Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon

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Abstract: Reproductive development and energy stores were characterized for sockeye salmon (*Oncorhynchus nerka*) maturing in the wild (Pick Creek, Bristol Bay, Alaska). Between freshwater entry and the start of spawning, ovaries increased in mass by 87.1% and secondary sexual characters increased in linear dimension by 13.0–47.4%. Between the start of spawning and death, secondary sexual characters decreased in relative size by 3.3–12.7%. Mass-specific somatic energy declined from freshwater entry (6.7% fat, 20.6% protein, 6.6 kJ·g^{-1}) to the start of spawning (1.6% fat, 18.0% protein, 4.5 kJ·g^{-1}) and finally to death (0.1% fat, 14.4% protein, 2.9 kJ·g^{-1}). Stored fat appeared to be used primarily for upriver migration and egg production, whereas stored protein appeared to be used primarily for the development of secondary sexual characters and metabolism during spawning. Most development of secondary sexual characters occurred late in maturation, perhaps to forestall deterioration of muscle tissue. Relative to populations with long freshwater migrations, Bristol Bay sockeye salmon stored less fat before entering fresh water and used less fat before death. The total energy cost of reproduction (freshwater entry until death, including gonad investment) was 74.1% for females and 66.1% for males, higher than levels typically reported for iteroparous salmonids.

Résumé : Le développement du système reproducteur et les réserves énergétiques ont été étudiés chez le Saumon rouge (*Oncorhynchus nerka*) au cours de la maturation, en nature (Pick Creek, baie de Bristol, Alaska). Entre le moment de leur en eau douce et le début de la fraye, la masse ovarienne des saumons augmente de 87,1% et leurs caractères sexuels secondaires augmentent de 13,0–47,4% dans leur dimension linéaire. Entre le début de la fraye et la mort, la taille relative des caractères sexuels secondaires diminue de 3,3–12,7%. L'énergie somatique spécifique à la masse diminue depuis l'entrée en eau douce (6,7% de graisses, 20,6% de protéines, 6,6 kJ·g^{-1}), jusqu'au début de la fraye (1,6% de graisses, 18,0% de protéines, 4,5 kJ·g^{-1}) et finalement jusqu'à la mort (0,1% de graisses, 14,4% de protéines, 2,9 kJ·g^{-1}). Les graisses de réserve semblent utilisées surtout au cours de la migration vers l'amont et servent à la production d'oeufs, alors que les réserves de protéines sont utilisées surtout à la production des caractères sexuels secondaires et au métabolisme durant la fraye. La plupart des caractères sexuels secondaires apparaissent tard au cours de la maturation, peut-être pour retarder la détérioration du tissu musculaire. Comparativement aux populations qui font de longues migrations en eau douce, les Saumons rouges de la baie de Bristol accumulent moins de graisses avant leur entrée en eau douce et en utilisent moins jusqu'à leur mort. Le coût énergétique total de la reproduction (de l'entrée en eau douce jusqu'à la mort, en comptant le coût de formation des gonades) a été évalué à 74,1% chez les femelles et à 66,1% chez les mâles, valeurs plus élevées que celles qui prévalent généralement chez les salmonidés itéropares.

[Traduit par la Rédaction]

Introduction

The most taxing period of life for many organisms is reproduction, when resources are diverted from procuring food and into tasks necessary for successful breeding. As a result, energetic constraints are often associated with reproduction, and these constraints are particularly evident in species with low energy intake and high energy expenditure during breeding. Sockeye salmon (*Oncorhynchus nerka*) migrate long distances from feeding areas in the open ocean to their natal spawning sites in streams or lakes (Burgner 1991). Females develop large gonads (about 25% of their body mass; Hendry et al. 1999) and engage in vigorous competition for access to spawning sites (Foote 1990). Males undergo extensive morphological changes (Davidson 1935) and fight incessantly for access to spawning females (Quinn et al. 1996). Feeding ceases at entry into fresh water, often several months before spawning commences (capital breeding), and all fish die after a single spawning season (semelparous). Given severe limitations on available energy and conflicting demands for that energy, natural selection should tend to optimize patterns of reproductive development and energy allocation. We investigated these patterns in the context of five specific objectives.

Our first objective was to document the temporal sequence of development for secondary sexual characters, traits that typically differ between the sexes and influence "the advantage which certain individuals have over other

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individuals of the same sex and species, in exclusive relation to reproduction" but "are not directly connected with the act of reproduction" (Darwin 1871*a*). Darwin suggested that exaggerated male traits in salmon evolved through intrasexual competition (Darwin 1871*b*), and recent research has confirmed that particular morphological features influence mating success (Fleming and Gross 1994; Quinn and Foote 1994). Quantifying temporal changes in the expression of secondary sexual characters is important for inferring selective forces that influence their evolution. For example, traits that increase considerably in relative size with maturation are likely to be those that are detrimental in the prebreeding state but necessary for successful breeding.

Our second objective was to examine linkages between energy use and reproductive development. The four major types of reproductive investment in salmon (migration, gonads, secondary sexual characters, and spawning competition), involve different energy requirements. Similarly, fat and protein have different properties (fat has a higher energy content, whereas protein serves a structural role; Jobling 1994), and muscle and viscera have different storage potential (more energy can be stored in the muscle but depletion of muscle tissue may negatively impact physical performance). As a result, mobilization of different energy sources should be tied to aspects of reproductive development in ways that promote efficient energy transfer. By identifying types of reproductive investment coincident with the use of specific energy sources, we could generate insights into adaptive aspects of energy storage and mobilization.

Our third objective was to explicitly consider energetics for sockeye salmon that undertake short freshwater migrations. The current view of reproductive energetics in Pacific salmon derives primarily from a study of three sockeye salmon populations that undertake exceptionally difficult migrations up the Fraser River, British Columbia (Idler and Clemens 1959; reanalyzed by Gilhousen 1980; reviewed by Brett 1995). Less detailed studies of a few other populations have been undertaken, but these studies were limited to only a few stages of maturation, sample sizes were usually small (3–5 individuals of each sex at each stage), and long migrations were still overrepresented (Appendix). The Fraser River populations were originally chosen for study specifically because their upstream migrations were expected to exact a high energy cost. Most sockeye salmon populations, however, undertake upstream migrations that are far easier (Burgner 1991, pp. 7–8). Disproportionate reliance on the Fraser River research may have led to an incomplete picture of energetics for maturing Pacific salmon (i.e., the extreme is viewed as the norm).

Our fourth objective was to estimate the energy cost of reproduction in sockeye salmon. Quantifying the cost of reproduction is an important component of the application of life-history theory and optimality models (Sibly and Calow 1986; Stearns 1992). For example, semelparous species are expected to expend more energy during reproduction than species with the potential for iteroparity. We compared the energy cost of reproduction in the population we studied with values calculated using other studies of semelparous and iteroparous salmonids (Appendix).

Our final objective was to integrate patterns of morphological change and energy depletion to provide a better pic-

ture of senescence. Pacific salmon show a remarkable senescent decline from maturity to death, a period of time typically ranging from a few days to several weeks (McPhee and Quinn 1998; Hendry et al. 1999). As part of this deterioration, individuals of both sexes shrink in size and secondary sexual characters become smaller (Quinn and Blair 1992). Somatic water content increases, while somatic fat content, protein content, and energy density decrease (Gilhousen 1980). Only one study has measured shape changes that accompany senescence (Quinn and Blair 1992), only a few studies have measured energy loss in naturally spawning Pacific salmon (e.g., Gilhousen 1980), and no study has systematically measured these correlated changes within the same population.

Methods

Sample collection

Attaining our objectives required a temporal sequence of samples, one that would be as representative as possible of changes in a single population. To generate such a sequence, fish must be sampled long before they reach their natal spawning sites. Biases could be introduced into such studies if samples include fish with migratory patterns different from those of the target population. One way to alleviate this problem is to sample populations that migrate at distinctive times, such as the early-migrating Fraser River sockeye salmon (Idler and Clemens 1959; Gilhousen 1980). Another way is to collect fish from a complex of populations that migrate at similar times and places and have equivalent migration distances. We applied the latter approach to the sockeye salmon of Bristol Bay, Alaska.

Sockeye salmon returning to spawn in the lake systems that drain into Bristol Bay migrate past Port Moller (Fig. 1) during a short period of time (80% of the fish pass during a 2-week period; Mundy 1979). A comparison of average migration distances and elevations to Bristol Bay lakes (from Burgner 1991, pp. 7–8) with the average number of spawners returning to those lakes for the years of the present study (1993, 1995, and 1996; Fisheries Research Institute, University of Washington, unpublished data; Alaska Department of Fish and Game, unpublished data), revealed that only about 10% of Bristol Bay sockeye salmon migrated farther than 150 km from the ocean and only about 10% migrated to elevations higher than 70 m asl. The "average" Bristol Bay sockeye salmon migrated 94 km in fresh water to an elevation of 28 m asl. The population chosen for the present study (Pick Creek, 98 km to an elevation of 22 m asl; Fig. 1) was therefore representative of Bristol Bay sockeye salmon considered.

In 1996, we collected a temporal sequence of samples (Table 1, Fig. 1). Fish were sampled (*i*) approximately a week before leaving the ocean (Port Moller, "coastal"), (*ii*) immediately after entry into fresh water (Lake Aleknagik, "freshwater entry"), (*iii*) at the start of spawning (at entry into Pick Creek, "spawning"), and (*iv*) at death (Pick Creek, "death"). The samples at Port Moller were collected in a test fishery (for details on the test fishery see Helton 1991); the samples at Lake Aleknagik were collected by seining fish that were entering the lake; the samples at the start of spawning were collected by sampling tagged fish as they entered Pick Creek (the fish begin spawning when they first enter the creek; Hendry et al. 1999); and the samples at death were collected by surveying Pick Creek and collecting fish that had just died of senescence (indicated by bright red gills and no obvious wounds; Hendry et al. 1999). We augmented the temporal sequence of 1996 samples with collections made from these locations in previous years (Table 1).

Fig. 1. Sampling sites for determining the temporal sequence of reproductive development and energy stores. (A) General location of Bristol Bay relative to Alaska. (B) Location of the Port Moller sampling site (✱) and the Wood River Lakes. (C) Sampling site at the outlet of Lake Aleknagik (✱), the sampling site at the mouth of Pick Creek (✱), and Pick Creek.
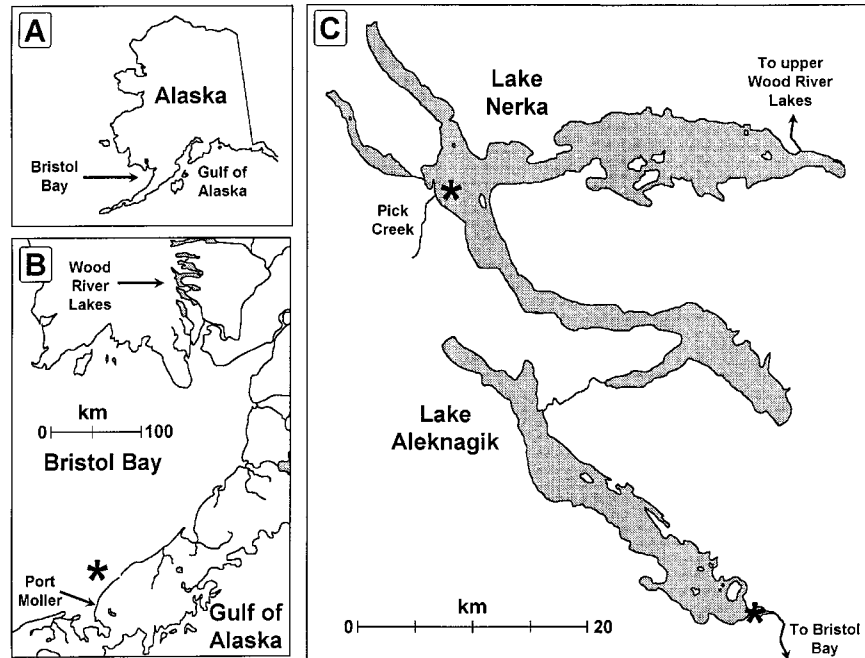

Table 1. Stages of maturation, collection dates and locations (see Fig. 1), sample sizes, and characteristics of sampled fish.

Stage	Location	Date	Sex	N	Length (mm)	Mass (g)	Gonads (g)
			1996 collections				
Coastal	Port Moller	1–2 July	F	10	485±24	2632±334	174.3±38.9
			M	10	493±21	2845±396	85.2±27.2
Freshwater entry	Aleknagik	7 July	F	10	459±29	2460±569	231.6±100.2
			M	10	487±42	3003±886	106.3±39.5
Spawning	Pick Creek	21 July – 12 August	F	30	449±29	1953±438	387.9±97.7
			M	30	473±37	2610±694	60.4±11.7
Death	Pick Creek	4–15 August	F	23	447±31	1459±321	—
			M	23	464±40	2109±554	14.9±6.8
			Supplemental collections				
Coastal	Port Moller	23 June – 4 July 1993	F	49	505±27	2623±523	186.9±60.0
			M	51	532±30	3224±102	101.8±39.8
Coastal	Port Moller	17 June – 8 July 1995	F	20	500±30	—	—
			M	20	506±30	—	—
Shoaling[a]	Pick Creek	8 July 1995	F	20	500±15	2707±332	471.2±68.1
			M	20	522±26	3487±477	62.9±8.6

Note: Values are given as the mean ± SD.

[a]Sample was obtained using a seine net to capture fish shoaling off the mouth of Pick Creek prior to spawning.

Morphological change

We measured various aspects of body shape (Fig. 2), including body length (middle of the eye to the end of the hypural plate), snout length (tip of the snout to the middle of the eye), caudal peduncle depth (at its shallowest point), body depth (anterior insertion of the dorsal fin to the bottom of the abdomen perpendicular to the lateral line), hump height (portion of body depth above the lateral line), and adipose-fin length (anterior insertion to posterior margin). Measurements were made using calipers, to the nearest millimetre for body length and the nearest 0.1 mm for all other traits. Owing to time limitations at Port Moller in 1995, only body length, body depth, and snout length were measured.
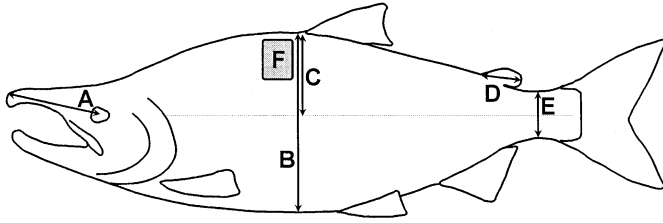
Analysis of covariance (ANCOVA) was used to assess morphological change, independent of variation in body length. All mea-surements were log_{10}-transformed, and the relationship between each trait and body length was tested for heterogeneity of slopes among the seven collections. When the slopes did not differ, the interaction term was removed from the ANCOVA model and adjusted means were calculated using the common within-group slope (Huitema 1980). Adjusted means from ANCOVA were antilogged for presentation. Similar statistical procedures were used to analyze changes in gonad mass (measured as described below).

Proximate composition

In 1996, each fish was divided into somatic tissues (all body parts excluding the gonads) and gonadal tissues, which were homo-genized separately by chopping with a knife and then grinding in a

Fig. 2. Morphological measurements taken on male and female sockeye salmon: snout length (A), body depth (B), hump height (C), adipose-fin length (D), and caudal-peduncle depth (E). The shaded rectangle (F) indicates the location of the muscle sample taken in 1995.

drill-powered meat grinder. Samples of homogenate were stored at –20°C until analysis. We determined energy content using proximate analysis, in which the main chemical constituents (water, protein, fat, and ash) are estimated. We ignored carbohydrates because they constitute <0.5% of the somatic tissue of salmonid fishes (e.g., Jonsson et al. 1991; Jonsson et al. 1997). Water content was measured by drying about 10 g of each homogenate at 55°C for 2 weeks (constant mass was attained). Fat content was determined gravimetrically following extraction of the dried samples in a solvent composed of five parts petroleum ether and one part chloroform (Berg et al. 1998). Fat extraction was carried out in two steps (3 + 3 days), using fresh solvent for each step. Ash content was determined by combustion of the fat-free samples at 550°C for 12 h. Fat and ash proportions by dry mass were multiplied by the proportion of dry material in the original sample (percent solids) to determine proportions by wet mass.

We estimated by subtraction (% protein = 100 – % water – % fat – % ash) because (*i*) protein content estimated this way is usually within a percentage point of that estimated using the standard Kjedahl procedure (e.g., Table 1 in Jonsson et al. (1991) and Tables 17 and 18 in Williams et al. (1986)), (*ii*) the Kjedahl procedure is subject to considerable error, and subtraction may actually be a more reliable way to estimate protein content, and (*iii*) by forgoing the expensive and time-consuming Kjedahl procedure, we could increase our sample sizes. Energy density (kJ·g^{-1}) of the soma and gonads was calculated by multiplying the percentage of fat and protein (by wet mass) by the energy equivalents reported by Brett (1995), 36.4 kJ·g^{-1} for fat and 20.1 kJ·g^{-1} for protein. Energy content estimated using proximate analysis (with correct energy equivalents) is essentially the same as that estimated using bomb calorimetry (Craig et al. 1978; Glebe and Leggett 1981), and is the standard approach in studies of salmonid reproductive energetics (Appendix).

Tissue samples were also obtained during the 1995 supplemental collections (Table 1). A piece of skeletal muscle (excluding the skin and dorsal fat deposit) was dissected from the left side of the hump just anterior to the dorsal fin (Fig. 2). We used these "standard" muscle samples rather than homogenizing the entire carcass because it saved considerable time and space during field collection and sample processing. The viscera (intestines, liver, stomach without stomach contents) and gonads were dissected free and weighed separately. The muscle, gonad, and viscera samples were frozen at –20°C until analysis. Water content was determined by drying to constant mass at 105°C, and fat content of the dried samples was determined by Soxhlet extraction using methylene chloride as the solvent. These water- and fat-estimation procedures are standard for the National Marine Fisheries Service laboratory in which they were performed (e.g., Shearer et al. 1997).

The different procedures used in 1995 and 1996 were complementary but precluded direct quantitative comparison between the years. First, the solvent used to extract fat in 1995 (methylene chloride) extracted total lipids (neutral storage lipids and structural phospholipids), whereas the solvent used in 1996 (petroleum ether and chloroform) extracted only neutral lipids. Estimates of fat content using the two solvents would be very similar, however, because phospholipids compose only ~0.5% by wet mass of the muscle tissue of sockeye salmon (Hatano et al. 1995). Second, the 1995 samples were of muscle and viscera tissue, whereas the 1996 samples were of the entire homogenized soma (including viscera, muscle, skeleton, skin, and brain). Despite these differences, similar temporal trends revealed by the two approaches lend support to the repeatability of our findings.

Energy cost of reproduction

The energy cost of reproduction in salmonids is typically estimated by subtracting the energy content of a sample of fish after reproduction from the energy content of a sample of fish before reproduction. Determining the starting point for calculating energy loss is not a trivial decision, because samples taken near spawning (e.g., in the river) miss energy invested in reproductive development or migration that took place earlier, whereas samples taken long before spawning (e.g., in the ocean) ignore energy acquired by feeding prior to freshwater entry, or expended earlier in migration and reproductive development. The starting point chosen for quantifying energy costs of reproduction in salmonids varies from coastal waters to just before spawning (Appendix). We used freshwater entry (Lake Aleknagik) as the starting point because (*i*) it unambiguously marks the time when feeding stops; (*ii*) it is consistent with other studies of Pacific salmon (Appendix); and (*iii*) if our coastal samples had been used as the starting point, energy invested in migration would have still been missed (primary ocean foraging areas for Bristol Bay sockeye salmon are thousands of kilometres from Port Moller; Burgner 1991). Nonetheless, we also calculated energy costs using the coastal samples (Port Moller) for comparison purposes.

To estimate energy stores before reproduction, we first multiplied the mass-specific somatic energy of each fish captured at the outlet of Lake Aleknagik (freshwater entry) by its somatic mass. To this value we added the total amount of gonadal energy contained in each fish (mass-specific gonadal energy multiplied by total gonad mass), thereby including in our estimate of reproductive cost the energy that was invested in the gonads before freshwater entry. To estimate energy stores required after reproduction, we multiplied the mass-specific somatic energy of each fish collected at death by its total somatic mass. To estimate the energy cost of reproduction, we compared the relationships between body length and energy (log10-transformed) before and after reproduction for each sex (comparison of the differences in elevation between the relationships before and after reproduction reveals energy loss; e.g., Jonsson et al. 1997).

For females, the slope of the relationship between body length and energy did not differ between freshwater entry and death (P = 0.252, from ANCOVA). This allowed a comparison of adjusted means to determine total energy loss for females (common slope = 0.002855, freshwater entry intercept = 2.903, death intercept = 2.345). For males, however, the slope of the relationship between body length and energy differed between freshwater entry and death (P = 0.004, from ANCOVA). Thus, we needed to calculate energy loss for males of a range of sizes, based on the individual regression relationships (freshwater entry: slope = 0.004298, intercept = 2.169; death: slope = 0.002818, intercept = 2.469). Using the coastal samples (Port Moller) as the starting point, length–energy slopes did not differ for females (P = 0.928, common slope = 0.002630, coastal intercept = 3.019, death intercept = 2.445) or males (P = 0.302, common slope = 0.002721, coastal intercept = 2.954, death intercept = 2.514).

The above procedure (as applied by Jonsson et al. 1997 and others) assumes that fish do not change in length. Sockeye salmon

Table 2. ANCOVA results for $\log_{10}$-transformed morphological traits on $\log_{10}$-transformed body length.

	Collection (F)	Length (F)	Interaction (F)	Slope coefficient	Adjusted mean (F)	Model R^2
Females						
Gonad mass	2.54*	28.35***	2.58*	3.203***	115.13***	0.80
Body depth	4.93***	238.16***	4.95***	—	—	—
Hump height	1.15	97.07***	1.18	1.154***	26.86***	0.87
Snout length	2.30*	101.66***	2.33*	1.239***	69.50***	0.76
Adipose-fin length	4.34*	1.14	18.47***	—	—	—
Caudal depth	1.49	98.15***	1.53	1.058***	2.52*	0.78
Males						
Gonad mass	0.90	8.83**	0.90	1.947***	86.82***	0.83
Body depth	13.05***	137.24***	0.47	1.230***	41.8***	0.77
Hump height	1.70	143.86***	1.72	1.334***	53.74***	0.82
Snout length	2.19*	105.98***	1.89	1.362***	167.57***	0.87
Adipose-fin length	3.22*	63.98***	3.04*	1.086***	35.59***	0.76
Caudal depth	1.79	93.11***	1.76	1.000***	6.26***	0.78

Note: The first three columns show statistics for the full model (including an interaction to test for slope heterogeneity). For those traits for which slopes did not differ greatly among collections ($P > 0.01$), the interaction term was removed to calculate adjusted means. The last three columns show slope coefficients and statistics for models without the interaction term. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

(and likely other species) violate this assumption, showing significant shrinkage during spawning (Quinn and Blair 1992). To correct for this effect we measured changes in body length of 174 females and 81 males between entry into Pick Creek and death. Fish were individually tagged and measured when they entered the stream and then measured again after they had died of senescence (for details of the tagging study see Hendry et al. 1999). We found that the average decrease in body length was 9.85 mm (SD = 9.59 mm) for females and 6.12 mm (SD = 7.20 mm) for males. We used these values to adjust our comparisons of energy stores before and after reproduction. For example, an average Pick Creek female was 472.5 mm in length before spawning (averaged across 2 years; Table 1 in Hendry et al. 1999) and had 17 864 kJ of energy at freshwater entry (using 472.5 mm length in the equations above), whereas the same female would be about 9.58 mm shorter at death, with 4633 kJ of energy, for an estimated energy loss due to reproduction of about 74.1%.

Results

Morphological change

Morphological-trait sizes were correlated with body length across all collections, and slopes for most of these relationships did not vary among collections (Table 2). Significant heterogeneity of slopes was detected for female body depth and female adipose-fin length and, accordingly, adjusted values were not calculated for these traits. Comparison of adjusted means for the other traits revealed that trait size usually varied dramatically among the collections and that these differences, combined with body length, explained most of the variation in trait size ($R^2 = 0.76–0.87$).

Changes in trait size (relative to body size) varied between the sexes and among the traits. Most traits increased only modestly between the coastal samples and freshwater entry (Table 3), consistent with the short length of time between these stages. Only gonad mass increased considerably during this period (+51.9% for females; +28.2% for males). Between freshwater entry and spawning, most male traits increased markedly in size (Table 3); snout length (+47.4%, Fig. 3A); body depth (+19.0%, Fig. 3B); hump height

(+13.0%); adipose-fin length (+20.8%). The only female traits that showed a substantial increase over this period were snout length (+23.6%; Fig. 3C) and gonad mass (+87.1%; Fig. 3D). From the onset of spawning (creek entry) until death, most traits decreased in relative size (Table 3). Female snout length decreased by 3.7%, and male traits showed greater decreases in relative size: body depth –9.4%, hump height –12.7%, snout length –8.8%, and adipose-fin length, –3.3%.

Proximate composition

Proximate composition (percent water, percent fat, and percent protein in somatic and gonadal tissues) was not correlated with body length (ANCOVA, $P > 0.10$ for each). Comparisons were therefore made on a mass-specific basis without adjusting values to a common body size. The major constituent of the wet soma (Table 4) at each stage was water (68.4–83.3%), followed by protein (14.4–21.2%), fat (0.1–8.4%), and ash (1.9–2.3%). The composition of the gonads differed markedly between the sexes but water was always the largest constituent (Table 4).

Changes in proximate composition (1996 samples) were similar for males and females (Table 4). As the fish approached maturity, the proportions of fat and protein decreased, while relative water content increased. From the coast (Port Moller) to freshwater entry (Lake Aleknagik), relative fat content decreased by 22.7% in males and 16.5% in females, whereas relative protein content decreased by only 1.9% in males and 3.2% in females. From freshwater entry until the onset of spawning (entry into Pick Creek), relative fat content decreased a further 77.9% in males and 75.8% in females (Table 4). From creek entry to death, relative fat content changed little (Table 4), while relative protein stores continued to decrease (a further 21.4% in males and 18.5% in females).

When the muscle and viscera were considered separately (1995 samples), the general pattern of change in proximate composition was comparable to that in the overall soma. This result suggests that the proximate composition of a

Fig. 3. Variation in male snout length (A), male body depth (B), female snout length (C), and female gonad mass (D) for collections of fish at Port Moller in 1993 (◇), at the mouth of Lake Aleknagik in 1996 (●), shoaling at the mouth of Pick Creek in 1995 (×), and at the onset of breeding in Pick Creek in 1996 (○).
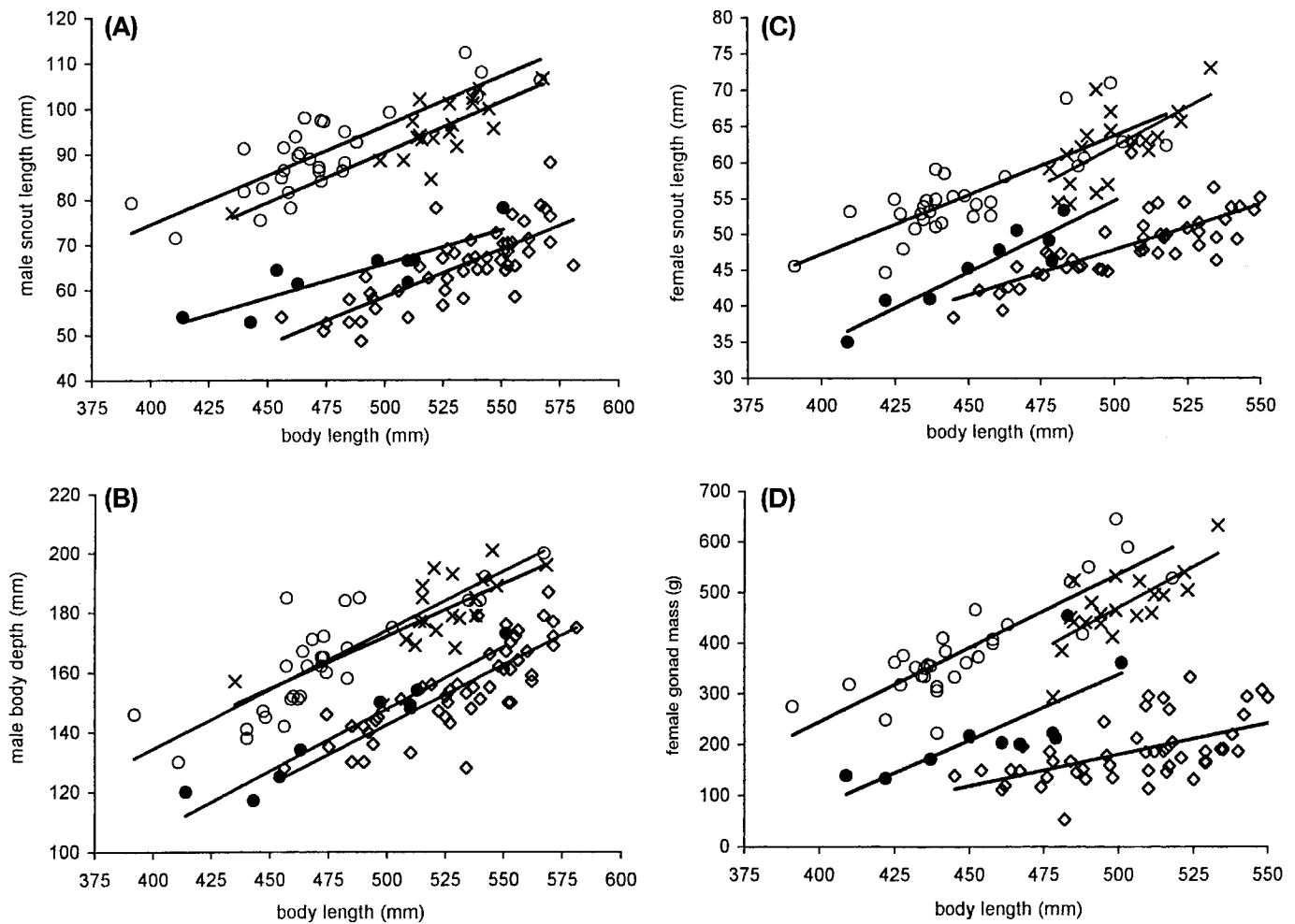

Table 3. Gonad mass (g) and morphological trait size (mm) after standardizing to a common body length (479.3 mm for females; 500.1 mm for males).

	Females				Males					
	Gonad mass	Hump height	Snout length	Caudal depth	Gonad mass	Body depth	Hump height	Snout length	Adipose-fin length	Caudal depth
Coastal										
1993	155.0	64.1	45.1	—	83.9	143.6	72.1	59.6	—	—
1995	—	—	48.1	—	—	147.2	—	61.7	—	—
1996	168.8	65.2	45.6	27.7	82.5	146.4	74.9	59.4	31.9	42.2
Freshwater entry, 1996	256.4	—	48.4	30.3	105.8	146.8	78.2	66.1	34.6	43.1
Shoaling, 1995	417.7	60.0	58.9	31.5	57.3	170.6	86.7	89.8	43.2	45.4
Spawning, 1996	479.7	58.4	59.8	28.4	66.6	174.7	88.4	97.4	41.8	44.7
Death, 1996	—	54.4	57.6	28.5	15.8	158.3	77.2	88.8	40.4	42.6

Note: Values are antilogged adjusted means from the log–log relationships used in ANCOVA (Table 2). Adjusted means for body depth and adipose-fin length were not calculated for females because slopes varied among the collections (Table 2).

sample of dorsal muscle is a reasonable surrogate for proximate composition in the entire soma, at least when relative changes over time are considered (absolute values differ between the techniques). Some subtle differences were evident between the muscle and the viscera (Table 5). From the coast to Pick Creek, maturing fish used energy from both muscle and visceral tissue, but the resulting increase in water content was much higher for muscle (from about 68% to about 78%) than for the viscera (from about 76% to about 79%). Over the same period, losses in fat content were roughly comparable for the muscle and viscera (about 2–4%). Thus, fat loss accounted for most of the loss of solids

Table 4. Proximate composition (by wet mass) of sockeye salmon at different stages of maturation in 1996.

	Soma				Gonads			
	Water (%)	Fat (%)	Protein (%)	Energy (kJ·g^{-1})	Water (%)	Fat (%)	Protein (%)	Energy (kJ·g^{-1})
	Females							
Coastal	68.2±1.2	8.8±1.5	21.1±0.4	7.6±0.4	57.2±0.7	5.1±0.9	35.8±1.4	9.0±1.5
Freshwater entry	70.6±1.4	6.8±1.4	20.7±0.5	6.8±0.5	57.9±1.3	3.2±0.6	37.7±1.2	8.6±0.4
Spawning	78.0±1.1	1.5±0.7	18.2±0.7	4.9±0.3	63.2±1.8	4.1±1.2	31.4±1.3	7.8±0.5
Death	83.4±1.3	0.2±0.1	14.3±1.1	2.9±0.2	—	—	—	—
	Males							
Coastal	68.7±1.5	7.9±1.8	21.3±0.5	7.0±0.6	81.8±0.7	0.4±0.9	15.4±0.5	3.2±0.1
Freshwater entry	70.7±2.1	6.6±2.3	20.6±0.6	6.4±0.8	82.6±0.4	0.5±0.2	14.8±0.5	2.8±1.0
Spawning	78.4±1.2	1.6±0.7	17.8±0.7	4.2±0.3	78.7±2.1	2.1±0.4	15.5±1.4	3.9±0.4
Death	83.2±0.9	0.1±0.1	14.5±0.7	3.0±0.1	85.0±2.0	2.1±1.1	10.9±3.5	3.0±0.9

Note: Values are given as the mean ± SD for subsamples of soma or gonad homogenate. Protein content was determined as 100 – % water – % fat – % ash.

Table 5. Water and fat contents of the muscle, viscera, and gonads of fish at Port Moller (coastal) and shoaling off the mouth of Pick Creek (shoaling) in 1995.

	Water (%)			Fat (%)		
	Muscle	Viscera	Gonads	Muscle	Viscera	Gonads
	Females					
Coastal	68.4±3.8	75.4±1.9	56.1±5.7	6.8±1.9	4.6±1.5	11.0±2.1
Shoaling	77.7±0.9	78.8±0.8	60.6±1.9	2.2±0.6	1.8±0.3	6.7±0.6
	Males					
Coastal	68.7±4.6	76.8±1.2	81.9±2.7	5.6±2.3	3.4±0.8	0.6±0.2
Shoaling	78.6±1.8	79.2±0.8	77.6±1.8	—	1.6±0.2	2.2±0.4

Note: Values are given as the mean ± SD for pieces of muscle tissue taken from the dorsal hump (muscle) and subsamples of the homogenized viscera and gonads. Similar muscle samples were also collected from freshly dead fish in Pick Creek in 1995 and 1996 (not shown in Table 1). The water content of these muscle samples was 87.1 ± 1.9% ($N = 68$, 1995) and 85.3 ± 3.3% ($N = 115$, 1996) for females, and 85.1 ± 3.3% ($N = 35$, 1995) and 85.2 ± 3.3% ($N = 77$, 1996) for males.

from viscera but not from muscle, the discrepancy being attributable to a major loss of protein from muscle.

Energy cost of reproduction

Mass-specific somatic energy decreased by 57.4% for females and 53.1% for males between freshwater entry and death (from Table 4). Somatic fat constituted 64.4% of this loss for females and 65.9% for males. Taking into account the loss of body mass over this period, the total energy cost of reproduction between freshwater entry and death (including the energy invested in the gonads before freshwater entry) was 74.1% of a female's initial energy stores. The corresponding value for males depended on body size, with larger males expending a greater proportion of their initial energy before they died. The energy cost of reproduction for males of 425, 450, 475, 500, and 525 mm (representative lengths) was 54.9, 58.6, 62.0, 65.1, and 68.0%, respectively. Pick Creek males averaged 491 mm in length at creek entry (the average of mean values for 2 years; from Table 1 in Hendry et al. 1999), and a male of this size would incur an estimated energy cost of 66.1%. When energy cost was calculated in a similar manner using the coastal samples (Port Moller) as the starting point, the energy cost of reproduction was 74.9% for females and 65.1% for males, body size having no effect on proportional energy costs for either sex.

Discussion

Development of secondary sexual characters

Between freshwater entry and the beginning of spawning (approximately 14–24 days), male body depth increased by 19.0%, hump height by 13.0%, and snout length by 47.4% (Table 3). These increases in relative trait size are consistent with evidence that sexual selection resulting from competition among male salmon favors individuals with deeper bodies (Quinn and Foote 1994) and longer snouts (Fleming and Gross 1994). Changes in other morphological traits in males may also reflect sexual selection. For example, the adipose fin is sexually dimorphic in maturing salmon (Beacham and Murray 1986), and Järvi (1990) suggested that female Atlantic salmon (*Salmo salar*) select mates on the basis of relative adipose-fin size. In the present study, the adipose fin of males increased in size by 20.8% from freshwater entry to spawning, which suggests that it is either sexually selected or pleiotropically linked to other characters (sensu Falconer 1989, p. 313). In the latter case, adipose-fin size could increase with maturation, and be correlated with competitive ability, simply because it is developmentally tied to other secondary sexual characters.

Some female traits also may reflect direct sexual selection. Females compete intensely for spawning sites, and the

same morphological traits that influence competitive ability in males may perform a similar function in females (Fleming and Gross 1994). In the present study, female snout length increased by 23.6% from freshwater entry to spawning, consistent with suggestions that this trait may be a sexually selected character (Fleming and Gross 1989; Quinn et al. 1995). In contrast, female hump height and adipose-fin length did not increase, which suggests that they may not be sexually selected. The decoupling of temporal size changes among different female traits supports the assertion of Fleming and Gross (1994) that female snout length is directly responsive to sexual selection rather than being the product of a genetic correlation between male and female characters (sensu Lande 1987). If female traits simply reflected selection on male traits, we would also have expected increases in female hump height and adipose-fin length, instead of just in snout length.

Energy and development

Although the sexes were externally distinguishable in the final oceanic phase of their migration (see also Beacham and Murray 1986), most development of secondary sexual characters took place after the fish entered fresh water (Table 3, Fig. 3). An obvious explanation for this delay in shape change is that secondary sexual characters would hinder life in the ocean. This explanation is not entirely sufficient, however, because the same traits would be at least as detrimental to survival and swimming efficiency in fresh water as they are in the marine environment.

We suggest that development of secondary sexual characters may be delayed because of differential benefits and costs associated with consuming different types of energy stores. Elongation of the snout and the development of the hump involves the deposition of cartilage (Davidson 1935), which is made up of protein. Fat cannot be converted to protein, so mobilization of muscle protein would be necessary for structural change to occur. Indeed, most development of secondary sexual characters occurs when muscle protein is the major energy source (compare Tables 3 and 4). Thus, development of secondary sexual characters may be delayed because the depletion of muscle protein early in maturation would unduly hamper physical performance. For example, spawning salmon cannot swim as well as maturing salmon, and post-spawning salmon are even weaker (Williams et al. 1986; Williams and Brett 1987). The precise link between development of secondary sexual characters and energy use remains to be elucidated, and our intent here is to suggest a hypothesis that warrants future investigation.

Influence of migration distance

One of our objectives was to consider patterns of energy use in a population migrating a short distance in fresh water, in contrast to the populations hitherto considered representative of Pacific salmon energetics. Pick Creek fish migrate only 98 km in fresh water to an elevation of 22 m asl, whereas the intensively studied Fraser River populations migrate over much greater distances and to higher elevations (Stuart River, 977 km and 678 m; Chilko River, 644 km and 1172 m; Adams River, 483 km and 347 m). General patterns of change in proximate composition were similar for Pick Creek and Fraser River fish: water content of the soma in-

creased and fat content decreased from the ocean to death (Fig. 4). Despite this general similarity, the fat content of Pick Creek fish was considerably lower than that of Fraser River fish at every stage of maturation except death, indicating that the Pick Creek fish stored less fat while in the ocean and then used less fat during maturation and spawning. These differences in fat storage and use fit the expectation that populations migrating greater distances will store a greater proportion of their energy as fat. Fat is a more concentrated energy source than protein and can be readily mobilized to provide metabolic fuel (Jobling 1994; Brett 1995). Moreover, mobilization of muscle protein to fuel migration would compromise swimming ability.
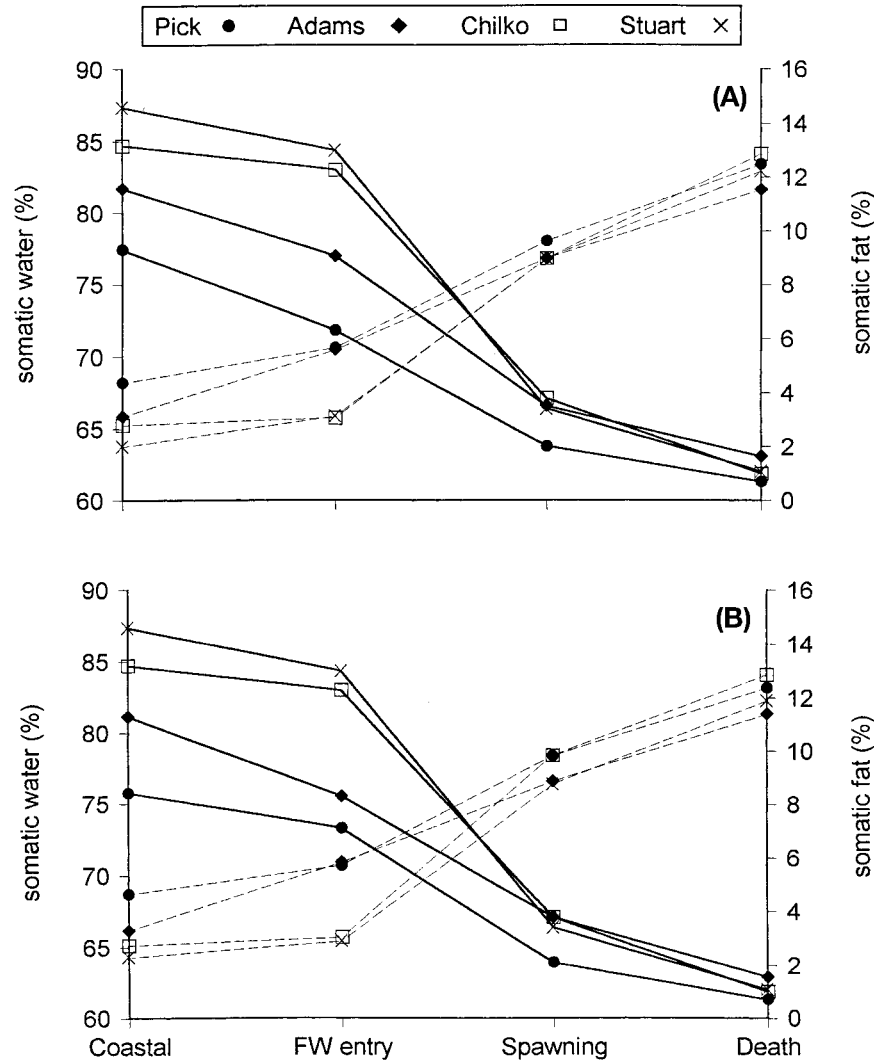
Increased energy use for migration might be accomplished at the expense of energy available for investment in egg production by females or secondary sexual characters by males. In accord with this expectation, the total mass of eggs of mature Pick Creek sockeye salmon (479.7 g at a body length of 479 mm; Table 3) was higher than that of the Fraser River populations (Early Stuart, 327.7 g; Chilko, 278 g; Adams, 440.5 g; from Table 9 in Linley 1993), despite the fact that Fraser River females were typically as large or larger (Early Stuart, 503 mm; Chilko, 477 mm; Adams, 493 mm; from Table 9 in Linley 1993, after conversion to post-orbit hypural length using the "all stocks" conversion in Linley 1993, p. 12). Other studies have shown that salmon populations that migrate longer distances have smaller eggs (Beacham and Murray 1993), fewer eggs (Beacham and Murray 1993), and smaller secondary sexual characters (Moore 1996).

Energy cost of reproduction

Reproduction in sockeye salmon is characterized by a dramatic depletion of energy stores. Fat content, protein content, and somatic energy stores decreased from the final stages of marine migration through freshwater entry, spawning, and death (Tables 4 and 5). Females lost 74.1% of their total somatic energy between freshwater entry and death (including energy invested in egg production before freshwater entry) and males of average size for Pick Creek (491 mm in length) lost 66.1% of their total somatic energy. The lower energy cost for males, which has also been found for all other surveyed sockeye salmon populations (Appendix), may be illusory, because males have probably used more energy in the construction of secondary sexual characters. The cost of developing secondary sexual characters has never been quantified in salmonids, and it may be quite high.

Our calculations of the energy cost of reproduction (and estimates from similar studies given in the Appendix) underestimate the true total energy expenditure because oceanic migrations are also costly (Brett 1995, pp. 30–31) and because some development of secondary sexual characters takes place prior to freshwater entry (Table 3; Beacham and Murray 1986). Energy costs calculated using our coastal samples (74.9% for females; 65.1% for males) were very similar to those calculated using our freshwater entry samples (74.1% for females; 66.1% for males), which suggests that energy costs incurred during the final phase of oceanic migration can be offset by the acquisition of energy by feeding during that period. In fact, Bristol Bay sockeye salmon are known to eat large amounts of prey with high caloric

Fig. 4. Water content and fat content of the soma of female (A) and male (B) sockeye salmon from Pick Creek (from Table 4) and three Fraser River tributaries (Early Stuart in 1956, Chilko in 1959, and Adams in 1958; the most complete years were chosen). The four broken lines show percent water (left-hand axis) and the four solid lines show percent fat (right-hand axis). Values for the Fraser River tributaries were calculated by considering the composition of the eviscerated carcass (Table 13 in Gilhousen 1980), the composition of the viscera (values for Chilko from Fig. 13 in Gilhousen (1980) were used for all populations), and the proportion of the body composed of viscera (Fig. 3 in Gilhousen 1980). To account for phospholipids not extracted with our solvent, fat contents for Pick Creek were increased by 0.5%. (FW, fresh water.)

value during the final stages of their marine migration (Nishiyama 1977). These observations argue for the use of freshwater entry as an appropriate standard for comparing energy costs of reproduction among populations or species of anadromous salmonids, despite the fact that doing so underestimates total cost.

Higher energy costs during breeding are expected to reduce post-reproductive survival. For example, anadromous populations of American shad (*Alosa sapidissima*) that use more energy during spawning have fewer individuals return to spawn a second time (Glebe and Leggett 1981). A negative correlation between energy use and post-reproductive survival has also been documented for Atlantic salmon (Jonsson et al. 1997) and brown trout (Berg et al. 1998). By extension, greater energy losses should be associated with semelparity than with iteroparity. For salmonids, levels of energy depletion do seem to be higher for semelparous spe-

cies, but some exceptions are striking (Appendix). For example, surprisingly high energy costs have been reported for a population of Atlantic salmon (60–70%), whereas moderate costs (from freshwater entry to death) have been reported for a sockeye salmon population (62.5% for females; 53.1% for males).

A bias that remains in such comparisons is that energy use in semelparous salmonids has typically been measured in populations migrating long distances (usually >200 km), whereas energy use in iteroparous salmonids has typically been measured in populations migrating short distances (<20 km for all but one; Appendix). Lengthy migrations are known to increase energy use (Gilhousen 1980; Glebe and Leggett 1981; Brett 1995), and the apparently higher energy cost of reproduction in semelparous salmonids might arise in part from this bias. Although the data we collected on Pick Creek sockeye salmon seem to suggest that even semel-

parous populations migrating short distances (98 km) use more energy than iteroparous species, a definitive standardized comparison has yet to be attempted.

Senescence

The reproductive life-span of Pick Creek sockeye salmon (from the start of spawning to death) averaged 17–20 days (Hendry et al. 1999). During this period, humps, snouts, adipose fins, and caudal peduncles shrank in linear dimension (relative to body size) by 3.7–6.8% for females and 3.3–12.7% for males (Table 3). The magnitude of this shrinkage is comparable to that observed in the only other salmon population for which it has been quantified (Quinn and Blair 1992), and we are the first to do this for naturally spawning salmon. Relative hump and snout sizes are positively correlated with mating success in male Pacific salmon (Fleming and Gross 1994; Quinn and Foote 1994), and shrinkage would reduce competitive ability. Accordingly, male reproductive status generally declines with time during spawning (Quinn and Foote 1994). Although shrinkage seems to be at odds with an individual's efforts to maximize reproductive success, evolutionary theory provides an explanation for why organisms deteriorate after they first mature.

The longer a salmon spends in a spawning stream, the higher its cumulative probability of death due to predation. In some streams, predation rates are so high that a large fraction of the salmon are killed after only a few days (Hanson 1992). Under such age-specific selection intensities, traits that increase reproductive success at the start of spawning would be subject to stronger selection than traits that increase reproductive success later (Williams 1957; Hamilton 1966). One adaptation that facilitates early success might be display and fighting behavior, because salmon usually exhibit high rates of aggression when they start spawning (Quinn et al. 1996; Quinn and McPhee 1998). Displays and fighting are energetically expensive, so fighting would rapidly deplete energy stores (e.g., *Tilapia zillii*, Neat et al. 1998; Atlantic salmon, A.P. Hendry, unpublished data). Fat stores are depleted by the time salmon commence spawning (Table 4), and somatic protein must be broken down to fuel reproductive behavior. We suggest that this loss of protein, in combination with other factors, leads to shrinkage of secondary sexual characters (Table 3), declines in aggression rates in females (Quinn and McPhee 1998), reduced mating success in males (Quinn and Foote 1994; Quinn et al. 1996), and finally death.

Synthesis

Pacific salmon cease feeding more than a month before spawning, but then migrate upstream, develop large ovaries (females) or secondary sexual characters (males), and compete for spawning sites (females) or mates (males). Large amounts of energy are stored in the somatic tissues before maturation commences and are almost entirely used by the time of death. The early stages of maturation are coincident with migration and initial gonad development, for which fat is the primary energy source. The later stages of maturation are coincident with continued development of the ovaries and secondary sexual characters, for which muscle protein is an increasingly important energy source. Accordingly, populations that migrate long distances store and use more fat,

whereas populations that migrate short distances are more dependent on protein. The total energy cost of reproduction in Pacific salmon is very high, contributing to their senescence and ultimate death.

> These and other extremes of reproductive effort are clearly adaptive in a fish for which the one opportunity will be its last (Williams 1966, p. 175).

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Appendix

Table A1. Estimated energy costs of reproduction in different populations of iteroparous and semelparous salmonids. "Start" and "end" denote the stages between which energy cost was estimated (FW, fresh water), "months" indicates the length of time between the starting and ending samples, "migration" indicates the distance that fish migrate in fresh water to reach their spawning sites, "method" indicates the technique used for estimating energy loss, either proximate analysis (PA) or bomb calorimetry (BC), "tissue" indicates whether a sample of muscle tissue (M), the entire soma (S), or the soma and the gonads (S + G) was used for calculating specific loss, "specific loss," is the proportional decrease in mass-specific somatic energy, and "total cost" is the proportional decrease in total energy (including mass-specific energy loss, overall loss of body mass, and energy invested in the gonads).

Species	Source	Start	End	Months	Migration (km)	Method	Tissue	Life history	Sex	Specific loss (%)[a]	Total cost (%)
Iteroparous species											
Salmo salar	1	Coastal	Spent	4–8	15–30	PA	S + G	Anadromous	Female	47	60–70
									Male	45	60–70
	2	Prespawning	Spent	2–5	<1	PA	S	Anadromous	Female	25.0	51.8
									Male	35.6	51.4
Salmo trutta	3	Prespawning	Postspawning	1–4	<1	PA	S + G	Lake, virgin	Female	22.1	32.9
									Male	9.3	14.3
								Lake, repeat	Female	17.2	28.9
									Male	11.2	12.5
	4	Immature	Spent	?	<1?	BC	S + G	Lake	Female	32.3	48.1
									Male	32.3	44.3
Salvelinus alpinus	5	Prespawning	Postspawning	12	19	PA	—	Anadromous	Both	—	52
Semelparous species											
Oncorhynchus nerka	6	FW entry	Death	1	98	PA	S	Anadromous	Female	57.4	74.1
									Male	53.1	66.1
	7	FW entry	Death	1–1.5	1087	PA	S	Anadromous	Female	62.6, 61.5	76.8, 73.4
									Male	59.1, 58.8	67.2, 61.2
	8	FW entry	Death	2	628	PA	S	Anadromous	Female	66.8, 64.9	78.5, 74.4
									Male	59.5, 62.4	63.2, 65.2
	9	FW entry	Death	1–2	483	PA	S	Anadromous	Female	51.0	62.5
									Male	50.4	53.1
Oncorhynchus keta	10	FW entry	Mature	2.5	845	PA	M	Anadromous	Male	46.0	56.0
	11	Coastal	Dying	~1?	1150	PA	M	Anadromous	Female	63.9	78.8
									Male	64.0	77.2
Oncorhynchus gorbuscha	12	Coastal	Spent	1	<10	PA	M	Anadromous	Female	19.4	47.6
									Male	30.7	41.4
	13	FW entry	Spent	<1	328	PA	S	Anadromous	Female	37.9	49.1
									Male	40.5	40.6
Oncorhynchus tshawytscha	14[b]	FW entry	Spawning	4–5	209	PA	M	Anadromous	Both	60.7	—
	15[b]	FW entry	Spawning	?	~375	PA	M	Anadromous	Both	60.1	—

Note: The sources of data cited are as follows (the tables, figures, and page numbers are for the paper cited): 1, Jonsson et al. (1997): River Drammen: specific loss (SL) is from the text (p. 431) and total cost (TC) from the abstract; 2, Jonsson et al. (1991): River Imsa: SL is from Table 1 and TC from Table 2; 3, Berg et al. (1998): Estenstaddammen (lake): values are for first-time spawners (virgin) and repeat spawners (repeat) and SL is from Table 3; for TC see footnote *c*; 4, Lien (1978): Øvre Heimdalsvatn (lake): SL values for both sexes are pooled from Table 1 and TC is from Table 2; 5, Dutil (1986): Nauyuk Lake: SL is not reported and TC is from the text (p. 950); 6, present study: Pick Creek; 7, Gilhousen (1980): Forfar Creek (Early Stuart, Fraser River) in 1956, 1958: for SL see footnote *d* and for TC see footnote *e*; 8, Gilhousen (1980): Chilko (Fraser) River in 1956, 1959: for SL see footnote *d* and for TC see footnote *e*; 9, Gilhousen (1980): Adams (Fraser) River in 1958: for SL see footnote *d* and for TC see footnote *e*; 10, Thurston and Newman (1962): White (Columbia) River: SL is from Table 3; for TC see footnote *e* (omitting gonad components); 11, Pentegoff et al. (1928): Amur River: SL and TC are calculated from the English summary; 12, Ando et al. (1985): Yurappu River: SL is from Table 2 (spawning migration to spent); for TC see footnote *e*; 13, Williams et al. (1986): Thompson (Fraser) River: SL is from Tables 17 and 18 (Fort Langley to Ashcroft-spawned, see footnote *f*); for TC see footnote *e*; 14, Greene (1926): Willamette (Columbia) River: SL is from Table 4 (Ilwaco to Cazadero); 15, Greene (1926): McCloud (Sacramento) River: SL is from Table 3 (tidewater to spawning grounds).

[a]Energy equivalence values from Brett (1995) were used when energy was calculated from proximate composition (36.4 kJ·g^{-1} fat; 20.1 kJ·g^{-1} protein).
[b]Data from Greene (1926) should be viewed with caution because they do not represent a clear temporal sequence.
[c]Total cost was calculated from raw data (O.K. Berg, unpublished data), based on the procedure used in this paper (without the correction for decreases in body length).
[d]Mass-specific somatic energy loss (SL) is calculated as

$$SL = [EE_1 (1 - PV_1) + VE_1 (PV_1)] - [EE_2 (1 - PV_2) + VE_2 (PV_2)]$$

where EE is mass-specific energy in the eviscerated carcass (using (see footnote a) Tables 13, 14, and 16 in Gilhousen 1980), VE is mass-specific energy in the viscera (using (see footnote a) Fig. 13 in Gilhousen 1980), and PV is the proportion of the total somatic mass composed of visceral tissue (using Figs. 3 and 4 in Gilhousen 1980); subscript 1 denotes freshwater entry (Albion, 64 km upstream of the Fraser River mouth) and subscript 2 denotes death (Forfar Creek: dead, fresh; Chilko River: dead, fresh; Adams River: dead, spent).
[e]Total energy costs of reproduction are calculated as

$$TC = SE_1 (M_1 - G_1) + (G_1SG_1) - [SE_2 (M_2(L_1/L_2)^{3.5} - G_2)]$$

where TC is total cost, SE is mass-specific energy of the soma, M is total body mass, G is total gonad mass, SG is mass-specific energy of the gonad (values from the present paper were used when values were not provided in the original papers), L is body length, and subscripts 1 and 2 denote values for starting and ending times, respectively. The first term of the equation estimates total somatic energy in fish at freshwater entry, the second term estimates energy invested in the gonads prior to freshwater entry, and the third term estimates somatic energy at death (adjusting total mass at time 2 to the average length of the fish at time 1; after Gilhousen 1980).
[f]The starting location for the Thompson River series (Fort Langley) was 58 km upstream of the mouth of the Fraser River. If the coastal site (Johnstone Strait) was used as the starting location, starting location, specific energy loss would be estimated at 46.2% for females and 48.0% for males.