Trends in Female Northern Fur Seal, *Callorhinus ursinus*,

Feeding Cycles Indicated by Nursing Lines

in Juvenile Male Teeth

by

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Abstract

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Northern fur seal (*Callorhinus ursinus*) teeth were examined for evidence of changes in the number of feeding trips made by lactating females from St. Paul Island, Alaska, during 1949-81. Teeth from 3-year-old males were sectioned and examined under transmitted polarized light. Lines formed in the dentin during the nursing/fasting cycles between birth and weaning were counted. A negative correlation was found between the number of nursing lines (or feeding trips) and the number of pups born. Increasing numbers of nursing lines during an extensive harvest of adult females during 1956-68 suggest that the number of feeding trips or trip duration reflect changes in per capita food availability for northern fur seals. Trends in nursing lines are not consistent with the hypothesis that a population decline following the female harvest was due to food limitation in the Bering Sea during the rearing season.

Significant correlations between the number of feeding trips and pup weight, juvenile size and survival indicate that the period of maternal care is a critical time which significantly influences the future of the pup. Nursing lines in teeth may be a useful tool for monitoring population status and indicating cohort strength.

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INTRODUCTION

Forty years ago Scheffer (1950) discovered that annuli in the canine teeth of northern fur seals (*Callorhinus ursinus*) represent a year's growth and could therefore be used to age individuals. Since that time, teeth and other hard tissues have been used to determine age in a wide variety of mammals. In addition, growth lines and patterns of tooth structure have been used to gain a variety of other information about free-ranging animals, including growth rates, foraging behavior, age at sexual maturity, and season of birth/death (Bengtson and Siniff 1981, Hewer 1964, Klevezal 1988).

Among the tooth structures identified as containing information on the life history of northern fur seals are "nursing lines" in the dentin. After giving birth on land, the female suckles her single pup for several days. She then begins a cycle of several-day feeding trips at sea and visits to shore during which she nurses her pup. This cycle continues until the pup weans at 3-4 months of age (Bartholomew and Hoel 1953). Because the mother exclusively suckles her own pup, her nursing pattern imposes on the pup a cycle of feeding and fasting while the mother is on land and at sea, respectively.

Scheffer and Peterson (1967) concluded that a pattern of regular lines observed within the area of dentin laid down between birth and one year of age was a reflection of these nursing cycles. That is, each time the mother is onshore and suckling her pup, a distinct and permanent growth layer forms in the dentin of the pup's teeth. As the pup fasts between the females' visits, another distinct layer forms.

Scheffer and Peterson's conclusion was based on the location of these nursing lines and the observation that they occur in numbers very similar to the number of feeding trips typically made by female fur seals. However, the theory was not proven until Bengtson (1988) showed, through the use of tetracycline marking, that nursing lines in Antarctic fur seals (*Arctocephalus gazella*) are indeed records of feeding/fasting events.

After confirming the formation of nursing lines, Bengtson (1988) carried out a study wherein the mean number of feeding trips made by females per season was estimated by counting the nursing lines in teeth. The number of trips made was interpreted as an index of food availability. Longer trips were considered to result from low food availability, so that fewer trips can be made before the time of weaning.

The first part of this study was to demonstrate that nursing lines in the teeth of juvenile male northern fur seals can be consistently identified and reliably counted in a standard way. Then, information on nursing lines was related to the population history of northern fur seals from

St. Paul Island, Alaska. Specifically, trends in nursing lines are related to: 1) possible changes in intraspecific competition during an extensive harvest of females during 1956-68, 2) population trends before and after the female harvest, and 3) observed changes in juvenile survival and body size.

These analyses were based on changes in the number of feeding trips (nursing lines) made annually by lactating female fur seals over a 33-year period (1949-1981) of dynamic population change. The St. Paul Island population of northern fur seals reached a maximum in the mid 1950's, then began to decline, and did not stabilize until the early 1980's (York and Kozloff 1987). A commercial harvest of females (1956-1968) precipitated the decline, but the level to which the population finally fell was far below that which could be explained by the effect of the female harvest alone (York and Hartley 1981). The cause of the decline has not been clearly identified (York and Kozloff 1987).

The period of the female harvest (1956-1968) provides an opportunity to test a hypothesis concerning intra-specific competition among lactating female fur seals feeding in the Bering Sea around St. Paul Island. A total of 253,049 females were killed on St. Paul Island. If these females were competing for food, their removal ought to have lowered the degree of competition. This situation would presumably allow females to make feeding trips shorter in duration and, consequently, more total nursing cycles. Therefore, the number of nursing lines present in teeth should have increased among the cohorts born during the female harvest. Testing this hypothesis was an objective of this study. The utility of feeding cycles as an index of per capita food availability is also discussed.

Nursing lines were also examined for cohorts born prior to and after the female harvest. Previously noted density dependence indicates that food limitation was probably not a factor in the population decline which extended into the 1980's (Fowler 1987; Baker and Fowler 1990). Another objective of this study is to determine what trends in nursing lines indicate regarding possible changes in abundance of food available specifically to lactating fur seals in the Bering Sea in summer and fall during the population decline.

Survival estimates of male fur seal pups from weaning to age 2 range from 18-49% (Lander 1979), and most of the mortality is believed to occur during the first winter at sea as pups struggle to survive the transition to independence (Kenyon et al. 1954). Previous work indicates that the condition (body weight) in which fur seal pups leave their islands of birth affects their subsequent survival and their body size later in life (Antonelis et al., in press; Baker and Fowler in press). A final objective of this study is to examine relationships between nursing lines, survival, and body size.

METHODS

Selection of teeth for study

Teeth were selected from among a large sample of upper right canines which were collected during the commercial harvests of juvenile male northern fur seals on St. Paul Island, Alaska from 1952-1984. Ages of harvested males ranged from 1 to over 5 years old, though 3-year-olds were by far the most abundant age class. To avoid any influence of age at death while retaining the largest possible pool of teeth from which to select, only teeth from 3-year-olds were included in this study.

Juvenile male fur seals congregate at areas called haulouts, which are adjacent to the 14 breeding rookeries on St. Paul Island. During the commercial harvest, seals from nearby haulouts were killed on the same days (Lander 1980). Therefore, teeth extracted from males from various haulouts were mixed and stored together according to date of harvest and the haulouts harvested that day. Over the years, various combinations of haulouts were harvested together. However, there are five haulout groupings which were consistently kept separate during the harvest, and which correspond to distinct geographical areas of the island

Table 1. Location names corresponding to distinct geographical areas of St. Paul Island, Alaska, and the rookeries associated with these locations

Location Name	Associated Rookeries
Reef	Gorbatch, Ardiguen and Reef
English Bay	Tolstoi, Zapadni, Little Zapadni, and Zapadni Reef
Northeast Point	Morjovi and Vostochni
Lukanin-Kitovi	Lukanin and Kitovi
Polovina	Polovina, Little Polovina and Polovina Cliffs

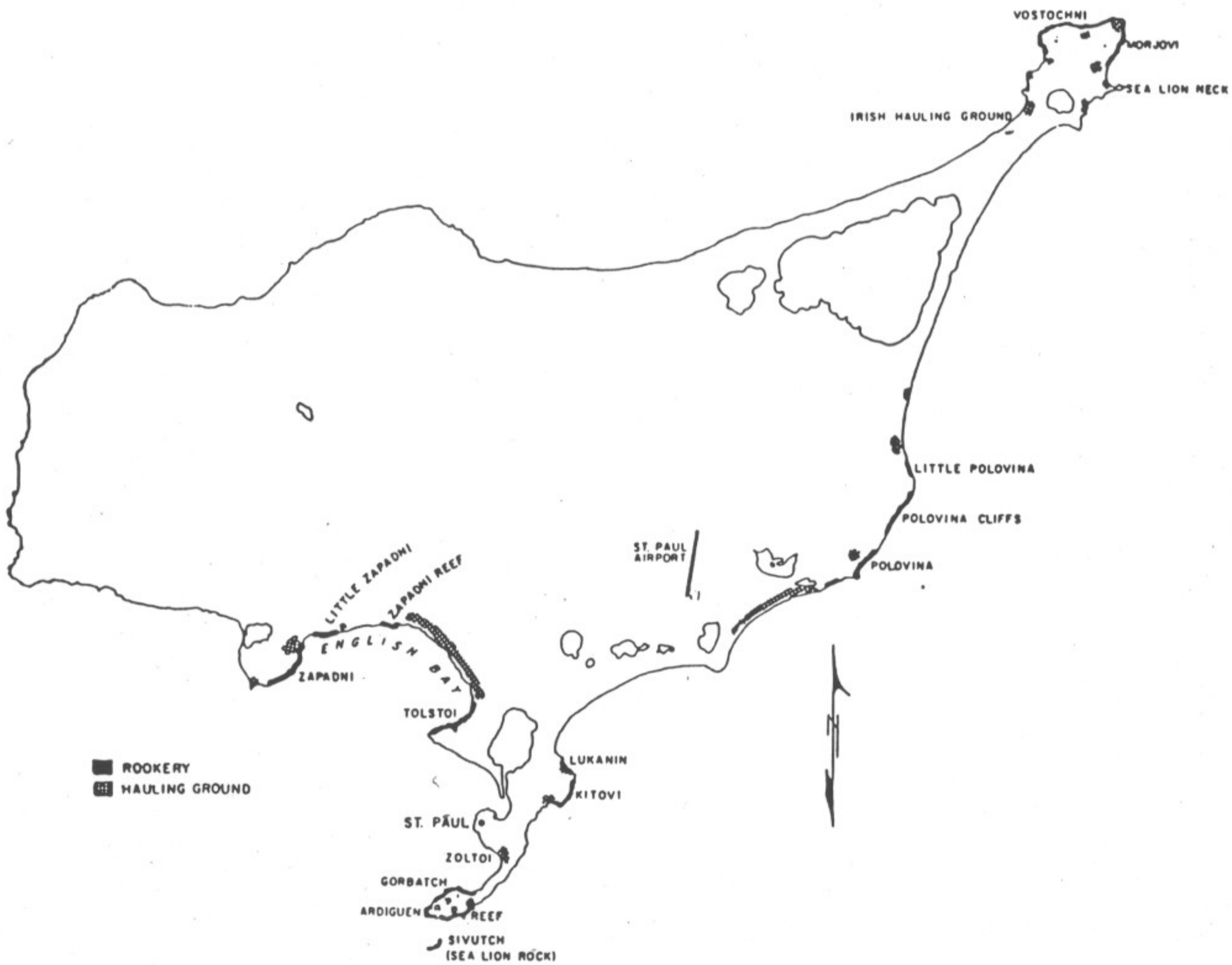

Figure 1. Locations of northern fur seal rookeries and haulouts on St. Paul Island, Alaska.

(Table 1, Figure 1). For this study, teeth were selected systematically from each of these locations within a year. When all locations were not available, the sampling was spread as evenly as possible over the available locations. Also when possible, teeth were chosen from various harvest dates.

Within year and location, teeth were selected randomly and first aged by counting external annual growth rings on the whole tooth (Scheffer 1950). A total of 194 teeth were sectioned from all cohorts 1949-1981 with the exception of 1959-1960, from which no teeth were available. All were 3-year-olds except one which was determined to be a 4-year-old after it was sectioned. This tooth was included in analyses. Originally, four teeth from each year were sectioned and the nursing lines counted. However, although trends were apparent, statistical power of some preliminary regression analyses was low. Samples were added especially for years when estimated numbers of pups born were near their lowest and highest levels during the particular years being tested. This maximized the increases of statistical power resulting from additional sampling for tests involving numbers of pups born.

Preparation of teeth and counting nursing lines

Two, and sometimes three, longitudinal thin sections were cut as near to the center as possible for each tooth using a diamond blade saw (Tyslide by Tycet Limited, Hemel Hempstead, Herts., UK). The sections were then stored in vials containing 70% alcohol. Most of the teeth were also weighed whole on a digital scale accurate to 0.01 g prior to being sectioned.

Each tooth section was examined under 50 x magnification and transmitted polarized light to enhance distinction of layered dentin. The age determined from the whole tooth was double-checked. When counting nursing lines, the reader was blind to all information about the teeth (year, location, etc.). Each section from a single tooth was examined simultaneously to arrive at a best estimate of the number of nursing lines, which was determined in the following way. First, the neo-natal line was located. Then, beginning with the next line interior to the neo-natal line, all subsequent lines up to and including the weaning line were counted and recorded as the total number of nursing lines (Figure 2). The entire sample of teeth was read four times, the reader always blind to previous counts.

Data analysis

The first reading of nursing lines was considered an exercise in learning to recognize tooth microstructures and standardizing counting technique. The resulting data were

Figure 2. A) Longitudinal thin section of a 3-year-old male northern fur seal's upper right canine tooth. The section was photographed using transmitted polarized light.

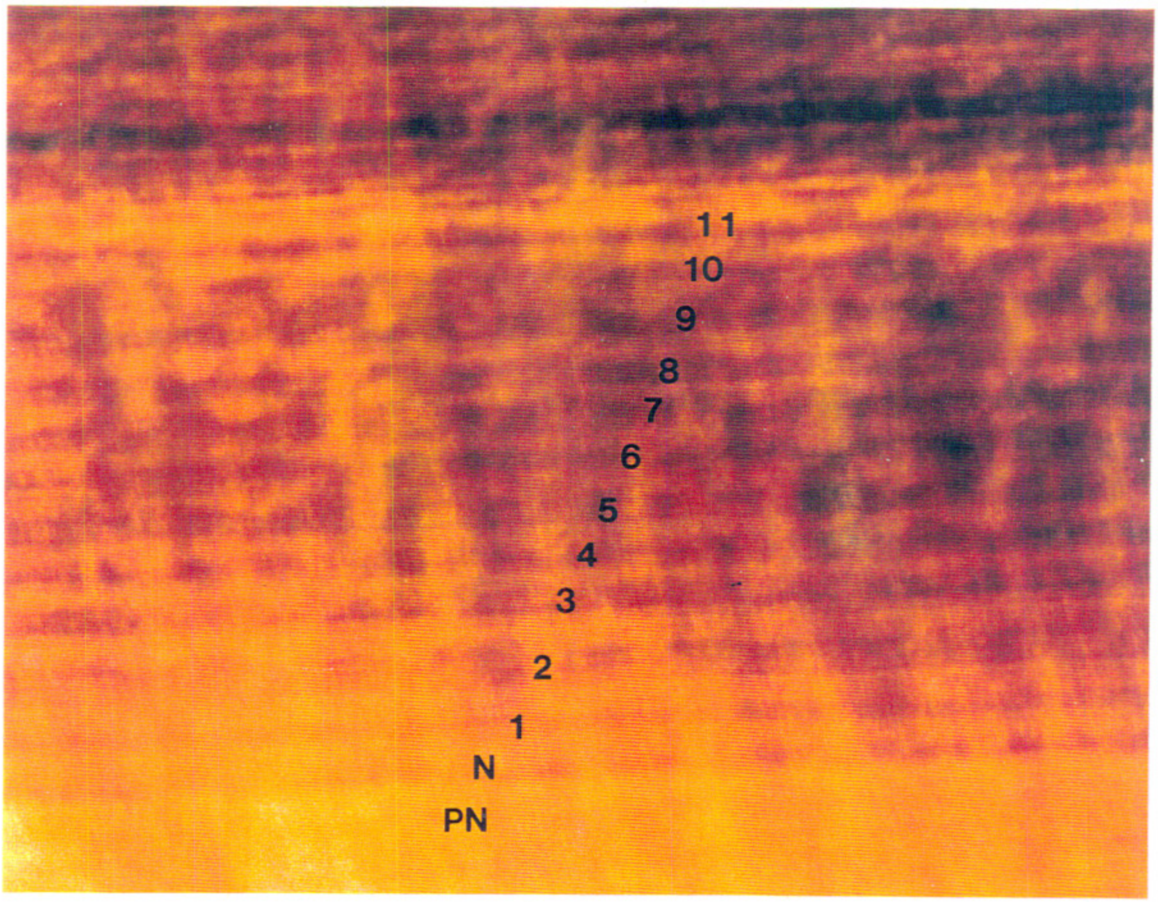

Figure 2. B) Nursing lines in the dentin of a 3-year-old male northern fur seal's upper right canine tooth, viewed with transmitted polarized light. Pre-natal dentin (PN) and the neo-natal line (N) are shown. Eleven nursing lines were counted in this tooth. Note that the last line counted (11) is the weaning line which is the last in the series of distinct and evenly spaced nursing lines.

excluded from analyses and only the second, third and fourth counts were used. Certain teeth were more difficult to count than others, due to the quality of the longitudinal sections. A set of screening criteria was established in order to minimize error variance by excluding from analyses those teeth for which a consistent estimate of the number of nursing lines could not be made. A tooth was included in analyses if:

1) at least one section was readable on at least two of the three times it was examined, and

2) the difference among counts for the three readings was not greater than four lines.

Nursing lines could not be counted more than once on sections from 21 teeth, and these were excluded from analyses. Only five teeth had counts differing by more than four lines. All of these had two counts that were either equal or differed by one line, while a third was wildly different. In such cases the divergent count was discarded and the tooth was read once more (again, without knowledge of the previous counts). The tooth was used if this count fell within four lines of either of the two counts which were similar.

For each tooth which passed the screening criteria, a mean of the estimated number of nursing lines counted during the three readings was calculated. The sample variance between readings was also calculated for each tooth. The mean variance among all teeth was considered to be the expected measurement error among multiple readings. Data were analyzed using multiple linear regression. When the number of nursing lines was the dependent variable, this mean measurement error was added to the mean squared error of the regression to account for this variance between readings.

The estimated numbers of pups born (Lander 1980, York 1985) were used as estimates of the number of lactating females present on St. Paul Island. In analyses involving estimated cohort survival on land and at sea, published survival estimates were employed (Lander 1979, York 1985). In analyses of pup weights, data for untagged male pups weighed close to the end of August were used (National Marine Mammal Laboratory data base). In all statistical tests performed, a critical value of $p = 0.05$ is considered significant.

To identify factors which possibly affect the number of nursing lines in teeth, multiple regression analyses were conducted for three time periods separately and for all years 1949-1981 combined, with the number of nursing lines as the dependent variable. Independent variables included year, number of pups born on St. Paul Island, date of harvest, indicator variables for five harvest locations, and two interactions (year x date of harvest, number of pups born x date of harvest).

RESULTS

Identifying and counting nursing lines

Nursing lines were clearly visible between the pre-natal dentin and the line marking the end of the first year of life. The neonatal line was usually easily distinguishable, and marked the beginning of a series of regularly spaced nursing lines. The weaning line was slightly more difficult to determine than the neo-natal line, because it is followed by subsequent lines, whereas the neo-natal line is the first very pronounced line in the dentin (Figure 2). The weaning line was often determined by its being an abrupt and distinct last line of a series of evenly spaced lines. Alternatively, it was less distinct but was followed by even less pronounced and more erratically spaced lines. Between these two endpoints the nursing lines could be counted as described in the Methods section. Difficulties arose when some or all of the nursing lines were obscured, perhaps due to the quality of the cut. In general, when two sections were cut from a tooth, one could be read and the other could not. What made one section good and another bad was not entirely clear. However, thickness of the section definitely was important. On a very thin section nursing lines were faint and indistinct. On an overly thick section, the alternating dark and light bands became uniformly dark. On a good section the nursing lines were sharply defined and visible along their entire length from the tip of the crown to their termination at the dentin-cementum border.

Of the 194 teeth sectioned, 173 (89%) passed the screening criteria and were used in analyses. Table 2 summarizes the nursing line data for each year. The between-reading sample variance for an average tooth was 0.92. The number of nursing lines was approximately normally distributed, with a slightly positive skew (Figure 3). The overall mean was 12.3 nursing lines and the standard deviation was 2.1.

Regression analyses

1949-1955

This was the period prior to the female harvest. The population was possibly showing an increasing trend as the number of nursing lines was falling sharply (Figure 4). For this period, year was significantly negatively correlated with the number of nursing lines ($r^2 = 0.22$, $p = 0.008$). There was a similar, but weaker, negative relationship between the number of pups born and nursing lines ($r^2 = 0.10$, $p = 0.08$). No other variables besides year were significantly related to the number of nursing lines.

Table 2. Summary of data on numbers of nursing lines on fur seal teeth from years 1949-1981. The mean between-reading variance was 0.92

Year	Number of Teeth	Mean Number of Nursing Lines	Standard Deviation
1949	8	13.3	1.6
1950	5	13.3	0.8
1951	4	12.3	2.3
1952	5	12.2	1.6
1953	5	11.3	2.2
1954	4	9.7	1.4
1955	8	11.5	2.2
1956	9	9.7	1.3
1957	4	12.4	0.6
1958	8	13.5	2.3
1961	5	10.5	0.6
1962	4	12.1	0.7
1963	5	13.1	1.4
1964	4	11.1	0.8
1965	4	13.8	1.4
1966	4	11.7	2.0
1967	4	15.2	1.3
1968	7	12.6	1.6
1969	4	12.1	1.0
1970	6	14.0	2.9
1971	4	12.0	2.2
1972	4	11.3	1.3
1973	4	12.9	1.7
1974	4	13.1	2.0
1975	4	10.9	2.1
1976	9	11.8	1.3
1977	6	12.6	3.0
1978	9	14.1	1.4
1979	5	12.1	1.5
1980	9	13.3	2.1
1981	8	11.9	2.4
All	173	12.3	2.1

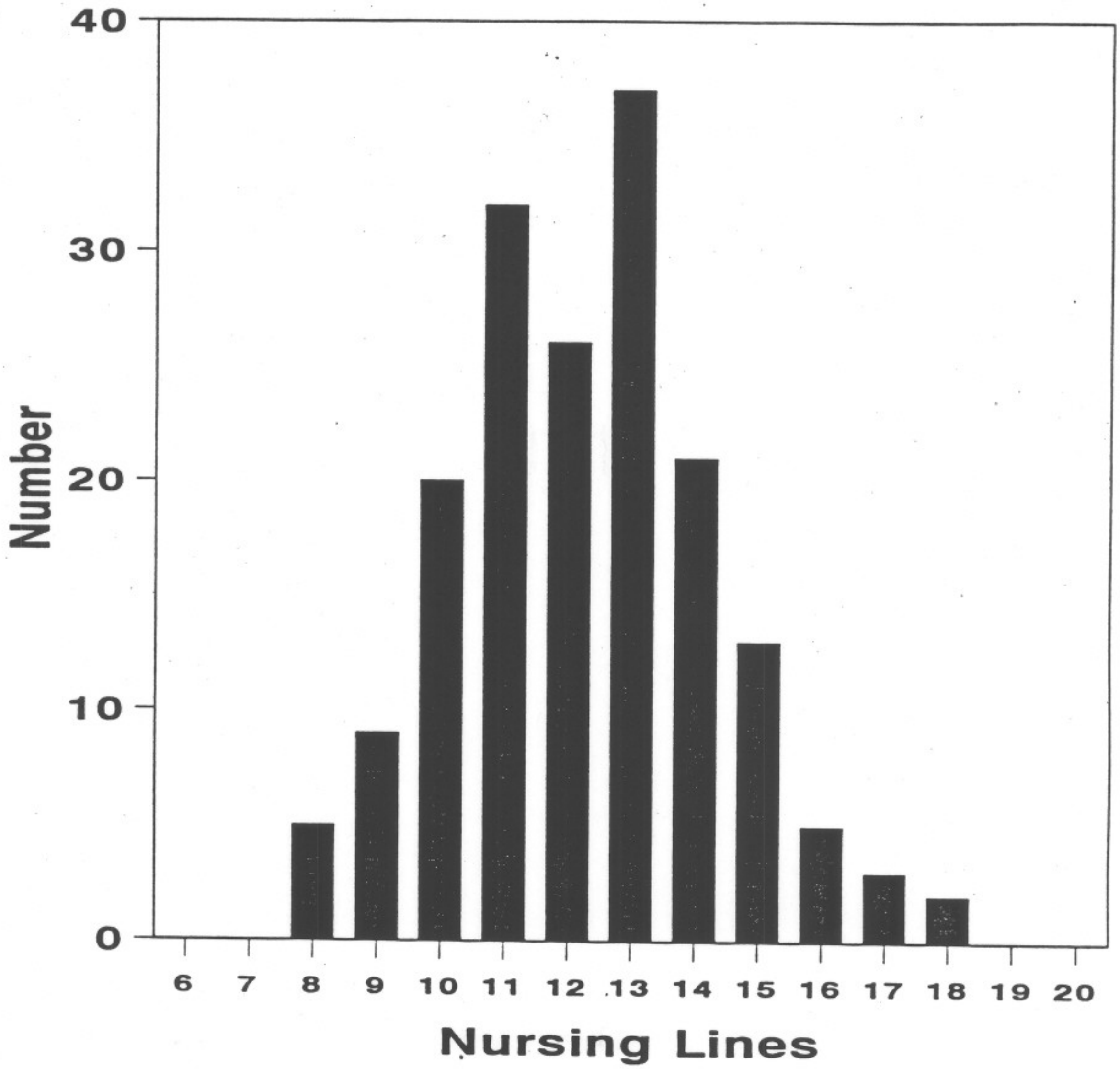

Figure 3. Frequency distribution of numbers of nursing lines on 3-year-old male northern fur seal teeth from years 1949-1981. (Mean number of lines = 12.3, standard deviation = 2.1, n = 173).

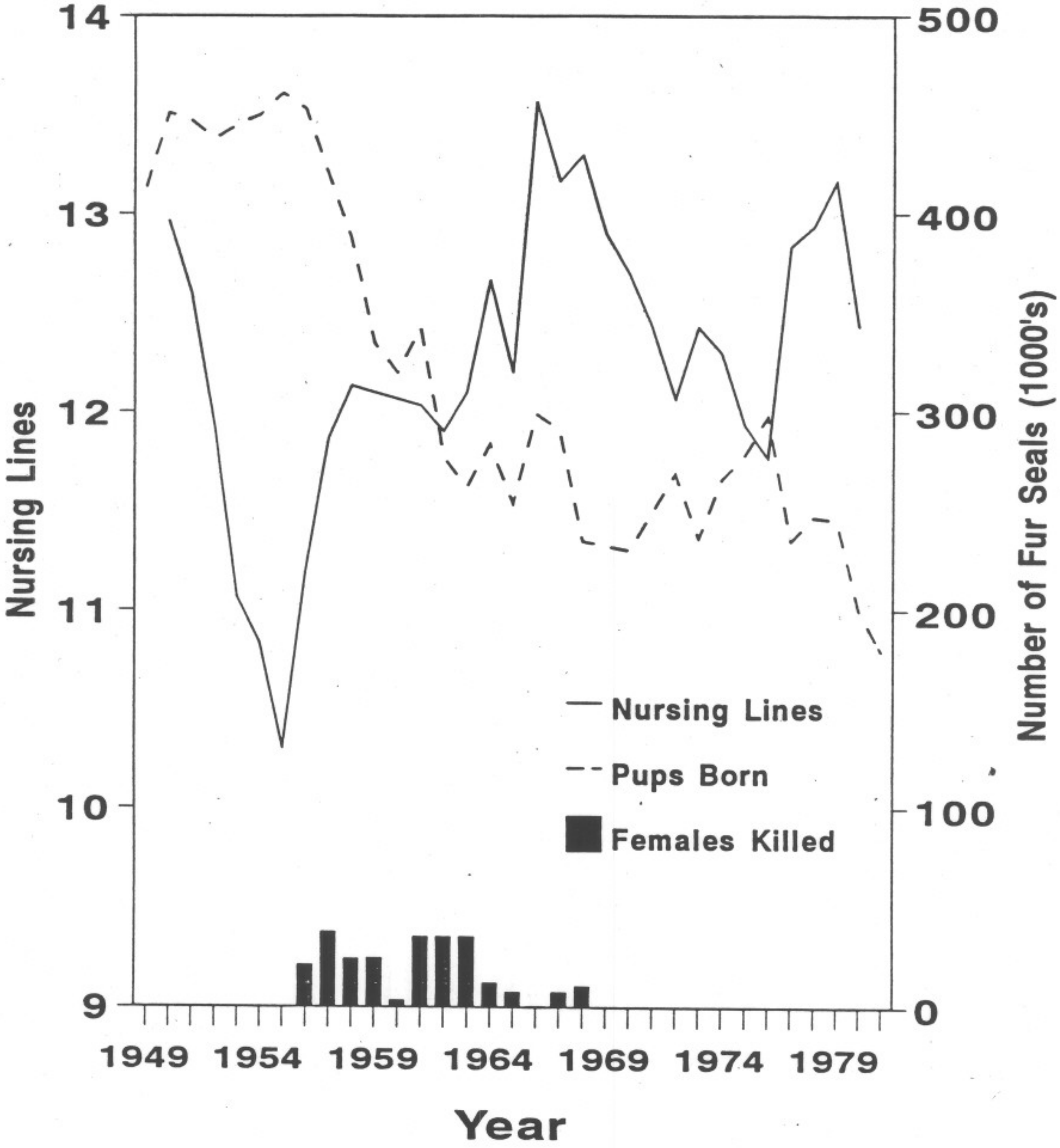

Figure 4. Time series of: Mean number of nursing lines on teeth smoothed by a running mean of three, numbers of pups born, and numbers of females killed on St. Paul Island, Alaska, for years 1949-1981.

1955–1968

This period includes one year prior to, and all years of the commercial harvest of female northern fur seals. There was a significant negative linear relationship between the number of nursing lines and the number of pups born (r^2 = 0.13, p = 0.003). There was likewise a significant positive relationship between the number of nursing lines and year (r^2 = 0.12, p = 0.004). However, for this period, year and the number of pups born were highly negatively correlated (r^2 = −0.89) due to the female harvest (Figure 4). No other variables were significantly related to nursing lines.

1969–1981

This period followed the cessation of the female harvest. No single or combination of independent variables showed a significant linear relationship with the number of nursing lines for these years. There appeared to be a negative relationship between nursing lines and the number of pups born up until 1981 (Figure 5). When the regression was conducted excluding data for 1981, there was a significant negative relationship with the number of pups born (r^2 = 0.08, p = 0.035). Other variables remained uncorrelated with the number of nursing lines when data for 1981 were removed.

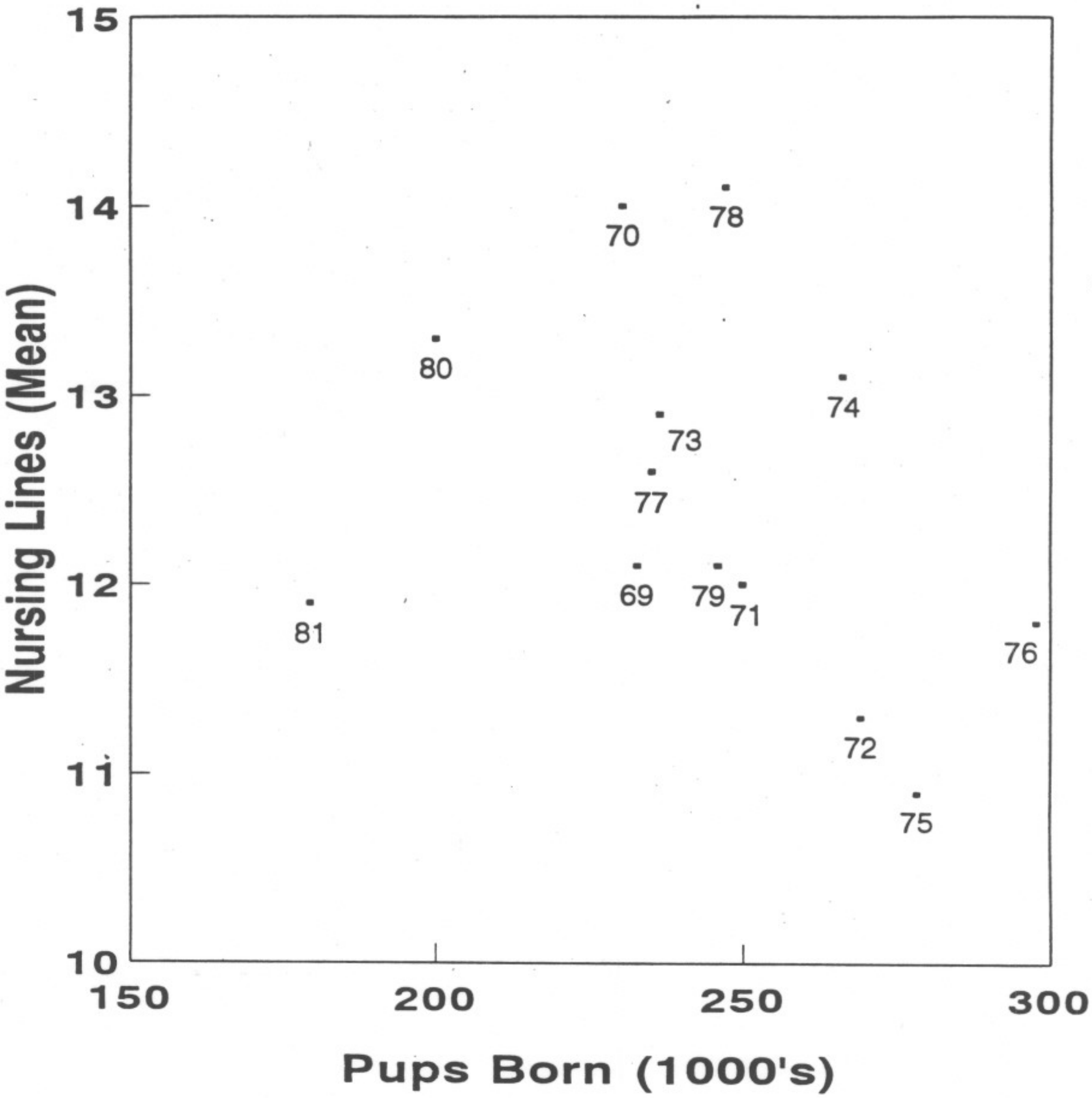

Figure 5. Mean number of nursing lines plotted against the number of pups born on St. Paul Island, Alaska, for years 1969-1981. Note that the data for 1981 depart from the trend.

All years 1949-1981

There is a negative correlation between the number of nursing lines and the number of pups born when all years were combined ($r^2 = 0.05$, $p = 0.007$, see Figure 6). Also, the English Bay location had a significantly higher mean number of nursing lines (13.1) compared to the other four locations (12.2 lines, $r^2 = 0.03$, $p = 0.036$). However, this location alone explained less of the variance in the number of nursing lines than did the number of pups born. In a regression model including the number of pups born and location English Bay, the former was highly significant ($p = 0.007$) and the latter was almost significant ($p = 0.065$, for the whole model $r^2 = 0.07$).

Number of nursing lines as the independent variable

The analyses presented thus far have been directed toward identifying possible factors which influence the number of nursing lines or the number of feeding trips made by lactating female fur seals. The following analyses are intended to reveal the possible influence of the number of feeding trips on other parameters.

Mean weights of male pups weighed near the end of August were available for several years (1957-1958,1961-1971). Regression analysis indicated a highly significant relationship between the number of nursing lines on each

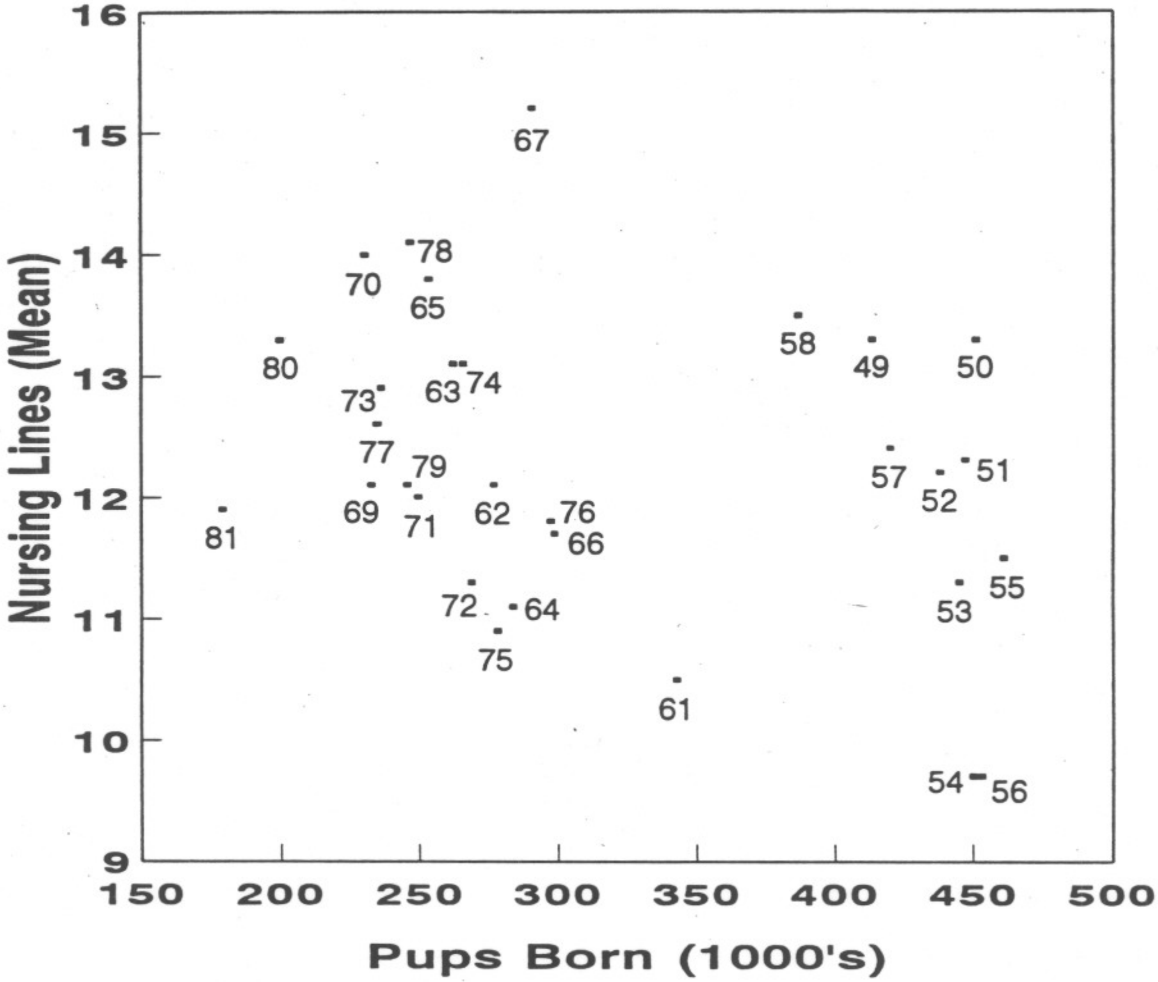

Figure 6. Mean number of nursing lines plotted against the number of pups born on St. Paul Island, Alaska, for years 1949-1981.

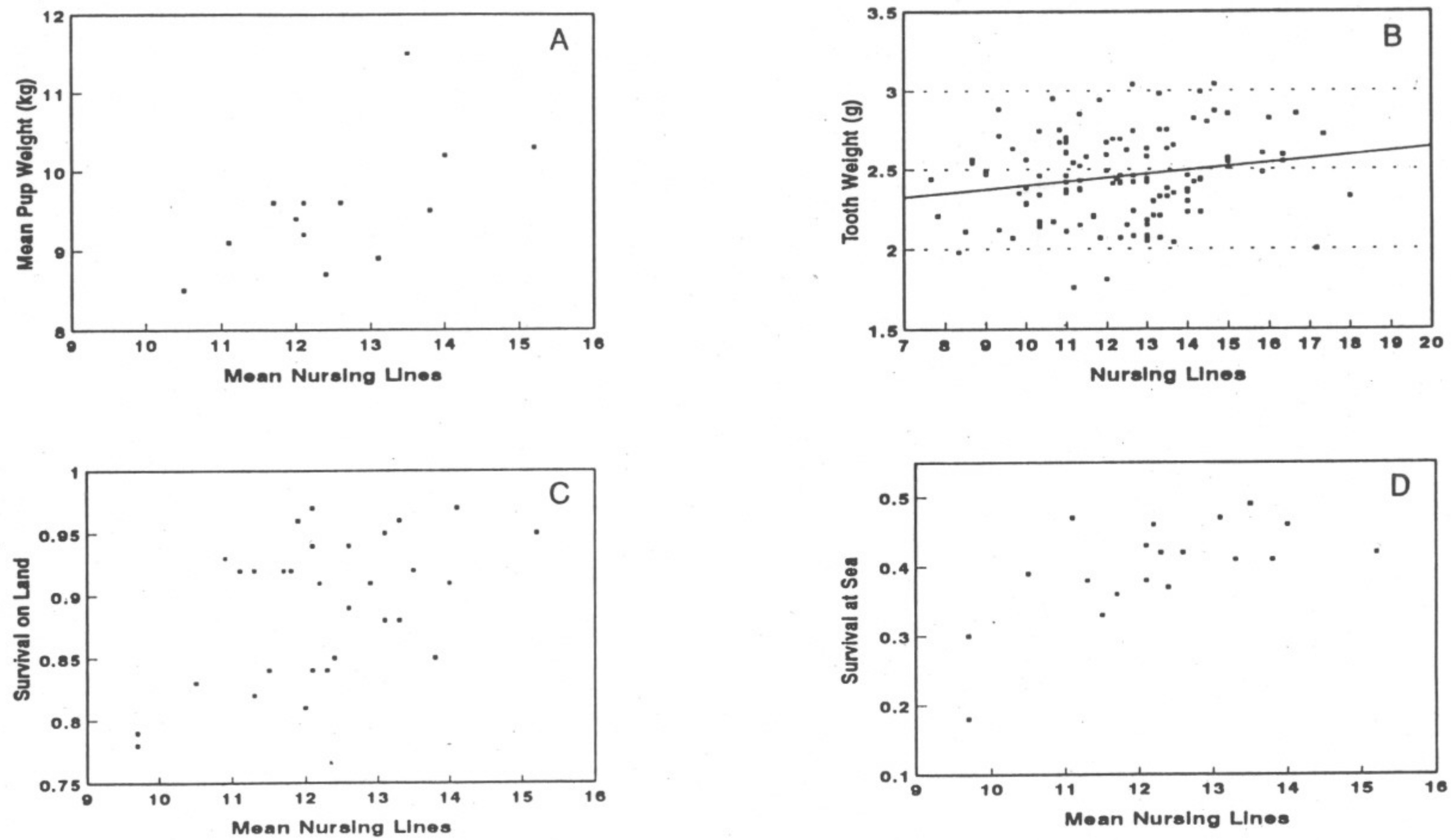

Figure 7. A) Mean weight (kg) of pups near the end of August plotted against the mean number of nursing lines for years 1957-1958, 1961-1971; B) Weight (g) of 3-year-old upper canine teeth plotted against the number of nursing lines on the same teeth (with regression line, n = 121); C) Estimated pre-weaning survival rates on land plotted against the mean number of nursing lines for years 1950-1981; D) Estimated post-weaning survival rates during the first 20 months at sea plotted against the mean number of nursing lines for years 1950-1970.

tooth and mean weight of pups born in those years ($r^2 = 0.14$, $p = 0.002$, Figure 7a).

A total of 121 teeth used in analyses had been weighed before they were sectioned. Tooth weight is an index of body size (Baker and Fowler 1990). A significant positive linear relationship was found between the number of nursing lines formed on a tooth and the weight of the same tooth three years later ($r^2 = 0.04$, $p = 0.039$, Figure 7b).

The number of nursing lines was also significantly related to estimated cohort survival prior to and after weaning. The relationships between the number of nursing lines on each tooth and pre-weaning survival on land (1950-1981) and post-weaning survival for the first 20 months at sea (1950-1970) were both highly significant ($r^2 = 0.14$ and 0.24 respectively, $p < .001$ for both, Figures 7c-d).

DISCUSSION

Identifying and counting nursing lines

Bengtson (1988), in a study on Antarctic fur seals, verified Scheffer and Peterson's (1967) interpretation of a regular pattern of lines in the dentin of northern fur seals as nursing lines. This study has demonstrated that for this species it is also practical to study the life history information these nursing lines represent. The requirements of practicality in this case involved balancing several interdependent factors which influence statistical power: sample size, the level of natural variance in the number of nursing lines, and the level of human error in counting the lines.

To process a sufficient number of teeth, a technique which is reliable, inexpensive and rapid was necessary. The methods employed in this study were simple: thin sectioning, examination with polarized transmitted light microscopy, and storage of sections in vials with 70% alcohol. These methods eliminated much of the time consuming procedures involved in alternative tooth preparation techniques such as staining, mounting of sections on slides, and electron microscopy. Most importantly, while minimizing processing time, reliable results were obtained.

To detect statistically significant trends, or to have confidence in the lack of trends, a sufficiently large sample of teeth was required to overcome natural variance and human error. Both sources of error were of sufficiently low magnitude that the number of teeth required (194) was manageable. Because the mean between-reading measurement error was added to the mean squared error in the statistical tests performed, the significant relationships observed were detected above the noise of human error in counting nursing lines. The screening criteria eliminated teeth which could not be read in more than one independent trial, or which had counts which ranged over more than four lines. This minimized the mean between-reading error to 0.92 while still allowing 89% of the teeth to be used in analyses. This high success rate and low reader error show that nursing lines are sufficiently distinct and can be reliably counted.

The application of a standardized method for identifying the neo-natal and weaning lines and for counting the nursing lines helped to minimize the between-reading error. Standardization also confers comparability to counts among teeth. For example, Bengtson (1988) showed that the number of feeding trips completed between injections of tetracycline corresponded to the number of nursing lines laid down between the corresponding tetracycline marks visible on the teeth. However, because pups go to sea upon weaning and their teeth cannot be examined, the line corresponding to that event must be estimated. Including the weaning line in the total number of nursing lines may bias the estimate of the number of feeding trips made by the mothers. However, because the counting method was standardized, the counts can be compared and conclusions drawn about differences in the number of feeding trips.

Nursing lines, duration of trips, and food availability

Because nursing lines represent the growing pup's feeding and fasting regime imposed by the mother's suckling and feeding cycle, a change in the mean number of nursing lines is equivalent to a change in the mean number of feeding trips made by females. What do such changes represent in the foraging behavior and ecology of lactating fur seals? A first step in answering this question is to relate the number of trips made to time spent foraging.

Bengtson (1988) showed that there was a significant negative relationship between the total number of trips made by lactating Antarctic fur seals and the duration of those trips. Gentry and Holt (1986) presented data on mean number of feeding trips made and mean duration of trips for northern fur seals at Kitovi rookery on St. Paul Island. The greater the number of trips made, the shorter the mean trip duration was. This relationship makes intuitive sense; to fit more cycles into a fixed period of time, the average cycle must be shorter. A greater number of feeding trips could be made without decreasing trip duration, if the visits to shore were shorter. However, Gentry and Holt

(1986) found that the duration of shore visits was less variable than trip duration. They also found that females from St. Paul Island made longer and fewer feeding trips than females from nearby St. George Island, but that those on St. Paul also made longer shore visits. Boyd *et al.* (1991) also found that longer feeding trips were associated with longer shore visits for Antarctic fur seals. Therefore, it seems unlikely that more feeding trips are made by decreasing time ashore.

Another possibility is that more feeding trips could be made in an extended rearing season. Early mean birth dates and/or late weaning dates might be dependent on weather. Data do not exist to test this possibility. On the other hand, regardless of whether the total duration of the rearing season influences the mean number of feeding trips, data do support an inverse relationship between mean number of trips and trip duration. The significant increase in the number of nursing lines observed during 1955-1968 indicates that feeding trips became shorter.

By the early 1950's the northern fur seal population had reached a maximum. During 1956-1968, a total of 253,049 female fur seals were removed from the population (York and Hartley 1981). The highly significant relationship found between the number of nursing lines and the number of pups born for these years indicates a density dependent response due to an easing of competition, i.e., an increase in food available per capita. Females' feeding trips are characterized by transit to a foraging area which may be located over 350 km from St. Paul Island, followed by alternating feeding and resting periods before returning to the rookery (Gentry *et al.* 1986; Loughlin *et al.* 1987). Bengtson (1988) suggested that female Antarctic fur seals probably feed until some physiological condition is attained, upon which they return to nurse their pups. When food is scarce more time would be required to attain satisfactory condition, and feeding trips would be longer in duration. During the summer and fall, fur seals occur at their highest densities on land and at sea, while they breed and rear their young. Competition for food is a plausible result of this concentration of numbers. Under crowded conditions feeding trips could be lengthened as a result of either more time required to feed, or greater distance required to travel, or both (Chapman 1961).

Still, it is questionable to ascribe the observed increase in number of feeding trips to lower competition (higher per capita food resources) when availability of food cannot be independently evaluated. Recognizing this, the case presented here has some special characteristics which make the food resource interpretation plausible.

The Pribilof Island fur seal population is thought to have been near its biological maximum in the early 1950's (Smith and Polachek 1981). K-selected species such as the northern fur seal are expected to exhibit most density-dependence at or near the carrying capacity (Fowler 1981, 1988). Thus density-dependent change would be expected to occur as females were unnaturally removed in large numbers from the fur seal population when it was near its carrying capacity, so long as the carrying capacity itself was relatively constant. In considering the duration or number of feeding trips made as a density-dependent parameter, the carrying capacity is dependent on food availability in the foraging area of lactating females. Walleye pollock (*Theragra chalcogramma*) is the single most important prey species for northern fur seals in summer (Kajimura 1985, Lowry *et al.* 1988). During the female harvest (1956-1968), there was little human exploitation of pollock resources in the eastern Bering Sea; the pollock fishery only began there in 1964 (Bakkala *et al.* 1987). It is therefore reasonable to assume that there was a trend toward more food per capita as females were removed. The increase in number of trips made, and inferred decrease in trip duration, seems a likely result of less competition.

In the argument presented above, absolute abundance of prey is assumed to be relatively constant while the number of fur seals changes, thus altering per capita food availability. Absolute prey abundance may vary significantly, and numbers of single prey species clearly fluctuate. Bakkala *et al.* (1987) present estimates of pollock abundance showing a dramatic increase in the eastern Bering Sea starting in 1964 and peaking in the early 1970's. Regression analyses showed no relationship between the mean number of pups born and estimated pollock abundance for the years 1964-1982 ($p = 0.71$). This may indicate the difficulty in trying to relate absolute prey abundance to parameters concerning predators. A change in prey abundance may not always indicate a change in prey availability, especially for generalists like northern fur seals. In addition to considerations of age (size) structure of prey, and patterns of prey distribution, this is further complicated when several prey species are involved. For example, during the increase in pollock abundance after 1964, Pacific herring (*Clupea harengus pallasi*) showed a major decline (Wepestad and Fried 1983). Herring is one of the several principle species taken by fur seals in the Bering Sea (Kajimura 1985).

Maternal age affects duration of feeding trips in northern fur seals, as older females make shorter duration trips than young females (Goebel 1988). Age structure of the population could therefore influence the number of nursing lines. For example, the observed increase in feeding trips might be related to maternal age if the female harvest resulted in an older age structure among females. To test for this possibility, age structure data from pelagic sampling during 1958-1974 (Eberhardt 1981) were summarized with a calculated mean age of females. There was no relationship between mean age of females and number of nursing lines ($p = 0.53$).

This study provides evidence that the number of feeding trips made by lactating females (estimated with nursing lines) is an indicator of food availability. Bengtson (1988) concluded the same for Antarctic fur seals. In general, when looking at changes in foraging cycles between years, researchers examine a negative correlate of the number of feeding trips, i.e. trip duration. Studies thus far have yielded conflicting results regarding the utility of trip duration as an index of food resources. Doidge *et al.* (1986) reported an increase in Antarctic fur seal feeding trips in a year when prey was evidently less abundant. Antonelis and DeLong (1985) found that trip durations of northern fur seals breeding on San Miguel Island, California, increased in an El Niño year when food was scarce. Loughlin *et al.* (1987) found differences in trip length among years for northern fur seals and suggested changes in prey availability as an explanation. Yet Gentry and Holt (1986) concluded that differences in trip durations they found among years were due to discrepancies in data collection procedures and that "for feeding generalists, such as northern fur seals, the duration of foraging trips is not a good indicator of fish abundance except when catastrophic declines occur, such as in the 1983 El Niño conditions." Goebel *et al.* (1991) also cautioned that trip duration may only reflect large changes in prey abundance. Boyd *et al.* (1991), in a study on Antarctic fur seals, expressed similar sentiments. Their confidence in trip duration as an index of food abundance was eroded by the finding that while trip duration differed significantly between two years, there was no corresponding difference in growth rates of offspring. It had been expected that pups would grow more rapidly when their mothers made shorter trips. This result is countered by two contrary findings for northern fur seals. First, this study found a significant relationship between the number of nursing lines and the mean weight of pups, indicating that pups do grow faster when their mothers' feeding cycles are shorter. Second, Gentry and Holt (1986) found that females from St. George made shorter trips than those from St. Paul. Although the St. Paul females spent more time with their pups on each visit, the pups on St. George still grew at a higher rate.

There are probably a large number of factors which could affect trip duration, and consequently, the number of nursing lines on teeth. Yet all researchers seem to agree that there is some point at which a change in prey will influence trip duration in a measurable way. The results of this study suggest that the change in prey need not be "catastrophic" to be detected by studies of fur seal feeding cycles. Reasonably long time series may be necessary to detect trends obscured by annual variation.

Trends in nursing lines

When regression analyses were conducted on nursing lines for all years combined, the number of pups born was the most significant variable. This reinforces the notion that the number of nursing lines is a density-dependent parameter. The significantly higher number of nursing lines (about one line) for seals killed at English Bay may have been an artifact of the years sampled since the *p*-value associated with the variable for this location increased to $p = 0.065$ when number of pups born was also in the regression model. If the location effect is indeed real, it is difficult to explain. Young males move from place to place on the breeding islands but tend to spend more time near their natal rookery (Antonelis *et al.* in press). Therefore, the trend in nursing lines seen among males killed at English Bay may reflect a trend among those born in English Bay. If females segregate according to rookery when feeding at sea, the greater number of nursing lines from English Bay might indicate that females from there fed closer to shore or had more abundant food resources. At present this scenario is merely speculative, because there has been little investigation of segregation by rookery at foraging locations (Loughlin *et al.* 1987).

Separate analyses of nursing lines during the periods before and after the female harvest were intriguing. Prior to 1956 the number of nursing lines was dropping rapidly (Figure 4) and was more closely correlated with year than with the number of pups born. Estimates of pup production in these years were very high and showed a somewhat erratically increasing trend. These estimates are considered to be somewhat unreliable and have been revised from earlier values which showed a more dramatic increase (Chapman 1964, 1973). It seems possible that the population was actually continuously increasing until the female harvest, and the weak relationship between nursing lines and pup numbers is due to error in estimates of pup numbers. Numbers of adult males on St. Paul Island, another population size index which was estimated more precisely than pup counts at the time, increased every year from 1949-1955 (Lander 1980). Another possibility is that the population of fur seals, which had been rapidly increasing since 1912 (York 1987), was actually depressing fish stocks. The steady decrease in nursing lines might reflect a depletion of food resources due to fur seal predation.

Fowler (1990) presents a summary of data on increased growth and survival, and lowered age at maturity, as evidence that the fur seal decline which continued following the female harvest was not a result of food limitation. Based on these density-dependent responses, he concludes that the Pribilof Island population has been reduced to below its carrying capacity. Loughlin *et al.* (1987) suggested that changes in duration of feeding trips may have been a density-dependent response to population decline.

This study indicates density-dependent changes in the number of nursing lines, not only since the beginning of the female harvest, but from its cessation until 1980. Figures 4 and 6 demonstrate the relationship between the number of nursing lines and pup production. Immediately following the female harvest the population began to recover, but fell again after the mid 1970's (Figure 4). During the recovery period females began to make fewer trips, a trend which reversed following the renewed decline.

Density-dependent parameters such as weight at age, survival, and age at maturity indicate population status based on the experience of individuals living in their habitats (which may include distant migrations) for several years. The trends in nursing lines, insofar as they are associated with per capita food availability, are much more specific in that they reflect the experience of females feeding around St. Paul Island in the Bering Sea in summer and fall. The observed density-dependence of nursing lines following the female harvest is consistent with the conclusion that food limitation did not cause the population decline. Females were probably not food limited while rearing their pups.

While the population seems to be below the carrying capacity as defined by summer and fall food resources, this does not mean that the carrying capacity is unchanged. Fisheries may have seriously altered the Bering Sea ecosystem in localized areas, perhaps to the detriment of other pinnipeds such as northern sea lions (Loughlin and Merrick 1988). Absolute food resources for northern fur seals may have declined since the early 1950's, but the decline of the seal population may have kept it always below a decreasing carrying capacity. This could explain why the most recent years' values for mean number of nursing lines are not much higher than several years in the early 1950's when the population was very high (Figure 6).

Sample sizes in this study are sufficient to detect long term trends. However, the samples are too small to allow paired year comparisons. Therefore, it is difficult to interpret the breakdown in the relationship between nursing lines and pup production when data from 1981 are included in the post-female harvest period. Teeth extracted from seals found dead may be used to continue monitoring trends in feeding cycles since the commercial harvest ended in 1984.

Importance of the interval from birth to weaning

The correlation between nursing lines and pup weight indicates that short trips (as a result of abundant food) allow females to transfer more food to the pups, which leads to greater growth. It is true that nursing lines are counted for the whole season while pup weights were measured in late August, only about half way through the rearing period. The correlation is still meaningful, since females which complete more total trips likely complete more by mid-season as well. This relationship between nursing lines and pup growth is consistent with Gentry and Holt's (1986) finding that northern fur seal pups grew faster on an island where females made shorter trips. On the other hand, Doidge and Croxall (1989) found the unexpected result that the number of trips made did not influence weaning weights of Antarctic fur seals. They suggested that females were effectively swamped by the current high abundance of krill, making foraging ability an unimportant factor in pup growth.

Tooth weight is an index of body size for juvenile male northern fur seals (Baker and Fowler 1990). The relationship of the number of nursing lines to tooth weight at age three for the same individual may indicate that the foraging ability of the female when rearing her pup affects her offspring's size until at least three years of age. This interpretation is consistent with another study which found that differences in weight among pups are maintained for several years (Antonelis *et al.* in press). On the other hand it seems likely that the number of nursing lines would be correlated with the amount of dentin formed during the first year. Therefore, it is possible that the correlation between the number of nursing lines and tooth weight at age three is due solely to tooth growth in the first year rather than to growth through the third year.

Baker and Fowler (in press) found that heavier male northern fur seal pups have a higher probability of post-weaning survival. They suggested that the condition of the pup upon weaning probably is critical for surviving the difficult transition to independence during the first winter of life. This study found that the number of nursing lines was significantly correlated with estimated cohort survival rates both prior to weaning and during the first 20 months at sea.

The correlation between nursing lines and survival reveals a bias in this study's estimates of the mean number of feeding trips. Teeth from males which survived until age three were examined, excluding all those who may have died in part due to inadequate maternal care. Survivors to age three were almost certainly not representative of the cohort as a whole in terms of numbers of nursing lines. Clearly there must be some minimum number of feeding trips required for survival. At the extreme, if fed only once or twice prior to weaning no pup could survive. Thus, a given year's mean ought to be less than that estimated from survivors. Consistent with this expectation, the mean number of feeding trips estimated by visual observations for three years on

St. Paul Island (Gentry and Holt 1986) were all lower than estimates for the same years based on nursing lines in survivors' teeth. The effect of a minimum required number of feedings may be apparent in the slight skewness in the distribution of nursing line numbers in Figure 3. Apparently this minimum requirement is low enough so that survivors still reflect differences in feeding trips among years. It is difficult to conceive of a way that the correlations found in this study between nursing lines and population size, pup weight, etc. could be artifacts of sampling survivors to age three. On the contrary, the exclusion of pups which were seldom fed and died would seem to make the detection of the trends observed more difficult.

The relationships between the number of feeding trips made by females and pup weight, juvenile size and survival, all lead to the conclusion that the interval from birth to weaning is a critical time which significantly influences the future of the pup. The ability of the mother to physically prepare her pup for independence is a significant element in spite of all the chance occurrences that might influence a weaned pup's survival over the next several years. This conclusion suggests the utility of monitoring the number of nursing lines in teeth as at least a partial indicator of cohort strength for northern fur seals. The demonstrated density-dependent nature of changes in the number of nursing lines may also, by way of long-term

monitoring, provide information on population status in relation to carrying capacity.

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