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

Andrew P. Hendry and Ole K. Berg

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.

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..."
individuals of the same sex and species, in exclusive relation to reproduction" but “are not directly connected with the act of reproduction” (Darwin 1871a). Darwin suggested that exaggerated male traits in salmon evolved through intrasexual competition (Darwin 1871b), 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 picture 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 seineing 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).
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 measurements 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 homogenized separately by chopping with a knife and then grinding in a homogenizer. The homogenized tissues were freeze-dried and weighed, then measured for proximate composition.

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

<table>
<thead>
<tr>
<th>Stage</th>
<th>Location</th>
<th>Date</th>
<th>Sex</th>
<th>N</th>
<th>Length (mm)</th>
<th>Mass (g)</th>
<th>Gonads (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal</td>
<td>Port Moller</td>
<td>1–2 July</td>
<td>F</td>
<td>10</td>
<td>485±24</td>
<td>2632±334</td>
<td>174.3±38.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>10</td>
<td>493±21</td>
<td>2845±396</td>
<td>85.2±27.2</td>
</tr>
<tr>
<td>Freshwater</td>
<td>Aleknagik</td>
<td>7 July</td>
<td>F</td>
<td>10</td>
<td>459±29</td>
<td>2460±569</td>
<td>231.6±100.2</td>
</tr>
<tr>
<td>Spawning</td>
<td>Pick Creek</td>
<td>21 July – 12 August</td>
<td>F</td>
<td>30</td>
<td>449±29</td>
<td>1953±438</td>
<td>387.9±97.7</td>
</tr>
<tr>
<td>Death</td>
<td>Pick Creek</td>
<td>4–15 August</td>
<td>M</td>
<td>23</td>
<td>473±37</td>
<td>2610±694</td>
<td>60.4±11.7</td>
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</tbody>
</table>

Supplemental collections

<table>
<thead>
<tr>
<th>Stage</th>
<th>Location</th>
<th>Date</th>
<th>Sex</th>
<th>N</th>
<th>Length (mm)</th>
<th>Mass (g)</th>
<th>Gonads (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal</td>
<td>Port Moller</td>
<td>23 June – 4 July</td>
<td>F</td>
<td>49</td>
<td>505±27</td>
<td>2623±523</td>
<td>186.9±60.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>51</td>
<td>532±30</td>
<td>3224±102</td>
<td>101.8±39.8</td>
</tr>
<tr>
<td>Coastal</td>
<td>Port Moller</td>
<td>17 June – 8 July</td>
<td>F</td>
<td>20</td>
<td>500±30</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>20</td>
<td>506±30</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Shoaling</td>
<td>Pick Creek</td>
<td>8 July 1995</td>
<td>F</td>
<td>20</td>
<td>500±15</td>
<td>2707±332</td>
<td>471.2±68.1</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>20</td>
<td>522±26</td>
<td>3487±477</td>
<td>62.9±8.6</td>
</tr>
</tbody>
</table>

Note: Values are given as the mean ± SD.

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

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.
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 and used prior to freshwater entry or expended 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 all coastal samples had been used as the starting point, energy invested in migration would still have been missed (primary ocean foraging areas for Bristol Bay sockeye salmon are thousands of kilometres from Port Moller; Burgher 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 Port Moller by its total somatic mass. To estimate the energy cost of reproduction, we compared the relationships between body length and energy required after reproduction (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
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 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).

<table>
<thead>
<tr>
<th></th>
<th>Females</th>
<th></th>
<th></th>
<th>Males</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gonad mass</td>
<td>Hump height</td>
<td>Snout length</td>
<td>Caudal depth</td>
<td>Gonad mass</td>
<td>Body depth</td>
</tr>
<tr>
<td>Coastal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>155.0</td>
<td>64.1</td>
<td>45.1</td>
<td>−</td>
<td>83.9</td>
<td>143.6</td>
</tr>
<tr>
<td>1995</td>
<td>−</td>
<td>−</td>
<td>48.1</td>
<td>−</td>
<td>−</td>
<td>147.2</td>
</tr>
<tr>
<td>1996</td>
<td>168.8</td>
<td>65.2</td>
<td>45.6</td>
<td>27.7</td>
<td>82.5</td>
<td>146.4</td>
</tr>
<tr>
<td>Freshwater entry, 1996</td>
<td>256.4</td>
<td>−</td>
<td>48.4</td>
<td>30.3</td>
<td>105.8</td>
<td>146.8</td>
</tr>
<tr>
<td>Shoaling, 1995</td>
<td>417.7</td>
<td>60.0</td>
<td>58.9</td>
<td>31.5</td>
<td>57.3</td>
<td>170.6</td>
</tr>
<tr>
<td>Spawning, 1996</td>
<td>479.7</td>
<td>58.4</td>
<td>59.8</td>
<td>28.4</td>
<td>66.6</td>
<td>174.7</td>
</tr>
<tr>
<td>Death, 1996</td>
<td>−</td>
<td>54.4</td>
<td>57.6</td>
<td>28.5</td>
<td>15.8</td>
<td>158.3</td>
</tr>
</tbody>
</table>

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.
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 increased 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

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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 species, 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 Blažk 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 zilli). 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).

Acknowledgements

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Nishiyama, T. 1977. Food-energy requirements of Bristol Bay sockeye salmon Oncorhynchus nerka (Walbaum) during the last marine life stage. In Fisheries biological production in the subarctic Pacific region. Spec. Vol. 1977, Research Institute of North Pacific Fisheries, Faculty of Fisheries, Hokkaido University, Research Institute of North Pacific Fisheries, Faculty of Fisheries, Hokkaido University, Hokodate, Japan.


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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).

<table>
<thead>
<tr>
<th>Source</th>
<th>Start</th>
<th>End</th>
<th>Months</th>
<th>Migration (km)</th>
<th>Method</th>
<th>Tissue</th>
<th>Life history</th>
<th>Sex</th>
<th>Specific loss (%)</th>
<th>Total cost (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Salmo salar</em></td>
<td>1</td>
<td>Coastal</td>
<td>Spent</td>
<td>4–8</td>
<td>15–30</td>
<td>PA</td>
<td>S + G</td>
<td>Anadromous</td>
<td>Female</td>
<td>47</td>
</tr>
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<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>Male</td>
<td>45</td>
<td>60–70</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Prespawning</td>
<td>Spent</td>
<td>2–5</td>
<td>&lt;1</td>
<td>PA</td>
<td>S</td>
<td>Anadromous</td>
<td>Female</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td>Male</td>
<td>35.6</td>
<td>51.4</td>
</tr>
<tr>
<td><em>Salmo trutta</em></td>
<td>3</td>
<td>Prespawning</td>
<td>Postspawning</td>
<td>1–4</td>
<td>&lt;1</td>
<td>PA</td>
<td>S + G</td>
<td>Lake, virgin</td>
<td>Female</td>
<td>22.1</td>
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<td>9.3</td>
<td>14.3</td>
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<td></td>
<td>4</td>
<td>Immature</td>
<td>Spent</td>
<td>?</td>
<td>&lt;1?</td>
<td>BC</td>
<td>S + G</td>
<td>Lake</td>
<td>Female</td>
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<td></td>
<td>Male</td>
<td>32.3</td>
<td>44.3</td>
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<tr>
<td><em>Salvelinus alpinus</em></td>
<td>5</td>
<td>Prespawning</td>
<td>Postspawning</td>
<td>12</td>
<td>19</td>
<td>PA</td>
<td>—</td>
<td>Anadromous</td>
<td>Both</td>
<td>52</td>
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<tr>
<td><em>Oncorhynchus nerka</em></td>
<td>6</td>
<td>FW entry</td>
<td>Death</td>
<td>1</td>
<td>98</td>
<td>PA</td>
<td>S</td>
<td>Anadromous</td>
<td>Female</td>
<td>57.4</td>
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<td></td>
<td>7</td>
<td>FW entry</td>
<td>Death</td>
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<td>1087</td>
<td>PA</td>
<td>S</td>
<td>Anadromous</td>
<td>Female</td>
<td>62.6, 61.5</td>
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<tr>
<td></td>
<td>8</td>
<td>FW entry</td>
<td>Death</td>
<td>2</td>
<td>628</td>
<td>PA</td>
<td>S</td>
<td>Anadromous</td>
<td>Female</td>
<td>66.8, 64.9</td>
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<tr>
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<td>9</td>
<td>FW entry</td>
<td>Death</td>
<td>1–2</td>
<td>483</td>
<td>PA</td>
<td>S</td>
<td>Anadromous</td>
<td>Female</td>
<td>59.5, 62.4</td>
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<td>10</td>
<td>FW entry</td>
<td>Mature</td>
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<td>845</td>
<td>PA</td>
<td>M</td>
<td>Anadromous</td>
<td>Female</td>
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<td></td>
<td>Male</td>
<td>50.4</td>
<td>53.1</td>
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<tr>
<td><em>Oncorhynchus keta</em></td>
<td>11</td>
<td>Coastal</td>
<td>Dying</td>
<td>~1?</td>
<td>1150</td>
<td>PA</td>
<td>M</td>
<td>Anadromous</td>
<td>Female</td>
<td>63.9</td>
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<tr>
<td></td>
<td>12</td>
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<td>Spent</td>
<td>1</td>
<td>&lt;10</td>
<td>PA</td>
<td>M</td>
<td>Anadromous</td>
<td>Female</td>
<td>64.0</td>
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<td></td>
<td>Male</td>
<td>30.7</td>
<td>41.4</td>
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<tr>
<td><em>Oncorhynchus gorbuscha</em></td>
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<td>FW entry</td>
<td>Spent</td>
<td>&lt;1</td>
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<td>PA</td>
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<td>37.9</td>
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<td>40.5</td>
<td>40.6</td>
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<td><em>Oncorhynchus tsawusica</em></td>
<td>14</td>
<td>FW entry</td>
<td>Spawning</td>
<td>4–5</td>
<td>209</td>
<td>PA</td>
<td>M</td>
<td>Anadromous</td>
<td>Both</td>
<td>60.7</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>FW entry</td>
<td>Spawning</td>
<td>?</td>
<td>~375</td>
<td>PA</td>
<td>M</td>
<td>Anadromous</td>
<td>Both</td>
<td>60.1</td>
</tr>
</tbody>
</table>

**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): Estenstadiammnen (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): Adams (Fraser) River in 1958: for SL see footnote d and for TC see footnote e; 9, Thurston and Newman (1962): White (Columbia) River: SL is from Table 3; for TC see footnote e (omitting gonad components); 10, Greene (1926): Willamette (Columbia) River: SL is from Table 4; 11, Greene (1926): McCloud (Sacramento) River: SL is from Table 3 (tidewater to spawning grounds).
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).

Data from Greene (1926) should be viewed with caution because they do not represent a clear temporal sequence.

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).

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 footnote a Tables 13, 14, and 16 in Gilhousen 1980), VE is mass-specific energy in the viscera (using 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).

Total energy costs of reproduction are calculated as

\[ TC = SE_1 (M_1 - G_1) + (G_1 SG_1) - [SE_2 (M_2 L_1 / L_2)^{3.5} - G_2] \]

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).

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, specific energy loss would be estimated at 46.2% for females and 48.0% for males.