Effects of Growth and Reproductive History on the Egg Size-Fecundity Trade-off in Steelhead

Thomas P. Quinn\textsuperscript{a}; Todd R. Seamons\textsuperscript{a}; Leif Asbjørn Vøllestad\textsuperscript{b}; Elisabeth Duffy\textsuperscript{a}

\textsuperscript{a} School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA
\textsuperscript{b} Center for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, Blindern, Oslo, Norway

First published on: 15 February 2011

To cite this Article Quinn, Thomas P., Seamons, Todd R., Vøllestad, Leif Asbjørn and Duffy, Elisabeth(2011) 'Effects of Growth and Reproductive History on the Egg Size-Fecundity Trade-off in Steelhead', Transactions of the American Fisheries Society, 140: 1, 45 — 51, First published on: 15 February 2011 (iFirst)

To link to this Article: DOI: 10.1080/00028487.2010.550244

URL: http://dx.doi.org/10.1080/00028487.2010.550244
ARTICLE

Effects of Growth and Reproductive History on the Egg Size–Fecundity Trade-off in Steelhead

Thomas P. Quinn* and Todd R. Seamons
School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

Leif Asbjørn Vøllestad
Center for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, Post Office Box 1066, Blindern, N-0316 Oslo, Norway

Elisabeth Duffy
School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

Abstract

The allocation of energy by females into different components of reproduction is critical and includes trade-offs between egg size and number. In anadromous salmonids, it is unclear whether the allocation patterns are determined by the growing conditions experienced when the fish are in freshwater or at sea or by the female’s reproductive history. We collected data on length, egg size, and fecundity from female steelhead Oncorhynchus mykiss that had spent 1 year in freshwater and then 2 (designated 1.2) or 3 years at sea (1.3) before spawning for the first time. We also collected the same data from females spawning for the second time but of the same age as those spawning after 3 years for the first time (1.1S1). The older females were longer than the younger ones, but there was considerable overlap in length. The repeat-spawning fish were shorter than fish of the same age that were spawning for the first time, which reflected the reduction in growth associated with the previous spawning migration and reproductive event. Fish length was positively correlated with egg size and fecundity, but the 1.2 females had smaller eggs for their size than did the 1.3 fish, which implied an effect of growth rate at sea. We then measured scales from a subset of the fish as an index of individual fish size at the time of seaward migration and size after their first year of growth at sea. Fish that matured first after 2 years at sea were slightly larger as smolts but grew significantly more in their first year at sea than did those maturing a year later. However, neither measure was related to egg size or egg number after adjustment for length. The processes controlling the egg size–fecundity trade-off in steelhead and other salmonid species remain unclear, but the present evidence is incompatible with the hypothesis that growth in freshwater as juveniles determines reproductive trade-offs at maturity by females.

*Corresponding author: tquinn@u.washington.edu
Received May 30, 2010; accepted October 26, 2010
Salmonids (salmon, trout, and char) produce much larger eggs than most other teleost fish (Wootton 1984; Winemiller and Rose 1992), resulting in comparatively large offspring. Fecundity increases with body size in female salmonids (Rounsefell 1957), but growth rate itself also affects egg production. Specifically, experimental results indicated that better-fed females grew faster and produced more numerous but smaller eggs than did females on a reduced ration (Bagenal 1969). A number of studies have associated rapid growth in freshwater with higher fecundity but smaller eggs for a given length (Thorpe et al. 1984; Morita et al. 1999; Gregersen et al. 2006), and Jonsson et al. (1996) reported that the growth of Atlantic salmon Salmo salar in freshwater (but not that at sea) affected their egg size–fecundity relationship. One explanation for this phenomenon is that females reproducing in poor growth environments have a fitness advantage by producing larger, competitively superior offspring, whereas those in environments that are food rich (that is, where the female herself grew faster) maximize fitness by increasing fecundity because even small offspring will grow rapidly and competition will be weak (Einum and Fleming 1999, 2000).

However, contradictory patterns have been reported in two Pacific salmon species: sockeye salmon Oncorhynchus nerka (Rounsefell 1957) and Chinook salmon O. tshawytscha (Donaldson and Menasveta 1961). Females of a given length that spent fewer years at sea (and therefore grew faster) tended to produce more eggs than did older (slower-growing) females. The positive effect of marine growth on fecundity as well as the absence of a relationship to growth in freshwater was also reported for Chinook salmon and coho salmon O. kisutch (Quinn et al. 2004). Moreover, Chinook salmon populations that grow slowly in their natural environment and spend a full year in freshwater before seaward migration produce smaller, not larger, eggs than those in environments in which they grow faster (Healey 2001; Kinnison et al. 2001). These findings are generally consistent with evidence from Atlantic herring Clupea harengus showing that females undergoing energetic stress may reduce fecundity by oocyte resorption, resulting in larger size at maturity for the remaining eggs (Hay and Brett 1988; van Damme et al. 2009; Kennedy et al. 2010). Laboratory research also indicated that energy allocation plays an important role in expression of female reproductive traits for coho salmon (Campbell et al. 2006). Experimental removal of one ovary (Tyler et al. 1996; Luckenbach et al. 2008) elicited compensatory responses by females to the artificial reduction in number of oocytes.

Though the relationship between growth rate, energy, and the egg size–fecundity trade-off has been extensively researched in salmonid fish, there are still many uncertainties. It is not clear whether the egg size–egg number trade-off is set early in life while fish are in freshwater as an adaptation to enhance female fitness through offspring survival, or late in life as a proximate response to the female’s energetic status. In addition, there is little information on the relationship between previous reproductive history and current investment. Reproductive history might affect size if the previous spawning event and associated migration reduced growth during that year relative to females that did not reproduce. Thus, we would predict that repeat spawners would be smaller for their age than first-time spawners. But how would this affect their reproductive investment? Reduced overall marine growth might result in larger but fewer eggs for their size if they follow the pattern displayed by several semelparous Pacific salmon Oncorhynchus spp. On the other hand, if freshwater growth was most important then there might be no difference in egg size and fecundity as a function of reproductive history unless freshwater growth affected probability of repeat spawning. The objective of this study was to test these hypotheses by comparing the relationships between body size, egg size, and fecundity for female steelhead O. mykiss of different marine ages (age 2 versus age 3) on their first spawning event, and by comparing females of the same marine age (age 3) that were on their first and second spawning events.

METHODS

Steelhead were sampled at the Forks Creek Hatchery near Raymond, Washington. The hatchery, operated by the Washington Department of Fish and Wildlife (WDFW), is located approximately 34 km from Willapa Bay at an elevation of 56 m. The steelhead hatchery program at Forks Creek Hatchery began with the release of steelhead smolts (seaward-migrating age-1 juveniles) in the spring of 1994 and 1995. These fish were not derived from the native Forks Creek population but were from the widely distributed hatchery broodstock originating from Chambers Creek, which flows into Puget Sound, Washington (see Mackey et al. 2001 for further details). These and all subsequent generations of hatchery-produced smolts were marked by removal of the adipose fin to allow separate management of wild (unmarked) and hatchery (marked) fish.

Mature adult steelhead returned to the Forks Creek Hatchery from November through May, but primarily in December and January (Mackey et al. 2001). A weir across the river diverted the steelhead into the hatchery. All steelhead were inspected by hatchery personnel and those fish with intact adipose fins (indicating wild origin) were returned to the river upstream from the weir to spawn naturally, and those with missing adipose fins (indicating hatchery origin) were killed, and some were used as broodstock. Since the winter of 1995–1996 we have sampled a large fraction of the hatchery steelhead. During that time we recorded sex and fork length (FL; mm), removed a sample of scales for age determination and a piece of fin tissue for DNA analysis, and sampled females for reproductive investment. In this study we weighed the entire mass of eggs in a colander after draining the ovarian fluid and then weighed (to the nearest 0.01 g) and counted a subsample of about 50 eggs. This subsample
TABLE 1. Numbers of steelhead sampled for reproductive traits, by the year in which they were produced (brood year). Fish that spent 1 year in freshwater and 2 or 3 years at sea are designated as 1.2 and 1.3, respectively. Fish that spent 1 year in freshwater and 1 year at sea before returning in their second year to spawn and then again in their third year are designated as 1.1S1.

<table>
<thead>
<tr>
<th>Brood year</th>
<th>1.2</th>
<th>1.3</th>
<th>1.1S1</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>1994</td>
<td>50</td>
<td>10</td>
<td>3</td>
<td>63</td>
</tr>
<tr>
<td>1995</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>1996</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>1997</td>
<td>13</td>
<td>17</td>
<td>2</td>
<td>32</td>
</tr>
<tr>
<td>1998</td>
<td>9</td>
<td>12</td>
<td>2</td>
<td>23</td>
</tr>
<tr>
<td>1999</td>
<td>41</td>
<td>31</td>
<td>5</td>
<td>77</td>
</tr>
<tr>
<td>2000</td>
<td>51</td>
<td>33</td>
<td>0</td>
<td>84</td>
</tr>
<tr>
<td>2001</td>
<td>2</td>
<td>10</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>2002</td>
<td>19</td>
<td>20</td>
<td>1</td>
<td>40</td>
</tr>
<tr>
<td>2003</td>
<td>55</td>
<td>78</td>
<td>13</td>
<td>146</td>
</tr>
<tr>
<td>2004</td>
<td>19</td>
<td>35</td>
<td>1</td>
<td>55</td>
</tr>
<tr>
<td>2005</td>
<td>70</td>
<td>59</td>
<td>9</td>
<td>138</td>
</tr>
<tr>
<td>2006</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Total</td>
<td>348</td>
<td>310</td>
<td>45</td>
<td>703</td>
</tr>
</tbody>
</table>

yielded what was essentially a mean egg mass without an estimate of variance, and the total number of eggs (fecundity) was estimated from the weights of the total egg mass, the subsample of eggs, and the number of eggs in the subsample.

Age determination was based on examination of scales taken from the region above the lateral line and posterior to the dorsal fin (Bernard and Myers 1997). Scales were collected from the preferred area (Walker et al. 1998), placed on gummed cards with the sculptured surface up, and impressed in transparent acetate. Freshwater and saltwater ages were determined from the scales and validated by DNA parentage analysis as described in Seamons et al. (2009). After starting exogenous feeding in March, all fish had spent a full year in the hatchery before being released to sea during the last 2 weeks of April in the following year. Most females had then spent 2 or 3 years at sea; these age-groups were designated 1.2 and 1.3, respectively. Scales were also examined for the presence of a “spawning check,” a series of rough or uneven circuli near the edge of the scale where some of the saltwater circuli were resorbed during periods of high calcium demand experienced during sexual maturation, spawning, and associated periods of fasting (Persson et al. 1995). In principle, all hatchery-produced adults should have been on their first spawning migration because none were released after spawning. However, steelhead can spawn elsewhere in the Willapa River system or, if river flows permit, jump over the weir and spawn in Forks Creek above the hatchery, as indicated by our sampling in the stream itself as well as at a downstream trap at the hatchery. Fish were designated 1.1S1 if they had spent their first year in the hatchery, returned to spawn after 2 years at sea, and then returned again after another year at sea (see Dauer et al. 2009 for further details on scale pattern identification of repeat-spawning fish). Those fish would be the same age as a 1.3 fish, but unlike 1.3 fish they had made a spawning migration in the year before they were sampled. The use of scale patterns to indicate reproductive history was validated by DNA parentage analysis in another steelhead population (Seamons et al. 2009).

To study life history effects on reproductive investment, we first examined the relationships between length, fecundity, and average egg mass using all the data on fish of known age. We analyzed data on 703 fish of age-groups 1.2, 1.3, and 1.1S1 (Tables 1, 2) for which we had complete data; the other age-groups were not represented by enough fish for analysis. We then selected two brood years (2003 and 2005) that produced the highest number of returning females in the three life history categories (Table 1) and randomly selected scales that were in sufficiently good condition (1.2, n = 72; 1.3, n = 85; 1.1S1, n = 15) for further analysis. The fish from each brood year experienced common environmental conditions in the hatchery and went to sea in the same year. Individual fish were spawned and later began exogenous feeding on different dates, and freshwater rearing conditions were controlled only to the extent that water conditions and food availability in the hatchery were uniform within brood years. Thus, conditions in the hatchery were similar but not identical for all fish within a brood year, and environmental conditions after release were entirely uncontrolled, so there was variation in growing conditions among individuals within and between brood years.

TABLE 2. Summary statistics (mean ± SD) for length and reproductive traits for female steelhead of three different life history types. Fish that spent 1 year in freshwater and 2 or 3 years at sea are designated as 1.2 and 1.3, respectively. Fish that spent 1 year in freshwater and 1 year at sea before returning in their second year to spawn and then again in their third year are designated as 1.1S1. F-values from one-way ANOVAs are given. In each column, estimates with different letters are significantly different (P < 0.05; Tukey’s HSD post hoc test).

<table>
<thead>
<tr>
<th>Life history type</th>
<th>Length (mm)</th>
<th>Egg size (g)</th>
<th>Fecundity</th>
<th>Gonad mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.2 (n = 348)</td>
<td>662.7 ± 33.5 x</td>
<td>0.101 ± 0.016 y</td>
<td>4,335 ± 1128 y</td>
<td>431.9 ± 100.7 y</td>
</tr>
<tr>
<td>1.3 (n = 310)</td>
<td>765.8 ± 42.2 z</td>
<td>0.128 ± 0.018 z</td>
<td>5,706 ± 1557 z</td>
<td>721.2 ± 181.1 z</td>
</tr>
<tr>
<td>1.1S1 (n = 45)</td>
<td>739.3 ± 45.7 y</td>
<td>0.125 ± 0.023 z</td>
<td>5,364 ± 1901 z</td>
<td>633.6 ± 161.0 z</td>
</tr>
<tr>
<td>F</td>
<td>598.0</td>
<td>197.3</td>
<td>81.4</td>
<td>328.8</td>
</tr>
<tr>
<td>P</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
We measured the radius of each scale (the same scales used for age determination) from the focus to the smolt check as an index of growth during freshwater and that from the smolt check to the first winter annulus as an index of growth during the first year at sea. Acetate impressions of the scales (see Seamons et al. 2009) were viewed under a video microscope (Leica MZ6 with attached RS Photometrics camera) at a magnification of 10×. Digital images were captured with a computerized video digitizing system (Image-Pro Plus, version 4.5.1.22, Media Cybernetics; www.mediacy.com/index.aspx?page = IPP). Scales were measured along the anterior–posterior axis (choosing the longest radius, \( r \), often offset about 25° from the perpendicular) from the middle of the focus to the scale edge, the most commonly used measurement (Martinson et al. 2000). By means of the caliper tool, measurements (calibrated from an image of a stage micrometer) were made from the focus to the saltwater entry check (at the last circulus before circuli spacing widens, indicating ocean growth) (\( r_s \)) and from the focus to the beginning of the first ocean annulus (\( r_{marine} \)). Marine growth rate during the first year at sea was estimated as the difference between these two measurements (\( r_{marine} - r_s \)).

We analyzed the variation in mean egg mass, total gonad mass, and total fecundity using general linear mixed models (GLMMs). Based on preliminary investigation of the data it was evident that reproductive investment varied among years. To account for this variation, which might be due to a number of unmeasured environmental factors, we used brood year (BY, i.e., the year in which the fish was born/spawned) as a random factor in our analyses. The overall model structure was

\[
Y = \alpha + \beta_1 LH + \beta_2 FL + \beta_3 (LH \times FL) + \zeta_1 BY - \zeta_2 (BY \times LH).
\]

The main fixed factor in the analyses was life history type (LH) and fork length (FL) was a covariate; \( \alpha \) is the intercept, the \( \beta_i \) are the slopes of the fixed factors, and the \( \zeta_i \) are the slopes of the random variables. All response variables and FL were loge transformed before analysis.

RESULTS

Female steelhead returned to spawn when they reached lengths of 592 to 885 mm. As expected, first-spawning females that had spent 2 and 3 years at sea differed in mean length (662.7 and 765.8 mm, respectively), though there was some overlap (Table 1; Figure 1). Females on their second return migration were smaller than those of the same age that had not spawned (739.3 and 765.8 mm, respectively). In addition, there was a general increase in fecundity and average egg weight with increasing length (Figure 2), as well as an increase in total gonad mass (not shown) for first-spawning females that had spent 2 and 3 years at sea.

Total investment in gonads varied strongly among brood years. Brood year and the brood year \( \times \) life history interaction were therefore used as random factors in the GLMM analysis, with total gonad mass (loge transformed) used as the response variable and life history type (1.2, 1.3, or 1.1S1) and FL (loge transformed) as fixed factors. The interaction between life history type and FL was not significant (\( F_{2, 664} = 2.05, P = 0.130 \)). The variance component for the brood year \( \times \) life history type interaction was low, accounting for only 0.76% of the total variance, whereas the brood year component accounted for 53.78%. This brood year effect was mainly because the 2005 brood year was an outlier; fish from that year produced relatively light gonads. The full mixed model explained 70.7% of the variance in total gonad mass.
total gonad mass with a highly significant effect of life history type ($F_{2,664} = 17.72, P < 0.001$) and FL ($F_{1,664} = 11955, P = 0.001$). Length-adjusted least-square mean (LSM ± SE) total gonad mass (g, on log scale) was lower for the 1.2 females (6.15 ± 0.06) than for the 1.3 (6.33 ± 0.06) and 1.1S1 females (6.30 ± 0.07), and the latter two groups did not differ significantly (Tukey’s honestly significant difference [HSD] post hoc test).

Length-adjusted fecundity also varied strongly among years (total model $R^2 = 0.542$), but there was no difference in fecundity between the life history types ($F_{2,664} = 0.002, P = 0.998$), nor was there an interaction between life history type and FL ($F_{2,664} = 0.777, P = 0.460$). The positive length effect was highly significant ($F_{1,664} = 76.81, P < 0.001$). The brood year variance component accounted for 56.1% of the total variance, whereas the brood year × life history type interaction term accounted for less than 0.01% of the total variance. The 2005 brood year was again an outlier with very low fecundity (as expected given the low total gonad mass).

The effects of life history type ($F_{2,664} = 31.17, P < 0.001$) and FL ($F_{1,664} = 4.24, P = 0.040$) on average egg mass were highly significant, with 1.2 fish (log$_e$ transformed LSM egg mass at mean FL of 710 mm ± SE, −2.283 ± 0.028 g; back-transformed egg mass, 0.102 g) having significantly smaller eggs than 1.3 fish (−2.100 ± 0.028; back-transformed egg mass, 0.122 g) and 1.1S1 fish (−2.123 ± 0.035; back-transformed egg mass, 0.120 g) after adjusting for gonad investment and fork length effects (Tukey’s HSD post hoc test). The brood year variance component explained 22.7% of the total variance, whereas the brood year × life history type interaction only explained 3.9%. Interestingly, the 2005 brood year was not an outlier year in this analysis.

Given that fecundity did not vary among life history types and that the differences in gonad mass seemed to be driven by egg mass in the full data set, we examined the variation in egg mass in more detail for the 2003 and 2005 cohorts for which we had scale measurements. For these years, as with the full data set, egg mass increased considerably with fish size ($r^2 = 0.505, P < 0.0001, n = 172$). We then analyzed the data for variation in egg mass (log$_e$ transformed) using a GLMM, with length (log$_e$ transformed) as a covariate, brood year as a random factor, and life history type as a fixed factor. This model explained 64% of the variation in egg mass, with a nonsignificant length effect ($F_{1,165} = 3.58, P = 0.060$) and a highly significant life history effect ($F_{2,165} = 18.63, P < 0.0001$). Egg mass for the various life history types differed, with the 1.2 fish having smaller length-adjusted eggs (LSM at mean length of 659 mm, −2.253 ± 0.033; back-transformed mean, 0.105 g) than both the 1.3 fish (−2.079 ± 0.031; back-transformed mean, 0.125 g) and 1.1S1 fish (−2.154 ± 0.038; back-transformed mean, 0.116 g). The interaction between length and life history type was not significant ($F_{2,163} = 32.51, P = 0.084$) and was deleted from the model before estimating the egg mass differences.

To further investigate the links between reproduction and growth, we first examined the scale radius to the sea winter check (as an index of smolt size), the difference between that radius and the radius to the first saltwater check (as an index of initial marine growth), and the total radius to the first sea winter check (as an index of overall size at that age). There was a weak but nonsignificant tendency for early-maturing fish (1.2 and 1.1S1 fish versus 1.3 fish) to be larger as smolts (one-tailed $t$-test: $t = 1.42, df = 268, P = 0.079$) and a stronger link between early marine growth and age at first maturity ($t = 2.23, df = 268, P = 0.013$). The two measurements combined (i.e., the radius from the focus of the scale to the first sea winter check, including a few fish for which the smolt check was ill-defined) also indicated that early-maturing females were larger after 1 year at sea than those that matured a year later ($t = 2.51, df = 276, P = 0.006$). We then tested the hypothesis that egg mass was affected by growth during the first year at sea or size at smolt transformation, using the same scale measurements as additional covariates in the analysis with length. In either case there was no effect of growth (smolt size: $F_{1,166} = 0.0001, P = 0.942$; first year’s marine growth: $F_{1,166} = 0.004, P = 0.835$) on egg mass.

**DISCUSSION**

As expected, females that spent 2 years at sea were smaller than those spending 3 years before returning to freshwater to spawn. There was considerable overlap in length of these two groups (Figure 1), probably because the individuals that remained at sea for a third year were the slower-growing members of the cohort (Burgner et al. 1992). The smaller size of the repeat spawners, compared with females of the same age that had not spawned (Figure 1), probably resulted from three factors. First, there was presumably some redirection of energy from growth to gonad development. Second, the return migration would have taken the fish from the productive feeding grounds offshore back into the natal river for spawning, where fish rarely feed, and thus the fish lost some feeding opportunities. Third, repeat-spawning steelhead do not seem to be distributed as far offshore as first-spawning fish (Burgner et al. 1992), and if the more distant waters are better for feeding, the repeat spawners probably had less access to those areas.

Given these factors, it is perhaps surprising that the repeat spawners were only slightly shorter (by 26.5 mm) than first-spawning females of the same age (739.3 versus 765.8 mm; Figure 1; Table 1). Interestingly, males in this population showed a greater difference in size between 1.1S1 and 1.3 fish (753.9 ± 78.7 mm [mean ± SD], n = 11, versus 811.3 ± 71.7 mm, n = 100; difference = 57.4 mm; T. P. Quinn and T. R. Seamons, unpublished data). The implication that males experience a greater energetic demand during reproduction than females is counter-intuitive because female gonads are so much larger and higher in energy density than male gonads (reviewed by Fleming and Reynolds 2004). However, the males may spend longer on the spawning grounds than do females or otherwise experience a more stressful period; this is supported by the much lower rate
of repeat spawning by males compared with females in this and other populations (Seamons and Quinn 2010).

We also found that the females returning to spawn after 2 years at sea rather than 3 years had been slightly larger as smolts and had grown significantly faster in their first year at sea, as indicated by scale measurements. This is consistent with evidence from various salmon species indicating an inverse relationship between growth or size at age and age at maturity (Quinn et al. 2009). We also found variation among years in growth, which is consistent with Acheson (2010) who reported that variation in the growth of steelhead in the first year was related to sea surface temperatures and diet.

As hypothesized, there were significant positive relationships between body length and both egg mass and fecundity. However, within each age-group these relationships were not strong, and females varied greatly in both traits. All of the fish had been reared in the hatchery during their first year of life, during which time they were fed a nutritious diet and grew rapidly compared with wild fish (which in this population typically spend 2 years growing in the river before their seaward migration). Thus, to the extent that freshwater growth determined egg mass, our prediction (e.g., based on Einum and Fleming 1999, 2000) was that all the females would have produced numerous small eggs and shown little variation among individuals. Instead, we observed that the 1.2 fish had significantly smaller eggs than the 1.3 fish for a given length. This is consistent with reports that younger (faster growing) female Chinook salmon of a given length had smaller eggs (Donaldson and Menasveta 1961; Quinn et al. 2004). Interestingly, the eggs of the repeat-spawning females were more similar in size to those of similarly aged fish (1.3 fish), but not to fish that also migrated back to spawn first after 2 years at sea (1.2 fish). We were not able to directly compare egg production by the same female on two spawning events, but such data might help resolve the question of how the reproductive allocation in the second event is determined.

Even so, the general effect of marine growth on egg mass inferred from the length and age data was not supported by the scale measurements. Neither growth in freshwater (smolt size, as indicated by scale radius) nor the growth during the first year at sea (distance between smolt check and the check indicating the first winter at sea) was correlated with egg mass or fecundity. As these results did not support either hypothesis regarding the mechanisms controlling reproductive trade-offs, it remains unclear when the patterns within individuals were fixed. However, there seems to be no support for the model that an early experience in freshwater by the female has an adaptive link to her reproductive traits at maturity years later. Among salmonid fish there may be a continuum of control mechanisms. We hypothesize that pink salmon *O. gorbuscha* and chum salmon *O. keta*, which have essentially no period of freshwater growth at all, would show the strongest relationship between marine growth and reproductive traits, and species with progressively greater reliance on freshwater for rearing might show different patterns. In this regard, wild steelhead that spent 2 (or more) years in the river might have shown different patterns from those seen in hatchery-reared fish that had experienced faster growth before their seaward migration.

Finally, this study was conducted in a hatchery population, and Heath et al. (2003) previously reported that Chinook salmon displayed rapid evolution toward smaller egg size in the hatchery environment. Those authors argued that the relaxation of selection favoring large offspring shifted the optimum toward a greater number of smaller eggs to maximize female fitness. However, this is not a general pattern in salmonids (i.e., hatchery populations do not, as a rule, evolve smaller and more numerous eggs; Quinn et al. 2004; Beacham 2010). Overall, we conclude that the evidence, at least in Pacific salmon and steelhead, is not consistent with control of egg size early in the female’s life as a juvenile in freshwater. Rather, we concur with Hay and Brett (1988:404), who concluded that

> [t]he role of atresia as a regulator of fecundity in teleosts is unclear, but ... it may be a widespread mechanism that allows some species to develop an appropriate number of optimally sized eggs in accordance with their growth and food supply during maturation.

**ACKNOWLEDGMENTS**

Sampling was conducted by many individuals over the years of the project, but we especially thank Greg Mackey, Justin Rhodes, Jennifer McLean, and Michael Dauer for their efforts. We thank the Washington Department of Fish and Wildlife for permission to work at the Forks Creek Hatchery and the hatchery staff (especially Rob Allan, Kevin Flowers, and Dave Shores) for assistance. Funding has been provided by the Weyerhaeuser Company Foundation, the National Science Foundation, the H. Mason Keeler Endowment, the Hatchery Science Reform Group in Washington State, and the Bonneville Power Administration.

**REFERENCES**


Elgar, M. A. 1990. Evolutionary compromise between a few large and many small eggs: comparative evidence in teleost fish. Oikos 59:283–287.


