Technical Report 2005-08 Draft

IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

# Energy use, migration times, and spawning success of adult spring-summer Chinook salmon returning to spawning areas in the South Fork Salmon River in Central Idaho.

**2002 and 2003**

A report for Project ADS-P-00-13, ADS-00-1; ADS-00-2; ADS-00-5

by

A.M. Pinson, C.A Peery, and J.L. Congleton
U.S Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit
University of Idaho, Moscow, Idaho 83844-1141

and

M. Moser
Northwest Fisheries Science Center
NOAA Fisheries
2725 Montlake Blvd. East, Seattle,

for
U.S Army Corps of Engineers
Portland and Walla Walla Districts

and
Bonneville Power Administration
Portland, Oregon

2006

## Preface

Adult Chinook salmon, *Oncorhynchus tshawytscha*, must pass eight hydroelectric dams and reservoirs and migrate over 1000 river kilometers from the Pacific Ocean to reach spawning areas in the South Fork Salmon River in central Idaho. Behavior during migration, the rate at which energy is depleted, and ultimately reproductive success may be affected by river conditions (temperature and flow) and dam operations (e.g., spill) occurring during the spawning migration. In this study we examined the energy use of adult Chinook salmon migrating through the Columbia and Snake Rivers to reach spawning areas to address several objectives. First, we determined the metabolic costs of migration to assess potential detrimental effects of dam and reservoir passage at the population level. Second, we explored non-lethal techniques for estimating energy content of adult migrating fish so that we could describe energy expenditures for an individual from start of migration to death on the spawning grounds. Third, we related the migration histories, including travel time and temperature exposures, of individual fish to energetic expenditures and final fate. Study objectives reported here relate to RPAs 107 and 118 in Section 9.6.1 of the Federal Columbia River Power System Biological Opinion (NMFS 2000).

## Acknowledgements

Many people assisted in data collection for this project. Brad Herauf, Chuck Boggs, Darin Jones, Chris Caudill, Brad Winans, Mike Jepson, George Naughton, and Ade Snider of the University of Idaho, assisted in data collection on the South Fork Salmon River and Steve Lee, Megan Heinrich, and David Griffith assisted at Bonneville Dam. Kim Apperson, Gene McPherson, and Joel Patterson of Idaho Department of Fish and Game and Jay Hesse of the Nez Perce Tribe provided helpful insight, logistical support, and cooperation on the South Fork Salmon River. A. Matter, NOAA Fisheries, managed the radiotelmetry database. Proximate Analysis was determined by the Washington State University Wildlife Habitat Lab under the supervision of Bruce Davitt. This project was funded by the U.S. Army Corps of Engineers.

## Table of Contents

Preface i

Chapter 1: Changes in body composition and energetic costs of the spawning migration for spring-summer Chinook salmon of the South Fork Salmon River population.

Abstract ..... viii
Introduction ..... 1
Methods ..... 3
Results ..... 6
Discussion ..... 16
References ..... 23

Chapter 2: Use of non-lethal techniques for assessing migratory and reproductive costs of Chinook salmon.

Abstract ..... 28
Introduction ..... 29
Methods ..... 30
Results ..... 32
Discussion ..... 36
References ..... 41

Chapter 3: Migration time, energy use, and spawning success of long distance migrating adult Chinook salmon.

Abstract ..... 43
Introduction ..... 44
Methods ..... 44
Results ..... 48
Discussion ..... 56
References ..... 62

Appendix ..... 64

## List of Tables

**Chapter 1**

Table 1.1 ANOVA P value and Mean (SE) for fork length and mass for males and females at four stages of the spawning migration.……7

Table 1.2 Results from canonical variate analysis for proximate composition (arc sine square root transformed muscle, skin, viscera and gonad lipid, moisture, ash and protein) of females and males by stage of migration with ranks in parentheses.…….....7

Table 1.3 Lipid, protein, and moisture (percent wet mass) for female and male Chinook salmon in 2002 with standard deviations in parentheses. (H = adipose clipped, hatchery origin; W = non-adipose clipped, wild origin) ……..9

Table 1.4 Mean contribution (percent) of muscle, skin, viscera, and gonads to total body mass in 2003 (standard deviation in parentheses) ……..……10

Table 1.5 Comparison (by ANCOVA) of mean length-controlled lipid and protein masses (g) for tissues of adult Chinook salmon sampled at four stages of migration. …….....11

Table 1.6 Comparison (by ANCOVA) of mean length-controlled lipid and protein masses (g) for tissues of wild adult Chinook salmon sampled at two stages of migration (pre-spawning death, post-spawning death).…….....12

Table 1.7 Total somatic and gonad energy (kJ) with percentage of initial somatic energy used as a source for swimming and gonad development in parentheses for adult Chinook salmon of 70, 80, 90 and 100 cm and for mean fork lengths (82 cm for females and 82.5 cm for males) sampled at four migration stages.....…….14

Table 1.8 Comparison (by ANCOVA) of mean length-controlled snout length, hump height, and gonad mass ($log_{10}$) on fork length ($log_{10}$). Antilogs of mean ($log_{10}$) snout length (mm), ($log_{10}$) hump height (mm) and ($log_{10}$) gonad mass (g) for four stages of migration are shown.……..16

**Chapter 2**

Table 2.1 Summary of best two models for estimating lipid content (%) of the somatic tissues (muscle, skin, viscera), total lipid mass, somatic lipid mass, somatic energy (kJ), total body energy (kJ), water content (%), total water mass of the

somatic tissues, and total body water mass (TBW). $R^2$, AIC, and Δi (AICi – AICmin) values are shown……33

**Chapter 3**

Table 3.1 Regression models for estimating percent lipid of muscle, somatic energy (kJ), and total energy (kJ) with coefficient of determination. Independent variables include body mass in kg (wt), fork length in cm (Lf), hump height in mm (Hh) and body depth at the anal fin in mm (Da).[a]……..47

Table 3.2 Travel times between Bonneville and Lower Granite Dams (BON-LGR), Lower Granite Dam and the SFSR receiver site (LGR-SFSR), Bonneville Dam and the SFSR receiver site (BON-SFSR), percentage lipid of the muscle tissue, mass specific somatic energy and mass specific total energy for two fish with radio transmitters recaptured after spawning in 2002…….48

Table 3.3 Migration time and energy content for radio-tagged fish recaptured at the trap on the SFSRin 2002 including tag date and location (BON = Bonneville dam, LGR = Lower Granite Dam) migration time from tagging location to the fixed antennae receiver site on the SFSR, muscle lipid (%), and derived estimates of mass-specific somatic and mass specific total energy (kJ $g^{-1}$ )……..49

Table 3.4 Migration times and percent lipid at death (Lipid f; where applicable) for radio-tagged fish with known spawning success in 2002…..…….53

Table 3.5 Tagging date, migration time, estimated initial percent muscle lipid at the start of freshwater migration (Lipid i), estimated final percent muscle lipid of the at death on the spawning grounds (Lipid f), and estimated somatic and total energy expended by death for fish with radio transmitters that were recaptured for energy use estimates in 2003. Migration times include days taken to migrate from Bonneville Dam (BON) on the Columbia River to the South Fork Salmon River (SFSR), and from the SFSR to death on the spawning grounds. Prediction intervals (95%) for estimated lipid are shown in parentheses after estimate..…….55

Table 3.6 Migration times and percent lipid (Lipid i = initial lipid, Lipid f = final lipid) with 95% prediction interval in parentheses for fish with known spawning success in 2003……...57

**Appendix**

Table 1. Regressions of energy content on fork length (Lf)…….....64

## List of Figures

**Chapter 1**

Figure 1.1 Figure 1. Section of muscle taken for proximate analysis (from Magie and Mesa 2004)…….4

Figure 1.2. Regressions of log somatic energy on log fork length (females, upper figure; males lower figure) at four stages of migration in 2002: the nominal start of migration = diamonds, arrival at the spawning stream = x, pre-spawned death = triangles, post-spawned death = squares..…….13

Figure 1.3 Percentage use of somatic energy (from Bonneville Dam) at arrival at the SFSR (South Fork Trap, diamonds), at death prior to spawning (squares), and at death after spawning (triangles) in 2002 estimated for 70, 80,90 and 100 cm fish.……..…...15

**Chapter 2**

Figure 2.1 Simple linear regressions of A) percent moisture (Y) over resistance (x), and B) percent moisture (Y) over conductor volume (x)…….**.....**35

Figure 2.2 Linear regressions of A) total body water (Y) over resistance (x), and B) percent moisture (Y) over conductor volume (x)……..…...37

Figure 2.3 Quadratic regressions of A) lipid content (Y) on moisture of content a 50-g homogenized muscle sample (x), and B) lipid content of a 50-g homogenized muscle sample (Y) on a moisture content of a 1-g sample of muscle tissue (x)……..…....38

Figure 2.4 Linear regression of moisture percentage of a 50-g muscle tissue sample (Y) on moisture percentage of a 1-g muscle sample (x)……..……39

**Chapter 3**

Figure 3.1 Study area including eight dams and receiver locations used for estimating migration time……..…...45

Figure 3.2 Pearson's correlation between migration time and percent muscle lipid for PIT-tagged fish at arrival at the SFSR in 2002…….…….. ……50

Figure 3.3 Pearson's correlation between A) migration time (Y) and river Temperature (x) and B) percent muscle lipid (Y) and river temperature (x) for 25 PIT-tagged fish at arrival at the SFSR in 2002……51

Figure 3.4 Frequency of pre-spawning mortalities observed in 2003 and maximum daily temperatures (USFS data logger) at the weir on the SFSR……59

## Abstract

Adult salmon do not feed during the spawning migration and rely on lipid and protein stores for energy to swim upstream and spawn. Behavior during migration, the rate at which energy is depleted, and ultimately reproductive success may be affected by river conditions (temperature and flow) and dam operations (e.g., spill, proportion of powerhouse flow, etc.) occurring during the spawning migration. Adult Chinook salmon, *Oncorhynchus tshawytscha*, must pass eight hydroelectric dams and reservoirs and migrate over 1000 river kilometers to reach spawning areas in the South Fork Salmon River in central Idaho. The goal of this study was to determine relationships between estimates of energy use, migration time, and reproductive success of adult Chinook salmon.

Chinook salmon originating in the South Fork Salmon River were sampled at four stages of migration: the nominal start of migration (arrival at Bonneville Dam 235 km upstream from the mouth of the Columbia River), arrival at the South Fork Salmon River, after pre-spawning death and after post-spawning death in the South Fork Salmon River. The lipid and protein reserves of the skin, muscle, viscera, and gonad tissue of all study fish were quantified to determine how these reserves were utilized to meet the costs of migration and reproduction. Energy content was compared for each stage. Energy content and reproductive costs were related to fish length (fork length) for both sexes. Energy for migration and for gamete development during migration was supplied primarily by lipid reserves. In addition, female Chinook salmon used protein reserves to some degree prior to completion of migration. More than half of the initial energy reserves were used during migration. After arrival at the spawning stream, energy for final gamete development and reproductive behavior was obtained largely from metabolism of protein reserves. Females expended up to 90% and males up to 80% of initial energy reserves from the beginning of the spawning migration to the completion of spawning. The observed decrease in energy reserves during migration and spawning was in the upper range of that reported for other salmonid stocks making long migrations in unimpounded rivers. The relatively large proportion of initial energy reserves used during migration and high total energetic requirements of migration and spawning suggest that increases in energetic expenditures during migration or reductions in initial reserves caused by changing ocean conditions could affect reproductive success during some years.

A non-lethal method for determining the energy content of individual fish during the spawning migration at several sampling locations was developed to relate migration patterns, energy use and reproductive success. Three non-destructive methods (morphometrics, bioelectrical impedance analysis [BIA], and biopsy) were assessed using linear and quadratic regression. Morphometrics alone estimated lipid and energy content with reasonable accuracy ($R^2 = 0.90$). Measures of BIA were poor to reasonable estimators of water content: single variable regressions accounted for 12 to 72% of the variance in water content. However, BIA measures did not contribute significantly to multiple regression models that also included morphometrics. Using muscle biopsy,

percent muscle lipid was estimated from percent muscle moisture of a small tissue biopsy with quadratic regression ($R^2 = 0.75$). We concluded that morphometric data (including body mass) provided the best non-lethal method to estimate energy condition of live fish in the field. This method could be improved by using standardized photographs of fish in the field; morphometrics could then be determined at a later time, reducing handling of fish. Morphometrics should prove to be a useful, non-lethal tool for further investigations into the relationship between energy expenditure, migration behavior, and reproductive success of adult Chinook salmon. Continued use of morphometrics and other recently developed technologies to monitor the initial condition of adults as they enter the hydrosystem will help determine to what degree variation among individuals in initial energetic conditions is associated with migration success. Comparisons of mean initial condition among years should also assist managers in forecasting in-river performance by adults, assuming a causal relationship between energetic condition and migration and reproductive success exists.

Migration times and rates for radio-tagged and PIT-tagged Chinook salmon migrating upstream to spawning grounds on the SFSR were compared with indices of energy condition and spawning success. The migration time (d) from Bonneville to Lower Granite Dam was negatively correlated with the mass specific energy content of PIT-tagged fish upon arrival at the spawning stream: slower migrating fish expended 39% of mass-specific somatic energy to develop gametes and migrate to the SFSR, while faster migrating fish expended only 29%. In some cases, percentage muscle lipid was similar for pre-spawning and post-spawning mortalities (males in 2002) suggesting that energy content was a factor for pre-spawning death. However, understanding the relationship between energy use and spawning success is complicated by variations in run timing, time spent in the spawning stream, reproductive behavior, and the limited number of fish returning to a single population. Small sample sizes, thus far, limit the ability to reach robust conclusions. Overall, patterns observed are consistent with the results of the population-level energetic work described above, patterns between passage time and migration success in the Columbia-Snake system, and recent studies on Sockeye salmon in the Fraser River system. Clearly, a mechanistic understanding of the relationships between initial condition, migration behavior, migration success, and reproductive success are needed given recent observations of high pre-spawn mortality on spawning grounds and the potential for future increases in the energetic costs of migration.

**Chapter 1: Changes in body composition and energetic costs of the spawning migration for spring-summer Chinook salmon of the South Fork Salmon River population.**

## Introduction

Adult salmon do not feed during the freshwater component of the spawning migration (Mommsen et al. 1980; Brett 1995) and rely on endogenous energy stores to meet the demands of upstream migration, gonad maturation, competition for mates (males), redd-building (females), spawning, and defense of spawning sites from competing fish (males and females) (Mommsen et al. 1980; Guderley et al. 1986; Hendry et al. 2000). Of these demands, the largest energetic costs are for swimming and gonad maturation (Brett 1995). In some species the cost of developing male secondary sexual characteristics outweigh the cost of gonad maturation (Kinnison 2003). Energy expended during migration depends on the difficulty of the migration (Idler and Clemens 1959; Brett 1995), and reflects the evolution of migratory and reproductive behavior (Brett 1995; Dodson 1997; Hendry et al. 2000; Crossin et al. 2003). The cost of the migration and the amount of somatic energy stores determine the adequacy of pre-migratory energy reserves for successful reproduction (Brett 1995).

Snake River spring and summer wild Chinook salmon populations have declined significantly from historical levels (Chapman 1986) and are currently listed as threatened under the Endangered Species Act (Petrosky et al. 2001). These declines have been attributed in part to construction of mainstem dams in the system (Ruckelshaus et al. 2002). Relevant to this study, migration conditions for fish in the Columbia River Basin have been altered dramatically since the completion of the Federal Columbia River Power system: adult salmon must now pass eight dams to reach spawning areas in Idaho and encounter altered flow and thermal regimes.

Potential difficulties of upstream migration associated with dams include the physiological effects of increased water temperatures, supersaturated dissolved gas, physical exertion of dam passage, and the possibility of fallbacks over dams (Bjornn and Peery 1992). Although impoundments reduce river velocity, higher metabolic costs associated with warmer water temperatures and dam passage may require more expenditure of energy than is saved by the reduction in velocity (Brett 1995). Fish are delayed below dams as they search for entrances to fishways, and may orient ineffectively in the spill. Delays may range from a few hours to several days at each dam (Keefer et al. 2004). For these reasons, mean pre-dam migration rates (km $d^{-1}$) for summer Chinook salmon are estimated to be 70 to 100 percent of what they are today (Keefer et al. 2004). Currently the Columbia River warms faster, attains higher maximum temperatures, and remains warm longer into the fall than prior to construction of mainstem dams and resulting flow manipulations (Quinn and Adams 1996; Quinn et al. 1997). Delays associated with dam passage and exposure to warmer water temperatures may increase energy expenditures during the spawning migration, and consequently limit reproductive success and increase the likelihood of pre-spawning mortality (Dauble and Mueller 2000; Geist et al. 2000).

Previous field studies of migrating adult salmon in natural river conditions have addressed the effects of gradient, flow and distance or travel time on energy costs. Reproductive energy expenditures associated with dam and reservoir passage have not been investigated until recently. The present study was designed to address the concern that delays in migration and physiologically stressful conditions in an impounded system may cause energy expenditures that are detrimental to the completion of migration, and ultimately detrimental to reproductive success.

Morphological and body compositional changes during the spawning migration can best be described by sampling from one population, so that all fish have similar migration distances, run timing, genetic composition, and energetic needs. Chinook salmon of the South Fork Salmon River (SFSR) population migrate past Bonneville Dam on the Columbia River between mid-May and mid-June. This population was chosen because they are long distance freshwater migrants (~1150 km), their spawning areas have been well documented, and because an Idaho Department of Fish and Game weir and trap on the South Fork Salmon River could be used to sample fish upon arrival at the spawning stream.

As noted above, energy consumption while migrating will be significantly affected by prevailing water temperature conditions. In 2002, mean river water temperatures at the nominal start of migration (Bonneville Dam, 235 rkm upstream from the ocean) were 12 °C in May, 15 °C in June, and 19 °C in July (USACE 2002-2003). Mean river temperatures at the SFSR weir were 16 °C in July (following July 16) and decreased to 13 °C in August, and 10 °C in September (USFS, unpublished data). Maximum daily temperatures were above 20 °C for five days in late-mid to late July (USFS, unpublished data). In 2003, mean river temperatures at Bonneville Dam were 12 °C in May, 16 °C in June and, 20 °C in July (USACE 2002-2003); mean river temperatures at the SFSR weir were 15 °C in July (following July 16) and decreased to 14 °C in August, and 12 °C in September (USFS, unpublished data). Maximum daily temperatures were above 20 °C for seven days in late-mid to late July (USFS, unpublished data).

*Objectives*

The first objective was to measure the lipid and protein reserves of the skin, muscle, viscera and gonad tissue, and to determine how these reserves were used to meet the costs of migration and reproduction. Fish with long, difficult spawning migrations must use fixed energy stores efficiently to reproduce successfully. Fish undergoing long migrations typically have high initial levels of muscle lipid and rely heavily on metabolism of this lipid to complete migration and spawn. Lipid stores hold the most energy per unit mass (Brett 1995), and are most efficiently used during the early stages of the spawning migration. Metabolism of muscle protein stores during migration may limit migration efficiency (Davison and Goldspink 1977) because of muscle deterioration, and are generally mobilized only after lipid stores have been depleted. We hypothesized that salmon migrating 920 kilometers through the Columbia and Snake Rivers would have large initial stores of lipid; that lipid from the viscera and skin would be valuable sources of energy during early

migration, but would be quickly depleted; and that muscle lipid would be the major source of stored energy.

The second objective was to determine the cost of migration and spawning by comparing the energy content of SFSR summer Chinook salmon near the start of freshwater migration, after arrival at the spawning stream, and after death on the spawning grounds (both before and after spawning). Semelparous fish species with long spawning migrations typically use the majority of energy reserves for migration, leaving less energy for gamete development, reproductive behavior, and development of secondary sexual characteristics (Kinnison et al. 2001). We hypothesized that migration would be the largest reproductive cost for SFSR Chinook salmon, despite the decreased river velocity caused by impoundments, and that a minimum amount of reserves would be needed upon arrival at spawning areas to complete spawning.

If the last hypothesis is true, then fish arriving at the SFSR with energy stores below a threshold level would likely die before spawning. Therefore, the third objective was to compare the final energy content of fish that died before and after spawning. We hypothesized that fish would have similar amounts of energy at death regardless of spawning success, suggesting that energy limitation is a factor in pre-spawning mortality.

## Methods

Fish were collected at four stages of migration: the nominal start of upstream migration (Bonneville Dam; the first dam on the Columbia River), arrival at the spawning grounds, and after death on the spawning grounds (before and after spawning). Hatchery Chinook salmon (denoted by adipose fin clips) were collected while migrating past Bonneville Dam during the peak of the McCall Hatchery run (some returning McCall adults could be identified by passive integrative transponder (PIT) tags placed in smolts prior to release from the hatchery) in late May to mid-June in 2002. Other spring-summer Chinook stocks passing Bonneville Dam (in lower abundance) during the sampling period included those from Pahsimeroi Hatchery, Sawtooth Hatchery, and Imnaha River Hatchery. Because these fish migrate extensive distances to hatcheries on tributaries of the Snake River and must pass the same series of dams and reservoirs as fish returning to the SFSR, their energetic needs should be similar to those of SFSR fish.

In 2002, fifty-seven fish were sampled at Bonneville Dam, 53 fish were sampled at the SFSR weir (operated by the Idaho Department of Fish and Game, rkm 1156.4), and 87 carcasses were collected from spawning areas in the SFSR (rkm 115-1159). Of the 87 fish collected from spawning areas, 36 (41%) had died prior to spawning and 51 (59%) had spawned. Fish that died before spawning were defined as those with greater than 75% of the expected pre-spawning gamete mass remaining after death (J. A. Hesse, Nez Perce Tribe, personal communication).

All fish sampled at Bonneville Dam were adipose clipped, indicating hatchery origin. However, we collected both hatchery and wild (unmarked) carcasses from the spawning

grounds. Of the 36 fish that died prior to spawning, 22 were female (16 hatchery, 6 wild) and 14 were males (9 hatchery, 5 wild). Fifty-one fish that died after spawning were collected: 25 females (18 hatchery, 7 wild) and 26 males (10 hatchery, 16 wild). Wild and hatchery fish were analyzed separately unless stated otherwise.

In 2003, ten (three females, seven males) salmon were sacrificed and carcasses were sampled near the start of migration at Bonneville Dam, 11 salmon were sacrificed and carcasses were sampled at the SFSR weir (five females, six males), and 20 carcasses were collected from spawning areas in the SFSR. Of the 20 fish collected from spawning areas, ten (five females, five males) had died prior to spawning and ten (seven females, three males) had spawned.

*Proximate Composition*

Muscle, skin, viscera and gonad tissue were collected for determination of lipid, protein, ash and moisture content. A rectangular piece of muscle was dissected from the left side of each fish just anterior to the dorsal fin (Figure 1.1), following Magie and Mesa (2004). The skin was removed from the muscle so the two tissue samples could be analyzed separately. The entire viscera, excluding the kidney, and gonad tissue were removed and weighed. All four tissue samples were immediately homogenized separately in a commercial Warring blender. An approximate 50 g sub-sample of each tissue type was then removed, weighed on digital scale and stored at -20 °C in polyethylene bags until transported to the laboratory for proximate analysis.

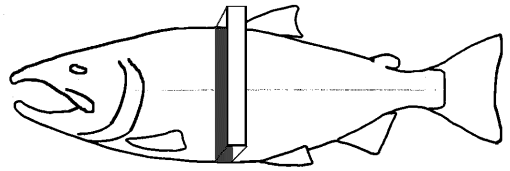

Figure 1.1. Section of muscle taken for proximate analysis (from Magie and Mesa 2004).

Lipid, protein, ash and moisture content of the muscle, skin, viscera, and gonads were determined by personnel of the Washington State University Wildlife Habitat Laboratory (Pullman, WA). Moisture content was determined by freeze-drying tissue samples and subtracting dry weight from wet weight. Lipid content was determined using Soxhlet extraction with anhydrous diethyl ether as the solvent. Ash weight was determined by weighing the sample before and after heating at 600 °C for 12 hours (Craig et al. 1978). Protein content was determined by subtraction (% protein =100 - % water - % fat - % ash), as in other studies on salmon energetics (Berg et al. 1998; Hendry and Berg 1999; Hendry et. al 2000). Carbohydrate stores in migrating salmonids are small and inconsequential relative to lipid and protein stores (Idler and Clemens 1959), and therefore were not determined in this study.

*Body Composition*

In 2002, viscera (minus kidney), gonads and whole body weights were determined for each fish sampled. In 2003, all skin and muscle tissue was removed as completely as possible from the carcasses of forty fish (ten at each of the four migration stages) and weighed. Skin and muscle mass, as a percentage of total body mass, was calculated for each fish. Mean values for percent skin and percent muscle at each migration stage were used to estimate tissue masses in all fish collected in 2002 at each stage of migration.

*Energy Estimations*

Energy content was calculated for each tissue type and summed to estimate somatic (muscle, skin, and viscera) and total body (muscle, skin, viscera, and gonad) energy for each fish. Mass-specific energy content ($kJ\ g^{-1}$) of each tissue was estimated using energy equivalents for fat and protein of 36.4 $kJ\ g^{-1}$ (8.66 $kcal\ g^{-1}$) and 20.1 $kJ\ g^{-1}$ (4.9 $kcal\ g^{-1}$) from Brett (1995), multiplied by the appropriate percentages (x0.01) of lipid and protein and summed. "Mass specific" energy of the somatic tissues (muscle, skin, and viscera) was multiplied by the mass of each tissue and summed to find somatic energy (kJ). Total body energy (kJ) was estimated by the same procedure except that gonad tissue was also included.

*Statistical Analysis*

Multivariate analysis of variance (MANOVA; proximate composition = migration stage) was used to test for differences ($P \leq 0.05$) in proximate composition (percent moisture, lipid, protein, and ash of each tissue) among migration stages. All data were arcsine square root transformed. Males and females were analyzed separately because of a significant interaction between sex and sampling location. Canonical variate analysis was used to determine the relative importance of biochemical constituents (protein, lipids, etc.) within body compartments (skin, muscle, etc.) among the four stages of migration for males and females separately.

Separate one-way ANOVA tests were used to test for differences in percent moisture, lipid, and protein of the constituents among migration stages. All data were arcsine square root transformed. When significance was detected, least squared mean estimations and Fisher's Least Significance Difference (LSD) tests ($P < 0.05$) were used to test for differences in percent lipid over each of the four migration stages (6 pair-wise comparisons).

Protein masses and lipid masses of each tissue were compared over migration stages using analyses of covariance (ANCOVA, type III sums of squares, SAS PROC GLM, SAS Institute Inc., Carey, NC) with fork length as the covariate. When assumptions of linearity and homogeneity of slopes were met, the interaction term (fork length by location) was removed from the model and the mean length-controlled protein and lipid content of each tissue was calculated. Fisher's LSD tests were used to determine differences between means.

Absolute values of somatic and total energy content could not be compared among migration stages using ANCOVA because migration stage by fork length interactions were significant for both females and males ($P<0.05$). Somatic energy content was calculated for fish of mean fork length with energy vs. fork length regressions at all four stages of migration (Appendix Table 1). In addition, to describe differences in energy use by fish of different fork lengths, somatic energy content was calculated for fork lengths of 70, 80, 90 and 100 cm for both males and females at each migration stage (Jonsson et al. 1997; Hendry and Berg 1999). Somatic energy, total energy, and fork length were log transformed to fit an allometric relationship and antilogs were compared to determine absolute energy loss in kilojoules. To determine the differential costs of gamete development and migration, the somatic energy expended on gamete production was estimated as the gain in energy of the gametes between the start of migration and arrival at the SFSR. The cost of active metabolism (costs of swimming and reproductive behavior) was determined by subtracting the gain in gonad energy from the loss of somatic energy occurring between two stages of migration (Crossin et al. 2004a).

*Secondary Sex Characteristics*

In 2002, snout length (distance from tip of snout to mid-eye), and hump height (perpendicular distance from anterior insertion of dorsal fin to lateral line) were measured with calipers to the nearest 0.01 mm for all fish collected. Fork length and length to hypural plate were measured to the nearest mm with a measuring stick or board. Mid-eye to hypural length was calculated from the measurements above.

All measurements were log transformed and ANCOVA was used to determine changes in morphology during migration and reproduction while controlling for variations in body length. Assumptions of linearity and homogeneity of slopes were tested and met for all tests. The interaction term was removed from the ANCOVA model and adjusted means were calculated using the common slope. The antilog of adjusted means was used to estimate changes in morphological characteristics.

## Results

*Changes in Body Length and Mass*

Fork lengths did not differ between migration stages for either females or males (Table 1.1); however, mean body mass decreased significantly for both male and female fish as they moved upstream. Body mass decreased 20% for both males and females during migration to the SFSR. After spawning, males weighed 11% less and females weighed 45% less than fish near the start of migration.

*Changes in Proximate Composition of Tissues*

Proximate composition (percent moisture, lipid, and ash of the muscle, skin viscera and gonads) differed significantly over migration stages for both females and males (Wilks

Lambda $P < 0.0001$). Canonical variate analysis indicated that differences between locations for males was due primarily to increased moisture and declining lipid content of muscle, skin and viscera as males migrated and spawned (Table 1.2). Decreased gonad protein and lipid also contributed to the difference in body composition among sample locations, but to a lesser extent. Similar results were found for females, except that differences among migration stages in lipid and moisture content of the viscera were smaller than for male fish.

Table 1.1 ANOVA P value and mean (SE) for fork length and mass of males and females at four stages of the spawning migration in 2002.

| | | Migration Stage[1.] | | | |
|---|---|---|---|---|---|
| | ANOVA P-value | Bonneville | Arrival SFSR | Pre-spawn Mortality | Post-spawn mortality |
| Females n = 91 | | | | | |
| Length (cm) | 0.46 | 83.0 (7.1) | 81.0 (5.3) | 81.0 (6.0) | 81.0 (6.0) |
| Mass(kg) | < 0.0001 | 8.0 (2.0)[a] | 5.9 (1.1)[b] | 5.5 (1.3)[b] | 4.4 (0.8)[c] |
| Males n = 67 | | | | | |
| Length(cm) | 0.08 | 82.0 (8.0) | 80.0 (5.5) | 83.0 (11.0) | 89.0 (11.0) |
| Mass (kg) | 0.006 | 7.8 (2.4)[a] | 5.7 (1.4)[b] | 5.8 (2.5)[b] | 6.9 (2.5)[ab] |

[1.] means with superscripts in common did not differ significantly (Fisher's LSD, $p < 0.05$)

Table 1.2. Results from canonical variate analysis for proximate composition (arc sine square root transformed muscle, skin, viscera and gonad lipid, moisture, ash and protein) of females and males by stage of migration with ranks in parentheses.

| Variable | Females Within CAN 1 (rank) | Standardized CAN 1 (rank) | Males Within CAN 1 (rank) | Standardized CAN 1 (rank) |
|---|---|---|---|---|
| Skin moisture | -0.7037 (1) | -5.2876 (3) | -0.5920 (2) | -4.2636 (4) |
| Muscle moisture | -0.6964 (2) | -2.0100 (6) | -0.6268 (1) | 0.3871 (14) |
| Skin lipid | 0.6321 (3) | -4.0114 (4) | 0.5314 (3) | -4.9048 (3) |
| Muscle lipid | 0.6283 (4) | -0.0795 (14) | 0.5282 (4) | 2.5926 (6) |
| Viscera moisture | -0.3001 (5) | 1.6574 (8) | -0.3469 (6) | 1.5547 (9) |
| Skin protein | -0.2216 (6) | -1.5514 (9) | -0.2121 (7) | -2.0953 (7) |
| Viscera lipid | 0.2140 (7) | 1.7221 (7) | 0.4054 (5) | 1.6211 (8) |
| Gonad lipid | 0.2028 (8) | -2.4056 (5) | -0.1400 (9) | -0.8226 (11) |
| Gonad moisture | -0.1711 (9) | -8.7054 (1) | -0.0553 (13) | -6.3670 (1) |
| Viscera protein | 0.1511 (10) | 1.2981 (10) | 0.0878 (10) | 0.8889 (10) |
| Muscle protein | 0.1410 (11) | -0.8480 (13) | 0.0014 (15) | 0.7343 (2) |
| Gonad protein | 0.1186 (12) | -6.2582 (2) | 0.0114 (14) | -4.9154 (2) |
| Muscle ash | 0.0842 (13) | 0.0779 (15) | 0.0841 (11) | 0.1046 (16) |
| Skin ash | -0.0398 (14) | 0.0639 (16) | 0.0628 (12) | 0.2630 (15) |
| Viscera ash | 0.0235 (15) | 0.1911 (12) | 0.0072 (16) | 0.6053 (13) |
| Gonad ash | 0.0001 (16) | -0.5669 (11) | -0.1560 (8) | -3.0263 (5) |

*Percent Lipid.*— Lipid content (as percent wet mass) of muscle, skin, viscera and gonads differed ($P < 0.0001$ for all ANOVAs) over migration stages for both males and females (Table 1.3). Between the start of the migration and arrival at the SFSR, the lipid content of the muscle, skin and viscera decreased significantly for males and females (Fisher's PLSD test). Lipid content of the gonads, on the other hand, increased for both females and males during migration. Between arrival at the SFSR and death after spawning, the lipid content of muscle and skin continued to decline ($P < 0.0001$) for both males and females. Remnant gonad tissue in post-spawning females was significantly reduced in lipid content from that at arrival on the spawning grounds (2.8% vs. 8.0%), but the already low lipid content of male gonads remained unchanged after spawning. Visceral lipid was reduced to about 1% of visceral mass in fish arriving at the SFSR and remained unchanged in fish after spawning. In fish that died before spawning, muscle, skin and viscera lipid content decreased from that at arrival at the spawning grounds for males and females, but lipid content of the gonads remained unchanged. Females that died before spawning had more muscle and skin lipid but similar visceral lipid than females that died after spawning. Males had similar lipid content of the muscle and skin and viscera regardless of whether they had spawned or not. Remnant gonad tissue of males and females after spawning was lower in lipid content than in those that died before spawning.

*Percent Protein.*— Protein content (as percent wet mass) of the muscle, skin, viscera and gonads differed ($P < 0.0001$ for all comparisons) over migration stages for both males and females (Table 1.3). During migration to the SFSR, the protein content of the muscle, skin, and gonads increased for both males and females, and viscera protein increased only for males. Between arrival at the SFSR and spawning, the protein content of the muscle and viscera tissue decreased, and protein content of the skin remained similar for both males and females. Remnant gonadal tissue in post-spawning males and females was significantly reduced in protein content. In fish (both males and females) that died before spawning, the protein content of the muscle and viscera decreased, but the protein content of the skin and gonads did not. The protein content of the muscle and viscera was higher in fish that died before spawning than those that died after spawning. Skin protein did not differ. However, protein of the remnant gonad tissue was significantly lower in males and females that died after spawning than in males and females that died before spawning.

*Percent Moisture.*— Moisture content was inversely correlated with lipid content ($r = -0.73$ to $-0.96$) at all four stages of migration.

*Proportional Changes in Tissue Mass.*— Muscle made up about 60% of total body mass near the start of migration, 65% at arrival at the SFSR and 40% after death for both females and males (Table 1.4). Female gonads, which were 4% of female body mass near the start of migration, increased to 10% at arrival at the SFSR and to about 19% prior to spawning. Male gonads were 1.5% body mass near the start of migration, increased to 3% at arrival at the spawning stream, and remained 3% prior to spawning.

Table 1.3. Lipid, protein, and moisture (percent wet mass) for female and male Chinook salmon in 2002 with standard deviations in parentheses. (H = adipose clipped, hatchery origin; W = non-adipose clipped, wild origin)

| | | | Females | | | | Males | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Location | Origin | Constituent | N | Lipid (%) | Protein (%) | Moisture (%) | N | Lipid (%) | Protein (%) | Moisture (%) |
| Bonneville | H | Muscle | 32 | 21.5(3.4) | 19.3(2.0) | 57.9(2.3) | 25 | 22.4(4.3) | 19.1(2.8) | 57.3(2.5) |
| | | Skin | | 40.7(3.2) | 17.6(3.0) | 40.4(2.4) | | 38.2(5.2) | 19.3(2.8) | 41.2(3.1) |
| | | Viscera | | 4.4 (3.5) | 20.4(2.0) | 73.8(2.6) | | 5.7(3.1) | 19.8(1.9) | 73.2(3.0) |
| | | Gonad | | 10.2 (2.6) | 32.3(2.4) | 56.0(2.4) | | 0.8(0.3) | 18.6(3.8) | 78.4(3.8) |
| SFSR Trap | H | Muscle | 25 | 7.9(2.5) | 20.8(1.7) | 70.1(3.1) | 27 | 10.3(3.2) | 20.7(1.9) | 67.8(3.1) |
| | | Skin | | 13.7(5.4) | 26.3(4.1) | 58.5(4.7) | | 16.2(6.4) | 25.1(3.6) | 57.4(5.0) |
| | | Viscera | | 0.8(0.3) | 21.0(1.6) | 76.7(1.8) | | 1.0(0.4) | 20.8(1.6) | 76.8(1.8) |
| | | Gonad | | 8.0(3.1) | 36.2(3.0) | 53.8(1.4) | | 1.2(0.3) | 20.5(2.5) | 74.4(2.6) |
| Pre-spawning | H | Muscle | 16 | 3.8(2.1) | 16.6(1.1) | 78.7(2.6) | 8 | 5.6(3.6) | 18.2(1.4) | 75.3(3.5) |
| | | Skin | | 7.3(6.2) | 24.7(3.5) | 66.5(4.7) | 9 | 1.1(0.4) | 25.4(2.6) | 65.6(4.6) |
| | | Viscera | | 0.9(0.4) | 18.1(1.6) | 79.7(1.6) | 9 | 0.7(0.1) | 17.7(1.6) | 80.5(1.5) |
| | | Gonad | | 7.0(1.6) | 33.7(2.0) | 57.3(2.7) | 9 | 1.5(0.5) | 21.4(3.1) | 72.0(2.8) |
| | W | Muscle | 6 | 3.0(1.8) | 16.3(1.8) | 79.9(3.3) | 5 | 6.4(2.4) | 19.4(1.9) | 73.2(4.4) |
| | | Skin | | 4.1(2.8) | 25.3(2.5) | 69.2(4.4) | | 8.5(3.1) | 26.8(2.2) | 63.6(3.0) |
| | | Viscera | | 0.7(0.2) | 17.1(1.5) | 80.9(1.8) | | 0.9(0.3) | 18.0(0.8) | 80.1(1.0) |
| | | Gonad | | 5.6(0.9) | 33.4(2.6) | 59.0(2.8) | | 1.0(0.3) | 19.1(3.6) | 74.9(3.8) |
| Post Spawning | H | Muscle | 18 | 1.1(1.1) | 15.1(2.0) | 83.0(2.9) | 26 | 3.4(3.3) | 16.7(1.9) | 79.0(4.0) |
| | | Skin | | 1.3(1.5) | 25.4(1.5) | 72.0(1.4) | | 5.5(5.5) | 26.6(6.9) | 67.0(5.8) |
| | | Viscera | | 0.9(0.2) | 16.0(1.3) | 82.0(1.4) | | 0.8(0.2) | 16.5(1.1) | 81.6(1.1) |
| | | Gonad | | 2.6(2.0) | 16.9(10.0) | 79.5(12.5) | | 0.9(0.2) | 14.5(3.6) | 81.8(5.4) |
| | W | Muscle | 7 | 3.8(2.1) | 16.6(1.1) | 78.7(2.6) | 10 | 2.9(2.6) | 16.3(1.6) | 79.9(3.8) |
| | | Skin | | 7.3(6.2) | 24.7(3.5) | 66.5(4.7) | | 5.6(3.8) | 26.0(3.4) | 67.5(3.8) |
| | | Viscera | | 0.9(0.4) | 18.1(1.6) | 79.7(1.6) | | 1.0(0.3) | 17.1(1.7) | 80.9(1.7) |
| | | Gonad | | 7.0(1.6) | 33.7(2.0) | 57.3(2.7) | | 0.9(0.3) | 13.1(5.2) | 83.7(6.6) |

Table 1.4. Mean contribution (percent) of muscle, skin, viscera, and gonads to total body mass in 2003 (standard deviation in parentheses).

| Location | N | Muscle (%) | Skin (%) | Viscera (%) | Gonad (%) |
|---|---|---|---|---|---|
| Females | | | | | |
| Bonneville | 3 | 61.6 (1.75) | 7.00(0.94) | 3.28( 0.43) | 4.20 (1.17) |
| South Fork Trap | 5 | 65.0 (12.3) | 6.44 (0.93) | 3.01 (0.66) | 10.30 (1.41) |
| Pre-spawning | 5 | 38.6 (1.34) | 5.71 (0.38) | 2.52 (0.78) | 19.4 (3.67) |
| Post-spawning | 7 | 42.1 (2.87) | 7.47 (0.92) | 2.53 (0.25) | 2.82 (1.85) |
| Males | | | | | |
| Bonneville | 7 | 58.6 (2.90) | 8.11 (1.11) | 3.13 (0.66) | 1.46 (0.46) |
| South Fork Trap | 6 | 65.3 (19.4) | 7.14 (0.51) | 2.26 (1.01) | 3.15 (0.34) |
| Pre-spawning | 5 | 42.9 (2.08) | 7.92 (0.81) | 2.42 (1.41) | 3.21 (0.72) |
| Post-spawning | 7 | 45.1 (6.14) | 7.91 (0.89) | 2.48 (0.18) | 1.22 (0.43) |

*Changes in Lipid and Protein Mass.*— Length-controlled lipid mass of the muscle, viscera, and gonads differed significantly over stages of migration for hatchery males and females (Table 1.5), and length-controlled skin lipid mass differed for females. Comparisons of skin lipid among migration stage could not be made for males due to heterogeneity of slopes. Both males and females lost significant amounts of lipid stores from muscle and viscera tissues during migration (Fisher's PLSD tests). Skin lipid decreased significantly for females. Gamete lipid, on the other hand, increased significantly for both males and females during migration. Muscle lipid continued to decrease in females after arriving at the SFSR. However, viscera lipid in males and females, muscle lipid in males, and skin lipid in females did not change between arrival at the SFSR and after spawning. Remnant gonad tissue in females after spawning had significantly less lipid than gonad tissue of females at arrival at the SFSR. Between arrival at the SFSR and death before spawning, muscle and viscera lipid mass did not differ significantly for females or males and skin lipid did differ in females. However, the lipid content of the remaining gametes was significantly less in fish that died before spawning than in fish arriving at the SFSR ($P<0.0001$ for males and females). Lipid contents of muscle, viscera, and gonads did not differ significantly between males or females that spawned and those that died prior to spawning. Females that spawned had significantly lower amounts of lipid in the skin than females that died prior to spawning (Table 1.5). Wild females that died before and wild females that died after spawning did not differ significantly in muscle, skin, or viscera lipid mass (Table 1.6). Wild males that died prior to spawning had significantly higher amounts of muscle and skin lipid mass, but similar amounts of viscera lipid mass as males that died after spawning.

Protein mass of the muscle, skin, viscera and gonad tissue differed significantly over migration stages for hatchery females and skin and gonad protein (g) differed significantly for hatchery males (Table 1.5). During migration to the SFSR, visceral

protein stores decreased for females. No other significant changes in protein mass were found during migration. Between arrival at the SFSR and spawning, muscle protein decreased and skin protein increased significantly for females. Muscle protein did not differ significantly between arrival at the spawning stream and after spawning for males. Skin protein content decreased significantly for males, while viscera protein remained similar for males and females. Remnant gonads in females and males after spawning had lower protein than at arrival at the SFSR. During the period between arrival at the spawning stream and death before spawning, protein (g) of the skin increased for females and males. Protein of the muscle and viscera tissue did not significantly differ between arrival at the spawning stream and death before spawning for females or males. Gamete protein decreased significantly between arrival at the SFSR and death prior to spawning

Table 1.5. Comparison (by ANCOVA) of mean length-controlled lipid and protein masses (g) for tissues of adult Chinook salmon sampled at four stages of migration.

| | | Migration Stage [1.] | | | |
|---|---|---|---|---|---|
| | ANCOVA P | Bonneville | Arrival at SFSR | Pre-spawning death | Post-spawning death |
| Hatchery Females (n = 91) | | | | | |
| Muscle lipid | < 0.0001 | 765.2 [a] | 251.0 [b] | 169.1 [bc] | 32.2 [c] |
| Muscle protein | 0.0300 | 680.7 [a] | 639.7 [a] | 652.7 [a] | 453.4 [b] |
| Skin lipid | < 0.0001 | 180.7 [a] | 43.1 [b] | 50.4 [b] | 6.17 [c] |
| Skin protein | < 0.0001 | 77.0 [a] | 81.4 [a] | 140.5 [b] | 116.4 [c] |
| Viscera lipid | < 0.0001 | 8.38 [a] | 1.44 [b] | 1.99 [b] | 1.63 [b] |
| Viscera protein | 0.0060 | 44.0 [a] | 34.0 [bc] | 41.4 [ab] | 27.1 [c] |
| Gonad lipid | < 0.0001 | 21.6 [a] | 55.6 [b] | 9.97 [c] | 4.96 [c] |
| Gonad protein | < 0.0001 | 63.9 [ac] | 244.7 [a] | 50.3 [b] | 33.3 [bc] |
| Hatchery Males (n = 67) | | | | | |
| Muscle lipid | < 0.0001 | 840.4 [a] | 318.9 [b] | 209.1 [c] | 100.7 [bc] |
| Muscle protein | 0.67 | 667.8 [a] | 649.2 [a] | 778.2 [a] | 565.9 [a] |
| Skin lipid [2] | — | 172.7 | 53.0 | 31.2 | 30.3 |
| Skin protein | < 0.0001 | 87.7 [a] | 87.1 [a] | 145.1 [b] | 131.7 [b] |
| Viscera lipid | < 0.0001 | 11.3 [a] | 1.60 [b] | 1.55 [b] | 1.81 [b] |
| Viscera protein | 0.25 | 43.2 [a] | 36.4 [a] | 43.9 [a] | 31.3 [a] |
| Gonad lipid | < 0.0001 | 2.16 [a] | 8.34 [b] | 1.46 [a] | 1.40 [a] |
| Gonad protein | < 0.0001 | 49.6 [a] | 149.4 [b] | 23.2 [a] | 22.2 [a] |

[1.] Means in each row with superscripts in common did not differ significantly (Fisher's LSD, P <0.05)

[2.] A significant fork length by migration stage interaction precluded comparison of means by ANCOVA. Means shown were calculated from the lipid mass vs. length regression for each stage (mean fork length = 82.5 cm).

for both males and females. Female that spawned had lesser amounts of protein in the muscle, skin, and viscera and similar gamete lipid (g) as females that died prior to spawning. Protein contents of muscle, skin, viscera and gamete tissue did not differ

between males that spawned and males that died prior to spawning. Wild females that spawned had similar muscle, skin, viscera, and gonad protein mass as wild females that died prior to spawning (Table 1.6). Comparisons for protein content of the tissues could not be made for wild males due to heterogeneity of slopes.

*Energetic Costs of Migration and Reproduction*

Absolute values of length-controlled somatic energy content could not be compared among migration stages using ANCOVA because migration stage by fork length interactions were significant for both females and males ($P<0.05$; Figure 1.2). Regression slopes differed significantly from zero at the nominal start of migration (Bonneville Dam), arrival at the SFSR (SFSR Trap), and at death prior to spawning for both males and females, but not at death after spawning for males or females (Appendix Table 1). Somatic energy content was calculated for fish of mean fork length with energy vs. fork length regressions at all four stages of migration (Table 1.7). In addition, to describe differences in energy use by fish of different fork lengths, somatic energy content was calculated for fork lengths of 70, 80, 90 and 100 cm for both males and females at each migration stage (Table 1.7; Jonsson et al. 1997; Hendry and Berg 1999).

Table 1.6. Comparison (by ANCOVA) of mean length-controlled lipid and protein masses (g) for tissues of wild adult Chinook salmon sampled at two stages of migration (pre-spawning death, post-spawning death).

| | | Migration stage | |
|---|---|---|---|
| | ANCOVA P | Pre-spawning death | Post-spawning death |
| Wild Females (n = 13) | | | |
| Muscle lipid | 0.24 | 98.2 | 48.7 |
| Muscle protein | 0.28 | 510.6 | 661.8 |
| Skin lipid | 0.11 | 20.9 | 8.69 |
| Skin protein | 0.43 | 118.6 | 148.0 |
| Viscera lipid | 0.39 | 1.38 | 1.75 |
| Viscera protein | 0.32 | 33.7 | 32.3 |
| Gonad lipid | 0.78 | 8.65 | 6.65 |
| Gonad protein | 0.39 | 48.6 | 35.9 |
| Wild Males (n = 21) | | | |
| Muscle lipid | 0.001 | 321.2 | 66.5 |
| Muscle protein[1.] | — | 740.7 | 398.0 |
| Skin lipid | 0.007 | 57.4 | 21.3 |
| Skin protein[1.] | — | 135.6 | 99.4 |
| Viscera lipid | 0.220 | 2.40 | 1.53 |
| Viscera protein[1.] | — | 35.6 | 24.8 |
| Gonad lipid | 0.22 | 1.04 | 1.40 |
| Gonad protein[1.] | — | 19.0 | 21.5 |

[1.] A significant fork length by migration stage interaction precluded comparison of means by ANCOVA. Means shown were calculated from the protein mass vs. length regression for each stage (mean fork length = 86.6 cm).

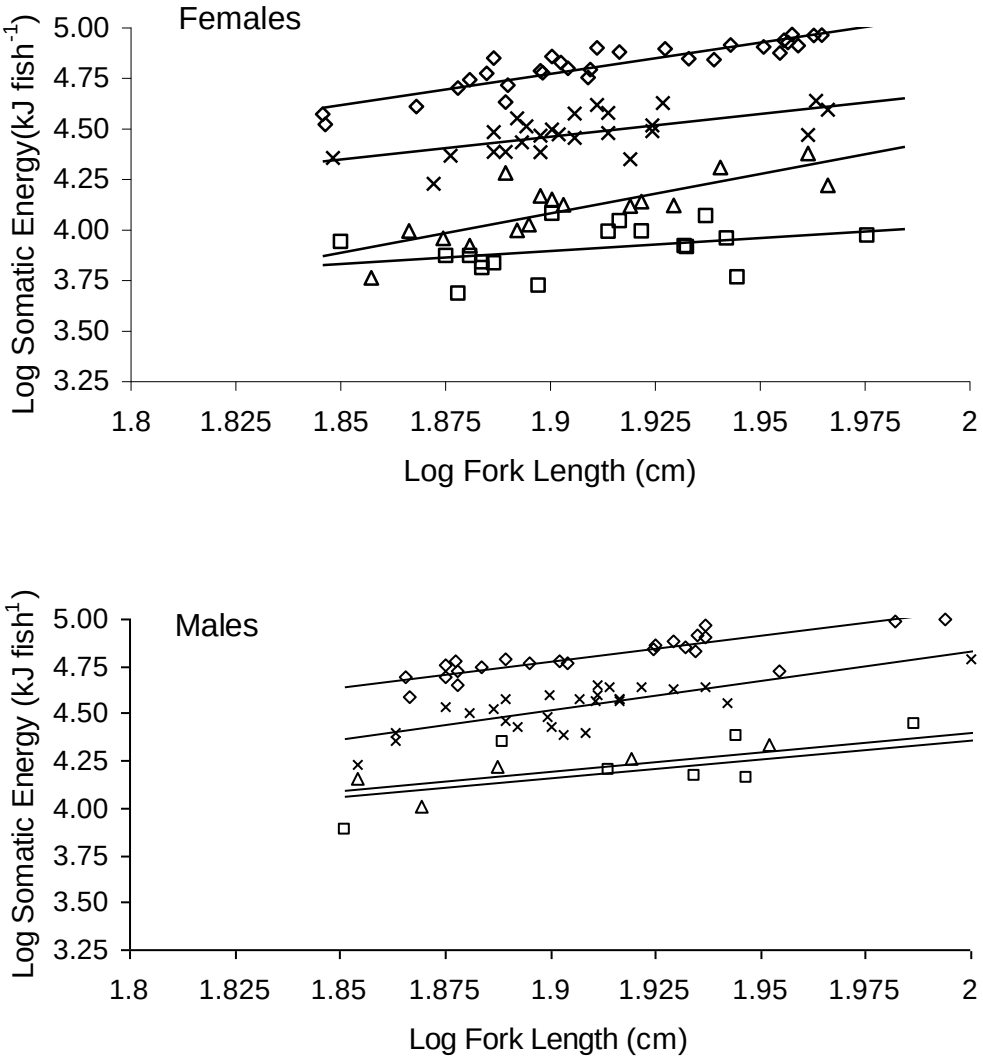


Figure 1.2. Regressions of log somatic energy on log fork length of females (top) and males (bottom) at four stages of migration in 2002: the nominal start of migration = diamonds, arrival at the spawning stream = x, pre-spawned death = triangles, post-spawned death = squares.

Energetic costs (as percentage of initial somatic energy stores) during migration to the SFSR were dependent upon fork length for both females and males, and were higher for longer females and shorter males (Figure 1.3). Females used 20 to 78 kJ $km^{-1}$, depending on fork length, to migrate 920 river kilometers from the nominal start of migration at Bonneville Dam to the Idaho Department of Fish and Game Weir on the SFSR. Males used 22 to 48 kJ $km^{-1}$, depending on fork length. During migration, females of mean fork length used 52% (including 6% for gamete development), and males of mean fork length used 44% (including 0.9% for gamete development) of initial somatic energy stores.

Between arrival at the SFSR and death before spawning, females of mean fork length used an additional 27% (including 4.7% for gamete development) and males used 30% of their initial somatic energy. Between arrival at the SFSR and death after spawning, males and females of a mean fork length used 32 and 35% of their initial somatic energy stores.

Reproductive costs were greater for females than males of similar fork lengths. Males of mean fork length (82.5 cm) used 77% of their initial somatic energy stores to migrate and spawn while females of mean fork length (82 cm) used 87% (Table 1.7). At death after spawning, 82 cm females had about half as much somatic energy remaining as males of a similar fork length.

Table 1.7. Total somatic and gonad energy (kJ) with percentage of initial somatic energy used as a source for swimming and gonad development in parentheses for adult Chinook salmon of 70, 80, 90 and 100 cm and for mean fork lengths (82 cm for females and 82.5 cm for males) sampled at four migration stages.

| | | Migration Stage | | | |
|---|---|---|---|---|---|
| | Fork length | Bonneville | Arrival at SFSR | Pre-spawning death | Post-spawning death |
| Females | | | | | |
| Soma | 70 | 40048 | 21739 (42,4) | 7374 (71,10) | 6692 (73,10) |
| Gonad | | 1979 | 3439 | 6051 | 3777 |
| Soma | 80 | 60477 | 29399 (46,5) | 12412 (70,10) | 7945 (77,10) |
| Gonad | | 2386 | 5616 | 8640 | 3653 |
| Soma | 82 | 65267 | 31078 (46,6) | 13666 (68,11) | 8201 (76,11) |
| Gonad | | 2455 | 6131 | 9212 | 3620 |
| Soma | 90 | 86993 | 38316 (49,7) | 19648 (67,11) | 9243 (78,11) |
| Gonad | | 2674 | 8468 | 11658 | 3466 |
| Soma | 100 | 120429 | 48561 (52,8) | 29632 (65,10) | 10582 (81,10) |
| Gonad | | 2771 | 12065 | 15015 | 3222 |
| Males | | | | | |
| Soma | 70 | 42304 | 22039 (47,0.8) | 12172 (70,0.8) | 11118 (73,0.8) |
| Gonad | | 466 | 803 | 768 | 480 |
| Soma | 80 | 60914 | 33589 (44,1) | 16897 (73,1) | 14521 (75,1) |
| Gonad | | 503 | 1054 | 971 | 505 |
| Soma | 82.5 | 66252 | 37014 (43,1) | 16943 (73,1) | 15442 (75,1) |
| Gonad | | 505 | 1118 | 1025 | 507 |
| Soma | 90 | 84018 | 48709 (41,1) | 21380 (75,1) | 18377 (77,1) |
| Gonad | | 490 | 1312 | 1194 | 504 |
| Soma | 100 | 112021 | 67920 (38,1) | 26391 (76,1) | 22682 (79,1) |
| Gonad | | 411 | 1561 | 1436 | 474 |

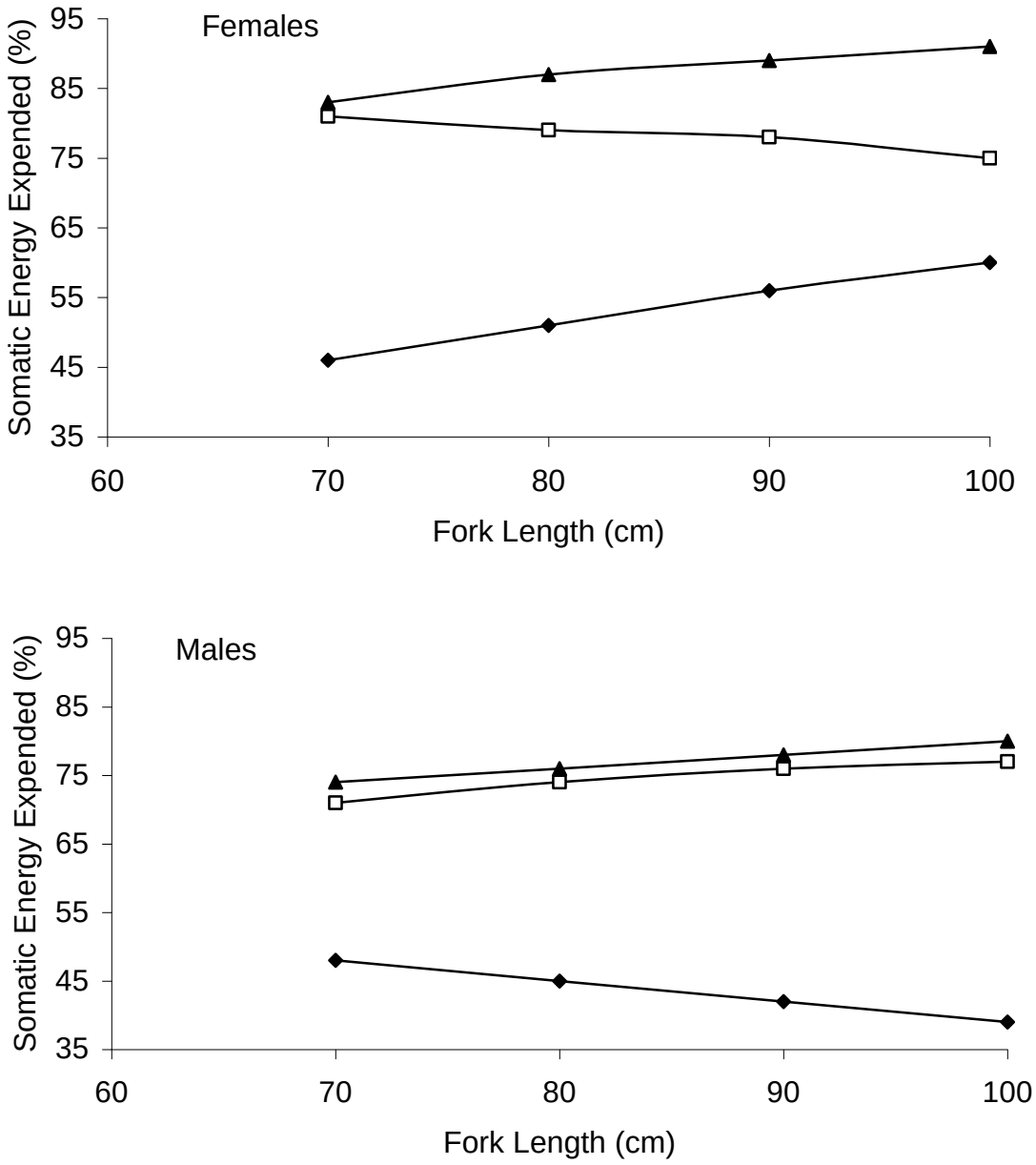


Figure 1.3. Percentage use of somatic energy (from Bonneville Dam) at arrival at the SFSR (South Fork Trap, diamonds), at death prior to spawning (squares), and at death after spawning (triangles) in 2002 estimated for 70, 80,90 and 100 cm fish.

*Secondary Sex Characteristics and Gonad Development*

Male snout length (controlled for fork length) increased by 34% between the start of migration and death after spawning (Table 1.8). About half of the total increase in snout length occurred between the start of migration and arrival at the spawning stream. Snout length increased 22% between the start of migration and death prior to spawning. Female snout length did not change significantly. Male hump height decreased 18% between the start of migration and arrival at the spawning stream, 21% between the start of migration and death after spawning, and 23% between the start of migration and death before spawning. Female hump height decreased by 20% of its initial size between the start of migration and arrival at the spawning stream, 31% between the start of migration and death after spawning, and 28% between the start of migration and death before spawning.

Fork-length-adjusted gonad mass increased 168% for males and 158% for females between the start of migration and arrival to the spawning stream. Between the start of migration and death prior to spawning, female gonad mass had increased 327% and male gonad mass had increased 141%.

Table 1.8. Comparison (by ANCOVA) of mean length-controlled snout length, hump height, and gonad mass ($log_{10}$) on fork length ($log_{10}$). Antilogs of mean ($log_{10}$) snout length (mm), hump height (mm) and gonad mass (g) for four stages of migration are shown.

| | | Migration stage [1.] | | | |
|---|---|---|---|---|---|
| | ANCOVA P | Bonneville | Arrival at SFSR | Prespawning death | Postspawning death |
| Females (n = 91) | | | | | |
| Snout length | <0.0001 | $71.8^{a}$ | $72.2^{a}$ | $70.7^{b}$ | $73.2^{a}$ |
| Hump height | <0.0001 | $100.5^{a}$ | $80.9^{b}$ | $72.5^{c}$ | $69.6^{d}$ |
| Gonad mass | <0.0001 | $216.6^{a}$ | $558.13^{b}$ | $924.4^{c}$ | $125.6^{d}$ |
| Males (n=67) | | | | | |
| Snout length | <0.0001 | $74.9^{a}$ | $87.1^{b}$ | $91.7^{bc}$ | $100.4^{c}$ |
| Hump height | <0.0001 | $103.9^{a}$ | $84.5^{b}$ | $80.5^{c}$ | $82.3^{bc}$ |
| Gonad mass | <0.0001 | $86.3^{a}$ | $231.4^{b}$ | $208.4^{bc}$ | $129.4^{ac}$ |

[1.] Means in each row with superscripts in common did not differ significantly (Fisher's LSD, $p < 0.05$)

## Discussion

*Initial Energy*

In 2002, Chinook salmon of the South Fork Salmon River population began their freshwater migration with large stores of readily mobilized somatic energy, primarily in the form of muscle lipid. Even though fish had already traveled 235 km from the mouth

of the Columbia River to reach the first sampling location, estimates of lipid mass as a percentage of somatic mass were in the upper range of those reported in other studies for interior salmon populations near the start of migration (reviewed in Brett 1995), and similar to other Columbia River Chinook salmon populations studied by Greene (1926) and Magie and Mesa (2004). These high proportions of somatic lipid (16% of body mass) near the start of up-river migration were likely related to good ocean productivity during 2001 and 2002 (Crossin et al. 2004b). In addition, earlier work has suggested that there is a correlation between the difficulty of freshwater migration (river discharge, distance, and elevation) for a particular stock and expendable energy content (Brett 1995; Crossin et al. 2004a).

*Cost of Reproduction*

*Body Mass.*— In this study, total body mass decreased 20% for both males and females during migration and 45% for females after spawning. Although decreases in body mass in females and males during migration were much greater than fish migrating 500 rkm past 5 dams to the Yakima River, a Columbia River tributary, in another study (3 to 10% depending on sex; Magie and Mesa 2004), the total loss in body mass in females after spawning was similar to that reported in other studies (31 to 46%; Love 1980; Magie and Mesa 2004). However, males sampled at death after spawning in the SFSR weighed only 11% less than males near the start of migration. This is likely due, in part, to the larger (though not significantly larger) size of males sampled after spawning.

*Lipid and Protein Use.*— In the present study, percent muscle, skin, and viscera lipid decreased significantly during migration. Viscera lipid was depleted to less than 1% for males and females during migration to the SFSR. Percent muscle and skin protein increased for both females and males and viscera protein increased for males during migration, likely as a result of the rapid depletion of lipid and corresponding decrease in body weight during migration. A similar increase in percent protein was reported for adult sockeye salmon (*Oncorhynchus nerka*) migrating in the Fraser River (Hendry et al. 2000). "Mass specific" somatic energy (kJ $g^{-1}$) decreased 51% for males and 63% for females, a much greater loss than reported for Yakima River spring Chinook salmon (6 to 17% of mass-specific energy depending on sex and migration speed, Magie and Mesa 2004). However, to better determine the total loss of lipid and protein, both information on the lipid and protein content per unit weight and decrease in tissue mass should be considered (Jonsson et al. 1997). Taking both of these into consideration, length-controlled muscle lipid mass decreased 67%, skin lipid mass decreased 76%, and viscera lipid mass decreased 83% from the start of migration to arrival at the spawning stream, indicating that lipid was a major source of energy for migration and gamete development. Females also used some visceral protein to fuel migration and gamete development, as indicated by a 23% decrease in length-controlled visceral protein mass. These estimates are consistent with values reviewed by Crossin et al. (2004a) where sockeye salmon used 60 to 86% of somatic lipids and 7 to 23% of somatic proteins during migration, depending on stock and migratory difficulty. However, in the present study, skin protein increased after arrival at the SFSR, perhaps indicating a relocation of protein stores to

increase skin strength for protection during activities such as redd building (females) and mate competition (males). Gonad lipid and protein increased during migration, indicating some somatic lipid and protein relocation.

Percent muscle and skin lipid and muscle and viscera protein continued to decrease in both females and males between arrival at the SFSR and death after spawning. Percent viscera lipid and skin protein did not change for either males or females. "Mass specific" somatic lipid and protein (kJ $g^{-1}$) decreased 76% and 29% for males and 91% and 47% for females between arrival and death after spawning. These results are similar to those reported for Yakima River Chinook salmon where mass-specific muscle and viscera lipid decreased 99 and 81%, and mass-specific muscle and viscera protein decreased by 30 and 16% after arrival at the spawning grounds (Magie and Mesa 2004). Considering both loss of mass and loss of protein and lipid per unit weight, females used 87% of their remaining muscle lipid mass and 29% of their muscle protein mass between arrival at the SFSR and spawning, while skin and viscera lipid and protein remained unchanged. The muscle, skin, and viscera lipid and protein stores of males also remained the same. The portion of energy stores used after arrival at the spawning stream is much greater than that reported for sockeye salmon in the Fraser River system, which expended 30 to 50% of remaining lipids and 10 to 25% of remaining proteins from arrival at the spawning stream to death after spawning (Crossin et al. 2004a). Changes in proximate composition observed in the present study are similar to the patterns of energy use described in other studies of salmonid energetics during the spawning migration reviewed by Brett (1995) and support the first hypothesis that muscle lipid is the greatest source of stored energy throughout migration, and protein stores are used during the later stages of migration and spawning.

The amount of lipid and protein loss at each stage of migration reflected the reproductive behaviors and energetic needs of semelparous fish that undergo long, difficult migrations. The loss of lipid and protein in hatchery females, wild females and wild males indicates that use of these energy stores was required to maintain position on the spawning grounds, continue to develop gametes, compete for spawning sites and mates, and spawn. The lack of lipid and protein loss in hatchery males suggests that they invested less energy in spawning behavior than wild males.

*Energy Use.*— Taking energy per unit weight (kJ $g^{-1}$) and total body weight loss (g) into consideration, female salmon expended about 46 to 60% (from shortest to longest fork length) of initial somatic energy (kJ) reserves to migrate to the SFSR. Males expended 39 to 48% (from longest to shortest fork length) of their initial somatic energy reserves to complete migration. These values are comparable to estimates of migratory cost for sockeye salmon where 30 to 53% of initial somatic energy reserves were spent to migrate 161 to 1089 km and 10 to 1158 m in elevation (Crossin et al. 2004a), and twice that of pink salmon (*Oncorhynchus gorbuscha*) that used only 11 to 22% of initial energy reserves to migrate 520 kilometers and 664 m in elevation (Crossin et al. 2003). Energy loss attributed to migration (920 km from Bonneville to the South Fork Trap) for fish of mean length and body mass in this study was about 3814 kJ $kg^{-1}$ (930 kcal $kg^{-1}$; 1.01

kcal kg $^{-1}$ km $^{-1}$) for females and 3670 kJ kg $^{-1}$ (895 kcal kg $^{-1}$; 0.97 kcal kg $^{-1}$ km $^{-1}$) for males. These results are similar to the absolute somatic energy loss of 990 kcal kg$^{-1}$ reported for fish collected in the Columbia River estuary in August and compared with fish from spawning grounds (340 km upstream) in July, and fish collected 1130 km upstream compared with fish collected 210 km upstream on the spawning grounds (Greene 1926; reviewed in Brett 1995). In the present study, total somatic energy loss (including energy used for gamete development) during migration was 4273 kJ g $^{-1}$ (1042 kcal kg$^{-1}$; 1.13 kcal kg $^{-1}$ km $^{-1}$) for females 3748 kJ g $^{-1}$ (914 kcal g $^{-1}$; 0.99 kcal kg $^{-1}$ km $^{-1}$) for males. These results are comparable to a total somatic energy loss (including energy spent on gamete development) of 1250 kcal kg$^{-1}$ for Sacramento River Chinook salmon (Greene 1926; reviewed in Brett 1995). Data reported in the present study are comparable to specific rates of energy loss for Amur River chum salmon (migrating 1150 km), Fraser River pink salmon (migrating 250-300 km), Columbia river sockeye salmon (migrating 832 km), and female Fraser River sockeye to migrate to the spawning grounds (0.69 to 1.74 kcal kg $^{-1}$ km $^{-1}$; reviewed in Brett 1995). After spawning, females in this study had expended 83 to 91% and males had expended 74 to 80% of initial energy stores (depending on size); these estimates are consistent with estimates for other Pacific semelparous salmonids that expend up to 80% of somatic energy stores (Brett 1986).

*Differential Energy Costs.*— We expected that migration would require the greatest proportion of available energy for Chinook salmon migrating 920 kilometers to spawning areas. Of the total somatic energy used while migrating, females used 87 to 91% (smaller females used a higher proportion) for active costs of swimming and 9 to 13% for gamete development. Males used 97 to 98% (smaller males used a higher proportion) of energy for swimming; the remaining 2 to 3% was used for gamete development. Of the gross somatic energy used from start (Bonneville Dam) to death after spawning, females used 51 to 57% (larger females used a higher proportion) for the active costs of swimming during migration (excluding gonad development) and males used 48 to 64% (smaller males used a higher proportion). These estimates of energy use while migrating are overestimates because we could not partition out costs associated with development of secondary sexual characteristics, primarily lengthening of the snout in this instance. Likewise, values reported here likely underestimate the proportion of energy expended on gamete development since considerable gamete development should have occurred before the fish were sampled near the start of migration, especially for females. This is supported from similar work on salmon populations migrating comparable distances. Sockeye salmon and pink salmon, monitored from freshwater entry to death on the spawning grounds, expended half of somatic energy stores on active costs of swimming, and half on reproductive development (Crossin 2003; Crossin et al. 2004a). The small proportion of energy used on gamete development by Chinook salmon in this study relative to sockeye salmon may also be explained by species (size) and life history differences. For example, Chinook salmon in this study may expend a much greater proportion of energy to develop gametes after reaching the spawning stream. We were not able to address this question in the current study because live fish were not sampled prior to spawning. Between arrival at the spawning stream and post-spawning death, females expended 37 to 31% (more for smaller females) and males 26 to 41% of their

initial energy stores for further development of gametes, reproductive behavior, and spawning accounting for 35 to 51% of the somatic energy use from the start of migration to death, depending on size and sex.

*Energy Use and Fork Length.*— Larger females used a greater percentage of initial energy reserves to migrate to the spawning stream than smaller females, and larger males and females used a higher proportion of initial energy than shorter fish between the start of migration and death after spawning. Positive relationships between fish length and energy use have also been reported for populations of sockeye salmon (Hendry and Berg 1999) and Atlantic salmon (*Salmo salar*; Jonsson et al. 1997). On the other hand, the proportion of energy used for activity was negatively related to fork length in this study: that is, longer females devoted a larger proportion of initial energy stores in to gamete production than shorter fish. Longer males used a smaller percentage of initial energy stores to migrate to the SFSR. A similar relationship between fish length and energy use were reported for male sockeye salmon (Hich and Rand 1998) where shorter sockeye salmon males swam faster than longer males. Hinch and Rand (1998) hypothesized that small males may swim faster in order to arrive on the spawning grounds at a similar time as large males and not lose spawning opportunities. In the present study, shorter males used an equal to larger proportion of energy on gamete development than longer males. After arrival at the SFSR, a negative association between fork length and percentage of initial energy used was observed in this study for females. Shorter females used a higher proportion of energy than longer females to develop eggs, secure a spawning site, and dig and guard redds from other females. In contrast, longer males expended a higher percent of initial energy than shorter males to develop gametes and compete for females on the spawning grounds. Reproductive tactics and energetic needs may be associated with size. For example, small males may be more likely to exhibit "sneaker" behavior during spawning, while large males use more overt aggressive behavior while competing for females, expending a more energy. The amount of gamete development occurring immediately before spawning was unknown for Chinook salmon in this study and comparisons between relative energy used between activity and gamete development between arrival at the SFSR and after spawning could not be determined.

Previous studies have reported both positive (Bernatchez and Dodson 1987; Jonsson et al. 1991; Dodson 1997) and negative associations (Crossin et al. 2004a) between fish length and migratory difficulty. Positive associations have been reported between migration distance, discharge, and fish length for Atlantic salmon (Jonsson et al. 1991), migratory distance and fish length for brown trout (*Salmo trutta;* L'abee Lund 1991), and river current and fish length for American shad (*Alosa sapidissima*; Glebe and Legett 1981). In those studies longer fish used energy more efficiently, possibly related with better swimming ability and larger stores of expendable energy that can be used for migration (Bernatchez and Dodson 1987). In contrast, studies on Pacific salmon (sockeye, chum (*O. keta*), and coho (*O. kisutch*) salmon) that typically migrate greater distances than Atlantic salmon, brown trout and American shad, have reported a negative relationship between fish length and migration distance or time, elevation or flow, and temperature in order to conserve energy during migration to spawning areas (reviewed in

Crossin 2004a). In the present study, smaller females used a lower proportion of initial energy to complete migration and were therefore more energy efficient. However larger females used a higher proportion of initial energy to develop gametes during migration and thus could have greater reproductive success if similar proportions of their gametes survived. The opposite was true for males where smaller fish used a higher proportion of initial energy reserves to complete migration and about an equal to lower proportion to develop gametes during migration. Both larger females and males used a higher proportion of available energy for swimming. To properly address the relationship between fish length and migratory difficulty for fish in the Columbia River basin, different stocks of fish with various degrees of migratory difficulty should be compared.

Flow velocities have been reduced in much of the Snake and Columbia Rivers due to impoundment, though a significant portion of SFSR salmon migration is still in unimpounded river segments. If current is a critical factor determining migration difficulty, decreased river velocities in reservoirs may be relaxing selection against large fish. However, if time to migrate is a more critical factor for salmon, longer passage times may put large fish at a disadvantage. Moreover, since fish with longer fork lengths have the ability to swim faster (Brett and Glass 1963; Webb 1995), longer fish that are not delayed in the hydrosystem may be arriving at the spawning stream earlier than historically and may be exposed to high temperatures for longer durations on the spawning stream. It is unclear how current selective pressures may be acting on fish body length in the Columbia River basin. An evaluation of the relationship between fish length and flow was outside the scope of this study.

### *Spawning Success*

If energy depletion was the cause of death, we would expect salmon that died before and after spawning to have similar low energy levels. We founds that length-adjusted muscle and viscera lipid mass was similar between hatchery females that died before and after spawning and length controlled muscle, skin, and viscera lipid was similar between wild females that died before and after spawning. On the other hand, length- adjusted protein mass was significantly higher for females (both hatchery and wild) that died before than for those that died after spawning. Length-adjusted lipid mass of the muscle, skin and viscera was similar between pre- and post-spawned hatchery males. Protein composition was also similar between hatchery males that died before and after spawning. This could indicate that energy limitation may be a factor in the ability for hatchery male Chinook salmon from this population to spawn. Since only dead salmon were sampled, we do not know how much energy was available just prior to the initiation of spawning for successful fish. Fish were collected during the same time period, and similarities of lipid stores in pre- and post-spawned females and of lipid and protein stores in pre- and post-spawned males may be a factor more accurately correlated with time spent in fresh water. In previous studies on sockeye salmon, premature death on the spawning stream has been attributed to difficult migratory conditions, temperature, disease, premature arrival, suspended sediments, and dissolved gas supersaturation (Gilhousen 1990). Comparisons between successful and unsuccessful migrants of initial

energy reserves, and of energy used during migration could provide further insight into the relationship between energy use during migration and spawning success.

Since fish in the present study may be exposed to higher temperatures than occurred prior to development of the FCRPS, describing energy expenditures for fish with various temperature exposures among and within years may provide insight into the effects of dams on bioenergetics of adult Pacific salmon during upstream migration. Higher river water temperatures increase the energetic demands of fish during migration and, along with flow and turbidity, have been reported to influence migration behavior (e.g. the start of upstream migration and the rate of migration; Quinn et al. 1997). Crossin (2004a) reported that migratory degree days accumulated by sockeye salmon of the Fraser River system was correlated with somatic energy stores at river entry, though not as strongly as migratory distance, elevation, river slope and work. Fish in this study migrated upstream during a year (2002) with relatively normal river temperatures (for the current system) and had the advantage of good ocean conditions during the years before migration. Fish migrating upstream from the ocean during years of extreme river temperatures and/or following years with less productive ocean conditions may experience greater migratory difficulty and higher rates of pre-spawning mortality.

*Secondary Sex Characteristics*

Hump height (mm) decreased for both males and females during migration and after arrival at the SFSR. For Chinook salmon of the SFSR population and other stocks with long difficult spawning migrations, the cost of developing a pronounced hump may be greater than the benefits (i.e. sexual selection). In this study, migration was completed at the expense of energy that would have been otherwise available for a pronounced hump. However, snout length increased significantly in male fish during migration, and continued to increase after they reached the spawning grounds. Elongated snout length in males suggests that this trait is a desirable characteristic and is sexually selected for, despite the cost of development.

*Summary*

In summary, lipid was the major source of energy used to migrate to the spawning grounds. Some visceral protein was used during migration by females, but the majority of protein use occurred after reaching the spawning stream and after muscle lipid was depleted. Energy near the start of migration and use of energy to migrate and spawn was positively related to fork length. Most of the available energy was used for migration: a much smaller percent of initial energy stores was expended for gamete development during migration than has been reported in other studies. However, energy used to develop gametes was likely underestimated because gametes were partially developed prior to the location of the first sampling event. Because of fish handling restrictions, this study did not include sampling of live fish just prior to spawning, so we could not estimate energy expended on gamete development after arrival at the spawning stream. Fish in this study expended 74 to 91% of initial energy reserves (depending on sex and fork length) to migrate 920 river kilometers, climb 1890 meters in elevation, pass 8 dams,

and spawn. The proportion of initial energy used to migrate and spawn was within the upper range of that described for other interior stocks in free-flowing rivers.

To better understand the effects of dams and impoundments (possible delays in migration and exposure to high temperatures) on reproductive energy expenditures, it is necessary to monitor energy condition, migration patterns, and spawning success of individual fish during migration. This possibility will be explored in the following chapters.

## References


Berg, O. K., E. Thronaes, and G. Bremset. 1998. Energetics and survival of virgin and repeat spawning brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic ciences 55:47-53.

Bernatchez, L. and J. J. Dodson. 1987. Relationship between bioenergetics and behavior in anadromous fish migration. Canadian Journal of Fisheries and Aquatic Sciences 44: 399-407.

Bjornn, T.C. and C.A. Peery. 1992. A review of literature related to movements of adult salmon and steelhead past dams and through reservoirs in the lower Snake River. U.S. Army Corps of Engineers Tech. Rep. 92-1. Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow.

Bjornn, T.C., J.P. Hunt, K.R. Tolotti, P.J. Keniry, and R.R. Ringe. 1994. Migration of Chinook salmon past dams and through reservoirs in the lower Snake River and into tributaries--1992. U.S. Army Corps of Engineers, Walla Walla, Washington.

Brett, J.R. 1986. Production energetics of populations of sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Zoology 64:555-564.

Brett, J.R. 1995. Energetics. Pages 1-66 in C. Groot, L. Margolis, and W.C. Clarke, editors. Physiological Ecology of Pacific Salmon. University of British Columbia Press, Vancouver.

Brett, J.R. and N.R.Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon, *Oncorhynchus nerka*, in relation to size and temperature. Journal of Fisheries Research Board of Canada 30:379-387

Chapman, D.W. 1986. Salmon and Steelhead Abundance in the Columbia River in the Nineteenth Century. Transactions of the American Fisheries Society 115:662-670.

Craig, J.F., M.J. Kenley, and J.F. Talling. 1978. Comparative estimations of energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. Freshwater Biology 8:585-590.

Crossin, G.T., S.G. Hinch, A.P. Farrell, M.P.Whelly, and M.C. Healey. 2003. Pink salmon (*Oncorhynchus gorbuscha*) migratory energetics: response to migratory difficulty and comparisons with sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Zoology 81:1986-1995.

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

Crossin, G.T., S.G. Hinch, A.P. Farrell, D.A. Higgs, and M.C. Healey. 2004b. Somatic energy of sockeye salmon, *Oncorhynchus nerka,* at the onset of upriver migration: a comparison among ocean climate regimes. Fisheries Oceanography 13:5, 354-349.

Dauble, D.D. and R.P. Mueller. 2000. Difficulties in estimating survival for adult Chinook salmon in the Columbia and Snake Rivers. Fisheries Management 25(8):24-34.

Davison, W. and G. Goldspink. 1977. The effect of prolonged exercise on the lateral musculature of the brown trout (*Salmo trutta*). Journal of Experimental Biology 70:1-12.

Dodson, J.J. 1997. Fish migration: an evolutionary perspective. Pages 10-36 in Fean-Guy J. Goodin editor. Behavioral Ecology of Teleost Fishes. Oxford University Press, Oxford.

Geist, D.R., C.S. Abernethy, and S.L. Blanton. 2000. The use of electromyogram telemetry to estimate energy expenditure of adult fall Chinook salmon. Transactions of the American Fisheries Society 129:126-135.

Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. Int. Pac. Salmon Fish. Comm. Bull. No 22.

Gilhousen, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. Int. Pac. Salmon Fish. Comm. Bull. No 26.

Glebe, B.D. and W.C. Legett. 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.

Greene, C.W. 1926. The physiology of the spawning migration. Physiological Review 6:201-241.

Guderley, H., P. Blier, and L. Richard. 1986. Metabolic changes during the reproductive migration of two sympatric coregonines, *Coregonus artedii* and *Coregonus clupeaformis*. Canadian Journal of Fisheries and Aquatic Sciences 43:1859-1865.

Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 312-393, in C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, Vancouver.

Hendry, A.P. and O.K Berg. 1999. Secondary sexual characteristics, energy use, senescence, and the cost of reproduction in sockeye salmon. Canadian Journal of Zoology 77:1663-1675

Hendry, A.P., A.H. Dittman, and R.W. Hardy. 2000. Proximate composition, reproductive development, and a test for trade-offs in captive sockeye salmon. Transactions of the American Fisheries Society 129 (5): 1082-1095.

Idler, D.R., and W.A. Clemens. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart lakes. Inter. Pac. Salmon Fish. Comm. Prog. Rep. 6:80 p.

Jonsson, N., B. Jonsson and L.P Hansen. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology 39: 739-744

Jonsson, N., L.P. Hanson, and B. Jonsson. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river dishcharge. Journal of Animal Ecology 60:937-947.

Jonsson, N., B. Jonsson, and L.P Hanson.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

Keefer, M.L., C.A Peery, T.C. Bjornn, M.A. Jepson, and L.C. Stuehrenberg 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. Transactions of the American Fisheries Society 133:1413-1439.

Kinnison, M.T., M.J.Unwin. A.P. Hendry, and T.P. Quinn. 2001. Migratory costs and evolution of egg size and number in introduced and indigenous salmon populations. Evolution 55(8):1656-1667.

Kinnison, M.T., M.J. Unwin, and T.P. Quinn. 2003. Migratory costs and the contemporary evolution of reproductive allocation in male Chinook salmon. Journal of Evolutionary Biology 16:257-1269.

L' abee-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.

Love, R.M.1980. The chemical biology of fishes. Academic Press, London, UK.

Magie, C.D. and M.G. Mesa. 2004. Evaluation of energy expenditure in adult spring Chinook salmon migrating upstream in the Columbia River basin: an assessment

based on sequential proximate analysis. Final Research Report. U.S. Geological Survey, Columbia River Research Laboratory. Cook, Washington.

Mommsen, T.P., C.J. French, and P.W. Hochachka. 1980. Sites and patterns of protein and amino acid utilization during the spawning migration. Canadian Journal of Zoology 58:1785-1799.

Petrosky, C.E., H.A. Schaller, and P. Budy. 2001. Productivity and survival rate trends in the freshwater spawning and rearing stage of Snake River Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 58:1196-1207.

Quinn, T.P., and D.J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151-1162.

Quinn T.P., S. Hodgson and C. Pevans. 1997. Temperature, flow, and the migration of adult sockeye salmon (*Onchorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Science 54:1349-1360.

Ruckelshaus, M.H., P. Levin, J.B. Johnson, and P. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33:665-706.

USACE (U.S. Army Corps of Engineers) 2002-2003. Annual fish passage reports. U.S. Army Engineer Districts, Portland, Oregon and Walla Walla, Washington.

Webb, P.L. 1995. Locomotion. Pages 71-99 in C. Groot, L. Margolis, and W.C. Clarke, editors. Physiological Ecology of Pacific Salmon. University of British Columbia Press, Vancouver.

**Chapter 2: Use of non-lethal techniques for assessing migratory and reproductive costs of Chinook salmon.**

## Abstract

Three methods—morphometrics, bioelectrical impedance analysis (BIA), and muscle biopsy—were explored to develop a non-lethal technique for estimating the energy content of adult Chinook salmon returning to spawning areas in central Idaho, over 1000 km from the Pacific Ocean. Regression models were developed from morphometric data to estimate muscle, skin, and viscera lipid and protein (mass and percentage wet mass), somatic energy, and total body energy. Data from BIA were used in models to estimate tissue water content. Moisture content was determined for a small tissue biopsy and then related to lipid content of a larger tissue sample representative of the entire body. The best models to estimate energy content using morphometric and BIA data were determined using AIC selection. Morphometric variables alone estimated lipid and energy content with reasonable accuracy ($R^2$ = 0.90). Bioelectrical impedance data (resistance, conductor volume) were poorer estimators of water content, accounting for 12 to 72% of the variance, and did not contribute significantly to multiple regression models containing morphometric and BIA measures. Using muscle biopsy, percent muscle lipid was estimated from percent muscle moisture of a small tissue biopsy with quadratic regression ($R^2$ = 0.75). We concluded that morphometric data (including body mass) provided the best non-lethal method to estimate energy condition of live fish in the field. This method could be improved by using standardized photographs of fish in the field; morphometrics could then be determined at a later time, reducing handling stress. Morphometric data should prove to be useful, non-lethal tools for meaningful investigations into the relationship between energy expenditure, migration behavior, and reproductive success of adult Chinook salmon.

## Introduction

Successful reproduction for Chinook salmon (*Oncorhynchus tshawytscha*) requires upstream migration to spawning streams, development of gametes and secondary sexual characteristics, competition for spawning substrate and redd construction (females), or competition for females on the spawning grounds (males). Because Chinook salmon must pass eight dams and reservoirs to reach spawning areas in Idaho, delays associated with dam passage may prolong migration time by up to 30% for summer Chinook salmon (Keefer et al. 2004), and consequently increase energy needed for migration. Altered temperatures in hydrosystem reservoirs resulting from the development and management of dams may further affect energetic costs for adult migrants. Excessive use of energy stores, such as from increased migration times, may limit energy available for gamete development and spawning behavior. In unaltered river systems, costs associated with ascending natural obstructions under low discharge and high temperature conditions could also affect escapement and reproductive success.

The importance of energy allocation between migration and reproduction has recently been implicated as an evolutionary basis for the development of various life history strategies for Pacific salmon (Hendry and Berg 1999; Crossin et al. 2003). Previous studies along this line of research have required lethal sampling to assess energetic conditions of fish at different stages of migration. A reliable, non-lethal method that allows repeat sampling of individual fish is needed to fully describe energy consumption during migration. The ability to evaluate the adequacy of energy stores for various reproductive behaviors would enhance our understanding of the bioenergetics of migratory fish.

Several non-invasive techniques have been used to estimate the lipid content of a variety of vertebrates. Three techniques were investigated in this study: morphological assessment, bioelectrical impedance analysis, and moisture analysis of a muscle sample obtained by biopsy. Each measure was related to chemical analysis of salmon sampled from stages of the migration and spawning period. Relationships between morphometrics and energy condition have been studied with juvenile fish (Simpson et al. 1992; Adams et al. 1995; Rikardsen and Johansen 2003), but this technique has not been attempted with migrating adult Pacific salmon. Bioelectrical impedance analysis (BIA) is a technique developed for determining total body water (an indirect indicator of energy) content in humans and has been successfully applied to grey seals (*Halichoerus grypus*; Bowen et al.1999), black, brown and polar bears (*Ursus americanus, U. arctos*, and *U. maritimus;* Farley and Robbins 1994), and just recently to brook trout (*Salvelinus fontinalis*; Cox and Hartman 2005). Measurements obtained from BIA include resistance (ohms) and reactance (ohms) between two pairs of electrodes spaced a known distance apart. Resistance is related to the dissipation of energy in a conductive medium and is inversely related to lipid content (non-conductor) and directly related to water content. Reactance is the component of impedance related to storage of energy in a conductive medium and is also inversely related to lipid content and directly related to water. Moisture proportions have been shown to increase during migration and reflect changes in

proximate composition (decreased lipid and protein) during the upstream salmon migration (Brett 1995; see also Chapter One). This relationship suggests that the water content of a small muscle biopsy could be used to estimate the whole body energetic condition of salmon.

The study objective was to develop a predictive model of body composition using non-lethal techniques that are sensitive to changes in lipid, water, and energy content during the spawning migration. Non-lethal measures of body composition would allow determination of changes in the body composition of an individual fish over time, and thus provide a description of energy use during freshwater migration and spawning. By quantifying energy use for individual fish, we hope to be able to draw inferences about the relationship between migratory patterns, changes in energy content, and reproductive success in future studies of Pacific salmon that undergo long distance, freshwater migrations.

## Methods

Chinook salmon originating from the SFSR were targeted for sampling at a nominal start of freshwater migration as they ascended the adult ladder on the Washington shore of Bonneville Dam (river kilometer [rkm] 235) in May and June of 2002. Hatchery Chinook salmon (denoted by adipose fin clip) were collected during the peak of the run of McCall Hatchery fish (identified by PIT-tag detections from mid-May to mid-June). Fish were also sampled at arrival at the SFSR spawning grounds (Idaho Department of Fish and Game weir at rkm 1156.4) during July. Finally, carcasses were collected from the spawning grounds in August. A more complete description of fish collection techniques is described in Chapter One. All fish sampled at the start of freshwater migration were adipose clipped, indicating hatchery origin. Both clipped and unclipped (potentially wild) carcasses were collected from the spawning grounds. Of the 36 fish collected that died before spawning, 22 were female (16 hatchery and 6 wild) and 14 were male (9 hatchery and 5 wild). Fifty-one fish were collected after they had spawned: 25 females (18 hatchery and 7 wild) and 26 males (10 hatchery and16 wild). Because un-clipped fish were not sampled at Bonneville Dam, they were excluded from analysis. For purposes of this evaluation, data for male and female hatchery fish were pooled for all analyses.

### *Morphology*

Twelve linear measurements of morphology were made on fish sampled at each stage of migration. Measurements included snout length (distance from tip of snout to mid eye), hump height (perpendicular distance from anterior insertion of dorsal fin to lateral line), and body depth and width at the operculum, dorsal fin, anus, and caudal peduncle (Simpson et al 1992; Adams et al 1995; Rikardsen and Johansen 2003). These measurements were taken to 0.01 mm. Fork length and length from mid-eye to caudal-fin fork were measured to 0.1 cm with a measuring stick or board. All fish were weighed

to 0.01 kg. Fulton's Condition Factor was estimated ($K= (W \div L^3) X 100,000$; Anderson and Neumann 1996) using body mass in grams (W) and fork length in millimeters (L).

Sixteen multiple regression models with various combinations of morphological traits were compared using Akaike's Information Criterion (AIC) model selection, which allowed selection of the model of best fit, with the fewest number of independent variables included. Comparisons were made between models with combinations of the following independent variables: body mass, fork length, body depth at the anus, hump height, and condition factor. Condition factor was not included in models that contained body mass and fork length. These variables were chosen because they decreased during migration and were correlated with energy and lipid content loss. AIC values were calculated from the regression output from procedure REG in SAS: AIC = n * ln (MSE) + 2K, where n was the sample size, K was the number of parameters, and MSE was $\sigma^2$ (Burnham and Anderson 2002). The lowest AIC value indicates the best relative model among those tested. Burnham and Anderson (2002) suggest that models with AIC values that differed by amounts between 0 an 2 provide substantially similar descriptions of the data as the model with the lowest AIC, and that $\Delta_i = 4$ or greater indicates considerably less empirical support that model *i* is the best model**.**

*Biolectrical Impedance Analysis*

Each fish was measured for whole body resistance and reactance (both in ohms) using an impedance plethysmograph (Quantum II body composition analyzer, RJL Systems, Clinton Township, MI). This instrument works by applying a 800 microamp current (50 KHz) through two electrodes and measuring the amount and type of current that reaches a secondary set of electrodes placed at the distal end of an organism. The original alligator clip electrodes were replaced with 20 gauge needles, similar to those used by Bowen et al. (1999) in a study with pinnipeds. One pair of electrode probes was inserted into the fleshy area just posterior to the opercle, and the second pair was placed in the fleshy area just anterior to the hypural plate. The electrodes were inserted about one centimeter apart in a ventral to dorsal direction, just underneath the skin and parallel to the long axis of the fish. Fish were placed on a dry, nonconductive plastic sheet during measurement to minimize leakage of electrical current to the ground (Farley and Robbins 1994; Bowen et al. 1999). Resistance and reactance between the electrode pairs were measured and recorded once the measurements stabilized or after 5 seconds. The distance between the electrode pairs was also recorded. This procedure (including placement of electrodes) was repeated three times for each fish to evaluate variability in BIA readings; only the initial measurement, however, was used in regression models because it was representative of what would be possible with constraints for handling anaesthetized fish in the field.

Eleven regression models using various combinations of BIA measures (resistance and conductor volume), and morphometrics (body mass and fork length) were compared for estimating water content (muscle, skin, and viscera water (% and mass) and total body water mass) using AIC model selection technique. Resistance was used in the equation

as an approximation for impedance (impedance = (resistance + reactance) $^{0.05}$), because the contribution of reactance to the bioelectrical impedance is negligible (Lukaski et al. 1986). Conductor volume was calculated: vol ($cm^{2} \cdot ohms^{-1}$) = $L^{2} \cdot Rs^{-1}$**,** where L was distance between electrodes in centimeters and Rs was bioelectrical resistance in ohms (Farley and Robbins 1994; Bowen et al. 1999). Conductor volume is an accurate estimator of total body water content in mammals (Kushner and Schoeller 1986; Bowen et al. 1999).

*Tissue Biopsy*

Approximately one gram of muscle tissue was removed with a scalpel from each fish from midway between the anterior insertion of the dorsal fin and the lateral line. Samples were sealed in polyethylene bags, weighed to 0.01 grams, and stored at -20°C. Because of the strong correlation ($r$ = 0.96) between muscle moisture and muscle lipid content found by proximate analysis of fish sampled at all four stages of migration, tissue biopsies were analyzed for percent moisture so that this value could be used to predict lipid content. Moisture analysis was performed by personnel at the Wildlife Habitat Laboratory at Washington State University, Pullman, WA, by freeze drying each sample and comparing initial and final weights. Moisture content of 50 gram and 1 gram tissue (biopsy) samples for each fish were compared with simple linear regression. All assumptions associated with regression analysis, linearity and normality, were met. Percent muscle moisture was related to percent muscle lipid using quadratic regression because of the non-linear relationship.

Lipid, moisture and ash contents were determined by proximate analysis of viscera (excluding kidney), gonad, skin, and muscle tissue. Protein content was determined by subtraction (% protein =100 - % water - % fat - % ash), as in other studies on salmon energetics (Berg et al. 1998; Hendry and Berg 1999; Hendry et al. 2000). Further explanation of proximate analysis can be found in Chapter 1.

## Results

*Morphology*

Percent muscle and skin lipid were best estimated by a model that included fork length, hump height and body depth (Table 2.1). Inclusion of body mass did not significantly increase the accuracy of either model for muscle or skin lipid. Percent viscera lipid was most accurately predicted using two variables: fork length and hump height. The best regression model identified using the AIC criterion for estimating somatic lipid mass, total lipid mass, and somatic energy (kJ) included fork length, body mass, body depth, and hump height. Total body energy was best described by the variables fork length, body mass, and body depth. Condition factor was not a predictor variable in any of the "best" models.

Table 2.1. Summary of best two models for estimating lipid content (%) of the somatic tissues (muscle, skin, viscera), total lipid mass, somatic lipid mass, somatic energy (kJ), total body energy (kJ), water content (%), total water mass of the somatic tissues, and total body water mass (TBW). $R^2$, AIC, and $\Delta i$ ($AIC_i - AIC_{min}$) values are shown.

| Dependent Variable | $R^2$ | AIC | $\Delta i$ | Model* |
|---|---|---|---|---|
| Muscle lipid (%) | 0.82 | 421 | 0 | lipid = 20.8 - 0.78L + 0.41Hh + 0.27Da |
| | 0.81 | 424 | 3 | lipid = 21.1-0.78L+0.03W+0.41Hh+0.27Da |
| Skin lipid (%) | 0.83 | 597 | 0 | lipid = 38.3-1.43L+0.86Hh+0.35Da |
| | 0.83 | 597 | 0 | lipid = 61.2-1.68L+1.92W+0.73Hh+0.29Da |
| Viscera lipid (%) | 0.53 | 215 | 0 | lipid = 1.56 -0.16L +0.16Hh |
| | 0.53 | 217 | 2 | lipid =3.94 – 0.18L + 0.20W + 0.14Hh |
| Somatic lipid (g) | 0.87 | 1683 | 0 | lipid = 1692-52.73L +189.6W +15.38Hh+9.968Da |
| | 0.86 | 1691 | 8 | lipid = 2221-57.27L+230.9W+18.60Hh |
| Total lipid (g) | 0.88 | 1679 | 0 | lipid = 2012-55.44L +215.8W+12.70Hh+9.831Da |
| | 0.97 | 1687 | 8 | lipid = 2534-59.92L+256.5W+15.87Hh |
| Somatic E (kJ) | 0.92 | 2836 | 0 | E = 62524-2100L+9438W+547Hh+583Da |
| | 0.91 | 2852 | 16 | E = 113435 – 2590L +13885W + 706Da |
| Total E (kJ) | 0.92 | 2823 | 0 | E =118350-2571L +14136W+630Da |
| | 0.92 | 2824 | 1 | E =102192415L + 12724.3W + 591.6Da + 173.6Hh |
| Muscle water (%) | 0.73 | 519 | 0 | water = -23.4 + 1.64L - 6.74W |
| | 0.73 | 520 | 1 | water = -26.8 + 0.58Cv – 6.16W + 1.70L |
| Skin water (%) | 0.75 | 575 | 0 | water = -54.3 + 2.01L -8.68W |
| | 0.75 | 578 | 28 | water = -54.3 + 0.0001Cv – 8.68W + 2.01L |
| Viscera water (%) | 0.63 | 263 | 0 | water = 45.1 + 0.57L - 2.41W |

| | | | | |
|---|---|---|---|---|
| | 0.63 | 294 | 31 | water = 44.5 - 0.12Cv – 2.29W + 0.59L |

Table 2.1. Continued

| Dependent Variable | $R^2$ | AIC | $\Delta i$ | Model |
|---|---|---|---|---|
| Muscle water (g) | 0.82 | 1824 | 0 | water = -29.3 - 1.42Rs+256W+15.3 L |
| | 0.82 | 1827 | 3 | water = 830 -1.13Rs +30.3W |
| Skin water (g) | 0.40 | 1313 | 0 | water= -277-0.32Rs -16.1W + 9.30L |
| | 0.36 | 1319 | 6 | water = -190-0.14Rs + 6.21L |
| Viscera water(g) | 0.77 | 1085 | 0 | water = 99.1 + 0.12Rs + 35.0W - 2.57L |
| | 0.75 | 1088 | 3 | water= 135 - 2.23L + 31.4W |
| TBW (g) | 0.78 | 1891 | 0 | water = -450Rs -1.51W +29.3L |
| | 0.77 | 1893 | 3 | water = -902 + 25.0 L+ 294W |

*E = energy (kJ), L = fork length (cm), W = body mass, Da = body depth at anus, Hh = hump height,Rs = resistance, Cv = conductor volume.

*Bioelectrical Impedance Analysis*

Throughout migration, the initial resistance measurement ranged from 214 to 548 ohms, with subsequent measurements differing from the initial value by 1 to 34 ohms. Both resistance and conductance were more highly correlated with water mass than with percent water, and conductor volume was a better predictor of water mass than resistance (Figures 2.1 and 2.2). In single-variable regressions, resistance accounted for 23 to 31% of the variance in percent water values and 13 to 44% of the variance in water mass, while conductor volume accounted for 12 to 17% of the variance in percent water and 23 to 72% of water mass. When selecting models from various combinations of morphometrics and BIA measures, however, resistance and conductor volume did not significantly improve models to predict percent water or water mass.

The best models selected to estimate percentage water of the muscle, skin and viscera included only body mass and fork length and accounted for 73, 75, and 63% of the variance in muscle, skin, and viscera water content. Including conductor volume did not substantially improve model fit for estimating percentage water of the muscle skin, and viscera. Total body water, muscle water, skin water and viscera water mass were best estimated by models including resistance, body mass, and fork length, and explained 40 to 82% of the variance.

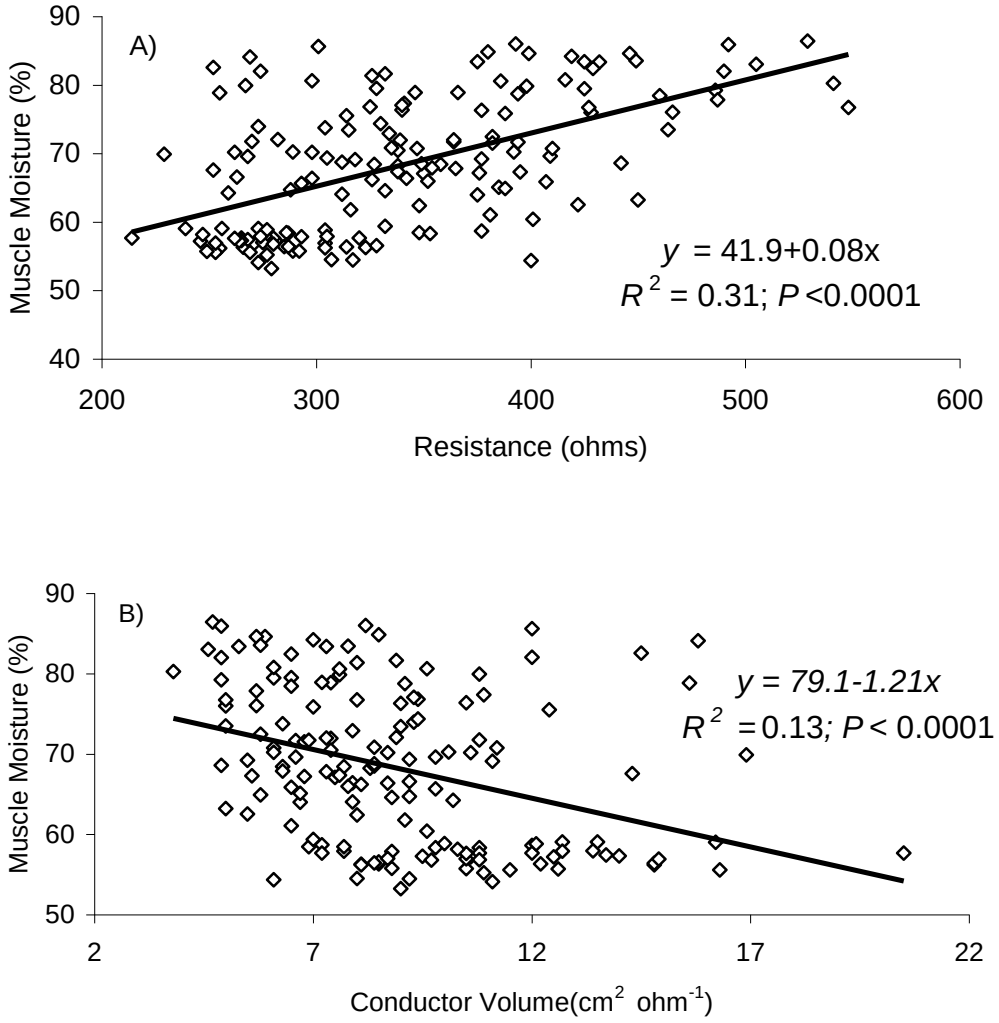


Figure 2.1. Simple linear regressions of A) percent moisture (Y) over resistance (x), and B) percent moisture (Y) over conductor volume (x).

*Tissue Biopsy*

Percent moisture of homogenized 50-g muscle tissue samples were strongly correlated ($R^2 = 0.96$) with percent muscle lipid. The relationship between lipid and moisture was non-linear, and was best represented by quadratic regression (Figure 2.3A).

The relationship between percent lipid of the homogenized 50-g muscle tissue sample and percent moisture of a 1-g biopsy sample was also quadratic but more variable ($R^2$ = 0.75; Figure 2.3B). Analysis of residuals confirmed model assumptions were met. There was a linear relationship ($R^2$ = 0.82; Figure 2.4) between percent moisture of the 50-g sample and the 1-g biopsy sample.

## Discussion

### *Morphology*

Morphometric variables estimated lipid masses and energy content of adult Chinook salmon with reasonable accuracy, accounting for 87 to 92% of the variance in somatic lipid mass, total lipid mass, somatic energy, and total energy content. In addition, morphometric variables estimated the percent lipid of muscle and skin reasonably well ($R^2$ = 0.82 and 0.83), but were relatively poor for predicting percent lipid of the viscera ($R^2$ =0.53). These findings are consistent with the findings of Adams et al. (1995), who developed equations that accounted for 65% of the variance in mesenteric fat mass and 85% of the variance in whole body lipid mass of Arctic charr (*Salvelinus alpinus*). However, visceral lipid is a relatively small portion of whole body lipid content for adult salmon and whole body lipid was reasonably predicted by morphometric measures.

Results reported here were from measurements made on dead fish; there is some concern that the extra handling needed to make a series of morphological measurements on live fish may be excessively stressful. However, with practice, key morphometric data can be collected on anesthetized fish quickly and without noticeable side effects (C. Peery, University of Idaho, unpublished data). Alternatively, some measurements could be made from standardized photographs with digitizing software such as described by Rikardsen and Johansen (2003).

### *Bioelectrical Impedance Analysis*

In single-variable regressions, resistance accounted for 13 to 44% (depending on tissue and measurement; % or mass) of the variance in moisture content. Conductor volume correlated well with muscle and total body water mass, but relationships with percent water of somatic tissues and water mass of skin and viscera were weak. These results are in agreement with those of Robinson and Farley (1994) and Bowen et al. (1999), who found that BIA measures were better at predicting water mass than percent moisture in mammals. However, in contrast to studies using BIA measures to estimate the lipid content of mammals, measures of BIA were poor predictors of water content in adult salmon. Bioelectrical impedance data in this study were also relatively poor predictors of energy content when compared to results reported for growing brook trout (Cox and Hartman 2005), indicating that BIA may not be as successful a predictor of energy change in fasting Chinook salmon. BIA measures contributed little to multiple regression models using combinations of BIA measures and morphometrics. Based on

AIC selection, fork length and body mass alone provided the best model for estimating percent moisture, and although the best model estimating water mass included measures of resistance, AIC values between the top three models (at least one of which that did not contain BIA measures) were similar. We concluded that the use of BIA did not improve water content estimation and may be difficult to use in the field on live adult salmon.

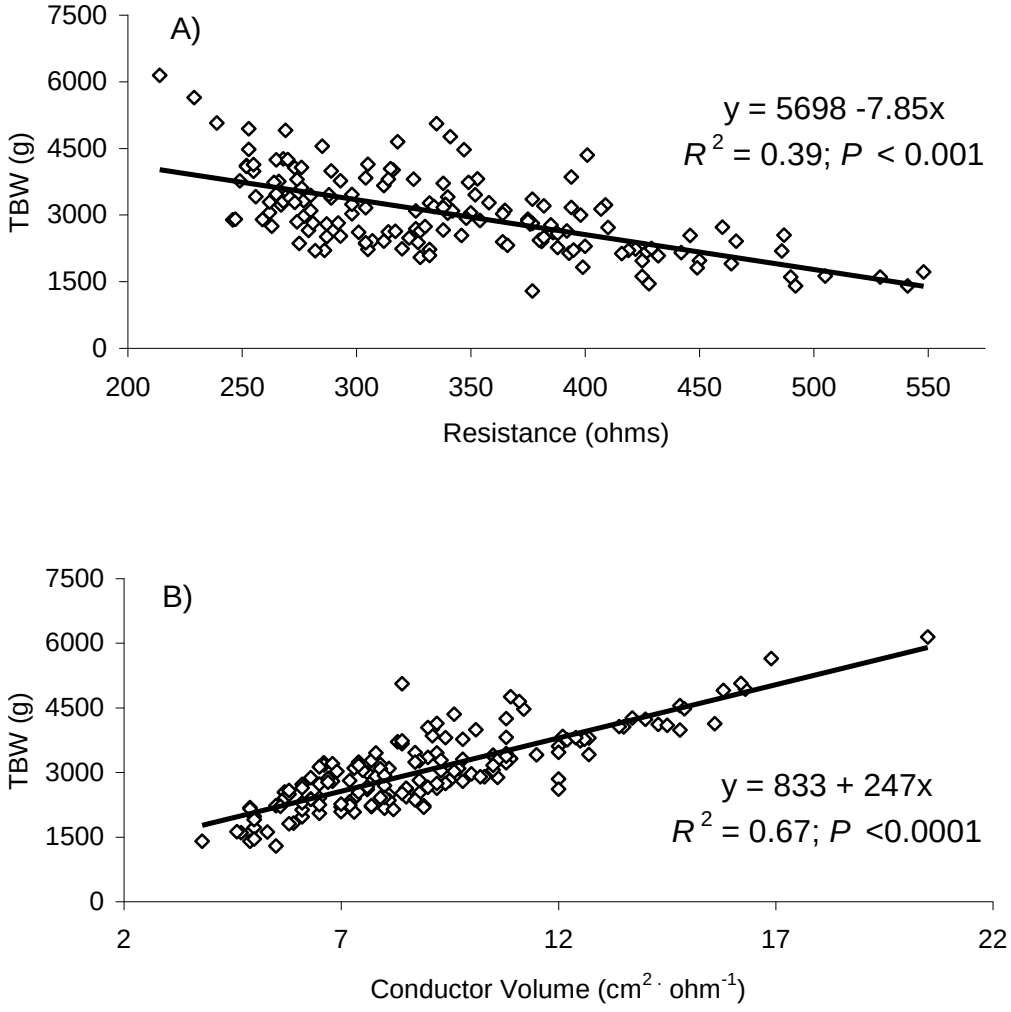


Figure 2.2. Linear regressions of A) total body water (Y) over resistance (x), and B) percent muscle moisture (Y) over conductor volume (x).

Improvements in methodology may increase the success of BIA on fish. In this study, some current may have traveled between the pairs of electrodes along the wet exterior of the fish rather than through the body tissues. Attachment of nonconductive material near the top of the electrode probes may improve the accuracy of the measurement by insulating the electrode probes (i.e. the portion that makes physical

contact with fish skin) and prevent current from running along the outside surface of the fish. Alternatively, a recently developed technique using low-energy microwaves to infer lipid content by estimating muscle water content has been successfully applied to salmonids (e.g., Hendry and Beall 2004, Crossin and Hinch 2005). We are currently exploring the ability of this technique to rapidly and non-destructively assess energetic status in migrating adults.

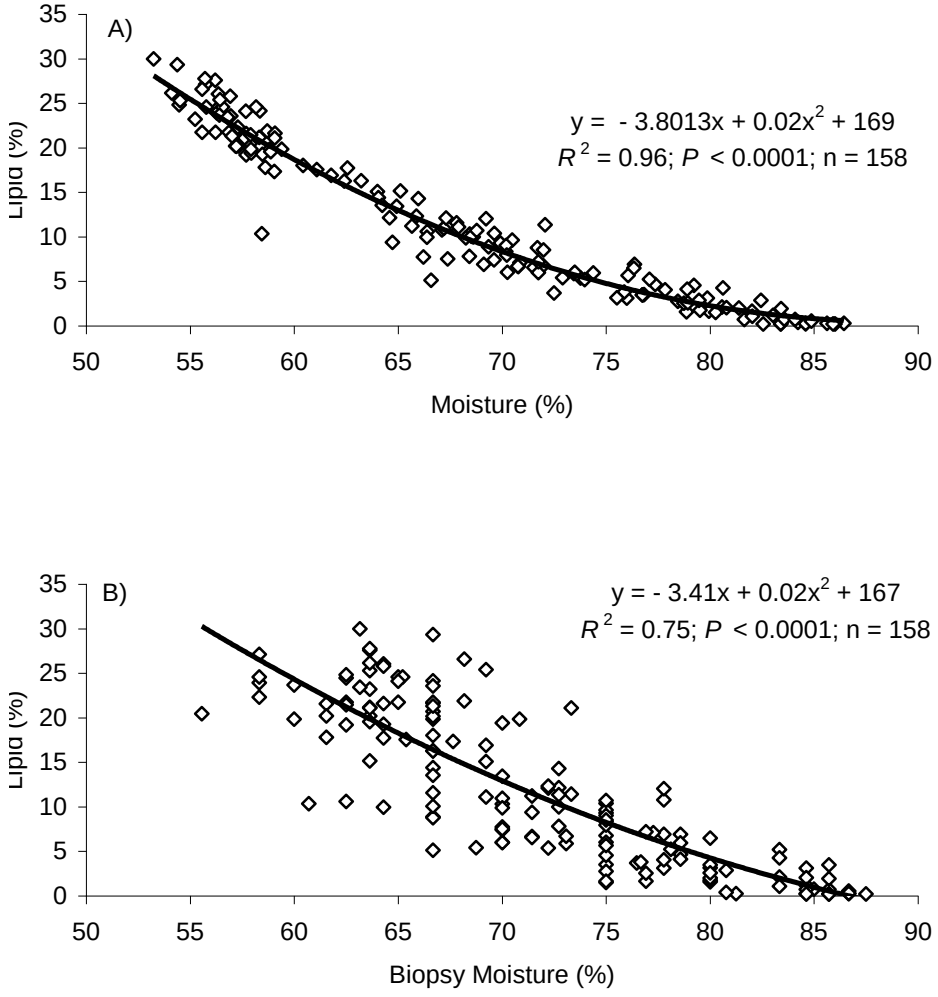


Figure 2.3. Quadratic regressions of A) lipid content (Y) over moisture of a 50-g homogenized muscle sample (x), and B) lipid content of a 50-g homogenized muscle sample (Y) over moisture content of a 1-g sample of muscle tissue (x).

*Tissue Biopsy*

Percent moisture of a biopsied tissue sample was tested as a potential predictor of moisture and lipid content. This method is potentially an inexpensive, non-lethal alternative to proximate analysis. Although small tissue samples were removed from dead fish with a scalpel, small tissue samples could be taken from live fish with biopsy needles. The moisture content of biopsied tissue samples was a reasonable predictor of whole muscle moisture ($R^2 = 0.82$), which in turn is highly correlated with muscle lipid ($R^2 = 0.96$). Moisture content of the 1-g biopsy sample accounted for 75% of the variance of lipid content of the larger muscle tissue sample. Although tissue biopsy could provide a quick inexpensive alternative to morphometrics for assessing energy content of live adult salmon, the impacts of tissue extraction on live fish should be monitored before its usefulness can be determined.

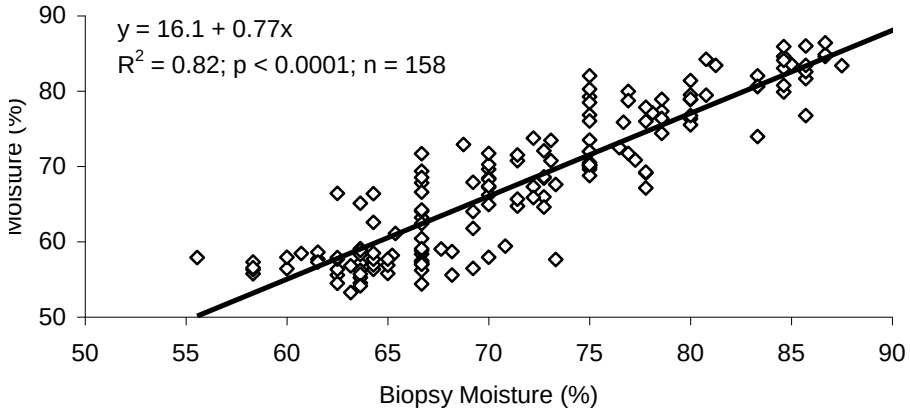


Figure 2.4. Linear regression of moisture percentage of a 50-g muscle tissue sample (Y) on moisture percentage of a 1-g muscle sample (x).

*Summary*

In summary, this study compared three non-destructive techniques for estimating the lipid, energy, and moisture contents of adult Chinook salmon returning to a central Idaho stream. We determined that morphometrics produced the best predictability of energy content for live adult fish sampled in the field. Such non-destructive measurements may be useful for describing the changes in energy condition of individual fish from other populations as well. Due to potential variability in the relationship between morphometrics and energy content among populations and years with different environmental conditions, the reported relationships should be confirmed through further sampling. Nonetheless, the ability to rapidly assess initial energetic state using

morphometrics or other developing technologies (BIA, the Lipidmeter) should provide a useful tool to assess the condition of fish returning after years of differing ocean conditions (e.g., Crossin et al. 2004) and to determine the relationship between individual initial energetic status and migration and reproductive success (Chapter 3).

## References


Adams, C.E., F.A. Huntingford, and M. Jobling. 1995. A non-destructive morphometric technique for estimation of body and mesenteric lipid in Arctic charr: a case study of its application. Journal of Fish Biology 47:82-90.

Anderson, R.O and R.M. Neumann. 1996. Length, weight, and associated structural indices. In *Fisheries Techniques* (Brian R. Murphey and David W. Willis , ed) 2nd edn, pp 447-482. American Fisheries Society, Maryland.

Bowen, W.D., C.A. Beck, and S.J. Iverson. 1999. Bioelectrical impedance analysis as a means of estimating total body water in grey seals. Canadian Journal of Zoology 77:418-422.

Berg, O. K., E. Thronaes, and G. Bremset. 1998. Energetics and survival of virgin and repeat spawning brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 55:47-53.

Brett, J.R. 1995. Energetics. (C. Groot, L. Margolis, and W.C. Clarke, ed). In *Physiological Ecology of Pacific Salmon*. pp 1-66. University of British Columbia Press, Vancouver.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information –theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cox, M.K. and K.J. Hartman. 2005. Nonlethal estimation of proximate composition in fish. Canadian Journal of Fisheries and Aquatic Sciences 62:269-275.

Crossin, G.T., S.G. Hinch, A.P. Farrell, M.P.Whelly, and M.C. Healey. 2003. Pink salmon (*Oncorhynchus gorbuscha*) migratory energetics: response to migratory difficulty and comparisons with sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Zoology 81:1986-1995.

Crossin, G. T., S. G. Hinch, A. P. Farrell, D. A. Higgs and M. C. Healey (2004). Somatic energy of sockeye salmon *Oncorhynchus nerka* at the onset of upriver migration: a comparison among ocean climate regimes. Fisheries Oceanography 13(5): 345-349.

Crossin, G. T. and S. G. Hinch (2005). A non-lethal, rapid method for assessing the somatic energy content of migrating adult Pacific salmon. Transactions of the American Fisheries Society 134: 184-191.

Farley, S.D. and C.T. Robbins. 1994. Development of two methods to estimate body composition of bears. Canadian Journal of Zoology 72:220-226

Hendry, A.P. and O.K Berg. 1999. Secondary sexual characteristics, energy use, senescence, and the cost of reproduction in sockeye salmon. Canadian Journal of Zoology 77:1663-1675

Hendry, A.P., A.H. Dittman, and R.W. Hardy. 2000. Proximate composition, reproductive development, and a test for trade-offs in captive sockeye salmon. Transactions of the American Fisheries Society 129(5):1082-1095.

Hendry, A. P. and E. Beall (2004). Energy use in spawning Atlantic salmon. Ecology of Freshwater Fish 13(3): 185-196.

Keefer, M.L., C.A Peery, T.C. Bjornn, M.A. Jepson, and L.C. Stuehrenberg 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. Transactions of the American Fisheries Society 133:1413-1439.

Kushner, R. F. and D.A. Schoeller. 1986. Estimation of total body water by bioelectrical impedance analysis. American Journal of Clinical Nutrition 44:417-424.

Lukaski, H.C., W.W. Bolonchuk, C.B. Hall, and W.A. Siders. 1986. Validation of tetrapolar bioelectrical impedance methods to assess human body condition. Journal of Applied Physiology 60:1327-1332.

Naughton, G.P, C.C. Caudill, M.L. Keefer, T.C. Bjornn, L.C. Stuehrenberg, and C.A. Peery. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 62: 30-47.

Rikardsen, A.H. and M.Johansen. 2003. A morphometric method for estimation of total lipid level in live Arctic Charr: a case study of its application on wild fish. The Fisheries Society of the British Isles. Journal of Fish Biology 62:724-734.

Simpson, A.L., N.B. Metcalfe, and J.E. Thorpe. 1992. A simple, non-destructive biometric method for estimating fat levels in Atlantic salmon, *Salmo salar.* Aquaculture and Fisheries Management 23:23-29.

## Chapter 3. Migration time, energy use, and spawning success of long distance migrating adult Chinook salmon


### Abstract

Spring-summer Chinook salmon (*Oncorhynchus tshawytscha*) must migrate over 1,000 river kilometers from the Pacific Ocean and pass eight mainstem dams and associated reservoirs to reach spawning areas on the South Fork Salmon River in central Idaho. We compared migration time, energy content, and reproductive success of radio-tagged or PIT-tagged fish in 2002 and 2003 to address concerns that fish delayed in their migration while passing dams may exhaust energy reserves prior to being able to successfully reproduce. Migration time and energy content were negatively correlated for PIT-tagged fish upon arrival at the spawning stream; slow migrating fish expended an estimated 39% of initial mass-specific somatic energy to develop gametes and migrate to the SFSR, while fast migrating fish expended only 29%. Similarities in energy content between pre-spawning and post-spawning mortalities from the general population were found for males in 2002, suggesting that energy content was a factor for pre-spawning death. However, understanding the relationship between energy use and spawning success is complicated by variations in run timing, time spent in the spawning stream, reproductive behavior, and the limited number of fish returning to a single population. Data from multiple years for a single population or for multiple populations within one year are needed before robust inferences can be made.

## Introduction

Difficulties associated with upstream migration of adult Pacific salmon (*Onchorhynchus spp*.) may include distance traveled, elevation changes, high or low flows, abnormal temperatures, dissolved gas supersaturation and natural and/or man-made obstacles such as waterfalls or dams. Chinook salmon returning to the South Fork Salmon River (SFSR) in central Idaho to spawn, must migrate over 1000 river kilometers and pass eight dams and associated reservoirs. Migration times (often used as a surrogate for migration distance) through an impounded river may be increased by time required to pass dams (Boggs et al. 2004; Keefer et al. 2004). Delays that prolong migration for fish with long difficult spawning migrations may cause excessive energy use and reduce energy available for migration, gamete development, and spawning. Results from recent studies on Pacific salmon suggest that excessive use of energy stores, such as from increased migration times, during the freshwater migration can limit gamete development and negatively affect spawning success (Rand and Hinch 1998; Geist et al. 2000). The purpose of the present study was to relate migration times to energy expenditures and spawning success for fish migrating long distances through an impounded river.

The objectives were to 1) determine migration times of radio-tagged and passive integrative transponder (PIT)-tagged adult salmon returning to spawning areas on the South Fork Salmon River in central Idaho, 2) use radio-telemetry to characterize migration behavior and recapture individual fish after death in the SFSR, 3) compare migration histories with final energy condition and spawning success, and 4) use estimates of energy content to describe the use of energy by individual fish during the spawning migration. The research hypothesis was that fish delayed in their migration to the spawning stream have lower energy content at arrival, and are more likely to die prior to spawning.

## Methods

### *Study Area*

Chinook salmon returning to the SFSR to spawn, pass four lower Columbia River dams (Bonneville, The Dalles, John Day, and McNary), four Lower Snake River dams (Ice Harbor, Lower Monumental, Little Goose, and Lower Granite) and climb 1,890 meters to reach spawning areas in the South Fork Salmon River (Figure 3.1). Once past Lower Granite Dam (river kilometer [rkm] 695) and reservoir, fish move through about 450 km of unimpounded river segments.

### *Fish Tagging and Telemetry Monitoring*

Adult Chinook salmon used for this evaluation were collected and tagged at Bonneville Dam (rkm 235). Fish were diverted from the Washington shore fish ladder to an anesthetic tank containing 22 mg/L clove oil (Peake 1998) and outfitted with radio transmitters (Lotek wireless, Inc., New Market, Ontario) before being released into the

tailrace or forebay at Bonneville Dam. Tagging was part of a telemetry study conducted by the University of Idaho and NOAA Fisheries. Fish tagged with radio transmitters were selected based on PIT-tag codes found by an automated PIT-tag detection system (McCutcheon et al. 1994), as well as from the general population of fish with similar run timing.

As fish progressed upstream, they were monitored using an array of receivers located at all eight dams, in reservoirs, and in major tributaries of the Columbia, Snake and Salmon rivers (Figure 3.1). A receiver with an aerial antenna was located at rkm 1,098 on the SFSR, and detections by this receiver were used to calculate migration time from Bonneville Dam to the SFSR. Migration times were calculated for three river segments: from the first telemetry record at Bonneville Dam to the last record at Lower Granite Dam (460 km), from the last record at Lower Granite Dam to the first record at the SFSR fixed receiver site (400 km), and from the first record at Bonneville Dam to the first record at the SFSR fixed receiver site (860 km). Time spent in fresh water was estimated for radio-tagged fish which had known dates of death on the spawning grounds.

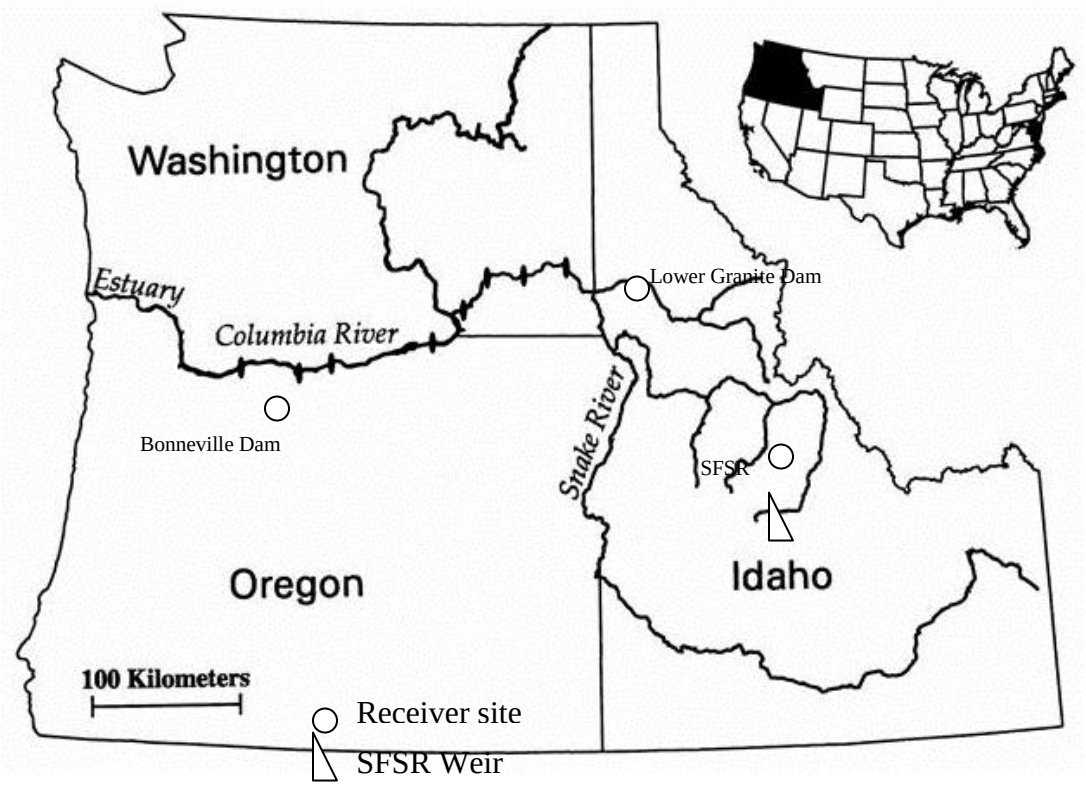


Figure 3.1. Study area including eight dams and receiver locations used for estimating migration time

*Fish Sampled*

Adult Chinook salmon en route to the South Fork Salmon River (SFSR) were targeted for sampling at Bonneville Dam, a nominal start of freshwater migration. During 2002, fish were sampled during the segment of the summer run when SFSR salmon were known to be passing the dam, based on detections of a separate group of SFSR fish that had been PIT tagged as juveniles. A sample of 57 fish was selected for proximate analysis (see Chapter 1) and to develop methods for non-lethal estimation of energy condition (see Chapter 2). Proximate analysis involved the determination of percent lipid, protein, ash and moisture of the muscle, skin, viscera and gonad tissue. Energy content was calculated for each tissue type and summed to estimate somatic (muscle, skin, and viscera) and total body (muscle, skin, viscera, and gonad) energy for each fish. To estimate the mass-specific energy content (kJ $g^{-1}$) of each tissue, energy equivalents for fat and protein of 36.4 kJ $g^{-1}$ (8.66 kcal $g^{-1}$) and 20.1 kJ $g^{-1}$ (4.9 kcal $g^{-1}$) from Brett (1995) were multiplied by the appropriate percentages (x0.01) of lipid and protein and summed. "Mass specific" energy of the somatic tissues (muscle, skin, and viscera) was multiplied by the mass of each tissue and summed to estimate somatic energy (kJ) for each fish. Total body energy (kJ) was estimated by the same procedure except that gonad tissue was also included.

A second group of salmon was radio-tagged and monitored as they migrated upstream for separate passage evaluations (Boggs et al.; Keefer et al. 2004). These fish were later searched for in the SFSR spawning areas during July and August of 2002.

Fifty-three fish were collected at the Idaho Department of Fish and Game weir on the South Fork Salmon River (rkm = 1,156) during July and early August, and 87 (36 pre-spawning and 51 post-spawning) carcasses were sampled on the spawning grounds during August. All freshly dead fish were weighed, measured for 12 linear morphological measurements (Chapter Two), and sampled for proximate analysis (Chapter One). Freshness was noted by firmness of body and red or pink color to the gills. Fish that died before spawning were defined as those with greater than 75% of the expected pre-spawning gamete mass remaining after death (J. A. Hesse, Nez Perce Tribe, personal communication).

*Estimation of Energy Content by Morphometrics*

Non-lethal estimates of energy content (based on results from proximate analysis in 2002) were obtained in 2003 for 163 fish sampled at Bonneville Dam by measuring body mass (kg), fork length (cm), hump height (mm) and body depth at the anus (mm) on fish being outfitted with radio-transmitters between the end of May and the first week of July. Morphometric data were used in multiple regression models (Table 3.1) to estimate total and somatic energy and percent muscle lipid (for fish sampled at Bonneville and on the SFSR). Since absolute values of energy were highly correlated with fork length of fish at start of migration, absolute values were only compared when describing energy use of individual fish. Because percent muscle lipid and mass-specific energy were not related

to fish size, these indices of energy were used to compare fish that died before spawning and fish that died after spawning. Further details of morphological measurements and model selection are given in Chapter Two. Spawning ground surveys were conducted daily on the South Fork Salmon River to locate radio-tagged and PIT-tagged fish, measure morphometrics of fresh carcasses, assess degree of pre-spawning mortality in the river, and estimate total energy consumption for select individuals.

Table 3.1. Regression models for estimating percent lipid of muscle, somatic energy (kJ), and total energy (kJ) with coefficient of determination. Independent variables include body mass in kg (wt), fork length in cm (Lf), hump height in mm (Hh) and body depth at the anal fin in mm (Da).[a.]

| Model | $R^2$ |
|---|---|
| Lipid (%) = 20.8 + -0.778Lf + 0.409Hh + 0.271Da | 0.82 |
| Total Energy (kj) = 118350 -2571Lf +14136wt +630Da | 0.92 |
| Somatic Energy (kj) = 62524 – 2100Lf + 9438wt +547Hh + 583Da | 0.92 |

[a.] Regression models from Chapter Two.

*River Water Temperature*

Temperature data was collected by the US Army Corps of Engineers at the Columbia and Snake River Dams in 2002 and 2003. Previous analysis has shown that of the temperature data collected at the dams on the Columbia and Snake Rivers, data at Bonneville Dam (the first dam on the Columbia River) provide a reasonable indicator of temperatures encountered by fish during upstream migration through the reservoirs of the Columbia and Snake Rivers (unpublished analyses, Naughton et al. 2004). Mean daily river water temperatures at Bonneville Dam, on the date the fish passed the dam, were compared to migration time (d) and energy content at arrival at the SFSR for 25 PIT-tagged fish.

*Statistical Analysis*

Because sample sizes were relatively small, the majority of analyses involved simple descriptive statistics. Correlation coefficients (Pearson's) were calculated between energy indices (log transformed percent muscle lipid, mass-specific total energy, and mass-specific somatic energy) and migration times, log transformed percent muscle lipid and mean river water temperature on the day of dam passage, and migration time and mean river water temperature on the day of dam passage for 25 PIT-tagged fish collected at the SFSR trap in 2002. Data were log-transformed to fit the assumptions of linearity for correlation analysis.

Separate independent *t* tests were used to test the null hypotheses that pre- and post-spawning mortalities had equal amounts of 1) percent muscle lipid, 2) mass-specific somatic energy, and 3) mass-specific total energy in 2002. Tests of significance were performed at $P \leq 0.05$. Males and females were analyzed separately. Since unequal variances were found between pre- and post-spawning females, Satterthwhaite's approximation (a *t* distribution with modified degrees of freedom; Ott and Longnecker 2001) was used to test for differences between pre- and post-spawning mortalities for mass-specific somatic energy, mass-specific total energy and muscle lipid in 2002.

## Results

*Travel Times and Sampling Locations (2002)*

In 2002, 85 radio-tagged salmon were recorded at the SFSR receiver site. Median travel time from release at Bonneville Dam to the fixed antennae receiver site was 32.7 days, and ranged from 20 to 54 days ($n$ = 56). Median travel time to pass the eight dams and associated reservoirs (Bonneville to Lower Granite) was 15.0 days, and ranged from 8.5 to 31.0 days ($n$ = 56). Median travel time to pass from Lower Granite Dam to the receiver site on the SFSR (free-flowing except for the lower 52 km) was 15.9 days, and ranged from 9.7 to 44.1 days ($n$ = 83).

Of the 85 radio-tagged fish known to return to the SFSR in 2002, eight were known to spawn and one died before spawning. Four of the radio-tagged fish that had spawned were recovered from the spawning stream during carcass surveys in 2002: two of these fish were suitable for analysis of proximate composition (one male and one female; Table 3.2), but two were deteriorated and partially eaten by predators. Nez Perce Tribe

Table 3.2. Travel times between Bonneville and Lower Granite Dams (BON-LGR), Lower Granite Dam and the SFSR receiver site (LGR-SFSR), Bonneville Dam and the SFSR receiver site (BON-SFSR), percentage lipid of the muscle tissue, "mass specific" somatic energy and "mass specific" total energy for two fish with radio transmitters recaptured after spawning in 2002.

| Tagging date | Travel time (days) | | | Lipid (%) | Somatic E (kJ $g^{-1}$) | Total E (kJ $g^{-1}$) | Sex |
|---|---|---|---|---|---|---|---|
| | BON-LGR | LGR – SFSR | BON-SFSR | | | | |
| 25 May | 23.9 | 14.5 | 38.5 | 1.45 | 2.5 | 2.5 | M |
| 4 Jun | __ | 16.1 | __ | 0.27 | 1.6 | 1.5 | F |

biologists recovered five radio-tagged carcasses (four fish that died after and one that died before spawning) during carcass surveys. Twenty-one were caught during the fishery and the transmitters were returned to us. Thirteen fish were trapped by Idaho

Department of Fish and Game at the SFSR trap; of these, four (all males) were killed and sampled for proximate analysis (Table 3.3). Nine radio tags were found on the river bank or river bottom. Eight fish were last mobile tracked in tributaries of the SFSR (East Fork South Fork Salmon River, Johnson Cr., Lake Cr., or Secesch R.). The fates of 21 of the 85 fish were unknown.

Table 3.3. Migration time and energy content for radio-tagged fish (all males) recaptured at the trap on the SFSR in 2002 including tag date and location (BON = Bonneville dam, LGR = Lower Granite Dam) migration time from tagging location to the fixed antennae receiver site on the SFSR, muscle lipid (%), and derived estimates of mass-specific somatic and mass-specific total energy (kJ $g^{-1}$ ) using proximate analysis.

| Tagging Location | Tagging Date | Migration Time (days) | Muscle Lipid (%) | Somatic E (kJ $g^{-1}$) | Total E (kJ $g^{-1}$) |
|---|---|---|---|---|---|
| LGR | 28 Jun | 11.0 | 5.2 | 4.4 | 4.5 |
| BON | 17 Jun | 23.0 | 5.4 | 4.9 | 5.0 |
| LGR | 10 Jun | 16.9 | 10.3 | 5.9 | 6.1 |
| BON | 21 Jun | 20.3 | 7.2 | 4.4 | 4.6 |

*Travel Times and Energy Content (2002)*

All four of the radio-tagged fish trapped by Idaho Department of Fish and Game and sampled for proximate analysis were males (Table 3.3). Two were tagged at Bonneville Dam and took 20 to 23 days to migrate to the SFSR fixed receiver site; two were outfitted with radio-transmitters at Lower Granite Dam and took 11 to 17 days to migrate to the SFSR. The lipid content of the muscle ranged from 5.2 to 10.3%, and mass-specific somatic energy (energy content of the skin, muscle, and viscera) ranged from 4.6 to 6.1 kJ $g^{-1}$ for these four fish.

Thirty-two PIT-tagged fish were sampled and analyzed for proximate composition at the trap on the SFSR. Of these 32 fish, 25 had records at the adult PIT detection sites at Bonneville and Lower Granite Dams, allowing for calculation of travel time between the two locations. Median time to travel between detections at Bonneville and Lower Granite dams was 12.3 d and ranged from approximately 10 to 20 d. Median travel time was 13.0 d for females ($n$ = 13, range= 9.7 to 20.0 d), and 11.9 d for males ($n$ = 12; range = 9.9 to 17 d).

Mean (SE) muscle lipid content for PIT- tagged fish at arrival at the spawning stream was 9.3 (3.3) %. Mean mass-specific somatic energy was 5.8 (0.8) kJ $g^{-1}$and mass-specific total energy was 6.4 (0.7) kJ $g^{-1}$. For females ($n$ =13), mean muscle lipid was 7.9 (2.5) %, mass-specific somatic energy was 5.4 (0.7) kJ $g^{-1}$, and mass-specific total energy was 6.4 (0.7) kJ $g^{-1}$. For males ($n$ = 12), mean muscle lipid was 10.8 (3.4) %,

mass-specific somatic energy was 6.3 (0.7) kJ $g^{-1}$, and mass-specific total energy was 6.4 (0.7) kJ $g^{-1}$.

We observed a negative relationship between travel time and percent muscle lipid, mass-specific somatic energy, and mass-specific total energy for PIT-tagged fish in 2002. Travel time was negatively correlated with log-transformed muscle lipid ($r$= -0.67, $n$ = *25, P* = 0.0002; Figure 3.2), mass-specific somatic energy ($r$ = -0.60, $P$ = 0.002, $n$ = 25) and mass-specific total energy($r$ = -0.57, $P$ = 0.003, $n$ = 25). Fish with travel times shorter than the median (12.3 d) had 32% more muscle lipid upon arrival at the SFSR than fish with travel times longer than the median. Mean percent muscle lipid, with standard deviation in parentheses, was 7.5% (2.3%) for slow migrating fish, and 11.0% (2.3%) for fast migrating fish. Mean mass-specific somatic energy was 5.3 kJ $g^{-1}$ for slow and 6.22 kJ $g^{-1}$ for fast migrating fish. Mass-specific total energy was 6.1 kJ $g^{-1}$ for slow and 6.7 kJ $g^{-1}$ for fast migrating fish. Based on mean levels for fish measured at Bonneville Dam, slow migrants expended 31 and 39% of their initial mass-specific total and somatic energy stores to migrate, while faster migrants expended 25 and 29% of their mass-specific total and somatic energy to migrate to the SFSR. Temperature near the start of the spawning migration, at Bonneville Dam, was not correlated with migration time (d) or muscle lipid remaining at arrival at the SFSR (Figures 3.3.).

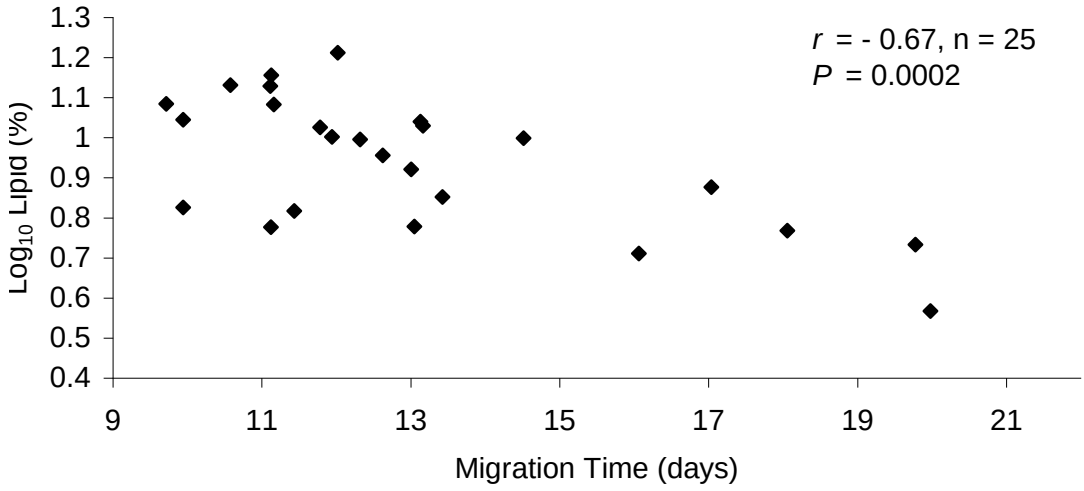


Figure 3.2. Pearson's correlation between migration time and percent muscle lipid for PIT-tagged fish at arrival at the SFSR in 2002.

*Spawning Success (2002)*

In 2002, 36 pre-spawning mortalities (22 females, 16 hatchery and 6 wild; 14 males, 9 hatchery and 5 wild) and 51 post-spawning mortalities were observed and sampled for proximate body composition in the spawning area. Of the 51 post-spawning mortalities, 25 were females (18 hatchery and 7 wild) and 26 were males (10 hatchery and 16 wild).

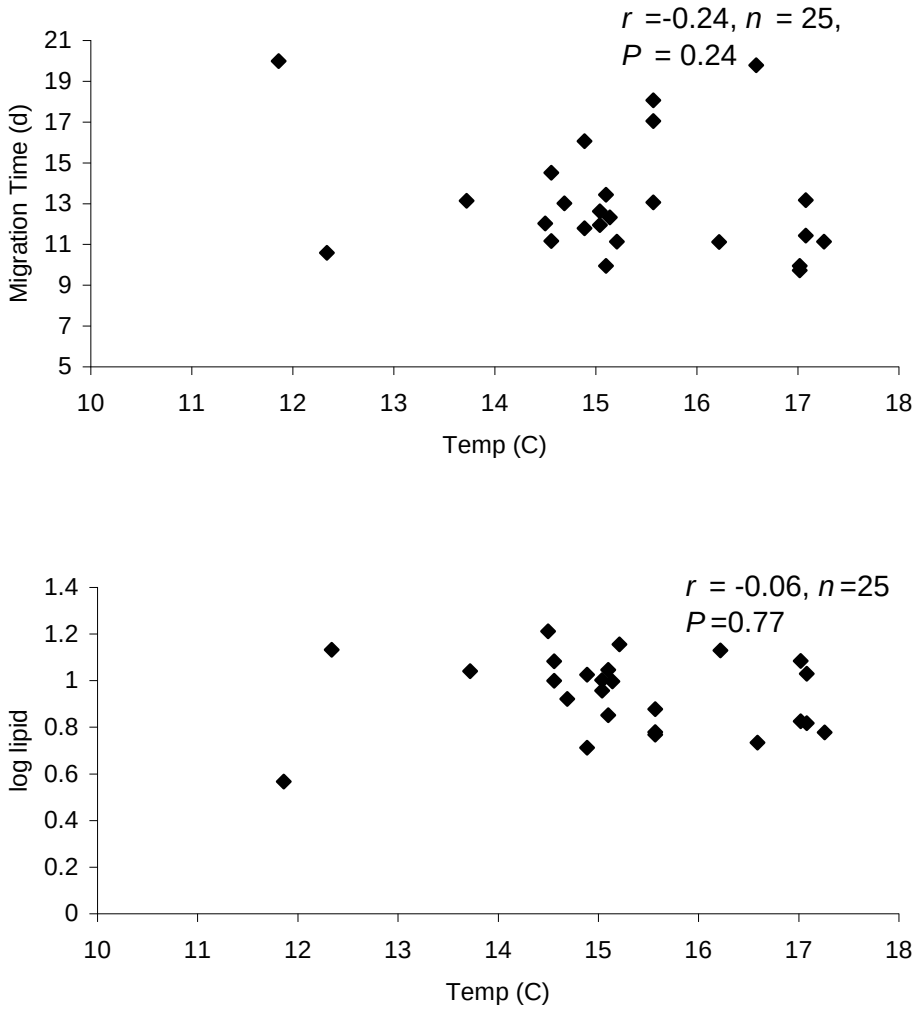


Figure 3.3. Pearson's correlation between A) migration time (Y) and river temperature (x) and B) percent muscle lipid (Y) and river temperature (x) for 25 PIT-tagged fish at arrival at the SFSR in 2002.

Percentage muscle lipid and mass-specific somatic energy were not significantly different ($t$ = -0.99, $df$ =13, $P$=0.34; $t$ = -1.1, $df$ = 13, $P$ = 0.29) between pre- and post-spawning males. Values were generally lower for post-spawning females (percentage

lipid Satterthwaite $t$ = -4.72, $df$ = 22.5, $P$<0.0001, mass-specific somatic energy Satterthwaite $t$ = -9.25, $df$ = 28, $P$ < 0.0001).

Two radio-tagged fish were obtained from the SFSR spawning areas for evaluation of energy content in 2002 (Table 3.3). Both had spawned. Two PIT-tagged fish were also found on the spawning grounds (one pre-spawning female and one post-spawning jack salmon). The female that died before spawning took 9.9 days and the jack salmon that spawned took 13.0 days to migrate between the impounded reaches of the lower Columbia and Snake Rivers and spent 85 and 75 days respectively from detection at Bonneville Dam to death on the spawning grounds. Muscle lipid content was estimated to be 6% for pre-spawning and 11% for post-spawning mortalities.

Spawning success of five additional fish (one pre and four post-spawning) was determined during spawning ground surveys conducted by Nez Perce Tribe biologists. The one fish that died prior to spawning was outfitted with a radio transmitter at Lower Granite Dam. Final energy content of the pre-spawning mortality was unknown, as was the travel time between Bonneville Dam and the receiver site on the SFSR. However, migration time through the free-flowing stretch (Lower Granite Dam to the receiver site on the South Fork Salmon River) was much longer than total time for all other fish to migrate from Bonneville to the spawning stream (Table 3.4). The four fish that died before spawning spent 13 to 24 days migrating between Bonneville and Lower Granite dams, 13 to 26 days to migrate the unimpounded segment between Lower Granite Dam and the fixed receiver site on the SFSR, and a total 78 to 101 days in freshwater between the start of migration and death on the SFSR.

Table 3.4. Migration times and percent lipid at death (Lipid f; where applicable) for radio-tagged fish with known spawning success in 2002.

| Tagging Date | Time (d) | | | | Lipid f (%) |
|---|---|---|---|---|---|
| | BON-LGR | LGR-SFSR | BON-SFSR | BON-death | |
| | | | Pre-spawning Females | | |
| 8 Jul | _ | 44.1 | _ | _ | _ |
| | | | Successful Females | | |
| 4 Jun | _ | 16.1 | _ | _ | 0.27 |
| 21 May | – | 20.8 | _ | _ | _ |
| 7 Jun | 12.8 | 13.1 | 25.9 | 88.2 | _ |
| 11 May | _ | 25.7 | _ | _ | _ |
| | | | Successful Males | | |
| 25 May | 24 | 14.5 | 38.5 | 97.0 | 1.45 |
| 6 Jun | 13.6 | 13.4 | 27 | 90.6 | _ |
| 19 Jun | 15.3 | _ | _ | 77.7 | _ |
| 21 May | 15.7 | 20.2 | 35.9 | 101.3 | _ |

*Travel Times and Sampling Locations (2003)*

In 2003, 65 fish outfitted with radio transmitters between 15 April and 15 July migrated past the fixed receiver site on the SFSR. Median travel time between Bonneville Dam and the SFSR fixed receiver site was 33.7 d ($n$ = 54; range = 17.4 to 59.1 d). Median travel time through the Columbia and Snake River dams was 16.7 d ($n$ = 55; range = 9.66 to 34.6 d). Median travel time through the unimpounded river segment was 16.4 d ($n$ = 61; range = 9.89 to 47.0 d). Females that spawned ($n$ = 7) spent 23.1 to 71.9 d in freshwater between Bonneville Dam and death on the spawning grounds with a median of 53.0 d. Males ($n$ = 7) spent 30.1 to 64.4 d in freshwater, with a median of 56.4 d.

Of the 65 fish detected in the SFSR, 14 were known to spawn in the SFSR. Eleven carcasses were obtained for energy estimates and three were observed spawning, but

taken by predators before carcasses could be retrieved (remains and transmitters were located away from the river). Six radio-tagged fish were collected for brood stock by Idaho Department of Fish and Game personnel, and five radio-tagged salmon died before spawning (two of the five were measured for energy estimates). The fates of 20 radio-tagged salmon were unknown, eight radio-tagged Chinook salmon were captured in the fishery, and six were captured by IDFG at the trap (two released, four ponded for spawning: two of which we were able to measure for energy estimates after being spawned by IDFG). One transmitter was found out of the water without the fish. Six fish migrated up tributaries of the SFSR. Two transmitters were found and returned to the University of Idaho without information (time of death or spawning success) and one transmitter was pulled from a fish that was caught and released during the fishery.

*Travel Times and Energy Content (2003)*

Of the 65 fish that migrated successfully to the SFSR receiver site, morphological measures had been made for 38 fish at Bonneville Dam at the time of radio-tagging. Travel time to the SFSR receiver site and estimated initial lipid (%) of the muscle tissue were not significantly related ($r = 0.12$, $n = 28$, $P = 0.537$).

Fifteen of the 65 fish that migrated successfully to the SFSR receiver site were measured for estimates of final energy content after death in the spawning stream. The correlation between final lipid of the muscle tissue and travel time was similar in trend observed in 2002, but the relationship was not significant ($r = -0.46$, $n = 10$, $P = 0.17$).

Of the 38 fish measured at Bonneville Dam, nine were located and re-measured after death on the spawning grounds and six (two pre-spawning and four post-spawning) had body mass, fork length, hump height measured at both the start of migration and after death on the spawning stream, allowing for estimation of muscle lipid, total energy and somatic energy (Table 3.5) and energy expended to migrate and spawn. Total body mass, hump height, and body depth at the anus decreased by 34, 25 and 22% for females and 28, 24, and 18% for males. Individual fish expended 74 to 93% of their estimated initial somatic energy reserves to migrate and spawn, with the female that spawned expending the highest proportion of energy. The two fish that died before spawning expended 58 and 66% of their initial somatic energy reserves (Table 3.5).

Table 3.5. Tagging date, migration time, estimated percent muscle lipid at the start of freshwater migration (Lipid $_i$), estimated final percent muscle lipid at death on the spawning grounds (Lipid $_f$), and estimated somatic and total energy expended by death for fish with radio transmitters that were recaptured for energy use estimates in 2003. Migration times include days taken to migrate from Bonneville Dam (BON) on the Columbia River to the South Fork Salmon River (SFSR), and from the SFSR to death on the spawning grounds. Prediction intervals (95%) for estimated lipid are shown in parentheses after estimate.

| Tag Date | Time (d) | | Lipid $_i$ | Lipid $_f$ | Energy Used | |
|---|---|---|---|---|---|---|
| | BON-SFSR | BON-death | (%) | (%) | Somatic (%) | Total (%) |
| | | | Pre-spawning Females | | | |
| 21 Jun | 28 | 75.8 | 21.3(7.4) | 3.9(7.4) | 66 | 54 |
| | | | Successful Females | | | |
| 20 Jun | 52 | 75.2 | 20(7.4) | 1.2(7.4) | 93 | 95 |
| | | | Pre-spawning Males | | | |
| 28 May | 34.5 | 62.6 | 16.5(7.4) | 4.6(7.4) | 58 | 58 |
| | | | Successful Males | | | |
| 10 Jun | 26.1 | 87.2 | 21.2(7.4) | 4.7(7.4) | 77 | 82 |
| 29 Jun | 38.8 | 68.9 | 17.8 (7.4) | 0.58(7.4) | 77 | 81 |
| *10 Jun | 29.5 | 84.2 | 20.8(7.4) | 1.5(7.4) | 74 | 76 |

* Fish was captured by Idaho Department of Fish and Game for spawning and sampled for energy use estimate after being spawned by hatchery personnel.

*Spawning Success (2003)*

Prespawn mortality during the study was high (71.3%). Three hundred and sixty-seven fish carcasses from the general population were inspected during spawning ground surveys in July, August, and September, 2003. The spawning success of 25 fish was undeterminable due to carcass deterioration. Of the remaining 342, 244 died prior to spawning (142 females: 68 hatchery, 71 wild and 3 unknown origin; 86 males: 31 hatchery, 50 wild and 5 unknown origin), and 98 were determined to have spawned.

The spawning success of 19 (and 6 hatchery spawned) radio-tagged fish was tracked in 2003: 5 fish died prior to spawning and 14 spawned (Table 3.6). Median travel time from Bonneville Dam to the receiver site on the SFSR for fish that died before spawning was 30.9 days and ranged from 27 to 38 days. Median travel time to complete migration to the spawning stream for fish that spawned was 31.9 ($n$ = 13, range = 23 to 55 days).

Initial energy condition was estimated for 11 fish and final energy condition was estimated for 11 naturally spawning fish (Table 3.6). Both initial and final estimates of energy content were estimated for six fish (five naturally spawned; one hatchery spawned) with morphometric data (Table 3.5). Of these six fish, there was one female that died before spawning and one female that spawned. The two females were tagged within one day of each other and spent about 75 days in freshwater from the start of migration at Bonneville Dam to death on the SFSR. At the start of migration estimated lipid content of the muscle tissue was 20%. However, the fish that died prior to spawning expended substantially less (30%) energy than the one that lived to spawn. The female that died before spawning took almost half the amount of time to migrate to the SFSR and was exposed to high temperatures in the SFSR, while the fish that spawned fell back over The Dalles Dam and reascended and took more time to migrate to the SFSR. One male died prior to spawning and three males spawned. The male that died before spawning started migration earlier with relatively less initial lipid stores (16.5%) and died on the spawning grounds in late July. Travel time for the male that died before spawning was just above the median for fish in 2003.

Final energy content was estimated from six PIT-tagged carcasses (five pre-spawning and one post-spawning) found on the spawning grounds. Median travel time from Bonneville to Lower Granite Dam for fish that died before spawning was 18 days and ranged from 11 to 24 days. The fish that spawned took 16.1 days to migrate through the impounded reaches of the lower Columbia and Snake Rivers. Mean percent muscle lipid was estimated to be 6.0%, for the five fish that died before spawning. The fish that spawned was left with an estimated 0.5% muscle lipid.

## Discussion

*Energy and Migration Patterns*

Energy content of PIT-tagged fish was negatively correlated with migration time upon arrival at the spawning stream in 2002. Fish taking longer than the median travel time between Bonneville and Lower Granite Dam (12.3 days) in 2002 used an estimated 39% of mass-specific somatic energy; faster migrating fish used only an estimated 29% of mass-specific somatic energy. This suggests that fish that spend a greater amount of time migrating past eight dams and associated reservoirs have less energy (per unit mass) upon arrival at the spawning grounds available for gamete development, site selection, competition, and spawning. Magie and Mesa (2004) found a similar negative relationship between energy use and time to migrate to spawning areas on the Yakima River: slow migrants used 5-8% more (depending on sex) mass-specific energy from muscle tissue than faster migrants. However, a cause and effect relationship between

Table 3.6. Migration times and estimated percent lipid (Lipid i = initial lipid, Lipid f = final lipid) with 95% prediction interval in parentheses for radio-tagged fish with known spawning success in 2003.

| Tag Date | Travel Time (days) | | | | Lipid(i) (%) | Lipid(f) (%) |
|---|---|---|---|---|---|---|
| | BON-LGR | LGR-SFS | BON-SFS | BON-death | | |
| | | | Pre-spawning Females | | | |
| 31 May | 11.1 | 19.8 | 30.9 | 45.6 | – | 8.9(7.4) |
| 21 Jun | 17.1 | 10.9 | 28 | 75.8 | 21.3(7.4) | 3.9(7.4) |
| | | | Successful Females | | | |
| 21 May | 21.7 | 18.3 | 40 | 111.8 | _ | _ |
| 14 Jun | 17.9 | 16.4 | 34.3 | 86.9 | 19.3(7.4) | _ |
| 20 Jun | 29.9 | 22.1 | 52 | 75.2 | 20(7.4) | 1.2(7.4) |
| 30 Apr | 22.1 | 33.3 | 55.4 | 119.6 | _ | -0.3(7.4) |
| 14 Jul | 13.4 | 15.6 | 29 | 53.8 | _ | -1.7(7.4) |
| 3 May | _ | 38.5 | _ | _ | _ | 5.6(7.4) |
| 19 May | 22 | 16 | 38 | 91 | _ | -4.6(7.4) |
| | | | Pre-spawning Males | | | |
| 28 May | 16.1 | 18.4 | 34.5 | 62.6 | 16.5(7.4) | 4.6(7.4) |
| 22 May | 19.2 | 18.3 | 37.5 | 67.7 | _ | _ |
| 10 Jun | 14.1 | 13.2 | 27.3 | 63.7 | 22.7(7.4) | _ |
| | | | Successful Males | | | |
| 22 Jun | 12.6 | 10.3 | 22.9 | 79.2 | 18.5(7.4) | _ |
| 23 Jun | 10.5 | 13.4 | 23.9 | 69.7 | 3.4(7.4) | _ |
| 10 Jun | 10.6 | 15.4 | 26 | 87.2 | 21.1(7.4) | 4.7(7.4) |
| 16 Jun | 11.9 | 13.4 | 25.3 | 78.9 | _ | 2.6(7.4) |
| 29 Jun | 14.3 | 24.5 | 38.8 | 68.9 | 17.8(7.4) | 0.6(7.4) |
| 5 Jun | 15 | 16.9 | 31.9 | 96.3 | 19.0(7.4) | _ |
| 6 Jun | 13.5 | 17.8 | 31.3 | 95.3 | 17.3(7.4) | _ |

longer migration time and lower energy reserves requires the assumption that all fish sampled in 2002 had similar energy reserves at the start of migration, expended similar amounts of energy reserves for reproductive development during migration, and migrated during comparable environmental conditions. Without initial estimates of energy to provide a point of comparison, any indication of increased energy use with increased migration time at this point is only a correlation. Different reproductive behavior such as migration timing, speed, maturation level, and time spent in the spawning stream play an important role in energy demands during migration. Earlier migrants might encounter high flow conditions, which would increase energy required to migrate upstream. Keefer et al. (2004) found that rate of travel of adult Chinook salmon was correlated with flow and temperature: within years, spring-summer Chinook salmon migrated faster as water temperature and date of migration increased, but among years, migratory rates were slower during years with higher discharge. In this study temperature was not correlated with migration time (d) or muscle lipid remaining at arrival at the SFSR.

A non-significant correlation between initial energy stores (estimated from morphometrics) and migration time was found in 2003, though the relatively small sample size ($n$ = 28) may have been inadequate to detect a relationship given the large variability in migration behavior.

*Energy and Spawning Success*

In 2002, muscle lipid, mass-specific somatic energy and mass-specific total energy were higher for females that died prior to spawning (pre-spawning fish) compared with fish that died after spawning, suggesting that prespawn mortality was not directly associated with the exhaustion of energy reserves. In contrast, muscle lipid, mass-specific somatic energy and mass-specific total energy were similar between males at pre-and post-spawning death, and in agreement with Magie and Mesa (2004) who found similar energy condition between pre- and post-spawning Chinook salmon in the Yakima River in 2002. Reasons why energy levels did not differ significantly between males that died before and after spawning in this study include: 1) fish died from exhaustion of energy reserves, or 2) small sample size may have affected the ability to detect significant differences.

The majority of fish that died before spawning (both male and female) in 2003 were found in July, prior to the main spawning period in the SFSR (mid-August to mid-September). The relationship between migration time and run timing could not be examined because of the small sample size of radio-tagged fish. However, the high pre-spawning mortality in July 2003 coincided with unusually high water temperatures (Figure 3.4).

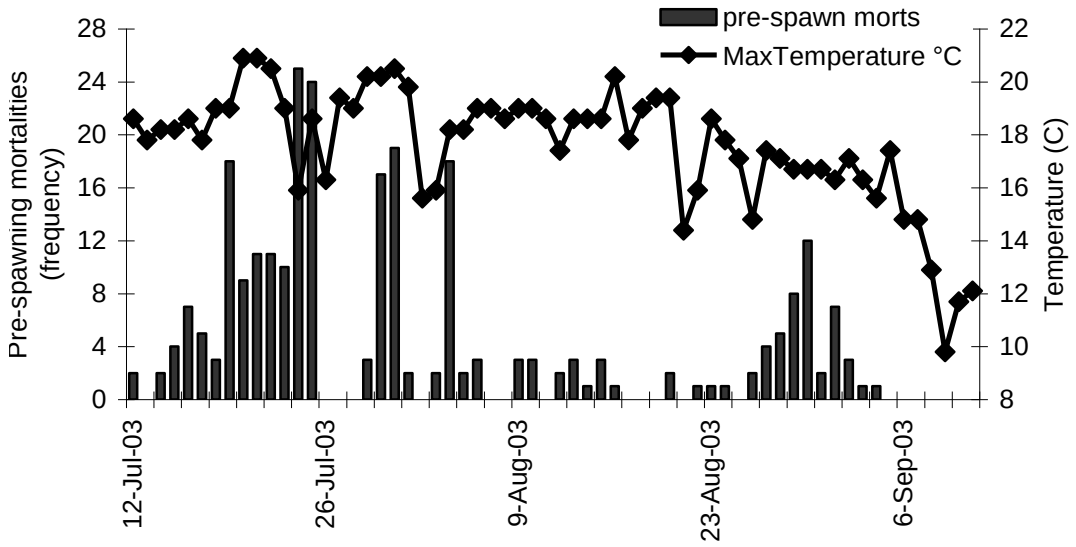


Figure 3.4. Frequency of pre-spawning mortalities observed in 2003 and maximum daily temperatures (USFS data logger) at the weir on the SFSR.

We only studied mortality after arrival at the spawning stream, and did not consider *en route* mortality. *En route* mortality has been related to exhausted energy stores in sockeye salmon during years of high temperature and discharge (Hinch and Rand 1998) and the onset of stressful temperatures in Columbia River sockeye salmon (Naughton et al. 2005) and should be considered in the future when assessing mortality due to energy use during migration.

*Energy Expenditures, Migration History, and Spawning Success*

Comparisons of energy content (either after death on the spawning grounds or at the start of migration) with migration patterns for fish that did and did not spawn were insightful but sample sizes in 2002 and 2003 were not adequate for describing the relationship between migratory uses of energy reserves and spawning success. Additional information on initial energy condition, energy used to migrate and spawn, detailed descriptions of migratory behavior, and confirmed spawning success of individuals are needed to properly address the relationship between energy use, migratory patterns, and spawning success.

To date, we have obtained initial energy condition, final energy condition, travel time and spawning success for six fish (four fish died before and two died after spawning), and consequently, we can only make anecdotal observations about the relationship between condition and reproductive success. One female that died before spawning and one female that died after spawning were observed at Bonneville Dam and again after death on the spawning stream. Migration timing (tag date), initial lipid content of the muscle

tissue and time spent in fresh water (Bonneville Dam to death on the SFSR) were similar for the two females. The fish that spawned fell back over The Dalles Dam and took almost twice as long as the fish that died before spawning to complete migration to the SFSR. The fish that spawned had expended an estimated 95% of its initial somatic energy, and the fish that died before spawning expended 66% of its energy by the time of death. Both fish spent an estimated 75 days in freshwater. Observations from these two fish do not support a relationship between migration behavior, energy expenditure and spawning success. The fish that died before spawning was adipose-clipped indicating hatchery origin, while the fish that spawned lacked clips or markings and was likely of natural origin. The fish that died before spawning arrived at the spawning stream much earlier than the fish that spawned, and was exposed to abnormally warm temperatures during that period.

There was one male that died before spawning that had energy estimates from the start of migration and after death on the spawning grounds. This fish began migration earlier than males that spawned and expired on 30 July 2003, following 62.6 days in freshwater. At death, the male that had not spawned had expended 58% of its initial energy reserves. It is possible that the early run-timing and early arrival at the spawning stream in 2003 was disadvantageous for this individual.

In summary, more data are needed to address the relationship between migration behavior, energy use, and spawning success. A relationship was found between slower migration speed and lower energy content at arrival at the spawning grounds in 2002, but there were many confounding factors and a cause and effect relationship is uncertain. Energy limitation may be a factor in decreased reproductive success in situations where migration is delayed, especially following periods of decreased ocean productivity, and physiologically stressful situations such as extreme river temperatures. In contrast, the hydrosystem may be causing selection against early migrating spring-summer Chinook salmon (those that are able to avoid fallback and other sources of delay during migration), because these fish may arrive at the spawning grounds earlier than is advantageous in years of high mid-summer temperatures.

*Management Implications:*

The energetic costs of migration and spawning for salmonids returning to the interior Columbia Basin is high. Results suggest a threshold level of initial energetic reserves exists which individuals must possess to successfully migrate and spawn. These data and other lines of evidence suggest that the level of this threshold will be affected by in-river migration conditions in the hydrosystem and spawning tributaries, migration behavior, and on conditions in spawning tributaries during pre-spawn holding and spawning. For instance, Naughton et al. (2005) observed increased *en route* mortality in Columbia River sockeye at the onset of stressful temperatures and Caudill et al. (in prep) observed that slow migrants in the hydrosystem were less likely to successfully reach spawning tributaries. Importantly, the proportion of the returning adult population with energetic reserves above the energetic threshold probably varies among years as ocean

productivity and subsequent salmon growth fluctuate. For example, initial energetic levels in Fraser River sockeye salmon can vary by ~15% between decades with differing ocean regimes and ~9% between years with different ocean conditions (Crossin et al. 2004).

Consequently, we suggest that successful management of adults in the hydrosystem and on the spawning grounds will require reliable information on the true level of the energetic threshold, the mean condition of stocks as they enter the river and the relative costs of migrating through the hydrosystem in years with different environmental and operational conditions. In particular, flow and temperature conditions will probably affect the costs of migration, with high costs incurred at high flow because of higher current velocities encountered, and at higher temperatures because of the direct effects of temperature on metabolic activity and indirect costs caused by slowed migration as adults seek cold-water refuges (e.g., Goniea et al. *in press*; High et al. *in press*). Providing adequate passage conditions in terms of energetic costs will become increasingly important if predictions of regional climate warming hold because metabolic costs during migration through the hydrosystem and during pre-spawn holding will rise as water temperatures warm (e.g., Naughton et al. 2005). Exposure to warm water in spawning tributaries has been implicated with increases in pre-spawn mortality (e.g., Figure 3.4).

Monitoring of initial lipid content of returning fish using non-lethal methods will provide a rapid indication of initial energetic state and the potential for interior stocks to successfully spawn. In years that fish return with low energetic reserves, efforts should be made to maximize escapement by adjusting fisheries and hydrosystem operations. Ongoing studies attempting to determine if initial energetic condition is related to migration success will improve estimates of the minimum energetic threshold for interior stocks and how the level of this threshold varies as freshwater conditions change.

## References


Bjornn, T.C., J.P. Hunt, K.R. Tolotti, P.J. Keniry, and R.R. Ringe. 1994. Migration of Chinook salmon past dams and through reservoirs in the lower Snake River and into tributaries--1992. U.S. Army Corps of Engineers, Walla Walla, Washington.

Boggs, C.T., M.L. Keefer, C.A. Peery, T.C. Bjornn, and L.C. Stuehrenberg. 2004. Fallback, Reascension, and Adjusted Fishway Escapement Estimates for Adult Chinook Salmon and Steelhead at Columbia and Snake River Dams. Transactions of the American Fisheries Society 133:932-949.

Brett, J.R. 1995. Energetics. Pages 1-68 in C. Groot, L. Margolis, and W.C. Clarke, editors. Physiological Ecology of Pacific Salmon. University of British Columbia Press, Vancouver.

Geist, D.R., Abernethy, C.S., and S.L. Blanton. 2000. The use of electromyogram telemetry to estimate energy expenditure of adult fall Chinook salmon. Transactions of the American Fisheries Society 129:126-135.

Goniea, T.M., C.A. Peery, D.H. Bennett, M.L. Keefer, L.C. Stuehrenberg, and T.C. Bjornn. *In press*. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society.

High, B., C.A. Peery, and D.H. Bennett. *In press*. Temporary staging of Columbia River summer steelhead in cool-water areas and its affect on migration rates. Transactions of the American Fisheries Society.

Hinch, S.G. and P.S. Rand. 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

Keefer, M.L., C.A Peery, T.C. Bjornn, M.A. Jepson, and L.C. Stuehrenberg 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. Transactions of the American Fisheries Society 133:1413-1439.

Magie, C.D. and M.G. Mesa. 2004. Evaluation of energy expenditure in adult spring Chinook salmon migrating upstream in the Columbia River basin: an assessment based on sequential proximate analysis. Final Research Report. U.S. Geological Survey, Columbia River Research Laboratory. Cook, Washington.

McCutcheon, C.S., E.F. Prentice, and D.L. Park. 1994. Passive monitoring of migrating adult steelhead with PIT-tags. North American Journal of Fisheries Management 14:220-223.

Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn and L. C. Struehrenberg (2005). Late season mortality during migration of radio-tagged adult sockeye salmon (*Onchorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 62: 30-47.

Ott, R. L and M. Longnecker. 2001. An introduction to statistical methods and data analysis: 5th edition. Duxbury, California.1152 p.

Peake, S. 1998. Sodium bicarbonate and clove oil as potential anesthetics for nonsalmonid fishes. North American Journal of Fisheries Management 19:919-924.

Rand, P.S. and S.G. Hinch. 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.

Webb, P.W. 1995. Locomotion. Pages 71-99 in C. Groot, L. Margolis, and W.C. Clarke, editors. Physiological Ecology of Pacific Salmon. University of British Columbia Press, Vancouver.

Appendix Table 1. Regressions of energy content (E) on fork length (Lf).

| Dependent Variable | Sex | Location | $R^2$ | df | P | Equation |
|---|---|---|---|---|---|---|
| Total Energy | Female | Bonneville | 0.86 | 31 | <0.0001 | E = -131618 + 2454.2(Lf) |
| | | South Fork Trap | 0.38 | 24 | <0.0001 | E = -49036 + 1058.9(Lf) |
| | | Pre-spawn | 0.75 | 15 | <0.0001 | E = -46887 + 857.5(Lf) |
| | | Post -Spawn | 0.07 | 17 | 0.74 | E = 5611.24 + 49.82(Lf) |
| | Male | Bonneville | 0.76 | 23 | <0.0001 | E = -133144 + 2447.57(Lf) |
| | | South Fork Trap | 0.68 | 26 | <0.0001 | E = -75292 + 1385.54(Lf) |
| | | Pre-spawn | 0.84 | 5 | 0.01 | E = -16849 + 426.98(Lf) |
| | | Post -Spawn | 0.34 | 8 | 0.10 | E = -9989.00 + 329.34(Lf) |
| Somatic Energy | Female | Bonneville | 0.86 | 31 | <0.0001 | E = -131668 + 2425.19(Lf) |
| | | South Fork Trap | 0.51 | 24 | 0.001 | E = -34905 + 811.90(Lf) |
| | | Pre-spawn | 0.60 | 15 | <0.0005 | E = -35856 + 611.50(Lf) |
| | | Post -Spawn | 0.12 | 17 | 0.15 | E = -1784.17 + 124.58(Lf) |
| | Male | Bonneville | 0.76 | 23 | <0.0001 | E = -133923 + 2451.16(Lf) |
| | | South Fork Trap | 0.67 | 26 | <0.0001 | E = -73822 + 1354.14(Lf) |
| | | Pre-spawn | 0.82 | 5 | 0.01 | E = -15874 + 402.75(Lf) |
| | | Post -Spawn | 0.38 | 8 | 0.08 | E = -10942 + 333.78(Lf) |