

Pink salmon (*Oncorhynchus gorbuscha*) migratory energetics: response to migratory difficulty and comparisons with sockeye salmon (*Oncorhynchus nerka*)

G.T. Crossin, S.G. Hinch, A.P. Farrell, M.P. Whelly, and M.C. Healey

Abstract: Pink salmon (*Oncorhynchus gorbuscha*) are generally considered weak upriver migrants relative to sockeye salmon (*Oncorhynchus nerka*), though this assertion is largely anecdotal. To assess energy-use patterns during migration, we collected pink salmon from two major Fraser River stocks (Weaver and Seton in British Columbia, Canada) in 1999 at three times and locations: (1) at the start of freshwater migration, (2) at the end of migration before spawning, and (3) immediately after spawning. We calculated the energy content of somatic and reproductive tissues, recorded several body measurements, and conducted both intraspecific (between pink stocks) and interspecific analyses with co-migrating Fraser River sockeye salmon collected during the same season. We found that between pink salmon stocks, there were no significant energetic or morphological differences either at river entry or upon arrival at spawning areas regardless of the level of migratory difficulty encountered. When compared with sockeye salmon, however, we found that pink salmon began upriver migration with significantly smaller somatic energy reserves but made up for this deficiency by minimizing absolute transport and activity costs, presumably by seeking out migratory paths of least resistance. This energetic efficiency comes at a cost to reproductive output: relative to sockeye salmon, pink salmon diverted less absolute energy to egg production, producing smaller ovaries and fewer eggs. We speculate that fundamental differences in behaviour shape the migratory energetic tactics employed by pink salmon.

Résumé : Par comparaison aux saumons rouges (*Oncorhynchus nerka*), les saumons roses (*Oncorhynchus gorbuscha*) sont considérés comme des migrants faibles vers l'amont des rivières, bien que cette affirmation repose surtout sur des preuves anecdotiques. Dans le but d'évaluer les patterns d'utilisation de l'énergie durant la migration, nous avons récolté des saumons roses appartenant à deux stocks importants du fleuve Fraser (Weaver et Seton, en Colombie Britannique, Canada) en 1999 à trois sites et périodes, soit (1) au départ de la migration en eau douce, (2) à la fin de la migration avant la fraye et (3) immédiatement après la fraye. Nous avons déterminé le contenu énergétique des tissus somatiques et reproducteurs, mesuré plusieurs dimensions du corps et procédé à diverses analyses comparatives intrasécifiques (entre les stocks de saumons roses) et intersécifiques (avec des saumons rouges migrants récoltés aux mêmes endroits et durant la même saison dans le Fraser). Il n'existe pas de différence significative d'énergie ou de morphologie entre les stocks de saumons roses, ni à l'embouchure de la rivière, ni aux sites de fraye, quel que soit le degré de difficulté rencontré durant la migration. Cependant, par comparaison aux saumons rouges, les saumons roses débutent leur migration vers l'amont avec des réserves énergétiques somatiques significativement plus petites, mais ils compensent pour cette déficience en minimisant leurs coûts absolus de transport et d'activité, probablement en cherchant les voies de migration qui offrent une résistance moindre. Cette efficacité énergétique entraîne cependant un coût en ce qui a trait au rendement reproductif : par comparaison aux saumons rouges, les saumons roses canalisent moins d'énergie absolue vers la production d'oeufs et ils ont des ovaires plus petits et un nombre d'oeufs réduit. Nous croyons que ce sont des différences fondamentales de comportement qui expliquent les tactiques énergétiques du saumon rose durant la migration.

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Introduction

Upon return from the ocean, Pacific salmon (*Oncorhynchus* spp.) stop feeding and rely solely on endogenous somatic energy reserves to fuel upriver migration, final maturation, and spawning (Gilhousen 1980; Linley 1993; Moore 1996; Hendry and Berg 1999; Kinnison et al. 2001; Quinn et al. 2001; Crossin 2003; Kinnison et al. 2003). For species on a fixed energy budget, the relative difficulty of upriver migration can be a significant factor shaping the evolution of life history characteristics. In salmon, for example, among-stock variation in pre-migratory somatic energy reserves as well as allocation patterns between somatic and reproductive compartments while en route to spawning areas have been correlated with measures of migratory difficulty (Kinnison et al. 2001, 2003; Crossin 2003). In sockeye salmon (*Oncorhynchus nerka*), somatic energy is accrued in the ocean in direct proportion to the degree of migratory difficulty encountered when migrating through the Fraser River in British Columbia, Canada (Hendry and Berg 1999; Crossin 2003). Likewise, reproductive trade-offs (i.e., between somatic storage and egg production) occur in sockeye salmon (Crossin 2003) and in chinook salmon (*Oncorhynchus tshawytscha*) (Kinnison et al. 2001, 2003), presumably as a compensatory mechanism through which energy can be conserved for the physical demands of difficult migrations. When upriver migrations are relatively easy, selection for energy efficiency appears to be relatively weak (Crossin 2003).

Pink salmon (*Oncorhynchus gorbuscha*) are the most abundant members of the genus *Oncorhynchus*, supporting the second largest salmon fishery in British Columbia, yet we know very little about their migration ecology. Most of our understanding about the migration ecology of Pacific salmon has been derived from studies of chinook and sockeye salmon. However, these two species possess very different life histories than pink salmon, spending substantial periods of their life cycles in fresh water (with some exceptions, i.e., ocean-type, fall chinook salmon) and showing much greater variation in the size and age at maturity than pink salmon. Pink salmon spend less time in fresh water after emerging from natal gravels, migrating directly to the sea, and returning 2 years later to spawn. Because of their shorter life span (about half that of most other Pacific salmon), pink salmon are generally the smallest salmon species. However, they undertake upriver migrations that can be as energetically demanding as those undertaken by some long-distance chinook and sockeye salmon stocks (Williams et al. 1986).

Given the pronounced influence that migration has on the energetic and reproductive patterns of sockeye salmon, one might expect similar patterns to emerge in pink salmon because they are closely related, occupying the same phylogenetic branch of the *Oncorhynchus* tree. (McKay et al. 1996; Domanico et al. 1997). However, it is a commonly held belief that pink salmon are inferior in migratory ability, unable to travel as far as sockeye salmon and generally poorer at negotiating rapids and river obstacles (as per Williams et al. 1986; Williams and Brett 1987; Heard 1991) and generally regarded as the weakest, or at least most "inefficient" in terms of swim capacity, of all anadromous salmonids. Brett

(1982), for example, reported that sockeye salmon outperformed pink salmon in prolonged and burst-swim trials. However, his analysis compared members of each species that differed greatly in maturity and in the temperature of acclimation; thus, the comparison was not entirely valid. Additionally, conclusions about swimming ability did not take into consideration differences in migratory difficulty. More recent electromyogram radiotelemetry studies in the Fraser River Canyon have clearly revealed that pink salmon can be as energetically efficient as sockeye salmon, if not more efficient. It is also clear that pink salmon and sockeye salmon behave differently when swimming up the Fraser River (Hinch et al. 2002; Standen et al. 2002). Thus, assertions that pink salmon are inferior migrants are brought to question, but to date, no thorough comparison between species has been conducted.

In this study, we had two objectives. The first was to determine how two stocks of Fraser River pink salmon differ energetically and morphologically by contrasting an upriver, interior stock and a lower river, coastal stock. Specifically, we looked for differences in the way that pink salmon stocks partition somatic energy at the onset of upriver migration (river entry), differences in energy-use patterns between river entry and arrival at spawning areas, and differences in morphology. We also contrasted egg production between river entry and spawning ground arrival and looked for evidence of reproductive trade-offs in pink salmon making difficult migrations. Given the greater energetic demands associated with difficult migrations, we predicted that the upper river pink salmon stock would be more energy efficient, having lower transport costs than the lower river stock. Additionally, we predicted that the upper river stock would invest less in egg production and secondary sexual characteristics than the lower river stock.

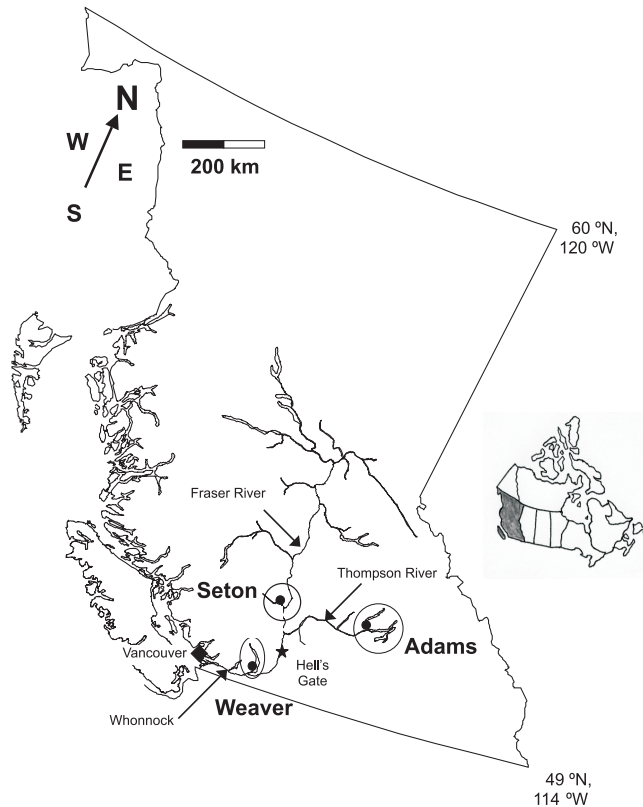
Our second objective was to compare these data with identical data collected from two co-migrating Fraser River sockeye salmon stocks that encounter similar levels of migratory difficulty and to determine how pink salmon respond differently to a common selective agent. These sockeye salmon data represent a small subset of data presented in Crossin (2003). Although pink salmon have a shorter life span and are generally smaller than sockeye salmon, pink salmon can migrate as far upriver as some sockeye salmon stocks. Because smaller fish generally contain less absolute energy than larger fish, we predicted that pink salmon would be more efficient than sockeye salmon making similar migrations, having smaller upriver transport costs but investing less to egg production and secondary sexual characteristics.

Materials and methods

Study system

The Fraser River watershed drains nearly a third of the province of British Columbia and is the largest producer of Pacific salmon in Canada (Dorcey 1991). Extending from headwater streams in the Rocky Mountains, the main stem runs 1378 km to its mouth at Vancouver, B.C. (Fig. 1), and traverses a range of elevations, from high inland plateau and mountain areas to low coastal areas. Because migration is a strong selective agent operating on wild salmon, we generated a composite migratory difficulty index (MDI) as a way

Fig. 1. Map of British Columbia, with inset of Canada, indicating the Fraser River pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*Oncorhynchus nerka*) spawning systems examined in this study (encircled). Black dots indicate the general sampling location within each system. The star indicates Hell's Gate, a region of difficult passage. The square indicates Vancouver, B.C.



to consider adaptive differences among populations. We defined the index as migratory distance by elevation ($MDI = \text{distance} \times \text{elevation}$). Migratory distance can be considered a surrogate for the time needed to complete a migration and elevation gained a surrogate for general current velocity encountered (see Crossin 2003). Both have been shown to affect energy expenditure rates in migrating salmon (Hinch and Rand 1998; Rand and Hinch 1998). In the Fraser River, salmon that migrate long distances also tend to climb high elevations, two environmental variables that are highly correlated (Moore 1996). Because they are correlated, the composite MDI may best reflect their possible joint influence. From work on sockeye salmon, MDI was found to best explain among-stock morphological and energetic variation (Crossin 2003). However, distance and elevation, whether considered a composite variable or individual variables, are both important in explaining among-stock variation and are strong selective agents shaping the evolution of life-history characteristics in Pacific salmon (Moore 1996; Hendry and Berg 1999; Kinnison et al. 2001, 2003; Crossin 2003). In this study, the upper river pink salmon and sockeye salmon stocks travel slightly different distances and elevations to reach spawning areas but encounter similar MDIs.

Sample collection

In 1999, we intercepted two stocks of migrating pink salmon and two stocks of migrating sockeye salmon entering the Fraser River. We targeted interior and coastal stocks from both species to provide good contrasts of migratory difficulty (Table 1). Pink salmon were collected from the Weaver Creek and Seton River stocks (a coastal and an interior stock, respectively). Sockeye salmon were collected from the Weaver Creek and Adams River stocks (again, coastal and interior stocks, respectively). All Fraser River entry salmon, collected at Whonnock, B.C., were captured by gill net by test fishing vessels administered by the Pacific Salmon Commission (PSC). Several hundred pink and sockeye salmon were collected and stored on ice until identified to stock by PSC. Because Fraser River salmon stocks enter the river in an annual sequence that is relatively well understood by PSC and by Fisheries and Oceans Canada, identities were determined in part by run timing. In recent years, some segments of late-run Fraser River sockeye salmon stocks have been migrating 2–6 weeks earlier than historical norms; however, our samples were obtained during times that conformed to historical norms. The identity of salmon collected at target times was confirmed through additional methods: by scale annuli pattern analyses and by parasite analysis at PSC (Cook and Guthrie 1987; M. Lapointe, personal communication). Once positively identified, 10 males and 10 females were collected for analysis.

The identity of returning Fraser River pink salmon, however, cannot currently be determined through scale or parasite analyses. Generally, however, interior (or upriver) Fraser pink salmon stocks typically begin their migrations 2–4 weeks earlier than coastal stocks (Heard 1991). There is currently no evidence to indicate that the 1999 pink salmon have changed their migration timing from the historic norm. Thus, run timing was used to target upper and lower river stocks at river entry. One hundred pink salmon were collected by gill net on each date (Table 1) and were held on ice until electrophoretic analyses were conducted in an effort to determine stock identity (B. White, personal communication). However, maximum-likelihood estimation of the data indicated that there was insufficient genetic variability in the pink salmon loci examined to effectively differentiate stocks of origin. Thus, 10 males and 10 females were randomly drawn from each collection pool of 100 salmon and classified as river entry “Weaver” and “Seton” pink salmon based on collection date.

For both species, an additional 10 male and 10 female salmon were collected by dip net upon spawning ground arrival and on the spawning ground immediately after spawning (Fig. 1). All river-entry, spawning-ground arrival, and postspawned salmon were collected at peak abundance dates estimated from historical trends by PSC and Fisheries and Oceans Canada. Only postspawned females that had released 90%–100% of their eggs were collected. Likewise, only postspawned males with reduced, shrunken testes were collected.

Body morphology and reproductive attributes

For each fish, we measured whole and eviscerated mass (whole less gonads and viscera) and the separate mass of the

Table 1. Peak dates of entry into the Fraser River and of arrival at spawning grounds and environmental characteristics of the migration routes of pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon stocks under study in 1999.

	Fraser River entry	Spawning ground arrival	Days to reach spawning grounds	Migratory distance (km)	Migratory elevation (m)	Migratory difficulty
Pink salmon						
Weaver ^a	29 Sept.	8 Oct.	9	161	10	1
Seton ^a	13 Sept.	7 Oct.	26	323	664	215
Sockeye salmon						
Weaver	18 Sept.	8 Oct.	20	161	10	1
Adams	15 Sept.	6 Oct.	21	484	366	177

^aAlthough the identity of river-entry pink salmon was not possible in this study, upper river (i.e., Seton) pink salmon stocks generally initiate upriver migration earlier than lower river stocks (i.e., Weaver). Thus, dates of Fraser River entry for each stock group were forecasted by the Pacific Salmon Commission using historical records.

gonads and viscera. We measured postorbital to hypural length, 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), all to the nearest millimetre. The ratio between body width to body depth was termed the "o-index" (Crossin 2003). Ovary mass and testis mass were measured and the gonadosomatic index was calculated as the quotient of ovary mass to eviscerated body mass multiplied by 100.

Before we could compare either body shape (e.g., width, depth) or reproductive attributes (e.g., fecundity, individual egg mass, ovary mass, testis mass) among stocks and relate them to MDI, we had to first correct for allometric differences attributed to body size. We corrected for body size with analysis of covariance (ANCOVA) (using type III sums of squares) wherein stock was the class variable, body length (postorbital to hypural length) was the covariate, and the dependent variable was the body shape or reproductive attribute of interest (Hendry and Berg 1999; Crossin 2003). A term examining the potential interaction between body length and stock was added to the ANCOVA model. In all cases, no body length by stock interactions were found; thus, the term was removed from the model. We found homogeneous slopes for each shape and reproductive attribute analysis ($P < 0.05$). Therefore, we used least squares means to generate length-corrected means and standard errors, which were then used in subsequent analyses and figures.

We conducted a length to mass comparison of all river-entry pink salmon through ANCOVA to look for differences based on river-entry date.

Proximate constituent analyses

Eviscerated carcasses and gonads were homogenized, separately, with an industrial food processor (Robot Coupe Blixer BX6V). A 250-g subsample of carcass homogenate and the entire gonad homogenate were packed separately in air-tight plastic freezer bags and stored at -20°C until proximate analyses were conducted. Proximate constituency (lipid, protein, water, and ash) was assessed in the carcasses and ovaries of all salmon according to the methods outlined by Higgs et al. (1979) and modified by Crossin (2003). Lipid percentages were determined through 1:1 chloroform:methanol extractions and converted to energetic equivalents by multiplying the percentage (by wet mass) by $0.03954\text{ MJ}\cdot\text{kg}^{-1}$ for lipid (see Higgs et al. 1979). We calcu-

lated protein percentage in testes as the difference between 100 and the summed water, ash, and lipid percentages. Protein percentages were converted to their energetic equivalents by multiplying the percentage (by wet mass) by $0.02364\text{ MJ}\cdot\text{kg}^{-1}$. This indirect method of protein determination has been employed in previous studies (Berg et al. 1998; Hendry and Berg 1999; Hendry et al. 1999; Crossin 2003) and has been shown to be accurate (Crossin 2003).

As with the body morphology and reproductive attributes described above, we used ANCOVA to correct stock-specific energy densities for body size. Also as above, we found homogeneous slopes in each analysis ($P < 0.05$). Therefore, least squares means were used to generate length-corrected energy density means and standard errors.

Somatic energy partitioning during migration

While migrating upstream, sockeye salmon partition somatic energy reserves to a number of tasks (e.g., standard metabolism, active metabolism, gonad maturation, development of secondary sexual characteristics). The two largest energetic needs are active metabolic costs of swimming and gonad maturation (Rand and Hinch 1998). We estimated energy investment during the migration into these two tasks with a linear regression technique used in previous salmon energetic studies (e.g., Jonsson et al. 1997; Hendry and Berg 1999). Using data from river entry and spawning ground arrival for each stock, we natural log (ln) transformed mass-specific somatic energy levels and regressed these against body length. ANCOVA tested for heterogeneity of slopes between these two collections. When 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 egg production (ovarian investment) was done in an identical manner, comparing the intercepts between river-entry and spawning-ground ovarian energy when regressed against body length. Energy costs estimates calculated in this way are inferential, determined by the amount of energy lost from the somatic tissues minus that diverted into the ovaries, which we could measure directly. Having accounted for ovarian investment, and knowing that losses from standard metabolism are relatively small in migrating sockeye salmon (Rand and Hinch 1998), any further somatic energy loss was most likely attributable to swimming activity costs and morphological change (secondary sexual characteristics).

Results

Pink salmon morphology

Comparison of ln-transformed lengths and masses of river-entry pink salmon from both river-entry gillnet collections revealed no significant difference between groups (ANCOVA, $P = 0.934$, $n = 200$). Additionally, ANCOVA revealed no significant group differences in river-entry ovary mass ($P = 0.341$) and the mean mass for 10 individual eggs ($P = 0.100$). No significant group differences were revealed in mean dorsal hump height ($P = 0.811$ for males and $P = 0.628$ for females) or in o-index measures ($P = 0.584$ for males and $P = 0.622$ for females). Testis mass did differ between river-entry groups ($P < 0.05$) but was not related to migratory difficulty (male salmon generally show a high degree of variation in testis mass at any given stage of migration). Given these results and that little allozymatic heterogeneity exists among these Fraser River pink salmon (B. White, personal communication), the somatic and ovarian energy signals in both river-entry groups were pooled and used as a starting energy value for both the Seton and Weaver river-entry groups.

There were no significant differences in dorsal hump and o-index measures between spawning ground Seton and Weaver pink salmon (female dorsal hump $P = 0.852$ and o-index $P = 0.723$; male dorsal hump $P = 0.156$ and o-index $P = 0.323$). Additionally, ovary mass did not differ between Seton and Weaver prespawning females ($P = 0.355$); prespawning testis mass also did not differ between males of each stock ($P = 0.226$).

Pink salmon somatic energy partitioning and egg production

Proximate analysis of river-entry pink samples showed that water was always the greatest constituent in both somatic and reproductive tissues (75%–77% in soma and 58% in ovaries) followed by protein (17%–18% in soma and 27% in ovaries), lipid (4%–5% in soma and 12% in ovaries), and ash (2%–3% in soma and 2% in ovaries) (Table 2, Fig. 2). ANCOVA revealed no sex effect on gross somatic energy, lipid, and protein concentrations at each sampling location ($P > 0.05$; Table 2). Although the Seton stock traveled more than 200 km farther than the Weaver stock to reach spawning areas, both stocks arrived on the spawning grounds with the same somatic energy densities ($P = 0.954$) (Table 2, Fig. 2b). Somatic lipid and protein concentrations were also the same for both upon spawning-ground arrival (both $P > 0.05$) (Table 2, Fig. 2a). Comparisons with sockeye salmon indicated that initial gross somatic energy concentrations were significantly lower in pink salmon ($6.2 \text{ MJ}\cdot\text{kg}^{-1}$) relative to both Weaver ($7.1 \text{ MJ}\cdot\text{kg}^{-1}$) and Adams ($8.3 \text{ MJ}\cdot\text{kg}^{-1}$) sockeye salmon (Fig. 2b). Despite this difference, Weaver and Seton pink salmon arrived on spawning grounds with energy levels nearly identical to those of Weaver and Adams sockeye salmon (all $P > 0.05$). All postspawning (moribund) pink salmon and sockeye salmon had somatic energy levels near $4 \text{ MJ}\cdot\text{kg}^{-1}$ (Fig. 2b).

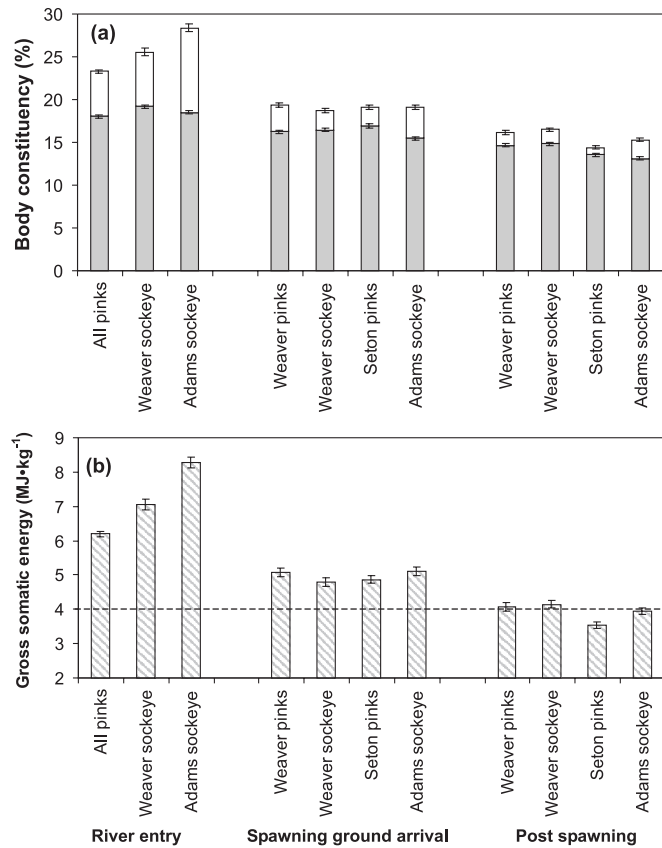
When traveling from river-entry to spawning-ground sites, Weaver pink salmon expended 2%–6% of somatic proteins and 23%–61% of somatic lipids. Seton expended 2% of somatic proteins and 39%–61% of somatic lipids. Depending

Table 2. Proximate composition (by wet mass) of somatic and ovarian tissues and gross somatic energy densities (GE) ($\text{MJ}\cdot\text{kg}^{-1}$) in upriver migrating Fraser River pink salmon (Weaver and Seton stocks) collected in 1999.

	Female soma						Male soma						Ovaries						
	protein		lipid		ash		protein		lipid		ash		protein		lipid		ash		
	Percent	GE	Percent	GE	Percent	GE	Percent	GE	Percent	GE	Percent	GE	Percent	GE	Percent	GE	Percent	GE	
River entry	17.80	5.44	74.48	2.28	2.64	6.36	16.70	3.72	77.05	2.53	2.53	5.42	27.31	12.18	58.07	2.45	11.27		
Weaver before spawn	16.83	3.40	77.12	2.64	2.79	5.32	15.62	2.85	78.96	2.57	2.57	4.82	26.85	11.78	59.21	2.16	11.01		
Weaver after spawn	14.84	1.34	81.04	2.79	2.75	4.04	14.50	1.54	80.97	3.00	3.00	4.04							
Seton before spawn	17.40	2.13	77.72	2.75	2.81	4.96	16.42	2.25	78.86	2.47	2.47	4.77	23.81	14.55	57.97	3.67	11.38		
Seton after spawn	13.69	0.86	82.64	2.81	2.81	3.58	13.39	0.81	82.88	2.92	2.92	3.48							

Note: Values are corrected for body length (see text for details).

Fig. 2. Comparison of mean (± 1 SE) somatic lipid (open bars) and protein (shaded bars) (a) and gross somatic energy concentrations (b) of Fraser River pink salmon and sockeye salmon collected in 1999. The sexes are pooled. Sample size (n) for each bar is 20. The broken horizontal line in Fig. 2b is our speculation at the approximate energetic threshold to sustain life in sockeye salmon (see Crossin 2003).

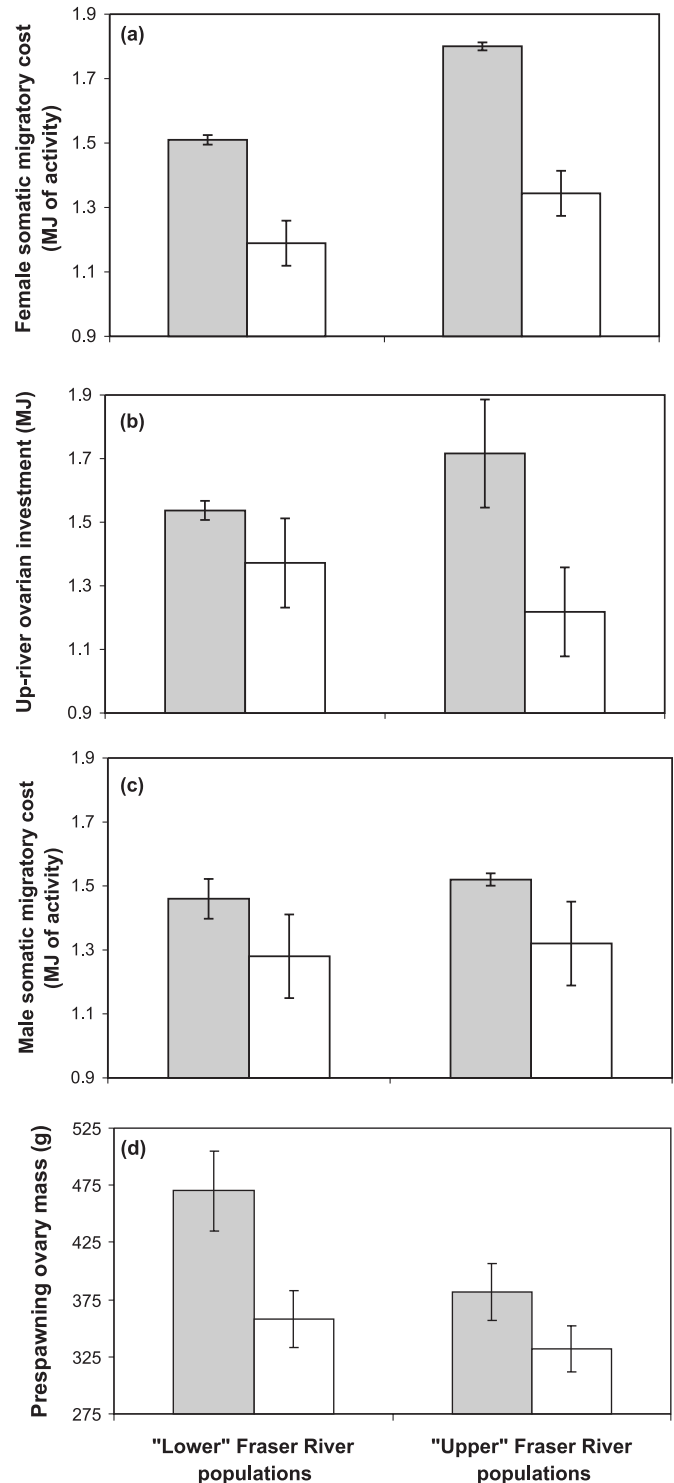


on the stock, this represented an 11%–16% loss of gross somatic energy reserves in Weaver pink salmon and a 12%–22% loss in Seton pink salmon (see Table 2), which is less than half of the range observed among sockeye salmon stocks (30%–53% loss). From spawning-ground arrival to death after spawning, pink salmon expended 7%–21% of their remaining somatic proteins and 46%–64% of remaining lipids. This represented a loss of 16%–28% of gross somatic energy, a range that was comparable with that of sockeye salmon (15%–30%).

Comparative somatic energy partitioning and egg production

Of the total somatic energy spent during upriver migration (i.e., transport costs), female Seton and Weaver pink salmon partitioned approximately half into swimming and other active metabolic processes (46% for Weaver and 52% for Seton) and half into egg production (54% for Weaver and 48% for Seton) (see Figs. 3a and 3b). After length corrections, males of both species channeled slightly more to upriver swimming costs than females (Figs. 3a and 3c). When compared by units of migratory difficulty, Weaver pink salmon had lower transport costs (i.e., they expended less somatic energy between Fraser River entry and spawning ground arrival) than Weaver sockeye salmon (Figs. 3a–

Fig. 3. Mean ($\pm 95\%$ confidence interval (CI)) somatic energy used for standard and active metabolic processes during upriver migration by female sockeye salmon (shaded bars) and pink salmon (open bars) (a) and male sockeye salmon and pink salmon (c), mean ($\pm 95\%$ CI) somatic energy used for egg production (ovarian investment) during upriver migration (b), and mean (± 1 SE) length-corrected ovary mass of spawning ground sockeye salmon and pink salmon females (d).



3c). Likewise, Seton pink salmon had lower transport costs than Adams sockeye salmon (stocks with similar degrees of migratory difficulty) (Figs. 3a–3c). Weaver pink salmon invested less energy into egg production than Weaver sockeye salmon (Figs. 3b and 3d), and likewise, Seton pink salmon invested less than Adams sockeye salmon (Figs. 3b and 3d). These energy estimations are derived from length versus absolute energy relationships in a given tissue group (i.e., soma or ovaries) (see Jonsson et al. 1997; Hendry and Berg 1999). When pink salmon length was scaled up to match that of their sockeye salmon counterparts, the relationship between pink salmon and sockeye salmon did not change, although absolute energy values changed slightly in pink salmon (Figs. 3a–3c).

Gross energy concentrations in the ovaries did not change substantially from river entry to spawning ground arrival (Table 2). However, ovarian mass (grams) increased substantially over this period (18% increase for Seton and 26% for Weaver). Length-corrected egg number (fecundity) of Seton and Weaver females upon spawning-ground arrival did not differ ($P = 0.546$). However, prespawning egg number and ovary mass in Weaver pink salmon were significantly smaller than in Weaver sockeye salmon (both $P < 0.01$). Likewise, both attributes were also smaller in Seton pink salmon relative to Adams sockeye salmon (both $P < 0.01$) (for prespawning ovaries) (Fig. 3d).

Discussion

This study details the energetic strategies employed by two stocks of migrating adult Fraser River pink salmon and makes comparisons with co-migrating adult sockeye salmon. From our results, two important conclusions can be drawn. (1) Unlike sockeye salmon, no significant energetic and (or) morphological differences were observed between the two stocks of Fraser River pink salmon that we examined, despite encountering substantially different levels of migratory difficulty en route to spawning areas. (2) When compared with stocks of sockeye salmon making similar migrations, pink salmon were much more energy efficient, minimizing transport costs by expending less somatic energy per unit of migratory difficulty and using less total energy to reach common spawning areas. These two conclusions provide new insights into the migratory ability of pink salmon and are discussed below.

Though it is commonly known that the earliest returning pink salmon to the Fraser River each year are generally bound for spawning areas in the upper regions of the watershed (J. Woodey, personal communication), analysis of river-entry pink salmon collected from both the leading and the trailing edges of the 1999 summer run revealed no significant energetic or morphological differences among river-entry collections. This was contrary to our prediction that river-entry pink salmon stocks would judiciously partition their finite somatic energy among fitness-related tasks, as sockeye salmon do, in direct proportion to the degree of migratory difficulty that they will encounter en route to spawning areas. That the two pink salmon stocks were energetically and morphologically indistinguishable at the onset of upriver migration suggests that, regardless of “stock” (or ultimate spawning location), all returning pink salmon have

the capacity to reach upriver spawning areas, although many ultimately spawn in downriver areas. This suggests further that pink salmon may be a highly exploratory species, well equipped energetically to seek out and colonize new spawning areas. It is generally accepted that pink salmon stray more than other Pacific salmon (as per Horall 1981; Heard 1991). A species that exhibits a high degree of straying (i.e., high gene flow) should be more genetically homogenous than a highly philopatric species, and indeed, a high degree of genetic homogeneity has been measured in Fraser River pink salmon and even among Fraser River, Puget Sound, and other non-Fraser British Columbian pink salmon (Beacham et al. 1985; Heard 1991). Thus, pink salmon may indeed stray more than other Pacific salmon. That we could detect no discernable morphological and energetic differences among *all* river-entry pink salmon collected, and even among pink salmon spawning in up- and down-river locales, suggest that Fraser River pink salmon may not be a collective of discernable, locally adapted stocks as in other Pacific salmon species. Three alternative explanations are possible: (1) Fraser River pink salmon are structured more like a single, large stock of salmon composed of generalists who exhibit little genotypic and phenotypic diversity and who tend to stray more than other Pacific salmon; (2) Fraser pink salmon are in the process of diversification, radiating toward new locally adapted forms; or (3) Fraser pink salmon are indeed a collective of distinct stocks but we have yet to identify traits to differentiate them.

Though scientific studies of Fraser pink salmon straying behaviour are scarce, anecdotal evidence supports the possibilities listed above. In 1913, a rockslide at Hell’s Gate in the Fraser Canyon of British Columbia (Fig. 1) made upriver passage nearly impossible for Fraser sockeye salmon and effectively eliminated passage of pink salmon for more than 30 years (Heard 1991), suggesting that pink salmon were weaker migrants. In the years that followed, small numbers of sockeye salmon were able to pass under their own power, and others were assisted by the International Pacific Salmon Fisheries Commission who caught sockeye salmon with dip nets and transported them past the barrier (Roos 1991). Thus, modest upstream passage for sockeye salmon was able to continue.

Only after the completion of fishways in 1945 were pink salmon able to recolonize upriver areas (Vernon 1962). Modest escapement past Hell’s Gate was recorded in the initial years after fishway completion (1000–2000; Roos 1991). By the mid-1950s, however, spawning at Seton River was again negatively impacted by the construction of the Seton River hydroelectric dam. Whether pink salmon that were displaced by this project died without spawning or spawned in adjacent upriver regions along the Fraser mainstem is unknown. However, total Fraser River pink escapement declined during this period, suggesting that these upriver pink salmon were not spawning successfully (Roos 1991). Not until the Seton spawning channels were built in the early 1970s did spawning fish return in significant numbers. Pink salmon escapements above Hell’s Gate eventually increased, numbering in the millions by the late 1970s and reaching tens of millions by 2001. There seems little doubt that current upriver spawning stocks in the Fraser River are derived from straying downriver pink salmon stocks (Heard 1991). Thus,

one might assume that the extent of straying in Fraser pink salmon may be much higher than previously suspected, providing a possible explanation for their allozymatic and phenotypic homogeneity.

Regardless of their ultimate spawning destination, female pink salmon from both river-entry collections (targeting up and down river stocks) (*i*) had roughly equal somatic energy levels, (*ii*) invested equal levels of energy into egg production (equal fecundities and ovarian mass), and (*iii*) expressed secondary sexual characteristics to the same degree (i.e., dorsal hump height). Male pink salmon followed the same pattern. This was contrary to our predictions that pink salmon would partition somatic energy in a way similar to that observed in other Pacific salmon making difficult migrations (see Kinnison et al. 2001, 2003). That pink salmon neither partitioned somatic energy nor expressed morphological characteristics in proportion to the degree of migratory difficulty encountered en route to spawning areas suggests that they are much less locally adapted than sockeye salmon (although in other geographic regions, pink salmon stocks show discernable local adaptation (i.e., run timings and fecundity; Smoker et al. 1998)).

Evolutionary theory predicts reproductive trade-offs (i.e., reduced secondary sexual characters and reduced egg production) to occur in organisms making difficult migrations (Stearns 1992), a process that has been well documented among stocks of other Pacific salmon and shows both genetic and plastic components (Kinnison et al. 2001, 2003). Theory argues that reproductive trade-offs are driven by a necessity to free energy for peripheral functions that directly affect fitness (i.e., locomotion). The magnitude of such a trade-off is generally proportional to the relative difficulty of the migration. For example, in this study, river-entry Fraser sockeye salmon accrue somatic energy in direct proportion to migratory difficulty but produce smaller and fewer eggs as migrations become more difficult (although egg number tends to be favoured over egg size (see Kinnison et al. 2001; Crossin 2003)). But pink salmon do not appear to conform to this model. Regardless of their ultimate spawning destination, pink salmon showed no significant differences in the amount of somatic or ovarian energy partitioned prior to migration. If difficult migrations do indeed select for energy efficiency (Kinnison et al. 2001; Crossin 2003), pink salmon appear to achieve this without limiting egg production.

Male and female pink salmon expended less energy per unit of migratory difficulty than male and female sockeye salmon making similarly demanding migrations. This is profound given that both the Weaver and Seton pink salmon began their upriver migrations with significantly smaller gross (and total) somatic energy concentrations ($6.2 \text{ MJ}\cdot\text{kg}^{-1}$) than Weaver and Adams sockeye salmon (7.1 and $9.8 \text{ MJ}\cdot\text{kg}^{-1}$, respectively). There is a mounting body of evidence to suggest that pink salmon may achieve higher energy efficiency by being more behaviourally efficient than sockeye salmon. For example, a recent electromyogram telemetry study of upriver migrating salmon shows that Fraser River pink and sockeye salmon swim at similar speeds and spend similar amounts of time in both aerobic and anaerobic metabolism when passing through the Fraser Canyon, a region of exceedingly difficult passage (Hinch et al. 2002). Both species successfully negotiated these turbulent waters, but behav-

ourally, they exhibited very different swim strategies. Pink salmon tended to swim closer to shore, and perhaps made better use of microenvironments (reverse flow fields, back eddies); they took a more "direct", steady path through the river, presumably finding and utilizing pathways of least resistance as a means to conserve their smaller relative and absolute somatic energy reserves. Indeed, pink salmon rarely displayed energetically costly burst-swim behaviours. In contrast, sockeye salmon, possessing greater somatic reserves and a more hydrodynamic body shape, were less direct than pink salmon, frequently crossing the river's main channel and exhibiting behaviours that were more costly and variable (burst and coast) as they made their way upriver. Standen et al. (2002) also found that sockeye salmon were much less energy efficient than pink salmon when migrating through river constrictions. Given that swim-tunnel respirometry studies show no difference (at a given temperature) between pink salmon and sockeye salmon in cost of transport (milligrams of oxygen per kilogram per metre), metabolic scope (milligrams of oxygen per kilogram per minute), and maximum sustained swimming speed (U_{crit}) (MacNutt 2003), we speculate that behavioural efficiency in pink salmon is the basis for their energetic efficiency. If we assume that the swimming behaviours observed in pink and sockeye salmon in the Fraser Canyon are representative of those used by both species over the full course of migration, this could explain the lower transport costs that we estimated in pink salmon relative to sockeye salmon at the whole-river scale.

Between river-entry and spawning-ground arrival, male pink salmon expended slightly more energy than females. We speculate that the expression of secondary sexual characteristics in migrating pink salmon, which was significantly greater in males (i.e., larger dorsal humps), reduces hydrodynamic efficiency and result in slightly higher transport costs (see Crossin 2003).

Collectively, results presented here, and results from the aforementioned studies, suggest that pink salmon are much stronger migrants than once suspected. That pink salmon did not pass through Hell's Gate after the 1913 rockslide was probably because of their unwillingness to burst swim rather than a presumed inferior migratory ability. Once the constriction was widened in the 1940s, pink salmon passed through in great numbers and have since been observed making exceptionally difficult migrations to the upper reaches of the Fraser watershed (upwards of 1000 km upriver), although numbers swimming this far are generally low (T. Cone, personal communication). An unwillingness to burst swim may ultimately limit their upriver distribution, as may their smaller somatic energy reserves at river entry.

Differences between pink salmon and sockeye salmon distributions may be attributed, in part, to differences in life history. For some stocks of sockeye salmon, life history necessitates long migrations to distant lake systems that serve as nurseries for sockeye salmon fry. Fraser River pink salmon do not rely on lakes as nurseries, and thus do not have to migrate far upriver for access to suitable spawning habitat and can spawn extensively on the banks of the lower Fraser and Thompson rivers.

In conclusion, we have identified some fundamental differences in the way that pink salmon and sockeye salmon

partition somatic energy for upriver migration. Given that pink salmon attain mature sizes that are only slightly smaller than mature sockeye salmon, and do so in half the generation time, pink salmon appear to favour growth over somatic energy storage and egg production relative to sockeye salmon. However, within species, we were unable to detect energetic and reproductive trade-offs in pink salmon. Regardless of the difficulty of migration, Weaver and Seton pink salmon stocks partitioned an equal amount of somatic energy to upriver activity demands and egg production.

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