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The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*)

Thomas P. Quinn, Andrew P. Hendry and Lisa A. Wetzel

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Egg size is a critical life history trait, reflecting female investment and affecting offspring fitness. We investigated several factors which may influence variation in egg weight for sockeye salmon (*Oncorhynchus nerka*). Comparisons were based on collections from 18 Alaskan populations, among which adult migration distance and juvenile rearing habitat were similar but the size composition of incubation gravels was different. Among populations, most of the variation in egg weight could be explained by a positive correlation with different measures of the size composition of incubation gravels (Pearson's $r = 0.45\text{--}0.91$). In contrast, egg weight was poorly correlated with female body length and with female snout length, a morphological feature used during intra-sexual competition. Within each of the Alaskan populations, however, egg weight and snout length were positively correlated with female body length and hence with each other. A positive association between snout length and egg weight was still evident even after the effects of covariance with body size were removed using residuals analysis: for all of the fish pooled and within 6 of the 16 populations. A significant relationship was not detected in the other populations but the trend was nevertheless positive in 8 of the other 10. Examination of reproductive traits (gonad weight, egg weight, egg number, snout length and hump size) within another population identified a trade-off between egg weight and egg number for females of a given body length. In contrast, positive correlations between reproductive traits were more common, suggesting that energy-rich individuals produce large eggs and large secondary sexual characteristics rather than sacrificing one for the other.

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Egg production is closely linked to individual fitness through direct selection on traits such as gonad size, egg number, and egg size (see reviews in Roff 1992 and Stearns 1992). Other components of fitness, including breeding success and the cost of maternal investment, are also important during reproduction and can initiate indirect selection on aspects of egg production (Bell 1980). Intra-specific variation in egg size has been the subject of considerable research, much of which has focused on mechanisms which maintain variation within

and among populations. Theoretical and empirical research has identified an interaction between energetic limitations, maternal phenotype and the environment in determining local egg size optima (Smith and Fretwell 1974, Parker and Begon 1986, Lloyd 1987). For example, the ability or opportunity to acquire energy may differ among females. Energy limitations could then be manifested as a trade-off between different forms of maternal investment such as egg size and number (Svärdson 1949, Smith and Fretwell 1974, Winkler and Wallin

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1987, Elgar 1990), secondary sexual characteristics (Fleming and Gross 1989), or parental care (Sargent et al. 1987). Egg size and patterns of energy allocation should vary depending on the number of reproductive episodes, the length of time before maturation, and the size of females (Gadgil and Bossert 1970, Bell 1980, Thorpe et al. 1984, Parker and Begon 1986, Hutchings 1994). Patterns of egg size variation are also linked to selection during early life history stages, particularly through the effects of size- and stage-dependent juvenile mortality (e.g., Shine 1978, Winemiller and Rose 1993).

Relative to other vertebrates, teleost fishes generally have small, numerous eggs (Winemiller and Rose 1993). Among fishes, however, Pacific salmon (*Oncorhynchus* spp.) have relatively few (1 500–9 000), large (90–500 mg) eggs; the range of which depends largely on female size (Wootton 1984, Hutchings and Morris 1985, Beacham and Murray 1993). Another defining feature of salmonid life history is the unusually long period (3–8 months) when embryos are maintained solely on endogenous food reserves. During these pre-feeding stages, the embryos incubate in stream or lake gravels for a period of time that depends primarily on water temperature (Wootton 1984, Beacham and Murray 1990). The salmonid pattern contrasts with the high egg number, small eggs, brief incubation period, and dependence on food-rich environments typical of most fish species (Hutchings and Morris 1985, Winemiller and Rose 1992, 1993). For Pacific salmon, the apparent premium on the value of individual offspring, relative to the tendency in other fishes to produce many small offspring, likely reflects the importance of selection on components of fitness which are directly associated with early life history stages.

The evolution of egg size in Pacific salmon

Pacific salmon spawn at their natal sites, thereby maintaining reproductive isolation from other conspecific groups (Quinn et al. 1987, Varnavskaya et al. 1994). Natal homing ensures that parents and progeny are exposed to similar selective regimes during several key life history stages, providing an opportunity and an impetus for the evolution of local adaptations (Taylor 1991, Levings 1993, Wood 1995). Egg size differs greatly among salmonid populations and is commonly interpreted as resulting from local patterns of selection (e.g., Fleming and Gross 1989, 1990, Hutchings 1991, Beacham and Murray 1993). In other animals, large eggs appear to confer an advantage during certain key life history stages (e.g., Semlitsch and Gibbons 1990, Williams 1994). In salmonids, egg size and juvenile size are positively correlated (e.g., Thorpe et al. 1984, Hutchings 1991). Accordingly, size-dependent survival and growth of juveniles (e.g., Bagenal 1969, West and Larkin 1987) may indirectly select for egg size (Ruggerone 1989, Linley 1993). For example, large juveniles, and hence large

eggs, might evolve in high predation environments because such fish are less susceptible to many predators (Ruggerone 1989, L'Abée-Lund and Hindar 1990, but see Fresh and Schroder 1987). Large juveniles also enjoy a significant advantage over even slightly smaller conspecifics in competition for feeding territories (Chapman 1962, Abbott et al. 1985). In contrast, a strategy comprised of many small eggs might evolve where increased productivity of the rearing environment reduces predation on juveniles and/or competition among them (Hutchings 1991, Linley 1993, Winemiller and Rose 1993).

While post-emergent growth and survival often favor large eggs, opposing selection (*sensu* Schluter et al. 1991) during incubation may place a balancing constraint on increasing egg size. Sub-optimal incubation substrates (i.e., those with a high proportion of fine sediment, limited intra-gravel water movement, and low dissolved oxygen levels; reviewed in Chapman 1988) may select against large eggs due to their higher metabolic oxygen demand and less efficient surface-to-volume ratio (Sargent et al. 1987). Thus, smaller eggs, which require less oxygen and are more efficient at acquiring it, have been hypothesized to evolve in populations which spawn in finer gravels (van den Berghe and Gross 1989) because the embryos would experience reduced water flow and limited oxygen availability (Chapman 1988). Certain aspects of this hypothesis have been invoked in many studies attempting to explain patterns of life history variation in salmonids (e.g., Holtby and Healey 1986, Sargent et al. 1987, van den Berghe and Gross 1989, Fleming and Gross 1989, 1990, Quinn and Bloomberg 1992). Nonetheless, a positive association between egg size and substrate size has not been explicitly demonstrated.

While the evolution of egg size can reflect abiotic (e.g., gravel porosity and dissolved oxygen) and biotic (e.g., predator and prey distributions) factors acting directly on offspring survival, energetic demands on females may also be important. Anadromous Pacific salmon cease feeding when they return to fresh water. Subsequent metabolic activity and reproductive development are carried out on a fixed energy budget, which is reflected in the depletion of energy reserves in salmon from river-entry to death (Idler and Clemens 1959, Gilhausen 1980). Variation in gonad mass, egg size and egg number among salmon populations has been interpreted as a function of energy allocation strategies. For example, egg production has been shown to be inversely correlated with the distance adults must travel to reach their natal spawning sites, suggesting that energy consumed when undertaking an arduous migration is then unavailable for reproductive development (Fleming and Gross 1989, Beacham and Murray 1993, Linley 1993).

The evolution of life history and morphology in Pacific salmon also appears to be influenced by breeding competition (Holtby and Healey 1986, Fleming and Gross 1994). Fleming and Gross (1989) reported a nega-

tive correlation between female gonad weight and estimated levels of competition among populations. They interpreted this pattern as evidence for a trade-off between reproductive requirements which compete for limited energy resources. Specifically, energy consumed while defending nest sites from intruders would reduce that available for investment into egg production. Furthermore, Fleming and Gross (1989) noted a negative correlation between egg size and the intensity of breeding competition among populations. To explain this trend they suggested that a larger proportion of females in populations exposed to high levels of competition would be forced into marginal habitats, where smaller eggs would evolve because large eggs would have low survival in the fine substrate.

Approach and objectives

Inter-population comparisons of life history traits to habitat features can provide valuable insights into mechanisms of selection and related processes of evolution (Endler 1986). However, patterns of differential energy allocation and life history trade-offs are less well investigated using this approach because they can be confounded by many other selective factors that differ among populations (e.g., energy availability and migration distance for adults, and/or predation and competition regimes experienced by offspring). Individuals within populations are exposed to a more common selection regime than those among populations. Accordingly, the examination of trade-offs among life history traits may be best conducted within populations. To date, however, the investigation of reproductive trade-offs within salmonid populations has been restricted to that between egg size and egg number (e.g., Bromage et al. 1990, Quinn and Bloomberg 1992).

Egg production can be evaluated in the context of gonad size, egg number, and egg size; each of which can be quantified in terms of their absolute number or size (i.e., length, diameter, or weight). On the other hand, maternal investment is a function of the energy content of eggs and gonads as well as the endogenous reserves consumed during maturation; expenditures which cannot be precisely delineated simply by weighing gonads and counting eggs. Nevertheless, the size of eggs is positively correlated with their energy content (e.g., Smirnov et al. 1968, Hislop and Bell 1987, Lahti 1991) and so, if other extrinsic factors are considered equal, egg size and number can provide a coarse estimate of relative energy expenditure. Within our study area, the size of individual sockeye salmon eggs was directly and positively correlated with their total caloric content (L. Wetzel unpubl.). Among populations, however, caloric content for a given egg size did not differ (Wetzel 1993). Therefore, while we refer specifically to the size of certain traits throughout this paper, most notably the weight of individual eggs; we will also infer a relationship to energy expenditure.

Our objectives were to quantify egg size variation both among and within populations of sockeye salmon (*O. nerka* Walbaum) and to test for a relationship between egg size and specific abiotic and biotic factors. Among-population variation was examined through a comparative survey of 18 Alaskan populations, selected for similar adult migration patterns and juvenile rearing habitats but for different spawning and incubation environments. Among these populations, we tested the following predictions: (1) egg weight is positively correlated with body length, (2) egg weight is positively correlated with snout length, and (3) egg weight is positively correlated with gravel size. Within each of these populations, we tested for correlations among female body length, egg weight and snout length. Correlations among a larger suite of reproductive traits (gonad weight, egg weight, egg number, snout length and hump size) were then examined within a population of sockeye salmon from the Cedar River, Washington.

Methods

Study sites and collection schedule

We examined variation in the egg weight of sockeye salmon from 2 lake systems which drain into Bristol Bay, Alaska (Iliamna Lake and the Wood River Lakes). Within each lake system there is considerable variation in the environments where adults spawn and embryos incubate (Demory et al. 1964, Bishop 1990, Blair et al. 1993, Wetzel 1993). After the incubation period, juveniles from the different spawning sites rear in their respective nursery lakes for 1 or 2 yr and then migrate to the sea at about the same date (Woolington et al. 1990). After several years of ocean residence, adults from the different populations return synchronously (Burgner 1980, Jensen and Mathisen 1987). Migration arduousness and the period of fasting before spawning differs only slightly among the populations (Jensen and Mathisen 1987) in comparison to the full range experienced within the species (Burgner 1991). Consequently, variation in egg weight among populations probably reflects adaptations to the incubation environment rather than inter-population variation in post-emergent conditions for juveniles or in the energy available to adults.

Collection locations included 8 populations (groups of adults spawning in discrete creeks, rivers or beaches) in the Iliamna Lake system (Fig. 1) and 10 populations in the Wood River Lakes system (6 in Lake Aleknagik and 4 in Lake Nerka; Fig. 2). The Aguluwak River was considered to be a Lake Aleknagik population because that is where its juveniles likely rear. In Iliamna Lake, adult females were collected at Woody Island, Fuel Dump Island and Knutson Bay in 1988 and in each year from 1990 through 1993. Sampling took place in 3 of these years at the Tazimina River and at Chinkelyes Creek, and in 2 of the years at the Copper River, Gibralt-

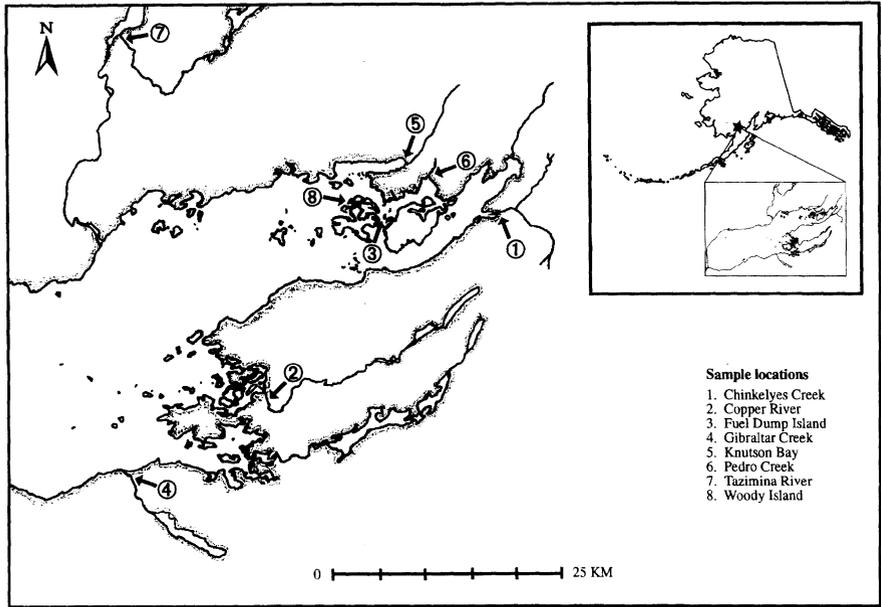


Fig. 1. Populations of sockeye salmon sampled for egg size in Iliamna Lake, Bristol Bay, Alaska.

tar Creek and Pedro Creek. Sample sizes ranged from 10–50 females at each location within each year. In Lake Aleknagik, eggs were collected from 18–27 females in both 1990 and 1993 at 3 spawning locations (Bear, Hansen and Happy creeks), from 25 females in 1990 at

the Agulowak River, and from 19 and 28 females in 1993 at Yako and Mission creeks, respectively. In Lake Nerka, 24–27 females were sampled in 1990 from each of the 4 locations. The intensive examination of reproductive traits (gonad weight, egg number, egg weight, snout length and hump size) was conducted for sockeye salmon from the Cedar River, Washington, in November 1993. For this location, females of wild origin were used for hatchery egg collection, allowing for the measurement of many reproductive traits and a large sample size ($n = 73$).

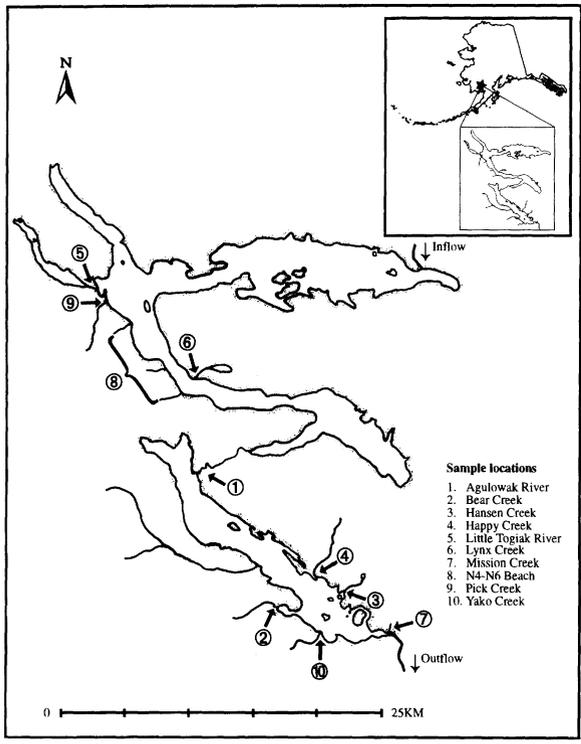


Fig. 2. Populations of sockeye salmon sampled for egg size in the Wood River Lakes (Aleknagik and Nerka), Bristol Bay, Alaska.

Sampling and characterization of incubation gravels

Spawning locations were categorized as creeks (<20 m wide and <50 cm deep), rivers (>20 m wide and >50 cm deep) or beaches, based on average width and depth reported in Demory et al. (1964) and Bishop (1990). In using these criteria, the spawning locations were classified independent of their gravel size distribution, which varied considerably within each habitat type. In 1993 and 1994, the size composition of incubation gravels was quantified for all of the collection locations in the Wood River Lakes and for 5 of the collection locations in Iliamna Lake (Table 1). Gravel was not collected from the Copper, Gibraltar and Tazimina rivers due to difficulty in obtaining representative samples from these large, heterogeneous spawning areas with deep, rapidly flowing water. Two correlated and complementary methodologies were used to quantify the size distribution of incubation gravels. These included the Wentworth pebble count (Wolman 1954) which was used to characterize surface gravels and the use of a McNeil core sampler

Table 1. Habitat type classifications (after Demory et al. 1964 and Bishop 1990) and the size composition of incubation gravels for spawning locations in lakes Iliamna, Aleknagik and Nerka. Bulk samples (McNeil and Ahnell 1960) were used to calculate the geometric mean particle size (Platts et al. 1979), the Fredle Index (Lotspeich and Everest 1981), and the percentage of particles, by weight, less than three sieve sizes (e.g., Young et al. 1991). The geometric mean was also calculated from surface pebble counts (pebble).

Spawning location	Habitat type	Geometric mean	Fredle index	% fines <3.3	% fines <1.7	% fines <0.85	geo. mean (pebble)
<i>Iliamna</i>							
Chinkelyes	creek	—	—	—	—	—	17.54
Fuel Dump	beach	32.05	32.05	0	0	0	77.83
Knutson Bay	beach	1.18	0.67	87.25	76.84	47.13	1.63
Pedro	creek	0.90	0.39	90.57	82.65	61.67	1.80
Woody	beach	26.50	23.59	0	0	0	72.06
<i>Aleknagik</i>							
Agulowak	river	—	—	—	—	—	27.84
Bear	creek	6.77	3.64	27.35	16.23	7.81	12.29
Hansen	creek	8.44	5.49	18.98	10.28	3.92	14.24
Happy	creek	8.07	4.58	21.57	12.60	5.88	12.97
Mission	creek	9.70	6.85	17.07	9.55	4.30	35.40
Yako	creek	10.22	7.71	16.06	9.06	4.06	36.13
<i>Nerka</i>							
Little Togiak	river	—	—	—	—	—	19.74
Lynx	creek	10.80	8.06	13.46	7.68	3.48	26.38
N4-N6	beach	—	—	—	—	—	4.21
Pick	creek	5.83	2.64	30.52	19.36	9.26	18.36

(McNeil and Ahnell 1960) to collect sub-surface gravels. The pebble count characterized a large area based on a limited number of particles whereas coring evaluated many particles from a few discrete sites within each collection location. The pebble count was relatively insensitive to variation in the smaller particle sizes but was particularly useful for sampling large rivers where bulk sampling was not possible.

For the pebble count, at least 100 particles (usually more than 200) were collected at random from the surface substrate within the area used for spawning at each site. The median axis of each rock was then measured to the nearest mm (Wolman 1954, Kondolf and Li 1992). For bulk sampling, 5 cores (30 cm deep by 15 cm in diameter) were taken at each location from areas used by females for spawning. The bulk samples were dried and then shaken through a series of 9 sieves of decreasing mesh size (mm): 38.1, 19.1, 13.33, 6.68, 3.33, 1.70, 0.83, 0.495 and 0.300. The sediment which collected on each sieve, and that which passed through the smallest sieve, was weighed to the nearest 0.1 g and averaged over the 5 samples for each location.

Variation in gravel size among locations was investigated using 5 indices, two which were based on measures of central tendency and 3 which were based on the proportion of sediment less than certain size classes. The geometric mean particle size (Platts et al. 1979) was calculated for each location from both pebble count and bulk samples. The Fredle Index (Lotspeich and Everest 1981), for which the geometric mean gravel size was divided by a sorting coefficient, was calculated from bulk samples. The proportions by weight of sediment less than 3.33, 1.70 and 0.85 mm were determined for each location from the bulk samples. Each of these indices

correlates with the rate of survival-to-emergence for salmonid embryos (Chapman 1988, Young et al. 1991) and some have been used in other studies pertaining to egg size (e.g., Holtby and Healey 1986, van den Berghe and Gross 1989).

Sampling of adult females

Females were collected by beach seine (primarily on beaches and at the mouths of some creeks), gill-net (primarily in rivers) or hand spear and landing net (primarily in small creeks). Females that had not completed spawning were measured from the middle of the eye's orbit to the end of the hypural plate (the last bone in the spinal column). This measurement was appropriate for determining body size without the confounding effect of morphological changes associated with maturation (notably extension of the upper jaw) or senescence (primarily fraying of the tail). The middle of the eye's orbit, rather than the pre-orbit or post-orbit points, was used as a landmark to facilitate the comparison of our results to those previously obtained from the same geographical area (Blair et al. 1993, Wetzel 1993, Quinn and Foote 1994). Egg weight was estimated from a sub-sample of at least 40 eggs taken from each female and preserved in buffered formalin (Fleming and Ng 1987). Within a week of collection each sub-sample was drained, blotted dry, and weighed to the nearest mg. The eggs were then counted and the average egg weight for each female was calculated by dividing the total weight of each sub-sample by the number of eggs contained therein. Weight was used in the specification of egg size as this measure correlates well with other related metrics (e.g., egg diame-

ter) and varies the least after collection (Fleming and Ng 1987). Snout length, the distance from the tip of the upper jaw to the middle of the eye (Blair et al. 1993, Wetzel 1993), was measured on a subset of females in some of the populations (listed in Table 4). Estimates of egg number could not be reliably obtained from the Alaskan populations because females began to deposit their eggs soon after maturation was complete.

Collection procedures on the Cedar River, Washington, allowed for accurate estimates of gonad weight, egg weight, egg number, snout length and hump size from wild adults. In 1993, migrating females were collected at a weir and retained in circular tanks, where they were checked daily for ripeness. All females were fully ripe, yet un-spawned, at the time of sampling, effectively minimizing potential variation in the size of reproductive traits due to senescence (Quinn and Blair 1992). All eggs were removed from each female and the entire egg mass was weighed to the nearest 0.1 g (fresh wet-weight). Average egg weight for each female was estimated using the same procedure as that for the Alaskan populations. Egg number was estimated by dividing the total weight of the egg mass by the average egg weight for each female. Morphological measures included body length (mid-orbit to the end of the hypural plate), hump height (anterior insertion of the dorsal fin to the lateral line, perpendicular to the lateral line) and snout length (mid-orbit to the tip of the upper jaw).

Egg weight and snout length indices

Analysis of variation in egg weight among populations was based on 3 indices: (1) mean egg weight, (2) egg weight adjusted to the long-term average body length of the population, and (3) egg weight standardized to a common body length of 450 mm. Mean egg weight was the arithmetic mean for females from each population. Variation in age-at-maturity and size-at-age is common in these systems, hence the females collected in any given year may not have accurately represented the long-term population averages. Therefore, long-term data on age composition and age-specific lengths (Blair et al. 1993, Wetzel 1993) were used to calculate the long-term average body length of females for each population. This was accomplished by multiplying average age-specific lengths by the proportion of the population in each age category and then summing these products (e.g., Blair et al. 1993). An allometric adjustment equation (see below) was then used to adjust the egg weight of individual females to the long-term average body size of females in each population, providing an estimate of the long-term average egg size.

Previous studies have shown that female body size and egg size are positively correlated (e.g., Thorpe et al. 1984, Beacham and Murray 1993). In our study, body length varied considerably among populations and hence variation in egg weight could have reflected covariation

with fish size. Allometric adjustments can be used to standardize the size of specific traits and allow for comparisons among groups, independent of differences in body size (Reist 1985, 1986). This technique has been applied to the analysis of differences in egg weight among salmon populations (e.g., Fleming and Gross 1989, Beacham and Murray 1993, Blair et al. 1993). We chose the mean length of all female sockeye collected in this study (450 mm) as the common body length for standardizing egg weights. The adjustment coefficient we used (1.185) was based on the 'common-within group' slope of log₁₀ values for egg weight on log₁₀ values for body length. This procedure calculated the common-within group slope using ANCOVA to allow for different intercepts while maintaining a common slope (Reist 1986). The adjustment equation used was that which is commonly applied to the standardization of salmon egg size (e.g., Fleming and Gross 1989, Beacham and Murray 1993, Blair et al. 1993). The equation, initially presented in Ihssen et al. (1981) was:

$$E_{std} = E_o(L/L_o)^b,$$

where: E_{std} = standardized egg weight, E_o = observed egg weight, L = mean body length of all collected fish (450 mm), L_o = observed body length, and b = adjustment coefficient from the common-within group slope (Reist 1986) of log₁₀ observed egg weight on log₁₀ observed body length (from ANCOVA).

A subset of the females sampled for egg weight were also measured for snout length in some of the populations (listed in Table 4). For this subset ($n = 494$), each of the egg weight indices was again calculated using the above procedures and the common within-group adjustment coefficient was calculated to be 1.172. Mean snout length and standardized snout length were also calculated for each of these collections using the same procedures as those for egg weight (the snout length adjustment coefficient was 1.421).

Analysis of variation among and within populations

The 3 indices of egg weight were compared among lakes, habitat types, populations, and years using the ANOVA model:

$$Y_{ijkl} = \mu + L_i + H_j + P_k + Y_l + PY_{kl} + e_{ijkl};$$

where: Y_{ijkl} = observed value for a given egg size index (egg weight, standardized egg weight, average egg weight), μ = mean, L_i = effect of lake (i = Iliamna, Aleknagik, Nerka), H_j = effect of habitat type (j = river, creek, beach), P_k = effect of population (k = 'see column 1 in Table 2), Y_l = effect of year (l = 1988, 1990, 1991, 1992, 1993), PY_{kl} = interaction between population and year, e_{ijkl} = error term.

Table 2. Comparison of body length and egg weight among populations of sockeye salmon from lakes Iliamna, Aleknagik and Nerka. Body length (mid-eye to the end of the hypural plate) and mean egg weight were arithmetic means for all sampled females. Long-term length was derived from the long-term average age composition and age-specific lengths for each population (Blair et al. 1993, Wetzel 1993). Average egg weight was the arithmetic mean when the egg weight of each female was allometrically adjusted to the long-term average length for each population. Standardized egg weight was the arithmetic mean when the egg weight of each female was allometrically adjusted to a common body length of 450 mm. Values are for all years pooled and standard errors are shown in parentheses.

Population	N	Body length	Long-term length	Mean egg weight	Average egg weight	Standardized egg weight
<i>Iliamna</i>						
Chinkelyes	26	474.0 (7.1)	456	96.3 (2.9)	92.0 (2.2)	90.5 (2.2)
Copper	32	456.4 (6.4)	447	113.0 (2.6)	110.9 (2.0)	110.0 (2.0)
Fuel Dump	100	437.3 (3.6)	427	112.2 (1.5)	109.0 (1.1)	116.1 (1.1)
Gibraltar	37	460.5 (6.0)	466	96.6 (2.4)	97.9 (1.8)	94.0 (1.8)
Knutson Bay	118	471.7 (3.4)	455	96.9 (1.4)	92.7 (1.0)	91.5 (1.0)
Pedro	29	434.9 (6.8)	–	84.5 (2.7)	–	87.9 (2.1)
Tazimina	46	475.0 (5.4)	464	104.2 (2.2)	101.0 (1.6)	97.4 (1.6)
Woody	150	442.5 (3.0)	427	113.5 (1.2)	108.8 (0.9)	115.8 (0.9)
<i>Aleknagik</i>						
Agulowak	25	452.4 (7.3)	462.0	113.4 (2.9)	115.8 (2.2)	112.3 (2.2)
Bear	46	441.0 (5.4)	443.5	101.6 (2.2)	102.0 (1.6)	103.8 (1.6)
Hansen	47	434.4 (5.3)	444.5	94.4 (2.1)	96.8 (1.6)	98.2 (1.6)
Happy	45	434.1 (5.4)	467.9	99.4 (2.2)	108.5 (1.7)	103.6 (1.7)
Mission	28	441.5 (6.9)	–	96.7 (2.8)	–	98.9 (2.1)
Yako	19	430.1 (8.4)	–	96.6 (3.4)	–	101.7 (2.5)
<i>Nerka</i>						
Little Togiak	25	459.4 (7.3)	440.7	107.4 (2.9)	102.4 (2.2)	104.9 (2.2)
Lynx	24	437.3 (7.4)	443.2	100.9 (3.0)	102.7 (2.3)	104.5 (2.3)
N4-N6	27	457.7 (7.0)	449.0	105.5 (2.8)	103.2 (2.1)	103.5 (2.1)
Pick	24	442.1 (7.4)	454.3	99.9 (3.0)	104.2 (2.3)	103.1 (2.3)

Pearson's product-moment correlation coefficient was used to test for a relationship between measures of egg weight and biotic (body length, snout length) and abiotic (gravel size) factors which varied among populations. For 23 collections (comprised of 16 populations – Table 4), data had been collected on female length, snout length and egg weight. These collections were used to test: (1) whether mean egg weight was correlated with the mean body length of females or with the mean length of their snouts, and (2) if standardized egg weight was correlated with standardized snout length. For the full suite of egg collections which had corresponding gravel size estimates (those populations listed in Table 1), each egg weight index was compared to each gravel size index. Sample sizes for these analyses varied because some populations did not have data for calculating long-

term average egg weight (see Table 2) and others did not have data for all of the gravel size indices (see Table 1). The former analyses (1) were conducted on individual collections (population- and year-specific) because each had discrete and independent measures of both egg weight and snout length for each year of collection. The latter analyses (2) were conducted on pooled data for each population and, separately, on a data set comprised of all the individual collections (population- and year-specific).

Correlations between body length and reproductive development (egg weight and snout length) were defined for each Alaskan collection (population- and year-specific) using simple linear regression. To compare variation in the size of traits independent of covariation with body length (e.g., Reist 1985, 1986, Fleming and Gross

1994, Quinn and Foote 1994), residuals from the above relationships were then regressed on each other for (1) all fish pooled, (2) all of the fish within each population, and (3) each individual collection (population- and year-specific). A positive slope between residuals indicated that individuals with heavier than average eggs also had longer than average snouts and a negative slope an inverse relationship. For the Cedar River population, simple linear regressions were again used to define relationships between body length and each of the reproductive traits (gonad weight, egg number, egg weight, snout length and hump size). Regressions of residuals from each of these relationships were then used to test for correlations between traits independent of the effect of body size.

Results

Variation among populations

The egg weight of the 848 collected sockeye salmon females ranged from 62 to 153 mg (mean = 103.7 ± 0.6 S.E.). Mean egg weight differed among lakes ($F = 5.34$, $df = 2$, $p = 0.005$), among habitat types ($F = 19.02$, $df = 2$, $p < 0.001$), and among populations ($F = 10.34$, $df = 13$, $p < 0.001$) but not among years ($F = 2.11$, $df = 4$, $p = 0.078$); with an interaction between population and year ($F = 3.48$, $df = 17$, $p < 0.001$). Among the populations, the smallest eggs by at least 11.8 mg were found in females from Pedro Creek (84.5 mg) and the heaviest eggs (> 107 mg) were found in 3 river populations and the 2 island beaches. Within the Iliamna Lake system the largest eggs were found at Woody Island (113.5 mg), Fuel Dump Island (112.2) and the Copper River (113.0 mg). For Lake Aleknagik and Lake Nerka, the largest eggs were found in river spawning females from the Agulowak River (113.4 mg) and the Little Togiak River (107.4 mg).

Egg weight adjusted to the long-term average female

body length for each population did not differ among lakes ($F = 1.58$, $df = 2$, $p = 0.207$) or among habitat types ($F = 0.18$, $df = 2$, $p = 0.836$) but varied among populations ($F = 15.91$, $df = 10$, $p < 0.001$) and among years ($F = 3.39$, $df = 4$, $p = 0.009$); with an interaction between population and year ($F = 2.24$, $df = 16$, $p = 0.004$). Long-term average egg weight was greatest, by at least 4.9 mg, for the Agulowak River females (115.8 mg) due to a large long-term average body length (462.0 mm) and large eggs in our collections (113.4 mg). In contrast, females from the island beaches in Iliamna Lake (Woody and Fuel Dump), while characterized by mean egg weight similar to females from the Agulowak River, had a small long-term average body size (427 mm) and hence smaller long-term average egg sizes (108.8 and 109.0 mg, respectively) than the Agulowak River fish.

Egg weight standardized to a common body length of 450 mm differed among lakes ($F = 10.33$, $df = 2$, $p < 0.001$), among habitat types ($F = 40.37$, $df = 2$, $p < 0.001$), and among populations ($F = 27.54$, $df = 13$, $p < 0.001$), but not among years ($F = 1.70$, $df = 4$, $p = 0.148$); with an interaction between population and year ($F = 2.12$, $df = 17$, $p = 0.005$). In general, sites with a large mean egg weight also had a large standardized egg weight. However, the females from island beaches in Iliamna Lake had smaller than average body lengths yet large eggs, hence they had considerably greater adjusted egg weights than the other populations. Conversely, the Knutson Bay females and Chinkelyes Creek females in our collections were very large (471.7 and 474.0 mm, respectively), resulting in small standardized egg weights (91.5 and 90.5 mg, respectively) relative to their mean egg weights (96.9 and 96.3 mg, respectively).

Values for Pearson's product-moment correlation coefficient (r_p) can range between -1 and $+1$, where -1 represents a perfect negative correlation, $+1$ a perfect positive correlation and 0 no correlation whatsoever. For the 16 Alaskan populations with body length, snout length and egg weight data, mean egg weight was not correlated with mean female body length ($r_p = 0.35$, $p =$

Table 3. Pearson's product-moment correlation coefficient (r_p) for the relationship between each egg weight index and each gravel size index. On the left side of the table are the results when all collections are considered (i.e., years are not pooled for each population) and on the right side are the results when data for all years are pooled within each population. Egg weight indices were arithmetic mean egg weight (mean), egg weight adjusted to the long-term average female body length of the population (average), and egg weight adjusted to common body length of 450 mm (standard). Bulk samples (McNeil and Ahnell 1960) were used to calculate the geometric mean particle size (Platts et al. 1979), the Fredle Index (Lotspeich and Everest 1981), and the percentage of particles, by weight, less than three sieve sizes (Young et al. 1991). The geometric mean was also calculated from independently collected pebble counts (pebble).

Gravel size index	All collections			Pooled years		
	Mean	Average	Standard	Mean	Average	Standard
geometric mean	0.79*	0.74*	0.91*	0.86*	0.70	0.90*
Fredle Index	0.77*	0.70*	0.88*	0.83*	0.64	0.90*
% < 3.3 mm	-0.69*	-0.79*	-0.86*	-0.71*	-0.79*	-0.85*
% < 1.7 mm	-0.66*	-0.78*	-0.83*	-0.66*	-0.77*	-0.81*
% < 0.85 mm	-0.65*	-0.76*	-0.80*	-0.66*	-0.75*	-0.79*
geo. mean (pebble)	0.67*	0.60*	0.80*	0.61*	0.45	0.70*

* $p < 0.05$.

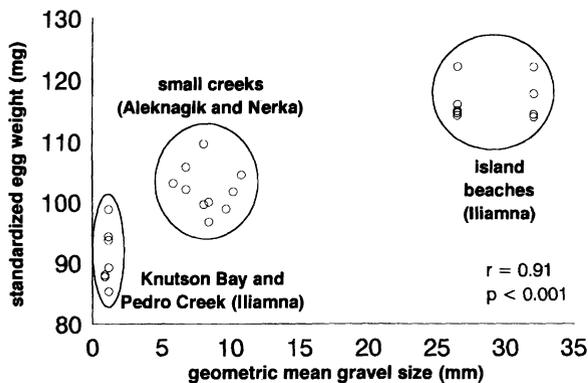


Fig. 3. The relationship between standardized egg weight (allometrically adjusted to a common body size of 450 mm) and geometric mean gravel size (Platts et al. 1979) calculated from samples obtained using a McNeil bulk substrate corer (McNeil and Ahnell 1960).

0.103) or with mean female snout length ($r_p = 0.16$, $p = 0.305$) among populations. Furthermore, standardized egg weight was not correlated with standardized snout length ($r_p = 0.09$, $p = 0.68$) among populations. For the populations with body length, egg weight and gravel size data available, the egg size indices were positively correlated with the size of surface and subsurface gravels and negatively with the percentage of fine sediments (Table 3). Pearson's correlation coefficients ranged from 0.65 to 0.91 and only 3 of the 36 correlations were not statistically significant. The non-significant correlations were for average egg weight in the years-pooled analysis

compared to the geometric mean gravel size from the pebble count and the geometric mean gravel size and the Fredle Index from bulk samples. Of the egg weight indices, standardized egg weight correlated best with the gravel size indices. Of the gravel size indices, geometric mean gravel size calculated from bulk samples correlated best with the egg weight indices. The correlation between gravel size and egg weight was largely determined by 3 population groups (Fig. 3). The smallest eggs and gravels were found at Knutson Bay and Pedro Creek in Iliamna Lake and the largest eggs and gravels were found at island beaches in Iliamna Lake (Fuel Dump and Woody). The sampling sites in lakes Aleknagik and Nerka were mostly small creeks; they all had gravel sizes between the extremes mentioned above and most had intermediate egg sizes.

Variation within populations

Within each collection of Alaskan females (i.e., population- and year-specific), egg weight was positively correlated with body length ($r^2 = 0.21 - 0.76$, $p < 0.05$ for 22 of the 23 collections), snout length was positively correlated with body length ($r^2 = 0.29 - 0.91$, $p < 0.05$ for 22 of the 23 collections), and snout length was positively correlated with egg weight ($r^2 = 0.20 - 0.80$, $p < 0.05$ for 20 of the 23 collections). Residuals were then used to compare trait development independent of covariation with body size. When the residuals for all 493 females were analyzed together, there was a positive rela-

Table 4. The results of tests for a relationship between residual snout length and residual egg weight within populations of Alaskan sockeye salmon. Residuals were calculated from population- and year-specific regression equations between body length and each trait (snout length and egg weight). Residual egg weight was then regressed on residual snout length within each population. Values for the slopes represent the increase in egg size (mg) for a given increase in snout length (mm). A positive slope indicates that for individuals of a given size, those with larger eggs also had larger snouts and vice versa.

Population	N	slope	F	p	r ²
<i>Iliamna</i>					
Copper	16	-0.26	0.29	0.60	0.02
Fuel Dump	40*	-0.18	0.17	0.69	0
Knutson Bay	53*	0.66	4.76	0.03	0.09
Pedro	28*	0.36	3.71	0.06	0.12
Tazimina	23	0.98	2.27	0.14	0.10
Woody	25*	1.16	6.42	0.02	0.21
<i>Aleknagik</i>					
Agulowak	25	0.60	0.28	0.60	0.01
Bear	46*	0.46	2.97	0.09	0.06
Hansen	47*	0.47	1.94	0.17	0.04
Happy	44*	0.99	7.01	0.01	0.14
Mission	28	0.65	4.24	0.04	0.14
Yako	19	0.39	0.79	0.39	0.04
<i>Nerka</i>					
Little Togiak	25	0.92	6.10	0.02	0.21
Lynx	24	0.78	1.96	0.18	0.08
N4-N6	27	1.25	20.70	<0.01	0.43
Pick	23	0.67	1.27	0.27	0.05

* populations for which 2 years of data were used.

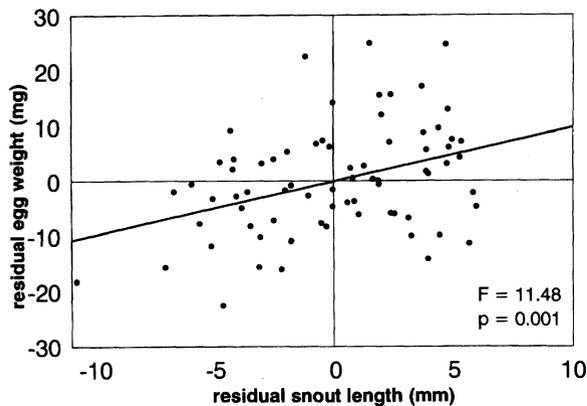


Fig. 4. The relationship between residual snout length and residual egg weight for 73 females from the Cedar River. Residuals were calculated based on regression equations between female body length and each of the traits. The trend line was generated using simple linear regression to define the relationship between residual egg weight and residual snout length.

relationship between snout length and egg weight (slope = 0.62, $F = 41.74$, $p < 0.001$, $r^2 = 0.08$). When residuals were considered at the population level, 6 of the 16 demonstrated a significant positive relationship and in all but 2 of the others, the trend was also positive although not significantly so (Table 4). When each of the 23 collections were considered individually (population- and year-specific), 5 had significant positive slopes ($p < 0.05$) and all but 2 of the other slopes were positive. The two collection-specific regressions which were negative were both far from significant ($p > 0.05$).

For the Cedar River females, body length was positively correlated with all of the measured traits (gonad weight: $r^2 = 0.58$, egg number: $r^2 = 0.45$, egg weight: $r^2 = 0.23$, snout length: $r^2 = 0.59$ and hump size: $r^2 = 0.68$, $p < 0.001$ for all traits). Each trait was positively correlated with every other trait ($r^2 = 0.21$ – 0.74 , $p < 0.001$ for all comparisons) except for egg weight vs egg number ($r^2 = 0.02$, $p = 0.18$). Considered independently of their covariation with body size, significant positive relationships prevailed for most pair-wise comparisons between traits. Residual hump size was positively correlated with residual snout length ($F = 18.55$, $p < 0.01$), residual gonad weight ($F = 11.76$, $p < 0.01$), residual egg weight ($F = 4.46$, $p = 0.04$) and residual egg number ($F = 4.64$, $p = 0.03$). Residual gonad weight was also positively correlated with residual egg weight ($F = 18.78$, $p < 0.01$) and egg number ($F = 80.36$, $p < 0.01$). Residual snout length was positively correlated with residual egg weight (Fig. 4), but was not correlated with residual gonad weight ($F = 1.37$, $p = 0.25$) or residual egg number ($F = 1.41$, $p = 0.24$). The only relationship which was negative was that between residual egg weight and residual egg number ($F = 5.13$, $p = 0.03$).

Discussion

Fleming and Gross (1989, 1994) suggested that breeding competition influences the morphology and life history of salmonids. They found that the intensity of breeding competition among coho salmon (*O. kisutch* Walbaum) populations was positively correlated with snout length and negatively correlated with egg weight (Fleming and Gross 1989), implying a negative correlation between egg size and snout size. We found no evidence for such a relationship among the sockeye salmon populations we investigated, even after removing possible effects of variation in the body length of females by standardizing egg weight to a common body size. We do not have direct estimates of differences in the intensity of competition among populations, but spawner densities were similar among the populations we sampled (Demory et al. 1964) and were much higher than those which would typically occur in coho salmon. The interaction between breeding competition and the development of reproductive traits has yet to be adequately explained for Pacific salmon.

Neither body length nor snout length correlated well with egg weight among populations. In contrast, correlations between egg weight and measures of the size composition of incubation gravels were very high, ranging between 0.65 and 0.91 based on Pearson's correlation coefficient (Table 3). Further examination of the association between egg size and gravel size at specific sites was particularly informative. At Knutson Bay and Pedro Creek, gravel sizes were much smaller (geometric mean ≈ 1.0 mm with 87–91% of the gravel < 3.33 mm) than those commonly used by salmon for spawning (Kondolf and Wolman 1993) and much smaller than those generally considered suitable for embryo incubation (Chapman 1988). At a common body length, females at these 2 sites had smaller eggs (91.4 and 88.0 mg, respectively) than most sockeye salmon throughout their range (Burgner 1991, Beacham and Murray 1993). These sites are fed by groundwater and the gravel has little silt (< 0.300 mm), which may explain why embryos are able to incubate successfully in such fine substrate. At the 2 sites with the heaviest eggs (island beaches at Woody and Fuel Dump; see also Mathisen and Gunnerød 1969), incubation gravels were very large (geometric mean > 25 mm) and devoid of fine sediments (see also Kerns and Donaldson 1968). Thus, our results confirmed the prediction that egg size is positively correlated with the size of incubation gravels. This relationship was most evident at the extremes of gravel size and may not be detectable over smaller ranges (Fig. 3).

The positive association between gravel size and egg weight was clearest when egg weight was standardized to a common body length (Table 3). We conclude that natural selection caused by, or associated with, gravel size acts on the evolution of egg size per se rather than indirectly through covariation with body size. For example, at island beaches which had the largest gravel, fe-

males were small-bodied yet had the largest eggs. Although the positive correlation between egg weight and gravel size was examined as a linear relationship it may conform better to a curvilinear function. When the size of incubation gravels decreases at the low end of the range, the added constraint on egg size is likely to be most severe. At very large gravel sizes, the relationship should approach an asymptote as the incremental benefit of large eggs is exceeded by the reduction in fitness associated with reduced egg number (*sensu* Lloyd 1987).

The relationship between egg weight and gravel size may stem from a mechanism whereby oxygen limitations in finer gravels select for smaller eggs through reduced oxygen demand and more efficient surface-to-volume ratios. This oxygen-limitation theory has had many proponents (Holtby and Healey 1986, Sargent et al. 1987, van den Berghe and Gross 1989, Fleming and Gross 1989, 1990, Quinn and Bloomberg 1992) but we acknowledge two alternative yet complementary explanations. At the lower end of the gravel size continuum large fry, which arise from large eggs (Hutchings 1991), may be at a disadvantage because they may have more difficulty emerging through fine gravels (Koski 1975, but see Crisp 1993). At the upper end of the gravel size continuum small eggs may be selected against because they are more susceptible to gape-limited predators such as sculpins which can penetrate large gravels (Phillips and Claire 1966). The latter theory may be especially relevant for the Iliamna Lake island beaches because sculpin densities are very high and egg consumption is substantial (Kerns and Donaldson 1968; C. Foote, School of Fisheries WH-10, Univ. of Washington, Seattle, WA 98195 unpubl.).

In contrast to the differences among populations, 21–76% of the intra-population variation in egg weight could be explained through covariation with body length, a result consistent with previous research (van den Berghe and Gross 1989, Quinn and Bloomberg 1992, Beacham and Murray 1993). One explanation for the increase in egg weight with body size relates to the optimal tradeoff between egg size and egg number. The ratio of gonad weight to body weight can be fairly constant among salmon of different sizes within populations (Quinn and Bloomberg 1992, but see Holtby and Healey 1986). The constancy of gonad to body weight ratio for sockeye salmon of differing sizes is supported by data from a separate collection of 82 females from the Cedar River in 1994 (Hendry and Quinn unpubl.). By inference, the limited resources available for egg production must be partitioned between egg size and number. The sacrifice in egg number necessary for small females to produce large eggs would likely result in fewer surviving offspring and reduced fitness.

In females from the Cedar River, an interaction between the expression of different reproductive traits was identified. All of the traits examined were positively correlated with body length and hence with each other. Most of these positive correlations remained after the ef-

fect of covariation with body size was removed: individuals which had greater development of a particular trait for a given size also had greater development of the other traits. We hypothesize that for a given body size, energy availability varies among individuals (see also Healey and Heard 1984), allowing increased development of a full suite of reproductive traits in energy-rich individuals and restricting the development of such traits in energy-poor individuals. Consistent with this hypothesis, Quinn and Foote (1994) found that female sockeye salmon that were heavier than average for their length also had larger than average snouts. Egg size and egg number were inversely related for a given body size in the Cedar River fish, consistent with previous evidence of a trade-off between these traits (e.g., Bromage et al. 1990, Quinn and Bloomberg 1992).

An alternative explanation for the positive covariation between egg size and body size may be that optimal egg size differs for fish of varying size. Increasing body size in Pacific salmon females has been related to success in obtaining a high quality nest site (Schroder 1981, Foote 1990, Quinn and Foote 1994), preparing the site for embryo deposition, and providing parental care in the form of nest defense (van den Berghe and Gross 1984, 1986, 1989, Fleming and Gross 1994). As nest site quality increases, oxygen availability may cease to be a limiting factor for developing embryos (Chapman 1988), resulting in a relaxation of selection against increasing egg size (see also Holtby and Healey 1986). By this mechanism, larger eggs could evolve in larger females because these fish can obtain and prepare a better incubation environment, within which their eggs will have increased survival despite their large size.

Both egg weight and snout length were positively correlated with each other due to their association with female body size. Considered independent of this association, individuals with larger snouts generally had heavier than average eggs. This relationship was (1) highly significant when all fish were pooled, (2) significant within 6 of the 16 Alaskan populations, and (3) positive although not significantly so in 8 of the other 10. Thus, the weight of evidence supports a positive association between these traits rather than a negative one. Had our sample sizes been larger within each population, statistical significance might have been the norm. Supporting this contention, the 73 Cedar River fish were characterized by many significant relationships between reproductive traits including egg weight and snout length, even considered independently of covariation with body size. Increased development of secondary sexual characteristics for a given body size enhances competitive ability in male salmon (humps: Quinn and Foote 1994, and snouts: Fleming and Gross 1994). In female salmon, snout length has been related to mating success (females use their snout and enlarged teeth during intra-sexual aggression) but its importance has yet to be separated from the correlation with body size (van den Berghe and Gross 1989, Fleming and Gross 1994, Quinn and Foote

1994). If snout length is directly associated with competitive ability, females with larger snouts for a given body size might obtain better nest sites. The eggs of these competitively superior individuals would be less constrained by oxygen limitations, allowing increased egg size.

Synthesis

This study documented variation in egg weight within and among populations of sockeye salmon from a restricted geographical area (Bristol Bay, Alaska). The level of variation we recorded was comparable to that previously recorded for this species throughout its range (Burgner 1991, Beacham and Murray 1993, Linley 1993). Post-emergent juveniles and pre-spawning adults from these populations were likely exposed to similar selective regimes, and we tested predictions that egg size would be related to specific physical and biological features of the spawning and incubation environment. Among populations, most of the variation in egg weight was explained through a strong positive correlation with the size composition of incubation gravels. This correlation likely relates to dissolved oxygen availability and surface-to-volume ratio constraints for eggs. Within populations, both egg weight and snout length were positively correlated with body length and hence with each other. Independent of their correlation with body length; some evidence indicated that egg weight and snout length also covaried positively. Positive associations between body size, egg weight and snout length; and between egg weight and snout length, independent of body length, may reflect: (1) an interaction between competitive ability and the quality of the incubation environment and/or (2) the ability of energy-rich females to invest in the development of both gonads and secondary sexual traits. Lending additional credence to the latter hypothesis was the observation that within populations only egg weight and egg number reflected a trade-off.

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References

- Abbott J. C., Dunbrack R. L. and Orr, C. D. 1985. The interaction between size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). – Behaviour 108: 104–113.
- Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. – J. Fish Biol. 1: 349–353.
- Beacham, T. D. and Murray, C. B. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. – Trans. Am. Fish. Soc. 119: 927–945.
- and Murray, C. B. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). – J. Fish Biol. 42: 485–508.
- Bell, G. 1980. The costs of reproduction and their consequences. – Am. Nat. 116: 45–76.
- Bishop, S. M. 1990. Morphometric differences among spawning populations of sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lake system. – Master's thesis, Univ. of Washington.
- Blair, G. R., Rogers, D. E. and Quinn, T. P. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. – Trans. Am. Fish. Soc. 122: 550–559.
- Bromage, N., Hardiman, P., Jones, J., Springate, J. and Bye, V. 1990. Fecundity, egg size and total egg volume differences in 12 stocks of rainbow trout, *Oncorhynchus mykiss* Richardson. – Aquacult. Fish. Manage. 21: 269–284.
- Burgner, R. L. 1980. Some features of ocean migrations and timing of Pacific salmon. – In: McNeil, W. J. and Himsworth, D. C. (eds), Salmonid ecosystems of the North Pacific. Oregon State Univ. Press, Corvallis, OR., pp. 153–164.
- 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). – In: Groot, C. and Margolis, L. (eds), Pacific salmon life histories. UBC Press, Vancouver, pp. 3–117.
- Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. – J. Fish. Res. Bd Can. 19: 1047–1080.
1988. Critical review of variables used to define effects of fines in redds of large salmonids. – Trans. Am. Fish. Soc. 117: 1–21.
- Crisp, D. T. 1993. The ability of U.K. salmonid alevins to emerge through a sand layer. – J. Fish Biol. 43: 656–658.
- Demory, R. L., Orrell, R. F. and Heinle, D. R. 1964. Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. – U. S. Fish Wildlife Service Special Scientific Report, Fisheries No. 488.
- Elgar, M. A. 1990. Evolutionary compromise between a few large and many small eggs: comparative evidence in teleost fish. – Oikos 59: 283–287.
- Endler, J. A. 1986. Natural selection in the wild. – Princeton Univ. Press, Princeton, NJ.
- Fleming, I. A. and Ng, S. 1987. Evaluation of techniques for fixing, preserving, and measuring salmon eggs. – Can. J. Fish. Aquat. Sci. 44: 1957–1962.
- and Gross, M. R. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). – Evolution 43: 141–157.
- and Gross, M. R. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. – Ecology 71: 1–11.
- and Gross, M. R. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. – Evolution 48: 637–657.
- Foote, C. J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. – Behaviour 115: 283–314.
- Fresh, K. L. and Schroder, S. L. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. – Can. J. Fish. Aquat. Sci. 44: 236–243.

- Gadgil, M. and Bossert, W. H. 1970. Life historical consequences of natural selection. – *Am. Nat.* 104: 1–24.
- Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. – *Int. Pac. Salmon Fish. Comm. Bull.* 22.
- Healey, M. C. and Heard, W. R. 1984. Inter- and intra-population variation in the fecundity of chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. – *Can. J. Fish. Aquat. Sci.* 41: 476–483.
- Hislop, J. R. G. and Bell, M. A. 1987. Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. – *J. Fish Biol.* 31: 1–20.
- Holtby, L. B. and Healey, M. C. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). – *Can. J. Fish. Aquat. Sci.* 43: 1946–1959.
- Hutchings, J. A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. – *Evolution* 45: 1162–1168.
- 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. – *Oikos* 70: 12–20.
- and Morris, D. W. 1985. The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. – *Oikos* 45: 118–124.
- Idler, D. R. and Clemens, W. A. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Stuart and Chilko lakes. – *Int. Pac. Salmon Fish. Comm. Prog. Rept.* 6.
- Ihssen, P. E., Evans, D. O., Christie, W. J., Reckahn, J. A. and DesJardine, R. L. 1981. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. – *Can. J. Fish. Aquat. Sci.* 38: 1790–1807.
- Jensen, K. A. and Mathisen, O. A. 1987. Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983. – *Can. Spec. Publ. Fish. Aquat. Sci.* 96: 101–109.
- Kerns, O. E., Jr. and Donaldson, J. R. 1968. Behavior and distribution of spawning sockeye salmon on island beaches in Iliamna Lake, Alaska, 1965. – *J. Fish. Res. Bd. Can.* 25: 485–494.
- Kondolf, G. M. and Li, S. 1992. The pebble count technique for quantifying surface bed material size in instream flow studies. – *Rivers* 3: 80–87.
- and Wolman, M. G. 1993. The sizes of salmonid spawning gravels. – *Water Resour. Res.* 29: 2275–2285.
- Koski, K. V. 1975. The survival and fitness of two stocks of chum salmon (*Oncorhynchus keta*) from egg deposition to emergence in a controlled-stream environment. – Ph.D. thesis, Univ. of Washington.
- L'Abée-Lund, J. H. and Hindar, K. 1990. Interpopulation variation in reproductive traits of anadromous female brown trout, *Salmo trutta* L. – *J. Fish Biol.* 37: 755–763.
- Lahti, E. 1991. The energy content and chemical composition of eggs, muscle and liver in winter spawning vendace (*Coregonus albula* L.) before spawning. – *Arch. Hydrobiol.* 122: 373–379.
- Levings, C. D. 1993. Requirements for genetic data on adaptations to environment and habitats of salmonids. – In: Cloud, J. G. and Thorgaard, G. H. (eds), *Genetic conservation of salmonid fishes*. Plenum Press, New York, pp. 49–66.
- Linley, T. J. 1993. Patterns of life history variation among sockeye salmon (*Oncorhynchus nerka*) in the Fraser River, British Columbia. – Ph.D. thesis, Univ. of Washington.
- Lloyd, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. – *Am. Nat.* 129: 800–817.
- Lotspeich, F. B. and Everest, F. H. 1981. A new method for reporting and interpreting textural composition of spawning gravel. – USDA Forest Service Research Note, PNW-369.
- Mathisen, O. A. and Gunnerød, T. 1969. Variance components in the estimation of potential egg deposition of sockeye salmon escapements. – *J. Fish. Res. Bd. Can.* 26: 655–670.
- McNeil, W. J. and Ahnell, W. H. 1960. Measurement of gravel composition of salmon stream beds. – Fisheries Research Institute, Univ. of Washington, Circular 120.
- Parker, G. A. and Begon, M. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. – *Am. Nat.* 128: 573–592.
- Phillips, R. W. and Claire, E. W. 1966. Intragravel movement of the reticulate sculpin, *Cottus perplexus* and its potential as a predator on salmonid embryos. – *Trans. Am. Fish. Soc.* 95: 210–212.
- Platts, W. S., Shirazi, M. A. and Lewis, D. H. 1979. Sediment particle sizes used by salmon for spawning with methods for evaluation. – U.S. Environmental Protection Agency, EPA-600/3-79-043.
- Quinn, T. P. and Blair, G. R. 1992. Morphological changes in senescing adult male sockeye salmon (*Oncorhynchus nerka* Walbaum). – *J. Fish Biol.* 41: 1045–1047.
- and Bloomberg, S. 1992. Fecundity of chinook salmon (*Oncorhynchus tshawytscha*) from the Waitaki and Rakaia rivers, New Zealand. – *New Zealand J. Mar. Freshwater Res.* 26: 429–434.
- and Foote, C. J. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. – *Anim. Behav.* 48: 751–761.
- , Wood, C. C., Margolis, L., Riddell, B. E. and Hyatt, K. D. 1987. Homing in wild sockeye salmon (*Oncorhynchus nerka*) populations as inferred from differences in parasite prevalence and allozyme allele frequencies. – *Can. J. Fish. Aquat. Sci.* 44: 1963–1971.
- Reist, J. D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. – *Can. J. Zool.* 63: 1429–1439.
- 1986. An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. – *Can. J. Zool.* 64: 1363–1368.
- Roff, D. A. 1992. The evolution of life histories. – Chapman and Hall, New York.
- Ruggerone, G. T. 1989. Coho salmon predation on juvenile sockeye salmon in the Chignik Lakes, Alaska. – Ph.D. thesis, Univ. of Washington.
- Sargent, R. C., Taylor, P. D. and Gross, M. R. 1987. Parental care and the evolution of egg size in fishes. – *Am. Nat.* 129: 32–46.
- Schluter, D., Price, T. D. and Rowe, L. 1991. Conflicting selection pressures and life history trade-offs. – *Proc. R. Soc. Lond. B* 246: 11–17.
- Schroder, S. L. 1981. The role of sexual selection in determining overall mating patterns and mate choice in chum salmon. – Ph.D. thesis, Univ. of Washington.
- Semlitsch, R. D. and Gibbons, J. W. 1990. Effects of egg size on success of larval salamanders in complex aquatic environments. – *Ecology* 71: 1789–1795.
- Shine, R. 1978. Propagule size and parental care: the “safe harbor” hypothesis. – *J. Theor. Biol.* 75: 417–424.
- Smirnov, A. I., Kamyshnaya, M. S. and Kalashnikova, Z. M. 1968. Dimensions, biochemical characteristics and caloric values of mature eggs of members of the genera *Oncorhynchus* and *Salmo*. – *J. Ichthyol.* 8: 524–530.
- Smith, C. C. and Fretwell, S. D. 1974. The optimal balance between size and number of offspring. – *Am. Nat.* 108: 499–506.
- Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press, New York.
- Svärdson, G. 1949. Natural selection and egg number in fish. – *Inst. Freshw. Res. Drottningholm Rep.* 29: 115–122.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. – *Aquaculture* 98: 185–207.
- Thorpe, J. E., Miles, M. S. and Keay, D. S. 1984. Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. – *Aquaculture* 43: 289–305.
- van den Berghe, E. P. and Gross, M. R. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). – *Can. J. Fish. Aquat. Sci.* 41: 204–206.

- and Gross, M. R. 1986. Length of breeding life of coho salmon (*Oncorhynchus kisutch*). – Can. J. Zool. 64: 1482–1486.
- and Gross, M. R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). – Evolution 43: 125–140.
- Varnavskaya, N. V., Wood, C. C., Everett, R. J., Wilmot, R. L., Varnavsky, V. S., Midanaya, V. V. and Quinn, T. P. 1994. Genetic differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*) within large lakes of Alaska, British Columbia and Kamchatka. – Can. J. Fish. Aquat. Sci. 51 (Suppl. 1): 147–157.
- West, C. J. and Larkin, P. A. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. – Can. J. Fish. Aquat. Sci. 44: 712–721.
- Wetzel, L. A. 1993. Genetic, morphometric and life history characteristics of sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lake system, Bristol Bay, Alaska. – Master's thesis, Univ. of Washington.
- Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. – Biol. Rev. 68: 35–59.
- Winemiller, K. O. and Rose, K. A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. – Can. J. Fish. Aquat. Sci. 49: 2196–2218.
- and Rose, K. A. 1993. Why do most fish produce so many tiny offspring? – Am. Nat. 142: 585–603.
- Winkler, D. W. and Wallin, K. 1987. Offspring size and number: a life history model linking effort per offspring and total effort. – Am. Nat. 129: 708–720.
- Wolman, M. G. 1954. A method of sampling coarse river-bed material. – Trans. Am. Geo. Union 35: 951–956.
- Wood, C. C. 1995. Life history variation and population structure in sockeye salmon. – In: Neilsen, J. (ed.), Evolution and the aquatic ecosystem. – Trans. Am. Fish. Soc. (in press).
- Woolington, J. D., Cross, B. A., Stratton, B. L. and Bue, B. G. 1990. Bristol Bay sockeye smolt studies for 1988. – Alaska Dept. Fish. Game, Tech. Rep. 90–16.
- Wootton, R. J. 1984. Introduction: strategies and tactics in fish reproduction. – In: Potts, G. W. and Wootton, R. J. (eds), Fish reproduction: strategies and tactics. Academic Press, New York, pp. 1–12.
- Young, M. K., Hubert, W. A. and Wesche, T. A. 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. – N. Am. J. Fish. Manag. 11: 339–346.