Estimating the Juvenile Survival Rate of Male Northern Fur Seals (*Callorhinus ursinus*)

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Three methods for estimating the survival rate of juvenile northern fur seals (*Callorhinus ursinus*) are developed from the earlier works of Chapman, Smith and Polacheck, and Lander. Each of the methods I propose divides the estimated number of males alive at 2 yr of age by the estimated number of pups born in their year class. The number of surviving juveniles are reconstructed by back calculation using the number of males killed during the commercial harvest and the subsequent counts of bulls. The three methods differ in their assumptions concerning subadult survival and escapement from the harvest, although all produce similar estimates when applied to the St. Paul Island fur seals. These new estimates of juvenile survival (1950–80) are strongly correlated with the ratio of cohort kill to pup production and with estimates from the currently-used Lander procedure. This is because the harvest mortality of males is large compared with natural mortality. The new methods perform acceptably over a wider class of data than Lander's. Their greatest advantage over current procedures is that they provide a better insight into the reliability of the survival estimates they produce.

Trois méthodes pour estimer le taux de survie des jeunes adultes d'otarie à fourrure (*Callorhinus ursinus*), ont été mises au point d'après les travaux antérieurs de Chapman, Smith et Polacheck, et Lander. Chacune des méthodes proposées divise le nombre estimé de mâles vivants à l'âge de deux ans, par le nombre estimé de jeunes nés dans leur classe annuelle. Le nombre de jeunes adultes survivants est calculé rétrospectivement à partir du nombre de mâles tués au cours de la récolte commerciale et du dénombrement subséquent de pachas. Les trois méthodes diffèrent quant à leur hypothèse concernant la survie des jeunes adultes et l'échappement de la récolte, bien que toutes trois permettent d'obtenir des estimations semblables lorsqu'elles sont appliquées aux otaries à fourrure de l'île Saint-Paul. Ces nouvelles estimations de la survie des jeunes adultes (1950–80) présentent une forte corrélation avec le rapport d'abattage de la cohorte à la production de nouveaux-nés, et avec les estimations obtenues par la méthode de Lander actuellement en usage. Ce phénomène s'explique par la mortalité élevée des mâles à cause de la récolte comparativement à la mortalité naturelle. Appliquées à une série plus étendue de données que celle de Lander, les nouvelles méthodes donnent des résultats acceptables. Leur plus grand avantage comparativement aux méthodes actuelles est de fournir une meilleure évaluation de la fiabilité des estimations de survie.

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In large mammal populations such as pinnipeds, juvenile survival is a key component of population dynamics and a potential indicator of population status (Eberhardt 1981). Eberhardt and Siniff (1977) have shown how the survival over the first 2 yr of life can account for changes observed in the size of four different pinniped species. Increases in population size were shown to occur when juvenile survival was high, while prolonged periods of low juvenile survival caused the populations to decline.

Estimates of juvenile survival rates for male northern fur seals (*Callorhinus ursinus*) have been widely used. They have been incorporated into mathematical models to examine the decline of the Pribilof population (Eberhardt 1981; Smith and Polacheck 1984; Trites and Larkin 1989) and to study the effect of the female harvest on pup production (York and Hartley 1981). They have also been used to predict maximum sustainable yield (Eberhardt 1981), to identify possible years of heavy net entanglement mortality (Fowler 1985), and to interpret the changing ages of first reproduction (York 1983). Furthermore, the Lander method has been applied to Soviet populations to model the effect of changing juvenile survival on pup production and bull numbers (Frisman et al. 1982).

The reliability of the fur seal survival estimates and estimators requires careful consideration because of their wide use and their importance in interpreting population dynamics. Currently, there are three sets of estimates for the Pribilof population, corresponding to three procedures for estimating the survival rate of juvenile males (Chapman 1961, 1964, 1973; Smith and Polacheck 1981, 1984; and Lander 1975, 1979). Comparing these estimates is complicated because they were not all determined for the same years and because many of the data used in the original publications were later revised. Furthermore, Lander estimated juvenile survival from birth to age 2, whereas the other authors estimated juvenile survival until 3 yr of age. The most widely used estimation procedure is that of Lander, which has apparently replaced the Chapman procedure. The method proposed by Smith and Polacheck has never been fully used, to my knowledge.

Details and a critique of all three methods are contained in the adjoining appendix. The general conclusion is that the three sets of previously published estimates of juvenile survival should be revised by combining the merits of the current procedures. In particular it is desirable to bound the estimate as in the Chapman and Lander methods, while striving to use all the available information concerning a year class as shown by Smith and Polacheck. Current estimates from the Chapman and Smith–Polacheck procedures are justifiable, but should only be considered as minimal values. However, the widely accepted Lander estimates are biased and the derivation contains a mathematical error.

The strengths and general methodology of the current procedures to estimate juvenile survival are combined in this paper to generate three alternate methods that differ in their underlying assumptions concerning subadult survival and escapement from the harvest. The proposed estimators are closely related and can be easily adapted if model assumptions are altered.

Biology and Management

Fur seals occur on the Pribilof Islands from late May until early November (Peterson 1968). The first animals to arrive are the adult males (7+ yr old). They defend breeding space on the rookery and await the return of the females in late June and early July. Pups are born shortly after the females arrive on land. They nurse for 2 d while their mother is on shore, and fast for the next 4–8 d that she is absent (Bartholomew and Hoel 1953; Costa and Gentry 1986). No other care is received by the pup while the mother is at sea. The harem structure begins to break down in August as the fur seals start their southward migrations.

Young males haul out in decreasing order of age and size from June until mid-August (Bigg 1986). These subadults band together in separate hauling grounds because of their inability to enter the rookery defended by harem bulls. It is from the class of subadult animals that harvests are made. The selective congregation of immature fur seals makes it possible to drive and kill primarily the valuable 3- and 4-yr olds without interfering with the breeding animals. These subadult males are harvested during a 5-wk period usually beginning July 1 (Lander 1980). Fourteen major areas on St. Paul Island, consisting of approximately 32 haulout sites, are visited once a week. The juveniles (0–2 yr) are rarely found on the hauling grounds during the harvest because few return during the summer following birth and the 2-yr olds tend to come back to the hauling grounds late in the season.

Fur seal managers count the adult males and estimate the numbers of pups born each year (Roppel 1984; Scheffer et al. 1984). They also age and count the number of males taken in the commercial harvest. The age composition of the subadult kill has been based on tooth annuli since 1950 and is considered reliable. The count of adult males on the rookeries is broken into harem bulls (defending a territory containing one or more females) and idle males (7 yr and older with no territory). Harem bull counts are considered accurate because the breeding animals are conspicuous. There is more uncertainty in the idle bull counts because some may be in the water at the time of the count. Furthermore the distinction between immature males and idle bulls is a subjective one and may vary between counters. Pup numbers have been estimated from mark–recapture studies (York and Kozloff 1987). From 1947–68 pups were tagged and subsequently recaptured as subadults in the harvest. Since 1960, pups have been sheared and counts made 2 wk later of the marked/unmarked ratios in subsamples. These pup numbers have been widely accepted although there exists some controversy over the 1950–60 estimates which were based on reconstructing the adult female population (Smith and Polacheck 1984). Adult females were derived from the estimated number of males that survived to age 4 and then multiplied by 0.6 (the average pregnancy rate) to yield the estimated number of pups born (Chapman 1964). Thus any estimates of survival rates with these estimates in the denominator will involve some circularity and confounding. Counts of dead pups are taken in mid to late August after most of the land mortality has occurred. The most complete set of data for pups, bulls, and harvest are from the 1950–83 year classes born on St. Paul Island (Tables 1 and 2).

TABLE 1. Numbers of harem and idle bulls on Saint Paul Island by year of count. Lander (1980).

Year	Harem	Idle
1950	9 292	3 102
1951	9 434	3 581
1952	9 318	4 717
1953	9 848	5 912
1954	9 906	6 847
1955	9 034	8 650
1956	9 384	9 016
1957	9 582	10 060
1958	9 970	9 510
1959	10 003	11 485
1960	10 247	10 407
1961	11 163	11 791
1962	10 332	9 109
1963	9 212	7 650
1964	9 085	7 095
1965	8 553	5 616
1966	7 925	5 931
1967	7 230[a]	4 439[a]
1968	6 176[a]	3 100[a]
1969	5 657	2 208
1970	4 945	1 666
1971	4 200[a]	1 900[a]
1972	3 738[a]	2 384[a]
1973	4 906[a]	2 550[a]
1974	4 563[a]	1 782[a]
1975	5 018	3 535
1976	5 324	4 041
1977	6 457	3 845
1978	6 496	3 908
1979	6 242	4 457
1980	5 490[b]	4 248[b]
1981	5 120[b]	4 003[b]
1982	5 767[b]	4 009[b]
1983	4 827[b]	4 242[b]
1984	4 803[b]	3 977[b]
1985	4 372[c]	3 363[d]
1986	4 603[c]	1 865[d]
1987	3 636[d]	1 892[d]

[a]Lander and Kajimura 1982.
[b]York and Kozloff 1985.
[c]York and Kozloff 1987.
[d]C. Fowler, pers. comm., NMML, NOAA, Seattle, WA.

Methods

Procedures for estimating three sets of juvenile survival rates for male northern fur seals are outlined in this section, and can

TABLE 2. Estimates of the number of pups born (male and female) and the number of dead pups subsequently counted on Saint Paul Island. The number of males killed from each year class is recorded by age. Lander (1980).

Year Class	Pups born	Dead pups	Age when killed 2	3	4	5	6
1950	451 000	53 420	855[a]	40 656[a]	15 365[a]	332[a]	0
1951	447 000	70 663	1 384[a]	32 350[a]	18 083[a]	3 057	0
1952	438 000	40 800[a]	1 735[a]	30 773[a]	31 448	675	0
1953	445 000	78 212	839[a]	38 290	8 855	54	9
1954	450 000	96 178	2 859	23 473	5 599	554	10
1955	461 000	75 544	1 015	27 863	10 555	115	0
1956	453 000	98 707	885	10 671	2 762	532	0
1957	420 000	61 662	2 590	24 283	15 344	733	68
1958	387 000	31 187	1 977	48 458	14 149	1 587	122
1959	335 000	39 964	2 820	26 456	14 184	1 764	73
1960	320 000	62 828	1 619	14 310	10 533	1 240	0
1961	342 336	57 867	1 098	22 468	12 046	1 270	96
1962	277 078	45 268	2 539	19 009	12 156	1 287	92
1963	262 498	32 598	1 264	25 535	11 785	1 542	121
1964	283 922	21 572	3 143	26 991	13 279	1 469	17
1965	253 768	39 124	2 200	18 706	10 565	731	190
1966	298 931	21 414	1 673	17 826	11 548	1 338	53
1967	291 000	14 076	2 640	22 176	12 503	2 185	22
1968	235 000[a]	25 298	1 725	12 888	14 932	721	135
1969	232 670	13 279	323	15 024	10 800	1 631	95
1970	230 485	20 581	916	16 337	15 533	1 402	19
1971	249 742[b]	46 439	577	14 652	10 768	722	9
1972	269 000	22 649	1 025	15 186	8 050	707	45
1973	236 420[c]	21 500[c]	1 642	13 397	9 421	598	18
1974	266 000	13 200[c]	893	16 476	8 955	470	33[d]
1975	278 261	20 625	1 783	13 752	7 918	725[d]	19[d]
1976	298 000	23 676	1 479	15 245	8 183[d]	651[d]	15[d]
1977	235 210[c]	14 083	2 051	13 157[d]	6 714[d]	511[d]	20[d]
1978	247 132[c]	8 073	2 180[d]	14 224[d]	7 016[d]	414[d]	20[d]
1979	245 932	6 444	2 284[d]	15 123[d]	6 644[d]	304[d]	0[f]
1980	203 825[c]	7 859[d]	2 065[d]	15 587[d]	4 601[d]	4[f]	0[f]
1981	179 444[c]	6 798[d]	3 047[d]	13 976[d]	496[f]	5[f]	
1982	203 580[c]	7 301[d]	3 133[d]	2 645[f]	81[f]		
1983	165 941[c]	5 997[d]	234[f]	542[f]			
1984	173 274[c]	6 115[d]	521[f]				
1985	182 258[e]	5 226[e]					
1986	167 656[e]	7 771[e]					
1987	171 422[f]	7 667[f]					

[a]Lander 1979.
[b]Mean number of pups born in 1970 and 1972.
[c]York and Kozloff 1985.
[d]Kozloff 1986.
[e]York and Kozloff 1987.
[f]C. Fowler, pers. comm., NMML, NOAA, Seattle, WA.

be contrasted with those of Chapman, Smith–Polacheck, and Lander which are contained in the appendix.

The survival rate of juvenile males (S_J) from birth till 2-yr old, is equal to the number of male fur seals alive at 2 yr of age, divided by the number of male pups born in each year class (N_0). The number of juveniles that survive until age 2 is reconstructed from the number of males killed at age a during subsequent commercial harvests (K_a: $a = 2,\ldots,6$). There are several ways to reconstruct the 2-yr old population. All begin by establishing plausible upper and lower estimates of juvenile survival (denoted $\bar{S}_J$ and $\underline{S}_J$). Note that these are not strict limits, but plausible values. The "best" estimate (S_J) is taken to be the mean of the two extremes:

(1) $$S_J = \frac{\bar{S}_J + \underline{S}_J}{2}$$

The minimum and maximum estimates of males alive at age 2 is derived from the number of males killed and the natural annual survival rate of the subadults (S_A). I made two assumptions about the kill process in order to fix the estimates. For the lower estimate of juvenile survival, I assumed that no seals escaped the harvest. The upper estimate was the consequence of assuming that at least 50% of the 4-yr old males were killed under management policies (Lander 1975). Thus

(2a) $$\underline{S}_J = [K_2 + K_3 S_A^{-1} + K_4 S_A^{-2} + K_5 S_A^{-3} + K_6 S_A^{-4}]/N_0$$

and

(2b) $$\bar{S}_J = [K_2 + K_3 S_A^{-1} + 2K_4 S_A^{-2}]/N_0$$

The exploitation rate has been set at 50% in equation 2b. The actual range of the upper and lower estimates will depend upon what assumptions are invoked to determine the subadult rates (S_A). Two reasonable sets of assumptions are as follows.

In the first case, values of S_A are chosen to make $\bar{S}_J$ as high as possible and $\underline{S}_J$ as low as possible. Thus, the lowest possible estimate of juvenile survival (equation 2a) occurs if all subadult animals survive under natural conditions ($S_A = 1.0$). The highest estimate of juvenile survival (equation 2b) uses an estimate of S_A based on the assumption that subadult survival will never be less than juvenile survival. The lower estimate of subadult survival is therefore set at $S_A = \sqrt{\bar{S}_J}$. Because juvenile survival is measured over a 2-yr period rather than 1, the annual rate of juvenile survival is assumed to be $\sqrt{\bar{S}_J}$. Equations 2a and b are rewritten to reflect these assumptions as follows:

(3a) $\underline{S}_J = [K_2 + K_3 + K_4 + K_5 + K_6]/N_0$

and

(3b) $\bar{S}_J = [K_2 + K_3\bar{S}_J^{-0.5} + 2K_4\bar{S}_J^{-1}]/N_0$.

This set of estimators is referred to as method 1.

In the second case, the upper and lower estimates of juvenile survival were tightened considerably by using more precise estimates of subadult survival. Fur seal life tables indicate annual male survival over the ages 2 to 6 is quite stable at $S_A = 0.80$ (Lander 1981). Substituting this value into equations 2a and b produced a second set of juvenile survival estimates (method 2).

A third case of tightening the limits improved the lower estimate of juvenile survival by including information on the abundance of harem and idle bulls in the calculations for numbers of 2-yr olds. The Lander life tables indicate that males become bulls at about age 7 (based upon average male weight per age) and that the proportion of total bulls surviving from one year to the next is $S_B = 0.74$. The two classes of mature males are harem bulls (H) and idle bulls (I). Thus the lower estimate of juvenile survival was written for year class t as

(4a) $$\underline{S}_J = \frac{K_2 + K_3S_A^{-1} + K_4S_A^{-2} + K_5S_A^{-3} + K_6S_A^{-4} + BS_A^{-5}}{N_0}$$

where

$$B = (H_t + I_t) - S_B(H_{t-1} + I_{t-1}).$$

An implicit assumption of the equation is that escapement does not change much from year to year. The upper estimate was set according to equation 2b with $S_A = 0.80$. This third set of estimators is referred to as method 3.

Results

Estimates of juvenile survival were calculated for male fur seals born on St. Paul Island using the three methods. The estimates are based on the pup estimates, commercial harvest records, and bull counts contained in Tables 1 and 2. The number of male pups was assumed to equal 50% of the total number of pups born, although there may in fact be a slight (50.65%) prevalence of males (Fowler 1987).

The estimates of juvenile survival are refined as more information about the male component of the herd is incorporated into the estimation procedure. The range of the original estimates (equations 3a and b) plotted in Fig. 1A was reduced when subadult survival was fixed at 80% (Fig. 1B). Even tighter estimates were obtained (Fig. 1C) when the counts of idle and harem bulls were used to estimate escapement from the harvest. The mean survival rates from birth to 24 mo are contained in Table 3 and are plotted in Fig. 2 for the purpose of comparison.

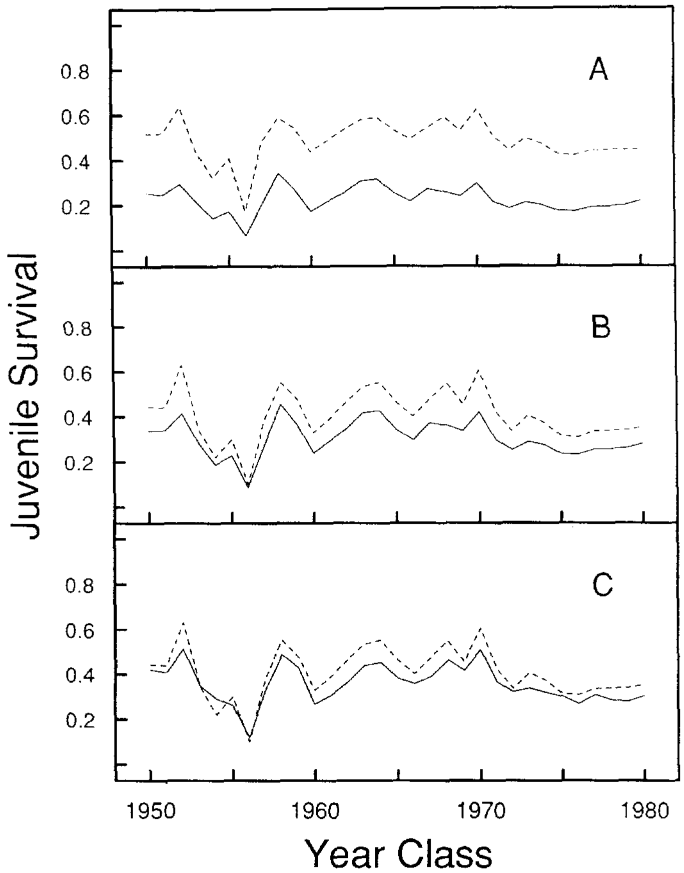

FIG. 1. Three sets of survival estimates for juvenile males. Each panel indicates an upper (broken line) and lower (solid line) estimate for the rate of survival over the first two years of life. The assumptions of the model have been refined in each successive panel. The lower estimates in panel A are the result of assuming no natural mortality of subadults, while the upper estimates assume that the annual survival rate from birth until 6 yr of age was constant (method 1). The upper and lower estimates in panel B assumes that the annual rate of survival of subadult males is 80% (method 2). Panel C also assumes 80% survival but uses the changing bull count as representative of year class strength to fix the lower estimates (method 3).

I believe that this last set of survival rates (method 3) is the best set of estimates because it incorporates the most information about the year class.

The inclusion of bull counts caused the lower survival estimate to exceed the upper estimate for 1953, 1954, and 1956. This might mean that the recruitment of males into the breeding reserve has been misrepresented by the above calculations or that exploitation patterns have changed since the 1950s. Since this difference between the upper and lower survival estimates is small, it is not considered significant. Estimates contained in Table 3 for these 3 yr are lower estimates and not mean values.

In general the parameter limits for the period 1953 to 1958 are much narrower than during the 1960s and 1970s for all three sets of revised estimates. This may indicate incorrect assumptions regarding the exploitation pattern or the survival rates. For example the assumption that 50% or more of the 4-yr old males are killed each year may only be true for the last two decades. It is equally true that subadult survival rates may have been higher during the 1950s than the rate of 80% I used. These changes in assumptions would widen the upper and lower juvenile survival estimates for this period.

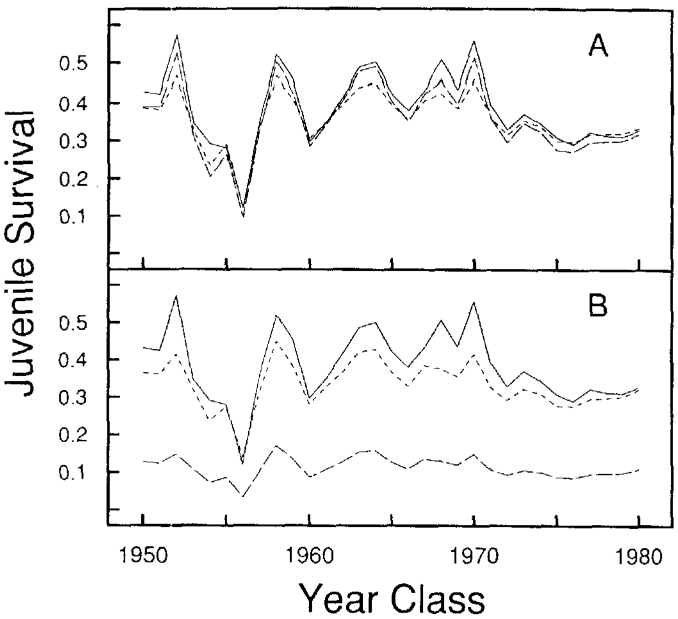

FIG. 2. Mean survival estimates for juvenile males. Panel A compares the estimated rate of juvenile survival from method 1 (short-dashed line), method 2 (long-dashed line), and method 3 (solid line). Panel B contrasts the Lander estimates (short-dashed line) with the results of method 3 (solid line). Both sets of estimates appear to mimic the ratio of total cohort kill to pups born (long-dashed line).

TABLE 3. Revised estimates of land survival (0–4 mo) and total juvenile survival (0–24 mo) for fur seals born on Saint Paul Island. The three sets of survival estimates result from the three methods outlined in the text.

Year class	0–4 mo	0–24 mo		
		Method 1	Method 2	Method 3
1950	0.882	0.386	0.390	0.431
1951	0.842	0.382	0.390	0.424
1952	0.907	0.465	0.523	0.572
1953	0.824	0.328	0.312	0.347[a]
1954	0.786	0.233	0.204	0.291[a]
1955	0.836	0.290	0.263	0.280
1956	0.782	0.119	0.094	0.120[a]
1957	0.853	0.343	0.332	0.359
1958	0.919	0.465	0.503	0.521
1959	0.881	0.407	0.424	0.454
1960	0.804	0.306	0.284	0.297
1961	0.831	0.350	0.343	0.349
1962	0.837	0.394	0.405	0.414
1963	0.876	0.442	0.476	0.487
1964	0.924	0.452	0.489	0.502
1965	0.846	0.394	0.404	0.424
1966	0.928	0.355	0.351	0.380
1967	0.952	0.407	0.425	0.434
1968	0.892	0.424	0.457	0.507
1969	0.943	0.385	0.396	0.436
1970	0.911	0.459	0.513	0.558
1971	0.814	0.361	0.359	0.393
1972	0.916	0.315	0.295	0.329
1973	0.909	0.354	0.347	0.371
1974	0.950	0.337	0.323	0.345
1975	0.926	0.299	0.275	0.308
1976	0.921	0.296	0.271	0.290
1977	0.940	0.316	0.296	0.322
1978	0.967	0.318	0.298	0.313
1979	0.974	0.321	0.301	0.311
1980	0.961	0.333	0.317	0.328
1981	0.962			
1982	0.964			
1983	0.964			
1984	0.965			
1985	0.971			
1986	0.954			
1987	0.955			

[a]Lower limits.

It is important to be aware of the possible biases arising from the model assumptions and the data base used. Unmeasurable bias can occur if escapement from the harvest is not constant, but varies in some systematic way. Similarly, fixing subadult survival rates may also introduce unmeasurable bias into the estimate. Furthermore, use of the harvest data and bull counts means that survival estimates for cohorts become statistically dependent on each other. Survival estimates are also strongly affected by the initial estimate of pup numbers. As previously noted, the survival estimates and pup numbers from 1950–60 are not entirely independent of each other given the method used to estimate their numbers.

The sensitivity of the mean estimates of juvenile survival to changes or errors in model assumptions is shown in Fig. 3 as a percent change. Altering only the assumed exploitation rate of 4-yr olds by ±20%, changes the juvenile survival estimates of method 1 by less than 5% (panel A) and the estimates of methods 2 and 3 by 10–15% (panel B). The juvenile survival estimates also appear robust to errors in the assumed rate of bull survival (method 3, panel C). The most significant parameter in methods 2 and 3 is subadult survival. Decreasing subadult survival from 0.80 to 0.70 increases the mean estimate of juvenile survival by about 25%.

The estimates of juvenile survival always lie between 0.0 and 1.0 over the range of model assumptions examined. The upper estimate in methods 2 and 3 could only exceed unity if subadult survival was less than 0.5 and the utilization of 4-yr olds was less than 20%. These conditions appear unlikely to arise.

The assumptions I have used are based upon the best information available. Unfortunately, the point estimates for survival of adults and bulls (methods 2 and 3), although considered adequate, are based on limited data. The third assumption of 50% utilization (method 1) was based on Lander's insight into the harvest rather than on data, and may be viewed as a best guess. However, the estimates of juvenile survival appear robust to errors in this parameter.

In general, the estimates of survival rate by each method are quite similar for any given year (Fig. 2A). The progressive refining of assumptions or addition of information concerning subadult survival and the escapement from the commercial harvest tends to increase the estimate of juvenile survival. The survival estimates from method 3 are constrasted in Fig. 2B with those of Lander (recalculated using the revised data contained in Table 2). They tend to exceed the Lander estimates by a factor of approximately 1.1, varying for only a few years. Interestingly, the new estimates exhibit the same trend over time as those of Lander (Pearson $r = 0.965$). The consistency of the Lander estimates is intriguing, considering the shortcomings of the method outlined in the appendix and illustrated by Fig. 4. The similarity in results is explained by the variation in the magnitude of the kill. The ratio of total kill to pups born exhibits essentially the same trends as the estimates of juvenile survival (Fig. 2B).

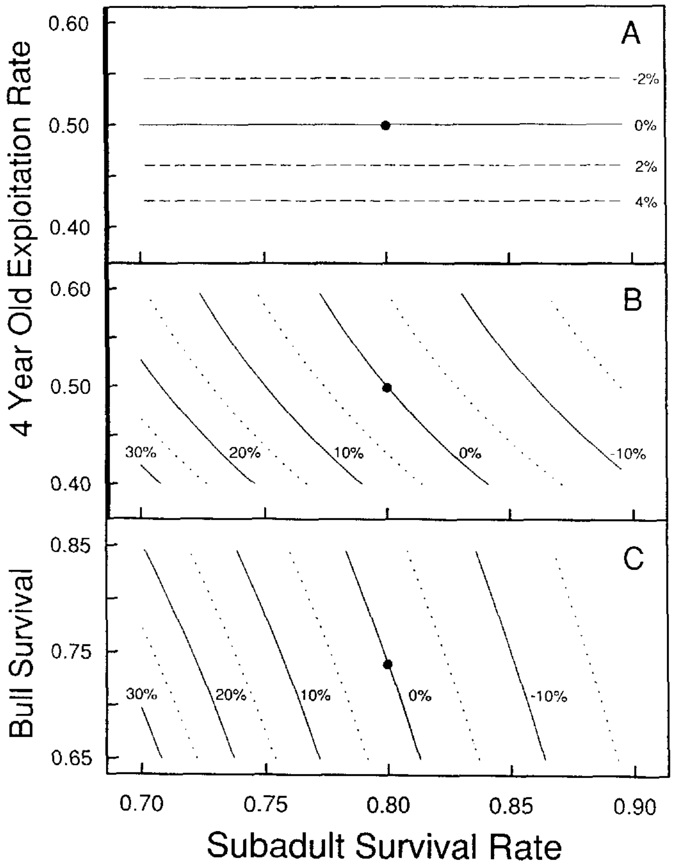

FIG. 3. Sensitivity of juvenile survival estimates to changes or errors in model assumptions. The contours indicate the percent changes that occur in the mean estimates of juvenile survival when the rates of subadult survival (S_A) and bull survival (S_B), or exploitation of 4-yr olds (U_4) are altered. Panels A, B, and C correspond to methods 1, 2, and 3, respectively. The sensitivity of method 3 was explored using $U_4=0.50$ (panel C). The combined effects of altering U_4 and S_A when $S_B=0.74$ (method 3) is similar to that shown in panel B. The dot at the center of each panel indicates the combination of parameters used in the original estimators.

Survival inevitably will be close to or proportional to the ratio of kill to pups born if kill mortality is large compared with natural mortality. This enables the Lander procedure to produce estimates which are proportionally correct despite the logical errors inherent in the method.

Discussion

Fur seal managers in the United States and the U.S.S.R. currently use the Lander procedure to estimate the survival of juvenile northern fur seals. These estimates indicate the trend in juvenile survival in the same way that the ratio of total cohort kill to the number of pups born does. The Lander procedure is complicated and should be rejected considering the mathematical error and the misuse of algebraic limits in the estimator (see appendix for details). The fact that the Lander estimates appear to be reasonable does not validate the procedure. In contrast to the Lander procedure, the methods 1, 2, and 3 outlined in this paper are relatively transparent so that assumptions can be easily modified and examined. Simple methods such as these, enhance our understanding of the estimates and in particular improve our insight into their reliability.

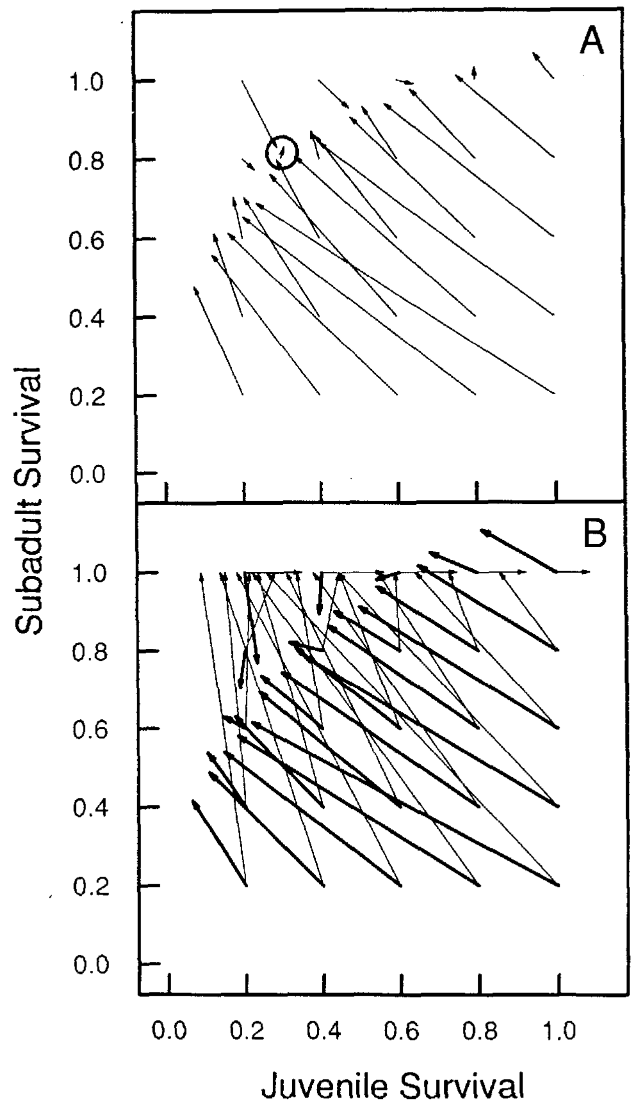

FIG. 4. Results of the Lander estimator applied to a simulated population with known rates of juvenile survival and adult survival. The simulated population was harvested at age specific rates of 0.05, 0.50, 0.70, and 0.20 for ages 2–5, respectively. The origin of each vector (tail) indicates the true combination of parameter values for one simulation run. Each vector points to the estimated rates of survival (arrow head). Panel A contains the mean estimates. The circled vector shows the combination of parameters chosen in Lander (1979) to illustrate the small bias of the procedure. Panel B indicates the upper (thin vector) and lower limits (thick vector) of the estimates and shows how the lower limit can exceed the upper limit for some combinations of parameters.

The revised methods of estimation show that the survival of juvenile males may be higher than has been acknowledged in the past. This has bearing upon the survival of juvenile females which has been previously assumed to exceed that of males by a constant factor ranging from 1.05–1.10 (Chapman 1961, 1964, 1973; York and Hartley 1981; Eberhardt 1981). Higher male survival estimates mean that the fur seal life table could be balanced by assuming that males and females experience similar rates of juvenile survival. It is certainly not unreasonable to expect that juvenile male and female fur seals are subject to similar sorts of mortality.

The major weakness of all the methods for estimating juvenile survival lies in the many years of harvest data required to reconstruct the historical population. The commercial harvest may no longer be a source of data because harvests since 1985 have been at subsistence levels, which are insufficient to derive estimates of juvenile survival beyond 1980. Therefore future efforts should be directed towards an alternative and more immediate means of estimating juvenile survival. One possibility is to concentrate subsistence harvests on selected rookeries, rather than spreading the kill over the entire island population. Monitoring sources of juvenile mortality (net debris, weather conditions) and examining the dynamics of other species that share the same ecosystem (sea birds) may be alternative approaches for getting indications of annual survival rates. These possibilities should be investigated considering the importance of juvenile survival to the ensuing demography of fur seal populations.

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Appendix: Review of Current Estimators

Three current methods (Chapman, Smith–Polacheck, and Lander) for estimating the survival of juvenile northern fur seals are reviewed here. Each method divides the number of fur seals that were alive at two or three years of age by the number of pups born in each year class (N_0). The surviving juveniles are reconstructed by back calculation using the number of males killed at age a during the commercial harvest (K_a: $a = 2,\ldots,5$). The methods differ in their treatment of escapement from the harvest and whether the estimated number of seals surviving is a mean value or an upper and lower estimate.

Chapman

Chapman (1961, 1964, 1973) determined the minimum number of three year olds that would have been alive in the absence of a kill at age 2. He did this by adding a measure of escapement to the total kill taken from each year class. Survival over the first 3 yr of life (S_J) was thus estimated from

$$(4)\quad S_J = \frac{K_2 + K_3 + K_4 + \epsilon K_4}{N_0}$$

The escapement rate (ϵ) was usually set at 0.40 but varied slightly depending upon the length of the harvest season.

Juvenile survival estimates of Chapman should be considered as lower parameter bounds. Their overall acceptability depends largely upon the assumption of a fixed rate of recruitment into the breeding reserve. Work by Smith and Polacheck (1984) suggests that escapement has probably varied considerably over time. It is therefore more reasonable to estimate escapement based on actual counts of bulls rather than assuming it to be a constant function of total kill. In this regard the analysis of Smith and Polacheck is superior to that of Chapman.

Smith–Polacheck

Smith and Polacheck (1984) modified the Chapman calculation by including age specific survival rates (S_a: $a=2,\ldots,5$) and determined the number escaping (E_5) into the breeding reserve using counts of mature males. They used two categories of males; those defending a territory containing one or more females (Harem Bulls, H) and those that held a territory with no females (Idle Bulls, I). Thus survival over the first 3 yr of life (S_J) for a given year class y was estimated as

$$(5)\quad S_J = \frac{K_2S_2 + K_3 + K_4S_3^{-1} + K_5S_3^{-1}S_4^{-1} + E_5S_3^{-3}S_4^{-1}S_5^{-1}}{N_0}$$

where

$$(6)\quad E_5 = H_y + I_y - S_B(H_{y-1} + I_{y-1}).$$

The number escaping (E_5) was derived from the difference between the total number of bulls belonging to year class y and the number surviving from previous cohorts ($y-1$). Bull survival (S_B) was assumed to be constant.

Smith and Polacheck did not evaluate the levels of escapement. Instead they published lower bound estimates of survival, obtained by dividing the total kill by the number of pups born (Smith and Polacheck 1981). Both the Chapman and the Smith and Polacheck sets of estimates calculated survival of young from birth to age 3 even though a substantial harvest begins at age 2. This may be because at the time of the original Chapman work, the specific age of kill was not known.

The major weakness of the Smith and Polacheck procedure arises from difficulties in accurately parameterizing subadult and adult survival rates. This may be why no firm estimates have been published for this estimator. Instead these authors have restricted themselves to producing a lower juvenile survival bound determined by dividing total year class kill by pups born (Smith and Polacheck 1981). Their estimates represent minimal values and should be refined.

Lander

Lander (1975, 1979) identified the upper and lower extremes of survival rates that could account for the observed male kill from a particular cohort. Best parameter estimates were taken within these limits. These are essentially two sets of estimates produced: an upper, mean, and lower estimate for juvenile survival ($\bar{S}_J$, S_J, and $\underline{S}_J$) and an upper, mean, and lower estimate for subadult survival ($\bar{S}_A$, S_A, and $\underline{S}_A$). Fur seals were considered juveniles from birth to age 2 and as subadults from 2 to 5 yr of age.

The first step in the method is to bound juvenile survival. At one extreme is the possibility that no animals escaped the harvest. Thus,

$$(7)\quad \underline{S}_J = \underline{F}(S_A) = \frac{K_2 + K_3S_A^{-1} + K_4S_A^{-2} + K_5S_A^{-3}}{N_0}$$

At the other, Lander assumed that the exploitation of 4-yr olds exceeded 50% such that

$$(8)\quad \bar{S}_J = \bar{F}(S_A) = \frac{K_2 + K_3S_A^{-1} + K_4S_A^{-2} + (K_4 + K_5)S_A^{-3}}{N_0}$$

Lander considered the mean of the lower and upper limits to be a good estimate of juvenile survival (S_J). This was presumably because the error in using a point estimate was minimized.

The process of setting parameter limits was also used to fix subadult survival. In this case the upper limit was arbitrarily set at unity ($\bar{S}_A = 1.0$) while the lower bound ($\underline{S}_A$) was written as a function of juvenile survival. Defining annual survival rates in terms of average monthly mortalities clarifies the calculation of $\underline{S}_A$.

Fur seal mortality from birth to age 5 is broken into a juvenile (birth − age 2) and subadult (ages 2–5) component. Average monthly mortality over the first 24 mo of life (M_J) is expressed as a function of juvenile survival (S_J) where

$$(9)\quad M_J = \frac{-\ln S_J}{24}$$

Subadult monthly mortality (M_A) is assumed to remain constant for ages 3, 4, and 5 and is calculated for 11 mo given insignificant natural mortality during the month of land harvest.

$$(10)\quad M_A = \frac{-\ln S_A}{11}$$

Combining juvenile and subadult mortality gives the total mortality from birth to age 5,

$$(11)\quad M_T = \frac{-\ln(S_JS_A^3)}{57}$$

which is related to the previous stages by the assumption that

$$(12)\quad M_J \geqslant M_T \geqslant M_A$$

The lower estimate of subadult survival $\underline{S}_A$ is contained within the left hand side of equation 12. If

$$(13)\quad M_J = M_T$$

then

$$(14)\quad \frac{-\ln \bar{S}_J}{24} = \frac{-\ln(\underline{S}_J\underline{S}_A^3)}{57}$$

Substituting equations (7) and (8) into equation (14) leaves one unknown, $\underline{S}_A$, which can be solved numerically. Note that appropriately bounded subadult survival rates must be substituted into the juvenile survival equations (i.e. $\bar{S}_J = \bar{F}(\underline{S}_A)$ and $\underline{S}_J = \underline{F}(\bar{S}_A)$). In this regard, Lander is incorrect in using $\underline{S}_J = \underline{F}(\underline{S}_A)$. This error means that the $\underline{S}_A$ estimated by Lander is too low and produces final estimates of juvenile survival that are too high.

Lander estimated the survival rate of subadults from the ratio of 4- to 3-yr olds rather than taking the mean of $\underline{S}_A$ and $\bar{S}_A$. The ratio is presumed to give better estimates because the 3- and 4-yr olds account for about 90% of the commercial kill and are taken in sufficient numbers to provide tight limits on the numbers that must have been present. Lander calculated the mean number of 4-yr old seals that were alive before the commercial harvest and the mean number of 3-yr olds that were alive after the kill in the previous year such that

$$(15)\quad S_A = \frac{[(K_4 + K_5)\,\bar{S}_A^{-1} + (K_4 + K_5)\,\underline{S}_A^{-1} + K_4]/2}{[(K_4 + K_5)\,\bar{S}_A^{-1} + (K_4 + K_5)\,\underline{S}_A^{-2} + K_4\underline{S}_A^{-1}]/2}$$

or

$$(16)\quad S_A = \frac{\bar{S}_A^{-1} + \underline{S}_A^{-1} + K_4(K_4 + K_5)^{-1}}{\bar{S}_A^{-1} + \underline{S}_A^{-2} + K_4(K_4 + K_5)^{-1}\underline{S}_A^{-1}}$$

The estimated rate of subadult arrival (S_A) is substituted into equations 7 and 8. Taking the geometric mean of these limits gives the best estimate of subadult survival:

$$(17) \quad S_J = (\underline{S}_J \bar{S}_J)^{.5}$$

Thus the Lander procedure has estimated juvenile and subadult survival rates by placing bounds on them to account for the the observed birth of male pups and the subsequent kill of the particular cohort.

Lander Evaluation

The alegbraic manipulations of the Lander procedure complicate a simple analytic evaluation. I therefore conducted a numerical analysis using simulation models. The technique was to apply the Lander procedure to hypothetical populations with known survival and exploitation rates. The simulated numbers at birth and subsequent male kill were used to predict the juvenile and subadult survival rates of the simulated population.

All simulation runs used a constant pup production of 100 000 males and 100 different combinations of juvenile ($S_J = 0.1, 0.2, \ldots, 1.0$) and subadult ($S_A = 0.1, 0.2, \ldots, 1.0$) survival rates. The runs differed by various age specific exploitation rates ($U_a{:}a = 2, \ldots, 5$). A typical simulation exhibiting the behaviour of the Lander estimator incorporated exploitation rates of 0.05, 0.50, 0.70, 0.20. Here for example $U_3 = 0.70$ means a harvest of 70% of 3-yr old males. This set of exploitation rates is the same one used by Lander (1975) to illustrate the small bias in calculating S_J and S_A.

The behaviour of the Lander procedure is illustrated by vectors in Fig. 4. The tail of each vector indicates the true combination of S_J and S_A of the simulated population that the Lander method is supposed to predict. The arrow head indicates the set of estimates that the Lander procedure actually produced (Fig. 4A). Fig. 4B indicates the upper and lower parameter estimates of the Lander method that gave rise to the mean values shown in panel A.

The Lander estimates fall on a set of unique lines that correspond to particular combinations of exploitation rates $U_2 - U_5$. The method performs well for combinations of exploitation and survival rates which happen to lie near the line. The circled vector in Fig. 4A is one such example. These are the values used in Lander (1979) to illustrate the small bias of this procedure. The overall ability of the Lander method to produce accurate survival estimates depends upon the relationshp between survival and exploitation. A population experiencing given rates of S_J and S_A must be exploited at precise age specific rates for the estimation technique to produce zero error. Unfortunately all simulations examined in this analysis suggest no obvious dependence between these two factors, thereby placing the validity of the estimation procedure into question.

Examination of the upper and lower estimate bounds casts further doubt upon the validity of the Lander procedure. Predictions of the lower subadult survival bound exceed the upper limit for populations experiencing juvenile rates in excess of 0.60 (Fig. 4B). This inconsistency arises from the incorrect manipulation of upper and lower survival bounds as algebraic symbols in equation 14. The error is analogous to assuming $a > b$, then erroneously permitting $-a > -b$. Equation 14 is also responsible for the quadratic shape of the lower bound and ultimately the line of best estimates.

The conclusion of this study is that the Lander procedure does not estimate juvenile survival but rather selects parameter values from a line determined by unique sets of exploitation rates. It is important to recognize that the area bounded by reasonable upper and lower survival estimates is quite restrictive. Within this region the Lander estimator generally predicts high survival associated with a large kill and low survival for small harvests. It is thus possible for the kill schedule to produce survival estimates from the Lander procedure which appear to be "in the right ball park," despite the error in calculating subadult survival rates and the incorrect use of parameter bounds.