Spawning behaviour and success of mature male Atlantic salmon (*Salmo salar*) parr of farmed and wild origin

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Abstract: We examined genetic differences in the reproduction of an alternative maturation phenotype in Atlantic salmon (*Salmo salar*) by comparing the spawning behaviour and success among farmed, first-generation hybrid, and wild mature male parr raised in similar environments. Parr competed for spawning opportunities in the presence of either wild or farmed large males. There were no consistent differences among groups in aggression; however, there were differences in spawning participation with respect to large male origin and among parr types. There was a strong negative temporal effect on mature male parr spawning participation that differed by parr type; wild and farmed parr were most likely to participate in early spawnings, with hybrids being the most likely to participate in late spawnings. Overall, parr were also less likely to participate in spawnings involving large farmed males. Variance in reproductive success was higher among parr than among large males. Our results are consistent with the hypothesis that there are genetically based behavioural differences among mature male parr of farmed and wild origin that may potentially lead to differences in reproductive success.

Résumé : Nous avons examiné les différences génétiques lors de la reproduction d'un phénotype mature de rechange du saumon atlantique (*Salmo salar*) en comparant le comportement de fraye et le succès de la fraye chez des tacons mâles matures hybrides de première génération de pisciculture et des tacons mâles matures sauvages élevés dans des conditions similaires. Les tacons font compétition pour obtenir des occasions de frayer en présence de mâles de grande taille provenant soit du milieu naturel, soit de pisciculture. Il n'y a pas de différences soutenues dans l'agression entre les groupes; il y a cependant des différences dans la participation à la fraye, en fonction de l'origine des grands mâles et des types de tacons. Il y a un fort effet temporel négatif sur la participation des tacons mâles matures à la fraye qui varie en fonction du type de tacon; les tacons du milieu naturel et de pisciculture sont plus susceptibles de participer à des frayes hâtives, alors que les hybrides le sont pour les frayes tardives. En général, les tacons sont moins susceptibles de participer à des frayes qui impliquent de grands mâles de pisciculture. La variance dans le succès de la reproduction est plus élevée chez les tacons que chez les grands mâles. Nos résultats s'accordent avec l'hypothèse qui veut qu'il y ait des différences de comportement génétiquement déterminées chez les tacons matures provenant du milieu naturel et de pisciculture qui mènent potentiellement à des différences de succès reproductif.

[Traduit par la Rédaction]

Introduction

Mating systems, being highly diverse among fishes, frequently involve alternative reproductive strategies (Taborsky 2001). These strategies are thought to be maintained in populations along some sort of evolutionarily stable continuum, resulting in approximately equal average fitness among individuals adopting either strategy at equilibrium (Gross 1985; Hutchings and Myers 1994). Among fish species, Atlantic salmon (*Salmo salar*) males express one of the most extreme size differences among alternative reproductive morphs (Hutchings and Myers 1994; Fleming 1996). This life his-

tory variability results in two distinct male maturation phenotypes: anadromous males and mature male parr (Jones 1959). Both phenotypes spend juvenile stages in fresh water; the former mature at a large size (~50–100 cm) following migration and feeding at sea, whereas the latter mature in fresh water at a considerably smaller size (~7–15 cm), whereafter they may or may not migrate to sea.

During the reproductive season, mature male parr sneak spawnings by darting under the female and attempting to fertilize eggs while anadromous males are releasing sperm (Jones 1959). For mature male parr, interactions with large fish can be injurious or fatal (sea trout (*Salmo trutta*): Bohlin

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1154

Can. J. Fish. Aquat. Sci. Vol. 62, 2005

1975; Atlantic salmon: Hutchings and Myers 1987; brown trout (*S. trutta*): Broberg et al. 2000). It is generally held that mature male parr establish dominance hierarchies behind females (Jones 1959; Myers and Hutchings 1987) and that parr closest to females at the time of spawning realize the highest fertilization success (Jones 1959). However, to our knowledge, there has been no empirical study of mature male parr behaviour immediately prior to the release of sperm.

In contrast with the paucity of behavioural information about mature male parr during spawning, several studies have assessed their relative reproductive success (e.g., Hutchings and Myers 1988; Jordan and Youngson 1992; Thomaz et al. 1997). In some cases, this has led to estimates of the contribution of mature male parr to the genetic variability and effective population size of natural salmon populations (L'Abée-Lund 1989; Jones and Hutchings 2001, 2002). Such genetic contributions by parr may be important in maintaining the genetic variability, or reducing its rate of decline, as the size of the anadromous population declines, a demographic imbalance now common throughout much of the species' range (Parrish et al. 1998).

Among several potential threats to the persistence of salmon populations are concerns about the impact of escaped farmed fish on the genetic structure and demography of wild populations (Hindar et al. 1991; Hutchings 1991). Considering the high potential for genetic contribution from mature male parr during spawning, they might represent a primary means of introgression of foreign genes from escaped farmed fish into wild populations. In a controlled experiment, Garant et al. (2003) found that mature male parr of farmed origin were extremely successful in fertilizing eggs when competing with their wild counterparts. They suggested that behavioural differences, such as increased aggression among farmed juveniles, provided one potential explanation for the observed success of farmed parr.

We document behavioural interactions and quantify fertilization success of mature male parr of wild, hybrid, and farmed origin in competition with either wild or farmed large males in a simulated natural environment. Specifically, we compare and contrast mortality, wounding, aggression, spawning participation, and fertilization success among mature male parr of different genetic origin raised under similar hatchery conditions.

Materials and methods

Experimental groups and treatments

The experiment was conducted at the Norwegian Institute for Nature Research field station in Ims, Norway, from 6 November to 14 December 2001 in four 47-m^2 outdoor spawning arenas (Fleming 1996). Wild parr originated from the Imsa River; farmed parr originated from a Norwegian aquaculture strain called AquaGen. Hybrids were first-generation crosses of Imsa and AquaGen individuals. All parr were raised from eggs at the hatchery under similar environmental conditions. Prior to the experiment, all farmed and hybrid fish were sampled from separate stock tanks, of which 50 of 3000 AquaGen and 60 of 2270 Imsa × AquaGen parr were mature males. Imsa parr were sampled

from a separate tank until approximately 100 mature males had been collected.

Mature males were distributed among the four arenas such that each contained 30 parr with equal numbers of Imsa, Imsa × AquaGen hybrids, and AquaGen individuals. Mature male parr were marked with a 5-mm white plastic bead in one of three locations, at the back of the dorsal fin on the right side of the fish, at the front of the dorsal fin on the left side of the fish, or at the front of the dorsal fin on the right side of the fish, to identify Imsa, hybrid, or AquaGen individuals, respectively. Large fish were from two different environments. Imsa wild fish were caught in a fish trap during their autumn migration; AquaGen fish were raised at the field station. Twenty-four Imsa females and 24 AquaGen females were placed in the arenas, six of each type in each arena. Two arenas each held 12 Imsa large males, while the other two arenas each held 12 AquaGen large males. Henceforth, we refer to the arenas containing only Imsa anadromous males as Imsa 1 and Imsa 2 and those with only AquaGen large males as AquaGen 1 and AquaGen 2. Anadromous fish were marked with 3.5-cm tags for individual identification. Prior to tagging, weight (grams) and fork length (centimetres) were recorded for all fish. Fin tissue samples were obtained and preserved in 95% ethanol for genetic analysis of parentage.

All mortalities were removed from the arenas and frozen for measurement at the end of the experiment. Parr recovered during and at the end of the experiment were photographed and examined for wounds. We classified the parr as wounded if the marks on their bodies included gashes that were characteristic of anadromous fish lingual and mandibular teeth (Hutchings and Myers 1987).

Behavioural observations

Parr and anadromous fish activity in each arena was monitored for 16 h daily from an observation tower. Each day, four 5-min periods of live observations of aggressive interactions among mature male parr and between anadromous fish and mature male parr were recorded at least 3 h apart. During these observation periods, we recorded the origin of the mature male parr initiating and receiving aggression. When anadromous fish were involved in interactions, their identity was recorded. Aggressive behaviours among parr consisted mainly of chases, whereby one individual swims rapidly toward another causing the latter to change direction, charges, which differ from chases in that the receiver of aggression does not flee, and bites. Anadromous fish were observed either chasing or biting mature male parr.

In addition to live observations, we videotaped behaviour at most nests from the time when a female had started digging until a few minutes after the time of egg release (*t*). We took 5-min samples of parr aggression beginning at $t - 10$ min and ending at $t - 5$ min. During these videotape sampling periods, we identified to group the initiator and receiver of each aggressive behaviour, noted whether the aggressor or receiver left the nest following a chase or bite, quantified the number of mature male parr of different origin present at the nest, and recorded the identity of anadromous fish present when the attack occurred. Maximum and minimum number of parr at the nest and the length of time the

female was present during the 5-min sample were also recorded. Encounters occurred when two or more parr were at the nest at a given time. One minute prior to spawning and at the time of spawning, we recorded the number of mature male parr of each origin and the identity and number of anadromous males present at the nest.

Genetic analyses

All egg nests in each arena (n_{nests} = 165, n_{eggs} = 50 745) were recovered between 25 February and 28 February 2002. Based on the range in spawning dates and the water temperatures in the arenas during winter, eggs were between approximately 140 and 330 degree-days old at the beginning of the excavation period and were at the "eyed" stage. Eyed and noneyed eggs were sorted and counted, and eggs containing live embryos were preserved in 95% ethanol for parentage analysis and transported to Dalhousie University, Halifax, Nova Scotia.

DNA was extracted from fin tissue using Qiagen DNeasy™ tissue extraction kits (Qiagen Inc., Mississauga, Ontario). Eggs were dissected and embryo heads were removed and placed in 100 µL of eyeball buffer (10 mmol Tris·L^{-1}, 50 mmol KCl·L^{-1}, 0.5% Tween 20) with 2 mg proteinase K·mL^{-1}. Samples were digested overnight at 55 °C and vortexed prior to denaturing the proteinase K at 95 °C for 15 min. We froze the samples at –20 °C after centrifuging at 2000 r·min^{-1} (1 r = 2π·rad) or 20000g for 2 min. Individuals were genotyped at five microsatellite loci: Ssa197 (O'Reilly et al. 1996), SSsp2213, SSsp2215, SSsp2216, and SSsp2210 (Paterson et al. 2004). One primer of each set was labelled with fluorescein or hexachlorofluorescein at the 5′ end. Polymerase chain reactions were carried out in 10-µL total volumes consisting of 2.0 µL of template DNA, 3.5 µL of double-distilled water, 1.0 µL of 10× *Taq* DNA polymerase buffer, 1.5 µL of 15 mmol MgCl$_2$·L^{-1}, 1.0 µL of 2 mmol dNTP·L^{-1}, 0.5 µL of 10 mmol forward primer·L^{-1}, 0.5 µL of 10 mmol reverse primer·L^{-1}, and 0.5 U (1 U ≈16.67 nkat) of *Taq* DNA polymerase. Polymerase chain reaction profiles for all loci were designed as follows: denaturation at 95 °C for 3 min followed by 35 cycles of 30 s at 95 °C, 30 s at 58 °C, 30 s at 72 °C, and a final extension for 30 min at 72 °C. Samples were run on 6% acrylamide gels and visualized using an FMBIO scanner (Hitachi Software Engineering America Ltd., Mirai Bio Division, Alameda, California). Individuals were genotyped against standard samples with known sizes, and each individual was rescored three times. All potential parents were amplified twice and genotyped four times.

Statistical analyses

Differences in body weight, length, and body condition among arenas and parr of different origin were tested using factorial ANOVAs with arena and origin entered as main factors. We used χ^2 tests to investigate differences in the numbers of recaptured and wounded parr of different origin among the four arenas. Aggressive behaviour initiated by mature male parr and large fish was analysed using χ^2 contingency tests or Fisher's exact tests for both live observations and aggression at nests prior to spawning, excluding instances when parr of a given origin were not present dur-

ing the interactions. The number of nests attended by mature male parr of different origin was also analysed using χ^2 tests, with the expected values being equal for parr of different origin. To examine the effects of anadromous male and parr origin on the number of parr participating in spawnings, we constructed generalized linear models (GLMs) using S-Plus 6.1, specifying Poisson error and the log link function. Significance for all tests was set at α = 0.05.

Offspring were assigned parents based on the maximum likelihood procedures of PAPA 1.1 (Duchesne et al. 2002). Video footage was used to corroborate ambiguous parentage assignments. As the focus of the genetic analysis was to determine group success among mature male parr, we verified through exclusion that offspring assigned to more than one most likely father of the same origin had no other potential fathers of different origin. Offspring that were not unambiguously assigned to fathers of only one origin were excluded from the analysis. As genotyping errors are not uncommon, analyses were carried out specifying an error rate across loci of 0.01 and an error distribution among alleles of 5 (Duchesne et al. 2002). Exclusion probabilities for potential parents were calculated using CERVUS 2.0 (Marshall et al. 1998). We used χ^2 tests to determine differences in fertilization success among groups and nonlinear regression analyses to examine changes in fertilization success of the different groups over the course of the spawning season.

Results

Body size and mortality

There were no size differences in parr among the arenas (ANOVA: length, $F_{[3,108]}$ = 0.035, P = 0.99; weight, $F_{[3,108]}$ = 0.014, P = 0.99; condition (grams per cubic centimetre × 100), $F_{[3,108]}$ = 0.12, P = 0.95) (Table 1) or among the parr of different origin (ANOVA: length, $F_{[2,108]}$ = 0.11, P = 0.90; weight, $F_{[2,108]}$ = 0.391, P = 0.68; condition, $F_{[2,108]}$ = 3.08, P = 0.05). In addition, there were no arena by parr type interactions affecting body size (ANOVA: length, $F_{[6,108]}$ = 0.026, P > 0.99; weight, $F_{[6,108]}$ = 0.052, P = 0.99; condition, $F_{[6,108]}$ = 0.84, P = 0.44). The number of parr recovered at the end of the experiment did not differ among arenas (χ^2 test: χ^2 = 0.836, df = 6, P = 0.99) (Table 1), nor were there differences in the incidence of wounding with respect to arena and parr origin (χ^2 test: χ^2 = 6.27, df = 6, P = 0.39). One Imsa parr, one Imsa × AquaGen parr, and one AquaGen parr were found in the stomachs of three different Imsa females.

Aggressive interactions

Aggressive interactions against parr initiated by anadromous fish differed between sexes and among arenas. Attacks by males and females differed among arenas (Fisher's exact test: P = 0.0002) such that large males in Imsa 1 and AquaGen 1 were observed attacking mature male parr more often than females, whereas the opposite was true in AquaGen 2. However, there was no tendency for large fish in the different arenas to attack mature male parr of a given origin more frequently (Fisher's exact test: P = 0.50).

Similarly, parr–parr aggression differed among arenas. Total mature male parr aggression tended to be higher in are-

Table 1. Length (cm), weight (g), and condition (g·cm^{-3} × 100) of parr (n = 10 per type) at the beginning of the experiment, number of parr recaptured from each arena at the end of the experiment, and number of wounded parr of Imsa, Imsa × AquaGen, and AquaGen origin in each of the four experimental arenas.

Variable	Imsa 1	Imsa 2	AquaGen 1	AquaGen 2
Imsa				
Length	11.62±0.37	11.63±0.41	11.67±0.46	11.73±0.36
Weight	20.21±2.16	19.86±2.21	20.28±2.30	20.39±1.85
Condition	1.24±0.02	1.21±0.02	1.22±0.02	1.23±0.02
Recaptures	9	9	8	9
Wounded	5	4	5	5
Imsa × AquaGen				
Length	11.76±0.46	11.73±0.35	11.72±0.33	11.73±0.34
Weight	21.49±2.68	21.58±1.91	20.98±1.66	20.64±1.66
Condition	1.25±0.02	1.30±0.03	1.27±0.02	1.25±0.03
Recaptures	9	8	10	10
Wounded	3	2	3	6
AquaGen				
Length	11.77±0.47	11.87±0.46	11.66±0.50	11.91±0.47
Weight	21.19±2.29	21.61±2.60	21.01±2.35	22.32±2.77
Condition	1.24±0.03	1.23±0.03	1.28±0.04	1.25±0.02
Recaptures	8	9	6	8
Wounded	0	5	3	3

Table 2. Total nests sampled from videotape recordings (n), total nests with encounters and aggression, and the number of nests at which parr of a given origin initiated aggression.

	n	Encounters	Aggression	Imsa	Imsa × AquaGen	AquaGen
Imsa 1	22	14	10	2 (8)	3 (8)	8 (9)
Imsa 2	27	12	6	5 (6)	1 (4)	2 (4)
AquaGen 1	37	14	9	5 (8)	3 (9)	1 (8)
AquaGen 2	43	17	14	5 (8)	7 (12)	6 (8)

Note: Data in parentheses indicate the number of samples during which parr of a particular origin were observed at the nest. The number of nests with aggression is lower than the sum total of the number of nests at which parr of a given origin was aggressive because parr of different origin may have initiated aggression at the same nest.

nas with Imsa anadromous males and differed among arenas (χ^2 test: χ^2 = 11.09, df = 3, P = 0.01). The number of aggressive interactions initiated by mature male parr of different origin varied among arenas (χ^2 test: χ^2 = 17.32, df = 6, P < 0.01); AquaGen parr were most aggressive in the presence of Imsa large males in the Imsa 1 arena and Imsa parr were most aggressive in AquaGen 1. The number of aggressive interactions received did not differ among parr of different origins or among arenas (χ^2 test: χ^2 = 8.41, df = 6, P = 0.21).

Video footage of parr behaviour at nests 5 min prior to spawning was available for 22, 27, 37, and 43 nests in Imsa 1, Imsa 2, AquaGen 1, and AquaGen 2, respectively (Table 2). There were no differences in the number of encounters among the four arenas (χ^2 test: χ^2 = 4.36, df = 2, P = 0.22). Encounters resulted in aggression in 71%, 50%, 64%, and 82% of cases in Imsa 1, Imsa 2, AquaGen 1, and AquaGen 2, respectively, and did not differ significantly among arenas (Fisher's exact test: P = 0.89). Similar to the live observations, the number of nests at which parr of a given origin were aggressive varied among arenas (Table 2), and differences in aggression with respect to parr origin were found only in Imsa 1 (Fisher's exact test: P = 0.02) in

which AquaGen parr attacked more frequently than Imsa or Imsa × AquaGen individuals.

Mature male parr spawning participation

To determine whether mature male parr origin affected positioning near the female before egg release, we recorded the group identity of the individual closest to the female 1 min prior to spawning and found some differences among arenas with respect to the origin of the parr closest to the female. In the Imsa 1, Imsa 2, and AquaGen 2 arenas, there were no differences among groups in proximity to the female, including only cases where two or more types of parr were present (Fisher's exact test: Imsa 1, P = 0.51; Imsa 2, P = 0.16; AquaGen 2, P > 0.9) (Table 3). However, in AquaGen 1, Imsa parr attained a closer position to females than other types of parr (Fisher's exact test: P < 0.01).

Overall, parr participated in 68%, 70%, 68%, and 73% of observed spawning events in Imsa 1, Imsa 2, AquaGen 1, and AquaGen 2 arenas, respectively (Table 3), and there were differences in parr attendance at spawnings within arenas. Parr of each origin were equally likely to be present at spawnings attended by at least one parr in arenas with Imsa anadromous males (χ^2 test: Imsa 1, χ^2 = 3.91, df = 2, P =

Table 3. Total number of videotaped spawnings analysed, total number of spawnings with parr, number of spawnings at which parr of a given origin were closest to the female 1 min prior to spawning, and number of spawnings attended by parr of different origin in the four arenas.

	Total no.	No. with parr	Origin	No. closest	No. of spawnings attended
Imsa 1	25	17	Imsa	4 (3)	15 (9)
			Imsa × AquaGen	4 (4)	10 (8)
			AquaGen	7 (4)	13 (11)
Imsa 2	27	19	Imsa	10 (4)	17 (9)
			Imsa × AquaGen	5 (5)	12 (9)
			AquaGen	1 (1)	14 (10)
AquaGen 1	40	27	Imsa	11 (5)	14 (5)
			Imsa × AquaGen	13 (2)	23 (6)
			AquaGen	2 (0)	7 (6)
AquaGen 2	44	32	Imsa	5 (3)	15 (8)
			Imsa × AquaGen	19 (4)	27 (9)
			AquaGen	3 (3)	18 (8)

Note: The number of spawnings for which these data were obtained differs slightly from those in Table 2 because some spawning events did not contain adequate footage prior to female egg release for aggression data to be collected. For the same reason, the closest parr 1 min prior to spawning was not attainable for all nests sampled. Figures in parentheses exclude cases where parr of a single origin only were observed and thus refer to the number of nests at which parr of two or three different origins were present.

0.14; Imsa 2, $\chi^2 = 3.60$, df = 2, $P = 0.17$) (Table 3). However, there were differences among the three parr types in arenas with AquaGen large males (χ^2 test: AquaGen 1, $\chi^2 = 19.85$, df = 2, $P < 0.001$; AquaGen 2, $\chi^2 = 10.40$, df = 2, $P < 0.01$) (Table 3), where hybrid parr consistently attended more nests than Imsa or AquaGen parr.

To control for arena differences in number of spawnings, we analysed the number of parr of different origin at nests with respect to spawning number using only the first 25 spawnings in each arena. Spawnings were numbered sequentially from 1 to 25 from the first observed spawning and occurred over a period lasting between 20 and 22 days. Overall spawning attendance differed between arenas containing Imsa or AquaGen large males (GLM: $F_{[1,94]} = 13.45$, $P < 0.001$) (Fig. 1). Interestingly, there was a strong temporal decline in parr spawning, as indicated by a highly significant negative effect of spawning number on the total number of parr attending spawnings (GLM: $F_{[1,94]} = 60.13$, $P < 0.001$).

There was a three-way interaction among spawning number, parr origin, and large male origin (GLM: $F_{[2,279]} = 3.35$, $P = 0.036$) (Fig. 2) on the number of parr attending spawning events. To examine differences among parr of different origin, we removed the effect of large male origin by analysing the AquaGen and Imsa treatments separately. In arenas containing AquaGen large males, there was also an interaction between parr origin and spawning number on parr attending spawnings (GLM: $F_{[2,141]} = 6.16$, $P < 0.01$), where more hybrids participated in spawning later in the experiment. In arenas with Imsa large males, more Imsa and AquaGen than Imsa × AquaGen individuals were involved in spawnings (GLM: $F_{[2,140]} = 4.84$, $P < 0.01$), and the number of parr of every origin per spawning decreased with increasing spawning number (GLM: $F_{[1,140]} = 94.61$, $P < 0.001$).
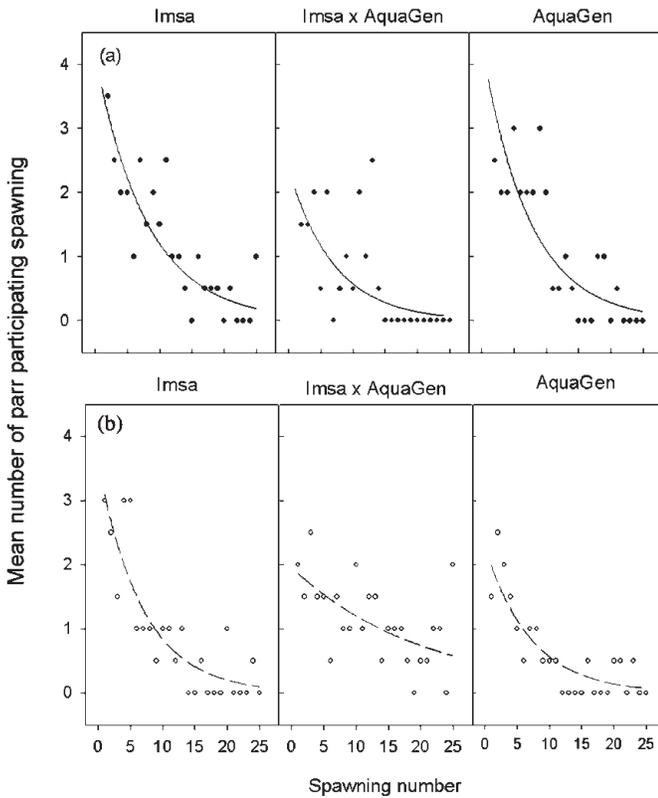
Genetic analysis

Embryo survival was extremely poor, with very few surviving in Imsa 1 and AquaGen 1; only a few nests from

Fig. 1. Mean ± SE of the total number of mature male parr attending per spawning for the first 25 spawnings in arenas with (*a*) Imsa or (*b*) AquaGen large males.
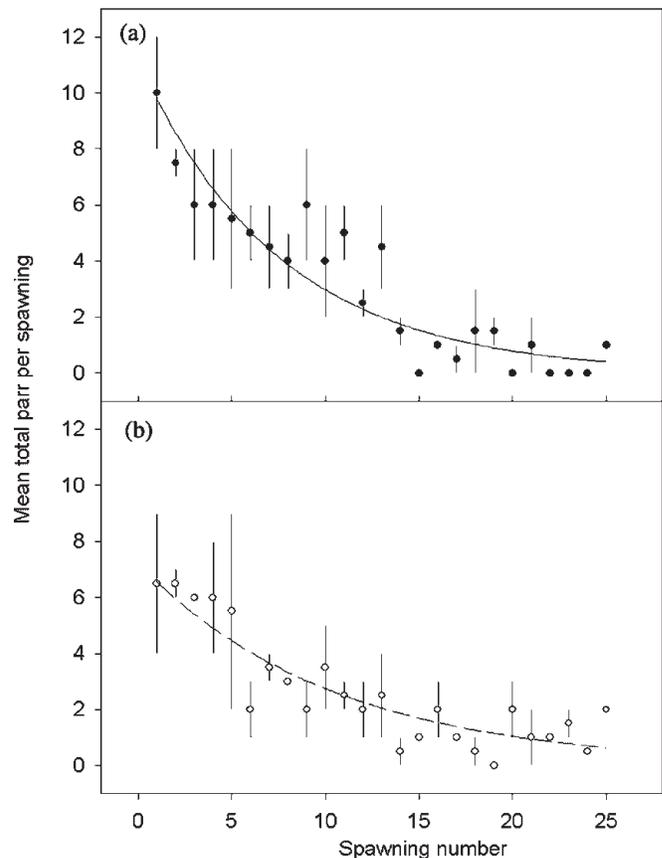
Imsa 2 and AquaGen 2 could be analysed for parentage assignment. Nests were analysed if more than 20 embryos survived, and in all but two cases, the number of eggs analysed per nest was greater than 90. In these two cases, be-

1158

Can. J. Fish. Aquat. Sci. Vol. 62, 2005

Fig. 2. Mean number of Imsa, Imsa × AquaGen, and AquaGen mature male parr per spawning for the first 25 spawnings in arenas with (*a*) Imsa or (*b*) AquaGen large males.

Fig. 3. (*a*) Proportion of total fertilization success among males and (*b*) CV ($s/\bar{x}$ × 100) (%) of group fertilization success in arenas with Imsa (solid circles) or AquaGen (open circles) large males.

havioural observations confirmed that only large fish were present at the nest and thus obtained 100% fertilization success. Five nests and a total of 816 embryos were genotyped from Imsa 2 and three nests for a total of 415 embryos were genotyped from AquaGen 2. Of these, 757 and 387 offspring could be unambiguously assigned to mothers and fathers of a given origin in Imsa 2 and AquaGen 2, respectively. Overall exclusion probability among possible parents was 0.998 in both Imsa 2 and AquaGen 2 and there were no deviations from Hardy–Weinberg equilibrium among potential parents.

In light of the poor embryo survival in the experiment, our estimates of fertilization success are based on overall success within either Imsa 2 or AquaGen 2. There were differences between the arenas with respect to the proportion of eggs sired by males of different origin (Fig. 3*a*). Imsa large males in Imsa 2 were assigned 77% of the offspring, while Imsa, Imsa × AquaGen, and AquaGen mature male parr fathered 6%, 13%, and 4% of offspring, respectively. In contrast, 15%, 28%, and 8% of offspring were fathered by Imsa, Imsa × AquaGen, and AquaGen parr in AquaGen 2, respectively, with the remaining 49% assigned to AquaGen large males. Although the proportion of eggs fertilized by mature male parr of different origin differed between arenas, the rank order of fertilization success remained the same; Imsa × AquaGen had the highest fertilization success followed by Imsa and AquaGen parr. Overall, mature male parr fertilized a higher proportion of eggs in the presence of AquaGen large males. More interestingly, there was a large range in individual fertilization success of the different parr groups
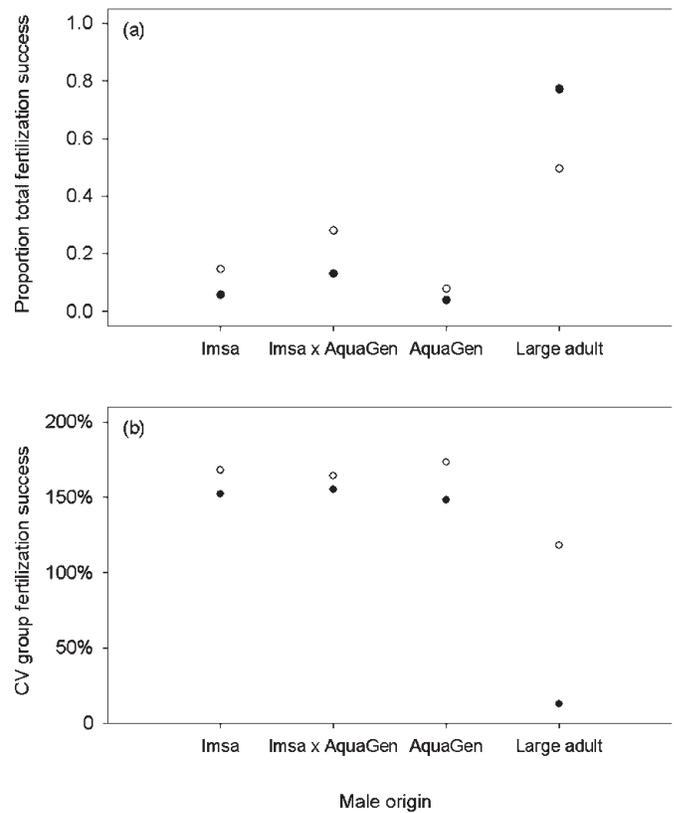
among nests (Imsa 2: Imsa, 0%–12%; Imsa × AquaGen, 0%–16%; AquaGen, 0%–6%; AquaGen 2: Imsa, 0%–42%; Imsa × AquaGen, 0%–100%; AquaGen, 0%–23%). In Imsa 2, variance in fertilization success was an order of magnitude higher within groups of mature male parr (CV = ($s/\bar{x}$) × 100%; CV: Imsa, 152; Imsa × AquaGen, 155; AquaGen, 148) than large Imsa males (CV = 13) (Fig. 3*b*). In contrast, the high variation in fertilization success per nest among AquaGen large males in AquaGen 2 (CV = 118) was closer to that expressed within groups of mature male parr (CV: Imsa, 168; Imsa × AquaGen, 164; AquaGen, 173).

Discussion

Our findings provide insight into the spawning behaviour and fertilization success of mature male parr of different genetic origin. We document differences in behaviour among mature male parr of different genetic origin and a strong negative temporal effect on spawning participation. Our results also indicate a high variance in fertilization success among mature male parr and that parr of farmed origin can successfully fertilize eggs in competition with wild parr. We found no consistent differences in either aggression or proximity to females prior to spawning among mature male parr of different genetic origin. By contrast, there were some notable differences in spawning participation among the three parr types. Interestingly, although the number of hybrids participating per spawning event tended to be lower than ei-

ther of the pure crosses, their participation persisted over a longer period of time in the presence of AquaGen large males. Prolonged participation by hybrid parr could have been attributable to high female activity in the arenas containing AquaGen large males (Weir 2003). Mature male Atlantic salmon parr show a hormonal response and increased milt production when exposed to the sound of female digging (Moore and Waring 1999), and male salmonids are known to respond behaviourally (Takeuchi et al. 1987) and hormonally (Rouger and Liley 1993) to spawning females. Thus, higher levels of female nesting activity in the arenas containing AquaGen males may have triggered participation by mature male parr for a longer period of time than in the arenas containing less active females. The lower number of hybrids participating early in the spawning season, when Imsa and AquaGen parr were present at high numbers, may have enabled them to partake in spawning for a longer period of time.

The similarity in spawning participation between Imsa and AquaGen male parr was unexpected based on previous comparisons of either hatchery and wild or farmed and wild juveniles: one group is usually reported to outperform the other. However, this similarity in behaviour may also signify similarities in the mode of competition among farmed and wild mature male parr during spawning. There may be many reasons why the documented differences in aggression did not result in parallel trends in spawning participation, and one likely explanation may be that mature male parr use scramble rather than interference competition during spawning. Parr spawning participation occurred mainly at the beginning of the experiment, when parr were associated near spawning females in groups. Large numbers of competitors are often associated with low individual aggression, as the defence of a resource against many competitors may not be economical (Brown 1964; Warner and Hoffman 1980; Grant et al. 2000). Although spawning in larger numbers may negatively affect individual parr reproductive success, the early participation by parr may have allowed them to avoid prolonged interactions with large fish, given that attacks from large fish can result in parr mortality (Hutchings and Myers 1987; Broberg et al. 2000; present study).

Indirect evidence of a reduction in parr participation over time has been reported in some experiments estimating fertilization success of mature male parr (Hutchings and Myers 1988; Thomaz et al. 1997). Given that our experiment was a closed system in which parr were not free to leave or enter the spawning grounds, we cannot conclusively infer that there is a negative temporal effect of parr participation under natural conditions. However, based on the sole study of parr migration to spawning grounds, evidence suggests that mature male parr migrate to natural spawning grounds at the beginning of the spawning season and that the likelihood of new parr arriving on the spawning grounds diminishes rapidly over time (Hutchings 1986) (Fig. 4).

Our behavioural data suggest that Imsa and AquaGen male parr spawning participation decreased over time, as did their fertilization success. Conversely, Imsa × AquaGen parr had the highest fertilization success among groups of mature male parr, and this success may be partly attributable to the fact that they tended to participate in spawning later in the experiment, when competition among parr was lower. Con-

Fig. 4. Average number of mature male parr moving out of Wings (solid circles) or Bluehill (shaded circles) Pond into streams in the autumn of 1982 in the Wings Brook system, Bonavista Bay, Newfoundland. Spawning usually occurs in late October – early November in the system. Data are from J.A. Hutchings (unpublished data).
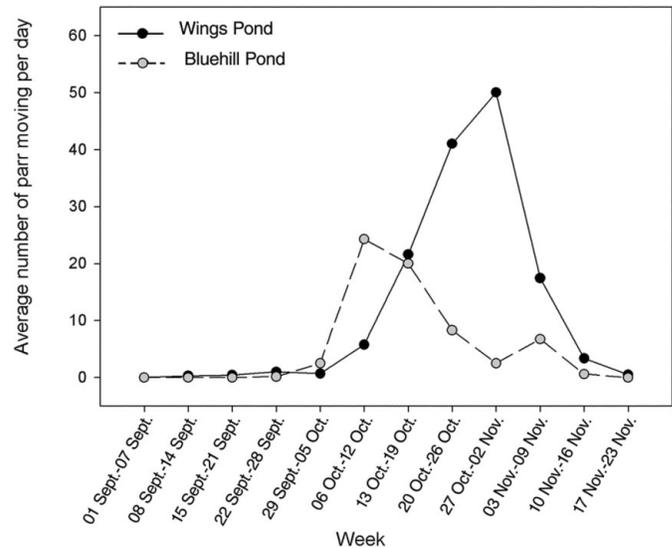
sequently, hybrid parr fertilized more eggs as participation by Imsa and AquaGen parr decreased, particularly in the presence of AquaGen large males. The relatively high mature male parr success in competition with AquaGen large males can probably be attributed to less frequent sperm release during spawning by farmed large males (Weir et al. 2004) and to our observation that mature male parr spawning success was significantly higher in the presence of farmed than wild large males. Although we cannot draw firm conclusions regarding relative fertilization success among parr of different origin owing to unfortunately small sample sizes, they do corroborate the results of our behavioural data and allow for some extrapolation of those results to sources of potential differences in fertilization success. The ranks in parr fertilization success were consistent between the two arenas, with hybrids consistently fertilizing more eggs than wild and farmed parr. Furthermore, an interesting and robust result is the high variance in parr fertilization success, a finding consistent with previous studies (Jones and Hutchings 2001, 2002).

We conclude that behavioural differences among mature male parr of different genetic origin can result in differences in reproductive success. Moreover, parr of farmed origin can adequately compete with wild parr and succeed in fertilizing eggs. Thus, in addition to making them a potential source of introgression of farmed genes into wild populations, parr of farmed origin may increase the intergenerational rate at which such introgression occurs, given that they mature earlier than their large counterparts.

Acknowledgements

1160

Can. J. Fish. Aquat. Sci. Vol. 62, 2005

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