GENETIC AND ENVIRONMENTAL FACTORS AFFECTING GROWTH, PHYSIOLOGY AND REPRODUCTIVE PATTERNS IN TWO FORMS OF ATLANTIC SALMON SALMO SALAR (LINNAEUS) 1758, IN NEWFOUNDLAND

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GENETIC AND ENVIRONMENTAL FACTORS AFFECTING GROWTH, PHYSIOLOGY AND REPRODUCTIVE PATTERNS IN TWO FORMS OF ATLANTIC SALMON *SALMO SALAR* (LINNAEUS) 1758, IN NEWFOUNDLAND

by

© Donald A. MacLean, B.Sc.

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

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April, 1984

St. John's Newfoundland

ABSTRACT

Newfoundland has numerous populations of landlocked Atlantic salmon (Salmo salar). Several of these populations are stunted, exhibiting a marked reduction in size at any age compared with other anadromous and landlocked populations. A population of stunted landlocked salmon from 5 Mile Pond East on the Avalon Peninsula was investigated. Data collected on ecology and life history reveal the population to be an extremely slow-growing, short lived form of Atlantic salmon.

Anadromous and landlocked Atlantic salmon examined at the smolt stage revealed a difference in the degree of smoltification and salinity tolerance exhibited by the two forms. Anadromous fish had a decrease in lipid, increase in water content and the increased salinity tolerance characteristic of true smolts. While wild landlocked 5 Mile Pond East fish experienced a similar reduction in lipid and increase in water, neither they, nor cultured landlocked salmon survived a challenge to sea water.

The two pure lines and the reciprocal hybrids between the early maturing, stunted 5 Mile Pond East fish and a later maturing anadromous form were reared in the laboratory for a period of 2.5 years. Ninety percent of female parr of the dwarf landlocked strain matured at age 2+ while no females of the anadromous form matured at this time. Ovary weight differed in the two pure forms at age 0+ and the numbers, size and stages of previtellogenic oocytes also differed at age 1+. Ovarian patterns of development and the time of onset of sexual maturation in the two hybrid forms appeared intermediate to that of the parental forms.

ACKNOWLEDGEMENTS

My deepest appreciation is extended to my thesis supervisor, Dr. A.M. Sutterlin, for his friendship, guidance and invaluable assistance during the course of this study.

Thanks are also extended to my advisory committee, Drs. R. Haedrich and D. Larson who provided constructive assessment of the project and critically read the manuscript.

I wish to express my thanks to Dr. D.R. Idler, director of the Marine Science Research Laboratory, for making the facilities of the lab available to me. I am very grateful to J. Mercer, E. Downton, M. Clark and the staff of the Marine Lab who provided technical expertise and equipment throughout the course of this study.

Special thanks are due Mr. C. Couturier for aid in field sampling, data collection and assistance in the preparation of this thesis. Thanks are also extended to J. Devereaux, D. Whitten and G. Russell who assisted in field work and to Dr. R. Thompson who provided equipment and advice for the biochemical and statistical analysis. Graham Hillier kindly photographed the figures.

I owe a debt of gratitude to W. Bruce, Dr. M. O'Connell and G. Whelan of the Department of Fisheries and Oceans for providing samples, valuable discussions and assistance in field sampling. The assistance of J. Davis and D. Scott in field collection of Exploits fish is gratefully acknowledged.

Thanks are also extended to E. Dalley, S. Barbour and J. Ritter for providing unpublished fecundity and maturity data.

I wish to express special thanks to my wife Judy for her patience and understanding during my research and especially for her support during the writing of this thesis.

Financial support for this study was provided by a Natural Sciences and Engineering Research Council grant to Dr. A.M. Sutterlin. The author was supported by a Graduate Fellowship from Memorial University.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

LIST OF FIGURES

GENERAL INTRODUCTION

The family Salmonidae originated in freshwater during the Pleistocene and later acquired anadromy as part of a life history strategy in order to exploit the marine environment (Tchernavin, 1939). The Atlantic salmon, *Salmo salar* Linnaeus 1758, is endemic to the Atlantic temperate and sub-arctic region (McCrimmon and Gots, 1979) and displays wide interpopulation variation in ecology and life history throughout its range.

In addition to anadromous Atlantic salmon populations, there are, in both North America and Europe, Atlantic salmon that spend their entire life cycle in fresh water. These fish are commonly called ouananiche (McCarthy, 1894) and sebago salmon (Girard, 1854) in North America and blege (Dahl, 1927) and smalback (Berg, 1953) in Europe. These populations are often referred to as "landlocked" but as several authors have suggested the term is a misnomer (Leggett, 1965; Havey and Warner, 1970). While the term implies the fish are physically denied access to the sea, in many cases freshwater populations do have access. The fact that they do not migrate to sea suggests physical factors alone fail to explain the solely freshwater life style of these populations.

On insular Newfoundland almost every body of water 20ha or larger and many flowing systems support ouananiche (Scott and Crossman, 1964). The origin and distribution of these freshwater populations can best be explained with reference to the Pleistocene and the events which preceded it (Power, 1958). The fourth and last glacial period of the Pleistocene era, the Wisconsin, is currently believed to have started 50,000 years before present (BP) and lasted until 10,000 years BP. The Wisconsin glaciation is divided into two main stages, early and late. The late Wisconsin climax occurred about 20,000 BP and most ice had disappeared by 7,000 BP (Prest, 1970).

The late Wisconsin glaciation appears to have been limited in its extent over insular Newfoundland (Rogerson, 1981). Deglaciation of the Avalon peninsula is as yet undated but data obtained from lake sediment cores indicate an ice free status about 10,000 BP (Henderson, 1972). While the late Wisconsin glacial advance was limited in its extent in Newfoundland, it does appear to have been sufficient to cause a downwarping of the earth's crust. With thinning of the ice the earth's crust rebounded in proportion to the thickness of the previous ice cover. (Andrews, 1970).

As the late Wisconsin ice sheets retreated, areas were exposed into which euryhaline forms of salmon from coastal or oceanic refugia entered. (McPhail and Lindsey, 1970).

Atlantic salmon penetrating the interior of the island by way of coastal rivers fed by glacial meltwater would become effectively landlocked when the land rose through isostatic rebound as the ice thinned. Power (1958) suggested that, in order to be perpetuated as a race, these fish would have to be isolated from the normal anadromous population. A period of spatial and temporal reproductive isolation has been suggested as being necessary before any significant genetic divergence could occur between populations (Mayr, 1963).

In Atlantic salmon, males commonly mature as parr (Jones, 1959) and spawn with anadromous females. While mature female parr are not usually found in anadromous populations they are common in landlocked populations (Bruce, 1976). Once females began to mature as parr, the requirements for a sea phase in their life cycle would be eliminated. Power (1969) pointed out that in their northern range the freshwater stage of Atlantic salmon is prolonged to such an extent that sexual maturity may occur before migration to sea and the distinction between an anadromous and freshwater life style is not clear cut.

Genetic variation among anadromous stocks has been reported for electrophoretically detectable proteins (Moller, 1970), body morphology and migratory activity (Riddell and Leggett, 1981) and life history traits (Schaffer and Elson, 1975). However, there is a paucity of information on the distinction between genetic influences on trait differences versus phenotypic plasticity between stocks of landlocked and anadromous salmon.

In my investigations I examined the relative role of genotype and phenotype in the expressions of growth, sexual maturity, oocyte recruitment patterns and salinity tolerance in 1, a dwarf form of landlocked salmon, 2, anadromous grilse population and 3, the reciprocal hybrids between the two forms. Available evidence suggests the Avalon Peninsula of Newfoundland was ice free 10,000 years BP. The hypothesis to be tested in this study was that in the interim period landlocked Atlantic salmon populations developed quantitatively different, genetically fixed mechanisms to deal with a non-anadromous life style. Such long term, presumably adaptive changes may have resulted in life history and reproductive tactics compatible with the existing environment.

ECOLOGY AND LIFE HISTORY TACTICS

INTRODUCTION

Newfoundland has numerous populations of landlocked Atlantic salmon, Salmo salar, known locally as ouananiche. To date nine life history studies have been carried out on ouananiche populations in insular Newfoundland involving 30 lake or stream systems (Leggett, 1965; Andrews, 1966; Wiseman, 1971, 1973, 1974; Wiseman and Whelan, 1974; Lee, 1971; Bruce, 1976; Barbour et al., 1979). Of these, the literature enumerates 4 systems which have populations that have been referred to as stunted (5 Mile Pond East, 5 Mile Pond West, Soldiers Pond and Candlestick Pond). While originally thought to be restricted to the Avalon Peninsula, the recent record from Candlestick Pond on the Great Northern Peninsula (Barbour et al., 1979) has raised speculation that stunted ouananiche may exist in any number of the approximately 10,000 ponds on Newfoundland.

The occurrence and cause of reduced growth in Salmonid populations has been the subject of speculation for some time. The importance of food availability as a factor in fish growth was recognized early (Dahl, 1910) while genetic and environmental factors were also implicated with regards to growth in fish populations exhibiting reduced size (Alm, 1946). Alm suggested that growth was primarily dependent on the environment while genetic factors were more important in the occurrence of sexual maturity. Ouananiche populations in Newfoundland reveal wide inter-population variation in age and growth as well as age at maturity. Fluctuations, and/or limitations in the environment, competition, predation and a lack of suitable forage have all been implicated as factors influencing growth in these populations.

The term stunted or dwarfed, while used to refer to ouananiche populations exhibiting reduced growth and size, is also used when referring to Atlantic salmon males which mature precociously (Osterdahl, 1969; Saunders and Sreedharan, 1977). Variation in age and size at sexual maturity has been reported for both anadromous and non-anadromous populations of male Atlantic salmon. The general trend by both sexes toward early maturity and smaller size at first maturity was noted for stunted forms early (Dahl, 1917; Huitfeldt, 1927) from field sampling. Ouananiche may have evolved maturation at a small size and early age to maximize reproductive success in rigorous environments.

Fecundity, defined as the number of developing eggs in the ovary immediately prior to spawning, is one of the fundamental factors determining population density and serves as an indication of the reproductive potential of a population (Bagenal, 1973). Inter-population differences in Atlantic salmon fecundity have been reported for both anadromous (Pope et. al., 1961) and landlocked (Baum and Meister, 1971) forms. Fecundity of Newfoundland ouananiche populations reveals wide inter-population variation from high egg number in populations exhibiting rapid growth and attaining large size (Leggett, 1965) to low fecundity in slow growing dwarf populations (Bruce, 1976).

Teleosts employ a wide range of life history tactics to ensure that the maximum number of progeny survive to reproduce again. Reproductive strategies of fish generally involve a trade off between reproductive effort and adult survival. The existence of an optimal reproductive effort for fish was suggested by Svardson (1949) who felt a trade off existed between present and future spawning. A high reproductive effort endangered future spawning by diverting energy resources away from maintenance with resulting high mortality.

This study examined the ecology and life history tactics of a population of stunted ouananiche from 5 Mile Pond East. Data collected on age, growth, fecundity and size and age at maturity were compared with other populations of anadromous and landlocked Atlantic salmon. Possible significance of population specific traits was discussed and compared with current generalizations in life history theory.

MATERIALS AND METHODS

Study areas

Ouananiche used in this study were collected from 5 Mile Pond East, an oligotrophic pond located 50km south-west of St. John's Newfoundland (Figure 1). The drainage area lies in a region of Precambian volcanic and sedimentary rock and the pond itself is shallow with a maximum depth of 7m (Figure 2).

For purposes of brevity ouananiche will subsequently be referred to in this thesis as landlocked salmon and abbreviated to LL salmon.

Anadromous Atlantic salmon samples were collected from the Exploits River in Central Newfoundland (Figure 1). The Exploits, Newfoundland's longest river, supports a primarily grilse (one sea winter fish) population. Mature fish used in fecundity determinations were collected at Noel Paul Brook while smolts and migrating adults were captured at the Bishops Falls counting fence and fishway.

Sample collection

Fish samples from 5 Mile Pond East Pond were collected using lake trap nets. Five nets were fished overnight in water 1-3 meters deep. Sampling was carried [illegible] Oct. 7 - Nov. 20, 1980; May 15-30, 1981 and Oct. 12 - Nov. 15, 1981.

Additional samples of LL salmon were available at the Marine Sciences Research Laboratory of Memorial University. Three year classes, progeny of wild 5 Mile Pond East fish were used to determine fecundity, egg size and incidence of sexual maturity.

Samples of Exploits River fish were collected by Department of Fisheries and Oceans personnell.

Measurements

LL salmon samples were examined fresh shortly after capture, while samples from anadromous fish were frozen within several hours of capture and examined at a later date. Fork length was measured to the nearest millimeter while body weight was measured to the nearest 0.01 gram using a Mettler 4400 balance.

Fulton's condition factor "K" was determined using the equation: $K = W100/L^3$ where W = body weight in grams and L = fork length in centimeters (Ricker, 1975).

The gonadosomatic index (G.S.I.) was calculated as: G.S.I. = GW100/BW where GW = gonadweight and BW = body weight in grams (Vladykov, 1956).

Egg dry weight was determined after drying at 40^0C for 24 hours and then weighing to 10^{-4} grams on a Sartorius analytical balance. Energy content of dried egg

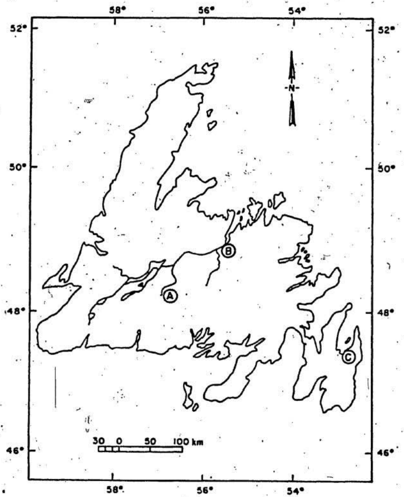


Figure 1. Locations in insular Newfoundland where samples were collected. A. Noel Paul Brook, B. Bishops Falls and C. 5 Mile Pond East.

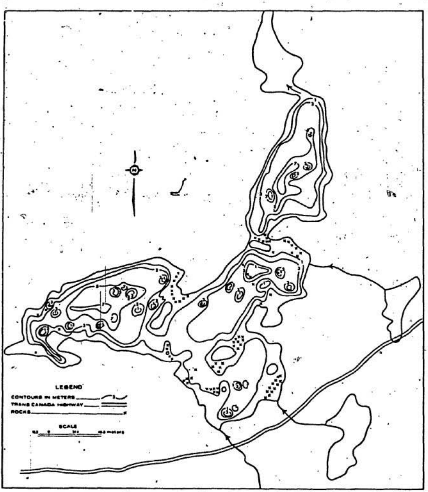


Figure 2. Bathymetric map of 5 Mile Pond East.

samples were measured using a Phillipson micro-bomb calorimeter.

Fecundity

Fish used in fecundity measurements were collected as close to spawning as possible and all eggs were examined fresh. Eggs from 5 Mile Pond East and Marine Sciences Research Lab fish were enumerated by direct count. Fecundity of Exploits salmon was determined volumetrically (Burrows, 1951).

Egg diameter was measured using a von-Bayer trough. Measurements were made on two 20 egg samples to an accuracy of 0.01mm. Egg samples were frozen (-20^0C) for later determination of caloric content.

Maturity and Sex ratio

All fish were sexed following dissection by visual inspection with the exception of the 1+ age class of 5 Mile Pond East fish. Immature females could be distinguished by the presence of small ova while immature males had long, thin gonads with no evidence of spermatogenesis. Mature females were determined by the size of the maturing eggs and males were judged to be mature based on enlargement of the testes as spermatogenesis progressed. Females which had spawned previously could be distinguished by the presence of unshed ova in the body cavity.

Ageing

Scale samples were taken from the left side of each fish, posterior to the dorsal fin and above the lateral line. Scales were aged using a Bausch and Lomb microprojector (43X) according to the annulus method validated by Havey (1959). Scales from both LL salmon and anadromous salmon were examined for the presence of spawning checks as evidence of past spawning.

Analysis

Sex ratio of the LL salmon sample and for the Exploits smolt sample were tested with a chi-square goodness of fit test (Sokal and Rohlf, 1969) to determine if they differed significantly from a 1:1 ratio.

Length and weight comparisons were made using a Students t- test in the case of two groups. When more than two groups were involved a one-way analysis of variance was used.

Fecundity-length relationships were determined using a Log-Log Regression with length as the independent variable (X) and weight the dependent variable (Y).

RESULTS

Species Collected

A total of 162 LL salmon were collected from 5 Mile Pond East. In addition 225 brook trout, Salvelinus fontinalis, 1 American eel, Anguilla rostrata and approximately 500 rainbow smelt, Osmerus mordax were captured. The majority of LL salmon were collected on shoal areas of the pond (<2m) as opposed to either inlet or outlet streams.

Age and growth

The results of growth and age composition data collected on 5 Mile Pond East LL salmon (Table 1 and Figure 3) reveals no significant difference between the sexes with the exception of 3+ females which were significantly longer and heavier than 3+ males ($P<.05$). A comparison of growth of 5 Mile Pond East fish with other Newfoundland populations of landlocked salmon (Figure 4) shows them to be the slowest growing population yet recorded.

Five Mile Pond East LL salmon are relatively short lived as revealed by ageing data. Although one fish, a male aged 6+ was collected, the dominant age group (48.17%) was 3+.

Age and growth data from on 38 Exploits River smolt from the Bishops Falls counting fence was compared with another sample of Exploits smolt from Noel Paul Brook (Davis and Farwell, 1974). The results (Table 2), indicate the majority of fish sampled in both studies were 4+ with a mean fork length of 16.8 and 15.1 cm respectively.

Marked seasonal differences were observed in the condition factor "K" of landlocked and anadromous salmon collected during this study. As Table 3 and Figure 5 indicate LL salmon in May had a very low (x=0.65) condition factor compared with anadromous adults and smolts (x=1.14 and 0.95 respectively). During the summer LL salmon were able to regain lost condition. Samples collected in the fall had condition factors (x=1.08) similar to those of anadromous fish (x=1.01).

Sex ratio, maturity and fecundity

The sex ratio (male:female) for the combined sample of 5 Mile Pond East LL salmon was 0.54 : 1. While there was no significant difference in the ratio of the 2+ age class, there were significantly more females in the 3+ age class (P<.05) and a highly significant difference (P<.001) in the sex ratio of the 4+ age class where there were 10 times as many females as males (Table 4).

Table 1. Mean (± Standard Deviaiton, in brackets) of Body Weight (gm), Fork Length (cm) and Condition Factor of 5 Mile Pond East LL salmon collected Fall 1980, 1981.

Age Class	Sex	N	Body Weight	Fork Length	Condition Factor
1+	not sexed	12	1.941 (0.418)	5.932 (0.426)	0.926 (0.139)
2+	Female	17	9.941 (2.46)	9.792 (0.655)	1.039 (0.090)
	Male	18	9.782 (1.81)	9.645 (0.790)	1.092 (0.149)
3+	Female	42	18.478 (3.46)	12.342 (0.559)	0.979 (0.144)
	Male	24	16.515* (4.36)	11.927* (0.611)	0.963 (0.173)
4+	Female	21	26.479 (5.01)	13.452 (0.587)	1.084 (0.157)
	Male	2	24.030 (13.80)	13.405 (0.997)	0.949 (0.359)
6+	Male	1	60.77 ---	17.10 -	1.215 -

*Significant Difference Between Means (t-test, $P<0.05$)

Table 2. Mean (± Standard Deviation, in brackets) of Body Weight (gm) and Fork Length (cm) for Exploits River smolts. Data for Bishops Fall (This Study); Noel Paul Brook (Davis and Farwell, 1974).

	Bishops Falls			Noel Paul Brook		
Age Class	N	Body Weight	Fork Length	N	Body Weight	Fork Length
3	5	34.03 (8.66)	14.39 (0.74)	23	18.8	12.5
4	22	45.44 (10.97)	16.79 (0.97)	141	30.0	15.1
5	8	54.07 (10.61)	17.79 (0.69)	19	43.5	17.1
6	3	63.39 (13.87)	19.27 (0.23)	-	-	-

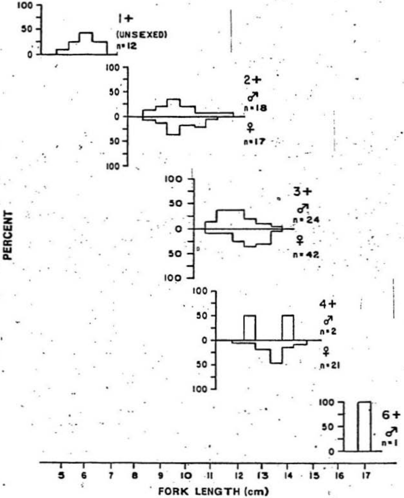


Figure 3. Age, length and sex composition of 5 Mile Pond East LL salmon collected in this study.

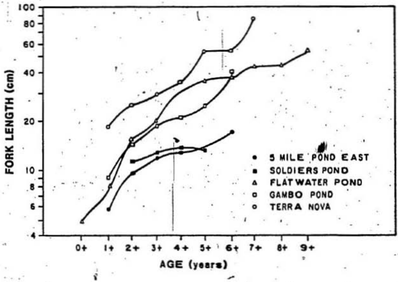


Figure 4. Comparison of growth of several Newfoundland LL salmon populations. Data for 5 Mile Pond East (This Study); Soldiers Pond (Bruce, 1976); Flatwater and Gambo Pond (Leggett and Power, 1969) and Terra Nova (Andrews, 1966).

Sex composition of Exploits River smolt collected at Bishops Falls were compared with smolt samples from northern Newfoundland (Chadwick, 1981). The results (Table 5) indicate a high proportion of smolt from both populations are females. Females made up 73.68% of the Exploits smolt sample and the male:female ratio (0.35 : 1) is the same as that recorded by Chadwick (1981) in his 1979 data from Western Arm Brook.

Data collected on age of maturity (Table 4) reveals that LL salmon males matured one year earlier than females. At age 2+, 82.35% of males were mature while no ripe 2+ females were encountered. The majority of males and females were sexually mature at 3+ and 4+.

While scales did not provide an accurate indicator of past spawning history due to the absence of spawning checks, the presence of unshed ova in the body cavity provided an indication of previous spawning in females. Mended LL salmon kelts made up 34.48% of the maturing female population. The presence of retained ova in two, 3+ females suggests maturation at 2+ occurs but is uncommon.

Changes in the ratio of female gonad weight to total body weight, the gonadosomatic index (G.S.I.), (Table 6 and Figure 6) revealed seasonal variations. Both landlocked and anadromous females had very similar G.S.I.'s in the spring ($\bar{x}$=0.98 and 1.10) respectively. In contrast anadromous smolt had a G.S.I. of $\bar{x}$=0.36. However, in the fall mature female LL salmon G.S.I. (x=11.41) was approximately one half that of anadromous females (x=19.87).

Egg counts were made on 43 LL salmon collected from 5 Mile Pond East. A comparison with fecundity data from other wild Newfoundland populations (Table 7 and Figure 7) reveal the mean number of eggs per fish (x=58) to be the second lowest egg number recorded for LL salmon. Only Bruce (1976) recorded a lower egg number (x=49) in his work on Soldiers Pond.

Additional data on fecundity, collected from several year classes of cultured LL salmon (progeny of wild 5 Mile Pond East), and wild Exploits River anadromous salmon were compared with data from 5 Mile Pond East fish. The results (Table 8) indicate eggs from wild salmon were significantly smaller, both in diameter and weight, than eggs from anadromous fish. Results from cultured LL salmon reveal a gradation in egg number, size and weight with fish size. Determination of caloric and lipid content (Table 8) indicate similar content on a per unit weight basis.

Regression of egg number on length was carried out for wild 5 Mile Pond East LL salmon, wild Exploits grilse and several year classes of cultured LL salmon (Figure 8 and Table 9). A comparison of the regression lines from the two groups of wild fish reveal significant difference in origin,

Table 3. Mean (±Standard Deviation (S.D.)), Variance $(S.D.)^2$ and coefficient of variation (C.V.) for Individual Condition Factor "K" of 5 Mile Pond East LL salmon and Exploits River Anadromous salmon collected in the Spring (May) and Fall (October) 1981.

	Spring			Fall	
	LL salmon	Anadromous Adults	Smolts	LL salmon	Anadromous Adults
$\bar{X}$	0.646	1.137	0.953	1.082	1.010
S.D.	0.118	0.088	0.156	0.101	0.050
$S.D.^2$	0.014	0.008	0.024	0.010	0.002
C.V.	18.29	7.803	16.365	9.33	4.97
N	13	8	46	24	7

Table 4. Age and Sex composition and incidence of maturity (in brackets) for LL salmon collected from 5 Mile Pond East, Fall 1980, 1981.

		Age Class				
		1+	2+	3+	4+	6+
Male & Females	#	12	35	66	23	1(1)
	%	8.76	25.54	48.18	16.79	0.73(100)
Male	#	*	17(14)	24	2(2)	1(1)
	%		38.64(82.35)	54.55	4.54(100)	2.27(100)
Female	#	*	18(0)	42(38)	21(20)	-
	%		22.22(0)	51.85(90.48)	25.93(95.24)	-
Chi-Square		-	0.028	4.37	14.08	-
P		-	P>0.25	P<.05	P<.001	-

* Not sexed

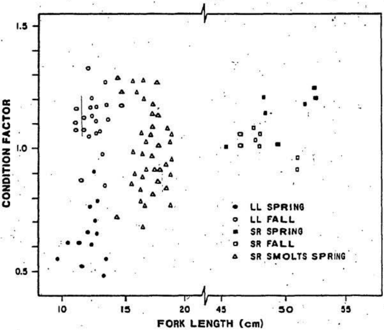


Figure 5. Seasonal changes in condition factor of landlocked (LL) 5 Mile Pond East and searun (SR) Exploits fish.

Table 5. Sex composition and fork length (cm), (mean ($\bar{x}$) and standard deviation (S.D.)) for smolts from the Exploits River and Western Arm Brook. Data for Exploits River (this study); Western Arm Brook (1979 data from Chadwick, 1981).

	Exploits River						Western Arm Brook					
	Male			Female			Male			Female		
Age Class	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.
3	2	13.97	0.27	3	14.67	0.82	13	17.30	11.70	32	17.40	14.20
4	5	16.64	1.17	17	16.84	0.89	36	18.00	13.00	99	17.80	16.40
5	2	17.10	0.30	6	18.02	0.69	1	18.20	-	10	18.50	29.80
6	1	18.80	-	2	20.15	1.56	-	-	-	-	-	

Table 6. Mean (± Standard deviation (S.D.), variance ($S.D.^2$)) and coefficient of variation (C.V.) for individual gonadosomatic index (G.S.I.) of 5 Mile Pond East LL salmon and Exploits River anadromous females collected in the spring (May) and fall (October) 1981.

	Spring			Fall	
	LL salmon	Anadromous Adults	Smolts	LL salmon	Anadromous Adults
$\bar{X}$	0.979	1.101	0.364	11.408	19.869
S.D.	0.104	0.512	0.116	3.916	0.704
$S.D.^2$	0.011	0.262	0.014	15.339	0.496
C.V.	10.578	46.538	31.950	34.326	3.540
N	5	8	18	23	7

but not in slope. A plot of body weight, fecundity and egg volume for the two wild groups and 5 age classes of cultured landlocked salmon (Figure 9) reveals a similar gradation of egg number and volume with fish size.

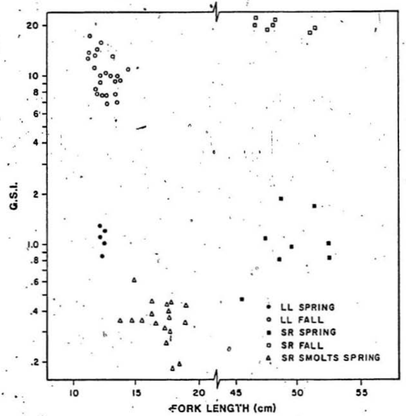


Figure 6. Seasonal changes in female gonadosomatic index (G.S.I.) of landlocked (LL) 5 Mile Pond East and searun (SR) Exploits fish.

Table 7. Mean size (fork length (cm) and weight (gm)) and fecundity of several Newfoundland LL salmon populations. (n=sample size).

Study Area	N	Fork Length	Weight	Fecundity	Reference
Five Mile Pond East	43	12.71	22.55	58	This Study
Soldiers Pond	39	NA	NA	49	Bruce, 1976
Ocean Pond	77	27.40	254.00	346	Lee, 1971
Forest Pond	77	23.00	153.00	279	Lee, 1971
Candlestick Pond	13	21.60	118.60	182	Barbour et al.,1979
Platwater Pond	32	20.07	209.29	318	Leggett, 1965
Several Avalon Lakes	361	NA	NA	517	Wiseman, 1971

NA - not available.

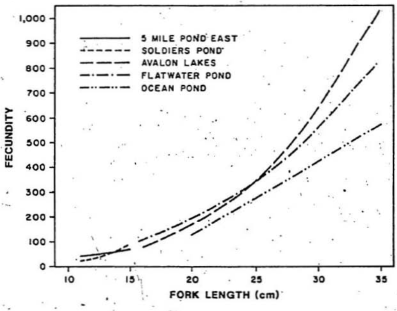


Figure 7. Fecundity curves for several Newfoundland LL salmon populations. Data for 5 Mile Pond East (This Study); Soldiers Pond (Bruce, 1976); Avalon Lakes (Wiseman, 1973); Flatwater Pond (Leggett and Power, 1969) and Ocean Pond (Lee, 1971).

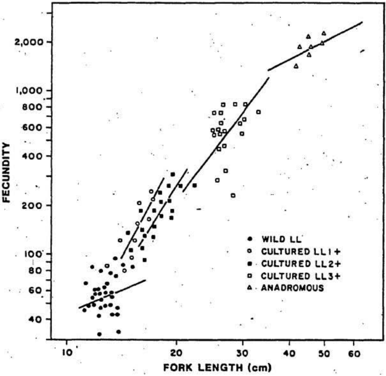


Figure 8. Fecundity-fork length regression for wild landlocked fish, cultured fish (age 1+, 2+ and 3+) and anadromous Exploits fish.

Table 8. Summary of data collected in fecundity study of wild and cultured LL salmon and wild anadromous salmon. Mean ($\bar{x}$), standard deviation (S.D.), coefficient of variation (C.V.) and sample size (n)

		Wild	Cultured			Anadromous
			1+	2+	3+	
Egg Number	$\bar{x}$	57.58	143.49	208.25	592.72	1987.14
	S.D.	16.49	68.66	103.27	188.41	110.96
	C.V.	28.64	47.85	49.59	31.79	5.58
	n	43	53	20	92	7
Total Wet body Weight (gms)	$\bar{x}$	24.47	41.72	103.03	306.41	1145.36
	S.D.	5.32	13.56	24.24	66.67	95.03
	C.V.	21.69	32.51	23.53	21.76	8.29
	n	43	77	20	92	7
Fork Length (cm)	$\bar{x}$	12.98	14.71	20.84	27.86	48.40
	S.D.	0.69	1.47	1.05	1.84	1.89
	C.V.	5.36	9.98	5.02	6.61	3.90
	n	43	77	20	92	7
Egg#/ gram Body Wt.	$\bar{x}$	2.60	3.26	2.02	1.96	1.738
	S.D.	0.68	0.86	0.91	0.46	0.06
	C.V.	26.14	26.26	45.11	23.43	3.71
	n	43	53	20	92	7
Egg Diameter (mm)	$\bar{x}$	4.63	4.14	5.24	5.58	5.74
	S.D.	0.51	0.24	0.31	0.28	0.26
	C.V.	11.03	5.73	5.83	5.06	4.56
	n	20	18	20	20	15
Egg Volume (mm^3)	$\bar{x}$	48.62	37.55	76.07	91.79	99.46
	S.D.	18.48	5.95	11.94	13.67	13.05
	C.V.	38.00	15.85	15.69	14.89	13.12
	n	20	18	20	20	15
Egg Dry Wt. (mg)	$\bar{x}$	24.60	17.09	35.07	40.77	44.27
	S.D.	8.01	2.73	4.06	3.90	4.60
	C.V.	33.00	15.96	11.56	9.79	10.49
	n	20	26	20	20	15
Joeles/gm Dry Wt. Egg	$\bar{x}$	22,357.27	-	-	-	23,024.24
	S.D.	1683.04				959.93
	C.V.	7.53				4.17
	n	10				10

Table 9. Least square regression of fecundity data for anadromous and landlocked Atlantic salmon collected for this study, a and b are parameters fitted to the equation y=log a + b log x, where y = number of eggs; X = fork length, r^2 = is the coefficient of determination represent the proportion of the total variance in the dependent variable that is explained by the regression equation. (n=sample size);

Group	n	b	a	r^2
Wild LL	43	1.15	0.47	.0519
Cultured LL 2+	53	3.90	-2.46	.6431
Cultured LL 3+	58	3.26	-1.80	.3300
Cultured LL 4+	92	2.83	-1.33	.3030
Wild Anadromous	7	1.13	1.38	.6047

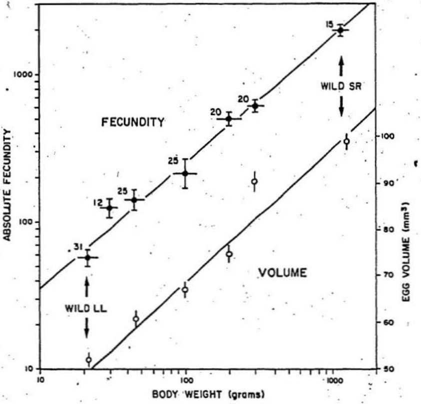


Figure 9. Body size, fecundity (●) and egg volume (o) of wild and cultured salmon. The extreme points represent the wild landlocked (LL) and anadromous (SR) salmon, and the 5 intermediate points were derived from cultured landlocked salmon of age 1-5 yrs. The number of fish sampled, the mean and 95% confidence limits, are shown. Lines fitted by eye.

DISCUSSION

Age and growth

Results of this study indicate LL salmon in 5 Mile Pond East are slow growing and short lived relative to other Newfoundland landlocked populations. The short life span, (the oldest fish collected was 6+), is similar to findings reported for other dwarf populations (Bruce, 1976; Barbour et al., 1979). In contrast Wiseman and Whelan (1974) reported 24 out of 29 Avalon Peninsula lakes had LL salmon older than 6 years with a maximum age of 11. Leggett and Power (1969) comparing LL salmon from two lakes in central Newfoundland reported maximum ages of 9+ and 10+. Freshwater Atlantic salmon in Maine generally live longer with fish as old as 13+ being reported. (Warner, 1961).

Growth data from LL salmon populations in Newfoundland (Wiseman, 1971, 1972, 1973) and Maine (Havey and Warner, 1970) suggest LL salmon attain their largest size and maximum age when forage species, principally smelt, are present. The importance of forage species as a factor in the growth rates of landlocked salmon was recognized early by Stillwell and Smith (1879) who stressed the role played by smelt in the large size attained by salmon in Sebago Lake, Maine. Studies by Fuller and Cooper, (1946) and Cooper, (1940) revealed that smelt may contribute 66-99% of the food volume in the salmon diet.

Smelt were very abundant during sampling carried out at 5 Mile Pond East and available evidence suggests that while brook trout may be benefitting (several specimens in excess of 500 grams were collected), the smelt may in fact be competing with LL salmon for zooplankton (Scott and Crossman, 1973). An analysis of food habits of LL salmon from 5 Mile Pond West (Wiseman, 1973) revealed that the small fish relied heavily on zooplankton as a food source while large individuals consumed a greater proportion of benthic and terrestrial organisms.

Sexual maturity

Another factor implicated in the reduced growth of fish populations is the onset of sexual maturity. Dahl (1917) was one of the early investigators to observe the incidence of early maturity and smaller size at first maturity in stunted forms. Leggett (1965) implicated early sexual maturity as a growth inhibitor in a study of landlocked salmon from Flatwater Pond in central Newfoundland. Age at first maturity of Newfoundland LL salmon populations reveal considerable inter-population variation. Landlocked salmon from Candlestick Pond (Barbour et al., 1979) matured as males for the first time at age 4 while females matured for the first time at age 5. A relatively fast growing population from central Newfoundland (Leggett and Power, 1969) matured as 2+ males and 3+ females. Similar ages at first maturity were reported by Blair (1937); Warner (1962) and Bruce (1967). The age at first maturity of 5 Mile Pond East LL salmon (2+ in males and 3+ in females) is similar to that reported in other Newfoundland LL populations. The presence of unshed ova in the body cavity of several 3+ females suggests maturity at 2+ is an uncommon occurrence.

Little of information exists on age at maturity of Newfoundland anadromous salmon populations. The age and incidence of sexual maturity in male parr from anadromous stocks was examined by Belding (1937) who reported the majority of 3+ parr from west coast rivers were male and Pepper (1976) observed 85% of male parr in the Gander River were mature. A survey by Dalley (1978) revealed variation in the incidence of precocity in male parr from several Newfoundland rivers. Dalley reported from 16% to 100% maturity in 1+ males, with 1+ being the earliest observed age at maturity. Dalley suggested maturity at 0+ by male parr was rare in Newfoundland rivers.

While maturity in presmolt female parr has not been reported, a very high percentage of returning adult Atlantic salmon in Newfoundland are grilse, and the sex ratio of these grilse is in favour of females (Moores et al., 1978). Davis and Farwell (1975) reported 85.7% of 24 fish returning to Grand Falls on the Exploits were female, and data from Western Arm Brook in northern Newfoundland (Chadwick et al., 1978) revealed 76% of returning fish were females.

The high percentage of returning females in Newfoundland anandromous salmon populations can be traced to the smolt sex ratio. The sex ratio of Exploits smolts collected in this study revealed the majority (74%) were females. A similar sex ratio was reported by Chadwick (1981) in Western Arm Brook, Newfoundland. The low number of male smolt can probably be attributed to early maturity of male parr accompanied by reduced growth and high post spawning mortality. Mortality in precocious male Atlantic salmon has been reported by Jones and Orton (1940) and Mitans (1973). Power (1969) in his work on Ungava salmon suggested the higher mortality of precocious males relative to immature females could be expected as a result of exposure of males to predators on the spawning grounds and the depletion of their body reserves for maturation.

The sex ratio of 5 Mile Pond East LL salmon, which was highly in favour of females after age 2+ suggests that a similar pattern of male mortality may be occurring. The stress of spawning followed by over wintering in an oligotrophic environment apparently results in a major depletion of somatic resources which is also reflected in the low condition factor of fish collected in the spring. The large number of LL salmon females spawning for the second time (mended kelts made up 34% of the female spawning population) indicates that female post spawning survival may be high relative to male survival.

Fecundity

The fecundity ($\bar{x}$=58) of wild 5 Mile Pond East LL salmon is the second lowest reported for landlocked salmon. Atlantic salmon egg numbers ranging from 920-1694/kg have been reported (Jones and King, 1946) and Jones (1959) suggested the range for Atlantic salmon was 1430-1540/kg. Differences in fecundity among stocks of anadromous and landlocked salmon have been reported (Pope et al., 1961; Baum and Meister, 1971), but to date no study has been carried out to examine the genetic and environmental contribution to this trait (Saunders, 1981). However, a significant genetic component was demonstrated for egg size by Aulstad and Gjedrem (1973).

The literature on LL salmon fecundity suggests low egg number was due to fish size, and that fecundity was actually similar, on a per unit weight basis, to that of anadromous populations (Barbour et al., 1979; Lee, 1971; Leggett and Power, 1969). Data on fecundity collected from both wild and cultured LL salmon and anadromous grilse in this study revealed wide intraspecific variation in egg number and size. An examination of absolute fecundity versus fork length and body weight (Figure 8 and Figure 9) however, indicates a contineum ranging from wild 5 Mile Pond East fish to Exploits grilse exists for both egg number and volume. Pope et al. (1961) reported a similar pattern in anadromous Atlantic salmon where, while the intercept varied between rivers the slope did not, suggesting the rate of change of fecundity was the same.

Life history tactics

The adaptive significance of life history tactics is based on the concept that a trade off exists between present and future spawnings. Energy expended on reproduction reduces the resources available for future spawning (Williams, 1966; Stearns, 1976). North temperate species, which spawn in the fall generally display a low gonadosomatic index from the post spawning period until mid-summer when a rapid increase occurs prior to spawning (Wooton, 1979). Wooton suggests somatic maintenance and growth have priority during winter, spring and early summer in these populations, with the priority switching to ovarian development in the late summer and fall.

Ovarian development may extract a large proportion of the yearly production of a population (LeCren, 1962). Energy changes in soma and ovaries of perch, Perca fluviatilis were measured by Craig (1977) who found that large maturing fish showed little somatic growth in a year, rather energy was partitioned between maintenance and ovarian development.

The slow growth rate, coupled with high relative fecundity of 5 Mile Pond East LL salmon indicates a similar pattern of resource allocation. While fish collected in the spring displayed low condition factor, the ratio of gonad weight to total weight (G.S.I.) was relatively high. This pattern suggests ovarian maintenance is a priority in this population, even during periods of major drain on somatic resources. The summer feeding period is sufficient to provide the resources for maturation and survival for the females, as evidenced by the high percentage of mended kelts, but not for either growth or male survival.

The pattern of high fecundity in slow growing populations has been reported for shad, Alosa sapidissima (Leggett and Carscadden, 1978) and anadromous Arctic charr, Salvelinus alpinus (Moore, 1975). These, and other studies on geographic differences in reproductive characteristics have suggested the differences were genetically based adaptations to the reproductive environment. That population life history characteristics were adaptations to their environment was recognized early (Fisher, 1930; Cole, 1954) and inter-geographic variation in fish life history traits have been reported by Murphy (1968); Schaffer and Elson (1975); Carscadden and Leggett (1975) and Leggett and Carscadden (1978).

Age of maturity for stunted LL salmon from 5 Mile Pond East appears to be a response to the environment they occupy. Factors such as a marginal environment (low pH, oligotrophic ponds), lack of forage species and inter-specific competition (brook trout and smelt) all contribute to make a rigorous environment. Where reproductive success is unpredictable, life history theory suggests that repeat spawning, iteroparity, increased population stability and would be selected for (Charnov and Schaffer, 1973; Schaffer, 1974).

The results of this study suggest 5 Mile Pond East LL salmon are "bet-hedging" in their life history response to the environment. Although actual egg-numbers are low, early maturity coupled with a high incidence of repeat spawning appear to compensate for the potential reduction in lifetime egg production.

SMOLTIFICATION AND SALINITY TOLERANCE

INTRODUCTION

The parr-smolt transformation (smoltification) in Atlantic salmon is characterized by morphological, physiological and behavioural changes which prepare the fish for entering a marine environment. The many processes involved in smoltification and the development of salinity tolerance in salmonids have been the subject of intensive research in recent years and have been reviewed by Hoar (1976); Knutsson (1979); Saunders (1979); Folmar and Dickhoff (1980); Wedemeyer et al. (1980) and have been the subject of a recent symposium (Bern and Mahnken, 1982).

Two of the most obvious morphological changes occurring during smoltification are body silvering and change in body shape. Juvenile salmon parr are distinguished by the presence of pigmented bars along the side of the body. During smoltification these parr-marks are masked by increased purine deposition in the scales (Johnson and Eales, 1967). Blackening of the fin margins is another characteristic often used as a criteria for smoltification (Wedemeyer et al. 1980). Change in body shape and condition factor (ratio of length to weight) results in a fusiform fish. The change in condition factor results from a rapid increase in fish length accompanied by a slower increase in weight (Komourdjian et al., 1976; Hoar, 1939). The period of rapid growth in length is accompanied by a reduction in total lipid and its replacement with water. Komourdjian et al. (1976) demonstrated that total lipid content of Atlantic salmon smolts was significantly lower than in non-smolted controls.

Parry (1960) concluded that both the onset of smoltification and the ability of salmoids to osmoregulate is dependent on the size and age of the fish. The minimum size threshold for smoltification to occur in wild anadromous Atlantic Salmon appears to be 12-13 cm., although most smolts are 14-17 cm in length (Wedemeyer et al., 1980). Atlantic salmon parr which are 10 cm in length are capable of adapting to salinities as high as 22 ppt (Saunders and Henderson, 1969) but smolts will survive a salinity challange as high as 40 ppt (Komourdjian et al., 1976, Saunders and Henderson (1978).

Smoltification and salinity tolerance are two separate processes which develop independently over time. Salinity tolerance often develops several months prior to smoltification (Wagner, 1974) and is marked by an increase in salinity tolerance of large parr (Farmer et al., 1978). Smoltification, the rapid transformation of parr to smolts prior to their migration to the sea (Hoar, 1976) is a transitory process and smolts prevented from entering seawater will revert back to a physiological state similar to that of parr (Farmer et al., 1978).

A paucity of information however, exists on smoltification and salinity tolerance in landlocked forms of normally anadromous salmonids. The only work which has examined this question in Atlantic salmon is that of Evropeytsevia (1962); Leduc (1972); Sutterlin et al. (1977, 1978) and Barbour (1979). Several of these studies suggested differences existed between the anadromous and non-anadromous forms.

This study examined smoltification and salinity tolerance in three groups of Atlantic Salmon, wild LL, cultured LL and anadromous smolt. Differences in the degree of smoltification, survival to challenges of high salinities and possible antagonistic effects betwee
and smoltification are discussed.

MATERIALS AND METHODS

Sample collection

Anadromous Atlantic salmon smolts from the Exploits River were collected at the Bishops Falls counting fence on June 2, 1981 and transported by tank truck to the Marine Sciences Research Lab. Wild LL salmon were collected May 15–30, 1981 from 5 Mile Pond East using lake traps and were held, along with the Exploits smolts in freshwater (ambient T^0, natural photoperiod) at the Marine Lab in $1m^2$ fiberglass tanks. Cultured LL Salmon (age 3+) were third generation progeny of 5 Mile Pond East fish, which had been reared on freshwater at the Marine Lab (ambient T^0, natural photoperiod and excess ration).

Biochemical analysis

Moisture and lipid determinations were conducted on 18 fish from each group. Fish were removed from the holding tanks, killed by a blow to the head and weight and length recorded. Samples were stored in plastic bags at -20^0C prior to being analysed. Moisture content was determined by drying to a constant weight in a drying oven at 80^0C. Moisture content was expressed as percentage wet weight. Carcass lipid content was determined using the extraction method of Bligh and Dyer (1959). Lipid content was expressed as a percentage of the dry weight of the carcass.

Salinity tolerance tests

Three fish from each group were tested in a series of two replicates. Seventy-five liter glass aquaria were filled with water of the desired salinity (0, 20, 30 and 40 ppt). Aquaria were immersed in a temperature controlled water bath (6^0C) and test fish were held under a natural photoperiod regime prior to and during testing. Aquarium grade sea salt was added to sea water (32 ppt) to produce the desired 40 ppt salinity. Fish were transferred directly from the holding facility to the test aquariums without an acclimation period. Observations were made at regular intervals and the time to death, fork length and weight of each fish was recorded. Cessation of opercular movement was selected as the criteria for death.

Analysis

One way analysis of variance was used to detect significant differences and a Student Newman Keuls multiple range test (Steel and Torrie, 1960) was used to isolate the differences. Arcsine transformations (Sokol and Rohlf, 1969) were carried out on percentage data prior to analysis.

Fulton's condition factor, K, was determined using the equation: $K = W100/L^3$ where W=body weight in grams and L=fork length in centimeters (Ricker, 1975).

RESULTS

Smolt colouration

Both wild and cultured LL salmon developed a degree of silvering similar to wild anadromous smolt (Figure 10). However, at death the silvering faded in fish from these two groups and revealed underlying parr marks. Also, blackening of the fin margins, which was obvious in the anadromous smolts, was poorly developed in the cultured and absent in the wild landlocked fish.

Length-weight relationship and condition factor

Cultured landlocked salmon were heavier than anadromous smolt of comparable length (Figure 11). This is also apparent in Figure 12 where the cultured LL salmon had a significantly (P<.001) higher condition factor than either the wild LL salmon or wild smolt.

Lipid-moisture content

Cultured LL salmon had significantly (P<.01) higher lipid, and significantly lower moisture (P<.01) than either of the other two groups (Figure 13). There was no significant difference (SNK P<.05) in lipid or moisture levels of the wild landlocked and wild smolt.

Figure 10. Differences in colouration of true smolt (top), cultured LL salmon (middle) and wild LL salmon (bottom) collected in May.

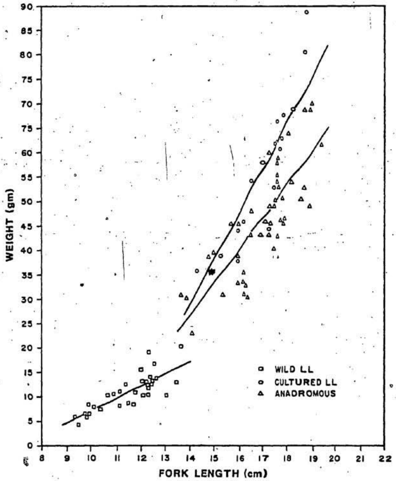


Figure 11. Length-weight relationship for anadromous smolt and cultured and wild-landlocked "smolt" in May.

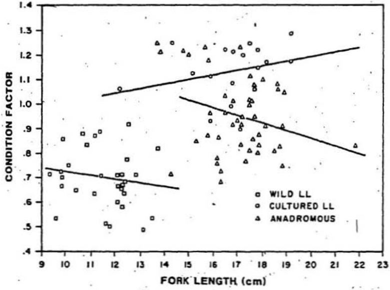


Figure 12. Condition factor - length relationship for anadromous smolt and cultured and wild landlocked "smolt" in May.

Salinity tolerance

No mortalities occurred in the three groups of control fish held in fresh water (Table 10). At 20 ppt salinity both the wild and cultured landlocked salmon experienced low (16%) mortality while mortality was 100% after three days in the same groups at 30 and 40 ppt. In contrast all the anadromous smolts were still alive after seven days in water of 20 and 30 ppt and anadromous smolts were also more resistant to 40 ppt (Figure 14).

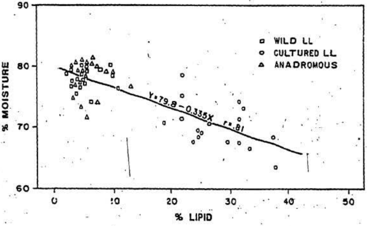


Figure 13. Lipid - water content of anadromous smolt and cultured and wild landlocked "smolt" in May.

Table 10. Survival time (in minutes) of the three forms of Atlantic salmon at four salinity levels. Number of fish in brackets.

Group

Salinity	Wild LL salmon	Cultured LL salmon	Anadromous Smolt
0 ppt	10,000 + (6)	10,000 + (6)	10,000 + (6)
20 ppt	996 (1)	6,510 (1)	10,000 + (6)
	10,000 + (5)	10,000 + (5)	
30 ppt	1035(1)	1290(1)	10,000 + (6)
	1050(1)	2430(1)	
	1290(1)	2730(1)	
	1740(1)	2895(1)	
	1755(1)	3416(1)	
	2370(1)	4110(1)	
40 ppt	560(1)	1050(1)	660(1)
	590(1)	1140(1)	852(1)
	650(1)	1170(1)	2775(1)
	660(1)	1290(1)	3510(1)
	810(1)	2730(1)	3870(1)
	1230(1)	4110(1)	10,000 + (1)

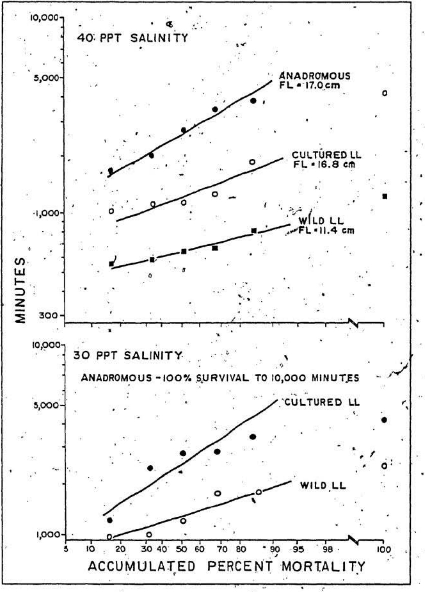


Figure 14. Log - probit plot of time to death for anadromous smolt and cultured and wild landlocked "smolt" at 30 and 40 ppt salinity.

DISCUSSION

The results of this study suggest that anadromous and freshwater forms of Atlantic salmon differ in their degree of smoltification and salinity tolerance. While LL salmon undergo a degree of smoltification which manifests itself in body silvering, their survival at high salinities relative to wild andromous smolt was low. Silvering of wild LL salmon, similar to that observed in this study has been reported by Barbour et al., (1979), and silvery parr have been observed in hatchery stocks of both anadromous (Wedemeyer et al., 1980) and freshwater (Sutterlin et al., 1977) stocks of Atlantic salmon. This widespread phenomenon of body silvering in anadromous and freshwater forms of Atlantic salmon suggests they are responding to the same environmental cues, photoperiod and temperature (Wagner, 1974).

The wild LL salmon used in this study appear to undergo certain physiological changes similar to anadromous smolts, (reduction in condition factor, increase in moisture and a reduction in lipid content) however their salinity tolerance was low. It is possible that the physiological changes observed in these fish are the result of overwintering in a rigorous pond environment or it could be argued that the wild LL salmon are in fact undergoing an incomplete form of smoltification and their reduced salinity tolerance is due to their small size (x = 11.53 cm) compared to the larger (x = 17.0 cm) anadromous smolts. In wild populations of Atlantic salmon the minimum size threshold for smolting is 12-13 cm although most smolts are 14-17 cm in length (Wedemeyer et al., 1980). In Newfoundland smolts tend to be fairly large with mean smolt fork lengths recorded ranging from 14.9 cm (Murray, 1968) to 17.5 cm (Chadwick, 1981).

The failure of cultured LL salmon to tolerate high salinities cannot be explained on the basis of size, as there was no significant difference (P<.05) in the length of the cultured LL salmon and the anadromous smolts (x F.L.=16.76 and 17.02 cm respectively). The reduced survival of the cultured LL salmon at 30 and 40 ppt salinity and their failure to undergo the same physiological changes as both groups of wild fish must therefore be due to other factors.

The wild anadromous smolts used in the 40 ppt salinity tests exhibited greater tolerance then both groups of LL salmon but, did not exhibit the high tolerance characteristic of true smolts (Saunders and Henderson 1978). This reduced level of tolerance observed in the wild Exploits smolts may be attributed to handling stress associated with collecting and transporting the smolts from the river to the Marine Sciences Research Lab. Bouck and Smith (1979) showed that disruption of the skin-scale complex in coho salmon (<u>Oncorhynchus kisutch</u>) resulted in 75% mortality within 10 days at 28 ppt salinity.

Alternative evidence exists which suggests that freshwater forms of Atlantic salmon may retain their ability to adapt to a hyperosmotic medium. Leduc (1972) found that parr of anadromous and freshwater resident Atlantic salmon reacted in the same way to short-term exposure to diluted sea water through changes in blood chloride and plasma osmotic concentration. Sutterlin et al. (1978) successfully reared freshwater Atlantic salmon from Chamcook Lake, New Brunswick in full strength sea water and Roberts (1971) working on a freshwater population of Arctic charr which had been landlocked for approximately 10,000 years found they possessed a high degree of salinity tolerance although it was variously developed among individuals. Roberts suggested the euryhalinity expressed by the population was characteristic of the ancestral stock.

Smoltification is reversible (Hoar, 1976) and is maintained by exposure to saltwater. Smolts retained in freshwater undergo desmoltification (Evropeytsevea, 1957; Zaugg and McLain, 1970). The process of desmoltification has been suggested as a possible mechanism for the development of residual or landlocked forms from normally anadromous salmonids (Conte et al., 1966). It appears that freshwater populations of Atlantic salmon in Newfoundland may have been isolated for as many as 10,000 years (Behnke, 1972; Grant, 1977). During the interim, although they have retained some features (silvering, dark fin margins) related to smoltification, the ability to adapt to a hyperosmotic medium has been reduced. Barbour (1979) suggested the observed differences in salinity tolerance between anadromous and freshwater populations of Atlantic salmon had a genetic basis and was adaptive.

Another factor which may serve to regress the development of true smoltification in Newfoundland ouananiche populations is the possible antagonistic effect of early maturation and smoltification. The relationship between early gonad ripening and smoltification has been little studied in Atlantic salmon and has been confined to males. Evropeytsevea (1960) suggested, based on histological studies and proximate composition, that precocious sexual maturity and smoltification were biologically incompatible and could not occur simultaneously.

Bailey et al. (1980) observed that there was a critical size threshold below which Atlantic salmon would not mature; there is also a critical size that must be attained before salmon will smoltify (Elson, 1957) and this critical size has been shown to vary between families (Thorpe et al., 1980). Thorpe and Morgan (1980) proposed that when the size threshold for maturation was higher than that for smolting, populations which had these thresholds would smoltify rather than mature.

Available information on Newfoundland LL salmon populations indicates the size threshold for maturation is low (Bruce, 1976). Fish from 5 Mile Pond East examined in this study matured at both an early age and small size. Males matured at 2+, (F.L. = 9.64 cm) and females matured at 3+ (F.L. = 12.34 cm). In contrast most Newfoundland anadromous smolts are 4+ with a fork length exceeding 14 cm. Having matured once, LL salmon may be committed to a strategy of maturing every year there after and such processes likely preclude complete or "normal" smoltification.

GROWTH, SEXUAL MATURITY AND OOCYTE RECRUITMENT PATTERNS IN DIFFERENT FORMS OF CULTURED ATLANTIC SALMON

INTRODUCTION

The term precocity in Atlantic salmon refers to the onset of sexual maturity at an early age. This phenomenon is common in male parr in anadromous populations (Jones and King, 1950); precocity is also observed in males of landlocked populations (Warner, 1962) as well as in females of both groups (Regan, 1938; Havey and Warner, 1970). It has been known for some time that precocious male Atlantic salmon produce viable milt (Shaw, 1836; Brown, 1862; Jones and King, 1950; Thorpe, 1975), and the functional significance of precocious maturation of male parr has been discussed by Jones (1959) and Osterdahl (1969). Precocious parr of anadromous populations commonly attempt to spawn with mature females (Jones and King, 1952) and may be the principle male spawners in populations where anadromous males are few in number (Leyzerovich, 1973; Lee and Power, 1976).

Interpopulation variation in the incidence of mature parr has been reported for Newfoundland rivers. Pepper (1976) found 85% of the male parr in the lower Gander River were mature and Dalley (1978) observed precocity ranging from 0-100% in male parr from several Newfoundland rivers.

Although precocity in female anadromous parr is rare, Regan (1938) reported the occurrence of ripe female parr. Jones (1959) however attributed the onset of maturity to the large size and age of these fish (F.L. = 30.48 cm and age 4+). Jones felt that female salmon parr rarely became sexually mature in the river.

The general occurrence of female precocity in landlocked populations is poorly documented. Havey and Warner (1970) reported that female sebago salmon which exhibited rapid growth matured at age 2+, although the majority spawned for the first time at 3+. Data on Newfoundland landlocked populations indicate females mature for the first time at 3+ (Bruce, 1976; Leggett and Power, 1969) and the presence of unshed ova in several females collected from 5 Mile Pond East during this study indicates that spawning at 2+ may occur.

Ovarian development in Atlantic salmon can be classified as group synchronous in that distinct cohorts of elements (oogonia, resting oocytes and vitellogenic follicles) can be observed prior to ovulation (Wallace and Selman, 1981; van den Hurk and Peute, 1979; Thurow, 1966). If the age and size of maturation differ among stocks and are under genetic control then it may be possible to detect differences in the number of ovarian elements and their pattern of recruitment in juvenile fishes from different races. The expression of genes in early life could be a prerequisite in arriving at the required fecundity at the appropriate time.

In species with a wide geographic range, body size is one of the most variable characters (Iles, 1974). Interpopulation variation in growth rate, size at first maturity and body size are common in fish (Alm, 1959; Iles, 1974), and as MacPhail (1977) suggests, such differences may be due to either environmental, genetic or a combination of both factors.

This study examined growth, sexual maturity and ovarian development in two races of cultured Atlantic salmon, (anadromous and landlocked) and their reciprocal hybrids. The role of genotype and phenotype in the expression of these traits and their adaptive significance is discussed.

MATERIAL AND METHODS

Characteristics of the salmon races

The anadromous salmon used in this study were obtained as eggs from Exploits River females. The Exploits supports a predominately grilse population which smoltify at age 4+, spend one winter at sea and return to spawn the following summer. Approximatly 10% of the fish survive to spawn a second time the following year (Figure 15D).

The dwarf landlocked salmon from 5 Mile Pond East were selected as an extreme representative of salmon maturing at a small size and young age. Age and growth data collected on this population during the course of this study indicate females spawn at age 3+ at a length of 12 cm (Figure 15A)). The dwarf form has been routinely cultured at the Marine Sciences Research Lab for 6 years using either a natural temperature cycle or warm water during the winter. Under natural temperature conditions approximately 6% of females mature at age 1+ and 90% at age 2+. If eggs are incubated at 8^0C and the fish subsequently maintained on heated water (15^0C) during the second winter, 90% of females will mature at age 1+ (Figure 15C).

Similarily a larger proportion (30%) of males can be induced to mature 1 year earlier when accelerated as above (Figure 15B and C). Post spawning mortality is greater in

Figure 15. Parental stock history, size structure and breeding scheme.

A. Donor wild LL stock captured at Five Mile Pond.

B. F_1 generation cultured from gametes from A.

C. F_2, LL x LL cultured using 8°C water for egg incubation and 15°C water during summer and second winter.

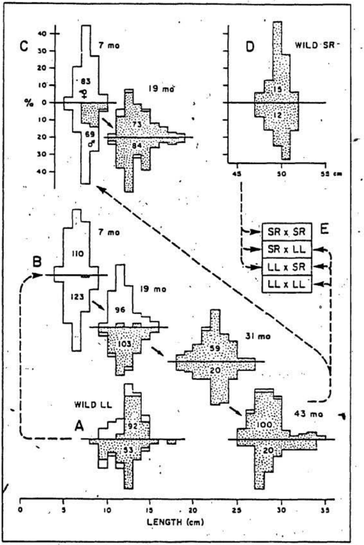
D. Donor wild SR stock captured in Exploits River.

E. Diallele crossing scheme using pooled gametes from B and D.

Shaded portions of histograms represent mature or maturing fish with females above and males below axis. The age and numbers of fish examined are indicated. LL = dwarf, landlocked salmon, SR = anadromous salmon.

Solid lines connect the same group of fish between growth intervals and dotted lines indicate the flow of gametes.

Except for D, the length scale on the bottom is common to all histograms.


C
%
40
30
20
10
0
10
20
30
40
7 mo
83
♀
69
♂
19 mo
73
84
D
WILD SR
15
12
45
50
55 cm
E
SR x SR
SR x LL
LL x SR
LL x LL
7 mo
110
B
123
19 mo
96
103
31 mo
59
20
WILD LL
A
92
53
43 mo
100
20
0
5
10
15
20
25
30
35
LENGTH (cm)

males than females, and most females have spawned 3-4 consecutive times while kept in captivity.

Hybrid crosses and culture conditions

In early November 1980, the eggs from 10 anadromous females that had returned from the sea were pooled as was milt from 10 males. Similarily the eggs and milt from 40 females and 20 male landlocked salmon were pooled. The landlocked parents were derived from gametes taken from wild 5 Mile Pond East fish 4 years earlier. A full diallel cross, using pooled gametes, was made resulting in triplicate groups of each of the 2 hybrid forms and 2 pure lines (Figure 15E).

Eggs were incubated in Heath Techna incubators under an ambient temperature regime. After hatching the alevins were reared in $1m^2$ fiberglass tanks. The tanks were filled to a depth of 25 cm with fresh water at 10-12 l/min. The fish were fed to satiation 4 times a day with a homemade moist pellet. Similar rearing densities were maintained for the four groups.

Sampling methods

Sampling of the different genetic groups began in July, 1981 and continued at monthly intervals. A sample of 50 fish were taken at random from each tank, anesthesized in

1-3% tert-amyl alcohol, and length and weight measurements taken. Fork length was measured to the nearest 0.1 cm and weight to the nearest 0.01 gm on a Mettler 4400 balance.

The incidence of precocity among 0+ males was examined in December, 1981 during monthly sampling. Mature males could be distinguished by their distended bellies, dark colour and the issue of milt when the fish was gently squeezed. In July 1982, water line failure resulted in the death of 3 tanks of replicates. These fish were measured for length, weight and the gonadsomatic index (G.S.I.) as well as condition factor (K) was calculated. At the time of the loss of these fish an additional 25 fish from the remaining replicates were killed and also sampled. In November 1982, mature female parr (1+) from the LL x LL cross were spawned and fecundity determination carried out by actual count.

Histological procedures

Ovaries from fish in each group were collected periodically, examined with a binocular microscope, weighed, and preserved in Bouin's fixative. Each ovary was cleared, embedded in paraffin, sectioned transversally (7um) and stained with hematoxylin and counterstained with eosin.

The ovaries of 6 fish from each of the 4 genetic groups were examined and approximately 30 sections, taken at 3 different transects extending the length of the ovary, were selected for analysis. These sections were projected on paper, and the outline of 100 oocytes of each stage was traced. The developmental stage of each oocyte was noted according to the following classification described for rainbow trout by van den Hurk and Peute (1979).

<u>Stage</u>	<u>Oocyte diameter</u>
1. Nucleus with one large nucleolus	0.01-0.02 mm
2. Numerous small nucleoli in the periphery of the nucleus; dark staining Balbiani bodies around nucleus	0.02-0.10
3. Balbiani bodies dispersed as "yolk" nuclei to the periphery of the ooplasm. Cytoplasm loses basophilic character; theca and granulosa layer apparent	0.10-0.30
4. Chromophobic "yolk vesicles" formed in cytoplasm	0.4 -1.1
5. Eosinophilic yolk granules formed in periphery of ooplasm	0.5 -1.5
6. Yolk granules aggregate and migrate to center of ovum	1.5 -3.0

The relative abundance of each of the oocyte stages was estimated by counting only those oocytes of each stage in which the nucleus was present. As no corrections were made to account for differences in nuclear diameter, the abundance of later stage oocytes are overestimates.

A Zeiss magnetically operated planimeter (MOP) was used to determine the circumference of oocytes. The oocyte was assumed to be spherical, and calculations of oocyte diameter (D), based on MOP - determined circumference (C), was arrived at by $D = C\pi^{-1}$. Only those oocytes which were sectioned through the nucleus were used to determine oocyte diameter. For analysis of serial sections, the nucleus was found to be centrally located and the ratio of nuclear to oocyte volume for oocyte stages 2, 3, 4 and 5 was 0.13, 0.079, 0.028 and 0.008, respectively. By restricting the MOP analysis to oocytes in which the nucleus was present, an average error in underestimating true diameter of oocyte stages 2, 3, 4 and 5 was 10, 6.5, 3.2 and 1.2%, respectively. This error was considered acceptable in arriving at approximate oocyte diameter.

RESULTS

Sexual maturity: males

The incidence of precocity in 0+ males examined in December, 1981 varied between groups. The incidence ranged from no mature parr (0%) in (giving female first) the SR x LL cross to 0.67% in both the LL x LL and LL x SR cross and 1.34% in the SR x SR cross. A fifth group comprised of LL x LL which had been reared under accelerated conditions (incubation and early rearing at $10^{0}C$) had a much higher incidence (16%) of precocity of 0+ males. (Figure 16).

In groups containing ripe male parr the precocious males were significantly longer and heavier in 3 out of 4 cases (Table 11). Condition factors were lower in immature than mature parr although the difference was significant only in the case of the LL x LL cross reared under accelerated conditions.

Sampling carried out in July 1982 revealed a significant difference in the incidence of mature male parr among groups. The LL x LL and LL x SR cross had significantly more mature parr than did the SR x SR or SR x LL cross. An examination of the size at maturity (Table 12) showed that mature 1+ parr were larger than immature parr in two groups and smaller in two although the difference was significant only in the SR x LL and LL x SR cross where

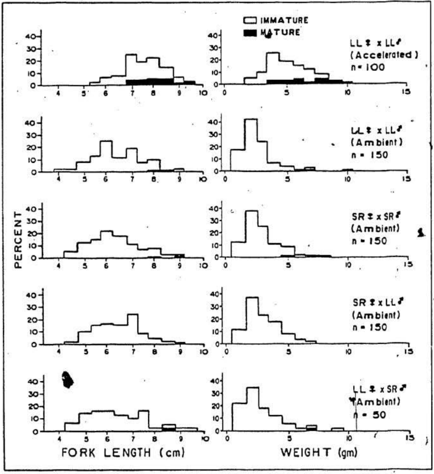


Figure 16. The size structure of 0+ parr of the 4 genetic groups. The accelerated group was incubated at 8°C and reared at 15°C. Shaded portions of the histograms represent mature 0+ male parr.

Table 11. Mean (±standard deviation) of body weight (gm) and fork length (cm) of precocious male and immature (unsexed) male and female Atlantic salmon parr, age 0+.

Cross (Giving first)	Rearing T°	Group	n	Body Weight	Fork length
LLxLL	Accelerated	Precocious	16	5.87± 1.73	8.01±0.72
		Immature	84	4.53± 1.49**	7.44±0.81*
LLxLL	Ambient	Precocious	1	4.77 -	7.80 -
		Immature	149	2.88± 1.36	6.45±0.99
LLxSR	Ambient	Precocious	1	6.74 -	8.5 -
		Immature	49	2.71± 1.71	6.32±1.16
SRxSR	Ambient	Precocious	2	6.63± 2.24	8.55±0.92
		Immature	148	2.71± 1.17**	6.41±0.89**
SRxLL	Ambient	Immature	150	2.56± 1.06	6.26±0.81

* Significant difference between means (t-test, $P<0.05$).

** Highly significant difference between means (t-test, $P<0.01$).

precocious males were significantly longer and heavier than immature male parr.

A comparison of the gonadosomatic index between groups revealed as expected, significantly larger values in mature than in immature male parr; there was no significant difference in the condition factor of mature and immature fish (Table 17).

Sexual maturity: females

The incidence of precocity among 0+ females was first examined in December, 1981 and no mature female parr were observed in any of the 4 groups.

Sampling carried out at age 1+ in July, 1982 identified mature female parr in only one cross (LL x LL) in which 6% of the females were mature. While mature females in this group were not significantly longer or heavier than immature females (Table 13), the gonadosomatic index of mature females was greater than that of immature females (1.6062 vs. 0.2014). These females were spawned 2.5 months later and yielded an average of 130 eggs per fish.

At age 2+ years, 90% of LL x LL females matured while no female SR x SR matured as either parr or post smolt. The SR x LL hybrids appeared intermediate in that 53% of females matured (Figure 17 and 18).

Table 12. Mean (±standand deviation) of body weight (gm), fork length (cm), gonad weight (gm) and gonadosomatic index (G.S.I.) of precocious and immature male Atlantic salmon parr, age 1+.

Cross (Giving first)	Group	n	Body Weight	Fork length	Gonad Wt.	G.S.I.
LLxLL	Precocious	88	23.51 ±10.60	11.80 ±1.65	0.2547 ±0.15	1.14 ±0.59
	Immature	2	26.06 ± 8.01	12.60 ±2.40	0.0118 ±0.01**	0.04 ±0.03**
LLxSR	Precocious	21	26.43 ±13.90	12.31 ±2.25	0.9016 ±0.65	3.22 ±1.47
	Immature	2	16.21 ± 4.16*	10.65 ±1.06*	0.0194 ±0.02**	0.10 ±0.13
SRxSR	Precocious	97	18.29 ± 6.20	10.86 ±1.26	1.3236 ±0.68	6.78 ±2.74
	Immature	47	21.29 ±11.91	11.29 ±2.25	0.0108 ±0.01**	0.06 ±0.07**
SRxLL	Precocious	91	16.77 ± 6.00	10.69 ±1.39	0.4801 ±0.31	2.49 ±1.46
	Immature	26	13.86 ± 5.39*	10.03 ±1.37	0.0047 ±0.01	0.03 ±0.01**

* Significant difference between means (t-test, P<0.05).

** Highly significant difference between means (t-test, P<0.01).

Table 13. Mean (±standard deviation) of body weight (gm), fork length (cm), gonad weight (gm) and gondosomatic index (G.S.I.) of precocious and immature female Atlantic salmon parr, age 1+.

Cross (Giving first)	Group	n	Body Weight	Fork length	Gonad Wt.	G.S.I.
LLxLL	Precocious	4	25.75 ±2.51	13.00±0.24	0.4119±0.03	1.61±0.15
	Immature	67	25.40±13.50	12.19±2.02	0.0476±0.02**	0.20±0.08**
LLxSR	Immature	18	21.72±13.80	11.69±2.49	0.0503±0.03	0.18±0.05
SRxSR	Immature	99	23.73 ±9.71	12.06±1.84	0.0574±0.02	0.24±0.11
SRxLL	Immature	97	18.59± 7.52	11.24±1.61	0.0432±0.01	0.21±0.05

** Highly significant difference between means (+-test, P<0.01).

Figure 17. The size structure and incidence of sexual maturity in the 4 genetic groups. Equal numbers of fish from each replicate were combined to produce each histogram. August and November histograms were obtained from sacrificed or spawned fish; the remaining histograms were constructed by sampling live fish with adjustments being made for known mortalities and sex ratios determined for fin clipped males. Shaded portions of histograms represent mature or maturing fish with females above, and males below. The sampling date, age and number of fish examined are indicated. The scale for length is the same for all histograms.

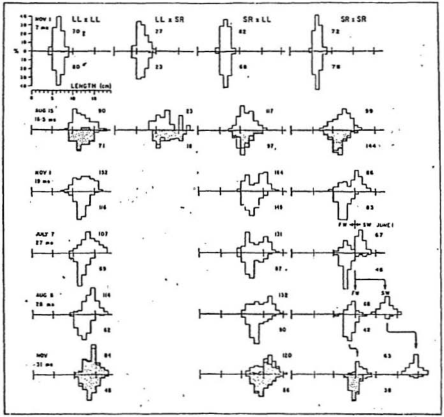
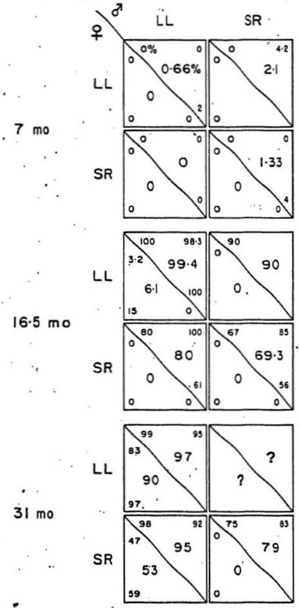

NOV 1
7 mo
LL x LL
LL x SR
SR x LL
SR x SR
%
40
30
20
10
0
10
20
30
40
70
80
27
23
82
68
72
78
LENGTH (cm)
0
5
10
15
AUG 15
15.5 mo
90
71
23
18
117
97
99
144
NOV 1
19 mo
152
116
164
149
86
83
FW
SW
JUNE 1
JULY 7
27 mo
107
69
131
87
67
46
AUG 8
28 mo
114
62
132
90
FW
SW
68
42
NOV
31 mo
84
48
120
86
63
38

Figure 18. Percentage of males and females in each group maturing during their first, second or third summer. Males are represented in a triangle diagonally above the triangle for females. The mean of each replicate is shown as a percentage in the corner of each triangle, and the overall mean of all replicates is shown in the center of the triangle.


♂
♀
LL
SR
7 mo
LL
0%
0
0
0·66%
0
2
0
0
0
4·2
0
2·1
0
SR
0
0
0
0
0
0
0
0
0
0
0
1·33
0
4
0
0
16·5 mo
LL
100
98·3
3·2
99·4
6·1
100
15
0
90
0
90
0
SR
80
100
0
80
0
61
0
0
67
85
0
69·3
0
56
0
0
31 mo
LL
99
95
83
97
90
97
?
?
SR
98
92
47
95
53
59
75
83
0
79
0
0

In groups of LL x LL reared previous to this study, at the Marine Sciences Research Lab, over 85% of females matured at age 2+ and again at 3+ and 4+, producing 144, 215 and 600 eggs per fish respectively.

External appearance and growth

Based on general external appearance it was impossible to distinguish between the 4 groups of fish prior to the onset of sexual maturity. At maturity males in all groups displayed distended abdomens and a darkening in colour.

Both the LL xLL and LL x SR fry were smaller than SR x SR and SR x LL fry (Table 14). This difference persisted for 3 months following swimup and is attributed to the small eggs produced by LL dams. However, by 5 months post swim up (September 1) the differences in the size of the parr among groups were no longer apparent. No difference in weight, length or condition factor was apparent either between replicates of the same group or among groups from age 5 to 17 months.

A degree of bimodality had developed in the length frequency distribution of female SR x LL and SR x SR parr by early November (age 1+) which persisted throughout the winter. The upper mode (>15cm), at least in the SR x SR groups is presumed to have given rise to the 60% of females that smoltified in May and were placed in sea water in early June (Figure 17). Only 8% of SR x SR males were judged to

Table 14. Mean (±standard deviation, S.D.) and coefficient of variation (C.V.) of total length (mm), body weight (mg) and yolk weight (mg) of the four groups at A. 50% hatch and B. swim up.

A. 50% Hatch

Cross(first)		SR x SR	SR x LL	LL x LL	LL x SR
n		25	25	25	25
Total Length (mm)	$\bar{x}$	18.46	17.44	15.56	16.67
	S.D.	0.4567	0.5405	0.7180	0.7987
	C.V.	2.47	3.10	4.61	4.79
Total Dry Wt. (mg)	$\bar{x}$	44.9	45.9	30.3	31.8
	S.D.	1.3	1.7	3.4	3.6
	C.V.	2.95	3.67	11.21	11.30
Dry Body Wt. (mg)	$\bar{x}$	5.6	4.2	2.8	4.3
	S.D.	1.1	0.5	0.6	0.9
	C.V.	19.28	12.50	19.90	20.27
Dry Yolk Wt. (mg)	$\bar{x}$	39.3	41.8	27.5	27.5
	S.D.	1.90	1.6	3.2	3.7
	C.V.	4.81	3.95	11.51	13.61
Yolk Wt. as % Body Wt.		87.39	90.91	90.54	86.18
B. Swim Up					
n		25	25	25	25
Fork Length (mm)	$\bar{x}$	26.43	26.13	23.30	26.92
	S.D.	0.4657	0.5693	1.1660	0.8024
	C.V.	1.76	2.18	5.00	2.98
Total Dry Wt. (mg)	$\bar{x}$	24.4	25.7	15.8	20.6
	S.D.	1.6	1.5	4.1	1.3
	C.V.	6.74	6.01	25.61	6.49

be smolts at this time and they were also placed in seawater. Both male and female SR x SR smolts exhibited a growth rate during the summer in seawater that far exceeded their SR x SR counterparts in freshwater (Figure 17).

Few LL x LL or SR x LL "smolts", although silvery in colour, would tolerate a direct transfer to seawater. Their subsequent growth rate during the summer in seawater was less than half that of the SR x SR smolts.

Gonadosomatic index

The gonadosomatic index of all groups of salmon remained below 1.0 until 5-6 months prior to spawning, then rapidly increased to levels exceeding 10% (Figure 19).

At age 5 months differences in G.S.I. among the genetic groups could be detected in that SR x SR and SR x LL females had ovaries nearly twice as large as ovaries from LL x LL and LL x SR groups. At age 16.5 months (August) differences in G.S.I. among non-maturing females in the 4 groups were no longer apparent. At this time a small percentage of maturing LL x LL were detected in that the G.S.I. ranged between 1.5 and 2. These fish may represent a portion of the 6% maturing females which spawned that fall.

At age 25 months (April), the G.S.I. in LL x LL females destined to mature during the summer increased to 0.91 and was significantly higher than in SR x SR or SR x LL females (Figure 19). Between April (25 months) and August

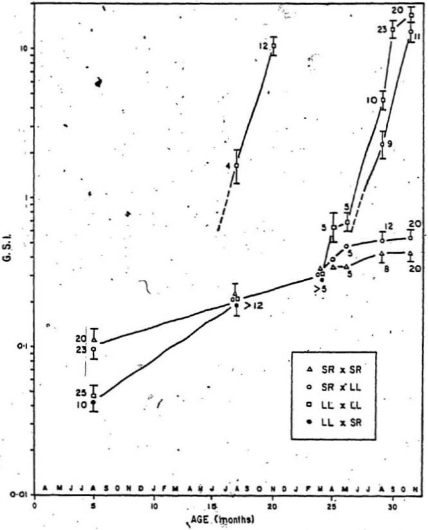


Figure 19: Changes in gonadosomatic index of maturing and non-maturing groups of salmon. Dotted lines indicate indeterminate projections. The number of fish examined, the mean and 95% confidence limits, are shown.

(29 months) the value of the G.S.I. began to differ between maturing and immature SR x LL females. The increase in G.S.I. of maturing SR x LL females continued to lag behind that of LL x LL females and the spawning time of SR x LL females was delayed 2 weeks. At age 29 months and 31.5 months there was no difference in the G.S.I. of non-maturing SR x LL and SR x SR females. The G.S.I. of wild Exploits female salmon captured in the river as returning grilse was 1.2% in early June and 21% at spawning 5 months later.

Oocytes in fresh ovaries

When examining the four groups at 16.5 months (August) in order to determine the onset of sexual maturity, it became apparent using a binocular dissecting microscope that the granular nature of the ovaries of non-maturing LL x LL and SR x SR females differed. The LL x LL ovaries, although the same size as the SR x SR ovaries, possessed larger oocytes.

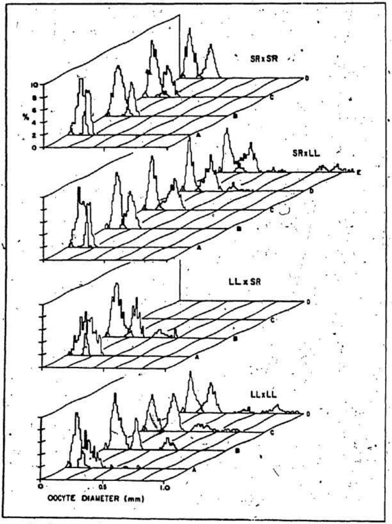
The fresh ovaries of 20 females from each of the 4 groups were again viewed through a dissecting microscope when the fish were age 23.5 months (March). Oocytes larger than 0.5mm were present in all LL x LL and LL x SR females, no oocytes greater than 0.5mm were present in either SR x SR or SR x LL females. Females from all groups were becoming silvery at this time and it was impossible to distinguish between the 4 forms based on external appearance.

At the end of April (25 months) the ovaries of LL x LL females could be distinguished from the ovaries of SR x SR and SR x LL females without the aid of a microscope. The largest oocytes in LL x LL ovaries were 3 times the size of the oocytes in the other two groups. By June (26 months) the ovaries of SR x LL females were variable in oocyte size and intermediate in appearance between SR x SR and LL x LL ovaries.

Histology of ovaries

Although 5 month old SR x SR and SR x LL females had larger ovaries than the LL x LL and LL x SR (Figure 19), there was no difference in either the relative number or size of stage 1 and 2 oocytes. Stage 3 oocytes were absent in 5 month old females from all groups.

Among the 16.5 month old SR x SR and SR x LL ovaries, there was no difference in relative number or size of stage 1, 2 or 3 oocytes (Figure 20). Stage 4 oocytes were absent in both these groups. Four of the six LL x LL ovaries sectioned contained large (0.31-0.60 mm diameter) stage 4 oocytes, and all 6 ovaries contained greater numbers of large (>0.25 mm diameter) stage 3 oocytes than ovaries of either SR x SR or SR x LL females (Figure 20). Ovaries of LL x SR females contained no stage 4 oocytes, but large (>0.2 mm diameter) stage 3 oocytes were abundant in the ovaries of all 6 fish (Figure 20). Peripheral yolk granules


SR x SR
SR x LL
LL x SR
LL x LL
A
B
C
D
E
%
10
8
6
4
2
0
0
0.5
1.0
OOCYTE DIAMETER (mm)

characteristic of stage 5 were absent in all ovaries examined.

Histological examination of the ovaries of 2 maturing 16.5 month LL x LL females which had elevated G.S.I. showed the presence of a proportion of large (>1.5 mm diameter) stage 5 and 6 oocytes that had reached the yolk nuclei and yolk coalescent stage. These fish probably represented the small proportion of LL x LL females that ovulated 3 months later (Figure 17, 18 and 19). In late April (age 25 months), oocytes in ovaries of 3 of the 6 LL x LL females examined had advanced to stage 5 (Figure 20), and all ovaries in this group contained stage 4 oocytes. The SR x SR and SR x LL ovaries were indistinguishable from each other in that the oocytes had not advanced past stage 3 (Figure 20).

At the beginning of June (age 26 months), all ovaries from 6 LL x LL females contained large stage 5 oocytes. Stage 3 oocytes in SR x SR ovaries exhibited some growth during the previous month but none had advanced to stage 4. Oocytes in 2 of 6 SR x LL ovaries contained stage 4 oocytes, and the remaining 4 ovaries were indistinguishable from SR x SR ovaries with stage 3 oocytes. In mid June (age 26.5 months), 6 overies of 14 SR x LL females examined appeared more developed when viewed under a dissecting microscope and these were sectioned. All 6 ovaries contained stage 5 oocytes suggesting that this fraction of maturing fish represents a subsample of the 53% of the SR x LL females that ovulated 4.5 months later.

DISCUSSION

While many factors may influence the onset of sexual maturity in Atlantic salmon, age, growth rate and genetic factors are often considered to be the most important. The results of the rearing experiments carried out in this study demonstrate a genetic as well as an environmental component, both of which contribute to interpopulation differences in size and age of first maturity and in oocyte recruitment patterns. The striking difference in age of maturity in the two cultured forms of salmon (landlocked and searun) correlate well with the differences observed in wild populations of these two forms of salmon (Figure 15 and 17). This suggests the minimum size of age at maturity has an adaptive basis.

Elson (1957) and Refstie et al. (1977) concluded that Atlantic salmon must reach a size threshold in stream and hatchery conditions respectively before they could smoltify. Bailey et al. (1980) hypothesized that a minimum size also existed for maturation in Atlantic salmon. They suggested the threshold for maturation was lower than that for smoltification and that a "decision" of male parr to mature at age 0+ and to smoltify at age 1+ must be made independently.

That the first individuals to mature in salmonid species are usually the fastest growing has been known for some time (Alm, 1959). Leyzerovich (1973); Mitans (1973); Glebe et al. (1978); Lundquist (1980) and Saunders et al. (1982) have shown that precocious male Atlantic salmon are derived from the fastest growing segment of the male population. Mature males in the present study were also significantly larger and had higher condition factors than immature fish.

By age 1+ however, the size difference between immature and mature males was less pronounced. Mature males in the pure crosses, (LLxLL; SRxSR), were smaller than immature males while mature males from the hybrid crosses (SRxLL; LLxSR) were larger than immature males. The reduced growth of mature males in the pure crosses may be a result of a switch of energy away from somatic growth to the gonads. The results suggest that while the fastest growing individuals may be the first to mature at age 0+ the resulting drain on resources results in a reduction in growth the following year.

Maturation of male parr requires a major energy investment and it has been proposed that diversion of energy results in increased mortality in male parr relative to female parr (Power, 1969). Evropeytseva (1959) stated that sexual maturation and smoltification were biologicially incompatible processes since they depend on the same energy stores of lipid which is inadequate to meet both needs. In my study, males in all groups which had matured the previous fall, were smaller than females within that group, suggesting that growth in these males was retarded following maturation. Males also experienced higher mortality in all groups during the winter resulting in females becoming 10-20% more prevalent than males in all groups by the following spring.

The ambient temperature regime used in this study employed approximately 3000^{0}C days per year which is conducive to producing predominately 2 year old anadromous smolts. The high incidence of male precocity in age 1+ and 2+ SR x SR Exploits River parr obtained in this study is similar to that in many Newfoundland anadromous populations in which few male parr survive to smoltify. Most smolts are 3-4 year old females, and returning adults also consist primarily of female grilse (Davis and Farwell, 1975; Chadwick et al., 1978; Moores et al., 1978; Dalley et al., 1983).

Very little information is available on the factors governing maturation in female parr. While maturation of presmolt female parr is rare in searun forms it is more common in landlocked populations. A small percentage (6%) of females in the LL x LL cross matured at age 1+ and the majority of the females from this cross (90%) matured at 2+. The attainment of 90% maturity at age 2+ by landlocked female salmon has not been reported in either cultured or wild anadromous salmon parr in freshwater, nor does it usually occur in anadromous post-smolts females living in seawater for one summer. Some exceptions to this however, have been recorded (Power and Shooner, 1966; Sutterlin et al., 1978; Brozet, 1981).

Sutterlin et al. (1978) observed maturation in an appreciable number of male and female salmon of both a landlocked and searun stock in a saltwater impoundment. They had been reared under an accelerated regime to produce large 1+ smolts and Sutterlin et al. (1978) explained the anomaly on the basis of altered presmolt history. Thorpe et al. (1982) hypothesized that the energetic cost of production of ovaries was much greater than the production of testes and that it was possible that the riverine environment resources were inadequate to permit the female salmon to build ovarian tissue as parr.

It is unlikely that this latter hypothesis explains the mechanism operating in Newfoundland populations of dwarf landlocked salmon. The environment in which many of these populations are found, (shallow, oligotiophic ponds with a lack of forage species) is rigorous, and the propensity of these fish, both male and female, to mature at a small size and early age would not be explained by the hypothesis of Thorpe et al., (1982).

That variations in age of maturity in Atlantic salmon are adaptive was suggested by Schaffer and Elson (1975). They considered that the decision of whether or not to spawn after one or more years at sea was a trade off between the probability of mortality before the next spawning season and the likelyhood of continued growth and enhanced reproductive output. A similar mechanism was postulated for young salmon in fresh water by Thorpe et al. (1982). They suggested that if conditions ceased to be favourable for somatic growth at a time in the season when gonadal development was susceptible to triggering, then the fish would allot resources to gonadal growth at the expense of somatic tissue.

Knutson and Grav(1976); Thorpe and Morgan (1978, 1980); Bailey et al. (1980) and Thorpe et al. (1982) showed that bimodal length frequency distributions develop under certain hatchery regimes by the end of the first growing season. In my study, a degree of bimodality had developed in the length-frequency distribution of female SR x LL and SR x SR parr by early November (age 19 months) which persisted throughout the winter. The length-frequency distribution of LL x LL parr however, remained unimodal throughout this period. Results similar to this were reported by Eriksson et al. (1979) for Baltic salmon parr where they found a uni-modal size distribution. They suggested that genetic factors rather than relative size determined year of precocity in this population. Further evidence of a genetic basis for age at maturity was shown by Naevdal et al. (1978) who reported on variation in age at first maturity of Atlantic salmon adults which they attributed to a genetic basis that originated as an adaptation to different river conditions.

The difference in age of first maturity in both LL x LL males and females when reared under different thermal regimes (Figure 15B and C), illustrates the difficulty in using such discontinuous or threshold dependent characters in quantitative genetics. However, an examination of oocyte recruitment patterns in the different forms of salmon (Figure 20) indicates that the mode of inheritance of such "quasi-continuous variations" is likely to be similar to that of a continuously varying character (Falconer, 1960).

The larger size of ovaries of 5 month old SR x SR and SR x LL crosses may be related to the fact that these fish are destined to mature at a later time and larger size than the LL x LL and LL x SR fish. Since neither the size nor relative abundance of oocytes among the 4 groups differed at this time, the larger ovaries of 5 month old offspring derived from the SR dams presumably contain twice as many stage 1 and 2 oocytes. The absolute fecundity of wild LL x LL at first spawning is about 50 eggs. In contrast, wild 3 year old SR x SR smolts are destined to produce about 2000 eggs at age 4+, or had they smoltified at age 2, they would likely have produced approximately the same number of eggs at age 3+. The differences in ovarian weight between the groups at age 5 months could represent the early expression of a maternally inherited approach to "family planning". The G.S.I. of all groups was identical at age 16.5 and 23.5 months (Figure 19), but the relative abundance and size of the oocytes among the groups was quite different (Figure 20).

Although the data for the LL x SR hybrid is incomplete, the 4 patterns of ovarian development in Figure 20 appear to represent a continuum in which the rate of recruitment is proceeding most rapidly in the LL x LL ovaries with decreasing rates in LL x SR and SR x LL ovaries and at a very low rate in SR x SR ovaries. Based upon the presence of stage 4 oocytes in LL x SR ovaries in March (age 15 months), had these fish lived, a high incidence of maturing females would have been expected the following summer.

The different rates of oocyte recruitment among the 3 surviving groups correlate well with the incidence of maturing females among these groups. Both lines of evidence suggest that the age at first maturity in females is under genetic control and that in the case of the LL x SR hybrid, maternal factors appear dominant while maternal and paternal factors appear additive in the SR x LL hybrid.

The intervening process of smoltification in searun forms complicates any simple comparisons between the characteristics of maturity of the SR and LL forms. Despite several attempts to introduce male or female 26 month old, 12-18 cm LL x LL "smolts" directly into sea water during the spring, they seldom live longer than 4 days. Despite a silvery appearance, LL x LL "smolts" have a high condition factor and low salinity tolerance perhaps more typical of presmolt parr. The predestination of the LL x LL "smolts" to spawn 5 months after this "pseudo smoltification" and the advanced ovarian development observed 2 and 14 months previously suggests that the earlier "decision" to mature precludes certain physiological changes that normally accompany smoltification in non-maturing anadromous females. This hypothesis might not be applicable to other forms of female landlocked salmon that mature at a larger size. The retention of such characteristics as body silvering in landlocked forms would appear adaptive in their migration from a fluvial to pelagic existence in lakes. Barbour and Garside (1983) noted similar differences between landlocked and anadromous salmon.

These results suggest that the "yolk" vesicle stage (stage 4) prior to June is a prerequisite for vitellogenesis and maturation to occur that summer. Stage 4 oocytes were present in the ovaries of LL x LL and LL x SR females as early as the previous March, but did not develop in the SR x LL ovaries until some time in May (Figure 20).

If the presence of stage 4 oocytes is indicative of spawning 5-14 months later in Atlantic salmon, the physiological and biochemical factors responsible for the recruitment of oocytes to this stage have not been established. Stage 4 oocytes are usually considered previtellogenic although presence of "yolk" vesicle has, in some cases, been used as evidence in support of the production of endogenous yolk. Wallace and Selman (1981), however, emphasize that such "yolk" vesicles appear to become the cortical alveoli, are subsequently extruded after fertilization and should therefore not be considered true yolk.

Biochemical and histological studies (Idler et al., 1981) on anadromous salmon returning from sea in June in preparation for spawning the following October, indicate that oocytes of these fish had surpassed stage 4 in development and the oocytes of most fish had advanced to the midprimary yolk stage (2 stages more advanced than the yolk vesicle stage, according to the classification of Ishida et al., 1961). These fish had G.S.I.'s exceeding 0.30 and plasma vitellogenin above 100 ug/ml. Studies by Thurow (1966) and Templeman (1967) had previously provided evidence, based on oocyte diameters of salmon captured at sea in November and April, that differences were taking place within the ovaries of presumptive spawners and non-spawners in advance of the hormonal and biochemical differences noted above by Idler et al. (1981). In November, Thurow (1966) could distinguish between ovaries taken from large and small salmon. The oocytes of small salmon were all below 0.9 mm diameter while a proportion of these from large salmon were greater than 1.2 mm diameter. He suggests that these two groups of fish represented 2 and 3 sea winter fish, respectively, that were destined to spawn 1 and 2 years later. Histological staging, however, was not conducted by Thurow.

Oocyte stages of development progressing from the yolk vesicle to the oil globule and early primary yolk stage reported by Idler et al. (1981) in prespawning salmon in June, have not been completely accounted for in anadromous Atlantic salmon. Ishida et al. (1961) have shown that oocytes in the group synchronous ovary of the Kokanee salmon (landlocked sockeye) had surpassed the yolk vesicle and reached the oil globule stage (stage 4.5) at least 8 months in advance of spawning. Recent studies of North sea capelin (Forberg, 1982) designate the onset of the yolk vesicle stage as being critical in predicting spawning within the year.

In Atlantic salmon, two critical phases of ovarian recuritment may be taking place several months apart. The first might relate to the commitment to mature or not (recruitment to "yolk" vesicle stage), and the second is perhaps fecundity related (number of oocytes ultimately recruited into vitellogenesis). Both processes are likely to be influenced by somatic energy reserves <u>vs</u> expenditures as well as genetic factors. Under conditions of accelerated growth, cultured LL x LL females can be made to mature at a comparable size but 2 years earlier than their wild counterparts. However, the eggs taken at first spawning from accelerated females over 3 successive years could never be fertilized. Similarly, eggs produced by the small percentage of 1+ LL x LL mature females reared under ambient conditions were also infertile. The relative fecundity of these fish was higher and the egg volume lower than in groups which produced viable eggs. It would appear then that some uncoupling of gametic and somatic coordination has occurred during the accelerated rearing regime.

Experiments on sticklebacks by Wallace and Selman (1979) have shown that lower stage previtellogenic follicles ("yolk vesicle" and below) can be advanced to incorporate exogenous yolk when stimulated with human chorionic gonadotropin, regardless of the stage of oocytes in the leading clutch. However, this is not the case in all species. In juvenile male and female trout, luteinizing hormone-releasing hormone analogue is not effective by itself in stimulating gonadotrope activity (GtH production) nor the onset of sexual maturity. In male trout, steroid priming of the pituitary does elevate plasma GtH and advance sexual development; however, such priming of females elevates GtH but does not result in further ovarian development (Crim and Evans, 1983). Thus, it is not clear whether the brain is controlling the ovary or vice versa.

The relative importance of genetic and environment influences on the age and size at first maturity in female Atlantic salmon has been a source of speculation for many years (Gardner, 1976). Although different river stocks exhibit different incidences of maturation when reared under identical conditions (Naevdal, 1981), the heritability of maturation rates of females within a stock has not been easily established, nor has the relative contribution of maternal and paternal factors been especially apparent (Piggins, 1974). Environmental factors affecting presmolt history and subsequent marine growth rates can substantially modify the age at first maturation of females (Ritter, 1975; Thurow, 1966; Sutterlin et al., 1981). This source of variation, coupled with the overlap in ages of first maturity present within and between many anadromous stocks, had complicated most attemps at determining the heritability of such traits in Atlantic salmon.

Age of first maturity in male and female platyfish has been shown to be under the control of a limited number of sex-linked genes (Kallman and Brokoski, 1978) and the incidence of male precocity in Atlantic salmon progeny is, to an extent, influenced by the maturational characteristics of the male parent (Thorpe, 1975; Glebe et al., 1978). In this study however, the incidence of maturing males in LL x LL and LL x SR groups was greater than in the SR x SR and SR x LL groups (Figure 18), which indicates the presence of a moderate maternal influence.

The selection of two diverse forms of salmon for use in this study may provide a better separation of genetic influences from those of the environment. However, due to the large differences in egg volume of the two parental dams (SR:LL = 3:2), it is impossible to separate the maternal genetic component from maternal environment. The larger egg size results in larger fry and this difference in size is maintained during the first 4 months of feeding. A second complicating factor arose from differences in mortality rates between the two hybrid groups. Pre-hatching mortality in the LL x SR eggs, measured for 3 successive generations, has been 10 time greater than in the remaining 3 groups, and might also be related to egg size. The possibility of linkage between mortality and other traits perhaps cannot be ignored (Payne, 1974).

Considerable effort is now being expended in breeding programs to develop late maturing lines of Atlantic salmon for use in mariculture. Based upon the additive effects noted in the present study, the commercial culture of F_1 hybrids derived from parental stocks with diverse characteristic of maturity is not likely to be beneficial without futher selection.

The extreme genetic differences in reproductive traits in the two forms of salmon used in this study may (Payne, 1974) or may not (Stahl, 1983 and Ryman, 1983) be similarly expressed as heterogeneities in other allele frequencies (enzyme polymorphisms). It is possible that genetic changes resulting in reproductively different phenotypes can occur more rapidly than changes in other perhaps "less adaptive" allele frequencies. Since traits such as age and/or size at first maturity can also effect growth and mortality rates as well as fecundity, the identification of closely linked biochemical markers would be especially useful.

Summary

1. The landlocked salmon population in 5 Mile Pond East is a slow-growing, short lived form of Atlantic salmon. They have evolved several traits (low fecundity, a high incidence of repeat spawning and early maturity) which enable them to successfully exploit a rigorous environment (oligotrophic ponds with a lack of forage species).

2. The landlocked and anadromous forms of Atlantic salmon differed in their degree of smoltification and salinity tolerance. While the landlocked forms appeared to respond to the environmental cues for smoltification their salinity tolerance was low. The poor survival of landlocked fish challenged to high salinities suggests there may be an antagonistic effect between precocious sexual maturation and smoltification.

3. The two pure lines and the reciprocal hybrids between the early maturing dwarf 5 Mile Pond East fish and the later maturing anadromous Exploits fish were reared for 2.5 years. Ninety percent of female parr of the dwarf landlocked form matured at age 2+ (fork length 15cm) while no females of the anadromous form matured at such a small size or young age. The weight of the ovary differed in the two pure forms at age 0+ and the number, size and sta[illegible] of previtellogenic oocytes also differed at age 1+. Ovarian pattern of

development and the time of onset of sexual maturation in the two hybrid forms appeared intermediate to that of the parental forms.

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