

The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon

NEIL B. METCALFE, SVEINN K. VALDIMARSSON* and IAN J. MORGAN

Fish Biology Group, Division of Environmental and Evolutionary Biology, Graham Kerr Building, Institute of Biomedical and Life Sciences, Glasgow University, Glasgow G12 8QQ, UK

Summary

1. Interactions between captive-reared and wild salmonids are frequent because hatcheries annually rear millions of fish for release in conservation programmes while many thousands of domesticated fish escape from fish farms. However, the outcome of competition between captive-reared and wild fish is not clear: wild fish may be smaller and less aggressive than hatchery fish, but they have more local experience and a prior residence advantage. Moreover, it is important to know whether any competitive differences are genetic (due to the process of domestication) or due to the rearing environment.

2. We therefore examined the factors influencing competition for feeding territories in juvenile Atlantic salmon. We studied the effect of domestication by using three independent stocks of both domesticated and wild-origin fish, all of which were reared in a common hatchery environment. We also used fish from the same wild stocks that had been living in the wild. Territorial contests were staged in stream tank compartments between pairs of fish differing in origin or rearing environment; the relative importance of body size and prior residence was also assessed.

3. All three stocks of domesticated fish were generally dominant over wild-origin fish when both had been raised in a common hatchery environment. If the wild-origin fish were given a 2-day period of prior residence on the territory this asymmetry in dominance was reversed. However, domesticated fish did not gain any additional advantage from being prior residents. The relative body size of the two contestants had a negligible effect on contest outcomes.

4. Truly wild fish (i.e. those of wild origin that had also grown up in the wild) were generally dominant over domesticated or wild-origin fish that had been hatchery-reared. Differences in body size between contestants had no effect on the outcome.

5. *Synthesis and applications.* These results show that, while juvenile farmed Atlantic salmon are inherently more aggressive than wild-origin fish, the hatchery environment reduces their ability to compete for territories with wild resident fish. Rearing salmon in conventional hatcheries for later release into the wild where natural populations already exist may not be a prudent conservation measure; it is preferable to plant eggs or first-feeding fry rather than attempt to 'help' the fish by rearing them through the early life stages.

Key-words: aquaculture, Atlantic salmon, captive breeding, enhancement, fish, reintroduction, territory.

Journal of Applied Ecology (2003) **40**, 535–544

Introduction

Reintroduction programmes have become an increasingly common tool in the conservation of rare and endangered populations (Ebenhard 1995; Sarrazin & Barbault 1996; Wolf *et al.* 1996). These generally involve the establishment of a captive breeding population, followed by the release of captive-born young into the wild, often alongside the remaining wild population. Such programmes are time-consuming and expensive, yet their success is rarely monitored in terms of the long-term viability and impact of the released animals (Ostermann, Deforge & Edge 2001). This has been especially evident in attempts to conserve fish populations: Waples, Ford & Schmitt (2003) reviewed 22 major 'supplementation' programmes (i.e. schemes to conserve wild stocks by the addition of captive reared individuals of the same genetic origin) for Pacific salmonids on the west coast of North America and found that not one involved the monitoring of the fitness of the released fish or their impact on the remnant wild population.

This is surprising, as it is possible that the process of rearing animals in captivity will lead to changes in phenotype (which can be either deliberate or unintentional) in comparison with their wild progenitors (Brown & Laland 2001). There are two separate causes of such effects. One is genetic selection for particular traits that are desired or favoured by captive conditions or genetically linked to such traits. This is the process of domestication, which can be unintentional as well as deliberate. The second is the effect of the environment on the phenotype. When it occurs this is usually a direct effect (the phenotype being altered by the environment in which it is reared) but intergenerational (maternal) effects are also possible, where the captive environment experienced by the parents influences the offspring's phenotype (Berejikian *et al.* 1999).

These changes in phenotype and/or genotype can cause problems when the captive-bred animals then come into contact with the wild population. While this may be deliberate, it can also be accidental, when farmed animals escape in an area containing their wild counterparts. These issues are perhaps most acute in the case of salmonid fishes, as millions of captive-reared fish are released each year into areas containing wild stocks, either intentionally, as part of conservation programmes (Einum & Fleming 2001; Levin, Zabel & Williams 2001; Waples, Ford & Schmitt 2003), or accidentally, as a result of escaping from intensive fish farms (Jonsson 1997). In the former case it is desirable for the released fish to perform as similarly as possible to the wild fish. In contrast, in the latter situation the ideal scenario is where the escaped fish are so outcompeted by the wild animals that their contribution to the future gene pool is minimal; in this way the local adaptations of the wild stocks are not diluted by the introgression of genes from domesticated animals.

While there is increasing concern over the impact of escaped or released fish on wild stocks (Levin, Zabel & Williams 2001), there is little quantitative information with which to evaluate the risks. The fate and impact of released or escaped captive-reared fish can be assessed at a population level by monitoring the relative abundance of either the animals themselves or their genes (Nickelson, Solazzi & Johnson 1986; Skaala, Jorstad & Borgstrøm 1996; Fleming *et al.* 2000). These approaches do not indicate the mechanisms behind any differences in fitness; for this it is necessary to examine the behaviour and performance of individual animals, in particular their competitive ability in comparison with that of wild conspecifics. However, the outcome of interactions between wild and captive-reared individuals is hard to predict. Animals that have been reared in captivity may be more aggressive, larger or (initially) better nourished than their wild counterparts, and so may outcompete them for scarce resources. Conversely, they may be inexperienced at finding or competing for food, seeking shelter or avoiding predators, and so may be at a disadvantage (Youngson & Verspoor 1998; Einum & Fleming 2001). Wild fish already established in a habitat may also have a prior residence advantage (Cutts, Metcalfe & Taylor 1999) in competition with intruders. There are therefore several competitive asymmetries that may act in different directions. Moreover, any of these traits may be affected either by domestication or by the rearing environment, and it is essential to know which process is most important because fish used in supplementation programmes tend to be genetically similar to the wild fish with which they may compete and have only experienced a different rearing environment, while escaped farmed fish are also at least partially domesticated.

While there have been several previous studies of the relative competitive abilities of wild and hatchery salmonid fish, they have produced ambiguous results. In some cases it was not possible to tell whether differences between fish were a result of domestication or the hatchery-rearing environment (Mesa 1991; Deverill, Adams & Bean 1999; Reinhardt, Yamamoto & Nakano 2001). Where these factors have been tested separately, the rearing environment has sometimes been found to have a negligible impact (Dickson & MacCrimmon 1982; Berejikian, Mathews & Quinn 1996) while in other cases the effect of the environment has been significant but contradictory (Rhodes & Quinn 1998, 1999; in comparison with Berejikian *et al.* 2000, 2001). Some of these discrepancies may have arisen because of small sample sizes or genetic differences between stocks (as salmonids are known to exhibit stock-specific differences in behaviour; Taylor 1991).

Therefore, this study used large sample sizes and a range of both farmed and wild stocks to look for general patterns of (i) how domestication has influenced the ability of juvenile Atlantic salmon *Salmo salar* L. to compete for territories; (ii) whether this competitive

asymmetry is influenced if wild-origin fish are already resident on a territory; and (iii) whether the rearing environment (hatchery vs. wild) also influences competitive ability. In all cases the importance of the relative body size of the two competitors was also assessed.

Methods

STOCKS OF HATCHERY-REARED FISH

Three sources of both domesticated (farmed) and wild-origin fish were reared in the hatchery, in order to be able to test for general differences between domesticated and wild fish. The domesticated stocks were two independent lines from Marine Harvest Ltd (Fort William, UK) and one from the Fisheries Research Services Marine Laboratory salmon hatchery at Aultbea, north-west Scotland. The first Marine Harvest stock (hereafter referred to as Farm1h, the 'h' denoting hatchery-reared) was a 'high grilse' line originally derived from salmon from Scottish highland rivers and subjected to six generations of selective breeding in aquaculture. The second Marine Harvest stock (hereafter Farm2h) was derived from a cross between a 'low grilse' line (farmed for c. 15 years in the UK but originally from Norwegian fish from the Namsen River and from the A/S Mowi Co., Bergen, Norway) and the standard stock used by the Booker McConnell Ltd farms (Edinburgh, UK) (derived from a mixture of Scottish and Norwegian fish). This stock had gone through seven farmed generations. The Aultbea stock (Farm3h) was based on the Norwegian A/S Mowi stock, and had been farmed for 10 generations. Because A/S Mowi was the major original source of fish for the UK salmon farming industry, while Booker McConnell and Marine Harvest were the major companies producing their own selected lines in the UK, these three farmed stocks were representative of the typical salmon currently farmed in the UK.

Each farmed stock was compared against a separate wild-origin stock; fish from these wild-origin stocks were either hatchery-reared (Wildxh) or had been living in the wild (Wildxw). Wild1h were the mixed family offspring of wild mature parents that had been caught during the breeding season in the River Braan, east Scotland, and stripped of eggs and sperm. Wild2h were similarly the offspring of wild spawning fish caught in the catchment of Loch Lomond, west Scotland, while Wild3h were the offspring of wild spawning parents from the River Almond, east Scotland.

All hatchery-reared stocks were raised from the fertilized egg stage in conditions resembling those in commercial hatcheries (i.e. in bare tanks at densities in excess of 500 fish m⁻², with commercial pelleted food supplied regularly by automatic feeders). Prior to testing they were also fed with bloodworms (chironomid larvae) dropped by hand onto the water surface; this is a preferred food type used later in the dominance trials.

STOCKS OF WILD-GROWN FISH

In order to investigate the effect of the rearing environment upon competitive ability, fish that had grown up in the natural environment were obtained for each of the wild-origin stocks. For the Wild1w and Wild3w stocks, these wild-grown fish were obtained by hand planting into streams from their natural catchment several thousand randomly selected eggs from the same families as were then raised in the hatchery. The 'nursery' streams were above an impassable waterfall and so contained no other salmon. The comparison between hatchery-reared and wild-grown fish for these two stocks was therefore between fish drawn from an identical genetic background. This procedure was not possible for the Wild2 stock and so the wild-grown fish (Wild2w) were caught in the same river as the parents of the hatchery-reared fish, so were presumed to be of similar genetic composition. All wild-grown fish were caught by electrofishing and taken to the same aquarium rooms on the Glasgow University campus, Scotland, as housed the hatchery-reared fish. Here they were placed in stock tanks and fed *ad libitum* on bloodworms dropped onto the water surface. They were allowed to settle for at least 3 weeks prior to being tested; this settling period was necessary to offset any effect of being electrofished, but was insufficient to cause the fish to behave like hatchery-reared fish (see the Results).

DESCRIPTION OF EXPERIMENTS

Experiment 1 was designed to investigate the effects of both domestication and relative body size in determining dominance in pairs of hatchery-reared fish. It was carried out on fish less than 2 months old, and pairs of fish were selected to create as large a range of relative body sizes (measured as wet mass) as possible. The majority of the pairings were between a farm and a wild-origin fish (Farm1h fish being paired with Wild1h, Farm2h with Wild2h, etc.), but for two representative stocks (Farm1h and Wild1h) pairs were also created using two fish from the *same* stock in order to establish the importance of body size in the absence of stock differences.

Experiment 2 tested how prior residence in a territory affected the outcome of dominance interactions between hatchery-reared fish. The same pairings were used as in Experiment 1 (including the two within-stock pairings), but this time one of the fish was intruding into the space that had already been occupied for 2 days by the other (see below for details). For the Farm1h–Wild1h pairing, both combinations of prior resident and intruder were tested. However, for the other pairings the farmed fish was used as the intruder and the wild-origin fish was used as the resident in order to reduce the number of possible combinations to manageable proportions (this combination being the most likely one to occur in nature). Experiment 2 was conducted on fish 2–3 months old.

Experiment 3 tested how the early environment affected the outcome of dominance interactions, using the same farm-wild origin stock pairings as the other two experiments. In this case the farm fish were from the same source of hatchery-reared fish as experiments 1 and 2 (i.e. Farm1h, Farm2h and Farm3h) but the wild fish were those that had grown in the wild (Wild1w, Wild2w and Wild3w). In addition, Wild1w fish were tested against Wild1h to examine the effect of rearing environment in the absence of stock differences. This experiment was carried out when the fish were 4–5 months old (i.e. when the wild-grown fish had approximately 3–4 months experience of feeding in the wild).

METHODOLOGY FOR TESTING RELATIVE DOMINANCE

All experiments were conducted in a purpose-built recirculating aquarium system, consisting of four linked glass channels (180 × 25 cm). Water was pumped to the uppermost of these and then flowed through them at 10–15 cm⁻¹ (at a depth of 10 cm) before returning to a filtration sump tank. This system was given a partial water change approximately weekly. The glass tanks were fitted with white plastic longitudinal and mesh transverse dividers to give a total of 60 smaller compartments (20 × 12.5 cm) for experiments 1 and 2, which used young fry, or 30 larger compartments (40 × 12.5 cm) for experiment 3 using larger fry. These compartment sizes ranged from 23% (experiment 3) to 76% (experiment 1) of the predicted territory size of average sized fish (Grant & Kramer 1990), so would induce the two fish to compete for a single territory rather than establish two separate territories. Because young salmon prefer a dark substrate, the floor of each compartment was covered with white gravel with a small patch of black gravel in the centre in order to produce a single preferred position (and so induce competition).

All experiments used pairs of fish in testing for dominance relationships. The two fish in a pair were distinguished on the basis of a single alcian blue dyemark on either the dorsal or caudal fin (chosen at random), administered under anaesthetic when the fish were weighed (to 0.01 g) prior to each experimental trial. In experiments 1 and 3 the two fish were then placed simultaneously in the same compartment and allowed to settle for 2 days prior to the 2 days during which behavioural observations were made. In experiment 2 (investigating the relative importance of prior residence) the two fish were placed in separate adjacent compartments and allowed to settle alone for 2 days. The opaque partition separating these two compartments was fitted with a sliding door that was opened on the morning of the third day, and one fish was prompted (using a transparent rod) to move through the opening. The door was then closed, so creating the situation of one fish (the intruder) entering the com-

partment that had been occupied by the other (the resident) for 2 days. In all experiments, the fish were fed periodically during the 2-day settling period by releasing single bloodworms with a pipette at the water surface at the upstream end of each compartment.

While dominance would ideally be quantified in terms of aggressive interactions, in practice pairs of juvenile salmon establish dominance relationships very quickly, after which point aggression rates decline markedly (O'Connor, Metcalfe & Taylor 1999). As a result, few interactions were noted during behavioural observations. Therefore, as in previous studies (Metcalfe *et al.* 1989; Johnsson, Jönsson & Björnsson 1996; Cutts, Metcalfe & Taylor 1999), dominance was measured in all experiments in terms of relative spatial positions in the tank. The positions of the two fish within the compartment were recorded five times on each observation day, with an hour between successive measurements. Spatial positions were quantified in three dimensions by marking each axis of a compartment into three equal lengths (to give 27 equal-sized cuboid zones, each larger than a test fish). The zone occupied by the eye of the fish was used as the measure of spatial position. Immediately after each recording of spatial positions a single bloodworm was released into the compartment using the same method as employed in the settling period. Fish were given additional bloodworms at the end of each observation day. At the end of the trial they were removed and replaced with new fish; no fish was used more than once in any experiment.

Previous research has shown that dominant juvenile salmonids occupy central-rear positions within simulated feeding territories, often maintaining position just off the substrate, while subordinates confined with a dominant usually remain on the periphery (Metcalfe *et al.* 1989; Johnsson, Jönsson & Björnsson 1996). Therefore spatial records in zones in the lower two-thirds of the water column at the centre and back of the compartment were given a score of +1, those in the corners of the compartment were given a score of -1, and all other positions were given a score of 0. The 2 days of observation yielded 10 records of spatial positions for each member of a pair of fish. The total scores for spatial positions could therefore range from -10 (for a fish always found in the most subordinate positions in a compartment) to +10 (a fish always found in the preferred positions). A fish was considered dominant over its partner if its position score was at least 4 points greater than that of its opponent, otherwise the outcome was regarded as inconclusive. Statistical analyses were restricted to contests with a conclusive outcome.

In order to examine the effect of relative body size on the likelihood of a fish becoming dominant, the outcomes of the within-stock pairings were analysed using stepwise logistic regression. One fish was chosen at random from each pair. The success of this fish was taken to be the dependent variable and was scored as 1 (if it was the dominant) or 0 (if it was the subordinate). The difference in body size (defined as the percentage

Table 1. Summary details of the three experiments, giving the total number of territorial contests, the number that had a conclusive outcome (i.e. where one fish was clearly dominant) and, for these conclusive contests, the mean mass of the two fish. See text for descriptions of the different salmon stocks (NA, not applicable)

Stock 1	Stock 2	Total <i>n</i>	Conclusive <i>n</i>	Mean mass (g) ± SE	
				Stock 1	Stock 2
Experiment 1. Effect of domestication and body size					
Farm1h	Farm1h	93	47	0.29 ± 0.01	NA
Wild1h	Wild1h	94	66	0.30 ± 0.01	NA
Farm1h	Wild1h	195	123	0.20 ± 0.01	0.20 ± 0.01
Farm2h	Wild2h	64	41	0.35 ± 0.01	0.34 ± 0.01
Farm3h	Wild3h	76	54	0.34 ± 0.01	0.34 ± 0.01
Experiment 2. Effect of prior residence (prior resident = stock 1)					
Farm1h	Farm1h	72	55	1.01 ± 0.09	1.20 ± 0.10
Wild1h	Wild1h	61	50	1.07 ± 0.06	1.29 ± 0.10
Wild1h	Farm1h	78	68	1.13 ± 0.07	1.32 ± 0.09
Wild2h	Farm2h	48	30	0.69 ± 0.03	0.70 ± 0.03
Wild3h	Farm3h	52	32	0.96 ± 0.03	0.96 ± 0.03
Farm1h	Wild1h	75	69	1.22 ± 0.09	1.41 ± 0.09
Experiment 3. Effect of rearing environment (hatchery-reared = stock 1)					
Wild1h	Wild1w	87	57	2.84 ± 0.09	2.38 ± 0.08
Farm1h	Wild1w	60	42	3.53 ± 0.12	3.72 ± 0.13
Farm2h	Wild2w	45	35	2.64 ± 0.08	2.63 ± 0.09
Farm3h	Wild3w	46	30	3.33 ± 0.12	3.24 ± 0.11

deviation in body mass of the target fish from its opponent) was used as the independent covariate.

Results

EXPERIMENT 1: EFFECT OF BODY SIZE AND STOCK ORIGIN

In total 522 pairs of fish were tested, of which 331 demonstrated conclusive dominance relationships (Table 1). Clear outcomes were obtained for 113 pairs of fish drawn from the same stock (either Farm1h or Wild1h). The difference in body size of the contestants (up to 59.3% in Farm1h and 182.4% in Wild1h fish) had no overall effect on the outcome of the contest ($P = 0.66$). However, there was a marginally significant interaction between the weight difference and the stock identity of the pair (Wald statistic = 3.95, 1 d.f., $P = 0.047$), indicating that the effect of relative body size was not the same in contests between pairs of Farm1h fish as it was between pairs of Wild1h fish. Further analysis on each stock separately showed that the relative body size of the two contestants had a marginally significant effect on the outcome in pairings of Farm1h fish (logistic regression, effect of size difference: Wald statistic = 3.97, 1 d.f., $P = 0.046$) but had no effect in pairings of Wild1h fish ($P = 0.81$).

Results of the mixed pairs (farm vs. wild-origin) were analysed in a similar manner. Logistic regression was again used, but this time the wild-origin fish was always taken to be the focal individual. In addition, 'stock pairing' (i.e. whether Farm1h–Wild1h, Farm2h–Wild2h or Farm3h–Wild3h) was included as a factor in

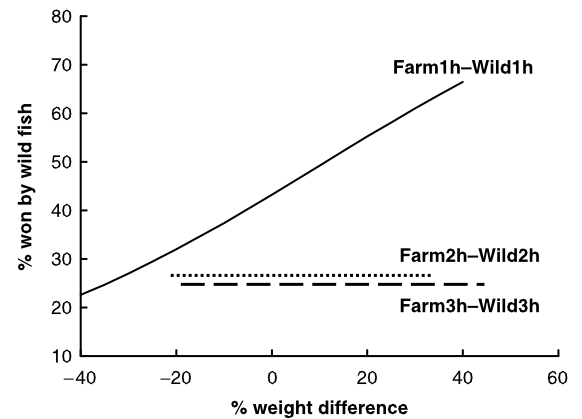


Fig. 1. Effect of the relative body weight of two salmon on the outcome of territorial contests in experiment 1; all fish were hatchery-reared and arrived simultaneously in the habitat. Results are shown separately for the three stock pairings of farm and hatchery-origin fish; the lines show the significant logistic regression line for the Farm1h–Wild1h pairs and the mean values for the other stock pairs in which the relative body size of the two contestants was not significant. See text for definitions.

the logistic regression, together with its interaction with size difference (with the two fish differing by up to 55.6%, 32.5% and 42.3%, respectively, for the three stock pairings). There was a significant effect of stock pairing (Wald = 6.58, 2 d.f., $P = 0.037$), with the wild-origin fish being more likely to be dominant in the Farm1h–Wild1h pairings than in any other farm–wild combination (Fig. 1). Moreover, there was a significant interaction between stock pairing and size difference (Wald = 6.74, 2 d.f., $P = 0.034$) but no overall effect of

size difference ($P = 0.94$). This was due to the relative size difference of the two fish having a strong effect in the Farm1h–Wild1h pairing (with the wild fish being increasingly likely to dominate as its size advantage increased) but no effect at all in the other two stock pairings (Fig. 1). The constant in the overall logistic regression was significantly less than 0.5 (Wald = 11.43, 1 d.f., $P = 0.001$), indicating that there was a general trend for the farmed stock fish to be dominant over the wild-origin fish; overall farmed fish dominated in 64.7% of resolved contests.

These results were confirmed in separate logistic regressions conducted on each stock pairing. Thus in the Farm1h–Wild1h pairs there was a significant effect of size difference ($P = 0.012$) while the constant was not different from 0.5 ($P = 0.15$), indicating that contests were usually decided on the basis of differences in body size rather than stock origin (Fig. 1). In contrast, in the other two stock pairings (Farm2h–Wild2h and Farm3h–Wild3h) there was no effect of size difference but the constant was in both cases significantly less than 0.5 ($P = 0.004$ and $P = 0.001$, respectively), indicating that the farmed fish tended to be dominant in approximately 75% of resolved contests irrespective of relative size differences (Fig. 1). In summary, the overall trend was for the relative body sizes of two contestants to play some role in determining dominance where the fish were from the same population, but this was of lesser significance than stock origin in mixed pairings, with farmed fish tending to dominate wild-origin opponents.

EXPERIMENT 2: EFFECT OF PRIOR RESIDENCE

A total of 386 separate trials was run, of which 304 gave a clear outcome (Table 1). The results of this experiment were also analysed using a logistic regression approach, this time taking the prior resident to be the focal fish. The first analysis was of the within-stock pairings (Farm1h–Farm1h and Wild1h–Wild1h), with size difference (up to 139.4% and 154.7%, respectively) as the independent variable and stock as a factor. Prior residents were more likely to be dominant than intruders (i.e. the regression constant was significantly different from 0.5, Wald = 10.01, 1 d.f., $P = 0.002$) but there was no effect of stock ($P = 0.38$) or relative size difference ($P = 0.12$), nor any interaction between stock and size difference ($P = 0.14$). When the analysis was repeated on each stock separately, the prior residence advantage was very pronounced in pairs of Wild1h fish (Wald = 7.54, 1 d.f., $P = 0.006$) but not significant in contests between Farm1h (Wald = 3.01, 1 d.f., $P = 0.08$), suggesting that the prior residence convention was more established in fish of wild origin (Fig. 2a). The effect of size differences was non-significant in both stocks.

Data on clear dominance relationships were obtained from 199 pairs where there was a stock difference between the two fish as well as an asymmetry in prior residence. Prior residents were significantly more

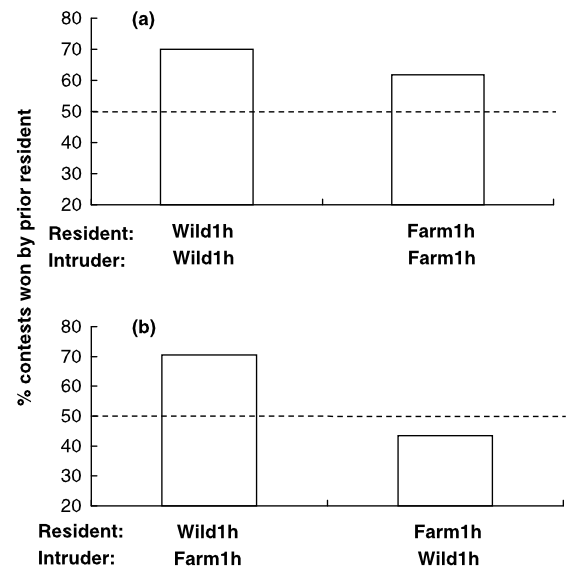


Fig. 2. The effect of prior residency on the outcome of territorial contests in experiment 2. (a) In contests between two Farm1h or two Wild1h fish, the wild-origin fish was dominant significantly more often than by chance if it was already resident on the territory, but the farmed fish gained no prior residency advantage. (b) A similar effect was found in between-stock contests, with prior residency affecting the outcome if the resident was of wild origin but not if it was farmed. The dashed line indicates the random expectation; see text for statistical analyses.

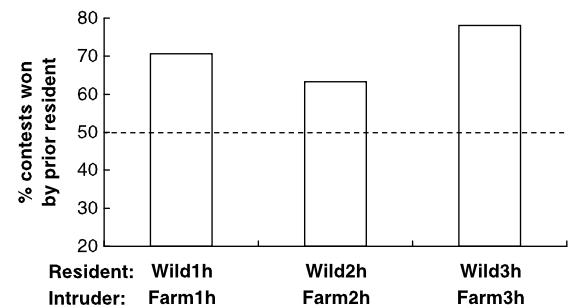


Fig. 3. Summary of territorial contests in experiment 2 between prior resident fish of wild origin and intruding farmed fish. The strength of the prior resident effect is evident from comparing these results with those for the same stocks of fish in Fig. 1, where the farmed fish tended to be dominant. See text for statistical analyses.

likely to be dominant than were intruders (logistic regression, Wald = 8.86, 1 d.f., $P = 0.003$) and this effect was independent of the size difference of the two fish (effect of size difference of up to 67.2%: $P = 0.29$). However, the strength of this effect differed between the stocks (Wald = 14.91, 3 d.f., $P = 0.002$), with farmed fish obtaining less of a benefit from prior residence than wild-origin fish ($\chi^2 = 15.58$, 3 d.f., $P = 0.001$; Fig. 2b). Thus if the wild-origin fish was the prior resident it became dominant on an average of 70.8% of the resolved conflicts [significantly different from a random 50% ($P < 0.01$) with no difference between the wild-origin stocks in the strength of this prior residence advantage; Fig. 3]. However, if the

farmed fish was the prior resident and the wild-origin fish was the intruder, then the farmed fish only became dominant on 43.5% of resolved conflicts (not significantly different from random). Again the relative size of the two contestants had no effect on the outcome in any of these comparisons ($P > 0.36$).

EXPERIMENT 3: EFFECT OF REARING ENVIRONMENT

A total of 240 separate contests between a hatchery-reared and a wild-grown fish were run, in 164 of which a clear dominant individual was identified. In the overall comparison the wild-grown fish were dominant in 72.0% of the contests with a clear outcome, significantly more than expected by chance (logistic regression, Wald = 14.92, 1 d.f., $P < 0.001$). Again the relative sizes of the two contestants did not influence the results ($P = 0.14$, despite the contestants differing by up to 157% in weight) but there was an effect of the stock identity of the fish (Wald = 23.35, 3 d.f., $P < 0.001$). This stock effect was due to the unusual results from one particular pairing. In three of the four pairings (Wild1w–Farm1h, Wild2w–Farm2h and Wild1w–Wild1h), the wild-grown fish were significantly more likely to be dominant than their hatchery-reared opponents, in 85.7%, 80.0% and 77.2% of resolved contests, respectively ($P < 0.01$). However, in the remaining pairing (Wild3w–Farm3h) the wild-grown fish only became dominant in 33.3% of such contests, not significantly different from random ($P = 0.074$). Circumstantial evidence of a lack of appetite while in the holding tank suggests that this may have been because the wild fish in this stock had not adjusted fully to the laboratory environment at the time of the tests. If this stock is ignored, the results indicate that fish that had grown up in the wild were more dominant.

This influence of rearing environment is seen most clearly if the results from experiment 1 are compared with those from experiment 3 for the same stock pairings (Fig. 4). Thus in contests between Farm1h and Wild1 fish, the wild-origin fish only dominated in

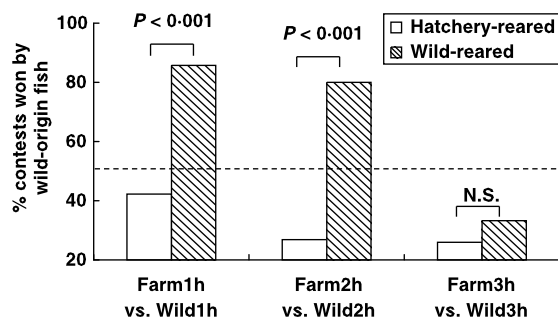


Fig. 4. Effect of the rearing environment of wild-origin fish on the outcome of territorial contests with farmed fish. When the wild origin fish had been reared in the hatchery (open bars, experiment 1) they tended to lose the encounters, whereas this was reversed in two of the three wild stocks if they had been reared in the wild (shaded bars, experiment 3).

42.3% of resolved contests if they had been reared in the hatchery (experiment 1), but 85.7% if they had grown up in the wild (experiment 3). Logistic regression (to control for the small effect of relative size in this stock pair) showed that the rearing environment of the wild fish had a highly significant effect on the outcome (Wald = 18.54, 1 d.f., $P < 0.001$). Similarly hatchery-reared Wild2 fish were dominant in only 26.8% of contests with Farm2 fish with a clear outcome, whereas wild-grown Wild2 fish were dominant in 80.0% of such contests against the same opponents ($\chi^2 = 19.29$, 1 d.f., $P < 0.001$).

Discussion

The results of this study have implications for both the likely adverse effect of escaped farmed salmon and the impact of releasing captive-reared fish in conservation programmes, as domestication and the rearing environment were found to have independent effects on the competitive ability of the fish. Ruzzante (1994) pointed out that the effect of domestication on behaviours associated with dominance will depend on the nature of the captive environment. In general, the process of domestication tends to involve selection for more rapid growth, but whether this leads to increased or decreased dominance behaviour depends on whether this is rewarded by greater access to food in the rearing environment. In the present study there was a consistent pattern for the domesticated stocks to be more dominant than the wild hatchery-reared fish. This is in line with most (but not all) of the previous studies that have teased apart the effect of domestication from that of the rearing environment (reviewed by Einum & Fleming 2001; Einum & Fleming 1997). Behavioural traits are quickly altered by domestication, usually by altering their intensities of performance or frequency of use rather than their nature (Ruzzante 1994). Greater aggression in hatcheries presumably has the benefit of ensuring greater access to predictably patchy food resources. While aggression in salmonids is positively linked to intrinsically higher standard metabolic rates (Metcalfe, Taylor & Thorpe 1995; McCarthy 2001), the fitness cost of an increased energetic expenditure is presumably lower under the *ad lib.* food regime of a hatchery than it is in the wild, so allowing the evolution of aggression rates to levels that would be detrimental to fitness in the wild.

There was a strong effect of prior residence, with fish that had already been present in the contested area for 2 days having a significant dominance advantage over newly arrived intruders. This is a widespread phenomenon in territorial animals (Baugh & Forester 1994; Tobias 1997; Olsson & Shine 2000) and has been documented in a range of salmonids (Chandler & Bjornn 1988; Cutts, Metcalfe & Taylor 1999; Johnsson, Nöbbelin & Bohlin 1999). Three explanations have been proposed for the phenomenon (reviewed by Tobias 1997). The resource-holding potential hypothesis

suggests that territory owners tend to defeat intruders because only individuals of superior quality will have obtained territories in the first place. The value asymmetry hypothesis suggests that the result is due to the territory being more valuable (or its value is more known) to the holder than to the intruder, so that the holder is prepared to fight harder. Finally the uncorrelated asymmetry hypothesis proposes that contests are determined by an arbitrary convention, such as 'owner always wins'. This is perhaps the least likely explanation because it is inherently unstable (Grafen 1987).

Because owners in the present study tended to defeat intruders despite having been allocated to their respective roles at random with respect to their inherent quality, the results cannot be explained by the resource-holding potential hypothesis. However, they do fit the value asymmetry hypothesis; moreover Johnsson, Carlsson & Sundström (2000) found that juvenile brown trout defended a territory more vigorously if it was in their preferred habitat, while Johnsson & Forser (2002) found that the tendency for them to defeat an intruder increased with their length of residency on the territory (and hence the greater their knowledge of its resource base). Therefore juvenile salmonids that have been resident on a feeding territory for just a few days (Cutts, Metcalfe & Taylor 1999; Johnsson & Forser 2002) become highly motivated to fight for it.

It is noteworthy that in almost all of the experiments and analyses the relative body size of the two contestants for a territory had no effect on the outcome, even when one fish was more than twice the mass of the other. This is a curious result as body size is a strong predictor of fighting ability in most animal groups (Huntingford & Turner 1987), but it is in agreement with other studies of Atlantic salmon (Huntingford *et al.* 1990; Metcalfe, Taylor & Thorpe 1995). Cutts, Metcalfe & Taylor (1999) did find a trend for larger intruders to displace residents in similar experiments using the same species, but here we have used a much larger sample size and variation in body size and found no trend, so if there is a size effect it cannot be strong. This is in contrast to the situation found in other species of fish, where intruders can displace residents if they have a sufficient size advantage (Rhodes & Quinn 1998; Johnsson, Nöbbelin & Bohlin 1999). The explanation for the tenacity of residents undoubtedly lies in the fitness consequences of losing a territory: Elliott (1994) concluded that dispersing trout fry that failed to establish themselves in a feeding territory within the first few months of life drifted downstream and died of starvation.

The prior residence effect more than offset that of domestication, so that while the farmed fish were dominant over the wild-origin fish in all three wild-farm comparisons when the fish were tested in a 'neutral' habitat this was reversed when the wild-origin fish were previously resident on a territory. Especially interesting was the fact that the domesticated fish did not obtain any additional advantage from prior residence: farmed

fish that had been resident on a territory did not defeat wild-origin intruders any more than would be expected by chance. As the prior ownership effect in salmonids seems to arise from an asymmetry in the value placed on the territory by the two fish, this indicates that the farmed fish did not perceive their territory as valuable and so did not match their defensive aggression to the perceived quality of the site. This suggests that domestication may have led to a reduced ability to establish territories and/or recognize suitable habitats.

A comparison of experiments 1 and 3 shows that the rearing environment generally had a strong effect on competitive ability. Salmon that had grown up in the wild tended to be dominant over hatchery-reared fish from the same genetic stock; similar results were obtained by Berejikian *et al.* (2000, 2001). Moreover, wild-origin fish that had been reared in the hatchery tended to be subordinate to farmed fish, whereas if they had lived in the wild they were usually dominant. It is increasingly being recognized that the effect of the early rearing environment on behaviour later in life can be complex and difficult to predict (Olla, Davis & Ryer 1998; Brown & Laland 2001; Wurbel 2001; Perrett *et al.* 2002). Fish reared in a hatchery do not gain experience of defending territories, and in fact may use aggression inappropriately because the high densities at which they have lived result in aggressive interactions being performed between unfamiliar opponents and over a very restricted spatial scale. Thus hatchery-reared fish may exhibit a similar level of aggressiveness as wild-grown fish (Berejikian, Mathews & Quinn 1996) but may behave differently in aggressive interactions (Fleming, Lamberg & Jonsson 1997; Berejikian *et al.* 2001) and so fail to win territorial contests.

While domesticated fish are usually inherently more aggressive or dominant than wild-origin fish reared in the same environment (Einum & Fleming 2001; this study), they tend not to be able to displace wild fish with a prior residence advantage, and the rearing environment also puts them at a disadvantage in comparison with wild-grown fish. These results suggest that juvenile Atlantic salmon that escape from fish farms may not be able to supplant wild conspecifics from freshwater feeding territories, especially as the greater size-at-age of farmed fish does not appear to give them any marked dominance advantage in this species. Moreover, the tendency of domesticated fish not to fight harder when territory owners may result in their not being able to retain feeding territories.

Therefore escapes of Atlantic salmon from fish farms at the juvenile freshwater stage of the life cycle may have less of an impact on wild populations than might be presumed from the relative abundance of the fish. However, even if their survival rate is lower than that of wild fish, they may still have a deleterious effect due to the scale of the number escaping. Moreover, it should be borne in mind that most escapes of farmed salmon occur during the marine phase, when damage by predators or storms to the net cages in which the fish

are usually reared can result in the simultaneous release of many thousands of fish. Because the fish are no longer territorial and have few predators at this stage of the life cycle they may be less disadvantaged in comparison with the wild fish, so leading to significant numbers of farmed fish surviving through to sexual maturation (Jonsson 1997).

Our results indicate that salmonid conservation programmes that are based on the captive-rearing of fish for later release into areas already containing wild populations are likely to be problematic. Even a period of a few months in the hatchery reduced the ability of the fish to compete for territories, which may explain the greater movement rate and poorer growth of hatchery trout stocked into streams in comparison with wild conspecifics (Bohlin *et al.* 2002). While experimental studies suggest that modifying the tank environment can partially reduce the deleterious effects of the hatchery (Berejikian *et al.* 2000, 2001; Brown & Laland 2001), no demonstration on the scale currently implemented by the major supplementation projects has occurred. Given that large-scale releases of hatchery fish may cause other problems for wild remnant populations (such as attracting predators or reducing the availability of food) (Einum & Fleming 2001; Levin, Zabel & Williams 2001), it may be more prudent to plant eggs or first-feeding fry rather than attempt to 'help' the fish by rearing them through the early life stages.

Acknowledgements

We thank Gordon Beaton at Marine Harvest's Invergarry hatchery, Phil McLaughlin at the FRS Marine Laboratory Salmon Hatchery at Aultbea, Mike Miles at the FRS Freshwater Laboratory Salmon Hatchery at Almondbank, Matt Stewart and Angus McRitchie of the Loch Lomond Angling Improvement Association and Keith Martin-Smith at Glasgow University for great help in obtaining the various stocks of fish. We are also grateful to Vivien Cameron and John Laurie for fish husbandry. Three referees made helpful comments on the manuscript. This study was funded by the Commission of the European Communities, Agriculture and Fisheries (FAIR) specific RTD programme CT-97-3498, 'Performance and Ecological Impacts of Introduced and Escaped Fish: Physiological and Behavioural Mechanisms'. This study does not necessarily reflect the view of CEC and in no way anticipates the Commission's future policy in this area.

References

Baugh, J.R. & Forester, D.C. (1994) Prior residence effect in the dart-poison frog, *Dendrobates pumilio*. *Behaviour*, **131**, 207–224.

Berejikian, B.A., Mathews, S.B. & Quinn, T.P. (1996) Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behaviour in steelhead trout (*Oncorhynchus mykiss*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 2004–2014.

Berejikian, B.A., Tezak, E.P., Flagg, T.A., LaRae, E.L., Kummerow, E. & Mahnken, C.V.W. (2000) Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 628–636.

Berejikian, B.A., Tezak, E.P., Riley, S.C. & LaRae, E.L. (2001) Competitive ability and social behaviour of juvenile steelhead reared in enriched and conventional hatchery tanks and a stream environment. *Journal of Fish Biology*, **59**, 1600–1613.

Berejikian, B.A., Tezak, E.P., Schroder, S.L., Flagg, T.A. & Knudsen, C.M. (1999) Competitive differences between newly emerged offspring of captive-reared and wild coho salmon. *Transactions of the American Fisheries Society*, **128**, 832–839.

Bohlin, T., Sundström, L.F., Johnsson, J.I., Höjesjö, J. & Pettersson, J. (2002) Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. *Journal of Animal Ecology*, **71**, 683–692.

Brown, C. & Laland, K. (2001) Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**, 471–493.

Chandler, G.L. & Bjornn, T.C. (1988) Abundance, growth, and interaction of juvenile steelhead relative to time of emergence. *Transactions of the American Fisheries Society*, **117**, 432–443.

Cutts, C.J., Metcalfe, N.B. & Taylor, A.C. (1999) Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar*. *Oikos*, **86**, 479–486.

Deverill, J.I., Adams, C.E. & Bean, C.W. (1999) Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout. *Journal of Fish Biology*, **55**, 868–875.

Dickson, T.A. & MacCrimmon, H.R. (1982) Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 1453–1458.

Ebenhard, T. (1995) Conservation breeding as a tool for saving animal species from extinction. *Trends in Ecology and Evolution*, **10**, 438–443.

Einum, S. & Fleming, I.A. (1997) Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *Journal of Fish Biology*, **50**, 634–651.

Einum, S. & Fleming, I.A. (2001) Implications of stocking: ecological interactions between wild and released salmonids. *Nordic Journal of Freshwater Research*, **75**, 56–70.

Elliott, J.M. (1994) *Quantitative Ecology and the Brown Trout*. Oxford University Press, Oxford, UK.

Fleming, I.A., Hindar, K., Mjølnerød, I.B., Jonsson, B., Balstad, T. & Lamberg, A. (2000) Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society of London B*, **267**, 1517–1523.

Fleming, I.A., Lamberg, A. & Jonsson, B. (1997) Effects of early experience on the reproductive performance of Atlantic salmon. *Behavioral Ecology*, **8**, 470–480.

Grafen, A. (1987) The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Animal Behaviour*, **35**, 462–467.

Grant, J.W.A. & Kramer, D.L. (1990) Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 1724–1737.

Huntingford, F.A. & Turner, A.K. (1987) *Animal Conflict*. Chapman & Hall, London, UK.

Huntingford, F.A., Metcalfe, N.B., Thorpe, J.E., Graham, W.D. & Adams, C.E. (1990) Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology*, **36**, 877–881.

- Johnsson, J.I. & Forser, A. (2002) Residence duration influences the outcome of territorial conflicts in brown trout (*Salmo trutta*). *Behavioral Ecology and Sociobiology*, **51**, 282–286.
- Johnsson, J.I., Carlsson, M. & Sundström, L.F. (2000) Habitat preference increases territorial defence in brown trout (*Salmo trutta*). *Behavioral Ecology and Sociobiology*, **48**, 373–377.
- Johnsson, J.I., Jönsson, E. & Björnsson, B.Th. (1996) Dominance, nutritional state, and growth hormone levels in rainbow trout (*Oncorhynchus mykiss*). *Hormones and Behavior*, **30**, 13–21.
- Johnsson, J.I., Nöbbelein, F. & Bohlin, T. (1999) Territorial competition among wild brown trout fry: effects of ownership and body size. *Journal of Fish Biology*, **54**, 469–472.
- Jonsson, B. (1997) A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES Journal of Marine Science*, **54**, 1031–1039.
- Levin, P.S., Zabel, R.W. & Williams, J.G. (2001) The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *Proceedings of the Royal Society of London B*, **268**, 1153–1159.
- McCarthy, I.D. (2001) Competitive ability is related to metabolic asymmetry in juvenile rainbow trout. *Journal of Fish Biology*, **59**, 1002–1014.
- Mesa, M.G. (1991) Variation in feeding, aggression, and position choice between hatchery and wild cutthroat trout in an artificial stream. *Transactions of the American Fisheries Society*, **120**, 723–727.
- Metcalfe, N.B., Huntingford, F.A., Graham, W.D. & Thorpe, J.E. (1989) Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London B*, **236**, 7–19.
- Metcalfe, N.B., Taylor, A.C. & Thorpe, J.E. (1995) Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behaviour*, **49**, 431–436.
- Nickelson, T.E., Solazzi, M.F. & Johnson, S.L. (1986) Use of hatchery coho salmon (*Oncorhynchus kisutch*) psmolts to rebuild wild populations in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 2443–2449.
- O'Connor, K.I., Metcalfe, N.B. & Taylor, A.C. (1999) Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Animal Behaviour*, **58**, 1269–1276.
- Olla, B.L., Davis, M.W. & Ryer, C.H. (1998) Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bulletin of Marine Science*, **62**, 531–550.
- Olsson, M. & Shine, R. (2000) Ownership influences the outcome of male–male contests in the scincid lizard, *Niveoscincus microlepidotus*. *Behavioral Ecology*, **11**, 587–590.
- Ostermann, S.D., Deforge, J.R. & Edge, W.D. (2001) Captive breeding and reintroduction evaluation criteria: a case study of peninsular bighorn sheep. *Conservation Biology*, **15**, 749–760.
- Perrett, D.I., Penton-Voak, I.S., Little, A.C., Tiddeman, B.P., Burt, D.M., Schmidt, N., Oxley, R., Kinloch, N. & Barrett, L. (2002) Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London B*, **269**, 873–880.
- Reinhardt, U.G., Yamamoto, T. & Nakano, S. (2001) Effects of body size and predators on intracohort competition in wild and domesticated juvenile salmon in a stream. *Ecological Research*, **16**, 327–334.
- Rhodes, J.S. & Quinn, T.P. (1998) Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. *Journal of Fish Biology*, **53**, 1220–1230.
- Rhodes, J.S. & Quinn, T.P. (1999) Comparative performance of genetically similar hatchery and naturally reared juvenile coho salmon in streams. *North American Journal of Fisheries Management*, **19**, 670–677.
- Ruzzante, D.E. (1994) Domestication effects on aggressive and schooling behaviour in fish. *Aquaculture*, **120**, 1–24.
- Sarrazin, F. & Barbault, R. (1996) Reintroduction: challenges and lessons for basic ecology. *Trends in Ecology and Evolution*, **11**, 474–478.
- Skaala, O., Jorstad, K.E. & Borgström, R. (1996) Genetic impact on two wild brown trout (*Salmo trutta*) populations after release of non-indigenous hatchery spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 2027–2035.
- Taylor, E.B. (1991) A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, **98**, 186–207.
- Tobias, J. (1997) Asymmetric territorial contests in the European robin: the role of settlement costs. *Animal Behaviour*, **54**, 9–21.
- Waples, R.S., Ford, M.J. & Schmitt, D. (2003) Empirical results from salmon supplementation: a preliminary assessment. *Ecological and Genetic Implications of Aquaculture Activities* (ed. T.M. Bert), in press. Kluwer Academic Publishers, Dordrecht.
- Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. (1996) Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology*, **10**, 1142–1154.
- Wurbel, H. (2001) Ideal homes? Housing effects on rodent brain and behaviour. *Trends in Neurosciences*, **24**, 207–211.
- Youngson, A.F. & Verspoor, E. (1998) Interactions between wild and introduced Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55** (Supplement 1), 153–160.

Received 5 September 2002; final copy received 11 February 2003