more rapid at recovering from a stressful experience, and more flexible in space use.

An alternative explanation that could explain our results is that small fish may be more motivated to fight compared to larger fish because small fish have lower energy status (Johnsson et al. 1996). However, we believe that this explanation is unlikely because the observed asymmetries in agonistic attacks arose despite there being no differences in condition factor between the fish from the two backgrounds.

Other studies that have observed varying levels of aggression in different groups of fish suggest that differences in territory holding behaviour are responsible for such differences, but this is not always the case. For example, Deverill et al. (1999) and Metcalfe et al. (2003) found effects of prior residence, growth and dominance in brown trout and Atlantic salmon, whereas the study of O'Connor et al. (1999a) reported no effect of prior residency alone on dominance in juvenile Atlantic salmon, but they found that prior residents did dart higher in the water column to feed and therefore grew faster. Another study reported that environmental enrichment in combination with prior residency influences aggression in seven species of freshwater fish (Nijman and Heuts 2000). In each of these species, prior residents were more dominant if they had been reared and tested in enriched environments (containing sand, pebbles and opportunities to shelter) compared to fish reared and tested in plain, impoverished aquaria.

It has previously been shown that wild cod tend to hold territories (Tupper and Boutilier 1995a) and that territorial behaviour is associated with size and length of time since settlement. Larger cod that settle early grow faster and hold larger territories than smaller cod that settled later. However, prior residency and size benefit cannot explain our observations. We designed our trials such that all fish entered the test tank within 5 min, thus it was not possible for fish to gain any prior residence advantage, and size did not have a significant effect on aggression. The underlying mechanism that influences the smaller juvenile HET-cod to develop an asymmetric aggression towards the larger HOM-cod is, as yet, unknown. One could argue that familiarity among fish could confound the results. However, the length of time fish spent together during treatments and until behavioural screening was, identical for HET and HOM-fish. It thus seems unlikely that familiarity effects can explain why HET fish directed asymmetric aggression towards HOM-fish.

Wild cod prefer habitats with complex vegetation consisting of macro algae, particularly during the daytime (Borg et al. 1997). It has also been observed that their survivorship depends on the complexity of the sea floor in their nursery habitats (Tupper and Boutilier 1995b; Lindholm et al. 2001), and survivorship increases with spatial complexity. Along the Norwegian coast macro algae biotopes represent the natural nursery habitats providing juvenile cod with prey as well as providing shelter opportunities from predation. Furthermore, survival differences between resident wild and released hatchery cod in these environments are considerable, and the ratio of hatchery/wild density decreases rapidly after hatchery fish are released (Nordeide et al. 1994). In general, hatchery-reared fish often do not avoid predators as well as wild fish do and, consequently suffer higher mortality rates (reviews in Olla et al. 1998 and in Weber and Fausch 2003). When the cod in our experiment were provided with shelter and a simulated predator attack, we observed that HET-fish had a higher probability of hiding and swam less than HOM-fish. This suggests that HET-fish were more skilled in using shelter. The results show that HOM-fish got access to shelter, but they were less successful than HET-fish in using it, this may be caused by the asymmetric aggressive attacks from HET-fish, but it was unfortunately not possible to track this once the fish moved into the cover. Although large fish generally have lower predation risks than smaller fish, size had no significant effect on our results, and therefore does not explain why HOM-fish used shelter less often than HET-fish. Field studies also reveal that cod reared in hatcheries tend to be more active post-release than similar sized wild fish (Svåsand et al. 2000).

The higher activity in HOM-fish may reflect escape behaviour from the aggressive interactions by HET-fish, but it could also be due to an inferior ability to use the "new" shelter opportunities in a flexible way. Nøstvik and Pedersen (1999) demonstrated using recapture data that released hatchery cod, which had been reared without enrichment, tended to stay shallower and be more active than resident wild cod, particularly if they were older than 1.5 years. Svåsand et al. (2000) speculated whether the time spent in captivity influenced the behavioral patterns after release. Our data suggest that it is not the time spent in captivity *per se* that generates this result, but rather, a combination of prior experience of spatial complexity, and differences in the social interactions between cod reared with different backgrounds.

It is possible that being reared with spatial structures allows the HET-fish to experience aggressive interactions associated with territory defence behaviour, and that this experience provides the fish with the necessary behavioural skills to avoid escalation of potential costly contests more efficiently than the HOM-fish. For example, the HET-fish may learn to show submissive behaviour more quickly than the HOM-fish. Or, perhaps the HET-fish's experience with a complex spatial environment provides them with skills associated with defense of potential territories, and interactions relating to territory boundaries. It may also be that HOM-fish do not signal submission towards dominant individuals as well as HET-fish. For example in juvenile Atlantic salmon, subordinate individuals produce signals of submission by darkening their body colour and use this to avoid potential costly escalated contests (O'Connor et al. 1999b, 2000). Cod also change colouration as a fright response (Salvanes unpublished observations), but we did not attempt to take visual communication into account in this study.

Predator avoidance behaviour in fish is partly innate and partly depends on environmental characteristics with respect to predation risk (Seghers 1974; Immelmann 1975; Giles and Huntingford 1984; Breden et al. 1987; Magurran 1990; Berejikian et al. 2003), but it can arise through experience (Kelley and Magurren 2003). Similarly, our results indicate that anti-predator behaviour is a combination of innate and environmental components. Given high predation risk of wild juvenile cod in Norwegian waters (annual natural instantaneous mortality rate for juveniles > 0.6 per year; Salvanes and Baliño 1998), it was not unexpected that responses to predators by cod would have a heritable component.

In summary, our results show that experience with spatial structures can influence the development of behaviors that are likely to be associated with survival in the wild. They demonstrate that if the complex spatial structures are absent in the nurseries of juvenile cod, fish tend to continue with a pelagic life style for longer, even if they interact with fish from other nursery backgrounds. Together, these findings have relevance for fisheries managers that use re-stocking, as well as for management of escapees from aquaculture. However, our results are also relevant for the management of marine protected areas because they suggest an important role for the conservation of the complexity of juvenile nursery habitats.

Acknowledgements This work was funded by the University of Bergen, the Research Council of Norway and The Leverhulme Trust (F/00158/N. AGVS thanks Jim Mallet and the Galton Laboratory, University College of London for providing an excellent working environment while completing the work. We thank D. Aksnes, Nick Colegrave, J. Giske, J. Krause and T. Nilsen for comments on the manuscript, Arild Folkvord, Karin Pittman for discussions, Saga Fjord Sea Farm A/S for providing the fish, and M. Hordnes, F. Midtøy, and J. Skadal for technical assistance. All experiments were carried out with the approval of The Norwegian Veterinary Authorities for Experimental Research; site licence number 18

References

Aprahamian MV, Smith KM, McGinnity P, McKelvey S, Taylor J (2003) Restocking of salmonids – opportunities and limitations. Fish Res 62:211–227

Basquill SP, Grant JWA (1998) An increase in habitat complexity reduces aggression and monopolization of food by zebra fish (*Danio rerio*). Can J Zool-Revue 4:770–772

Berejikian BA, Mathews SB, Quinn TP (1996) Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behaviour in steelhead trout (*Oncorhynchus mykiss*) fry. Can J Fish Aquat Sci 53:204–214

Berejikian BA, Tezak EP, Flagg TA, LaRae AL, Kummerow E, Mahnken CVW (2000) Social dominance, growth and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. Can J Fish Aquat Sci 57:628–636

Berejikian BA Tezak EP, Riley SC, LaRae AL (2001) Competitive ability and social behaviour of juvenile steelhead reared in enriched and conventional hatchery tanks and a stream environment. J Fish Biol 59:1600–161

Berejikian BA, Tezak EP, LaRae AL (2003) Innate and enhanced predator recognition in hatchery-reared chinook salmon. Environ Biol Fish 67:241–251

Borg A, Pihl L, Wennhage H (1997) Habitat choice by juvenile cod (*Gadus morhua* L) on sandy and soft bottoms with different vegetation types. Helgolander Meeresun 51:197–212

Braithwaite VA, Guilford T (1995) A Loft With A View: Does exposure to natural landmarks during development encourage adult pigeons to use visual landmarks during homing? Anim Behav 49:252–254

Braithwaite VA, Salvanes AG, (2005) Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. Proc. Roy. Soc. Lond B DOI:10.1098/rspb.2005.3062

Breden F, Scott M, Michel E (1987) Genetic differentiation for anti-predator behaviour in the Trinidadian guppy, *Poecilia reticulata*. Anim Behav 35:618–620

Bredy TW, Humpartzoomian RA, Cain DP, Meaney MJ (2003) Partial reversal of the effect of maternal care on cognitive function through environmental enrichment. Neuroscience 118:571–576

Britt A, Welch C, Katz A, et al. (2004) The re-stocking of captive-bred ruffed lemurs (*Varecia variegata variegata*) into the Betampona Reserve, Madagascar: methodology and recommendations. Biodiver Conserv 13:635–657

Brown C, Laland K (2001) Social learning and life skills training for hatchery fish. J Fish Biol 59:471–493

Carrol SP, Corneli PS (1999) The evolution of behavioural norms of reaction as a problem in ecological genetics: theory, methods and data. In: Foster S Endler JA (eds) Geographic variation in behaviour: Perspectives on evolutionary mechanisms. Oxford University Press, Oxford, pp 52–61

Conover DO, Schultz ET (1995) Phenotypic similarity and the evolutionary significance of counter-gradient variation. Tr Ecol Evol 10:248–252

Deverill JI, Adams CE, Bean CW (1999) Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout. J Fish Biol 55:868–875

Diggle PD, Liang KY, Zegher SL (1994) The analysis of longitudinal data. Clarendon Press, Oxford

Einum S, Fleming IA (1997) Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. J Fish Biol 50:634–651

Fleming IA, Einum S (1997) Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES J Mar Sci 54:1051–1063

Foster S, Endler JA (1999) Geographic variation in behavior. Perspectives on evolutionary mechanisms. Oxford University Press, Oxford

Giles N, Huntingford FA (1984) Predation risk and inter-population variation in anti-predator behaviour in the three-spined stickleback, *Gasterosteus aculeatus* L. Anim Behav 32:264–275

Godin JGJ (1978) Behaviour of juvenile pink salmon (*Onchorhynchus gorbuscha* Walbaum) toward novel prey: influence of ontogeny and experience. Environ Biol Fish 3:261–266

Hamilton LC (1992) Regression with graphics. Duxbury press, Belmont, California

Hilborn R (1998) The economic performance of marine stock enhancement projects. Bull Mar Sci 62:661–674

Hunter SA, Bay MS, Martin ML, Hatfield JS (2002) Behavioural effects of environmental enrichment on harbour seals (*Phoca vitulina concolor*) and grey seals (*Halichoerus grypus*). Zoo Biol 21:375–387

Höjesjö J, Johnsson J, Bohlin T (2004) Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. Behav Ecol Sociobiol 56:286–289

Immelmann K (1975) Ecological significance of imprinting and early learning. Ann Rev Ecol Sys 6:15–37

Imre I, Grant JWA, Keeley ER (2002) The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). Can. J Fish Aquat Sci 59:303–309

Johnsson JI, Jonsson E, Bjørnsson BT (1996) Dominance, nutritional state, and growth hormone levels in rainbow trout (*Oncorhynchus mykiss*). Horm Behav 30:13–21

Kelley JL, Magurran AE (2003) Learned predator recognition and antipredator response in fishes. Fish Fish 4:216–226

Kempermann G, Gast D, Gage FH (2002) Neuroplasticity in old age: sustained five-fold induction of hippocampal neurogenesis by long term environmental enrichment. Ann Neurol 52:135–143

Lindholm JB, Auster PJ, Ruth M, Kaufman L (2001) Modeling the effects of Fishing and implications for the design of marine protected areas: juvenile fish responses to variation in sea floor habitat. Conserv Biol 15:424–437

Machordom A, Garcia-Marin JL, Sanz N, Almodovar A, Pla C (1999) Allozyme diversity in brown trout (*Salmo trutta*) from central spain: genetic consequences of restocking. Freshwater Biol 41:707–717

Magurran A (1990) The inheritance and development of minnow antipredator behavior. Anim Behav 39:834–842

Metcalfe NB, Valdimarsson SK, Morgan IJ (2003) The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. J Appl Ecol 40:535–544

Nicoll MAC, Jones CG, Norris K (2003) Declining survival rates in a reintroduced population of the Mauritius kestrel: evidence for non-linear density dependence and environmental stochasticity. J Anim Ecol 72:917–926

Nijman V, Heuts BA (2000) Effect of environmental enrichment upon resource holding power in fish in prior residence situations. Behav Proc 49: 77–83

Nordeide JT, Fosså JH, Salvanes AGV, Smedstad O (1994) Testing if year-Class strength of coastal cod (*Gadus morhua* L) can be determined at the juvenile stage. Aquacult Fish Manage 25(Suppl 1):101–116

Nøstvik F, Pedersen T (1999) Movement patterns and growth of wild cod (*Gadus morhua* L) and hatchery reared cod released as 1-group. In: Howell BR, Moksness E, Svåsand T (eds) Stock enhancement and sea ranching. Fishing News Books, Blackwell Science Ltd, Oxford. pp.315–333.

O'Connor K, Metcalfe NB, Taylor AC (1999a) The effect of prior residence on behaviour and growth rates in Juvenile Atlantic salmon (*Salmo salar*). Behav Ecol 11:13–18

O'Connor K, Metcalfe NB, Taylor AC (1999b) Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? Anim Behav 58:1269–1276

O'Connor K, Metcalfe NB, Taylor AC (2000) Familiarity influences body darkening in territorial disputes between juvenile salmon. Anim Behav 59:1095–1101

Odling-Smee L, Braithwaite VA (2003) The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. Anim Behav 65:701–707

Olla BL, Davis MW. Ryer CH (1994) Behavioural deficits in hatchery-reared fish: potential effects on survival following release. Aquacult Fish Manage 25(Suppl 1):19–34

Olla BL, Davis MW, Ryer CH (1998) Understanding how the hatchery environment represses or promotes the development of behavioural survival skills. Bull Mar Sci 62:531–550

Phillipart JC (1995) Is captive breeding an effective solution for the preservation of endemic species? Biol Conserv 72: 281–295

Rabin LA (2003) Maintaining behavioural diversity in captivity for conservation: natural behaviour management. Anim Welfare 12:85–94

Rhodes JS, Quinn TP (1998) Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. J Fish Biol 53:1220–1230

Salvanes AGV, Baliño B (1998) Productivity and fitness in a fjord cod population: an ecological and evolutionary approach. Fish Res 37:143–161

Salvanes AGV, Skjæraasen JE, Nilsen T (2004) Sub-populations of coastal cod with different behaviour and life history strategies. Mar Ecol Prog Ser 267:241–251

Seghers BH (1974) Schooling behaviour in the guppy (*Poecilia reticulata*): an evolutionary response to predation. Evolution 28:486–489

Sundbaum K, Naslund I (1998) Effect of woody debris on the growth and behaviour of brown trout in experimental stream channels. Can J Zool.-Revue 76:56–61

Svåsand T, Kristiansen TS, Pedersen T, Salvanes AGV, Engelsen R, Nævdal G, Nødtvedt M (2000) The biological and economical basis of cod stock enhancement. Fish Fish 1:173–205

Swain DP, Riddel BE, Murray CB (1990) Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus-kisutch*) – environmental versus genetic origin. Can J Fish Aquat Sci 48:1783–1791

ten Cate C, Vos D (1999) Sexual imprinting and evolutionary processes in birds. Adv Study Behav 28:1–31

Tupper M, Boutilier RG (1995a) Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Mar Ecol Prog Ser 118:295–300

Tupper M, Boutilier RG (1995b) Effects of habitat on settlement, growth, and post settlement survival of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 52:1834–1841

Weber ED, Fausch KD (2003) Interactions between hatchery and wild salmonids in streems: differences in biology and evidence for competition. Can J Fish Aquat Sci 60:1018–1036.

Wiltschko W, Wiltschko R, Grüter M, Kowalski U (1987) Pigeon homing: early experience determines what factors are used for navigation. Naturwissenschaften 74:196–198

Winer BJ, Brown DR, Michels KM (1991) Biostatistical analysis. 3rd edn. Prentice-Hall INC, New Jersey