Effective Size of Fluctuating Salmon Populations

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ABSTRACT

Pacific salmon are semelparous but have overlapping year classes, which presents special challenges for the application of standard population genetics theory to these species. This article examines the relationship between the effective number of breeders per year (N_b) and single-generation and multigeneration effective population size (N_e) in salmon populations that fluctuate in size. A simple analytical model is developed that allows calculation of N_e on the basis of the number of spawners in individual years and their reproductive contribution (productivity) to the next generation. Application of the model to a 36-year time series of data for a threatened population of Snake River chinook salmon suggests that variation in population dynamic processes across years reduced the multigeneration N_e by ∼40–60%, and reductions may have been substantially greater within some generations. These reductions are comparable in magnitude to, and in addition to, reductions in N_b within a year due to unequal sex ratio and nonrandom variation in reproductive success. Computer simulations suggest that the effects of variable population dynamics on N_e observed in this dataset are not unexpected for species with a salmon life history, as random variation in productivity can lead to similar results.

IT has long been known that the genetic behavior of a population depends not on the number of individuals it contains (N) but rather on its effective population size (N_e; Wright 1931 and later). In an "ideal" population (random mating, binomial variance in reproductive success among individuals) N_e is equal to N, but in real populations N_e will generally be $<N$ because of unequal sex ratio (resulting in unequal reproductive success of the average male compared to the average female) and larger than binomial variance in reproductive success among individuals of the same sex. Wright (1938) also showed long ago that if population size varies over time, a population behaves genetically as if it had a constant N_e approximately equal to the harmonic mean of the single-generation N_e values.

This theory of effective population size was originally developed to model genetic processes in organisms with discrete generations. Since most species do not fit the assumptions of the discrete generation model, various authors have evaluated robustness of this theory for species with more complex life histories. In general, these studies have found that discrete-generation models for effective population size also provide a good description of processes of genetic change in organisms with overlapping generations, provided that demographic parameters of the population are stable (Felsenstein 1971; Hill 1972).

Demographic parameters are not stable, however, in populations that change in size. Fluctuating population size is an important consideration for evolutionary biologists because variability in N is one of the most important factors that determine extinction risk. Furthermore, because the rate and/or magnitude of most genetic processes are inversely related to N_e, the genetic effects of small population size are nonlinear; for example, although it may make little difference in the short term whether a population has N_e of 10^3 or 10^4, it can make a great deal of difference whether N_e is 10 or 10^2. It is important, therefore, to consider in more rigorous detail the concept of effective size for populations with complex life histories that are (or may become) relatively small and that also fluctuate in size.

Here I consider this topic for Pacific salmon (*Oncorhynchus* spp.). These species have an unusual life history that combines features of both discrete and overlapping generation models (Figure 1): Adults invariably die after spawning (so there is no overlap in the breeding population from one year to the next—a feature shared with discrete generation models), but most species and populations produce offspring that mature at a variety of ages (which means that breeding populations in different years are not connected by a first-order Markov process—a feature shared with overlapping generation models). Waples (1990a,b) modeled genetic changes over time in Pacific salmon populations and examined the relationship between the effective number of breeders per year (N_b) and the effective size per generation (N_e). He showed that when population size is constant, N_e per generation is simply the sum of the yearly N_b values over a period of a generation: $N_e = gN_b$, where g is the generation length (average age at spawning).

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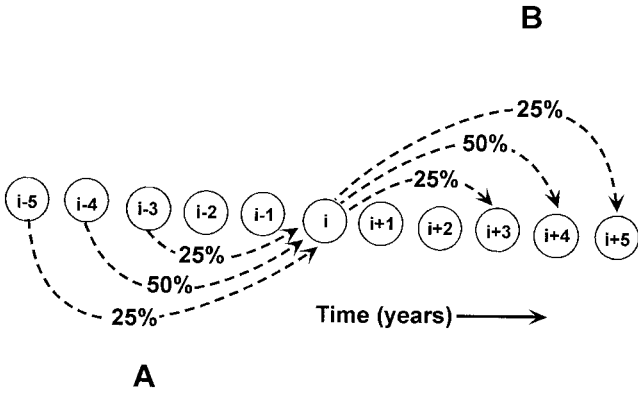E-mail: robin.waples@noaa.gov

B

A

FIGURE 1.—Schematic diagram showing Pacific salmon life history (modified from WAPLES 1990a). Each circle represents a spawning population in 1 year. In this example, progeny of fish spawning in year i mature at ages $k = 3$, 4, and 5 with probabilities $A_k = 0.25$, 0.5, and 0.25, respectively (maturity schedule B). In populations of constant size the average age of spawners in any year will also follow the same proportions (maturity schedule A), but this will not be true in populations that fluctuate in size. The simulation model used in this article followed maturity schedule B.

WAPLES (1990b) also performed a limited number of simulations with variable population size and concluded that N_e for Pacific salmon is a function of the harmonic mean of the N_b values in individual years:

$$N_e \approx g\tilde{N}_b. \tag{1}$$

This result is analogous to WRIGHT'S (1938) discrete-generation formula showing that multigeneration N_e is approximately the harmonic mean of the single-generation values.

It turns out, however, that Equation 1 is valid only for a particular demographic assumption implicit in Waples' model—specifically, that each year's spawning population contributes equally to the next generation regardless of the number of spawners. If instead we assume that each year's spawning population contributes to the next generation in direct proportion to the number of spawners, then (as is shown below) the relationship

$$N_e \approx \sum N_{bi} = g\overline{N}_b \tag{2}$$

holds, where N_{bi} is the effective number of breeders in year i, and $\overline{N}_b$ is the arithmetic mean of the N_{bi}. Equation 2 describes a linear relationship in which N_e per generation is an additive function of the yearly N_b values within a generation.

The harmonic mean is smaller than the arithmetic mean for any variable series, so N_e computed using Equation 1 will be less than the value obtained using Equation 2. The difference can be substantial, as illustrated by a simple time series of abundance data for a salmon population with mean generation length of 4 years: $N_1 = 100$; $N_2 = 100$; $N_3 = 10$; $N_4 = 100$. Assume for the

moment that $N_{bi} = N_i$ each year. The arithmetic mean for this data series is $\overline{N}_b = 77.5$ whereas the harmonic mean is only $\tilde{N}_b = 30.8$, leading to Equation 1, $N_e = g\tilde{N}_b = 4 \times 30.8 = 123$; and Equation 2, $N_e = g\overline{N}_b = 4 \times 77.5 = 310$. In this example, the computed N_e per generation differs by a factor of almost 3 depending on the demographic assumption used.

It is clear from this simple example that population dynamic processes can profoundly influence effective population size in species with Pacific salmon life histories. In particular, whereas N_b is a function only of demographic processes occurring within a single cohort, N_e per generation is also a function of the relative reproductive success (productivity) of different cohorts within a generation. In this article I examine this issue in more depth using both analytical and simulation approaches, with the objective being to determine which of these ways of computing N_e is more realistic for Pacific salmon.

METHODS

Definition of terms:

N_i is the number of spawners in year i

N_T is the total number of spawners in a generation ($= \Sigma N_i$ over a generation)

g is the generation length (average age at spawning)

N_{bi} is the effective number of breeders in year i

N_e is the effective population size in a generation

$N_{e(k)}$ is the effective population size over k generations (harmonic mean of single-generation N_e values)

R_i is the recruits = spawners in the next generation produced by spawners in year i

R_T is the total spawners in the next generation produced by all the spawners in the current generation ($= \Sigma R_i$ over a generation)

λ_i is the productivity of spawners in year i (R_i/N_i)

σ is the standard deviation of λ

X_i is the proportional contribution of spawners in year i to the next generation (R_i/R_T).

Analytical model: The genetic consequences of the contrasting demographic assumptions implicit in Equations 1 and 2 can be evaluated quantitatively by use of a model developed by RYMAN and LAIKRE (1991). Although their article focused on amplification of part of a population's gene pool through a captive breeding program, Ryman and Laikre also provided a more general formula for evaluating the genetic effects of differential reproductive success by different segments of a population,

$$N_e = 1/\sum (X_i^2/N_{bi}), \tag{3}$$

where N_e is the effective size of the population over a full generation, N_{bi} is the effective size of segment i, X_i is the proportional contribution of breeders in segment i to the next generation, and the summation is over all

years in a generation. Application of this model to a series of g years of data evaluated under the two demographic scenarios leads to the following results:

Scenario 1: Spawners in each year contribute an equal number of progeny to the next generation, regardless of N_{bi} or N_i. (All $X_i = 1/g$.)

$$N_e = \frac{1}{\sum[(1/g)^2/N_{bi}]} = \frac{1}{(1/g^2)\sum(1/N_{bi})}$$

$$= g\frac{1}{(1/g)\sum(1/N_{bi})} = g\tilde{N}_b.$$

Scenario 2: Spawners in each year contribute to the next generation in proportion to N_{bi}. ($X_i = N_{bi}/N_T$.)

$$N_e = \frac{1}{\sum[(N_{bi}/N_T)^2/N_{bi}]} = \frac{1}{\sum N_{bi}/(N_T)^2}$$

$$= \frac{N_T^2}{\sum N_{bi}} = N_T = g\overline{N}_b.$$

This demonstrates that, if population dynamics conform to Scenario 1, the harmonic mean method (Equation 1) is appropriate for estimating N_e, whereas the additive method (Equation 2) is appropriate if population dynamics conform to Scenario 2.

Equation 3 was used with empirical data for salmon to compute N_e for comparison with predictions based on Equations 1 and 2.

Empirical data: Marsh Creek, in central Idaho, is a tributary of the Middle Fork Salmon River, which flows into the Salmon River and thence the Snake River. All native chinook salmon populations in the Snake River were listed as threatened under the U.S. Endangered Species Act in 1992 (Federal Register 57(78):14653–14662, 22 April 1992). A time series (1958–1993) of abundance data for Marsh Creek spring chinook salmon (BEAMSDERFER *et al.* 1998 and unpublished data) was used to provide an example for analytical evaluation of single- and multigeneration N_e. The total number of spawning adults was estimated each year on the basis of expansions from sampling a portion of the population. Estimates of the age composition of the spawners each year, on the basis of lengths measured on a sample of returning adults, allowed a partitioning of the spawners into individual cohorts and, therefore, a reconstruction of the proportional contribution of each year to the next generation (X_i from Equation 3).

In the Marsh Creek population, the mean frequencies of spawners ages 3, 4, and 5 over the time series of data were 0.04, 0.25, and 0.71, respectively (BEAMSDERFER *et al.* 1998), leading to $g \approx 4.7$ years. The 3-year-old spawners are all males (called "jacks"), and the spawner-recruit relationships were based only on age 4 and age 5 spawn-

ers ("adults"). Therefore, to apply Equation 3 to these data, the time series was divided into either 4-year or 5-year segments, starting backward from the most recent year (1993) for which complete adult return data were available. These segments correspond roughly to salmon generations. For each generation, an estimate of N_e was computed in three ways, using Equations 1–3.

Computer simulations: To evaluate more generally the effects of population dynamic processes on N_e in Pacific salmon, I modified the computer model used by WAPLES (1990b). Each simulation was characterized by an initial number of spawners per year (N_0) and an average age distribution (progeny of spawners in year i matured at age $i + k$ with probability A_k; $\sum A_k = 1$; maximum age at spawning $= A_{max} = 5$). Thus, the demographic trajectory of the population followed maturity schedule B in Figure 1, which is more realistic for fluctuating populations than maturity schedule A (as considered by WAPLES 1990b). Each replicate was started by creating an initial population with A_{max} years of N_0 adults having allele frequency $P_0 = 0.5$.

The replacement rate, or productivity (λ), for each year was selected randomly from a lognormal distribution (PETERMAN 1981), with specified mean ($\overline{\lambda}$) and standard deviation (σ_λ). The product $N_i\lambda_i$ (rounded to the nearest integer) determined the number of individuals produced by that year that would mature in subsequent years. Random numbers were used to assign each of these $N_i\lambda_i$ individuals and their associated genes to subsequent years' spawners. This process modeled a population that fluctuated in size but otherwise was "ideal" ($N_{bi} = N_i$) within each year. To retain the fixed initial population size and allele frequency for one complete life cycle (A_{max} years), new adults maturing in years 2 to A_{max} were ignored. After allowing the system to "warm up" for 20 years to allow the random allele frequency changes among years to reach a dynamic equilibrium, population data were collected each year for up to 80 years. Because λ was chosen randomly from a series that often included both very high and very low values, N_{max} and N_{min} values were chosen to prevent the population from growing too large or going extinct.

At periodic intervals, allele frequencies in the current year were compared to those in the reference year ($A_{max} + 20$), and the difference was used to estimate F (NEI and TAJIMA 1981), the standardized variance of allele frequency change,

$$\hat{F} = \frac{(P_1 - P_2)^2}{(P_1 + P_2)/2 - P_1P_2},$$

where P_1, P_2 are the population allele frequencies at the two points in time. This formula is a special case of the more general formula provided by NEI and TAJIMA (1981) that is applicable to diallelic loci (as considered here).

F has been widely used in the temporal method for estimating effective population size from allele frequency change because its expectation is well known and independent of initial allele frequency. Waples (1990b) and Tajima (1992) showed that for species with Pacific salmon life history, the following describes the relationship between F and N_b:

$$E(\hat{F})\,(\text{salmon}) \approx 1 - [1 - 1/(2N_b)]^b. \qquad (4)$$

The value of b varies according to age structure and the number of years between samples; it can be interpreted as the number of generations that would be required to achieve a particular value of F in a population with discrete generations and effective size N_b. I used Tajima's (1992) algorithm to calculate b for each set of parameters used in the simulations. For each parameter set, I computed both the harmonic mean and the arithmetic mean of the simulated N_b values, and these values, together with the appropriate value of b, were used in Equation 4 to generate two $E(\hat{F})$ values. I then compared the observed $\hat{F}$ from the simulations with these two expectations to evaluate whether Equation 1 or Equation 2 more accurately predicted the genetic behavior of fluctuating salmon populations.

Each simulation was run 5000 times, and mean $\hat{F}$ values were computed for a range of numbers of years of elapsed time. Because the interest here is on parametric genetic processes, population allele frequencies, rather than samples thereof, were used in computing $\hat{F}$. Loss of alleles during the simulation could downwardly bias $\hat{F}$ and upwardly bias estimates of N_e (once an allele goes extinct it can no longer change in frequency), so the incidence of allelic extinction [defined as $P_i(1 - P_i) = 0$ in A_{max} consecutive years] was monitored in the simulations.

$\bar{\lambda}$ and σ_λ were chosen to keep mean N approximately constant over the course of the simulation. Under these circumstances, the variance in N increases over time (Pimm and Redfearn 1988), as does the likelihood of encountering extreme values (Ariño and Pimm 1995), and consequently the harmonic mean N decreases. Therefore, arithmetic and harmonic means of $N_i = N_{bi}$ were computed across all replicates separately for each number of elapsed years, with each mean value including all years spanned by the comparison.

RESULTS

Empirical data analysis: From the series of data for Marsh Creek chinook salmon on yearly spawner abundance and recruits (spawners in the next generation summed over all ages), it is possible to calculate recruits-per-spawner ratios, or productivities (λ), for each year and the relative contribution of that year to the next generation (X_i; see Table 1). The data shown in Table 1 are arranged in 4-year generation blocks to facilitate

analysis and discussion of the data; analysis based on 5-year segments would take a similar form. With the data arranged in this way, it is straightforward to compute estimates of N_e using the three methods (Table 2).

$\hat{N}_e$ values computed using the harmonic mean method (Equation 1) were always lower than using the additive method (Equation 2), and the magnitude of the difference between the two estimates was largest in the generations with the greatest annual variability in spawner counts. For example, in generation 6 the spawner counts ranged 30-fold among years, from 16 to 491. Whereas the arithmetic mean number of spawners per year in this generation was 176, the harmonic mean was only 47. As a result, $\hat{N}_e$ using the harmonic mean method (188) was less than one-third of the estimate from the additive method (705). In contrast, in generations 2–4 N_i was generally high with little annual variation, and $\hat{N}_e$'s based on the two methods were more similar.

Surprisingly, $\hat{N}_e$ based on Equation 3 was even lower than the estimate based on the harmonic mean method (Equation 1) in seven of the nine generations. This same result was found in six of the seven generations using a 5-year generation length (Table 2). Inspection of data for individual generations illustrates why these effects occurred. In generation 6, the range in productivity of cohorts (nearly 100-fold, from a low of $\lambda = 0.14$ in 1978 to $\lambda > 10$ in 1980) was even greater than the 30-fold variation in abundance. Furthermore, these population dynamic processes occurred in such a way that the year with the largest spawner escapement (1978) had the lowest λ and the year with the lowest escapement (1980) had the highest λ. As a result, the 16 spawners in year 1980 contributed 2.5 times as many total adults to the next generation as did the 491 spawners in 1978. Put another way, the 16 adults in 1980 represented just over 2% of the total spawners in the parental generation, but they were responsible for 35% of the genes transmitted to the progeny generation. These factors greatly increased the variance in reproductive success among individuals in different years (but within the same generation), thus by definition reducing N_e.

A different picture is seen in generation 8 (years 1986–1989). In this case, the yearly spawner counts were more stable, ranging from 80 to 395. Although λ was below replacement for all years in the generation, the values were roughly comparable, ranging only from 0.2 to 0.69. Furthermore, the highest λ occurred in the year with the largest population size, and the year with the lowest N_i had relatively low reproductive success. As a consequence, the contribution of spawners in each year to the next generation (X_i) was much closer to the relative size of N_i than was the case in generation 6, and $\hat{N}_e$ calculated by Equation 3 (762) was larger than the value (650) calculated using the harmonic mean method.

The total number of adult spawners within a genera-

TABLE 1

Spawner-recruit data for 36 years for Marsh Creek (Idaho) chinook salmon arranged into 4-year generations (BEAMSDERFER *et al.* 1998 and unpublished data)

Year	Spawners (N_i)	Recruits (R_i)	R_i/N_i (λ_i)	N_i/N_T	R_i/R_T (X_i)
1958	463	732	1.58	0.23	0.22
1959	155	1126	7.24	0.08	0.34
1960	506	809	1.60	0.25	0.25
1961	933	635	0.68	0.45	0.19
Gen 1 N_T, R_T	2057	3302			
1962	604	1207	2.00	0.19	0.37
1963	651	661	1.02	0.20	0.20
1964	1259	608	0.48	0.39	0.19
1965	686	766	1.12	0.21	0.24
Gen 2 N_T, R_T	3200	3241			
1966	724	547	0.76	0.24	0.23
1967	1099	558	0.51	0.36	0.23
1968	830	992	1.19	0.27	0.41
1969	390	317	0.81	0.13	0.13
Gen 3 N_T, R_T	3043	2414			
1970	829	459	0.55	0.30	0.38
1971	490	87	0.18	0.17	0.07
1972	555	72	0.13	0.20	0.06
1973	934	598	0.64	0.33	0.49
Gen 4 N_T, R_T	2808	1216			
1974	382	92	0.24	0.38	0.33
1975	358	17	0.05	0.36	0.06
1976	76	54	0.71	0.08	0.19
1977	178	118	0.66	0.18	0.42
Gen 5 N_T, R_T	994	281			
1978	491	70	0.14	0.70	0.14
1979	83	71	0.86	0.12	0.14
1980	16	178	10.86	0.02	0.35
1981	115	190	1.66	0.16	0.37
Gen 6 N_T, R_T	705	509			
1982	71	228	3.22	0.17	0.27
1983	60	472	7.86	0.14	0.56
1984	100	56	0.56	0.23	0.07
1985	196	86	0.44	0.46	0.10
Gen 7 N_T, R_T	427	841			
1986	171	102	0.59	0.19	0.23
1987	268	54	0.20	0.29	0.12
1988	395	273	0.69	0.43	0.61
1989	80	21	0.26	0.09	0.05
Gen 8 N_T, R_T	914	449			
1990	101	2	0.02	0.20	0.01
1991	72	5	0.07	0.14	0.02
1992	114	61	0.53	0.23	0.21
1993	216	225	1.04	0.43	0.77
Gen 9 N_T, R_T	504	293			

Gen, generation.

tion ($N_T = \Sigma N_i$) provides a benchmark for comparing N_e to N ratios within a generation. Because the effective size estimates shown in Table 2 assume "ideal" conditions within a year, they provide an indication of the reduction in N_e due entirely to the effects of annual variance in mean reproductive success. For the nine generations of data shown in Table 2, the estimates of N_e/N_T using $\hat{N}_e$ from Equation 3 ranged from 0.16 to 0.89—indicating that population dynamic processes among years can be a substantial factor in reducing

TABLE 2

**Estimates of N_e and N_e/N for Marsh Creek chinook salmon based on three methods (Equations 1–3)
using demographic data from Table 1**

Generation	Years	$\hat{N}_e$ Equation 1	Equation 2	Equation 3	$\hat{N}_e/N^a$
		Generation length 4 years			
1	1958–1961	1372	2057	986	0.48
2	1962–1965	2939	3200	2484	0.78
3	1966–1969	2640	3043	2723	0.89
4	1970–1973	2615	2808	2234	0.80
5	1974–1977	662	994	566	0.57
6	1978–1981	188	705	110	0.16
7	1982–1985	349	427	157	0.37
8	1986–1989	650	914	762	0.83
9	1990–1993	430	503	321	0.64
Harmonic mean $\hat{N}_{e(9)}$ (9 generations)		584	964	376	0.39
		Generation length 5 years			
1	1959–1963	1970	2849	1516	0.53
2	1964–1968	4349	4598	3975	0.86
3	1969–1973	2879	3198	2556	0.80
4	1974–1978	953	1485	824	0.55
5	1979–1983	219	345	191	0.55
6	1984–1988	919	1130	990	0.88
7	1989–1993	503	583	361	0.62
Harmonic mean $\hat{N}_{e(7)}$ (7 generations)		716	992	607	0.61

A generation is assumed to include either 4 or 5 years of spawners. N_{bi}/N_i is assumed to be 1 each year.
[a] $\hat{N}_e$ from Equation 3 divided by $\hat{N}_e = N_T$ from Equation 2.

effective population size in Pacific salmon. Estimates of N_e/N based on the 5-year model were not as extreme, falling in the range 0.53–0.88 (Table 2). The difference in the estimates for the 4- and 5-year generation models can be attributed primarily to the different way years 1978 and 1980 were allocated into generations. In the 4-year model, these two years fell in the same generation, leading to the extreme contrast in productivity noted above and an estimated 84% reduction in N_e. In the 5-year model, these years fell in different generations within which there was much less variance in productivity among years.

Over the entire dataset (seven to nine generations), a long-term effective size can be calculated for each of the three methods using the harmonic mean of the estimates for the individual generations. If the assumptions behind the additive model are met, then $N_e = N_T$ within each generation, and the genetic behavior of the population over the 36-year period will be a function of the harmonic mean of the single-generation N_T values. These multigeneration estimates of effective size using Equation 2 are $\hat{N}_{e(9)} = \tilde{N}_{T(9)} = 964$ for the 4-year generation model and $\hat{N}_{e(7)} = \tilde{N}_{T(7)} = 992$ for the 5-year generation model (Table 2), the small difference being due to 1 more year of data in the 4-year model. These values

provide a benchmark for comparing the long-term $\hat{N}_{e(k)}$ values computed using the demographic data (Equation 3). For the 4-year model we can estimate the long-term ratio $\hat{N}_{e(9)}/\tilde{N}_{T(9)}$ as $376/964 = 0.39$; for the 5-year model
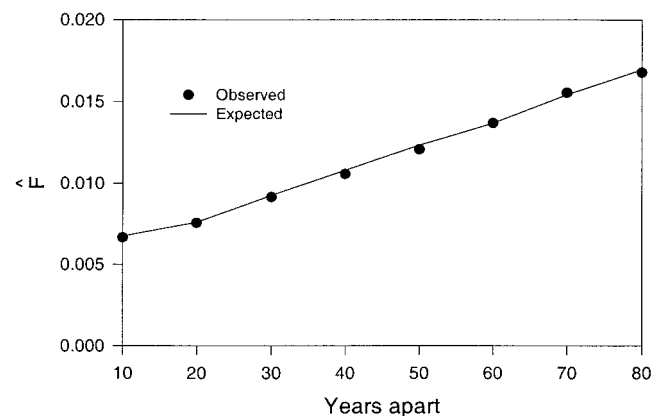

FIGURE 2.—Comparison of $\hat{F}$ from computer simulations (solid circles) with its expected value. With N_i held constant, $E(\hat{F})$ is the same for the additive and harmonic mean methods. Simulation conditions, $N_i = N_{bi} = 200$ every year; age structure, $A_k = 0, 0, 0.25, 0.5, 0.25$ for $k = 1 \ldots 5$. $\hat{F}$ values were computed for temporal comparisons of allele frequencies spanning up to 80 years and represent means over 5000 replicates.
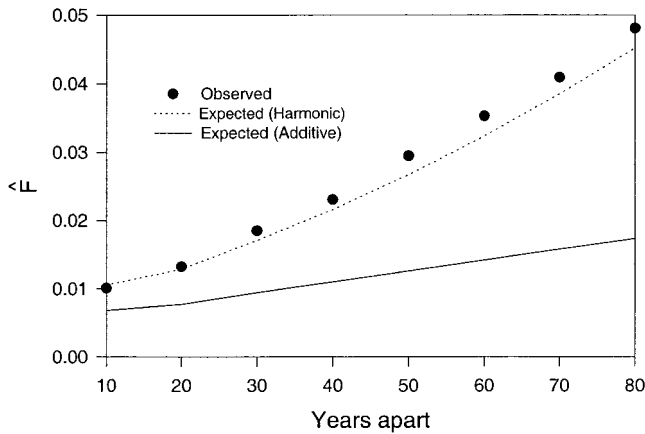
FIGURE 3.—Comparison of $\hat{F}$ from computer simulations (solid circles) with expectations based on the additive and harmonic mean methods. Simulation conditions are as follows: $N_0 = 200$; population productivity (λ) is drawn randomly each year from a lognormal distribution with $\bar{\lambda} = 1$ and $\sigma_\lambda = 0.5$; N_i is constrained to the range from $N_{\min} = 10$ to $N_{\max} = 10{,}000$; other conditions are as in Figure 2.

the estimate is $607/992 = 0.61$. Because to this point it has been assumed that $N_{bi} = N_i$ each year, these reductions in the N_e/N ratio are due entirely to annual differences in productivity. Data shown in Table 2 suggest that for Marsh Creek chinook salmon, these population dynamic processes have reduced effective size over a 36-year time period by ~40–60%.

Although $N_{bi}/N_i < 1$ was not formally considered in these analyses, all of the methods discussed here can easily accommodate annual estimates of N_{bi} if they are available. In that case, the estimates of N_e can be scaled by the factor N_{bi}/N_i in the individual years. For example, assuming $N_{bi}/N_i = 0.3$ each year (consistent with empirical estimates for Snake River chinook salmon; WAPLES *et al.* 1993; WAPLES 2002), the single-generation estimates of N_e in Table 2 would all be reduced by the factor 0.3, and single-generation N_e/N estimates for Marsh Creek chinook salmon would range from 0.05 to 0.27 (using the 4-year model) and from 0.16 to 0.26 (using the 5-year model).

Computer simulations: Figure 2 shows results of a simulation that mimicked parameters previously considered by WAPLES (1990a,b) in evaluating temporal change in Pacific salmon: $A_k = 0.25$, 0.5, 0.25 for ages $k = 3$, 4, and 5, respectively; $N_{bi} = N_i = 200$ every year. Because N_{bi} was constant, $\tilde{N}_b = \bar{N}_b$ for every time period considered and the expectations for long-term $N_{e(k)}$ and F under scenarios 1 and 2 are the same. Results shown in Figure 2 demonstrate that $\hat{F}$ values calculated from the simulations over periods ranging from 10 to 80 years (2.5 to 20 generations with $g = 4$) agree well with expectations for salmon populations, on the basis of previous work by WAPLES (1990a,b) and TAJIMA (1992).

When λ was allowed to vary randomly among years,

N_i and N_{bi} fluctuated over time, and empirical results from the simulations allowed a comparison of the long-term genetic behavior of the fluctuating population with expectations using the additive and harmonic mean methods. In the simulation shown in Figure 3, conditions were the same as in Figure 2 except that λ for each year was chosen from a log-normal distribution with $\bar{\lambda} = 1.0$ and $\sigma_\lambda = 0.5$. With this moderate level of variability ($\sigma_\lambda = 2.3$ for the Marsh Creek data), expectations under the two scenarios are quite different, and it is clear that $\hat{F}$ from the simulations agrees much better with the harmonic mean method than with the additive method. In fact, for every time period the observed $\hat{F}$ was even larger than expected under scenario 1, indicating that long-term $N_{e(k)}$ in the modeled population was lower than expected using the harmonic mean method and much lower than expected using the additive method.

To evaluate sensitivity of this result to particular values of key variables (initial N, σ_λ, age structure, generation length) I conducted additional simulations encompassing a wide range of parameter sets (data not shown). The following general results were obtained:

1. Larger variance in λ leads to larger $\hat{F}$ and smaller effective size. This result was found consistently across a wide range of age structures and other parameter values. Under most scenarios with $\sigma_\lambda > 1$, $\hat{F}$ was larger (and $\hat{N}_e$ lower) than predicted using the harmonic mean method.
2. For a given σ_λ, $\hat{F}$ was larger (and $\hat{N}_e$ lower) if the population had more than two age classes of spawners.
3. Reductions in N_e are greatest with an even age distribution and diminish if any single age class constitutes >70% of the spawners.

DISCUSSION

It might be assumed that an analysis that fully accounted for variable demographics would show that N_e for species with salmon-type life history falls in the range bounded by the additive and harmonic mean methods. Results presented here show that this assumption is not true, at least in a general sense. The additive method does provide an upper bound for N_e; if the genetic contribution of individual cohorts to the next generation is exactly proportional to N_{bi}, N_e cannot be increased further except by increasing N_{bi}/N_i within years. However, it is clear that the harmonic mean method does not provide a lower limit to N_e, which in some cases can be much lower than predicted by Equation 1. In fact, it is easy to show using Equation 3 that N_e for a generation can be as small as N_{bi} in a single year (*i.e.*, if $\lambda = 0$ in all other years). Years in which X_i (R_i/R_T) is large relative to N_{bi}/N_T are primarily responsible for these reductions in effective size. With random variation

in productivity, this phenomenon occurs frequently due to stochastic processes alone, and because the effects on N_e are nonlinear they are not completely offset by years in which X_i and N_{bi}/N_T are more similar.

The simulations evaluated how well $\hat{F}$ and long-term $N_{e(k)}$ were predicted by functions of the harmonic mean and arithmetic mean of the yearly N_{bi} values. Mathematically, taking the harmonic mean of a series of N_{bi} values (as in the simulations) is equivalent to first computing single-generation N_e values as the harmonic mean of the N_{bi} within a generation and then taking the harmonic mean of the generational N_e values (as in the analytical model; see Table 2). This is not true for the additive method, since even if N_e per generation were an additive function of the N_{bi} values within a generation, the long-term N_e must be a function of the harmonic mean N_e values per generation. Thus, we would expect that the additive method would overestimate $N_{e(k)}$ unless effective size were constant across generations.

Collectively, the results presented here lead to the following conclusions: (1) Variability across years in population dynamic processes can substantially reduce effective population size in Pacific salmon; (2) this reduction is in addition to, and can be comparable in size to, reductions in the ratio N_{bi}/N_i within individual years; (3) under most realistic conditions, the harmonic mean method is much better than the additive method in describing the relationship between N_b and N_e in Pacific salmon; (4) in Marsh Creek chinook salmon, temporal variance in productivity over a 36-year period has reduced effective size by an estimated 40–60%.

The simulation results corroborate these conclusions and provide more general insight into the effects of population dynamic processes on N_e in Pacific salmon. This is important because the analytical models all have limitations. First, the additive and harmonic mean methods make fixed assumptions about annual productivity that are unrealistic for most real populations. Equation 3 makes no assumptions about the nature of the variation in productivity, but it must be applied to a specific time series of data. The simulations allowed me to consider random variation in productivity and a large number of time series of data.

Second, the analytical approach is somewhat artificial in that no sharp temporal boundaries exist to indicate where one generation ends and another begins in Pacific salmon (except in pink salmon, which have a fixed 2-year life cycle). Estimates of N_e can differ depending on how the years are organized into generations (Table 2, results for the 4-year vs. the 5-year model). In contrast, the simulations do not deal with individual generations but instead provide information about the genetic behavior of a population over continuous periods of time.

Third, Equation 3, which was derived on the basis of the concept of identity by descent (RYMAN and LAIKRE 1991), applies to the inbreeding effective size, which will differ from the variance effective size in populations that vary in size (as do those considered here). The simulations, which focus on allele frequency change over time, provide information about the variance effective size of a population and thus provide a check for the general relevance of Equation 3.

Finally, the demographic data for Marsh Creek chinook salmon include an unquantified magnitude of uncertainty (measurement error in counting the fish and aging the spawners and sampling error associated with estimating the total number of spawners and age structure on the basis of sampling only a portion of the population). The simulations allowed an evaluation of genetic behavior of the population under a known set of parameters. The strong agreement of the analytical and modeling results suggests that the analytical approach can provide useful insights in spite of some of its simplifying assumptions.

The simulation results show that reductions in N_e in Pacific salmon as large or larger than those found in Marsh Creek chinook salmon can occur through random variation in productivity among years. Collectively, the simulations show that N_e in Pacific salmon generally will be as low or lower than predicted using the harmonic mean method if σ_λ is high, if adults mature at three or more age classes, or if age distribution is even. The genetic consequences will be less severe if the variance in λ is low or if age at maturity is strongly unimodal.

Salmon are unusual, but not unique, in being semelparous yet having variable age structure; other species with these traits include opossum shrimps (MORGAN 1980) and a variety of monocarpic plants (DEJONG *et al.* 1987). In these species, annual variability in λ can be expected to affect N_e in a fashion similar to that for Pacific salmon. See NUNNEY (2002) for analysis of a closely related problem involving N_e in annual plants with seed banks. In general, however, the effects of fluctuating population size on N_e are expected to be less for iteroparous species because lifetime reproductive success will not be dominated so strongly by events that occur in only 1 year.

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Communicating editor: F. Tajima