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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: 2002–2007.

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

And
Bonneville Power Administration
Portland, Oregon
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USGS science for a changing world

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Preface

Adult Chinook salmon, *Oncorhynchus tshawytscha*, must pass eight hydroelectric dams and reservoirs and migrate more than 1000 river kilometers to reach spawning grounds in the South Fork Salmon River in central Idaho. Behavior during migration, energy depletion, and ultimately reproductive success may be affected by river conditions (e.g. temperature and flow) and dam operations (e.g. spill) within the migration corridor. In this study we examined the energy use of migrating adult Chinook salmon through the Columbia and Snake Rivers in order to investigate the relationships between initial fish condition, migration experience, and river conditions, and eventual migration and spawning success. As part of this research, we also tested non-lethal methods to estimate adult salmon energy condition.

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Chapter 1: Assessment of non-lethal energy estimates for Chinook salmon returning to the South Fork of the Salmon River, Idaho

Abstract

The accuracy and feasibility of multiple methods for determining energy condition in Chinook salmon were determined. These results were compared to proximate analysis of fish tissues, which represented the true value of energy content for these fish. Although all estimate methods produced results that were significantly correlated with proximate analysis, bioelectrical impedance and condition factor were less accurate than morphometrics and the Distell Fatmeter. Bioelectrical impedance did not seem to be as accurate in salmon as with other fish species, and is generally considered of better use for mammals. Although condition factor was included as a factor in many models to predict energy condition, its lipid estimation qualities by itself are suboptimal. From a series of 12 morphometric measures, breadth at anus, hump height and mideye to hyperal length together provided the best method for determining lipid content. These three measures were used in subsequent years. Although morphometrics proved to be the most accurate method for estimating energy condition, the Distell Fatmeter was also accurate, and had the added benefit of a reduced handling time. Either of these two methods are recommended to be used in further research when a quick and accurate measure of lipid content is needed.

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) depend on finite energy reserves when entering freshwater because they do not replace energy stores by feeding. This limited supply of energy is utilized for migration, development of gametes and secondary sexual characteristics (males) and spawning behavior (Brett 1995; Pinson 2005). Habitat alterations can increase the demand on energy reserves in several ways. These include increased temperature, which raises metabolic rates, installation of obstructions such as dams, which may increase energy consumption in passage, or changes in flow, which affect swimming costs. All of these alterations can be observed in impounded systems in the Pacific Northwest, and particularly in the Columbia River watershed where the installation of the mainstem dams began with Bonneville Dam in 1933 (Raymond 1988; Dauble and Mueller 2000; Peery et al. 2003).

There is concern that overcoming the potential effects of these anthropogenic changes on energy reserves of salmon may be at the expense of successful spawning. It is currently unclear whether salmonid energy stores are enough to facilitate successful spawning at the population level given changing migration factors and year-to-year differences in fish condition. Before one can understand how energy use plays a role in either migration or spawning success, however, non-lethal and non-invasive methods for the estimation of individual energy consumption are needed.

Most studies on anadromous salmonid energy condition have focused on juveniles (e.g., Sutton et al 2000; Rikardsen and Johansen 2003), but the importance of exploring energy conditions for adults has been the subject of several recent studies (e.g., Crossin and Hinch 2005; MacNutt et al. 2006; Young et al. 2006). Interest is especially high for salmon with long distance migrations, which potentially exhaust energy reserves during spawning migrations and completion.

A number of non-lethal lipid estimation techniques have been explored in the past, and the goal of this project was to weigh the feasibility of each method for research on salmonids in the Columbia River. Four different methods were analyzed, including: bioelectrical impedance analysis (BIA), morphometrics, the Distell Fatmeter, and Fulton's condition factor. Analysis of the efficiency and effectiveness of each estimation techniques was undertaken to minimize impacts on endangered or threatened stocks during future research.

BIA has been successfully used to determine lipid contents through the inverse relationship between lipids and body water content. It has been used in humans, 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 in 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.

Body morphometrics have also been used to evaluate lipid levels in fish. This technique uses various combinations of body morphology measures and multiple regression models to estimate total body lipid levels. It has been shown that morphometric models can provide accurate lipid estimates in salmonids (e.g., Adams et al 1995; Rikardsen and Johansen 2003), although stock-specific models would be useful and more accurate for most individual populations.

New technologies have also been used to estimate energy content in fish. Originally designed for the commercial fish companies, the Distell Fatmeter was developed to measure lipid content in fillets. The device uses low-energy microwaves to determine water content in muscle tissue. Its accuracy in estimating whole body lipid levels on live

fish has been tested in sockeye salmon (*O. nerka*) with promising results (e.g., Cooke et al. 2005; Crossin and Hinch 2005).

Condition factor (K) is a simple relationship between fish weight and length that has been a staple in fisheries research. The index is used to compare fishes' condition under the assumption that heavier fish of the same length have a higher overall condition. Although this method has been used for many years relatively few researchers have attempted to compare total body lipid levels to the condition factor, and the results of previous studies have indicated relatively little association (e.g., Peters et al 2003).

Our overall study objective was to develop a predictive model of adult Chinook salmon energy composition and to examine the effectiveness and ease of use in the field of these non-lethal energy estimation techniques. 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 for salmonids. This should lead to a better understanding of Pacific salmon physiology, migration behavior, and spawning ecology in the Columbia–Snake River system.

Methods

Collection

The Chinook salmon population used in this study migrates to the South Fork of the Salmon River (SFSR), Idaho. This migration covers > 1100 kilometers from the mouth of the Columbia River and a total elevation gain of approximately 1890 meters. Along the migration corridor, this population must pass eight dams and reservoirs (four on the Columbia River and four on the Lower Snake Rivers) in the Federal Columbia River Power System (Hydrosystem). Impoundments cover slightly more than half of the migration corridor beginning at Bonneville dam (river kilometer 235) and ending at Lower Granite Dam (rkm 695). The remainder of the migration (roughly 450 km) occurs in unimpounded sections of the Snake, Salmon, and SFS rivers (Figure 1.1). The headwaters of the SFSR are located approximately 75 kilometers east of Cascade, Idaho. The river flows north from its origin for approximately 200 km until it enters the main stem of the Salmon River at Mackay Bar. In the upper SFSR, substrate is dominated by gravel, cobble and boulders while the lower river is dominated by smaller gravel and sand. Much of the potential spawning habitat present in the SFSR is in the upper third of the river, primarily from Poverty Flats upstream to Stolle Meadows.

Chinook salmon originating from the SFSR were targeted for sampling as they ascended the adult ladder adjacent to the Washington shore at Bonneville Dam in May and June of 2002–2007. Hatchery Chinook salmon (denoted by adipose fin clips) were collected during the peak of the run of McCall Hatchery fish (identified by PIT-tag

detections). 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, salmon carcasses were collected from the spawning grounds in August. All fish sampled at the start of freshwater migration (i.e., at Bonneville Dam) were of hatchery origin.

Twenty thousand juvenile salmon were PIT-tagged specifically for this study and this number was augmented by other groups of PIT-tagged fish to increase the number of potential returning adults in the sample. Returning PIT-tagged adult salmon from these cohorts were sampled at the Adult Fish Facility (AFF) located adjacent to the Washington shore fish ladder at Bonneville Dam in the summers from 2002–2007. The fish were diverted from the ladder by a set of picket leads and redirected up a false ladder into a collection pool. The pool had two false weirs operated by AFF personnel. Fish passed through the weirs, down a flume and returned to the ladder, unless manually diverted. The lists of PIT-tag codes for the sample groups were entered into a computer linked to the PIT-tag detectors in the AFF. Detectors were programmed to trigger an alarm when a desired tag code was detected so the fish could be diverted to the anesthetic and sampling area.

Once anesthetized, fish were weighed and morphological measures were taken. Fish were then tagged by inserting a radio transmitter into the stomach through the mouth. Two tag sizes were used; both were LOTEK® radio tags. Attached to the antenna of the radio tags were temperature recorders. Additional external temperature tags were sutured to the base of the dorsal fins of subsample of the fish in 2005 to compare external and internal temperature exposures. Upon completion of the radio tagging, fish were allowed to recover in a pen before being returned to the fish ladder to continue upstream migration.

Proximate Analysis

In all years, some fish were lethally sampled to determine appropriate benchmark averages of lipid, protein, water, and ash amounts in the fishes' bodies. Processing fish entailed partitioning the fish carcass into 4 tissues; muscle, skin, viscera and gonads. Each of the tissues was removed as entirely as possible from a carcass, and weighed to the nearest gram to establish the total weight of each tissue type. Then each tissue was homogenized independently in a Cuisinart® food processor and a 50 gram subsample of the homogenate was taken. The samples were frozen and later transported to Washington State University where they underwent proximate analysis to determine the levels of lipid, protein, ash and water in the each of the tissues.

Proximate analysis was conducted on all tissue samples taken from the fish at Bonneville Dam and from the South Fork of the Salmon River. Lipid amounts were determined by passing volatized ether through a sample of tissue which removes all ether soluble products. Lipid is soluble in ether, allowing the removal from the sample. The lipid is then extracted from the ether, dried and weighed to determine the exact weight in the tissue sample (AOAC 1965).

Ash weights are determined by igniting the samples at 500–600 ºC to burn off all organic matter and the resulting remnants are considered ash. The samples are placed in crucibles in an oven and left over night at these temperatures, and then cooled and weighed the next day to determine exact ash weights (AOAC 1965). The percent of moisture in the samples was obtained by weighing a sample, placing it in a freeze drier at -40 ºC for 24 to 36 hours and weighing the same sample after drying. The total weight loss was recorded and percent moisture was determined. Protein content was determined by subtraction (% protein =100 - % water - % fat - % ash), as in other studies on salmon energetics (e.g., Berg et al. 1998; Hendry and Berg 1999; Hendry et al. 2000).

After lipid weights were determined for each 50 gram subsample, the total lipid amount per tissue was calculated and this was used to determine total body lipid levels. The percentage of lipid in each sample was used to determine the total weight in grams of lipid in each tissue. All the lipid weights for each of the 4 tissues were combined together and divided by the total weight of the fish to determine a whole body percent lipid.

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 ($kJ \bullet g^{-1}$) of each tissue type was estimated using energy equivalents for fat and protein of 36.4 $kJ \bullet g^{-1}$ (8.66 $kcal \bullet g^{-1}$) and 20.1 $kJ \bullet g^{-1}$ (4.9 $kcal\ g^{-1}$; Brett 1995), respectively, and multiplying by the appropriate proportions of lipid and protein in the tissue. Mass-specific energy of the somatic tissues (muscle, skin, and viscera) was multiplied by the mass of each tissue and summed to find total somatic energy (kJ). Total body energy (kJ) was estimated by the same procedure except that gonad tissue was also included.

Non-lethal Estimates of Energy Condition

In 2004-2007, several non-lethal techniques were used to estimate the total body lipid content of fish in order to gain an understanding of the energy condition of fish at the beginning of their migration. The three methods used in these years were the Distell Fish Fatmeter, a series of morphometric measures, and Fulton's Condition Factor. These methods were compared in this study and assessed for accuracy, practicality, and effectiveness. Fish were collected at Bonneville Dam, a representative starting point for in-river migration, and from the SFSR at the end of the migration. Fish processed at Bonneville Dam were obtained from a tribal fishery operating in the lower Columbia River in 2005 and were provided by the United States Fish and Wildlife hatchery on the Little White Salmon River in Washington approximately 25 miles upstream from Bonneville Dam in 2006. Fish processed on the SFSR were collected as pre- or post-spawning mortalities from the river. All fish used in this study objective had lipid levels estimated by all three non-lethal techniques and the results of each method were compared to those of individual fishes' proximate analysis results. Thus each method could be compared to the appropriate benchmark results of the proximate analysis.

Bioelectrical Impedance Analysis

In 2002 and 2003, 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 applyies an 800 microamp current (50 KHz) through two electrodes and measures 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 techniques. 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 as: vol ($cm^2 \bullet ohms^{-1}$) = $L^2 \bullet Rs^{-1}$, 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 considered an accurate estimator of total body water content in mammals (Kushner and Schoeller 1986; Bowen et al. 1999).

Morphometrics

In 2002, twelve linear measurements of morphology (+/- 0.1 mm) 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 breadth at the operculum, dorsal fin, anus, and caudal peduncle (Simpson et al 1992; Adams et al 1995; Rikardsen and Johansen 2003). 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 $K = (W \bullet L^{-3}) \bullet 100{,}000$; 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' (i.e., most parsimonious) 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 breadth 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 σ^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 and 2 provide substantially similar descriptions of the data as the model with the lowest AIC, and that models with AIC values greater than 4 over the lowest AIC have considerably less empirical support as the 'best' model**.** Based on the results in 2002, only hump height, breadth at anus, and mid-eye to hypural length along with weight and fork length were collected in 2003–2007 as these variables provided an accurate estimation of energy condition.

NOTE: Due to a clerical error during the original data collection which was transcribed to later years, the breadth at anus measurement was mistakenly documented as depth at anus and vice versa in previous reports of research on the South Fork of the Salmon River. The values listed in this report are correctly identified and reported, and fall within the typically reported range of values for breadths and depths of Chinook salmon.

Distell Fatmeter

Distell Fish Fatmeter model 692 was used to estimate energy condition in 2005-2007. This device is most commonly used in the commercial sector to grade fish quality without having to destructively sample from the group. The meter employs a low energy microwave oscillator (frequency 2 GHz ± 2,000 MHz, power 2 mW) which determines the percentage of water in the fish tissues (Distell Inc. West Lothian, Scotland 2007). Due to the inverse relationship between the water content of a fishes' tissue and the amount of lipid in the tissue (Brett 1995), the meter then uses the estimated water content to derive a percentage of lipid in the fish. The meter is calibrated for species-specific measurements and the Chinook calibration was used for this study. The meter is calibrated to determine the lipid percentages in two trimmed fillets (muscle tissue) but the majority of studies on the energy condition of migrating salmonids utilize total body lipid levels (e.g., Crossin and Hinch 2005) because of lipid deposition in the body cavity and subcutaneous tissues. It was shown by Pinson (2005), however, that the majority of lipid reserves occur in the muscle tissue for salmon at the beginning of their migrations. Thus it was hypothesized that for estimating lipid condition at the outset of the migration, the Fatmeter was an applicable method without a significant need for correction factors. The

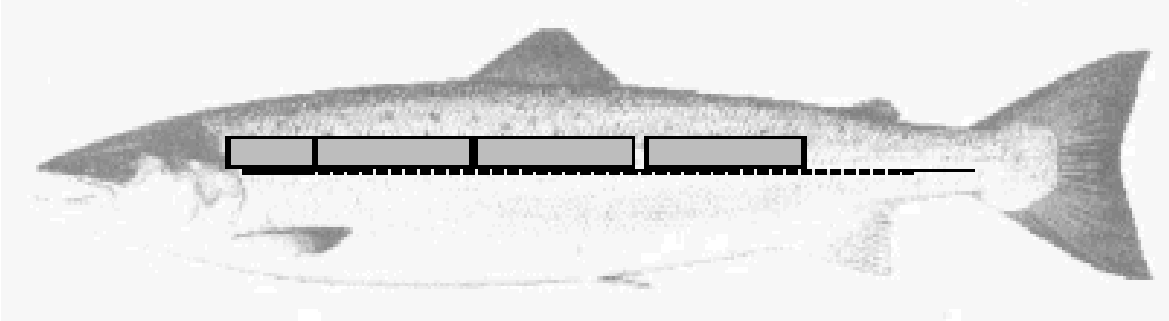

Figure 1.1. Representation of locations where readings were taken with the Fish Fatmeter.

estimates obtained with this method were compared to those from other methods and compared to the proximate analysis values.

To obtain an estimation the meter was allowed to warm up prior to use (as recommended by Distell), placed on the fish in the locations indicated in Figure 1.1. Four readings were taken on one side of the fish. Total time to take all readings rarely exceeded 10 seconds. The meter automatically calculated an average percent lipid from the four readings and this average reading was the reported estimated lipid level.

Condition Factor

Fulton's condition factor is method of estimating the overall condition of a fish by using a simple length-weight linear relationship. The Fulton's condition factor (K) was determined by a simple length weight relationship that is expressed in the model $K = (\text{Weight} \bullet \text{Length}^{-3}) \bullet 100{,}000$. Higher numbers indicate a higher "condition". Fulton created the ratio in 1904, and it has become a staple in fisheries research. The method produces a simple linear relationship between length and weight, and when used to estimate fish condition, it uses a standardized slope of 3 for the regression line (Cone 1989). This means that variations in either weight or length can impact the slope of the line used to evaluate the relationship. Some previous research has shown little relationship between the condition factor and total body lipid levels in adult Chinook salmon in the Great Lakes (Peters et al 2003). However, the body of research on adult salmon is relatively small.

Statistical Analysis

Multivariate analysis of variance (MANOVA) 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 with the model: proximate composition = migration stage. Stages were defined as: (1) at collection near Bonneville Dam; (2) at arrival at the SFSR weir; (3) pre-spawn mortality in the SFSR; and (4) after spawning (i.e., post-spawn

mortality). All four stages were evaluated in 2002–2003, while only the initial (Bonneville Dam) and final stages were evaluated in 2004–2006. 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, with males and females analyzed 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 ($P < 0.05$) was detected, least squared mean estimations and Fisher's Least Significance Difference (LSD) tests ($P < 0.05$) were used to evaluate 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 among 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×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 evaluate differences between means.

Absolute values of somatic and total energy content could not be compared among migration stages using ANCOVA because migration stage×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 versus fork length regressions at all four stages of migration (Appendix Table A.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, as described by Jonsson et al. (1997) and 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 (kJ). 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 (e.g., Crossin et al. 2004a).

Non-lethal methods for estimating energy condition were compared to the proximate analysis values through linear regression, and the morphometric model and the Fatmeter results were compared using log-linear and log-log regression. Due to the nature of the results derived from the Condition Factor model, log transformation was not possible. The results of the Fatmeter and the morphometric model were also compared to the proximate analysis values using a simple one-way ANOVA. Significance was

determined to the $\alpha = 0.01$ level. In addition to the ANOVA's, a Randomized Complete Block analysis was used to determine whether the results from each method differed significantly. Fish were used as the blocking variables and the lipid estimation methods were used as the treatment terms. Significance was determined at the $\alpha = 0.01$ level.

To evaluate the effect of various factors on spawning success (yes, no), a multiple logistic regression was used. The full model contained fish passage times, degree days, fallback events, initial fish condition (Fulton's Condition Factor K), and initial lipid levels. Multi-model selection with Akaike Information Criteria (AIC) was used to identify the most parsimonious model. Spawning success was the dependent variable with all other variables acting as independent terms in the model. Each independent variable was analyzed separately with a one-way ANOVA to determine if there were statistical differences between spawning and non-spawning groups.

Results

Proximate Analysis

2002

In 2002, 57 Chinook salmon were sampled near Bonneville Dam from local tribal fisheries, and 140 were sampled in the SFSR, either in-river or at the Idaho Fish and Game collection weir. In 2003, 10 fish were sampled near Bonneville Dam and 31 were sampled in the SFSR. In 2004, 110 fish were sampled near Bonneville Dam. In 2005, 12 fish were sampled near Bonneville Dam and 11 were sampled in the SFSR. In 2006, 10 fish were sampled near Bonneville Dam and 5 were sampled in the SFSR. No fish were sampled for proximate analysis in 2007.

Fork lengths did not differ between migration stages for either females or males in 2002 (Table 1.1); however, mean body mass (weight) decreased significantly for both male and female fish as they moved upstream. Average body mass for the population decreased by 20% for both males and females during migration to the SFSR. Comparing successful spawners, males weighed 11% less and females weighed 45% less than fish near the start of migration.

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, $P < 0.05$)

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 $P < 0.0001$). 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 males and females, except that differences among migration stages in lipid and moisture content of the viscera were smaller for females than for male fish.

Percent Lipid.— Lipid content (as a percentage of wet mass) of muscle, skin, viscera and gonads differed ($P < 0.0001$ for all ANOVAs) among migration stages for both males and females (Table 1.2). 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). In contrast, lipid content of the gonads 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 sexes. Remnant gonad tissue in post-spawning females was significantly reduced in lipid content from that at arrival on the spawning grounds (2.8% post-spawning vs. 8.0% upon arrival), 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 lipid content decreased by 4.2–15.1% from levels upon arrival at the spawning grounds, but lipid content of the viscera and gonads remained unchanged.

Females that died before spawning had about 2.3% more muscle and skin lipid on average but similar visceral lipid levels compared to females that died after spawning. Males had similar lipid content of the muscle, skin, and viscera regardless of whether they had spawned or not. Remnant gonad tissue of males and females after spawning was significantly 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 1.2). During migration to the SFSR, the protein content of the

muscle, skin, and gonads increased for both sexes, while 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 sexes. Remnant gonadal tissue in post-spawning males and females was significantly reduced in protein content. In fish (both sexes) 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 fish that died after spawning than in those that died before spawning (both sexes).

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

Table 1.2. Mean (SD) lipid, protein, and moisture (percent wet mass) for female and male Chinook salmon in 2002. (H = adipose clipped, hatchery origin; W = non-adipose clipped, wild origin)

Location	Origin	Constituent	Females				Males			
			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	1.7(1.3)	14.4(4.4)	76.4(21.4)	10	2.9(2.6)	16.3(1.6)	79.9(3.8)
		Skin		2.6(2.5)	23.4(6.1)	66.7(18.0)		5.6(3.8)	26.0(3.4)	67.5(3.8)
		Viscera		1.0(0.4)	15.8(4.6)	75.2(21.3)		1.0(0.3)	17.1(1.7)	80.9(1.7)
		Gonad		4.6(2.4)	23.0(11.6)	64.4(21.8)		0.9(0.3)	13.1(5.2)	83.7(6.6)

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 1.3), and length-controlled skin lipid mass differed for females. Comparisons of skin lipid among migration stages could not be made for males due to heterogeneity of slopes. Both sexes 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 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, but skin lipid differed 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 both sexes). Lipid contents of muscle, viscera, and gonads did not differ significantly between fish that spawned and those that died prior to spawning (both sexes). Females that spawned had significantly lower amounts of lipid in the skin than females that died prior to spawning (Table 1.3). Muscle, skin, and viscera lipid mass did not differ significantly for wild females that died before or after spawning (Table 1.4). 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 1.3). 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. Male muscle protein did not differ significantly between arrival at the spawning stream and after spawning. 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 both sexes. Protein of the muscle and viscera tissue did not significantly differ between arrival at the spawning stream and death before spawning for either sex. Gamete protein decreased significantly between arrival at the SFSR and death prior to spawning 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 1.4). Comparisons for protein content of the tissues could not be made for wild males due to heterogeneity of slopes.

Table 1.3. Comparison (by ANCOVA) of mean length-controlled lipid and protein masses (g) for tissues of hatchery adult Chinook salmon sampled at four stages of migration in 2002. SFSR = South Fork Salmon River.

		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×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)

Table 1.4. 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) in 2002.

		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).

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×fork length interactions were significant for both sexes ($P < 0.05$; 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, but not at death after spawning for both males and females (Appendix Table A.1). Somatic energy content was calculated for fish of mean fork length using energy vs. fork length regressions at all four stages of migration (Table 1.5). 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 1.5).

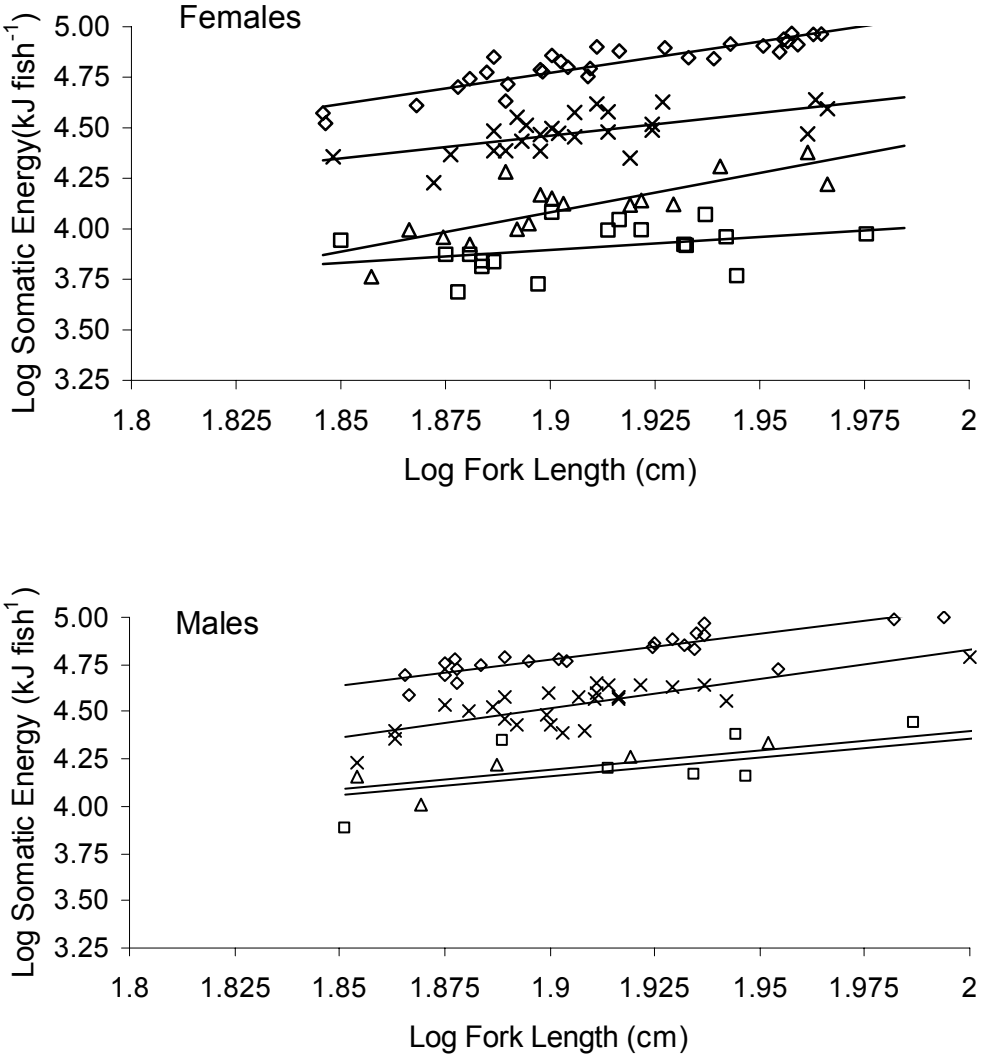

Figure 1.2. Regressions of log somatic energy and log fork length of females (top) and males (bottom) at four stages of migration in 2002: the nominal start of migration = diamonds, arrival at the spawning stream = x, pre-spawned death = triangles, post-spawned death = squares.

Energetic costs (as a percentage of initial somatic energy stores) during migration to the SFSR were dependent upon fork length for both sexes, but were higher for longer females and shorter males (Figure 1.3). Females used 20–78 kJ•km^{-1}, depending on fork length, to migrate 920 river kilometers from the nominal start of migration at Bonneville Dam to the SFSR collection weir. Males used 22–48 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, respectively.

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 1.5). At death after spawning, 82 cm females had about half as much somatic energy remaining as males of a similar fork length.

Table 1.5. Total somatic and gonad energy (kJ), with percentages of initial somatic energy used as a source for metabolism (standard and active combined) 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					
Somatic	70	40048	21739 (42,4)	7374 (71,10)	6692 (73,10)
Gonad		1979	3439	6051	3777
Somatic	80	60477	29399 (46,5)	12412 (70,10)	7945 (77,10)
Gonad		2386	5616	8640	3653
Somatic	82	65267	31078 (46,6)	13666 (68,11)	8201 (76,11)
Gonad		2455	6131	9212	3620
Somatic	90	86993	38316 (49,7)	19648 (67,11)	9243 (78,11)
Gonad		2674	8468	11658	3466
Somatic	100	120429	48561 (52,8)	29632 (65,10)	10582 (81,10)
Gonad		2771	12065	15015	3222
Males					
Somatic	70	42304	22039 (47,0.8)	12172 (70,0.8)	11118 (73,0.8)
Gonad		466	803	768	480
Somatic	80	60914	33589 (44,1)	16897 (73,1)	14521 (75,1)
Gonad		503	1054	971	505
Somatic	82.5	66252	37014 (43,1)	16943 (73,1)	15442 (75,1)
Gonad		505	1118	1025	507
Somatic	90	84018	48709 (41,1)	21380 (75,1)	18377 (77,1)
Gonad		490	1312	1194	504
Somatic	100	112021	67920 (38,1)	26391 (76,1)	22682 (79,1)
Gonad		411	1561	1436	474

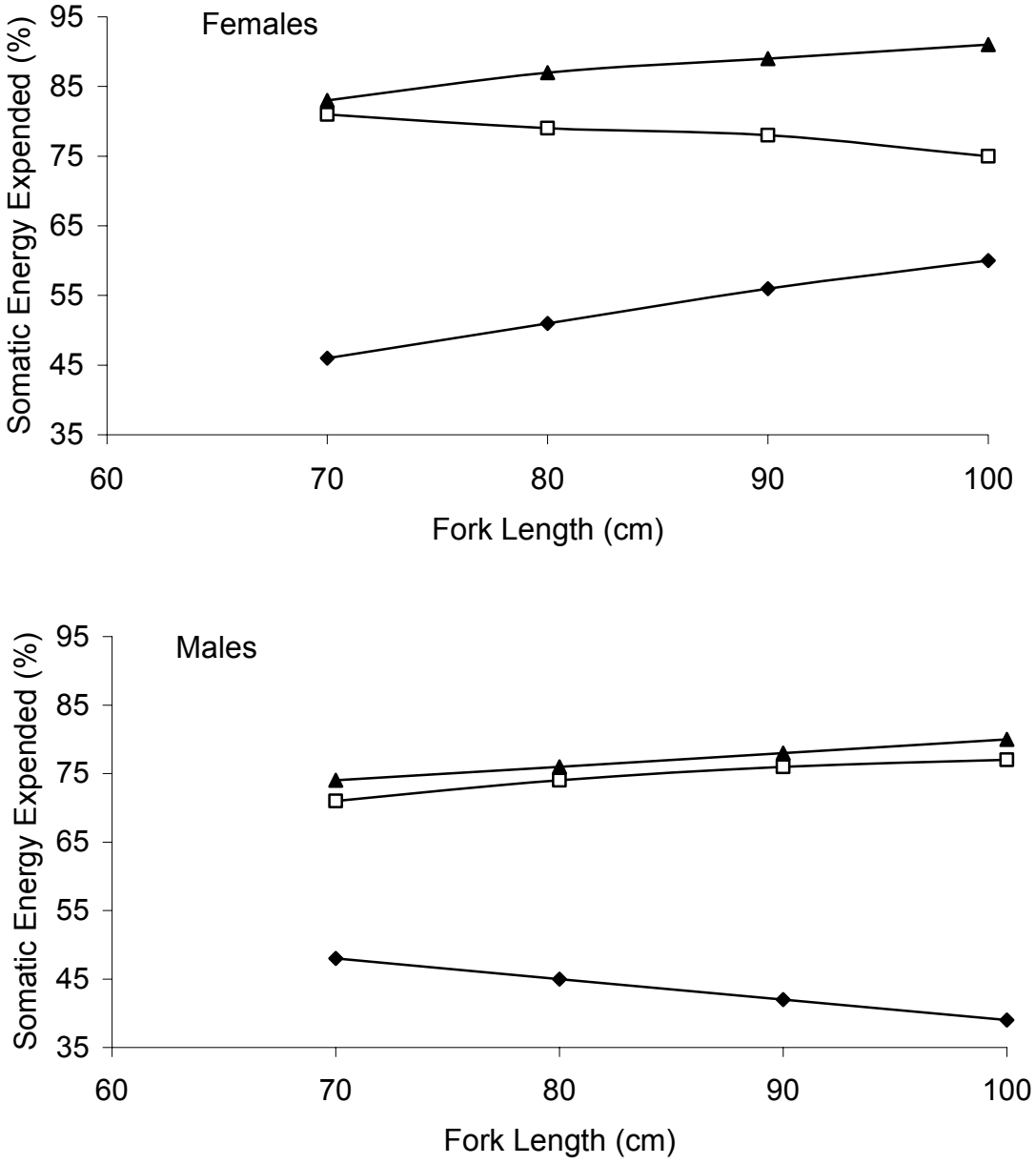

Figure 1.3. Percentage of somatic energy (from Bonneville Dam) used upon arrival at the SFSR (South Fork Trap, diamonds), death prior to spawning (squares), and death after spawning (triangles) in 2002 estimated for 70, 80,90 and 100 cm fish.

2003

Proportional Changes in Tissue Mass.— In 2003, 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 1.6). 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 1.6. Mean (SD) contribution (percent) of muscle, skin, viscera, and gonads to total body mass in 2003.

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 Weir	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 Weir	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)

2005

Proximate analysis was run in 2005 on test fish collected near Bonneville Dam and on fish recovered from the SFSR (Table 1.7). The percent of lipid dropped considerably in every tissue, which would be expected due to the expenditure of energy during migration. An increase in moisture content was also noted with a reduction of protein in all tissues except the skin.

Table 1.7. Mean (SD) lipid, protein, and moisture (percent wet mass) for Chinook salmon collected in 2005 at Bonneville Dam and the South Fork of the Salmon River.

Bonneville				
n = 12	% Moisture	% Ash	% Lipid	% Protein
Muscle	67.3(1.5)	1.5(0.5)	10.1(2.9)	21.0(2.7)
Gonad	71.2(13.2)	1.9(1.4)	4.4(4.3)	22.5(9.3)
Viscera	74.2(2.4)	1.7(0.8)	7.7(3.0)	16.5(2.0)
Skin	53.1(5.9)	1.1(0.2)	23.4(6.6)	22.4(3.7)

South Fork Salmon River				
n = 11	% Moisture	% Ash	% Lipid	% Protein
Muscle	83.5(3.6)	1.0(0.2)	1.0(1.4)	14.4(2.6)
Gonad	83.7(8.8)	1.7(1.2)	1.5(1.3)	13.2(7.2)
Viscera	83.1(2.2)	0.9(0.2)	1.2(0.4)	14.9(2.0)
Skin	72.8(3.8)	0.9(0.2)	1.4(1.3)	24.9(3.1)

2006

Proximate analysis was conducted again in 2006. Although sample sizes were smaller, the trends mirrored those seen in 2005 (Table 1.8). Lipid levels decreased significantly and moisture levels increased in all tissues. Again we saw a decrease in protein percentages in all tissues except for the skin. Lipid levels in gonads were higher in 2006 than in 2005, most likely due to the sexual maturity of fish that were chosen for sampling. As such, they may not be a representation of the overall run.

Table 1.8. Mean (SD) lipid, protein, and moisture (percent wet mass) for Chinook salmon collected in 2006 at Bonneville Dam and South Fork of the Salmon River.

Bonneville

n = 10	% Moisture	% Ash	% Lipid	% Protein
Muscle	68.7(2.7)	1.2(0.1)	8.8(2.3)	21.3(1.4)
Gonad	63.3(11.9)	1.9(0.4)	8.8(5.4)	26.0(6.7)
Viscera	78.3(1.5)	1.3(0.4)	2.3(0.8)	18.2(1.0)
Skin	57.9(3.9)	3.9(0.7)	22.6(4.9)	15.7(2.1)

South Fork Salmon River

n = 5	% Moisture	% Ash	% Lipid	% Protein
Muscle	83.2(3.1)	0.9(0.1)	0.9(0.8)	15.1(2.4)
Gonad	70.7(9.2)	3.8(3.4)	3.2(2.0)	22.3(7.4)
Viscera	82.7(3.1)	1.0(0.2)	1.1(0.5)	15.2(2.8)
Skin	74.9(3.0)	0.9(0.2)	1.3(0.5)	22.9(2.7)

Non-lethal Estimates of Energy Condition

Bioelectrical Impedance Analysis

2002

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 1.4 and 1.5). In single-variable regressions, resistance accounted for 23–31% of the variance in percent water values and 13–44% of the variance in water mass, while conductor volume accounted for 12–17% of the variance in percent water and 23–72% 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, respectively. Including conductor volume did not substantially improve model fit for estimating percentage water of the muscle, skin, or 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 40–82% of the variance.

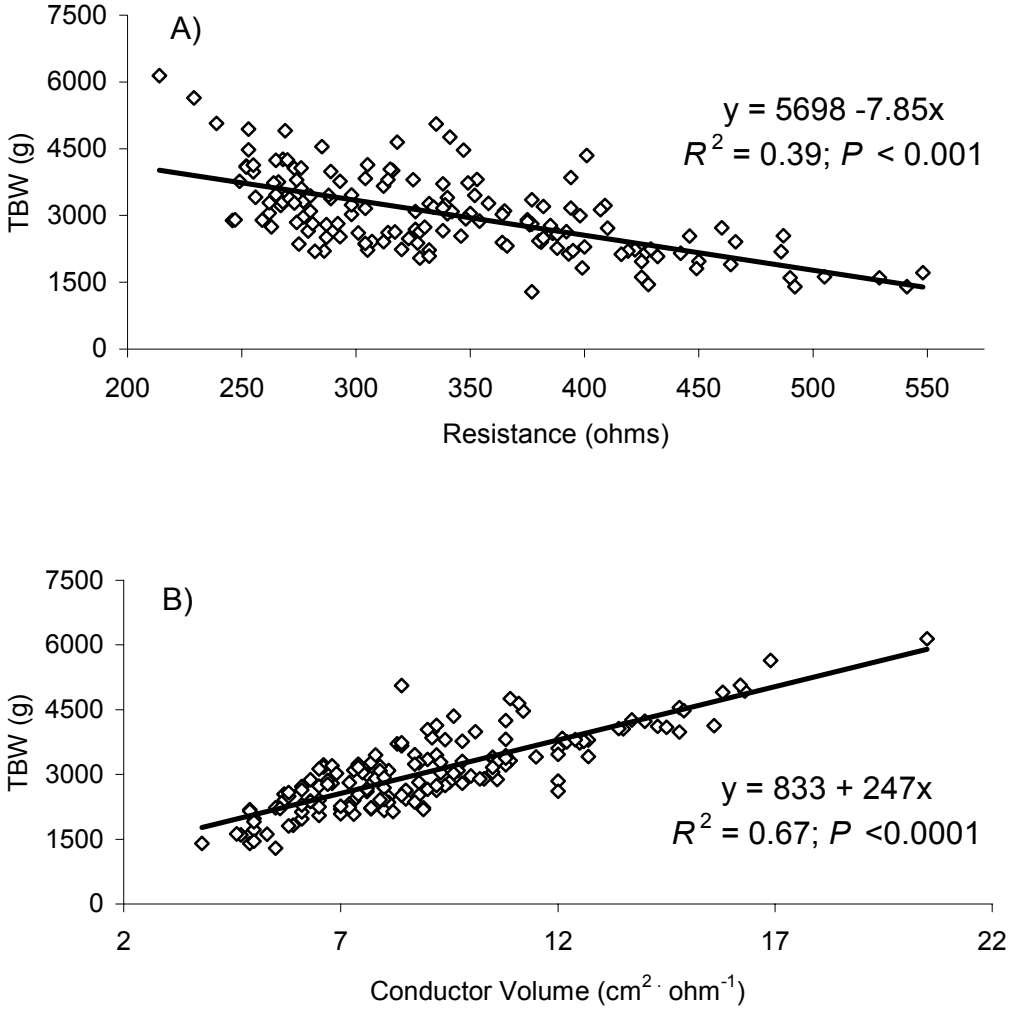

Figure 1.4. Linear regressions of: (A) total body water and resistance, and (B) total body water and conductor volume.

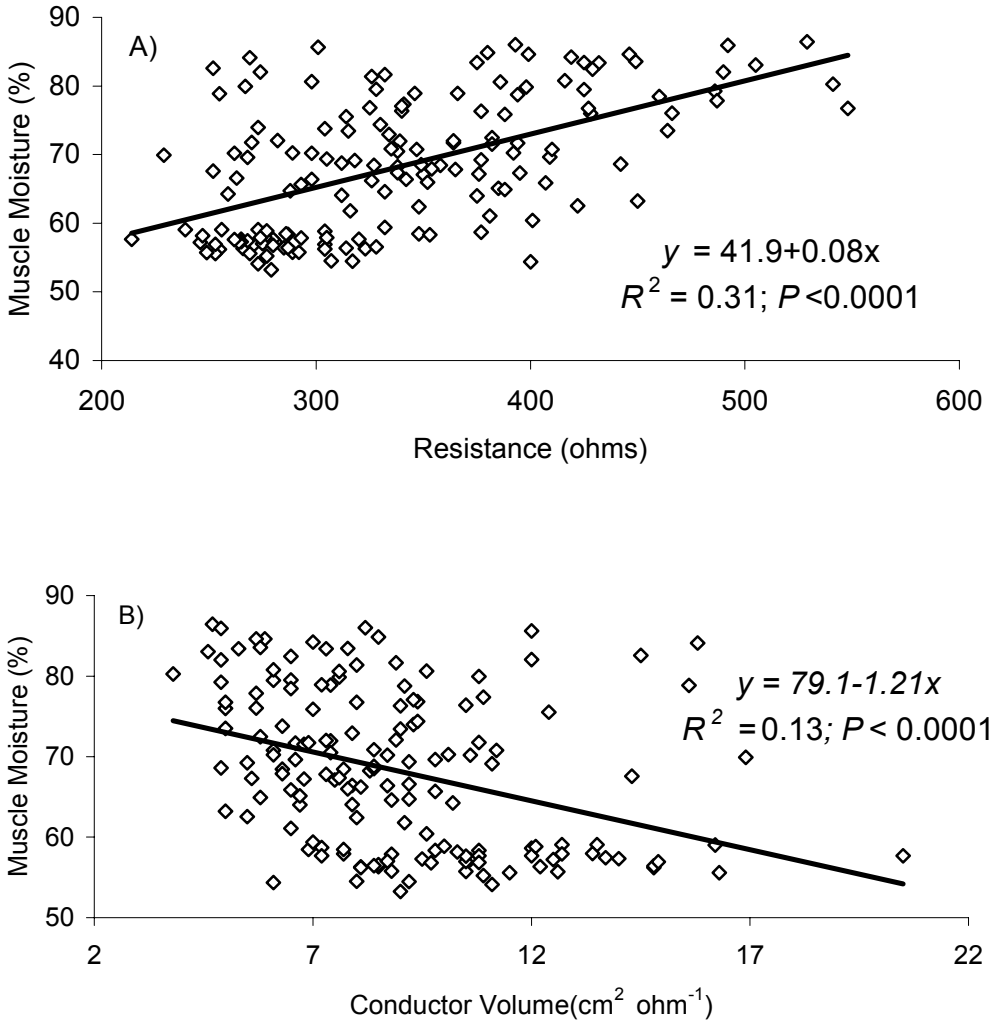

Figure 1.5. Linear regressions of: (A) percent moisture and resistance, and (B) percent moisture and conductor volume.

Morphometrics

2002

The twelve morphological measures taken were analyzed and used to create models to predict various lipid and energetic values for individual fish (Table 1.9). Percent muscle and skin lipid were best estimated by a model that included fork length, hump height and body breadth at anus (Table 1.10 and 1.11). 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 breadth, and hump height. Total body energy was best described by the variables fork length, body mass, and body breadth. Condition factor was not included as a predictor variable in any of the "best" models.

Table 1.9. Summary of the twelve morphological measures taken at Bonneville Dam in 2002. ME to Hyperal = Mid-eye to hyperal length, D_o = Depth at operculum, D_d = Depth at dorsal fin, D_a = Depth at anus, D_{cp} = Depth at caudal peduncle, B_o = Breadth at operculum, B_d = Breadth at dorsal fin, B_a = Breadth at anus, B_{cp} = Breadth at caudal peduncle

N = 57	Fork Length (cm)	Snout Length (mm)	ME to Hyperal (cm)	D_o (mm)	D_d (mm)	D_a (mm)	D_{cp} (mm)	B_o (mm)	B_d (mm)	B_a (mm)	B_{cp} (mm)	Hump Height (mm)
Average	82.75	74.58	69.94	166.12	197.45	145.53	63.97	109.31	110.44	80.38	40.71	103.37
St Dev	7.40	10.12	6.32	19.90	20.56	16.92	7.08	9.87	12.03	12.36	5.16	11.55
Max	100.5	100.84	83.2	220.8	272.04	209.44	95.48	132.46	135.58	101.18	57.92	144.72
Min	70.1	32.34	59	82.94	161.2	121.18	52.14	86.66	68.04	32.12	30.8	81.88

Table 1.10. 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 ($AIC_i - AIC_{min}$) values are shown. Model terms: E = energy (kJ), L = fork length (cm), W = body mass, Ba = body breadth at anus, Hh = hump height, Rs = resistance, Cv = conductor volume.

Dependent Variable	r^2	AIC	Δi	Model
Muscle lipid (%)	0.82	421	0	lipid = 20.8 - 0.78L + 0.41Hh + 0.27Ba
	0.81	424	3	lipid = 21.1-0.78L+0.03W+0.41Hh+0.27Ba
Skin lipid (%)	0.83	597	0	lipid = 38.3-1.43L+0.86Hh+0.35Ba
	0.83	597	0	lipid = 61.2-1.68L+1.92W+0.73Hh+0.29Ba
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+9.968Ba
	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+9.831Ba
	0.97	1687	8	lipid = 2534-59.92L+256.5W+15.87Hh
Somatic E (kJ)	0.92	2836	0	E = 62524-2100L+9438W+547Hh+583Ba
	0.91	2852	16	E = 113435 – 2590L +13885W + 706Ba
Total E (kJ)	0.92	2823	0	E =118350-2571L +14136W+630Ba
	0.92	2824	1	E =102192415L + 12724.3W + 591.6Ba + 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

Table 1.10. Continued

Dependent Variable	R^2	AIC	Δi	Model
Viscera water (%)	0.63	294	31	water = 44.5 - 0.12Cv – 2.29W + 0.59L
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

Table 1.11. Morphological measurements of Chinook salmon collected in 2002–2007.

	Year	*n*	Mid-eye to hypural (cm)	Hump height (mm)	Breadth at anus (mm)
Mean	2002	57	69.94	103.37	80.38
St Dev			6.32	11.55	12.36
Max			83.2	144.72	101.18
Min			59	81.88	32.12
Mean	2003	141	-	110.62	86.09
St Dev			-	13.23	10.13
Max			-	158.42	121.48
Min			-	78.82	67.26
Mean	2004	169	-	104.58	79.65
St Dev			-	14.56	11.81
Max			-	148	109
Min			-	71	48
Mean	2005	46	66.82	89.59	70.91
St Dev			4.85	7.77	7.68
Max			73.8	108	81
Min			49	68	46
Mean	2006	20	67.39	89.9	73.65
St Dev			4.01	7.11	7.04
Max			75.5	102	87
Min			56.4	76	60
Mean	2007	35	68.95	98.54	79.43
St Dev			4.97	9.76	8.86
Max			80.5	130	105
Min			56	80	59

2003–2007

Based on the results from 2002, mid-eye to hypural length, hump height, and breadth at anus were the morphological measurements that best predicted levels of lipid, total energy in the body. Thus, some or all of these measurements were collected in future years.

Morphometric means for fish from 2003 were larger than any other year sampled (Table 1.11). Proximate analysis was not taken at Bonneville Dam in 2004, so results were only used to compare to other years data.

Data from 2005 and 2006 were pooled due to small sample sizes. A highly significant linear regression was found between the morphometric and proximate analysis results for these years ($r^2 = 0.83$) indicating morphometric analysis was a reasonably accurate method from estimating lipid levels in muscle tissue (Figure 1.6).

Proximate analyses were not run in 2007, due to conclusive results in previous years. Results were compared to data from previous years.

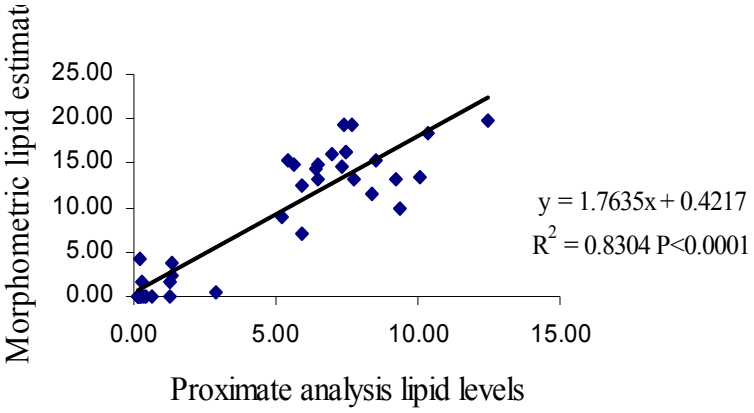

Figure 1.6. Linear regression results of the morphometric lipid estimates versus proximate analysis results in 2005 and 2006 (samples combined).

Year-to-Year Comparisons

A difference in the morphological measurements between years was observed. In general larger fish were tagged in the earlier years of the study, most notably in 2003. On average, smaller fish were tagged in 2005 and 2006 (Figures 1.7- 1.9). These size differences did not affect the estimates of lipid content from the morphological measures, however. In all years where proximate analysis was run (2002, 2005, 2006) morphological measures were significantly positively correlated with estimated lipid levels (e.g. 2005 and 2006, $r^2 = 0.83$).

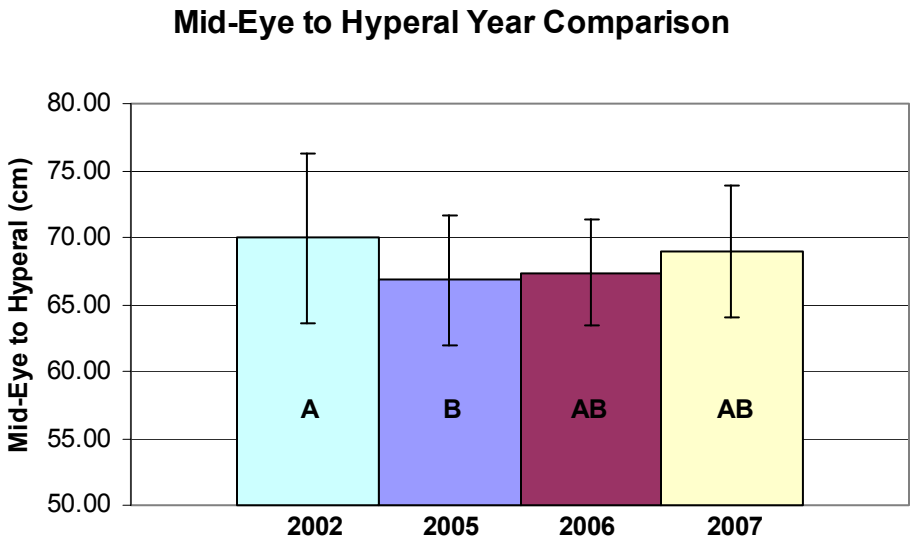

Figure 1.7. Mean (SD) annual mid-eye to hypural lengths of Chinook salmon. Bars with different letters indicate statistically significant differences (α = 0.05, Tukey's HSD test)

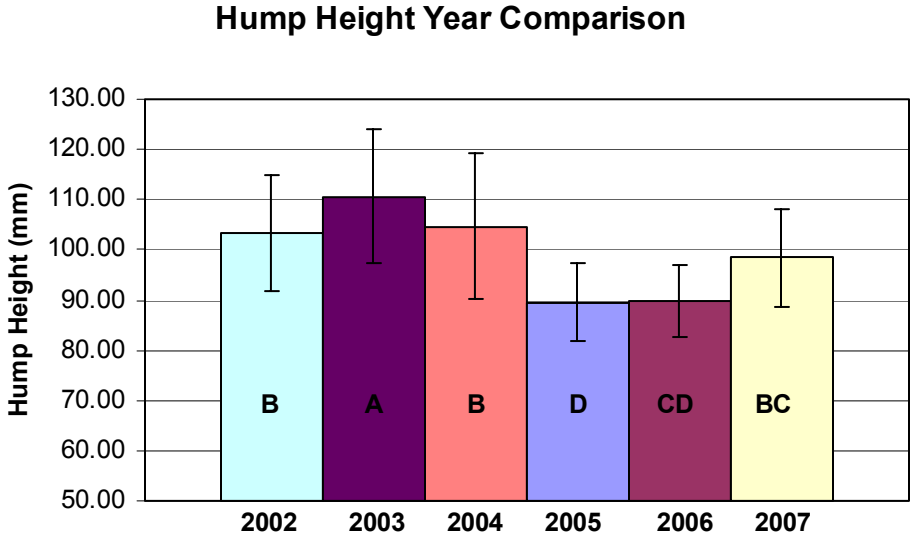

Figure 1.8. Mean (SD) annual Chinook salmon hump heights. Bars with different letters indicate statistically significant differences (α = 0.05, Tukey's HSD test).

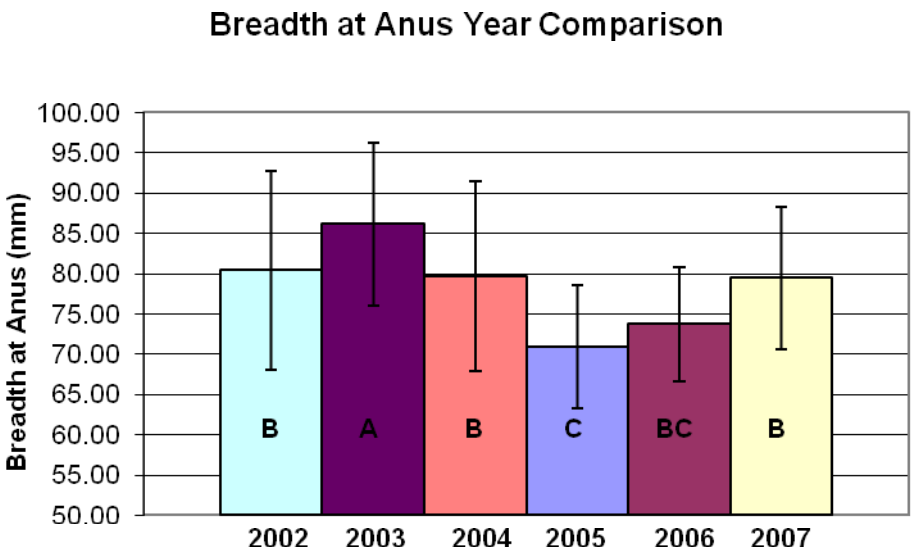

Figure 1.9. Mean (SD) annual Chinook salmon breadths at anus. Bars with different letters indicate statistically significant differences ($\alpha = 0.05$, Tukey's HSD test).

Distell Fatmeter

2005-2007

The Distell Fatmeter was a new method for estimating lipid content that was used for the first time in 2005. A total of 38 fish were measured and used to test the associations between the lipid estimation models and the proximate analysis results. A total of 22 fish were obtained at the beginning of the migration at Bonneville dam, 12 in 2005 and 10 in 2006. A total of 16 fish were recovered on the SFSR, 11 in 2005 and 5 in 2006. In 2007 an additional 65 fish were sampled with the fat meter at Bonneville Dam, with 15 of those fish recovered and sampled again at the SFSR.

Data from 2005 and 2006 were pooled due to small sample sizes. The relationship between the Distell Fatmeter estimates and the proximate analysis results for muscle lipid content was highly significant (Figure 1.10). Muscle lipid levels were positively correlated ($r^2 = 0.8281$, $P < 0.0001$) with proximate analysis results with a simple linear regression. The results of total body lipid levels compared to the Fatmeter readings were also significant ($r^2 = 0.8141$, $P < 0.0001$) (Figure 1.11).

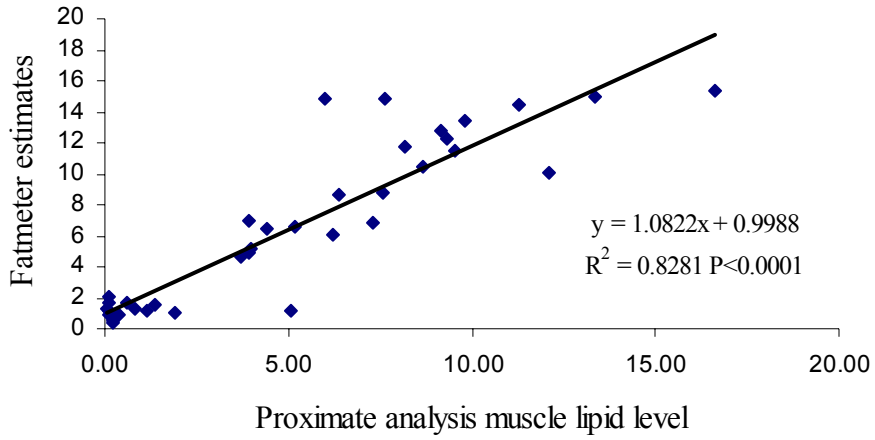

Figure 1.10. Simple linear regression of the Fatmeter results over muscle proximate analysis results in 2005 and 2006.

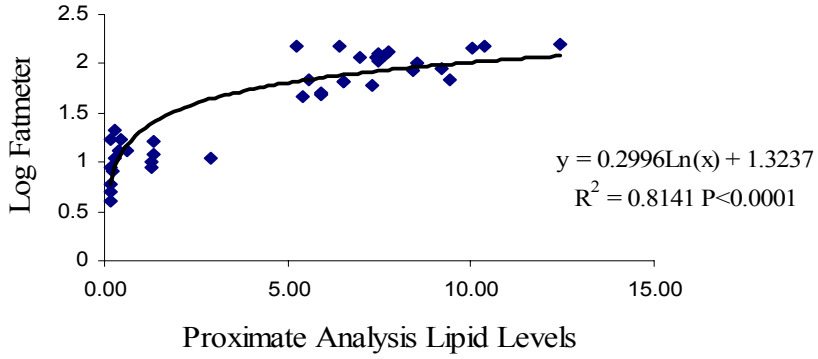

Figure 1.11. Log-linear regression of log-transformed Fatmeter results over whole body proximate analysis results for the combined 2005 and 2006 data.

Proximate analysis was not run in 2007. The 65 fish collected at Bonneville Dam had mean fat meter readings of 11.23 (SD = 1.89, *range* = 4.0–15.8). Results for the 15 fish recovered in the SFSR were: *mean* = 2.85 (SD = 3.22), *range* = 0.9–12.8. A breakdown of individual fish differences between starting and ending migration fat meter results is included in Chapter 2.

Year-to-Year Comparisons

Fatmeter results differed among years. A significantly higher percentage of muscle lipid levels was observed in 2005 compared to 2006 and 2007 (Figure 1.12). This was somewhat surprising given that the morphometric data showed that fish collected in 2005 were the smallest fish tagged, on average.

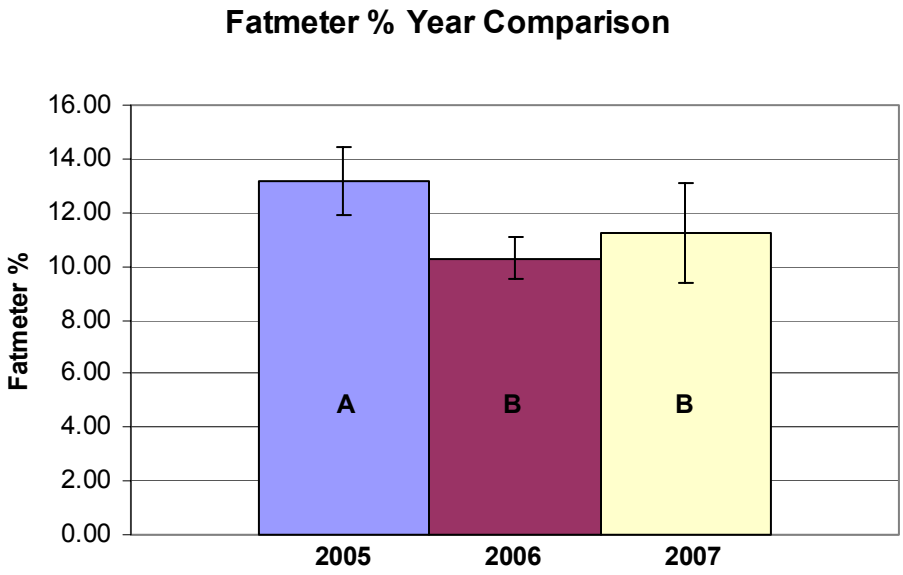

Figure 1.12. Mean (SD) annual Distell Fatmeter results for adult Chinook salmon collected at Bonneville Dam. Bars with different letters indicate statistically significant differences ($\alpha = 0.05$, Tukey's HSD tests).

Condition Factor

2002 and 2003

Condition Factor was included in models to estimate lipid content of somatic tissues outlined earlier. Condition factor was not found to be a predictor variable in any of the best models according to the AIC model comparison (Table 1.10)

2005 and 2006

Condition factors for the pooled 2005–2006 fish were compared to the proximate analysis of fish tissues. There was a significant linear relationship between condition factor and total body lipid content (Figure 1.13). This was in contrast with previous research which suggested no such relationship (Peters et al 2003).

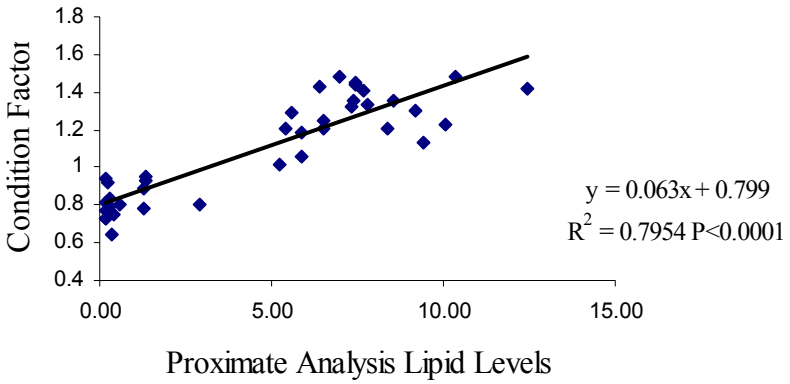

Figure 1.13. Simple linear regression results of Fulton's Condition Factor versus proximate analysis results for the combined 2005 and 2006 data.

Year-to-Year Comparisons

Interestingly, annual condition factor results mirrored the trends seen in the morphometric data (Figure 1.14). However only the 2003 results were significantly different from the other years sampled. It was unclear whether this was actually an indication that fish from 2003 were of higher condition. Examinations into the condition and overall reproductive success are examined in Chapter 2.

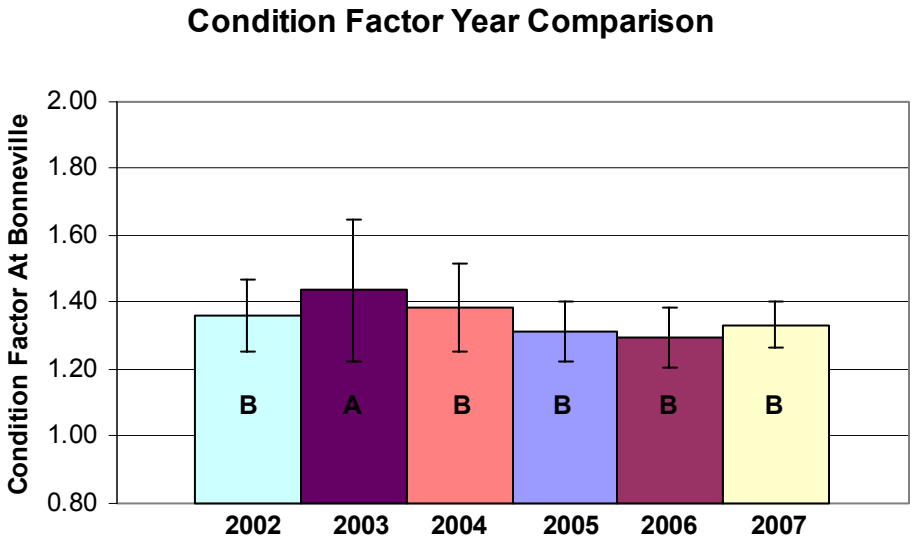

Figure 1.14. Mean (SD) annual Condition Factor results. Bars with different letters indicate statistically significant differences ($\alpha = 0.05$, Tukey's HSD test).

Discussion

A number of methods for estimating lipid levels in adult Chinook salmon were analyzed over multiple years of this study. These methods were compared to results from proximate analysis performed on tissues from lethally-sampled fish. Based on these results the accuracy and feasibility of each method was assessed.

Bioelectrical Impedance Analysis (BIA) was the first non-lethal energy estimation technique. In single-variable regressions, resistance accounted for 13–44% (depending on tissue type and measurement metric [% 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 consistent 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 results, 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 (including at least one 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.

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.

A series of morphometrics were also used to develop comparisons to the proximate analysis results. Morphometric variables estimated lipid masses and energy content of adult Chinook salmon with reasonable accuracy in 2002 and 2003, accounting for 87–92% 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 relatively poorly predicted percent lipid of the viscera ($r^2 = 0.53$). These findings are consistent with the results 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 char

(*Salvelinus alpinus*). However, we note that visceral lipid is a relatively small portion of whole-body lipid content for adult salmon and that whole-body lipid was reasonably predicted by morphometric measures.

Results from 2002 and 2003 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).

Although using morphometrics proved to be the most accurate method in comparisons with proximate analysis results, the handling time increases considerably when this method is employed (i.e., handling time can exceed 45 seconds for an inexperienced technician). Because one of the primary goals of comparing these methods was to determine what method was the most efficient and to reduce handling time of fish while maintaining accuracy this should be taken into account. In addition to increasing handling time, another limitation of the morphometric model was that it did a relatively poor job estimating lipid in fish with very low lipid levels and those of smaller size (i.e., precocious males).

The third non-lethal lipid estimation technique examined was the Distell Fatmeter. As a relatively new technology this method was only implemented in 2005-2007. The results from the Fatmeter were as expected from a review of previous studies. Similar to Crossin and Hinch (2005), the results of our study confirmed the applicability of the Fatmeter to field research even though the instrument was designed for commercial purposes. The relationship between the Fatmeter results and proximate analysis results was significant not only for muscle lipid estimation, but for whole-body lipid estimation with r^2 of both regressions being greater than 0.8.

Although previous research has been done with other species, including sockeye salmon, rainbow trout (*O. mykiss*), and American shad (*Alosa sapidissima*), the results of this study are a promising beginning for the use of the meter for Chinook salmon. The Fatmeter is simple to use and accurate in estimating fish lipid levels. We recommend that this method be employed in energetics studies, including on live individuals due to the ease of use, portability, and limited fish handling time. The use of this method during carcass surveys, fish tagging at dams, or collection/handling at weirs are also potentially useful applications.

The final energy estimation technique examined was Fulton's condition factor (K). Condition factor was included in the morphometric modeling done in 2002 and 2003, but was not a significant variable in any of the best models. The relationship between condition factor and lipid levels was analyzed separately in 2005-2006. These results were interesting because they displayed such a significant relationship while other studies have failed to show this. The issues of length and weight changes are especially

applicable to the results of this comparison when condition factor is considered for an estimate of lipid levels in adult Chinook salmon. Length changes in adult Chinook salmon occur most notably in males developing secondary sexual characteristics. Weight changes occur for both male and female fish during migration and during spawning activities. During these times, fish use lipid reserves that result in a decrease in weight (and concurrent decrease in condition factor). However, migrating fish using energy reserves have been shown to replace the lipid loss by maintaining or increasing tissue water levels, thereby helping the fish to maintain their fusiform shape (Brett 1995).

Fulton's Condition Factor was less accurate than morphometrics or the Fatmeter and was problematic when certain physiological changes in adult salmon were considered. We recommend that researchers continue to take length and weight measurements on adult Chinook salmon in the basin, but to use the relationship to determine overall lipid condition of fish would be inappropriate. A benefit of continuing to estimate condition factors using this method would be to track changes in the overall average condition of populations across years. This information would be of great value in understanding how changes in ocean condition influence changes in a populations' energetic condition (e.g., Crossin et al. 2004).

Over the years studied, condition factors seemed to mirror the trends seen in the morphometric data. In general, larger fish generally had higher condition factors, although only the 2003 mean was significantly different from the other years. The 2005 results were somewhat inconsistent with the general pattern, as fish had comparatively equal condition factors but low morphological measurements (i.e., good condition but smaller size). Perhaps higher energy/lipid levels indicated by the high Distell Fatmeter readings can account for this, although we only had three years of data to compare; additional sampling may help clarify the fish condition-fish size relationship across years.

In conclusion, the comparison of non-lethal methods of lipid estimation suggests that the morphological assessment was the most accurate. The Distell Fatmeter also proved to be accurate for both muscle and whole-body lipid levels and had the added advantage of minimal fish handling time (a few seconds) compared to the morphological assessment. Although BIA and condition factor methods successfully estimated lipid levels, these techniques were not as accurate as morphometrics or the Distell Fatmeter.

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Appendix A

Table A.1. Linear regressions of Chinook salmon energy content (E) and fork length (FL).

Dependent Variable	Sex	Location	R^2	df	P	Equation
Total Energy	Female	Bonneville	0.86	31	<0.0001	E = -131618 + 2454.2(FL)
		South Fork Trap	0.38	24	<0.0001	E = -49036 + 1058.9(FL)
		Pre-spawn	0.75	15	<0.0001	E = -46887 + 857.5(FL)
		Post -Spawn	0.07	17	0.74	E = 5611.24 + 49.82(FL)
	Male	Bonneville	0.76	23	<0.0001	E = -133144 + 2447.57(FL)
		South Fork Trap	0.68	26	<0.0001	E = -75292 + 1385.54(FL)
		Pre-spawn	0.84	5	0.01	E = -16849 + 426.98(FL)
		Post -Spawn	0.34	8	0.1	E = -9989.00 + 329.34(FL)
Somatic Energy	Female	Bonneville	0.86	31	<0.0001	E = -131668 + 2425.19(FL)
		South Fork Trap	0.51	24	0.001	E = -34905 + 811.90(FL)
		Pre-spawn	0.6	15	<0.0005	E = -35856 + 611.50(FL)
		Post -Spawn	0.12	17	0.15	E = -1784.17 + 124.58(FL)
	Male	Bonneville	0.76	23	<0.0001	E = -133923 + 2451.16(FL)
		South Fork Trap	0.67	26	<0.0001	E = -73822 + 1354.14(FL)
		Pre-spawn	0.82	5	0.01	E = -15874 + 402.75(FL)
		Post -Spawn	0.38	8	0.08	E = -10942 + 333.78(FL)

Chapter 2: Spawning success, and the effect of multiple factors on energy condition and migration experience, of summer Chinook salmon returning to Central Idaho

Abstract

Spawning success as it relates to energy condition and migration experience were studied over multiple years for a single population of summer Chinook salmon returning to the South Fork of the Salmon River (SFSR) in Central Idaho. In combination, about 400 salmon were radio-tagged at Bonneville Dam across six years in order to record migration histories and spawning success. Additional fish were PIT-tagged and many more were sampled on spawning grounds on the SFSR. 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 pre-spawn mortality was not directly associated with the exhaustion of energy reserves. Pre-spawn mortality did seem to be correlated with high temperature periods in the SFSR in early years of the study.

A series of logistic regression models which related spawning success to a multitude of factors of energy condition and migration success were built in 2005-2006. The most parsimonious model included only energetic condition of fish upon river entrance and total passage time. Every factor measured, however, did appear in at least one significant model suggesting spawning success is complex and potentially controlled my many factors. It is important for the successful management of this species to have accurate methods to determine 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. This is especially true in the face of changing climate and river environments in the Pacific Northwest.

Introduction

Snake River Chinook salmon (*Oncorhynchus tshawytscha*) must make long freshwater migrations as maturing adults in order to reach natal spawning grounds. Because salmon do not feed during freshwater migration, they are reliant on energy stores acquired during their time in the ocean. Adult salmon typically die within days to weeks of spawning, indicating these energy stores are usually just enough to allow fish to reach spawning habitat and complete reproduction. Because of changes in the migration corridor of many rivers of the Pacific Northwest resulting from climate change, habitat degradation, and hydroelectric installations, it is unknown whether current energy stores are enough to facilitate successful spawning at the population level.

Arguably, the greatest impact to the migration corridor of the Columbia and Snake Rivers has been the construction of the Federal Columbia River Power System (Hydrosystem). The demand for irrigation water, commercial navigation, and electricity has resulted in the construction of multiple dams on these rivers in the last century starting with Bonneville Dam in 1933. While these dams provide numerous benefits, they have also profoundly affected the natural functions and processes of these riverine systems. Dams inundate spawning and rearing habitats and interfere with natural movement patterns of migratory fish, such as anadromous salmonids *Oncorhynchus spp*. (Quinn et al. 1997, Dauble et al. 2000, Peery et al. 2003). In addition to the direct effects of passage blockage and the removal of spawning habitat, the operation of dams and reservoir for power production, navigation, and flood control can indirectly affect ecosystem functions and fish migration behaviors.

Some important indirect effects are the alteration of natural flow and temperature regimes within the river. Operating the dams for flood control has resulted in a more consistent flow regime throughout the year. There is no longer a large spike of flow during the spring-summer snowmelt runoff that occurred historically in the Columbia system. In addition, water retention during the summer effectively heats the water in the reservoirs. More specifically, peak water temperature dates in the Columbia River occur earlier in the year, and warm water remains later in the fall than historically (Quinn and Adams 1996; Quinn et al. 1997). The physiological effects of increased water temperatures, supersaturated dissolved gas, and physical exertion of dam passage adds to the potential difficulties of upstream migration by adult salmonids (Bjornn and Peery 1992). Although impoundments reduce river velocity, higher metabolic costs associated with warmer water temperatures and dam passage may require more energy expenditure than is saved by the reduction in water velocity (Brett 1995). This added energy cost may have negative consequences for other important physiological demands such as gonad production, potentially resulting in lowered reproductive fitness.

Construction of the Hydrosystem has coincided with a dramatic decrease in Pacific salmon populations in the inland Northwest (Chapman 1986) resulting in the listing of many populations as threatened under the Endangered Species Act (Petrosky et al. 2001; Good et al. 2005). Although ocean and climate changes have fluctuated during this time, it is important to explore what effects conditions in the migration corridor might have on a fish's energy condition and reproductive success. The effects of dams have been linked with a variety of changes in adult salmonid behavior, ranging from widely variable passage times at dams and in reservoirs (Keefer et al. 2004; Brown et al. 2006; Caudill et al. 2007), to temperature-avoidant thermoregulation (Goniea et al. 2006; High et al. 2006) and disorientation due to turbulence in tailraces, inundation of tributary confluences, or fallback events (Bjornn and Peery 1992; Boggs et al. 2004; Keefer et al. 2008a).

It is important to understand how changes along the migration corridor and behavioral responses affect the energy condition of migrating adult Chinook salmon and how these physiological changes influence the reproductive success of these species. To this end, we evaluated these relationships over a six year time period (2002-2007) on a single

population of Chinook salmon. Chinook salmon returning to the South Fork of the Salmon River (SFSR) were selected as a test population for several reasons. Their long (~1150 km) migration includes passage at eight main stem dams on the Columbia and Snake Rivers before reaching spawning habitat in central Idaho. Migration timing of SFSR fish occurs during mid-summer, exposing them to potentially stressful in-river conditions. Furthermore, the spawning areas of this population have been well documented and are accessible. An Idaho Department of Fish and Game (IDFG) weir and trap on the SFSR also made it possible to sample fish upon arrival near spawning grounds .

Several objectives were identified to examine the relationship between Hydrosystem conditions, energy expenditure, and spawning success. First, we determined energy conditions of fish at specific points of their migration by analyzing lipid and protein contents of the skin, muscle, viscera and gonad tissue. Second, we examined methods for non-lethal energy estimation for migrating adults (see Chapter 1). Third, we explored differences in energy conditions between successful and unsuccessful spawners. Fourth, we investigated the inter-relationships between initial fish condition, migration experience, and river conditions, and how these factors affected migration and spawning success.

Methods

A combination of radio tagging and PIT tagging was used to track fish tagged at Bonneville Dam as they passed through the Hydrosystem and were recovered in the SFSR at the IDFG weir and upon death. Energy condition at various points along the migration was determined for individual fish to reconstruct energy status through time. For a detailed explanation of energy/lipid estimation methods see Chapter 1.

Telemetry Monitoring

Radio-tagged fish were monitored during upstream migration through the Hydrosystem by a series of fixed receiver sites at hydroelectric dams, along reservoirs, and at major tributaries (e.g., Keefer et al. 2004). Salmon passage times through the Hydrosystem were calculated as the time from tagging at Bonneville Dam to the last telemetry record at Lower Granite Dam. Time to traverse the unimpounded river was calculated from the last record at Lower Granite to the first record on the SFSR fixed receiver site 95 km upstream from the SFSR confluence with the Salmon River main stem. Migration success was defined by the passage and residence of a tagged fish past the SFSR receiver site.

Carcass Collection

Fish that migrated successfully (i.e., passed the SFSR fixed receiver site) were monitored by foot and truck tracking. Foot tracking entailed using a mobile receiver (Lotek Wireless, Inc., Newmarket, Ontario) and a hand-held Yagi antenna. With this method, trackers were able to locate fish to within several meters. Truck tracking used a rotating mounted antenna and receiver to locate transmitters while traveling along a road adjacent to the river. This method provided approximate fish location of fish, typically to within 100 meters. Whenever possible, fish were observed daily until they died or could no longer be located in the study area.

After a fish died, either as a pre- or post-spawn mortality, the carcass was collected and taken to the IDFG weir on the SFSR where lengths, weights, morphological measurements and Fatmeter readings were taken. The body cavity was inspected to determine spawning success. A fish with less than 25% of gametes remaining was determined to have been a successful spawner, following the protocol of Pinson (2005). The fish was then processed for tissue samples as described in Chapter 1. The samples were frozen and transported to Washington State University for proximate analysis.

Statistical Analysis

Migration histories for each fish were reconstructed from telemetry or PIT-tag records. To evaluate the effects of various factors on spawning success, a multiple logistic regression was used. The full model contained passage times, degree days, fallback events, initial fish condition (Fulton's Condition Factor K) and initial lipid levels. Multi-model selection with the Akaike Information Criteria (AIC) was used to determine the 'best' model (Burnham and Anderson 2002). Spawning success was the dependent variable with all others acting as independent variables in the model. Each independent variable was also evaluated separately with a one-way ANOVA to determine if there were statistical differences between spawning and non-spawning groups.

Results

2002-2003

In 2002, 85 radio-tagged Chinook salmon were recorded at the SFSR telemetry site. Median travel time to pass the eight dams and associated reservoirs (Bonneville to Lower Granite) was 15.0 d, and ranged from 8.5–31.0 d (n = 56). Median travel time to pass from Lower Granite Dam to the SFSR receiver site (free-flowing except for the lower 52 km, in Lower Granite Reservoir) was 15.9 d, and ranged from 9.7–44.1 d (n = 83). Median travel time for the two segments combined was 32.7 d, and ranged from 20–54 days (n = 56) (Table 2.1).

Of the 85 successful migrants to the SFSR, eight were confirmed to have spawned, and one was a confirmed pre-spawn mortality. Four of the successful spawners carcasses were recovered from the river. Two of these underwent proximate analysis, while two were either partially eaten by predators or were too far deteriorated for analysis. Nez Perce Tribal biologists recovered five radio-tagged carcasses (four fish that died after spawning 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 IDFG at the SFSR trap; of these, four (all males) were killed and sampled for proximate analysis (Table 2.2). Nine radio tags were found on the river bank or river bottom. Eight fish were last mobile tracked in SFSR tributaries (East Fork South Fork Salmon River, Johnson Creek, Lake Creek, or Secesch River). The fates of 21 of the 85 fish were unknown.

Table 2.1. 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), for two fish with radio transmitters recaptured after spawning in 2002. Also shown are percentage lipid of the muscle tissue, mass-specific somatic energy and mass-specific total energy after death on the spawning grounds.

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

Table 2.2. 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 SFSR fixed receiver site, 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	10 Jun	16.9	10.3	5.9	6.1
BON	17 Jun	23.0	5.4	4.9	5.0
BON	21 Jun	20.3	7.2	4.4	4.6
LGR	28 Jun	11.0	5.2	4.4	4.5

Energy Condition (2002)

Thirty-two PIT-tagged fish were sampled and analyzed for proximate analysis at the trap on the SFSR. Of these 32, 25 had records at the adult PIT detection sites at Bonneville and Lower Granite Dams, allowing calculations of travel times between the two locations. Median time between the 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 –20.0 d), and 11.9 d for males (n = 12; range = 9.9–17 d).

Mean (SE) muscle lipid content for PIT-tagged fish at arrival at IDFG weir 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 $^{-1}$.

Travel time was negatively correlated with log-transformed muscle lipid (r = -0.67, n = 25, P = 0.0002; Figure 2.1), 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) for PIT-tagged fish in 2002. 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 was 7.5% (SD = 2.3%) for slow-migrating fish, and 11.0% (SD = 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 to the SFSR. In contrast, faster migrants expended 25 and 29% of their mass-specific total and somatic energy. Temperature near the start of the spawning migration at Bonneville Dam was not correlated with migration time (d) or muscle lipid remaining at SFSR arrival.

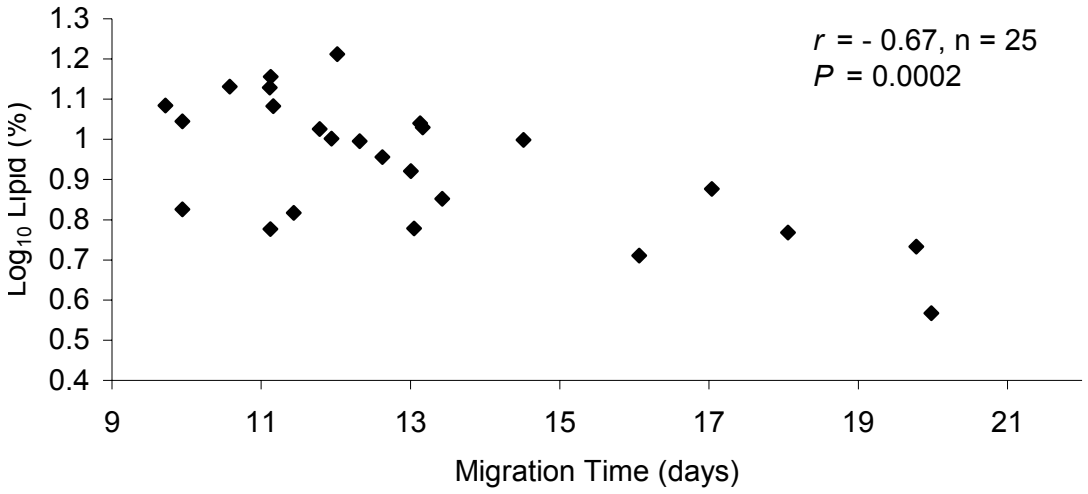

Figure 2.1. Pearson's correlation between migration time and percent muscle lipid for PIT-tagged fish at arrival at the SFSR in 2002.

Percent muscle lipid and mass-specific somatic energy were not significantly different between pre- and post-spawning males (t = -0.99, df = 13, P = 0.34; t = -1.1, df = 13, P = 0.29). However, values were 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 SFSR spawning areas for energy content evaluation in 2002 (Table 2.2). 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 through 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 Tribal 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 SFSR receiver site. However, migration time through the free-flowing stretch (Lower Granite Dam to the SFSR receiver) was longer than total time for all other fish to migrate from Bonneville to the spawning stream (Table 2.3). The four fish that died before spawning spent 13–24 days migrating between Bonneville and Lower Granite dams, 13–26 days to migrate from Lower Granite Dam to the SFSR receiver, and a total 78 to 101 days in freshwater between the start of migration and death in the SFSR.

Table 2.3. Migration times and percent lipid at death ($Lipid_f$) 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		
11 May	_	25.7	_	_	_
21 May	–	20.8	_	_	_
4 Jun	_	16.1	_	_	0.27
7 Jun	12.8	13.1	25.9	88.2	_
			Successful Males		
21 May	15.7	20.2	35.9	101.3	_
25 May	24.0	14.5	38.5	97.0	1.45
6 Jun	13.6	13.4	27.0	90.6	_
19 Jun	15.3	_	_	77.7	_

Energy Condition (2003)

In 2003, 65 fish that had received radio transmitters between 15 April and 15 July migrated past the SFSR receiver. Median travel time between Bonneville Dam and SFSR was 33.7 d (n = 54; range = 17.4–59.1 d). This was split between travel time through the Hydrosystem (16.7 d; n = 55; range = 9.66–34.6 d) and travel time through the unimpounded river segment (16.4 d; n = 61; range = 9.89–47.0 d). Females that spawned (n = 7) spent 23.1–71.9 d in freshwater between Bonneville Dam and death on the spawning grounds with a median of 53.0 d. Males that spawned (n = 7) spent 30.1–64.4 d from Bonneville to their death, with a median of 56.4 d. There was no significant difference in the median travel times between males and females.

Of the 65 fish detected in the SFSR, 14 were known to have spawned. Eleven carcasses were obtained for energy estimates and three fish 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 IDFG 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, and four retained for spawning; two of the retained fish were measured for energy estimates after being spawned by IDFG). One transmitter was found out of the water without the fish. Six fish migrated up SFSR tributaries. Two transmitters were found and returned to the University of Idaho without information (i.e., no time of death or spawning success) and one transmitter was pulled from a fish that was caught and released during the fishery.

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

Fifteen of the 65 fish that migrated to the SFSR receiver site were measured for estimates of final energy content after death in the river. The correlation between final muscle tissue lipid and travel time was similar to the 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. This allowed estimation of muscle lipid, total and somatic energy, and energy expended to migrate and spawn (Table 2.4). Total body mass, hump height, and body breadth at the anus decreased by 34, 25 and 22% for females and 28, 24, and 18% for males. Successful fish expended between 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 2.4).

Table 2.4. Tagging date, migration time, estimated percent muscle lipid at Bonneville Dam (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. Confidence 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	28.0	75.8	21.3(7.4)	3.9(7.4)	66	54
			Successful Females			
20 Jun	52.0	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.

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

The spawning success of 19 radio-tagged fish was tracked in 2003: 5 fish died prior to spawning and 14 spawned (Table 2.5). Median travel time from Bonneville Dam to

the SFSR receiver for fish that died before spawning was 30.9 days and ranged from 27–38 days. Median travel time to complete migration to the spawning stream for fish that spawned was similar at 31.9 d (n = 13, range = 23–55 days).

Initial energy condition was estimated for 11 fish and final energy condition was estimated for 11 naturally spawning fish (Table 2.5). However, we measured both initial and final energy condition for only six fish (five naturally spawned; one hatchery spawned) with morphometric data (Table 2.1). Of these six fish, one female died before spawning and one female that spawned. The two females were tagged within one day of each other and spent about 75 d between Bonneville Dam and death in the SFSR. At the start of migration, estimated lipid content of the muscle tissue was 20%. However, the female 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 as long 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. We measured both initial and final energy condition for four males: one died prior to spawning and three spawned. The male that died before spawning started migration earlier with relatively lower initial lipid stores (16.5%) than the successful male spawners. Travel time for the male that died before spawning slightly higher than the median for all 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 d (*range* = 11–24 d). 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 had an estimated 0.5% muscle lipid.

Daily maximum temperatures were recorded at the IDFG weir in 2003. Large prespawn mortality events appeared to coincide—in part—with times when river temperature was highest (Figure 2.2). Most of the pre-spawn mortality at the SFSR occurred in July, when temperatures were highest. Pre-spawn mortalities occurring *en route* in the Hydrosystem and downstream from the SFSR were not analyzed here. The mechanism(s) affecting both the pre-spawn and pre-SFSR mortality are not fully understood.

Table 2.5. 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)	_

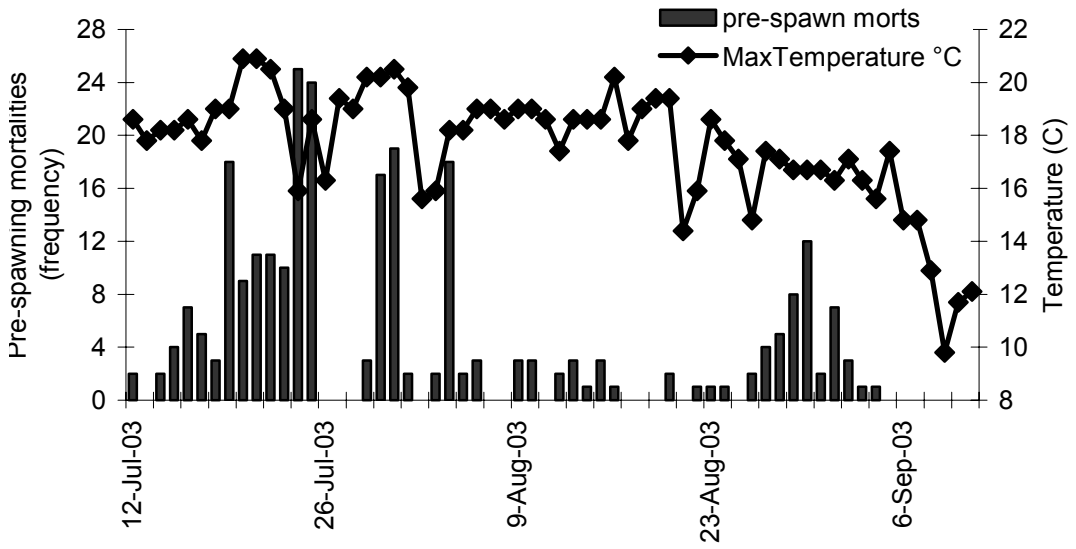

Figure 3.4. Frequency of pre-spawning mortalities observed in 2003 and maximum daily temperatures (USFS data logger) at the weir on the SFSR.

2004-2006

Sort-by-code methods were not employed at Bonneville Dam in 2004, so the total number of fish tagged specifically for the SFSR could not be determined for this year. A total of 47 fish were tagged in 2005 and 20 fish were tagged in 2006.

In 2005, a total of 42 fish successfully passed through the Hydrosystem (passed Lower Granite Dam), representing an 89% success rate from Bonneville Dam. Of the 42 fish that passed Lower Granite Dam, 41 (97.6%) fish passed the SFSR receiver. Overall migration success from Bonneville to the SFSR was 87% (41 out of 47 fish). The average passage time in the Hydrosystem in 2005 was 13.5 d (*range* 7–26 d). Average passage time in the unimpounded river was 15.1 d (*range* = 9–25 d).

In 2006, 16 of 20 (80.0%) radio tagged fish successfully passed Lower Granite Dam. Of the 16 that successfully passed Lower Granite, 15 (93.8%) passed the SFSR receiver.

Table 2.6. Radio tagged passage times from Bonneville Dam to Lower Granite Dam, from Lower Granite Dam to SFSR and from Bonneville to SFSR for 2005 and 2006.

Migration Stage	2005 *n* = 47	2006 *n* = 20
Mean Total Passage Time BON to SFSR	28.8d (±1.75)	28.1d (±2.71)
Mean Passage Time BON to LGR	13.5 d	15.2 d
Mean Passage Time LGR to SFSR	15.1 d	13.8 d
Maximum Passage Time BON to LGR	26 d	26 d
Minimum Passage Time BON to LGR	7 d	12 d
Maximum Passage time LGR to SFSR	25 d	16 d
Minimum Passage Time LGR to SFSR	9 d	9 d

In 2006, 16 of 20 (80.0%) radio tagged fish successfully passed Lower Granite Dam. Of 16 fish that successfully passed Lower Granite, 15 (93.8%) passed the SFSR receiver. A total of 15 of the 20 radio tagged fish successfully passed from Bonneville to the SFSR, for a 75% overall migration success rate. The average passage time in the Hydrosystem for radio tagged fish in 2006 was 15.2 d (*range* = 12–26 d). The average passage time in the unimpounded river section was 12.9 d (*range* = 9–16 d).

Table 2.7. Radio-tagged Chinook salmon migration success rates through the Hydrosystem, unimpounded river system and total migration 2005 and 2006.

	2005 *n* = 47	2006 *n* = 20
BON to LRG Migration Success	89.3% (42/47)	80.0% (16/20)
LRG to SFSR Migration Success	97.7% (41/42)	93.8% (15/16)
Total Migration Success	87.3% (41/47)	75.0% (15/20)

Energy Condition (2004-2006)

Lipid levels were estimated for 170 fish in 2004, 142 fish in 2005 and 371 fish in 2006 (Table 2.8). In 2004, lipid levels were estimated using morphometric measures, whereas the Distell Fish Fatmeter was used in 2005 and 2006. Average lipid estimates for all fish sampled were 17.07% (SD = 1.55%) in 2004, 13.2% (1.17%) in 2005, and 10.6% (1.08%) in 2007.

Table 2.8. Average, maximum and minimum estimated percent lipid for run-at-large fish and SFSR fish in 2004, 2005 and 2006.

	2004	2005	2006
Average % lipid with standard deviation	17.07(±1.55)	13.2(±1.17)	10.16(±1.08)
Maximum % lipid	26.92	22.2	17.7
Minimum % lipid	7.93	6.4	4.3
SFSR Average % Lipid	-	13.2(±1.26)	10.3(±0.76)
SFSR Maximum % Lipid	-	22.2	13.9
SFSR Minimum % Lipid	-	8.3	7.6

SFSR fish were analyzed separately from the run at large in 2005 and 2006 in an effort to evaluate what the energy condition of the stock was compared to other fish migrating at the same time. In 2005, the average estimated percent lipid for 47 SFSR fish was 13.2% (SD = 1.26%). In 2006, the average estimated lipid in 20 SFSR fish was 10.3% (0.76%). In both years, the results indicate that the SFSR population was very similar to the run at large with very low variability around the mean. In addition, the average energetic condition of fish decreased over the last 3 years studied.

Temperature Modeling

Temperatures were recorded for fish in 2004, 2005 and 2006, but the 2006 data were incomplete and were not used in the modeling. Temperature records in the Hydrosystem from 40 fish were used to build the temperature exposure model. Temperature profiles were analyzed to obtain the total number of degree days each fish accumulated in the Hydrosystem. These results were compared to temperature at tagging at Bonneville Dam and to the total number of days spent in the Hydrosystem.

Number of days spent in the Hydrosystem provided the best relationship with total degree days experienced. The 2004 and 2005 data were analyzed independently and together. The combined regression model provided an $r^2 = 0.9347$ ($P \leq 0.0001$). Each year had a similar strong relationship with little variation between slopes. This indicated little inter-annual variation, allowing the combination of data into a multi-year regression. The model was used to estimate the degree-day exposures of fish with no temperature profile and these estimated exposures were used in the total migration and spawning success multiple logistic regression models.

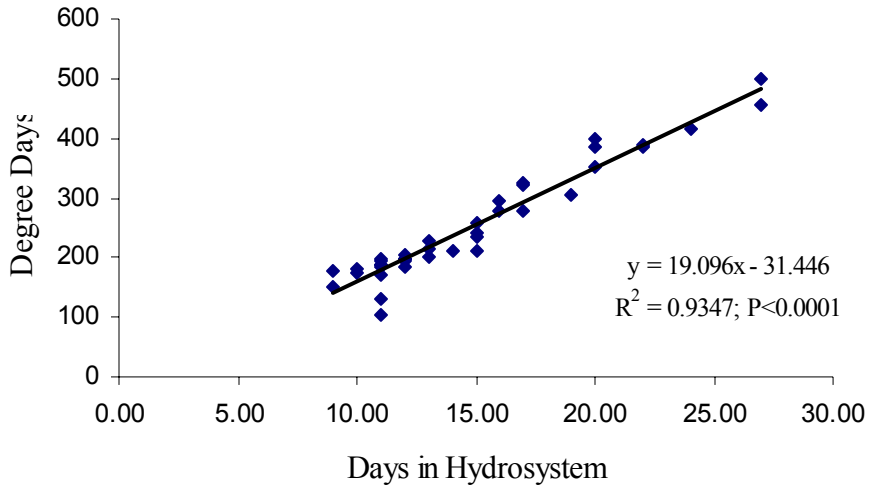

Figure 2.3. Linear regression of degree days experienced in the Hydrosystem and total days from tagging to Lower Granite Dam in 2004 and 2005.

Radio-tagged salmon migration success modeling

Multiple logistic regressions were used to evaluate if any factor or combination of factors was associated with unsuccessful migrations. The models used passage time, temperature exposure, beginning lipid levels, and beginning fish condition. All radio tagged fish from 2005 and 2006 (n = 67) were included in this analysis. A total of 11 fish were unsuccessful migrants, with 9 of those failing to migrate through the Hydrosystem. There were four fish recaptured in the Columbia and Snake Rivers, which affected the power of the model. In addition, 3 of the 6 unsuccessful fish failed to pass Bonneville Dam after tagging, making their use in the model impossible. After completing the analyses it was determined that the only variables that could be used in the model were initial lipid levels and initial condition. These two variables analyzed separately and combined were not significantly associated with migration success.

Radio tagged salmon spawning success modeling

A total of 20 radio-tagged carcasses were recovered upon death in 2004–2006. These fish had been radio–tagged at Bonneville Dam and monitored to the SFSR. These fish had estimates of beginning and ending lipid percentage, condition factor at the beginning and end of migration, passage times for all migration sections, temperature exposures in the Hydrosystem, and spawning success determined. None of the fish were recorded falling back at main stem dams, so the variable was removed from the model. These 20 individuals were used in the multiple logistic regression models to determine which variables were associated with spawning success (Table 2.9).

Table 2.9. Model results for the spawning success multiple logistic regression models with associated *P*-values, AIC values and Δi values. Only models with $\Delta i < 4$ are included here. A full list of models is included in the Appendix.

Dependent Variable	Model P-value	AIC value	Δi	Model
Spawning Success	0.0024	20.535	0	Spawning = Beginning fat condition+ Condition factor+ Total Passage Time
Spawning Success	0.0056	22.319	1.784	Spawning = Beginning fat condition + Condition factor + Total Passage Time + Degree Days
Spawning Success	0.0061	22.5	1.965	Spawning = Beginning fat condition + Condition factor + Hydrosystem Passage Time + Total Passage Time
Spawning Success	0.0114	23.866	3.331	Spawning = Beginning fat condition + Hydrosystem Passage Time + Total Passage Time
Spawning Success	0.0110	23.907	3.372	Spawning = Beginning fat condition + Total Passage Time
Spawning Success	0.0122	24.319	3.784	Spawning = Beginning fat condition + Condition factor + Hydrosystem Passage Time + Total Passage Time + Degree Days

A total of 30 models were developed with single or combined independent variables. Fifteen of the 30 models were significant to the $\alpha < 0.05$ level and one model was significant at $\alpha < 0.005$. All significant models contained multiple independent variables and all study variables were observed in the significant models. The most significant model included condition factor, starting lipid level, and total passage time. The next most predictive model included the same three variables plus degree days.

SFSR PIT-tagged salmon Hydrosystem passage times and migration Success

PIT tag records were used in 2004, 2005 and 2006 to evaluate SFSR population passage times and migration success through the Hydrosystem. Totals of 498, 56, and 152 fish were recorded in the three years, respectively. Average Hydrosystem passage time in 2004 was 12.7 d (*range* = 6–39 d). In 2005, the average was 14.4 d (*range* = 8–39 d). In 2006, the average time was 17.4 d (*range* = 8–56 d).

Table 2.10. Mean, maximum, and minimum passage times (d) for PIT-tagged SFSR Chinook salmon migrating through the Hydrosystem in 2004–2006.

	2004	2005	2006
n	498	56	152
Mean Passage time	12.7	14.4	17.4
Maximum passage time	39	39	56
Minimum passage time	6	8	8

Migration success through the Hydrosystem, defined as successful passage of Lower Granite Dam without evidence of fallback at that dam, was calculated for SFSR PIT-tagged fish in 2004–2006. Annual migration success rates ranged from 77.8–81.6% (Table 2.11).

Table 2.11. Hydrosystem migration success rates for SFSR PIT tagged fish in 2004, 2005 and 2006.

	2004	2005	2006
Total PIT tagged individuals	610	72	189
Successful Hydrosystem migrants	498	56	152
Success rates for Hydrosystem passage	81.6%	77.8%	80.4%

We also evaluated whether total Hydrosystem passage success was associated with successful passage past the lower 4 Columbia River dams. Passage of McNary Dam was a good predictor of overall Hydrosystem migration success in 2004 and 2006. In 2004, 102 of 112 (91.1%) fish that failed to pass the full Hydrosystem did not pass McNary Dam. In 2006, 41 of the 57 (71.9%) fish that failed to pass Lower Granite Dam did not pass McNary Dam. In the smaller 2005 sample, about half of the unsuccessful fish failed to pass McNary Dam and half failed between McNary and Lower Granite Dams.

2007

Work was continued in 2007 using similar techniques as in previous years. Initial conditions were sampled on 31 radio-tagged salmon and 36 PIT-tagged salmon at Bonneville Dam. The success rate to Lower Granite dam was 88%. Success rate was 58% from Bonneville to the SFSR. Travel time for all PIT-tagged fish ranged from 9.7–

34.4 d from Bonneville Dam to Lower Granite Dam with the mean of 16.1 d (SD = 5.4 d).

Energy Condition (2007)

Lipid levels were estimated using the Distell Fatmeter in 2007. Lipid levels ranged from 4.0–15.8% with a mean of 11.23% (SD = 1.89%). Condition Factors were estimated for the 31 radio-tagged fish only, and ranged from 1.24–1.51 with a mean of 1.33 (SD = 0.07). Both lipid level and condition factor means were average compared to previous years research (See Chapter 1).

Sixty-six fish were recovered from spawning surveys and radio tracking in the SFSR. Of these, we had initial conditions at Bonneville for 15 fish. Five of these were radio-tagged fish, and ten were PIT-tagged fish.

Multiple logistic regressions were run on the data to evaluate if spawning success was related to any migration or condition factors assessed for this population. Variables examined included travel time through the Hydrosystem, fallbacks, Fatmeter percentage, starting condition factor, and ending condition factor. Fatmeter percentage was the only factor that was significantly ($P < 0.1$) related to spawning success (Figure 2.3)

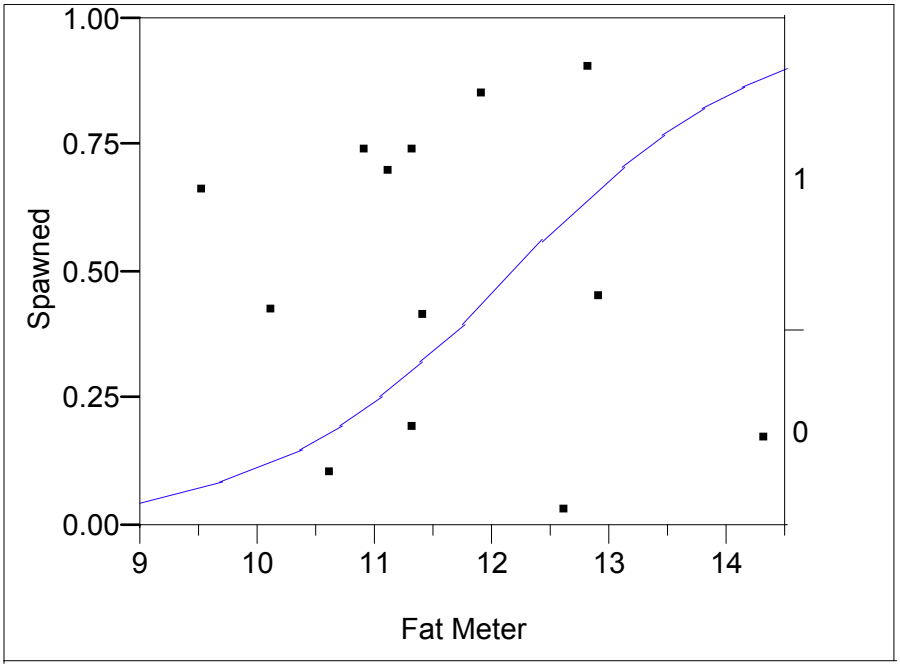

Figure 2.3. Logistic regression between Fat Meter percentage and spawning success. The model had a χ^2 value of 3.19 ($P = 0.074$, $n = 13$).

Discussion

Between river entry and death after spawning, Chinook salmon and other semelparous salmonids experience an almost complete exhaustion of lipids and considerable loss of protein (Gihousen 1980; Brett 1995; Jonsson et al. 1997; Hendry and Berg 1999). These physiological changes reflect the energetic demands of migration, maturation, competition for mates, redd construction, and spawning. The relatively high initial muscle lipid content in SFSR Chinook salmon (~22% for males and females, see Chapter 1) is at the high end of the observed range for Chinook salmon. The high initial fat content reflects the long migration distance for SFSR salmon (~1,150 rkm) and is consistent with estimates for long-distance migrants from other river systems (Iverson 1972; Brett 1995).

In a comparable study of Yakima River spring Chinook salmon, Mesa and Magie (2006) reported initial muscle lipid of 18–20% at Bonneville Dam. Between Bonneville Dam and post-spawning death in the Yakima River (~750 rkm from the Columbia River mouth), the Yakima salmon lost 95–99% of muscle lipid and 73–86% of visceral lipid. The Yakima results were generally consistent with the SFSR lipid results, particularly for fish that spawned. In the 2002 SFSR study, we found that 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 pre-spawn 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 SFSR males at pre-and post-spawning death. This may reflect similar levels of overall exhaustion of energy reserves, though it is more likely that small sample size affected our ability to detect significant differences between pre- and post-spawn groups.

In the first SFSR study years (2002-2003) observations of the condition of a small number (n = 6) both pre-spawn and post-spawn mortalities were conducted. Given the very small sample of radio-tagged fish in these years, results were largely anecdotal. Some inferences, however, can be made. Four recovered radio-tagged fish died prior to spawning, while two died post-spawning. Comparing two females with similar tagging date, initial lipid content, and migration timing, but with different spawning fates, we observed differences in percentage of energy consumption. The successful spawner fell back downstream over the Dalles Dam and spent twice as long as the other fish to reach the SFS from this point. The successful fish spent 95% of its initial energy content, while the unsuccessful spawner only spent 65%. Both fish spent about 75 days from Bonneville Dam to their death. Observations from these two fish do not support a relationship between migration behavior, energy expenditure and spawning success. It should also be noted that the successful spawner arrived much later to the SFS than the unsuccessful fish, so it is possible that arrival timing was more important than events during migration in downstream reaches.

In 2005-2006, additional effort was made to analyze specific migration histories of radio-tagged fish. Spawning success was not limited to assessments of initial and final

energy conditions, but also to migration experience and river conditions during migration. Through these correlative modeling efforts, migration experience, fish condition, and river conditions all showed significant relationships with the spawning success of adult salmon. No individual factors were dominant in predicting spawning success, but as one might expect when dealing with the complex Chinook salmon life history, many correlated factors seem to be related to spawning success in this population. The most predictive model included both the energetic condition of fish upon river entrance and total passage time. The next most predictive model also included temperature experienced during migration. In most models, the passage time relationship indicated higher lipid loss for slower-migrating individuals, which is a result also reported in the Yakima River study (Mesa and Magie 2006) and in Fraser River studies (e.g., Standen et al. 2002). However, we note that all of the variables investigated had some association with SFSR spawning success on some level. There was collinearity among the measured variables and unmeasured effects (e.g., disease status, temperature exposure) were also likely important, suggesting that additional studies including more detailed analysis of other potential causal factors may improve our understanding of the mechanisms affecting spawning success.

A critical question addressed by this study was whether SFSR Chinook salmon had sufficient energetic reserves to spawn once they reached the spawning grounds. Results were somewhat mixed. Many fish sampled at the SFSR weir had lipid reserves of 5–8%, indicating sufficient reserves. In fact, these levels were higher than those reported on river entry for some coastal salmon populations (Brett 1995). However, some pre-spawn mortality occurred in all years, some of which was presumably unrelated to energetic status (i.e., mortality was the result of injury, fungal infection or disease). Mortality related to causes other than energetic status was supported by the analyses that showed some pre-spawn mortalities with relatively high lipid content. Other pre-spawn mortality may have been due to energetic exhaustion, and continued proximate or fatmeter analyses of pre-spawn fish will establish how variable and how significant a contributor energetic exhaustion is to SFSR pre-spawn mortality across years. Interaction between energetic status and other factors are also possible and should be explored in future studies.

The ability to predict pre-spawn mortality rates would substantially affect in-season management plans for Columbia and Snake River Chinook salmon. Fish condition levels on the spawning grounds may be a useful predictor, particularly at sites (like the SFSR weir) where fish are routinely collected. More beneficial would be early season predictions based on fish condition at Bonneville or Lower Granite dams. Initial or mid-migration condition can be a very good predictor of eventual spawning success (Rand et al. 2006; Young et al. 2006). Routine measurement of fish condition at downstream sites, using the Fatmeter or other non-invasive techniques, would be useful for predicting escapement and spawning success. Having a baseline of initial condition data may be especially important if ocean conditions deteriorate from the relatively high productivity conditions that occurred during our study. Relatively cool ocean surface temperatures (SST) and good upwelling conditions during the study likely resulted in good overall condition for returning adult SFSR Chinook salmon (see Mantua and Hare 2002; Mueter et al. 2002; Beamish et al. 2004; Crossin et al. 2004; Scheuerell and Williams 2005;

Hodgson et al. 2006; Todd et al. 2008 for examples of ocean climate regime and productivity effects on salmon survival and condition). The variables investigated during this study provided interesting results beyond the spawning success modeling. Migration success rates for the SFSR population and the radio-tagged subset provided data about migration behavior and potential limiting areas in the migration corridor. Migration success through the Hydrosystem for PIT-tagged SFSR fish did not significantly change over three years of the study. Average success rates were consistently close to 80%, with the majority of the fish that failed to pass Lower Granite Dam last recorded in the Lower Columbia River. This is at least partially due to the higher tribal and sport fisheries effort in the lower river reservoirs, and is consistent with escapement results for the multi-stock spring and summer Chinook salmon runs in the Columbia River (e.g., Keefer et al. 2005). Radio tag records indicated that successful passage through the Hydrosystem was generally predictive of overall migration success and, like the PIT-tagged population, most unsuccessful fish failed to pass McNary Dam.

Small sample sizes in 2007 made it difficult to confirm results from previous years. From the logistic models, lipid content was the only factor statistically associated with spawning success in 2007. Migration success to the South Fork appeared to drop significantly in 2007 (to 57%, from 75–87%), but this may have resulted from our focus on the recovery of PIT-tagged fish to determine success rate and was most likely an underestimate.

Combining results across the entire duration of the study, it appears that monitoring lipid levels and energy condition of fish entering migration corridors can be a useful tool to determine how successful a year class may be. Furthermore, it is likely that successful management of adults in the Hydrosystem and on the spawning grounds can be improved by gathering reliable information on the true level of an energetic/lipid 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. This is particularly important in the face of changing ocean conditions, and the warming climate expected for the Pacific Northwest (Eaton and Scheller 1996; Mote et al. 2003).

Changing ocean and Pacific Northwest regional climate will undoubtedly affect the migration corridor. In particular, flow and temperature conditions will likely impact migration costs. Forecasts for decreasing total discharge may lower energetic demands, because of lower current velocities encountered. However, this may be offset by the forecast of higher temperatures, which would directly increase energetic demand by increasing metabolic activity. Increasing migration corridor temperatures may also add indirect costs via slowed or failed migration as adults seek cold-water refugia, as documented for Columbia and Snake River Chinook and steelhead runs (Goniea et al. 2006; Mann 2007; Keefer et al. *in press*) and both Columbia and Snake River sockeye salmon (Hyatt et al. 2003; Keefer et al. 2008b), runs that co-migrate with SFSR Chinook salmon. For both direct and indirect effects, monitoring population-level energy condition is important for understanding fitness responses to climate change, ocean

conditions, Hydrosystem operations, and environmental conditions salmon encounter along the Columbia–Snake River migration corridor.

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Appendix B

Table B.1. Model results for the spawning success multiple logistic regression models with associated *P*, AIC, and Δi values.

Dependent Variable	Model P-value	AIC value	Δi	Model
Spawning Success	0.0024	20.535	0	Spawning = Beginning fat condition + Condition factor + Total Passage Time
Spawning Success	0.0056	22.319	1.784	Spawning = Beginning fat condition + Condition factor + Total Passage Time + Degree Days
Spawning Success	0.0061	22.5	1.965	Spawning = Beginning fat condition + Condition factor + Hydrosystem Passage Time + Total Passage Time
Spawning Success	0.0114	23.866	3.331	Spawning = Beginning fat condition + Hydrosystem Passage Time + Total Passage Time
Spawning Success	0.0110	23.907	3.372	Spawning = Beginning fat condition + Total Passage Time
Spawning Success	0.0122	24.319	3.784	Spawning = Beginning fat condition + Condition factor + Hydrosystem Passage Time + Total Passage Time + Degree Days
Spawning Success	0.0168	24.845	4.31	Spawning = Beginning fat condition + Degree Days + Hydrosystem Passage Time + Total Passage Time
Spawning Success	0.0236	25.428	4.893	Spawning = Degree Days + Condition Factor
Spawning Success	0.0262	25.64	5.105	Spawning = Total Passage Time + Condition Factor
Spawning Success	0.0261	25.666	5.131	Spawning = Beginning fat condition + Condition factor + Degree Days
Spawning Success	0.0278	25.806	5.271	Spawning = Beginning fat condition + Condition factor + Hydrosystem Passage Time
Spawning Success	0.0290	25.899	5.364	Spawning = Beginning fat condition + Degree Days + Total Passage Time

Spawning Success	0.0329	26.175	5.64	Spawning = Degree Days + Total Passage Time + Condition Factor
Spawning Success	0.0416	26.563	6.028	Spawning = Hydrosystem Passage Time + Condition Factor
Spawning Success	0.0390	26.835	6.3	Spawning = Beginning fat condition + Condition factor + Hydrosystem Passage Time + Degree Days
Spawning Success	0.0521	27.198	6.663	Spawning = Degree Days + Hydrosystem Passage Time + Condition Factor
Spawning Success	0.0625	27.374	6.839	Spawning = Beginning fat condition + Degree Days
Spawning Success	0.0571	27.404	6.869	Spawning = Total Passage Time + Condition Factor + Hydrosystem Passage Time
Spawning Success	0.0662	27.546	7.011	Spawning = Total Passage Time
Spawning Success	0.0778	27.809	7.274	Spawning = Degree Days
Spawning Success	0.0795	27.846	7.313	Spawning = Beginning fat condition
Spawning Success	0.0875	28.056	7.521	Spawning = Beginning fat condition + Condition factor
Spawning Success	0.0663	28.121	7.586	Spawning = Degree Days + Total Passage Time + Condition Factor + Hydrosystem Passage Time
Spawning Success	0.1239	28.553	8.018	Spawning = Condition Factor
Spawning Success	0.1033	28.742	8.207	Spawning = Degree Days + Hydrosystem Passage Time + Total Passage Time
Spawning Success	0.1286	28.819	8.284	Spawning = Beginning fat condition + Hydrosystem Passage Time
Spawning Success	0.1332	28.88	8.345	Spawning = Degree Days + Total Passage Time

Spawning Success	0.1537	29.176	8.641	Spawning = Total Passage Time + Hydrosystem Passage Time
Spawning Success	0.1308	29.285	8.75	Spawning = Beginning fat condition + Degree Days + Hydrosystem Passage Time
Spawning Success	0.1818	29.511	8.976	Spawning = Degree Days + Hydrosystem Passage Time
Spawning Success	0.3021	29.856	9.321	Spawning = Hydrosystem Passage Time