Extreme *Salmo*: the Risk-Prone Life History of Marine-Phase Atlantic Salmon and its Implications for Natural Mortality

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Keywords: Atlantic salmon, life history, growth-mortality trade-off, fasting

Although life history variation in Atlantic salmon (*Salmo salar*) has been examined in scores of scientific papers, the most remarkable features of the species' life history have been ignored in the literature. This paper examines marine growth and pre-spawning fasting in Atlantic salmon, two traits which set Atlantic salmon radically apart from other fish species. Atlantic salmon pre-fishery abundance in the Northwest Atlantic has decreased markedly since the 1980s due to increased marine mortality (Cairns 2001). Understanding the life history strategies behind the Atlantic salmon's growth and fasting patterns may be the key to explaining the species' decline.

Juvenile Atlantic salmon grow at rates typical of other stream fishes, but growth rates increase dramatically after sea entry. Salmon in the Northwest Atlantic increase in weight 75-fold between river exit and return after 1 sea winter, and > 200-fold between river exit and return after 2 sea winters. These growth rates are two orders of magnitude faster than those of other fish (herring, mackerel, capelin) which occupy the same pelagic habitat (Fig. 1).

Atlantic salmon typically return to natal rivers in early summer (early run) or in fall (late run). Adult Atlantic salmon stop feeding before they enter rivers, and continue to fast during their time in fresh water. The pre-spawning fast typically lasts about five months in early run fish. Late-run fish spend the summer at sea. Although they have the opportunity to feed during the pre-spawning summer, late-run fish are not larger than early-run fish (Fig. 2). This suggests that they either have a slower overall growth trajectory, or that they do not eat during the pre-spawning summer. Circulii spacing patterns in scales collected from late-run salmon returning to the Margaree River, Nova Scotia, suggest that these fish did not grow in the summer prior to river entry (G. Chaput, personal communication). Hence it is possible that both early- and late-run Atlantic salmon fast in the summer prior to spawning.

Survivorship of Atlantic salmon between river exit and return after 1 sea winter is typically < 10% in eastern North American stocks (Table 1). Survivorships of other ocean fish of similar size, estimated from allometric equations that relate natural mortality to body weight (Lorenzen 1996), are about 50–60% (Fig. 3). Atlantic salmon marine survivorship

Fig. 1. Growth of three species of pelagic fish in the Northwest Atlantic. Salmon weights assume a smolt age of 3 years. Data are from Cairns and Reddin (2000) for salmon and from Scott and Scott (1988) for mackerel and herring.

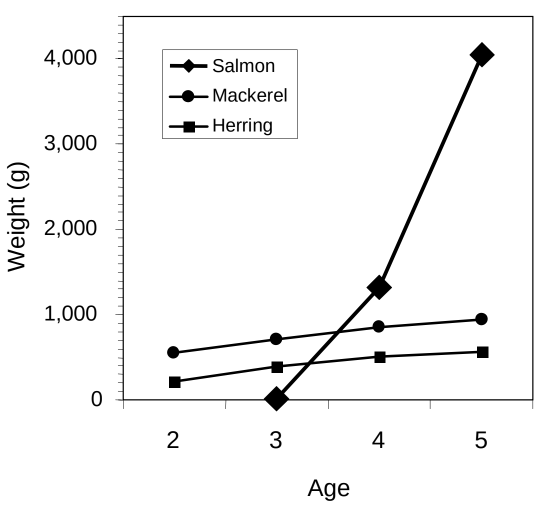

Fig. 2. Weights of 1SW and 2SW maiden Atlantic salmon vs. date of capture at the Millbank Trap, Miramichi River, 1986–1991. Data from G. Chaput.

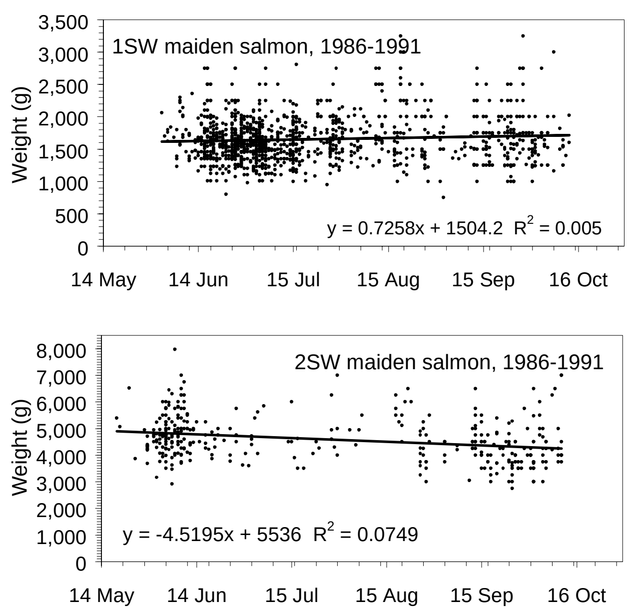

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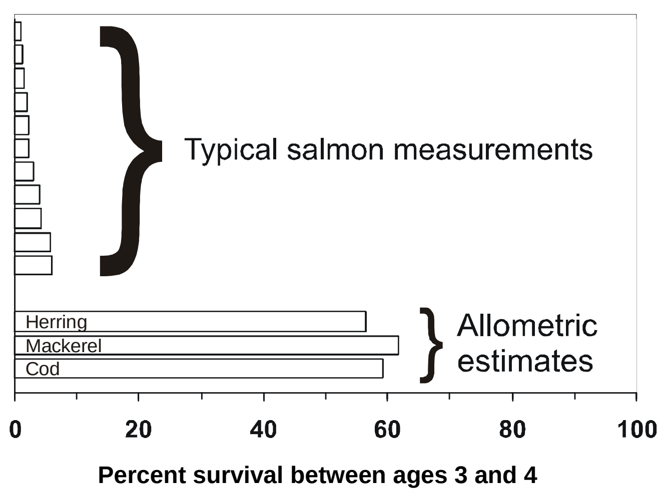
Table 1. Means, standard deviations, and coefficients of variation of annual sea survivals and sizes at return of Atlantic salmon in Eastern Canada.

Item	Location	Dates	Mean	SD	CV (%)	N	Mean of within-year CVs (%)
Size[a]							
Fork lengths (cm) of returning maiden 1SW salmon	Miramichi	1971-1999	53.6	2.0	3.7	29	5.6
Fork lengths (cm) of returning maiden 2SW salmon	Miramichi	1971-1999	73.8	1.6	2.2	29	4.5
Weights (g) of returning maiden 1SW salmon	Miramichi	1971-1991	1,578.0	78.9	5.0	21	16.9
Weights (g) of returning maiden 2SW salmon	Miramichi	1971-1991	4,468.1	224.8	5.0	21	15.7
Mortality[b]							
Survival between smolt exit and river return (%)	Bec-Scie	1988-1995	1.4	0.3	20.6	8	
Survival between smolt exit and river return (%)	de la Trinité	1984-1997	1.7	0.9	55.5	14	
Survival between smolt exit and river return (%)	Saint-Jean	1989-1996	0.4	0.1	24.3	8	
Survival between smolt exit and river return (%)	Catamaran	1990-1997	9.7	3.2	33.4	8	
Survival between smolt exit and river return (%)	Highlands	1993-1997	1.9	0.8	40.7	5	
Survival between smolt exit and river return (%)	Campbellton	1993-1997	6.6	2.3	34.4	5	
Survival between smolt exit and river return (%)	Western Arm Brook	1977-1997	4.8	2.8	58.3	21	
Survival between smolt exit and river return (%)	Northeast Trepassy	1986-1997	5.5	2.2	39.5	12	
Survival between smolt exit and river return (%)	Rocky	1990-1997	3.3	0.7	22.3	8	
Survival between smolt exit and river return (%)	Conne	1987-1997	5.3	2.4	45.8	11	

[a]Data from Moore et al. 1995 and G. Chaput.
[b]Data from compilation by Cairns and Reddin 2000

Fig. 3. Annual percent survival of marine-phase Atlantic salmon based on typical return rates of 1SW fish, and annual percent survival of Northwest atlantic fish based on Lorenzen's (1996) allometric estimates of natural mortality.



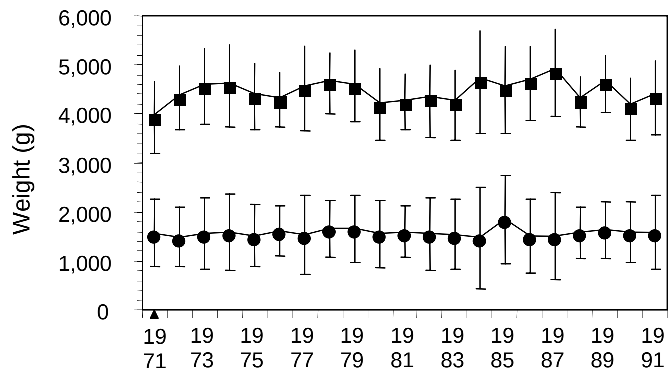
fluctuates greatly from year to year (CVs from 20.6% to 58.3%, Table 1). In contrast, sizes of returning adults show little inter-annual variation (CVs 5% or less, Table 1).

The following explanation of the Atlantic salmon's remarkable patterns of growth and fasting is proposed. Growth and mortality in fishes are thought to operate as trade-offs (Henning et al. 1993). Growth in fishes depends heavily on food availability and on water temperature. Water temperature is important because it influences the rate at which food can be procured and assimilated. The warmest temperatures in summer occur in the surface layer. To grow rapidly, salmon must feed aggressively, and also preferentially occupy the surface layer where warm temperatures enhance growth. But rapid growth is traded against higher mortality because vigorous feeding movements, especially in the photic zone near the surface, increases exposure to predation.

Food supplies and ocean temperatures fluctuate inter-annually, but sizes of returning Atlantic salmon show little inter-annual variability (Fig. 4). This suggests that Atlantic salmon have a target size at return, which they achieve by adjusting their feeding intensity and their use of the warm surface layer. These behaviours alter the risk of predation mortality. Thus in the face of fluctuating growth conditions, Atlantic salmon appear to adjust the mortality term, but not the growth term, of the growth-mortality trade-off.

Salmon that fast during the pre-spawning summer forego the opportunity for a major increase in somatic and gonadal weight which would increase their reproductive fitness. The timing of early runs cannot be attributed to the need to ascend obstacles when the spring run-off is high, because the spring run-off has usually finished before the run begins. Pre-summer fasting cannot be attributed to a need to physiologically prepare for spawning, because it is implausible that

Fig. 4. Mean (± SD) weights of maiden 1SW (circles) and 2SW (squares) salmon captured in assessment traps in the Miramichi River. Data from G. Chaput.



such a preparation period needs to be five months long. Many vertebrate animals fast for extended periods, but the reasons for these fasts are obvious (e.g. lack of food during winter hibernation, requirement to incubate eggs or guard harems, inability to fly because of wing moult). To fast for five months during the normal growing season, as pre-spawning Atlantic salmon often do, is an extraordinary aberrancy that may, among vertebrates, be unique to salmonids.

The only viable explanation of the Atlantic salmon's pre-spawning fast appears to be that feeding imposes a fitness cost that is even higher than the fitness cost of fasting. Atlantic salmon sit on the high-growth/high-mortality end of the growth-mortality spectrum. At a certain body size, the high mortality due to aggressive feeding and use of the warm surface layer overtakes the advantage of further growth. At this size, fitness is better served by fasting. The body size at which fasting becomes more advantageous than feeding appears to vary geographically. In the Northwest Atlantic, salmon destined to grow to 2SW size travel to the northern Labrador Sea or southern Greenland. Salmon that don't make this journey return to natal rivers as 1SW fish. Among 1SW returnees, early-run fish, and possibly late-run fish as well, fast during the pre-spawning summer.

The lifestyle of marine-phase Atlantic salmon is highly risk-prone. The annual income of a professional gambler is likely to be more variable than that of a steady wage-earner. In similar vein, marine survivorships of Atlantic salmon can be expected to be highly volatile, and dependent on poorly-understood relations with food supply, temperature, and predators.

This paper has pointed out extraordinary features of salmon life history, and offered preliminary explanations for the life history strategies that underlie them. If we want to determine why Atlantic salmon are in difficulty, theoretical, observational, and experimental investigations of these features and their fitness consequences should be a research priority.

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