

Behavioural syndromes in farmed fish: implications for production and welfare

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Summary

Consistent individual differences in behaviour have been described for several species of salmonid fish, the group that has been most intensively farmed. In particular, fish accept different levels of risk when competing for limited resources and, in nature, the different behavioural phenotypes seem to perform better in different environmental conditions. Studies of the behaviour of farmed fish can provide insights into the genetic basis of such differences and into their consequences for some components of fitness. Both deliberate selection for fast growth in farmed fish and inadvertent selection of fish that flourish in intensive aquaculture systems have generated inherited behavioural differences between farmed fish and the wild stocks from which they originated. Thus, fish from farmed stocks tend to be bolder and to take greater risks when foraging; they may also be more aggressive, depending both on conditions during selection and the environment used to screen aggressiveness. Such results indicate the existence of inherited variation in risk-taking and aggression in the populations from which today's farmed stocks were derived. They also suggest that fish from the risk-avoiding/non-aggressive end of the behavioural spectrum may fail to flourish in conditions that usually prevail in intensive husbandry systems. The implications of these findings for production and welfare in aquaculture are discussed.

Keywords: risk taking, competitive styles, domestication, welfare.

Introduction

As the other papers in this volume make clear, in species as different as rhesus monkeys (*Maccaca mulatta*) and sticklebacks (*Gasterosteus aculeatus*),

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individual animals show striking, consistent and inherited variation in their readiness to take risks. Such differences in 'personality' may be reflected in several different contexts, including exploration of unfamiliar environments and objects, interactions with potential predators and encounters with conspecific rivals (Wilson et al., 1994; Koolhaas et al., 1999; Gosling, 2001; Sih et al., 2004). There are a number of well studied systems (including mice, *Mus musculus*, Van Oortmerssen & Busser, 1989; rats, *Rattus norvegicus*, Koolhaas et al., 1999; pigs, *Sus scrofa*, Bolhuis et al., 2003 and great tits, *Parus major*; Drent et al., 2003) for which we know, to varying extents, about the causation, development and function of such behavioural variation. Studies on these systems tell us that the variation is often inherited and that spatial or temporal variation in selection regimes means that different behavioural phenotypes perform best in different conditions (van Oortmerssen & Busser, 1989; Dingemanse et al., 2004).

Here we briefly review the evidence that in wild salmonid fish in general (and Atlantic salmon, *Salmo salar*, in particular), individual fish use different strategies for gaining access to limiting resources and that in wild-derived fish the different behavioural phenotypes perform best in different environmental circumstances. The process of domestication of salmonids for the aquaculture industry has involved deliberate selection for desirable traits, such as fast growth performance. It has also involved inadvertent selection for traits that promote good performance under culture conditions in farms, namely high density, with abundant, predictable food in a homogeneous environment (Huntingford, 2004). This being the case, we expect that behavioural traits that maximize growth in such conditions may have been selected for during the domestication process. To examine this possibility, we also review the literature on the effects of domestication on the behaviour of farmed salmonids. This provides evidence for inherited variation in risk-taking and aggression in salmonid fish and sheds light on the circumstances in which risk-takers and risk-avoiders flourish. It also has implications for production and welfare in aquaculture, which we discuss.

Competitive styles in wild salmonid fish

Individual differences in risk-taking during fights and in other circumstances (controlling for past experience and current nutritional status and independent of gender and age) have been described in various species of salmonid

fish. For example, in groups of laboratory-reared Atlantic salmon, offspring of wild parents housed in tanks at high densities and fed at regular intervals from a fixed food source, individual fish compete for food in different ways that involve different degrees of risk. Some fish consistently fight for the favourable position just below the feeder, others consistently remain on the substratum, feeding largely on uneaten food falling to the bottom, while yet others consistently remain in the water column at a distance from the feeder, responding rapidly to each food delivery by intercepting pellets. The fish that fight for a position beneath the feeder get most food but receive many attacks, those that remain on the substratum gain little food but are rarely attacked, while the rapid responders are intermediate on both counts (Adams et al., 1998). Individual wild brown trout (*Salmo trutta*) differ markedly in their response to novel objects, some strongly avoiding and others attacking them. In pairwise tests, fish that react most boldly to novelty tend to become dominant regardless of body size, especially when the boldness difference is big (Sundstrom et al., 2004). In the wild, individual brook charr (*Salvelinus fontinalis*) show two distinct behavioural modes, being either aggressive or non-aggressive. This is associated in a complex way with activity levels; most fish are either largely inactive or highly active, with only a small number of fish showing intermediate activity levels. Only fish in the active and inactive categories showed significant levels of aggression, while fish in the intermediate-activity category were non-aggressive (McLaughlin et al., 1999).

Thus, the coexistence within the same population of individuals with different competitive styles seems to be quite common among salmonid fishes. In a few cases, something is known about the physiological processes that underlie such differences in risk taking. For example, strains of rainbow trout (*Onchorrhynchus mykiss*) selected for divergent cortisol response to a standard stressor confinement (Pottinger & Carrick, 1999) also differ in various aspects of behaviour, including aggressiveness during staged fights (Pottinger & Carrick, 2001) and cognitive function (Moreira et al., 2004). It is possible, though as yet untested, that difference in risk-taking may accompany inherited differences in stress responsiveness in other farmed species, such as the common carp (*Cyprinus carpio*; Tanck et al., 2001, 2002).

In terms of components of fitness in fish with such different competitive styles, a number of laboratory studies of juvenile Atlantic salmon held at high densities have shown that fish that aggressively monopolise a fixed,

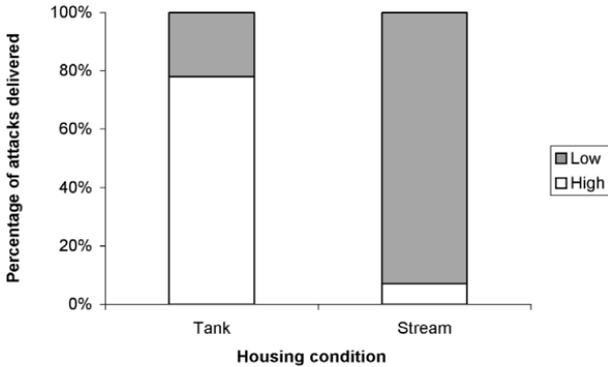


Figure 1. Comparison of the behaviour of the same individual juvenile Atlantic salmon held in groups of 10 in a bare laboratory tank at high densities and with a localised, predictable food supply and in an artificial stream, at natural densities, in a physically-complex environment and with dispersed, unpredictable food. Fish spent a 5 day period in isolation before transfer between testing conditions. Percentage of attacks delivered in the tank and in the stream in fish classified as showing high aggression (High: the top 50% of fish ranked by rate of observed attacks) and low aggression (Low: the bottom 50% of fish ranked by rate of observed attacks) in the tank trials (Adams & Huntingford, unpubl. data).

profitable feeding sites gain more food and grow better at high densities (e.g., Atlantic salmon: Metcalfe et al., 1990; MacLean & Metcalfe, 2000). However, these same aggressive fish do not necessarily do better in more natural conditions where the food supply is spatially and temporally unpredictable. For example, salmon that were able to dominate a localised food supply when held at high densities in tanks were not successful at acquiring feeding sites and getting food in an artificial stream with a dispersed food supply (Huntingford & Garcia de Leaniz, 1997). A similar result is shown in Figure 1, which summarises the behaviour of individually identified salmon observed in groups of 10 both in a bare laboratory tank (at high densities and with a localised, predictable food supply) and then (after a period held in isolation) in an artificial stream (at natural densities, in a physically-complex environment and with dispersed, unpredictable food). Fish that aggressively monopolised the localised food supply in the tank were unable to acquire feeding stations and showed very low levels of aggression in the stream. Aggressive fish ate 73% of the available food in the tank, but made only 39% of the observed feeding attempts in the stream. Comparable results were obtained when fish were screened for aggressiveness in the artificial stream and then moved to tanks (Adams & Huntingford, unpublished data).

Moving closer to fish in the wild, Höjesjö et al. (2002) captured wild brown trout and observed them during pairwise encounters in tanks. Fish that won such encounters grew better following release into their native stream than did those that lost. However, about 30% of the tested fish did not fight at all during the laboratory test and on release these non-aggressive fish grew just as well as the dominant fish. When Atlantic salmon of known social rank were released into the wild (Harwood et al., 2003) and into large stream enclosures (Martin-Smith & Armstrong, 2002), there was little or no association between social rank and growth rate. Aggressive brook char showed more foraging attempts than non-aggressive fish, allowing for differences in activity. Growth rate potential (measured by tissue concentration of RNA) was above average in active and in inactive fish, but below average in those showing intermediate rates of activity. Thus charr with the highest growth potential fell into those two categories in which aggressive behaviour was observed (McLaughlin et al., 1999).

Thus in several species of salmonid, fishes with different competitive styles coexist and the different behavioural phenotypes perform best in different selective environments. There is some evidence that such behavioural variation is inherited, for example, there are behavioural differences between selected strains of rainbow trout (Pottinger & Carrick, 2001). In general, though, since salmonids tend to be relatively long-lived, breeding programmes for purely scientific purposes are rarely possible. However, several well-documented breeding programmes for farmed fish have provided material for studies of the effects of domestication in farmed strains; such studies provide information on the inheritance of risk-taking and aggression in salmonid fishes.

Selection for boldness and aggression during domestication?

A number of 'common garden' experiments, in which effects of experience, nutritional status and other confounding variables are removed (Huntingford, 2004), have demonstrated differences in risk-taking between fish from lines that have been farmed for several generations and fish from the wild stock from which the farmed stock was originally derived, reared in identical conditions in the laboratory. To give just two of many possible examples, brown

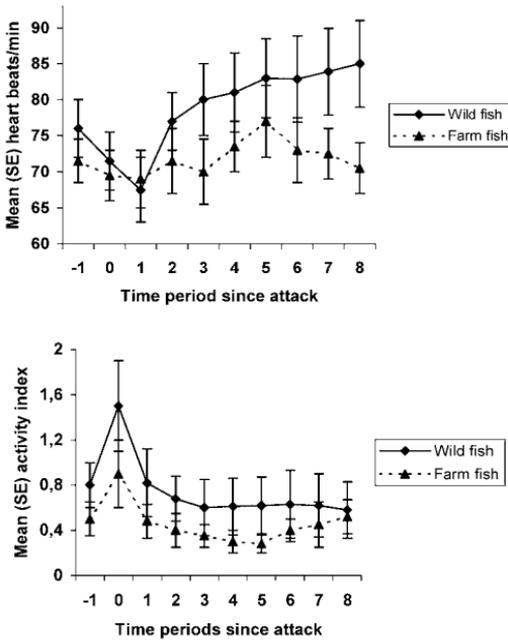


Figure 2. Rate of heart beat and a measure of activity in farmed Atlantic salmon (filled triangles) and hatchery-reared wild fish from the same stock (filled diamonds) before (–1) and after a simulated predatory attack (at time 0). Time scale runs from 3 minutes before attack to two hours after attack, with variable sampling intervals. After Johnsson et al. (2001).

trout fry from a sea-ranched strain (raised in production conditions until seaward migration for 5 generations) were faster to approach a novel (potentially dangerous) object and novel food than were hatchery-reared fish from the same original stock (Sundstrom et al., 2004). Juvenile Atlantic salmon in their second year of life from a farmed strain selected for fast growth had lower base level heart rates than their hatchery-reared wild counterparts (Figure 2a) and were less likely to respond to a simulated attack by a piscivorous bird; those that did respond showed weaker physiological arousal (Figure 2a) and resumed activity faster (Figure 2b). Differences in behaviour and physiology became weaker with age and experience, but the original stock effects in this common garden experiment indicate inherited differences in risk taking (Johnsson et al., 2001).

Caution is needed in interpreting the results of such common garden studies, since for logistic reasons possible effects of maternal nutrition/condition can rarely be ruled out. In general, however, it seems likely that generations of captive rearing has selected for fish that are more likely to take risks.

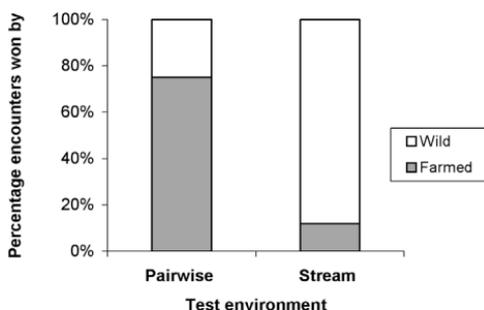


Figure 3. Outcome of dominance interactions between hatchery-reared juvenile Atlantic salmon of wild and farmed origin. Percentage of encounters won by each category of fish in pairwise tests in tanks and in stream channels (after Fleming & Einum, 1997; Einum & Fleming, 1997).

Comparison of aggressive behaviour in cultured and wild fish gives more variable results, depending both on the conditions in which fish are held during domestication and on the environment used to screen for aggressiveness. In pairwise tests in a neutral tank, domesticated Atlantic salmon usually dominated hatchery-reared fish of wild origin (Einum & Fleming, 1997; Figure 3; Metcalfe et al., 2003). Sea ranched brown trout also tended to defeat wild fish in fights, but here the effect depended entirely on the fact that, on average, farmed fish are larger than wild fish of the same age (Peterson & Järvi, 2000). No differences in aggressiveness or tendency to dominate were found between Masu salmon (*Onchorhynchus masou*) that had been farmed or sea ranch for 30 generations and wild fish (captured in the wild; Yamamoto & Reinhardt, 2003). Overall, the literature suggests that domestication (often including selection for fast growth at high densities) can sometimes influence aggressiveness, but that the direction of this effect depends on feeding regimes (Ruzzante, 1994). Using the medaka (*Oryzias latipes*) as a model, Ruzzante & Doyle (1991) showed (somewhat surprisingly) that selection for fast growth favours aggressive fish when food is dispersed, but not when it is clumped. The authors suggest that aggression may be too costly at the high densities that localised food generates (Ruzzante & Doyle, 1991). Overall, the fairly extensive literature on behavioural differences between fish of wild and domestic origin reared under the same conditions strongly points to the existence of inherited differences in risk-taking and aggression in the original stocks.

The effect of the environment in which fish are held when being screened for aggression throws light on the circumstances that favour the different

variable competitive styles described in the previous section. In pair-wise tests in simple tanks with a predictable food supply, farmed Atlantic salmon were marginally more aggressive than hatchery reared fish of wild stock and tended to dominate them in pairwise encounters. In contrast, wild fish won encounters in groups in more complex, stream-like tanks where densities were low and food unpredictable in space and time (Figure 3; Einum & Fleming, 1997; Fleming & Einum, 1997). The fact that farmed fish dominate in simple, pair-wise situations, but not in groups in more complex artificial streams, suggests that, in the conditions usually prevailing in intensive production systems, favour fish from the risk-taking, aggressive end of the behavioural spectrum.

Behaviour and growth in farmed fish; implications for production and welfare

Taken together, comparison of the behaviour of wild and farmed fish suggest that domestication (especially when accompanied by selection for fast growth in the farm environment) has resulted in the concomitant selection for the behavioural traits of high aggression and risk taking. This in turn suggests that risk-avoiding fish fare poorly in normal production conditions, which has implications for both production and welfare. What is the evidence that this is the case?

In all species of farmed fish, growth within a single cage or tank is often highly variable, however well matched the fish were to begin with and however much farmers try to provide standard conditions and sufficient food for all fish. Such variable growth has been particularly well documented for salmonid fish (Storebakken & Austreng, 1987a, b; Johansen & Jobling, 1998). Growth variation increases when fish are held on low rations (Storebakken & Austreng, 1987a, b; Damsgård et al., 1997), but it is still seen (though to a lesser extent) on high rations (Abbott & Dill, 1989; McCarthy et al., 1992). In adult Atlantic salmon, marked size differences develop quickly even on high rations and persist for months in the absence of grading. Size differences are relatively fixed, with some fish consistently growing very fast and other consistently growing slowly or losing weight (Cubitt et al., *subm.*). Do such differences in growth rate reflect different patterns of risk taking or aggression, with non-aggressive, risk-avoiders failing to gain access to food?

The causes of differential growth among farmed fish are still imperfectly understood and may include differences in efficiency of digestion or assimilation of food or in the allocation of the resulting nutrients. However, variable food intake arising from differences in competitive style is also a possible cause. Aggressive interactions are known to occur among farmed salmonids in production conditions (e.g., Kadri et al., 1997) and various indirect lines of evidence suggest that this can result in differential access to food. For example, among juvenile Atlantic salmon held at high densities, larger fish have relatively high levels of fin damage, probably incurred as a result of frequent aggressive interactions (MacLean & Metcalfe, 2000). McCarthy et al. (1999) showed that in the cichlid fish *Tilapia rendalii* dominant fish (identified indirectly via low daily variability in food intake) gained more food overall than subordinate fish (also identified indirectly) when fed from a point source. Direct observations of the behaviour of Atlantic salmon undergoing different rates of growth in production conditions show that fast-growing fish jostle for a position in the water column underneath the feeder, whereas non-growing fish avoid such interactions (Cubitt, 2002). Overall therefore, such evidence as we have suggests that at least some of the striking variation in growth rate among farmed fish is caused by behavioural differences. Where densities are high and food is predictable, as is usually the case in intensive husbandry systems, fish at the risk-avoiding/non-aggressive end of the spectrum may gain little food over long periods and grow poorly, if at all. The end result is loss of production and potentially compromised welfare, and it is worth considering whether we can use our understanding of behaviour to suggest remedial measures.

Possible remedial action

It is not a simple matter to decide what action we should take to prevent failure to thrive in risk-avoiding, low-aggressive fish held in intensive production systems, assuming (as seems to be the case) that such differences are at least partially inherited. In the first place, the best strategy will depend on the reasons why fish are being reared. If this is to provide large numbers of fish for restocking purposes, then arguably farmed populations should include fish from across the whole spectrum of risk-taking (Huntingford, 2004). If, on the other hand, fish are being farmed for food so production and welfare

are the main considerations, one approach might be to avoid placing low-risk taking fish in production systems, either by using domesticated strains (where these are available) or by pre-screening fish at the start of the production cycle. However, as described above, the performance of fish with different patterns of risk-taking is context-dependent, being influenced by many aspects of the competitive environment, particularly food distribution, environmental complexity and density. This being the case, trying to engineer the behavioural structure of farmed fish populations is not necessarily the best approach, at least in the short term until we know more about the species- and context-specific performance of risk-takers and risk-avoiders in different production systems.

An alternative, promising approach based on altering husbandry systems rather than altering fish, is to use our knowledge of the behavioural biology of fish to identify conditions that allow low-risk taking/low-aggression fish to gain access to food. For example, increasing the cost of fighting by raising current speed reduces aggression in farmed Arctic charr (*Salvelinus alpinus*; Adams et al., 1995), allowing otherwise slow-growing fish to do better. Likewise, by suppressing aggression at a population level, the presence of older companions promotes growth in juvenile Atlantic salmon (Adams et al., 2000). In *Tilapia rendalli*, the relationship between dominance and overall food intake described above is lost when food is well distributed and therefore cannot be monopolised by aggressive fish (McCarthy et al., 1999). Using 'smart' feeders that deliver food whenever fish are hungry rather than at pre-defined, predictable times of day creates a farm environment in which there is much less competition for food (Figure 4; Andrew et al., 2002) and low-risk/low aggression fish have opportunities to feed and grow (Noble, 2001).

Conclusion

As in many other groups of animals, fishes (including the intensively farmed salmonids) provide many examples of consistent individual differences in behaviour, over and above differences in age, experience and current nutritional status. In particular, individuals within the same population are often differentially responsive to risk and use different tactics to compete for limited resources. In some cases, such differences are related to differential responsiveness of the hypothalamic-inter-renal axis, are known to be inherited

Table 1. Representative examples of studies comparing the behaviour of domesticated salmonid fishes ('farmed fish') with that of offspring wild fish ('wild fish') from the original founder stock, reared in identical, hatchery conditions.

Species	History of farmed stock	Result	Authors
Brown trout (<i>Salmo trutta</i>)	Sea ranched for 5 generation.	Farmed fish approached novel objects and food more quickly.	Sundström et al., 2004
Brown trout	Sea ranched for 5 generation.	In stream channels, randomly-selected farmed fish dominated wild fish. No effect in size-matched fish.	Petersson & Jarvi, 2000
Brown trout	1 generation of hatchery-rearing.	Wild fish but not farmed fish become night-active in the presence of a predator.	Alvarez & Nicieza, 2003
Atlantic salmon (<i>Salmo salar</i>)	Selection for fast growth for 6 generations.	Farmed fish start moving more quickly after being attacked.	Einum & Fleming, 1997
Atlantic salmon	Selection for fast growth for at least 6 generations.	Fewer farmed than wild fish responded to an attack (72% v. 100%) and they reacted less strongly.	Johnsson et al., 2001
Atlantic salmon	Selection for fast growth for at least 6 generations.	Farmed fish are somewhat more aggressive and dominate wild fish in pair-wise tests in tanks.	Einum & Fleming, 1997
Atlantic salmon	Selection for fast growth for 6 generations.	Wild fish dominate farmed fish in stream channels.	Fleming & Eimun, 1997
Atlantic salmon	Farmed for 6 generations.	Farmed fish dominate wild fish in pair-wise tests in tanks, but this is overridden if wild fish have a prior residence advantage.	Metcalf et al., 2003
Steelhead trout (<i>Oncorhynchus mykiss</i>)	Farmed for more than 20 years.	Farmed fish forage closer to a predator than do wild fish.	Johnsson & Abrahams, 1991
Masu salmon (<i>Oncorhynchus masu</i>)	Sea ranched for 30 generations.	Farmed fish emerge from shelter faster than wild fish after exposure to chemicals from a predatory fish.	Yamamoto & Reinhardt, 2003
Masu salmon	Sea ranched for 30 generations.	No differences between farmed and wild fish in aggressiveness or ability to win fights.	Yamamoto & Reinhardt, 2003
Coho salmon (<i>Oncorhynchus kisutch</i>)	Farmed offspring from wild-caught females housed in culture from fry.	Newly hatched farmed fry won most fights against half-sib offspring of females captured as adults.	Berejikian et al., 1999

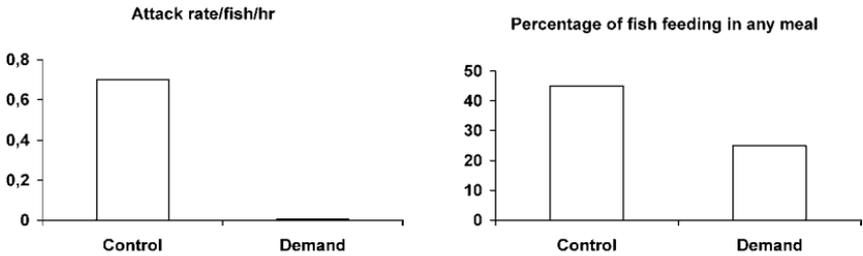


Figure 4. Rate of attacks (per fish per hour) and percentage of fish attempting to feed in any given meal in farmed Atlantic salmon held in production cages and fed either by an automatic feeder at fixed times (control) or by a 'smart' feeder in accordance with spontaneous appetite (demand). From Andrew et al., 2002).

and promote fitness in different environments. A robust finding of studies comparing the behaviour of domesticated salmonid fishes with that of wild-derived fish from the same stock reared in standard conditions is that domesticated fish are bolder in a variety of circumstances. They may or may not be more aggressive, depending on conditions during domestication and during behavioural screening. These findings strongly suggest that conditions normally prevailing in intensive husbandry favour risk-taking/aggressive fish. Such evidence as we have relating behaviour to growth in farmed fish suggests that this is indeed the case and that low-risk/low-aggressive fish may well fail gain food and grow and thrive. Arguably, the best way to avoid the welfare and production problems that this poses is either to screen juvenile fish for boldness and use only high-risk fish in intensive production or to adjust husbandry systems (and in particular to feed delivery) so as to give low risk fish opportunities to feed.

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