

Mating of anadromous Atlantic salmon, *Salmo salar* L., with mature male parr

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Sexually mature male parr successfully mated with female anadromous Atlantic salmon, *Salmo salar*, in the absence of anadromous males. There was no significant difference between the proportion of eggs fertilized by mature male parr and anadromous males. One of the demographic consequences of our observations is that overfishing could eventually eliminate anadromy in male members of a population.

I. INTRODUCTION

Jones (1959) stated that for the Atlantic salmon, *Salmo salar* L., anadromous males are required to stimulate anadromous females to spawn, despite the presence of mature male parr. However, there are populations of brown trout, *S. trutta*, (Barach, 1962; Svärdsen & Anheden, 1963) and possibly headwater populations of Atlantic salmon (Fritsch, 1893) in which all females are anadromous and all males mature in fresh water. This dichotomy warrants investigation because the proportion of male Atlantic salmon maturing as parr may be increasing in some populations, possibly as a result of increased fishing pressure (Gibson, 1978; Myers, 1983). Such increases are alarming because the mortality associated with parr maturation already leads to a loss of 60–70% of the male production in some commercial fisheries (Myers, 1984). If anadromous males are not necessary for the successful spawning of anadromous females, then increased fishing pressure could lead to the elimination of anadromous males from some populations.

In view of the economic importance of any change in the population structure of Atlantic salmon, we tested Jones' (1959) hypothesis that anadromous females will not spawn in the absence of anadromous males. We also examined the behaviour of mature male parr in the presence of spawning anadromous adults to determine whether Jones' (1959) observations on English salmon hold for North American populations.

II. METHODS

Wooden enclosures (0.85 × 2.5 m, set parallel to the stream flow) were constructed in a regulated flow channel in Noel Paul's Brook (48° 33'N, 56° 33'W), a tributary of the Exploits River, Newfoundland. Galvanized wire screening (6 mm square mesh) permitted the flow of water through the enclosures. Aprons of wire screening were stapled to the bottoms of the sheets of plywood separating the enclosures from one another, and covered

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with gravel to prevent fish passage between compartments. Mean water depth was 0.4 m (range 0.35–0.50 m). Average surface water velocity was 6.5 cm s^{-1} within the channel. Substrate composition (particle diameters) was as follows: 6–15 cm, 10%; 3–6 cm, 44%; 0.2–3 cm, 38%; and <0.2 cm, 8%.

Anadromous Atlantic salmon were collected ascending the fishway located at Grand Falls, Exploits River during the summer of 1984. All fish were aged as grilse (i.e., they had spent one winter at sea) and measured 48.0–55.4 cm fork length. A beach seine was used to collect mature male parr (fork length range 10.9–14.7 cm) from Noel Paul's Brook. One anadromous female and five mature male parr were placed in each of four enclosures on 26 October 1984. Two control enclosures contained a single anadromous female in each. An anadromous male and female were placed in a third control enclosure. There were no anadromous males immediately upstream or adjacent to the experimental enclosures.

The experiment was terminated on 14 November 1984. The experimental period encompassed the spawning dates of naturally reproducing Atlantic salmon in Noel Paul's Brook (Department of Fisheries and Oceans, St. John's, Newfoundland, Canada, unpublished data). The reproductive state of each fish was recorded and egg samples removed from the redds at the end of the experiment. Eggs were cleared and examined for cell division, following Velsen (1980).

The spawning behaviour of anadromous Atlantic salmon in the presence of mature male parr was examined at the stream tank facility in the Northwest Atlantic Fisheries Centre, St John's. The stream tank is 9.1 m long and 3.0 m wide, consisting of a circular wooden flume with recirculated water. A channel 1.2 m wide and another 0.6 m wide are 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). Mean flow rates in the narrow and wide channels were 15 and 11 cm s^{-1} , respectively. Photoperiod was kept constant with a light:dark cycle of 12:12 with twilight. Water temperature ranged from 5.0 to 8.0°C.

Eight sexually mature male parr were placed in the stream tank with an anadromous male and one anadromous female. Observations were made on a daily basis for 14 days.

III. RESULTS

Female anadromous salmon dug, spawned into, and covered redds in the two control enclosures with the single female, in the one control enclosure with the anadromous pair, and in all but one of the four experimental compartments. The proportions of eggs fertilized in the experimental enclosures (0.82, 0.92, 0.83) did not differ significantly from that of the control containing the anadromous pair (Fisher's exact test for independence, $n=144$, $\alpha=0.05$), and were similar to previously reported rates for salmonids (Warner, 1963). The eggs spawned by the lone anadromous females were not fertile. With the exception of the female in the experimental enclosure in which spawning did not occur, all fish were spent: i.e., neither eggs nor milt were extruded when pressure was applied to the fish abdomens.

The failure of an anadromous female to construct and spawn into redds in one of the enclosures may be attributable to the fineness of the substrate (predominantly sand) in this enclosure.

The male and female anadromous salmon spawned successfully in the stream tank in the presence of mature male parr. We were unable to detect any differences in the behaviour of the Newfoundland population from the English population described by Jones (1959). The anadromous male frequently chased parr that were swimming or maintaining position off the bottom. The attendant male did not attack parr that remained motionless on the substrate.

A linear dominance hierarchy was established amongst parr behind the anadromous female, with the largest of the parr nearest to the female. Any subdominant

parr swimming near the redd site were immediately chased and nipped by the dominant parr. Agonistic encounters among parr were restricted to those brief periods when the anadromous male was absent from the spawning site.

IV. DISCUSSION

Females will dig a redd, spawn, and cover eggs in the absence of anadromous males. Indeed, anadromous females will spawn and cover eggs in the absence of mature parr. Eggs deposited in the presence of male parr are fertile. The ability of parr sperm to successfully fertilize salmon ova and produce viable offspring has been well documented (Thorpe & Morgan, 1980). The ability of salmon parr to successfully mate with anadromous females is not surprising given that male ouananiche (non-anadromous *S. salar*) will mate with anadromous salmon despite the size differential between forms (Hutchings & Myers, 1985). Thus, there is the potential for populations to exist in which females are anadromous but males are not. Increased fishing pressure could result in such a change (Myers, 1983). However, quantitative predictions of the evolutionary consequences of increased fishing pressure are impossible without measurements of the reproductive contribution of mature male parr.

There are two mechanisms that may prevent all males from maturing only as parr. The first mechanism depends upon the linear dominance hierarchy established by mature male parr downstream of courting anadromous pairs (Jones, 1959; this study). If the reproductive success of mature parr depends upon order of nest entry, as it does for chum salmon, *Oncorhynchus keta*, (Schroder, 1982), then the average number of eggs fertilized by male parr will decrease as the proportion of mature parr in the population increases. This will reduce the mean fitness of mature parr, thus favouring maturation following migration to sea (Myers, 1983). The second mechanism depends upon the high mortality associated with parr maturation (Myers, 1984). This mortality among male parr has the effect of biasing the sex ratio of smolts toward females. Consequently, any increase in the proportion of mature parr in a population will result in an increase in the average number of matings per anadromous male. Again, the individual fitness of anadromous males will increase as the proportion of mature parr in a population increases. Either of the two mechanisms can result in an evolutionarily-stable (Maynard Smith, 1982) mixture of male maturation phenotypes (Gross, 1984; Myers, 1986).

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