National Research Council Canada
Conseil national de recherches Canada

Canada

Reprinted from
Réimpression du

Canadian Journal of Zoology

Journal canadien de zoologie

Mating between anadromous and nonanadromous Atlantic salmon, *Salmo salar*

J. A. HUTCHINGS AND R. A. MYERS

Volume 63 ● Number 9 ● 1985

Pages 2219–2221

Printed in Canada / Imprimé au Canada

NOTES

Mating between anadromous and nonanadromous Atlantic salmon, *Salmo salar*

J. A. HUTCHINGS

Department of Biology, Memorial University of Newfoundland, St. John's, Nfld., Canada A1B 3X9

AND

R. A. MYERS

Fisheries Research Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld., Canada A1C 5X1

Received March 6, 1985

HUTCHINGS, J. A., and R. A. MYERS. 1985. Mating between anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Can. J. Zool. **63**: 2219–2221.

Mating experiments were conducted to determine whether behavioural isolating mechanisms exist that would prevent interbreeding between anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Males of both forms attempted to stimulate females of the other form to spawn and females responded by digging redds, spawning, and covering redds. Viable eggs were produced in both cases. These forms probably represent within-population phenotypic variation where they co-occur. Interbreeding can be expected if anadromous salmon are introduced into areas formerly occupied only by the nonanadromous form.

HUTCHINGS, J. A., et R. A. MYERS. 1985. Mating between anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Can. J. Zool. **63**: 2219–2221.

Des expériences d'accouplements ont servi à déterminer s'il existe des comportements d'isolement qui empêchent les croisements entre les poissons anadromes et les poissons non anadromes chez le saumon de l'Atlantique, *Salmo salar*. Les mâles des deux formes ont tenté de stimuler les femelles de l'autre forme à déposer leurs oeufs et les femelles ont réagi en creusant des nids, en y déposant leurs oeufs et en les recouvrant. Des oeufs viables ont résulté des deux types de croisement. Ces formes représentent probablement des variantes phénotypiques au sein de la même population aux endroits où elles cohabitent. L'introduction de saumons anadromes dans des régions occupées exclusivement par des formes non anadromes auparavant résultera donc probablement en des croisements entre les deux formes.

[Traduit par le journal]

Introduction

Anadromous migrant and freshwater resident (ouananiche) forms of the Atlantic salmon, *Salmo salar*, co-occur in eastern North America (Behnke 1972; Riley et al. 1984) and northeastern Europe (Berg 1948). This phenomenon is particularly prevalent in Newfoundland (Leggett and Power 1969; Hutchings 1985; Department of Fisheries and Oceans, St. John's, unpublished data). It is not known whether differences in the life histories of these forms represent within- or between-population variation.

Salmon enhancement activities in eastern North America have resulted in the removal of many natural barriers to upstream migration, thus permitting access of anadromous *S. salar* to waters inhabited solely by ouananiche. To properly assess the effects of these introductions of anadromous salmon, and to aid in the management of systems in which both forms presently co-occur, it is important to know whether the two forms could interbreed with one another. We undertook this study to determine whether there are behavioural isolating mechanisms that would prevent reproduction between ouananiche and anadromous Atlantic salmon.

Methods

Anadromous Atlantic salmon ascending the Exploits River, Newfoundland, were collected at the Grand Falls fishway and transported to the spawning channel facility located on Noel Paul's Brook (48°33′ N, 56°33′ W) during the summer of 1984. These fish were aged as grilse (i.e., they had spent one winter at sea) and ranged from 46.9 to 53.2 cm in fork length (mean size did not differ between sexes). Sexually mature ouananiche were collected on October 26, 1984, over spawning substrate (geometric mean size 3–6 cm) at the outlet of Furriers Pond (48°31′ N, 56°37′ W), using a beach seine and electroshocking equipment. Females ranged from 29.9 to 37.0 cm in fork length, males from 20.0 to 30.7 cm. Fish were transported for a maximum of 7 h in refrigerated tanks. No mortalities or undue stress were observed.

Enclosures were constructed in a regulated flow channel in Noel Paul's Brook. Galvanized wire screening (6-mm square mesh) permitted the flow of water through the enclosures, each measuring 0.85 m in width and 2.5 m in length (set parallel to stream flow). Aprons of wire screening were stapled to the sheets of plywood separating the enclosures from one another and were covered with gravel to prevent passage of fish between compartments. Mean water depth measured 0.4 m (range 0.35–0.50 m) while mean surface current velocity was 6.5 cm/s within the channel. Substrate composition was as follows: cobble (6–15 cm) 10%, pebble (3–6 cm) 44%, gravel (0.2–3 cm) 38%, and sand (<0.2 cm) 8%.

Four experimental enclosures contained one anadromous male and one female ouananiche. Two male ouananiche and one anadromous female were placed in each of four other experimental enclosures to replicate the natural occurrence of multiple males at a mating. Two types of controls were used: (*i*) two enclosures each containing two male and one female ouananiche, and (*ii*) a single enclosure holding an anadromous pair. Male ouananiche were not placed upstream of the enclosures containing female ouananiche. Similarly anadromous females were not downstream of enclosures containing anadromous males.

Detailed behavioural observations on spawning activities were made twice daily on fish in a stream tank. The salmon had been transported from Noel Paul's Brook to the facility at the Northwest Atlantic Fisheries Centre, St. John's. The stream tank was 9.1 m long and 3.0 m wide, consisting of a circular wooden flume with recirculated water at an exchange of 10 L/min. A channel 1.2 m wide and another 0.6 m wide were joined by a pool section 1.5 m wide and deeper than the two channels by 30 cm (see Gibson (1981) for a detailed description of the stream tank). A total of 14.3 m^2 of substrate was available for spawning. Average flow rates in the narrow and wide channels were 15 and 11 cm/s, respectively. Photoperiod was kept constant with a light:dark cycle of 12:12 h with twilight. Water temperature fluctuated between 6.0°C and 9.0°C.

Two experiments, each 7 days in duration, were carried out in the stream tank. The spawning behaviour of two anadromous females with two male ouananiche was examined in the first experiment. Two female ouananiche were paired with two anadromous males in the second experiment.

The experiments in the field enclosures and in the stream tank were conducted from October 26 until November 14, 1984, an interval concomitant with the natural spawning period of Atlantic salmon in Noel Paul's Brook.

Eggs were collected from the redds and cleared using Stockard solution, 4–6 days after spawning had occurred in the stream tank and 7–14 days following reproduction in the field enclosures. Egg fertilization was determined following Velsen (1980). In addition, 400 eggs from each of the females in the stream tank were incubated at ca. 4°C.

Results

Stream tank facility

Male ouananiche and anadromous male salmon attempted to "stimulate" females to spawn within 2 h of being placed in the stream tank. Males were observed quivering against the sides of the females in a short series of rapid shudders. Jones (1959) described this behaviour in detail, noting that it was an integral part of the spawning act. Initially both males quivered intermittently on each side of the female that had begun to dig a redd. However, within 24 h one of the males became dominant over the other, i.e., it frequently nipped the fins of the subordinate male, chasing it from the spawning site. Female dominance was also observed in both experiments as digging females were seen to chase their subordinates from the spawning sites. Subordinate females made no subsequent attempts to dig a redd. Neither subordinate males nor females initiated any spawning activities for the duration of both experiments once dominance had been established.

Spawning began within 72 h of the initiation of each experiment, as indicated by the cleared sections of gravel immediately upstream of the previously dug redds. The anadromous female dug, spawned into, and covered three separate redds. These were located at the downstream end of the pool section and in the upstream section of the narrow channel. The female ouananiche spawned into a single redd located in the midsection of the pool. Following this, the female ouananiche began feeding on organic particulate matter drifting through the water column. (Anadromous females did not feed after spawning.) Egg fertility exceeded 95% in both experiments. Hatching occurred following an incubation period of 100–110 days.

Field enclosures

Spawning occurred in all experimental and control enclosures. There was no significant difference in the proportion of eggs fertilized between the control and experimental groups (Fisher's exact test for independence, $n = 237$, $\alpha = 0.05$). An interesting ancillary observation was that one of the ouananiche died during the course of the experiment in three of the six enclosures containing two male ouananiche. In each case it was the smaller of the two males that had died. It was not known whether they died before or after spawning. There were no other mortalities during the experiment.

Discussion

Anadromous and nonanadromous males can successfully spawn with females of the alternate form under simulated stream conditions in the field and laboratory. We find no evidence that behavioural isolating mechanisms prevent interbreeding between anadromous migrant and freshwater resident Atlantic salmon in nature. Temporal isolating mechanisms can also be discounted in this case because the spawning period of ouananiche in Furriers Pond encompassed that of naturally reproducing anadromous salmon in Noel Paul's Brook. Furthermore, the substrate over which ouananiche were spawning in Furriers Pond was not qualitatively different from that utilized by anadromous salmon. Thus, there is no evidence that choice of spawning substrate would serve to maintain reproductive isolation between forms. The viability of eggs artificially fertilized by ouananiche and anadromous salmon has been previously documented (Sutterlin et al. 1977), and it is known that such hybrids can mature and produce viable ova and spermatozoa (Sutterlin and MacLean 1984).

Females have limited control in selecting the males that fertilize her eggs. A dominant male guards and defends a female during courtship, however, other males dart in and shed sperm in competition with the dominant male at the time of egg extrusion (Jones 1959; Myers 1984). This sneaking behaviour has been observed for both mature parr, which are positioned on the substrate in close proximity to the female, and subdominant anadromous males located immediately downstream of the female or hidden behind rocks (Belding 1934; Ouellet 1977). Agonistic behaviour of dominant males toward subdominant males was observed in the stream tank, and probably caused the deaths of male ouananiche in the relatively small field enclosures.

The consequences of female territorial behaviour, particularly the lack of spawning by subordinate females (with 7.1 m^2 of substrate available per female), could significantly reduce the egg deposition for a population. More detailed observations of female–female interactions are needed to demonstrate whether this could have significant effects on the population dynamics of Atlantic salmon. Our observations are consistent with those of Schroder (1982) who found that some chum salmon, *Oncorhynchus keta*, females did not spawn at high densities, and that males preferred females (regardless of size) that were digging redds over those that were not sexually active.

There is no reason to believe that co-occurring resident and anadromous forms of *S. salar* do not interbreed unless spatial isolation during spawning can be demonstrated. Both forms spawn in the outlet streams of Wings and Bluehill ponds in eastern Newfoundland (Hutchings 1985). Mitochondrial DNA sequencing experiments suggest that these forms are from the same gene pool (U. Gyllensten, Department of Genetics, University of Stockholm, S-106 91 Stockholm, Sweden; personal communication). Mating between anadromous sockeye salmon and nonanadromous kokanee, *Oncorhynchus nerka*, has been observed in the Skeena River system in British Columbia (Hanson and Smith 1967). McCart (1970) presented evidence to show that co-occurring anadromous and resident *O. nerka* represent phenotypic polymorphism within a single population.

Based on our limited evidence, we conclude that co-occurring anadromous and nonanadromous Atlantic salmon probably represent within-population variation. Their co-occurrence may be evolutionarily stable through the differential operation of density-dependent factors acting on each form. For example, Myers (1985) presented the conditions under which redd superimposition could lead to such evolutionarily stable mixed strategies. Alternatively, the co-occurrence of anadromous and nonanadromous salmon could represent a transient phenomenon possibly resulting from human interference, e.g., habitat disturbance and overfishing (Hutchings 1985).

Interbreeding between forms can be expected when anadromous salmon are introduced into systems that formerly supported ouananiche. Consequently an unknown proportion of the offspring may remain in freshwater, or undertake alternate migration patterns, thus rendering standard stock-recruitment relationships inappropriate for such systems. Furthermore, interbreeding would likely reduce the population size of ouananiche. A more subtle consequence of interbreeding is its unknown effect on the expression of suites of previously coadapted traits in both populations. One important manifestation of this might be a significant reduction in mean egg size of anadromous females.

Acknowledgments

We thank C. Bourgeois, J. Davis, and J. Pratt for assistance at the Noel Paul's Brook spawning facility. J. Gibson, J. Kiceniuk, and S. Nettleton provided assistance at the stream tank facility. M. Shears identified egg developmental stages and J. Thorpe proffered advice on experimental design. J. Gibson and J. Green provided helpful comments on the manuscript. The work was supported by a contract from Fisheries Research Branch, Department of Fisheries and Oceans, St. John's Newfoundland.

BEHNKE, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Board Can. **29**: 639–671.

BELDING, D. 1934. The spawning habits of the Atlantic salmon. Trans. Am. Fish. Soc. **34**: 211–216.

BERG, L. S. 1948. Freshwater fishes of the U.S.S.R. and adjacent countries. Akad. Nauk SSSR Zool. Inst. Vol. I. 4th ed. (Translated from Russian by the Israel Program for Scientific Translations, 1962.)

GIBSON, R. J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and steelhead trout (*Salmo gairdneri*) at the juvenile fluviatile stages. Can. Tech. Rep. Fish. Aquat. Sci. No. 1029.

HANSON, A. J., and H. D. SMITH. 1967. Mate selection in a population of sockeye salmon (*Oncorhynchus nerka*) of mixed age-groups. J. Fish. Res. Board Can. **24**: 1955–1977.

HUTCHINGS, J. A. 1985. The adaptive significance of lakeward migrations by juvenile Atlantic salmon, *Salmo salar* L. M.Sc. thesis, Memorial University of Newfoundland, St. John's.

JONES, J. W. 1959. The salmon. Collins, London.

LEGGETT, W. C., and G. POWER. 1969. Differences between two populations of landlocked Atlantic salmon (*Salmo salar*) in Newfoundland. J. Fish. Res. Board Can. **26**: 1585–1596.

MCCART, P. J. 1970. A polymorphic population of *Oncorhynchus nerka* at Babine Lake, B.C., involving anadromous (sockeye) and non-anadromous (kokanee) forms. Ph.D. thesis, University of British Columbia, Vancouver.

MYERS, R. A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **41**: 1349–1353.

——— 1985. Game theory and the evolution of Atlantic salmon age at maturation. *In* Salmonid age at maturity. *Edited by* D. Meerburg. Can. Spec. Publ. Fish. Aquat. Sci. In press.

OUELLET, G. 1977. Fraie en groupe de quatre saumons atlantiques sur l'Ilê Anticosti. Nat. Can. (Que.), **104**: 507–510.

RILEY, S. C., A. T. BIELAK, and G. POWER. 1984. The Atlantic salmon stock of the Grand Watshishou River (Québec) — a historial perspective. Nat. Can. (Que.), **111**: 219–228.

SCHRODER, S. O. 1982. The influence of intrasexual competition on the distribution of chum salmon in an experimental stream. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium, June 1981. *Edited by* E. L. Brannon and E. O. Salo. University of Washington, Seattle. pp. 275–285.

SUTTERLIN, A. M., L. R. MACFARLANE, and P. HARMON. 1977. Growth and salinity tolerance in hybrids within *Salmo* sp. and *Salvelinus* sp. Aquaculture, **12**: 41–52.

SUTTERLIN, A. M., and D. MACLEAN. 1984. Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic salmon (*Salmo salar*) and their hybrids. Can. J. Fish. Aquat. Sci. **41**: 1139–1149.

VELSEN, F. P. J. 1980. Embryonic development in eggs of sockeye salmon, *Oncorhynchus nerka*. Can. Spec. Publ. Fish. Aquat. Sci. No. 49.