

Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*

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Summary

1. Variance in competitive ability among males should lead to a corresponding skew in reproductive success. Atlantic salmon (*Salmo salar*) males form dominance hierarchies during spawning, such that the dominant individuals are predicted to realize the highest reproductive success. However, the degree to which this occurs depends on various genetic and environmental factors.

2. We investigated the influence of the aquaculture environment on male Atlantic salmon behaviour during spawning in three experiments involving groups of either purely farmed or wild males, or mixed groups composed of equal numbers of farmed and wild fish. The objective of this study was to compare and contrast the formation of dominance hierarchies and relationships between aggression, courtship and spawning success in farmed and wild males.

3. Although farmed males did not establish dominance hierarchies as effectively as wild males, they courted and spawned with females in larger numbers and they frequently failed to release sperm when females released eggs.

4. Dominance structures established by wild males led to reliable behavioural correlates of spawning success; this was not the case among farmed males.

5. From the risk-assessment perspective, farmed males can be expected to have reduced spawning success, although the degree of reproductive inferiority of farmed relative to wild males depends upon rearing environment and the populations under consideration.

Key-words: domestication selection, farmed salmon, interbreeding, reproductive success, spawning behaviour.

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Introduction

Individual differences in reproductive success can often be attributed to competitive interactions for mates, expressed through a variety of phenotypic and behavioural characteristics (Andersson 1994). Consequently, high variance in competitive ability should be reflected by similarly skewed differences in individual reproductive success (e.g. Clutton-Brock, Albon & Guinness 1988; Davies 1991), notwithstanding the effects that various ecological and phylogenetic factors can have on fitness (Emlen & Oring 1977). Different

selection regimes resulting from varying ecological conditions among populations have been shown to influence characteristics directly involved in reproductive success, such as life-history traits (Reznick & Endler 1982), mating behaviour (Ptacek & Travis 1996; Van Parijs, Hastie & Thompson 2000) and incidence of multiple paternity (Kelly, Godin & Wright 1999). Adaptation to local environments owing to different selection pressures provides a potential means by which population differentiation may occur, such that differences within species can become genetically based (Roff 2002).

Domestication provides a striking example of the influence of intentional and unintentional selection on reproductive traits. Changes in age at maturity (Kallio-Nyberg & Koljonen 1997), spawning time (Webb *et al.*

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1991; Lura & Sægrov 1993), mating behaviour (Fleming & Gross 1992, 1993; Fleming *et al.* 1996, 1997; Berejikian *et al.* 1997; Berejikian *et al.* 2001a; Berejikian, Tezak & Schroder 2001b), and parental care (Spinka *et al.* 2000) have been documented in animals of farmed or hatchery origin. To date, most studies of the effect of domestication on behavioural traits have focused on differences between wild and domesticated groups of individuals rather than on differences in trait variance within groups.

Atlantic salmon (*Salmo salar* L.) is an ideal model organism in which to examine the behavioural causes of, and the effects of artificial selection on, individual variance in reproductive success. First, Atlantic salmon have undergone intense artificial selection in aquaculture facilities since the mid-1970s (see Gjedrem, Gjølén & Gjerde 1991 and Heggberget *et al.* 1993 for reviews) and have been raised in the hatchery environment for re-introduction programmes for decades. Differences in juvenile aggression (Fenderson, Everhart & Muth 1968; Einum & Fleming 1997; Fleming & Einum 1997), migratory behaviour (Jonsson, Jonsson & Hansen 1991; Jonsson, Hansen & Jonsson 1993), age at maturity (Jonsson *et al.* 1991; Kallio-Nyberg & Koljonen 1997) and spawning behaviour (Fleming *et al.* 1996; Fleming, Lamberg & Jonsson 1997) have been observed between groups of wild and farmed or hatchery-reared Atlantic salmon. Secondly, the mating system of Atlantic salmon is well known. The system is a polygamous one in which the primary mechanism of sexual selection is male contest competition (Jones 1959; Järvi 1990; Fleming 1996). Atlantic salmon anadromous males typically form a dominance hierarchy, in which one or a few individuals control access to females (Jones 1959; Järvi 1990; Fleming 1996) and the expected variance in individual reproductive success is correspondingly high (Jones & Hutchings 2001, 2002).

In the current study, we compare groups of farmed and wild Atlantic salmon in competition during spawning. Although some studies of this nature have been undertaken comparing hatchery and wild fish (e.g. Fleming & Gross 1992, 1993; Berejikian *et al.* 1997; Berejikian *et al.* 2001a), only one study has focused on interactions between fish farmed for aquaculture purposes and wild individuals (Fleming *et al.* 1996). The novelty of our approach lies in the fact that we are examining behaviour and spawning success in light of the behavioural and reproductive skew, or variance, among individuals. Furthermore, our study represents the most extensive analysis to date of behavioural interactions between farmed and wild Atlantic salmon during spawning. This approach is enlightening because Atlantic salmon males establish clear dominance relationships during spawning, such that the behaviour and success of one individual can greatly affect that of others. Moreover, variation among individuals is a key component in determining individual reproductive success and thus selection for reproductive traits.

Our objective was to quantify behavioural and reproductive skew and behavioural correlates of individual reproductive success, and to compare these between farmed and wild Atlantic salmon. To address this objective, groups of wild and farmed salmon were allowed to spawn undisturbed in an experimental stream environment in the autumn of 2001. To increase the breadth and power of our analyses, particularly in consideration of the trade-off in the number of replicates possible in large-scale studies, we also include data obtained from two earlier experiments in which behavioural differences among reproductive wild and farmed fish were quantified. Specifically, we re-analyse data from an experiment conducted in 1990 in which reproductive differences between groups of wild and farmed fish were documented (Fleming *et al.* 1996) and an experiment conducted on farmed individuals and wild fish from the same source river in 1999 (Ian A. Fleming & Sigurd Einum, unpublished data).

Materials and methods

EXPERIMENTAL SPAWNING ARENAS

Experiments were conducted at the Norwegian Institute for Nature Research (NINA) research station at Imsa, south-west Norway (58°59'N, 5°58'E), in four outdoor circular arenas, each containing 47 m² spawning substrate. Water was supplied continuously from Lake Liavatn located at the headwaters of the River Imsa. Gravel substrate, lighting and water velocities were similar to those described by Fleming *et al.* (1996), such that they simulated ambient conditions in the River Imsa. The arenas were divided into 1 × 1-m grids to identify the positions of fish and egg nests. Above- and underwater video cameras were used to record spawning activity.

PROTOCOL FOR THE 2001 EXPERIMENT

Experimental groups and treatments

The experiment was conducted from 6 November to 14 December 2001. Imsa fish were caught at a fish trap at the research station in autumn 2001, during their ascent up the River Imsa. Farmed fish were seventh generation individuals derived from the main Norwegian aquaculture strain, AquaGen, and were raised in a hatchery at the research station until the beginning of the experiment (Table 1).

The four arenas described above each held 24 anadromous salmon at a 1 : 1 sex ratio. Two arenas contained only Imsa anadromous males (hereafter referred to as Imsa1 and Imsa2); the other two arenas contained only AquaGen adult males (AquaGen1 and AquaGen2). Six Imsa and six AquaGen adult females were placed in each of the four arenas. Each arena also contained 30 mature male parr, comprised of equal numbers of Imsa, Imsa × AquaGen hybrids and AquaGen individuals.

Table 1. Year of experiment, duration, sex, mean \pm SE fork length (cm), body weight (g), condition factor ($k = g\text{ cm}^{-3} \times 100$), and number of mortalities for males and females in the four experimental arenas in the three experiments. Imsa fish in both 2001 and 1990 were wild-caught, Namsen fish in 1999 were raised in the hatchery environment. ANOVAs and *t*-tests were used to assess differences among arenas and between populations, respectively. Significant values ($P < 0.05$) are marked with an asterisk

Year	Duration	Sex	Variable	Population	Arena 1	Arena 2	Arena 3	Arena 4	<i>F</i>	<i>t</i>	
2001	38 days	Female	Number	Imsa	6	6	6	6			
				AquaGen*	6	6	6	6			
			Length	Imsa	58.82 \pm 0.61	58.48 \pm 0.99	57.20 \pm 2.30	56.00 \pm 2.4	0.54	11.41*	
				AquaGen*	47.23 \pm 0.94	46.13 \pm 1.02	45.68 \pm 0.74	46.20 \pm 1.33	0.40		
			Weight	Imsa	1863 \pm 81	1768 \pm 137	1781 \pm 190	1670 \pm 198	0.25	5.46*	
				AquaGen*	1356 \pm 80	1310 \pm 70	1290 \pm 82	1302 \pm 75	0.14		
			k	Imsa	0.91 \pm 0.08	0.89 \pm 0.02	0.93 \pm 0.02	0.93 \pm 0.02	0.30	14.28*	
				AquaGen*	1.28 \pm 0.04	1.34 \pm 0.03	1.34 \pm 0.03	1.32 \pm 0.05	0.42		
			Mortalities	Imsa	0	0	0	0			
				AquaGen*	0	0	0	1			
			Male	Number	Imsa	12	0	0	12		
					AquaGen*	0	12	12	0		
		Length		Imsa	55.25 \pm 1.05	–	–	55.71 \pm 1.00	15.8*	7.01*	
				AquaGen*	–	48.65 \pm 1.06	48.24 \pm 0.98	–			
		Weight		Imsa	1401 \pm 77	–	–	1396 \pm 77	0.04	0.24	
				AquaGen*	–	1393 \pm 81	1367 \pm 88	–			
		k	Imsa	0.82 \pm 0.02	–	–	0.80 \pm 0.01	118.43*	19.10*		
		AquaGen*	–	1.20 \pm 0.02	1.20 \pm 0.03	–					
Mortalities	Imsa	0	–	–	1						
	AquaGen*	–	7	10	–						
1990	27–39 days	Female	Number	Imsa	12	6	6	0			
				AquaGen†	0	6	6	12			
			Length	Imsa	52.63 \pm 2.76	51.90 \pm 3.79	53.6 \pm 3.41	–	0.05	1.31	
				AquaGen†	–	55.85 \pm 0.721	56.2 \pm 1.56	54.67 \pm 1.77	0.26		
			Weight	Imsa	2819 \pm 549	2722 \pm 676	3063 \pm 582	–	0.06	2.27*	
				AquaGen†	–	3767 \pm 169	3534 \pm 319	3741 \pm 236	0.20		
			k	Imsa	1.73 \pm 0.02	1.78 \pm 0.08	1.86 \pm 0.04	–	2.12	3.60*	
				AquaGen†	–	2.16 \pm 0.05	1.96 \pm 0.06	2.38 \pm 0.02	1.04		
			Mortalities	Imsa	0	0	0	–			
				AquaGen†	–	3	2	9			
			Male	Number	Imsa	12	6	6	0		
					AquaGen†	0	6	6	12	1.87	9.76*
		Length		Imsa	48.45 \pm 0.73	48.20 \pm 1.59	45.7 \pm 0.95	56.72 \pm 1.77	0.54		
				AquaGen†	–	57.92 \pm 0.86	58.7 \pm 1.05	–	1.26	11.12*	
		Weight		Imsa	2000 \pm 124	2019 \pm 264	1662 \pm 110	3742 \pm 236	0.76		
				AquaGen†	–	4035 \pm 178	4329 \pm 235	–	0.93	9.45*	
		k	Imsa	1.73 \pm 0.03	1.76 \pm 0.08	1.72 \pm 0.04	2.38 \pm 0.02				
		AquaGen†	–	2.07 \pm 0.04	2.13 \pm 0.05	–		1.43			
Mortalities	Imsa	3	2	3	–						
	AquaGen†	–	12	12	12						
1999	39 days	Female	Number	Namsen	–	–	Mixed3 6	–			
				AquaGen†	–	–	6	–			
			Length	Namsen	–	–	50.50 \pm 2.76	–	–	2.43*	
				AquaGen†	–	–	61.50 \pm 3.58	–	–		
			Weight	Namsen	–	–	1868 \pm 384	–	–	1.81	
				AquaGen†	–	–	2913 \pm 432	–	–		
			k	Namsen	–	–	1.36 \pm 0.06	–	–	1.55	
				AquaGen†	–	–	1.22 \pm 0.07	–	–		
			Mortalities	Namsen	–	–	0	–	–		
				AquaGen†	–	–	0	–	–		
			Male	Number	Namsen	–	–	6	–		
					AquaGen†	–	–	6	–		
		Length		Namsen	–	–	50.33 \pm 3.14	–	–	1.97	
				AquaGen†	–	–	61.00 \pm 4.41	–	–		
		Weight		Namsen	–	–	1677 \pm 331	–	–	1.69	
				AquaGen†	–	–	2852 \pm 614	–	–		
		k	Namsen	–	–	1.24 \pm 0.03	–	–	1.51		
		AquaGen†	–	–	1.15 \pm 0.05	–	–				
Mortalities	Namsen	–	–	0	–	–					
	AquaGen†	–	–	4	–	–					

*AquaGen fish raised in freshwater hatchery conditions only. †AquaGen fish raised in hatchery and sea-cage conditions.

Anadromous adults were photographed and tagged with 3.4 cm diameter disc tags for individual identification, following weight (g) and fork length (cm) measurements. Those that died during the experiment were frozen for later measurement. All fish were sacrificed at the end of the study.

Behavioural observations

Over a period of 16 h daily, we observed aggressive and spawning interactions in the arenas. Approximately every 4 h, 5-min periods of direct behavioural observations were used to identify the initiator and the receiver of each aggressive and courtship behaviour. We also recorded the location of male courtship and female digging behaviours throughout each 16-h period.

Aggressive behaviours fell into two major categories: chases and displays. A chase was defined broadly as a unidirectional burst of movement directed toward another individual and included biting, whereby one individual lunged with an open mouth toward another. Displays occurred when males swam next to one another with erect fins, and included the following behaviours: lateral display, whereby an anadromous male presented his lateral side with dorsal and anal fins extended; parallel swimming, whereby fish swam beside each other with dorsal fins erect; and head-down display, whereby a male raised his tail and lowered his head toward the substrate (Fleming 1996). The sum total of chases and displays undertaken by each individual over the course of the experiment were combined to obtain a measure of total aggression.

Male spawning behaviours included courting, whereby a male attended a female within two body lengths of her nest, and quivering, a short sequence of rapid shudders undertaken next to the female at her nest (Jones 1959). During a given observation, courtship of the female by an individual male was recorded as a single event. The spawning activity of each male was defined by the overall total frequencies of courting and quivering combined. The size of a courting group was defined as the number of males surrounding a female at a nest at any given time. The only female spawning behaviour recorded was digging, whereupon a female beats the substrate with her tail to create a depression into which she deposits her eggs.

We considered a female to be reproductively active on a given day if she was observed spawning, digging or being courted at her nest after she had been digging. Similarly, males were considered reproductively active if they initiated or received an aggressive act, or were observed courting or quivering next to a female. The sum total of aggression and courtship interactions was used for analyses of group and individual behaviour.

Spawning behaviour at each nest prior to egg deposition was continuously recorded on videotape for 24 h daily until either spawning had occurred or the nest was abandoned. The identity of individuals present at the time of spawning and the identity of males releasing

sperm at the time of egg release were obtained from the videotapes. Males were considered to have spawned successfully if quivering and sperm release were observed when the female deposited her eggs. Hereafter, we refer to presence at the time of spawning as a *spawning attempt*, and observation of sperm release and quivering commensurate with female spawning as *spawning success*.

PROTOCOL FOR THE 1990 EXPERIMENT

Groups of 24 fish (1 : 1 sex ratio) were comprised of either purely Imsa fish (Imsa3), purely AquaGen fish (AquaGen3) or a mixture of equal numbers of Imsa and AquaGen males and females (Mixed1 and Mixed2; see Fleming *et al.* 1996 for detailed methods). Fish from the River Imsa were collected during their upstream migration; fifth generation AquaGen individuals were raised in sea cages at a local fish farm and transported to the NINA research station at Ims, having spent a feeding season in a sea pen. Data regarding courting group size and spawning attempts were not collected for this experiment.

PROTOCOL FOR THE 1999 EXPERIMENT

The wild fish used in this experiment were obtained from the River Namsen, the principal founding source river of the AquaGen 'broodline one' strain (Gjedrem *et al.* 1991). Both Namsen and seventh-generation AquaGen broodline one individuals were raised from eyed eggs in a hatchery environment at the Ims research station beginning in the winter of 1996 (Fleming & Einum 1997; Fleming & Einum, unpublished observations). The single arena of experimental fish contained 12 males and 12 females; half the individuals of each sex were of Namsen origin and the other half were of AquaGen origin (Mixed3). Activity in the arena was observed continuously from 13 November to 15 December 1999. Although data on courting group size were collected for this experiment, data regarding spawning attempts were not.

STATISTICAL ANALYSES

For all three experiments, differences among arenas with respect to body weight, length, condition and sex were evaluated using factorial ANOVAS. Differences between groups of different origin were assessed using *t*-tests. Cumulative mortality among AquaGen males over time for each of the three experiments was compared by plotting the proportion of males alive each day after the beginning of the experiment and then fitting the data to logistic regressions. Frequency distributions of spawning, courtship, and total aggressive behaviours among males were described using measures of skew. Skew measures were also used to infer dominance relationships among males, such that positive skew would indicate that relatively few individuals

were performing the majority of behaviours in a group. Relationships among individual aggression, courtship and spawning success were determined using bivariate and partial correlations.

For the experiment conducted in 2001, regression models were used to relate spawning attempts and spawning success. Distributions of courting and spawning group sizes were described using measures of symmetry, and differences among these distributions were evaluated using Kolmogorov–Smirnov goodness-of-fit tests. Significance levels involving multiple comparisons were adjusted using sequential Bonferroni corrections.

Results

BODY SIZE AND MORTALITY

Design and duration of the three experiments are reviewed in Table 1. There were some differences among individuals in length, weight and condition factor in all experiments (Table 1). Mortality was considerably higher among AquaGen males when compared to Imsa or Namsen males, and varied among arenas and experiments. AquaGen male mortality in 1990 was very high; half the AquaGen males died between 9 and 10 days into the experiment, and all were dead within 14 days (Fig. 1). By comparison, AquaGen males in 2001 and 1999 experienced 50% mortality between 34 and 37 days into the experiment, and never attained 100% mortality (Fig. 1).

MALE GROUP AGGRESSION AND COURTSHIP BEHAVIOUR

The frequency distribution of courting group size in 2001 varied among arenas. Courting group size was positively skewed in Imsa1, Imsa2 and AquaGen1 (Table 2). Two-sample Kolmogorov–Smirnov goodness-of-fit tests indicated that neither the Imsa1 and Imsa2 groups ($ks = 0.138$, $P = 0.729$), nor the AquaGen1 and AquaGen2 groups ($ks = 0.130$, $P = 0.392$) differed in distribution of courting group size. Furthermore, when data from replicate arenas were combined, the distributions were significantly different between Imsa and AquaGen anadromous males ($ks = 0.376$, $P < 0.001$). Courting group size in 1999 was also positively skewed (Table 2).

MALE SPAWNING ATTEMPTS AND SUCCESS: 2001 EXPERIMENT

At a given spawning event, the number of males attempting to spawn with a given female tended to be higher in arenas containing AquaGen males than in arenas containing Imsa males (Table 2). There was positive skew in all four groups. The frequency distribution of spawning group size in AquaGen1 differed significantly from that in the arenas containing Imsa males (Imsa1:

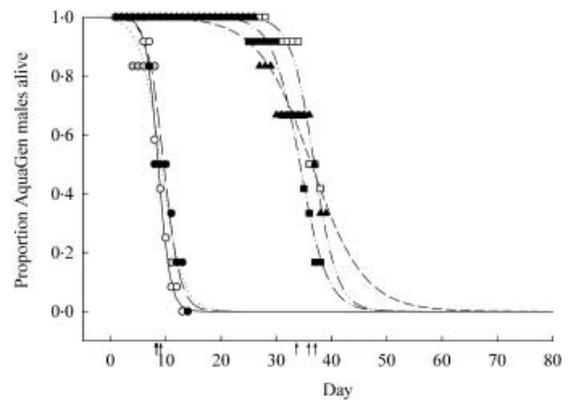


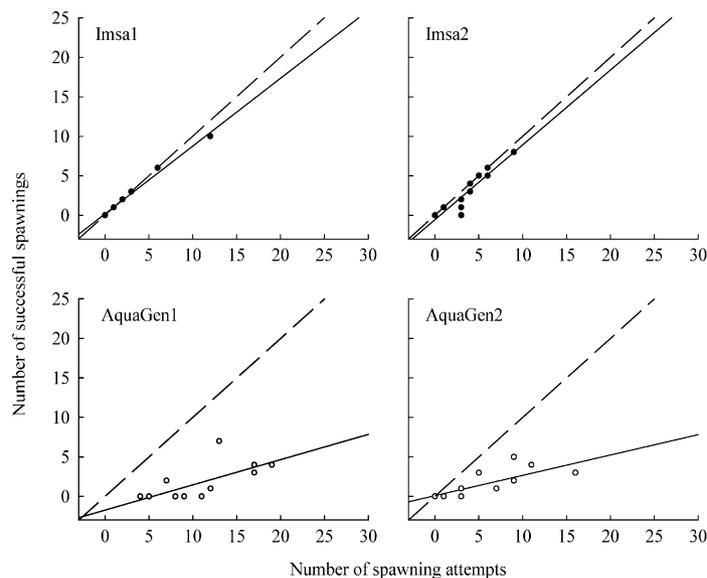
Fig. 1. Survival among AquaGen males as a function of day into the experiment in AquaGen3 (—○—); Mixed1 (—○—); Mixed2 (—●—); AquaGen1 (—□—); AquaGen2 (—■—); Mixed3 (—▲—). Lines are logit regressions. Arrows on the x-axis indicate days at which 50% mortality occurred or was expected to occur.

$ks = 0.673$, $P < 0.001$; Imsa2: $ks = 0.543$, $P < 0.001$), but not from that in AquaGen2 after sequential Bonferroni adjustment. Imsa1 and Imsa2 ($ks = 0.014$, $P = 0.906$) did not differ in the frequency distribution of spawning group size, nor did AquaGen2 and Imsa2 ($ks = 0.304$, $P = 0.060$), but Imsa1 differed from AquaGen2 ($ks = 0.434$, $P = 0.002$).

Notable differences in spawning success between Imsa and AquaGen males were observed. Spawning success in 2001 in the arenas with Imsa males was much higher than in arenas with AquaGen males, with at least one male observed quivering and releasing sperm in 92.3% and 100% of the observed spawnings in Imsa1 and Imsa2 groups, respectively. In the arenas containing AquaGen males, at least one male was seen releasing sperm in 50% and 47% of the observed spawnings in AquaGen1 and AquaGen2, respectively. Furthermore, there were differences between Imsa and AquaGen males with respect to spawning success and attempts. Among Imsa males, individuals who attempted to spawn most frequently were also the most successful at releasing sperm at the time of female egg release (simple regression ($b = \text{slope}$): Imsa1: $b = 0.859$, $P < 0.001$; Imsa2: $b = 0.948$, $P < 0.001$; Fig. 2). Similarly, among AquaGen males, individuals that attempted spawning most often also tended to successfully release sperm more frequently than others, but the slopes of these relationships were considerably less than 1, the expected value if each attempt resulted in sperm release (AquaGen1: $b = 0.320$, $P < 0.001$; AquaGen2: $b = 0.258$, $P < 0.001$). In Imsa1 and Imsa2, the most successful male was also the most aggressive (Fig. 3). In Imsa1, of the 25 instances when sperm release was observed, 10 were by the most aggressive males (40%). In addition, in Imsa2, of the 35 observed instances of sperm release, 23% of successful spawning attempts were by the most aggressive male, and 17% by the male who courted most often (40% combined). By contrast, among males in AquaGen1, the most aggressive male did not spawn successfully,

Table 2. Number of courting and spawning groups, mean (\pm SE), median (with upper and lower quartiles) and skew ($g_1 \pm$ SE) in courting and spawning group sizes. Significant values ($P < 0.05$) of skew are marked with an asterisk

	<i>n</i>	Mean	Median	g_1
Courting group size				
2001				
Imsa1	42	1.59 \pm 0.182	1 (1,2)	1.317 \pm 0.365*
Imsa2	44	2.05 \pm 0.187	2 (1,2)	1.451 \pm 0.357*
AquaGen1	93	3.68 \pm 0.240	3 (2,5)	0.850 \pm 0.250*
AquaGen2	78	3.05 \pm 0.19	3 (1,4)	0.332 \pm 0.272
1999				
Mixed3	110	2.50 \pm 0.141	2 (1,4)	0.758 \pm 0.230*
Spawning group size				
2001				
Imsa1	26	1.07 \pm 0.053	1 (1,1)	3.373 \pm 0.456*
Imsa2	29	1.52 \pm 0.241	1 (1,1)	3.215 \pm 0.434*
AquaGen1	40	3.33 \pm 0.379	2.5 (2,4)	1.000 \pm 0.374*
AquaGen2	45	1.80 \pm 0.181	1 (1,2)	1.272 \pm 0.354*

**Fig. 2.** Spawning success vs. spawning attempts in the four arenas in the 2001 experiment for Imsa (●) and AquaGen (○) males. The dashed line is the 1 : 1 line.

and the most successful male was relatively non-aggressive and courted the least. Similarly, in AquaGen2, the most successful male was neither the most aggressive nor the most active courter.

DISTRIBUTION OF INDIVIDUAL MALE AGGRESSION AND SPAWNING BEHAVIOURS

In the 2001 experiment, differences were found among arenas in the frequency distributions of aggression, courtship, spawning attempts and spawning success. Among Imsa males in Imsa1 and Imsa2, there was significant positive skew in total aggression, and in Imsa1 courting frequency, spawning attempts and successful spawnings were also positively skewed (Table 3). Among AquaGen males, the only significantly skewed distribution of behaviour was that for total aggression in AquaGen1.

In 1990, the distribution of behaviours among males also varied among arenas. Among Imsa males in Imsa3, Mixed1 and Mixed2 there was positive skew in the distribution of aggression (Table 3), and significant skew in the distribution of courtship among Imsa males in Mixed1 and Mixed2. Spawning success was positively skewed among Imsa males (Table 3). Among AquaGen males in Mixed2, there was significant positive skew in the frequency of courtship. Spawning success was not analysed for AquaGen males in 1990 as they were observed spawning 0, 1 and 1 times in Mixed1, Mixed2 and AquaGen3, respectively.

In contrast with the other experiments, there was no significant skew for frequencies of aggression or courtship within Namsen or AquaGen males in 1999. However, there was significant positive skew among AquaGen males in spawning success (Table 3).

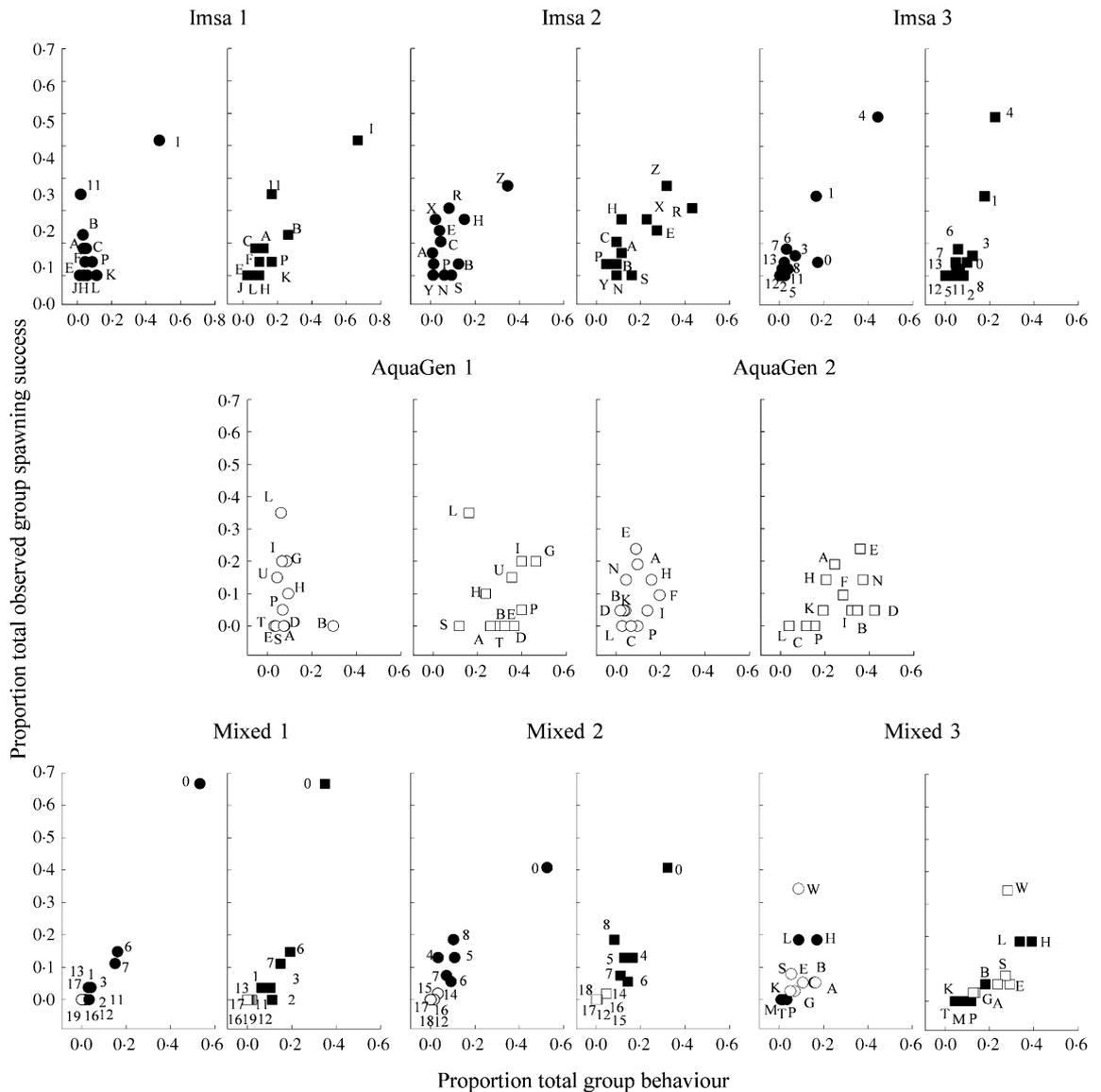


Fig. 3. Spawning success as a function of aggression (○) and courtship (□) for Imsa or Namsen males (black fill), and AquaGen males (white fill) in pure or mixed groups. Letters and numbers denote tag identifications for each male.

CORRELATES OF INDIVIDUAL MALE BEHAVIOUR

In the 2001 experiment, relationships between behaviours were more consistent among males in Imsa1 and Imsa2 than among males in AquaGen1 and AquaGen2. In Imsa1, aggression was positively related to courtship, and both aggression and courtship tended to be related to spawning success (Fig. 3; Table 4). Among males in Imsa2, aggression was not correlated with courtship, but both were correlated with spawning success. By contrast, among males in AquaGen1 and AquaGen2, there were no significant trends among aggression, courtship and spawning success.

Similar to the 2001 experiment, relationships among behaviours were consistent for the Imsa males in 1990. Among males in Imsa3, there was a positive relationship between aggression and courtship, and both

aggression and courtship frequencies were significant positive correlates of observed spawning success (Fig. 3; Table 4). Partial correlation analysis indicated that courtship was a significant correlate of spawning success when controlling for effects of aggression (partial $r = 0.686$, d.f. = 9, $P = 0.02$). Similarly, among Imsa males in Mixed1 and Mixed2, there were positive relationships among aggression, courtship and spawning success. Behavioural correlates among AquaGen males in 1990 were less consistent than those among Imsa males. In Mixed1 and Mixed2, aggression and courtship were weakly correlated with one another (Table 4). There was no correlation between aggression and courtship in AquaGen3.

Behavioural correlates in 1999 were not as clear as in 2001 or 1990. Correlations among aggression, courtship and spawning success among Namsen males indicated that individuals who courted the most often

Table 3. Skewness (g_1) for total aggression, number of courting groups, spawning attempts and successful spawnings in each of the arenas in the three experiments. SE of skewness is 0.637 for pure and overall mixed groups and 0.845 within populations in mixed groups. Significant values ($P < 0.05$) of skew are marked with an asterisk

	Origin	Total aggression	Courting groups	Spawning attempts	Successful spawnings
2001					
Imsa1	Imsa	3.185*	2.703*	2.25*	1.941
AquaGen1	AquaGen	3.002*	-0.512	0.336	1.225
AquaGen2	AquaGen	0.752	-0.375	0.538	0.762
Imsa2	Imsa	2.173*	1.217	0.362	0.515
1990					
Imsa3	Imsa	2.239*	1.195	–	2.450*
Mixed1	Mixed	2.760*	1.567*	–	3.082*
Mixed1	Imsa	1.961*	1.516	–	2.200*
Mixed1	AquaGen	0.140	1.494	–	N/A
Mixed2	Mixed	2.997*	1.374*	–	2.006*
Mixed2	Imsa	2.326*	1.853*	–	1.782*
Mixed2	AquaGen	1.031	2.393*	–	N/A
AquaGen3	AquaGen	0.592	0.139	–	N/A
1999					
Mixed3	Mixed	0.421	0.121	–	1.698*
Mixed3	Namsen	0.464	0.626	–	0.775
Mixed3	AquaGen	1.303	-0.731	–	2.309*

Table 4. Correlation coefficients for relationships among aggression, courtship and spawning success in the three experiments. Significant correlations after sequential Bonferroni correction for multiple comparisons are marked with an asterisk

	Origin	n	Aggression–courtship	Aggression–spawning	Courtship–spawning
2001					
Imsa1	Imsa	12	0.891*	0.749	0.896*
Imsa2	Imsa	12	0.365	0.596	0.753
AquaGen1	AquaGen	12	-0.108	-0.197	0.020
AquaGen2	AquaGen	12	-0.006	0.292	0.474
1990					
Imsa3	Imsa	12	0.889*	0.934*	0.890*
Mixed1	Mixed	12	0.934*	0.991*	0.934*
Mixed1	Imsa	6	0.978*	0.993*	0.959
Mixed1	AquaGen	6	0.851	N/A	N/A
Mixed2	Mixed	12	0.875*	0.933*	0.911*
Mixed2	Imsa	6	0.901	0.931	0.828
Mixed2	AquaGen	6	0.880	N/A	N/A
AquaGen3	AquaGen	12	0.419	N/A	N/A
1999					
Mixed3	Mixed	12	0.673	0.363	0.711
Mixed3	Namsen	6	0.768	0.694	0.997*
Mixed3	AquaGen	6	0.365	0.003	0.506

tended to be the most frequent spawners (Fig. 3, Table 4). There were no significant correlations among aggression, courtship and spawning success for the AquaGen males.

Discussion

Our individual-based comparisons between farmed and wild male Atlantic salmon behaviour have shown that: (1) in contrast with wild males, farmed males do not appropriately establish reliable dominance relationships; and (2) there is significant behavioural variation among and within groups of farmed and

wild fish, such that potential outcomes of interactions between farmed and wild groups are largely context-dependent, i.e. they will almost certainly depend on the rearing history and genetic and demographic origins of the affected individuals (Hutchings 1991).

MALE DOMINANCE STRUCTURE AND BEHAVIOURAL CORRELATES OF SPAWNING SUCCESS

Previous work suggested that farmed male Atlantic salmon are behaviourally inferior to wild males during spawning (Fleming *et al.* 1996). Our results are not

inconsistent with this hypothesis, but they do suggest that the mechanisms responsible for the competitive inferiority of farmed males may be more complex than previously thought. In addition, our re-analysis of data from Fleming *et al.*'s (1996) experiment indicates that high AquaGen male mortality, possibly attributable to their sea cage rearing environment, may have affected the observed differences in spawning behaviour and success between wild and farmed salmon.

The present study extends previous analyses of the spawning behaviour of farmed male Atlantic salmon (see also Fleming *et al.* 1996, 2000). Presence at spawning did not necessarily result in sperm release among individual farmed males, whereas there was a strong relationship between Imsa male spawning attempts and spawning success. Among salmonids in general, male success is also usually related directly to behavioural dominance (Fleming 1998). There was a large discrepancy between groups of AquaGen and Imsa or Namsen males in the reliability of behavioural correlates of spawning success. Among Imsa and Namsen males, courtship and/or aggression were good correlates of spawning success, whereas similarly reliable relationships were absent among AquaGen males.

Despite these behavioural differences between wild and farmed males, results from the 2001 study indicated that the AquaGen males, as well as the Imsa males, responded to female spawning activity. In fact, AquaGen males generally courted females in large groups. The large courting group sizes observed among AquaGen males are consistent with the hypothesis that they do not establish appropriate dominance hierarchies. In addition, the distribution of individual aggression, courtship and spawning success in farmed males did not consistently result in bias toward few individuals as expected in the instance of strong dominance relationships. An apparent lack of dominance hierarchies within groups of fish in hatchery conditions has also been noted among juvenile (Griffiths & Armstrong 2002) and adult Atlantic salmon (Fleming *et al.* 1997). Furthermore, hatchery fish have been noted to use aggression excessively when competing for food (Fenderson *et al.* 1968; Mesa 1991) or mates (Fleming *et al.* 1997), without necessarily gaining any advantage over others. Such indiscriminate aggression may have led to high levels of activity among AquaGen males that did not result in increased access to females.

Although AquaGen males did not establish strong dominance hierarchies, there was no evidence to suggest that females were unwilling to spawn with them. In fact, the large courting groups among AquaGen males may have had a positive effect on female spawning behaviour (see also de Gaudemar, Bozom & Beall 2000). However, in general the farmed males in our 2001 study either did not respond appropriately or in a timely fashion when the female released her eggs; at times, females were observed spawning with no males present. We suggest that the culture environment, where males are not required to perform any spawning

behaviour, almost certainly affects the ability of males to execute the appropriate behaviours required to spawn successfully with females in natural or seminatural conditions.

BEHAVIOURAL DIFFERENCES AMONG GROUPS OF FARMED AND WILD MALES

Changes attributable to artificial selection in animals have been documented for various behaviours including aggression (Mesa 1991; Ruzzante & Doyle 1991; Ruzzante 1994; Einum & Fleming 1997; Fleming & Einum 1997; Plusquellec & Bouissou 2001; Hedenskog, Petersson & Järvi 2002), foraging (Gustafsson *et al.* 1999), predator avoidance (Johnsson & Abrahams 1991; Johnsson *et al.* 1996; Einum & Fleming 1997; Fleming & Einum 1997), migration (Jonsson *et al.* 1993) mating (Webb *et al.* 1991; Lura & Sægrov 1993; Fleming *et al.* 1996, 1997; Berejikian *et al.* 1997, 2001a,b) and parental care (Spinka *et al.* 2000). Thus, it is not surprising that there are some behavioural differences between farmed and wild Atlantic salmon. However, inconsistencies in the literature, as well as in the present study, serve to emphasize the context-dependency of potential interactions between farmed and wild fish (reviewed by Saunders 1991 and Youngson & Verspoor 1998).

Further underscoring the potential for different outcomes of interactions between farmed and wild fish, the 1999 experiment, although unreplicated, indicated that captively reared Namsen and AquaGen males behave similarly. The lack of differences between groups may be attributable to genetic differentiation, rearing environment, or more probably some interaction between the two. AquaGen fish were derived mainly from the Namsen River, such that behavioural differences observed between AquaGen and Imsa individuals may be due to both population origin (Ptacek & Travis 1996; Van Parijs *et al.* 2000) and rearing environment (e.g. Fleming *et al.* 1997; Griffiths & Armstrong 2002). Dunmall & Schreer (2003) did not find any difference in swimming and cardiac performance between captively reared Namsen and AquaGen fish, and concluded that farmed individuals could compete effectively with Namsen fish during spawning. This suggestion was supported by the results of the 1999 experiment, especially given that the most successful individual was an AquaGen male.

Although AquaGen males did relatively well in competition with Namsen males, Fleming *et al.* (1996) reported them to be competitively inferior to Imsa males. One explanation for the difference in these outcomes is the fact that both Namsen and AquaGen males were captively reared, while Imsa fish were caught from the river during their upstream migration. Although we cannot separate the effects of rearing environment and genetics on the spawning behaviour of Namsen and AquaGen males in the 1999 experiment, we can infer a genetic basis to the observed differential

male mortality. Mortality among males occurred in all experiments (1990, 1999, 2001), reflecting the intense physical stress involved in competition among males during spawning. However, this mortality occurred almost exclusively among AquaGen males, suggesting differences in survival ability between farmed and wild fish. The higher mortality experienced by farmed males may be due to inherent performance differences, such that the AquaGen males were less able to survive the intense competition under the experimental conditions. In addition, generally high levels of aggression among hatchery juvenile Atlantic salmon have been considered a main cause of mortality under experimental conditions (Fenderson *et al.* 1968).

From a conservation perspective, the observed differences among experiments emphasize the degree to which the reproductive inferiority displayed by farmed fish relative to their wild counterparts can vary. Although the wild populations were most probably genetically different and the experiments varied slightly in design, there were broad qualitative similarities across studies with respect to correlates of spawning success. However, quantitative differences suggest that the spawning success of farmed males will depend upon the rearing history and genetic backgrounds of the farmed and wild populations. Furthermore, the relative spawning success of farmed fish in 2001 and 1999 was not as low as in 1990, suggesting that farmed males can have a greater impact on wild populations than suspected, based on estimates from Fleming *et al.* (1996). Hutchings (1991) predicted that the effect of interactions on wild population should depend upon the degree to which wild salmon are locally adapted, on the genetic differentiation between wild and farmed individuals, on the magnitude of outbreeding depression and on the size of the wild populations relative to their carrying capacities. Our results are consistent with these predictions in that they underscore the importance of adopting a case-dependent approach when assessing the effects that a given farmed population may have on the persistence of a particular wild population.

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References

- Andersson, M. (1994) *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Berejikian, B.A., Tezak, E.P., Park, L., LaHood, E., Schroder, S.L. & Beall, E. (2001a) Male competition and breeding success in captivity reared and wild coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 804–810.
- Berejikian, B.A., Tezak, E.P. & Schroder, S.L. (2001b) Reproductive behaviour and breeding success of captivity reared chinook salmon. *North American Journal of Fisheries Management*, **21**, 255–260.
- Berejikian, B.A., Tezak, E.P., Schroder, S.L., Knudsen, C.M. & Hard, J.J. (1997) Reproductive behavioral interactions between wild and captivity reared coho salmon (*Oncorhynchus kisutch*). *ICES Journal of Marine Science*, **54**, 1040–1050.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1988) Reproductive success in male and female red deer. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (ed. T.H. Clutton-Brock), pp. 325–343. University of Chicago Press, Chicago.
- Davies, N.B. (1991) Mating systems. *Behavioural Ecology: an Evolutionary Approach*, 3rd edn (eds J.R. Krebs & N.B. Davies), pp. 263–294. Blackwell Scientific Publishing, Boston.
- Dunmall, K.M. & Schreer, J.F. (2003) A comparison of the swimming and cardiac performance of farmed and wild Atlantic salmon, *Salmo salar*, before and after gamete stripping. *Aquaculture*, **220**, 869–882.
- 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.
- Emlen, S.T. & Oring, L.W. (1977) Ecology, sexual selection and the evolution of mating systems. *Science*, **197**, 215–223.
- Fenderson, O.C., Everhart, W.H. & Muth, K.M. (1968) Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. *Journal of the Fisheries Research Board of Canada*, **25**, 1–14.
- Fleming, I.A. (1996) Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fisheries and Fish Biology*, **6**, 379–416.
- Fleming, I.A. (1998) Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, **55** (Suppl. 1), 59–76.
- 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 Series B*, **267**, 1517–1523.
- Fleming, I.A. & Einum, S. (1997) Experimental test of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES Journal of Marine Science*, **54**, 1051–1063.
- Fleming, I.A. & Gross, M.R. (1992) Reproductive behavior of hatchery and wild coho salmon (*Oncorhynchus kisutch*): does it differ? *Aquaculture*, **103**, 101–121.
- Fleming, I.A. & Gross, M.R. (1993) Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecological Applications*, **3**, 230–245.
- Fleming, I.A., Jonsson, B., Gross, M.R. & Lamberg, A. (1996) An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *Journal of Applied Ecology*, **33**, 893–905.
- Fleming, I.A., Lamberg, A. & Jonsson, B. (1997) Effects of early experience on the reproductive performance of Atlantic salmon. *Behavioral Ecology*, **8**, 470–480.

- de Gaudemar, B., Bonzom, J.M. & Beall, E. (2000) Effects of courtship and relative mate size on sexual motivation in Atlantic salmon. *Journal of Fish Biology*, **57**, 502–515.
- Gjedrem, T., Gjoen, H.M. & Gjerde, B. (1991) Genetic origin of Norwegian farmed Atlantic salmon. *Aquaculture*, **98**, 41–50.
- Griffiths, S.W. & Armstrong, J.D. (2002) Rearing conditions influence refuge use among over-wintering Atlantic salmon juveniles. *Journal of Fish Biology*, **60**, 363–369.
- Gustafsson, M., Jensen, P., de Jonge, F.H. & Schuurman, T. (1999) Domestication effects on foraging strategies in pigs (*Sus scrofa*). *Applied Animal Behaviour Science*, **62**, 305–317.
- Heggerberget, T.G., Johnsen, B.O., Hindar, K., Jonsson, B., Hansen, L.P., Hvidsten, N.A. & Jensen, A.J. (1993) Interactions between wild and cultured Atlantic salmon: a review of the Norwegian experience. *Fisheries Research*, **18**, 123–146.
- Hedenskog, M., Petersson, E. & Jarvi, T. (2002) Agonistic behavior and growth in newly emerged brown trout (*Salmo trutta* L.) of sea-ranched and wild origin. *Aggressive Behaviour*, **28**, 145–153.
- Hutchings, J.A. (1991) The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. *Aquaculture*, **98**, 119–132.
- Jarvi, T. (1990) The effects of male dominance, secondary sexual characteristics and female mate choice on the mating success of Atlantic salmon *Salmo salar*. *Ethology*, **84**, 123–132.
- Jonsson, J.I. & Abrahams, M.V. (1991) Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 243–247.
- Jonsson, J.I., Petersson, E., Jonsson, E., Bjornsson, B.Th & Jarvi, T. (1996) Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1546–1554.
- Jones, J.W. (1959) *The Salmon*. Collins, London.
- Jones, M.W. & Hutchings, J.A. (2001) The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. *Heredity*, **86**, 675–684.
- Jones, M.W. & Hutchings, J.A. (2002) Individual variation in Atlantic salmon fertilization success: implications for effective population size. *Ecological Applications*, **12**, 184–193.
- Jonsson, N., Hansen, L.P. & Jonsson, B. (1993) Migratory behaviour and growth of hatchery-reared post-smolt Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, **42**, 435–443.
- Jonsson, B., Jonsson, N. & Hansen, L.P. (1991) Differences in life-history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, **98**, 69–78.
- Kallio-Nyberg, I. & Koljonen, M.L. (1997) The genetic consequence of hatchery-rearing on life-history traits of the Atlantic salmon (*Salmo salar* L.): a comparative analysis of sea-ranched salmon with wild and reared parents. *Aquaculture*, **153**, 207–224.
- Kelly, C.D., Godin, J.-G.J. & Wright, J.M. (1999) Geographical variation in multiple paternity within natural populations of the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London Series B*, **266**, 2403–2408.
- Lura, H. & Sægrov, H. (1993) Timing of spawning in cultured and wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the River Vosso, Norway. *Ecology of Freshwater Fishes*, **2**, 167–172.
- 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.
- Plusquellec, P. & Bouissou, M.F. (2001) Behavioural characteristics of two dairy breeds of cows selected (Herens) or not (Brune des Alpes) for fighting and dominance ability. *Applied Animal Behaviour Science*, **72**, 1–21.
- Ptacek, M.B. & Travis, J. (1996) Inter-population variation in male mating behaviours in the sailfin mollie, *Poecilia latipinna*. *Animal Behaviour*, **52**, 59–71.
- Reznick, D. & Endler, J.A. (1982) The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, **36**, 160–177.
- Roff, D.A. (2002) *Life History Evolution*. Sinauer Associates Inc., Sunderland.
- Ruzzante, D.E. (1994) Domestication effects on aggressive and schooling behavior in fish. *Aquaculture*, **120**, 1–24.
- Ruzzante, D.E. & Doyle, R.W. (1991) Rapid behavioral changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. *Evolution*, **45**, 1936–1946.
- Saunders, R.L. (1991) Potential interaction between cultured and wild Atlantic salmon. *Aquaculture*, **98**, 51–60.
- Spinka, M., Illmann, G., de Jonge, F.H., Andersson, M., Schuurman, T. & Jensen, P. (2000) Dimensions of maternal behaviour characteristics in domestic and wild × domestic crossbred sows. *Applied Animal Behaviour Science*, **70**, 99–114.
- Van Parijs, S.M., Hastie, G.D. & Thompson, P.M. (2000) Individual and geographical variation in display behaviour of male harbour seals in Scotland. *Animal Behaviour*, **59**, 559–568.
- Webb, J.H., Hay, D.W., Cunningham, P.D. & Youngson, A.F. (1991) The spawning behaviour of escaped farmed and wild adult Atlantic salmon (*Salmo salar* L.) in a northern Scottish river. *Aquaculture*, **98**, 97–110.
- Youngson, A.F. & Verspoor, E. (1998) Interactions between wild and introduced Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55** (Suppl. 1), 153–160.

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