

Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation

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Depending on population, wild Fraser River sockeye salmon *Oncorhynchus nerka* travel distances of <100 km to >1100 km and ascend elevations ranging from near sea-level to 1200 m to reach spawning areas. Populations embarking on distant, high elevation migrations (i.e. Early Stuart, Chilko and Horsefly populations) began their upriver spawning migrations with higher densities of somatic energy (c. 9.2 to 9.8 MJ kg⁻¹) and fewer eggs (c. 3200 to 3800) than populations making shorter, low elevation migrations (i.e. Weaver and Adams; c. 7.1 to 8.3 MJ kg⁻¹ gross somatic energy and c. 4300 to 4700 eggs). Populations making difficult upriver migrations also had morphologies that were smaller and more fusiform than populations making less difficult migrations, traits that may facilitate somatic energy conservation by reducing transport costs. Indeed, fish travelling long distances expended less somatic energy per unit of migratory difficulty than those travelling shorter distances (2.8 to 3.8 kJ v. 10–1400 kJ). Consistent with evolutionary theory, difficult migrations appear to select for energy efficiency but ultimately fish making more difficult migrations produce fewer eggs, even when differences in body length have been accounted for. Despite large among-population differences in somatic energy at the start of upriver migration, all populations completed migration and spawning, and subsequently died, with c. 4 MJ kg⁻¹ of energy remaining, a level which may reflect a threshold to sustain life.

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Key words: energetics; local adaptation; migration; *Oncorhynchus*; reproductive trade-offs; sockeye salmon.

INTRODUCTION

Adult Pacific salmon *Oncorhynchus* spp. begin fasting when they return to fresh water and will not eat again during the final phases of their life history. Once migration and spawning are finished, Pacific salmon in fact die. Because they have only one opportunity to migrate upriver and spawn successfully

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before their inevitable death (semelparity), it is profoundly important for them to have sufficient somatic energy reserves in place to fuel migration, complete sexual maturation, and support the behaviours and morphological changes associated with courtship and spawning (Burgner, 1991; Brett, 1995). Previous studies of body constituents show that such upriver migrations are energetically expensive, usually depleting >50% of a salmonid's total somatic reserve (Brett, 1995). Disproportionately high levels of energy use during migration has been known to cause premature mortality (Rand & Hinch, 1998a). Thus, natural selection should act strongly on traits and behaviours that help accrue energy in preparation for migration, and that conserve energy during upriver transport (swimming). Attaining energy efficiency, however, may come at a cost to egg production (Kinnison *et al.*, 2001) and to other functions peripheral to spawning (*i.e.* competition and defence). When migrations are relatively easy (*i.e.* short distances and low elevations), salmonids can invest more energy to such peripheral fitness-related activities. When migrations are more difficult, however, salmonids should possess adaptations for the more efficient use of swim-energy (*i.e.* lower transport costs) to ensure a timely arrival on spawning areas despite long and varied conditions. A review of anadromous fish bioenergetics and behaviour by Bernatchez & Dodson (1987) showed that interspecific differences in swim-energy use were in fact related to measures of migratory difficulty.

Few studies, however, have rigorously examined the hypothesis that intraspecific differences in energy allocation and expenditure exist. Previous among-population comparisons have been based on data collected in different years, which confounds interpretation as ocean climate and productivity regimes can vary two to three-fold among years (Rand & Hinch, 1998b). Somatic energy at the onset of upriver migration can thus vary considerably in relation to ocean climate (Crossin *et al.*, 2004), and among-years, within-population variation in adult body size is strongly related to oceanic conditions (Hinch *et al.*, 1996; Cox & Hinch, 1997). Nevertheless, body constituent analyses conducted in the 1950s on Fraser River sockeye salmon *Oncorhynchus nerka* (Walbaum) show that initial energy reserves were higher for populations that migrated far upriver compared to those migrating shorter distances (Gilhousen, 1980). Additionally, short distance Alaskan sockeye salmon examined in the 1990s had lower initial energy reserves than the long distance Fraser fish reported in Gilhousen (1980) (Hendry & Berg, 1999). In Norway, gonado-somatic indices were higher in anadromous male Atlantic salmon *Salmo salar* L. from a short distance river than from a long distance one (Jonsson & Jonsson, 2003).

Intraspecific differences in body morphology of adult sockeye salmon are well documented in coastal populations, which do not migrate far upriver (Blair *et al.*, 1993; Quinn *et al.*, 2001). The few studies that have compared the morphology of short and long distance migrants suggest that migratory distance can be a determining factor (Linley, 1993; Moore, 1996). These studies however included sockeye salmon sampled in different years and fish of hatchery origin, both of which can complicate interpretations about the role of migration on the evolution of body morphology. Long distance populations tend to be smaller and more streamlined than short distance populations, mechanical adaptations that may help them conserve energy for migration.

In the face of energetically costly migrations, life-history theory predicts reproductive trade-offs (Stearns, 1992). There is evidence that egg number (fecundity) and ovary mass decrease with migration distance (Linley, 1993), reflecting an energetic necessity to invest in other functions affecting reproductive success (*i.e.* upriver swimming). Though the net phenotypic response in long distance populations is a net decrease in ovarian mass and fecundity, these populations tend to have higher egg number-to-egg size ratios relative to shorter distance populations, suggesting that egg number is favoured over egg size when migrations are difficult (Kinnison *et al.*, 2001).

Previous studies suggest that upriver migration may impose a strong selective pressure on Pacific salmon such that populations undertaking 'difficult' migrations have energetic, morphological and reproductive adaptations for accruing energy prior to migration and conserving energy during migration. No thorough examination of energetics, morphology and reproductive trade-offs, however, have been examined in multiple wild populations within an individual watershed, in an individual year. To address the above hypothesis within a single year and watershed, energy levels in somatic and reproductive tissues and the morphologies of five sockeye salmon populations migrating through a broad spectrum of environmental conditions were examined. Several environmental variables reflecting aspects of the difficulty of migration were measured to explore whether populations with difficult migrations possess higher initial energy levels, smaller and more fusiform morphologies, and allocate less energy to gonad development (thus saving energy for locomotion) than populations with less difficult migrations.

MATERIALS AND METHODS

STUDY SYSTEM AND SAMPLE COLLECTION

Adult sockeye salmon were collected in 1999 from the five most productive populations (Early Stuart, Chilko, Horsefly, Adams and Weaver) that spawn in the Fraser River watershed, British Columbia (B.C.), Canada (Fig. 1). Among its many tributaries are several highly productive lake systems, lying at various distances from the ocean and elevations above sea level (Table I).

Sockeye from each population were collected three times: at the Fraser River mouth, at arrival on spawning grounds and on the spawning grounds after spawning (except for Early Stuart; Fig. 1). Ten males and 10 females were collected from each population at each time. Upon capture, fish were euthanized and sealed in airtight bags for transport to the laboratory. Sockeye salmon populations (or 'stocks') enter the Fraser River in a sequence that is relatively well understood by management agencies [Fisheries and Oceans Canada (DFO) and the Pacific Salmon Commission (PSC)]. Generally, the Early Stuart population enters the Fraser River in July, the Chilko and Horsefly populations in August, and the Adams and Weaver populations in September (Table I). The PSC test fisheries captured sockeye salmon at Whonnock, B.C. (Fig. 1) at times when study populations are historically migrating upriver. The PSC identified population origin using three methods: 1) river-entry timing, 2) scale patterns and 3) brain parasites. Though population mis-identification is possible, sockeye salmon migrating together are generally bound for similar upriver regions. Thus, if any fish were mis-identified, they were probably from populations bound for adjacent localities that experience similar degrees of migration difficulty (M. Lapointe, pers. comm.). As such, energetic and morphological variation among such populations should be minimal. Fish age was

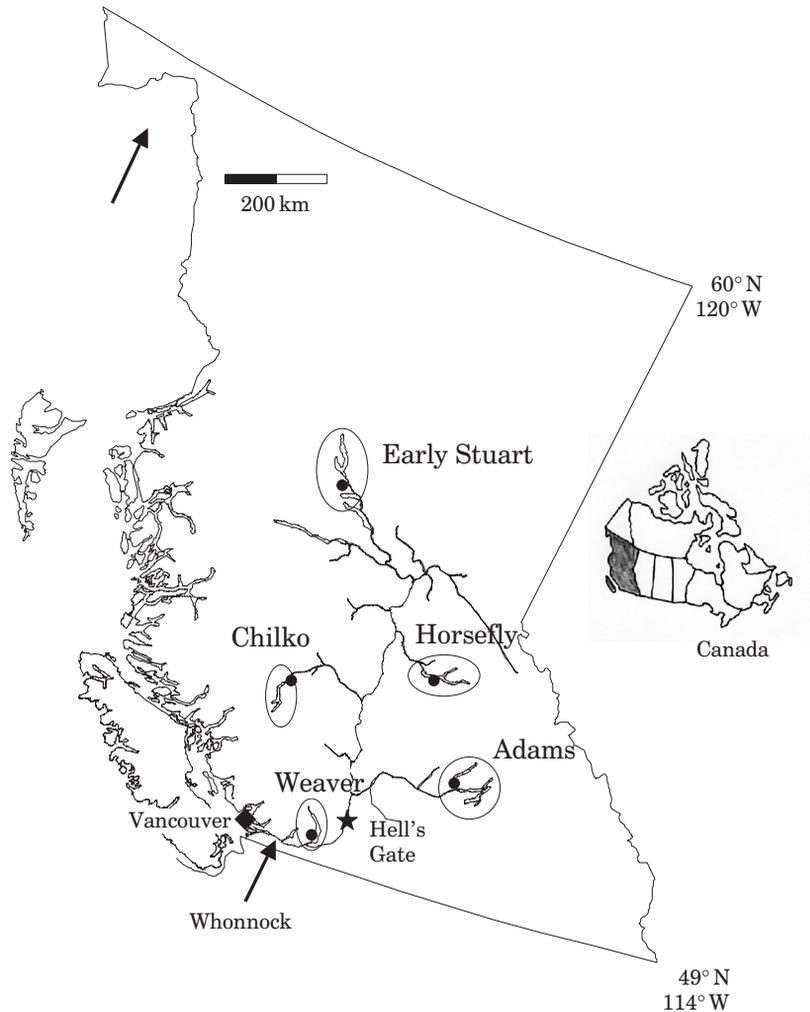


FIG. 1. Map of British Columbia, with inset of Canada, indicating the five most productive Fraser River sockeye salmon spawning systems (○), ●, spawning ground sampling locations.

determined by scale analyses. Only age 4₂ (4 years of age, 2 years reared in fresh water) individuals were used in this study. Generally, >98% of all Fraser sockeye salmon return at this age (M. Lapointe, pers. comm.).

In recent years, some segments of Fraser sockeye salmon populations (particularly Weaver and Adams) have been migrating upriver 4–8 weeks earlier than the historic norm (PFRCC, 2002). While it is unclear why this is happening, members of the Weaver and Adams populations were collected during the average historic range (Gilhousen, 1990). Their identity was cross-checked with scale pattern analyses.

With DFO assistance, prespawning sockeye salmon were beach-seined from the Early Stuart population at Kynoch Creek, the Chilko population on the Chilko River just downstream of the Chilko Lake outlet, and from the Adams population on the Adams River just upstream from its delta on Shuswap Lake (Fig. 1). Collections from the Horsefly and Weaver populations were made by dip-net at the gates to spawning channels lying adjacent to these tributaries (Fig. 1). Approximately 2 to 3 weeks after collecting prespawning fish, moribund, post-spawning carcasses were collected from

TABLE I. Dates of sampling and environmental characteristics of the migration route for the five populations of Fraser River sockeye salmon collected in 1999

Population	Peak Fraser River entry	Peak spawning ground arrival	Migration distance (D_M) (km)	Migration elevation (E_M) (m)	River slope ($E_M D_M^{-1}$) 500	Work ($0.001 E_M D_M$)	Migration degree-days ($^{\circ}C$)
Weaver	18 September	8 October	161	10	31	2	270
Adams	15 September	6 October	484	366	441	177	355
Horsefly	10 August	8 September	807	762	472	615	495
Chilko	10 August	2 September	629	1158	921	729	390
Early Stuart	10 July	12 August	1089	701	322	763	607

these same sites except for the Early Stuart carcasses which were not collected by DFO in 1999.

As a general note, energy stores and morphology of sockeye salmon are known to change dramatically among early and late spawners within a population (Hendry & Berg, 1999; Hendry *et al.*, 1999). All fish were collected at peak (50% of population) arrival times at each site.

INDICES OF DIFFICULTY OF MIGRATION

Three environmental variables with physiologic relevance to energetic studies were examined: migratory distance (D_M), spawning ground elevation (E_M) and migratory degree-days (*i.e.* thermal units accrued over the course of migration). Generally, these variables tend to be cross-correlated; assessing their independent roles is difficult, both from a statistical and conceptual perspective. Thus, these three measures were examined individually, as were combinations of distance and elevation: 500 ($E_M D_M^{-1}$) (river slope; Gilhousen, 1980) and 0.001 $E_M D_M$ (work) (Table I). River slope was multiplied by 500, and work was divided by 1000, to simplify presentation. As water temperatures strongly affect standard metabolic rates in fishes, accumulated migratory degree days were also examined for their relationship to pre-migratory energy reserves.

From topographic maps, upriver D_M and E_M were estimated from Whonnock, B.C. (Table I). Using DFO data, the number of migratory degree-days each population encountered while migrating from Whonnock to the spawning grounds was estimated (Table I). For the Adams, Horsefly and Chilko populations, migration routes were divided into three segments: 1) Whonnock to Qualark (*c.* 70 km upstream from Whonnock), 2) Qualark to tributary river arrival (*i.e.* the Quesnel, Chilcotin and Thompson Rivers) and 3) tributary river arrival to spawning ground arrival. Degree-days were calculated for each segment by multiplying the upstream temperature of each segment by the number of days spent within each segment (estimated from known spawning run-times). Segments were then summed to provide an estimate of the degree-days accumulated during migration.

A Pearson's correlation matrix was used to relate the five environmental variables to mean river-entry somatic energy density concentrations and the means of specific morphological and reproductive attributes in both sexes.

MORPHOLOGICAL AND REPRODUCTIVE ATTRIBUTES

For each fish, whole and eviscerated mass (M_E whole less gonads and viscera) were measured, as were the masses of ovaries (M_O) and testes (M_T) and the viscera. Post orbital-to-hypural length (L_{POH}), body depth (from the anterior insertion of the dorsal fin to the leading edge of the pelvic fin), and body width (horizontal cross-section at the lateral line intersection with the body depth line), were all measured to the nearest mm. The ratio between body width to body depth was termed the 'o-index'. Fecundity was determined for all females arriving at their spawning grounds by counting eggs within the ovary. Ovary mass was measured in all river-entry and spawning ground females. The gonado-somatic index (I_G) was calculated for river-entry and spawning ground females from $I_G = 100 M_O M_E^{-1}$. Individual egg mass was estimated for females at river-entry and spawning grounds weighing 10 eggs and calculating the average. M_T was determined for all river-entry and spawning ground arrival males.

Before comparisons between body shapes and reproductive attributes among populations could be made, data had to be corrected for allometric differences attributed to body size. Following Hendry & Berg (1999), data were corrected for L_{POH} with analysis of covariance (ANCOVA; using type III sums-of-squares) with population as a class variable, L_{POH} the covariate and the body shape and reproductive attributes of interest the dependent variables. Homogeneous slopes were found for each analysis ($P > 0.05$), therefore, least squares means were used to generate 'length corrected' means and s.e. which were used in subsequent analyses and figures. In all analyses, no significant interactions were found between L_{POH} and the attribute of interest, thus all least squares

means presented were calculated with the interaction term removed from the ANCOVA model. Linear regression analysis examined the relationship between an attribute of interest and different measures of migratory difficulty. Morphological analyses focussed on river-entry and prespawning sockeye salmon. Morphological changes that occurred on the spawning grounds were not examined.

PROXIMATE CONSTITUENT ANALYSES

Eviscerated carcasses and gonads were homogenized, separately, with an industrial food processor (Robot Coupe Blixer BX6V). A 250 g sub-sample of carcass homogenate and the entire gonad homogenate were packed separately in airtight plastic freezer bags and stored at -20°C until proximate analyses were conducted. Proximate constituency (lipid, protein, water and ash) was assessed for carcasses and gonads of all fish according to the methods outlined by Higgs *et al.* (1979). Water content was determined by drying a sample of each homogenate at 100°C for 24 h. Ash was determined by combusting the dried sample at 600°C for 2 h. Water and ash content were calculated as percentages by wet mass. Lipid content was determined as wet mass through a 1 : 1 chloroform-methanol extraction of a sample of each tissue homogenate. Protein content of somatic samples was calculated from the total per cent of Kjeldahl nitrogen (TKN-macro Kjeldahl procedure). Proximate constituency (lipid, protein, water and ash) was assessed for carcasses and gonads of all fish (Higgs *et al.*, 1979), and calculated as percentages and as g kg^{-1} . Protein and lipid concentrations (g kg^{-1}) were converted to their energetic equivalents by multiplying (by wet mass) by $0.02364 \text{ MJ kg}^{-1}$ for protein and $0.03954 \text{ MJ kg}^{-1}$ for lipid (Higgs *et al.*, 1979). The above protein conversion factor however inaccurately estimates the energy content (per cent and MJ kg^{-1}) of sockeye salmon testes (D. Higgs & J. Oakes, unpubl. data). Thus, protein percentages in testes were calculated as the difference between summed water, ash and lipid percentages and 100. This method has been employed in previous studies (Berg *et al.*, 1998; Hendry & Berg, 1999; Hendry *et al.*, 1999). Only lipid and protein results are presented.

As with the body morphology and reproductive attributes described above, ANCOVA was used to correct population energy densities for body size. As above, homogeneous slopes were found in each analysis ($P > 0.05$), thus least squares means were calculated, with the length-by-attribute interaction term removed, to generate size corrected means and S.E.

SOMATIC ENERGY PARTITIONING DURING MIGRATION

While migrating upstream, sockeye salmon partition somatic energy reserves to a number of tasks (*e.g.* standard and active metabolism, gonad maturation and secondary sexual characters). For female sockeye salmon, the two greatest energetic needs are the active metabolic costs of swimming and gonad maturation (Rand & Hinch, 1998*a*). For males, the two greatest needs are active metabolism and secondary sexual character development (Kinnison *et al.*, 2003). For each sex, energy invested into these tasks was estimated with a linear regression technique used in previous salmonid energetic studies (Jonsson *et al.*, 1997; Hendry & Berg, 1999). Using population data from river-entry and spawning ground arrival fish, mass-specific somatic energy data were ln-transformed and regressed against L_{POH} . ANCOVA was used to examine for heterogeneity of slopes between the river-entry and spawning ground arrival fish. As there was no significant interaction between L_{POH} and total energy, least squares means were calculated with the interaction term removed from the model. If slopes were homogeneous, the difference between the intercepts provided an estimate of the amount of energy partitioned to swimming activity during the migration. Estimation of ovarian and testicular investment was done in an identical manner, comparing the intercepts between river-entry and spawning ground energy levels in each tissue type. Activity costs were inferential, established by the amount of energy lost from the somatic tissues minus that diverted into the ovaries, which could be measured directly. Having accounted for ovarian investment, and

knowing that standard metabolism is small in migrating sockeye salmon, it was inferred that any further somatic energy loss is most likely attributable to swimming activity costs (Rand & Hinch, 1998a) and to the development of secondary sexual characteristics, particularly in males (Hendry & Berg, 1999).

RESULTS

INDICES OF DIFFICULTY OF MIGRATION

The five sockeye populations fell into three general levels of difficulty of migration. Weaver fish made the least difficult migrations (lowest elevation gain, shortest distance travelled and lowest 'work' demands). Horsefly, Chilko and Early Stuart fish made the most difficult migrations (highest elevation gain, longest distance travelled and greatest 'work' demands). Adams was intermediate in difficulty (Table I).

All five environmental variables showed strong correlations with size-corrected mean initial energy density, morphology and reproductive attributes (Table II). Of these variables, work (migratory distance-by-elevation) provided strong correlations across eight of nine energetic and reproductive attributes, and migration distance and elevation as individual variables generated some strong associations, but not as consistently across variables. Migratory degree-days consistently provided the weakest correlations (Table II). Thus, the work variable was used as an environmental correlate in analyses. As migratory 'work' is a new concept, other individual environmental measurements are also presented for comparison.

MORPHOLOGICAL AND REPRODUCTIVE ATTRIBUTES

The L_{POH} corrected data (ANCOVA) revealed that for all fish sampled, all intercept terms (*i.e.* all population attributes) were significant ($P < 0.01$). With the exception of river entry female body width, there were no significant slope-by-intercept interactions (all $P > 0.05$). Prespawning sockeye salmon attributes were regressed against migratory work: mean fecundity [$P = 0.032$, $r^2 = 0.83$, $n = 5$; Fig. 2(a)], mean ovary mass [$P = 0.03$, $r^2 = 0.83$, $n = 5$; Fig. 2(b)], mean individual egg mass [$P = 0.031$, $r^2 = 0.81$, $n = 5$; Fig. 2(c)], mean testes mass [$P = 0.362$, $r^2 = 0.28$, $n = 5$; Fig. 2(d)], mean female body length (L_{POH}) [$P = 0.012$, $r^2 = 0.86$, $n = 5$; Fig. 2(e)], mean female body depth and width [depth $P = 0.008$, $r^2 = 0.98$, $n = 4$; width $P = 0.018$, $r^2 = 0.96$, $n = 4$; Fig. 2(f), (g)], mean male body depth and width [depth $P = 0.149$, $r^2 = 0.73$, $n = 4$; width $P = 0.022$, $r^2 = 0.96$, $n = 4$; Fig. 3(h), (i)] and mean male body length (L_{POH}) [$P = 0.01$, $r^2 = 0.82$, $n = 5$; Fig. 2(j)].

The L_{POH} corrected data (ANCOVA) revealed that for fish sampled at the Fraser River mouth, all intercept terms (*i.e.* all population attributes) were significant ($P < 0.01$), as were all slope terms (*i.e.* body length covariate, all $P < 0.01$). Linear regressions of river-entry attributes produced the following values: mean ovary mass [$P = 0.005$, $r^2 = 0.95$, $n = 5$; Fig. 2(b)], mean individual egg mass [$P = 0.046$, $r^2 = 0.78$, $n = 5$; Fig. 2(c)], mean testes mass [$P = 0.178$,

TABLE II. Pearson's correlation matrix relating mean energetic, morphological and reproductive attributes of five Fraser River sockeye salmon populations at river entry to five environmental variables encountered along the migration route. Analysis used $n = 5$ for each attribute (mean of 10 fish in each of five populations by sex)

Energetic, morphological or reproductive attribute	Migratory distance (D_M)	Migratory elevation (E_M)	River slope 500 ($E_M D_M^{-1}$)	Work ($0.001 E_M D_M$)	Migratory degree-days ($^{\circ}C$)
Female somatic energy	0.73	0.95*	0.85	0.89*	0.62
Ovary mass	-0.89*	-0.92*	-0.73	-0.97**	-0.81
Female I_G	-0.89*	-0.92*	-0.72	-0.98**	-0.81
Average egg mass	-0.76*	-0.91	-0.80	-0.92*	-0.66*
Fecundity	-0.64	-0.99**	-0.91*	-0.92*	-0.52
Female L_{POH}	-0.65	-0.92*	-0.74	-0.93*	-0.58
Male somatic energy	0.81	0.97**	0.81	0.97**	0.71
Testis mass	-0.88	-0.53	-0.28	-0.71	-0.87
Male L_{POH}	-0.65	-0.86	-0.70	-0.91*	-0.56

* $P < 0.05$; ** $P < 0.01$.

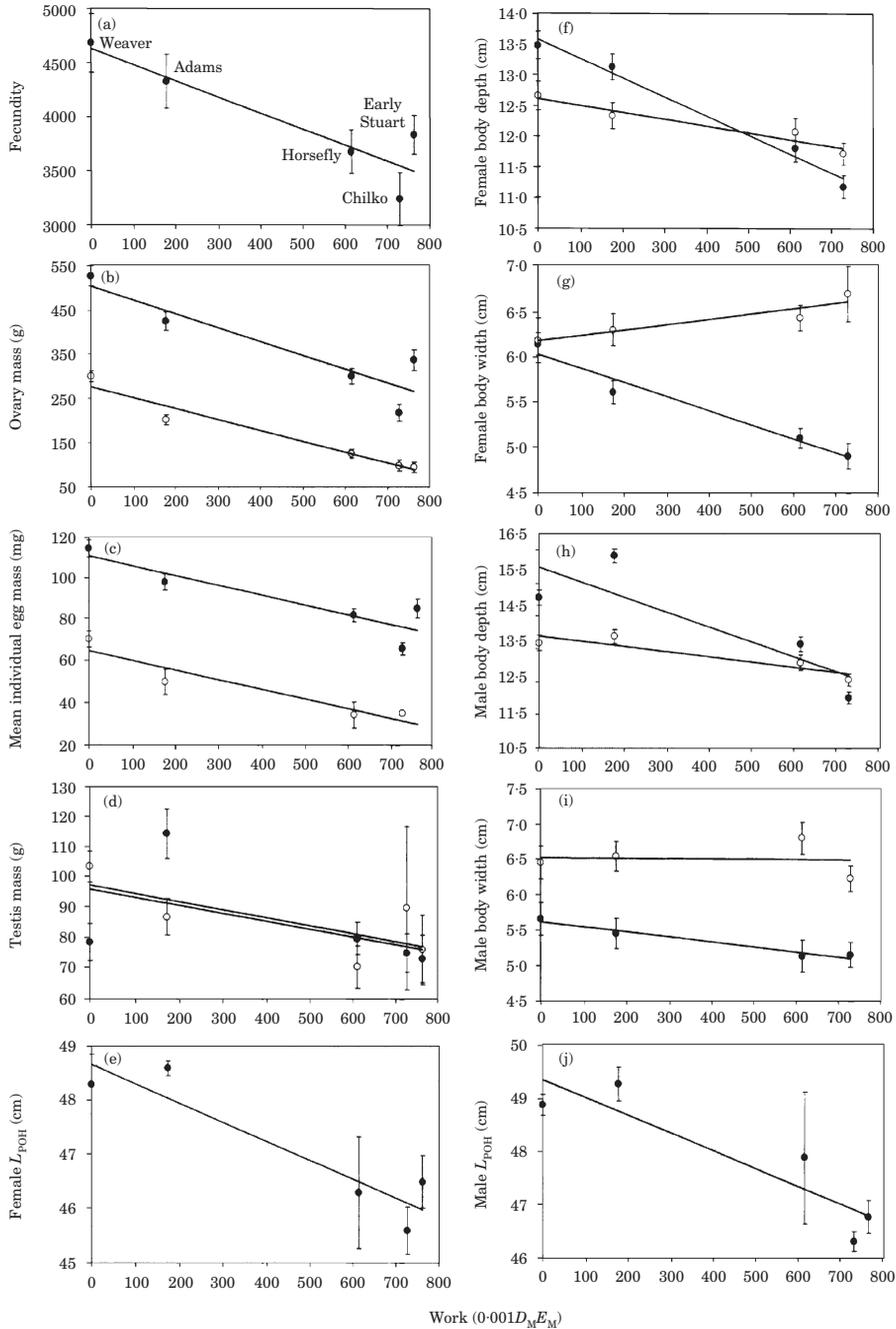


FIG. 2. Mean \pm 1 s.e. (a) fecundity, (b) ovary mass, (c) individual egg mass, (d) testes mass, (e) female body length, (f) female body depth, (g) female body width, (h) male body depth, (i) male body width and (j) male body length relative to work. Attributes in panels (a)–(d) and (f)–(i) are L_{POH} corrected. \bullet , spawning ground samples; \circ , Fraser River entry samples. Lines are best linear fit. The order of populations is given in (a) and is the same throughout. Early Stuart data are not presented in (f) to (i). D_M , migratory distance; E_M , migratory elevation.

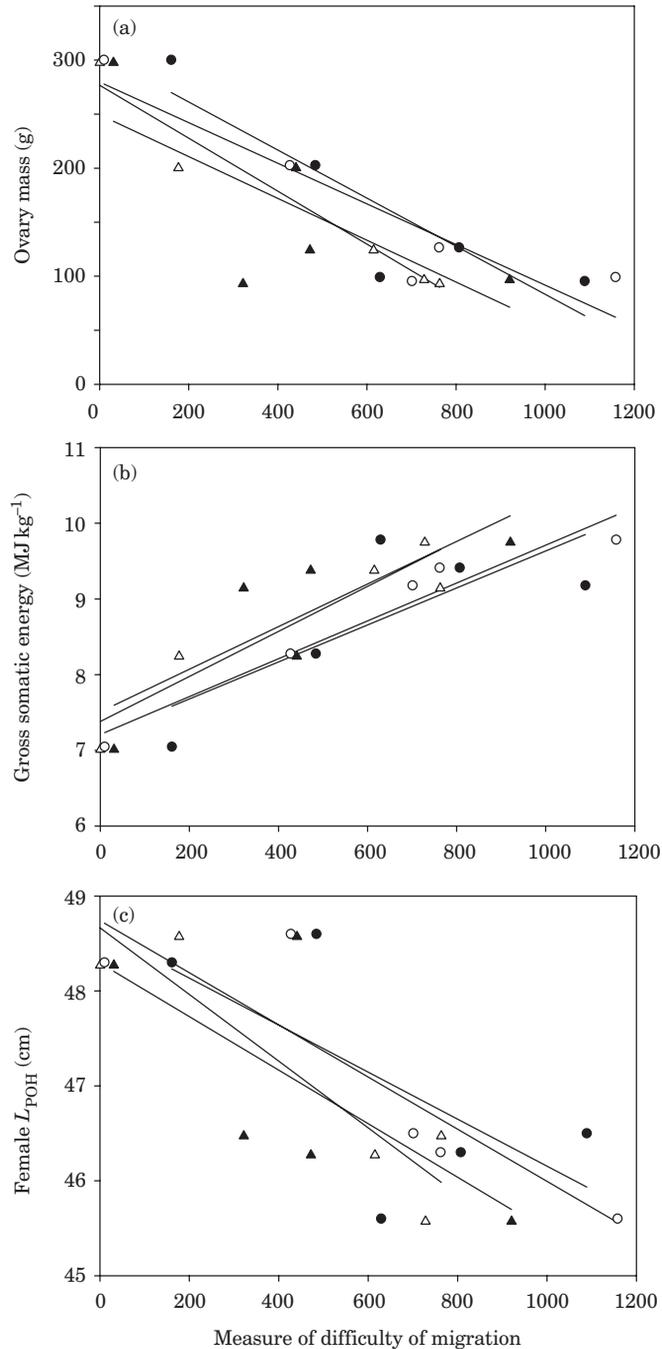


FIG. 3. The relationship between (a) mean ovarian mass, (b) female gross somatic energy and (c) female body length relative to various measures of migratory difficulty. ●, distance (D_M) (km) [$r^2 =$ (a) 0.79, (b) 0.60 and (c) 0.42]; ○, elevation (E_M) (m) [$r^2 =$ (a) 0.84, (b) 0.94 and (c) 0.79]; ▲, $500 (E_M D_M^{-1})$ (river slope) [$r^2 =$ (a) 0.51, (b) 0.68 and (c) 0.47]; △, $0.001 D_M E_M$ (work) [$r^2 =$ (a) 0.97, (b) 0.88 and (c) 0.86]. Linear regressions are fitted to the data.

$r^2=0.51$, $n=5$; Fig. 2(d)], mean female body depth and width [depth $P=0.039$, $r^2=0.92$, $n=4$; width $P=0.069$, $r^2=0.87$, $n=4$; Fig. 2(f), (g)] and mean male body depth and width [depth $P=0.089$, $r^2=0.83$, $n=4$; width $P=0.98$, $r^2=0.01$, $n=4$; Fig. 2(h), (i)].

Whether elevation, distance, slope or work was used as an index of difficulty of migration, L_{POH} corrected river entry ovary mass, female gross somatic energy and female L_{POH} all showed the same trends (Fig. 3).

Males and females from the Chilko, Horsefly and Early Stuart populations began their upriver migrations with more fusiform, torpedo-like shapes than those in Adams and Weaver populations, which were broader and deeper-bodied. The more difficult a population's migration route, the closer the ratio of depth-to-width approached one, and the closer body shape (when viewed head-on) became rounded. As width measurements were made at the sockeye salmon's lateral line, above the visceral cavity containing reproductive and internal organs, ovary mass did not affect this measurement. The L_{POH} corrected means of 'o-index' measures of river entry Weaver females were not different from those of Adams ($P=0.43$), but were from Chilko, Horsefly and Early Stuart (all $P<0.05$; Fig. 4). Adams values were intermediate and not different from either Weaver or the Chilko-Horsefly-Early Stuart group (all $P>0.05$; Fig. 4).

SOMATIC ENERGY PARTITIONING AND REPRODUCTIVE INVESTMENT

Proximate composition values for all samples showed that sockeye salmon populations making long distance and high elevation migrations (*i.e.* Early Stuart, Chilko and Horsefly) possessed greater gross somatic energy (*c.* 9.2 to 9.8 MJ kg⁻¹) and lipid (*c.* 12.0 to 13.6%) reserves at the start of upriver migration compared with populations making less distant, low elevation migrations (*i.e.* Weaver and Adams; 7.1 to 8.3 MJ kg⁻¹ gross somatic energy and 6.3 to 9.7% lipid) (Fig. 5). Regardless of starting somatic energy concentration, all populations arrived on the spawning grounds with similar energy densities, with the exception of Chilko sockeye salmon, which arrived with higher energy

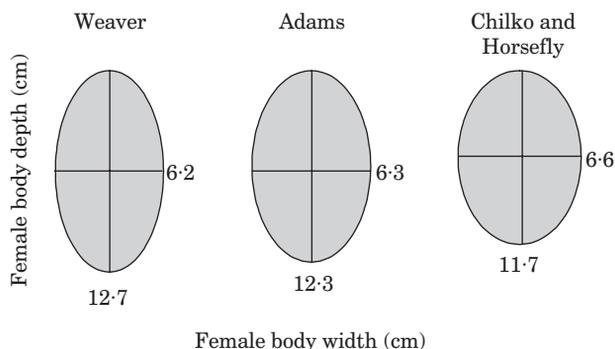


FIG. 4. A generalized schematic of female sockeye salmon shape, when viewed head-on, at the beginning of their upriver spawning migrations. Shapes are derived from mean depth and width measurements (lines).

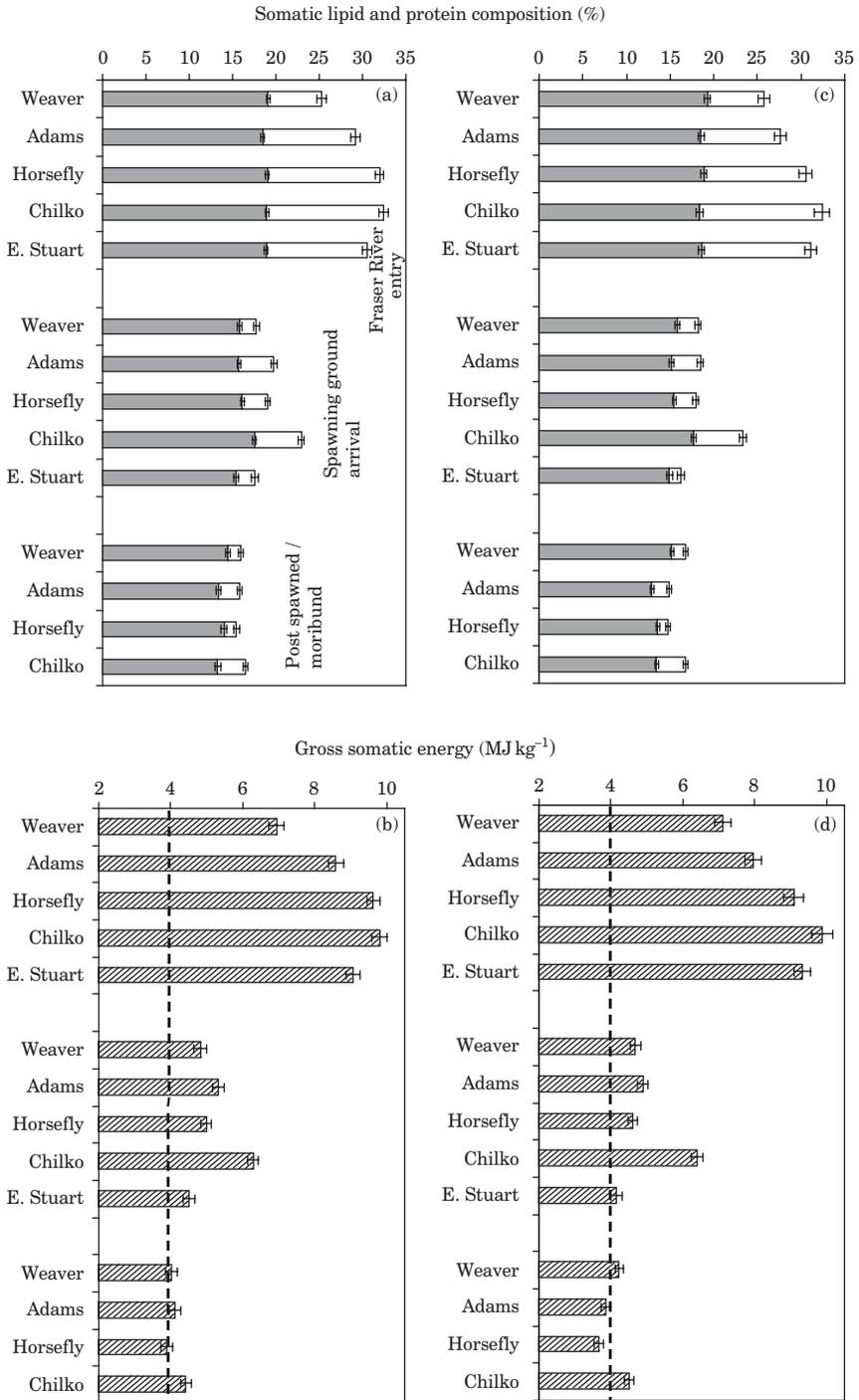


FIG. 5. Mean \pm 1 S.E. (a),(c) protein (\square) and lipid (\blacksquare) percentages and (b),(d) gross energy concentrations (MJ kg^{-1}) in the soma of female (a), (b) and male (c), (d) Fraser River sockeye salmon collected in 1999. Collection locations are given in (a). ---, the approximate energetic threshold to sustain life.

reserves relative to the others [Fig. 5(b), (d)]. There was no sex effect on gross somatic energy, lipid and protein concentrations at river-entry and at spawning ground arrival (ANCOVA, all $P > 0.05$).

At river-entry, water was always the greatest constituent in both somatic and reproductive tissues, mean levels ranging among populations from 65 to 82% in the soma and 55 to 62% in the gonads [water values from Crossin (2003)], followed by protein [13 to 20% in the soma and 19 to 25% in the gonads; Fig. 5(a)], lipid [1 to 14% in the soma and 1 to 16% in the gonads; Fig. 5(a)] and ash (2 to 3% in the soma and 2 to 7% in the gonads; ash values from Crossin (2003)]. When swimming from the Fraser River mouth to spawning grounds, sockeye salmon expended 7 to 20% of somatic proteins, and 60 to 86% somatic lipids; ranges are the maximum among-population differences. This represents, depending on population, a 30 to 53% loss of gross somatic energy reserves [Fig. 5(b), (d)]. From spawning ground arrival to death after spawning, depending on the population, sockeye salmon expended 10 to 25% of their remaining somatic proteins and 30 to 50% of lipids. This represents a loss of 15 to 30% of gross energy [Fig. 5(b), (d)]. At river entry, mean gross energy concentrations in the ovaries varied little among populations (11.18 to 12.16 MJ kg⁻¹), and had decreased slightly upon arrival at the spawning grounds (10.18 to 11.33 MJ kg⁻¹). Mean ovarian mass, however, changed substantially over this period (42 to 78%), and depending on the population, mass specific (total) ovarian energy increased from 40 (Weaver population) to 58% (Early Stuart population). For males, mean gross energy in the testes at river entry differed little among populations (3.68 to 3.83 MJ kg⁻¹), and mean mass specific energy changed little (0 to 2%), owing to the modest change in testes mass between river entry and arrival at the spawning grounds. Female mean I_G at river entry was inversely proportional to all measures of difficulty of migration (Table II). Between river entry and spawning ground arrival, mean female I_G increased from 40 to 74%. Mean male I_G at river entry differed little among populations and changed little between river entry and spawning ground arrival.

Of the total somatic energy spent on activity and gonad maturation during upriver migration, female sockeye salmon channelled approximately half to each compartment: means ranged among populations from 43 to 51% to swimming activity (active metabolism), and 49 to 56% to ovarian development (Table III). Absolute energy spent increased with increasing work (*i.e.* distance-by-elevation) demands. With the exception of Horsefly, males followed similar somatic energy use patterns as females (55 to 68% for swimming activity), but expended less on gonad development than females (31 to 44% to testicular development). As males expended less energy, surplus energy may have been available for other fitness related traits. Presumably, this energy went to secondary sexual character development, which is greater in migrating males than females. Horsefly males had higher testicular energy relative to the other populations, a difference that may have to do with their collection. Prespawning Horsefly sockeye salmon were collected at the mouth of the Horsefly spawning channels, which were shut by gates the day collection occurred. Thus, arriving fish congregated in great numbers at the channel entrance. Males were seen charging the gates, presumably ready to spawn and 'anxiously' trying to gain entry. Females were generally found further downstream, 'calmly' holding in

TABLE III. Absolute mean $\pm 95\%$ CI somatic energy (MJ) and relative mean somatic energy [$\text{kJ } (0.001E_M D_M)^{-1}$ or kJ work^{-1}] used for standard and active metabolic processes (upriver activity), and for reproductive tissue development (ovarian and testicular investment) during the upriver migration of five Fraser River sockeye salmon populations

Population	Females				Males			
	Absolute upriver cost (MJ)	Relative upriver activity cost [kJ work^{-1}]	Absolute ovarian investment (MJ)	Relative ovarian investment [kJ work^{-1}]	Absolute upriver cost (MJ)	Relative upriver activity cost [kJ work^{-1}]	Absolute testicular investment (MJ)	Relative testicular investment [kJ work^{-1}]
Weaver	1.50 \pm 0.02	1440.0	1.54 \pm 0.03	1560.0	1.46 \pm 0.10	1460.0	0.99 \pm 0.05	990.0
Adams	1.80 \pm 0.01	10.4	1.72 \pm 0.17	9.8	1.52 \pm 0.03	7.4	1.23 \pm 0.01	6.0
Horsefly	2.36 \pm 0.06	3.8	2.44 \pm 0.004	4.0	2.29 \pm 0.01	3.7	4.53 \pm 0.49	7.4
Chilko	2.10 \pm 0.02	2.8	2.16 \pm 0.04	3.0	2.19 \pm 0.01	3.0	1.03 \pm 0.001	1.4
Early Stuart	2.39 \pm 0.17	3.1	3.07 \pm 0.05	4.0	2.34 \pm 0.11	3.1	1.09 \pm 0.03	1.4

pools. The effort made by males may have caused greater testicular development, and a higher estimate of absolute investment (Table III).

Populations that encountered low difficulties of migration spent higher amounts of energy per unit work on ovarian investment and swimming activity. In relative terms, the energy allocated to various migratory components (*i.e.* ovarian, locomotor and morphological) showed strong associations with difficulty of migration (Table III).

Though sockeye salmon return to and initiate upriver migrations over a 3 month period each summer, differences in return timing probably would not confound estimations of somatic and reproductive energy densities in this study. Four of the study populations arrived within only a few weeks of one other. As >60% of a sockeye salmon's final mass is accrued in its last 6 months of ocean residency, development levels should be relatively similar among populations (Cox & Hinch, 1997). Moreover, the Early Stuart population, which arrived at the Fraser *c.* 1 month earlier than the other populations, had presumably less time to feed than the other populations, yet it had the highest energy density out of all the populations.

DISCUSSION

INDICES OF DIFFICULTY OF MIGRATION

This study details the energetic and morphological changes that occur in wild sockeye salmon during their freshwater spawning migrations, and provides some insight to the evolution of life-history traits among populations. One of this study's objectives was to determine the environmental characteristics that best explain the energetic and morphological patterns observed among Fraser River sockeye salmon populations. The impetus was to understand how natural selection has shaped the pre-migratory partitioning of somatic energy to best prepare fish for the challenges of upriver migration. Though migratory distance, elevation and various combinations of these correlated variables all provide reasonably good measures of the difficulty of migration, distance-by-elevation (*i.e.* work) provided the most number of significant correlations to the among-population morphological and energetic differences observed in the data. A consideration of how sockeye salmon conduct the work of migration is useful in explaining these findings.

In physical terms, work (W) is defined as the product of an applied force (F) over a given distance (d) such that $W = Fd$. In the context of a sockeye salmon's migration, the elevation of the spawning grounds (which influences average river velocities encountered) can provide a rough surrogate for encountered 'force', thus providing half of the work equation. Upriver migratory distances (a surrogate for travel time) are known, thus these two physiologically relevant variables (distance and elevation) can be used to provide an approximate estimate of the amount of work a salmonid must do to reach spawning areas. As migration distances and elevations increase, the accrual and partitioning of somatic energy at river-entry should evolve to satisfy the combined time-at-velocity demands experienced by each population, thus ensuring that the work

of migration is completed. This is especially important since sockeye salmon, as all Pacific salmon, are fuelling migration with fixed endogenous energy reserves. Partitioning this energy to ensure a timely arrival on spawning grounds and subsequent spawning has fitness consequences. No single index, however, can reflect fully the biological complexity of migration, which is probably subject to many biotic and abiotic factors not considered here. But analyses suggest that, regardless of the measure used, the physical difficulty of migration is probably a strong selective agent responsible for the among population differences in energetic and morphological attributes.

As an alternate hypothesis, it could be argued that Fraser River sockeye salmon are genetically predisposed to partition energy and develop morphologies in similar ways, and that the energetic and morphological differences observed among populations at river entry might be due to differences in maturity. As such, among population differences in energetics and morphology could occur without necessarily being adaptive traits. Given the pronounced differences in these traits between the Chilko and Horsefly populations, though they enter the Fraser River at the same time and presumably at approximately the same state of maturity, this seems an unlikely explanation. This also applies to the Weaver and Adams populations, which also enter at the same time, but show distinct energetic and morphological differences. Additionally, given that significant differences are evident among all populations upon arrival at the spawning grounds, when maturation is generally complete, this seems again an unlikely explanation.

SWIM ENERGY EFFICIENCY

Energy use analyses revealed that coastal, lower river populations of Fraser River sockeye salmon are much less energy efficient, expending more somatic energy per unit of difficulty of migration, than interior, upper river populations. For example, upper river Chilko sockeye salmon travelled 468 km further than lower river Weaver sockeye salmon to reach their spawning grounds, yet took only 3 days longer than Weaver to do so (23 v. 20 days respectively), and expended only $2.9 \text{ kJ } (0.001D_M E_M)^{-1}$ relative to Weaver which expended $>1400 \text{ kJ } (0.001D_M E_M)^{-1}$. Such energetic differences reflect fundamental differences between populations in swimming behaviour and secondary sexual character development, both of which influence swim performance. Other studies have examined the differences in swim performance between upper and lower Fraser River sockeye salmon populations. Through electromyogram telemetry, Cultus Lake sockeye salmon (a lower river population) were found to meander more and expended higher amounts of energy *en route* to spawning areas relative to upper river Early Stuart fish (S.G. Hinch, unpubl. data). Additionally, body constituent analyses revealed that Pitt River sockeye salmon (another coastal Fraser population) were less efficient in energy use relative to other upper Fraser populations (Gilhousen, 1980). Behavioural differences between lower and upper river populations have also been observed by fisheries managers and commercial fishermen who monitor Fraser River salmon (J. Woodey, pers. comm.). In a swim-tunnel respirometry study, Weaver sockeye salmon did not perform as well aerobically as other upper river Fraser populations (Lee

et al., 2003). These studies all serve to substantiate the hypothesis that energy efficiency is possibly more strongly selected in populations making difficult migrations. The relative 'inefficiency' of energy use by lower river, coastal populations, however, should not be interpreted as a fitness disadvantage. Coastal populations should be viewed as efficient relative to the specific migrations to which they are adapted. Free from the energetic demands made of fish making longer, more difficult migrations, lower river populations are free to invest more time and resources to egg production and other fitness related traits (*i.e.* secondary sexual characteristics, redd construction and defence and courtship). Indeed, lower river, coastal populations in this study had larger ovaries, greater egg numbers and larger egg sizes than upper river populations. Undoubtedly, there are fundamental behavioural and metabolic differences in the way populations approach upriver migration that appear related to the difficulty of migration.

REPRODUCTIVE TRADE-OFFS

In a reciprocal transplant experiment, Kinnison *et al.*, (2001) raised full-sib families from two populations of New Zealand chinook salmon *Oncorhynchus tshawytscha* (Walbaum) under common hatchery conditions and released them into spawning systems that differed in the difficulty of migration. They detected a reduction in ovarian investment among female chinook salmon, and also a reduction in energy reserves at spawning ground arrival. Likewise, males from the same families showed similar energetic patterns to females, and possessed shallower bodies when migration became more difficult (Kinnison *et al.*, 2003). Strikingly, common-garden rearing experiments with the same families indicate that long migrating populations are genetically predisposed to invest more energy to ovarian development despite having smaller ovaries in the wild (Kinnison *et al.*, 2001). Though these results provide strong evidence of the effects of migration on energy allocation in wild salmonids, the differences in migratory conditions experienced by New Zealand chinook salmon (17 to 100 km distance, 17 to 430 m elevation) are much smaller than those experienced by the Fraser sockeye salmon in this study, but migration distance appears to be the factor most directly responsible for the differences observed in this and other studies (Blair *et al.*, 1993; Bohlin *et al.*, 2001; Quinn *et al.*, 2001). The range of energetic and morphological attributes observed among sockeye salmon migrating across a broad environmental continuum supports Kinnison *et al.* (2001), and provides strong additional evidence for the effects of migration difficulty on salmonid energetics and morphology.

For the upper river sockeye salmon populations examined in this study, attaining high energy efficiency involved a reduction in egg production. Individuals must be judicious in their use of stored energy to ensure their arrival on the spawning grounds, but must also ensure that enough is left for the maturation of their reproductive tissues, as well as for courtship, redd construction, defence and spawning. Though upriver populations possessed high energy reserves at the start of migration, egg production was ultimately less than the lower river populations due to the expense of their difficult migrations (approximately

one-sixth fewer eggs and one-third less ovarian mass). From an evolutionary point of view, trade-offs between somatic and reproductive energy allocation are expected among highly philopatric populations (Stearns, 1992), as has been observed in chinook salmon (Kinnison *et al.*, 2001; Unwin *et al.*, 2001) and in sockeye salmon (Hendry *et al.*, 1999). In Pacific salmon, the magnitude of this trade-off is determined largely by the energetic constraints imposed by upriver migration. In the present study, ovarian mass, egg mass, and egg number (fecundity) all diminished, independently of body length (L_{POH}), as the difficulty of migration increased, indicating an energetically driven reproductive trade-off. Though egg numbers and sizes were smallest in populations making the most difficult migrations, a high ratio of egg number to egg size was observed in these populations (Pearson's $r=0.78$), a pattern that has also been observed in native and introduced chinook salmon and in wild sockeye salmon populations (Kinnison *et al.*, 2001). Though both egg number and size ultimately affect offspring survivorship, salmonids appear to favour offspring number over offspring size when migrations are difficult.

This study provides strong correlative evidence for the role of migration in the evolution of life history trade-offs in a wild salmonid species, but a strong genetic basis for such trade-offs can be found in Kinnison *et al.* (2001).

MORPHOLOGICAL DESIGN AND ENERGY EFFICIENCY

The results of morphological analyses [body depth, body width, ratio of body width-to-depth (o-index) and L_{POH}] suggests that natural selection correspondingly favours a shorter, more torpedo-like, hydro-dynamic body shape in sockeye salmon making long-distance migrations, a characteristic that may help minimize drag and upriver transport costs (Vogel, 1994). This characteristic was more striking in females than in males. Among population differences in the female o-index, however, cannot be attributed to the presence and size of ovaries. Width of river-entry females increased with migratory difficulty (a measure which did not differ between whole and eviscerated sockeye salmon), even while ovary mass decreased. Male body width and depth at river entry decreased with difficulty of migration, but the o-index differences among populations were not as striking, though the general trend was the same as for females. This may explain why recent electromyogram telemetry studies of migrating Fraser sockeye and pink salmon *Oncorhynchus gorbuscha* (Walbaum) found females to be more swim-energy efficient than males (Hinch & Rand, 1998; Standen *et al.*, 2002). In this study, only modest differences between sexes in estimates of upriver activity costs were observed, though estimates presented here are very rough approximations compared to those made by electromyogram telemetry. Lower river populations (*i.e.* Weaver) were deeper bodied and less streamlined, reflecting an increased investment in secondary sexual characteristics during upriver migration, and were less efficient swimmers. It seems adaptive for sockeye salmon making difficult migrations to possess a morphology that positively affects their ability to conserve energy *en route* to spawning areas. In a relative sense, less evolutionary emphasis is placed on swim energy efficiency in lower river populations, thus freeing resources for other fitness related traits.

A study of juvenile Fraser River coho salmon *Oncorhynchus kisutch* (Walbaum) found that upper river populations were more fusiform in shape, and had shallower bodies than coastal populations (Taylor & McPhail, 1985). Given that these structural differences were evident in juvenile salmonids prior to ocean residency, it is likely that salmonids have a genetic predisposition for hydrodynamic efficiency, determined in part by the characteristics of their natal watershed and the migrations they will inevitably make. Presumably, these innate morphological designs carry through to adulthood. If indeed morphological variation in sockeye salmon is not simply an expression of phenotypic plasticity (Moore, 1996), it is likely that a streamlined body shape has co-evolved with swim energy efficiency when migratory constraints are considerable.

In many anadromous fishes, body length increases in relation to upriver distance of spawning grounds. Atlantic salmon (Shaffer & Elson, 1975; Jonsson *et al.*, 1991), brown trout *Salmo trutta* L. (L'Abée-Lund, 1991) and American shad *Alosa sapidissima* (Wilson) (Glebe & Leggett, 1981) all show this positive relationship. One hypothesis for this phenomenon is that larger fishes are capable of storing more somatic energy and generating greater thrust per tail-beat, thus facilitating upriver migration. Bernatchez & Dodson (1987) showed that among anadromous species, increasing difficulty of migration was related to increasing body length and energy efficiency. Body length in sockeye salmon in this study, however, was inversely related to migratory distance, a characteristic also reported in other studies of Pacific salmon including coho (Fleming & Gross, 1989), chum (Beacham & Murray, 1987) and sockeye salmon (Linley, 1993; Moore, 1996). Thus, the Pacific salmon seem to deviate from the expectations of Bernatchez & Dodson (1987), due perhaps to differences in life-history (*i.e.* semelparity *v.* iteroparity). The distances that Atlantic salmon, shad and brown trout migrate upriver tend to be much shorter than those travelled by most Pacific salmon, particularly Fraser River sockeye. Selection may be acting differentially on species that travel only modest distances upriver, and ones that must conserve energy for the downriver return to the ocean.

Regardless of pre-migratory somatic energy concentrations and of difficulty of upriver migration, all five populations of Fraser sockeye salmon died when their somatic energy concentrations reached *c.* 4 MJ kg⁻¹. Previous studies (Gilhousen, 1980; Williams *et al.*, 1986; Hendry & Berg, 1999) also reported similar values, suggesting that this level is the approximate energetic threshold to sustain life in Pacific salmon. The same threshold has also been observed in chum, pink and coho salmon (G.T. Crossin, unpubl. data).

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