

MIGRATORY COSTS AND THE EVOLUTION OF EGG SIZE AND NUMBER IN INTRODUCED AND INDIGENOUS SALMON POPULATIONS

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Abstract.—The trade-off between reproductive investment and migration should be an important factor shaping the evolution of life-history traits among populations following their radiation into habitats with different migratory costs and benefits. An experimentally induced difference in migratory rigor for families of chinook salmon (*Oncorhynchus tshawytscha*), of approximately 86 km and 413 m elevation, exacted a cost to somatic energy reserves (~ 17% reduction in metabolizable mass) and ovarian investment (13.7% reduction in ovarian mass). This cost was associated with a reduction in egg size and paralleled the phenotypic pattern of divergence between two introduced New Zealand populations of common origin, presently breeding at sites with different migration distances. The genetic pattern of divergence of these same populations, detected under common rearing, was consistent with compensation for migratory costs (the population that migrates farther invested more in ovarian mass), but egg number more than egg size was associated with this evolution. These evolutionary patterns are consistent with what is known of the inheritance of these traits and with trade-offs and constraints favoring initial evolution in offspring number over offspring size. Analysis of egg number-size patterns of other Pacific salmon populations in their native range supported the hypothesis that migration strongly influences patterns of reproductive allocation, favoring a higher ratio of egg number to egg size with greater migration distance.

Key words.—Adaptation, divergence, migratory costs, rapid evolution, reproductive investment, trade-offs.

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For many animals (e.g., salmon, marine turtles, birds, and pinnipeds; Dingle 1996), migration involves extensive to-and-fro patterns from natal habitats. Such migrations are metabolically expensive, particularly if they are followed by reproduction (e.g., Blem 1980; Brett 1995; Sandberg and Moore 1996; Hendry and Berg 1999). Life-history theory suggests that other attributes of migratory animals (e.g., provisioning, body size, maturation timing, iteroparity) will co-evolve to maximize lifetime reproductive success (e.g., Leggett and Carscadden 1978; Leggett 1985; Roff 1988; Snyder and Dingle 1989; Sandberg and Moore 1996). The reproductive benefits associated with migration are well known and their role in the evolution of migratory life histories has been considered (e.g., Leggett 1985; Roff 1988; Gross et al. 1988). However, the related role of variation in migratory costs in shaping phenotypic and genetic patterns of reproductive investment among populations of migratory species has received little theoretical or empirical attention.

We contend that the energetic cost of migration (longer migration translates into reduced investment in other aspects of reproduction) can affect the evolution of allocation patterns among populations. Life-history theory generates predictions about the broad evolutionary patterns and trade-offs expected for reproductive investment (see reviews in Roff 1992; Stearns 1992). Within a limited energy budget, trade-offs are expected between egg size and number (Smith and Fretwell 1974; Lloyd 1987) and between ovarian investment and investment in other functions affecting reproductive suc-

cess (e.g., secondary sexual characters, intrasexual aggression, and parental care; for a review in fishes, see Wootton 1990). When migration predominates within a taxonomic group, differences in energetic costs caused by migratory rigor may impose energetic constraints that contribute to variation in allocation to other major “bins” such as total ovarian investment or parental care. Additional constraints, including phenotypic and genetic correlations, may determine which constituent traits within these bins (e.g., egg size vs. number; nest guarding vs. preparation) are most impacted or prone to evolve in response to these pressures. In migratory species, especially those with a high degree of philopatry, the cost of migration could drive initial divergence in reproductive allocation, with implications for longer-term patterns.

Most studies on the costs of migration have measured tissue composition and energy content within populations or among populations with different migration patterns, with assumed implications for energy reserves available for aspects of fitness such as parental care or survival (e.g., Brett 1995; Choinière and Gauthier 1995; Sandberg and Moore 1996; Hendry and Berg 1999). Some correlative studies have presented results consistent with among-population variation in ovarian investment associated with migratory rigor (e.g., Saldaña and Venables 1983; Beacham and Murray 1993; Linley 1993; Hendry and Berg 1999), but the effects of altered migration distance on reproductive investment, particularly direct costs on ovarian investment and allocation patterns, have not been experimentally examined. Likewise, empirical evidence and theory is lacking for how such costs influence evolutionary divergence in allocation strategies in new and long extant populations. Our objective in this paper was to address these issues via experimental and correlative analyses for a semelparous, anadromous fish. Three avenues of investigation were employed: (1) Experimental translocations

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of chinook salmon (*Oncorhynchus tshawytscha*) among river systems with different migratory conditions were performed to measure the phenotypic cost of migration on ovarian investment and how this cost is distributed among egg number, egg size, and tissue energy reserves. By splitting populations and families across sites, we controlled for genetic variation and measured realistic phenotypic costs imposed by altered migration patterns. (2) Representatives from the experimental populations and families were reared in a common-garden design to determine if genetic divergence in reproductive allocation has occurred between introduced populations evolving under different migratory conditions. Our design also allowed for assessment of phenotypic and genetic trade-offs that may have contributed to observed evolutionary patterns of investment in egg size and number. (3) Published data on egg number, egg size, and relative migration distance for indigenous North American populations of salmon were examined to determine whether the relationships between migration and ovarian investment revealed by our experiments contribute to long-term and large-scale patterns of reproductive allocation.

In combination our techniques examined phenotypic and genetic costs, trade-offs, and responses in manners akin to the four methods reviewed by Reznick (1985): phenotypic correlation (2 and 3 above), experimental manipulation (1), genetic correlation (2), and response to selection (2—we measure natural evolutionary divergence, rather than response to artificial selection). As indicated by Reznick (1985), the latter two genetic methods provide the most insight into how population life histories will evolve (or have evolved in our case). However, our insights would have been limited if we did not also use phenotypic correlations and experimental manipulation because these methods can prove valuable in understanding the plastic responses and costs in fitness that are imposed on genotypes subjected to new environments, a condition that likely arises whenever new populations are established.

MATERIALS AND METHODS

Experimental Organisms and Study Sites

Most anadromous Pacific salmon (genus *Oncorhynchus*) are semelparous, “capital” breeders (sensu Jönsson 1997) that cease feeding at approximately the time they re-enter fresh water on their return migrations from ocean to the breeding sites of their natal origins (Groot and Margolis 1991; Higgs et al. 1995). We consider egg number in salmonids to be largely set months (or longer) in advance of final maturation, consistent with the results of studies that manipulated feeding and growth prior to maturation (e.g., Bromage et al. 1992), and thus direct costs of migration are expected to be reflected more in egg size variation, given that eggs continue to gain mass until just prior to spawning. All species of salmon show strong philopatry, resulting in numerous localized breeding populations (Quinn and Dittman 1990). The large habitat range of each species and their philopatry combine to produce extensive intraspecific variation in phenotypic traits, including egg size and number (Groot and Margolis 1991). For example, natural spawning populations of chinook salmon range from central California to Kotzebue

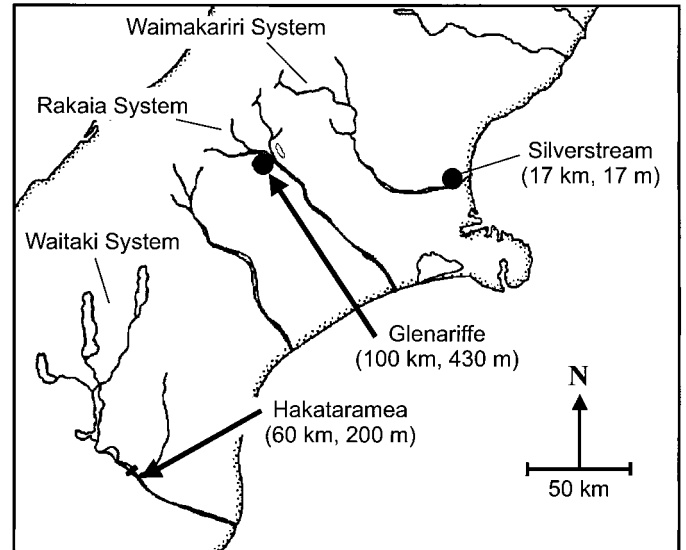


FIG. 1. The central South Island of New Zealand showing spawning sites of study populations (arrows) and experimental rearing and release sites (filled circles), with approximate distances (km) and elevations (m) to spawning grounds and release/recovery sites.

Sound in Alaska (with freshwater migration ranging from less than 1 km to 3200 km), commensurate with extensive variation in egg size (~ 120 – 470 mg) and number (~ 2000 – $17,000$ eggs; Healey and Heard 1984; Healey 1991). The life history of salmon makes them an interesting subject for examining reproductive trade-offs because there is considerable scope for phenotypic and genetic divergence and they can be studied without the confounding considerations of future reproductive investment and continued energy acquisition during the breeding season.

Most attempts to transplant anadromous Pacific salmon within and outside their natural range have failed (Withler 1982). Nonetheless, anadromous populations of chinook salmon were established in New Zealand (NZ) from releases to a single river system (the Waitaki) between 1901 and 1907 (McDowall 1994). The transplanted salmon were derived from a Sacramento River population (likely Battle Creek) that returned to fresh water in the fall of their spawning year (McDowall 1994; Quinn et al. 1996). Spawning chinook were noted in the Hakataramea River (the primary tributary of the Waitaki system) within a few years, and within 10 years in the other large, glacier-fed rivers on the east coast of the South Island, where spawning presently occurs from mid-April to early June (McDowall 1990). The NZ populations now phenotypically differ in morphometric and reproductive traits (Quinn and Bloomberg 1992; Kinnison et al. 1998a,b), but the genetic and environmental basis for variation in many traits, such as egg size and number, have not been studied in detail (but see Kinnison et al. 1998b,c).

Experimental fish in this study were derived from the Hakataramea population and from Glenariffe Stream, a spring-fed headwater tributary of the upper Rakaia River (Fig. 1). The Hakataramea joins the Waitaki River 60 km from the sea at approximately 200 m elevation, whereas the Glenariffe joins the Rakaia River at approximately twice the distance and elevation (100 km above the mouth at an altitude of

430m; Unwin 1986). Very little spawning habitat exists in the mainstems or in tributaries downstream of either of these tributaries, and most spawning takes place in the lower few kilometers within each one. To experimentally examine the costs of migration, we released and recovered Hakataramea and Glenariffe salmon from two sites: the mouth of Glenariffe Stream and the Silverstream Experimental Hatchery on the Kaiapoi River, 17 km from the coast in the Waimakariri River system at 17 m elevation above sea level (Fig. 1). The experimental sites were chosen for their permanent fish collecting facilities (to allow recapture of returning salmon) and to maximize the difference in migratory rigor between experimental groups (although the difference is modest with respect to the natural range encountered by the species).

Production of Experimental Fish

In 1994, mature fish were captured near the Hakataramea and Glenariffe mouths (Fig. 1). On 22 and 23 April we recorded female body length, body mass and reproductive trait data (ovarian mass, egg size, and egg number measured as described for experimental fish below and in Kinnison et al. 1998b). In combination, 72 experimental families of Hakataramea and Glenariffe origin were initially created using a half-sibling mating design (Kinnison et al. 1998b). Milt from each male fertilized ova from two females. Following initial rearing and culling for space limitations, we retained 29 full-sibling families nested within 15 half-sibling families for each population (two families were accidentally mixed and excluded from the design, resulting in one full-sibling family without half-sibling relatives in each population). Families were incubated, hatched, and reared at the Silverstream hatchery, and fry were fed to satiation with a commercially produced dry diet (for details, see Kinnison et al. 1998c).

Six months postfertilization (October 1994) all fry were marked with coded-wire (CW) micro-tags inserted into the cranial cartilage (Peterson et al. 1994), and assigned to one of two groups. One group, consisting of fry tagged to either family level (Glenariffe fry) or population level (Hakataramea fry), was transferred to the hatchery on Glenariffe Stream and pooled into a single raceway for common rearing. These fish (117,824 of Glenariffe origin and 23,655 of Hakataramea origin) were then released on 19 July 1995 to migrate and rear at sea (Glenariffe release). Fish in the second group (400 fry per family for both populations) were given family-specific CW tags and reared at Silverstream in circular tanks. Twelve months after fertilization (April 1995), 50 fish were randomly selected from each family, marked with individually encoded passive integrated transponder (PIT) tags (Peterson et al. 1994), transferred to Glenariffe, and pooled in a large raceway for rearing to maturity in freshwater (captive group). All remaining fish at Silverstream (13,709 fish, averaging 232 per family) were pooled and released on 31 July 1995 (Silverstream release).

In 1995 we replicated the 1994 release program using a full-sibling mating design to create 12 families of Hakataramea origin (on 1 May 1995) and 13 of Glenariffe origin (on 3 May 1995). In doing so we followed similar protocols for collecting gametes, incubating embryos, initial rearing at Silverstream, tagging, and additional rearing at the Glenariffe

hatchery. On 16 August 1996 we released 15,753 of these fish (average 630 per family) from Silverstream and on 20 August the remaining 68,547 fish (average 2742 per family) from Glenariffe Stream. Variation in release numbers among populations in 1994 and among cohorts reflected logistical constraints (rearing space was limited and permitting in 1994 required that we return a large proportion of Hakataramea fry to that river). The larger release numbers from Glenariffe reflected a decision to compensate for lower returns of fish released from that site.

Measurement of Experimental Fish

Most experimental salmon matured in 1997 and 1998. A few months prior to maturation, captive fish were sorted into two groups on the basis of obvious early morphological signs of maturation. Maturing captive fish were sorted into a separate raceway for repeated examination of maturity status during the spawning season, and the remainder was held for examination in subsequent years. CW-tagged fish returning to the Glenariffe and Silverstream weirs were checked for maturity status (indicated by the ability to express eggs from the vent). Individuals that were not fully mature were held and checked at approximately weekly intervals. Upon complete maturation, captive and release group fish were processed immediately for their reproductive trait data as described below.

Body length (tip of snout to fork of tail) and mass were recorded for each fish prior to removal of the ova. The ova, drained of ovarian fluid and consisting of loose eggs free from supportive tissues, were weighed (to 0.1 g; referred to as "ovarian mass"). A subsample of approximately 30 g of eggs was taken, weighed (to 0.01 g), and preserved with 5% buffered formalin. These subsamples were later counted and used to estimate the average number and size of eggs produced by each female (egg size = sample mass/sample count; egg number = ovarian mass/egg size). The mass of the ovaries was subtracted from body mass to estimate the somatic mass of females. The somatic mass was then used in further analyses, because it does not confound body mass with contributions from ovarian investment. A small sample of muscle tissue (~ 10–15 g without skin or subcutaneous fat) was cut from the largest muscle mass on the fish, anterior and ventral to the dorsal fin and ridge of the back (Hendry and Berg 1999). This tissue was packaged in a Whirl-pack (Nasco, Fort-Atkinson, WI) bag and frozen. Muscle samples were later weighed in the laboratory (to 0.0001 g), dried at 95°C for 24 h, and then reweighed to estimate the percent dry mass (percent muscle solids). This percentage is highly correlated with fat content in NZ salmon ($r = 0.87$, $n = 69$, $P < 0.001$; M. T. Kinnison and A. J. Hendry, unpubl. data), and dry weight is highly correlated with energy density in fish ($r = 0.97$; Hartman and Brandt 1995; see also, Hendry and Berg 1999; Unwin et al. 1999). Snouts were cut from returning fish and later dissected to recover CW tags for identification of population, family, cohort, and age.

Analysis of Experimental Data

Analyses were performed using SPSS version 7.5, except genetic correlations, which were estimated using S-Plus ver-

sion 4.5. Analysis of trade-offs can be confounded if one does not account for trait variation resulting from variation in body size (cf. Roff 1992). Because ovarian mass, egg size, and egg number all tend to increase allometrically with body size (Fleming and Gross 1990; Quinn et al. 1995; this study), trait variation was examined by analysis of covariance (ANCOVA) of \log_{10} (trait values) with \log_{10} (somatic mass) as the covariate or on size-standardized values computed from the allometric relationships estimated by such ANCOVAs. To determine the cost of migration, the following ANCOVA model was employed for each reproductive trait (Y):

$$Y_{ijkl} = \mu + W_i + O_j + A_k + L_1 + \text{interactions} + \epsilon_{ijkl}, \quad (1)$$

where μ is the overall mean, W_i is the somatic mass covariate, O_j is the population effect (fixed), A_k is the age effect (fixed), and L_1 is the site effect (fixed) for evaluating the influence of migratory costs. Age, brood year, and return year cannot all be simultaneously examined in the same ANOVA model because age = return year – brood year. Thus, of the three, age was considered in our primary analyses, although similar models with brood and return year effects were also run to determine if their contributions to trait variation were different than models with age. Only two-way interactions were examined; of these, the origin-by-age effect was excluded because only a single age 4 Hakataramea female was recovered (vs. 24 such Glenariffe females). Factor effects were tested in the absence of interaction effects when interaction effects were not significant, and the slope coefficients (common to the different factor levels) were used to standardize the trait values to the geometric mean somatic mass (3130 g) for further analyses requiring size-adjusted variates. We also performed pairwise t -tests between family mean values of fish that returned to the two release sites to further ensure that apparent migratory costs were not artifacts of different relative abundances of certain families or populations. The percent difference in the anti-logged estimated means ($\Delta\bar{x}$) or marginal means ($\Delta\bar{x}_m$; where marginal means are average values when all other factors and covariates are standardized) was computed as an indication of the effect magnitude.

Divergence between the two populations (Hakataramea and Glenariffe) and the influence of inheritance on trait variation were examined with the captive fish data in a model incorporating full-sibling and half-sibling effects. The full ANCOVA model may be written as:

$$Y_{ijklm} = \mu + W_i + O_j + A_k + S(O)_{l(j)} + D(S(O))_{m(l(j))} + \text{interactions} + \epsilon_{ijklm}, \quad (2)$$

where μ , W_i , O_j , and A_k are as defined above; $S(O)_{l(j)}$ is the effect of a given sire (random) within a population; $D(S(O))_{m(l(j))}$ is the effect of a given dam (random); and the interaction terms (two-way) are among W_i , O_j , and A_k . Slope coefficients for the somatic mass covariate (common to the different factor levels) were again used to allometrically standardize trait values to a geometric mean somatic mass of 1860 g for further analyses.

Restricted maximum likelihood (REML) was used to obtain estimates of sire and dam variance components and their associated sampling variances for estimation of narrow-sense heritability (h^2). Families without half-sibling counterparts

were excluded from these analyses. The number of families for each population represented a modest quantitative genetic design, hence variance components were estimated for captive females using two mixed ANCOVA models: one in which population was treated as a fixed factor, as shown above (without interaction terms—providing twice the sample size), and one in which each population was analyzed separately. Heritabilities were estimated using techniques described in Becker (1984) and Lynch and Walsh (1998). Genetic correlations among traits were estimated by pairwise covariance of half-sibling families (Lynch and Walsh 1998) using residuals from a reduced ANCOVA model with age and population as fixed effects and somatic mass as the covariate. The significance of the correlations were inferred from the separate P -values for the covariance of the traits across half-siblings (Lynch and Walsh 1998).

Phenotypic trade-offs were summarized by use of Pearson correlations on the size-standardized reproductive trait values within the captive group and Glenariffe site returns, although we also computed and presented correlations for the raw data. The ratio of egg number to egg size was calculated for raw and standardized values as a composite measure of the trade-off between these traits, for comparison with muscle energy density and to evaluate its utility before applying it to analyses of indigenous population patterns (see below). This variable was also suggested by preliminary analyses of the standardized gonadal traits with principal components analysis that showed a clear tendency for egg number and size to form a distinct “trade-off factor” (captive fish loadings: ovarian mass = -0.001 , egg size = 0.957 , egg number = -0.911).

Compilation and Analysis of Indigenous Population Data

To examine the generality of the patterns of migration distance, egg size, and number suggested by divergence of the NZ populations (see Results), we compiled published data on mean egg number, egg size, and relative migratory rigor experienced by Pacific salmon (*Oncorhynchus* spp.) populations. The data were selected with two primary criteria: (1) egg number, egg size, and migratory distance data could be readily obtained (some distances were estimated from maps); and (2) the data included at least four populations within a restricted and well-defined geographic area with a reasonable range of migratory distances. The latter criterion is important if one is to infer that trait variation derives from variation in freshwater migration rigor rather than other factors. Data on the five suites of populations obtained (from four studies) are likely to represent the majority of available data and to be representative of Pacific salmon in general. The population suites included Columbia River chinook salmon (Myers et al. 1998), Fraser River chinook salmon (Beacham and Murray 1993), Fraser River sockeye salmon (*O. nerka*; Linley 1993), and Fraser River and Puget Sound coho salmon (*O. kisutch*; Fleming and Gross 1990). For each suite we examined trends between migration distance and egg number, egg size, and the ratio of the two (see Appendix for details). Individual tests of correlation were made with Pearson or Spearman rank correlations as appropriate for the data. To evaluate the overall significance of distance-related trends across the five geographic systems, we performed a signs test (Zar 1984), under

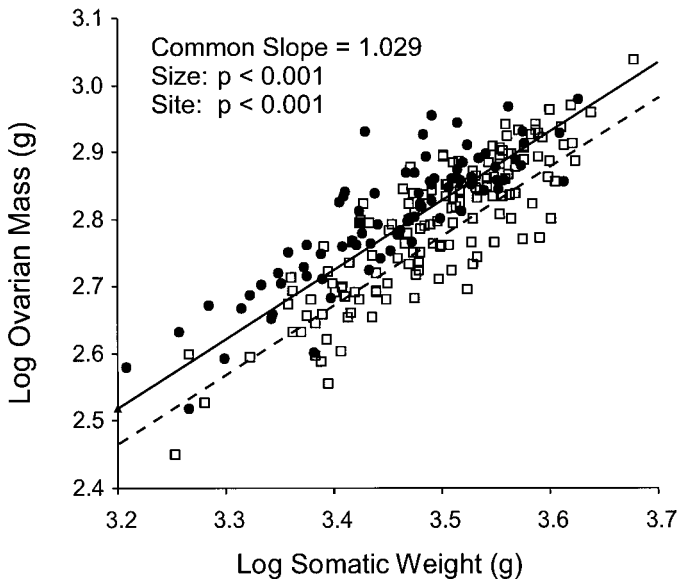


FIG. 2. Log ovarian mass relative to log somatic mass for three-year-old female chinook salmon returning to Glenariffe Stream (open squares) and the Silverstream Hatchery (filled circles). Dashed and solid lines represent the predicted ANCOVA relationships from the complete dataset.

the null hypothesis that equal proportions of positive and negative slopes would be obtained among systems assuming no significant tendency for the traits to increase or decrease with distance.

RESULTS

The Cost of Migration

ANCOVA confirmed that all traits (ovarian mass, egg size, egg number, percent muscle solids) increased with body size, both for captive fish and for fish recovered from the release groups ($P < 0.047$ for somatic mass in all ANCOVAs). ANCOVA using age or brood year and maturation year showed that each of these temporal factors had a similar pattern of influence on the study traits, confirming that these factors were related (for all three factors ovarian mass: $P \leq 0.047$, egg number: $P \geq 0.851$, egg size: $P \leq 0.084$, muscle solids: $P < 0.001$). Fish making the longer migration to Glenariffe were larger on average than their counterparts returning to Silverstream ($P < 0.001$ for somatic weight and length). However, based on analyses with somatic weight as a covariate, there were among-site effects for all traits at a given body size, including evidence of significant costs of migration on ovarian investment, egg size, and muscle energy ($P < 0.001$; Fig. 2). Salmon returning to Silverstream had larger ovarian masses ($\Delta\bar{x}_m = 13.2\%$), egg sizes ($\Delta\bar{x}_m = 18.9\%$) and percent muscle solids ($\Delta\bar{x}_m = 6.2\%$), but fewer eggs ($\Delta\bar{x}_m = 4.7\%$) at a given somatic mass than females from the same populations and families migrating to Glenariffe. The site effect on egg number ($P = 0.026$) was mostly associated with the Glenariffe population (Table 1; although no site-by-population effect was detected; $P = 0.12$).

Because egg size tends to trade off with egg number in salmonids (below; see also Jonsson and Jonsson 1999), we

sought to control for the small differences in egg number among sites to prevent bias of the estimated costs of migration (most egg number variation probably arose months before maturation; cf. Bromage et al. 1992). To do so we performed an ANCOVA on the size-adjusted egg size data, using egg number as a covariate with origin, age, and site effects. The results indicated that the longer migration to Glenariffe stream resulted in a 13.7% (by mass) reduction of egg size ($P < 0.001$) relative to fish returning to Silverstream.

Pairwise *t*-tests based on size-adjusted means for the same families at both sites (18 to 21 families, depending on trait) also indicated significant site effects for all traits ($P < 0.007$). Migration to Glenariffe decreased ovarian mass by 9.4%, egg size by 15.0%, muscle solids by 5.8%, and number-independent ovarian investment by 11.9% (egg number was 6.3% greater for Glenariffe fish). This paired analysis of family values confirmed that site effects were not due to differences in the family or population composition of returns.

Population Divergence

An interaction effect ($P = 0.006$) was detected between age and somatic mass for the percent muscle solids (energy density) of captive fish. Reduced ANCOVAs by year of return indicated that in both years muscle energy density increased with body size, but at a slightly higher rate in 1997 than in 1998 (slope = 0.093 vs. 0.067). Muscle data were size adjusted relative to the yearly slopes and ANOVA indicated that 1997 fish had more muscle solids (%) than 1998 fish ($P < 0.001$, $\Delta\bar{x}_m = 9.1\%$) at the geometric mean body size (1860 g), but no difference was detected between populations ($P = 0.910$). In a pattern countergradient to the environmental cost of migration, ovarian mass at a given somatic mass was genetically greater for the Glenariffe population (longer migration) than for Hakataramea fish ($P = 0.004$, $\Delta\bar{x}_m = 6.4\%$). Glenariffe females had more eggs ($P = 0.072$, $\Delta\bar{x}_m = 4.2\%$) but egg size did not differ under common rearing conditions ($P = 0.371$). All ovarian traits varied between years ($P < 0.001$), even after accounting for body size and population effects.

Marginal mean patterns for released salmon were consistent with trends detected between populations for the captive fish (Glenariffe > Hakataramea: ovarian mass: $\Delta\bar{x}_m = 2.3\%$, egg number: $\Delta\bar{x}_m = 3.3\%$), but tests of population effects were not significant. This lack of a significant population effect may have been due to limited power associated with small numbers of Hakataramea returns and environmental variability encountered by wild salmon, effects that were better controlled for under captive rearing.

Inheritance and Genetic Trade-offs

Population specific ANCOVA indicated significant sire effects (additive genetic variation) for the Glenariffe population (ovarian mass: $P = 0.004$; egg size: $P = 0.030$; egg number: $P = 0.041$; percent muscle solids: $P = 0.041$). There was less evidence of sire effects for the Hakataramea population (ovarian mass: $P = 0.091$, egg size: $P = 0.081$, egg number: $P = 0.780$, percent muscle solids: $P = 0.121$). Heritabilities largely followed the trends for sire effects, with higher heritabilities for Glenariffe fish than for Hakataramea fish (Table

TABLE 3. Bivariate (Pearson) correlations between muscle energy density (percent muscle solids), ovarian mass, egg number, egg size, and the ratio of egg number to egg size (a measure of their trade-off) for size-standardized (top value) and raw (bottom value) trait values. Above the diagonal are values for captive fish, below the diagonal are data for returns to Glenariffe Stream, and on the diagonal are sample sizes for a given trait (captive above, returns below). Sample size for a given correlation is the smaller sample size of the two traits.

	Muscle energy	Ovarian mass	Egg size	Egg number
Muscle energy	1009 139	-0.18** -0.11*	-0.44** -0.30**	0.30** 0.13**
Ovarian mass	0.07 -0.23*	1025 170	0.28** 0.73**	0.41** 0.78**
Egg size	0.12 -0.02	0.47** 0.52**	1007 162	-0.75** 0.16**
Egg number	-0.04 0.25*	0.45** 0.84**	-0.56** -0.002	1007 162

* $P < 0.05$, ** $P < 0.001$.

decrease with increasing muscle energy density in the captive fish. Similar trade-offs were not detected in the Glenariffe returns (Table 3).

North American Population Patterns

Our experimental results indicated that the phenotypic cost of increased freshwater migration is a decrease in egg size, whereas the evolutionary tendency, suggested by the population effect under captive conditions, is for increased investment in ovarian mass, manifested largely as an increase in egg number. The environmental and genetic effects are therefore predicted to increase the ratio of egg number to size with migration distance. Data on the five suites of salmon populations indicated a tendency for higher egg number/size trade-off values with increasing migratory rigor (Fig. 3). As expected, this trend resulted from a tendency for egg size to decrease with migration distance and for egg number to increase or remain constant with migration distance (Fig. 3). Although many of the individual relationships were not statistically significant, the appearance of the same directional trend (positive vs. negative slope) in all five cases for each type of relationship (distance vs. egg number, egg size, or their ratio) was significantly greater than expected by chance (sign test: $P = 0.03$ for each relationship type), indicating a general trend.

DISCUSSION

Investment in Introduced and Indigenous Populations

The cost of migration in salmon appears to come not only as a cost to tissue energy reserves, but also as a cost to ovarian investment, primarily in egg size. We experimentally demonstrated this cost and provided evidence of recent evolutionary compensation for it in new populations and for its role in contributing to differences among indigenous populations.

The migratory costs we documented were detected by considering similar genotypes measured under different environmental conditions (analogous to designs for studying phe-

notypic plasticity; Via et al. 1995), a situation that rarely presents itself to investigators studying migration in natural systems. However, such a design may be needed to critically evaluate the interactions of genotype and environment faced by new populations (e.g., with altered migratory routes).

Differences other than migration costs could contribute to ovarian differences between the experimental release sites, but we believe migration is the most likely explanation. Whereas Glenariffe fish were larger on average at return than Silverstream fish (Table 1), perhaps experiencing better growth at sea or stronger size dependent survival, our analyses considered investment relative to body size. Also the cost in egg size we found cannot be explained by a tendency for Glenariffe fish to produce slightly more, but smaller, eggs, perhaps associated with some growth differences; total ovarian mass was less for Glenariffe fish of a given body size, and an ANCOVA correcting egg size differences by their trade-off with egg number confirm that egg size was reduced beyond the innate trade-off between egg size and number observed in these salmon.

The pattern of ovarian trait values for wild Glenariffe and Hakataramea salmon returning to their respective rivers systems was entirely consistent with the migratory cost pattern we have demonstrated (Kinnison et al. 1998b; Fig. 4), providing further evidence that such costs act in the wild. Interestingly, wild Glenariffe fish differed about half as much in egg size and ovarian mass from wild Hakataramea River fish as did salmon experimentally released from Glenariffe and Silverstream (Kinnison et al. 1998b; Fig. 4). This pattern is consistent because the difference in migratory rigor (distance and elevation) between the Hakataramea and Glenariffe sites is about half the difference between Glenariffe and Silverstream (Fig. 1).

A substantial change in ovarian investment, manifested as a decrease in egg size, is likely to have fitness consequences and to thus play a role in the divergence of new populations. Egg size is strongly correlated with initial offspring (fry) size in salmonids (Pitman 1979; Kinnison et al. 1998c; Heath et al. 1999) and offspring size is in turn correlated with survival in salmon (Hutchings 1991; Einum and Fleming 2000a), other fishes (Ware 1975), and most organisms (Roff 1992). Survival of wild fry relative to their size has not been estimated for NZ salmon. However, examination of survival rates for 209 artificially reared fry groups released from Glenariffe Stream (between 1978 and 1990) has shown that a proportional increase (or decrease) in fry size results in more than an equivalent change in fry-to-adult survival (Unwin 1997).

Selection is thus expected to more strongly favor increased ovarian investment in Glenariffe fish relative to Hakataramea fish in a genetic pattern counter to the gradient of environmentally induced costs (i.e., countergradient variation: for review, see Conover and Schultz 1995). This was observed in the higher ovarian mass of Glenariffe salmon compared to Hakataramea salmon under experimental rearing conditions (Fig. 4). Because of the countergradient nature of the ovarian mass pattern and the potentially strong fitness consequences of variation in egg size, we attribute this divergence to local adaptation.

Without common rearing studies, we cannot directly ascertain whether "long-migration" populations, established

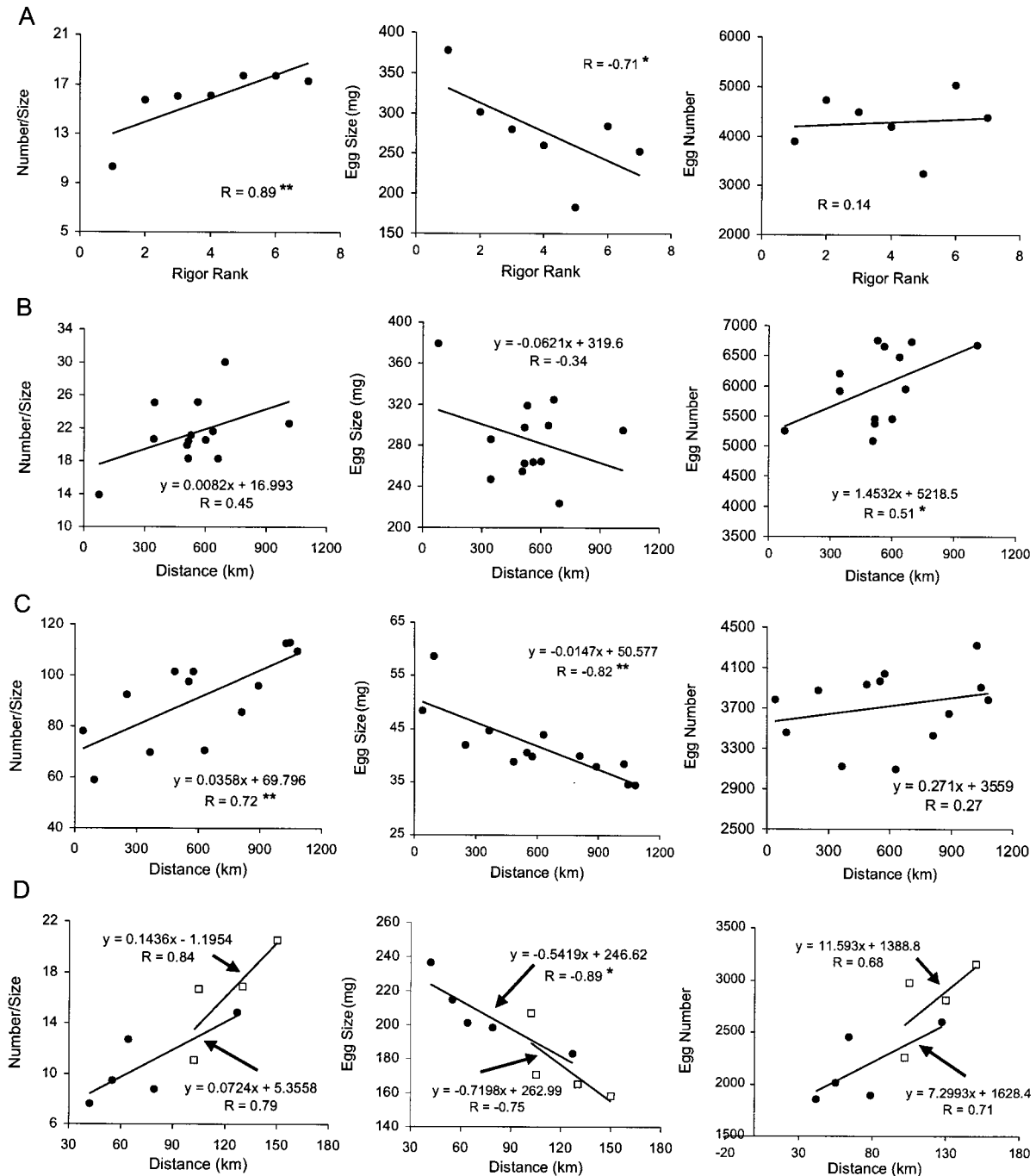


FIG. 3. Relationship between migratory rigor and reproductive traits (egg size, egg number, and their ratio) for chinook, sockeye, and coho salmon from five geographic population groupings. (A) Columbia River chinook, (B) Fraser River chinook, (C) Fraser River sockeye, (D) Fraser River (open squares) and Puget Sound (closed circles) coho salmon. Regression equations and bivariate Pearson correlations are presented except for Columbia River chinook in which only the Spearman (nonparametric) correlation is shown (see Appendix). * $P < 0.05$, ** $P < 0.01$ for one-tailed tests.

postglacially (i.e., diverging over longer periods), invest more in ovarian mass and egg size. It is clear, however, that full compensation in ovarian investment has not occurred: Two of the studies employed in our analyses indicated that phenotypic ovarian mass decreased with river distance in the wild (Beacham and Murray 1993; Linley 1993). Furthermore, examination of the trade-off between egg number and size

for five suites of populations (representing different species and geographic areas) suggested that a cost of migration persists on mean population egg size, whereas egg number tends to increase (or at least not decrease) with migration distance, consistent with our experimental results and hypotheses. Overall, the trade-off between egg number and size among populations exhibits a strong cogradient trend (Conover and

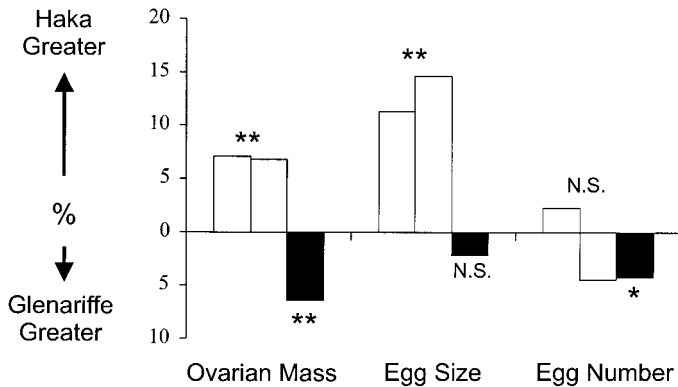


FIG. 4. Comparison of size-adjusted ovarian trait variation in wild and captive reared Hakataramea (Haka) and Glenariffe fish. Results are presented as the percent difference between populations for two years of wild fish data (open bars: 1994 and 1995 parents used to initiate this study) and the data from captive reared offspring (solid bars) from this study. Wild fish data are from Kinnison et al. (1998b) and are adjusted to a common length, except ovarian mass, which was expressed relative to weight. * $P < 0.1$, ** $P < 0.05$.

Schultz 1995) with migration distance in which the genetic and environmental trends may both favor an increased ratio of number/size. These patterns, which persist in populations potentially tens of thousands of years old, speak strongly to the generality and long-term role of migration in fashioning diversity in ovarian investment.

Factors in Egg Number and Size Allocation

Our results hint at a further interesting element in the evolutionary response to ovarian costs of migration: egg size does not appear to evolutionarily respond as much as egg number over short time frames, nor does it (or ovarian mass) appear to recover to comparable phenotypic sizes over longer time frames. Selection acting on egg and offspring size has been theorized to be the primary factor influencing the evolution of size-number strategies (Lloyd 1987) and to be the primary basis for other egg size-number trends in salmon (Fleming and Gross 1990). However, there are several viable hypotheses for the patterns we have observed, including quantitative genetic inheritance patterns, the energy-number effect and premigration provisioning, and variation in optimal sizes of ovarian masses and eggs. We now discuss our results in light of these hypotheses.

Several of our inheritance estimates (controlling for body size) were zero, extreme, or nonestimable for the Hakataramea population (perhaps associated with the modest sample size; Gjedrem 1983; Roff 1997). This was particularly true for estimates associated with egg number. For that reason our inferences regarding inheritance are based on estimates from Glenariffe fish (and the combined population data). Such inferences would be particularly appropriate if much of the evolutionary compensation for migration costs occurred in the Glenariffe population, in which selection from migration distance was likely strongest.

The generally high estimates for ovarian mass heritability in our study are consistent with our observation of a rapid evolutionary response. One mechanism favoring initial evolutionary compensation in ovarian investment via egg num-

ber, more than egg size, could be the relative inheritance of reproductive traits. If egg number had a higher genetic correlation with ovarian mass, then an evolutionary increase in ovarian mass investment would result in a greater correlated increase in egg number than egg size. Estimates of genetic correlations in the Glenariffe population appear to support this (Table 2; although statistical inference is not possible given that neither correlation was significant). However, Su et al. (1997), using a much larger quantitative genetic design (377 families, five generations, and three brood lines in *O. mykiss*), also found that egg number and size had comparable heritabilities (0.55 and 0.60, respectively) but estimated the genetic correlation between ovarian mass and egg number at approximately twice that with egg size (0.81 vs. 0.48, respectively). If such inheritance patterns are characteristic of salmonid fishes, evolution resulting in an increase in ovarian mass could result primarily in a correlated response in egg number following genetic lines of least resistance (*sensu* Schluter 1996).

Our second hypothesis for observed egg size-number patterns also concerns trait correlations and constraints. In particular it involves a correlated outcome of selection for individuals with more energy reserves at the onset of freshwater migration. Selection for more energy prior to migration, and thus for greater provisioning or growth leading up to migration, is perhaps the most likely mechanism by which migratory costs are ameliorated. Wild salmon with longer freshwater migrations, such as Yukon River chum salmon (*O. keta*) can have nearly four times the energy reserves (primarily fat content) found in salmon from coastal populations (Brett 1995). However, in salmonids there is also a tendency for increased egg number (and in some cases decreased egg size) in individuals experiencing better growth and energy conditions (see Bromage et al. 1992; Jonsson et al. 1996). For example, captive NZ chinook with higher muscle energy density at maturity tended to have more, but smaller, eggs at a given size (Table 3). Although this energy-number effect may be induced by environmental variation in feeding conditions (a plastic response), there is no reason to suspect it would not be expressed among individuals with different genetic propensities for provisioning and growth. Thus, this energy-number effect could initially constrain ovarian allocation, in favor of egg number, as a correlated physiological response to selection for individuals with greater premigration provisioning. We did not find significantly greater muscle energy for the captive Glenariffe population compared to Hakataramea fish at maturity. However, given the greater ovarian investment of Glenariffe fish, they may have possessed greater energy densities prior to maturation.

The assumptions of optimality theory (e.g., Smith and Fretwell 1974; Lloyd 1987; Einum and Fleming 2000b) would suggest that after an environmentally induced reduction in ovarian mass and egg size, a population should eventually evolve back to a phenotypically similar optimal ovarian mass and egg size, as long as the egg size/offspring fitness functions were unchanged. The failure of ovarian mass to fully recover and the observation that egg size did not evolve as much as egg number in NZ may reflect the short time scale and a nonequilibrium evolutionary state. However, patterns of egg size and number of indigenous populations tend to be

negatively correlated with migration rigor even after thousands of years, leading to the hypothesis that optimal ovarian mass and egg sizes are smaller for populations migrating farther.

One argument for reduced optimal ovarian mass with longer migration surrounds the hydrodynamics and energetics of swimming. The egg mass of female salmon commonly exceeds 20% of their body mass (Kinnison et al. 1998b; Healey 2001) and prominently affects their shape (increased cross-sectional area). Increasing ovarian investment may pose a twofold cost to migration efficiency: (1) a reduction in swimming efficiency with potential energetic and survival costs; and (2) a reduction in energy reserves available for swimming (we have shown phenotypic and genetic trade-offs between ovarian mass and muscle energy in Table 3; see also Hendry et al. 1999). Clearly, the energetic costs of migration increases greatly with distance, putting a premium on migration efficiency (see also Brett 1995; Hinch and Rand 1998). Using an estimate of 14% unmetabolizable solids at death for spawning salmon (see Hendry and Berg [1999], used similar muscle samples), the 6.0% difference in muscle solids from our migration cost experiment (contrasting Glenariffe and Silverstream returns) would translate into a difference of approximately 17% of energetically metabolizable dry mass (a substantial cost of the additional migration). Although some countergradient evolution may occur in response to costs of migration on total ovarian mass (e.g., NZ salmon), the hydrodynamic and energetic risks of mortality to females with larger ovaries may present a trade-off favoring smaller optimal ovarian masses in populations migrating farther upriver.

However, what about factors favoring a smaller optimal egg size (within a given ovarian mass)? Smaller eggs may be favored under oxygen-limited incubation conditions because smaller eggs have higher surface-to-volume ratios and potentially lower metabolic oxygen demands (Quinn et al. 1995; Hendry et al. 2001). There is little reason, however, to expect that upriver spawning grounds are innately more oxygen limited, unless low winter flows reduce subgravel circulation around the buried embryos (suggested by Healey 2001). Given that muscle energy reserves are positively correlated with the length of life on the spawning grounds (Hendry et al. 1999) and females expend energy obtaining, constructing, and defending quality nest sites, all of which can affect offspring mortality (van den Berg and Gross 1989; McPhee and Quinn 1998), longer migration might favor smaller eggs if females sacrificed nest quality. However, we are not aware of any substantial reduction of nest construction effort or duration of stream life in upriver populations. Regardless of what factors favor smaller optimum eggs in populations with longer migrations, fitness costs associated with smaller offspring may still accrue in later juvenile life stages, and increased egg number could compensate for such costs.

We have proposed adaptive constraints (e.g., genetic correlations or energy-number effect) and optimality arguments surrounding observed ovarian allocation patterns with migration distance. However, we believe it may prove very difficult to distinguish among such alternatives. Indeed it may be the synergy of multiple mechanisms, more than any one,

that make such patterns apparent over a range of time frames, species, and river systems.

Countervailing Pressures against Overinvestment

Because studies of population divergence integrate two or more evolutionary trajectories (one for each population), it is difficult to ascertain where and how rapidly evolution has occurred (Hendry and Kinnison 1999). For simplicity, the preceding discussion essentially rooted the ancestral state of NZ salmon near that of the present day Hukataramea population, with much of the divergence arising due to evolution under the more intense migratory conditions of the Glenariffe population. Our arguments would not require significant modification if the ancestral state were different, as long as one recognized the importance of countervailing selection pressures against excessive ovarian investment. For example, energy not used in ovarian development may provide significant fitness benefits via parental care; mechanical constraints (e.g., body cavity area or hydrodynamic limitations) may arise that place stabilizing effects on ovarian investment (for examples in insects and squamates, see Roff 1992); and larger eggs may suffer greater mortality in some incubation environments (Quinn et al. 1995; Peterson and Quinn 1996; Hendry et al. 2001). Thus, populations faced with shorter migrations than their ancestors may come under selection for reduction of ovarian investment.

Summary and Implications

Our study highlights several important issues in evolutionary ecology and life-history theory. Foremost, we provide experimental evidence that migration can enact a direct cost on ovarian investment. In this study, the phenotypic cost of migration was primarily reflected in decreased egg size (consistent with indigenous population patterns), whereas the suggested evolutionary compensation in ovarian investment primarily involved an increase in egg number. We present some data and theory that bear on three possible reasons for the observed pattern: (1) evolution along genetic lines of least resistance; (2) a correlated shift toward greater egg number under selection for premigratory provisioning; and (3) variation in optimal ovarian mass and egg size with migration distance. There is little reason to suspect that these mechanisms are mutually exclusive or represent the entirety of mechanisms driving ovarian allocation with migratory distance. Regardless of the exact mechanism, migratory differences among populations can result in divergence over very short time scales in a pattern consistent with trends of ovarian allocation that have arisen over geological time frames in indigenous populations. Taken together, these results provide a case study demonstrating the potentially strong role migration may play as both an element and determinant of the evolution of reproductive investment.

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APPENDIX

Notes on data used in examining migration rigor and reproductive trait allocation of North American salmon populations (Fig. 3).

Columbia River (USA) chinook.—Data were obtained from a status review of chinook salmon from Washington, Idaho, Oregon, and California (Myers et al. 1998) and consisted of average egg number and egg weight for seven populations (for which egg weights were directly measured). Populations were a priori ranked for migratory rigor, primarily on the basis of tributary distance from the Columbia River mouth. Data on both spring and fall returning populations were available for the Kalama River, and the spring-run fish were ranked for higher migratory rigor than the fall-run fish, due to their longer freshwater phase prior to spawning. Rank correlations are presented because exact distances to spawning grounds were unknown and because there is no clear conversion between migration distance and duration. Populations (season of freshwater entry): Cowlitz (fall), Kalama (fall), Kalama (spring), Klickitat (spring), Warm Springs (spring), Wells (summer), Methow (spring).

Fraser River (Canada) chinook.—Data (adjusted to 730 mm post-orbital to hypural length) were obtained from Appendix I of Beacham and Murray (1993). Egg sizes are mean water-hardened weights. Migration distances were estimated using a map-wheel on an International Pacific Salmon Fisheries Commission map (1:100000 scale) and map landmarks with published distances from the ocean. Populations: Bowron, Cottonwood, Chilko, Quesnel, North Thompson, Clearwater, Finn, Raft, Eagle, Salmon, Bonaparte, Chilliwack, Upper Cariboo, and Coldwater.

Fraser River (Canada) sockeye.—Data were available for 13 river spawning populations of sockeye salmon from the Fraser River system (Linley 1993). Egg number and size (milligrams dried weight), standardized for body length (approximately 543 mm from tip of snout to base of caudal peduncle), were obtained along with distances to spawning grounds. Populations: Early Stuart, Late Stuart, Nadina, Stellako, Adams, Horsefly, Shuswap, Seymour, Birkenhead, Chilko, Gates, Pitt, and Weaver.

Fraser River (Canada) and Puget Sound (WA, USA) coho.—Data on coho salmon were estimated from tables in Fleming and Gross (1990) for four Fraser River populations and five Puget Sound populations, whose migrations varied from 102 km to 150 km and from 42 km to 127 km, respectively. These were the only geographical sets in Fleming and Gross (1990) with four or more populations and migrations varying by more than 20 km. Of the Green River samples, only data for fish released and recovered at the Green River site were analyzed. Average egg number and egg size (non-water-hardened weights) were standardized to body lengths (post-orbital-hypural) of 465 mm (Puget Sound) and 488 mm (Fraser River). Puget Sound populations: Deer Creek Junior, Green, Issaquah, Skagit, and Skykomish. Fraser River populations: Chilliwack, Post Creek, Pye Creek, and Siddle Creek.