

## LIFE HISTORY TACTICS OF ATLANTIC SALMON IN NEWFOUNDLAND

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### Introduction

Popular articles about the Atlantic salmon (*Salmo salar*) usually state that 'the Atlantic salmon is an anadromous species', e.g. publications by the Atlantic Salmon Federation (North America), Atlantic Salmon Trust (UK), and WWF (World Wildlife Fund), and the life history is depicted as migration of juveniles from fresh water to the marine environment, with a return to where the fish were born as spawning adults. These publications and illustrations are well done and very informative, and sufficient for the messages the organisations wish to communicate. Nevertheless, as well as performing marvelous migrations, Atlantic salmon also show a wonderful range of life history tactics, and may be considered as a polytypic species.

The degree of anadromy and other traits displayed by Atlantic salmon is intermediate within the family Salmonidae (Marschall et al. 1998). Non-anadromous races of salmon (frequently referred to as 'landlocked salmon') are not found in the British Isles (Jones 1959), so are less known there. However, if the science of salmon had originally been studied from the Newfoundland and Labrador perspective (the same Province, consisting of the island of Newfoundland and what is sometimes referred to as the Labrador Peninsula), salmon, like trout, would have probably been regarded primarily as a freshwater species, but with interesting anadromous forms as well. In the remainder of this article we will consider primarily insular Newfoundland, which we will refer to as 'Newfoundland'.

Anadromous salmon, generally the form most desired by commercial fishermen and anglers, are abundant in many of the river systems in Newfoundland (the half not damaged by hydroelectric developments). Non-anadromous salmon are found more often in larger surface-area lakes (van Zyll de Jong et al. 2005) and are common in many river systems of Newfoundland, including the Humber River system of the west coast, but have not been recorded in some of the higher gradient rivers in the south-west part of the island. Non-anadromous salmon in Newfoundland most commonly are called 'ouananiche' (an aboriginal term), or occasionally 'salmon peel'. Scott & Crossman (1964) reported that ouananiche were widely distributed throughout the Island in those areas investigated, noting

that there had been no confirmed reports of ouananiche on the Great Northern Peninsula, but qualifying this as in all probability due to the lack of investigation. In fact ouananiche have recently been recorded from a number of river systems on the Great Northern Peninsula (personal communication, R. Perry, Senior Fisheries Biologist, Government of Newfoundland and Labrador). Due to Newfoundland's glacial history all freshwater fish species are euryhaline. Salmonids generally are the dominant fish species numerically and in biomass, with a few exotic introductions (Scott & Crossman 1964; van Zyll de Jong et al. 2004) of which the only significant successful species is the Atlantic salmon's congener, the brown trout, *Salmo trutta*. The indigenous salmonids are Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and Arctic charr (*Salvelinus alpinus*). All three species have both non-anadromous and anadromous forms. The brook trout is the most widespread and is found in most habitats. On the Island, Arctic charr are considered a glacial relict, occurring mainly in lakes, with few rivers having the anadromous form, although in Labrador the anadromous form is common (Scott & Crossman 1964). The presence of Arctic charr in insular Newfoundland went undetected until 1949. However, Hammar & Filipson (1985) in gill net testing across the Island recorded Arctic charr as rather common, and in fact dominant in some lakes.

### Salmonid life histories

The basic life history of the salmonids of the Province is similar, beginning in fresh water with egg deposition in late autumn. The eggs are deposited in the substratum, in a gravel-covered hollow (with a number of egg pockets) called a redd, in running water (salmon, brook trout, occasionally Arctic charr), or over coarse substratum in littoral areas of lakes (Arctic charr, occasionally brook trout and ouananiche). They then develop in the substratum and emerge in the spring as fry. Spawners of all three species may survive to spawn again, although a relatively small proportion with anadromous salmon. Anadromous salmon repeat spawners may spawn in consecutive seasons, or as alternate spawners after spending a year at sea, the relative proportions of types varying between rivers. The freshwater stage of young salmon following that of the fry (which is the term for 0+ salmon for their first season in Canada, but only until dispersion from the redd site in the UK) is termed 'parr', and the migratory form to sea is termed 'smolt'. The ecology of these species is well described in a number of publications (e.g. Crisp 2000; Waters 2000) so we do not go into detail of relative life histories here.

Atlantic salmon may be resident in the stream or lake with limited migration over the life period (potamodromous in streams and rivers, limnodromous in lakes), or migrate to spawn and rear in a tributary stream

with growth to maturity in a lake (adfluvial) or in the sea (anadromous), the latter usually spending at least one winter at sea, but some forms using the estuary or near marine habitat and returning to fresh water the same season. All these migratory tactics occur in the Province, and are illustrated in the three-part figure below (Fig. 1).

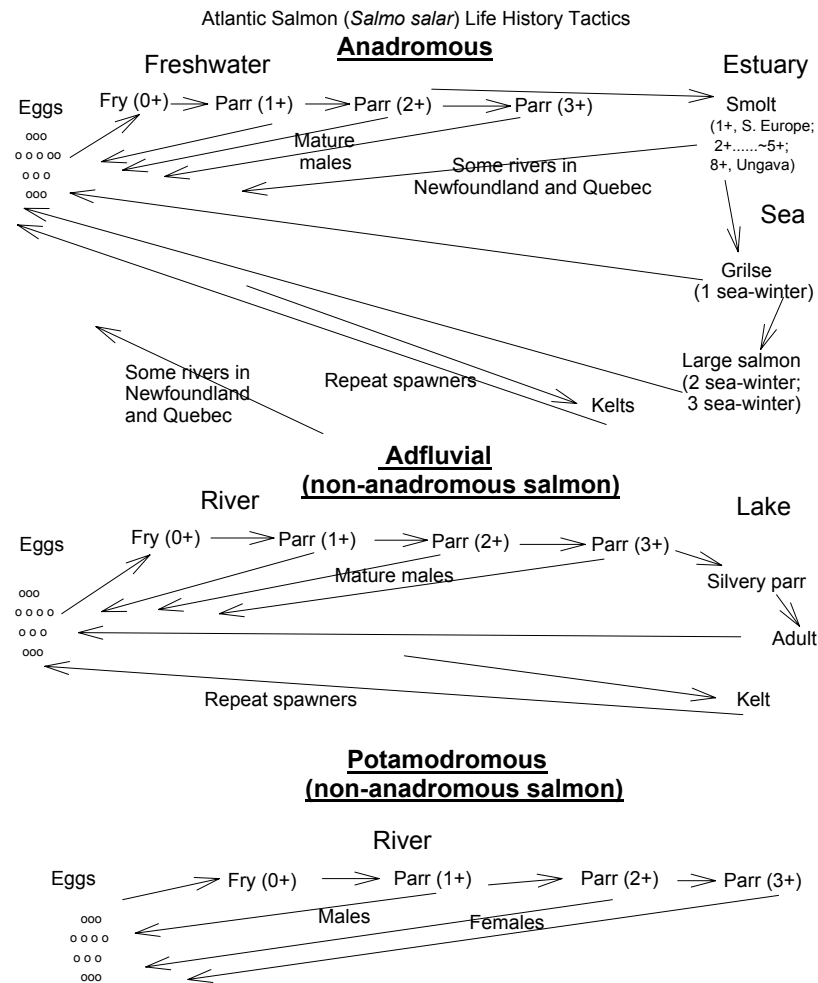


FIG. 1. Life history tactics found in salmon of Newfoundland.

**Ecology and life history tactics**

Anadromous salmon vary considerably in age at maturity, size, and timing of return to their home river (Fleming 1996). Hutchings & Jones (1998) note that the length of freshwater residence of anadromous salmon populations declines with increasing parr growth. In addition to being the prime determinant of smolt age, parr growth rate is also positively associated with the incidence of male parr maturity. Increased smolt-to-grilse survival reduces growth rate thresholds for maturation as grilse (1 sea winter fish, i.e. fish returning after one year at sea). If survival in both fresh water and the sea is low, females are favoured to mature as 2 sea winter fish, independent of growth rate. Similarly, if survival in both fresh water and the sea is high, maturation as grilse is favoured, the reduction in growth rate threshold being largely independent of fecundity. Most insular Newfoundland rivers are 'grilse' rivers, with a relatively small proportion of the adults as larger salmon. Rivers with a higher proportion of large salmon occur in the south-west part of Newfoundland, and also in Labrador. Grilse rivers generally have a high proportion of the adults (grilse) as females, and male parr that have matured in fresh water may contribute significantly to egg fertilisation (Jones & Hutchings 2001, 2002). Where the large salmon are predominantly females, the grilse are mainly males.

The ecology of juvenile salmon has been extensively studied (reviewed in: Gibson 1993; Heggenes et al. 1999). The preferred habitat (for juveniles of both the anadromous and non-anadromous forms) is generally described as being riffle habitat of the rhithron, with 0+ fish in shallower water with pebble substrate and the older parr in faster water with a coarser substratum, with some interaction between size classes affecting relative distributions. In general this is the case, and the riffle habitats may be the most productive areas of streams for juvenile salmon. However, young salmon are extraordinarily plastic in their habitat requirements. In Newfoundland piscine predators and competitors are few (although there can be interactions with the indigenous brook trout, depending on type of habitat – Gibson 1993), allowing an increase in niche breadth, so that the realized niche of young salmon is close to their fundamental niche, and with the absence of competing species salmon can be found occupying a range of water velocities in most habitats available in the river system, including the pools of tributaries and in lakes (Gibson 2002). Relative biomass in habitats of various systems in the Province can vary more than ten-fold, related to habitat variables, with water chemistry and stability of flows having the greatest influences. The relative abundance of prey affects production, so that for example, sections downstream from lakes, where filter feeding insects profit from exported seston, and rivers fertilised by nutrients and having high insect production, provide suitable

prey items resulting in relatively high biomass and production of salmonids (Gibson 2002). Models have been derived describing densities and biomass of juvenile salmon related to habitats for some systems, but due to the plasticity in use of habitats and interactive effects of physical, chemical and biological variables, few are applicable across systems. Similarly, for the same reasons, stock-recruitment functions (e.g. the oft-cited 240 eggs.100 m<sup>-2</sup> stocking rule) cannot generally apply between river systems. Milner et al. (2003) point out that stock-recruitment curves should be developed for key habitat types and be expressed on a scale compatible with the management regime. In addition, variability and abundance of the adult anadromous salmon are influenced by climatic and oceanic factors (Scarnecchia et al. 1989).

No significant morphometric differences have been found between anadromous and non-anadromous salmon (Wilder 1947; Riley et al. 1989). Although some populations of non-anadromous salmon (ouananiche) are found above obstructions to upstream migration, many are not and have access to the sea, so that strictly speaking to call them 'landlocked' is not always correct. Some ouananiche populations co-exist with anadromous strains, but spawn in different parts of the system (Verspoor & Cole 1989). Some populations can be either anadromous or resident as adults, representing within-population variation (Hutchings 1986). This raises interesting questions about the relative benefits of growth and survival towards maximizing fitness in freshwater and marine habitats. Anadromy is considered a response to allow utilisation of the higher productivity of the marine environment compared to the freshwater environment, but having the two life history tactics in the same system may suggest that the relative benefits vary between habitats, or that the non-anadromous strains benefit and can compete by having better survival in fresh water despite their lower fecundity. An interesting population of salmon that behaves like sea trout occurs on the east central part of Newfoundland, and in fact are locally known as 'sea trout'. Juvenile and adult salmon migrate to the estuary, and some a bit beyond, in the spring, but unlike the usual anadromous salmon, they do not usually overwinter there but return upriver in late summer and autumn, as both immature and mature salmon, and feed as adults in fresh water (Sutton 2000). These fish could possibly be termed 'amphidromous'. The discovery of populations like this in small river systems feeding lengthy estuaries in Newfoundland encourages the view that Atlantic salmon are best-considered a highly plastic species that displays a continuum of life history tactics ranging from sea-run on the high seas to completely fresh water.

As in anadromous salmon, ouananiche populations vary considerably in size, habitats and feeding. In net testing across Newfoundland, Hammar & Filipsson (1985) caught ouananiche up to 556 mm fork-length in size. The



FIG. 2. Probably the smallest salmon in the world? Mature ouananiche from a small stream in south-eastern Newfoundland. The upper parr was an immature female. (The graduations of the measuring board are in centimetres).

largest types are generally piscivorous, smaller ones being primarily insectivores. Many populations are adfluvial in that spawning, and rearing to small parr, is in a stream, with migration to a lake for growth to maturity. Potadromous salmon are fairly common. The smallest that we have found were entirely fluvial, going through their full life history above an obstruction, in a tiny tributary of a river in the southern Avalon Peninsula. The main river below the obstruction had both ouananiche and anadromous salmon. In the tributary the male salmon matured at 1+, and the females at 2+ and 3+. Mean fork length of mature males was 9.2 cm, and of mature females 10.2 cm (Gibson et al. 1996). This population is comprised of the smallest Atlantic salmon recorded (Fig. 2).

The extraordinary range of life history tactics displayed by Atlantic salmon displays as great and possibly a greater general plasticity in genotypes and ability of colonisation ability than do other salmonids. Pacific salmon, *Onchorhynchus spp.*, occupy a similar range of habitats, but they have accomplished this by evolving into at least six species. *Salmo* does the same through its plasticity, and it is interesting to note that the introduced brown trout, *S. trutta*, today displays in Newfoundland nearly the full range of phenotypes as found in Europe, from various landlocked types to sea-run strains. It is commonly postulated that Atlantic salmon have a marine origin. However, the ability of the species to successfully occupy many niches in fresh water, as demonstrated in Newfoundland, supports the idea of a freshwater origin. McDowell (2002) reviewed the debate on whether salmonids have a marine or freshwater ancestry. The range of life history tactics and divergence to utilise a wide variety of habitats in Newfoundland could be related to the absence of a

diverse indigenous freshwater fish fauna there. Such absence has allowed the genus to express its full evolutionary potential, one that is kept in check elsewhere through rigorous competition.

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