yielded age-specific-survival fractions (l_x) for females of each year class. R_0* for each year class ranged from 7,100 to 25,800 (Table 3). The reciprocal of these numbers, 0.000141 and 0.000039, respectively, indicate a survival rate ranging from 39 to 141 females, or 78 to 282 fish of both sexes, for each 1,000,000 eggs spawned.

Any estimate based in turn on a series of rather imprecise and arbitrary estimates must be viewed with caution, and this one is no exception. Yet it is in line with current knowledge that the survival rate of pelagic fish eggs is extremely low.

TABLE 3.—Net reproductive rates (R_0*) and their reciprocals ($1/R_0$*) for the 1954-63 year classes of Atlantic menhaden.

Year class	R_0*	$1/R_0$*	Year class	R_0*	$1/R_0$*
1954	16,546	0.000060	1959	22,297	0.000045
1955	7,109	0.000141	1960	10,120	0.000099
1956	25,932	0.000039	1961	14,073	0.000071
1957	11,850	0.000084	1962	11,024	0.000091
1958	21,856	0.000046	1963	11,181	0.000089

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ROLE OF LAND AND OCEAN MORTALITY IN YIELD OF MALE ALASKAN FUR SEAL, *CALLORHINUS URSINUS*

The annual commercial harvest of male fur seals has fluctuated widely and declined since the early 1950's. This has occurred despite a fairly stable harvesting regime and efforts to maintain the population near the level believed to be consistent with maximum sustainable productivity (Chapman 1961, 1964, 1973). Variations in early natural mortality are mainly responsible for these changes in the harvest of males which occurs at ages 2-5 yr (mostly 3-4 yr). Kenyon et al. (1954) and Chapman[1] emphasized that natural mortality between birth and age 3 yr is high and that most of it probably occurs during the first winter just after weaning.

This report gives estimates of male survival from natural mortality of pups on land and from the first 20 mo of life at sea, a total interval of approximately 2 yr. The importance of pup numbers and early survival rates in determining annual variations in abundance at age 3 yr is quantified also.

Methods

Data for survival estimates are in Table 1. The age composition of annual kills before 1950 cannot be determined accurately because an aging technique was not available until then (Scheffer

[1]Chapman, D. G. 1975. Methods of forecasting the kill of male seals on the Pribilof Islands. Background paper for the 19th Annual Meeting of the North Pacific Fur Seal Commission, 10 p. (Unpubl. rep.)

TABLE 1.—Estimated numbers of male pups (born, dead, and living at the time of migration) and age-specific commercial kill of males from the 1950-70 year classes on St. Paul Island, Pribilof Islands, Alaska.[1]

Year class	Number of pups (thousands)			Number killed at age				
	Born	Dead	Living	2	3	4	5	2-5
1950	225.5	26.7	199	855	40,656	15,365	332	57,208
1951	223.5	35.3	188	1,384	32,350	18,083	3,057	54,874
1952	219.0	20.4	199	1,735	30,773	31,410	675	64,553
1953	222.5	39.1	183	839	38,312	8,855	54	48,060
1954	225.0	48.1	177	2,918	23,473	5,599	554	32,544
1955	230.5	37.8	193	1,015	27,863	10,555	115	39,548
1956	226.5	49.4	177	885	10,671	2,762	532	14,850
1957	210.0	30.8	179	2,590	24,283	15,344	773	42,990
1958	193.5	15.6	178	1,977	48,458	14,149	1,587	66,171
1959	167.5	20.0	148	2,820	26,456	14,184	1,764	45,224
1960	160.0	31.4	129	1,619	14,310	10,533	1,240	27,702
1961	168.4	29.0	139	1,098	22,468	12,046	1,270	36,882
1962	139.2	22.6	117	2,539	19,009	12,156	1,287	34,991
1963	132.0	16.3	116	1,264	25,535	11,785	1,542	40,126
1964	142.5	10.8	131	3,143	26,991	13,279	1,469	44,882
1965	133.4	19.6	113	2,200	18,706	10,565	731	32,202
1966	150.0	10.7	138	1,673	17,826	11,548	1,338	32,385
1967	142.0	7.0	135	2,640	22,176	12,503	2,185	39,504
1968	117.5	12.6	105	1,725	12,888	14,932	721	30,266
1969	116.8	6.6	110	323	15,024	10,800	1,631	27,778
1970	115.8	10.3	105	916	16,337	15,533	1,402	34,188

[1]Sources for data in Table 1, and footnotes, are given below:
Pups born: 1950-60, table 112 from Chapman (1973); 1961-65 and 1969-70, table 14 from Marine Mammal Biological Laboratory (1971[a]); 1967-68, table 10 from Marine Mammal Division (1976[b]). A 1:1 sex ratio is assumed (Kenyon et al. 1954; H. Kajimura pers. commun.).
Dead pups: 1950-60 (except 1952), appendix table 39 from Marine Mammal Biological Laboratory (1961[c]); 1952, counts (from same source) on sample rookeries only, extrapolated to island total from average contribution of these rookeries to known totals in 1951 and 1953; 1961-69, table A-12 from Marine Mammal Biological Laboratory (1971). A 1:1 sex ratio is assumed (Kenyon et al. 1954; M. C. Keyes pers. commun.).
Living pups: Pups born less dead pups, rounded to nearest thousand.
Kill by age: 1950-56 year classes, table 1 from Marine Mammal Biological Laboratory (1961[c]); 1957-64 year classes, table 1 from Marine Mammal Biological Laboratory (1971); 1965-70 year classes, table 1 from Marine Mammal Division (1976[b]).

[a]Marine Mammal Biological Laboratory. 1971. Fur seal investigation, 1970. Unpubl. manuscr., 155 p. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, WA 98112.
[b]Marine Mammal Division. 1976. Fur seal investigations, 1975. Unpubl. manuscr., 115 p. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, WA 98112.
[c]Marine Mammal Biological Laboratory. 1961. Fur seal investigation, Pribilof Islands, Alaska. Unpubl. manuscr., 148 p. U.S. Fish Wildl. Serv., Bur. Commer. Fish.

1950). However, the average numbers of pups migrating from land and of seals harvested at age 3 yr are approximated for the 1920-22 year classes in order to include in the yield-pup relationship a data point for the relatively small pup population then present. It should be mentioned that basic data were not taken during 1925-46 from which to estimate annual pup production.

The 1920-22 averages are based on kill data from Lander and Kajimura[2] and on pup data from Kenyon et al. (1954). The average number of pups born annually on St. Paul Island during 1920-22 was approximately 150,700. Their mean mortality rate on land was 2.2%, so an average of about 74,000 male pups migrated to sea annually. Because the harvest always has been selective for animals the size of 3- and 4-yr-olds, these 1920-22 year classes contributed to the kills mainly in 1923-26. The annual average kill then was 14,300, of which about 9,100 were age 3 yr assuming the same average (64%) as in the kills from the 1950-70 year classes (Table 1).

[2]Lander, R. H., and H. Kajimura. 1976. Status of northern fur seals. Food and Agriculture Organization of the United Nations, Scientific Consultation on Marine Mammals, Bergen, Norway, August 31-September 9, 1976, 50 p. (Unpubl. rep.)

The kill of 3-yr-olds is used as an index of abundance at that age. The assumption is justified reasonably well by the generally stable harvesting regime and the usual predominance of this age group in the kills.

Annual population monitoring and behavioral data (Bartholomew and Hoel 1953; Peterson 1968) show the median date of birth on St. Paul Island is about 8 July, pup mortality on land is essentially over by mid-August, and the median date when pups migrate to sea is around 1 November. Survival of pups on land is calculated as the ratio of living pups to pups born (Table 1).

Few seals haul out on land until 24 mo of age, and survival is estimated for the first 20 mo at sea. These ocean survival rates are calculated from the data for living pups and age-specific kills (Table 1) and from the model of Lander (1975) with time intervals appropriately modified.

Results

Figure 1 shows wide fluctuations in the kill at age 3 yr around the regression line for pups born. After the effects of pup mortality on land are removed, high variability persists around the line

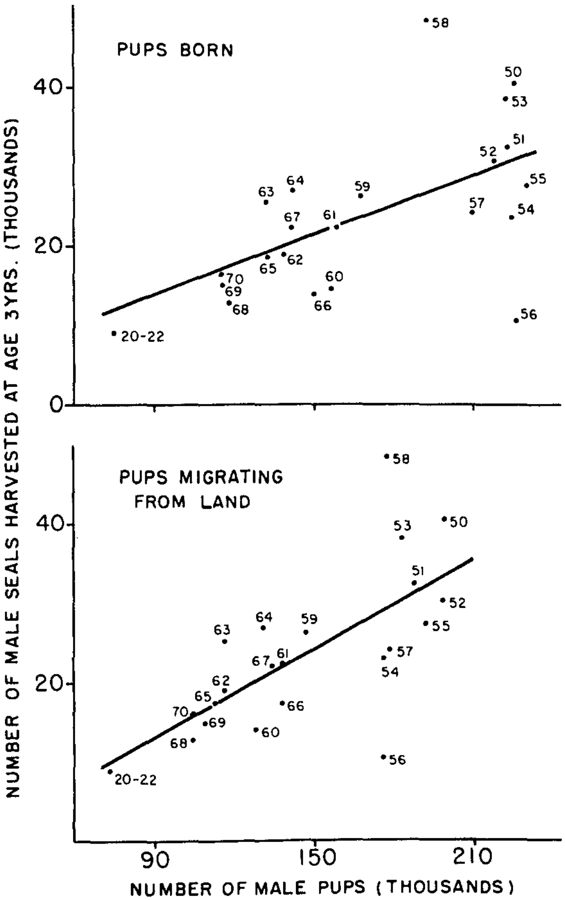

FIGURE 1.—Yield-pup relation for male fur seals of the 1920-22 and 1950-70 year classes from St. Paul Island. Least squares regression lines are shown for pups born (a = 2.341, b = 0.126) and for pups migrating from land (a = 3.740, b = 0.188).

for pups migrating from land. Most of the variation in abundance at age 3 yr is evidently due to changes in the ocean survival rate undergone by the different year classes, not to changes in the rate of pup survival on land.

Estimated survival rates for the 1950-70 year classes are in Table 2 (ocean survival could not be estimated for the 1920-22 year classes without age composition data). The means and ranges of survival estimates in Table 2 are 87% (78-95%) for pups on land, 40% (18-49%) for the first 20 mo at sea, and 35% (14-45%) for both stages between birth and 2 yr of age.

Figure 2 shows a statistically significant association between the ocean and land survival estimates (r = 0.67, P<0.01). Conditions of weather, feeding, and disease which promote good survival of pups on land apparently equip them to survive relatively well at sea. As in Figure 1, however, the wide scatter about regression is prominent—emphasizing again that events at sea contribute

TABLE 2.—Estimated natural survival rates of male fur seals from St. Paul Island in two stages from birth to age 2 yr, 1950-70 year classes.

Year class	Pups on land	First 20 mo at sea until start of kill at age 2 yr	Birth to age 2 yr
1950	0.88	0.41	0.36
1951	0.84	0.42	0.35
1952	0.91	0.46	0.42
1953	0.82	0.38	0.31
1954	0.79	0.30	0.24
1955	0.84	0.33	0.28
1956	0.78	0.18	0.14
1957	0.85	0.37	0.31
1958	0.92	0.49	0.45
1959	0.88	0.43	0.38
1960	0.81	0.34	0.28
1961	0.83	0.39	0.32
1962	0.84	0.43	0.36
1963	0.88	0.47	0.41
1964	0.92	0.47	0.43
1965	0.85	0.41	0.35
1966	0.92	0.36	0.33
1967	0.95	0.42	0.40
1968	0.89	0.42	0.37
1969	0.94	0.38	0.36
1970	0.91	0.46	0.42
All	0.87	0.40	0.35

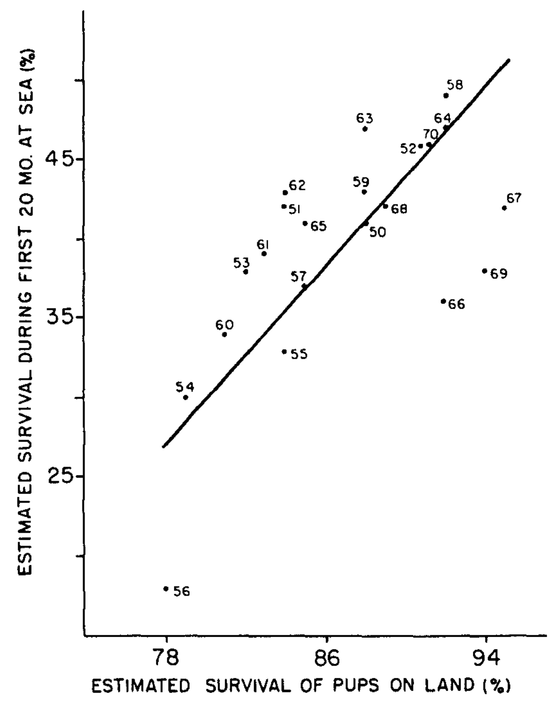

FIGURE 2.—Relation of estimated survival rate during first 20 mo at sea to estimated survival rate of pups on land for male fur seals of the 1950-70 year classes from St. Paul Island. Functional regression line shown (Ricker 1973) has intercept u = 0.830 and slope v = 1.425.

heavily to fluctuations in the survival of different year classes.

Values in Tables 1 and 2 were also analyzed under the multiple linear regression model

$$Y = A + B_1X_1 + B_2X_2 + B_3X_3 + E$$

where Y = kill at age 3 yr in thousands, X_1 = male pups born in thousands, X_2 = survival rate pups on land, and X_3 = survival rate during the first 20 mo at sea. E is a random error term; the intercept A and slopes B_i are parameters to be estimated.

Table 3 shows that multiple regression is highly significant (F = 26.60, P<0.001). Given that the pup survival rate on land is not significant (deletion of X_2 causes no change in R^2 here), 100 R^2 = 82% of the annual variation in estimated abundance at age 3 yr, as indexed by the kill, is explained by annual changes in pup production and in the survival rates of different year classes during their first 20 mo at sea. The remaining variability, 18%, is due to random sampling errors and possibly to systematic errors.

Discussion

This report helps to quantify the importance of early ocean mortality in determining the average number of males available for harvest at age 3 yr and their pronounced annual fluctuations. Kenyon et al. (1954) speculated that only half the pups survive the attempted transition from a milk diet on the Pribilof Islands to the quest for fishes and squids in a stormy environment after the islands are left behind. The authors stated that starvation during prolonged storms is a direct cause of death and noted that unusually large numbers of young seals from the 1949 year class were washed ashore on the Washington coast in emaciated condition during the severe winter of 1949-50. Ichihara (1974) postulated that the apparently higher mortality of males between birth and age 3 yr (Chapman 1964) was due to the greater proportion of males wintering in stormy northern areas than in calmer waters to the south where females predominate.

TABLE 3.—Statistics and tests for linear regression of male seals killed on St. Paul Island at age 3 yr (thousands) from the 1950-70 year classes (Y) on pups born (X_1, thousands), estimated survival rate of pups on land (X_2), and estimated survival rate during the first 20 mo at sea until age 2 yr (X_3).

Item	Calculated value
Source of sum of squares, degrees of freedom, and mean square:	
Multiple regression	1,531.60/3 = 510.53
Deviations	326.26/17 = 19.19
Total	1,857.86/20 = 92.89
Test of multiple regression	F = 510.53/19.19 = 26.60**
Square of multiple correlation	R^2 = 1,531.60/1,857.86 = 0.82
Parameter estimates and variances:	
a, s^2_a	−70.355, 533.294
$b_1, s^2_{b_1}$	0.203, 0.001
$b_2, s^2_{b_2}$	21.389, 753.857
$b_3, s^2_{b_3}$	103.012, 350.151
Tests of individual regresions	
Pups born:	$t_1 = 0.203/\sqrt{0.001} = 6.42$**
Land survival rate	$t_2 = 21.389/\sqrt{753.857} = 0.78$
Ocean survival rate	$t_3 = 103.012/\sqrt{350.157} = 5.50$**

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