ARRIVAL OF NORTHERN FUR SEALS, *CALLORHINUS URSINUS*, ON ST. PAUL ISLAND, ALASKA

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ABSTRACT

The age-specific arrival times and relative numbers of northern fur seals, *Callorhinus ursinus*, on St. Paul Island, Alaska, were determined from an analysis of kill data collected during 1956-82, and a review of the fur seal literature. Arrival times differed by sex, age, and reproductive state. Arrival took place progressively earlier with age in young males and females. Most males age ≥6 arrived by late June, while most males age 5 arrived by late June to early July, those age 4 by mid-July, those age 3 by late July, those age 2 by mid- to late August, and those age 1 by late September to early October. Females tended to arrive later than males of the same age. Nonpregnant females age ≥3 arrived by mid-August, while those age 2 arrived by mid- to late September, and females age 1 by October to early November. Pregnant females age ≥4 arrived mainly by mid-July, about 1 month before nonpregnant females of the same age. For both sexes, the number of seals returning increased between age 1 and age 3. Both sexes appeared to stop arriving earlier and in larger numbers at about the age of sexual maturity. The process of gradual maturation may play a role in inducing a cohort to undertake the return migration at earlier times with age, and to cause a greater proportion to return.

The northern fur seal, *Callorhinus ursinus*, inhabits the North Pacific Ocean mainly between lat. 32°N and 60°N (Fiscus 1978; King 1983). The species is migratory, being pelagic and widely dispersed in winter, and gathering on rookeries to give birth, mate, nurse, and rest in summer. Rookeries occur along the Asian coast on Robben, Kurile, and Commander Islands, and along the North American coast mainly on the Pribilof Islands and on San Miguel Island. The presence of large numbers of animals on Robben Island, Commander Islands, and the Pribilof Islands has allowed an annual commercial kill for pelts over many years.

The Pribilof Islands, in particular St. Paul Island and St. George Island has the largest stock of seals, numbering currently about 0.9 million (North Pacific Fur Seal Commission 1984a). The species has been harvested there almost every year since discovery in 1786 (Roppel and Davey 1965; Roppel 1984). Over the years, fishery managers learned to adjust the kill quite specifically for seals of a particular age and sex by making use of the arrival sequence of migrants and their preferences for haul-out sites. For example, Russians in the early 1800's took juvenile males on hauling grounds, and left the breeding adults and pups undisturbed on nearby rookeries. Americans in the late 1800's knew that the largest, and thus oldest, juvenile males arrived before small males (Jordan and Clark 1898). Following the discovery in 1950 that teeth could be used for aging, the kill was refined further to focus on 3- and 4-yr-old males. Although the kill has been directed primarily at young males since the early 1900's, females were taken during a herd reduction program from 1956 to 1968.

Behavioral studies on the Pribilof Islands have documented the arrival times for broad population categories, such as adult and juvenile males, and pregnant females (Jordan and Clark 1898; Bartholomew and Hoel 1953; Peterson 1965, 1968; Gentry 1981). However, these studies could not determine the age-specific arrival times because no method was available to distinguish the age of the live animals being observed. The widely accepted arrival sequence was for bulls to arrive on land first, followed by progressively younger males, progressively younger pregnant females, and later by mostly young nonpregnant cows (Kenyon and Wilke 1953; Fiscus 1978). This arrival sequence was deduced from preliminary examinations of the age and sex composition of commercial kills and from the arrival times of tagged individuals and to some extent from differences in body size, at least for the 1- and 2-yr-olds. There are no published analyses that describe age-specific arrival times, although some unpublished reports give information on arrival times.

In this study, I determine the arrival times for seals of each age, sex, and reproductive condition on hauling grounds and rookeries of St. Paul Island, the largest of the Pribilof Islands. The study is based

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mainly on an analysis of seasonal changes in the number of animals killed of each age during harvests. I examine the evidence for arrival times by order of decreasing age within each sex, and compare the relative numbers returning for each age of young seals. The published and unpublished literature on northern fur seals is reviewed for information on arrival times and abundance. The relationship between arrival schedules, relative number returning, and onset of sexual maturity is discussed.

METHODS

The kill data from St. Paul Island used in this study were collected during 1956-82 by the National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle. Most data up to 1979 were listed by Lander (1980), who noted the method of data collection and the number killed by age, sex, date, and location. Kozloff (1981[2], 1982, 1983) listed the data collected during 1980-82. Abegglen et al. (1956, 1957, 1958, 1959) determined the age-specific pregnancy rates of females killed during 1956-59. These authors considered a female to be pregnant when parous (carrying a term fetus), or recently postpartum (lactating or uterus involuting). They did not separate females into these two categories, or determine whether postpartum females were carrying a new conceptus.

Almost all males and females were killed on hauling grounds rather than on rookeries. No commercial kills for males took place on rookeries, and only a few took place for females. Typically, the kill of both sexes on hauling grounds was made between late June and mid-August. It consisted of a series of consecutive 5-d circuits, or rounds, of all hauling ground sites. During each round, a crew undertook one killing operation at each site, and killed all seals present of a particular sex and length. The body length limits for harvesting were set in inches (in) from nose to tip of tail, or from nose to base of tail. I converted all lengths to cm and standard length, using 1 in for tail length. Lander (1980) and the North Pacific Fur Seal Commission (1984b) noted the annual changes in management practices on St. Paul Island. The changes included variations in body length limits, kill dates, quotas, kill locations, and special kills for sex and age. I used only data that were collected under comparable management restrictions.

[2]P. Kozloff (editor). 1981. Fur seal investigations, 1980. NWAFC Processed Rep., 96 p. National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle.

Probit plots of age-specific cumulative length frequencies were used to determine the percentage of males and females of each age present in the kill for each set of length limits. Sufficient age-length data were not available for the plots from kills made on St. Paul Island, but were available from samples collected pelagically for research purposes by the United States and Canada under the terms of the North Pacific Fur Seal Commission. These data are on file at the Pacific Biological Station, Nanaimo, and at the National Marine Mammal Laboratory, Seattle. The age-length data used were from seals collected near St. Paul Island during June-August 1958-74. The lengths of females used were those of postpartum and nonpregnant seals, the main categories of females killed on land.

I assumed that seals were arriving on St. Paul Island when the number killed increased in successive rounds and that arrival was completed when the number killed reached an asymptote. These assumptions were valid only under certain circumstances. One was that all seals encountered of a designated sex and length were killed, which was the case. Another was that the number of seals hauled out, and thus available for killing, was a constant proportion of the number alive through the harvest season. The assumption seems reasonable in that Gentry (1981) estimated an average of about 19% of marked juvenile males were ashore at any one time on St. George Island. Finally, the proportion of a particular age and sex killed during each year must have been sufficiently small so as not to have substantially reduced cohort size, and thus altered the trend in numbers killed by round. This qualification was probably true for all ages, except perhaps for 4-yr-old males. Lander (1981) estimated the harvest utilization rate of males on St. Paul Island to be only 2.8% for age 2, 40.3% for age 3, 14.7% for age 5, but 57.3% for age 4. Escapement rates of females from the commercial harvest were not calculated, but were probably high. The females killed were mainly of ages 3 and 4 with the largest annual take for age 3 in the years studied being 9,700, and for age 4 being 6,300. These figures compared with about 55,000 and 48,000, respectively, for females present in the whole population, based on Lander's (1981) life table for the species.

The number killed of each age up to the last day of each round for each year was plotted to describe the seasonal change in numbers killed. For males, the most common last-day dates for each round were in the series of 5-d rounds ending between 1 July and 5 August. For years in which the dates for last-day rounds differed from this series, the number of

males killed was interpolated from the annual plots, so as to standardize the number killed by date. The mean number of males killed, and standard error of the mean, were determined for each date of the last-day of rounds. During 1965-72, a kill of males sometimes took place twice at a haul-out site in one round, but was missed at this site in the preceding or following round. In these cases, one of the two kills was selected randomly and transposed to the other round. Occasionally, sites were visited extra times without being missed in the adjacent round. These data were omitted.

The kill data used for females on hauling grounds were from years in which the kills on rookeries and hauling grounds were recorded separately, and in which the pregnancy rates were noted. Such kills took place only during 1956-59. These kills were made during the 5-d rounds with the last-day dates between 1 July and 20 August. The only kills on rookeries for which pregnancy data could be used were in 1956 and 1957. On 1-6 July 1956, a kill was made on Polivina rookery. All kills made in the region of this rookery on 1-21 July 1957 were in fact made only on the rookery (A. Roppel[3]). The number of females killed on rookeries was set by quota, rather than by all available animals being taken, as on hauling grounds. No body length limits were imposed on the kill of females on rookeries in 1956 and 1957.

To determine the relative number of each age that returned to St. Paul Island, I reviewed the largely subjective comments on abundance given in the literature, and also compared the number killed when arrival was believed to have been completed. For the latter, the only data used were from years when body length limits included at least 50% of the individuals of the relevant age and when the total number of living animals of a particular age did not change substantially between years. The main change in herd size was between 1956 and 1959, when pup production on St. Paul Island decreased by about 27% due to the killing of adult females during the herd reduction program (York and Hartley 1981; Fowler 1982). Pup production changed little between 1960 and 1980, although declined slightly in 1981-82. The cumulative effect of harvesting a cohort over several years was considered when comparing the relative number of each age killed. The relative numbers of females of each age killed between 1956 and 1959 were biased slightly downward with time by the herd reduction program during the intervening years. The bias was only slight because of the years and ages selected for analysis, the lack of time for the herd reduction program to have potentially changed age distribution, and the fact that most seals ages 1 and 2 remained at sea.

[3]A. Roppel, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. July 1983.

RESULTS

Effect of Body Length Limits

The lower length limit of 107 cm for males included essentially no individuals age 1, few age 2, but most of those ≥3 yr (Table 1). The upper length limit varied by year, with the smallest upper limit including a few ≥4 yr, and the largest, a few ≥6 yr. I used kill data collected from the years 1969-82 to describe arrival times and relative numbers of males ages 1 and 2. Data from the years 1962-82 were used to describe the arrival time and relative number of 3-yr-olds. For males ≥4 yr, the relative numbers returning by age could not be compared with one another, or with younger males, because of the cumulative reduction in the size of a cohort by the harvest, and the exclusion of seals by upper length limits. I used data from the years 1963-72 and 1980-82 to describe the arrival schedule for age 4, and 1964-71 for ages 5, 6, and ≥7.

The lower length limit of 104 cm for females included most individuals ≥4 yr, while the upper length limit of 116-117 cm included mostly ≤5 yr. Data collected in 1956 were used to describe the arrival schedules for females ≥4 yr, and 1958-59 for those ≤5 yr. The number of females killed at age 3 during 1959 was not used due to an unusually low pup survival in 1956 (Abegglen et al. 1959; Lander 1979).

Arrival of Males on Hauling Grounds

1-Year-Olds

No yearling males were taken in the kill by 5 August, and thus none were likely to have been on hauling grounds up to this time. However, few yearling males apparently go to hauling grounds. Osgood et al. (1915) and Roppel et al. (1965a) indicated that yearlings of both sexes preferred rookery edges, near cows and pups, and only occasionally went to hauling grounds (see section on Arrival of Males on Rookeries).

2-Year-Olds

Very few 2-yr-old males arrived by 1 July (Fig.

TABLE 1.—Percent of each age included in standard length restrictions for kills of male and female northern fur seals on hauling grounds. Percentages determined from Probit plots of age-length cumulative length frequencies of seals collected at sea near St. Paul Island by the United States and Canada. Sample sizes are in parentheses.

Length limit (cm)	Years	Age (yr) 1	2	3	4	5	6	≥7
		Males						
		(24)	(166)	(251)	(117)	(48)	(20)	(43)
107-119	1956-58, 1960	1.6	27.7	71.0	44.2	5.0	3.0	0.0
107-121	1959	1.6	27.9	76.5	55.7	8.3	4.0	0.0
107-124	1961-63	1.6	28.0	79.5	71.2	15.5	6.5	0.0
107-[1]135	1964-68	1.6	28.0	82.0	96.8	64.0	28.0	≤1.2
[1]≤135	1969-71	100.0	100.0	100.0	98.6	64.0	28.0	≤1.2
≤124	1972, 1980-82	100.0	100.0	97.5	73.0	15.5	6.5	0.0
≤117	1973-75	100.0	99.2	82.0	35.0	3.0	1.5	0.0
≤119	1976-79	100.0	99.5	86.0	40.0	4.0	2.0	0.0
		Females						
		(18)	(69)	(297)	(465)	(301)	(136)	(530)
≥104	1956	0.0	16.0	48.0	89.0	97.0	99.4	≥99.9
≤116	1958	100.0	99.8	98.4	80.0	54.0	31.5	≤12.0
≤117	1959	100.0	99.9	99.0	84.0	63.0	40.0	≤16.0

[1]Upper body size was the presence of a mane. A. Roppel (National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, WA 98115, pers. comm. July 1983) felt that the mane developed at a body length of about 135 cm.

1). Numbers began to increase in early July and continued to increase up to 5 August. This age group began to arrive earlier than the yearlings. Osgood et al. (1915) observed the first branded 2-yr-old individuals on 12 June, about 1½ mo before the first branded yearling males on rookeries. As found in the current study, Kenyon and Wilke (1953) noted that 2-yr-olds were quite common by the end of July, and after 1 August became increasingly abundant.

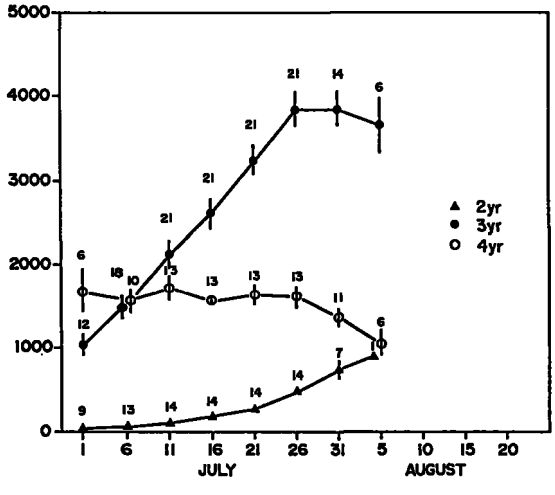

FIGURE 1.—Mean number, and standard error, of northern fur seal males killed of age 2-4 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle. Number of years of data for each date indicated above means.

The date of peak numbers, and thus the date when most arrived, was probably after early August. The date when most would have arrived may be determined by assuming that the interval between the time when seals clearly began to increase in number and the time when essentially all seals had arrived was the same for 2-yr-olds as for bulls and cows. Observations by Peterson (1968) suggested that this interval was about 1-1½ mo for bulls and pregnant females. Because the number of 2-yr-old males began to increase in early July, the arrival time for most was probably mid- to late August. A similar arrival time was also indicated by subtracting 1-1½ mo, the interval separating the first sightings of tagged yearlings and 2-yr-olds, from the arrival time of late September to early October for yearling males on rookeries.

The number of 2-yr-olds returning appeared to be greater than that for yearlings, but less than that for 3-yr-olds. Roppel (fn. 3) felt that more 2-yr-old males returned than yearling males, and Kenyon et al. (1954) noted that many 2-yr-olds remained at sea.

3-Year-Olds

The 3-yr-olds were already quite abundant by 1 July and reached a peak in numbers by late July (Fig. 1), suggesting that arrival was completed by late July. Kenyon and Wilke (1953) similarly noted the maximum number of 3-yr-olds on hauling grounds was after mid-July. This age group

appeared to have the largest number of males returning.

4-Year-Olds

The number of males killed of age 4 remained essentially constant during July, except for a decrease in late July (Fig. 1). Although no distinctive peak in numbers was evident, several factors suggest the main arrival was probably completed by mid-July. First, the number killed in the first round (i.e., up to 1 July) was likely to have been too large relative to later rounds because of an accumulation of males that arrived before the kill began. This situation was most obvious for kills of males ages 5 and 6 (Fig. 2), but also could have existed to some extent for the kill of males ages 2 and 3. For ages 2 and 3, the accumulation would not have been as obvious because the main arrival time was after kills began. Secondly, the true peak in number killed of 4-yr-olds was probably flattened by the high harvest utilization rate of this age. Finally, an examination of the trend in numbers killed by round for individual years indicated the seasonal pattern was quite variable, ranging between that noted for males age 3, and that for males age 5. For example, the arrival time for 4-yr-olds in 1971 was similar to that seen for the typical 3-yr-olds; it was similar for the typical 5-yr-olds in 1968; and in 1980 it was intermediate, with a distinctive peak in mid-July. Such variations tended to dampen the peak. Kenyon and Wilke (1953) remarked that the maximum number of males older than 3 yr arrived before mid-July. Fewer age-4 males returned than age-3 males, probably due to the large kill at age 3.

5-Year-Olds

Most 5-yr-olds appeared to have already arrived by early July (Fig. 2). However, as noted for 4-yr-olds, the kill by 1 July was probably large relative to the number killed in later rounds. Most males probably arrived by late June to early July, assuming the time in peak numbers of 5-yr-olds was earlier than mid-July, but not earlier than for territorial bulls (≥7 yr) on rookeries. Fewer 5-yr-olds returned than 4-yr-olds because of the large kill of males at age 4.

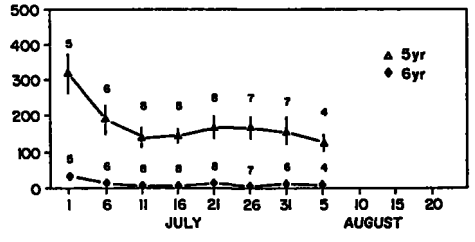

FIGURE 2.—Mean number, and standard error, of northern fur seal males killed of age 5-6 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle. Number of years of data for each date indicated above means.

6-Year-Olds

As with 4- and 5-yr-olds, the first kill was likely too large. Most 6-yr-olds probably arrived by late June. Gentry (1981) tagged juvenile males on hauling grounds of St. George Island in 1977 and counted them during late May to mid-August 1980. Although the ages were not known with certainty, the most common age in 1977 was likely 3 yr, with a range of 2-5 yr (R. Gentry[4]), and thus most males in 1980 were probably 6 yr of age. His counts indicated numbers began to increase in late May, reached a peak on 19-28 June 1980, and declined thereafter.

≥7-Year-Olds

No males older than 6 yr of age were taken in the annual kills on hauling grounds. This was because the upper length limits excluded these ages from kills, and because many males of these ages go to rookeries for breeding rather than to hauling grounds.

Arrival of Males on Rookeries

1-Year-Olds

Behavioral studies suggest most yearling males probably arrived on rookeries by late September to early October, and the number returning was the smallest of any age group of males. Osgood et al. (1915) reported that branded male yearlings were rarely seen between late July and mid-August but became more numerous later, although they always remained small in number. Kenyon and Wilke (1953) mentioned yearlings of unspecified sex returned principally in September to November, and that only a few individuals were involved. Using counts of tagged yearlings seen on rookeries between 17 September and 17 October, Roppel et al. (1965a)

[4]R. Gentry, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. February 1984.

suggested that the largest number of yearlings of unspecified sex was present on 27 September to 11 October. These animals were predominantly males, as indicated by the recorded sex ratio of 84% males in a sample of 356 yearlings seen during 1961-65 (Roppel et al. 1965a, 1965b, 1966). Osgood et al. (1915) noted all yearlings examined during his study were males. Surveys by Abegglen et al. (1961) indicated very few yearlings of either sex were present on rookeries after early November.

≥7-Year-Olds

Essentially all males present on rookeries during the pupping season were bulls (Jordan and Clark 1898). According to Johnson (1968), the age of such bulls would have been ≥7 yr. Peterson (1965, 1968) noted that bulls began to arrive on rookeries in mid-May, reached peak numbers by late June, and declined in numbers after mid-July. No data exist on whether old bulls arrived before young bulls.

Arrival of Females on Hauling Grounds

Pregnant, ≥4 Years

Very few females younger than 4 yr give birth (Lander 1981). Pregnant females age ≥4 were rarely taken on hauling grounds during July, but were increasingly common during 1-15 August (Fig. 3). Using the trend in the number of 4- and 5-yr-olds killed after 15 August, most pregnant females probably arrived by mid-August. Because essentially all pregnant females gave birth in July, the pregnant females killed on hauling grounds during August would have been postpartum. An examination of the median dates for collection of pregnant females suggested that arrival times on hauling grounds of age ≥4 did not differ among ages (Table 2).

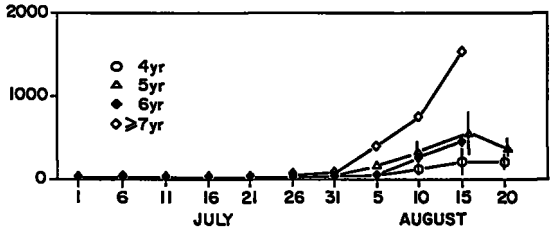

FIGURE 3.—Mean number, and range, of pregnant females of northern fur seal killed of age ≥4 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle.

Nonpregnant

1-YEAR-OLDS.—As with yearling males, yearling females apparently preferred rookeries to hauling grounds (Jordan and Clark 1898; Roppel et al. 1965a). No yearling females were taken on hauling grounds during the commercial kill for females up to 20 August.

2-YEAR-OLDS.—Jordon and Clark (1898) and Osgood et al. (1915) suggested 2-yr-old females also preferred rookeries to hauling grounds. However, a few were taken on the hauling grounds during the harvest for females. Numbers began to increase in mid-August (Fig. 4), and thus increases began about 1 mo later than males of the same age. Assuming a 1-1½ mo interval for essentially all animals to arrive, as assumed for 2-yr-old males, then 2-yr-old females probably arrived by mid- to late September.

≥3-YEAR-OLDS.—Very few nonpregnant females ≥3 yr were taken on hauling grounds in July, but many were present by 15 August (Figs. 4, 5). Based on the trend in the number of females killed at 3-5 yr, the arrival of ages ≥3 yr was essentially completed by mid-August. Support for this conclusion comes from Peterson (1965, 1968), who counted

TABLE 2.—Median dates of collection of pregnant and nonpregnant females of northern fur seals taken during 1956, 1958, and 1959 on hauling grounds of St. Paul Island. All dates are in August. Data from annual reports of the National Marine Mammal Laborabory, National Marine Fisheries Service, NOAA, Seattle.

		Age (yr)							
Year	State	3	4	5	6	7	8	9	≥10
1956	Pregnant	—	11	11	9	11	10	10	9
	Nonpregnant	12	11	11	10	11	10	10	9
1958	Pregnant	—	9	9	9	8	10	15	10
	Nonpregnant	13	11	10	10	8	10	10	8
1959	Pregnant	—	13	12	12	12	12	12	13
	Nonpregnant	14	13	13	12	12	13	11	12

"nonbreeders" on hauling grounds and the inland edges of rookeries. "Nonbreeders" were thought to consist of idle females and young males. He observed a sharp increase in numbers in early August and that most arrived by mid-August. The current study indicated the female component of Peterson's "nonbreeders" were mainly nonpregnant females, plus a few postpartum females. Abegglen et al. (1956) noted an increase in the number of seals on hauling grounds and rookery edges between 15 August and 4 September. While this increase may have resulted from a continued influx of nonpregnant females at ⩾3 yr, it may also have been due, at least in part, to the arrival of some 2-yr-old males and females.

The increase in number of nonpregnant females during August consisted primarily of 3- and 4-yr-olds. A comparison of the median dates for collection of nonpregnant females at ⩾3 yr on hauling grounds suggests that arrival times were similar for each age (Table 2).

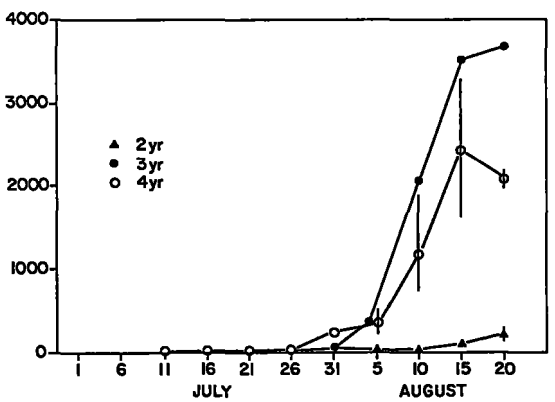

FIGURE 4.—Mean number, and range, of nonpregnant females of northern fur seal killed of ages 2-4 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle.

Arrival of Females on Rookeries

Pregnant, ⩾4 Years

Females gave birth on St. Paul Island during 15 June to 10 August, with about 90% of all births completed by 20 July (Bartholomew and Hoel 1953; Peterson 1965, 1968). The general belief that pregnant females arrived by order of decreasing age apparently originated from Wilke (1953). He collected 571 females on rookeries from 15 June to 4 September and showed the median date of collection for each age became progressively earlier with age. For example, the median collection date for females at ⩾10 yr was 7 July, while that for females at 3 yr was 23 August. However, Wilke did not separate pregnant and nonpregnant females in his calculations. The large shift in median dates probably resulted mainly from an influx of young nonpregnant females on rookeries during August, as took place on hauling grounds.

An analysis of arrival times for pregnant females of each age should not include seals that are nonpregnant. Such an analysis can be made using data collected by Wilke between 15 July and 22 July 1953 (Table 3). Although Wilke did not record pregnancy

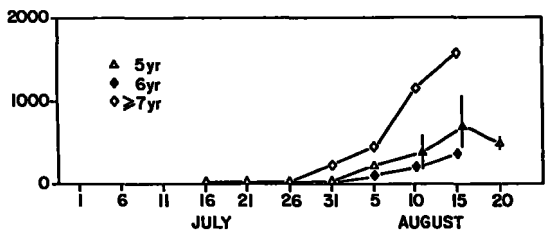

FIGURE 5.—Mean number, and range, of nonpregnant females of northern fur seal killed at age ⩾5 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle.

TABLE 3.—Median dates of collection of northern fur seal females on rookeries of St. Paul Island during 17 June to 22 July 1953. Data from Wilke (1953) and the current study.

	Number collected by age							
Date Age (yrs):	4	5	6	7	8	9	⩾10	*n*
17 June	0	2	2	1	0	0	20	25
22 June	1	0	7	3	2	2	22	37
27 June	0	2	3	1	1	3	26	36
2 July	0	4	5	7	5	5	23	49
7 July	0	2	6	3	3	6	20	40
12 July	1	3	5	1	1	0	2	13
17 July	2	2	5	3	5	5	21	43
22 July	3	9	8	7	6	1	16	50
Median date	16 Jul	10 Jul	6 Jul	4 Jul	9 Jul	.3 Jul	29 Jun	

rates for this sampling period, the rates were probably 90-100%, as will be shown later on rookeries for the period 1-21 July. A comparison of median collection dates suggests arrival may have taken place slightly earlier with increasing age, but no clear shift in arrival times was evident, as previously believed. Unfortunately, the true age-specific arrival times of parous females cannot be determined readily from these data. The main difficulty is that the pregnant females used in the analysis included not just parous seals, but postpartum seals as well. Postpartum seals usually remain on land for 2 d, then go to sea to forage for 8 or 9 d, and repeat this pattern about 10 times throughout the nursing period (Peterson 1958; Gentry and Holt in press). The potentially complex effect that returning postpartum females could have on the trend in the number of parous females arriving of a particular age must be considered. Other difficulties were the small sample sizes, and the fact that the sample sizes taken on each date did not reflect the increase in numbers on rookeries. At this time, while a slight shift in arrival times of parous females may exist with age, more research is needed for confirmation.

Nonpregnant

1-YEAR-OLD.—Jordan and Clark (1898) felt yearling females did not arrive on rookeries before September. As noted earlier for yearling males, Kenyon and Wilke (1953) felt yearlings returned to the Pribilof Islands mainly during September to November, and only a few individuals were involved. The date of arrival for most yearling females is unclear, although it is probably after yearling males, during October to early November. Only a small number of yearling females had arrived by late September to early October compared to males. However, they arrived presumably no later than early November, because few yearlings were present on the rookeries after that time.

2-YEAR-OLDS.—The arrival of 2-yr-old females on rookeries began in August, a similar time to that seen on hauling grounds. Branding studies by Osgood et al. (1915) suggested a few individuals began to arrive about one month after males. The first branded 2-yr-old female was seen on 19 July compared to 12 June for males age 2. Thus, arrival was probably completed also a month later than males, by mid- to late September. Jordan and Clark (1898) reported that 2-yr-old females began to increase in numbers by about 1 August, while Kenyon and Wilke (1953) noted they did not begin until late August, and the current study suggested arrival on hauling grounds began in mid-August. Kenyon and Wilke (1953) believed the largest number were present in October, slightly later than suggested by the current study. Based on the comments by Kenyon and Wilke (1953) and Kenyon et al. (1954), fewer 2-yr-olds returned than 3-yr-olds, but more 2-yr-olds returned than yearlings.

≥4-YEAR-OLDS.—A total of 1,533 females were collected on rookeries during 1-6 July 1956 and 1-21 July 1957, a period covering the main pupping season. All females were ≥4 yr of age. Of these, only 2% were nonpregnant, a low rate compared to 31% nonpregnancy for the population as a whole, based on the life table derived by Lander (1981). The low rate likely resulted from the small number of nonpregnant females on the rookeries, as was found on

TABLE 4.—Summary of the times of arrival and relative numbers for males and females of northern fur seal rookeries and hauling grounds of St. Paul Island, based on the current study and a review of the literature.

Sex	Site[1]	State[2]	Age (yr)	Arrival time[3]	Abundance
Male	R		1	late Sept. to early Oct.	few
	HG		2	mid- to late Aug.	2 yr > 1 yr
	HG		3	late July	3 yr > 2 yr
	HG		4	mid-July	—
	HG		5	late June to early July	—
	HG		6	late June	—
	R		≥7	late June	—
Female	R	NP	1	Oct. to early Nov.	few
	HG,R	NP	2	mid- to late Sept.	2 yr > 1 yr
	HG	NP	≥3	mid-Aug.	3 yr > 2 yr
	HG	P	≥4	mid-Aug.	—
	R	P	≥4	mid-July	—

[1]R = rookery; HG = hauling grounds.
[2]NP = nonpregnant; P = pregnant.
[3] Date when essentially all seals would have arrived.

the hauling grounds at this time (Figs. 4, 5). The rate was probably biased downward by the fact that nonpregnant females stayed on land for a slightly shorter period of time than nursing females. Using data given by Gentry and Holt (in press), nonnursing females appeared to stay on shore for only about 64% as long as nursing females. Nonnursing females make about half as many visits to land as nursing females, but stay about one-third longer for each visit.

A gradual increase in the nonpregnancy rate took place on Polivina rookery during early to mid-July: 1 July = 0% (n = 280), 6 July = 2% (734), 11 July = 1% (198), 16 July = 3% (148), and 21 July = 6% (173). When weighted for the shorter period of stay on land by nonpregnant females, the rates increased from 0% by 1 July to 10% by 21 July. Presumably, the increasing rate during July resulted from the arrival of more nonpregnant females age ≥4. Numbers of nonpregnant females began to increase particularly by mid-July.

DISCUSSION

Northern fur seals arriving on St. Paul Island can go first to rookeries located on beaches just above high tide, or to hauling grounds more inland. The typical arrival sequence (Jordan and Clark 1898; Kenyon and Wilke 1953; Peterson 1965, 1968) is for the bulls to establish territories for breeding on rookeries in May-June. Pregnant females arrive next on rookeries to pup, mate, and nurse in harems within the territories. Subadult males arrive mainly during the pupping season and go to hauling grounds rather than rookeries. Although young males of different sizes (i.e., ages) tend to arrive in successive waves with time, studies of marked seals (Gentry et al. 1979) indicate that arrival times of individual subadult males can be quite variable between years. In early August, harem bulls abandon their territories, and the social structure of the rookery disintegrates. Nursing cows then tend to disperse more widely on land, and nonterritorial bulls and some subadult males move on rookeries from hauling grounds. The mixing of seals between rookeries and hauling grounds after July results in less site distinction. The literature is unclear as to the arrival times of subadult and nonpregnant adult females after July, and whether these seals go first to rookeries or to hauling grounds, or go to both simultaneously. Age 2 females arrive later in the season, and go to rookeries and hauling grounds, while yearlings of both sexes arrive last, and go mainly to rookeries. Seals begin leaving St. Paul Island for the southern migration in October to November (Roppel et al. 1965a; Kenyon and Wilke 1953). Few remain on the hauling grounds after mid-October, and few on rookeries after early November.

Table 4 summarizes the age-specific arrival times and relative numbers of seals seen on rookeries and hauling grounds, based on information given in the Results. Two arrival times existed for pregnant females, one by mid-July on rookeries and the other by mid-August on hauling grounds. The second date no doubt resulted from the movement of some postpartum females from the rookeries to the hauling grounds after the harems disintegrated. Thus, the arrival time on St. Paul Island was by mid-July, rather than mid-August.

The arrival times for nonpregnant females at ≥3 yr on to St. Paul Island was less certain than for pregnant females because age-specific data on arrival times existed from hauling grounds up to mid-August, but not from rookeries after mid-July. Also it was not known whether nonpregnant females went first to rookeries or to hauling grounds. The main arrival time was probably by mid-August, as was found on hauling grounds. This was likely because nonpregnant females began to increase in numbers on rookeries in early to mid-July, and an interval of 1-1½ mo was probably needed for essentially all arrivals to be completed. Also, Abegglen et al. (1956) felt that most females on the hauling grounds during August came directly from the sea, although some came from rookeries. From the current study, some postpartum females go from rookeries to hauling grounds. Perhaps most nonpregnant females go first to the hauling grounds.

Nonpregnant females ≥3 yr arrived about 1 mo later than pregnant females. According to R. Gentry (fn. 4), marked adult females on St. George Island also arrived later when nonpregnant, although only about 10 d later. The reason for the differences in length of delay caused by nonpregnancy found in the two studies is unclear at this time. The answer may come when details of the study by Gentry are reported, or perhaps when more is known about movement patterns of adult females between rookeries and hauling grounds.

The finding that nonpregnant females arrived after pupping suggests nonpregnancy delayed the date of mating. A delay in mating has been reported previously for maturing females, but not for nonpregnant cows. Because parous females pup about 1 d after arrival, and mate 5-6 d after pupping (Peterson 1968; Gentry and Holt in press), essentially all females that pup will have mated by mid-

to late July. Assuming a similar interval between arrival and mating for nonpregnant females, most nonpregnant females would be mated by mid- to late August. Jordan and Clark (1898) stated that young females were impregnated in early August, after old females, and Abegglen et al. (1958) observed that females ages 3 and 4 bred after the harems disbanded. Also, Craig (1964) reported females ovulated for the first time in late August or September. The only evidence that I could find of late mating in a nonpregnant cow was by Osgood et al. (1915), who observed a harem bull mating a female that was "not very young" on 21 August.

A comparison of the age-specific arrival times for each sex on St. Paul Island (Table 4) largely confirms the comments by Kenyon and Wilke (1953) and Fiscus (1978) that arrival began progressively earlier with increasing age. However, the current study indicated that this phenomenon was obvious only for young ages. It was seen in nonpregnant females ages 1-3 and in males ages 1-6. Although no differences in arrival times were shown for older males and nonpregnant females, differences could exist, but would be small. The differences in arrival times became progressively less with age for males between 1 and 6 yr and apparently for females between 1 and 3 yr.

A comparison of the relative numbers returning to St. Paul Island (Table 4) suggests that progressively more males and females returned between ages 1 and 3. The cumulative effect of the kill on males of 2 and 3 yr prevented comparisons of abundance with males ≥4 yr. For females, the number of 4-yr-olds returning was probably not greater than 3-yr-olds, as suggested by the similarity in the number of 3- and 4-yr-olds killed on hauling grounds by mid-August (Figs. 3, 4). However, pregnancies complicate comparisons of abundance on hauling grounds between females 3 yr and older. Between ages 4 and 10, an increasing proportion of females become pregnant (Lander 1981) and thus go to rookeries rather than hauling grounds.

The data collected in this study suggest that, with age, young seals of both sexes arrive progressively earlier, and in progressively larger numbers. The reason for these changes in arrival schedules lies in an understanding of the mechanism that controls the migration schedule. However, little is known about this mechamism in the northern fur seal. The mechanism, if it is like that of other vertebrates (see Gauthreaux 1980; Baker 1978), is probably complex. It could involve selective factors, such as food supply and climate, and numerous environmental and physiological factors, such as photoperiod, reproductive hormones, and endogenous rhythms. For northern fur seals, learned and innate components are likely to be involved. There are several examples of where learning has been suggested to be involved in migration. When the species leaves the Pribilof Islands for the southern migration, juveniles tend to disperse widely in the North Pacific Ocean, pregnant females tend to travel to the coastal waters off California, and adult males generally remain in the northern Gulf of Alaska (Baker et al. 1970; Fiscus 1978). Baker (1978) has suggested that the juvenile northern fur seals may explore the habitat, and, with age, eventually learn the best wintering areas. Also, an increasing proportion of immature seals return to their natal sites on Pribilof Islands with age (Kenyon and Wilke 1953), although sometimes the natal site is abandoned and a new colony is established, such as at San Miguel Island, CA (Peterson et al. 1968). Baker (1978) has proposed that site recognition may be learned shortly after birth, and with time, the site is usually relocated. However, other components of migration may be innate. For example, the annual timing of arrival for pregnant females on St. Paul Island is remarkably precise. Peterson (1968) calculated the mean arrival date to be 30 June for each of 3 years. Such precision seems unlikely to be the result of only learning. Keyes et al. (1971) examined the pineal gland of this species for seasonal variations in hydroxy-indole levels for various ages of males and females, and postulated photoperiodic regulation of the reproductive cycle.

A physiological event in the lives of young males and females which coincides with the cessation of arriving earlier and returning in greater numbers is the attainment of sexual maturity. Baker (1978) pointed out that sexual maturation controls the initiation of migration in many vertebrates. While a few male northern fur seals begin to produce sperm at 3 yr, most do not do so until about 5 yr (Kenyon et al. 1954; Murphy 1969, 1970). The average female conceives for the first time on her 5th birthday, although typically ovulates for the first time on her 4th (Craig 1964; York 1983). Thus, it was during the years of immaturity that young seals gradually synchronized their arrival schedules with that of the adults. Perhaps the gradual process of gonad maturation in both sexes over several years plays a role in inducing a cohort to migrate progressively earlier in the year and in causing a greater proportion to return to breeding sites.

A relationship between sexual maturity and changes in arrival times on St. Paul Island could explain two other arrival phenomena noted in this study. In the first case, considerable annual varia-

tion was noted in the seasonal pattern of arrival for 4-yr-old males, ranging from the typical pattern seen in 3-yr-olds to that seen in 5-yr-olds. Such differences in the arrival pattern may indicate that the age at which males reach sexual maturity differs between cohorts, a possibility worth further investigation. Variations in the age at sexual maturity could result from annual variations in body growth rate caused in turn by fluctuations in food supply. In the second case, pregnant females at ≥4 yr may have arrived slightly earlier with increasing age. This would take place if the first conception resulted in a later date of parturition than in subsequent years. This is a possibility because, according to Craig (1964), the first ovulation appears to be later than subsequent ovulations. The age of primiparous females spans mainly between 4 and 10 yr (York 1983), and thus the age at first ovulations presumably also spans a similar number of years. Arrival times would tend to be slightly earlier with age from the increased proportion of mature females.

An alternate explanation for seals arriving in progressively larger numbers, may lie in the energetic costs of the return migration from the North Pacific Ocean to the Bering Sea. For yearlings, the energetic costs may be too large for all but a few individuals to return. With age, the relative costs may be more favorable and permit an increased proportion to return.

For each age, males tended to arrive before females. This situation could result if, through selection or learning, the time of the return migration was ultimately established for each sex by the adults. The mechanism controlling the timing of migration in young seals would gradually shift arrival times with age to eventually synchronize with those of the adults. However, because the arrival times of adult males was earlier than that of cows, the arrival times of immature males would also be before those of immature females. The fact that nonpregnant adult females arrived after parous females could be the result of nonpregnant females gaining some advantage in the energetic costs of migration. Since presumably competition exists for food around the Pribilof Islands during the summer, perhaps survival of nonpregnant adult females is enhanced by feeding elsewhere, thus delaying the return migration by 1 mo.

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