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Reproduction of Aquaculture Atlantic Salmon in a Controlled Stream Channel on Vancouver Island, British Columbia

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Abstract.—Sightings and captures of Atlantic salmon *Salmo salar* that have escaped from aquaculture facilities have become common in coastal British Columbia, Canada. A lack of empirical data has prevented the forecast of what effects may result from the presence of this species in the Pacific Northwest. A first step towards this objective is to evaluate the spawning potential of escaped Atlantic salmon. We report results from a study of Atlantic salmon spawning in a simulated stream channel at the Little Qualicum River, British Columbia. Adults were obtained from a local commercial marine net-pen operation; 17 of 19 males and 24 of 30 females matured sexually, and up to 9 females successfully deposited eggs in six redds, five of which yielded viable progeny when the eggs were collected and incubated in Heath trays. Results suggest Atlantic salmon escaping from aquaculture facilities are likely to experience low spawning success in coastal British Columbia. However, based on the high proportion of sexual maturation, and even though successful spawning may be limited, we conclude that adult Atlantic salmon escapees, particularly those observed in freshwater, should be considered potential spawners.

The coastal marine waters of southern British Columbia (B.C.) around Vancouver Island support one of the world's most prolific salmon culture industries. Over 47,000 metric tons of salmon were produced by B.C. salmon farmers in 1999, 81% of which was Atlantic salmon *Salmo salar,* an exotic species in this region. Atlantic salmon cultured in B.C. are a composite of strains imported from Scotland, Ireland, USA, and New Brunswick (Atlantic Canada; Alverson and Ruggerone 1997). Eleven private hatcheries (mostly on Vancouver Island) select broodstock and supply smolts to marine grow-out facilities (Alverson and Ruggerone 1997).

Atlantic salmon were first imported for commercial culture in 1984 (Keller and Leslie 1996), and free ranging escapees have been reported in both the marine and freshwater environments since 1987 (McKinnell et al. 1997). During the following 11 years a total of 236,974 Atlantic salmon have been reported to have escaped (Thomson and Candy 1998). It is likely additional fish have been lost due to ''leakage'' (i.e., chronic, undocumented loss of fish; Alverson and Ruggerone 1997; Moring 1989). The adjacent waters of Washington State also support Atlantic salmon culture facilities. Three recent events occurring over 3 years liberated an estimated 591,000 Atlantic salmon into coastal Washington waters (Amos and Appleby 1999).

These escaped fish have prompted debate over the colonization potential of Atlantic salmon in the Pacific Northwest. On the Atlantic Coast, spawning success of farm-raised Atlantic salmon escapees has been shown to be inferior relative to wild counterparts (reviewed by Fleming et al. 1996). In a Norwegian study, farm-raised females retained more eggs, had greater egg mortality, and overall were 20–40% as successful as wild females (Fleming et al. 1996). Restrained and inappropriate behaviors of farm-raised males resulted in less than 3% of the success of wild males (Fleming et al. 1996). Poor spawning performance and presumed poor competitive ability of any wild-reared Atlantic salmon progeny have led to suggestions that escapees from aquaculture facilities pose little threat to native species in coastal B.C. (Needham 1995; Alverson and Ruggerone 1997).

Atlantic salmon reproduction in the wild has been documented in B.C. (Volpe et al. 2000); how-

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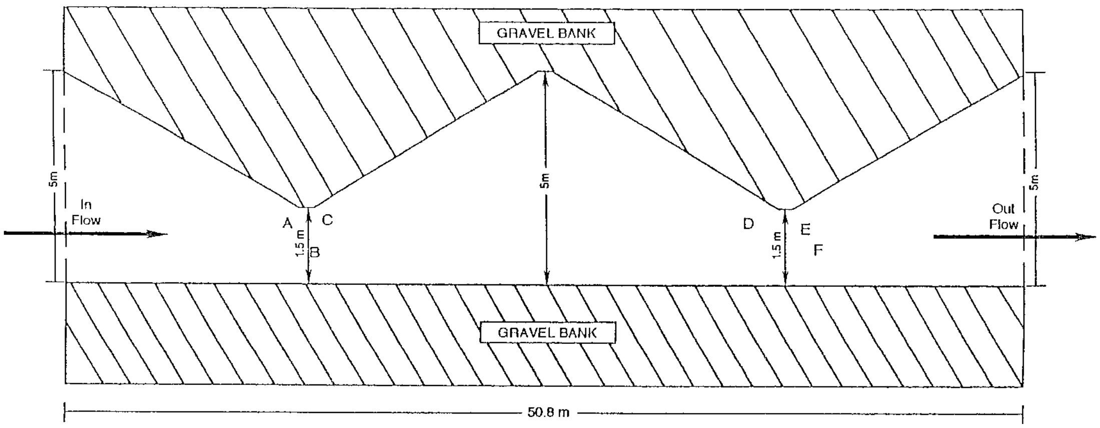

FIGURE 1.—Schematic representation of the experimental spawning channel for farm-reared Atlantic salmon. Redd sites are lettered A to F.

ever, the reproductive potential of B.C. Atlantic salmon in a natural environment has not been evaluated. The objective of this work was to assess the reproductive potential of B.C. aquaculture production stock in a simulated natural environment and apply the findings to the ongoing debate regarding the colonization potential of Atlantic salmon in the northeastern Pacific region.

Methods

The study was conducted between October 1997 and February 1998 at the Little Qualicum Project, Canada Department of Fisheries and Oceans, in Qualicum Beach, B.C. Physical containment of the Atlantic salmon was a high priority in choosing a venue for this work. A fully contained rearing pond was re-engineered to serve as a spawning channel. Approximately 352 m^3 of river gravel (mean diameter $\pm$ SD = 17.5 $\pm$ 2.5 cm) was used to create a 50-m-long channel of various depths (0–40 cm), widths (1.5–5.0 m), and water velocities, providing heterogeneous holding and spawning habitats (Figure 1). Water diverted from the Little Qualicum River passed through the channel at velocities ranging from about 0–0.42 m/s, depending on location in the channel (maximum velocities at the two narrowest points). The minimum gravel depth was approximately 40 cm at mid-channel. Gravel banks sloped from the water's edge to a depth of 40 cm at mid-channel. No instream structure was provided.

Adult aquaculture production fish were collected from an offshore marine grow-out facility off Tofino, B.C., on January 14, 1997. All fish (30 females, 20 males) were silvery and bright; however, some showed early signs of sexual maturation, particularly kype formation in some males. Transfer from marine to freshwater was rapid to minimize osmotic shock; we loaded the fish into a hatchery transport truck with an 80:20 mix of marine: freshwater (salinity was not measured). Total transport time from the offshore farm site to the Little Qualicum site was 5.3 h. Fish were released into the channel immediately upon arrival, without additional intermediate acclimatization to freshwater.

After a 96-h acclimatization period to freshwater and the new environment, behavioral observations began. Fish were not individually marked but sexes were distinguishable. Individuals were observed from a stepladder atop the channel bank (approximately 4 m above and 3 m back from the waters edge), and behavioral data were collected between dawn and dusk. Focal individuals were chosen randomly, and behavior was recorded for 15 min. Counts of cruising (nondirected movement), agonism (attacks, front or lateral displays), and mating behaviors (digging and courted by females, quivering and courting by males) were recorded. A total of 19.5 h of data were collected in 78 observation sessions.

At the end of the experiment, redd lengths and widths were measured from the center of the two most distant egg clusters. Lengths were measured on the long axis parallel to water flow and widths were measured at the widest point and at right angles to length. Egg samples were removed from each redd and transported to the University of Victoria for observation and to assess viability.

Moribund fish were removed from the channel and weighed, measured, and examined for fungal infection and wounds. Fungal infections were

TABLE 1.—Behavioral data of adult male and female Atlantic salmon in an artificial spawning channel. All data are mean counts (±SD) per observation period except mean cruising distance, which is expressed in meters.

Behavior	Females	Males
Agonism	0.20 (0.40)	0.36 (0.49)
Cruise	1.36 (1.92)	2.39 (1.73)
Mean cruise distance (m)	3.42 (1.18)	3.22 (1.04)
Female dig	0.12 (0.33)	
Female courted	0.08 (0.27)	
Male quiver		0.04 (0.19)
Male court		0.07 (0.26)
Total observations	50	28

scored (no infection; <40% body coverage, >40% body coverage). Level of sexual maturation was assessed in both sexes, and degree of gamete retention was estimated in females that showed evidence of spawning (retention of some ripe eggs, extended ovipositor). The physical condition of spawners versus nonspawners was compared using the log-transformed ratio of dried (60°C, 48 h) heart mass to somatic mass (Farrell et al. 1988; Fleming et al. 1996).

Results

Conditions in the channel remained constant throughout the experiment. Weather was seasonally normal, and mean ± SD water temperature was 3.9°C ± 0.64 (range 1.5–6.4°C). At 4 d post-introduction some fish began to show signs of an epidermal fungal infection, which we attributed to extensive handling required during transport and the rapid transition from marine to freshwater. The number infected and intensity of infection increased throughout the experiment.

Within 5 d of introduction, females began to defend territories and showed little interest in areas other than riffle head or tails where putative redd sites were located (Figure 1). Females were inactive unless digging or defending a putative redd. Males were more evenly distributed throughout the channel and were not significantly more agonistic ($\chi^2 = 1.5735$, df = 1, $P = 0.2097$) than females, nor more likely to cruise ($\chi^2 = 12.0828$, df = 7, $P = 0.0979$; Table 1). Almost all agonistic behaviors were directed at individuals of the same sex, males competing for access to mates and females defending territories.

All fish were dead by day 33 of the experiment (February 15). All but two individuals exhibited heavy fungal infection at the time of death (Table 2), which confounded our results and prevented attributing a cause of death for most individuals. One male was lost to predation by a bald eagle. Nine females showed evidence of spawning but only six redds were identified. Many opaque, nonviable eggs were observed on top of the substrate throughout the channel; 2,348 of these eggs were recovered but many more probably remained beneath the substrate. At time of death nearly all fish had sexually matured, but less than half of those females showed signs of egg deposition (Table 2). Wide variation in egg maturation was noted among the 21 females that did not spawn; 15 had fully mature ova, whereas the 6 others held immature eggs in their ovaries and would not have matured for many weeks, if at all (Table 2). Of the nine females that spawned, only two were completely devoid of eggs; the rest retained numerous eggs, but no evidence of egg resorbtion was noted before they died. Fecundity of mature females that did not spawn varied so greatly that no relationship was found between fork length and gonad weight ($r^2 = 0.14$, $N = 15$). Physical condition of spawning and nonspawning females did not differ in the ratio of log-transformed dried heart mass to somatic mass ($t = 1.107$, df = 28, $P = 0.277$) or in condition factor ($t = 0.877$, df = 28, $P = 0.3878$).

The distribution of eggs in the redds was not typical of discrete nests; instead, there were areas of localized concentration surrounded by diffusely scattered eggs. The six redds averaged 1.56 ± 0.42

TABLE 2.—Results of postmortem examination of adult Atlantic salmon held in a spawning channel. Length is mean (±SD) postorbital–hypural (O–H) distance; weight is mean (±SD) total body mass including gonads. Reproduction status abbreviations are as follows: I = immature gonads (males not ripe and females with eggs in skein); R = ripe gonads (not applicable (na) for males, females ripe or almost ripe but no evidence of spawning [all eggs retained]); M = mature gonads (males ripe and females ripe with at least partial egg release). Fungal infection ratings are based on fungal coverage.

Sex	N	O–H length (cm)	Total weight (g)	Gonad weight (g)	Reproduction status			Fungal infection		
					I	R	M	0%	<40%	>40%
Males	19	57.3 ± 5.0	4,240 ± 1,504.0		2	na	17	0	0	19
Females	30	58.2 ± 3.1	4,364.7 ± 1,029.4	631.6 ± 337.0	6	15	9	2	7	21

m long and 0.77 ± 0.07 m wide; the midpoint of egg masses was 23 ± 7 cm below the substrate surface. Viable eggs were recovered from five of the six redds; all eggs in one redd (C in Figure 1) had been infected by fungus and were not viable. We were unable to enumerate eggs in the redds.

Because of other fish culture activities at the Little Qualicum project, we could not allow the eggs to incubate and hatch in the channel. Therefore, we transported a sample of 50 viable eggs from each redd to the University of Victoria, Aquatic Research Facility, for incubation. Mean mass of the retrieved eggs was 105 ± 16 mg. Because the parentage of each redd was unknown and possibly contained eggs of more than one female, we combined the eggs in a single standard Heath incubator tray. At 10°C, 88% successfully hatched at between 455 and 510 thermal units (number of days between spawning and hatching times water temperature), the range being produced by the days separating first and last observed spawning. The hatched fry, reared at the University of Victoria, smoltified at 20 months and are currently maintained in salt water, indicating typical and continuing development.

Discussion

Our results show that commercially reared Atlantic salmon will sexually mature and spawn successfully in a simulated natural environment but that per capita reproductive success is low. Although most females matured, the majority did not spawn. Those females that did spawn exhibited considerable egg retention, poor redd construction, and limited egg viability. Because of the confounding influence of the fungal infections, we cannot be certain that ovaries of the nonspawning females would not have continued to mature (no evidence of egg resorbtion was noted), nor that the spawning females would have continued to spawn had they survived longer. Nearly all males matured but showed subdued breeding behavior compared with typical wild Atlantic salmon (Gibson 1993; Fleming 1996). Spawning was restricted to areas most closely resembling typical Atlantic salmon spawning habitat described by (Fleming 1996); all spawning events occurred in habitat predicted a priori as being optimal based on published values. This may be useful in identifying potential spawning areas in natural river systems where Atlantic salmon activity has been reported. Even at a low per capita success rate, the increasing presence of adult migratory Atlantic salmon observed in British Columbia river systems (Volpe 1998; 1999; 2000) could to some extent ameliorate poor spawning performance by feral fish.

Within the native range of Atlantic salmon, farm-reared Atlantic salmon have been shown to successfully reproduce in the wild (Lura and Sægrov 1991; Webb et al. 1993; Carr and Anderson 1997). However, when compared to wild counterparts, adult farmed salmon displayed inferior competitive ability and inappropriate behavior resulting in lower reproductive success (Fleming et al. 1996). The present data support these observations. Examination of the six spawning sites suggest the females we observed lacked normal spawning ability. Under normal circumstances a female Atlantic salmon would be expected to construct an average of five or more discrete egg pockets or nests per redd (Fleming 1996 and references therein; but see Lura et al. 1993). All six redds we observed were constructed as a single, large deposition of eggs with no evidence of discrete egg pockets. The overall size and depths of the redds were within published ranges from other studies (reviewed by Fleming 1996), but many eggs were found to be nonviable. Fleming et al. (1996) attributed poor performance of farm-raised fish to behaviors altered by domestication, poor physical condition, and eroded caudal fins.

We observed no differences in physical condition between spawning and nonspawning females. Wild Atlantic salmon have been shown to posses greater physical condition than farm-reared counterparts (Fleming et al. 1996). Relative spawning ability of farm-reared and feral Atlantic salmon in British Columbia has not been investigated to date.

Spawning performance was probably compromised by the fungal infection, particularly with respect to caudal fins, most of which were heavily infected by the end of spawning activity. Many nonviable eggs were found in clusters directly atop of the substrate, considerable distances from any identifiable redd sight, indicating females had oviposited directly onto the substrate without preparation of a redd. We do not know if they were accompanied by a male during this period, but no fertilized eggs were found among these surface clusters.

Reproductive success was further reduced by egg retention; only two of nine spawning females were devoid of eggs. Because there was no relationship between female size and fecundity, we were unable to estimate what proportion of total fecundity was retained by each female that did spawn. Fecundity estimates from 12 wild Atlantic salmon populations (1996) adjusted to the mean length of our females (58 cm) produced an average fecundity of 4,004 eggs (range 2,496–4,767). If we use the regression of fork length to gonad weight of our ripe females, the mean number of eggs spawned per female would be 3,448 (range of 1,028–6,333). This translates to a mean retention by spawning females in this experiment of 46.4% (ranged of 0–76.4%). Although there is significant residual error associated with this estimate because of the low r^2 (0.14) of the original correlation, it is a more conservative estimate than simply subtracting the mean retained gonad weight from the mean total gonad weight.

Male spawning behavior in this experiment was very similar to that reported for farm-reared males in competition with wild males (Fleming et al. 1996), except that males in this experiment were more agonistic and more likely to cruise, perhaps due to the absence of wild males. Behaviors directly related to mating, specifically counts of courting and quiver, were very similar to those reported by Fleming et al. and significantly lower ($P < 0.001$) than corresponding their counts for wild fish. Fleming et al. concluded that subdued male behavior contributed to the poor overall spawning success of the farm-raised fish relative to their wild counterparts.

Our experimental environment lacked potential competitor species such as coho salmon *Oncorhynchus kisutch* and steelhead trout *O. mykiss*, both of which prefer spawning habitats similar to Atlantic salmon (Scott and Crossman 1973; Sandercock 1991; Gibson 1993). Atlantic salmon show considerable variation in spawning time, and although our fish did not initiate spawning behavior until early winter (19 January), it is still well within the observed range of wild Atlantic salmon populations (Mills 1989; Fleming 1996). In late January, coho salmon would have largely completed spawning (Sandercock 1991), and steelhead probably would not have begun. Thus, midwinter spawning Atlantic salmon may face reduced competitive interference from native salmonids. Redd destruction and superimposition by later spawning steelhead may act to reduce this advantage; however, the magnitude of the effect would be density dependent, and steelhead are currently at all-time lows in B.C. (Slaney et al. 1996). To date, potential interspecific effects on spawning success, with regard to the presence of Atlantic salmon in B.C., remain uninvestigated.

Putatively low reproductive success of farm-reared Atlantic salmon observed here and elsewhere does not rule out the possibility of successful colonization in B.C. Successful reproduction in three Vancouver Island rivers has already been documented (Volpe 2000; Volpe et al. 2000). Two of these systems currently support at least two year-classes of juveniles and therefore do not represent isolated incidents. Atlantic salmon culture is currently expanding in British Columbia, which may result in an increase in escape numbers. Neither the actual number of current escapees nor the proportion of escapees that survive to ascend coastal rivers is known. However, the number of adults observed in coastal freshwaters during annual river surveys continue to increase (Volpe 1998, 1999, 2000). Undetected spawning has occurred and will probably continue, so successful colonization is possible. How the presence of competitor or predator species in a natural, more heterogeneous environment may alter our findings also remains to be investigated. Numbers of Atlantic salmon adults in many Vancouver Island rivers are now adequate to undertake such natural experiments. Our results suggest that although *per capita* success is low, escaped Atlantic salmon that survive to ascend coastal B.C. rivers are capable of successfully excavating redds and spawning viable eggs.

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