The need to understand the behaviour of fish reared for mariculture or restocking

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Following severe stock collapses in many natural populations, efforts are now being invested in farming marine species, and in rehabilitating populations through controlled releases. While the development of cod farming is still relatively new, it may be wise to consider some of the problems other fish farming industries have encountered. For example, farmed fish generally have a different genotype from that of local wild populations, and these artificially selected fish are typically bigger and more aggressive than wild fish. These differences can be problematic if farmed fish escape and begin breeding with local wild populations. An alternative approach to farming is to rehabilitate local wild populations through restocking. To date, however, this approach has had mixed success. Fish behaviour develops during early life stages through a combination of innate characteristics and experience. Apparently, the capacity for behavioural flexibility later in life is affected by the early experiences of juvenile fish. Here, we review the literature concerning the role of population origin and juvenile experience on fish behaviour. We highlight our recent studies on Atlantic cod, which demonstrate that variability in the nursery habitat generates behaviourally flexible fish. We discuss these issues in the context of gadoid mariculture and restocking. We conclude that behavioural studies are an important part of applied research for developing an industry of fish farming in gadoids, as well as for research concerning restocking and conservation of marine resources.

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Introduction

Many marine fish species have experienced dramatic declines in spite of considerable efforts to manage their populations (Pauly *et al.*, 2002; Dulvy, 2003). Despite numerous restocking attempts, wild populations have shown few signs of recovery (Hutchings, 2000), and there are few data demonstrating that releases of hatchery-reared fish actually benefit wild stocks (Hilborn, 1992; Coronado and Hilborn, 1998; Salvanes, 2001). It seems that the majority of release programmes fail because released individuals suffer higher mortality compared with wild fish of the same age (Godin, 1978; Nordeide *et al.*, 1994; Phillipart, 1995; Olla *et al.*, 1994, 1998; Hilborn, 1998; Brown and Laland, 2001). Issues in addition to those mentioned above include criticism of the fish farming industry for perceived problems associated with the domestication process

selecting for aggressive fish and the fear that escapees may breed with wild fish, potentially weakening the genetic structure of wild populations (Bekkevold *et al.*, 2006). Given these concerns and the problems associated with previous restocking programmes, it seems appropriate to ask whether there is a future for rehabilitating natural populations through managed releases of hatchery-reared stocks. And, if this approach is worth pursuing, can we identify methods of good practice that would avoid previous mistakes made in other areas of aquaculture, or stock enhancement?

The farming of marine species like cod is a relatively young industry, but one that is growing. This expansion is occurring regardless of several unanswered questions. Why has restocking of marine populations previously failed, and what potential negative effects do wild populations face if hatchery-reared fish are released or escape? For example, previous restocking experiments failed

juvenile cod, large enough to have passed through the bottleneck of high early life mortality, were released (Svåsand *et al.*, 2000). Owing to predation, the released cod perished, being too small and too young to elevate the cod biomass (Nordeide and Salvanes, 1991; Nordeide *et al.*, 1994). There are a number of reasons why this rehabilitation programme may have failed. Typically, however, all these point to the rearing environment being inadequate to generate fish with behavioural skills necessary to survive in the wild (Brown and Laland, 2001). It has been shown that hatchery cod are less efficient in prey capture (Steingrund and Fernø, 1997), as well as being predator-naïve staying, closer to predators than those with prior experience of predators (Nødtvedt *et al.*, 1999). There are several examples of deficits in feeding behaviour, anti-predator responses, and social interactions in several species of hatchery fish (of recent wild ancestry), and these deficits appear to be the result of the nursery rearing environment (review in Huntingford, 2004). Recent experiments with cod, in which juveniles are reared for most of their nursery period in enriched conditions (an environment characterized by variability), have shown promising results. Juvenile cod reared in enriched tanks develop more flexible behaviour than fish reared in standard hatchery conditions (Braithwaite and Salvanes, 2005; Salvanes and Braithwaite, 2005). This suggests that experiencing enrichment and variability has an impact on adult behavioural phenotype as they develop. This emphasizes the importance of the quality of early life environment and how this shapes fish behaviour. These are messages that could be valuable to the current cod farming industry as it develops. Do we have sufficient knowledge of natural, wild cod behaviour to be able to properly evaluate the possible effects of escapees from fish farms? Is our knowledge sufficient to evaluate their impact on wild stocks if hatchery cod are used for restocking? Is there a chance that providing fish with environmental enrichment will improve behavioural skills and survival in cod used for restocking? Or, if reared for mariculture, would cod reared with enrichment pose less of a threat to wild populations if they were to escape from fish farms? To date, most behavioural studies on fish species of commercial value have focused on salmonids owing to the long history of restocking and farming in this taxonomic group. Therefore, it may be worth considering whether the lessons learned in salmon rearing (whether for restocking, or for farming), are applicable to other species like cod.

Similarly, we should consider how issues relating to escapees from fish farming are associated with those of restocking. This could highlight which basic behavioural skills are necessary for survival and growth. Quantitative traits in natural populations depend on individual behaviours, and behaviours vary as do life history traits in a complex interaction between the population's genotype and the environment (Huntingford and Wright, 1989, 1992, 1993; Fuiman and Magurran, 1994; Carroll and Corneli, 1999; Salvanes *et al.*, 2004). Populations adapt to local selection pressures, and phenotypic traits are expressed differently in different areas. For example, acquired anti-predator skills can reflect the evolutionary history of their populations or species (Huntingford and Wright, 1989, 1992, 1993). This phenotypic plasticity (Thompson, 1991) allows individuals to develop behavioural repertoires appropriate for growing and surviving in their local habitat (Fuiman and Magurran, 1994). Here, we review the literature concerning the effects of enrichment and fish origin on fish behaviour and present, in particular, two recent studies on Atlantic cod in which we have demonstrated that nursery habitat variability generates behaviourally flexible individuals. We suggest that fish behaviour studies should be part of applied research for developing an industry of cod farming, as well as for research concerning restocking and conservation of marine resources.

Problems encountered when juvenile fish are reared in hatcheries

Fish reared and released for the purpose of rehabilitating populations have been housed in predator-free conventional hatchery environments with plenty of food. Such an environment allows better survival through the earliest life stages than nature does. However, these early rearing experiences do little to prepare the fish for the natural environment. To survive they need basic behavioural skills that allow them to find suitable food and avoid predation. Current evidence suggests that a hatchery environment does little to promote these behavioural abilities (Brown and Laland, 2001; Braithwaite and Salvanes, 2005). For example, cod reared in a pond on pelleted food learned to feed on live gobies (fish prey) when they were first offered, but they were much less efficient at capturing them than wild cod (Steingrund and Fernø, 1997). Moreover, cod reared in ponds without any previous experience of predators initially approached a predator (behind glass) and got closer to it than those with experience of predators (Nødtvedt *et al.*, 1999). Many of the behavioural deficits observed in fish reared in hatcheries appear to be exacerbated by the impoverished hatchery environment (Brown and Laland, 2001; Braithwaite and Salvanes, 2005). For example, hatchery-reared fish generally fail to avoid predators, and consequently, suffer higher mortality rates (reviews in Olla *et al.*, 1998; Weber and Fausch, 2003). Growing and developing in a hatchery, therefore, does little to prepare fish for the transition to a variable natural environment. A hatchery provides safe housing and a plentiful supply of highly nutritious pellets, so there is little need to search actively for food (Olla *et al.*, 1998). Once released, however, the fish must learn to capture live prey, a task that many fish fail to master (e.g. Ersbak and Haase, 1983; Ellis *et al.*, 2002). In some cases, released fish are so poor at negotiating this dietary transition that they consume small stones and pebbles which resemble the food pellets they ate in the hatchery (Ellis *et al.*, 2002).

The poor post-release survival of hatchery fish has led to a range of rearing studies that have attempted to train hatchery fish a short period before they are released into the wild (Olla *et al.*, 1994; Berejikian, 1995; Brown and Laland, 2001), but these studies report limited success on post-release survival. More recently, Braithwaite and Salvanes (2005) hypothesized that these training attempts may have mixed success because the fish still experienced constant unchanging conditions that are unlikely to promote learning and variable behaviour. To investigate this, we reared cod with and without experience of environmental variability. We found that simple enrichment in hatchery tanks from the post-larval stage (8 weeks post-hatch) until fish were tested 14, 20, and 26 weeks later, promoted flexible behaviour (Braithwaite and Salvanes, 2005; Salvanes and Braithwaite, 2005). These results suggest that intensive training programmes used prior to release may be insufficient to compensate for the hatchery generated behavioural deficiencies.

Identifying factors that influence behaviour

A fishery can disrupt a population's genotype, and it can alter life history evolution in harvested stocks as it typically removes individuals in a selective way. Such changes occur over only a few generations (Stokes *et al.*, 1993; Law, 2000; Conover and Munch, 2002; Olsen *et al.*, 2004). Similarly, salmonids escaped from fish farms that interbreed with wild stocks can cause disturbances by lowering long-term reproductive success (Hindar *et al.*, 1991; Fleming *et al.*, 1996, 1997; Jonsson, 1997; Skaala *et al.*, 2004). This has the potential to push local wild populations to extinction. This is an aspect which is difficult to explore owing to the complex interactions between genetic and environmental factors.

There are a variety of ways in which experience shapes behaviour, including environmental effects on the development of the neuro-endocrine and sensory systems and specific learning effects (Bateson and Martin, 1999; Huntingford, 2004; Braithwaite, in press). These types of processes are at work during development of fish (Huntingford, 2004; Braithwaite, in press). For example, there are studies illustrating how simple enrichment of the rearing environment affects learning ability, foraging skills, social behaviour, predator avoidance, aggression, and reproductive success (Fleming *et al.*, 1997; Berejikian *et al.*, 2000; Brown *et al.*, 2003; Braithwaite and Salvanes, 2005; Salvanes and Braithwaite, 2005). Since hatchery and wild fish grow up in very different environments, differential experience is likely to generate behavioural differences. Behaviours achieved early in life are likely to influence behaviour at later stages. Hence, deficiencies generated in early life are likely to affect later success.

Cultivating fish can potentially generate behavioural differences in three interlinked ways: differential experience,

different mortality, and survival of behavioural phenotypes within a single generation and over several generations (Huntingford, 2004). To understand these processes, we need to disentangle genetic background from environmental influences while quantifying effects of enrichment on the development of behaviour. Natural fish habitats represent more than just the physical properties of water masses. They include the topographical variation in the spatial landscape, such as predation risk, prey opportunities, and other stimuli that fish perceive. The natural environment is therefore complex and variable. Work with other captive vertebrates such as birds and mammals has already demonstrated that increasing complexity of the captive environment increases both behavioural and neuronal plasticity, improves cognitive performance, and increases survival of reintroduced species (Hunter *et al.*, 2002; Kempermann *et al.*, 2002; Bredy *et al.*, 2003; Rabin, 2003). Experience with a variable environment is also known to promote learning, a behaviour that allows an animal to adapt to its current situation (Papaj, 1986; Odling-Smee and Braithwaite, 2003). Therefore, from the perspective of rearing fish for rehabilitation of populations, experience of variation would seem to be important.

For fish, environmental variables consist of more than just physical properties of the water, predation risk, and food. Although some studies of cod have evaluated habitat choice and survival probabilities in habitats that differ with respect to bottom type or degree of algal cover (Tupper and Boutilier, 1995; Borg *et al.*, 1997; Gotceitas *et al.*, 1997; Gotceitas and Brown, 1998; Lindholm *et al.*, 2001; Linehan *et al.*, 2001), the influence of spatial landscape on the development of behaviour has received less attention. The recent results of Braithwaite and Salvanes (2005) and Salvanes and Braithwaite (2005) indicate that juvenile cod benefit from experiencing a spatial landscape during the hatchery-rearing phase, in that they develop flexible behaviour and are capable of enhanced social interactions. Nursery habitat quality, therefore, may be more important than previously thought, and an approach with more emphasis on behavioural and evolutionary ecology may provide a better understanding of the development of fish behaviour.

Determining nursery environment effects

Huntingford (2004) points out that many studies comparing hatchery and wild fish fail to recognize the influence of maternal effects on egg quality that can cause divergence in survival and can affect the behaviour of young and adult stages. Thus, comparing behaviours of fish with different parents is likely to be confounded. However, one approach would be to randomly divide offspring from the same parental stock into different types of nursery environments, and then later test how these rearing treatments generate differences in behaviour. Such an approach gives insight into which environmental characteristics influence behaviour. We divided offspring from the same parents into

several types of nursery environments to examine how different combinations of presence/absence of spatial cues and constant/variable food deliveries affected subsequent behaviour (Braithwaite and Salvanes, 2005; Salvanes and Braithwaite, 2005).

Using cod, we carried out four rearing treatments that consisted of (i) an environment identical to a normal hatchery tank, providing constant food and no spatial cues, (ii) an environment in which fish experienced variation in food availability but had no spatial cues, (iii) an environment in which fish had variable spatial cues but constant food input, and (iv) an environment in which fish experienced both variable food and spatial cues. Pebbles and rocks (cobble) and a plastic model of kelp on the base of the holding tank provided spatial cues. Their positions were changed randomly once a week. Cod reared with no spatial cues were reared in plain tanks that were cleaned at the same time as the landmarks were moved in the other tanks to control for this disturbance. The spatial variability created was chosen to mimic natural cod nursery habitats. Food variability was created by a variable feeding regime. Food could be presented in four possible 2-h intervals during the day. A pseudo-random sequence provided variable schedules, fish could receive food in one meal in the first 2 h, or this could be spread across two, three, or four feeding intervals. Feeding regimes varied between days and weeks, and ran over a 4-week cycle. In addition, the position at which food was introduced also changed on a daily basis. Fish reared with constant food cues were fed small amounts of food pellets continuously between 08:00 and 16:00 at a fixed position that remained constant throughout rearing. All rearing tanks received the same total quantity of food daily. Fish from these treatments were assayed for behaviour after 14 weeks (22 weeks post-hatch), and for a further set of replicate tanks after 20 weeks (28 weeks post-hatch) of experiencing their respective treatments. These assays quantified propensity to explore a novel area, how quickly fish recovered after a mildly stressful experience, response to live prey, and how quickly they transferred to a diet of wild prey. Together, these assays revealed a complex interaction between experience of different types of environmental heterogeneity and subsequent behavioural responses (Braithwaite and Salvanes, 2005). The results are in line with enrichment experiments on other higher vertebrates (Gomez-Pinilla *et al.*, 1998; Sackett *et al.*, 1999; Allen *et al.*, 2003), and they reveal that it is possible to alter cod behaviour by manipulating the rearing environment. Cod reared in conditions that most closely resemble a plain hatchery tank were found to behave poorly across all of the behavioural assays. In contrast, fish reared with experience of different levels of environmental variability appeared to have more flexible behavioural repertoires. Early experience with both variable spatial and food cues consistently produced cod that were faster in their attraction to, and their consumption of, live prey; in their speed of exploration of a new

environment, and in their recovery from a stressful experience. Prey were two-spotted small fish goby (*Gobiusculus flavescens*) and mysid shrimps, both natural prey for juvenile cod in western Norway.

In a further common garden experiment, we compared social interactions between juvenile cod of the same parental stock that had been reared in two contrasting environments. Here, each rearing environment had access to variable food input (as described above), but one of the groups was also exposed to variable spatial cues as well. We compared the aggressive behaviour of the two groups after 28 weeks (36 weeks post-hatch) in different rearing treatments. Fish that had experienced variable spatial cues directed relatively more agonistic attacks toward fish reared in a plain environment, however, the fish from the plain environment showed little discrimination in selecting the target of their aggression. Furthermore, cod reared in the impoverished hatchery environments spent less time in shelter, were more active, and showed weaker anti-predator responses than fish reared with access to variable spatial cues. These results suggest that the constant, plain environments of standard fish hatcheries influence a range of behavioural traits, including social behaviour.

Such common garden experiments are therefore a useful way of assigning the relative roles for genetic or environmental effects, and they have been successfully used in a range of studies (e.g. Trexler, 1990; Fuiman and Magurran, 1994; Conover and Schultz, 1995). In this instance, they have provided a versatile method with which to localize the effects of the environment while controlling for other factors (e.g. maternal or genotype).

Determining genetic effects

To identify the influence of genetic effects over other influences, it is necessary that fish with different origins are reared from the egg stage in a common environment, though it is also important to control maternal factors. Moreover, egg batch effects within a female can also influence progeny fitness, and thus, holding females from different populations in the same conditions does not control this completely, and if the parental feeding conditions were to be eliminating, the next generation should ultimately be used. Nevertheless, as an approximation, maternal effects can be minimized by ensuring that the mothers receive identical treatment to avoid the possibility that confounding factors associated with maternal rearing conditions will influence egg quality (cf. Huntingford, 2004). Such an approach was used by Salvanes *et al.* (2004). Here, juvenile cod reared from eggs from "northern" (70°N) and "southern" (60°N) Norway were compared in (i) feeding behaviour, growth, and food conversion efficiency and (ii) energy allocation between skeletal growth and storage tissues. Consistent differences imply adaptation to different environments and, hence, sub-populations. Offspring from fish from north and south were reared initially in a common

environment typical of the southern strain from the egg stage. When the fish were 15-months old, they were tagged to allow individual identification. In trials run in aquaria housing mixed groups, the fish were allowed to interact and compete for a food source over an 8-month period. Offspring reared from the northern population were more successful in food competition when food was restricted, and they had a larger energy allocation to storage tissues, as suggested by the greater increase in condition. This was interpreted as an adaptation to the high latitude environment for northern cod and counter-gradient variation and the existence of genetically distinct sub-populations along the Norwegian coast (Salvanes *et al.*, 2004; see also Jørstad *et al.,* 2006, for an examination of stock differentiation of cod along the Norwegian coast and northeast Arctic).

Another study of genetic divergence, this time for salmon, was performed by Fleming *et al.* (1997). Here, they compared a seventh-generation strain of farmed fish from Sunndalsøra with its principal founder population from River Nansen. The fish were reared from eyed eggs to juveniles in the same types of environment and, thereafter, they were assessed for genetic divergence by several fitness-related traits. The authors report that farmed juveniles were more aggressive in tank environments typical of hatcheries, while wild juveniles dominated in test environments that resembled a natural stream. Farmed salmon were more risk prone and re-appeared from cover more quickly than wild fish after a simulated predator attack (Fleming *et al.*, 1997).

Shaping behaviour in hatcheries — why does it matter?

The interaction between the behaviour of individuals and the quantitative traits of populations can occur through foraging behaviour, risk taking, anti-predator responses, and aggressive or social interactions. Populations are characterized by large individual variations in both behaviour and life history traits (growth, maturation age, fecundity, and survival). During domestication, the frequency distributions of various behavioural traits change partly as a result of the selection process; many fish normally selected out of the population thrive in the predator-free and food-rich hatcheries, partly because hatchery nursery environments fail to shape behaviour appropriately. The traditional way of culturing fish in hatcheries is to use conventional, non-enriched hatchery tanks in which intended and unintended selection occurs. In the last two decades, there has been a drive to improve the survivorship of released fish by attempts at remedial training, after rearing them in a poor environment. These approaches have had mixed success. However, we suggest that a combination of enriched rearing environments followed by a short pre-release training programme may provide more consistent, positive effects.

Training fish reared in standard nursery environments prior to release

Given that finding food and avoiding being eaten are two basic requirements for growth and survival in a natural setting, researchers began to devise various ways of training hatchery fish to prepare them for life in the wild (Olla *et al.*, 1998). Again, the majority of these studies to date have been with salmonids. Hatchery fish have been provided with live prey in an effort to improve their ability to sustain transfer from an artificial diet to a natural one. However, these studies report mixed results, and compared with wild fish, the hatchery fish are often slower in switching to new prey items as they become abundant (Olla *et al.*, 1994), or they never reach the same feeding efficiency as the wild fish (Steingrund and Fernø, 1997; Sundstrøm and Johnsson, 2001). Brown *et al.* (2003) investigated the effects of feeding live prey to juvenile salmon in enriched glass aquaria. Their results suggest a positive effect of exposure to live prey, but the data are difficult to interpret as the control fish, without enrichment or access to live prey, were reared in large plastic hatchery-like tanks that are not readily comparable to the enriched glass aquaria. Similarly, a number of studies have begun to investigate ways to train fish about the risks of predation (Berejikian, 1995; Nødtvedt *et al.*, 1999; Brown and Laland, 2001). Again, these approaches have had variable success in finding effects on anti-predator behaviour. Some studies showed an effect which could have a positive influence on survival (Brown and Smith, 1998; Nødtvedt *et al.*, 1999; Mirza and Chivers, 2000; Hossain *et al.*, 2002), while others found no effect (Johnsson and Abrahams, 1991; Vilhunen and Hirvonen, 2003). One study on anti-predator behaviour in cod has reported effects similar to those reported for salmon. Nødtvedt *et al.* (1999) investigated the behaviour of wild-caught cod and cod reared for 2 months in a predator-free marine pond before being transferred into net-pens and then tested. They found that, initially, the pond-reared cod had little respect for potentially dangerous predators and had a reduced tendency to perform predator inspection compared with wild fish. Direct experience with a predator, however, rapidly induced a much higher respect distance suggesting that cod surviving initial predatory attacks can possibly learn appropriate anti-predator responses.

Why do some training programmes appear to have more success than others? We suggest that the effects of training may lie in the fact that an ability to forage or to avoid a predator often requires more than just an ability to recognize food or a threat. Rather, it requires the fish to respond in a flexible manner and to show a propensity to learn and adapt to new situations. Given that many of the studies were performed on fish reared in standard, non-enriched hatchery tanks, it is possible that many of the fish had only a low capacity for learning. If the fish have a limited ability to learn, pre-release training may take both longer and have limited success.

Braithwaite and Salvanes (2005) showed that juvenile cod reared (from 8 weeks post-hatch) for 14 weeks in the constant environment of a standard hatchery tank are behaviourally less flexible than cod reared for the same length of time but with experience of environmental complexity. Furthermore, they found differences in the learning propensities of these different groups in terms of feeding on live prey. These results suggest that relatively simple manipulations of the uniform fish farm environment generate fish with advanced learning capacities. However, more assays are required to address this directly.

Aggressive behaviour and social interactions are also influenced by the early rearing environment

Behavioural patterns during fights are often similar in cultured and wild fish (Mork *et al.*, 1999). However, domestication can select for increased intensity of aggression (Huntingford, 2004), and environmental enrichment in the rearing environment has also been shown to influence aggression in fish (Fleming *et al.*, 1997; Deverill *et al.*, 1999; Nijman and Heuts, 2000; Berejikian *et al.*, 2001; Metcalfe *et al.*, 2003; Sundstrøm *et al.*, 2003; Salvanes and Braithwaite, 2005). How are agonistic behaviours displayed? What cues are used among individuals to signal dominance or subordinate behaviours, and are these different in wild or cultured fish? These questions are of general interest for behavioural ecology, but they are also highly relevant both to determine the fate of hatchery-reared fish and to maintain groups of fish for mariculture. Despite the clear value of detailed examination of behavioural interactions in such fish as salmon and cod, there have been, as yet, only a small number of studies. Although signals could be provided through a range of sensory systems, for example, olfactory or auditory, most of the studies on social interactions have concentrated on visual cues. Here, the sorts of signals that could be used include changes in body coloration or particular postures (e.g. O'Connor *et al.*, 1999a).

A number of factors that may influence levels of aggression have been proposed. For example, in different species of fish, it has been suggested that differences in territorial holding behaviour may be responsible for differences in aggression, 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 (*Salmo trutta*) and Atlantic salmon, whereas the study of O'Connor *et al.* (1999b) reported no effect of prior residence on dominance in juvenile Atlantic salmon, but found that prior residents did dart higher in the water column to feed and, therefore, these individuals grew faster. Another study reported that environmental enrichment in combination with prior residency influenced 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 with fish reared and tested in plain, impoverished aquaria. However, the effects from the rearing and testing environment could not be separated, making it unclear which factors generated asymmetry in the aggressive interactions. More recently, Salvanes and Braithwaite (2005) found that the presence or absence of spatial cues in the rearing environment created asymmetries in agonistic behaviour. Fish reared in the presence of spatial cues showed a better level of discrimination in their agonistic behaviour than fish reared in a standard hatchery tank. Fish reared with spatial cues were less likely to initiate an aggressive interaction with a fish also reared in a similar way, but were more likely to initiate aggressive interactions with fish reared in a standard, plain rearing tank (Salvanes and Braithwaite, 2005).

Detailed studies of signalling during social interactions have yet to be undertaken for cod. In juvenile Atlantic salmon, subordinate individuals produce signals of submission by darkening their body colour, and they use this to avoid potential costly escalated contests (O'Connor *et al.*, 1999a, b). Cod also change colour as a fright response (Salvanes, unpublished observations), but it is not clear whether this represents a stress response, camouflage, social signalling, or a combination of these. We suggest that further studies on social interactions among cod from a variety of origins (wild-caught populations and hatchery-reared cod) would be a useful next step to increase our understanding of the behaviour of this species.

Concluding remarks

Culturing gadoids such as cod for the fish farming industry or for restocking, requires careful planning in terms of sourcing the broodstock and creating appropriate nursery environments for culturing juveniles. Behaviours that fish learn early in life are likely to influence their skills later. Recently, it was shown that enrichment in rearing tanks generates fish with more flexible behaviour than conventional rearing tanks. These fish have the potential for greater survival if released for restocking as enriched environments may generate more suitable feeding behaviour, anti-predator responses, and social behaviour for the wild. However, it remains to be determined how well this increased behavioural flexibility improves post-release survival. Selection of broodstock collected for hatcheries is important and should take into account the fact that many populations of fish are locally adapted to a particular environment. It would be timely to pay attention to how the genotype and environment interact to create locally adaptive populations. Armed with such knowledge, it may be feasible to restock fish that have high survivability or to farm fish that will be of little threat to a local population if they escape. We therefore suggest that if managed correctly, restocking could be used as a technique to enhance wild populations.

However, as we have argued above, we stress the need for an interdisciplinary approach and associated research to make such techniques viable. Moreover, we suggest that behavioural studies should be part of applied research for developing an industry farming gadoids, as well as for research concerning restocking and conservation of marine resources.

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