

**EFFECTS OF MIGRATORY CONSTRAINTS AND OCEAN CLIMATE ON THE BIOENERGETICS,  
FECUNDITY, AND MORPHOLOGY OF  
WILD, HOMING FRASER RIVER SALMON**

by

*GLENN T. CROSSIN*

B.A. The University of Maine, 1992  
B.Sc., Hon., The University of New Hampshire, 1995

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF  
MASTER OF SCIENCE

In

*The Faculty of Graduate Studies*  
(Department of Forest Sciences)

We accept this thesis as conforming  
to the required standard

.....  
.....  
.....  
.....

*The University of British Columbia*

June 2002

© Glenn T. Crossin, 2002

## Thesis abstract

*Adult sockeye salmon (Oncorhynchus nerka) depend on fixed somatic energy reserves to fuel their upriver migrations to spawning grounds and to complete sexual maturation before their inevitable death. These endogenous reserves are developed while feeding at sea, and are influenced by oceanographic factors (ocean currents and upwelling, temperature, zooplankton production). Upon return to the Fraser River, sockeye travel distances of <100 to >1100 km, and ascend elevations ranging from near sea-level to 1200 m to reach their spawning grounds throughout the diverse Fraser River watershed in British Columbia, Canada. I calculated the energy content of somatic and reproductive tissues and took several morphometric measurements in five populations of sockeye to examine how both energetic condition and morphology was influenced by migratory difficulty. Sockeye traveling to high and distant spawning grounds began their migration with higher levels of somatic energy and were smaller and more fusiform than those traveling to lower, less-distant grounds. The former were also less sexually developed at the start of migration, presumably a means for conserving energy necessary for upriver migration. These patterns were strongly correlated with the degree of upriver migratory difficulty each populations faces. Collectively, results suggest that upriver populations of sockeye are under strong selective pressure for bioenergetic efficiency. The importance of this efficiency diminishes as the difficulty of migration diminishes. Additionally, selection appears to favour an energetically efficient fusiform morphology in upriver populations.*

*Comparing recent bioenergetic and morphological data from five Fraser River sockeye and pink salmon (O. gorbuscha) populations and with data collected for each in the 1950s and in 1983 respectively, I looked to see whether a decadal-scale energetic shift has occurred in the energetic provisioning of salmon just prior to upriver spawning migration, and to associate these energetic shifts, if present, to conditions in the ocean environment. Historically, the climate of the North Pacific Ocean is known to oscillate between period of high and low pressure. However, since 1977, changes in ocean climate have been linked to anthropogenic CO<sub>2</sub> emissions. The affect on the ocean environment has resulted in broad-scale bio-physical changes that ultimately seem to affect both the acquisition and storage of somatic energy in Pacific salmon. I detected a decline in somatic energy in two upriver populations of Fraser River sockeye salmon between sampling decades, and show that in El Niño years, that this decline is amplified. I discuss these results in light of the recent climatological and oceanographic literature.*

## Table of Contents

Thesis abstract	2
Table of contents	3
List of Figures	5
List of Tables	6
Acknowledgements	8

Thesis overview	9
-----------------	---

### Chapter 1

<b>ENERGY ALLOCATION AND MORPHOLOGY OF WILD, ADULT SALMON: THE EFFECTS OF UPRIVER MIGRATORY DISTANCE AND ELEVATION</b>	<b>10</b>
--	-----------

Chapter abstract	10
------------------	----

Introduction	11
--------------	----

Methods	16
---------	----

Study system and development of migratory difficulty index	16
--	----

Sample collection	17
-------------------	----

Morphological measurements and analysis	18
---	----

Proximate analyses	19
--------------------	----

Upriver somatic energy partitioning	20
-------------------------------------	----

Results	21
---------	----

Migratory indices	21
-------------------	----

Morphological analyses	22
------------------------	----

Somatic energy partitioning and reproductive investment	13
---	----

Discussion	24
------------	----

Selection for energy efficiency and evidence for an energetic-morphological feedback mechanism	24
--	----

The role of body length in energy efficiency	29
--	----

Conclusion	30
------------	----

Literature cited	32
------------------	----

## Chapter 2

<b>CLIMATE CHANGE AND INTER-DECADAL SHIFTS IN PACIFIC SALMON BIOENERGY PRIOR TO UPRIVER MIGRATION</b>	<b>50</b>
Abstract	50
Introduction	51
Methods	53
Inter-decadal energy partitioning of river entry salmon	53
Energy partitioning during upriver migration	54
Results	55
Inter-decadal analysis: river entry sockeye and pink salmon	55
Inter-decadal analysis: partitioning between upriver activity and ovarian development in sockeye	56
Discussion	56
Bioenergetic changes associated with climate change	56
El Niño effects	57
Effects of anthropogenic climate change	59
Is climate change causing late-run Fraser River sockeye populations to migrate early?	61
Literature cited	64

## Chapter 3

<b>EVOLUTION OF BODY SIZE AND EGG SIZE IN PACIFIC SALMON, AND FUTURE WORK</b>	<b>74</b>
Literature cited	78

## List of Figures:

- Figure 1.1: Map of British Columbia, Canada, indicating the five major Fraser River sockeye spawning systems (areas encircled). 36
- Figure 1.2: Fraser River sockeye spawning ground elevations and distances. 37
- Figure 1.3: External morphological measurement made on sockeye salmon in this study. 38
- Figure 1.4: Fecundity (A), mean egg weight (B), and ovarian mass (C) of female sockeye in relation to migratory difficulty. Order of population points in each plot is: Weaver, Adams, Horsefly, Chilko, Early Stuart. Migratory difficulty index = migratory distance \* migratory elevation / 1000. Error bars are +/-SEM. All  $P < 0.01$ . 39
- Figure 1.5: Populations differences in body depth and girth upon arrival on the spawning grounds for females (A) and males (B). Error bars are +/-SEM. All  $P < 0.01$ . 40
- Figure 1.6: The relationship between body length and migratory distance in pre-spawning male ([B] POH: post orbital-to-hypural.) and female ([B] standard length: snout-to-hypural) Fraser River sockeye populations. Male plot is a re-analysis of data presented in Moore (1996), and focused on wild Fraser River sockeye only in years 1992-94. Triangles represent populations under examined in this study. Circles represent other Fraser River sockeye populations examined by FOC. 41
- Figure 1.7: A generalized schematic of female sockeye shape, when viewed head-on, at the beginning of their upriver spawning migrations. Shapes are derived from depth and width measurements. Termed o-index, values represent the quotient of body width and depth. O-index values are printed above each shape. Asterisks (\*) indicate populations that are statistically significant from one another ( $P < 0.01$ ). 42
- Figure 1.8: Protein and lipid percentages (A), gross energy concentrations (B), and gross energy depletion (C) in the soma of Fraser River sockeye populations collected in 1999. Dashed lines in B and C represent the approximate energetic threshold between life and death for most sockeye. Sexes are pooled. Error bars are +/-SEM. 43
- Figure 1.9: Rates of somatic expenditure (swimming expenditure) and ovarian investment from time of Fraser River entry to arrival on spawning grounds. Error bars are +/-SEM. 44
- Figure 1.10: Conceptualization of an adaptive energetic-morphological feedback mechanism, driven by selection for energy efficiency, designed to enhance the

fitness of upriver migrating sockeye salmon.	45
FIGURE 2.1: Scatterplot of scores for the first two PC axes. The first axis represents sites ranging from low to high GSI scores. The second axis represents sites ranging from low to high somatic lipid concentrations. Points represent stock-sex-year means. Ellipses were drawn around population groups. Dark circles represent 1950s data. Open circles are for 1999 and 2000 data.	68
Figure 2.2: Mean (+/- SE) gross somatic energy concentrations in Fraser River entry Chilko sockeye salmon. Values printed in bars are mean monthly SSTs at a coastal BC lighthouse station for a six month period prior to upriver migration. Raw data for 1959 were not available so SE could not be calculated.	69
Figure 2.3: Inter-decadal comparison of somatic energy expenditure as a function of migratory distance from the mouth of the Fraser River in the Early Stuart sockeye population. 1956 data point to the left of the y-axis present sockeye collected in the marine environment. Dark symbols are for sampling years in the 1950s. Open symbols are for recent collections. Dashed line represents the approximate energetic threshold between life and death for sockeye salmon.	70
Figure 2.4: Percent somatic protein and lipid concentrations in Fraser River pink salmon measured at the Fraser River entry in 1983 and 1999. Error bars are +/-95% confidence intervals.	71
Figure 2.5: Mean (+/-) somatic energy partitioning during upriver migration in female Fraser River sockeye.	72

**List of Tables:**

Table 1.1: Run times, spawning ground characteristics, and river temperatures specific to the Fraser River sockeye populations sampled in 1999.	46
Table 1.2: Linear R <sup>2</sup> values for river-entry and pre-spawning female energetic and morphological attributes regressed against migratory difficulty, distance, elevation, degree-days, and mean river temperature.	47
Table 1.3: Proximate composition (by wet mass) of somatic and reproductive tissues, and gross somatic energy densities in upriver migrating Fraser River sockeye collected in 1999.	48
Table 1.4: Somatic energy used for swimming and standard metabolic processes	

and for reproductive tissue development during the upriver migration of five Fraser River sockeye populations. Units are  $\mu\text{J}$  / unit of migratory difficulty. 49

Table 2.1: Pearson correlation coefficients (upper value) and associated probabilities (lower value) relating log10-transformed somatic protein, lipid, GSI, and length values in sockeye at end of ocean residency, with PC1 and PC2 factor scores from interdecadal PCA analysis. 73

## **Acknowledgements**

This broad-scale project was made possible with the help of many people. I'd like to extend particular thanks to my advisor Scott Hinch for providing sound direction, and to committee members Michael Healey, Kathy Martin, and Dave Higgs. Thanks also to Tony Farrell and Andrew Lotto for various insights. Jim Woody, Mike Lapointe, and Jim Cave at the Pacific Salmon Commission also provided many valuable insights.

Thanks to FOC personnel Ian Barnes, Vic Euwert, Colin Harrison, Doug Lofthouse, Ken Peters, and Pieter Van Will for help with river sampling and logistics. Tracy Cone provided me with historical biological and environmental data. Jan Carlson and his crew provided help with gill-net sampling in the lower Fraser. Steve Macdonald and Dave Patterson provided data and insights regarding Early Stuart sockeye. Mamhoud Rowshandeli and Janice Oakes at the West Vancouver Laboratory provided logistical and lab assistance. Jim Helfield provided feedback and comments. Cheryl Bullock, Shannon Maclaughlin, Elena Middlecamp, Trevor Nowak, Yuho Okada, Kate Shapiro, Jason Turner, and Mark Whelly provided lab and field assistance. The HHH group at UBC and Pete Rand provided many additional insights. Funding for the research was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Grant to Mike Healey, Scott Hinch and Anthony Farrell, and an NSERC Research Grant to Scott Hinch. My stipend was provided by the Strategic Grant and a partial international student tuition waiver by the Faculty of Forestry, University of British Columbia.

## Thesis overview

In this thesis, I set out to describe how the energetic and morphological characteristics of Fraser River sockeye salmon (*Oncorhynchus nerka*) populations are affected by two sets of environmental conditions: 1) upriver migration distance and spawning ground elevation, and 2) ocean climate.

Chapter 1 examines the responses of five populations of Fraser sockeye to constraints imposed on upriver migration by the distance traveled, and the elevation gained *en route* to spawning grounds. The populations under study traverse a broad range of distances (100km to excess of 1200km upriver), and elevations (near sea level to 1200m), which has allowed life-history variation to evolve. Because sockeye rely solely on endogenous energy reserves to provide the metabolic fuel for migration, and because they are semelparous with a single life-time opportunity to spawn, migratory difficulty imposes significant selective pressure on the energetic tactics used when migrating upriver. I found evidence of reproductive trade-offs among populations with respect to the degree of migratory difficulty that each faces *en route* to spawning grounds. These trade-offs involved an increase in somatic energy in populations making arduous migrations, but a reduction in reproductive investment (i.e., egg production and expression of secondary sex characteristics).

Chapter 2 examines the influence of ocean climate on the provisioning of somatic energy needed for upriver migration. Since the 1950s, the North Pacific Ocean has experienced two substantial climatological shifts, the first in 1977 and the second around 1989. Evidence for a third shift in 1997 has recently surfaced. Associated with these changes in climate are changes in ocean upwelling, primary production, and sea-surface temperature. Comparing energetic and morphological data from Chapter 1 with that of sockeye collected in the 1950s, I discussed how these bio-physical changes occurring in the ocean environment have influenced the provisioning of somatic energy reserves in sockeye between sampling decades. I also collected Fraser River pink salmon (*Oncorhynchus gorbuscha*) in 1999 and compared data with those of pink salmon collected in 1983. Since the 1950s, I have observed a decline in energy partitioning in sockeye, which seems the result of both diminished zooplankton production and increases ocean temperatures. Energetic data collected during the 1959, 1983, and 1997 El Niño events for both species revealed that energy levels were further reduced relative to 1999 reductions, indicating that these anomalously strong climatological events have additionally pronounced effects on

aspects of the ocean environment that influence the acquisition and storage of somatic energy in Pacific salmon.

Chapter 3 is a discussion of the factors affecting the evolution of egg sizes in Pacific salmon, and highlights some of the recent literature on this difficult topic. Future avenues of research are proposed to address this topic, which ultimately is related the evolution of body sizes in salmon.

## CHAPTER 1

### ENERGY ALLOCATION AND MORPHOLOGY OF WILD, ADULT SALMON: THE EFFECTS OF UPRIVER MIGRATORY DISTANCE AND ELEVATION

Published as Crossin, G.T., S.G. Hinch, A.P. Farrell, D.A. Higgs, A.G. Lotto, J.D. Oakes, and M.C. Healey. (2004) Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology* 65:788–810.

#### ABSTRACT

Adult sockeye salmon (*Oncorhynchus nerka*) depend on fixed somatic energy reserves developed during ocean residency to fuel their upriver migrations to spawning grounds and to complete sexual maturation. Depending on population, Fraser River sockeye travel distances of <100 to >1100 km, and ascend elevations ranging from near sea-level to 1200 m to reach their spawning grounds throughout the Fraser River watershed in British Columbia, Canada. In 1999, I collected live sockeye from five major populations arriving at the Fraser River mouth and on the spawning ground, as well as post-spawning moribund carcasses. I calculated the energy content of somatic and reproductive tissues of these sockeye and made several morphometric measurements to examine how energetic condition and morphology was influenced by migratory difficulty. Sockeye travelling to high and distant spawning grounds began their migration with higher levels of somatic energy, were smaller and more fusiform than those travelling to lower, less-distant grounds, and had diverted less somatic energy to ovarian development relative to coastal sockeye, presumably a means for conserving energy necessary for upriver migration. Migratory difficulty (a composite index of distance and elevation) was found to be strongly associated with initial energetic state and was a stronger predictor of en-route energy-use than either migratory distance or elevation individually, and mean migratory degree-days. Collectively, these results suggest that upriver populations of sockeye are under strong selective pressure for bioenergetic efficiency, and energy reserves prior to upriver migration are likely genetically predetermined. The importance of this efficiency diminishes as the difficulty of migration diminishes. In upriver populations, ovarian investment is traded for energy efficiency to make available the free energy needed for difficult upriver runs. Additionally, selection appears to favor an energetically efficient fusiform morphology in upriver populations.

## INTRODUCTION

The tendency for organisms to occupy new niches and expand their breeding distributions is fundamental to the evolutionary process (Stearns 1992). Homing by Pacific salmon (*Oncorhynchus* spp.) to their natal freshwater systems provides a window through which to observe an important component of this process, that of local adaptation. Though local adaptation is somewhat difficult to measure empirically, homing has resulted in the formation of discrete breeding populations whose phenotypic signatures often correlate strongly with features of the natal environment (Taylor and McPhail 1985; Quinn and Dittman 1990). Such correlations offer us small glimpses into the theoretical workings of adaptive radiation, and beyond toward evolution. From an energetic and morphological point of view, this is well illustrated in migrating, adult sockeye salmon (*O. nerka*).

Each year, adult sockeye swim long distances from oceanic feeding grounds in the North Pacific to their natal streams and lakes where they court and spawn (Burgner 1991). Because most sockeye populations are dependent on lake systems for the rearing of their fry, sockeye may swim as little as 10 km to as much as 1150 km upriver, depending on the accessibility of suitable lakes. Though the bulk of the world's sockeye populations spawn in coastal lake systems, with migration distances typically under 100 km and elevations near sea level, the Fraser River in British Columbia contains populations that swim great distances and ascend high elevations, providing a broad environmental gradient upon which natural selection can operate.

Regardless of the relative difficulty of a sockeye's migration path, upriver runs to spawning grounds are energetically demanding (Burgner 1991; Hinch and Rand 1998). Sockeye typically expend 75-95% of their somatic lipid reserves, and 40-60% somatic protein (Gilhausen 1980; Hendry and Berg 1999). Furthermore, sockeye begin fasting when they return to freshwater and remain non-consumptive throughout the course of their spawning migration. Coupled with the fact that they, as all Pacific salmon, have only one opportunity to migrate upriver and spawn successfully before their inevitable death (semelparity), it is profoundly important for them to have sufficient somatic energy reserves in place to fuel migration, complete sexual maturation, and support the behaviors and morphological changes associated with courtship and spawning (Burgner 1991; Brett 1995). Because sockeye are highly fidelitous to their streams of origin, the selective pressures operating within each population's natal watershed, and *en route* to these watersheds, should allow adaptive distinctions between

populations to emerge, and a streamlining of energy allocation to these tasks (Idler and Clemens 1959; Fleming and Gross 1989).

Variation in somatic energy reserves at the onset of upriver migration has been documented previously among Pacific salmon populations. Somatic energy reserves between coastal and upstream populations of chum salmon (*O. keta*) show a high degree of variability (Brett 1995). Studies of Fraser River sockeye in the 1950's suggest that energy reserves for salmon travelling on long upriver migrations may be higher relative to those populations making shorter migrations (Idler and Clemens 1959, reviewed by Gilhousen 1980). A bioenergetic review by Bernatchez and Dodson (1987) compared somatic costs of short- and long-distance anadromous fish and found that long-distance fish, particularly Pacific salmon, minimized energetic transport costs by swimming at optimal speeds. A more recent study by Hendry and Berg (1999) examined in detail the partitioning of somatic energy among short distance sockeye populations in Alaskan streams. They compared their results with those from the 1950's work and showed that relative to long distance Fraser populations, coastal populations began upriver migration with much smaller somatic energy reserves. However, inconsistencies in sample collection and method in the 1950's studies have precluded any in-depth analysis among populations; sockeye were sampled at varying stages of migration and maturity (sometimes in small samples sizes), were sampled in different years and watersheds, and in some studies, hatchery populations were considered. Comparisons between studies have proved insightful, but as there is much year-to-year variability in ocean climate, influencing oceanic density dependent mechanisms and the size-at-maturity of sockeye (Cox and Hinch 1997), and potentially the energetic signatures at the start of upriver migration (G.T. Crossin, unpublished data), it has been difficult to piece together a comprehensive picture of the adaptive patterns that emerge among wild, migrating sockeye populations.

Variation in morphology among populations has also been documented in sockeye, revealing that coastal sockeye tend to be deeper bodied and larger than their longer-distance migrating, upriver relatives (Moore 1996; Blair et al. 1993; Hendry and Berg 1999). A suite of selective forces can contribute to variation in morphology. Determining which are at play however depends on context. Studies of sockeye populations migrating through small, coastal watersheds, have identified migratory distance as well as stream characteristics, predation, and sexual competition as strong selective pressures that can influence morphology (Blair et al. 1993;

Quinn et al. 1995; Woody et al. 2000). Morphological variation has also been linked to breeding competition (Fleming and Gross 1989), as well as the rigors of migration (Taylor and McPhail 1985) in coho salmon (*O. kisutch*). Constraints associated with migratory distance have also shaped morphological differences among populations of juvenile Atlantic salmon (*Salmo salar*; Riddell and Leggett 1981). In the context of the Fraser River however, where massive pre-spawning mortality can occur *en route* (see Macdonald et al. 2000), the severe energetic constraints associated with sockeye migration may supercede those imposed by other selective agents, particularly in populations making difficult migrations.

Morphological changes occurring during migration tend to occur late in upriver migration, after energy has first been channeled to the physical demands of migration (Moore 1996; Hendry and Berg 1999). Migrating sockeye gradually lose their streamlined, ocean morphology as they approach the spawning grounds, and develop the humped backs, hooked snouts, red bodies, and green heads characteristic of spawning salmon. These new traits are necessary for the complexities of courtship, redd construction, and redd defense, but their expression probably diminishes the hydrodynamic benefits associated with their once fusiform, oceanic body shape. Thus, it would be energetically adaptive for sockeye to delay both the expression and magnitude of those traits until the constraints imposed by upriver migration have been overcome.

I propose that the constraints associated with migration are the principal drivers of energetic and morphological variation among Fraser River sockeye populations. To examine this, I had three objectives. First was to understand how migratory difficulty has shaped the pre-migratory partitioning of somatic and reproductive energy among different populations of adult sockeye to best prepare them for the environmental features that they will encounter when homing to their natal systems. Two of the most conspicuous environmental characteristics encountered along a population's migration path are the distance to and elevation of the spawning grounds. Both have physiological relevance: spawning ground elevation provides a relative estimate of river gradient and currents regimes likely to be encountered, and migratory distance provides an estimate of the time, as well as total effort, spent traversing that gradient. Migratory distance has been used traditionally as the chief measure of migratory difficulty in studies of fish migratory energetics (Gilhousen 1980; Brett 1995; Hendry and Berg 1999). Migratory elevation has been examined in only one previous Pacific salmon energetic study

(Gilhousen 1980) and one morphological study (Moore 1996), but its role as a physical constraint to migration received little discussion, mostly because migratory distance better explained the differences observed among populations. Because river gradient and discharge are likely related to spawning ground elevation, and as long distance migrants generally spend more time traversing a river gradient relative to short distance migrants, I suspect that both migratory distance and elevation will do well in explaining the energetic and morphological differences observed among populations.

Water temperature is also known to affect metabolic rates in fish, but usually involves increases in standard metabolism. Its affect as a migratory constraint, and on the expenditure of finite energy reserves, is probably negligible. Simulations of metabolic power consumption in migrating Early Stuart sockeye found river temperature to be a fairly insensitive parameter relative to river discharge rates, which are indirectly determined by elevation (Rand and Hinch 1998). Nevertheless, I examined its affect as a possible migratory constraint in addition to migratory distance and elevation.

Our second objective was to examine morphological changes among and within populations at the start of upriver migration and upon arrival at the spawning grounds. It has been shown that female sockeye gradually develop their ovaries as they make their way upriver, and that the expression of secondary sexual characteristics of males and females are similarly delayed with freshwater migration distance (Gilhousen 1980; Moore 1996; Hendry and Berg 1999), presumably to ensure that the demands of swimming are first met. Rearing experiments by Moore (which involved only male sockeye) found that morphological variation among males met two of three criteria for it to be deemed adaptive (as defined by Taylor 1991), suggesting that phenotypic variation among male sockeye is not simply an expression of plasticity. Considering that females are generally under more restrictive energy budgets than males, I predicted that morphological variation in both females and males would be expressed as an inverse function of the energetic constraints imposed along each populations migratory route.

Our third objective was to trace the partitioning of somatic energy into both ovarian development and upriver swimming among populations, and to look for evidence of reproductive trade-offs in relation to migratory constraints. I also considered these patterns relative to other species and to predictions of energy allocation in life-history theory. Complementary to my predictions of morphological variation, I predicted that energy allocated

ovarian development (i.e. egg production) would be diminished in the face of difficult upriver migrations.

## METHODS

### *Study system and development of migratory difficulty index*

I examined the influence that local environmental features have on the morphology of upriver migrating, wild adult sockeye, and the patterns of somatic and reproductive energy allocation *en route*, by systematically sampling sockeye from five populations in the Fraser River watershed of British Columbia, Canada (Figure 1). The Fraser River offers a good natural laboratory for studies of this sort as native populations traverse a broad environmental gradient when homing to their spawning systems, ranging from low coastal systems to inland plateau and mountain systems.

The Fraser River watershed drains nearly a third of the province of BC and is the largest producer of sockeye in Canada (Dorcey 1991). Extending from headwater streams in the Rocky Mountains, the mainstem runs 1378 km to its mouth at Vancouver. Among its many tributaries are several highly productive sockeye lake systems, lying at various distances from the ocean and at various elevations above sea level (Figure 2). Because most sockeye rely on lakes as nurseries for their young, a broad range of migratory distances and elevations are traversed for access to these lakes. Additionally, there is a broad range of temperatures encountered in the various tributaries leading to these nursery lakes (Table 1).

I sought to determine which environmental variables had the greatest effect on the partitioning and expenditure of somatic energy as sockeye make their way upriver: migratory distance, migratory elevation, migratory distance-by-elevation, and degree-days accumulated while *en route*. Migratory distance and elevation are two variables that have great physiological relevance, and have presumably affected the evolution of pre-migratory partitioning of somatic and reproductive energy, and rates of somatic expenditure and ovarian investment. Thus, I developed a composite variable by multiplying distance and elevation to explore the effect of these correlated environmental characteristics. Because distance provides a surrogate for total migratory time and effort, and because elevation is a surrogate for current velocity, time-at-velocity, a multiplicative function, describes a range of energetic constraints salmon will encounter when migrating upriver.

Using upriver distances and elevations published in Gilhousen (1980), I regressed population specific energetic and morphological attributes against migratory distance, elevation, and distance\*elevation to view among population patterns that have presumably evolved through divergence and reproductive isolation. Whonnock, BC was the point of river-entry from which upriver migratory distances were calculated (Figure 1).

Using temperature data provided by Fisheries and Oceans Canada (FOC), who maintain temperature data loggers at several stations along the Fraser River mainstem and spawning tributaries (see Macdonald et al. 2000), I calculated the number of migratory degree days encountered by each population in the 1999 season. Sockeye data were regressed against these variables in a manner identical to that listed above.

In total, I regressed four variables (migratory distance, migratory elevation, migratory distance-by-elevation, and degree-days accumulated while *en route*) against sockeye morphological attributes to determine which best explained the variation observed among populations (i.e. best  $R^2$ ; Table 2).

### *Sample collection*

In 1999, I collected migrating sockeye from five populations that differ in their total upriver migratory distance, elevation, and encountered river. Salmon were collected at Fraser River entry, spawning ground arrival, and immediately post-spawning (Figure 1). All spawning ground Early Stuart sockeye were collected by FOC, and were taken from the Kynoch Creek sub-population. Spawning ground Chilko sockeye were collected from the spawning grounds located at the Chilko lake outlet. Spawning ground Adams sockeye I collected in the along the Adams river, just upstream from its delta on Shuswap Lake. Spawning ground Horsefly and Weaver sockeye were collected at the spawning channels maintained by FOC. Because FOC and the Pacific Salmon Commission (PSC) manage Fraser River sockeye largely by population (or stock) groupings, population run-times are well known (see also Hodgson and Quinn 2002). To successfully collect river-entry sockeye for this study, a PSC test fishery gill-net vessel operating at Whonnock, BC, targeted upriver migrating stock groups that historically contain the populations of interest to this study. The identity of each individual fish from the gill-net catch was then determined by scale and internal parasite analyses at the PSC laboratory. As most sockeye spend their first year and sometimes second years of life in lakes, their first and second

scale annuli show patterns that reflect the temperature regimes specific to their natal lakes (Cook and Guthrie 1987). Additionally, internal parasites unique to each lake system (affecting sockeye fry) can also reveal population identity (Mike Lapointe, Pacific Salmon Commission, Vancouver, BC, personal communication; see also Bailey et al. 1988).

All river-entry sockeye were collected through the gill-net test fishery administered by the PSC at Whonnock, British Columbia. When caught, all fish had numbered tags attached to their gill operculi, and tissue and scale samples were taken for stock identification by the PSC. Each fish was then packed on ice. Once identified to stock, I retrieved 10 males and 10 females from each population of interest. I also collected fish from each population upon their arrival on the spawning ground, and another set of fish from these areas immediately after spawning (termed moribund carcasses). From each sampled set, 10 males and 10 females were collected on site by dipnet, placed in sealed plastic bags, and packed in ice until processing.

#### *Morphological measurements and analyses*

For each individual fish, I recorded whole and eviscerated weights (whole less gonads and viscera) to the nearest gram. Body measurements included fork length (tip of snout to tail fork), post-orbital hypural length (POH), body depth (perpendicularly from the anterior insertion of the dorsal fin to the abdomen), and body width (horizontal cross-section at the lateral line, perpendicular to anterior insertion of the anal fin), all measured to the nearest millimeter (Figure 3). The ratio between body width and body depth I termed the “o-index”. This morphological index reflects two important energy investment pathways: body depth as a qualitative measure of investment to secondary sexual characteristics, and body width as a measure of the somatic lipids stored for the coming migration.

Eggs measurements were taken for all river-entry and spawning ground arrival females. From each female, 10 fresh eggs were removed and weighed to the nearest milligram (see Fleming and Ng 1997). After dissection, reproductive and visceral tissues were weighed individually, packed in air-tight plastic freezer bags, and stored at -20°C for proximate analysis. Gonado-somatic index (GSI) was calculated as the quotient of gonad mass to eviscerated body mass, multiplied by 100. Eviscerated carcasses were homogenized with an industrial food processor (Robot Coupe Blixer BX6V). A 250 g sub-sample of the homogenate was removed, packed in airtight plastic freezer bags, and stored at -20°C until analysis.

Additional data for exploring among-stock relationships were provided by FOC. These included spawning ground female standard length data (1992), male post-orbital length data (1992-3), and fecundity data (1999).

When making comparisons among populations, data were analyzed by the general linear models analysis of covariance (proc glm, ANCOVA, Type III Sums-of-squares, SAS Institute, Inc. 1988) to remove the allometric effects associated with body length. In these analyses, individual morphological features were the dependent variable, and length was the independent variable. If the test for heterogeneity of slopes proved non-significant, then the interaction term was removed from the model. Alpha was set a 0.05. Least squares means comparisons were used as the *a posteriori* method.

### *Proximate analyses*

All somatic and reproductive samples were analyzed for their respective concentrations of proximate constituents (lipid, protein, water and ash) according to the methods outlined by Higgs et al. (1979). Water content was determined by drying 2.0 g of each homogenate at 100°C for 24 hours. Ash was determined by combusting the dried sample at 600°C for two hours. Water and ash content were calculated as percentages by wet weight. Lipids were determined by wet mass through a 1:1 chloroform-methanol extraction of 2.0 g sample of each tissue homogenate (Bligh and Dyer 1959). The protein content of each 0.5 g somatic sample was determined as total (%) Kjeldahl nitrogen (TKN-macro Kjeldahl procedure). Protein and lipid percentages were converted to their energetic equivalents by multiplying percent (by wet mass) by 0.02364 MJ kg<sup>-1</sup> for protein and 0.03954 MJ kg<sup>-1</sup> for lipid (Higgs et al. 1979).

Somatic energy values determined through proximate analysis are believed comparable to values derived through direct bomb-calorimetry, which is believed a more accurate method for energetic determinations. A subset of samples was analyzed through bomb-calorimetry to ensure that the proximate method generated comparable and accurate values (D. Higgs and J. Oakes, West Vancouver Laboratory, West Vancouver, BC, unpublished data). By doing so, it was discovered that the Kjeldahl method underestimated the protein content of sockeye testes, primarily due to the energy conversion factor used to estimate testicular protein concentrations. In general, percent Kjeldahl nitrogen in biological samples represents 16% protein, thus a factor of 6.25 is used to convert percent nitrogen to percent protein. However, amino acid profiles of

the testes revealed that this conversion factor is inaccurate for estimation of testicular protein concentrations (D. Higgs and J. Oakes, West Vancouver Laboratory, West Vancouver, BC, unpublished data). Owing to the expense of using total amino acid levels as a reliable method for protein estimation in the testes, the following indirect method was employed. In proximate analysis, the sum of water, ash, protein and lipid equals 100% (carbohydrates contribute negligibly at <0.05%). Thus, by subtracting water, ash, and lipid percentages from 100, protein percentages can be indirectly determined. This method has been employed in previous studies (Berg et al. 1998; Hendry and Berg 1999; Hendry et al. 1999), and values reported were within one percentage point of those determined through the Kjeldahl method (Jonsson et al. 1991). A preliminary comparative analysis of the 1999 somatic data was nearly identical to that of Jonsson: in all cases, protein values calculated indirectly from somatic data were within one percentage point of values determined through the Kjeldahl method, thus I felt confident using the indirect protein determination method for reproductive tissues. Statistical comparison of proximate compositions among the five sockeye populations were made through ANCOVA in a manner identical to that used in the morphological analyses listed above.

Preliminary analyses of sub-samples of visceral tissues revealed that gross somatic energy densities (that included both soma and viscera) were nearly identical to those of somatic tissues alone (less viscera). Because visceral energy made such a small contribution to total energy, I did not consider them in further analyses.

#### *Upriver somatic energy partitioning*

While migrating upstream, sockeye partition somatic energy to a number of tasks. Energy is needed for standard metabolism, swimming and other behaviors, gonadal maturation, and development of secondary sexual characteristics. Because sockeye are capital breeders, relying on fixed somatic energy reserves to accomplish these tasks, the amount of energy invested in the gonads when homing upriver comes directly from somatic reserves. Employing a regression technique used in previous salmon energetic studies, I estimated the amount of somatic energy partitioned to swimming activity within each population during upriver migration by regressing  $\log_{10}$  transformed mass-specific somatic energy (at river-entry and spawning ground arrival) against body length (Jonsson et al. 1997; Hendry and Berg 1999). ANCOVA was used to detect heterogeneity of slopes between the river-entry and spawning

ground arrival somatic sample. If no significant effect was detected, the difference in intercepts between river-entry and pre-spawning, somatic, mass-specific energy can be used to estimate the amount of energy partitioned to general upriver swimming activity (active and standard metabolism). Estimation of ovarian investment was done in an identical manner, comparing the intercepts between river-entry and spawning ground ovarian energy.

## RESULTS

### *Migratory indices*

The highest  $R^2$  values for energetic and morphological variables were consistently generated when regressed against the composite migratory distance-by-elevation variable. Migratory degree days provided only modest fits to the data. Migratory distance and elevation both provided reasonably good fits. However, these two variables were highly correlated, precluding their use as complementary independent variables. Thus, all somatic energetic and morphological data presented forthwith were compared with the composite distance-by-elevation variable, which I will refer as the “migratory difficulty index” (Table 1).

The five populations that I sampled fell into three general levels of migratory difficulty: Weaver sockeye make the least difficult migrations, Chilko, Early Stuart, and Horsefly sockeye cluster together at the more difficult end, and Adams is intermediate (Table 1 and Figure 2). Though Chilko, Early Stuart and Horsefly occupy spawning grounds that differ in migratory distance and elevation, the relative distance of each plotted point from the graph’s origin is roughly the same. Thus, they cluster into a common category of difficulty.

### *Morphological analyses*

ANCOVA revealed that all morphological attributes were associated with body length within populations (all  $P < 0.05$ ). However, slopes were homogenous among populations and collection locations. Within each population, body depth for both males and females, ovarian mass, individual egg mass, and egg number increased between river-entry and spawning ground arrival (Figures 4 a,b,c and 5 a,b). Among populations however, these attributes were negatively associated with migratory difficulty (ANCOVA, all  $P < 0.05$ ; Figures 4 a,b,c and 5 a,b). Body width generally decreased between river-entry and spawning round arrival (Figure 5 a,b). Among populations, the largest traits were expressed by Weaver sockeye, and the smallest by

Chilko and Early Stuart, following the migratory difficulty index (Figures 4 a,b,c and 5 a,b). Depending on the population, ovarian weight increased 43-72% from river-entry to spawning ground arrival. Additionally, egg weight increased by 38-60%, and egg number (fecundity) increased by 10-41%. Female body depth increased by 1-3%, but body width decreased from 3-26%. Males followed similar overall trends but with much more variability in some traits (body depth increased by 1-16%, body width decreased by 12-24%, see Figure 5b). Both male and female body length showed a strong negative association with migratory difficulty (male  $R^2=0.86$ , female  $R^2=0.83$ . Figure 6 a,b). Figure 6a is a re-analysis of data presented in Moore (1996) and is restricted to wild Fraser River populations only in years 1992-94 when ocean climate (which have known effects on size at maturity) was comparable (see Chapter 2). Data for figure 6b are from FOC Stock assessment for the same years.

Both males and females from the Chilko and Early Stuart populations began their upriver migrations with a more fusiform, torpedo-like shape than the broader, deeper-bodied Weaver sockeye (ANCOVA of o-index measures,  $P<0.05$ , Figure 7). Among populations, the magnitude of body depth was greatest when migratory difficulty was low, and body width was greatest when difficulty was high. Thus, the more difficult a population's migration route, the closer the ratio of depth-to-width approached one, and the closer body shape (when viewed head-on) approximated a circle. This measure did not differ between whole and eviscerated sockeye, thus ovary mass, which can be quite substantial, did not affect this measure. O-index measures of Weaver were not significantly different from those of Adams, but were from Chilko and Early Stuart ( $P<0.05$ ); Adams was intermediate between the two.

#### *Somatic energy partitioning and reproductive investment*

Proximate composition values for all samples showed that sockeye populations making long distance and high elevation migrations possessed greater energy reserves, particularly lipid reserves, at the start of upriver migration compared with populations making less distant, low elevation migrations (Figure 8a). Regardless of somatic starting energy concentration, all populations arrived on the spawning grounds with near similar energy levels, with the exception of Chilko sockeye, which arrived with smaller ovaries and higher energy reserves relative to the others. There was no sex effect on gross somatic energy, lipid, and protein concentrations in river-entry sockeye, nor on gross somatic energy and lipids in spawning ground arrival sockeye,

(all  $P > 0.05$ , Table 3). However, a sex-effect was detected among spawning ground arrival protein concentrations ( $P = 0.045$ ), due to the difference observed between Weaver males and females (Table 3). Nevertheless, sexes were thus pooled in comparisons among river-entry, spawning ground arrival, and post spawned moribund sockeye (Figure 8 a,b,c). In Figure 8c, the first point on each populations line is river-entry gross somatic energy, the second point is at spawning ground arrival, except for Early Stuart which is at Hell's Gate, and the last point is post-spawned moribund. Post spawned Early Stuarts were not collected in 1999, thus the third point is spawning ground arrival.

Water was always the greatest constituent in both somatic and reproductive tissues (64-82% soma, 55-82% gonads), followed by protein (13-20% soma, 56-62% gonads), lipid (1-13% soma, 12-16% gonads), and ash (2-3% soma, 2-5% gonads) (Table 3). From river-entry to spawning ground arrival, sockeye expended 7-20% of somatic proteins, and 60-86% somatic lipids when traveling from river-entry to the spawning grounds. This represents a 30-53% loss of gross somatic energy reserves. From spawning ground arrival to death after spawning, sockeye expended 10-25% of their remaining somatic proteins and 30-50% of lipids, representing a loss of 15-30% gross energy (Table 3).

Gross energy concentrations in the both the ovaries and testes did not change substantially from river-entry to spawning ground arrival. However, ovarian weight changed substantially over this period, thus mass specific (total) energy increased from 40-58% for females, but only about 2% for males (Table 3).

Of the total amount of somatic energy spent during upriver migration, migrating female sockeye channeled approximately half into ovarian development, and half into other activities (predominantly swimming activity costs) (49-56% and 43-51% respectively; Figure 9), regardless of population. I must caution that activity costs are inferential, determined by the amount of energy lost from the somatic tissues minus that diverted into the ovaries which I could measure directly. Having accounted for ovarian investment, and knowing that standard metabolism is small in migrating sockeye, any further somatic energy loss is most likely attributable to swimming activity costs (Hinch and Rand 2000). However, there were population-specific differences in the absolute amounts of energy expended to each task. Weaver females, for example, allocated 1.44 MJ of somatic energy into upriver activity, while Chilko females allocated 2.02 MJ to the same task (Figure 9). Rates of energy expenditure and

ovarian investment however differed significantly among populations ( $P < 0.01$ ), becoming increasingly more efficient as migratory difficulty increased. Chilko and Early Stuart sockeye channeled 2.8  $\mu\text{J}$  and 3.1  $\mu\text{J}$  of energy per unit of migratory difficulty toward upriver activity, compared to Weaver sockeye which channeled 1440.0  $\mu\text{J}$  per unit of migratory difficulty. However, Weaver and Chilko/Early Stuart represent just two extremes in the migratory continuum. Rates of upriver somatic energy expenditure and ovarian investment became exponentially more efficient, per unit of migratory difficulty, along the migratory difficulty continuum (Table 4).

## DISCUSSION

### *Selection for energy efficiency and evidence for an energetic-morphological feedback mechanism*

This study details the energetic and morphological changes that occur in wild sockeye during their freshwater spawning migrations. One of my objectives was to develop an index that identifies which environmental characteristics best explain the energetic and morphological patterns I observed among Fraser River sockeye populations. The impetus was to understand how natural selection has shaped the pre-migratory partitioning of somatic energy to best prepare sockeye for the challenges of upriver migration. The composite migratory difficulty index I developed provided the best physiological explanation for the variability observed by estimating the time-at-velocity a salmon encounters when swimming upriver. Because sockeye are fueling migration with finite somatic energy reserves, partitioning of somatic energy at river-entry should be sufficient to satisfy time-at-velocity demands experienced by each population. Other measures, like distance and elevation as individual variables, provided good estimates, but not as good as those provided by the composite migratory difficulty index. The number of thermal units accumulated over the course of migration showed only moderate associations with these attributes. These results suggest that the energetic constraints imposed by physical difficulty of migration strongly influence patterns of somatic and reproductive energy allocation in wild sockeye, and suggest further that bioenergetic efficiency is likely the chief attribute under natural selection in populations making difficult migrations (e.g. Chilko, Early Stuart, and Horsefly populations).

Energetic comparisons show that Weaver sockeye are apparently much less efficient migrants, expending more somatic energy per unit of migratory difficulty, than upriver populations like Chilko and Early Stuart. For example, Chilko sockeye traveled 468 km further than Weaver sockeye to reach their spawning grounds, yet took only three days longer than Weaver to do so (23 vs. 20 days respectively). Weaver's apparent swimming "inefficiency" however is accompanied by the possession of larger ovaries and greater egg numbers than Chilko and other upriver populations. Thus, it is important to note that this relative inefficiency doesn't necessarily equate to reduced fitness. Nevertheless, electromyogram (EMG) telemetry studies of migrating Fraser sockeye (e.g. Hinch and Rand 1998) show that coastal salmon meander more and expend higher amounts of energy while swimming upriver relative to Early Stuart sockeye (S.G. Hinch, Forest Science Department, University of British Columbia, unpublished data). Such differences in swimming behavior have also been observed by scientists and commercial fishermen who monitor Fraser River salmon (Jim Woodey, Pacific Salmon Commission, Vancouver, BC, personal communication). Clearly, there are some fundamental behavioral and physiological differences in the ways these populations migrate upriver. The relatively short distance that Weaver sockeye travel does not require the same energy efficiency required by the other upriver populations (Adams, Horsefly, Chilko and Early Stuart), all of whom swim greater distances, ascend higher elevation, and must pass through Hell's Gate, a region of exceedingly difficult passage in the Fraser Canyon (Hinch and Bratty 2000). Swim-tunnel respirometry studies also reveal that Weaver sockeye do not perform as well aerobically as upriver populations (C.G. Lee, Biology Department, Simon Fraser University, personal communication), providing additional evidence that energy efficiency is likely more strongly selected in upriver populations. Thus, Weaver sockeye may perceive a reduced sense of energetic urgency when migrating upriver, freeing time and resources for the development of reproductive tissues and secondary sexual characteristics in preparation for spawning.

Though ovary mass, egg size, and egg number showed inverse associations with migratory difficulty among populations, these all increased within population from time of river-entry to spawning. In fact, rates of somatic energy depletion and ovarian investment among all five populations show a strong negative association with migratory difficulty. But the rate of somatic energy expenditure estimated for Weaver sockeye (calculated as the amount of somatic energy lost per unit of migratory difficulty) may be slightly over-estimated given that their slow river

meandering probably exceeds the simple linear distance between the Fraser mouth and the spawning grounds (Table 4).

In a reciprocal transplant experiment, Kinnison et al. (2001) raised full-sib families from two populations of New Zealand chinook salmon (*O. tshawytscha*) under common hatchery conditions and released them into spawning systems that differ in migratory difficulty. They detected a reduction in ovary mass and egg size among female chinook, and also a reduction in energy reserves upon arrival at spawning areas. Additionally, males from the same populations had smaller humps as migration became more difficult (Kinnison et al. 2002). Though these results provide some direct experimental evidence of the effects of migration on energy allocation in wild salmon, the migratory conditions experienced by chinook in this study (17-100 km distance, 17-430 m elevation) are much smaller than those traveled by sockeye in this present study. Watershed differences other than migratory costs can contribute to differences among populations with near-similar migrations distances (Quinn et al. 1995; Woody et al. 2000, Quinn et al. 2001). The dramatic energetic and morphological patterns I have observed among the five populations in this study, as a result of a broad continuum of migratory conditions, find support in the Kinnison et al. (2001, 2002), and provide strong evidence for the effects of migration on sockeye energetics.

For the upper river sockeye populations examined in this study, attaining high energy efficiency involved a reduction in reproductive effort. Upriver sockeye must be judicious in their use of stored energy to ensure their arrival on the spawning grounds, but they must also ensure that enough is left for the maturation of their reproductive tissues, as well as for courtship, redd construction/defense, and spawning. Though these populations possess high energy reserves at the start of upriver migration, their ultimate investment in reproduction is less than lower river populations due to the great expense of their difficult runs (approximately 1/6<sup>th</sup> fewer eggs and 1/3<sup>rd</sup> less ovary mass). From an evolutionary point of view, trade-offs between somatic energy allocation and total reproductive (ovarian) investment are expected among highly philopatric populations (Roff 1992; Stearns 1992), as was observed in chinook by Kinnison et al. (2001). In salmon, the magnitude of this trade-off is determined largely by the energetic constraints imposed by upriver migration. In the present study, ovarian mass, egg mass, and egg number (fecundity) all diminished, independently of body length, as migratory difficulty increased, indicating an energetically driven reproductive trade-off.

The results of morphological analyses (o-index measures, body depth, body width, and body length) further support the assertion that energy efficiency is under strong selection in sockeye making difficult upriver migrations, and suggest that natural selection correspondingly favors a shorter, more torpedo-like, hydro-dynamic body shape in these salmon, a characteristic that may help optimize energy efficiency by minimizing surface drag and transport costs (as per Vogel 1994; Webb 1995; Hinch and Rand 2000). This characteristic was more striking in females than in males. However, greater body width does not appear linked to the possession of ovaries. Width of female sockeye at river-entry increased with increasing migratory difficulty (a measure which did not differ between whole and eviscerated sockeye), even while ovary mass decreased. Male width and hump height also increased with migratory difficulty, but o-index measures were not different among populations, though the general trend was for an increasing o-index with migratory difficulty. This may help explain why long distance migrating female sockeye were more energy efficient than male sockeye in recent EMG studies of migrating Fraser sockeye (Hinch and Rand 1998; Standen 2002). Coastal populations however (e.g. Weaver) are deeper bodied and less streamlined, reflecting an increased investment in secondary sexual characteristics during upriver migration. Because coastal sockeye undertake less difficult migrations, it is possible that selection for energy efficiency is not as strong. It seems adaptive that sockeye possess a body shape that positively affects their ability to conserve energy, particularly when the demands of upriver migration are high (see Kinnison et al. 2001).

A study of juvenile Fraser River coho also found that upriver populations were more fusiform in shape, and had shallower bodies than their coastal relatives (Taylor and McPhail 1985). Given that these differences were evident in juvenile salmon, prior to their ocean residency, it is likely that salmon have a genetic predisposition for hydrodynamic efficiency, determined in part by the characteristics of their natal watershed. Presumably, these innate morphological designs carry through to adulthood. If indeed morphological variation in sockeye is not simply an expression of phenotypic plasticity (Moore 1996), it is likely that a streamlined body shape is co-selected with energy efficiency when migratory constraints are substantial.

Because sockeye are under strong selective pressure to spawn when temperatures in their natal streams are favorable for egg and alevin development (Macdonald et al. 1998; Hodgson and Quinn 2002), it seems adaptive for sockeye to possess both an innate capacity for energy efficiency and a hydro-dynamically favorable body shape to ensure a timely arrival on the

spawning grounds (thus bolstering fitness), particularly in populations with difficult upriver migrations. Given the grave fitness consequences that delayed migrations can incur (i.e. exhaustion of energy reserves and consequent pre-spawning mortality), it is apparent from the results of this study that upper Fraser River sockeye are generally well adapted to contend with severe and variable hydrodynamic conditions. This is particularly so with Chilko sockeye, who were identified as the most energy efficient migrants. In populations making less difficult migrations however (i.e. Weaver and, to a lesser extent, Adams), the importance of energetic and morphological attributes facilitating energy efficiency wanes, and other selective pressures are likely to affect body shape and energy allocation patterns.

Collectively, these results provide evidence that a complex energetic-morphological feedback mechanism may have evolved in sockeye as a way to bolster upriver migratory success and reproductive fitness (Figure 10). Driving this adaptation is the necessity to overcome migratory constraints and spawn in early summer so that sufficient degree-days can be accumulated for egg and alevin development (Macdonald et al. 1998; Hodgson and Quinn 2002). By accumulating sufficient degree-days to initiate hatching before the onset of winter freeze-up, mobile alevins may be at lesser risk of ice-mortality than stationary eggs. Working in synergy with the components of this mechanism, and with perhaps equal weighting, are the energetically efficient swimming behaviors exhibited by sockeye, a topic of considerable interest which has been receiving recent attention (Hinch and Rand 2000; Hinch et al. 2002; Standen 2002). Hinch and Rand (2000) used underwater stereo videography to document many energy saving swim tactics employed by Chilko, Early Stuart, and Horsefly sockeye. They found that upriver sockeye minimize migratory transport costs per unit distance traveled by swimming at metabolically optimal speeds, and by locating and exploiting small-scale reverse flow fields. They also found that Chilko sockeye in particular seemed capable of generating greater stride lengths per tail-beat relative to Early Stuart and Horsefly. This finding supports my results and suggests that Chilko sockeye are exceptionally efficient swimmers.

In migratory contexts where energy efficiency for swimming is not a principal selective agent, a high degree of morphological variation can be observed. For example, among coastal Alaskan populations, where migratory constraints are much less pronounced than in the Fraser River, migratory efficiency is likely less involved in shaping morphological variation among populations. Differences in spawning stream hydrology and substrate, predation, and

intraspecific spawning competition (or sexual selection) may have a much stronger influence (Quinn et al. 1995; Woody et al. 2000). It is likely that a number of selective pressures, in addition to migratory difficulty, are working synergistically to drive pre-migratory somatic and ovarian provisioning, and the morphology of mature sockeye. However, the present study provides strong correlative evidence that migratory difficulty figures significantly in the evolution of energy partitioning in Fraser River sockeye (see also Kinnison et al. 2001).

#### *The role of body length in energy efficiency*

Sockeye body length may be an important component of the energetic-morphological feedback model presented in this study, and its possible role in achieving high energy efficiency warrants discussion. It has been generally accepted that for anadromous fish, body length tends to increase with migratory distance, presumably because larger fish can store more somatic energy and generate greater thrust per tailbeat. Atlantic salmon (*Salmo salar*, Jonsson et al. 1991), brown trout (*Salmo trutta*, L'Abée-Lund 1991), and American shad (*Alosa sapidissima*, Glebe and Leggett 1981) all show this positive relationship. However, body length tends to be inversely related to migratory distance in Pacific salmon, most notably in coho (Fleming and Gross 1989), chum (Beacham and Murray 1987; Beacham et al. 1988; Beacham and Murray 1993), and sockeye (Moore 1996; this study). This may be due to fundamental differences in life history (i.e. semelparity versus iteroparity).

In preparation for upriver spawning migration, sockeye channel some of their consumed energy away from growth and into somatic storage. In length, the smallest sockeye in this study (Chilko and Early Stuart) possessed the highest somatic energy concentrations, suggesting that the feeding opportunities available to them while at sea are at least equal, if not greater, than those available to the other lower river populations making less difficult migrations. Thus it seems likely that upriver sockeye have a genetic predisposition for smaller body length at maturity, and higher somatic lipid concentrations, perhaps, as the data presented in this study suggest, to assist in the energetic feedback mechanism. The genetic coupling of high lipid reserves and shorter body length likely enhance fusiform body shape, hydro-dynamic performance, and the energy efficiency needed for difficult upriver migrations (Figure 10).

Being iteroparous, Atlantic salmon, shad, and brown trout experience different sets of selective pressures compared with Pacific salmon. For example, should they deem conditions

for spawning inappropriate, iteroparous species can choose whether or not to spawn, and can also feed during upriver migrations. Whether they spawn or not however, many will try to return to the ocean, though return mortality is usually high. Increasing body length could allow these fish to possess higher total energy reserves, which may be important for the return trip downriver. The absolute distances that these species migrate are also far shorter than those traveled by sockeye in this study. Thus, local adaptation likely plays a large role in shaping differences between iteroparous and semelparous body size. Regarding sockeye, there is the possibility that body length may have a threshold value beyond which hydrodynamic energy efficiency is sacrificed. There may also be a local adaptation to the size of redd-gravels in spawning areas (Quinn et al. 1995; see Chapter 3).

Decreasing body size in sockeye may also be the result of oxygen uptake efficiency and oxygen permeability, both of which tend to be greater in small bodies than in larger ones. Across taxa, standard metabolic rates and metabolic rates during exercise are higher in small animals than in large animals, and in fish, several studies show that oxygen uptake efficiency improves with diminishing size (Degani et al. 1989). Pauly (1981) suggested that large fish are unable to metabolize stored energy as efficiently as small fish due reduced oxygen uptake efficiency. Thus, the ability to mobilize and metabolize stored energy, an absolute requirement for semelparous migrations, may additionally select for smaller body size as migrations become more difficult. This possibility may indeed work synergistically within the energetic-morphological feedback mechanism proposed here.

### *Conclusion*

The present study argues that selection for energy efficiency shapes the morphological and energetic patterns observed among populations of Pacific salmon. Of particular interest is the reduction in reproductive output (ovarian investment) observed in populations making difficult migrations. Though these differences suggest a genetic predisposition, it is clear that significant ovarian investment is made *en route* to spawning areas. This raises an interesting and unanswered question: if a genetic trade-off between somatic energy reserves/energy efficiency, and ovarian investment occurs, does interannual variation in environmental parameters not considered here (river discharge rates, river temperature, see Macdonald et al. 2000) significantly affect ovary mass and egg number within population? This could be a possible

explanation for the adapted states observed here.

Literature cited:

- Bailey, R.E., Margolis, L., and Groot, C. 1988. Estimating stock composition of migrating juvenile Fraser River (British Columbia) sockeye salmon, *Oncorhynchus nerka*, using parasites as natural tags. Canadian Journal of Fisheries and Aquatic Sciences 45:586-591
- Beacham, T.D., Murray, C.B., and Withler, R.E. 1988. Age, morphology, developmental biology, and biochemical genetic variation of Yukon River fall chum salmon, *Oncorhynchus keta*, and comparisons with British Columbia populations. Fisheries Bulletin 86: 663-674.
- Beacham, T.D. and Murray, C.B. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44: 244-261.
- Beacham, T.D. and Murray, C.B. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). Journal of Fish Biology 42: 485-508.
- Bernatchez, L., and Dodson, J.J. 1987. Relationship between bioenergetics and behaviour in anadromous fish migrations. Canadian Journal of Fisheries and Aquatic Sciences 44: 399-407.
- Berg, O.K., Thornæs, E., and Bremset, G. 1998. Energetics and survival of virgin and repeat spawning brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 55: 47-53.
- Blair, G.R., Rogers, D.E., and Quinn, T.P. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. Transactions of the American Fisheries Society. 122: 550-559.
- Bligh, E.G. and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. Can. Journal of Biochemistry and Physiology 37: 911.
- Brett, J.R. 1995. Energetics. *In: Physiological ecology of Pacific salmon*. Eds. C. Groot, L. Margolis and W.C. Clarke. University of British Columbia Press. Pps. 3-68.
- Burgner, R.L. 1991. Life history of sockeye salmon. *In: Pacific salmon life histories*. Edited by C. Groot and L Margolis. UBC Press, Vancouver. Pps. 3-117.
- Cook, R.C. and Guthrie, I. 1987. In-season stock identification of sockeye *salmon* (*Oncorhynchus nerka*) using scale pattern recognition. *In: Sockeye salmon population biology and future management*. Canadian Special Publication of Fisheries and Aquatic Sciences 96:327-334.
- Degani, G., Gallagher, M.L., and Meltzer, A. 1989. The influence of body size and temperature on oxygen consumption of the European eel, *Anguilla anguilla*. Journal of Fish Biology 34: 19-24.

- Dorcey, A.H.J. 1991. Water in the sustainable development of the Fraser River Basin. *In*: Water in sustainable development. Westwater Research Centre, Faculty of Graduate Studies, University of British Columbia, Vancouver. Pps. 3-18.
- Fleming, I.A. and Gross, M.R. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution* 43: 141-157.
- Fleming, I.A. and Ng, S. 1997. Evaluation of techniques for fixing, preserving, and measuring salmon eggs. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1957-1962.
- Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. *International Pacific Salmon Fisheries Commission Bulletin No. 22*.
- Glebe, B.D. and Leggett, W.C. 1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 806-820.
- Hendry, A.P. and Berg, O.K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Canadian Journal of Zoology* 77: 1663-1675.
- Hendry, A.P., Berg, O.K., and Quinn, T.P. 1999. Condition dependence and adaptation-by-time: breeding date, life history, and energy allocation within a population of salmon. *Oikos* 85: 499-514.
- Higgs, D.A., Markert, J.R., MacQuarrie, D.W., McBride, J.R., Dosanjh, B.S., Nichols, C., and Hoskins, G. 1979. Development of practical dry diets for coho salmon, *Oncorhynchus kisutch*, using poultry-by-product meal, feather meal, soybean meal and rapeseed meal as major protein sources. *In* *Finfish Nutrition and Fishfeed Technology*, Vol. 2 (Edited by J.E. Halver and K. Tiews). pp. 191-218. Heenemann Verlagsgesellschaft MbH., Berlin.
- Hinch S.G. and Bratty, J. 2000. Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Transactions of the American Fisheries Society* 129: 598-606.
- Hinch, S.G., and Rand, P.S. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): Role of local environment and fish characteristics *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1821-1831.
- Hinch, S.G., and Rand, P.S. 2000. Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviors of upriver-migrating adult salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 2470-2478.
- Hodgson, S. and Quinn, T.P. 2002. The timing of adult sockeye salmon migration to fresh water: adaptations by population to prevailing thermal regimes. *Canadian Journal of Zoology* 80: 542-555.

- Idler, D.R. and Clemens, W.A. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. International Pacific Salmon Fisheries Commission Progress Report No. 6.
- Jonsson, N., Hansen, L.P., and Jonsson, B. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *Journal of Animal Ecology* 60: 937-947.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* 66: 425-436.
- Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* 55: 1656-1667.
- Kinnison, M.T., Unwin, M.J., and Quinn, T.P. 2002. Travel and sex on a tight budget: migratory costs and contemporary evolution of reproductive allocation in male salmon. *Evolution*, in review.
- L'Abée-Lund, J.H. 1991. Variation within and between rivers in adult size and sea age maturity of anadromous brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1015-1021.
- Macdonald, J.S. (editor) 2000. Mortality during the migration of Fraser River sockeye salmon (*Oncorhynchus nerka*): a study of the effect of ocean and environmental conditions in 1997. Canadian Technical Report for Fisheries and Aquatic Sciences 2315. Pps. 119.
- Macdonald, J.S., Scrivener, J.C., Patterson, D.A., and Dixon-Warren, A. 1998. Temperatures in aquatic habitats: the impacts of forest harvesting and the biological consequences to sockeye salmon incubation habitats in the interior of BC. Proceedings of the Forest-Fish Conference, May 1996, Calgary, Alberta. Natural Resources Canada, Canadian Forest Service, Northern Forest Centre, Edmonton, Alberta. Report NOR-X-356. Pps 313-324.
- Moore, K. 1996. The adaptive significance of body size and shape in sexually mature sockeye salmon (*Oncorhynchus nerka*). M.S. thesis, University of Washington, Seattle.
- Quinn, T.P., and Dittman, A.H. 1990. Pacific salmon migrations and homing: mechanisms and adaptive significance. *Trends in Ecology and Evolution* 5: 174-177.
- Quinn, T.P., Hendry, A.P., and Wetzel, L.A. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos* 74: 425-438.
- Quinn, T.P., Wetzel, L., Bishop, S., Overberg, K., and Rogers, D.E. 2001. Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Canadian Journal of Fisheries and Aquatic Sciences* 79: 1782-1793.

- Rand, P.S. and Hinch, S.G. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1832-1841.
- Riddell, B.E. and Leggett, W.C. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 38: 303-320.
- SAS Institute. 1988. SAS/STAT user's guide, version 6.03. SAS Institute, Cary, N.C.
- Smith, C.C. and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108: 499-505.
- Standen, E. 2002. Effects of hydraulic characteristics on energy use and behaviour of adult upriver migrating sockeye and pink salmon. MSc. thesis, University of British Columbia, Vancouver.
- Stearns, S.C. 1992. The evolution of life histories. Oxford University Press.
- Taylor, E.B. and McPhail, D. 1985. Variation in body morphology among British Columbia populations of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 42:2020-2028.
- Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98: 185-207.
- Vogel, S. 1994. Life in moving fluids. The physical biology of flow. Second edition. Princeton University Press.
- Webb, P.W. 1995. Locomotion. In *Physiological ecology of Pacific salmon*. Edited by C. Groot, L. Margolis, and W.C. Clarke. University of British Columbia Press, Vancouver, B.C. pp. 71-99.
- Woody, C.A., Olsen, J., Reynolds, J., and Bentzen, P. 2000. Temporal variation in phenotypic and genotypic traits in two sockeye salmon populations, Tustumena Lake, Alaska. *Transactions of the American Fisheries Society* 129: 1031-1043.

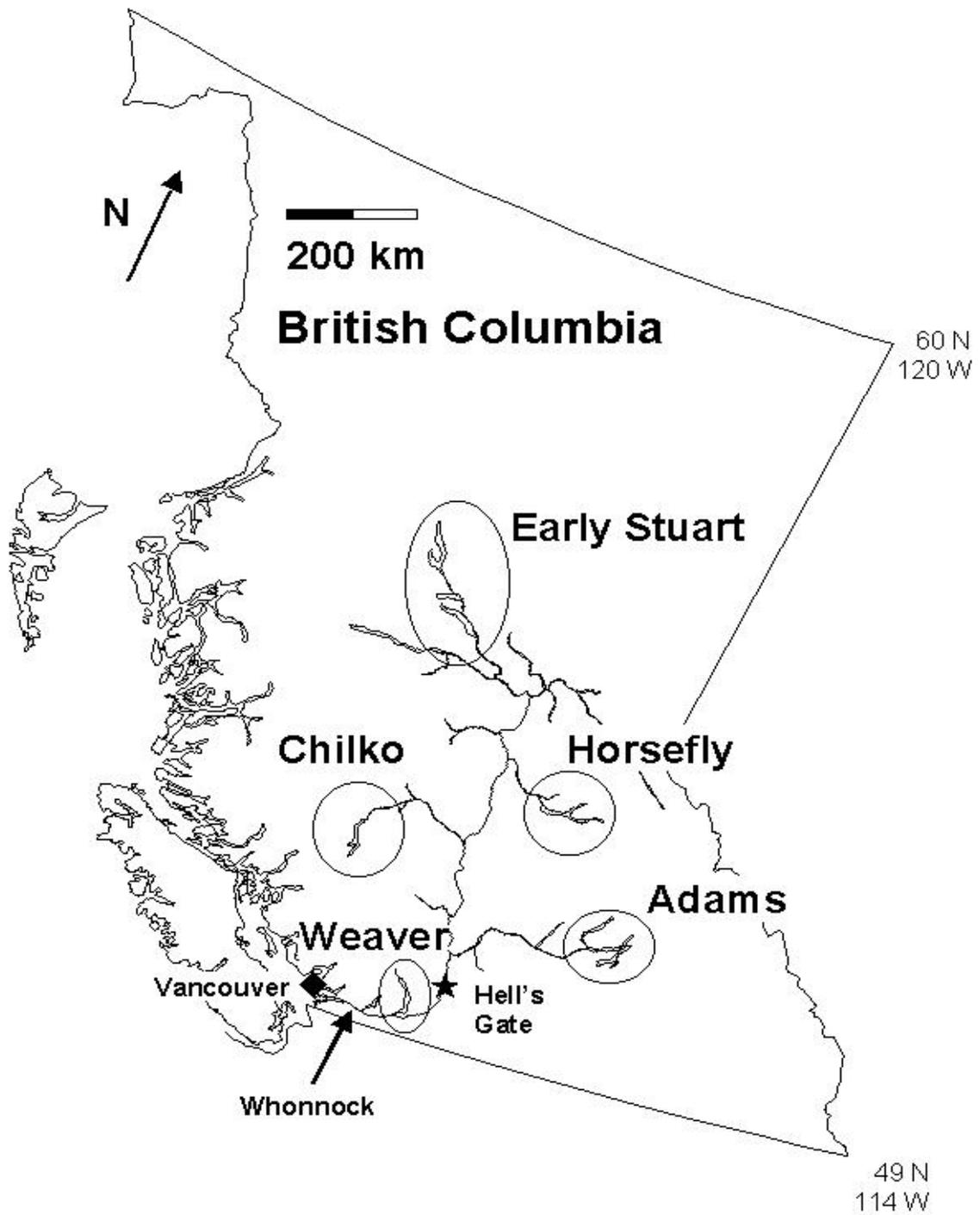


Figure 1.1: Map of Fraser River sockeye spawning systems.

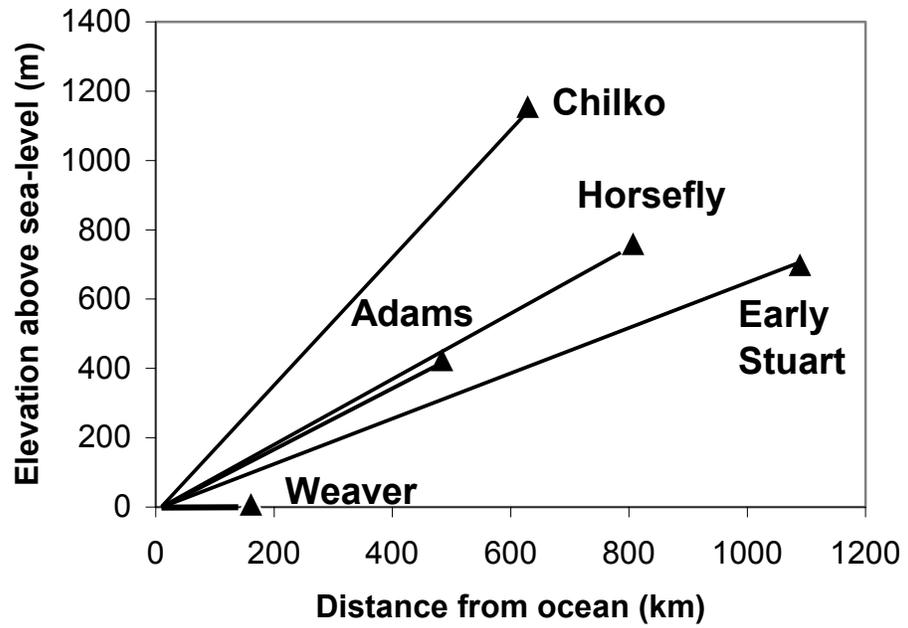


Figure 1.2: Fraser River sockeye spawning ground elevations and distances.

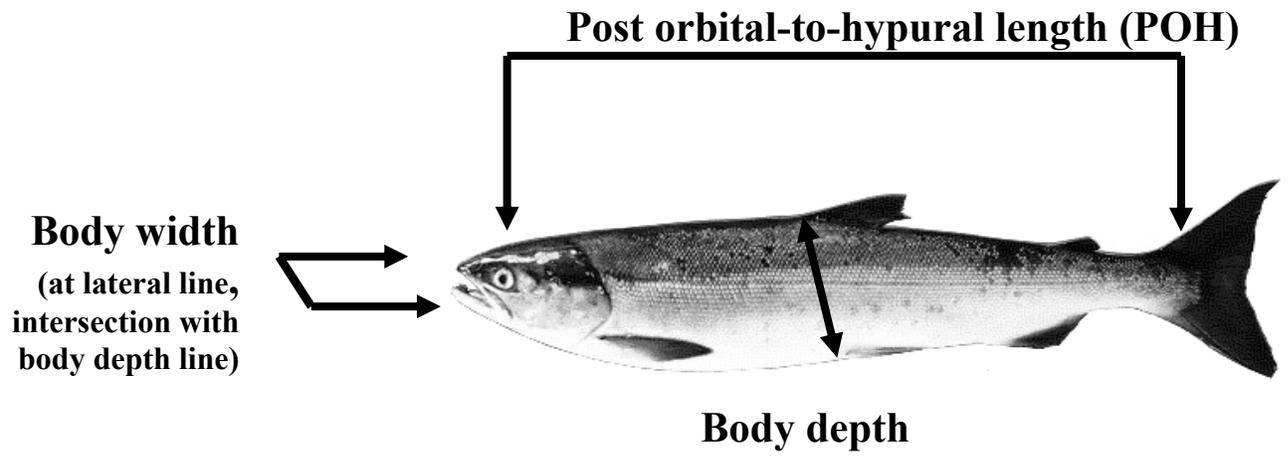


Figure 1.3: External morphological measurement made on sockeye salmon in this study.

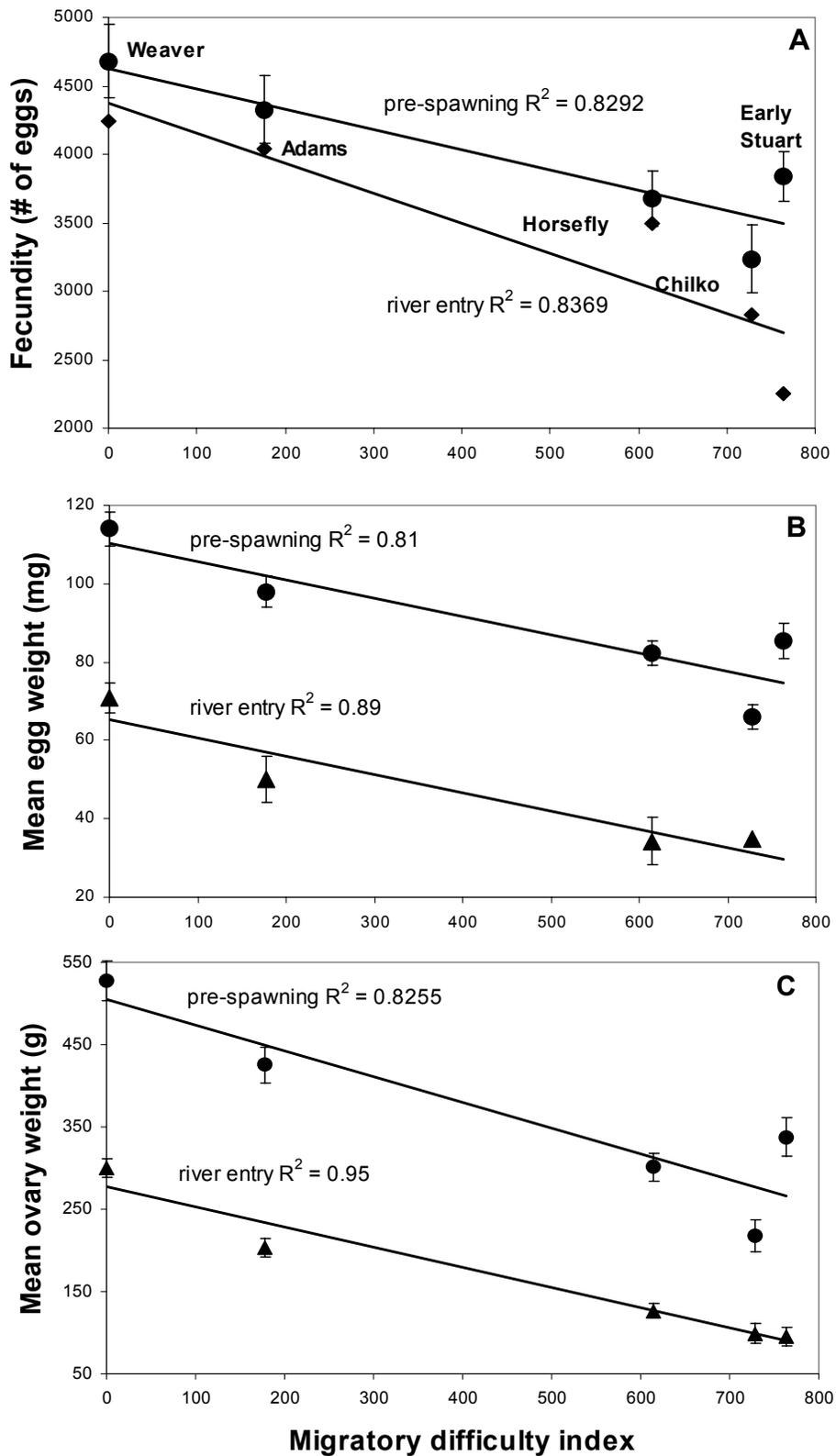


Figure 1.4: Fecundity (A), ovarian mass (B), and mean egg weight (C) of female sockeye in relation to migratory difficulty. Order of population points in each plot is: Weaver, Adams, Horsefly, Chilko, Early Stuart. Migratory difficulty index = migratory distance \* migratory elevation / 1000. Error bars are +/-SEM. All  $P < 0.01$ .

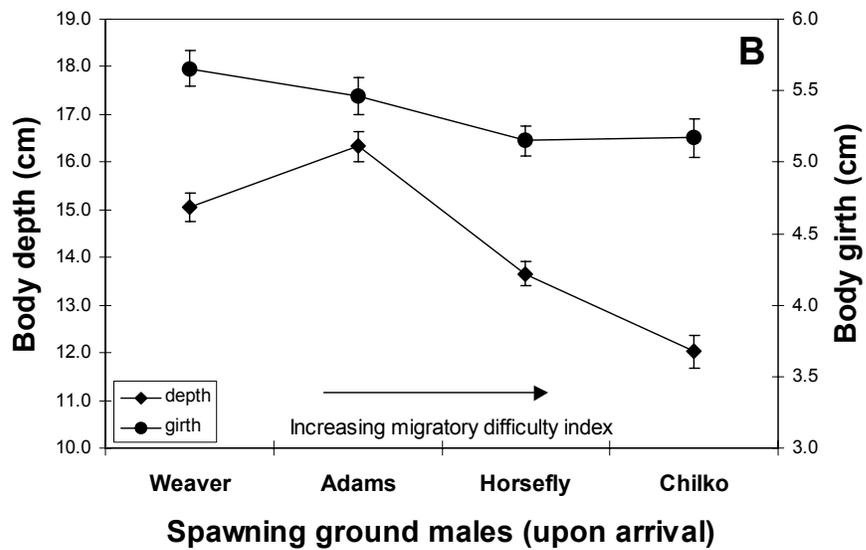
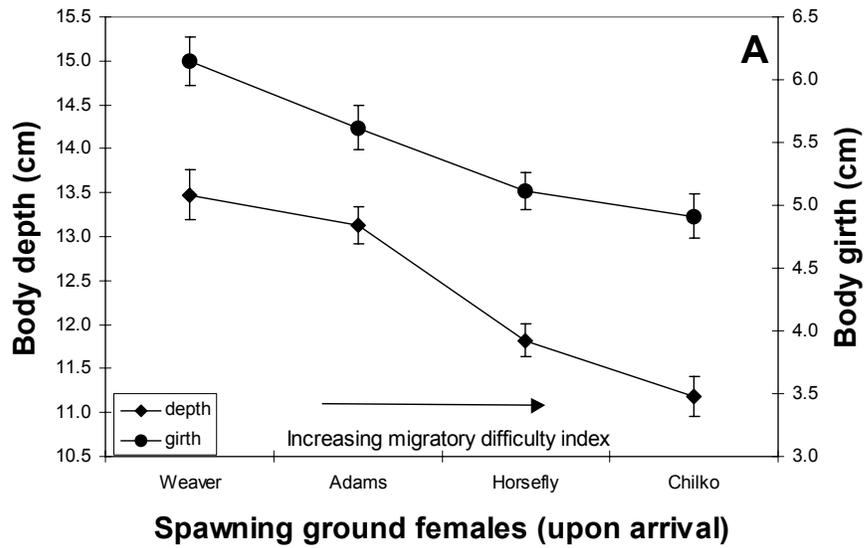


Figure 1.5: Populations differences in body depth and width upon arrival on the spawning grounds for females (A) and males (B). Error bars are +/-SEM. All  $P < 0.01$ .

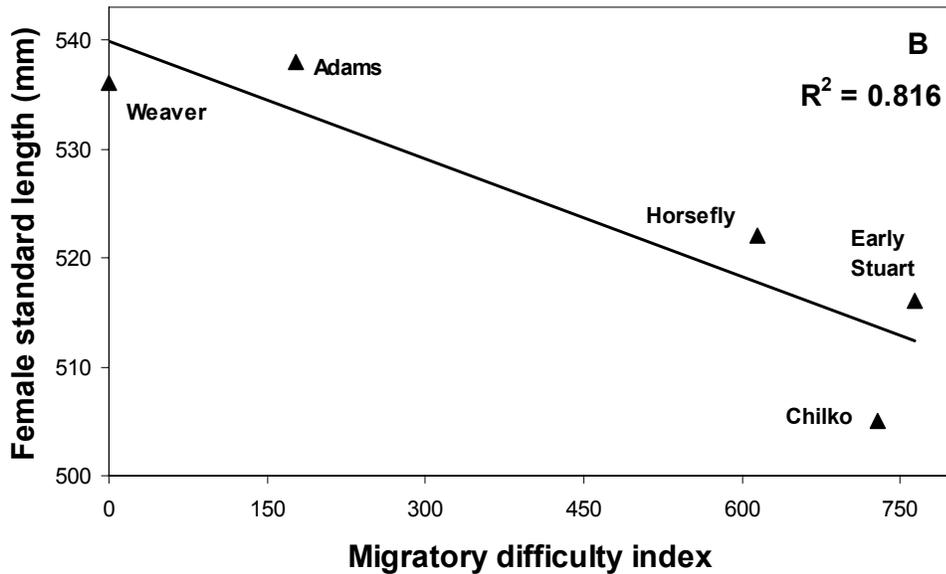
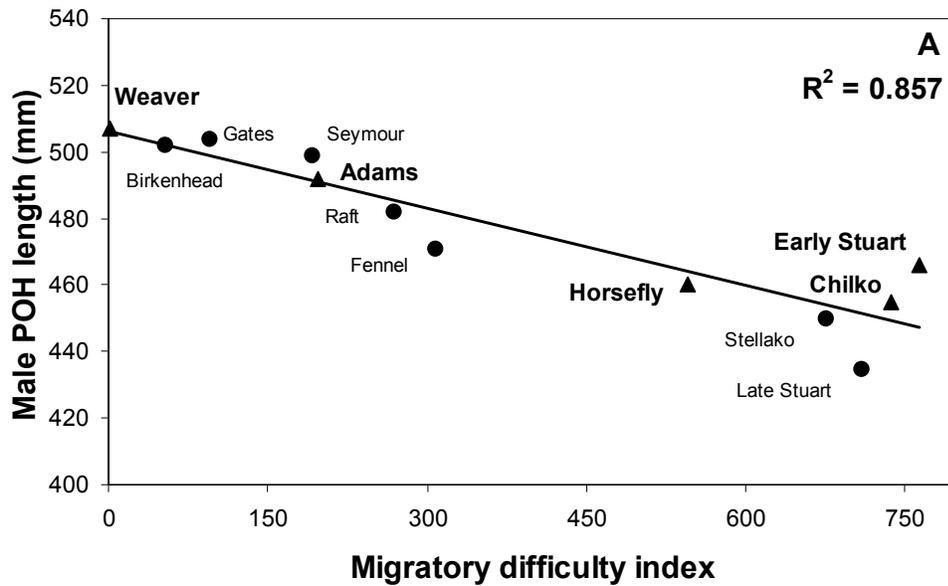


Figure 1.6: The relationship between body length and migratory distance in pre-spawning male ([B] POH: post orbital-to-hypural.) and female ([B] standard length: snout-to-hypural) Fraser River sockeye populations. Male plot is a re-analysis of data presented in Moore (1996), and focused on wild Fraser River sockeye only in years 1992-94. Triangles represent populations under examined in this study. Circles represent other Fraser River sockeye populations examined by FOC.

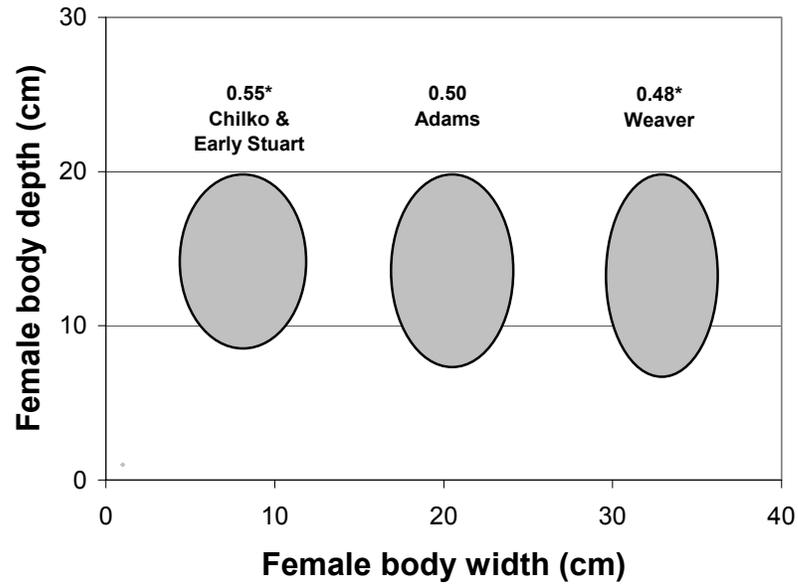


Figure 1.7: A generalized schematic of female sockeye shape, when viewed head-on, at the beginning of their upriver spawning migrations. Shapes are derived from depth and width measurements. Termed o-index, values represent the quotient of body width and depth. O-index values are printed above each shape. Asterisks (\*) indicate populations that are statistically significant from one another ( $P < 0.01$ ).

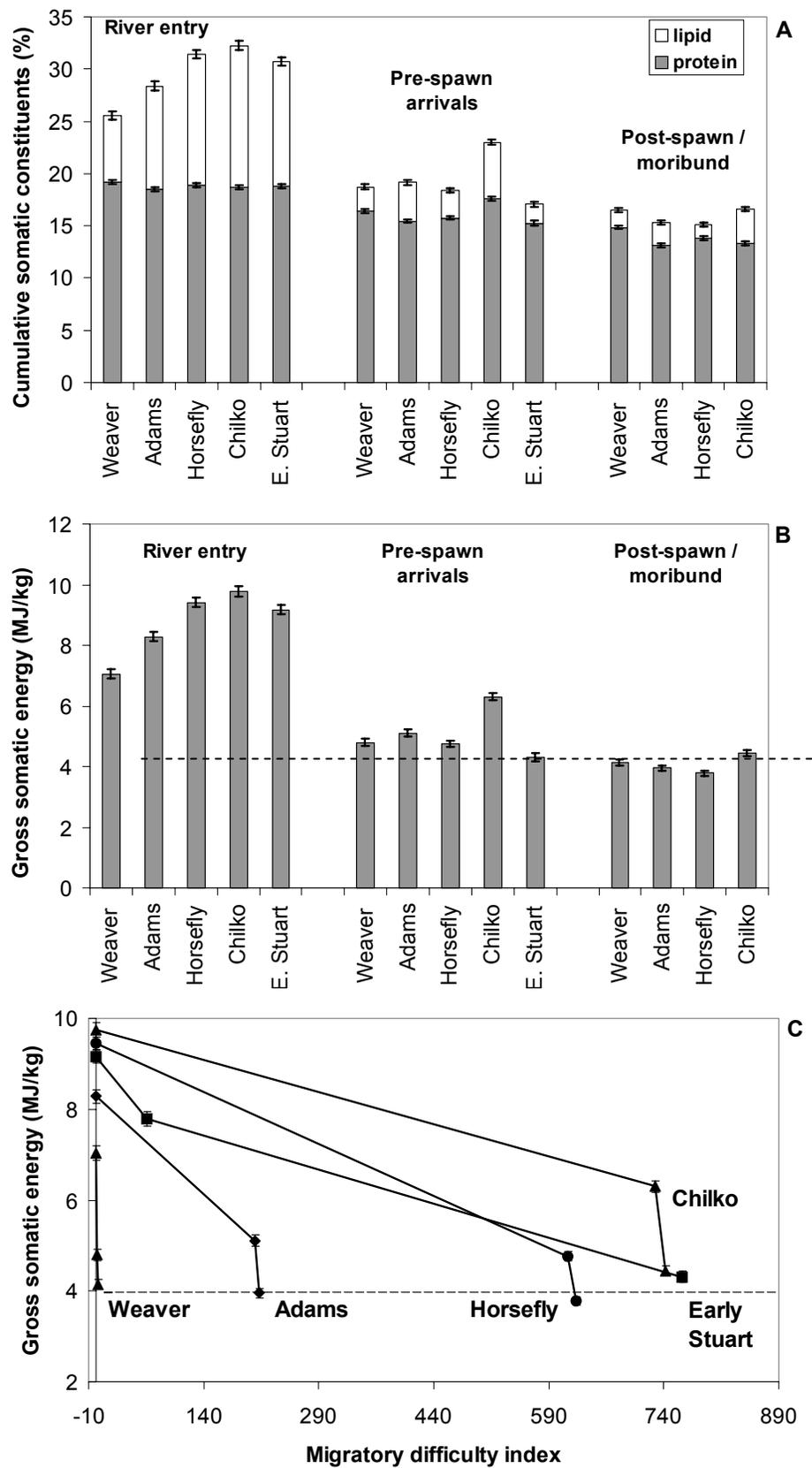


Figure 1.8: Protein and lipid percentages (A), gross energy concentrations (B), and gross energy depletion (C) in the soma of Fraser River sockeye populations collected in 1999. Dashed lines in B and C represent the approximate energetic threshold between life and death for most sockeye. Sexes are pooled. Error bars are +/-SEM.

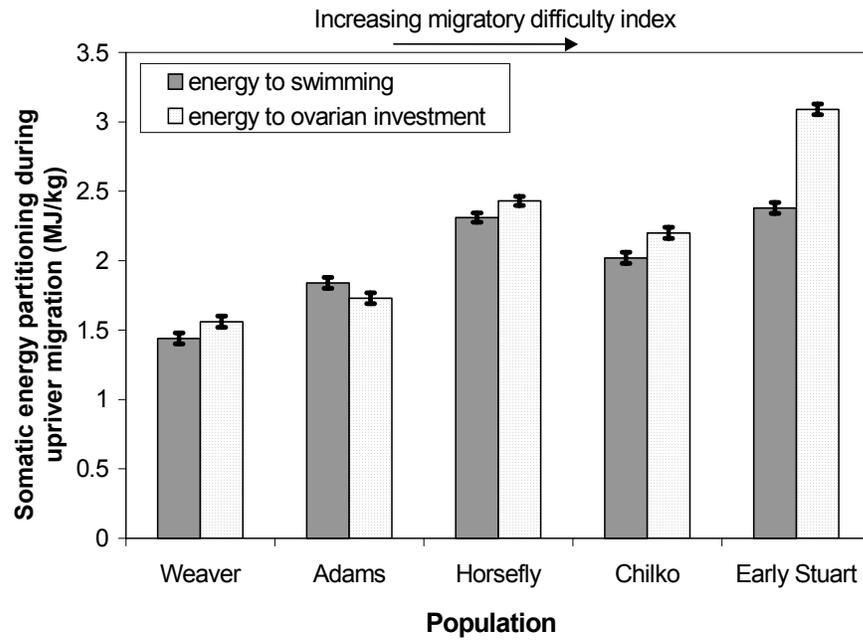


Figure 1.9: Rates of somatic expenditure (swimming expenditure) and ovarian investment from time of Fraser River entry to arrival on spawning grounds. Error bars are +/-SEM.

**ADAPTATIONS:**

**SOCKEYE ADAPTATIONS:**

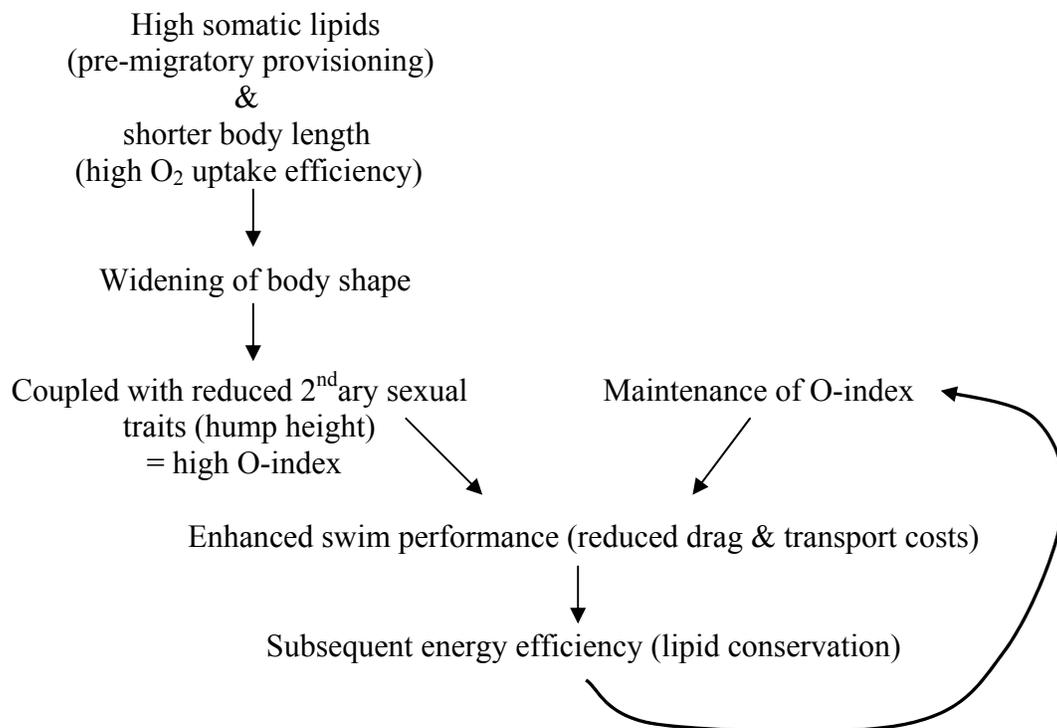


Figure 1.10: Conceptualization of an adaptive energetic-morphological feedback mechanism, driven by selection for energy efficiency, designed to enhance the fitness of upriver migrating sockeye salmon.

Table 1.1: Run times, spawning ground characteristics, and river temperatures specific to the Fraser River sockeye populations sampled in 1999.

Population	Arrival at Fraser mouth	Spawning ground arrival	Days to spawning grounds	Migratory distance (km)	Migratory elevation (m)	Migratory difficulty	Migratory degree-days
Weaver	18-Sep	8-Oct	20	161	10	1	270
Adams	15-Sep	6-Oct	21	484	366	177	355
Horsefly	10-Aug	8-Sep	29	807	762	615	495
Chilko	10-Aug	2-Sep	23	629	1158	729	390
Early Stuart	10-Jul	12-Aug	33	1089	701	763	607

Table 1.2: Linear  $R^2$  values for river-entry and pre-spawning female energetic and morphological attributes regressed against migratory difficulty, distance, elevation, degree-days, and mean river temperature.

Female attribute	Migratory distance	Migratory elevation	Migratory difficulty index	Migratory degree-days
At river-entry:				
Somatic energy	0.60	0.94	<b>0.89</b>	0.45
Ovary mass	0.79	0.84	<b>0.95</b>	0.65
Egg weight	0.94	0.86	<b>0.90</b>	0.80
Fecundity	0.74	0.52	<b>0.84</b>	0.68
Gonado-somatic index	0.80	0.83	<b>0.94</b>	0.66
Body length	0.37	0.81	<b>0.82</b>	0.27
Pre-spawning:				
Ovary mass	0.43	0.99	0.83	0.30
Egg weight	0.41	0.99	0.81	0.27
Fecundity	0.40	0.98	0.83	0.28
Gonado-somatic index	0.56	0.97	0.90	0.41
Egg number/egg size	0.23	0.94	0.61	0.11

Table 1.3: Proximate composition (by wet mass) of somatic and reproductive tissues, and gross somatic energy densities in upriver migrating Fraser River sockeye collected in 1999. Values are length corrected.

		FEMALE SOMA				Gross energy (MJ/kg)	MALE SOMA				Gross energy (MJ/kg)	
	Population	% Protein	% Lipid	% H2O	% Ash		% Protein	% Lipid	% H2O	% Ash		
Fraser River	Weaver	19.23	6.13	72.04	2.47	6.97	19.74	5.96	72.08	2.42	7.02	
	Entry	Adams	18.43	10.67	68.73	2.59	8.57	18.51	9.12	69.58	2.34	7.98
		Horsefly	18.82	13.00	66.32	2.69	9.59	18.65	12.21	66.76	2.60	9.23
		Chilko	19.12	13.45	65.33	2.59	9.84	18.60	13.41	65.79	2.38	9.70
		Early Stuart	18.96	11.62	66.23	2.17	9.08	18.73	12.20	66.31	1.88	9.25
Hell's Gate	Early Stuart	18.71	8.84	70.06	2.69	7.92	18.42	8.32	70.56	2.62	7.64	
Spawning ground arrival	Weaver	17.13	2.43	78.23	2.59	5.01	15.70	2.31	78.37	2.36	4.62	
	Adams	15.76	3.87	77.11	2.38	5.26	15.21	3.42	78.50	2.22	4.95	
	Horsefly	16.10	3.12	77.56	2.30	5.04	15.42	2.26	78.98	2.42	4.54	
	Chilko	17.55	5.28	74.14	2.57	6.24	17.71	5.59	73.86	2.48	6.40	
	Early Stuart	15.51	1.81	79.20	2.50	4.38	15.09	1.58	79.70	2.15	4.19	
Post spawn moribund	Weaver	14.58	1.67	80.53	2.86	4.11	15.15	1.62	80.69	2.62	4.22	
	Adams	13.34	2.27	81.18	2.75	4.05	12.94	2.03	81.33	2.97	3.86	
	Horsefly	14.04	1.54	81.09	2.80	3.93	13.76	1.17	81.61	2.44	3.72	
	Chilko	13.24	3.10	80.66	2.46	4.35	13.37	3.37	80.67	2.27	4.49	
		OVARIES				Gross energy (MJ/kg)	TESTES				Gross energy (MJ/kg)	
	Population	% Protein	% Lipid	% H2O	% Ash		% Protein	% Lipid	% H2O	% Ash		
Fraser River	Weaver	24.42	14.34	57.21	4.00	11.44	13.12	1.67	79.25	5.96	3.76	
	Entry	Adams	25.13	15.73	56.41	2.84	12.16	12.90	1.60	79.50	6.00	3.68
		Horsefly	22.99	15.27	57.91	3.84	11.47	13.12	1.83	80.33	4.72	3.83
		Chilko	21.92	15.17	58.95	3.96	11.18	13.64	1.29	80.89	4.19	3.73
		Early Stuart	25.87	14.38	57.92	1.82	11.80	13.92	1.04	81.73	3.31	3.70
Spawning ground arrival	Weaver	19.98	15.43	60.76	3.83	10.82	15.25	2.57	75.23	6.96	4.62	
	Adams	23.31	12.32	59.75	4.62	10.38	13.39	2.16	76.83	5.94	4.02	
	Horsefly	19.09	15.23	61.03	4.66	10.53	12.08	2.58	79.17	6.18	3.87	
	Chilko	25.06	13.66	57.57	3.71	11.33	13.80	2.12	76.85	7.24	4.10	
	Early Stuart	23.89	11.47	62.22	2.43	10.18	14.09	1.82	78.15	5.94	4.05	

Table 1.4: Somatic energy used for swimming and standard metabolic processes and for reproductive tissue development during the upriver migration of five Fraser River sockeye populations. Units are mJ / unit of migratory difficulty.

Female Population	Upriver activity: swimming and standard metabolism	Ovarian investment
Weaver	1440.0	1560.0
Adams	10.4	9.8
Horsefly	3.8	4.0
Chilko	2.8	3.0
Early Stuart	3.1	4.0

**CHAPTER 2**  
**CLIMATE CHANGE AND INTER-DECADAL SHIFTS IN PACIFIC**  
**SALMON BIOENERGY PRIOR TO UPRIVER MIGRATION**

Published as Crossin G.T., S.G. Hinch, A.P. Farrell, D.A. Higgs, and M.C. Healey. (2004) Somatic energy of sockeye salmon at the onset of upriver migration: a comparison among ocean climate regimes. *Fisheries Oceanography*. 29:22-33.

**ABSTRACT**

Since the mid 1950s, the climate of the North Pacific Ocean has shifted twice and broad-scale oceanographic and biological changes have occurred. Associated with these shifts have been changes in production at many trophic levels, and changes in ocean thermal regimes. Both have been linked with changes in the distribution, abundance, and production of Pacific salmon (*Oncorhynchus* spp.). Comparing recent bioenergetic and morphological data from Fraser River sockeye (*O. nerka*) and pink salmon (*O. gorbuscha*) populations with data collected for each in the 1950s and in 1983 respectively, I explored inter-decadal somatic energy patterns in salmon just prior to upriver spawning migration. I also explored whether conditions in the ocean environment have influenced these patterns. Results of principal components analysis revealed that, compared to the 1950s, a reduction in somatic lipid concentrations and gonado-somatic index has occurred, particularly in upriver sockeye populations (Chilko and Early Stuart). However, recent pink salmon have showed an energetic increase compared to 1983, an El Niño period. Data on sockeye energy from two additional El Niño periods (1959 and 1997) indicate that El Niño events may play a role in sockeye energy partitioning. Reduced somatic energy at the onset of upriver migration puts salmon at risk of in-river energy exhaustion and pre-spawning mortality, particularly in years of high river discharge rates. Increases in sea-surface temperatures and summer river discharge, as predicted by climate change models, may threaten the long-term fitness of Fraser River salmon populations.

## INTRODUCTION

Reports describing the effects of global climate change on phenology and migration are numerous in both the scientific and the popular literature. Recent scientific reports describe advances in the spring arrival and laying date of migratory birds (Sparks 1999; Both and Visser, 2001), in the date of first reproduction in amphibians (Forchhammer et al. 1998), and in the date of emergence from hibernation in small mammals (Inouye et al. 2000). Additionally, coherent patterns of broad scale ecological change are now visible from polar terrestrial to tropical marine environments (Walther et al. 2002). Large-scale atmospheric phenomena affecting global temperature patterns have generally been attributed as the principal drivers of these biological variations.

Among the growing list of affected species are the Pacific salmon (*Oncorhynchus* spp.). There is growing evidence that the climate of the North Pacific Ocean oscillates between periods of warming and cooling on a decadal timeframe (Beamish et al. 1999). These climatological shifts are connected to air-sea heat flux anomalies that eventually lead to changes in oceanic pressure fields, ocean upwelling, primary and zooplankton production, and sea-surface temperatures (SST). Changes in zooplankton production have been associated with changes in the size-at-maturity of Pacific salmon (Hinch et al. 1995; Welch et al. 2000). Changes in SST have been associated with changes in the distribution, abundance, and survival (Welch et al. 1998; Beamish et al. 1999; McFarlane et al. 2000), and with a decline in the size-at-maturity, of Pacific salmon (Cox and Hinch 1997). Hinch et al. (1995) found a negative correlation between the weight of sockeye (*O. nerka*) a month prior to upriver migration and average SSTs. Indeed, several modeling studies warn that if ocean temperatures in the North Pacific warm above their 'natural' range in the next half-century, resulting from climate change, the long-term productivity of Pacific salmon populations could be put at risk (Hinch et al. 1995; Welch et al. 1998). The broader implications that climate-related changes in the ocean environment pose for reproductive success, however, are largely speculative.

Understanding how shifts in ocean climate may affect reproductive fitness in Pacific salmon requires an understanding of the constraints that limit the provisioning of somatic energy needed for upriver migration. Pacific salmon rely solely on fixed somatic energy reserves, acquired while feeding at sea, to fuel upriver migrations to natal spawning areas, and to complete the maturation of their reproductive tissues. Variation in ocean climate that affects both the

distribution and abundance of salmon and their prey-base may diminish the ability of salmon to capture and store consumed energy.

In the mid-1950s and in 1983, the International Pacific Salmon Fisheries Commission conducted extensive bioenergetic studies of Fraser River sockeye (Idler and Clemens 1959, reviewed by Gilhousen 1980) and pink salmon (*O. gorbuscha*; Williams et al. 1986). In 1999, I conducted a more extensive bioenergetic study of Fraser River sockeye (Chapter 1) and pink salmon (data presented here). As indicated by two complimentary climatological indices (Beamish et al. 1999), the climate of the North Pacific has shifted twice, once in 1977 and again in 1989. Evidence for a third shift occurring in 1997 is now being considered (Thompson 2002). The data from the 1950s, the 1983, and the 1999 studies provided an excellent opportunity to explore inter-decadal variation in somatic energy partitioning just prior to upriver migration, and to determine whether such variation, if detectable, could be explained by changes in the ocean environment.

In this study, I had two objectives. My first objective was to determine whether population-specific energetic and (or) morphological shifts have occurred in sockeye and pink salmon at the beginning of their upriver spawning migrations (at end of ocean residency). I accomplished this by comparing historical energetic data for five sockeye populations (Idler and Clemens 1959, reviewed by Gilhousen 1980) and one pink salmon population (*O. gorbuscha*; Williams et al. 1986) with data I collected for both species in 1999 and 2000. Because shifting ocean climates can influence a broad range of oceanographic (atmospheric pressure fields, upwelling rates, SST) and biological processes (primary and secondary production), I predicted that shifts in ocean climate would affect the somatic energy signatures of sockeye and pink salmon at the end of ocean residency. My goal was to detect whether there have been inter-decadal changes in the amount of energy that salmon stored for their upriver spawning migrations and explain these difference in light of interdecadal oceanographic changes in the North Pacific Ocean.

Were I to indeed detect an energetic and (or) morphological change between sampling decades, my second objective was to explore differences in energy partitioning between two migratory tasks in sockeye: upriver swimming activity and ovarian development. If sockeye have experienced a reduction in starting somatic energy over the past fifty years, the total amount of energy allocated to these two tasks may also have been reduced. Reduced energy for

upriver migration, and reduce reproductive output could pose potential threats to reproductive fitness, particularly in populations making energetically difficult migrations. This analysis utilized multi-year data from two upriver populations (Chilko and Early Stuart).

## METHODS

### *Inter-decadal energy partitioning of river entry salmon*

Recent and historical proximate compositional and morphological data were analyzed through principal components analysis (PCA) to explore trends among populations over time. Sockeye data represented six collection years: 1956, 1957, 1958, 1959, 1999 and 2000. Energetic and morphological data for two Fraser River sockeye populations in 1956 (Early Stuart and Chilko) were taken from Idler and Clemens (1959). Additional data for the Chilko (1959), Early Stuart (1957 and 1958), and Adams (1958) populations were taken from Gilhousen's 1980 review of Fraser River sockeye energetics. Recent data from five Fraser River populations (Weaver, Adams, Horsefly, Early Stuart, and Chilko), were reported in Chapter 1. The data matrix contained five log-transformed variables: somatic protein, lipid, and water concentrations, length (POH) and gonado-somatic index. Cases represented population-sex-year means.

Only mean data from the 1957, 1958, and 1959 sockeye studies, and from the 1983 pink salmon study, were available. Thus, PCA explored differences among population-sex-year means. PCA was performed on a covariance matrix. A scatter plot of PC 1 versus PC2 factor loading scores was generated to visualize trends by population and decade. Group differences were explored by ANOVA of PC scores by population and year.

An ANCOVA of length-corrected river-entry somatic energy concentrations in Chilko sockeye were explored for years 1956 (from Idler and Clemens 1959), and 1999-2000 river-entry somatic values (Chapter 1). Unlike PCA, this univariate analysis was run to explore annual differences in somatic energy within a single population rather than multiple populations. Mean data for 1959 Chilko were taken from Gilhousen (1980).

Somatic energy data for 1956, 1957, 1958, 1997 and 1999 Early Stuart river-entry and spawning-ground arrival sockeye were plotted against migratory distance to explore interdecadal trends in river energy expenditure. Data for 1956 Early Stuart were from Idler and Clemens (1959). Data for 1957 and 1958 were from Gilhousen (1980). Data for 1999 were taken from

Chapter 1. Data for 1997 were from analysis of sockeye fillets rather than whole bodies (Higgs et al. 1999). A comparison between whole body and fillet protein and lipid concentrations in individual sockeye indicates that fillets have higher protein concentrations relative to whole body concentrations ( $P < 0.01$ ), but lipid concentrations between soma and fillets were not significantly different ( $P = 0.21$ ). Gross energy concentrations in each sample type, calculated from lipid and protein concentrations, were also not significantly different ( $P = 0.64$ ) (G.T. Crossin, unpublished data). Thus, 1997 fillet energy values can be used in comparisons with whole body energy values.

### *Energy partitioning during upriver migration*

During upriver migration to spawning areas, sockeye partition somatic energy to a number of tasks. Energy is needed for standard metabolism, swimming and other behaviours, gonadal maturation, and development of secondary sexual characteristics. Because sockeye are capital breeders, relying on finite, endogenous energy reserves to accomplish these tasks, the amount of energy invested in the gonads when migrating upriver is derived directly from somatic protein and lipid catabolism. Energy partitioned to swimming activity within each population during upriver migration was estimated by regressing  $\log_{10}$  transformed mass-specific somatic energy (at river-entry and at spawning ground arrival) against body length (as per Jonsson et al. 1991; Hendry and Berg 1999; Chapter 1). ANCOVA (Proc GLM, SAS Institute, Inc. 1988) was used to explore heterogeneity of slopes between the river-entry and spawning ground arrival somatic samples. If slopes were homogenous, then the difference in intercept values between river-entry and pre-spawning somatic energy (MJ) serves as an estimate of the amount of energy partitioned to general upriver swimming activity (i.e. active and standard metabolism; see Chapter 1). Estimates of ovarian investment are made in an identical manner, comparing the intercepts between river-entry and spawning ground ovarian energy from regressions against body length (Jonsson et al. 1997; Hendry and Berg 1999; Chapter 1). However, spawning ground ovarian energy data were unavailable. Assuming that there is a minimum level of investment to produce a viable egg, I estimated total ovarian energy in 1956 Chilko and ES eggs by regressing ovary mass (g) against gross ovarian energy for all 1999 and 2000 sockeye.

Regression analyses of this sort require the raw data for each individual fish in a population. Raw data were only available for 1956 Chilko and Early Stuart sockeye populations

(published in Idler and Clemens 1959), and for 1999 (Chapter 1). Thus, inter-decadal analysis of upriver activity and ovarian energy partitioning was restricted to these two populations in the 1956 and 1999.

## RESULTS

### *Inter-decadal analysis: river entry sockeye and pink salmon*

Principal components 1 and 2 accounted for 97% of the total variance in the sockeye dataset (80 and 17%, respectively). Pearson correlations between original PCA variables and PC scores revealed strong correlations between PC1 and GSI ( $r = 0.99$ ,  $P < 0.01$ ), and between PC2 and somatic lipid concentrations ( $r = 0.84$ ,  $P < 0.01$ ) (Table 2.1). A scatter plot of PC1 against PC2 revealed specific groupings of GSI and lipid signatures among the five populations (Figure 2.1). Populations fell into three groupings (Chilko-Early Stuart-Horsefly, Adams, and Weaver), and suggest a separation between sampling decades in the Chilko-Early Stuart-Horsefly group. Two factorial ANOVAs, designating PC1 and PC2 as separate dependent variables, revealed significant effects of both population and year ( $P < 0.01$  for both), but no significant population\*year interaction ( $P > 0.06$  for both).

ANCOVA revealed that somatic energy concentrations in 1956 Chilko females returning from ocean residency were significantly different from 1999 and 2000 females ( $P < 0.05$ ), and showed an inverse association with sea-surface temperature (printed on figure bars; Figure 2.2). Only mean somatic energy data for 1959 Chilko were available, so it was not included in the analysis but is presented in Figure 2.2 for comparison. Relative to 1956, 1957, and 1958, starting somatic energy concentrations in Early Stuart sockeye were lower in 1999, and lower still in 1997 (Figure 2.3). Energy reserves upon spawning ground arrivals in the 1990s Early Stuarts were lower than in the 1950s.

Pink salmon somatic energy measured at the mouth of the Fraser River was lower in 1983 than in 1999. Raw data for the 1983 pink salmon were not available, thus length corrections were not possible between years (Figure 2.4). However, 95% confidence intervals show no overlap between lipid concentrations, suggesting a potential difference between years.

*Inter-decadal analysis: partitioning between upriver activity and ovarian development in sockeye*

Partition analyses showed that in 1999, female Chilko sockeye used substantially more somatic energy to reach the spawning grounds, and invested more to ovarian development, than in 1956 (Figure 2.5). Early Stuart females, however, differed little between 1956 and 1999.

## DISCUSSION

### *Bioenergetic changes associated with climate change*

Somatic energy reserves in Fraser River sockeye, measured at the end of their period of ocean residency, have declined between the 1950s and the present. This decline was most evident in the two populations, Chilko and Early Stuart, for which I have extensive interannual data. In addition to somatic declines, energy allocated to ovarian development has also declined in these populations. Recent large-scale climatological changes in the North Pacific Ocean, which can affect nutrient upwelling, primary production, and sea-surface temperatures regimes, have been implicated in the reduced survival of all Pacific salmon (Welch et al 1998; Welch et al. 2000). These changing conditions may be affecting the ability of sockeye to both acquire and store energy prior to their upriver spawning migrations, thus potentially reducing survival.

Since the 1950s, two significant climatological shifts have occurred in the North Pacific Ocean (see Welch et al. 2000), and evidence for a third shift is beginning to surface (Thompson 2002). The first, occurring around 1977, resulted in substantial changes in zooplankton production, and in the production and survival of Pacific salmon. Though zooplankton biomass increased between 1977 and the late 1980s, its spatial distribution changed, shifting from the central Gulf of Alaska to coastal areas through advection (Brodeur and Ware 1992). The aggregation of zooplankton in coastal areas presumably offered juvenile salmon good feeding and growth opportunities, boosting them past the critical life-history stage when mortality is size-dependent, and is perhaps a reason for the increased survival of salmon up into the 1980s. However, declines in size-at-maturity in Fraser River sockeye were observed during this time (Cox and Hinch 1997), suggesting that conditions for adults were not entirely favourable. SSTs for a region of the Gulf of Alaska south of Kodiak Island show a pattern of increase from 1950 to 1990, as do SSTs recorded at several coastal BC lighthouse stations (<http://www.pac.dfo-mpo.gc.ca/sci/pages/lighthousedata.htm>). Though upwelling generally brings cool, nutrient rich

water to the surface, the distribution of that water is dynamic and affected by many interacting variables (wind and current velocities, temperature, variations in length of day and Earth's rotation). The survival of juvenile salmon in coastal areas probably increased through the enhanced growth opportunities offered by high zooplankton concentrations. However, most salmon move to off-shore regions as adults. It is in these open ocean regions where greater than 90% of sockeye growth occurs. Thinner zooplankton densities and higher SSTs in the central Gulf may have constrained growth, leading to the observed declines in size-at-maturity in sockeye

Further declines in the size-at-maturity and survival of Fraser River sockeye were observed in the 1990s by Welch et al. (2000). The 1989 climate shift was accompanied by a shallowing of the mixed layer-depth in the Gulf of Alaska and a shift from a characteristically iron-limited ecosystem to a nitrate-limited one. As a result, large reductions in both primary and secondary production occurred, and salmon survival declined. Until the North Pacific shifts back to a more productive and stable pre-1977 state, salmon, and presumably many other species, may suffer energetically.

There are two potential mechanisms through which the reduction in somatic bioenergy that I observed in sockeye between the 1950s and 1999-2000 may have occurred. First, the recent reduction in zooplankton biomass observed in the Gulf of Alaska may currently be at levels insufficient to allow optimal foraging. The energy spent in pursuit of scarce zooplankton prey may thus exceed energy consumed, leading to a reduction in somatic energy reserves prior to upriver migration. Second, the thermal boundaries that limit the distribution of salmon in the North Pacific may be shifting in response to climate change, thus reducing the functional area of ocean habitat that supports sockeye growth (Welch et al. 1999). Assuming that zooplankton are not confined by the same thermal boundaries that limit sockeye distribution, zooplankton concentrations, which declined in the Gulf of Alaska following the 1989 climate shift, would be further reduced as metabolically unfavourable habitats expand, thus reducing sockeye forage opportunities. The observed decline in size-at-maturity observed in Fraser River sockeye prior to the 1990s (Cox and Hinch 1997), and during the 1990s (Welch et al. 2000), support these two mechanisms.

*El Niño effects*

Associated with the recent climatological shifts in the North Pacific are increases in the frequency and intensity of El Niño events, and precipitation (as per Trenberth 2001 a,b). Bioenergetic data for sockeye and pink salmon collected from two recent El Niño years (1983 and 1997) show that relative to data collected in 1999 (Figures 3 and 4), somatic energy reserves in both species were reduced.

In 1983 and 1997 the Northeast Pacific was subjected to anomalous, high atmospheric pressure systems that prevented the formation of storm events, and subsequently warmed the mixed layer (Stabeno et al. 2001). In 1997, euphasiids (*Thysanoessa* spp.), which constitute the bulk of sockeye diet, responded by moving deeper into the water column of the Bering Sea than had been observed in previous years, perhaps a thermoregulatory response. Thus, the large surface spawning aggregates that typically occur in May and June were not present (see Baduini et al. 2001). It is likely that the large-scale changes in zooplankton densities and behaviour occurring in the Bering Sea in 1997 also occurred in the adjacent Gulf of Alaska, giving cause for the energetic reduction I observed in 1997 sockeye. It is probable that the depressed pressure fields and warm ocean temperatures associated with the 1983 El Niño also lead to zooplankton reductions and the subsequent energy reductions in pink salmon. In 1983, there was widespread mortality of short-tailed shearwaters (*Puffinus tenuirostris*) extending across a 2736 km arc in the northern and western Gulf of Alaska, as a result of starvation (Hatch 1987). These seabirds migrate from Antarctic waters during the austral winter to the North Pacific and Bering Sea where they feed primarily on euphasiids during the boreal summer. Hundreds of thousands were estimated to have died from anomalously warm ocean conditions and subsequent reductions in prey availability (Baduini et al. 2001). In 1997, hundreds of thousands died again in the Bering Sea and in parts of the northern Gulf of Alaska, all from starvation precipitated by declines in euphasiid abundance and movement from the surface ocean to deeper waters (Baduini et al. 2001). Presumably, sockeye and pink salmon have a feeding advantage over seabirds, able to move vertically in the water column with greater ease. However, salmon tend to be strongly surface oriented, and there is currently no evidence that they have changed their behaviour in recent years to seek out prey in deeper waters (see Welch et al. 1998). Whether they have or not however, the massive upriver mortality of Early Stuart sockeye in 1997 in the face of severe river discharge lends support to the hypothesis that sockeye were unable to acquire sufficient energy at sea to fuel upriver migration (Macdonald et al. 2000).

Energy levels measured in Chilko sockeye during the 1958-1959 El Niño were also diminished relative to three years prior in 1956. Thus, even in decades with relatively favourable ocean conditions (strong upwelling, higher primary and secondary production, as in the pre-1977 North Pacific), El Niño effects may possibly lead to substantial somatic energy losses. Somatic energy levels in 1959 Chilko sockeye, measured during a relative 'stable' period, were similar to those measured in 1999 and 2000, non- El Niño periods.

### *Effects of anthropogenic climate change*

There is broad scientific consensus that CO<sub>2</sub> emissions are causing global climate patterns to change (McBean 1990, and references therein; Trenberth 2001b). Though natural decadal-scale variation in ocean climate has always occurred, anthropogenic emissions are for the first time having an important impact on global atmospheric circulation patterns and will likely be the dominant climate affector in the coming centuries (McBean 1990). There has been much speculation about how anthropogenic climate change will affect the success of upriver migration and reproduction in future Pacific salmon populations. From an energetic point-of-view, Healey (1986) speculated that decreases in body weight, resulting primarily from rising SST effects on standard metabolism, will negatively affect egg production and the ability of salmon to migrate successfully upriver. Assuming that salmon have a minimum size and (or) energetic condition needed for successful migration and reproduction, energetic and reproductive shortcomings may be offset by feeding an additional year at sea, thus boosting growth potential and fecundity (Mangel 1994; Cox and Hinch 1997). But an increase in the age-at-maturity has not been observed in sockeye over the last fifty years (Helle and Hoffman 1995), lending support to the assertion that this would lead to a reduction in reproductive potential through an increase in generation time (*sensu* Cox and Hinch 1997). The results of principal components analysis presented in this study demonstrate that in recent years, Fraser River sockeye populations (Chilko and Early Stuart) are instead beginning their spawning migrations in a diminished energetic and reproductive condition relative to fifty years ago. Thus, it is possible that shifting thermal boundaries, increased SSTs, reduced nutrient upwelling, and reduced zooplankton production in the North Pacific are collectively affecting the survival of Pacific salmon, presumably, as this study suggests for sockeye, by affecting the procurement of bioenergy.

The way in which Chilko and Early Stuart sockeye partitioned somatic energy while migrating to their spawning areas underscores how potentially dangerous a changing ocean climate is to reproductive fitness. Between 1956 and 1999, I found no discernable difference in the absolute amount of energy that Early Stuart females allocated to both upriver swimming and ovarian development while migrating upriver. However, in 1999, Early Stuart sockeye began their upriver migration with 22% less somatic energy than in 1956. As a result, they arrived on the spawning grounds with 27% less energy than in 1956, close to the 4 MJ/kg line in Figure 2.4, which is the approximate threshold between life and death for most sockeye (Gilhousen 1980; Hendry and Berg 1999; Chapter 1). Thus, 1999 Early Stuart females were at extreme risk of pre-spawning mortality.

However, a trend for increasing precipitation is also predicted with global climate change, as is a trend for increased spring air temperatures, both of which can affect the magnitude and timing of spring freshets (Trenberth 2001 a,b). In recent years, snowpack has increased substantially in the headwater mountains of the Fraser River watershed. Following a record-setting El Niño and high SSTs in 1997, which presumably depressed river-entry somatic energy concentrations, Fraser River discharge rates reached their highest recorded level and coincided with the upriver run of the Early Stuart population. As a result, energy reserves were exhausted prematurely in the face of these high discharge rates, leading to massive pre-spawning mortality (Macdonald et al. 2000). However, analysis of the individuals that swam successfully upriver shows that, between 1956 and 1999, there were no discernable differences in the amount of energy spent on upriver swimming, though poorer-condition fish died *en route* (Rand et al. 2002). EMG telemetry work by Hinch and Rand (1998) revealed that the most energetically successful swim strategies employed by upriver salmon were those that chose not to swim anaerobically. Thus, it seems safe to assume that the depressed starting somatic energy concentrations put sockeye at exceptional risk. Given that climatological models do not predict a reversal of ocean conditions to pre-1977 conditions, but do predict that SSTs will continue to rise over the next 100 years (Welch et al. 1998), resulting in a possible increase of 2-4°C (Boer et al. 1992), the concentration of stored somatic energy in all salmon may approach critical threshold levels, below which successful upriver migration and reproductive fitness may be critically jeopardized. If these models prove correct, the future for Early Stuart sockeye may be a bleak one.

Though also threatened by climate change, Chilko sockeye do not appear to be in as severe a predicament. Unique among Fraser River sockeye populations, Chilko sockeye have been identified as “superoptimal” migrants, utilizing less energy per unit of migratory difficulty, than other Fraser populations (Hinch and Rand 2000; Chapter 1). However, the fact that they spent more energy on upriver swimming and on egg production in 1999 than in 1956, and that Early Stuart showed no difference in both tasks between years, suggests that in-river migration conditions were perhaps more difficult for Chilko sockeye in 1999. It is possible that they may have encountered more severe discharge rates in their specific migration route relative to Early Stuart. Chilko Lake is a glacially fed system high in the Coast Mountains of British Columbia, lying nearly twice the elevation of the Stuart-Takla system (1158m vs. 701m above sea-level). Data from several Coast Mountain monitoring stations show that snowpack in the mountains adjacent to the Chilko Lake region in 1999 was substantially higher than the long-term average. Snowpack adjacent to the Stuart Takla region however was only slightly above the long-term average (data compiled by the Government of British Columbia, <http://srmwww.gov.bc.ca/aib/wat/rfc/index.htm>). Thus, spring discharge rates may have indeed been more substantial in the Chilko and Chilcotin River drainages than in the upper reaches of the Fraser/Stuart-Takla drainages, leading to potentially higher migratory energy costs for 1999 Chilko sockeye.

Upriver sockeye populations are under strong selection for energy efficiency (Chapter 1). Relative to other upriver populations (Early Stuart and Horsefly), Chilko sockeye appear to have adapted a greater capacity for energy efficiency, perhaps because of the high elevation of their spawning system. This capacity serves as an “evolutionary insurance policy” for coping with the severe discharge levels that can presumably occur through this steep tributary system. Though Chilko sockeye arrived on the spawning ground in 1999 with 6.3 MJ/kg of somatic energy (nearly 2.5 MJ/kg higher than the terminal 4 MJ/kg line), this was still 25% lower than arrival concentrations in 1956 ( $\approx 8.0$  MJ/kg). Chilko sockeye may be better adapted to contend with high variation in spring freshets, but in a changing climate their long-term fitness may be put at risk.

*Is climate change causing late-run Fraser River sockeye populations to migrate early?*

There is growing evidence that a recent climatological shift may have occurred in 1997 in the North Pacific Ocean, one which may be having critical impacts on late run Fraser River sockeye (Thompson 2002). Since 1997, late summer-runs of Fraser River sockeye (which include the Weaver and Adams populations) have begun their upriver migrations three to six weeks earlier than was historically recorded, and are coincident with massive pre-spawning mortality (PSC 2002). In 2000 and 2001, Weaver sockeye returned nearly six weeks earlier than historically noted and 90% of the population died before spawning. These early runs may be linked to worsening bio-physical conditions in the North Pacific Ocean following the 1997 shift. Though a parasitic infection is believed the proximate cause of death in these sockeye, many speculate that climate-related reductions in somatic bioenergy (caused by changes in SSTs and zooplankton production) may be the ultimate cause.

Late run Fraser River sockeye populations begin upriver migration with smaller energy reserves relative to upriver populations, and, unlike upriver populations, generally hold for approximately two weeks at the mouth of the Fraser River, presumably awaiting an endogenous and (or) environmental cue to initiate upriver migration. If these populations are experiencing critical climate-related declines in somatic energy prior to upriver migration as discussed in the previous sections for Chilko and Early Stuart populations, there may be two possible ways to compensate for this energetic shortcoming: 1) by diverting less somatic energy to reproductive compartments thus making more energy available for migration, and (or) 2) by beginning upriver migration earlier than usual to avoid wasting energy. The first explanation seems unlikely as reproductive allocation in salmon is under genetic control. The second explanation seems an attractive candidate for study. Because run timing and holding behaviours in sockeye have evolved to synchronize their arrival on the spawning grounds when stream temperatures are most favourable for egg and alevin development (Macdonald, et al. 1998), it would take a very strong signal to override this endogenous and (or) environmental migratory cue and advance upriver run timing. If sockeye can somehow 'sense' during this time that their somatic energy reserves are dwindling toward levels that are insufficient for the completion of the upriver migration to which they have evolved, this may be just such a signal. However, there is recent evidence that sockeye populations are aerobically adapted to specific river temperature ranges (Lee et al. in prep). If late run Weaver and Adams sockeye are migrating early into unfavourable thermal river conditions, this could metabolically exacerbate their already diminished energetic state,

making them more prone to parasitic infection, and contributing to the massive pre-spawning mortalities observed in recent years. Additionally, earlier than normal migrants face higher discharge rates in the Fraser River. Recently, both Rand et al. (??) and Macdonald (J.S. Macdonald, Fisheries and Oceans Canada, unpublished data) have shown direct links between high river discharge and *en route* mortality. An energetic mechanism may be responsible for these losses. I suggest that this line of inquiry be investigated in greater detail.

In this chapter, I present data that suggests a climatological link to decreases in somatic energy observed over the last fifty years. Because salmon die when they reach a body energy density of about 4 MJ/kg (Chapter 1, and Figure 4), and that aspects of reproductive behaviour are related to the concentration of energy reserves on the spawning grounds (Mehranvar, in prep.), continued declines in somatic energy at the onset of upriver migration may contribute to pre-spawning mortality (Rand & Hinch 1998; Hinch & Bratty 2000). This may have profound implications for spawning success, and may provide a clue why late-run Fraser River sockeye have changed their migration timing.

Literature cited:

- Baduini, C.L., Hyrenbach, K.D., Coyle, K.O., Pinchuk, A., Mendenhall, V., and Hunt, G.L. 2001. Mass mortality of short-tailed shearwaters in the south-eastern Bering Sea during the summer of 1997. *Fisheries Oceanography* 10: 117-130.
- Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., and Kurashov, V. 1999. The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56: 516-526.
- Boer, G.J., McFarlane, N.A., and Lazare, M. 1992. Greenhouse gas-induced climate change simulated with the CCC second generation general circulation model. *J. Clim.* 5: 1045-1077.
- Both, C. and Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296-298.
- Cox, S.P. and Hinch, S.G. 1997. Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952-1993) and associations with temperature. *Can. J. Fish. Aquat. Sci.* 54: 1159-1165.
- Forchhammer, M.C., Post, E., and Stenseth, N.C. 1998. Breeding phenology and climate... *Nature* 391: 29-30.
- Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. *Int. Pac. Salmon Fish. Comm. Bull. No. 22.*
- Hatch, S.A. 1987. Did the 1982-1983 El Nino-Southern Oscillation affect seabirds in Alaska? *Wilson Bull.* 99: 468-474.
- Healey, M.C. 1986. Optimal size and age at maturity in Pacific salmon and effects of size-selective fisheries. *In Salmonid age at maturity. Edited by D.J. Meerburg. Can. Spec. Publ. Fish. Aquat. Sci. No. 89. pp. 39-52.*
- Helle, J.H. and Hoffman, M.S. 1995. Size decline and older age at maturity in two chum salmon (*Oncorhynchus keta*) stocks in western North America. *In Climate change and northern fish populations. Edited by R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 245-260.*
- Hendry, A.P. and Berg, O.K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Can. J. Fish. Aquat. Sci.* 77: 1663-1675.
- Higgs, D.A., Rowshandeli, M., Greig, M., Barnes, D.P., and Macdonald, J.S. 2000. Changes in the levels of proximate constituents and gross energy in the muscle (fillet) of four year old Early Stuart sockeye salmon (*O. nerka*) during the 1997 upstream Fraser River spawning migration. *Can. Tech. Rep. Fish. Aquat. Sci.* 2315: 91-103.

Hinch, S.G., Healey, M.C., Diewert, R.E., Thomson, K.A., Hourston, R., Henderson, M.A., and Juanes, F. 1995. Potential effects of climate change on marine growth and survival of Fraser River sockeye salmon. *Can. J. Fish. Aquat. Sci.* 52: 2651-2659.

Hinch, S.G., Healey, M.C., Diewert, R.E., and Henderson, M.A. 1995. Climate change and ocean energetics of Fraser River sockeye (*Oncorhynchus nerka*). In *Climate change and northern fish populations*. Edited by R.J. Beamish. *Can. Spec. Publ. Fish. Aquat. Sci.* No. 121. pp. 439-445.

Hinch, S.G., and Rand, P.S. 2000. Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. *Can. J. Fish. Aquat. Sci.* 57: 2470-2478.

Hsieh, W.W. and Boer, G.J. 1992. Global climate change and ocean upwelling. *Fisheries Oceanography* 1: 333-338.

Idler, D.R. and Clemens, W.A. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. *Int. Pac. Salmon. Fish. Comm. Prog. Rep.* No. 6.

Inouye, D.W., Barr, B., Armitage, K.B., and Inouye, B.D. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences* 97: 1630-1633.

Jonsson, N., Hansen, L.P., and Jonsson, B. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *J. Anim. Ecol.* 60: 937-947.

Lee, C.G., Farrell, A.P., Hinch, S.G., and Healey, M.C. in prep. ...

McBean, G.A. 1990. Possible impacts of climate change on the North Pacific Ocean and its marine resources. *Transactions of the Royal Society of Canada* 1: 435-452.

McFarlane, G.A., King, J.R., and Beamish, R.J. 2000. Have there been recent changes in climate? Ask the fish. *Progress in Oceanography* 47: 147-169

Macdonald, J.S., Foreman, M.G.G., Farrell, T., Williams, I.V., Grout, J., Cass, A., Woodey, J.C., Enzenhofer, H., Clarke, W.C., Houtman, R., Donaldson, E.M., and Barnes, D. 2000. The influence of extreme water temperatures on migrating Fraser River sockeye salmon (*Oncorhynchus nerka*) during the 1998 spawning season. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2326.

Macdonald, J.S., Scrivener, J.C., Patterson, D.A., and Dixon-Warren, A. 1998. Temperatures in aquatic habitats: the impacts of forest harvesting and the biological consequences to sockeye salmon incubation habitats in the interior of B.C. *Proc. Forest-Fish Conf.*, May 1-4, 1996, Calgary, Alberta. *Nat. Resour. Can, Can. For. Serv., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-356.* Pps 313-324.

- Mangel, M. 1994. Climate change and salmonid life history variation. *Deep-Sea Res.* 41: 75-106.
- Mehranvar, L. A genetic evaluation of the breeding system of sockeye salmon. Zoology Department, University of British Columbia. MSc. thesis, in preparation.
- Namais, J., Yuan, X., and Cayan, D.R. 1988. Persistence of North Pacific sea surface temperature and atmospheric flow patterns. *J. Clim.* 1: 682-703.
- Pacific Salmon Commission. Agenda: 3<sup>rd</sup> Late-run Sockeye Salmon Workshop. Sponsored by the Fraser River Panel, Pacific Salmon Commission, Vancouver, BC. Jan 2002.
- SAS Institute. 1988. SAS/STAT user's guide, version 6.03. SAS Institute, Cary, N.C.
- Stabeno, P.J., Bond, N.A., Kachel, N.J., Salo, S.A., and Schumacher, J.D. 2001. On the temporal variability of the physical environment over the southeastern Bering Sea. *Fisheries oceanography* 10: 81-98.
- Sparks, T.H. 1999. Phenology and the changing pattern of bird migration in Britain. *Int. J. Biometeorol.* 42: 134-138.
- Thompson, R. 2002. Late-run early-migration: a response to an abrupt climate-scale shift in estuarine exchange between the Strait of Georgia and adjoining coastal waterways. Presentation given to 3<sup>rd</sup> Late-run Sockeye Salmon Workshop. Sponsored by the Fraser River Panel, Pacific Salmon Commission, Jan 2002.
- Trenberth, K. E., 2001a. How should rainfall change as climate changes: Prospects for increases in extremes? *The Climate Report*. Ed: Maryam Golnaraghi, Climate Risk Solutions, Inc. 2, 1, 11-13.
- Trenberth, K. E., 2001b. The IPCC assessment of global warming 2001. *The Forum for Environmental Law, Science, Engineering and Finance (FAILSAFE) electronic journal spring (March) issue*, <http://www.felsef.org/spring01.htm#3>, pps. 8-26.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.
- Welch, D.W., Ishida, Y., and Nagasawa, K. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): Long-term consequences of global warming. *Can. J. Fish. Aquat. Sci.* 55: 937-948.
- Welch, D.W., Ward, B.R., Smith, B.D., and Eveson, J.P. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. *Fisheries Oceanography* 9: 17-32.

Williams, I.V., and 15 others 1986. The 1983 early run Fraser and Thompson River pink salmon; morphology, energetics and fish health. *Int. Pac. Salmon. Fish. Comm. Bull.* XXIII. Pps 55.

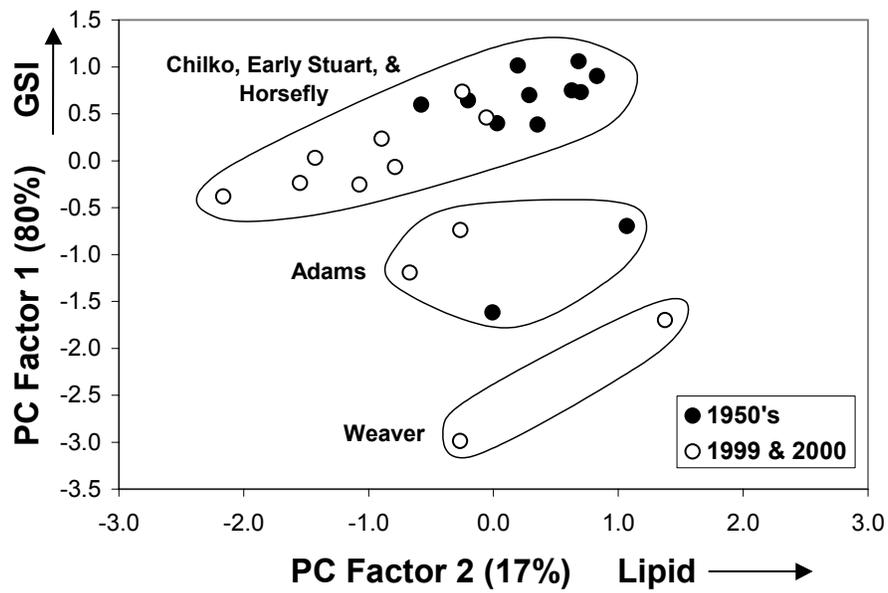


Figure 2.1: Scatterplot of scores for the first two PC axes. The first axis represents sites ranging from low to high GSI scores. The second axis represents sites ranging from low to high somatic lipid concentrations. Points represent stock-sex-year means. Ellipses were drawn around population groups. Dark circles represent 1950s data. Open circles are for 1999 and 2000 data.

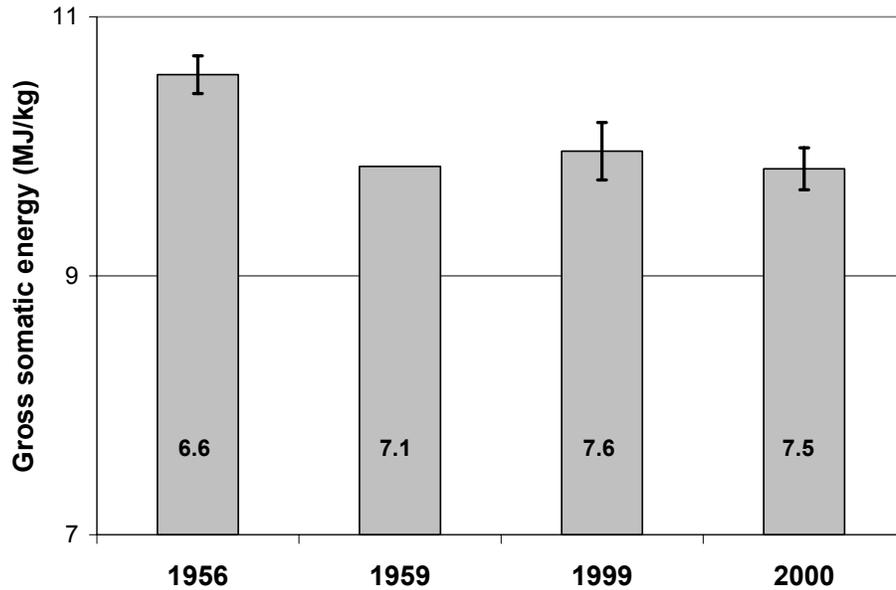


Figure 2.2: Mean (+/- SE) gross somatic energy concentrations in Fraser River-entry Chilko sockeye salmon. Values printed in bars are mean monthly SSTs at a coastal BC lighthouse station for a six month period prior to upriver migration. Raw data for 1959 were not available so SE could not be calculated.

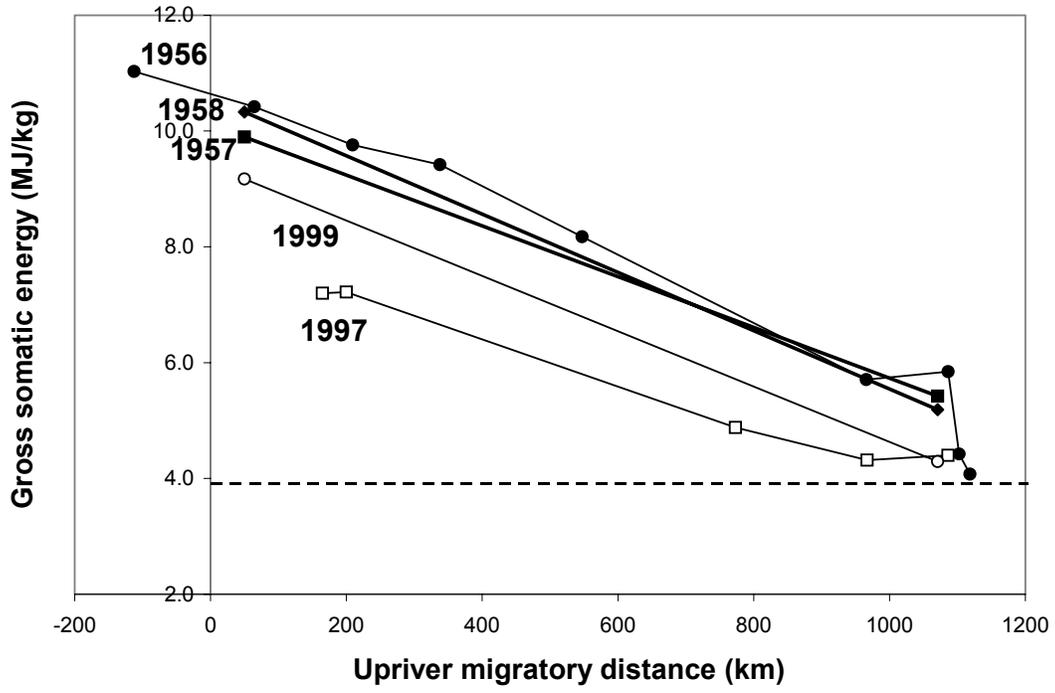


Figure 2.3: Inter-decadal comparison of somatic energy expenditure as a function of migratory distance from the mouth of the Fraser River in the Early Stuart sockeye population. 1956 data point to the left of the y-axis present sockeye collected in the marine environment. Dark symbols are for sampling years in the 1950s. Open symbols are for recent collections. Dashed line represents the approximate energetic threshold between life and death for sockeye salmon.

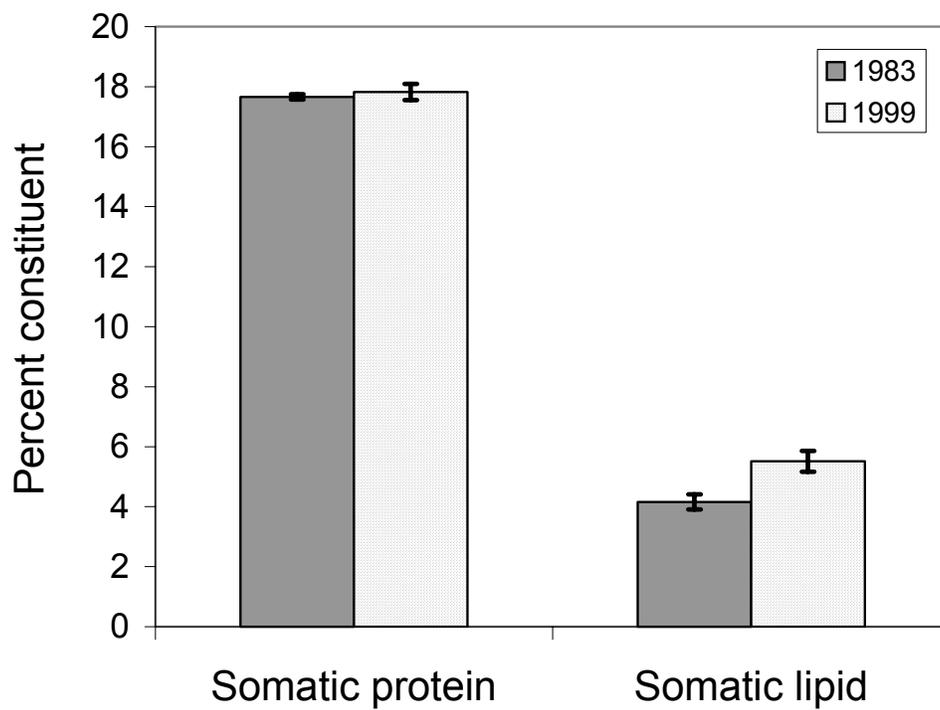


Figure 2.4: Percent somatic protein and lipid concentrations in Fraser River pink salmon measured at the Fraser River entry in 1983 and 1999. Error bars are +/-95% confidence intervals.

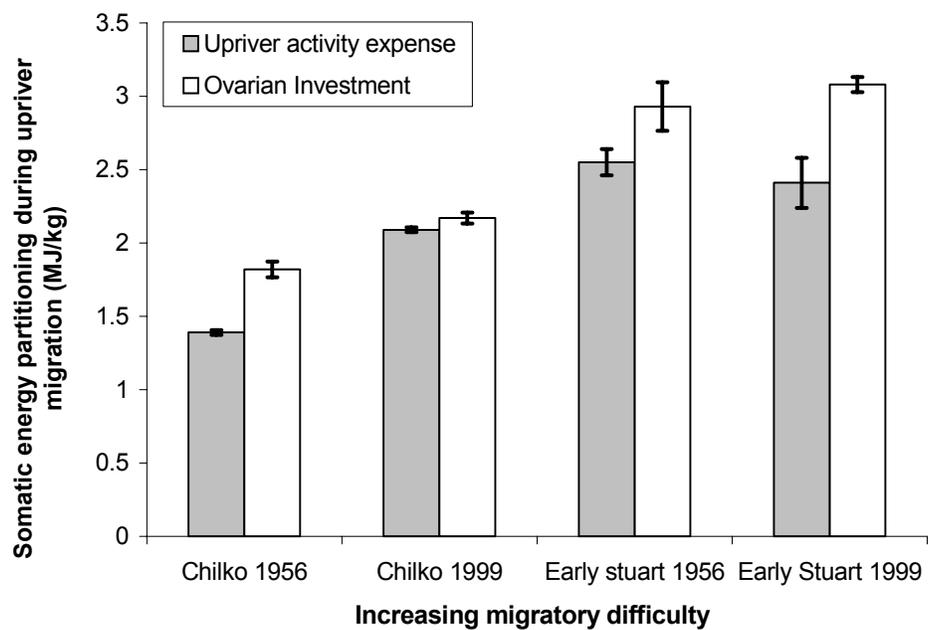


Figure 2.5: Mean (+/-) somatic energy partitioning during upriver migration in female Fraser River sockeye.

Table 2.1: Pearson correlation coefficients (upper value) and associated probabilities (lower value) relating log10-transformed somatic protein, lipid, GSI, and length values in sockeye at end of ocean residency, with PC1 and PC2 factor scores from interdecadal PCA analysis.

	PC1	PC2
Protein	-0.1692 0.4087	-0.1366 0.5059
Lipid	-0.5429 0.0042	<b>0.8398</b> <b>0.0001</b>
GSI	<b>0.9901</b> <b>0.0001</b>	0.1402 0.4944
Length	-0.2935 0.1456	-0.0437 0.8323

## CHAPTER 3

### EVOLUTION OF BODY SIZE AND EGG SIZE IN PACIFIC SALMON AND FUTURE WORK

The vast and varied terrain found throughout the Fraser River watershed present a diverse array of habitats for spawning sockeye. In Chapter 1, I attributed, in part, the diversity of body shapes and sizes, and the diversity of energetic and reproductive tactics observed throughout the watershed, to two specific features of the natal environment: upriver distance and spawning ground elevation. However, when migratory constraints are eased, their strength as selective agents diminishes, allowing other forces to influence body size in sockeye. Such is the case among coastal lake systems, where high variation in body size generally can be observed (Quinn et al. 1995; Woody et al. 2000). This variation shows correlations with measures of stream hydrology, predatory pressure, and sexual selection. However, there is some confusion in the literature about what factors are most responsible for variation in body size (e.g. length). In Chapter 1, I provide strong correlative evidence that when migratory constraints are great, a smaller body facilitates upriver energy efficiency. When migratory constraints are low however, body size seems unrelated to migratory difficulty. The literature points to two selective forces that influence egg size (incubation temperature and incubation gravel sizes), which may account for the high variation in adult body sizes among populations with low degrees of migratory difficulty (Gillooly and Dodson 2000; Quinn et al. 1995).

As with body length, egg sizes among populations in Chapter 1 were inversely related to migratory difficulty (Chapter 1, Figure 4), suggesting a possible energetic link. However, a wide range of stream incubation temperatures were observed among the spawning systems considered in Chapter 1. Considering the strong influence that temperature has on standard metabolism, incubation temperatures within natural spawning environments may influence egg size.

There is a strong positive relationship between egg size and the number of thermal units required for embryonic development that spans a wide range of taxa (Gillooly and Dodson 2000). Temperature is an important variable that affects enzymatic activity, gas transport, and gas solubility within a developing embryo. Because small eggs contain relatively less yolk than large eggs, fewer accumulated thermal units (ATUs, or degree-days) are required for development, especially at cold temperatures (0-4°C) when enzymatic activity rates are sub-optimal. Emergence timing of fry from redds is considered the major evolutionary force

influencing the timing of sockeye migrations and spawning, and coincides with optimal growth potential and food availability in the adjacent lakes where young sockeye live for two years before migrating to sea (Brannon 1984). Essential to this synchronization are rates of embryonic development, which are largely controlled by incubation temperature.

However, incubation gravel sizes may indirectly constrain egg size, largely through their influence on the permeability of dissolved oxygen (DO) to interstitial gravel spaces (see Quinn et al. 1995). In ectothermic vertebrates, the coupling of cardiac activity and convective blood-oxygen transfer is not established until late in embryonic development. Respiration in early development is therefore dependent on oxygen diffusion across egg capsule membranes and into developing tissues (Pelster 1999). An argument for smaller egg selection in habitats where mean gravel sizes are small draws support from the fact that small eggs have larger surface-to-volume ratios than large eggs, which may offset any diffusive limitations to oxygen consumption imposed by small gravels.

In a recent review of embryonic development in fish, Pelster (1999) notes that embryonic fish are generally considered “oxy-conformers”, able to adjust to wide variation in stream DO, and possessing a strong capacity for anaerobic respiration. In fact, unpublished results cited in this review found that Arctic char embryos (*Salvelinus arcticus*) were capable of surviving eight hours of anoxia in laboratory experiments. Thus, salmonids seem well suited to cope with wide fluctuations in DO that may occur naturally in redds. In line with this observation, Peterson and Quinn (1996) observed that DO concentrations in natural chum (*O. keta*) redds appeared to fluctuate more often in the early stages of incubation than in the later, though long-term averages were still better from fertilization to hatch than from hatch to emergence. Interestingly, the time when DO concentrations were poorest in this study (hatch to emergence, winter to spring) occurred after the chum embryos had hatched, perhaps at which point they are free to behaviourally oxy-regulate within the redd, seeking out pockets where DO concentrations are more favourable. Developmentally, cardiac output and convective blood transport become coupled in salmonid embryos sometime prior to hatching, shifting respiration from diffusive uptake to gill transport in preparation for a mobile life (Pelster 1999, Rombough 1999).

Wild salmon generally construct their redds in pool-riffle channels and pool tailouts (Schuett-Hames et al. 2000), regions where oxygen-rich surface stream water downwells into the oxygen-poor hyporheic zone, presumably because these offer suitable incubation conditions.

These conditions are enhanced during redd construction, when, with powerful tail sweeps, female salmon remove the finer particles thus enhancing gravel permeability (Peterson and Quinn 1996). Peterson and Quinn (1996) found that DO concentrations within wild chum redds were not correlated with the gravel composition of the redd. Furthermore, they found no correlation between egg burial depth and DO concentrations. Possible explanations were drawn from studies showing that the relationship between fine sediments and DO is often weak (Shapley and Bishop 1965), and that DO concentrations may not depend on gravel size (Sowden and Powder 1985). If DO concentrations are not affected by gravel sizes within the range of those found naturally in a typical, undisturbed redd, then the influence of gravel size on eggs size may be weak.

In my research, I found a strong positive correlation between developmental ATUs (acquired from peak spawning/fertilization to peak to emergence) and egg size (mg) (Pearson's  $r = 0.67$ ,  $P < 0.05$ ), a relationship that has been well studied and that synchronizes key life-history stages in salmon to important environmental events (warm stream temperatures from fertilization to hatching; hatching and mobility when winter DO levels are naturally low and when storm cycles ensue; emergence when spring lakes turn-over and productivity blooms). Unfortunately, I did not measure gravel sizes at the spawning grounds in this study. Thus, I am unable to comment directly on the effect of gravel size on egg size.

A study by Rombough (1989) found that area-specific oxygen conductance across the egg capsules of embryos varied little among all six Pacific salmon species, though egg sizes differed substantially. Sockeye eggs for example were smaller than pink salmon eggs (63 and 71 mm diameters respectively). Due perhaps to some unidentified structural difference between the eggs of these species, area-specific oxygen conductance is similar between eggs that differ considerably in size. It is unclear how different egg sizes within a species are affected by DO concentrations. A controlled survivorship experiment, in which a range of eggs sizes were exposed to different DO concentrations, would be informative.

Quinn et al. (1995) found a strong positive correlation between gravel sizes and egg sizes among several populations of coastal sockeye in Alaskan lakes systems, and speculated that *in situ* DO concentrations (and potentially natural levels of egg predation) influence egg size. Given these results, I wonder if there is some geomorphological link through which stream-bed

morphology and temperatures may co-vary. Unfortunately, their study did not examine water temperatures within the different habitats.

A comprehensive analysis of *in situ* DO concentrations, gravel sizes, and temperatures throughout the course of development would help identify the selective forces most directly influencing egg size among populations, and may provide some insight to the evolution of body size in sockeye.

Literature cited:

- Brannon, E.L. 1984. Mechanisms stabilizing salmonid fry emergence timing. *Can. Spec. Publ. Fish. Aquat. Sci.* 96: 120-124.
- Gillooly, J.F. and Dodson, S.I. 2000. The relationship of egg size and incubation temperature to embryonic development time in univoltine and multivoltine aquatic insects. *Freshwater Biology* 44: 595-604.
- Pelster, B. 1999. Environmental influences on the development of the cardiac systems in fish and amphibians. *Comp. Biochem. Physiol.* 124A: 407-412.
- Peterson, N.P. and Quinn, T.P. 1996. Spatial and temporal variation in dissolved oxygen in natural egg pockets of chum salmon, in Kennedy Creek, Washington. *J. Fish Biol.* 48: 131-143.
- Quinn, T.P., Hendry, A.P., and Wetzel, L.A. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos* 74: 425-438.
- Rombough, P.J. 1989. Oxygen conductance values and structural characteristics of the egg capsules of Pacific salmonids. *Comp. Biochem Physiol.* 92A: 279-283.
- Rombough, P.J. 1994. Energy partitioning during fish development: additive or compensatory allocation of energy to support growth? *Functional Ecology* 8: 178-186.
- Rombough, P.J. 1999. The gill of fish larvae. Is it primarily a respiratory or an ionoregulatory structure? *J. Fish Biology* 55: 186-204.
- Schuett-Hames, D.E., Peterson, N.P., Conrad, R., and Quinn, T.P. 2000. Patterns of gravel scour and fill after spawning by chum salmon in a western Washington stream. *Nor. AM. J. Fish. Mgmt.* 20: 610-617.
- Shapley, S.P. and Bishop, D.M. 1965. Sedimentation in a salmon stream. *Journal of the Fisheries Research Board of Canada* 22: 919-928.
- Sowden, T.K. and Powder, G. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. *Trans. Am. Fish. Soc.* 114: 804-812.
- Woody, C.A., Olsen, J., Reynolds, J., and Bentzen, P. 2000. Temporal variation in phenotypic and genotypic traits in two sockeye salmon populations, Tustumena Lake, Alaska. *Trans. Am. Fish. Soc.* 129: 1031-1043.