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Reprinted from the
Alaska Fishery Research Bulletin
Vol. 7, Summer 2000

The Alaska Fishery Research Bulletin can found on the World Wide Web
at URL: http://www.state.ak.us/adfg/geninfo/pubs/afrb/afrbhome.htm .

Alaska Fishery Research Bulletin 7:44–50. 2000.

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ABSTRACT: We studied genetic variation of fitness traits in a population of salmon that is not captive but spawns naturally and grows to maturity in nature. Additive genetic variation contributed significantly to variation of fecundity, a trait closely related to fitness, but not to variation of egg size (another trait closely related to fitness) in families drawn from an anadromous population of salmon and measured after growing to maturity in the wild. Greater fecundity-at-length in families drawn from the early-spawning component of the population suggests that variation of fecundity is itself adaptive. The families were generated by hierarchical mating of 60 male pink salmon to 120 females randomly chosen from the odd-year population at Auke Creek, Juneau, Alaska, 2 females to each male. Half were from the early (August-spawning) component and half from the late (September-spawning) component. The families were incubated separately, tagged with coded microwires, released during emigration of naturally-spawned fry (~1,000 unfed fry per family), and recovered at maturity when they returned to Auke Creek after 16 months at liberty (119 of the 120 families had surviving female members). Body size (length), egg number, and egg size (weight) were measured in 2 females sampled at random from those members having intact ovaries (i.e., before ovulation and retaining all eggs) in each returning full-sib family. Heritability (estimated from the paternal component of variation) of number of eggs was 0.8 (standard error, SE = 0.3). The estimate of genetic correlation of body length and egg number was imprecise (0.4, SE = 0.5). Mean egg number (adjusted for body size) was greater in families from the early component of the population than in families from the late component (1,501 vs. 1,351, $P < 0.01$). Egg size did not differ between components. Maternal effects contributed significantly to variation of egg size, suggesting the importance of special maternal environments (e.g., yolk accumulation) or nonadditive genetic effects. Our observations suggest that variations of fitness-related traits can be maintained from generation to generation in fluctuating environments by genetic variation and are important to the adaptability and persistence of salmon populations.

INTRODUCTION

Maintenance of genetic variation in salmon populations has often been invoked as a necessary condition for the conservation and persistence of populations, and the likely presence of genetic variation of fitness traits is the basis for concern about conservation practices. One example concerns the widespread declines of body size in Pacific salmon stocks in recent decades (e.g., Ishida et al. 1993), which some have hypothesized to have been caused in part by artificially selective harvest practices (Ricker 1981; McAllister and Peterman 1992). Correlated losses of fecundity and egg size have been proposed as likely mechanisms of loss of fitness in stocks whose average size has decreased (Helle and Hoffman 1995; Bigler et al. 1996). A different view is that genetic variation might be exploited through artificial selection of growth and related traits in sea-ranching culture (e.g., Gjedrem 1986). Such artificial selection is generally avoided in Pacific salmon culture out of concern for unintended detrimental effects of selection (e.g., ADF&G 1985).

Direct estimates of genetic parameters in populations of salmon growing in nature are rare but are required by these applications of genetic theory to salmon management and conservation, that is, by these pre-

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Acknowledgments: This research was supported by the Alaska Sea Grant College Program, cooperatively sponsored by NOAA, Office of Sea Grant and Extramural Programs, U.S. Department of Commerce under grant number NA81-AA-D-00009, project number R/02-11, and the University of Alaska with funds appropriated by the state. The U.S. NOAA Fisheries Auke Bay Laboratory, the Alaska Department of Fish and Game, and the Territorial Sportsmen, Inc., cooperated with the University of Alaska in our use of the Auke Creek weir and hatchery. The Alaska Department of Fish and Game Tag Laboratory decoded tags. We especially thank F. P. Thrower, S. Lane, M. James, M. Thomason, S. Shirley, K. M. Iverson, J. Joyce, and J. James for assistance.

dictions that artificial selection can change body size in salmon stocks and simultaneously can cause a correlated change of fecundity. Genetic parameter estimates from captive populations may not indicate typical values in populations growing at sea. For instance, because these populations complete their lives at sea in an uncontrolled environment, ranging over thousands of kilometers of ocean, environmental variation may contribute more to phenotype variation than it would in controlled laboratory or farm environments, and genetic contributions to variation may be relatively reduced. Direct estimates of genetic parameters in anadromous populations are difficult to obtain because, even though large arrays of families of embryos can be readily generated by external fertilization and artificial incubation, families of adults are difficult to observe. Identifying marks or tags are not easily applied to large arrays of families of larval salmon, and survival of cohorts of released fish in the sea is low and variable, often 1% or less. Both of these factors tend to reduce the statistical power of experiments. Most studies of populations growing in nature have been limited to embryonic and larval stages (McIntyre and Blanc 1972; McIntyre and Amend 1978; Smoker 1986; Beacham and Murray 1988a, 1988b). A few studies have demonstrated between-family variation of survival at sea of anadromous salmonids (McIntyre et al. 1988; Jonasson et al. 1997) including families of pink salmon *Oncorhynchus gorbuscha* studied here (Geiger et al. 1997). Similarly there are few genetic studies of body size of adult anadromous salmon (McIntyre et al. 1988; Hankin et al. 1993; Smoker et al.1994). Studies of size-related traits such as fecundity and egg size in anadromous salmonids have been lacking.

By means of a hierarchical mating design we studied genetic variation of fitness traits in a population of salmon that is not captive but spawns naturally and grows to maturity in nature. We estimated heritability of fecundity and egg size, and estimated the genetic correlation of those traits with each other and with body size by analyzing variation of these traits in families drawn from a population of odd-year spawning pink salmon at Auke Creek, Juneau, Alaska. Our analysis of body size (Smoker et al. 1994) found: late-returning (September) salmon of both genders were longer and heavier than early-returning (August) salmon; a significant paternal effect (indicative of additive genetic variation) contributed to body-size variation of males; and both phenotypic and additive genetic variation of body size were greater among males than among females. Our analysis of return timing demonstrated that genetic variation is an important basis for the phenotypic variation of that component of fitness (Smoker et al. 1998). Here we report our analysis of fecundity and egg size as they relate to timing and body size.

METHODS

We used a hierarchical mating design to generate 120 full-sib (60 half-sib) families of pink salmon at Auke Creek, Alaska. Because the populations of pink salmon in Auke Creek return to the stream in early (August) and late (September) subpopulations, we generated the families in 2 corresponding groups. We mated 30 males randomly chosen from early-returning males to 60 females randomly chosen from early-returning females, and we mated 30 males randomly chosen from late-returning males with 60 females randomly chosen from late-returning females. Each male was mated to 2 females, each female to only one male. Two equal portions of each family of embryos were incubated in replicate cells randomly assigned to an array of incubators. At completion of embryonic development and before first feeding, a sample of 1,000 fry from each family (approximately 0.25-g body size) were tagged with coded microwires. The families were released to sea immediately after being tagged in early spring. Surviving adults were recovered at the mouth of the stream 16 months later during late summer of the next year. Our experimental design, and methods of fish culture, tagging larvae, recovering adults, and analysis are also reported in Smoker et al. (1994), Geiger et al. (1997), and Smoker et al. (1998).

Nearly all (119) of the families had 2 or more surviving female members. In addition to body size and date of return, we observed, in 2 randomly chosen females in each family, fecundity (counts of individual eggs in both ovaries before ovulation) and mean egg size (wet weights, to the nearest 0.001 gram, of a sample of >20 eggs not exposed to water).

We tested hypotheses about genetic effects and estimated genetic parameters for the entire population, including in our statistical model the fixed effect of date of spawning to account for variation due to the 3-week separation between early and late components. The parameters included heritabilities of traits and genetic correlations between them. Because late-returning pink salmon at Auke Creek on average have been at sea and have grown for 5 weeks longer than early-returning salmon, explaining at least in part why they are larger (Smoker et al. 1994), we expected them to be more fecund. We expected greater fecundity in these older, larger fish because body size is well known in Pacific salmon to correlate positively with both fecundity and egg size. Therefore, we tested hypotheses

Table 1. Analysis of variance of fecundity (egg counts) in families of pink salmon drawn from the odd-year population at Auke Creek, Alaska, released as fry and observed as returning adults. Mean square (MS) was based on type III sum of squares. Denominator of approximate F test and probability associated with the ratio are given.

Source	df	Mean Square	F Denominator	Pr > F
Date of spawning	1	233,815	0.8335*MS(Sire(Date)) + 0.0186*MS(Dam(Sire*Date)) + 0.1479*MS(Error) =82,882 df = 69.36	0.0975
Sire (Date)	57	91,683	0.9685*MS(Dam(Sire*Date)) + 0.0315*MS(Error) = 41,449 df = 50.61	0.0028
Dam (Sire*Date)	47	41,233	MS(Error)	0.7258
Error	152	48,101		

about differences of fecundity or egg size between early and late components by analyzing a model including body length as a covariate.

We used a hierarchical or nested statistical model to analyze variation in fecundity and egg size[1]

$$Y_{ijkl} = \mu + P_i + S_{j(i)} + D_{k(ji)}[+L_{ijkl}] + e_{ijkl} ,$$

where Y is the response variable (fecundity or egg size) measured in a female member of a family, μ is the population mean fecundity or egg size, P_i is the fixed effect of the ith date of spawning (by the parents of the observed fish), $S_{j(i)}$ is the random effect of the jth sire within the ith date of spawning, $D_{k(ji)}$ is the random effect of the kth dam mated to the jth sire, and e_{ijkl} is residual error associated with the lth offspring in each family. The term $[+ L_{ijkl}]$ represented body length of female offspring when appropriate. We used the GLM procedure in SAS (Version 6, 1989) to compute all analyses of variance.

We tested significance of effects by approximate F tests (Searle 1971, ch. 6; generated by the SAS GLM option *Test* in the *Random* statement). We estimated components of variance of, heritabilities of, and the genetic, environmental, and phenotypic correlations between fecundity, egg size, and body size, and standard errors of those parameters, from the intraclass correlations according to formulas given in Becker (1984).

We estimated heritability from intraclass correlations as the ratio of additive genetic variance to total phenotypic variance, $h^2 = V_A / V_P$, where, in the absence of nonadditive genetic effects, $V_A = 4\ \sigma_s^2$ or 4 times the sire component of variance and $V_P = \sigma_s^2 + \sigma_d^2 + \sigma_e^2$ or the sum of the sire, dam, and error components of variance. Formulas for standard errors are given in Becker (1984, pp. 53–63). Formulas for estimating genetic correlation (r_G) and its standard error are also from Becker (1984, p. 111ff).

RESULTS

The effect of sires nested within spawning date contributed significantly to variation of fecundity but not to variation of egg size (Tables 1 and 2). The effect of dams contributed significantly to variation of egg size (Tables 1 and 2). The intraclass correlation estimate of heritability of fecundity, 0.84 (SE = 0.32), was higher than that of body size, 0.27 (SE = 0.21), but neither is precise. The estimate of genetic correlation between fecundity and body size, 0.35 (SE = 0.45), was also imprecise.

Offspring of early-spawned (17 August) pink salmon were more fecund, 1,501 eggs (SE = 29.9) adjusted for body size of the same individual female, than late-spawned (20 September) salmon, 1,351 eggs (SE = 29.1, $P < 0.0009$, test of equality of least squares means using mean square due to sires within date as the error term; Table 3). Offspring of early-spawned salmon had eggs that were the same size, 0.155g (SE = 0.0024), as those of late-spawned salmon, 0.158g (SE = 0.0023, $P < 0.3620$; Table 4).

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[1] We reported analysis of body size data in Smoker et al. 1994; here we report analysis of size in the subset of records of females that included measures of all 3 variables size, fecundity, and egg size.

Table 2. Analysis of variance of egg size in families of pink salmon drawn from the odd-year population at Auke Creek, Alaska, released as fry and observed as returning adults. Mean square (MS) was based on type III sum of squares. Denominator of approximate *F* test and probability associated with the ratio are given.

Source	df	Mean Square	*F* Denominator	Pr > *F*
Date of spawning	1	0.00059974	0.8299*MS(Sire(Date)) + 0.0227*MS(Dam(Sire, Date)) + 0.1475*MS(Error) = 0.0004019349 df = 69.03	0.2260
Sire (Date)	57	0.00043938	0.9555*MS(Dam(Sire(Date))) + 0.0445*MS(Error) = 0.0004353822 df = 44.66	0.4917
Dam (Sire*Date)	43	0.00044709	MS(Error)	0.0001
Error	133	0.00018423		

DISCUSSION

We expected, from studies of other salmonids, to find evidence of additive genetic variation of both fecundity and egg size and a negative genetic correlation between fecundity and egg size (e.g., Huang and Gall 1990). One explanation of our contrary result follows from the likelihood that nutrition, which determines egg size during the final weeks of maturation after egg number is determined, is probably highly variable among females foraging at sea compared to the nutrition of fish raised in captivity. The result of variable nutrition might be relatively high maternal environmental variation of egg size in wild salmon and its predominance among components of their egg-size variation. Such high maternal environmental variation might mask genetic variation of egg size and its genetic correlation with fecundity. Under this scenario of high maternal environmental variation of egg size, detection of additive genetic variation of (sire effect on) egg size would be less likely than it would if the salmon matured in a homogenous nutritional environ-

Table 3. Analysis of covariance of fecundity (egg counts) and length in families of pink salmon drawn from the odd-year population at Auke Creek, Alaska, released as fry and observed as returning adults. Mean square (MS) was based on type III sum of squares. Denominator of approximate *F* test and probability associated with the ratio are given.

Source	df	Mean Square	*F* Denominator	Pr > *F*
Date of spawning	1	857,830	0.7476*MS(Sire(Date)) + 0.0205*MS(Dam(Sire*Date)) + 0.2319*MS(Error) = 58,045 df = 77.35	0.0002
Sire (Date)	57	66,290	0.9551*MS(Dam(Sire*Date)) + 0.0449*MS(Error) = 35,524 df = 46.85	0.0147
Dam (Sire*Date)	43	35,622	MS(Error) = 33,443 df =132	0.3832
Length	1	147,729	MS(Error) = 33,443 df =132	0.0001
Error	132	33,443		

Table 4. Analysis of covariance of egg size and length in families of pink salmon drawn from the odd-year population at Auke Creek, Alaska, released as fry and observed as returning adults. Mean square (MS) was based on type III sum of squares. Denominator of approximate F test and probability associated with the ratio are given.

Source	df	Mean Square	F Denominator	Pr > F
Date of spawning	1	0.00037566	0.7476*MS(Sire(Date)) + 0.0205*MS(Dam(Sire*Date)) + 0.2319*MS(Error) = 0.0003696397 df =76.49	0.3166
Sire (Date)	57	0.00042490	0.9551*MS(Dam(Sire*Date)) + 0.0449*MS(Error) = 0.0004355006 df = 44.68	0.5392
Dam (Sire*Date)	43	0.00044731	MS(Error) = 0.00018459 df = 132	0.0001
Length	1	0.00013714	MS(Error) = 0.00018459 df = 132	0.3903
Error	132	0.00018459		

ment as they would in captivity. In support of this explanation we observed significant maternal effects on egg size, although they may also be explained by interactive genetic effects not detectable with our experiment design.

The estimate of heritability of fecundity is surprisingly high considering that the fish grew most of their lives in an uncontrolled oceanic environment in which environmental variability was probably high and considering that fecundity is closely related to fitness (Mousseau and Roff 1987). This, with the evidence for a moderate to high heritability of body size (Smoker et al. 1994) and our result that genetic correlation of body size and fecundity may also be high, suggests that artificial selection on body size, whether by broodstock management or by fishing gear, would be effective in changing both body size and fecundity. This prediction should serve as a caution to salmon resource managers and encourage them to avoid selective practices in their efforts to conserve natural diversity in salmon populations.

Two sources of evidence suggest that selection might not be effective, however. One is that records of body size of parents and their offspring in our experiment were not correlated with one another (Smoker et al. 1994; measurements of fecundity in the parents could not be made, and we are not able to make a similar analysis for fecundity). The lack of a significant parent–offspring regression of body size was probably a consequence of the parents having grown at sea during different years than those in which the offspring grew and of the different environmental conditions, physical and biological, that occurred during those sets of years. Geiger et al. (1997) observed evidence of different survival at sea of different families, supporting the hypothesis that different genotypes grow and survive with variable success in the different environments experienced by populations of salmon from year to year.

Additional evidence that selection on body size resulting in correlated responses of size and fecundity would not be effective is that body size has changed markedly in many populations of Pacific salmon in the absence of artificial selection, probably as a consequence of climate change. We say this despite the argument (e.g., Ricker 1981) that gear selectivity may have artificially selected for slower growth. Too many unselected populations have also experienced declining body size. At Auke Creek, for instance, mean length of pink salmon declined from over 520 mm in the 1970s to less than 440 mm in the 1990s (data on file, U.S. National Marine Fisheries Service Auke Bay Laboratory, Juneau, Alaska). Auke Creek pink salmon have not been exposed to any plausible artificial selection because harvest of Auke Creek pink salmon, when it occurs, is by purse seine, a nonselective gear. This suggests that environmental variation from generation to generation has been the important contributor to size variation over time in salmon populations. Even though corresponding historical records of fecundity from salmon populations are not available, it is reasonable to infer that fecundity also declined. During the period of declining body size, however, Pacific salmon populations have not become less reproductively successful over most of the species' ranges. Abundances, indicated by population censuses and by catch records, generally have increased markedly during the same years (e.g., Byerly et al. 1999). Whether or not fecundity has declined along with body size, reproductive fitness has not declined.

The difference of fecundity between early- and late-spawned pink salmon may represent genetically-based adaptive variation between subpopulations of Auke Creek pink salmon. Spawning efficiency (the proportion of potential eggs spawned by females, measured inversely by retention of eggs in samples of females at death) is lower in early-spawning females at Auke Creek than in late-spawning females (Fukushima and Smoker 1997). Survival during embryogenesis is probably less for August-spawned eggs than for September-spawned eggs in Auke Creek (unpublished data, AJG). Periods of elevated temperature (above 15°C) which may be detrimental to fertility or lethal to pink salmon embryos, are frequent in August but not in September in Auke Creek (Fukushima and Smoker 1997; Wing and Pella 1998). Episodes of low streamflow, which can inhibit successful spawning, are more frequent in August than in September (Fukushima and Smoker 1997; Wing and Pella 1998). A larger fecundity in August-spawning salmon would therefore tend to compensate for their reduced fitness in the August-spawning environment relative to the September-spawning environment. Adaptability of fecundity historically may have allowed the achievement of greater fecundity by August-spawning salmon, which may have permitted that component of Auke Creek pink salmon to respond to selection in favor of earlier spawning (Smoker et al. 1998; the agent of selection on spawning time may have been redd superposition by later-spawning salmon). That response to selection for earlier spawning in a component of Auke Creek pink salmon may have lead to the protracted period of spawning, including both early and late components, that is observed not only in the odd-year population but also in the even-year population. Our view is that maintenance of significant genetic variability of body size and fecundity has been important to the long-term adaptability and persistence of Auke Creek pink salmon, and by extension to the persistence of other salmon populations. Our view is that the presence of a diversity of genotypes enables the population to persist in a fluctuating environment and that conservation of that diversity should be a primary goal of resource managers.

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