THE CONTRIBUTION OF ENVIRONMENT AND HEREDITY TO DIFFERENCES IN FRESHWATER GROWTH BETWEEN BIRKENHEAD RIVER AND WEAVER CREEK SOCKEYE SALMON (*ONCORHYNCHUS NERKA*)

BY

James Douglas Cave

B. Sc. University of British Columbia 1978

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

June 1988

APPROVAL

Name: James Douglas Cave

Degree: Master of Science

Title of Thesis:

THE CONTRIBUTION OF ENVIRONMENT AND HEREDITY TO DIFFERENCES IN FRESHWATER GROWTH BETWEEN BIRKENHEAD RIVER AND WEAVER CREEK SOCKEYE (ONCORHYNCHUS NERKA)

Examining Committee:

Chairman: Dr. L.M. Dill, Professor

Dr. B. Hartwick, Associate Professor,
Senior Supervisor

Dr. R. Peterman, Professor, Natural
Resource Management, SFU

Dr. J. Woodey, Chief, Management Div.,
Pacific Salmon Commission, Vancouver

Dr. B. McKeown, Professor, Biological
Sciences, S.F.U., Public Examiner

Date Approved 27 June 1988

PARTIAL COPYRIGHT LICENSE

Title of Thesis/Project/Extended Essay

The contribution of environment and heredity to differences in freshwater growth between Birkenhead River and Weaver Creek sockeye (*Oncorhynchus nerka*)

Author: ______________________

(signature)

James Douglas Cave

(name)

June 30/1988

(date)

ABSTRACT

The Harrison - Lillooet Lake sockeye salmon (Oncorhynchus nerka) population of the Fraser River watershed presented an opportunity to use scale data and laboratory studies to investigate environmental and hereditary differences in growth of sockeye. Scale data indicated that Weaver Creek sockeye, which rear entirely in Harrison Lake, grow significantly more in their first-year in freshwater than Birkenhead River sockeye, which rear in both Harrison and Lillooet Lakes. Available limnological data from the watershed indicated that conditions for sockeye growth in Lillooet Lake are less suitable than in Harrison Lake.

Freshwater growth of both Weaver Creek and Birkenhead River sockeye declined as density increased. This effect of density on growth was greater in Lillooet Lake than in Harrison Lake. The proportion of Birkenhead fry estimated to have reared in Lillooet lake declined as total return increased. As Birkenhead fry output increases, a strong effect of density on growth may cause an emigration from Lillooet Lake into Harrison Lake.

In laboratory studies, fry from both populations were reared under variable temperature and feeding regimes to test the hypothesis that genetic differences in growth exist between Birkenhead and Weaver sockeye. I found significant differences in growth between the study populations. While these differences under controlled laboratory conditions were not as great as observed in the wild, a hereditary contribution to differences in growth was indicated. Relative differences in freshwater growth between the two populations were reflected in differences in circulus spacing, circulus number and overall measurement of the fresh-

freshwater zone. Growth rate affected relationships between scale variables and size.

I concluded that heredity and environmental conditions combine to cause Weaver Creek sockeye to have substantially greater first-year freshwater growth than Birkenhead River sockeye. Environmental factors were concluded to be the principal cause of these differences in growth. However, Weaver sockeye may have evolved behavioural or physiological mechanisms that lead to faster freshwater growth than Birkenhead sockeye exhibit in their normal habitat.

ACKNOWLEDGEMENTS

I would like to express my thanks to the staff of the International Pacific Salmon Fisheries Commission and the Pacific Salmon Commission for their help during the completion of this work. In particular, Fred Andrew, Dave Blackbourn, Rodney Cook, Mike Fretwell, Jim Gable, Philip Gilhousen, Greta Grant, Matthew Graves, Ian Guthrie, John Roos, Paul Ryall, Bill Stevenson, Ross Stewart, and Ian Todd were very helpful. The staff of the Sweltzer Creek Laboratory, in particular, Dave Barnes, Herman Enzenhofer, Bob Gordon, Al Lesberg, Chris Mack, Dennis Martens, Ken Morton, Mike Peters, Earle Stewart, Jim Servizi, and Ian Williams assisted with the laboratory study. Betty Tasaka provided valuable help with scale readings and Steve Cox-Rogers reviewed the manuscript and provided helpful comments.

I gratefully acknowledge the financial support of the International Pacific Salmon Fisheries Commission and the Pacific Salmon Commission throughout this work.

I wish to thank my family for their understanding.

Finally, I wish to express my sincere thanks to my supervisory committee, Dr. Randall Peterman, Dr. James Woodey and especially to my supervisors, Dr. Glen Geen and Dr. Brian Hartwick for their guidance, and patience from the initiation of the project to its completion.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

GENERAL INTRODUCTION

The Birkenhead River and Weaver Creek sockeye salmon (Oncorhynchus nerka) populations of the Fraser River system in British Columbia show distinctly different freshwater growth patterns on the scales of adult fish although as juveniles they may rear in the same lake. Weaver Creek sockeye rear entirely in Harrison Lake (Brannon, 1972). Birkenhead River sockeye begin their lacustrine life history in Lillooet Lake but many individuals complete their lake growth in Harrison Lake (Killick and Goodlad, unpublished manuscript, 1954). However, no adequate freshwater studies of these populations have been conducted to provide evidence as to what mechanisms could be responsible for these distinct differences in growth. In this thesis, I report the results of studies on the contribution of environment and heredity to differences in freshwater growth between these two populations and discuss the implications of the results on sockeye growth and ecology.

Variation of morphological and behavioral characteristics in salmon populations is a result of the interaction of two principal mechanisms: heredity and environment (Ricker, 1972). Heredity is responsible for variation in morphology (Neave, 1944; Smith, 1969), colour (Ricker, 1938) age of smolts and returning adults (Robertson, 1957; Foerester, 1968), migratory behaviour of fry (Brannon, 1972) and adults (International Pacific Salmon Fisheries Commission - I.P.S.F.C., unpublished data). Environment has been shown to influence growth (Brett et al., 1969; Bilton, 1974), age at return (Bilton et al., 1982), meristics (Lindsey, 1981), and homing (Hasler et al., 1978).

Variation in growth, particularly in early life history, is an important variable distinguishing populations of sockeye. Environmental parameters such as temperature and food (Brett et al., 1969), density and lake structure (Goodlad et al. 1974; Biette and Geen, 1980; Hyatt and Stockner, 1985) have significant effects on sockeye salmon growth. The effect of heredity on salmon growth is more difficult to demonstrate. However, its effects must underlie expressions of growth in populations as the "scope for growth" (Brett, 1976) must in some way be genetic. Heredity has been shown to affect growth in Atlantic salmon _Salmo salar_ (Thorpe, 1977; Refstie and Steine, 1978) and in rainbow trout _Salmo gairdneri_ (Austreng and Refstie, 1979).

Growth, age and other life history events of salmon populations can be assessed directly or indirectly through techniques involving the examination of hard body parts such as scales (Gilbert, 1919; Van Oosten, 1929; Clutter and Whitesel, 1956; Henry, 1961; Bilton, 1974; Boyce 1985) or otoliths (Neilson 1984; Bradford, 1985; Campana and Neilson 1985). Sockeye scales are flat calcified structures that lie in pockets in the skin (Figure 1). They increase in area and thickness with the growth of the fish. A series of concentric ridges or circuli, that increase with body growth, are formed on the anterior portion of the scale. The circuli formed in freshwater are discernable from those formed in the ocean by their spacing and the depth of the ridges. Winter checks or annuli are series of closely spaced circuli and are formed on the scale when growth of the scale begins to increase although the exact time of formation may vary (Bilton and Robins, 1971b). Other types of checks may be formed on the scales of fish during other life history events such as migration and smoltification. Feeding level also influences the formation of checks (Bilton, 1974; Boyce, 1985).

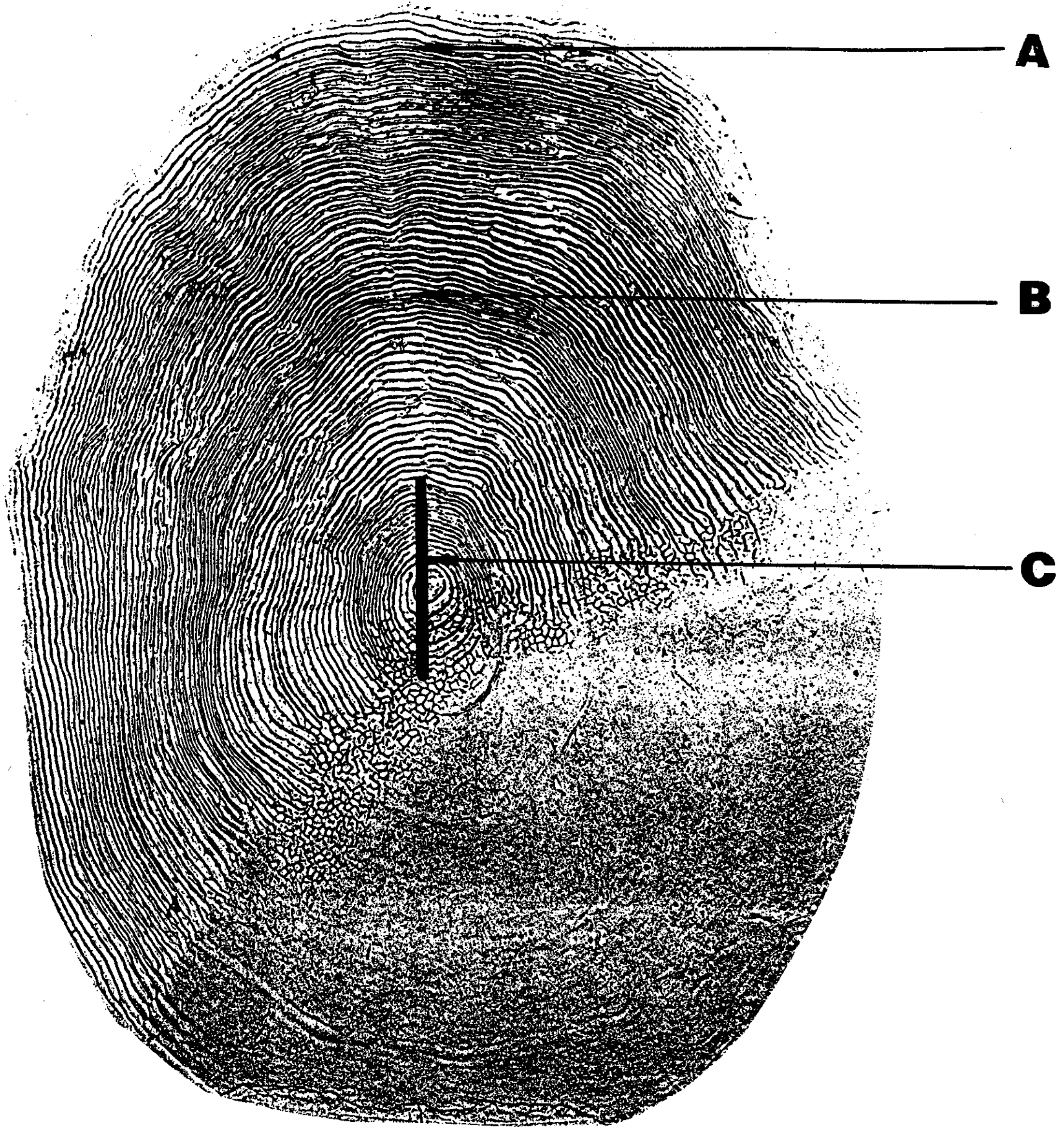

Figure 1A: Photo-micrograph of an acetate impression of a scale taken from an age 4_2 Fraser River sockeye. A: Second marine annulus. B: First marine annulus. C: Freshwater zone.

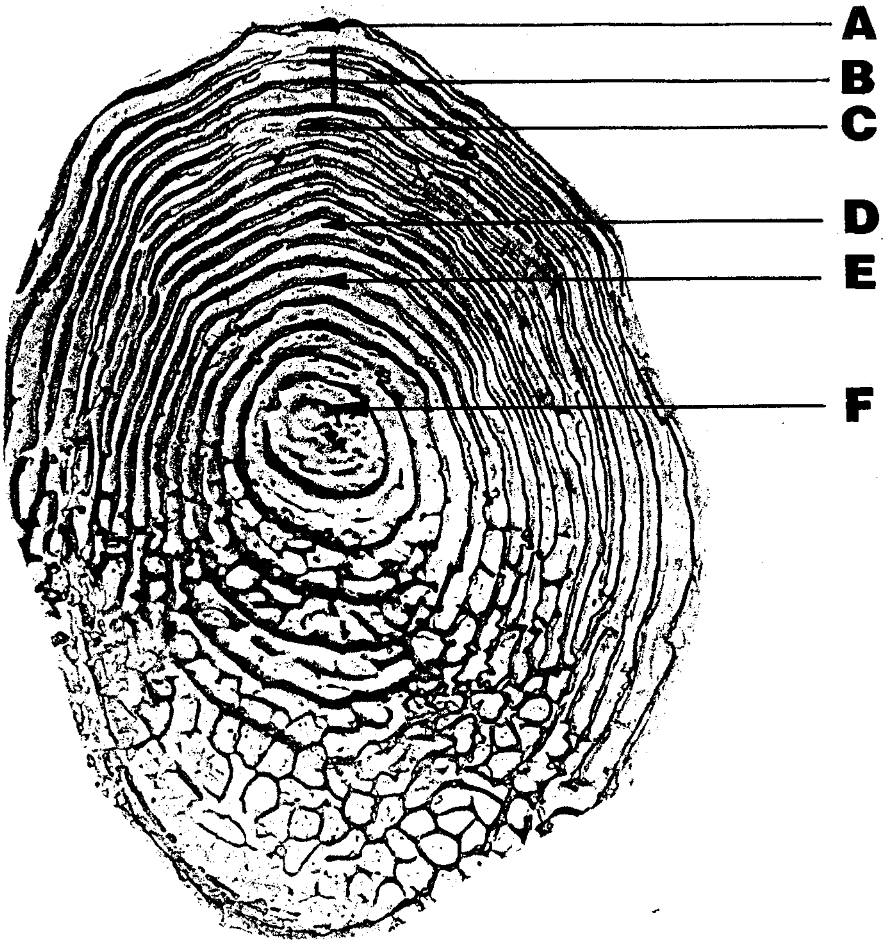

Figure 1B: Detail of Freshwater zone of the same scale in Figure 1A (mirror image). A: First marine circulus. B: spring growth circuli. C: Freshwater annulus. D: Space between circuli. E: Freshwater circulus. F: Focus of the scale. This scale has 14 circuli to the freshwater annulus and 4 spring growth circuli.

Circuli number, scale diameter, scale radius and scale area are significantly correlated with fork length (Clutter and Whitesel, 1956; Bilton, 1974; Boyce, 1985). Environmental conditions have a greater effect on intra-annual variation in the number of freshwater circuli within and among stocks than does racial heritage (Clutter and Whitesel, 1956). As evidence of this the wide differences in circuli number between dominant and off-year Adams River sockeye can be noted. Also, transplanted sockeye often had quite different circuli number than fish from the donor stocks. Bilton (1974) found that circuli spacing and number as well as scale radius were positively correlated with feeding level.

The following assumptions are implicit in studies where size and growth rates are back-calculated from scale - body length relationships:

1) Event markers on the scale such as annuli are formed at the same time within the study and are readily discernable from other checks.

2) The spacing between event markers on the scale accurately reflects proportionate body growth.

Validation of size back-calculation methodologies is important if the techniques are to be of value to biological management (Carlander, 1981). For example, growth rate affects the relationships between scale variables and body size (Boyce, 1985) and resulting inferences about the growth of individuals in a population may be incorrect. Also, Lee's phenomenon (Van Oosten, 1929; Smale and Taylor, 1987) can affect these relationships .

In Chapter I, I investigated adult scale data and limnological information for contribution of the environment to relative differences in freshwater growth of Weaver and Birkenhead sockeye fingerlings. Also I examined the effect of density and subsequent growth on the proportion of Birkenhead fingerlings which rear in Lillooet Lake. The following working hypotheses were investigated:

1) Main hypothesis: Environmental conditions for growth are less suitable for Birkenhead sockeye than for Weaver sockeye.

a) Subsidiary Hypothesis: Sockeye fingerling density affects the growth of fingerlings of both sockeye populations in the Harrison-Lillooet lake system.

b) Subsidiary Hypothesis: As fry density increases, the contribution of Lillooet Lake to abundance of adult returns of Birkenhead sockeye decreases.

In Chapter II, I examined the possible genetic differences in growth between the Birkenhead River and Weaver Creek sockeye populations in the laboratory. Also, I examined the validity of some of my assumptions in the inference of relative differences in growth from adult scale data in Chapter II. The following working hypotheses were investigated:

1) Main Hypothesis: Weaver Creek and Birkenhead River sockeye have genetically different freshwater growth.

a) Subsidiary Hypothesis: Relative differences in growth between the study populations are reflected in differences in circuli spacing, circuli number and overall measurement of the freshwater zone of the scale.

b) Subsidiary Hypothesis: Growth rate affects relationships between scale variables and size.

The effect of contribution of environment and heredity on differences in freshwater growth between Birkenhead River and Weaver Creek sockeye is determined through examination of the above hypotheses. Also, I discuss the application of methods used in this study in the assessment of the potential adult returns of these stocks.

CHAPTER I:

CONTRIBUTION OF ENVIRONMENT TO DIFFERENCES IN FRESHWATER GROWTH BETWEEN BIRKENHEAD RIVER AND WEAVER CREEK SOCKEYE

INTRODUCTION

Sockeye growth rates are influenced by changes in environmental variables. Brett et al. (1969) showed that specific growth in weight (percent increase in weight/day) in the laboratory was related to food intake (up to satiation) and to temperature, up to a physiological optimum of 15° C. At temperatures greater than 15° C, growth rate declined. In the wild, sockeye growth rate is inversely related to fingerling density and directly related to zooplankton abundance (Goodlad et al. 1974; Hyatt and Stockner, 1985).

Typically, sockeye growth is greater in more eutrophic or mesotrophic lakes than in glacial, oligotrophic conditions. However, comparisons of sockeye growth between lakes are difficult for a number of reasons. Biette and Geen (1980) suggested that the interrelationships of food and temperature on growth may be quite complex, depending on thermal stratification of the lake, as diel migrations of sockeye between temperature zones affects food conversion efficiency. Goodlad et al. (1974) suggested that lake temperature depth structure rather than average temperature may be important in the determination of growth in the wild. Eggers (1978) explored the alternate hypothesis for diel migrations and showed that predator populations influence diel migrations and ultimately growth rates of sockeye. This theory is supported by sockeye data from the Fraser River watershed. Sockeye growth in Anderson Lake in the Fraser River watershed is poor (Geen and Andrew, 1961) despite low fingerling density and high zooplankton abundance. This is thought due to the fingerlings inhabiting deeper and colder water within the lake in an attempt to avoid predation by piscivorous fish, thereby affecting foraging (J.C. Woodey, Pacific Salmon Commission, Vancouver, B.C. pers. comm.).

In this chapter, I examined some environmental factors which might be responsible for differences in freshwater growth observed between Weaver Creek and Birkenhead River sockeye populations, both of which ultimately rear in the same lake system. I hypothesized that environmental conditions for growth are less suitable for Birkenhead than for Weaver sockeye. Second, I investigated abundance of adult returns and scale growth information to explore the hypothesis that fingerling density affects the growth of sockeye of both populations in the Harrison system. Finally, I explored the hypothesis that contribution of Lillooet Lake to abundance of adult returns of Birkenhead sockeye decreases as the abundance of those returns increases.

STUDY POPULATIONS

The Lillooet Lake - Harrison Lake watershed includes two principal tributaries: the Lillooet and Birkenhead Rivers, which flow into Lillooet Lake (Figure 2). This lake is drained by the lower Lillooet River into Harrison Lake, which is in turn drained by the Harrison River into the Fraser River, 100 km from the ocean. Weaver Creek is a small tributary of the Harrison River.

The two major sockeye populations in the Harrison Lake - Lillooet Lake watershed are the Birkenhead River and Weaver Creek stocks. Schaefer (1951) reviewed the biology and history (since the beginning of the 1900's) of these and other, smaller populations in the Harrison system. Returning Birkenhead River adult sockeye arrive at the mouth of the Fraser River during August and delay 1 to 2 weeks before continuing upstream to spawn. These fish may delay in Lillooet Lake before entering the spawning grounds during September. Peak spawning generally occurs near the last week of September. Weaver Creek sockeye generally overlap with the Birkenhead River sockeye during migration through the coastal marine areas, but characteristically delay near the Fraser River mouth for approximately 4 to 6 weeks. Weaver Creek sockeye begin to arrive on the spawning grounds in the first week of October and are at their peak of spawning during the third week of October. Sockeye fry production from Weaver Creek is enhanced by an artificial spawning channel constructed in 1965. Fry production and adult returns have increased greatly since that facility has been operational (Cooper, 1977).

The age and growth dynamics of Birkenhead sockeye are quite complex. Following the age designations according to the Gilbert method

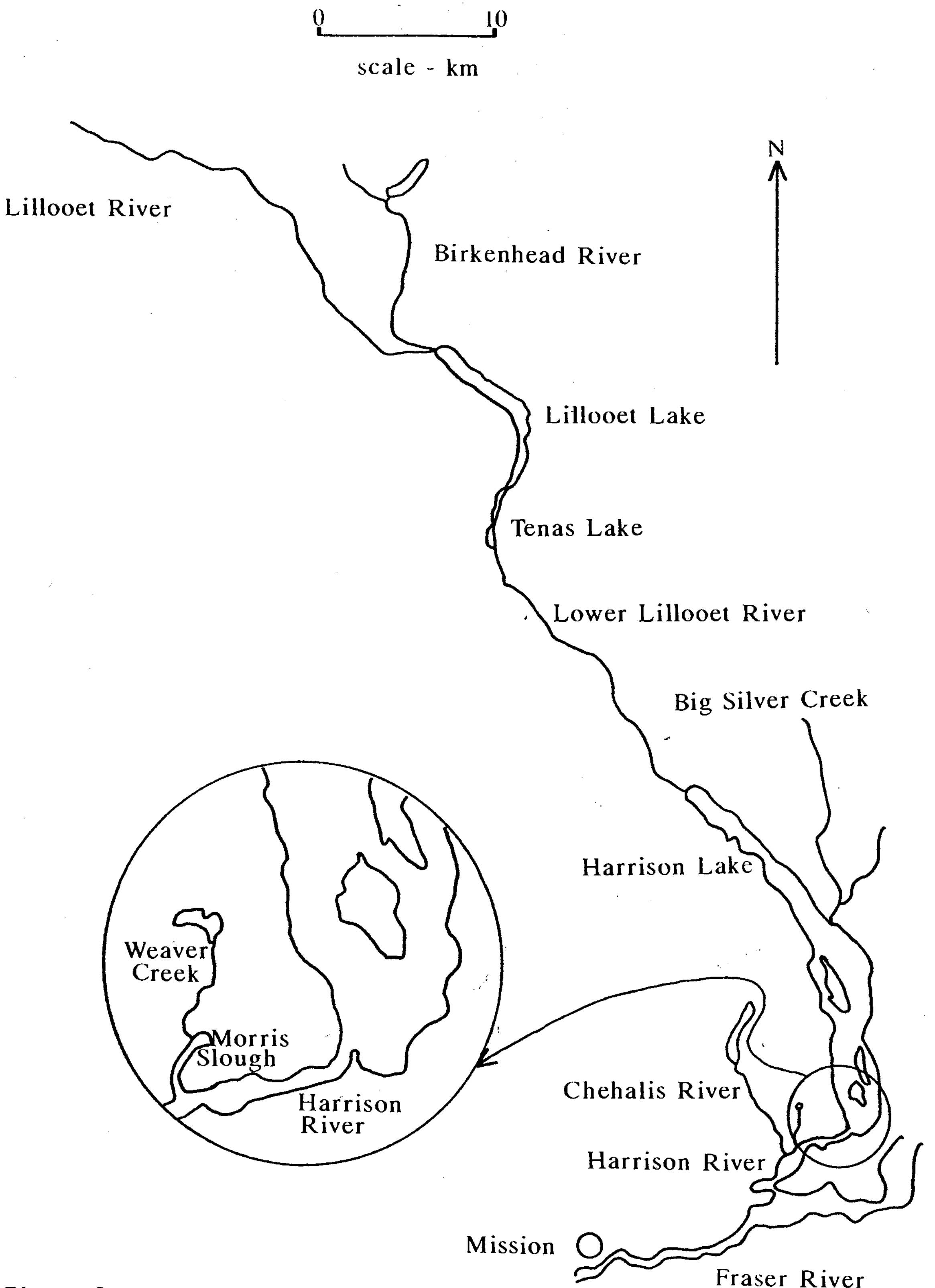

Figure 2: Map of Harrison - Lillooet River System, showing location of lakes and streams.

(Gilbert, 1914-1925) average brood year returns by age class are as follows:

3_2:	10.3%
4_2:	66.8%
5_2:	15.6%
4_3:	1.5%
5_3:	5.5%
6_2 & 6_3:	0.3%

Jacks (age 3_2 and 4_3 males) may contribute up to 20% of any given brood year recruitment return, more than any other large population in the Fraser River watershed. Also unusual with this population is the occurrence of two size ranges of age 4_2 males. Weaver Creek sockeye average brood year returns by age class are as follows:

3_2:	1.2%
4_2:	89.2%
5_2:	9.0%
5_3:	0.6%

Weaver Creek sockeye fry migrate downstream into Morris Slough soon after emergence, feeding primarily on pre-emergent insects (Brannon, unpublished data). When the fry reach the Harrison River, they change their orientation towards the current (Brannon, 1972) and migrate upstream to Harrison Lake in approximately 3 days. During this migration, they have access to good food reserves, mainly dipterans. The south end of Harrison Lake is shallow and plankton populations are augmented by insect larvae. The fry spend an estimated 30 - 45 days in the shallow bay and shore area before assuming a pelagic behaviour.

The Birkenhead River is productive in its lower reaches where it meanders through a fertile delta. However, it empties into Lillooet Lake, the principal tributary of which is the glacial, upper Lillooet River. Birkenhead River sockeye fry bound for Harrison Lake must migrate through this lake and the lower Lillooet River. The duration of the Birkenhead sockeye fry migration through Lillooet Lake is quite variable. Some fry remain for a period of one year (Killick and Goodlad, unpublished manuscript, 1954), as smolts have been collected from the lower Lillooet River in May. However, other fry and fingerlings pass through the lake over a variable length of time, from within a few days of entering the lake to possibly the fall months. There is no direct information on the proportion of the fry-of-the-year rearing in Lillooet Lake as studies on the total fry produced from the Birkenhead River and subsequent migration from Lillooet Lake in any one year have not been undertaken.

Gilbert (1913, 1914 and 1925) and Schaefer (1951) analyzed scale growth of Harrison system sockeye and concluded that Birkenhead River sockeye have narrowly spaced, irregular circuli and a small freshwater scale region. The freshwater "nucleus" of Birkenhead sockeye scales have many breaks and interruptions. Scales from Weaver Creek sockeye have widely spaced and more numerous and regular circuli and a much larger freshwater scale region than Birkenhead sockeye. Goodman reviewed information on Birkenhead sockeye and concluded that 4_3, 5_3 and 6_3 age classes tend to spend their first year in Lillooet Lake and the second year in either Lillooet or Harrison Lake (Goodman, I.P.S.F.C. unpublished data). Elsewhere Goodman notes that "...as much as 60% of the population goes directly into Harrison Lake some years." Bimodality is often evident in the Birkenhead River freshwater circuli frequency distribution, both in the number of circuli to the 1st annulus and to the end of the freshwater growth. The general conclusion from the scale data is that some Birkenhead River sockeye rear entirely in Lillooet Lake while others rear partially in Lillooet Lake and subsequently in Harrison Lake.

MATERIALS AND METHODS

Water temperature, physical and hydrological characteristics, water quality and zooplankton information were collected from Lillooet and Harrison lakes in 1975 by the International Pacific Salmon Fisheries Commission (I.P.S.F.C.). Additional limnological information was obtained by the Department of Fisheries and Oceans, Canada (Stockner and Shortreed, 1983). This information was used to determine the suitability of these lakes for growth of Birkenhead sockeye as compared with conditions for Weaver Creek sockeye.

I examined scale information in order to investigate differences in growth between Weaver and Birkenhead sockeye. Scales have been taken from adult and jack sockeye from Birkenhead River and Weaver Creek spawning grounds from 1955 to the present. Preparation, interpretation and measurement methods were as outlined by Clutter and Whitesal (1956). Sample size varied with age composition but 60 to 550 age 4_2 scales were available from each population each year (mean = 293; S.E. = 27.3). The freshwater zone of each scale was examined along the dorsal 20° axis (Figure 1) of the scale for the number of circuli from the focus to the annulus (without spring growth after the annulus - WOSG) and for the number of circuli to the end of the freshwater zone (with spring growth after the annulus - WSG). One experienced scale reader read all scales. Means and frequency distributions of circuli counts were then calculated. Scales taken from yearling Lillooet Lake smolts captured in 1966 were processed using the same methods.

Measurements of circuli spacing were obtained from scales of age 4_2 sockeye of both stocks (1973 and 1978) by the same scale reader. The scale measurement information from 1973 was used originally in a racial analysis study (Cave and Woodey, unpublished manuscript) and information from 1978 was used for comparison with 1975 Harrison Lake fingerlings (I.P.S.F.C. unpublished data). Measurements were made by projecting the image of the scale magnified 250 times onto paper and marking off the required sections. The measurements were then reduced back to actual size for analysis and presentation. For the 1973 samples, measurements from the focus of the scale to the 10th freshwater circulus, to the freshwater annulus and to the end of the freshwater growth were recorded. Measurements from the focus of the scale to each freshwater circulus were obtained from 1978 scales. Distances from the focus to the tenth freshwater circulus have been recorded from scales taken from age 3_2 sockeye for years 1977 - 1978.

A maximum likelihood analysis of the age 4_2 WOSG circuli frequency distributions was used to estimate the proportion of Birkenhead River sockeye rearing in Lillooet and Harrison lakes for each year. The method involves fitting mixtures of normal distributions to grouped data by maximum likelihood and has been used in the investigation of length frequency data (Macdonald and Pitcher, 1979; Macdonald and Green, 1985). Since specific circuli count data from smolts of Birkenhead sockeye were unavailable from each lake, I used modal points on the frequency distributions corresponding to the two lakes for the analysis. For 20 of the 33 years, the modes were quite distinct. For the remaining 13 years, the Lillooet Lake mode was less obvious but I searched for obvious inflections in the frequency distributions approximately 4 circuli lower than the dominant Harrison Lake mode. This procedure was validated by comparison of the age 4_2 WOSG data with Lillooet Lake smolt data where available (years 1953 and 1966) from the same brood. The initial value for the standard deviation was estimated from scale data from Lillooet Lake smolt and Weaver Creek adults and was set at 1.8 for both modes. For each year, the proportions of Birkenhead River sockeye rearing in each of the two lakes were first estimated by the maximum likelihood method with means and standard deviations held fixed. An iterative method was then used to refine estimates of means and standard deviations with fixed proportions. This procedure was repeated until chi-square goodness of fit (observed circuli count frequency distribution minus expected circuli count frequency distribution) was maximized.

Long-term information on the number of fry, fingerlings or smolts was unavailable for the two stocks therefore, estimates of the abundance of adult returns for each stock (source: I.P.S.F.C. archives) were used as indices of sockeye productivity by stock in the Harrison system. These included the sum of all catch and spawning ground escapement data following methodology of Henry (1961).

I assembled the abundance of adult returns and scale data for each population as follows. Brood year (year t), following the terminology of the I.P.S.F.C. and Walters and Staley (1987), signifies the year in which a year-class was deposited as eggs, for example 1982 (Figure 3). The first year of freshwater growth for this brood or year-class would have occurred during year t+1 or 1983 in this example. Yearling smolts would have left the lake in the spring of 1984, year t+2 (hence called sub-2's following the Gilbert system). Two year old smolts (sub-3's) would have left the lake in 1985 or year t+3. Adult returns (including jacks) would occur from year t+3 (1985) to year t+6 (1988). Adult returns of Birkenhead sockeye which had utilized Harrison and Lillooet lakes each year were estimated by multiplying the total adult returns

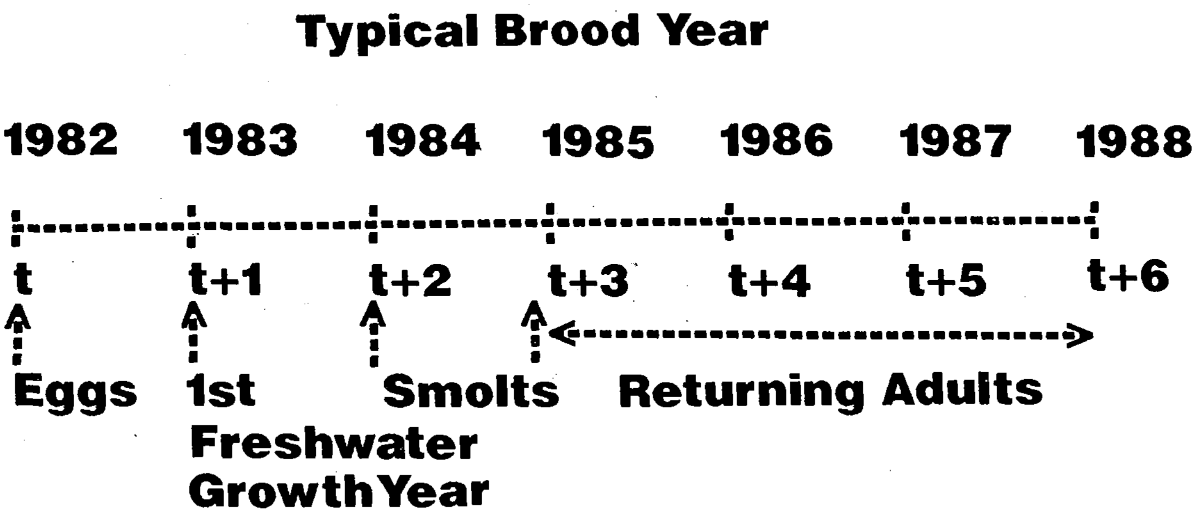

Figure 3: Schematic diagram of the sockeye life-history for the 1982 brood year. See text for explanation.

<u>Returning Adults:</u>

t+3: 3_2 return year
t+4: 4_2 and 4_3 return year
t+5: 5_2 and 5_3 return year
t+6: 6_2 and 6_3 return year

for the brood year by the proportions for each lake estimated from the maximum likelihood analysis. Scale data for this brood year, for comparison with total adult returns, would be collected from age 4_2 sockeye on the spawning grounds in year t+4 or in 1986.

I tested the following working hypotheses using least squares regressions:

1) Freshwater scale growth of sockeye in year t+1 for each lake is correlated with total abundance of adult returns of that brood year (years t+3 to t+6). Sockeye growth is density-dependent.

2) The proportion of the Birkenhead sockeye population which rears in Lillooet lake in year t+1 is related to the subsequent total abundance of adult returns of Birkenhead sockeye of that brood year in years t+3 to t+6.

In these analyses, I make the assumption that the abundance of adult returns from a given brood year is linearly related to the fingerling or smolt abundance for each stock in that brood year.

The main hypothesis that environment is responsible for the differences in freshwater growth observed between the study populations was tested by inference from several studies:

a) The examination of the limnological data.

b) The examination of the Birkenhead circuli frequency distributions and relative differences in overall scale growth between the two populations.

c) Analysis of covariance to determine if growth in Lillooet Lake declined more rapidly with density than in Harrison Lake.

RESULTS

a) Limnological information. I investigated the available limnological information to determine if Lillooet Lake was less productive than Harrison Lake. Although the data are incomplete, the available evidence indicates that Lillooet Lake is a less favourable environment for sockeye growth than Harrison Lake. First, Lillooet Lake is colder at most depth strata during the growing season than Harrison Lake (Table 1). Secchi depths were less in Lillooet Lake indicating less light penetration because of the glacial silt. The flushing rate is greater for Lillooet Lake than Harrison Lake (Table 2). Also zooplankton biomass was less in Lillooet Lake. Phytoplankton and zooplankton productivity estimates were unavailable.

b) Scale growth information. Three variables were examined for differences in scale growth between Birkenhead River and Weaver Creek sockeye: circuli number to the freshwater annulus, distance from the focus to the freshwater annulus and circulus spacing as indicated by the distance from the focus to the tenth freshwater circulus. ANOVA's indicated significant main effects of stock ($P < 0.001$) for all variables (Table 3). Weaver sockeye had significantly higher circuli counts, greater distances to the freshwater annulus and wider circuli spacing than Birkenhead sockeye. In particular, circuli spacing, as represented by distance from the focus to the tenth circulus (Figure 4) showed little overlap between the two stocks and this was found to be the case for every year which was investigated. Circuli number to the annulus of Weaver and Birkenhead sockeye has been quite similar in some years. Weaver sockeye had 37% greater distance to the freshwater annulus than Birkenhead sockeye.

Table 1: Secchi measurement and temperature by depth stratum. (Data from I.P.S.F.C. archives except as noted.)

			Temperature (C)			
		Secchi	Depth in meters.....			
Lake	Date/Source	Depth (m)	0-15	16-30	31-46	47-61
Harrison	24-Apr-75	10.7	6.9	6.6	6.5	6.2
Lillooet	30-Apr-75	4	6.3	5.6	5.5	Na
Harrison	18-Aug-75	2.1	16.6	13.3	10.3	8.4
Lillooet	02-Sep-75	1.8	12.5	11.2	8.6	6.3
Harrison	14-Jun-76	9.2	10.4	8.9	7.2	6.6
Lillooet	22-Jun-76	2.3	10.2	8.1	6.6	5.3
Harrison[1]		4.1	12.2	Surface		
Lillooet[1]		0.3	9.7	Surface		

[1] Stockner and Shortreed, 1983

Table 2: Summary of physical, water quality and biological characteristics.

	Harrison Lake	Lillooet Lake
Physical Characteristics[3]:		
Elevation (m)	10	196
Watershed (km^2)	8440	5180
Surface Area (km^2)	218	35
Mean Depth (m)	151	62
Flushing Rate (y)	2.3	0.6
Water Quality[4]:		
Compensation Depth (m)	10	2
pH	7.2	7.5
Alkalinity (mg $CaCO^3/l$)	13	14
Biological Characteristics:		
Bacteria[4] (no./ml)	1.20×10^6	1.10×10^6
Chlorophyll[4] (ug/l)	0.80	0.85
Zooplankton Biomass[4] (mg/m^2)	220	150
Zooplankton Communities[3]: % Numeric Composition		
Bosmina:	0.80	0.12
Daphnia:	0.03	2.67
Leptodora:	0.07	0.00
Epishura:	14.02	73.74
Cyclops:	13.54	0.79
Diaptomous:	71.54	22.68
Total:	100.00	100.00

---

[3] I.P.S.F.C. Archives.

[4] Stockner and Shortreed, 1983.

Table 3: Analyses of variance of the main effect of stock on freshwater scale variables:

(1) number of circuli to the freshwater annulus (CCANN)
(2) distance from the focus to the freshwater annulus (DANN)
(3) distance from the focus to the tenth freshwater circulus (DTEN)
for combined years 1973, 1978.

			Main effect of stock:		
Test	Variable	d.f.	F-Ratio	Probability	d.f.
1	CCANN	396	71.17	< 0.001	1
2	DANN	396	734.09	< 0.001	1
3	DTEN	396	1277.07	< 0.001	1

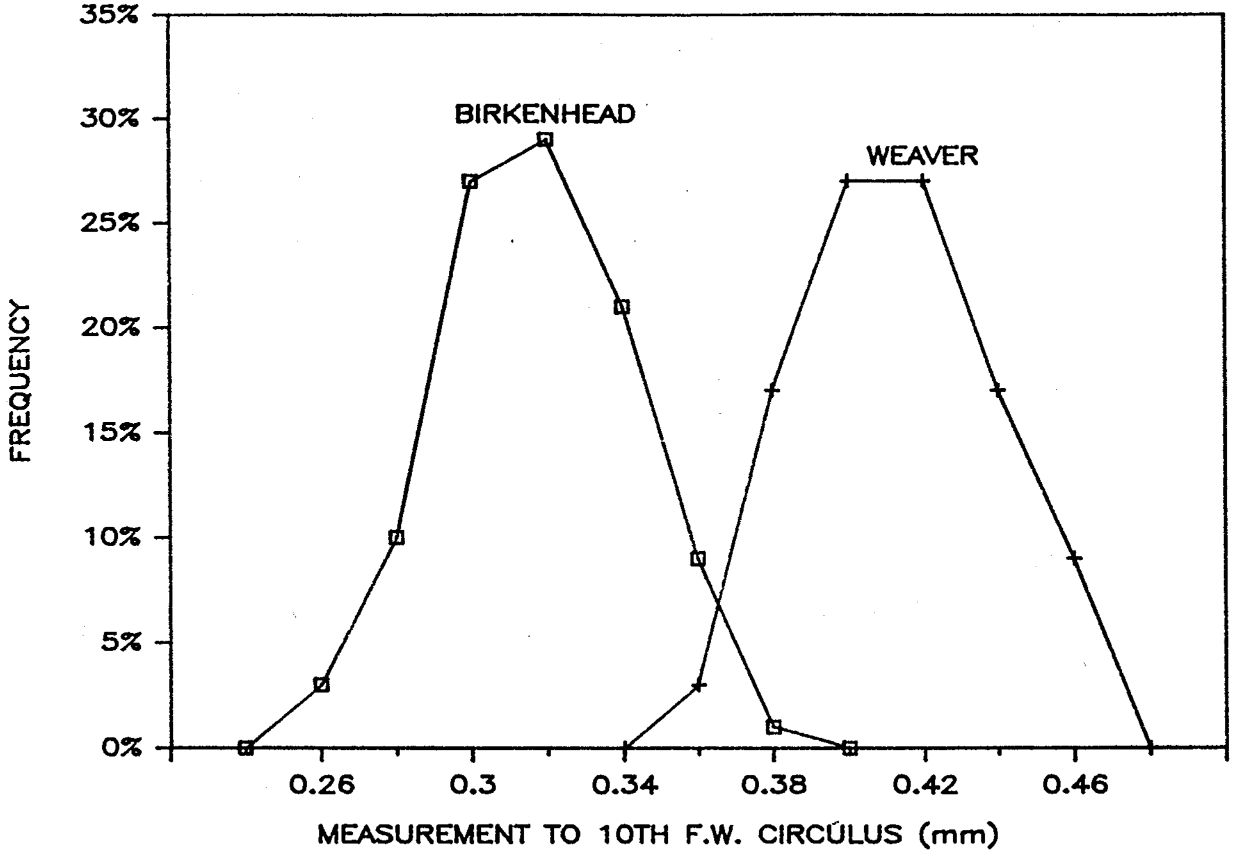

Figure 4: Frequency distribution for measurement to the tenth freshwater circulus for 1973 Birkenhead River and Weaver Creek age 4_2 adult sockeye.

The growth differences between the two stocks were very apparent in the measurement from the focus to the freshwater annulus data. This was the most representative measure of growth in the first year in freshwater. However, I needed to establish a linkage between circuli counts and growth for the productivity differences between the two lakes and concluded that the ANOVA for effect of stock on the circuli data was necessary (Table 3). The ANOVA of the effect of stock on the measurement from the focus to the tenth freshwater circulus demonstrates that the spacing data from a consistent zone of the scale showed a strong effect of stock.

Birkenhead sockeye usually have more spring growth circuli than Weaver fish. However, analysis of spring growth circuli was difficult as not all fish showed spring growth and the data were not normally distributed. Investigation of spring growth was not a goal of this study.

Before the maximum likelihood procedure was used to estimate the proportion of adult returns of Birkenhead sockeye which reared in Lillooet Lake, I needed to determine if this information could be established from the circuli data. The frequency distributions of circuli counts of Birkenhead sockeye were strongly bimodal on some years, however this was not always the case. Circuli count frequency distributions for Weaver sockeye were never bimodal. Frequency distributions of circuli counts to the freshwater annulus for 1968 age 4_2 Birkenhead and Weaver adults and for smolts caught at the outlet of Lillooet Lake in 1966 demonstrate the effects of rearing lake on scale growth (Figure 5). The smolts showed a strong mode at 11 circuli. The Birkenhead adults also showed a mode at 11 - 12 circuli and a second, slightly stronger mode at 17 circuli. The higher mode was more similar to the circuli

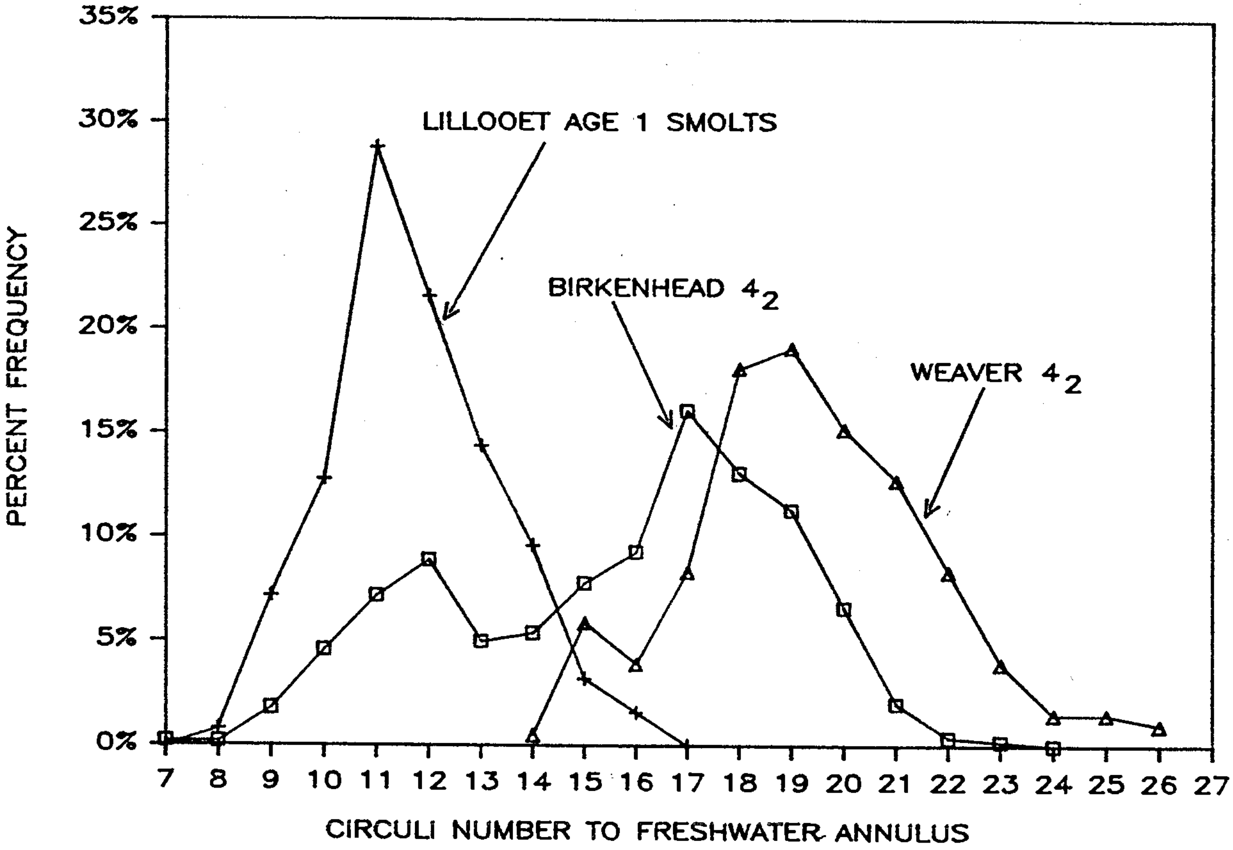

Figure 5: Frequency distributions of circuli number to the freshwater annulus for 1966 Lillooet lake age 1 smolts, 1968 Birkenhead River and Weaver Creek age 4_2 adults. The left mode of the Birkenhead River age 4_2 frequency distribution represents sockeye which reared in Lillooet Lake while the right mode represents fish which reared in Harrison Lake. Weaver Creek fish rear entirely in Harrison Lake.

count frequency distribution for Weaver Creek sockeye, which rear entirely in Harrison Lake. I conclude that the lower circuli count mode of the age 4_2 adult Birkenhead sockeye represents fish which reared in Lillooet Lake (Figure 6). The upper mode represents fish which reared in Harrison Lake.

Plots of the spacing between circuli versus circulus number or position on the scale for Birkenhead and Weaver age 4_2 adult sockeye for the 1978 return year are shown in Figures 7 and 8. Typically, circuli spacing decreases as spacing position increases in distance from the focus of the scale. These distributions demonstrate checks, annuli and spring growth on the scale. Birkenhead sockeye on average showed a check at the fifth circuli, but no indication of a similar marker was apparent in the circuli spacing of Weaver sockeye. The position of this check on Birkenhead sockeye scales varied between the third and tenth circulus

c) Adult Return Information:

i) Growth in Lillooet Lake vs. density. Annual summaries of total return for Birkenhead sockeye, Lillooet Lake mode circuli data, and the results of the maximum likelihood analysis are shown in Table 4. Using these data, I investigated the effect of density on growth of sockeye which rear in Lillooet Lake. First-year freshwater growth of Lillooet Lake sockeye in year t+1, as measured by circuli number to the freshwater annulus (Y) was inversely related to estimated adult returns of the same brood year (return years t+3 to t+6) of Birkenhead sockeye produced in Lillooet Lake (X). The abundance of adult return information was used as an index of brood year fry abundance rearing in Lillooet Lake. The relationship appeared to be fitted equally well by either a

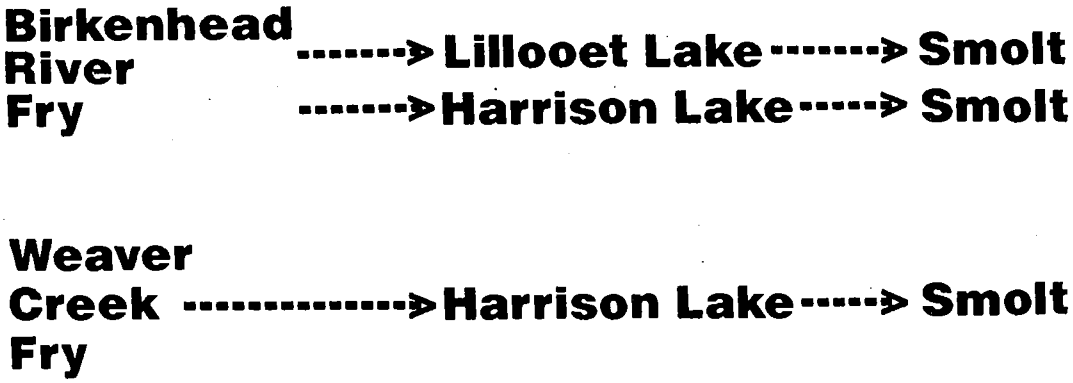

Figure 6: Schematic diagram of the freshwater life-history types in the Harrison-Lillooet system.

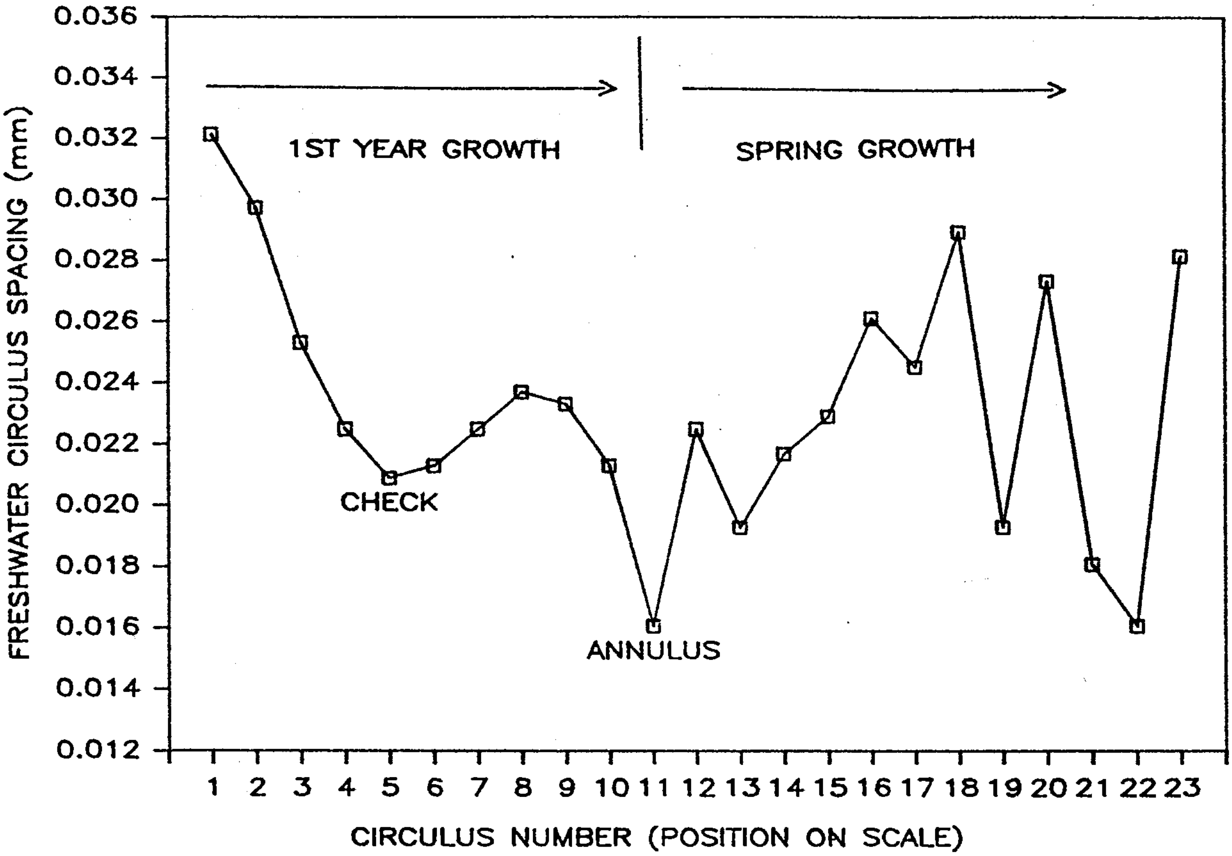

Figure 7: Plot of mean freshwater circulus spacing (mm) against circulus number or position on the scale for 1978 Birkenhead River age 4_2 adult sockeye. n = 100.

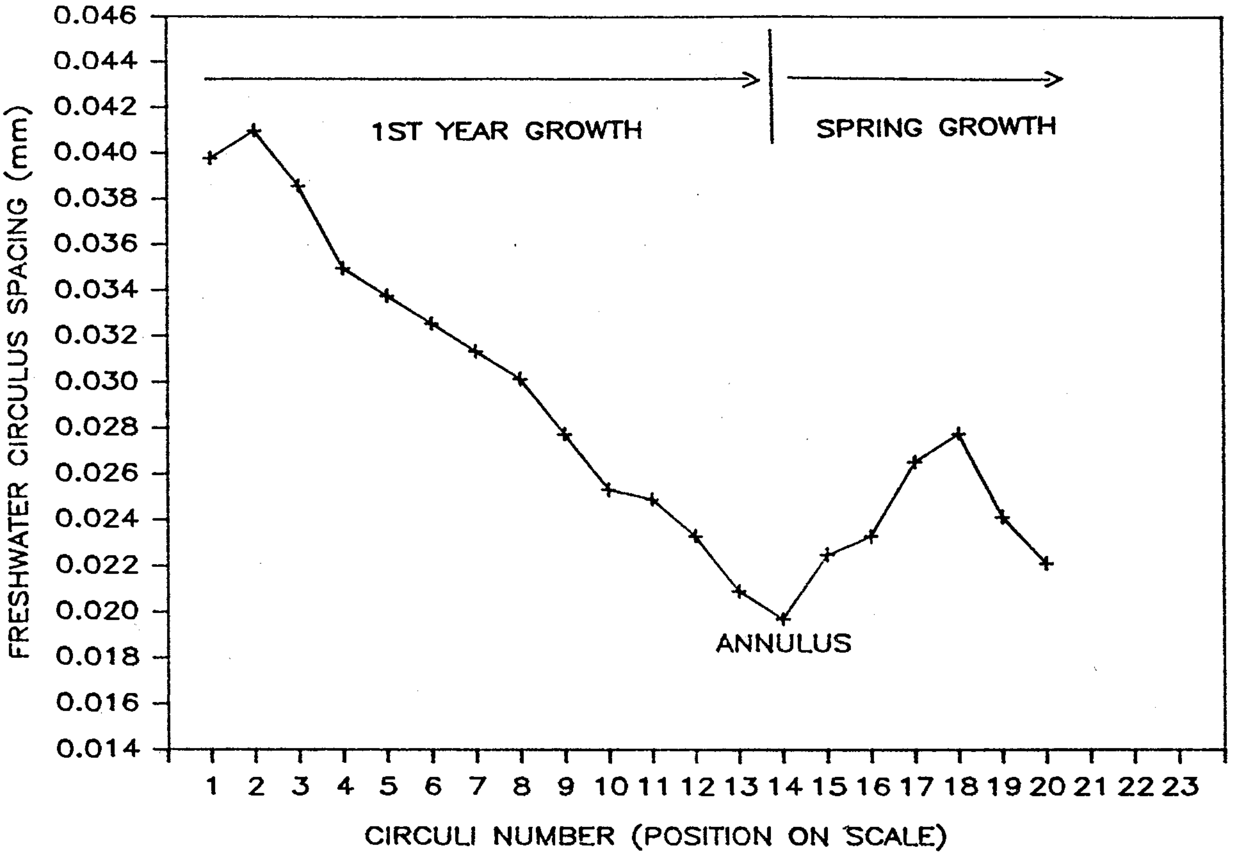

Figure 8: Plot of mean freshwater circulus spacing (mm) against circulus number or position on the scale for 1978 Weaver Creek age 4_2 adult sockeye. n = 100.

Table 4: Birkenhead sockeye adult returns and estimates of the fractions which reared in Lillooet Lake, densities and circuli counts.

Brood Year	Birkenhead Total Return (a)	Percent Lillooet Reared (b)	Lillooet Reared Total Return (c)	Lillooet Sockeye Density (d)	Lillooet WSG CC Mode (e)	Lillooet WOSG CC Mode (f)
1951	216,719	30%	65,016	1858	14.0	11.2
1952	244,678	45%	110,839	3167	13.0	11.8
1953	156,143	80%	125,227	3578	13.0	12.4
1954	175,704	60%	105,422	3012	14.0	12.4
1955	280,383	81%	228,232	6521	12.0	12.0
1956	279,109	83%	231,940	6627	14.0	12.2
1957	75,666	71%	53,950	1541	14.0	12.4
1958	130,934	51%	66,514	1900	16.0	12.8
1959	268,572	67%	178,869	5111	12.0	11.1
1960	168,936	69%	115,721	3306	14.0	13.2
1961	131,851	54%	70,936	2027	16.0	13.6
1962	103,783	42%	43,381	1239	16.0	15.0
1963	455,775	25%	115,311	3295	16.0	13.6
1964	365,993	31%	114,556	3273	13.5	11.2
1965	163,901	44%	72,116	2060	16.5	15.0
1966	317,710	24%	76,250	2179	16.0	12.9
1967	492,216	31%	155,048	4430	16.0	13.0
1968	285,925	41%	118,373	3382	16.0	13.7
1969	791,710	29%	225,637	6447	13.0	10.1
1970	736,305	32%	237,827	6795	12.5	10.3
1971	371,401	24%	90,622	2589	15.0	12.9
1972	515,310	26%	132,435	3784	13.5	12.7
1973	328,391	14%	46,632	1332	14.5	13.9
1974	918,986	9%	82,709	2363	13.5	12.5
1975	127,367	20%	25,983	742	16.0	13.8
1976	632,531	18%	113,856	3253	11.5	10.0
1977	460,202	39%	177,638	5075	14.5	11.9
1978	776,704	12%	90,098	2574	14.0	10.7
1979	511,682	23%	118,710	3392	16.5	13.2
1980	169,738	32%	53,807	1537	17.0	15.7
1981	143,790	20%	28,327	809	18.0	14.3
1982	1,736,177	9%	156,256	4464	17.0	12.0
MEAN:	391,700	29	113,400	3200	14.6	12.6

(a) Abundance of adult returns estimated according to Henry (1961).
(b) Contribution of Lillooet Lake to the total return of Birkenhead River sockeye estimated by maximum likelihood method according to Macdonald and Green (1985).
(c) Total Birkenhead River adult returns estimated to have reared in Lillooet Lake. (Column (2) X Column (3)).
(d) Density of total returns reared in Lillooet Lake (fish / km^2).
(e) Circuli number (CC) to the freshwater annulus.
(f) Circuli number (CC) to the end of the freshwater growth.

multiplicative or reciprocal model. The reciprocal model is shown in Figure 9 ($r = -0.584$, $P < 0.001$)[1]. I could not reject the working hypothesis that scale growth of sockeye in Lillooet Lake is density-dependent. Growth declines rapidly from 13.8 circuli to 10.9 circuli as abundance or density increases from 25,000 to 260,000 returning adults (700 to 7,400 returning sockeye / km^2 lake surface area).

ii) Proportion of the Birkenhead population rearing in Lillooet Lake vs. density. The strong effect of density on sockeye growth in Lillooet Lake may be a mechanism triggering an early emigration of fry from this lake to Harrison Lake. If this were the case, the proportion of Birkenhead sockeye fry which had reared in Lillooet lake in year t+1 should be related to the total abundance of adult returns of Birkenhead sockeye of the same brood year, (return years t+3 to t+6, within that brood). The adult returns were used as an index of the total brood year fry abundance entering in Lillooet Lake. The arcsine percentage of Birkenhead sockeye fry reared in Lillooet Lake (Y), was inversely related to the total adult return of Birkenhead sockeye of the same brood year (X) (Figure 10). The relationship was clearly non-linear and the reciprocal model most accurately fit the data ($r = -0.758$, $P < 0.001$). Lillooet Lake contribution decreases rapidly as total run size increases: I cannot reject my working hypothesis that the proportion of adult returns produced in Lillooet Lake is related to the total adult return of Birkenhead sockeye.

The relationship shown in Figure 10 could be caused by processes other than density. I therefore plotted estimated Lillooet contribution

---

[1] The linear model parameters were estimated using the reciprocal transformation of the dependent variable (Polhemus, 1985).

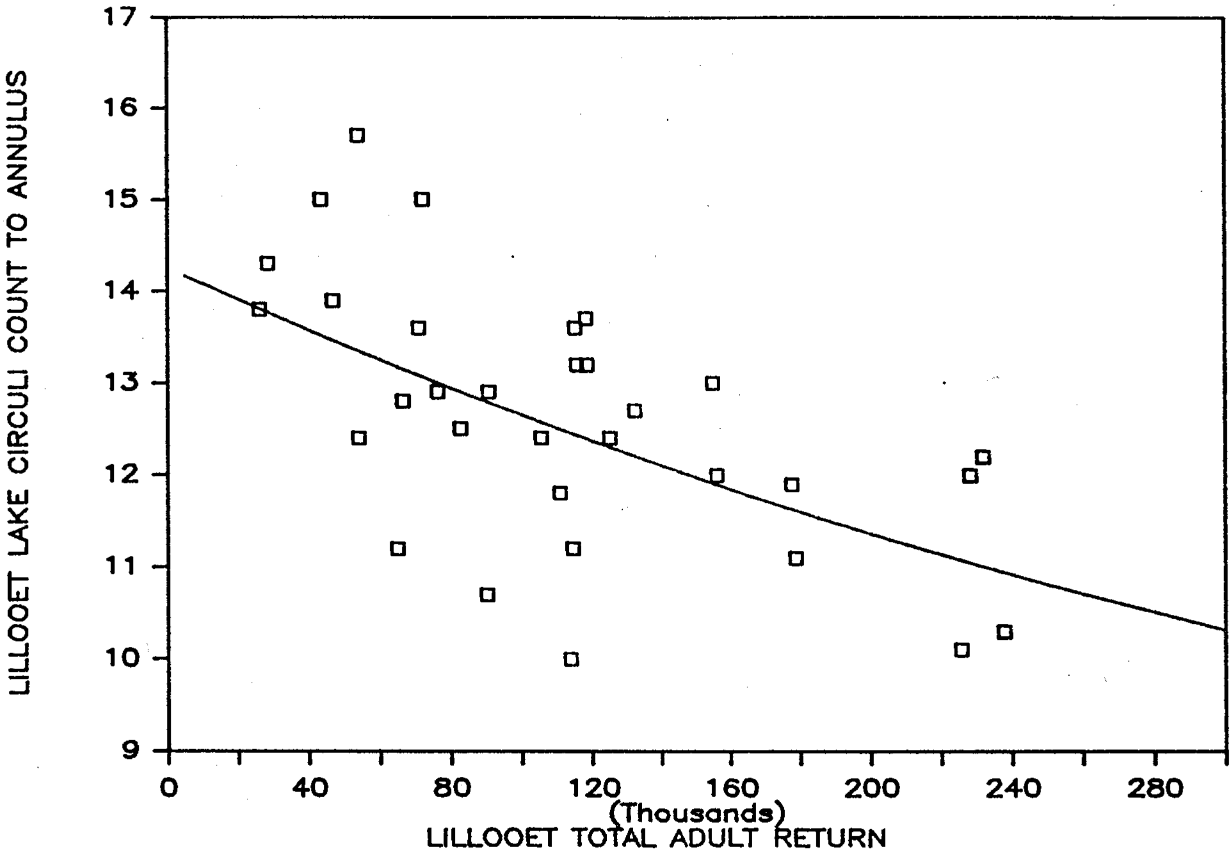

Figure 9: Relationship between freshwater scale growth of Lillooet Lake sockeye (year t+1) and estimated adult returns of Birkenhead River sockeye produced in Lillooet Lake (years t+3 to t+6). The linear model parameters were estimated using the reciprocal transformation of the dependent variable, $Y^{-1} = a + bX$, (Polhemus, 1985).

$Y = (0.070 + 8.98 \times 10^{-8} X)^{-1}$ $r = {}^{-}0.5843$, $P < 0.001$, d.f. = 31.

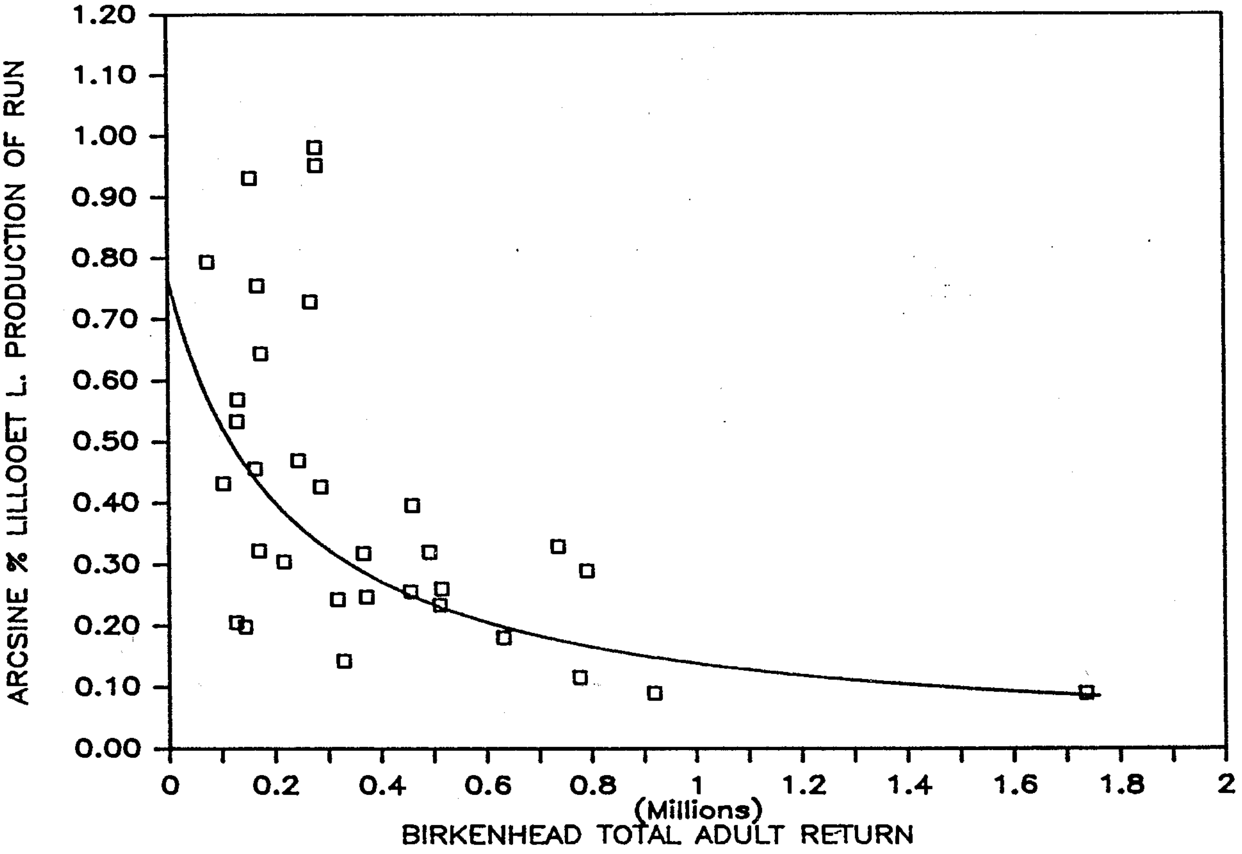

Figure 10: Relationship between the arcsine transformation of the percentage Birkenhead sockeye reared in Lillooet lake (year t+1) and the total adult return of Birkenhead sockeye (years t+3 to t+6). The linear model parameters were estimated using the reciprocal transformation of the dependent variable $Y^{-1} = a + bX$, (Polhemus, 1985).

$Y = (1.30 + 5.97 \times 10^{-8}X)^{-1}$ $r = ^{-}0.7580$, $P < 0.001$, d.f. = 31.

by brood year to investigate possible time trends. A time-trend towards decreased Lillooet Lake contribution to the production of total adult returns of Birkenhead sockeye was apparent (Figure 11). The trend was still evident after the Birkenhead sockeye adult returns were stratified into low, medium and high abundance. There was no relationship between percent Lillooet Lake contribution to the abundance of adult returns of Birkenhead (Y), and Lillooet Lake scale growth as measured by number of circuli to the annulus ($r = -0.020$).

iii) Growth in Harrison Lake vs. density. Annual estimates of the total returns of Weaver Creek and Birkenhead River sockeye which had reared in Harrison lake, were summed to obtain an index of total Harrison Lake juvenile abundance (Table 5). These annual estimates of the abundance of adult returns produced by Harrison Lake sockeye were examined to determine the degree of density-dependent growth in Harrison Lake. Summaries of Harrison Lake circuli count data for Birkenhead and Weaver sockeye are shown in Table 6. First-year freshwater growth of Harrison Lake sockeye in year t+1, as measured by circuli number to the annulus of Weaver Creek sockeye (Y) was negatively correlated with the combined abundance of adult returns (years t+3 to t+6) of Weaver and Birkenhead sockeye estimated to have reared in Harrison Lake of the same brood year (X), (reciprocal model, $r = -0.796$, $P < 0.001$, Figure 12). The abundance of adult returns were used as an index of brood year fry abundance rearing in Harrison Lake. Growth declines from 19.7 circuli to 13.8 circuli as the abundance of adult returns increases from 30,000 to 2,600,000 (140 - 11,900 sockeye / km^2 lake surface area). I could not reject the working hypothesis that scale growth of sockeye in Harrison Lake is density-dependent.

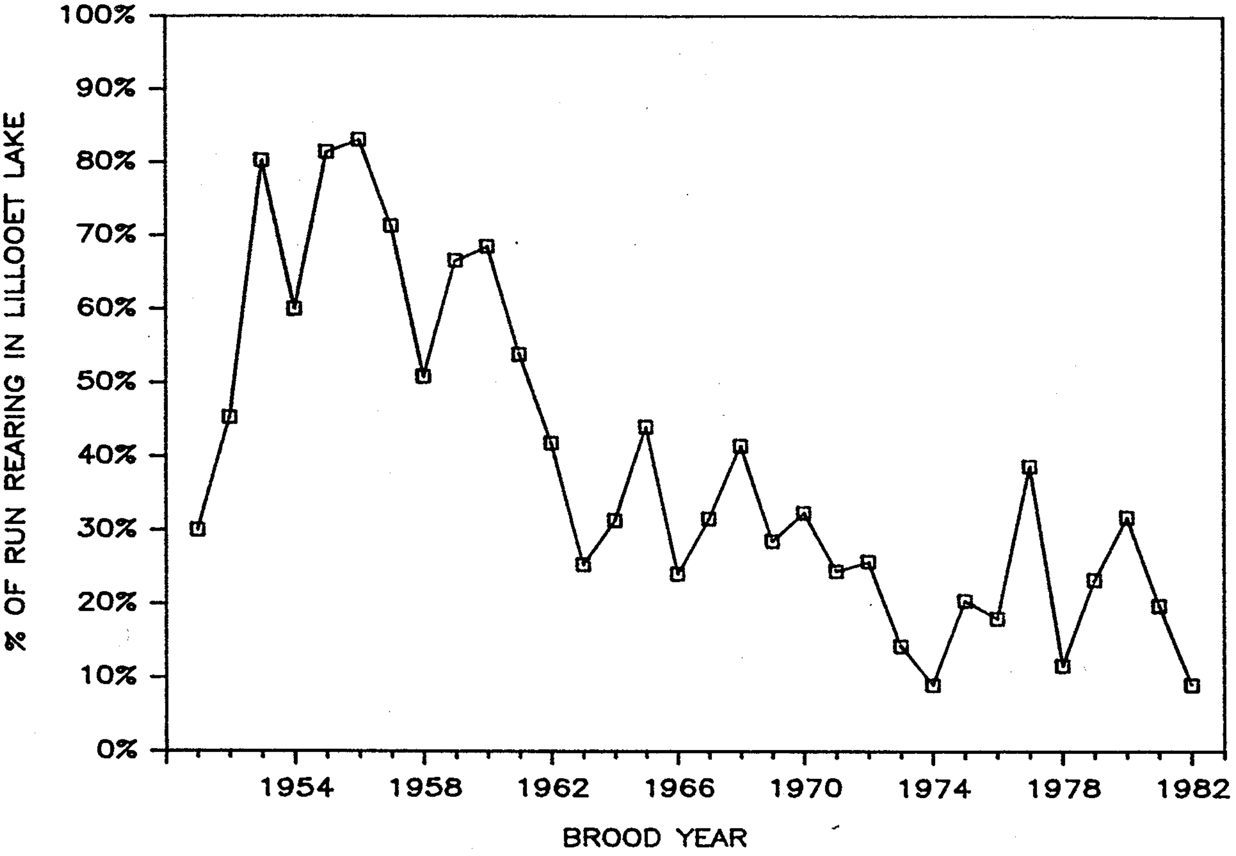

Figure 11: Time trend of the percentage of Birkenhead River sockeye recruitment rearing in Lillooet Lake.

Table 5: Harrison Lake adult return data.

Brood Year	Weaver Total Return (a)	Harrison Rear. Birkenhead (b)	Combined Harrison Total Return (c)	Harrison Sockeye Density (d)
1951	117,511	151,703	269,214	1235
1952	11,006	133,839	144,845	664
1953	218,207	30,916	249,123	1143
1954	235,297	70,282	305,579	1402
1955	72,848	52,151	124,999	573
1956	21,608	47,169	68,777	315
1957	8,842	21,716	30,558	140
1958	31,072	64,420	95,492	438
1959	39,259	89,703	128,962	592
1960	4,623	53,215	57,838	265
1961	57,809	60,915	118,724	545
1962	47,938	60,402	108,340	497
1963	166,479	340,464	506,943	2325
1964	25,040	251,437	276,477	1268
1965	205,659	91,785	297,444	1364
1966	76,161	241,460	317,621	1457
1967	88,405	337,168	425,573	1952
1968	155,396	167,552	322,948	1481
1969	412,913	566,073	978,986	4491
1970	384,038	498,478	882,516	4048
1971	155,255	280,779	436,034	2000
1972	342,374	382,875	725,249	3327
1973	355,612	281,759	637,371	2924
1974	276,337	836,277	1,112,614	5104
1975	145,953	101,384	247,337	1135
1976	304,515	518,675	823,190	3776
1977	234,642	282,564	517,206	2373
1978	1,123,838	686,606	1,810,444	8305
1979	175,741	392,972	568,713	2609
1980	401,285	115,931	517,216	2373
1981	290,888	115,463	406,351	1864
1982	1,012,233	1,579,921	2,592,154	11891
MEAN:	225,000	278,300	503,300	2309

(a) Abundance of adult returns estimated according to Henry (1961).

(b) Contribution of Harrison Lake to the total return of Birkenhead River sockeye estimated by maximum likelihood method according to Macdonald and Green (1985).

(c) Total Harrison Lake contribution to total adult returns of Weaver Creek and Birkenhead sockeye.

(d) Density of total returns reared in Harrison Lake (fish / km^2).

Table 6: Mean circuli counts for Birkenhead River age 4_2 sockeye reared in Harrison Lake and Weaver Creek age 4_2 sockeye. WOSGCC: Circuli number to the freshwater annulus. WSGCC: Circuli number to the end of the freshwater growth.

Brood Year	Harrison WSG CC Mode	Harrison WOSG CC Mode	Weaver WSG CC	Weaver WOSG CC
1951	19.0	18.2	21.5	21.1
1952	17.5	16.9	21.9	21.5
1953	17.0	16.7	19.3	18.9
1954	17.0	14.1	18.9	18.7
1955	15.3	15.3	19.9	18.7
1956	19.0	15.8	20.6	19.4
1957	18.0	17.2	19.7	18.3
1958	19.0	15.7	21.0	19.0
1959	17.0	14.9	20.4	19.6
1960	19.0	16.7	22.6	20.3
1961	21.5	17.2	22.7	19.8
1962	20.5	18.1	21.4	20.3
1963	18.5	15.1	20.5	18.8
1964	19.5	17.0	21.0	19.3
1965	21.0	19.0	20.8	18.5
1966	19.5	16.8	19.5	18.1
1967	21.0	19.2	21.5	19.6
1968	21.0	18.1	21.3	19.6
1969	18.5	15.4	19.1	16.2
1970	18.0	15.4	18.2	17.3
1971	21.0	18.4	19.5	18.8
1972	17.0	14.4	18.6	16.4
1973	18.5	15.9	20.0	17.6
1974	17.0	13.7	17.0	15.8
1975	21.0	18.1	21.5	20.1
1976	18.5	14.1	17.3	16.0
1977	19.0	16.0	18.4	15.6
1978	18.0	15.3	16.5	14.5
1979	20.5	17.0	20.8	18.9
1980	21.5	18.0	21.8	19.0
1981	22.0	16.8	21.1	18.3
1982	20.0	15.0	18.8	15.4
MEAN:	19.1	16.4	20.1	18.4

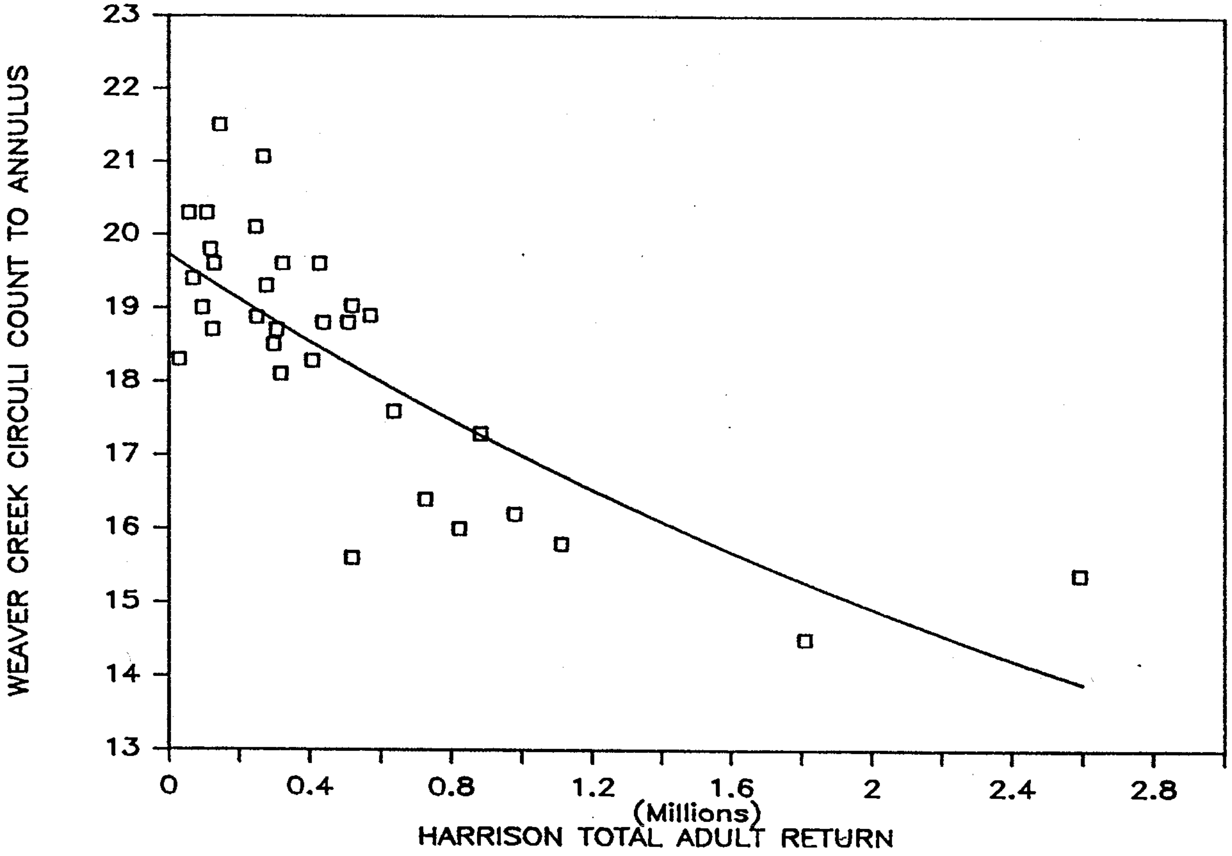

Figure 12: Relationship between freshwater scale growth of Harrison Lake sockeye, as measured by circuli number to the annulus of Weaver Creek sockeye (year t+1) and estimated combined adult returns of Weaver and Birkenhead sockeye produced in Harrison Lake (years t+3 to t+6). The linear model parameters were estimated using the reciprocal transformation of the dependent variable, $Y^{-1} = a + bX$, (Polhemus, 1985).

$Y = (0.051 + 8.98 \times 10^{-9} X)^{-1}$ $r = {}^{-}0.7959$, $P < 0.001$, d.f. = 31

Much of the variability in scale growth of Weaver sockeye, however, could be explained by the abundance of Weaver adult returns alone (reciprocal model, relationship not shown, $r = -0.777$, $P < 0.001$). Also, the apparent effect of density on first-year freshwater growth of Harrison-reared Birkenhead sockeye appeared to be more variable than was evident for Weaver sockeye. The relationship between Harrison Birkenhead sockeye WOSG circuli versus Harrison adult abundance was non-linear and was best fitted by the reciprocal model, $r = -0.419$, $P = 0.017$. The effect that the fry of one population may have on the growth of the other population in Harrison Lake is unclear; however, first-year scale growth of Weaver sockeye was correlated with first-year scale growth of Birkenhead sockeye (Figure 13), suggesting that some mechanism may be operating. However, incremental growth was not equal. Birkenhead (Harrison only) sockeye scale growth to the annulus was similar to Weaver sockeye at the lower end of the range (14 circuli) but the slope of the regression ($b=0.519$) showed Birkenhead sockeye added growth at one-half the rate of Weaver sockeye.

iv) Comparison between lakes of Birkenhead sockeye growth vs total sockeye density (adults/km^2 lake rearing area). The magnitude of the effects of density on scale growth differed between the two lakes. Analysis of covariance on the response of Birkenhead sockeye scale growth (number of circuli to annulus) to lake density of sockeye return showed a main effect of lake on the relationship (d.f. = 61, $F = 16.75$, $P < 0.001$)[2]. Harrison lake sockeye showed more scale growth at a given density than Lillooet Lake sockeye (Figure 14).

---

[2] The analysis of covariance was estimated after first taking the reciprocal transformation of the dependent variable.

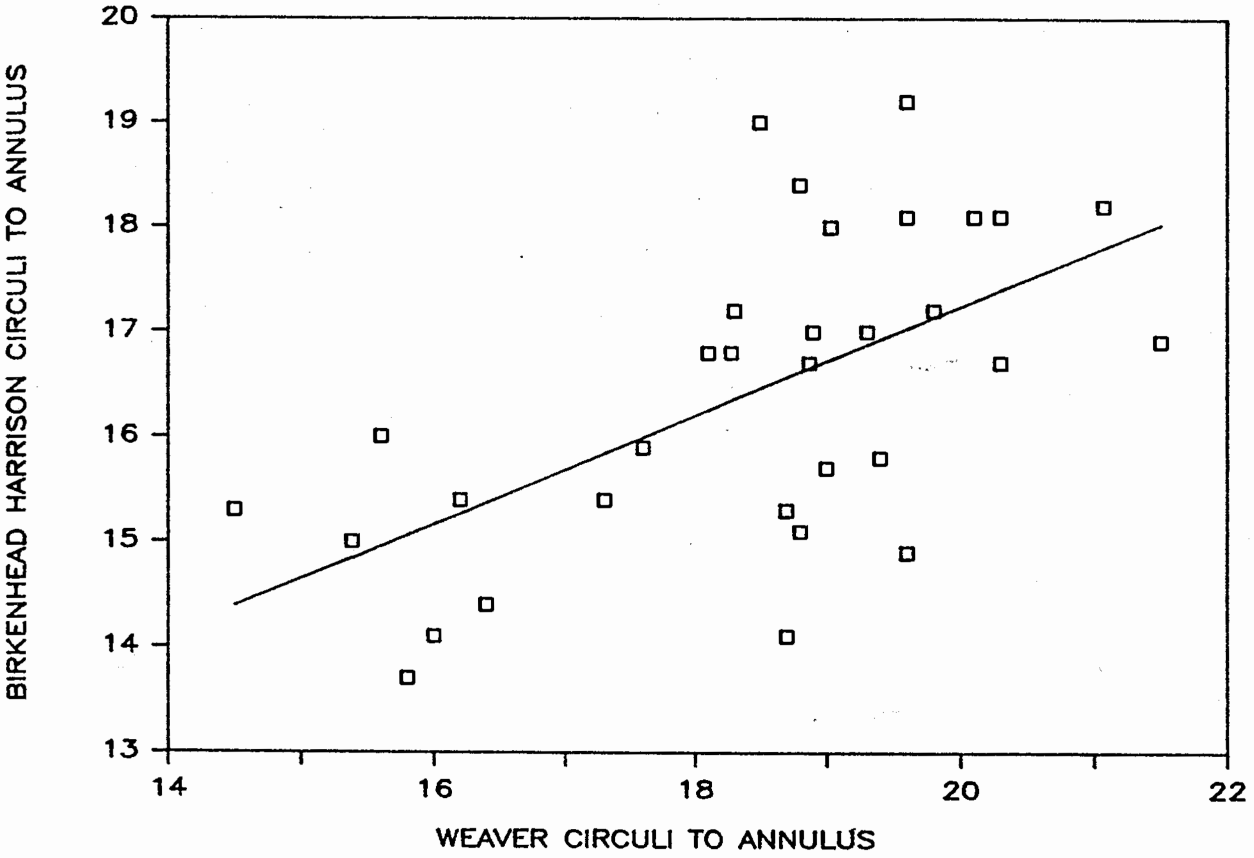

Figure 13: Relationship between Birkenhead age 4_2 adult sockeye Harrison mode circuli count to the annulus and mean Weaver sockeye circuli count to annulus.

$Y = 6.86 + 0.519 X$ $r = 0.5992$, $P < 0.001$, d.f. = 31

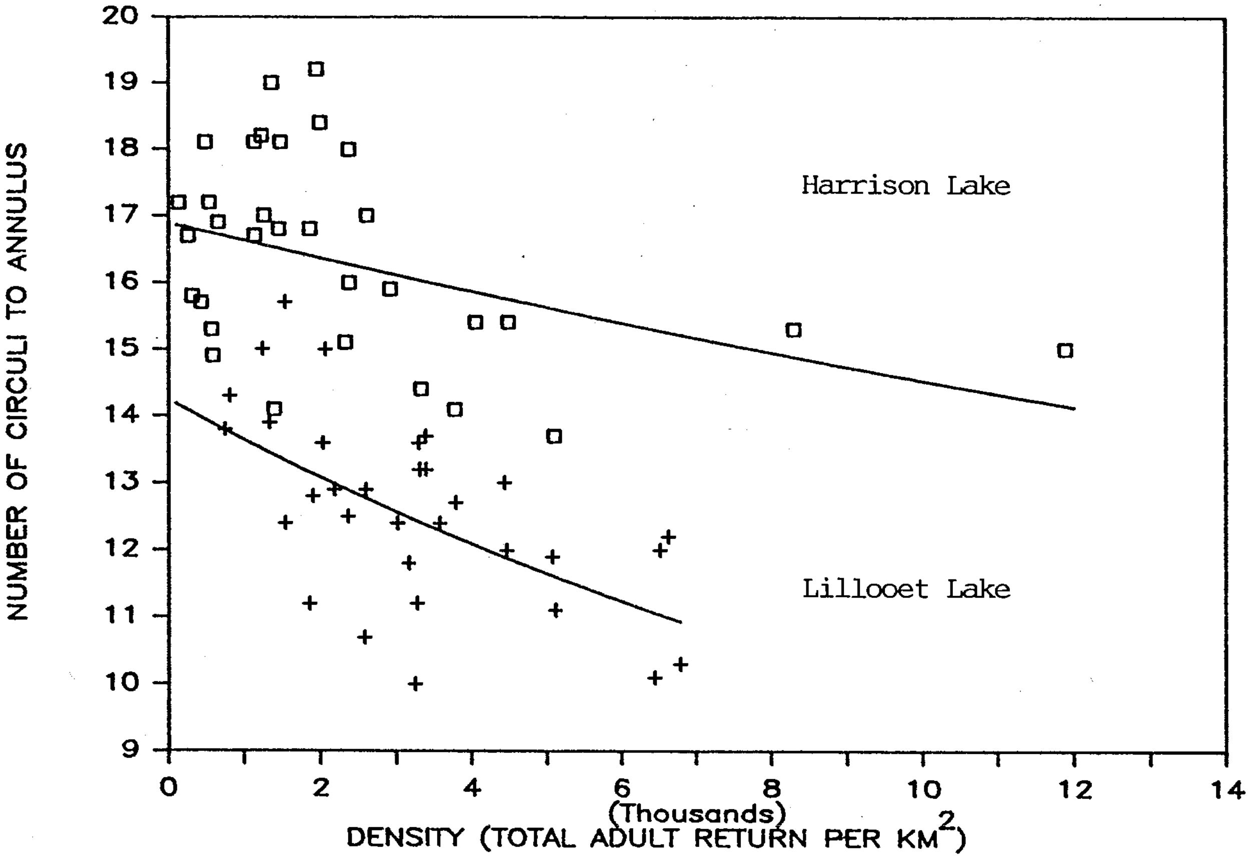

Figure 14: Comparison between Lillooet Lake and Harrison Lake in the relationship between freshwater sockeye scale growth to the first annulus (year t+1) and estimated density of adult returns produced by each lake per km^2 lake area (year t+3 to t+6). The linear model parameters were estimated using the reciprocal transformation of the dependent variable, $Y^{-1} = a + bX$, (Polhemus, 1985).

Lillooet Lake:
$Y_1 = (0.070 + 3.14 \times 10^{-6} X_1)^{-1}$ $r = -0.5843$, $P < 0.001$, d.f. = 31
Y_1 = freshwater scale growth of Lillooet Lake sockeye
X_1 = estimated density of adult returns of Birkenhead River sockeye produced in Lillooet Lake.

Harrison Lake:
$Y_2 = (0.059 + 9.61 \times 10^{-7} X_2)^{-1}$ $r = -0.4187$, $P = 0.017$, d.f. = 31
Y_2 = freshwater scale growth of Birkenhead sockeye in Harrison Lake.
X_2 = estimated density of combined adult returns of Birkenhead and Weaver sockeye produced in Harrison Lake.

The results and conclusions of this chapter are summarized in Table 7.

Table 7: Summary of working and null hypotheses tested in Chapter I together with results.

H: Freshwater scale growth of juvenile sockeye in year t+1 for each lake is correlated with total abundance of adult returns of that brood year (years t+3 to t+6). Sockeye growth is density dependent.

H_0: There is no relationship between freshwater scale growth and abundance of adult returns.

Results: First-year freshwater growth of Lillooet Lake sockeye, as measured by circuli number to the freshwater annulus (Y) is inversely related to estimated adult returns of Birkenhead sockeye produced in Lillooet Lake (X), (reciprocal model, $r = -0.758$, $P < 0.001$, Figure 9). Reject H_0.

Results: First-year freshwater growth of Harrison Lake sockeye, as measured by circuli number to the annulus of Weaver Creek sockeye (Y) is negatively correlated with combined adult returns of Weaver and Birkenhead sockeye estimated to have reared in Harrison Lake (X), (reciprocal model, $r = -0.796$, $P < 0.001$ Figure 12). Reject H_0.

H: The proportion of the Birkenhead sockeye population which rears in Lillooet lake in year t+1 is correlated with total adult returns of Birkenhead sockeye of that brood year (years t+3 to t+6).

H_0: There is no relationship between the proportion of the Birkenhead population which rears in Lillooet Lake and total adult return of Birkenhead sockeye.

Results: The percentage of adult returns of Birkenhead sockeye produced from Lillooet Lake (Y), was inversely related to the total adult returns of Birkenhead sockeye (X) (reciprocal model $r = -0.758$, $P < 0.001$, Figure 10). Reject H_0.

H: Environment is responsible for differences in freshwater growth observed between the study populations.

H_0: Environment is not responsible for differences in freshwater growth observed between the study populations.

Evidence: 1) Limnological information indicates that Lillooet Lake is less productive than Harrison Lake.

2) Environment seems to be responsible for a wide range of freshwater growth within the Birkenhead sockeye population, as evidenced by the bimodal circuli frequency distributions.

3) ANCOVA on the response of scale growth (number of circuli to annulus) on the covariate of lake density of sockeye return showed a main effect of lake. Harrison lake sockeye showed more scale growth at a given density than Lillooet Lake sockeye.

DISCUSSION

The effect of environment on growth of sockeye has been documented in many studies. Fingerling density, zooplankton abundance and lake temperature either singly or together affect sockeye growth in lakes (Goodlad et al., 1974; Hyatt and Stockner, 1985). In the present study, the main hypothesis was that environment is responsible for differences in freshwater growth observed between the study populations. Secondly, I hypothesised that sockeye growth is affected by density of fingerlings in each lake which also affects the proportion of fingerlings which remain in Lillooet lake.

The limnological data indicate that conditions for growth are less suitable for Birkenhead than for Weaver sockeye during the early stages of lake residence. Birkenhead fry spend a portion of their early life in Lillooet Lake, if only during passage to Harrison Lake. Lower maximum summer temperatures in Lillooet Lake result in more rapid mixing and cooling to homothermal fall and winter temperatures (Goodlad et al. 1974). This would result in Lillooet Lake having a shorter growing season than Harrison Lake. Also low light penetration and high flushing rates probably contribute to lower productivity and subsequent growth of sockeye. While zooplankton biomass is lower in Lillooet Lake, this statistic is not a reliable measure of differences in zooplankton productivity between the two lakes because predation and recruitment of zooplankton is not necessarily equal in the two lakes (Wetzel, 1977). Also, no information on zooplankton size distribution is available with which to determine the value of the zooplankton to sockeye.

Yearling smolts caught at the outlet of Lillooet Lake had a frequency distribution of freshwater circuli number which was nearly identical to the lower mode of the circuli frequency distributions of returning Birkenhead age 4_2 adults (Figure 5). The lower circuli count mode of the age 4_2 adult Birkenhead sockeye represents fish which have reared in Lillooet Lake. The upper mode of the circuli frequency distributions of returning Birkenhead age 4_2 adults represents fish which have reared in Harrison Lake. The differences in growth are clearly linked to the Birkenhead fingerlings rearing in the different lakes.

Environment is the most tenable cause of the inter-lake variability in freshwater growth of Birkenhead sockeye. A genetic cause of this variability is unnecessary to postulate. First, it is clear the two growth modes are formed in separate lakes. For a genetic theory to be true, there would have to be sub-populations within the Birkenhead stock which have genetically different freshwater growth rates and which rear in different lakes. Maintenance of genetic integrity of these sub-populations would require assortative mating on the spawning grounds. Spawning ground scales have been collected by time period and area within the Birkenhead population (I.P.S.F.C. archives). There was no evidence that circuli count distributions varied during the course of spawning or between sub-areas on the spawning grounds. My conclusion from the scale growth data and limnological data is that the environment is responsible for the wide range in freshwater growth within the Birkenhead sockeye population.

The comparison of frequency distributions of circuli number to the freshwater annulus of smolts with those of age 4_2 adults indicates that some Birkenhead sockeye rear entirely in Lillooet Lake while others rear partially in Lillooet Lake and subsequently in Harrison Lake. This second group probably includes a range of growth patterns relating to the period in which the individuals entered Harrison Lake. I originally believed that the pre-annulus check observed on Birkenhead sockeye scales was formed as a result of growth disruption associated with migration into Harrison Lake during the early rearing period. The position of this check varies between the third and tenth circulus indicating that a migration may either occur during a protracted growth period or at the same time over a range of sizes. However, some fish which apparently remained in Lillooet Lake had the check. If the check is formed in both lakes, it may be the result of physiological or environmental stress. Ball (1969) showed that circuli deposition was affected by hormones. Boyce (1985) found that checks could be formed on scales of steelhead (Salmo gairdneri) by simulating seasonally elevated water temperature during summer (12° to 24° to 12°C) even though fish were fed to satiation. Such wide shifts in temperature are probably unlikely in Lillooet or Harrison Lakes. However in Lake Washington, fall turnover may be responsible for checks in the freshwater zone of scales of sockeye which rear in that lake (Woodey, pers. comm.). Bilton and Robins (1971) found that variation in feeding level influenced the formation of checks.

Weaver sockeye had greater first-year scale growth (higher circuli counts and circulus spacing) than Birkenhead fish. In juvenile salmonids, scale radius and body length are highly correlated (Clutter and Whitesel, 1956; Bilton, 1974; Boyce, 1985). Weaver sockeye show greater scale radius growth to the freshwater annulus than do Birkenhead sockeye. The results are consistent with those of Gilbert (1913; 1914 and 1925) and Schaefer (1951). Therefore, I can conclude that Weaver sockeye have greater first-year freshwater growth than Birkenhead sockeye. This was the case even for the 1978 return of age 4_2 adults when most of the Birkenhead adult return was produced from Harrison Lake (Table 6).

By using scale measurements to test for relative differences in growth between the two stocks, I assume that scale measurement is equally proportional to length in the two populations. Bradford (1985) examined growth of daily growth rings on otoliths and showed that changes in fish growth rate are not always recorded on the otolith. Bradford concluded that this "uncoupling" of growth was not a concern in the investigation of growth over longer time periods. Uncoupling of fish and otolith growth have also been shown by Campana and Neilson (1985) and is referred to as false Lee's phenomenon or back-calculation error (Smale and Taylor, 1987). Bilton (1974) and Boyce (1985) found that growth also affected scale - body length relationships.

I also assume that the annulus is formed at the same time in the two populations. Cooper (1951) showed that the time of annulus formation can vary by up to one month between years within local populations. I have not looked for possible differences in time of annulus formation between the two populations. Considering the magnitude of the differences in scale measurement (37%) between the two populations, this assumption is probably valid. However, the possible effect of growth rate on body length - scale relationships may bias my conclusions and I examine this concern in the next chapter.

True Lee's phenomenon is the apparent change of length at age with increasing age of capture as a result of size selective mortality or sampling (Ricker, 1969; Smale and Taylor, 1987). Sampling of adult sockeye for scales on the spawning grounds may be size selective; however freshwater scale measurements are not correlated with sockeye size at return (I.P.S.F.C. unpublished data). Therefore, size-selective sampling is an unlikely bias in the study of freshwater growth parameters. Differential size-selective mortality may occur between the stocks, particularly as juvenile Weaver sockeye would be much larger than Birkenhead fish. Although a much more detailed review of this phenomenon is necessary, the prevailing view is that for fish of the same age, smaller sockeye have higher mortality rates than larger sockeye (Healey, 1982; Hyatt and Stockner, 1985; West and Larkin, 1987). If this were the case, one would expect that the smaller fingerlings in the Birkenhead sockeye population would exhibit a greater degree of size-selective mortality than those from the Weaver Creek population. This would drive the size distribution of Birkenhead sockeye (as inferred from scale data) towards that of Weaver sockeye. If size selective mortality were to exist in these populations, it has not masked the obvious differences in growth between the populations.

The percentage of adult returns of Birkenhead sockeye which reared in Lillooet Lake can also be assessed with parasite information. Bailey (Pacific Biological Station, Nanaimo, B.C., pers. comm.) found that the swim bladder nematode Philonema and plerocercoids of the gut cestode Diphyllobothrium were common in juvenile sockeye in Harrison Lake but were virtually absent in Lillooet Lake juveniles. Of the Birkenhead jacks recovered in 1985, 35% had Philonema and 49% had Diphyllobothrium. Since the probability of infection increases with time, smolts from Lillooet Lake passing through Harrison Lake would probably not acquire these parasites as readily as fry which spent an entire year in the lake. Using parasite data, Bailey estimated a minimum of 70 to 80% of the 1982 brood year of Birkenhead sockeye would have reared in Harrison Lake, compared to the scale analysis estimate of 91%. The similarity of the two estimates suggests that the maximum likelihood method of estimation of the proportion of fish rearing in Lillooet Lake is reasonable.

In my examination of the effects of density on growth, I make the assumption that adult returns are linearly related to fingerling or smolt abundance for each stock. These data were used because long-term information on the number of fry, fingerlings or smolts is unavailable. Peterman (1982) observed significant within-stock non-linear marine mortality which tended to obscure the adult-abundance-to-smolt-abundance relationship in Babine sockeye. For Fraser River sockeye, sufficient data exist only for the Chilko population. In this population, the relationship between the abundance of adults and the abundance of smolts appears to be linear (I.P.S.F.C. unpublished data). If abundance of adult returns is non-linearly related to the fingerling or smolt abundance in the Harrison system populations, density-dependent effects on growth may be over-estimated. For example, if the abundance of adult returns indicate less fingerlings than were actually there during years of high abundance, the actual relationship between freshwater growth and fingerling abundance would have less slope than would be predicted from the adult return data. In this situation, the relationships shown in Figure 14 would not be affected equally. Harrison Lake produces much greater adult returns than Lillooet Lake and Consequently may have a flatter distribution than apparent in Figure 14.

Size-selective mortality may also affect the two lake populations differentially. If smaller smolts have greater marine mortality than large smolts, the relationship between Lillooet Lake sockeye growth and abundance actual smolt circuli counts would be lower and smolt abundances would be greater, shifting the relationship in Figure 14 accordingly. In view of these possibilities, conclusions from Figure 14 are necessarily preliminary, pending further investigations.

Goodlad et al. (1974) used the number of female spawners in the brood year per hectare as a measure of sockeye density in the lake. However, the relationship between spawners and fry production is highly variable in coastal sockeye populations such as Weaver Creek and Birkenhead River because of frequent flooding during incubation. The measure of Weaver Creek effective females is biased because of steady degradation in the wild spawning ground habitat and subsequent implementation of the artificial spawning channel. Also, there is strong evidence of considerable non-linearity in the relationship between fry abundance and the abundance of brood year spawners (Foerester, 1968). Although there are estimates of Weaver Creek fry production, there are no comparable estimates for the Birkenhead River. Therefore, I could not use the number of fry as an estimate of in-lake abundance. Therefore, I considered that adult return data were probably best used in this study.

The variation in growth with changes in the environment is clearly evident in the occurrence of density-dependent growth in both lakes. The data support the hypothesis that as density of sockeye fingerlings increases, growth decreases. Hyatt and Stockner (1985) found that fish density in fertilized lakes was the single best predictor of smolt size. Goodlad et al. (1974) found similar results in studies on Cultus, Shuswap and Fraser Lakes. As fry abundance increases, growth in Lillooet Lake may deteriorate to a level where survival may be affected, if some compensating mechanism were not available. I conclude that higher levels of emigration from Lillooet Lake to Harrison Lake occur with the decreased growth brought about by increased competition in years of high Birkenhead fry output (Figure 10). The tendency toward emigration is probably hereditary, as it would be maladaptive in other populations where a downstream lake does not provide for successful rearing. Aggressive behaviour in juvenile coho salmon has been found to cause a downstream emigration of "nomads" of that species (Chapman, 1962). The Gates Creek sockeye population of the Fraser River watershed exhibit inter-lake migration, presumably to improve freshwater survival.

An alternate mechanism for the results shown in Figure 10 may be depensatory mortality (Walters and Staley, 1987), acting on fingerlings migrating from Lillooet Lake to Harrison Lake during the growing season. For example, the rate of mortality on fingerlings in the Lower Lillooet River and the north end of Harrison Lake may decrease with increased Birkenhead fry abundance, as predators become satiated. Consequently with low Birkenhead fry abundance, the proportion of fry attempting Harrison Lake rearing may be underestimated because of intense predation. Resolution of the two theories will require a field study designed to investigate the relative importance of predation rates on Birkenhead sockeye fry in Lillooet Lake versus the Lower Lillooet River and Harrison Lake.

A trend towards decreased Lillooet Lake contribution to the production of adult returns of Birkenhead sockeye over time is evident. Potential causes of this time trend are largely speculative. Adult returns of Birkenhead were higher in recent years and increased density over time may have caused the observed trend. However, the trend over time was evident even after I stratified the Birkenhead sockeye data into low, medium and high adult returns. This trend may also be caused by a change in the genetic propensity for Harrison Lake rearing in the Birkenhead stock. The random loss of genes in a population through genetic drift is unlikely to have occurred in this situation as Birkenhead sockeye spawning population levels are too high (Hedrick, 1983). However, this time trend may result from increased Birkenhead fry survival in that component of the population which has migrated to Harrison Lake.

If large fry outputs from the Birkenhead population result in reduced growth, causing an emigration from Lillooet Lake, I expected that there should be some relationship between scale growth to the annulus of Lillooet Lake reared sockeye and proportion reared in Lillooet Lake. This was not present. However, if the interlake migration response of the fry to low growth as a result of high density occurs early in the growing season, fish remaining in Lillooet Lake will have time to recover and continue their growth. Consequently a correlation need not exist between first-year scale growth and the proportion rearing in Lillooet Lake for this theory to be correct.

Density-dependent growth is also evident in Harrison Lake. However, the degree of interaction between the two stocks is uncertain. First, much of the variation in freshwater growth of Weaver sockeye in Harrison Lake could be explained by adult returns of Weaver sockeye alone. The correlation coefficient of this relationship was almost as high as in the relationship between freshwater growth of Weaver sockeye and the combined Harrison-reared adult returns. Second, the apparent effect of density on first-year freshwater growth of Harrison-reared Birkenhead sockeye appears to be more variable than evident for Weaver sockeye. Growth of Harrison-reared Birkenhead sockeye may be affected primarily by factors encountered before the fish enter Harrison Lake. However, growth of the two stocks is correlated (Figure 13) and they are probably similarly affected by environmental conditions.

I found that Birkenhead sockeye which had reared in Harrison Lake showed more growth at a given density than Lillooet Lake reared sockeye. This is consistent with the main hypothesis that environment is responsible for the differences in freshwater growth observed between the study populations.

I conclude that the environmental conditions, both physical (temperature and growing season) and biological (zooplankton and sockeye density) are responsible for at least some of the differences in freshwater growth between the study populations. First, limnological conditions for growth appeared to be less favourable for Birkenhead sockeye than for Weaver sockeye. Second, environment seems to be responsible for a wide range of freshwater growth within the Birkenhead sockeye population, as evidenced by the bimodal circuli frequency distributions. Third, as sockeye density increases, growth of sockeye in Lillooet Lake decreases more rapidly than in Harrison Lake. This results in an emigration of fingerlings from Lillooet Lake to Harrison Lake, as evidenced by the effect of sockeye density on abundance of adults which reared as fry in Lillooet Lake.

The alternate hypothesis that heredity may be responsible for some of the observed differences in freshwater growth in the study populations could not be investigated from the available field data collections. In the next chapter, I describe laboratory experiments designed to test the hypothesis that Weaver Creek and Birkenhead sockeye have genetically influenced differences in freshwater growth.

CHAPTER II:

CONTRIBUTION OF HEREDITY TO DIFFERENCES IN FRESHWATER GROWTH BETWEEN BIRKENHEAD RIVER AND WEAVER CREEK SOCKEYE

INTRODUCTION

In the previous chapter, I provided evidence supporting the hypothesis that differences in growth observed between Birkenhead River and Weaver Creek sockeye within Harrison Lake were in part due to environmental effects. However, I must determine if a genetic component is also present. Growth varies with body size, season and location. In addition, the Birkenhead River and Weaver Creek populations enter the Harrison Lake in different areas and probably at different times and varying body sizes. In order to minimize the effects of these variables, growth was examined in the laboratory, to determine if genetic differences in growth rate and scale parameters existed.

From the environmental data, I made conclusions about the differences in growth of these populations based on the observed differences in the freshwater zone of scales from returning adults. Validation of these conclusions about growth from scale data is important as growth can affect scale-body relationships (Carlander, 1981; Boyce, 1985).

I designed a laboratory study to investigate the following hypotheses:

(1) Main Hypothesis: Weaver Creek and Birkenhead River sockeye have genetically different freshwater growth.

I investigated the following subsidiary hypotheses in order to verify my conclusions about the differences in growth of these populations based on the observed differences in the freshwater zone of scales from returning adults.

(a) Subsidiary Hypothesis: Relative differences in growth between the study populations are reflected in differences in circuli spacing, circuli number and overall measurement of the freshwater zone of the scale.

(b) Subsidiary Hypothesis: Growth rate affects relationships between scale variables and size.

The study was conducted over a range of environmental conditions: Feeding level was varied during studies in 1983. Temperature was varied during studies in 1984.

MATERIALS AND METHODS

1983 Rearing Study

The purpose of the 1983 feeding study was to investigate possible genetic differences in growth between Weaver Creek and Birkenhead River sockeye under different food rations in controlled laboratory conditions.

On 18 - April, I collected sockeye fry from both Weaver Creek and Birkenhead River and transported them to Sweltzer Creek laboratory. These were introduced to rearing troughs, one for each stock. Both groups were fed freeze-dried *Calanus* and allowed to acclimate for a period of 5 weeks.

Six cylindrical fiber glass and six steel tanks were chosen for the experiments, with volume maintained at 120 l and flow rates of 10 l/min. The experimental design is shown below.

STOCK	REPLICATE	TANK	FEEDING REGIME	SAMPLE SIZE
Weaver	1st	FBG[1]	8% daily	500
Weaver	1st	FBG	8% every 2nd day	500
Weaver	1st	FBG	8% every 3rd day	500
Weaver	2nd	STEEL[2]	8% daily	500
Weaver	2nd	STEEL	8% every 2nd day	500
Weaver	2nd	STEEL	8% every 3rd day	500
Birkenhead	1st	FBG	8% daily	500
Birkenhead	1st	FBG	8% every 2nd day	500
Birkenhead	1st	FBG	8% every 3rd day	500
Birkenhead	2nd	STEEL	8% daily	500
Birkenhead	2nd	STEEL	8% every 2nd day	500
Birkenhead	2nd	STEEL	8% every 3rd day	500

[1] FBG: Fiberglass tank
[2] STEEL: Painted steel tank

The tanks were prepared to receive the fry on 20 - May. I found that 0.25 g fry were able to consume 8% of their wet body weight in dry weight of food over the course of 4 - 5 daily feedings. Since dry body weight is approximately 25% of wet body weight this converts to a ration of 30% dry body weight at satiation. This is consistent with estimates for fish of this size made by Brett et al. (1975) . The ration consisted of 67% freeze-dried Calanus and 33% mash diet (Silver Cup ^{TM}). The latter, being less palatable to sockeye was not well utilized. As fish grew and became less able to handle the 8% feeding level, mash was removed from the diet. Those fish fed every 3rd day were originally to be fed every fourth day, but weight loss was apparent so they were fed more frequently. Between sample periods, daily feeding levels for each tank were adjusted using growth rate information calculated from most recent sample data (Ricker, 1974):

$$G = (\ln W_2 - \ln W_1) / (t_2 - t_1)$$

where:

W_2 = mean weight for most recent sample period
W_1 = mean weight for 2nd most recent sample period
$t_2 - t_1$ = days between samples (W_2 & W_1)

then:

$$W_3 = e^{(G \times (t_3 - t_2) + \ln W_2)}$$

where:

W_3 = Estimated mean weight at t_3
$t_3 - t_2$ = days since most recent sample (t_2)

then:

$$F = W_3 \times R \times n$$

where:

F = weight of food
R = ration (% body weight)
n = number of fry in tank

Although mortalities were generally low, a Costia infestation was identified in all tanks during June. I treated this with the standard formalin - malachite treatment over 3 days. The regular feeding regime had to be interrupted because of this treatment. Although growth during this time was likely reduced, scale formation would have been negligible in all cases and the formation of false checks on scales was not apparent. The Costia infestation was most noticeable for Weaver fish reared under the third regime and moderate mortalities were recorded.

I removed random samples of 50 fry from each tank at the start of the experiment and at eight regular intervals thereafter (Appendix 1.3). The exceptions to this were the Weaver tanks in the third regime which had fewer fry than the other tanks due to mortality. Only 25 fry were sampled from these tanks on each sample date through July and August in order to bring the densities more in line with the other tanks in the study. The study was terminated on October 2 after 135 days.

1984 Rearing Study

The purpose of the 1984 temperature study was to investigate possible genetic differences in growth between Weaver Creek and Birkenhead River sockeye under different temperature regimes in controlled laboratory conditions.

I collected fry from both populations on 15 - April following procedure used in 1983 (acclimation was shortened to 2 weeks as fry were feeding well). Six 120 l circular fiberglass tanks were used, one for each stock - regime combination. Three different temperature regimes were set: Ambient, using unheated water from well below the thermocline in Cultus lake (6.5 - 7.5°C), 11°C and 15°C. The experimental design was as follows:

STOCK	TANK	TEMPERATURE REGIME	SAMPLE SIZE
Weaver	FBG	15°C	200
Weaver	FBG	11°C	200
Weaver	FBG	Ambient	200
Birkenhead	FBG	15°C	200
Birkenhead	FBG	11°C	200
Birkenhead	FBG	Ambient	200

The 11°C and 15°C water temperatures were achieved by heating ambient water with electric coils. I used a header box to maintain a constant flow of water into an electrically grounded 100 l stainless steel tank. Three 1000 watt coils and one 750 watt coil were suspended in the tank and allowed to operate continuously at full output. Water drawn from the bottom of the tank was raised to within approximately 15 cm of the top of the tank, allowing a constant water level in the tank.

I adjusted the flow into the steel tank so that the water leaving it maintained a constant temperature of 15°C. The heated water trickled down a 1.5 meter PVC pipe (8cm ID) filled with smooth stones. This degassing column reduced total gas saturation from 116.3% to an acceptable 104.5%. The heated, degassed water flowed into a second header box, and then was diverted into two more header boxes, one each for the 11°C and 15°C regimes. In the 11°C header box, the 15°C water was cooled to 11°C by the addition of cool ambient water. I controlled water flow at the exit of each header box by means of valves to ensure a continuous flow rate of 2.3 l/min to each tank. This allowed minimum turnover in excess of once per hour.

Temperature control was very reliable (standard deviation = 0.25°C). I adjusted incoming water flows to allow for changes in the ambient water temperature. The ambient water temperature was itself quite uniform, increasing slowly over the summer. Temperatures in each tank were measured twice daily and ambient flow rates were adjusted to maintain temperatures in the 11°C and 15°C regimes. The ambient temperature regime was allowed to fluctuate over the course of the study.

The food used in the study was freeze dried Euphausids. Feeding levels were kept at near satiation: 40% dry body weight per day at the start of the study for the 15°C group, 30% for the 11°C group and 24% for the ambient group. These percentages were revised throughout the study and reduced if food waste was excessive. I collected waste food on May 21 from all tanks and found it to be less that 5%. Thereafter, waste food was evaluated visually.

Initially, I adjusted feeding levels every two weeks using weight data from the entire population of each tank. This information was to be taken from anesthetised fish. Conspicuous black marks on the posterior areas of fish were noticed, indicating the fish were being stressed (I. Williams, Pacific Biological Station, Nanaimo, B.C., pers. comm.). I discontinued this method in order to minimize stress and used weight data from the preserved samples to adjust feeding levels.

The study began on May 1. I discontinued the 15°C temperature regime on June 6 because the fish had infectious haemopoetic necrosis (IHN), a viral infection which is considered to be incurable (I. Williams, pers. comm.). This regime was restarted on June 6, but was again terminated on July 2. Flows were then increased for the 11°C group using the excess heated water. The 11°C group suffered from a form of bacterial gill disease and a moderate mortality (2 - 6%/day) was recorded. This disease was successfully cured using para-toluene-sulphochloramide (Chloramine ^{tm}). These two instances of disease are almost certainly due to the lake water source. More sterile water such as spring water is advised for similar studies in the future.

Samples of 25 fish from each tank were collected approximately every 2 weeks over 7 regular intervals for the ambient temperature group, over 6 intervals for the 11°C group and 3 intervals for the 15°C group. The 11°C group was terminated on September 1 and the ambient group was terminated on September 30.

Length, Weight and Scale Data for 1983 and 1984 Studies

Samples were kept in formalin for 4 - 6 months before being processed to allow for stabilization of length and weights. Rogers (1965) found that most decrease in length with preservation had occurred by 100 days of preservation. He also found that weight initially increased then decreased, stabilizing after 100 days. My results were similar to Rogers', but I also discovered an effect of preservation on scale measurements, likely due to fixation of protein in the scale. Scale measurement decreased by 6.2% during the first 30 days of preservation.

Fork length to the nearest millimetre and wet weight to the nearest 0.01 gram were recorded from each fish. From selected samples, 4 scales (When present) were taken from the first or second row above the lateral line on either side of the diagonal originating from the posterior insertion of the dorsal fin. These were placed on gummed cards and an impression was made on an acetate strip using a heat press. Using a microscope projector the scale image on the acetate was projected onto a piece of paper (250 X magnification). From each fish, the best scale of the four was selected and the focal area, individual circuli and the end of the scale were marked off following the procedure of Clutter and Whitesal (1961). These were measured to the nearest millimetre, the edge of the focus being the first circulus. The measurements were then corrected to the original magnification for analysis and presentation. All data were itemized separately for each fish and stored in computer files for analysis. A data base was designed to accommodate the variables listed below by tank and sample date. Means and standard deviations were calculated for each variable.

Measured Variables:

Length (L)
Weight (W)
Number of Circuli (CC)

Measurements to:	1st Circulus	DONE
	2nd Circulus	DTWO
	3rd Circulus	DTHREE
	4th Circulus	DFOUR
	5th Circulus	DFIVE
	6th Circulus	DSIX
	7th Circulus	DSEVEN
	8th Circulus	DEIGHT
	9th Circulus	DNINE
	10th Circulus	DTEN
	End of the Scale	DEND

Derived Variables:

Distance between:	1st and 2nd Circuli	S2C
	2nd and 3rd Circuli	S3C
	3rd and 4th Circuli	S4C
	4th and 5th Circuli	S5C
	5th and 6th Circuli	S6C
	6th and 7th Circuli	S7C
	7th and 8th Circuli	S8C

Statistical Procedures for 1983 and 1984 Studies

Analyses of variables associated with growth were directed towards investigation of 3 hypotheses:

1) Main Hypothesis: Weaver Creek and Birkenhead sockeye have genetically different freshwater growth.

a) Subsidiary Hypothesis: Differences in circuli spacing, circuli number and overall measurement of the freshwater zone of the scale reflect differences in growth between the populations.

b) Subsidiary Hypothesis: Growth rate affects relationships between scale variables and length.

I calculated simple least squares regressions for scale parameters versus length. Unbalanced fixed effect factorial designs were analyzed using the ANOVA option in the APL STATGRAPHICS computer package (Polhemus, 1985). Main effects of stock and regime were examined for the indicated response variables. An analysis of covariance for unbalanced experimental designs (Winer, 1971) was used to examine the significance of main effects for response variables (Y) after the appropriate linear adjustments for covariates (X). A priori significance levels were set at 5%.

RESULTS

1983 FEEDING STUDY

The initial analysis was designed to determine if replication effects existed. Using analysis of variance tests, I could not find a main effect of replicate on the study variables. Consequently, replicates were pooled for subsequent analyses. Summaries of weight, length and scale data by sample period for pooled replicates are summarized in appendices 1.3 - 1.5.

I investigated the main effects of feeding regime and stock on fry growth. Results of ANOVA's on $\log_e$ weight and $\log_e$ length for each sample period are shown in Tables 8 and 9. The main effect of feeding regime on weight was highly significant for all sample periods ($P < 0.001$). As expected, fish fed daily were largest followed by those fish fed every second day. Those fish fed every three days were the smallest.

Mean weights of Weaver Creek and Birkenhead River fry were not significantly different ($P = 0.063$) at the start of the study although Weaver fry were larger from collection date to initiation of the study. Within a feeding regime, average fry weights of the two stocks were not significantly different for sample dates 0 to day 79 with the exception of day 63 ($P = 0.044$). On that day, Birkenhead fry were significantly heavier than Weaver fry. For sample days 99 to 135, the main effect of stock on $\log_e$ weight was significant (ANOVA results, table 8): Weaver fingerlings within a regime on average were heavier than Birkenhead fingerlings. An example of the divergence in growth of the two stocks (fish fed daily) is shown in Figure 15. This divergence in growth was

Table 8: Analysis of variance of $\log_e$ weight by day of sampling for the 1983 feeding study.

MAIN EFFECTS

		Regime			Stock			Interaction		
Day	d.f.	F-Ratio	Prob.	d.f.	F-Ratio	Prob.	d.f.	F-Ratio	Prob.	d.f.
0	98	-	-	-	3.57	0.062	1	-	-	-
17	591	65.28	<0.001	2	0.81	0.379	1	0.02	0.826	2
31	593	198.14	<0.001	2	<0.00	0.960	1	8.64	0.002	2
47	542	205.29	<0.001	2	0.03	0.870	1	0.17	0.841	2
63	540	151.15	<0.001	2	4.08	0.044	1	1.93	0.146	2
79	569	327.89	<0.001	2	0.42	0.841	1	1.19	0.305	2
99	568	189.85	<0.001	2	6.30	0.012	1	0.31	0.736	2
121	568	390.88	<0.001	2	26.61	<0.001	1	1.02	0.361	2
135	594	386.70	<0.001	2	85.07	<0.001	1	1.32	0.269	2

Table 9: Analysis of variance of $\log_e$ length by day of sampling for the 1983 feeding study.

MAIN EFFECTS

		Regime			Stock			Interaction		
Day	d.f.	F-Ratio	Prob.	d.f.	F-Ratio	Prob.	d.f.	F-Ratio	Prob.	d.f.
0	98	-	-	-	1.81	0.181	1	-	-	-
17	591	48.72	<0.001	2	7.00	0.008	1	0.20	0.815	2
31	593	133.52	<0.001	2	1.20	0.273	1	4.21	<0.001	2
47	542	158.55	<0.001	2	<0.01	0.987	1	0.49	0.611	2
63	540	154.41	<0.001	2	5.08	0.025	1	2.91	0.056	2
79	569	330.54	<0.001	2	0.90	0.354	1	1.19	0.305	2
99	568	210.74	<0.001	2	1.61	0.205	1	0.89	0.411	2
121	568	392.67	<0.001	2	15.46	<0.001	1	0.48	0.619	2
135	594	450.30	<0.001	2	26.61	<0.001	1	1.02	0.361	2

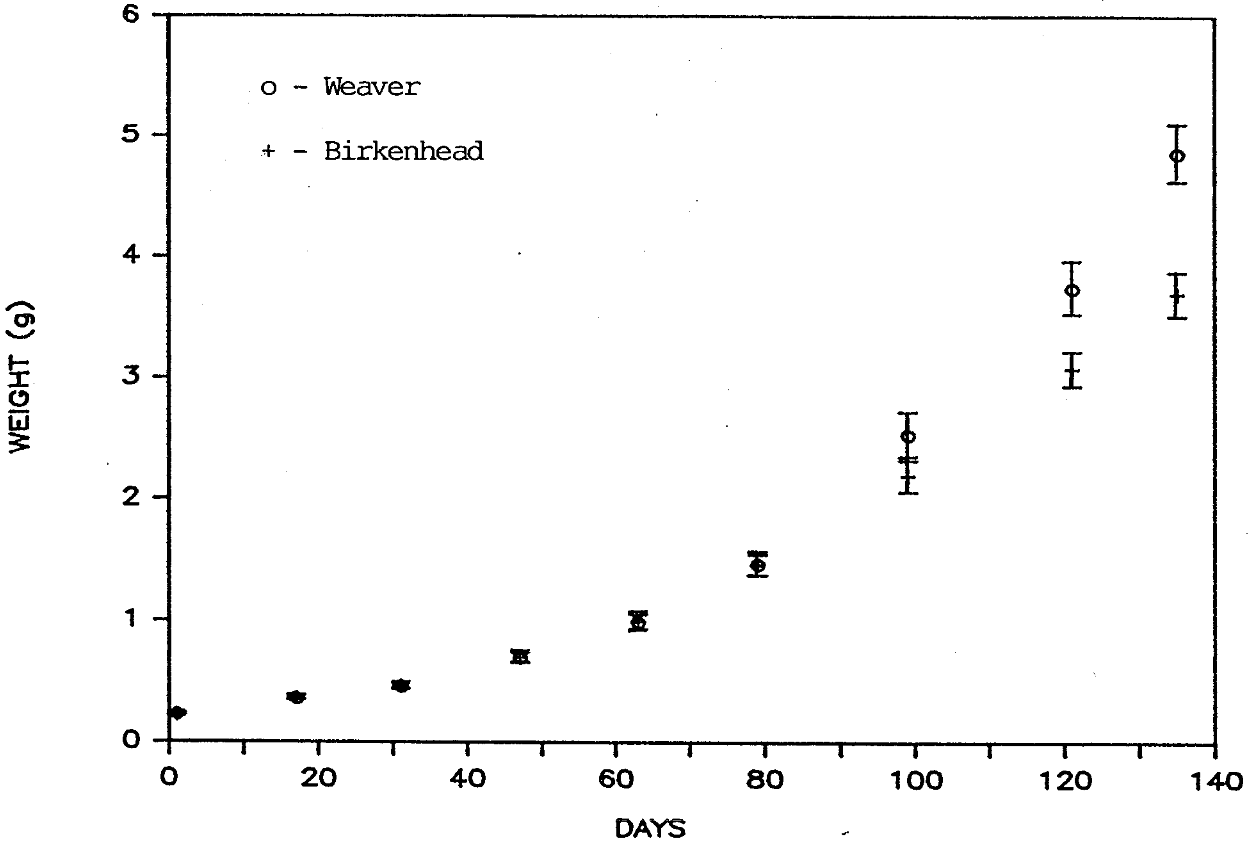

Figure 15: Increase in weight with time for fish fed daily. 1983 fry rearing study. Sample means ± standard error about the mean.

evident to a lesser extent in the other two regimes. Interaction between the main effects of stock and regime were minimized with the $\log_e$ transformation of weight, however significant interaction was apparent on day 31. In this instance, interaction was weak relative to the main effect of regime.

I calculated ANOVA's on $\log_e$ length data prior to investigation of the subsidiary hypotheses concerning the relationships between scale variables and length. ANOVA results on length closely paralleled those on weight. Significant main effects of stock on length occurred on day 17 and day 63 which were traced in turn to larger Weaver fry on day 17 and Birkenhead fry on day 63. Consistent and highly significant effects of stock became apparent on day 121 of the study (Table 9) when Weaver fry growth out paced Birkenhead growth. Significant interaction between stock and regime was again noticed on day 31.

I examined ANOVA's of circuli counts, scale radius and circuli spacing to determine if these variables reflected the observed differences in body growth between the two populations (table 10). Significant main effects of stock ($P < 0.001$) and regime ($P < 0.001$) on circuli number and scale radius were apparent at the completion of the study. Scales from Weaver fingerlings within a feeding regime had more circuli and greater scale radii than scales from Birkenhead fingerlings of the same age and feeding regime. Scales from fish fed daily also had the most circuli and greatest scale radii followed by those from fish fed every second day. Scales from fish fed every three days had the fewest circuli and smallest scale radii. Interaction between the main effects of stock and regime on circuli number was absent ($P = 0.490$). Interac-

Table 10: Analysis of variance of circulus spacing at each increment, circuli number and scale radius: sample day 135, 1983 feeding study.

MAIN EFFECTS

		Regime			Stock			Interaction		
Test	d.f.	F-Ratio	Prob.	d.f.	F-Ratio	Prob.	d.f.	F-Ratio	Prob.	d.f.
1	578	131.13	<0.001	2	39.54	<0.001	1	0.72	0.490	2
2	578	234.47	<0.001	2	45.87	<0.001	1	3.31	0.037	2
3	578	90.45	<0.001	2	0.12	0.731	1	0.67	0.511	2
4	576	104.49	<0.001	2	0.92	0.348	1	0.45	0.640	2
5	569	103.18	<0.001	2	4.61	0.032	1	0.74	0.476	2
6	556	99.70	<0.001	2	35.79	<0.001	1	2.85	0.059	2
7	522	101.03	<0.001	2	39.06	<0.001	1	5.63	0.004	2
8	365	24.95	<0.001	1	29.92	<0.001	1	-	-	-
9	317	21.83	<0.001	1	51.91	<0.001	1	-	-	-

Test: 1 - circuli number
2 - scale radius
3 - space between 1st and 2nd circulus
4 - space between 2nd and 3rd circulus
5 - space between 3rd and 4th circulus
6 - space between 4th and 5th circulus
7 - space between 5th and 6th circulus
8 - space between 6th and 7th circulus
9 - space between 7th and 8th circulus

tion between the main effects on scale radius was significant ($P = 0.037$), but weak relative to the main effects of stock and regime.

Results of ANOVA's on each incremental distance between circuli are shown in Table 10. I found a significant main effect of regime ($P < 0.001$) for spacing between each adjacent pair of circuli. A trend of increased spacing was apparent with increased feeding level. A main effect of stock was insignificant for the first two circuli increments, but was significant ($P < 0.032$) for the later increments. Scales from Weaver sockeye had significantly greater circuli spacing than scales from Birkenhead sockeye from the same feeding regime beyond the third circulus. Interaction was significant ($P = 0.004$) for spacing between 5th and 6th circulus but the F ratio was low relative to the main effects. Interaction between the main effects was not estimated for increments after the 6th circulus as the 3rd regime had insufficient observations from that portion of the scale to be included in the analysis.

In the next phase of the analysis, I examined whether growth affected the relationships between length and scale variables associated with growth. The scatter plots of scale radius on length indicated a linear relationship. These regressions are shown in Figure 16 for each stock and regime. Analysis of covariance indicated a significant main effect of regime ($F = 59.34$, $P < 0.001$) on the linear response of scale radius to length with scale radius for a given length being greater for feeding regimes 2 and 3 than for regime 1. Also, a significant main effect of stock ($F = 4.24$, $P = 0.040$) was evident on the relationship of scale radius with length: in all feeding regimes, scale radius for Birkenhead

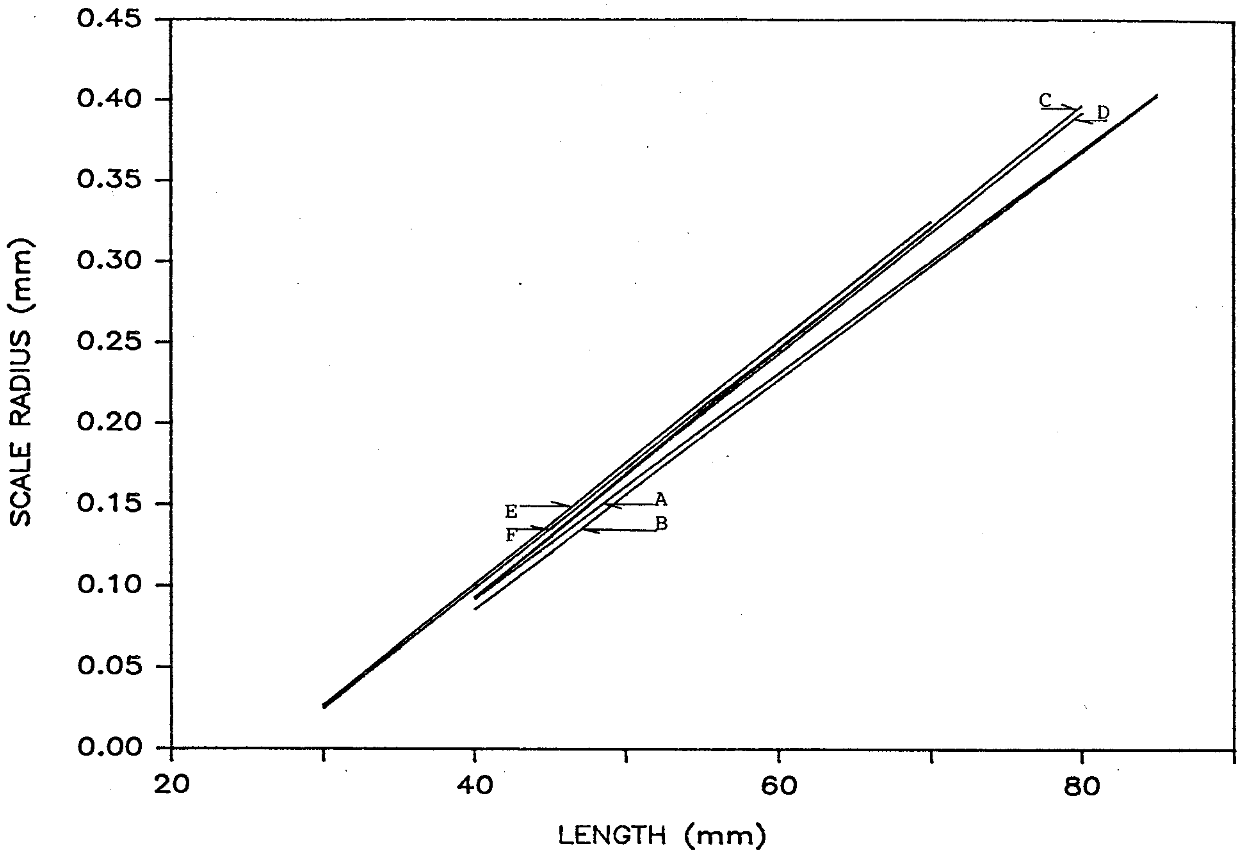

Figure 16: Relationship between scale radius and length by regime and stock for the 1983 growth study.

A: Birkenhead fry fed every day
$Y = 0.00694 X - 0.185$ $r = 0.9270$, $P < 0.001$, d.f. = 334

B: Weaver fry fed every day
$Y = 0.00705 X - 0.196$ $r = 0.9558$, $P < 0.001$, d.f. = 331

C: Birkenhead fry fed every second day
$Y = 0.00759 X - 0.211$ $r = 0.9272$, $P < 0.001$, d.f. = 188

D: Weaver fry fed every second day
$Y = 0.00748 X - 0.206$ $r = 0.9476$, $P < 0.001$, d.f. = 185

E: Birkenhead fry fed every third day
$Y = 0.00745 X - 0.197$ $r = 0.9037$, $P < 0.001$, d.f. = 178

F: Weaver fry fed every third day
$Y = 0.00739 X - 0.197$ $r = 0.9089$, $P < 0.001$, d.f. = 153

fish was slightly greater than for Weaver fish. Interaction between the main effects was not significant (F = 0.73, P = 0.473).

I could not determine an effect of stock or feeding regime on size at time of first scale formation. Scales were first apparent as chips on fish as small as 35 mm. All fish except pin-heads (chronic emaciated fish) had good scales by 39 mm. The first circulus was generally formed by 37 mm. Size at first scale formation was estimated to be 26 - 28 mm using regressions of scale radius on length with no obvious trends by stock or regime. These back-calculated estimates are likely too low, since fish less than 35 mm rarely had discernable scales.

The relationships between scale circuli number and length for each stock and regime are shown in Figure 17. The scatter plots of circuli count against length indicated a linear relationship. Analysis of covariance indicated a significant main effect of regime (F = 218.80, P = 0.001) on the relationship between circuli number and length: a general tendency for greater circuli number at a given length with decreased level of feeding and concomitant lower growth rate was apparent. No significant effect of stock on this relationship was evident (F = 1.18, P = 0.277). Interaction between the main effects was significant (F = 3.93, P = 0.029) but weak relative to the main effect of regime.

1984 TEMPERATURE STUDY

Results of the 1984 studies were adversely affected by the problems associated with disease which forced the termination of the 15°C groups on two separate occasions. Disease problems with the 11°C fish also affected the overall growth rate of the group. Consequently checks on the scales were apparent. Size selective mortality due to the disease

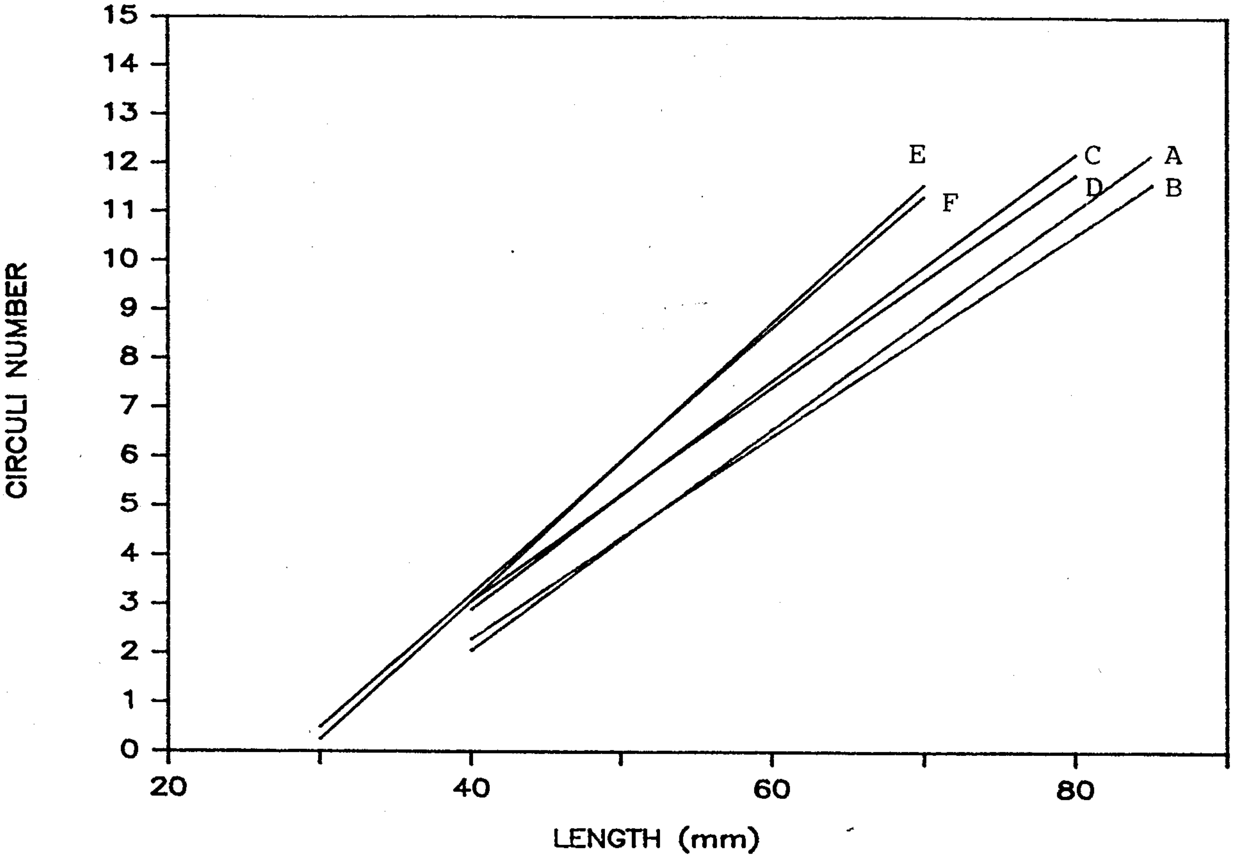

Figure 17: Relationship between circuli number and length by regime and stock for the 1983 growth study.

A: Birkenhead fry fed every day
$Y = 0.225\ X - 6.94$ $r = 0.9167$, $P < 0.001$, d.f. = 334

B: Weaver fry fed every day
$Y = 0.206\ X - 5.95$ $r = 0.9370$, $P < 0.001$, d.f. = 331

C: Birkenhead fry fed every second day
$Y = 0.233\ X - 6.44$ $r = 0.8684$, $P < 0.001$, d.f. = 188

D: Weaver fry fed every second day
$Y = 0.218\ X - 5.67$ $r = 0.8795$, $P < 0.001$, d.f. = 185

E: Birkenhead fry fed every third day
$Y = 0.283\ X - 8.25$ $r = 0.8354$, $P < 0.001$, d.f. = 178

F: Weaver fry fed every third day
$Y = 0.271\ X - 7.64$ $r = 0.8534$, $P < 0.001$, d.f. = 153

likely biased results in the 11°C group. In addition, the powdered freeze-dried Euphausids were less suitable for food than the Calanus used the previous year and growth rates for the ambient group were significantly lower than comparable groups reared during the previous year.

Because of these problems, statistical analyses are not valid, however, generalities are evident. Results were similar to 1983: Weaver Creek sockeye tended to grow faster than Birkenhead sockeye and tended to have greater scale radii and more circuli.

DISCUSSION

The principal purpose of the laboratory studies was to investigate the hypothesis that Weaver Creek and Birkenhead River sockeye have genetically different freshwater growth. I was unable to reject this hypothesis, although the between stock differences under the controlled conditions of the laboratory were not as large as I observed with the age 4_2 adult scale data (Figure 4). This supports the conclusions in Chapter 1 which indicated a strong environmental component to differences in freshwater growth observed in the adult sockeye. In addition, conditions for growth in the laboratory may have been more favourable for Weaver sockeye than for those from the Birkenhead River, by being closer to the temperature and feeding regime in Harrison Lake (laboratory artifact). Hybrid cross studies would also be subject to the same laboratory artifact which may have affected my study (E.L. Brannon, University of Washington, Seattle, Washington, pers. comm.). However, since the study involved large numbers of fry collected from the rivers, presumably from numerous parents, possible variation as a result of low genetic variability in the study can be discounted.

Hybrid crosses between Birkenhead River and Weaver Creek sockeye would have been difficult because of the small amount of overlap in spawning timing between the two populations. Since I did not run experiments using interstrain hybrids, I cannot determine the nature of the genetic differences in growth between the two populations (Withler et al., 1982). In particular, maternal effects, such as egg size, cannot be separated from other possible genetic differences (Refstie and Steine, 1978). Weaver Creek age 4_2 females are larger than Birkenhead 4_2 females, and fry sizes were close to being significantly different in my study. I feel however, that maternal effects in this study can be largely discounted because of the similarity of growth between the two populations early in the study. Also, the spawning population on the Birkenhead River on some years may comprise over 50% age 5_2 individuals (I.P.S.F.C. archives) and fry from these spawnings would be more similar in size to the Weaver Creek population.

Significant interaction between stock and regime was minimal in this study. Interaction of this nature would indicate that some of the genetic variance is nonadditive (Whithler et al., 1982). Significant interaction would also indicate that a population would grow better under certain environmental conditions, perhaps laboratory conditions, but perhaps not as well under other conditions (Austreng and Refstie, 1979). Weaver Creek sockeye may not grow well or alternatively survive in freshwater environments which Birkenhead River sockeye have by necessity become adapted.

Thorpe (1977) observed bimodal growth in sibling populations of juvenile Atlantic salmon reared under experimental conditions. The proportion of fish in the upper growth mode was strongly influenced by inheritance. Thorpe et al. (1980) concluded that these two modal groups diverged in growth in June-July. They concluded that the determination of the precise time of growth rate divergence could not be estimated by length frequency analysis because of the time lag between the physiological processes responsible and growth in length.

In the present study, the divergence in growth between the two stocks first noticeable at approximately day 100 (late August), suggests an adaptive physiological mechanism. Villarreal (1983; as cited by Thorpe, 1987) proposed that photoperiod synchronised a genetically determined endogenous rhythm in Atlantic salmon, which ultimately timed and caused bimodality in growth rates of juveniles. Thorpe (in press; as cited by Thorpe, 1987) found delayed photoperiod delayed the time when the separation into the two modal groups occurred. Photoperiod may have an effect on physiological processes in Birkenhead sockeye. If adequate size is not reached by a particular day length, possibly because of density-dependence (Chapter I), a further emigration from Lillooet Lake may be triggered. Alternatively, photoperiod may affect physiological control of growth differentially in the two stocks, explaining the divergence of growth in the laboratory.

Heggberget et al. (1986) also found several growth modes in Atlantic salmon within the River Alta system. Young salmon in the upper part of this river had better overall growth than those inhabiting downstream sections of the river. Estimated growth based on adult scales indicated corresponding river growth patterns from the three sections of the river. They also found electrophoretic differences in the three subpopulations of smolts and concluded that adults homed to the section of the river in which they had reared. The better growth in the upper part of the river was attributed to more favourable environmental conditions in that section but a genetic contribution to the differences in growth could not be precluded.

The effect of feeding regime on growth was expected: fish fed more (within the limits of satiation) should grow faster. This was consistent with the results of Brett et al. (1969) and Bilton (1974). The retardation in growth at lower rations affected the two populations similarly. Therefore, I could not explain the divergence in growth between the stocks in terms of food availability.

Scale radius and circuli number were also highly correlated with growth rate. Length, weight, scale radius and circuli number and circuli spacing for fish of the same age were all highly correlated with feeding level. Scale radius and circuli number were highly correlated with length. These results are consistent with those of Bilton (1974), Boyce (1985) and other workers. In addition, I found that differences in growth between Birkenhead and Weaver sockeye were reflected in the scale radius, circuli number and in the spacing of the later circuli increments. Consequently, I am unable to reject my subsidiary hypothesis that relative differences in freshwater growth in the wild in the study populations are reflected in relative differences in circuli spacing, circuli number and overall radius of the freshwater zone of the scale.

Growth rate appeared to affect the relationships between circuli number and length and between scale radius and length. These results are consistent with those of Boyce (1985) and Bilton (1974). Faster growing fish for a given length had fewer but wider spaced circuli than those from slower growth regimes. Lower scale radius for a given length was also evident. Bradford (1985) documented the "uncoupling" of otolith growth from changes in body growth. He found that otolith growth is conservative and does not record small or rapid changes in somatic growth. In my study, it is likely that scale growth could not keep pace with body growth in the daily feeding regime. The results show that I cannot reject my subsidiary hypothesis that growth rate can affect relationships between scale variables and size.

I could not find an effect of stock on the relationships of scale radius to fry length and circuli number to fry length. These relationships may differ between the two populations in the lake because of the effect that variable growth has on these relationships. Where possible, scale - length relationships should be determined for individual populations (Carlander, 1981). In the first chapter, I assume that the relative differences in freshwater growth of each population can be inferred from relative differences in freshwater scale growth (circuli number and total freshwater scale radius). If fast growing fish put on less scale growth for a given size than slow growing fish, scale growth would underestimate growth differences between the two stocks. Scale growth would probably catch up in the winter when body growth slows down. Consequently, I am probably correct in determining differences in first year growth in these populations using the method described in the first chapter. If growth rate comparisons between the populations are to be made over shorter time intervals, I would have to define the relationships between circulus spacing and growth rate and circulus spacing with time (Corley, 1985). Such analysis would likely be affected by the uncoupling of scale growth from changes in body growth rate.

Smale and Taylor (1987) examined sources of back-calculation error in estimating growth from scales. They determined that false Lee's phenomenon (LP or Lee's phenomenon caused by back-calculation error) could be distinguished from "true" LP (caused by size-selective sampling or mortality). If the estimated size at first scale formation (X intercept Figure 15) is either too small or too large, the percentage of the error will increase with age. They considered that other sources of error in scale radius-length relationships were seasonal non-linearity and early stanzas (differences) in scale growth relative to length. I found that size at first scale formation was underestimated by regression technique. In the very early stages scale growth is non-linear with growth in length. This is probably due to the lack of overlap of scales when they are first formed (Van Oosten, 1929) and a period of accelerated scale growth relative to growth in length. In my first chapter, I make an important assumption that size of first scale formation is the same for both stocks. This is probably reasonable as this size is about 35-40 mm in sockeye stocks which have been studied (Clutter and Whitesal, 1956).

In conclusion, the laboratory study provided evidence for the hypothesis that Weaver Creek and Birkenhead River sockeye have genetically different freshwater growth rates. Also I was unable to reject the hypothesis that relative differences in growth between the study populations are reflected in differences in circuli spacing, circuli number and overall measurement of the freshwater zone of the scale. This was an important assumption in Chapter I. Finally, growth rate was found to affect relationships between scale variables and body size.

GENERAL DISCUSSION

In this thesis, I provide evidence for the theory that the combination of environment and heredity result in Weaver Creek sockeye growing substantially more during their first year in freshwater than Birkenhead River sockeye. The contribution of environment to differences in freshwater growth between the study populations is supported by limnological evidence, the wide range of freshwater growth in the wild within the Birkenhead sockeye population, and evidence that the negative effect of sockeye density on growth is greater in Lillooet Lake than in Harrison Lake. In the laboratory, Weaver Creek and Birkenhead River sockeye were shown to have different freshwater growth rates in the same environment, possibly due to genetic differences. No accurate measure of the relative importance of the two effects was possible.

In Chapter I, I found that the freshwater scale radius of Weaver Creek sockeye was on average 37% greater than for Birkenhead River sockeye. In the laboratory studies, the scale radius of Weaver Creek sockeye was on average 11% greater than for Birkenhead River sockeye at termination of the 1983 study (day 135). However, it would be incorrect to calculate the relative contribution of environment and heredity to the observed growth differences in the wild using this information because one of the populations may be better adapted to growth under the experimental laboratory conditions than the other, for reasons unrelated to the wild situation. Considering the magnitude of the differences observed in the wild compared to the laboratory results, environment would seem to be the principal cause.

While environment seems to be the most likely cause of these differences in growth, Weaver sockeye could have evolved behavioural or physiological mechanisms to take advantage of the environment and optimize or maximize growth in Harrison Lake. Other environmental constraints on Birkenhead sockeye may have resulted in the evolution of a more conservative scope for growth. I can only speculate on the physiological or behavioural processes contributing to possible genetic differences in growth between the two study populations. These may be numerous and difficult to investigate because of the uncertain contribution of the laboratory environment to the results (Brannon, pers. comm.). For example in my study, Weaver Creek sockeye may have a lower basal metabolic rate than Birkenhead sockeye, resulting in greater food conversion efficiency (Brett, 1976). Second, under the limits of satiation, which were in place in this study, Weaver Creek sockeye may be able to physically hold more food or simply maintained a higher level of satiation than Birkenhead fry.

While freshwater growth of Weaver Creek sockeye was greater, this does not necessarily imply a competitive advantage over Birkenhead River sockeye. This is because large smolt size has not been shown to be of significant advantage in marine survival in Fraser River sockeye populations which have been studied. These sockeye are typically large as smolts compared to most coastal stocks in British Columbia (see for example, Hyatt and Stockner, 1985).

Studies dealing with the question of age at maturation indicate that heredity is a principal factor affecting growth, however ecological factors are also implicated and make results difficult to interpret (Naevdal, 1983). Ritter and Newbold (1977; as cited by Naevdal, 1983) found that in Atlantic salmon, grilse parents tend to produce offspring which return as grilse. They also found that 1-year-old smolts tended to produce comparatively fewer grilse than 2-year-old smolts of the same strain. These results contrast to Naevdal (1983) who found that 2-year-old smolts tended to produce less grilse. Thorpe (1987) found that slower growing Atlantic salmon fingerlings tended to remain in freshwater and mature the following year. The confusing results are probably related to stock specific differences and interaction between genotype and environmental factors (Naevdal, 1983). Refstie and Steine (1978) demonstrated the need to remove environmental effects in an analysis of genetic variation within or between strains of fish. From these studies it is increasingly clear that it is difficult to estimate the relative effects of environment versus heredity in the situation described in this thesis.

In this study, I have attempted to show the value of the long-term scale and adult return database in the investigation of the biology of Fraser River sockeye: in most Fraser populations, this is the only long-term information available. The scale database has considerable potential towards assessment of the carrying capacity of sockeye lakes if density dependent effects on growth are present. I have investigated the relationship between scale measurements and body size and the relationship between scale measurement and sockeye abundance. If marine mortality to smolt size relationships can be further developed, the critical smolt size in a specific population may be determined, below which increased marine mortality may affect the abundance of adult returns. Scale-measurements-to-adult-return relationships may assist in the assessment of potential adult returns in consideration of critical smolt size. Optimal fry output or escapements for a population can then be assessed by methods independent of spawner-recruit analysis. The value of such methodology may depend on an assessment of size-selective mortality, which has not been conclusively demonstrated to exist in Fraser River sockeye.

While growth differences between populations were the focus of the study, the impact of freshwater growth on the dynamics of the Birkenhead population was an additional finding. The proportion of Birkenhead sockeye fry estimated to have reared in Lillooet Lake declined as fry output (as indexed by total adult returns) increased. The effect of sockeye density on growth, while present in both lakes was greater in Lillooet Lake than in Harrison Lake.

In this thesis, I have found evidence for density-dependent growth as well as density-dependent migration in the Birkenhead River sockeye population. However, an assessment of the duration and timing of fry and fingerling emigrations from Lillooet Lake are required to test my theory that density affects the proportion of fry that continue to rear in the lake. This study should be augmented by lake studies to assess the vertical and horizontal distributions as well as spatial interactions of the Harrison system populations.

LITERATURE CITED

Austreng, E. and T. Refstie. 1979. Effect of varying dietary protein level in different families of rainbow trout. Aquaculture 18: 145-156.

Ball, J.N. 1969. Prolactin (fish prolactin or paralactin) and growth hormones. In: W.S. Hoar and D.J. Randall, ed. Fish Physiology, Vol. II. Academic Press, New York, pp. 207-240.

Biette, R.M. and G.H. Geen, 1980. Growth of underyearling salmon (*Oncorhyncus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquat. Sci. 37: 203-210.

Beamish, R.J. and G.A. McFarlane. 1983. The forgotten requirements for age validation in fisheries biology. Trans. Am. Fish. Soc. 112: 735-743.

Bhatia, D. 1931. On the production of annual zones in the scales of the rainbow trout (*Salmo irideus*) I. J. Exper. Zool. 59: 45-49.

Bhatia, D. 1931. Factors involved in the production of annual zones on the scales of the rainbow trout (*Salmo irideus*) II. J. Exper. Biol. 9: 6-11.

Bilton, H.T. 1974. Effects of starvation and feeding on circulus formation on scales of young sockeye salmon of four racial origins and one race of young kokanee, coho and chinook salmon. In: The aging of fish: T. Bagenal (ed), Unwin Bros., pp 40 70.

Bilton, H.T., D.F. Alderdice and J.T. Schnute. 1982. The influence of size and time at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426-447.

Bilton, H.T. and G.L. Robins. 1971a. Effects of feeding level on circulus formation on scales of young sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Can. 28: 861-868.

Bilton, H.T. and G.L. Robins. 1971b. Effects of starvation, feeding, and light period on circulus formation on scales of young sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Can. 28: 1749-1755.

Bilton, H.T. and G.L. Robins. 1971c. Response of young sockeye salmon (*Oncorhynchus nerka*) to prolonged periods of starvation. J. Fish. Res. Bd.Can. 28: 1757-1761.

Boyce, R.R. 1985. Effects of feeding level, temperature, and photoperiod on growth and selected scale characteristics of juvenile steelhead trout. M.Sc. Thesis. Oregon State Univ. 72 p.

Bradford, M.J. 1985. The use of otolith daily increment width to estimate the size and growth of juvenile chinook salmon (Oncorhynchus tshawytscha). M. Sc. Thesis. Simon Fraser Univ. 87 p.

Brannon, E.L. 1972. Mechanisms controlling migration of sockeye salmon fry. Internat. Pac. Salmon Fish. Comm. Bull. XXI, 86 p.

Brett, J.R. 1976. Scope for metabolism and growth of sockeye salmon, Oncorhynchus nerka, and some related energetics. J. Fish. Res. Bd. Can. 33: 307-313.

Brett, J.R., and J.E. Shelbourn. 1975. Growth rates of young sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Bd. Can. 26: 2363-2394.

Brett, J.R., J.E. Shelbourn and C.T. Shoop. 1969. Growth and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Bd. Canada 26: 2363-2394.

Burgner, R.L. 1962. Studies of red salmon smolts from the Wood River lakes, Alaska. Univ. of Wash. Publ. in Fisheries, New Series 1 (6): 247-314.

Campana, S.E. and J.D. Neilson. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42: 1014-1032.

Carlander, K.D. 1981. Caution on the use of the regression method of back-calculating length from scale measurements. Fisheries (Bethesda) 6 (1): 2-4.

Cave, J.D. and J.C. Woodey. 1982. Discriminant function analysis of sockeye scale data. Int. Pac. Sal. Fish. Comm. Unpublished manuscript, 9 p.

Chapman, D.W. 1962. Aggressive behavior in coho salmon as a cause of emigration. J. Fish. Res. Bd. Can., 19: 1047-1080.

Cooper, A.C. 1977. Evaluation of the production of sockeye and pink salmon at spawning and incubation channels in the Fraser River system. Int. Pac. Sal. Fish. Comm. Prog. Rept. 36, 80 p.

Corley, S.D. 1985. A proposal to define relations of intercircular distance to growth rate and intercircular distance to time for juvenile steelhead (Salmo gairdneri). Unpublished manuscript, cited with permission. N.M.F.S. 18 p.

Clutter, R.I. L.E. Whitesel. 1956. Collection and interpretation of sockeye salmon scales. Internat. Pac. Salmon Fish. Comm. Bull. IX, 159 p.

Cooper, E.L. 1951. Validation of the use of scales of brook trout, Salvelinus fontinalis, for age determination. Copeia 2: 141-148.

Eggers, D.M. 1978. Limnetic feeding behaviour of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnol. Oceanogr. 23 (6): 1114-1125.

Geen, G.H. and F.J Andrew. 1961. Limnological changes in Seton Lake resulting from hydroelectric diversions. Internat. Pac. Salmon Fish. Comm., Prog. Rept. 8, 76 p.

Foerster, R.E. 1968. The sockeye salmon. Fish. Res. Bd. Can. Bull. 162: 422 p.

Gilbert, C.H. 1914-1925. Contributions to the life-history of sockeye salmon, Nos. 1-10. Report Comm. Fish. B.C. 1913-1915, 1917-1919, 1921-1924.

Goodlad, J.C., T.W. Gjernes, and E.L. Brannon. 1974. Factors affecting sockeye salmon (Oncorhynchus nerka) growth in four lakes of the Fraser River system. J.Fish. Res. Bd. Can. 31: 871-892.

Goodman, J.C. Notes on Birkenhead sockeye. Unpublished manuscript.

Hasler, A.D., A.T. Scholz, and R.M. Horral. 1978. Olfactory imprinting and homing in salmon. Am. Sci. 66: 347-355.

Healey, M.C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (Oncorhynchus keta) during early sea life. Can J. Fish. Aquat. Sci. 39: 952-957.

Hedrick, P.W. 1983. Genetics of Populations. Science Books International. Boston. 629 p.

Heggberget, T.G., R.A. Lund, N. Ryman, and G. Ståhl. 1986. Growth and genetic variation of Atlantic salmon (Salmo salar) from different sections of the River Alta, North Norway. Can. J. Fish. Aquat. Sci. 43: 1828-1835.

Henry, K.A. 1961. Racial identification of Fraser River sockeye salmon by means of scales and its applications to salmon management. Internat. Pacific Salmon Fish. Comm., Bull. IX, 97 pp.

Hogman, W.J. 1968. Annulus formation on scales of four species of coregonids reared under artificial condition. J. Fish. Res. Bd. Dan. 25: 2111-2122.

Hyatt, K.D., and J.G. Stockner. 1985. Responses of sockeye salmon (Oncorhunchus nerka) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. 42.: 320 331.

Killick, S.R. and L.E. Whitesel. 1954. Study of sockeye fry and migrants at Lillooet Lake. Unpublished manuscript.

Lee, R.M. 1912. An investigation into the methods of growth determination in fishes. Conseil Perm. Intern. Explor. Mer, Publ. Circ. 63. 35 p.

Lindsey, C.C. 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. Can. J. Fish. Aquat. Sci 38: 1497-1506.

Macdonald, P.D.M., and P.E.J. Green. 1985. User's guide to mix: An interactive program for fitting mixtures of distributions. Ichthus Data Systems. 28 p.

Macdonald, P.D.M., and T.J. Pitcher. 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Bd. Can. 36: 987-1001.

Naevdal, G. 1983. Genetic factors in connection with age at maturation. Aquaculture, 33: 97-106.

Neave, F. 1944. Racial characteristics and migratory habits in Salmo gairdneri. J. Fish. Res. Bd. Can. 6 (3): 245-251.

Neilson, J.D. 1984. Formation of otolith growth increments and their potential for assessing the early life history of chinook salmon (Oncorhynhus tshawytscha) Ph.D. Thesis. Simon Fraser Univ. 167 p.

Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Bd. Can. 28: 1503-1510.

Peterman, R. M. 1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (Oncorhynchus nerka) and implications for other salmon populations. Can. J. Fish. Aquat. Sci. 39: 904-913.

Polhemus, N.H. 1985. STATGRAPHICS: Statistical Graphics System Version 1.3. Statistical Graphics Corporation. Princeton N.J.

Refstie, T. and Steine. 1978. Selection experiments with salmon. III. Genetic and environmental sources of variation in length and weight of Atlantic salmon in the freshwater phase. Aquaculture 14A: 221-234.

Ricker, W.E. 1938. "Residual" and kokanee salmon in Cultus Lake. J. Fish. Res. Bd. Can. 4 (3): 192-218.

Ricker, W.E. 1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. J. Fish. Res. Bd. Can. 19: 531-560.

Ricker, W.E. 1972. Hereditary and environmental Factors affecting certain salmonid populations. In: The stock concept in Pacific salmon, R.C. Simon and P.A. Larkin, (ed). H.R. MacMillan lectures in fisheries. U.B.C. pp 19-160.

Robertson, O.H. 1957. Survival of precociously mature king salmon male parr (Oncorhynchus tshawytscha Juv.) after spawning. Calif. Fish Game, 43 (2):119-129.

Rogers. D.E. 1965. Variability in measurement of length and weight of juvenile sockeye salmon and threespine stickleback. Univ. of Washington, College of Fisheries, Circ. No. 224, 23 p.

Saunders, R.L., and C.B. Schom. 1985. Importance of the variation in life history parameters of Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 42: 615-618.

Schaefer, M.B. A study of the spawning populations of sockeye salmon in the Harrison River system, with special reference to the problem of enumeration by means of marked member. Internat. Pac. Salmon Fish. Comm., Bull. IV, 207 p.

Skurdal, J. and R. Andersen. 1985. Influence of temperature on number of circuli of first year scales of brown trout, Salmo trutta L. J. Fish. Biol. 26: 363-366.

Smale, M.A., W.W. Taylor. 1987. Sources of back-calculation error in estimating growth of lake whitefish. In: Age and Growth of Fish. R.C. Summerfelt and G.E. Hall (ed) Iowa Univ. Press. pp. 189-202.

Smith, S.B. 1955. The relation between scale diameter and body length of Kamloops trout, Salmo gairdneri kamloops. J. Fish. Res. Bd. Can. 12 (5): 742-755.

Smith, S.B. 1969. Reproductive isolation in summer and winter races of steelhead trout. University of British Columbia, H.R. MacMillan Lectures in Fisheries, Symposium on Salmon and Trout in Streams, p. 21-38.

Stockner, J.G. and K.S. Shortreed. 1983. A comparative limnological survey of 19 sockeye salmon (Oncorhynchs nerka) nursery lakes in the Fraser River system, British Columbia. Can. Tech. Rep. Fish Aquat. Sci. 1190: 63 p.

Thorpe, J.E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (Salmo salar L.) under artificial rearing conditions. J. Fish Biol., 11: 175-184.

Thorpe, J.E., C. Talbot, C. Villarreal. 1982. Bimodality of growth in Atlantic salmon, Salmo salar L. Aquaculture, 28: 123-132.

Van Oosten, J. 1929. Life history of the lake herring (Leucichthys artedi Le Sueur) of Lake Huron as revealed by its scales with a critique of the scale method. Bull. U.S. Bur. Fish., 44: 265-448.

Walters, C.J. and M.J. Staley. 1987. Evidence against the existence of cyclic dominance in Fraser River sockeye salmon (Oncorhynchus nerka). p 375-384. In H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (Oncorhynchus nerka) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

West. C.J., and P. A. Larkin. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (Oncorhynchus nerka) in Babine Lake, British Columbia. Can. J. Fish. Aquat. Sci. 44: 712-721.

Wetzel, R.G. 1975. Limnology. Saunders, Toronto. 743 p.

Winer, B.J. 1971. Statistical principles in experimental design. McGraw-Hill, New York. 907 p.

Withler, R.E., M.C. Healey, and B.E. Riddell. 1982. Annotated bibliography of genetic variation in the family Salmonidae. Can. Tech. Rep. Fish. Aquat. Sci. 1098: 161 p.

Woodey, J.C. 1987. In-season management of Fraser River sockeye salmon (Oncorhynchus nerka): meeting multiple objectives. p. 367-374. In H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (Oncorhynchus nerka) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Appendix 1.1: Summary of age 4_2 adult scale data examined for differences in scale growth between Birkenhead River and Weaver Creek sockeye for years 1973 and 1978.

CCANN: number of circuli to the freshwater annulus
DTEN: distance from the focus to the tenth freshwater circulus
DANN: distance from the focus to the freshwater annulus

		Birkenhead Sockeye			Weaver Sockeye		
Year	Variable	Mean	SD	N	Mean	SD	N
1973:	CCANN	14.2	2.71	100	16.3	1.64	100
	DTEN	0.318	0.0244	100	0.415	0.0261	100
	DANN	0.399	0.0610	100	0.558	0.0547	100
1978:	CCANN	14.1	1.80	97	15.4	1.67	103
	DTEN	0.318	0.0206	97	0.407	0.0319	103
	DANN	0.395	0.0463	97	0.530	0.0543	103

Appendix 1.2: Correlation coefficients between scale variables for age 4_2 adult Birkenhead River and Weaver Creek sockeye for years 1973 and 1978.

CCANN: number of circuli to the freshwater annulus
DTEN: distance from the focus to the tenth freshwater circulus
DANN: distance from the focus to the freshwater annulus

		Birkenhead Sockeye		Weaver Sockeye	
Year	Variables	r	N	r	N
1973:	CCANN-DTEN	-0.0220 ns	100	0.0946 ns	100
	DANN-DTEN	0.4103	100	0.6303	100
	DANN-CCANN	0.8372	100	0.7081	100
1978:	CCANN-DTEN	0.0066 ns	97	-0.2919	103
	DANN-DTEN	0.5132	97	0.4443	103
	DANN-CCANN	0.8279	97	0.6681	103

Appendix 1.3: Summary of weight (g) data by sampling date and regime for the 1983 fry rearing study.
Regime 1: Fish fed every day.
Regime 1: Fish fed every second day.
Regime 1: Fish fed every third day.

Weaver Creek Sockeye

		Regime 1			Regime 2			Regime 3		
Date	Day	Mean	SD	N	Mean	SD	N	Mean	SD	N
20-May	1	0.24	0.041	100	0.24	0.041	100	0.24	0.041	100
06-Jun	17	0.37	0.104	99	0.32	0.077	99	0.27	0.070	100
20-Jun	31	0.47	0.139	99	0.39	0.137	100	0.24	0.077	100
06-Jul	47	0.71	0.253	100	0.50	0.206	100	0.32	0.133	50
22-Jul	63	1.00	0.402	98	0.69	0.317	100	0.40	0.156	50
07-Aug	79	1.48	0.499	100	1.10	0.407	100	0.56	0.264	75
27-Aug	99	2.54	0.940	100	1.75	0.809	100	1.06	0.396	75
18-Sep	121	3.75	1.118	100	2.54	0.893	100	1.30	0.590	75
02-Oct	135	4.87	1.225	100	3.40	1.086	100	1.88	0.783	100

Birkenhead River Sockeye

		Regime 1			Regime 2			Regime 3		
Date	Day	Mean Weight	SD	N	Mean Weight	SD	N	Mean Weight	SD	N
20-May	1	0.22	0.041	100	0.22	0.041	100	0.22	0.041	100
06-Jun	17	0.36	0.085	99	0.31	0.079	100	0.27	0.074	100
20-Jun	31	0.46	0.124	100	0.34	0.097	100	0.27	0.080	100
06-Jul	47	0.70	0.204	100	0.48	0.154	98	0.33	0.118	100
22-Jul	63	0.99	0.306	100	0.68	0.233	98	0.51	0.241	100
07-Aug	79	1.46	0.445	100	1.02	0.319	100	0.58	0.237	100
27-Aug	99	2.19	0.660	100	1.54	0.538	99	1.00	0.372	100
18-Sep	121	3.08	0.718	99	2.07	0.666	100	1.16	0.410	100
02-Oct	135	3.70	0.933	100	2.50	0.813	100	1.51	0.498	100

Appendix 1.4: Summary of length (mm) data by sampling date and regime for the 1983 fry rearing study.
Regime 1: Fish fed every day.
Regime 1: Fish fed every second day.
Regime 1: Fish fed every third day.

Weaver Creek Sockeye

		Regime 1			Regime 2			Regime 3		
Date	Day	Mean	SD	N	Mean	SD	N	Mean	SD	N
20-May	1	30.2	1.15	100	30.2	1.15	100	30.2	1.15	100
06-Jun	17	33.9	2.41	99	32.6	2.74	99	31.6	1.77	100
20-Jun	31	35.9	3.01	99	34.1	2.74	100	31.9	2.06	100
06-Jul	47	40.1	4.12	100	35.9	3.99	100	33.0	2.89	50
22-Jul	63	44.5	6.00	98	39.5	5.42	100	33.8	4.76	50
07-Aug	79	50.5	5.46	100	44.8	5.44	100	36.8	4.76	75
27-Aug	99	59.1	7.04	100	51.7	7.99	100	44.2	5.42	75
18-Sep	121	68.0	6.61	100	59.4	6.98	100	48.6	7.15	75
02-Oct	135	73.2	5.87	100	64.0	6.99	100	52.5	6.54	100

Birkenhead River Sockeye

		Regime 1			Regime 2			Regime 3		
Date	Day	Mean	SD	N	Mean	SD	N	Mean	SD	N
20-May	1	29.9	1.20	100	29.9	1.20	100	29.9	1.20	100
06-Jun	17	33.3	2.25	99	32.1	2.11	100	31.3	2.03	100
20-Jun	31	36.3	2.82	100	33.1	2.41	100	31.9	2.10	100
06-Jul	47	39.6	3.51	100	35.9	3.11	98	33.3	2.79	100
22-Jul	63	44.6	4.51	100	39.7	4.00	98	36.3	4.84	100
07-Aug	79	50.7	4.95	100	44.5	4.44	100	37.0	4.78	100
27-Aug	99	57.1	5.77	100	51.0	5.77	99	44.2	5.22	100
18-Sep	121	64.9	4.86	99	56.9	5.69	100	47.3	5.50	100
02-Oct	135	68.0	5.32	100	59.2	6.36	100	50.3	5.36	100

Appendix 1.5: Summary of scale data for day 135 of the 1983 fry rearing study.
Regime 1: Fish fed every day.
Regime 1: Fish fed every second day.
Regime 1: Fish fed every third day.

Weaver Creek Sockeye

	Regime 1			Regime 2			Regime 3		
Variable	Mean	SD	N	Mean	SD	N	Mean	SD	N
S1C	0.0312	0.0078	100	0.0280	0.0068	98	0.0217	0.0055	96
S2C	0.0314	0.0060	100	0.0284	0.0073	98	0.0217	0.0057	95
S3C	0.0295	0.0061	100	0.0274	0.0050	96	0.0210	0.0053	93
S4C	0.0286	0.0059	99	0.0279	0.0059	95	0.0213	0.0059	88
S5C	0.0276	0.0060	99	0.0271	0.0060	95	0.0200	0.0057	76
S6C	0.0277	0.0064	99	0.0246	0.0058	93	0.0184	0.0066	59
S7C	0.0276	0.0059	93	0.0247	0.0058	82	0.0181	0.0074	34
RADIUS	0.322	0.047	100	0.280	0.050	98	0.194	0.049	96
CIRCULI #	9.44	1.23	100	8.70	1.58	98	6.96	1.81	96

Birkenhead River Sockeye

	Regime 1			Regime 2			Regime 3		
Variable	Mean	SD	N	Mean	SD	N	Mean	SD	N
S1C	0.0301	0.0068	96	0.0282	0.0067	97	0.0220	0.0058	97
S2C	0.0310	0.0081	96	0.0271	0.0056	97	0.0218	0.0057	96
S3C	0.0279	0.0052	96	0.0263	0.0060	97	0.0207	0.0056	94
S4C	0.0271	0.0052	96	0.0237	0.0047	95	0.0186	0.0055	89
S5C	0.0264	0.0053	95	0.0221	0.0051	92	0.0170	0.0045	71
S6C	0.0243	0.0059	93	0.0210	0.0061	84	0.0162	0.0046	46
S7C	0.0229	0.0064	85	0.0192	0.0067	61	0.0165	0.0047	19
RADIUS	0.291	0.042	96	0.245	0.047	97	0.182	0.040	97
CIRCULI #	8.60	1.07	96	7.81	1.3	97	6.40	1.53	97

S1C: space between 1st and 2nd circulus
S2C: space between 2nd and 3rd circulus
S3C: space between 3rd and 4th circulus
S4C: space between 4th and 5th circulus
S5C: space between 5th and 6th circulus
S6C: space between 6th and 7th circulus
S7C: space between 7th and 8th circulus
RADIUS: scale radius
CIRCULI #: circuli number