Reproductive energy expenditure and changes in body morphology for a population of Chinook salmon *Oncorhynchus tshawytscha* with a long distance migration

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Energetic demands of a long freshwater migration, extended holding period, gamete development and spawning were evaluated for a population of stream-type Chinook salmon *Oncorhynchus tshawytscha*. Female and male somatic mass decreased by 24 and 21%, respectively, during migration and by an additional 18 and 12% during holding. Between freshwater entry and death after spawning, females allocated 14% of initial somatic energy towards gonad development and 78% for metabolism (46, 25 and 7% during migration, holding and spawning, respectively). Males used only 2% of initial somatic energy for gonad development and 80% on metabolic costs, as well as an increase in snout length (41, 28 and 11% during migration, holding and spawning, respectively). Individually marked *O. tshawytscha* took between 27 and 53 days to migrate 920 km. Those with slower travel times through the dammed section of the migration corridor arrived at spawning grounds with less muscle energy than faster migrants. Although energy depletion did not appear to be the proximate cause of death in most pre-spawn mortalities, average final post-spawning somatic energy densities were low at $3 \cdot 6 \, \text{kJ} \, \text{g}^{-1}$ in females and $4 \cdot 1 \, \text{kJ} \, \text{g}^{-1}$ in males, consistent with the concept of a minimum energy threshold required to sustain life in semelparous salmonids.

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INTRODUCTION

For semelparous Pacific salmon *Oncorhynchus* spp., individual lifetime fitness depends on maximizing reproductive output during a single event (Stearns, 1976; Bonnet *et al.*, 1998). Therefore, acquisition of sufficient energy reserves and the allocation of resources during reproduction can be critical to reproductive success (Crossin *et al.*, 2009). Upon return to fresh water as mature adults, *Oncorhynchus* spp. cease feeding and rely on endogenous energy stores acquired during ocean rearing to supply the energetic demands of upstream migration, gonadal maturation, development of secondary sexual characteristics, competition, spawning and maternal care in the form of redd guarding (Brett, 1995; Healey *et al.*, 2003; Quinn, 2005). The

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partitioning of energy among these different events can have strong effects on fitness, as energy allocation towards migration, gonad development or secondary sexual characteristics reduces energy reserves available for mating activities (Rand & Hinch, 1998; Kinnison *et al.*, 2003; Crossin *et al.*, 2004*b*). Insufficient energy reserves at the onset of migration or an excessive use of energy during one portion of the reproductive cycle may contribute to failed migration or spawning (Rand *et al.*, 2006; Young *et al.*, 2006; Hinch *et al.*, 2012).

Many populations of Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) undergo long migrations that can be energetically taxing (Mesa & Magie, 2006; Eiler *et al.*, 2015). Stream-type *O. tshawytscha* enter fresh water in the spring and summer, often arriving at spawning areas many weeks before they spawn (Healey, 1991). These *O. tshawytscha* require sufficient energy stores upon freshwater entry to survive both rigorous migrations and an extended holding period while fasting (Brett, 1995; Geist *et al.*, 2000). Contemporary energetic costs for *O. tshawytscha* during the adult freshwater phase may differ from historic costs due to anthropogenic or climatic changes to migration corridors and spawning habitats. For example, in the Columbia River basin of North America, many populations of *O. tshawytscha* must pass hydroelectric dams where they can be delayed as they search for fishway entrances, or they may fall back over dams and have to re-ascend (Boggs *et al.*, 2004; Keefer *et al.*, 2004*a*). Additionally, high stream temperatures along the migration route may slow migrations when *Oncorhynchus* spp. choose to hold in cooler water at the mouths of tributaries (Goniea *et al.*, 2006; Keefer *et al.*, 2009). Such migration delays could increase travel times and reduce available energy reserves prior to arrival at spawning grounds (Geist *et al.*, 2000; Mesa & Magie, 2006). Changes in run-timing as a result of increased temperatures and altered flow regimes may also affect reproductive development rates and the range of environmental conditions that fishes experience during migration, resulting in energetic demands to which a particular population is not well adapted (Cooke *et al.*, 2004; Crossin *et al.*, 2004*b*; Young *et al.*, 2006).

After arrival at spawning streams, energetic costs during the holding and spawning period may be increased by predation rates, fisheries interactions, pathogen exposure and handling at dams and weirs, in addition to water temperature (Berman & Quinn, 1991; Healey *et al.*, 2003; Wagner *et al.*, 2005). Insufficient energy has been hypothesized as one potential factor contributing to pre-spawning mortality, when adult salmonids die after reaching spawning grounds, but prior to successful reproduction (Gilhousen *et al.*, 1990; Mesa & Magie, 2006; Keefer *et al.*, 2010). Thus, knowledge of the energy required during upstream migration and holding after adults reach spawning grounds will increase understanding of constraints on energy allocation to different activities (*e.g.* migration, gamete maturation, redd building and guarding) and help managers evaluate the extent to which increased energetic costs might limit successful reproduction in vulnerable salmonid populations.

The primary goal of this research was to provide information on the patterns of energy use among different freshwater maturation stages of a spring–summer run *O. tshawytscha* population with a long migration and holding period. The study population originated in the South Fork Salmon River (SFSR) in central Idaho, part of the Snake River spring–summer *O. tshawytscha* evolutionarily significant unit, which is listed as threatened under the U.S. Endangered Species Act (ESA; NMFS, 2005). These *O. tshawytscha* enter fresh water in late spring, migrate long distances (>1000 km inland; >1500 m elevation gain) through eight dams and reservoirs in the Columbia and Snake

River hydro-system and then hold near spawning grounds for weeks or months prior to spawning in late August through to mid-September. Given the high energetic requirements of a rigorous migration and long maturation period in fresh water, this population may be particularly vulnerable to increased energetic costs during migration and holding as a result of management actions (*e.g.* fishing pressure and altered flow regimes) or climatic changes (Rand & Hinch, 1998; Rand *et al.*, 2006).

The first objective of this study was to evaluate changes in body mass, gonad mass and body morphology of *O. tshawytscha* during the maturation process to better understand how body size and shape differ among reproductive stages. The second objective was to estimate energy used during distinct stages of freshwater maturation based on sequential proximate analysis. Understanding how fishes partition energy during maturation can provide insights into how various stages might respond to environmental or phenological changes, such as increased water temperatures or earlier migration timing (Rand *et al.*, 2006; Crozier *et al.*, 2008). A third objective was to test whether energy depletion was a direct cause of pre-spawning mortality by comparing final energy content of *O. tshawytscha* that died on spawning grounds, but prior to spawning (pre-spawn mortalities), with *O. tshawytscha* that spawned successfully. To examine whether migration delays led to excessive energy expenditures and reduced fitness, a fourth objective was to evaluate associations between individual migration history and energy stores upon arrival at spawning grounds and the spawning success of *O. tshawytscha*.

MATERIALS AND METHODS

FISH COLLECTIONS

The SFSR is a tributary to the Salmon River, which flows into the Snake and then Columbia Rivers (Fig. 1). Adult *O. tshawytscha* were collected at Bonneville Dam (rkm 235 from the ocean), upon arrival at a weir within the SFSR spawning area (rkm 1155; elevation *c*. 1550 m) and on spawning grounds (20 km both downstream and upstream of the weir). *Oncorhynchus tshawytscha* returning to the SFSR travelled 460 km and gained 180 m elevation during passage of eight hydroelectric dams and seven reservoirs, from Bonneville Dam to Lower Granite Dam (695 rkm), the uppermost dam on their migration route and the last location where marked individuals were detected within the regulated migratory corridor (Fig. 1). They then travelled an additional 460 km with 1370 m elevation gain through the Lower Granite Dam reservoir, the lower Snake River and the free-flowing Salmon River to reach spawning grounds.

In 2002, *O. tshawytscha* were sampled for proximate analysis during four collection periods along their migration route and on spawning grounds and an additional collection was taken on the spawning area in 2014 (Table I). Owing to the protected status of Snake River spring–summer *O. tshawytscha*, collection permits only allowed for sampling of spawn-ready *O. tshawytscha* in 2014 as a follow-up to the original 2002 study. The first collection occurred between 19 May and 10 June 2002 at Bonneville Dam (Fig. 1), hereafter considered the migration start. *Oncorhynchus tshawytscha* ascending the dam *via* a fish ladder were diverted into a trapping and sorting facility where spring–summer *O. tshawytscha* of known origin were identified based on passive integrative transponder (PIT) tags that had been implanted in juvenile outmigrants (Keefer *et al.*, 2008). *Oncorhynchus tshawytscha* were trapped, anaesthetized and sacrificed in the same manner described by Mesa & Magie (2006). Sampled *O. tshawytscha* originated either from the SFSR, or from other drainages of the Snake and Salmon Rivers, locations that required passage of the same series of dams and migration of a similar distance. Hence, all *O. tshawytscha* in this collection were assumed to have similar energetic requirements and initial energy reserves at the start of upriver migration.

The second collection occurred between 3 and 23 July 2002 at a weir located within spawning habitat on the SFSR (termed arrival at spawning grounds) using the same method of lethal
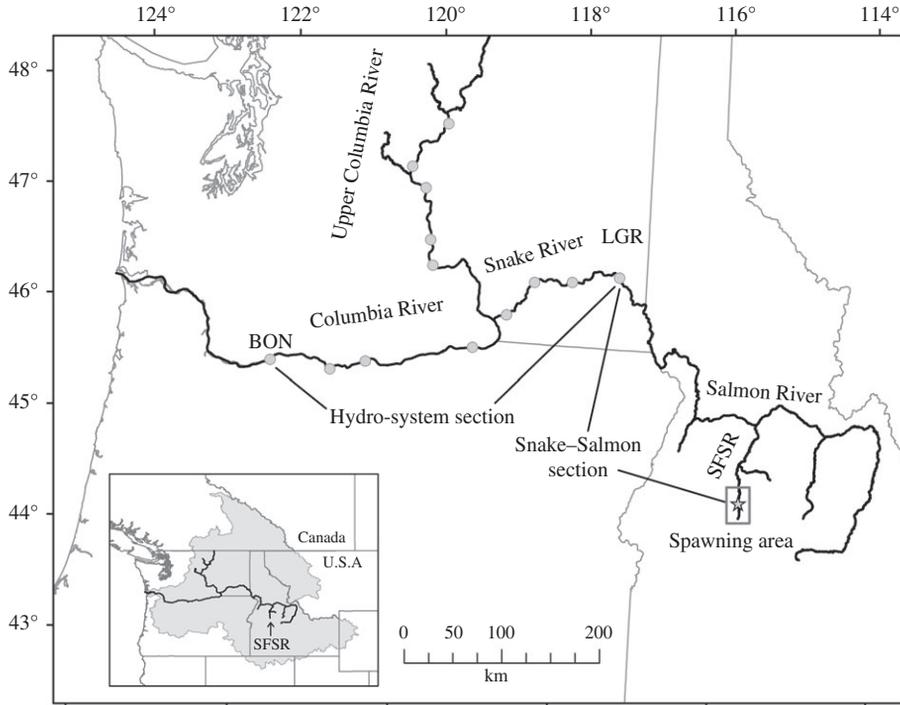
FIG. 1. Map of spring–summer *Oncorhynchus tshawytscha* collection sites at Bonneville Dam (BON) on the Columbia River (rkm 234), the South Fork Salmon River (SFSR) weir in central Idaho (rkm 1155; ☆) and the SFSR spawning area (rkm *c.* 1125–1175; ☐). The migratory corridor was divided into two distinct sections: the hydro-system section (rkm 234–695), with a series of eight dams (◎), and the Snake–Salmon section (rkm 695–1155) from Lower Granite Dam (LGR) to the SFSR weir. Inset shows the location of the SFSR within the Columbia River Basin (▭) on the border of the U.S.A. and Canada.

take as above. Collections three and four were composed of carcasses recovered from spawning grounds during the period of active spawning to evaluate energetic content of *O. tshawytscha* that died prior to release of gametes and thus had completed the holding period but failed to spawn (collection three; *i.e.* pre-spawning mortality) and those that had released gametes and presumably spawned successfully (collection four; *i.e.* post-spawning mortality). A carcass with >75% of expected gonad mass remaining after death was considered a pre-spawning mortality and a carcass with <25% gonad mass remaining a post-spawning mortality (Young & Blenden, 2011). Carcass sampling occurred during periods of observed spawning from 13 to 30 August 2002. All recovered carcasses were recent mortalities, as qualitatively determined by firm muscle, at least one clear eye and pink gill colour. Due to permitting restrictions, only known hatchery-origin *O. tshawytscha* with clipped adipose fins were included in collections from the first two locations, whereas recovered carcasses included individuals of both known hatchery and presumed natural origin (those with an adipose fin).

In 2014, a fifth collection was used to evaluate proximate composition of *O. tshawytscha* just prior to spawning activity (spawn-ready; Table I). Spawn-ready *O. tshawytscha* were not collected in 2002 due to permitting restrictions. The 2014 spawn-ready collection was used to test whether pre-spawning mortalities had similar mass and energetic composition to *O. tshawytscha* that survived to spawn (*i.e.* pre-spawning mortality *O. tshawytscha* were comparable with spawn-ready *O. tshawytscha*). The 2014 sample comprised *O. tshawytscha* that were taken at the weir and held in man-made ponds adjacent to the SFSR for use as brood stock at the McCall Fish Hatchery. Females were held until they were completely ripe (eggs were loose

TABLE I. Collection stage, sites and dates, sample sizes (n), fork length (L_F) and mass of female (F) and male (M) spring–summer *Oncorhynchus tshawytscha* returning to the South Fork Salmon River (SFSR), Idaho. A supplementary collection in 2014 comprised *O. tshawytscha* that were sampled at the onset of spawning (spawn-ready)

Collection	Location	Date	Sex	n	L_F Mean ± s.d. (mm)	Mass Mean ± s.d. (g)
Migration	Bonneville Dam	19 May–10 June 2002	F	32	831 ± 71	7961 ± 2040
			M	24	827 ± 78	7831 ± 2381
Arrival	SFSR salmon weir	3–23 July 2002	F	26	805 ± 55	5829 ± 1143
			M	24	809 ± 56	5864 ± 1429
Pre-spawning	Spawning grounds	13–30 August 2002	F	16	798 ± 65	5191 ± 1362
			M	12	761 ± 48	5360 ± 2008
Post-spawning	Spawning grounds	10–30 August 2002	F	23	837 ± 60	4676 ± 967
			M	17	903 ± 126	6907 ± 2705
Supplementary collection						
Spawn-ready	SFSR broodstock	14–21 August 2014	F	12	768 ± 47	4758 ± 998

Migration, *O. tshawytscha* at the start of freshwater migration; arrival, upon arrival at spawning grounds; pre-spawning, mortalities prior to spawning; post-spawning, mortalities after spawning; spawn-ready, *O. tshawytscha* that spawned successfully.

in the body cavity and ready to be expressed), at which time *O. tshawytscha* were euthanized and the eggs removed. The sample included both hatchery and natural-origin *O. tshawytscha* collected for analysis between 14 and 21 August 2014. Proximate analysis was conducted only on spawn-ready females, as the number of males was limited. Gametes were weighed but could not be evaluated for energy content because they were used by the hatchery.

MORPHOLOGICAL CHANGE

At each collection, various aspects of *O. tshawytscha* size and shape were measured to evaluate changes in body morphology during the reproductive period. Body fork length (L_F) was measured to the nearest mm, total mass to the nearest 10 g and gonad mass to the nearest g. Snout length (L_{Sn}, distance from tip of snout to middle of the eye) and hump height (H_H, portion of body depth from anterior insertion of dorsal fin to lateral line; Kinnison *et al.*, 2003) were measured with callipers to the nearest mm.

To assess morphological changes during migration and reproduction while accounting for trait variation resulting directly from body size, ANCOVA (type III sums of squares) was used to compare among 2002 collection locations, with L_F included as a covariate (Hendry & Berg, 1999; Crossin *et al.*, 2004b). The effect of collection location on morphological traits was evaluated with the ANCOVA model: $Y_{ij} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ij}$, where Y_{ij} was the response variable (somatic mass, gonad mass, hump height or snout length), α_i was the main effect of collection location, β_j was the L_F covariate, $\alpha\beta_{ij}$ was the interaction between collection and L_F and ε_{ij} was random error. Physical traits and L_F were $\log_{10}$ transformed in analyses (Hendry & Berg, 1999; Hendry *et al.*, 2000; Kinnison *et al.*, 2003) because physical trait variables increased allometrically with L_F (Kinnison *et al.*, 2001; Froese, 2006) and to meet ANCOVA assumptions of linearity and homogeneity of variance (Huitema, 2011). Levene's test was used to assess homogeneity of variance and residuals were examined to evaluate normality of error terms. In all cases, the slope of the relationship between L_F and morphological traits did not vary among collections (all interaction $P > 0.05$ in ANCOVA models), so the $L_F \times$ stage interaction term was removed and adjusted means were calculated based on the common slope (Huitema, 2011).

Adjusted means were back-transformed for presentation. Sexes were analysed separately and significant differences among collections were identified based on Tukey's HSD *post hoc* test with the package multcomp in R 3.1.1 (Torsten *et al.*, 2008). These and all subsequent statistical analyses were performed in R version 3.1.1 (www.r-project.org). Because of the confounding year effect, the 2014 spawn-ready collection was not included in the initial analysis. Instead, the 2002 pre-spawning and 2014 spawn-ready collections were compared independently with two separate ANCOVA models, with $\log_{10}$ somatic mass and $\log_{10}$ gonad mass as separate response variables, $\log_{10} L_F$ as the covariate and collection location as the independent variable.

PROXIMATE COMPOSITION AND ENERGY DENSITY

To evaluate the proximate composition and energy density for constituent parts of each *O. tshawytscha*, viscera (excluding kidney) and gonads were removed and a large, rectangular muscle sample (*c.* 70 mm × 120 mm, 150 g) was taken from the left side of the *O. tshawytscha* just anterior to the insertion of the dorsal fin and continuing to the centre of the abdomen (Mesa & Magie, 2006). Muscle and skin were separated and tissue samples of viscera, gonad, skin and muscle were each weighed and homogenized in a commercial-grade food processor. A 50 g subsample of homogenate from each tissue was retained and stored at −20° C until analysis. Equipment was washed and dried between samples.

For each tissue sample, lipid, protein, ash and moisture content was assessed by proximate analysis conducted at the Washington State University Wildlife Habitat and Nutrition Laboratory. Tissue samples were freeze-dried and dry mass was subtracted from wet mass to calculate water content. Lipid content was estimated using Soxhlet extraction with anhydrous diethyl ether as a solvent. Ash content was determined by heating a subsample of tissue at 600° C for 12 h. Lipid and ash percentages by dry mass were multiplied by per cent dry material in the original sample to estimate per cent wet-tissue mass (Jonsson *et al.*, 1997; Hendry & Berg, 1999). Following similar research, carbohydrates were ignored because they typically make up less than 0·5% of somatic tissue in salmonids and protein content was calculated based on % protein = 100 − % water − % lipid − % ash (Berg *et al.*, 1998; Hendry & Berg, 1999; Mesa & Magie, 2006). Energy density (kJ g^{-1}) of each tissue was calculated by multiplying the percentage of lipid and protein contents by their energy equivalents (36·4 kJ g^{-1} for lipids and 20·1 kJ g^{-1} for protein; Brett, 1995), commonly applied in proximate analyses (Hendry *et al.*, 2004; Mesa & Magie, 2006; Penney & Moffitt, 2014).

Initial analyses of both 2002 and 2014 samples for each sex showed that proximate composition of viscera, skin, muscle and gonad tissue was not correlated with L_F, nor was energy density of any tissue (all ANCOVA $P > 0·05$ for the covariate L_F), so L_F was not included in final analyses of proximate composition and energy density. ANOVA was used to evaluate differences in per cent moisture, per cent lipid, per cent protein and energy density among collection locations for each sex separately with the model: $Y_i = \mu + \alpha_i + \varepsilon_i$, where Y_i was the response variable (% moisture, % lipid, % protein or energy density), μ was the overall mean, α_i was the main effect of collection location and ε_i was random error. These analyses were repeated for each tissue (viscera, skin, muscle and gonad). Tukey's HSD *post hoc* test was again used to identify significant differences among collections. To test for differences in energy density between the 2002 pre-spawning and 2014 spawn-ready collections, separate two-sample *t*-tests were used for each tissue (viscera, skin and muscle).

ENERGETIC COSTS OF MIGRATION AND REPRODUCTION

The total energy in each major tissue component (gonad, viscera, skin and muscle) was calculated for each *O. tshawytscha* based on the energy density from proximate analysis multiplied by total mass of each tissue. Gonads, viscera and the remaining eviscerated body mass were weighed separately. For gonads and viscera, energy density was multiplied by observed tissue mass. Total mass of skin and muscle were estimated separately based on standard proportions of total eviscerated body mass from 10 *O. tshawytscha* of a range of sizes for each sex sampled at each collection location (*e.g.* muscle comprised 0·62 of female eviscerated body mass at migration start and 0·65 upon arrival at spawning grounds). Total skin and muscle energy were then estimated separately for each individual by multiplying the total eviscerated mass,

standard proportion of skin or muscle for collection location and the estimate of individual energy density of skin or muscle from subsamples analysed by proximate analysis. Total somatic energy per *O. tshawytscha* (kJ individual^{-1}) was calculated as the sum of total energy values in muscle, skin and viscera. To test whether pre-spawning mortalities had similar total energy to spawn-ready *O. tshawytscha*, $\log_{10}$ somatic energy was compared between 2002 pre-spawning and 2014 spawn-ready collections using ANCOVA with $\log_{10} L_F$ as a covariate and collection location as the independent variable.

Using a technique applied to similar studies of salmonid energetics (Jonsson *et al.*, 1997; Hendry & Berg, 1999; Crossin *et al.*, 2003, 2004*b*), the costs of active metabolism and gonad development were estimated for three different maturation stages by comparing mean energy values at beginning and ending collection locations while statistically controlling for body size. The three stages were (1) migration (from the start of migration to arrival at spawning grounds), (2) holding (from arrival at spawning grounds to pre-spawning mortalities) and (3) spawning (pre-spawning mortalities relative to post-spawning mortalities). For each sex, $\log_{10}$ gonad energy was regressed on $\log_{10} L_F$ at each collection location to estimate energy used for ovarian or testes development. Estimation of somatic energy use was done in the same manner, with sexes analysed separately. ANCOVA was used to assess heterogeneity of slopes between the four collection locations. For both sexes, the slope of the relationship between L_F and somatic or gonad energy did not differ among collection locations (ANCOVA, $P > 0.05$ for all interactions), so the difference between intercepts provided an estimate of the change in the amount of energy in gonads and soma during each maturation stage (Hendry & Berg, 1999; Hendry *et al.*, 2000; Crossin *et al.*, 2004*b*). Whereas gonad energy was measured directly, energy used for metabolism and development of secondary sexual characteristics during each stage was inferred based on the difference between intercepts in the somatic energy model minus energy diverted to gonad development during that stage (Hendry & Berg, 1999; Crossin *et al.*, 2003, 2004*b*). Estimates of metabolic energy use were primarily attributed to active metabolic costs, as standard metabolism comprises a relatively small percentage of the energy budget in migrating salmonids (*e.g.* 7%; Rand & Hinch, 1998). This procedure assumed that *O. tshawytscha* did not change in L_F between maturation stages and nor was the energy in bones and connective tissue labile. The former assumption was validated by comparing L_F measurements of individually marked *O. tshawytscha* at Bonneville Dam with measurements of those same *O. tshawytscha* recovered after death on spawning grounds ($n = 55$). Observed changes in L_F were similar to estimated measurement error (± 10 mm). The total cost of reproduction was calculated as the sum of energy used during all stages plus total energy allocated toward gonad production.

MIGRATION HISTORIES OF INDIVIDUALLY MARKED *O. TSHAWYTSCHA*

A subset of *O. tshawytscha* collected for analysis in this study were individually marked with PIT tags during outmigration as juveniles or with radio tags and PIT tags at Bonneville Dam as returning adults (Keefer *et al.*, 2004*b*). For these *O. tshawytscha*, migration time between Bonneville Dam and arrival at spawning grounds was calculated based on detections at a series of fixed PIT-tag antennas and radio telemetry receivers along the migration route (Keefer *et al.*, 2004*b*). Individually marked *O. tshawytscha* were identified upon arrival at the SFSR weir and when carcasses were recovered on spawning grounds. Travel time was also calculated for both halves of the migration (Fig. 1): from Bonneville Dam to Lower Granite Dam (hydro-system section) and from Lower Granite Dam to spawning grounds (Snake–Salmon section).

Twenty-five individually marked *O. tshawytscha* (13 females and 12 males) were collected for proximate analysis upon arrival at spawning grounds and their energetic values were compared with migration times. Linear regression was used to evaluate the relationship between energy density of muscle, viscera and skin as separate response variables and total migration time and migration date as predictor variables. Although migration rate is typically correlated with migration date (Keefer *et al.*, 2004*a, b*), it was not in this dataset, probably because all *O. tshawytscha* started migration within a relatively short time frame of 30 days. Migration date was therefore included as a predictor variable to account for potential abiotic variations in migration conditions that can affect migration rates (*e.g.* discharge and temperature). A second set of regression equations were used to evaluate the relationship between the same three response variables

and migration times within the two halves of the migration separately plus migration date as predictor variables, as described by: energy density$_{tissue}$ = migration time$_{hydro-system}$ + migration time$_{Snake-Salmon}$ + migration date + ε.

Individually marked *O. tshawytscha* were also recovered from spawning grounds after death; nine were pre-spawning mortalities and 14 were post-spawning mortalities. To assess the potential effect of travel and holding times on spawning success (*i.e.* pre-spawning mortalities *v.* post-spawning mortalities), four separate two-sample *t*-tests were used to compare the differences in (1) total travel times, (2) travel time in the hydro-system migration corridor, (3) travel time in the Snake−Salmon migration corridor and (4) time between arrival at spawning grounds and death (*e.g.* holding and spawning period).

RESULTS

MORPHOLOGICAL CHANGES

Morphological attributes were correlated with L_F across all collections. After controlling for the effect of L_F, trait sizes varied considerably among collections and collection and L_F combined explained most of the variation in trait size ($r^2 = 0.75-0.96$ except for male gonad mass; Table II). For females, somatic mass decreased by 24% during migration and by an additional 18% between arrival at spawning grounds and pre-spawning mortalities [Table II and Fig. 2(a)]. Male somatic mass decreased by 21 and 12%, respectively [Table II and Fig. 2(b)]. After controlling for L_F, somatic mass was similar between 2002 pre-spawning mortalities and 2014 spawn-ready *O. tshawytscha* ($F_{1,27} = 0.01$, $P > 0.5$).

Average female gonad mass more than doubled during migration and then nearly doubled again during the holding period, with a total increase of 392% between the start of migration and spawning [Table II and Fig. 2(c)]. There was no statistical difference in gonad mass between 2014 spawn-ready and 2002 pre-spawning mortality females ($F_{1,27} = 0.22$, $P > 0.5$). Male gonad mass increased by 178% during migration, but did not change substantively during the holding period (Table II). Male snout length increased by 10% during migration and by an additional 12% prior to spawning [Table II and Fig. 2(d)]. Hump height decreased during migration and holding for both males and females (Table II).

PROXIMATE COMPOSITION AND ENERGY DENSITY

With the exception of gonads, changes in proximate composition were similar for males and females. Both sexes used more than half of their lipid stores from muscle and skin and the majority of visceral lipid stores between the start of migration and arrival at spawning grounds (Table III). Muscle and skin lipids also decreased significantly between arrival on spawning grounds and pre-spawning death. Comparisons between pre-spawning and post-spawning mortalities suggested that both sexes metabolized muscle lipid, as well as protein from both muscle and visceral tissues during spawning (Table III). Per cent skin lipid was also significantly lower in post-spawning than pre-spawning females. Concurrent with decreases in per cent lipid and protein, the relative water content in tissues increased in each sequential collection.

For both males and females, muscle, viscera and skin energy densities all decreased significantly between the start of migration and arrival at spawning grounds (Table III). Between arrival and spawning, energy densities in all three tissues also decreased

TABLE II. ANCOVA results for somatic mass (M_S), gonad mass (M_G), dorsal hump height (H_H) and snout length (L_{Sn}) on fork length (L_F), including F-values for collection location and L_F and overall model coefficient of determination (r^2). No interaction term was included because slopes did not differ significantly among collection locations. Physiological traits and L_F were $\log_{10}$ transformed. Adjusted means were back-transformed to show predicted trait at each collection location for female (mean $\pm$ S.D. $L_F = 815 \pm 65$ mm) and male (mean $\pm$ S.D. $L_F = 830 \pm 94$ mm) spring−summer *Oncorhynchus tshawytscha* from the South Fork of the Salmon River, Idaho. Within-sex groupings with the same superscript lower case letter are not significantly different (Tukey's HSD test; $P > 0.05$)

	F			Adjusted mean trait size at collection			
Physiological trait	Collection (d.f.)	L_F (d.f.)	r^2	Migration	Arrival	Pre-spawning	Post-spawning
Females							
M_S (g)	303·19*** (3, 94)	878·74*** (1, 94)	0·95	7115[a]	5393[b]	4420[c]	4152[c]
M_G (g)	675·78*** (3, 88)	128·08*** (1, 88)	0·96	259[a]	577[b]	1014[c]	57[d]
H_H (mm)	308·80*** (3, 94)	210·78*** (1, 94)	0·93	101[a]	81[b]	72[c]	69[c]
L_{Sn} (mm)	1·69 (3, 94)	271·48*** (1, 94)	0·75	72[a]	73[a]	71[a]	73[a]
Males							
M_S (g)	122·87*** (3, 79)	1375·94*** (1, 79)	0·95	7453[a]	5861[b]	5157[c]	4726[c]
M_G (g)	35·46*** (3, 78)	5·46** (1, 78)	0·56	86[a]	239[b]	185[b]	75[a]
H_H (mm)	121·46*** (3, 79)	439·39*** (1, 79)	0·91	105[a]	85[b]	81[b]	79[b]
L_{Sn} (mm)	82·90*** (3, 79)	575·32*** (1, 79)	0·93	79[a]	87[b]	97[c]	100[c]

Migration, *O. tshawytscha* at the start of freshwater migration; arrival, upon arrival at spawning grounds; pre-spawning, mortalities prior to spawning; post-spawning, mortalities after spawning. **$P < 0.01$; ***$P < 0.001$.

in females and energy density of muscle and skin decreased in males. Energy density of viscera was higher in spawn-ready *O. tshawytscha* than pre-spawning mortalities ($t = 3.95$, d.f. $= 26$, $P < 0.01$), but there were no differences in energy density of muscle and skin between 2014 spawn-ready and 2002 pre-spawning mortalities females (muscle: $t = 0.87$, d.f. $= 26$, $P > 0.05$; skin: $t = 0.69$, d.f. $= 26$, $P > 0.05$). In contrast, pre-spawning mortalities had higher energy density in muscle tissue than did post-spawning mortalities (Table III). The average somatic energy density in metabolizable mass (*i.e.* viscera, muscle and skin combined, not including skeleton) remaining after death was 3·6 and 4·1 kJ g^{-1} for post-spawning females and males, respectively.

ENERGETIC COSTS OF MIGRATION AND REPRODUCTION

The estimated total cost of reproduction between freshwater entry and death, including initial gonadal energy at the start of migration, was 92% of initial energy
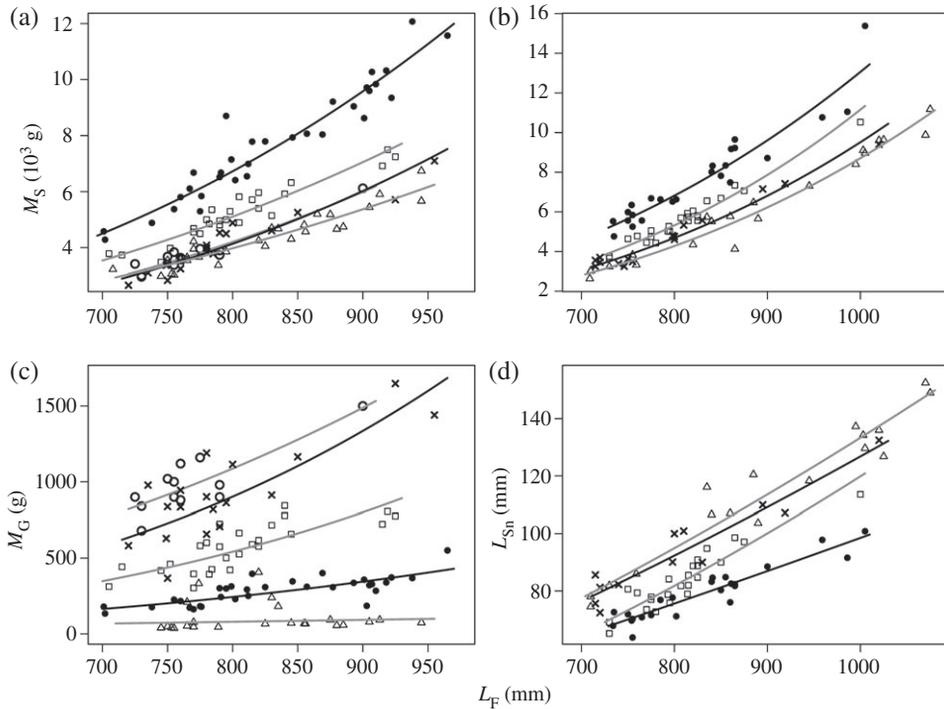
FIG. 2. The relationship between fork length (L_F) and (a) female and (b) male somatic mass (M_S), (c) female gonad mass (M_G) and (d) male snout length (L_{Sn}) for *Oncorhynchus tshawytscha* collected in 2002 at the start of migration [●; (a) $M_S = 2·95\ L_F - 7·74$; $r^2 = 0·92$; d.f. = 30; $P < 0·001$; (b) $M_S = 2·91\ L_F - 7·62$; $r^2 = 0·92$; d.f. = 22; $P < 0·001$; (c) $M_G = 2·95\ L_F - 6·16$; $r^2 = 0·59$; d.f. = 30; $P < 0\ 0·001$; (d) $L_{Sn} = 1·19\ L_F - 1·57$; $r^2 = 0·87$; d.f. = 22; $P < 0·001$], arrival at spawning grounds [□, (a) $M_S = 2·74\ L_F - 7·24$; $r^2 = 0·89$; d.f. = 24; $P < 0·001$; (b) $M_S = 3·32\ L_F - 8·91$; $r^2 = 0·95$; d.f. = 22; $P < 0·001$; (c) $M_G = 3·31\ L_F - 6·89$; $r^2 = 0·59$; d.f. = 24; $P < 0·001$; (d) $L_{Sn} = 1·71\ L_F - 3·06$; $r^2 = 0·84$; d.f. = 22; $P < 0·001$], pre-spawning mortalities [×, (a) $M_S = 2·97\ L_F - 8·01$; $r^2 = 0·91$; d.f. = 14; $P < 0·001$; (b) $M_S = 3·03\ L_F - 8·12$; $r^2 = 0·98$; d.f. = 10; $P < 0·001$; (c) $M_G = 2·84\ L_F - 5·25$; $r^2 = 0·63$; d.f. = 14; $P < 0·001$; (d) $L_{Sn} = 1·42\ L_F - 2·16$; $r^2 = 0·88$; d.f. = 10; $P < 0·001$] and post-spawning mortalities [△, (a) $M_S = 2·48\ L_F - 6·60$; $r^2 = 0·89$; d.f. = 23; $P < 0·001$; (b) $M_S = 2·97\ L_F - 7·97$; $r^2 = 0·95$; d.f. = 22; $P < 0·001$; (c) $M_G = 2·85\ L_F - 6·55$; $r^2 = 0·65$; d.f. = 13; $P < 0·001$; (d) $L_{Sn} = 1·49\ L_F - 2·35$; $r^2 = 0·92$; d.f. = 22; $P < 0·001$]. L_F, M_S, M_G, and L_{Sn} were log10 transformed in analyses and equations; data were back-transformed in plots for ease of interpretation. Females collected at the start of spawning in 2014 (○) were not included in statistical analysis (no model fit line) but are shown for reference.

stores for females, 78% of which was used for metabolism and 14% for ovarian development. Males used 82% of initial energy stores prior to death, 80% for metabolism and development of secondary sexual characteristics and only 2% for testes development. Females allocated 46% of initial somatic energy towards metabolism during migration, 25% during holding and 7% for spawning [Fig. 3(a)]. Males used 41, 28 and 11% of initial somatic energy during migration, holding and spawning, respectively [Fig. 3(b)]. The average energetic cost of reproduction was 8·4 and 7·3 kJ g^{-1} for females and males, respectively.

Total somatic energy of female 2014 spawn-ready *O. tshawytscha* was comparable to that of 2002 female pre-spawning mortalities ($F_{1,27} = 2·14$, $P > 0·05$). On

TABLE III. Mean ± S.D. proximate composition (per cent water, lipid and protein by wet mass) and energy density (kJ g^{-1}) of the muscle, viscera, skin and gonads of female and male spring–summer *Oncorhynchus tshawytscha* from the South Fork Salmon River, Idaho, at different collection locations: at the start of freshwater migration (migration), upon arrival at spawning grounds (arrival), at the onset of spawning (spawn-ready; females only), *O. tshawytscha* that died prior to spawning (pre-spawning mortalities) and *O. tshawytscha* that completed spawning (post-spawning mortalities). Within-sex groupings with the same superscript lower case letter are not significantly different (Tukey's HSD test; $P > 0.05$). Spawn-ready *O. tshawytscha* were collected in 2014, and were not included in the formal analysis but values are provided for comparison; all other samples were collected in 2002

Tissue	Stage	Females					Males				
		n	Water	Lipid	Protein	Energy	n	Water	Lipid	Protein	Energy
Muscle	Migration	32	57.9 ± 2.3[a]	21.5 ± 3.4[a]	19.3 ± 2.0[a]	11.7 ± 1.0[a]	24	57.3 ± 2.5[a]	22.9 ± 3.5[a]	18.7 ± 1.8[a]	12.1 ± 1.1[a]
	Arrival	26	70.0 ± 3.1[b]	7.8 ± 2.5[b]	21 ± 2.0[a]	7.1 ± 0.9[b]	24	67.1 ± 2.5[b]	10.9 ± 3.0[b]	20.8 ± 1.9[b]	8.2 ± 0.9[b]
	Spawn-ready	12	77.6 ± 1.2	1.2 ± 0.5	19.9 ± 1.0	4.4 ± 0.3	—	—	—	—	—
	Pre-spawning	16	80.1 ± 1.9[c]	2.8 ± 1.3[c]	16.2 ± 1.2[b]	4.4 ± 1.2[c]	12	73.9 ± 3.6[c]	5.9 ± 2.9[c]	19.2 ± 1.5[ab]	6.0 ± 1.2[c]
	Post-spawning	23	83.1 ± 3.0[d]	1.1 ± 1.1[d]	14.5 ± 2.2[c]	3.4 ± 0.7[d]	17	80.0 ± 3.9[d]	3.1 ± 2.9[d]	16.4 ± 1.7[c]	4.4 ± 1.2[d]
Viscera	Migration	32	73.8 ± 2.6[a]	4.4 ± 3.4[a]	20.4 ± 2.0[a]	5.7 ± 1.1[a]	24	73.1 ± 3.0[a]	5.9 ± 3.1[a]	19.7 ± 1.9[a]	6.1 ± 1.1[a]
	Arrival	26	76.7 ± 1.8[b]	0.8 ± 0.3[b]	21.0 ± 1.6[a]	4.5 ± 0.4[b]	24	76.7 ± 1.7[b]	1.0 ± 0.4[b]	20.9 ± 1.5[a]	4.6 ± 0.4[b]
	Spawn-ready	12	78.0 ± 0.8	1.1 ± 0.3	19.5 ± 1.0	4.3 ± 0.2	—	—	—	—	—
	Pre-spawning	16	80.3 ± 1.7[c]	0.9 ± 0.4[b]	17.6 ± 1.7[b]	3.9 ± 0.4[c]	12	79.5 ± 1.5[c]	0.9 ± 0.3[b]	18.6 ± 1.4[a]	4.0 ± 0.3[bc]
	Post-spawning	23	82.1 ± 1.3[d]	0.9 ± 0.2[b]	15.9 ± 1.3[c]	3.5 ± 0.3[c]	17	81.2 ± 1.5[c]	0.9 ± 0.2[b]	16.8 ± 1.5[b]	3.7 ± 0.3[c]
Skin	Migration	32	40.4 ± 2.4[a]	40.7 ± 3.2[a]	17.6 ± 3.0[a]	18.4 ± 0.9[a]	24	41.2 ± 3.1[a]	38.2 ± 5.2[a]	19.3 ± 2.8[a]	17.8 ± 1.4[a]
	Arrival	26	58.3 ± 4.7[b]	13.6 ± 5.3[b]	26.5 ± 4.1[b]	10.3 ± 1.6[b]	24	56.1 ± 3.4[b]	17.6 ± 5.1[b]	24.9 ± 3.7[a]	11.4 ± 1.4[b]
	Spawn-ready	12	64.4 ± 4.2	0.4 ± 0.4	30.6 ± 3.8	6.9 ± 0.7	—	—	—	—	—
	Pre-spawning	16	69.3 ± 3.5[c]	4.5 ± 3.4[c]	24.9 ± 2.5[b]	6.6 ± 1.2[c]	12	66.4 ± 3.2[c]	5.7 ± 2.9[c]	26.7 ± 1.9[b]	7.4 ± 1.1[c]
	Post-spawning	23	72.0 ± 3.5[d]	1.2 ± 1.4[d]	25.5 ± 1.8[b]	5.7 ± 0.5[c]	17	67.2 ± 4.6[c]	5.5 ± 4.5[c]	26.4 ± 4.9[b]	7.3 ± 1.4[c]
Gonad	Migration	32	56.0 ± 2.4[a]	10.2 ± 2.6[a]	32.3 ± 2.4[a]	10.2 ± 0.8[a]	24	78.3 ± 3.8[a]	0.8 ± 0.3[a]	18.7 ± 3.9[a]	4.1 ± 0.8[a]
	Arrival	26	53.8 ± 1.3[a]	7.9 ± 3.1[b]	36.3 ± 3.0[b]	10.2 ± 0.7[a]	24	74.8 ± 2.2[ab]	1.2 ± 0.2[b]	20.4 ± 2.4[a]	4.5 ± 0.5[a]
	Pre-spawning	16	58.3 ± 2.9[a]	6.4 ± 1.3[b]	33.4 ± 2.[2ab]	9.0 ± 0.7[a]	12	73.1 ± 3.6[b]	1.4 ± 0.5[b]	20.2 ± 3.0[a]	4.6 ± 0.7[a]
	Post-spawning	23	79.3 ± 11.3[b]	2.8 ± 2.0[c]	16.9 ± 9.4[c]	4.4 ± 2.6[b]	16	83.0 ± 6.2[c]	0.9 ± 0.3[a]	13.6 ± 4.7[b]	3.1 ± 1.0[b]
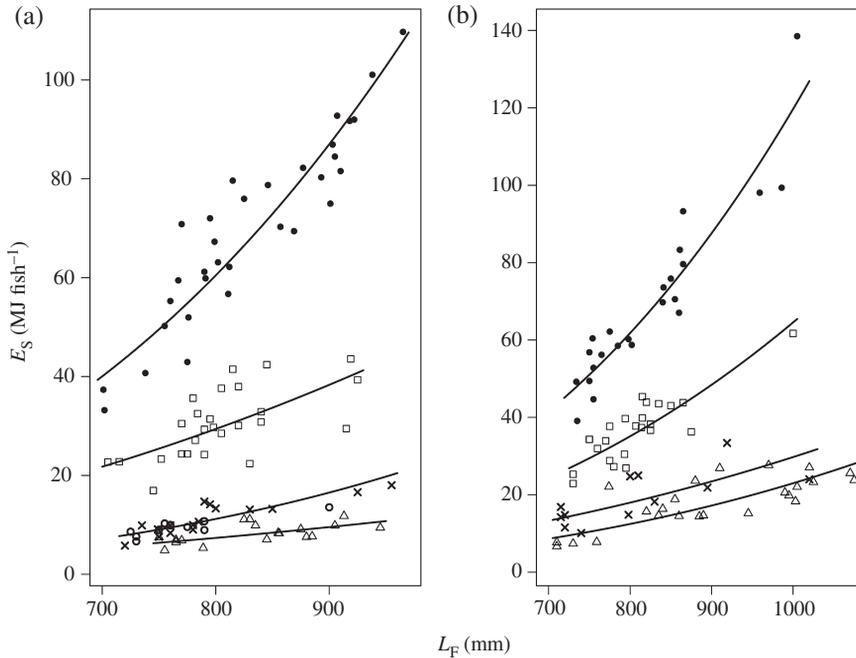
Fig. 3. Relationship between fork length (L_F) and total somatic energy (E_S) for (a) female and (b) male *Oncorhynchus tshawytscha* collected in 2002 at the start of migration [●, (a) $E_S = 3.09\ L_F - 7.18$; $r^2 = 0.84$; d.f. = 30; $P < 0.001$; (b) $E_S = 2.96\ L_F - 6.81$; $r^2 = 0.88$; d.f. = 21; $P < 0.001$], arrival at spawning grounds [□, (a) $E_S = 2.25\ L_F - 5.07$; $r^2 = 0.42$; d.f. = 24; $P < 0.001$; (b) $E_S = 2.73\ L_F - 6.37$; $r^2 = 0.67$; d.f. = 22; $P < 0.001$], pre-spawning mortalities [×, (a) $E_S = 3.31\ L_F - 8.55$; $r^2 = 0.72$; d.f. = 14; $P < 0.001$; (b) $E_S = 2.26\ L_F - 5.30$; $r^2 = 0.54$; d.f. = 10; $P < 0.01$] and post-spawning mortalities [△, (a) $E_S = 2.21\ L_F - 5.56$; $r^2 = 0.41$; d.f. = 16; $P < 0.01$; (b) $E_S = 2.74\ L_F - 6.87$; $r^2 = 0.66$; d.f. = 22; $P < 0.001$]. L_F and E_S were log10 transformed in analyses and equations; data were back-transformed in plots for ease of interpretation. Females collected in 2014 at the start of spawning (○) were not included in statistical analysis (no model fit line) but are shown for reference.

average, pre-spawning mortalities retained more somatic energy upon death than did post-spawning mortalities, although a few pre-spawning mortalities had final energetic values similar to those of post-spawning mortalities (Fig. 3).

MIGRATION HISTORIES OF INDIVIDUALLY MARKED *O. TSHAWYTSCHA*

Individually marked *O. tshawytscha* travelled through the hydro-system section of the migration corridor faster than the Snake–Salmon section (hydro-system: mean = 15 days, range = 9–26 days, rate = 18–51 km day^{-1}; Snake–Salmon: mean = 24 days, range = 15–53 days, rate = 9–31 km day^{-1}). Travel time through the hydro-system section of the migration route was not correlated with travel time through the Snake–Salmon reach (Pearson's $r = 0.2$, $P > 0.05$). Overall, both sexes took an average of 37 days (range = 27–53 days) to make the entire 920 km migration travelling at an average rate of 25 km day^{-1} (range = 12–34 km day^{-1}). After arrival at spawning grounds, marked *O. tshawytscha* spent between 19 and 53 days

(mean = 43 days) holding before death (including spawning, for post-spawning *O. tshawytscha*).

Travel time in the hydro-system section was negatively related to muscle energy density upon arrival at the SFSR spawning grounds ($r^2 = 0.22$, $P = 0.01$), after accounting for the effect of migration date and travel time in the Snake–Salmon section. There was no difference in skin or viscera energy density. Travel time in the Snake–Salmon section was not a significant predictor of energy densities in these same models. Muscle energy density was 7–16% lower upon arrival at spawning grounds for *O. tshawytscha* that had a migration rate below the median observed rate in the hydro-system section compared with those that migrated faster than the median. After controlling for migration date, total migration travel time between Bonneville Dam and the SFSR weir was not a significant predictor of muscle, skin or viscera energy densities of *O. tshawytscha* upon arrival at spawning grounds.

There was no difference in travel time between successful spawners and pre-spawning mortalities through the hydro-system reach ($t = -0.49$, d.f. = 17, $P > 0.05$), Snake–Salmon section ($t = -0.32$, d.f. = 13, $P > 0.05$) or from Bonneville Dam to spawning grounds ($t = -0.62$, d.f. = 10, $P > 0.05$). Likewise, there was no difference in the amount of time spent holding (days from arrival at spawning grounds to death) between pre-spawning and post-spawning *O. tshawytscha* (Welch's two-sample *t*-test for unequal variance: $t = -0.13$, d.f. = 13, $P > 0.05$).

DISCUSSION

MORPHOLOGICAL CHANGES

During their extended time in fresh water, adult SFSR spring–summer *O. tshawytscha* somatic mass decreased considerably, as lipids and proteins were used for metabolism and were re-allocated towards development of gonads and secondary sexual characteristics. Although some *O. tshawytscha* populations develop prominent dorsal humps prior to spawning, particularly in males, dorsal hump size decreased for both sexes in the SFSR population. This morphological change was probably the result of the high metabolic costs of a long-distance migration, as energy allocation towards reproductive traits has an inverse relationship with migratory rigour (Kinnison *et al.*, 2003). Males showed a significant increase in snout length, the majority of which occurred after arrival at spawning grounds. Delayed development of secondary sexual traits probably helps *Oncorhynchus* spp. maintain an energetically efficient shape during migration (Williams & Brett, 1987) and may allow plasticity in allocation of remaining resources after an energetically taxing migration (Hendry & Berg, 1999; Kinnison *et al.*, 2003).

MOBILIZATION OF LIPID AND PROTEIN STORES

The population of *O. tshawytscha* evaluated in this study initiated migration with large stores of readily mobilized somatic energy, primarily in the form of muscle lipid. Somatic lipid percentages were in the upper range of those reported in studies of other *Oncorhynchus* spp. populations at the start of upstream migration (Hendry *et al.*, 2000; Crossin *et al.*, 2004*b*; Mesa & Magie, 2006), consistent with expectations for a population that undergoes a long migration with substantial elevation gain (Brett, 1995;

Crossin *et al.*, 2004*b*). Additionally, high somatic lipid percentages observed in this study may have been related to high open ocean productivity in 2001 and 2002 (Crossin *et al.*, 2004*a*).

Stored lipids appeared to be the primary energy source for upstream migration and initial gonad development in SFSR *O. tshawytscha*, similar to observations of other *Oncorhynchus* spp. (Hendry *et al.*, 2000; Penney & Moffitt, 2014). Lipids were first depleted in visceral tissues (Rowe *et al.*, 1991), whereas *O. tshawytscha* retained some lipids in muscle and skin which, combined with an increase in water content (Crossin & Hinch, 2005), helped maintain a more efficient fusiform shape during migration (Kiessling *et al.*, 2004). Muscle and skin lipids were further depleted during the holding period. In contrast, protein stores were significantly reduced only in female pre-spawning mortalities and in post-spawning *O. tshawytscha* of both sexes, indicating that protein was metabolized during holding and spawning after fat reserves had been used (Hendry & Berg, 1999; Kiessling *et al.*, 2004). The observed increase in per cent skin protein has not been noted in similar studies, most likely because skin is rarely analysed separately from the rest of the soma. Retention of skin protein stores may help maintain skin strength in preparation for redd digging in females and for protection during acts of competitive aggression in males.

ENERGETIC COSTS OF REPRODUCTION

Between freshwater entry and death after spawning, SFSR *O. tshawytscha* used up to 92% of their initial energy, which is slightly higher than energetic costs reported for other semelparous *Oncorhynchus* spp., which range from 41 to 79% (Hendry & Berg, 1999). This considerable reproductive expenditure is consistent with semelparous fishes that undergo long-distance migrations, spend an extensive amount of time between freshwater entry and spawning and allocate substantial energetic resources towards fecundity (Glebe & Leggett, 1981; Crespi & Teo, 2002; Araújo *et al.*, 2013). The greatest percentage of initial energy was used during migration, followed by holding, while considerably less was used during spawning and for gonad development.

The average percentages of energy used during migration to the SFSR (46% for females, 41% for males) were comparable with estimated migration costs for several sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) populations within the Fraser River catchment, where 30–53% of somatic energy reserves were spent to migrate between 161 and 1100 km (Crossin *et al.*, 2004*b*). SFSR *O. tshawytscha* used an average of 28 and 24 kcal kg^{-1} day^{-1} for females and males, respectively, during migration to spawning grounds.

SFSR *O. tshawytscha* used large percentages of initial somatic energy on metabolism during holding (32% for females and 39% for males) and a smaller percentage for spawning (7 and 11%, respectively). Proportional holding costs were higher than those observed in Fraser River *O. nerka* (15–30%; Crossin *et al.*, 2004*b*) and pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792) (16–28%; Crossin *et al.*, 2003), whereas spawning costs were lower compared with *O. nerka* (up to 20% of initial energy reserves in *O. nerka*; Gilhousen, 1980). These proportional energy expenditures probably reflect the amount of time spent in each stage. Individually marked *O. tshawytscha* spent between 19 and 53 days from arrival at spawning grounds to death,

of which 7–15 days were probably spent on spawning and post-spawning activity (Brett, 1995).

Female SFSR *O. tshawytscha* allocated approximately seven times more available energy to gonadal development than males (14 *v.* 2% allocation for females and males, respectively). The percentage of energy used for ovarian development was relatively small compared with Fraser River *O. nerka* (Crossin *et al.*, 2004*b*) and *O. gorbuscha* populations (Crossin *et al.*, 2003), for which *c.* 50% of energy used during migration went to ovaries. This considerable difference in relative energy expenditure is probably a function of both species and population-specific traits. *Oncorhynchus tshawytscha* generally have lower fecundity relative to their mass compared with other *Oncorhynchus* spp. (Healey & Heard, 1984) and ovarian mass tends to decrease as migrations become more difficult (although fecundity may not; Beacham & Murray, 1993; Kinnison *et al.*, 2001). Thus, the relatively low proportional ovarian investment observed here is consistent with the hypothesis that for *O. tshawytscha*, a greater advantage may be conferred by the allocation of energetic resources towards body size than towards fecundity (Healey & Heard, 1984).

Initial and final energy densities of muscle, visceral and gonadal tissues in this study were similar to values reported in the only other recent publication on energy use in *O. tshawytscha*, conducted in the Yakima River (Mesa & Magie, 2006), another tributary to the Columbia River. Final energy densities in both of these studies were similar to the somatic energy threshold of *c.* $4.0 \, \text{kJ g}^{-1}$ to sustain life proposed by Crossin *et al.* (2004*b*) based on four *O. nerka* populations and lend credence to the concept of a minimum energy threshold for *Oncorhynchus* spp. Consistent estimates of a minimum threshold suggest that, regardless of fish size or initial total energy content, on average, fish die when energy levels are exhausted to a critical point.

This study provides some of the first empirical estimates of energy use during different stages of reproduction for *O. tshawytscha* based on samples from a single population, but a few study design limitations are worth noting. A comparison of live *O. tshawytscha* captured just prior to spawning relative to post-spawning moribund *O. tshawytscha* would provide a more accurate estimate of spawning costs than comparison with pre-spawning mortalities, which were used because of permitting restrictions. Comparisons between 2002 pre-spawning mortalities and 2014 spawn-ready females were used to support the assumption that pre-spawning mortalities were effective surrogates for live *O. tshawytscha* captured just prior to spawning. As these two collections occurred in different years, however, the possibility of a year effect cannot be ruled out. Second, when comparing among studies of energy budgets, potential discrepancies can arise from variations in sampling procedures (Brett, 1995). In this study, total somatic energy was estimated from subsamples of muscle and skin and somatic energy density did not include skeleton mass.

RELATIONSHIP BETWEEN MIGRATION RATES AND ENERGY RESERVES

Although SFSR *O. tshawytscha* began their migration with considerable energy stores, protracted migration times may have resulted in *O. tshawytscha* arriving at spawning grounds with suboptimal energy reserves, leaving less energy available for holding and spawning (Young *et al.*, 2006). *Oncorhynchus tshawytscha* that took longer to travel through the hydro-system portion of the migration route arrived at

spawning grounds with less energy than faster migrants, a pattern also observed in Yakima River spring *O. tshawytscha* (Mesa & Magie, 2006). Radio telemetry studies in the Columbia–Snake River hydro-system have demonstrated slower median travel times for *O. tshawytscha* that fell back and had to re-ascend at least one dam (Keefer *et al.*, 2004a). Thus, fallback at dams may have resulted in longer than average travel times and greater energy expenditure (Geist *et al.*, 2000).

Direct evaluation of the relationship between energy availability and passage times through specific portions of the migration route was somewhat confounded by variation in travel times through the two migratory sections. Sampling of individually marked *O. tshawytscha* at various points along the migration corridor (*e.g.* Lower Granite Dam) would improve the inference provided by the current study. Estimates of available energy were based on relative energy measures because proximate analysis relies on lethal sampling, precluding direct evaluation of energy content in individual fish at different maturation stages. This study failed to show a link between migration rate or holding time and spawning success, but a larger sample size might be needed to detect an effect.

ENERGY CONTENT OF PRESPAWN MORTALITIES V. SUCCESSFUL SPAWNERS

On average, *O. tshawytscha* that died prior to spawning had more absolute somatic energy than did post-spawning mortalities, indicating that factors other than energy depletion were the likely proximate cause of death in pre-spawning mortalities, a conclusion also reached for late-run Fraser River *O. nerka* stocks (Hinch *et al.*, 2012). The single year of data in this study may, however, have been insufficient to observe the effects of energetic constraints on survival, as pre-spawning mortality rates can vary substantially among years (Keefer *et al.*, 2010; Hinch *et al.*, 2012). A few of the pre-spawning mortalities did have somatic energy values similar to those of post-spawning *O. tshawytscha* and it is possible that mortality for those individuals was the result of energy exhaustion (Gilhousen *et al.*, 1990; Cooke *et al.*, 2004). Given the substantial energy requirements remaining after spring–summer *O. tshawytscha* arrive at spawning grounds, it seems likely that *O. tshawytscha* that complete their migration with larger energy stores will be more resilient to other factors that can lead to pre-spawning mortality, such as injuries and pathogens (Young *et al.*, 2006; Baker & Schindler, 2009; Keefer *et al.*, 2010) and would have more energy available for spawning activities that could contribute to reproductive fitness, including competitive interactions and redd guarding (Healey *et al.*, 2003; Hruska *et al.*, 2010).

SYNTHESIS

Individual *O. tshawytscha* entered fresh water with large reserves of stored energy, up to 90% of which were used prior to death after spawning. Postspawned *O. tshawytscha* died at a critical energy threshold of *c*. 4 MJ kg^{-1}. This considerable energy expenditure occurred within a regulated river system where *O. tshawytscha* negotiate dams, a fishery and were handled on spawning grounds and thus reflected both historical and more recent management-related energetic costs. Owing to the high energetic requirements of reproduction for SFSR spring–summer *O. tshawytscha*, additional stressors during migration and holding, such as increased migration times, holding times or water

temperatures, may further reduce energy stores and ultimately affect spawning success (Rand *et al.*, 2006; Crozier *et al.*, 2008). Estimates of energetic costs provided here can help managers evaluate how changes in migratory and holding conditions due to management actions or climatic changes could affect available energy prior to spawning.

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