Influences of Freshwater and Marine Growth on the Egg Size–Egg Number Tradeoff in Coho and Chinook Salmon

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Abstract.—How to partition a finite amount of energy into progeny is an important issue in evolutionary biology. Salmonids produce a small number of large eggs compared with other teleost fishes, and there are positive correlations between female size and both the size and number of eggs produced. We examined the temporal variation in reproductive investment (gonad mass, fecundity, and egg size) of coho salmon Oncorhynchus kisutch and Chinook salmon O. tshawytscha at the University of Washington hatchery over the last three to five decades. During this period, fish growth rates in freshwater and at sea varied greatly, allowing us to test the hypotheses that rapid early growth rate results in high fecundity and that hatchery populations evolve high fecundity over time. In the coho salmon, reductions in length, condition factor, and size-adjusted fecundity over the past decades combined to reduce overall average fecundity to only about half its former level. In Chinook salmon, age at maturity decreased as smolt size increased, so average size decreased over time but size at a given age did not decline. Reproductive investment (gonad size, corrected for body size) decreased for the coho salmon but not for the Chinook salmon. Egg size (adjusted for variation in fish size) did not vary with growth rate for either species or environment. Size-adjusted fecundity did not increase with increasing freshwater growth for either species, but it did increase with marine growth for the coho and age-3 Chinook salmon. These results contradict the prediction that females adjust egg size depending on the perceived quality of the juvenile habitat. Egg size is probably determined much later in life, corresponding to the number of remaining eggs and the energetic constraints at maturity. The results are also inconsistent with the hypothesis that hatchery populations will evolve small eggs and high fecundity as a result of a relaxed selection for large fry.

The question of how to partition a finite amount of energy into progeny is a very important issue in evolutionary biology. A large body of theoretical and empirical work has focused on the tradeoff between producing many small or few large offspring (Roff 1992; Stearns 1992). Most models for the evolution of egg size suggest that each population has an optimal size (Svardson 1949; Smith and Fretwell 1974), based on the assumption that evolution will maximize maternal—not progeny—fitness. Recently, empirical evidence supporting this contention was found in Atlantic salmon Salmo salar (Einum and Fleming 2000). Offspring survival was apparently sacrificed to maximize maternal fitness by producing more numerous but smaller progeny than would have been the case if juvenile survival (progeny fitness) were maximized. However, it is not evident that there should be a single optimal egg size within each population (Parker and Begon 1986; Sargent et al. 1987; Hendry et al. 2001; Sakai and Harada 2001).

Patterns of egg size and fecundity have been extensively studied in salmonid fishes. Larger females produce larger as well as more numerous eggs than smaller females (Beacham and Murray 1993; Quinn et al. 1995), and juvenile size at emergence is strongly correlated with egg size (Bea-
An alternative to the perspective that egg size is controlled by maternal growth rate comes from recent studies of hatchery-produced Chinook salmon *Oncorhynchus tshawytscha*. Heath et al. (2003) reported a decrease in egg size and a concurrent increase in fecundity with the number of generations of hatchery propagation. In the hatchery, natural selection favoring large eggs is relaxed; this allows fecundity selection to drive the evolution for small eggs. However, phenotypic plasticity or genetic correlation between traits may produce the same general trend under certain conditions, so the generality of this finding is unclear.

Anadromous salmonids present particularly good opportunities to test the prediction that females experiencing slow growth early in their lives should produce large eggs, whereas those growing faster should produce smaller eggs (Einum and Fleming 1999). They begin life in relatively growth-limited freshwater habitats which will be shared by mothers and their offspring, and then migrate to sea where growth opportunities are better and the fish are more dispersed. At what point in their life cycle is the egg size–egg number trade-off determined, and is it a stage where or when maternal experience will correlate with offspring experience? The relationships among growth, body size, and egg size are complicated by the fact that some female salmon are large because they are old, not because they grew fast. Indeed, as individuals maturing at an older age are often the slower growing individuals of their population (Groot and Margolis 1991), analyses of egg size need to consider both maternal size and growth history in freshwater and marine environments.

In contrast to the hypothesis that egg size is the fundamental trait, there are mechanistic reasons to believe that egg size is determined secondarily as a consequence of fecundity and energetic constraints. The recruitment of oocytes and the allocation of energy to each potential egg may be independent processes, as the growth and maturation of an individual egg can take 1 year or more (Brooks et al. 1997). The energetic costs of adult migration influence egg size; females with arduous migrations sacrifice egg size rather than egg number (Kinnison et al. 2001). Thus, it is reasonable to assume that variation in early growth rate influences the number of eggs recruited at each reproductive event, not their size per se. Egg size may be influenced by the level of surplus energy during later phases. Finally, the possible evolutionary trajectory of hatchery populations towards more numerous, but smaller, eggs (Heath et al. 2003) needs to be tested.

The purpose of this study was to test if and how egg size is phenotypically plastic in two species of semelparous Pacific salmon: coho salmon *O. kisutch* and Chinook salmon. The populations were established at the University of Washington hatchery in the 1950s (Chinook salmon) and 1960s (coho salmon). Over the period of record, growth rates in freshwater and salt water have varied, making it possible to examine patterns of reproductive investment under a range of growth regimes (e.g., fast in freshwater and slow at sea, or slow in freshwater and fast at sea) over several decades. Preliminary data analysis indicated that the growth of Chinook salmon in freshwater has become faster over the years, coho salmon growth has varied but not shown a trend over time, and growth of both species at sea has varied and probably declined over time. The years of fast and slow growth rates in the two environments may have led to changes in reproductive investment (Table 1), allowing three contrasting hypotheses for the controls over egg size to be tested. First, egg size may be directly controlled by early growth (i.e., fast growth leads to small eggs), as has been hypothesized for Atlantic salmon and brown trout *Salmo trutta*. In this case, the ratio between egg number and egg size in adult Chinook salmon should increase over the years (assuming that the relative investment into gonads does not vary) because the fish are growing faster in freshwater in recent years and so should produce more numerous, smaller eggs. This ratio should not show a time trend for coho salmon, but cohorts that grew rapidly in freshwater should have produced more eggs as adults. Alternatively, the association be-
Table 1.—Summary of predictions of the effects of variation in growth rate in freshwater or marine environments on the ratio of fecundity to egg size, according to the stage at which egg size is controlled. In these models, we assume that the relative reproductive investment does not change.

<table>
<thead>
<tr>
<th>Water stage</th>
<th>Growth rate</th>
<th>Egg number/egg size</th>
<th>Growth rate</th>
<th>Egg number/egg size</th>
<th>Growth rate</th>
<th>Egg number/egg size</th>
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<tr>
<td>Freshwater</td>
<td>Fast</td>
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<td>Slow</td>
<td>Low</td>
<td>Fast</td>
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<tr>
<td>Freshwater</td>
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* The indirect control is through differential recruitment of oocytes, and egg number is determined at an early stage (either in freshwater or early during marine life).

tween growth in freshwater and the egg number—egg size tradeoff may be spurious. Atlantic salmon and brown trout have protracted periods (i.e., 1–2 or more years) of rearing in freshwater prior to seaward migration. The tradeoff may be determined after 1–2 years of life, regardless of the environment, and the association is not fundamentally an adaptation to benefit offspring survival in competitive freshwater environments. Thus, the second hypothesis is that rapid growth at sea leads to high fecundity relative to egg size. If so, slow growth at sea should be accompanied by few, large eggs. Finally, there could be a third mechanism by which growth affects egg size. If egg number is more or less fixed early in life but egg size depends on energy available at the end of the marine growth period, then rapid growth at sea, as reflected by overall size and especially condition factor (weight at length) should result in larger eggs relative to fecundity. None of these patterns would produce the trend towards higher length-specific fecundity predicted by the evolutionary hypothesis unless there was a trend towards faster growth, allowing us to test this alternative hypothesis.

Methods

In the late 1940s, a salmon and trout hatchery was constructed on the University of Washington (UW) campus, located between Lake Washington and Lake Union, about 7 km upstream from Puget Sound. The first Chinook salmon were released in 1949. The hatchery was modified somewhat when a holding pond for adults was built in 1960, but it has otherwise been structurally similar over much of its existence. Coho salmon and sockeye salmon *O. nerka* experiments in the early years were not very successful, but starting in the late 1960s substantial numbers of coho salmon returned, along with the Chinook salmon. The stocks of Chinook and coho salmon were primarily from the Green River system (Soos Creek hatchery) in Puget Sound, though some exchange with other populations took place over the years, and the Green River population itself had exchanges with other populations. There is no spawning area for either salmon species in the vicinity of the hatchery, so the populations have evolved with minimal influence from wild populations since the hatchery was initiated. Since the early days of the hatchery, all returning salmon were identified, measured for fork length, weighed, and had their date of capture recorded, along with any marks or unusual circumstances. For a large number of the females, fecundity and egg size were measured.

The UW Chinook salmon are of the ocean type, meaning that they migrate to sea in their first year of life, as is characteristic of lowland Puget Sound populations (including the Green River; Myers et al. 1998). Juvenile coho salmon in the Puget Sound region typically migrate to sea in their second year of life (Weitkamp et al. 1995). However, the epilimnion of Lake Washington (the UW hatchery’s main water source) is too warm in the summer to rear Pacific salmon. Both the coho and Chinook salmon are incubated on an elevated temperature regime during embryonic development and fed heavily in the spring. The fish reach a suitable size for smolt transformation in their first spring of life (after about 5 months of growth). This is the natural life history pattern for the Chinook salmon but is a shorter (and faster growing) period in freshwater than is typical for coho salmon. The accelerated rearing program began with the 1967 cohort of coho salmon (Donaldson and Brannon 1976), and our analyses were restricted to data on adults since 1969.

Data collection and analysis.—Adult Chinook salmon returned to the hatchery and were spawned from early October to early December, and the
coho from early November to mid-December (Quinn et al. 2002). Three times each week (with some exceptions), each adult salmon was checked for ripeness to spawn. Ripe fish were killed, weighed to the nearest 0.01 kg, measured (fork length) to the nearest mm, and inspected for marks or tags. Eggs were taken from the females, fertilized with sperm from usually one male, and placed in vertical-stack, Heath tray incubators. Eggs from each female were typically placed in separate trays so that offspring corresponding to particular parents could be traced. Up to 25% of the female coho salmon (mean ± SD: 47 ± 30, minimum = 8, maximum = 131) and 45% of the Chinook salmon (124 ± 30, minimum = 0, maximum = 367) were measured for reproductive output during any given year. Fecundity and mean egg size were measured for individual females in a standardized manner (Allen 1958), facilitating comparisons among years. The volume of water displaced by the total mass of eyed eggs was recorded, and the average egg volume was estimated by counting the number of eggs needed to fill a 15-cm (6-in) trough (effectively a measure of average egg diameter). Dead eggs removed from the tray prior to these measurements were added to the total estimated fecundity.

Data were collected in 1999 to convert these volumetric estimates of egg size at the eyed stage to mass of fresh (unspawned) eggs, facilitating comparison with other studies. A sample of 50–100 fresh eggs (prior to water hardening) was weighed and counted, and the total egg mass was weighed. Fecundity (estimated from gravimetric data) and mean egg mass were compared with the volumetric estimates and diameters of eyed eggs measured as above on the same females. The relationship between the number of eggs per trough and fresh weight was very close; this was expected because the density of eggs is nearly constant, and the relationship between diameter and volume is constant for a sphere. Using data from both species, the average egg weight (g) was calculated (1567.3 * [number of eggs per trough]^{-2.922}, r^2 = 0.984) over a range of 0.40–0.15 g. Annual average fecundity and egg size were estimated and graphed over the years for Chinook (1954–1999) and coho salmon (1969–1999). The relationships among egg size, fecundity, and body size were examined to determine if the patterns of allocation of reproductive effort have changed with body size over time. Fecundity, egg size, and total fish mass were standardized to the overall mean fork length by removing the length effect using linear regression. Trait values were standardized to a mean body length (766, 830, and 545 mm for age-3 Chinook salmon, age-4 Chinook salmon, and coho salmon, respectively).

Smolt size data were collected for one or more groups of salmon from each cohort before their release from the hatchery. Smolt groups were distinguished by fin clips, brands, or coded wire tags identifying groups; thus there were no data on the freshwater growth rates of individual fish. Further, as scales and otoliths were not collected, it is not possible to indirectly estimate the smolt size of individual fish. Since 1990, 100 or more individual smolts were measured for length and weighed from each group. Prior to 1990, fish were weighed in bulk and counted to estimate the average mass per fish. In some years (1965–1967, 1970–1979, 1981, and 1984) the smolts comprised some fish from experimental treatments (including special temperature regimes, irradiation, nutritional adjustments, and an age-specific breeding scheme). Data from these experimental groups were analyzed, but data on releases of UW fish from locations other than the UW hatchery, as well as on releases of non-UW populations, were excluded. To avoid pseudoreplication we use the weighted annual mean smolt mass as our estimate of growth rate in freshwater for the different cohorts.

It was possible to assign an age to 7293 female coho salmon and 3224 female Chinook salmon based on tags or marks (group marks). Almost all the known-age female coho salmon (96.85%) returned after two summers and the rest after three summers. Given the great preponderance of age-2 female coho salmon, we assumed that all unmarked females were also of this age. Most female Chinook salmon returned after three (46.22%) or four (51.99) summers, but a few returned after two (0.03%) or five (1.78%) summers. No Chinook salmon were tagged or marked during most of the 1980s and 1990s, so there were no known-age females for this period. It was therefore not possible to examine the traits associated with individual size at age during this period.

We estimated the mean marine growth rate for each cohort and age-group within a cohort (Chinook salmon only) based on the mean smolt mass at release and the mean size at return to the hatchery for spawning. The usual measures of growth rate, such as the specific growth rate (g = [log(M2) – log(M1)]/time), may be correlated with size at the start of the experiment (M1). This was the case for our material and is probably due to an allometric relationship between growth efficiency and
body mass. We therefore used a standardized mass specific growth rate (Ω; Ostrovsky 1995):

$$\Omega = \frac{M_f^2 - M_i^2}{b \cdot \text{time}} \cdot 100,$$

where \( b \) is the allometric mass exponent for the relation between growth rate and body mass. This exponent has not been estimated for coho or Chinook salmon. However, since estimates obtained for brown trout (0.308) and Atlantic salmon (0.310) are very similar (Elliott et al. 1995; Elliott and Hurley 1997), suggesting that this exponent may be similar among salmonids, we set \( b = 0.31 \).

Results

The mean mass of the Chinook salmon smolts released each year during the period increased almost tenfold, from 2.5 to 23.3 g (linear regression of annual mean smolt size on time: \( r_{29} = 0.858, P < 0.001 \)). The mean mass of the coho salmon smolts varied from 6.7 to 22.4 g, but there was no significant time trend (\( r_{29} = 0.108, P = 0.576 \)).

The annual mean fork length and mass of all the spawning females (ignoring age) decreased during the study period in both species (Figure 1). The proportion of female Chinook returning after three summers rather than four increased over the years (\( r_{22} = 0.382, P = 0.031 \)), accounting for some of the reduction in mean size. A marginally significant positive correlation was observed between mean smolt mass and the proportion of female Chinook salmon of that cohort maturing after three summers at sea (\( r_{24} = 0.391, P = 0.059 \)). Almost all (96.85\%, \( n = 7,293 \)) of the known-age coho females spawned after two summers at sea. Variation with time in relative body mass at size (condition) was evaluated using an analysis of covariance (ANCOVA), with body mass as the dependent variable, fork length as the independent variable, and return year as the treatment. Both body mass and fork length were natural log-transformed before analysis. The least-square mean log-body mass decreased significantly with time for both coho and Chinook salmon (Figure 1). Thus the salmon have not only been growing slower at sea in terms of length but were also getting lighter for a given length. There were indications that the trend was not linear, so we fitted a piecewise linear regression to the data. For the coho salmon, no good piecewise linear model was found. However, for the Chinook salmon the model indicated that the decrease started in 1967 (±3 years).

The mean saltwater growth rate (\( \Omega \)) of known-age fish decreased with time for female coho salmon (\( r_{22} = -0.551, P = 0.008 \), but not for Chinook salmon (three summers at sea: \( r_{23} = -0.125, P = 0.578 \); four summers at sea: \( r_{24} = 0.258, P = 0.223 \)). It is important to note here that the data for the coho and Chinook salmon cover somewhat different time periods. Female Chinook salmon maturing after three summers at sea grew faster than the females maturing 1 year later (ANCOVA with time as covariate; \( F_{1,42} = 336.5, P < 0.001 \), though on an absolute basis the age-4 females were heavier than the age-3 fish.

For the female Chinook salmon, the mean annual reproductive investment (gonadosomatic index [GSI] = percent of the total mass in gonad) did not vary with time (ANCOVA; \( F_{1,42} = 2.62, P = 0.113 \)), nor did it differ between age-classes (ANCOVA; \( F_{1,42} = 0.689, P = 0.411 \)). Fecundity (\( F_{1,3148} = 832.9, P < 0.001 \)) and egg size (\( F_{1,2932} = 288.3, P < 0.001 \)) increased with fish length (all traits log\(_e\) transformed), but age-3 Chinook salmon had smaller (\( F_{1,2935} = 697.8, P < 0.001 \)) and more numerous (\( F_{1,3148} = 139.1, P < 0.001 \)) eggs than age-4 females of the same size. Due to significant age-length interaction effects (fecundity: \( F_{1,3148} = 26.8, P < 0.001 \); egg size: \( F_{1,2932} = 5.1, P = 0.024 \)), the data were analyzed for the two age-classes separately. Mean length-adjusted fecundity did not change with time (Chinook salmon three summers at sea: \( r_{22} = 0.252, P = 0.246 \); Chinook salmon four summers at sea: \( r_{26} = 0.254, P = 0.210 \)). Neither did we detect a change in length-adjusted egg size (three summers at sea: \( r_{22} = -0.099, P = 0.652 \); four summers at sea: \( r_{26} = 0.203, P = 0.319 \)) or in the ratio of egg number to egg mass (three summers at sea: \( r_{23} = 0.230, P = 0.291 \); four summers at sea: \( r_{26} = 0.123, P = 0.548 \)).

For the female coho, fecundity (\( r_{1055} = 0.774, P < 0.001 \)) and egg size (\( r_{1048} = 0.566, P < 0.001 \)) increased with fish length (all traits log\(_e\) transformed). GSI decreased significantly with time (\( r_{22} = -0.589, P = 0.004 \)) in addition to the decline in overall weight. Mean length-adjusted fecundity decreased with time (\( r_{22} = 0.750, P < 0.001 \)), and mean length-adjusted egg size increased (\( r_{22} = 0.553, P = 0.008 \)). This latter result reflects the fact that the absolute egg size has changed little and that body size has decreased, so the calculated egg size at a fixed body size increased. The ratio of egg number to egg mass also decreased with time (\( r_{22} = -0.767, P < 0.001 \)).

After adjusting for adult length, the correlations between the growth rate in freshwater and marine
environments and the fecundity and egg size of the salmon were compared (Figures 2 and 3). The growth rate in freshwater was not correlated with egg size or fecundity for either species. However, for the coho salmon and age-3 (but not age-4) Chinook salmon there were positive correlations between marine growth and fecundity and the fecundity-to-egg mass ratio.

**Discussion**

Our results revealed different temporal trends in female growth and reproductive investment in the UW coho and Chinook salmon. The growth rates of the coho salmon but not the Chinook salmon in saltwater have decreased with time. The growth rate in freshwater for the Chinook salmon but not the coho salmon increased during the 1960s and early 1970s, a result of higher water temperatures and increased quality of feed and husbandry designed to produce large smolts (Donaldson and Joyner 1983). Regardless of the reason for the differences in growth rate trends between the two species, neither showed the inverse correlation between freshwater growth rate (i.e., smolt size) and
Figure 2.—Relationship between size-adjusted mean egg size, fecundity, and the egg size/fecundity ratio and smolt size (g) for cohorts of coho and Chinook salmon at the University of Washington hatchery. Mean smolt size is measured at release of the various cohorts and is not necessarily the smolt size of the mature fish actually returning.

Egg size (adjusting for fish size and age) predicted by models of optimal egg size (Parker and Begon 1986). The growth rate in freshwater was also not associated with high fecundity in either species. This indicates that the time period in freshwater was too short for these populations to establish a relationship between growth and reproductive allocation. The period of freshwater rearing was accelerated for the coho salmon but was normal for the Chinook salmon, so in Chinook salmon at least we conclude that there is no fundamental relationship between growth in freshwater per se and egg size. Furthermore, egg size (adjusted for fish size) did not decrease with time, contradicting the observations for British Columbia Chinook salmon (Heath et al. 2003). The UW populations are almost entirely isolated from wild salmon influence, so, according to that hypothesis, these should have shown a dramatic decrease in egg size.

Uncertainty regarding the possible environmental and genetic factors that influence the decline in the adult body size of these (and other nearby) populations makes it difficult to interpret the reproductive patterns we observed. Nevertheless, no relationship between the growth rate at sea and egg size was observed in either species. In coho salmon and age-3 Chinook salmon, growth rate at sea was positively correlated with size-adjusted fecundity. Coho salmon body size has declined greatly while egg size has remained essentially constant, as though the population has reached some minimal egg size. The coho salmon have not only declined in length but also in condition (weight at length), and the gonad size relative to weight (GSI) has declined as well. Apparently, the fish are becoming so thin that a larger proportion of the body’s energy is needed for survival and migration, and gonad production must be sacrificed. These losses in gonad size are translated into reductions in fecundity, perhaps through atresia of eggs produced earlier in life. Whatever the reasons, such a reduction in fecundity might have
serious consequences for the productivity of a natural population.

In contrast to coho salmon, Chinook salmon commonly mature at more than one age within populations (Healey 1991; Roni and Quinn 1995). UW females maturing after four summers at sea produced significantly larger but fewer eggs than fish maturing after three summers (after adjusting for variation in size). This effect, first documented by Donaldson and Menasveta (1961), was especially marked for egg size and was clearly independent of freshwater growth rate since the analysis used cohort data. Thus, there was a strong age effect on egg size. Fish maturing after four summers at sea had been growing slower than fish maturing after three summers (on average), so it would seem that fast growth at sea was associated with high fecundity and small eggs. However, this effect was only evident when comparing the two age-groups. Within age-groups, there was no relationship between growth and the egg number-egg size tradeoff.

We propose the following model for the timing of events determining the egg size-egg number tradeoff in salmonid fishes. The number of eggs recruited (the maximum number that can eventually be spawned by an individual) is determined early in life, either during freshwater residence or early during the marine phase, depending on the species. If adverse environmental conditions are encountered, the number of eggs is reduced by atresia. Although this provides energy to benefit the female, even good growing conditions later will not increase egg number. Repeated sampling of pink salmon *Oncorhynchus gorbuscha* (Walbaum) at sea revealed that mean fecundity was stable until late winter, when it dropped sharply (Grachev 1971). Thus, the energy allocated to these eggs could have been reabsorbed by the female at the time when growth would be slow and other energy stores depleted, prior to an increased food availability in spring. In species with protracted freshwater rearing (such as Atlantic salmon and brown trout), the reduction in fecundity may...
occur in freshwater but is related to the fitness of the female, not the offspring. At maturity, egg size is determined by taking the surplus energy attained during the late marine phase and not depleted during upstream migration, divided among the remaining eggs. Thus females with few eggs for their size, because they experienced poor growth earlier, will have proportionally larger eggs at maturity because their surplus energy is divided among fewer eggs. This hypothesis accounts for the strong effect of age on fecundity in the UW Chinook salmon, the reduction in fecundity in the UW coho salmon, the reduction in egg size with increasing migration distance documented by Kinnison et al. (2001), and the linkage between freshwater growth and egg size in other species (e.g., Jonsson et al. 1996; Lobon-Cervia et al. 1997; Morita et al. 1999).

The growth rates of coho salmon but not Chinook salmon in salt water declined over the period of record, and the cause of the decline might influence interpretation of the results. Declines have also been observed in other Pacific salmon species and populations (Bigler et al. 1996; Helle and Hoffman 1998), and there are many possible contributing factors. Growth rates at sea have been correlated with a number of physical factors and with salmon density (e.g., Pyper and Peterman 1999). Environmental factors (such as sea level, salinity, temperature, and depth of the mixed layer) have been correlated with the growth of coho salmon at sea; the significant decline in size from 1974 to 1998 in populations from the Puget Sound–Strait of Georgia area suggests that the decline was not unique to the UW population (Hobday and Boehlert 2001). Our preliminary analysis indicated a significant correlation between the Pacific Decadal Oscillation (PDO, an index of region climatic–ocean variability that correlates with various aspects of Pacific salmon production; Mantua et al. 1997) and the growth of UW coho salmon but not Chinook salmon (our unpublished data).

In addition to the influence of environmental conditions, the decline in body size in the UW populations might have resulted from genetic effects. In most hatcheries, some form of nonrandom mating may occur, and when the population is small, this may lead to inbreeding. Inbreeding depression often is evident as a reduction in genetic variation and in trait means (Roff 2002). The reduction with time in the coho salmon GSI may indeed indicate that inbreeding is influencing this species. There are no data on the genetic variation of the two species, but the number of parental fish sustaining them has been small in some years. Perhaps more significantly, breeding protocols in the UW hatchery selected strongly against jacks (males of either species maturing at an early age). These males were almost never used in spawning, but as they typically represent the fastest growing members of their cohort, there was effectively selection for slow growth in male salmon. Correlated selection on female growth and reproductive traits may have also occurred, and it is unclear how this might affect reproductive tradeoffs. Finally, size-selective fisheries might also have affected average size. Most female coho and Chinook salmon are above the legal size limit in Washington’s recreational fisheries (currently 40 cm for coho and 60 cm for Chinook). However, the fishery will impose a selection against large size and thus old age. Many salmon populations (including both wild and hatchery fish over a wide geographic range) have shown declines in body size, so the trends are probably caused by a complex mixture of different factors.

Further, breeding and rearing practice in hatcheries means that the fitness benefits of large eggs are reduced compared with natural situations. This may lead to a relaxed selection on egg size, whereas selection on fecundity remains strong. This may, over time, lead to decreased egg size and increased fecundity as observed by Heath et al. (2003) for British Columbia Chinook salmon. Egg size is a trait with high heritability (Heath et al. 2003), and if the optimal egg size is moved due to changes in size-related mortality, rapid evolution is to be expected. However, as we did not observe this effect, its generality is open to question.

In summary, our observations from a long-term study on two salmon species were contrary to the expectations from various life history models (Parker and Begon 1986), and contrary to what has been reported previously for other salmonid species (Thorpe et al. 1984; Jonsson et al. 1996; Lobon-Cervia et al. 1997; Morita et al. 1999; Tame and Maekawa 2000). Thus the generality of the conclusion that maternal growth rate in freshwater controls egg size to accommodate the advantages of large progeny under growth-limited conditions has to be questioned. Although the mechanisms leading to a variation in the allocation of energy into egg production (number or size) are still largely unknown, we hypothesize that the fundamental phenomenon is the reduction in fecundity associated with poor growing conditions, either at sea or in freshwater, depending on the species. The diverse factors affecting the growth
trends of salmon (and other fishes) at sea complicate the use of time series data to resolve this question. Rather, controlled experiments with genetically similar groups of fish exposed to different growth regimes in freshwater and at sea are needed for testing these important hypotheses further.

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References


