TABLE 1. Sizes (fork length in cm) of anadromous males and mature male parr in the simulated streams

Facility	Anadromous male	Mature male parr	
		Dead parr	Group mean ± SD
Tank 1	50.4	—	15.1 (n = 1)
Tank 2	51.3	—	16.3 (n = 1)
Tank 3	54.6	14.3, 15.1, 15.9 16.3, 17.4	15.4±1.3 (n = 5)
Tank 4	52.0	15.3	17.2±1.8 (n = 10)
Tank 5	54.1	11.2, 14.4	15.6±2.1 (n = 15)
Stream tank	52.7	—	15.0±1.5 (n = 20)

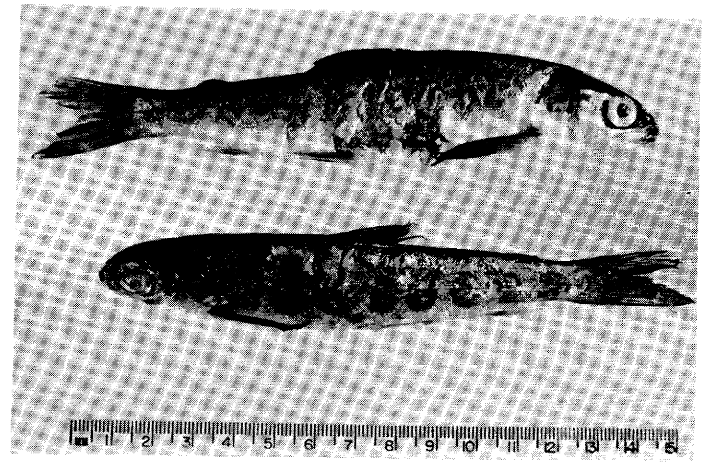

FIG. 1. Wounds in the musculature of mature male parr resulting from aggression by anadromous male Atlantic salmon.

substrate (geometric mean size 3–6 cm) available for spawning. The second type, a modified 2700-L holding tank, had water circulating around a cylindrical fiber glass container (77.5 cm diameter) over 1.8 m^2 of substrate (a 1:1 mixture of 1.9 and 3.8 cm washed stone).

Two modified holding tanks contained one anadromous male, one anadromous female, and one mature male parr. Three tanks held an anadromous pair with 5, 10, or 15 parr. The stream tank held 20 parr with an anadromous male and female. Fish were in the simulated streams 3–4 weeks prior to spawning. Observations were made once every 1–3 days for evidence of spawning activity. Fish remained in the simulated streams 2 months after spawning.

Results

Parr mortalities occurred in three of the modified holding tanks 1 to 3 days after spawning (Table 1). One parr died in the tank holding 10 parr, two died in the tank holding 15 parr, and all parr died in the tank containing 5 parr. Prior to death, wounded parr rarely swam and were not always able to maintain position in the current.

The dead parr possessed a characteristic wound on one side of the body directly below or immediately posterior to the base of the dorsal fin (Fig. 1). The wound consisted of three parallel cuts, each of which measured 9–11 mm long and 3–4 mm wide. The centres of the cuts were 5–6 mm apart and the entire length of the wound measured 15–20 mm, depending upon the degree to which the skin had been shredded. The hypaxial, or epaxial, musculature was exposed in all cases. None of the surviving parr was injured in this manner.

Anadromous males possess series of teeth on the floor and roof of the mouth and pharynx. The upper teeth (vomerine, maxillary, premaxillary) are not well developed. Conversely, the lower teeth (mandibular, lingual) are sharp and relatively long. In 50–54 cm long males, there is a separation of 3–4 mm between the two rows of lingual teeth and a distance of 6–8 mm between each row of lingual teeth and the mandibular teeth. The floor of the mouth measures 16–18 mm between the rows of mandibular teeth.

Discussion

There is strong evidence that parr injuries resulted from the aggressive behaviour of anadromous males during spawning. Spacing between the well-developed lingual and mandibular teeth of anadromous males corresponded closely with the spacing between the parallel cuts in the parr musculature. Anadromous males have been observed to shake parr vigorously while holding them between their jaws (unpublished observations). Subsequent parr mortalities were probably a function of stress and fatigue. Jones (1959) found that dominant parr will grasp subordinate parr behind the head to displace the latter from a redd. Anadromous male brown trout (ca. 40 cm), *S. trutta,* attack nonanadromous males in a similar manner during spawning, wounding the smaller males (ca. 15 cm) with two parallel cuts in the musculature (Bohlin 1975). It is not known whether these injuries proved fatal. Hutchings and Myers (1985) found that mate competition between two male ouananiche (nonanadromous Atlantic salmon) can lead to the death of the smaller male.

It is unlikely that parr mortalities were an artifact of the laboratory. First, the simulated streams provided spawning conditions (depth, temperature, current velocity, substrate, area available for spawning) that are well within the range observed for natural populations (Pratt 1968; R. J. Gibson, Fisheries Research Branch, P.O. Box 5667, St. John's, Nfld., Canada A1C 5X1, unpublished data). Second, anadromous male Atlantic salmon and brown trout have been observed to physically attack small mature males under natural conditions. Third, under natural or laboratory conditions, parr must expose themselves to potential attack by anadromous males if they are to successfully fertilize eggs.

Parr mortalities have not been reported in previous investigations of spawning behaviour under simulated natural conditions (Jones 1959; Myers and Hutchings 1987). This may be attributed to the comparatively short observation periods (1–4 days) in those studies (to minimize observation time, the sexes were held in isolation until natural spawning had commenced). Thus, there may have been insufficient time for male–male competitive interactions to become fully established. In contrast, all males used in the present study were held in the simulated streams 3–4 weeks prior to spawning, a period similar to the time spent by anadromous salmon and mature male parr on the spawning grounds prior to natural spawning (Hutchings 1986).

Parr maturation is associated with a higher mortality than that experienced by immature Atlantic salmon parr (Mitans 1973; Leyzerovich 1973; Dalley et al. 1983; Myers 1984). Myers

Escalation of an asymmetric contest: mortality resulting from mate competition in Atlantic salmon, *Salmo salar*

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Male anadromous Atlantic salmon, *Salmo salar*, fatally injured mature male parr during spawning. The wound consisted of three parallel cuts which exposed musculature on one side of the parr either directly below or immediately posterior to the base of the dorsal fin. The spacing of the cuts matched the spacing of the anadromous male's lingual and mandibular teeth. The wounding of parr in this manner is consistent with the observation of larger males vigorously shaking smaller males between their jaws. Mortality resulting from anadromous male aggression contributes to the low survival of mature male parr. Given the high mortality associated with parr maturation, if male parr must compete with anadromous males and other parr at all spawning sites, parr may be willing to risk escalated contests during mate competition with anadromous males to fertilize eggs.

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Des mâles anadromes du saumon atlantique (*Salmo salar*) peuvent infliger des blessures fatales aux tacons génésiques au cours de la fraye : il s'agit de trois coupures parallèles exposant la musculature d'un côté, immédiatement derrière la base de la nageoire dorsale ou en-dessous. La distance entre les coupures correspond à la distance entre les dents linguales et mandibulaires du mâle anadrome. Ce type de blessure correspond bien aussi au comportement des gros mâles qui secouent vigoureusement les petits mâles entre leurs mâchoires. La mortalité qui résulte des agressions des mâles anadromes contribue au faible taux de survie des tacons génésiques. C'est pour fertiliser les oeufs que les tacons génésiques sont prêts à prendre de grands risques puisque la mortalité associée à leur maturation est forte et qu'ils doivent faire compétition aux mâles anadromes et aux autres tacons à tous les sites de fraye.

[Traduit par la revue]

Introduction

Conflicts arising through competition for resources (such as mates) are often settled without physical contact through a range of displays and cues that transfer information between individuals concerning their relative chances of success (Maynard Smith 1982). Traits such as body size and body condition serve as important criteria in an individual's assessment of an opponent's strengths and weaknesses (Clutton-Brock and Albon 1979). Maynard Smith and Parker (1976) applied the concept of an evolutionarily stable strategy (ESS) to predict the outcomes of asymmetric contests. They demonstrated that the ESS in asymmetric contests is to permit the asymmetric cue to settle the contest without escalation unless the information transfer between individuals is imperfect. We discuss a case in which prior asymmetries (size and ownership) did not prevent escalation among intrasexual contests for mates.

Male Atlantic salmon, *Salmo salar*, mature as one of two life history forms that shed sperm in competition with each other during spawning. Male parr mature in fresh water and can be a year or more younger and considerably smaller (25–50 g vs. 1.5–10.0 kg) than anadromous males which mature following migration to sea (Jones 1959; Dalley et al. 1983; Saunders and Schom 1985). During spawning, male parr establish a linear dominance hierarchy immediately downstream of a courting anadromous male and female with the largest parr nearest the female (Jones 1959; Myers and Hutchings 1987). Male parr dart in close to anadromous pairs and shed sperm during oviposition. The ratio of mature male parr to anadromous males can exceed 20:1 on the spawning grounds (Hutchings 1986) and it is not uncommon for 80% of the males in a population to mature as parr (Myers et al. 1986). Dominant anadromous males exhibit a variety of threat displays and open-mouthed lunges against subordinate anadromous males and male parr during intrasexual competition for mates (Jones 1959). Myers and Hutchings (1987) found that parr were generally able to avoid attack by remaining motionless on the stream substrate.

During a study of the gametic contributions of anadromous male Atlantic salmon and male parr at spawning, we found that several parr had died as a consequence of spawning activities. Herein, we describe these parr mortalities, their probable causes, their importance to salmon demography, and their relationship to theoretical predictions in asymmetric contests.

Methods

Anadromous Atlantic salmon were dip-netted at the fishway on Great Rattling Brook, Nfld. (48°59′ N, 55°35′ W), in late September 1985, and immediately transported in a cooled, aerated 2700-L tank to holding facilities at the Northwest Atlantic Fisheries Centre (NAFC), St. John's, Nfld. Mature male parr were collected over spawning substrate in mid-October 1985, from the inlet stream of Junction Pond (Northeast River; 46°21′ N, 53°40′ W), using back-pack electroshocking equipment and an apron seine. Parr were transported to the NAFC facilities in cooled 900-L tanks shortly after capture.

Two types of simulated streams were used in our experiments. Both were recirculating systems with water replacement rates ranging from 10 to 18 L/min. Mean water depth was 30 cm (range 25–30 cm) and mean current velocity was 12–15 cm/s, well within the range of natural spawning conditions for Newfoundland populations (Pratt 1968). Water temperature ranged from 3 to 6°C. The first type of simulated stream, a stream tank, was 9.1 m long and 3.0 m wide, consisting of a wooden and glass flume with recirculated water. A channel 1.2 m wide and another 0.6 m wide were joined by a 1.5 m wide pool section (see Gibson (1981) for a detailed description), providing 14.3 m^2 of

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