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# PUPPING PHENOLOGY AND DEMOGRAPHY OF HARBOR SEALS (*PHOCA VITULINA RICHARDSI*) ON TUGIDAK ISLAND, ALASKA

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ABSTRACT

The number of seals on shore at Tugidak Island (Gulf of Alaska) declined 72%–85% between 1976 and 1988 and increased during the 1990s. We compared pupping phenology and the ratio of pupping-period counts to molting-period counts between declining (1976–1979) and increasing (1994–1998) years, and examined the sex/age structure of seals ashore during the 1990s. In the 1970s the onset and peak of pupping occurred 6–18 d later than in the 1990s. Rate of pup abandonment was higher in 1978 than in the 1990s. Between 1994 and 1995, the maximum and mean number of seals ashore increased >50%, largely due to an increase in non-pups. From 1995 to 1998, the sex/age structure of seals ashore was similar among years. We observed three to four times as many seals during the molting period than during the pupping period in the 1970s, whereas similar numbers were ashore during these periods in the 1990s, perhaps reflecting changes in demography and/or haul-out behavior. Changes in pupping phenology and demography may reflect environmental changes, such as food availability, and when monitored in conjunction with population counts, may help us better interpret changes in the number of seals ashore.

Key words: pupping phenology, demography, molting period, harbor seals, *Phoca vitulina richardsi,* population decline, Gulf of Alaska, food abundance and availability.

An estimated 15,000–20,000 harbor seals (*Phoca vitulina richardsi*) came ashore annually at Tugidak Island, 40 km south of Kodiak Island in the

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western Gulf of Alaska, during the late-1950s through the mid-1960s (Mathisen and Lopp 1963, Pitcher 1990). A commercial harvest during the 1960s through 1972 removed an estimated 18,000 seals from the island, about 90% of which were pups. The harvests likely were responsible for a decline in the number of seals through 1972. A simulation model of the effects of the harvest suggested that the population would stabilize by the mid 1970s and then slowly begin to increase (Pitcher 1990). Biennial counts conducted from 1976 through 1988, however, detected a 72%–85% decline in the number of harbor seals using the island (Pitcher 1990). A comparison of opportunistic counts of harbor seals along the Kodiak Archipelago during the 1970s to standardized counts made during August and September in the 1990s indicated that a major area-wide decline occurred.[2] Thus, seals on Tugidak Island did not simply move to nearby sites. Harbor seals declined elsewhere in Alaska during the same time period, including Nanvak Bay in northern Bristol Bay (Jemison and Pendleton, unpublished), Otter Island in the Pribilof Islands (Jemison and Kelly, unpublished), and Prince William Sound (Frost *et al.* 1999).

The harbor seal decline was not an isolated event, as Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*) also have declined in the Gulf of Alaska and the Bering Sea during the past 30 yr (Braham *et al.* 1980, Fowler 1982, Merrick *et al.* 1987, York and Kozloff 1987, Loughlin *et al.* 1992). Reduced food availability may have played a role in some of these declines (*e.g.,* Merrick *et al.* 1987, Trites 1992, Calkins *et al.* 1998, Pitcher *et al.* 1998). Merrick *et al.* (1997) found that Steller sea lions declined the least in areas where diet diversity was greatest. Alverson (1992) suggested that Steller sea lions suffered from dietary deficiencies when their diet shifted in the 1970s and 1980s to one dominated by walleye pollock (*Theragra chalcogramma*) and other low-calorie, low-fat fishes. In Alaska, considerable overlap exists in the diet of Steller sea lions and harbor seals (Pitcher 1980, 1981); thus, it is reasonable to presume that reductions in abundance or availability of important Steller sea lion prey could have had a negative impact on the harbor seal population. Anderson and Piatt (1999) describe changes in the fish community in the western and central Gulf of Alaska which may have precipitated a shift in pinniped diets in the 1970s.

Since 1994, the number of seals on Tugidak Island has increased (Jemison and Pendleton, unpublished). Repetitive counts of seals ashore during the pupping and molting periods have been essential in identifying population trends on Tugidak Island. To better understand these trends, we compared pupping phenology and the ratio of pupping period counts to molting period counts when the population was declining (1976–1979) and when it was increasing (1994–1998). Additionally, we examined the sex/age structure of seals on shore during the 1990s. We evaluated several possible factors that might explain observed differences, including changes in food abundance and/or availability, changes in haul-out behavior, and the impacts of human activities.

[2] Personal communication from Ken Pitcher, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska 99518, U.S.A., October 2000.

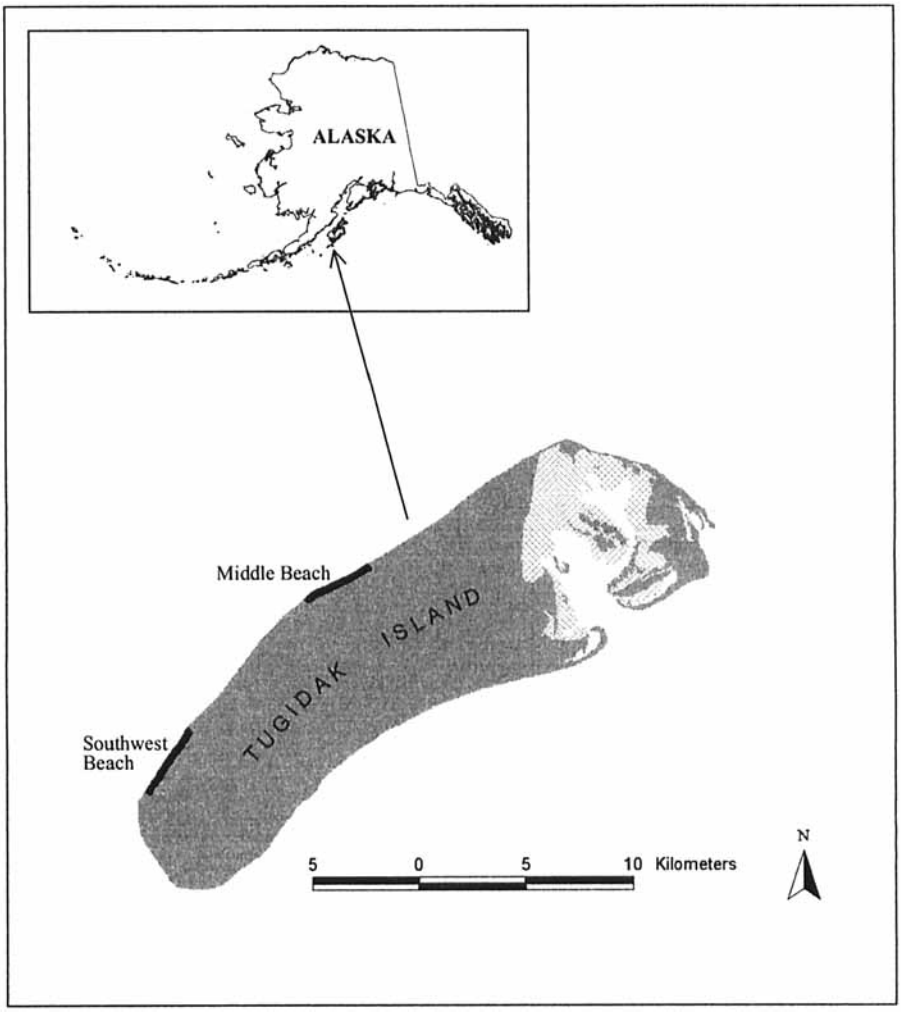


*Figure 1.* Location of study sites on Tugidak Island, Alaska.

## METHODS

We observed two peaks in the number of seals ashore from May through September. The first peak coincides with the birth of pups; we refer to this as the pupping period. The second peak corresponds to the time when a large portion of the population is molting; we refer to this as the molting period. We recognize that the molting period is longer than the pupping period and is not as easily defined, as the timing of the molt varies among sex and age classes (Thompson and Rothery 1987).

*Study area and timing*—We surveyed harbor seals on the southwestern and western shores of Tugidak Island (56°30′N, 154°40′W) (Fig. 1) during the pupping period in June, 1977–1978, and May and June, 1994–1998; addi-

tional surveys[3,4] were conducted during the pupping period in 1976 and 1979 and during the molting period in July–September of 1976, 1978, 1979, and 1996–1998. Additionally, we examined data collected in 1964 and reported by Bishop (1967). During 1976–1979, seals along the southwestern shore (SW Beach) were surveyed. Small numbers of seals hauled out sporadically on the central portion of the western shore (Middle Beach), but these seals constituted only a small fraction of the total number of seals. As they were not monitored regularly, they were not included in counts. In 1994–1998, similar numbers of seals used SW Beach and Middle Beach during the pupping period. During the molting period, however, seals primarily used SW Beach. Middle Beach was regularly monitored and these counts included in analyses.

*Data collection*—We used a spotting scope (20×) and binoculars (10 × 25) from atop 15–30-m cliffs to observe seals on beaches below. Photographs from a Polaroid camera were used to aid counting of especially large herds. Whenever possible, we conducted surveys within two hours of afternoon low tide, when typically the greatest number of seals were on shore. Low-tide surveys were not always possible, however, due to poor weather or the time of low tide. Seals on shore were easily counted during low and mid tides, when views of seals were unobstructed; during high tide, seals were limited to a narrow band of beach adjacent to the cliffs, making observations difficult. Surveys included counts of seals at SW Beach during the 1970s and SW and Middle beaches during the 1990s.

We categorized seals according to sex and age class during the pupping period in May and June. Sex was determined by the location of genitalia when the ventrum was visible or by association of a mother and pup. When sex could not be ascertained, the sex was recorded as unknown. We classified seals as either pups, yearlings, or older. Pups were easily identified by their small size, newly molted pelage, and association with their mother. Unattended pups that appeared too young to be weaned were recorded as lone pups. We defined yearlings as the smallest size class excluding pups; typically they had a uniform pelage on which the markings were obscured, as the hair was bleaching prior to molting. Any seal larger than a yearling we recorded as older, a category that included both immature and mature animals.

*Data analysis*—We analyzed pupping phenology (date of onset and maximum pup count), counts (total number of seals, number of pups, and number of non-pups), and demography (number of each sex/age class during the pupping period). Not all types of data were collected every year (Table 1). We defined the onset of pupping as the date when more than one attended pup was on shore and the peak of pupping as the date of the maximum pup count. We compared count and demographic data between years during a standardized peak pupping period. We visually examined plots of the number of pups

[3] Unpublished data provided by Brian and Pattie Johnson, 450 Walnut Drive South, Monmouth, Oregon 97361, U.S.A., January 1997.

[4] Unpublished data provided by the Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska 99518, U.S.A., December 1996.

*Table 1.* Harbor seal population data collected on Tugidak Island, Alaska, 1964, 1976–1979, and 1994–1998.

| | Observation period[a] | Pupping phenology | Count data | Demographic data |
|---|---|---|---|---|
| 1964[b] | 25 April–31 July | X | | |
| 1976[c] | 15 May–27 Sep. | X | X | |
| 1997[d] | 1 Jun–24 Aug. | X | | X |
| 1978 | 27 Apr.–5 Sep. | X | X[e] | X[f] |
| 1979[d] | 5 Jun.–13 Sep. | | X | |
| 1994 | 25 May–30 Aug. | X[g] | X | X |
| 1995 | 25 May–3 Sep. | X[g] | X | X |
| 1996 | 9 May–4 Sep. | X | X | X |
| 1997 | 13 May–3 Sep. | X | X | X |
| 1998 | 10 May–23 Sep. | X | X | X |

[a] Data collected within these dates; however, number of days that data were collected varied considerably among years.
[b] Bishop 1967.
[c] Unpublished data provided by Brian and Pattie Johnson, 450 Walnut Drive South, Monmouth, Oregon 97361. January 1997.
[d] Data were unusable for most analyses due to disturbances during the peak pupping period.
[e] Unpublished data provided by the Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, Alaska 99518, December 1996.
[f] Data were unusable for most analyses due to disturbances and incomplete surveys.
[g] Onset of pupping was not observed.

ashore and found that similar numbers of pups were on shore for about 9–10 d around the maximum pup count; thus, we defined the peak pupping period as a nine-day period centered around the maximum pup count. To compare counts of all seals on shore during the molting period, we used counts during a nine day period centered around the maximum count; we considered this the peak molting period.

We summarized and compared demographic data from 1994 to 1998 by forming the following indices: (1) *Index of abandonment*—Lone pups/total pups; (2) *Yearlings*—Yearlings/non-pups; (3) *Older males*—Older males/older seals. Sufficient data were available for us to calculate the index of abandonment in 1978 as well. Each index was computed for each day that data were available. For each index we compared yearly means using a 1-way linear model. Because the data within years are based on counts conducted close in time, and hence, residual errors might not be independent, we evaluated several within-year correlation structures when producing estimates, standard errors, and test statistics (Littell *et al.* 1996). We chose the model with the most appropriate error structure based on AICc (Burnham and Anderson 1998).

Typically, we determined the sex of 65%–80% of the older seals during each survey. To estimate the number of males and females in the unknown/older category, we used the ratio of older males to older females without pups. The estimated number of each sex was then added to the observed number of each sex as an estimate of the total number of older females and older males.

*Table 2.* Harbor seal pupping phenology on Tugidak Island, Alaska, 1964, 1976–1979, and 1994–1998.

| Year | Onset (> 1 attended pup) | Date of maximum pup count | Source |
|---|---|---|---|
| 1964 | 1–15 May | 13 June | Bishop 1967 |
| 1976 | 1 June | 22 June | B & P Johnson unpublished[a] |
| 1977 | 1 June | | this study |
| 1978 | 27 May | 22–25 June | this study & ADF&G unpublished |
| 1979 | | ≥20 June[b] | ADF&G unpublished |
| 1994 | | 11 June | this study |
| 1995 | | 11 June | this study |
| 1996 | 13 May | 12 June | this study |
| 1997 | 13 May | 11 June[c] | this study |
| 1998 | 21 May | 11 June | this study |

[a] Unpublished data provided by Brian and Pattie Johnson, 450 Walnut Drive South, Monmouth, Oregon 97361, January 1997.

[b] Maximum count on 20 June, but counts discontinued after 21 June, so date of peak number uncertain.

[c] Disturbance prior to count; estimated to be date of maximum pup count based on counts of pups on beach and in water just off shore.

Seals tended to separate into three haul-out areas, two of which were sex biased; seals of unknown sex were recorded in all three areas. We estimated the number of males and females in the unknown category for each of the three areas individually.

To examine the relationship between the number of seals ashore during the peak pupping and molting periods in 1976, 1978, 1979, and 1996–1998 we defined a pupping/molting ratio as follows: *mean number of seals during the peak pupping period/mean number of seals during the peak molting period.* An estimated variance for this ratio was calculated using a Taylor series approximation (Rice 1995). We assumed that counts conducted during the pupping and molting periods were independent of each other and thus set the covariance term to zero. Individual 95% confidence intervals were calculated.

## Results

*Onset of pupping*—The onset of pupping occurred approximately 6–18 d earlier in the mid-1990s than in 1976–1979. In 1976 pupping began on 1 June, when 11 pups were observed; the onset of pupping in 1977 and 1978 was similar to 1976 (Table 2). In 1994 and 1995 the onset of pupping was not observed, but pups were present during the first day of observations (25 May), and approximately 75 pups were on shore by 1 June. In 1996 two newborn pups were observed on 13 May, and by 1 June, 182 pups were on shore; timing of pupping in 1997 was nearly identical to 1996. In 1998 pupping began on 21 May, later than the previous two years, however, the number of pups increased rapidly and by 31 May 123 pups were on shore.

Bishop (1967) reported that a few pups were born on Tugidak Island during the first two weeks of May in 1964, however, these pups retained some or all of their lanugo which is normally shed *in utero* before birth, and most were eventually deserted. Most pups born in the latter half of May had shed their lanugo *in utero* and were attended by their mothers.

*Peak of pupping*—Peak pupping occurred 9–14 d earlier in 1964 and the mid-1990s than in 1976–1979. Timing of the maximum pup count was similar between years in the 1970s, occurring on 22 June in 1976 and between 22 and 25 June in 1978. The maximum number of pups ashore in 1977 and 1979 appears to have occurred during the same time period, however, disturbances in 1977 and limited survey days in 1979 resulted in incomplete data. From 1994 to 1998, the dates of the maximum pup counts were nearly identical and similar to the timing of the maximum pup count in 1964 (Bishop 1967). Whether the shift in the onset and peak of pupping was gradual, occurring over several years, or abrupt is unknown.

*Demographic changes*—Error structures we chose for these analyses were compound symmetry/heterogeneous (CSH) for the lone pup/total pup analysis and a spatial error structure (Gaussian) for both yearlings/non-pups and older males/older seals although other spatial structures provided very similar results (Littell *et al.* 1996). CSH implies equal correlation among residuals within years, but with differing variances among years. Spatial structure allows for residuals of observations collected closer in time to be more highly correlated than those farther apart.

The proportion of lone pups to total pups on shore in 1978 was significantly greater than all other years and the proportion in 1994 was significantly greater than in 1995–1998 (Table 3). The ratio of yearlings to non-pups was lower in 1994 than in all other years, but this difference was not significant ($P < 0.10$). The ratio of older males to older seals was significantly lower in 1994 than in 1995–1998. From 1995 to 1998, the ratios of yearlings to non-pups and older males to older seals were not significantly different between any two years.

*Trends in June counts during the 1990s*—The largest change in the number of seals ashore occurred between 1994 and 1995 when the mean number of seals increased 55% and the maximum number of seals increased 53% (Table 4). Changes in the annual maximum and mean counts from 1995 to 1998 were generally positive, but much smaller than the change between 1994 and 1995.

Maximum and mean number of pups on shore generally increased each year from 1994 to 1998 with an annual mean percentage change ranging from 2% to 14%. The number of non-pups increased dramatically between 1994 and 1995 with the mean number of non-pups increasing 78% and the maximum number increasing 70%.

*Pupping : molting ratios*—During 1976–1979 the number of seals was much higher during the molting period than during the pupping period, whereas in the 1990s the number of seals during pupping and molting were more similar (Fig. 2). The confidence intervals for the three years in the 1970s

*Table 3.* Estimates and *P*-values[a] associated with comparisons of the proportion of lone pups to total pups and of ratios of number of yearlings to non-pups and number of older males to older seals on Tugidak Island, Alaska, during peak pupping period in 1978 and 1994–1998.

| Year (n[b]) | | | Probabilities | | | | |
|---|---|---|---|---|---|---|---|
| | | Ratio [SE] | 1994 | 1995 | 1996 | 1997 | 1998 |
| 1978 (6) | Lone pups/total pups | 0.07 [0.003] | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| 1994 (6) | Lone pups/total pups | 0.04 [0.004] | | 0.008 | 0.002 | <0.001 | <0.001 |
| | Yearlings/non-pups | 0.04 [0.010] | | 0.063 | 0.093 | 0.012 | 0.052 |
| | Older males/older seals | 0.24 [0.024] | | 0.002 | <0.001 | 0.003 | 0.001 |
| 1995 (5) | Lone pups/total pups | 0.02 [0.003] | | | 0.569 | 0.020 | 0.108 |
| | Yearlings/non-pups | 0.07 [0.011] | | | 0.834 | 0.505 | 0.976 |
| | Older males/older seals | 0.36 [0.259] | | | 0.344 | 0.556 | 0.790 |
| 1996 (7) | Lone pups/total pups | 0.02 [0.003] | | | | 0.087 | 0.324 |
| | Yearlings/non-pups | 0.07 [0.011] | | | | 0.376 | 0.805 |
| | Older males/older seals | 0.39 [0.022] | | | | 0.086 | 0.167 |
| 1997 (9) | Lone pups/total pups | 0.02 [0.022] | | | | | 0.412 |
| | Yearlings/non-pups | 0.08 [0.010] | | | | | 0.511 |
| | Older males/older seals | 0.34 [0.019] | | | | | 0.703 |
| 1998 (9) | Lone pups/total pups | 0.02 [0.002] | | | | | |
| | Yearlings/non-pups | 0.07 [0.010] | | | | | |
| | Older males/older seals | 0.35 [0.019] | | | | | |

[a] Based on comparisons of yearly means using a 1-way linear model.
[b] Number of daily counts within the 9-day peak pupping period.

*Table 4.* Summary of maximum and mean daily counts of all harbor seals, pups[a], and non-pups on Tugidak Island, Alaska, during peak pupping period, 1994–1998.

| Year ($n$[b]) | | Max | Max % change[c] | Mean | SD | Mean % change[d] | Diff. in means[e] | SE of diff. in means |
|---|---|---|---|---|---|---|---|---|
| 1994 (6) | All seals | 652 | | 551 | 62.4 | | | |
| | Pups | 225 | | 197 | 19.6 | | | |
| | Non-pups | 459 | | 354 | 55.0 | | | |
| 1995 (5) | All seals | 995 | 53 | 856 | 138.9 | 55 | 305 | 67.1 |
| | Pups | 257 | 14 | 225 | 19.6 | 14 | 28 | 11.9 |
| | Non-pups | 780 | 70 | 631 | 129.4 | 78 | 277 | 62.1 |
| 1996 (7) | All seals | 1070 | 8 | 972 | 98.0 | 14 | 116 | 72.3 |
| | Pups | 292 | 14 | 251 | 26.6 | 12 | 26 | 13.3 |
| | Non-pups | 773 | −1 | 627 | 104.8 | −1 | −4 | 70.1 |
| 1997 (9) | All seals | 1124 | 5 | 912 | 118.4 | −6 | −60 | 54.1 |
| | Pups | 276 | −5 | 257 | 14.0 | 2 | 6 | 11.1 |
| | Non-pups | 719 | −7 | 605 | 94.1 | −4 | −22 | 50.5 |
| 1998 (9) | All seals | 1292 | 15 | 961 | 212.2 | 5 | 49 | 81.0 |
| | Pups | 313 | 13 | 271 | 40.5 | 5 | 14 | 14.3 |
| | Non-pups | 833 | 16 | 619 | 165.1 | 2 | 14 | 63.3 |

[a] Maximum pup and non-pup counts did not necessarily occur on same day during peak pupping period, nor do they necessarily correspond to highest daily count.
[b] Number of daily counts within 9-day peak pupping period.
[c] Percent change in maximum number of seals since previous year.
[d] Percent change in mean number of seals since previous year.
[e] Difference in mean number of seals since previous year.

overlapped with each other; between decades, only the confidence intervals for 1976 and 1998 overlapped. Ratios calculated using maximum pupping- and molting-period counts (1976 = 0.38, 1978 = 0.32, 1979 = 0.34, 1996 = 1.05, 1997 = 0.85, and 1998 = 0.92) were similar to those calculated using means.

## Discussion

Harbor seals on Tugidak Island gave birth earlier in 1964 and in the mid-1990s than in the mid- to late-1970s. Typically the timing of birth of most pinnipeds in temperate or higher latitudes does not vary greatly among years (*e.g.,* Bartholomew and Hoel 1953, Boyd and Campbell 1971, Boulva 1975, LeBoeuf and Briggs 1977, Coulson 1981, Stein 1989, Boyd 1991). Whereas both the onset and peak of pupping were earlier in the 1990s compared to the 1970s, the timing of pupping within the 1970s and within the 1990s was very consistent, suggesting that the forces influencing timing were affecting all females similarly. Changes in pupping phenology may be related to the age structure of the population, changes in the time when food is available, or changes in the quantity or quality of available food.

Changes in the age structure of pinniped populations may influence the timing of pupping, as older females tend to give birth earlier than younger

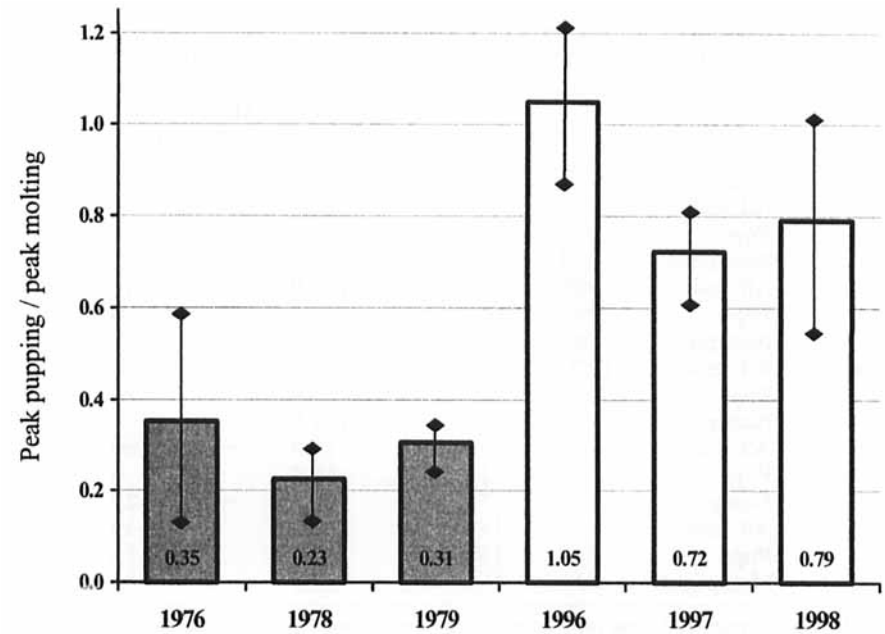


*Figure 2.* Ratios of mean number of seals during peak pupping period to mean number of seals during peak molting period. Gray shading indicates years in the 1970s. Error bars represent 95% confidence intervals.

females (Reiter *et al.* 1981, Lunn and Boyd 1993, Lunn *et al.* 1994, Boyd 1996). Due to heavy pup harvests in the 1960s through the early 1970s (Pitcher 1990), we suspect the harbor seal population on Tugidak Island was skewed toward older seals during the mid- to late-1970s. Because this should have resulted in an earlier pupping period it seems unlikely that changes in the age structure were the cause of later pupping in the 1970s.

Changes in the timing, quantity, or quality of prey available to harbor seals could influence the timing of implantation or the length of gestation, thus altering parturition dates. Temte (1994) proposed that the timing of pupping in Alaska was likely constrained by temperature, prey availability, and ice conditions. Boyd (1984) found that female gray seals (*Halichoerus grypus*) whose body condition increased earliest in spring had the earliest implantation dates. Stewart *et al.* (1989) proposed that implantation in Atlantic harp seals (*Phoca groenlandica*) occurred after females attained a certain level of body fat. In years of reduced food availability, Antarctic fur seal (*Arctocephalus gazella*) females returned to the breeding beaches later, gave birth later, were less likely to give birth and successfully wean their pups, and had longer pregnancies (Duck 1990, Lunn and Boyd 1993, Lunn *et al.* 1994, Boyd 1996). Studies of terrestrial mammals have linked food availability and/or female body condition with changes in timing of reproduction (Skogland 1984, Bowyer 1991, Rachlow and Bowyer 1991, Ruthven *et al.* 1994, Ben-David 1997).

The higher rate of pup abandonment on Tugidak Island in 1978 may be

evidence that females had difficulty obtaining food during that year. Reduced food availability may have been the cause of female Antarctic fur seals increasing their time at sea (Boyd *et al.* 1994) and having less success in raising their pups (Lunn *et al.* 1994). Alternately, disturbances to harbor seals during the 1970s, due to recreational and mining activities on Tugidak Island, resulted in frequent separations of mothers and pups which may have resulted in a higher rate of pup abandonment in 1978 (Jemison 1997). Very few human-caused disturbances were documented during the 1990s, as mining activities had greatly diminished and motor vehicle use on seal haul-out beaches was restricted (Jemison 1997).

We found similar patterns among years from 1995 to 1998 in the ratios of older males to older seals and yearlings to non-pups, and in the rate of pup abandonment. In 1994, however, the ratios of older males to older seals and yearlings to non-pups were lower than in later years, and the rate of abandonment was higher. Though it is difficult to interpret changes in the ratios, one explanation may be that environmental conditions, such as food availability, influence the haul-out patterns of sex and age classes differently. Perhaps when food is scarce, the sex/age classes with the greatest need to be on land at a particular time (*i.e.,* reproductive females during the pupping period) will make up a larger portion of the seals ashore than during years when food resources are not as limited. The lower ratios of older males to older seals, and yearlings to non-pups, in 1994 suggest that it may have been beneficial for yearlings and males to spend more time in the water, perhaps feeding.

The >50% increase in the number of seals ashore between 1994 and 1995 was too great to be explained by local production, suggesting that seals moved to Tugidak Island from other areas or that environmental conditions were conducive to more seals coming ashore. Perhaps a transition occurred around 1994 in the Tugidak Island area from a period of poor food availability, which may have started in the mid-1970s, to a period of better food availability. There is evidence of changes in feeding locations of seals tagged in Prince William Sound beginning in the fall of 1995.[5] Twelve of 14 seals tagged during 1993 and 1994 stayed within Prince William Sound during winter and spring, whereas 12 of 15 seals tagged in 1995 and 1996 left Prince William Sound to feed in the Gulf of Alaska and the Copper River Delta.

The number of seals on Tugidak Island declined from 1976 through the 1980s (Pitcher 1990), but population trends in southeastern Alaska have remained stable or increased since 1983.[6] Similar population trends have been documented for Steller sea lions, with populations declining in the western Gulf of Alaska and the Bering Sea (Merrick *et al.* 1987, Loughlin *et al.* 1992), but stable or increasing in southeastern Alaska (Calkins *et al.* 1999), suggesting these parallel trends may be influenced by some larger oceanic effect.

[5] Personal communication from Kathy Frost, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701, U.S.A., June 1997.

[6] Personal communication from Robert J. Small, Alaska Department of Fish and Game, 1255 West 8th Street, Juneau, Alaska 99802, U.S.A., October 2000.

Major physical and biological changes occurred in the Northeast Pacific Ocean beginning in the mid-1970s (*e.g.*, Trenberth and Hurrell 1994, Polovina *et al.* 1995, Anderson and Piatt 1999). A significant climatic change from about 1976 to 1988 was characterized in Alaska by a shift from cooler to warmer ocean and atmospheric conditions (Trenberth 1990, Trenberth and Hurrell 1994). Coincident with this shift was a dramatic reorganization in the community structure in the western and central Gulf of Alaska from a crustacean and forage fish dominated community to a pleuronectid and gadid fish dominated community. Bottom trawls in the western and central Gulf of Alaska were dominated by capelin (*Mallotus villosus*) and shrimp between 1972 and 1978, after which their abundance greatly declined coincident with large increases in pollock, cod, and flatfishes (Piatt and Anderson 1996, Anderson and Piatt 1999). Capelin was a top-ranked prey item of harbor seals in the Kodiak area during the 1970s (Pitcher 1980), and shrimp are likely an important prey for seals during summer months (Fisher 1952, Bigg 1973, Burns and Gol'tsev 1984). Spawning capelin may be an especially important food for pups and lactating females. Lactation and the first months of foraging by weaned pups coincide with the capelin spawn (June through August) in the Kodiak area.[7] Pollock was another top-ranked prey along the Kodiak Archipelago during the 1970s (Pitcher 1980). Although estimated pollock biomass in the western Gulf of Alaska was about four times greater from 1978 to 1982 than during the mid 1970s, pollock may have been less available to harbor seals in the Kodiak area after the climatic shift as the abundance of pollock appears to have shifted from the Kodiak area westward to the Shumagin Islands beginning in 1977 (Alton *et al.* 1987).

The influence of commercial fisheries on the availability of important prey resources of marine mammals in Alaska is unclear. Since the mid-1950s, fisheries off the coast of Alaska have grown at a tremendous rate. Large removals of certain fish and invertebrate species have likely changed predator/prey relationships, altering community structure and confounding interpretations of environmentally influenced changes. Harbor seals may have shifted to other prey sources or increased foraging effort as a result of ecosystem changes due to climate shift and/or commercial fisheries. Unfortunately, current data on the diet of harbor seals along the Kodiak Archipelago are limited.

During the 1970s on Tugidak Island, three to four times as many seals came ashore during the molting period as during the pupping period. However, in the 1990s, the number of seals ashore was more similar between the pupping and molting periods. Because timing of molting varies among sex and age classes, with pups molting first (*in utero*) (Scheffer and Slipp 1944), followed by yearlings, then older seals (Thompson and Rothery 1987), a change in the demographic structure of the population may partly explain the change in these ratios. During the 1970s there likely were fewer young animals in the population after the commercial pup harvests compared to the 1990s

[7] Personal communication from Paul Anderson, National Marine Fisheries Service, 301 Research Court, Kodiak, Alaska 99615, U.S.A., March 1997.

when there was a more typical age distribution. A population biased toward older animals would exhibit a large peak in numbers associated with the molt later in the summer. In contrast, a population biased toward young animals may not exhibit a large peak in numbers but, instead, show increased numbers ashore over an extended period of time. Additionally, changes in behavior could influence the relationship of pupping to molting numbers; for example, if older males and yearlings spent less time on shore during the peak pupping period when food was scarce, the pupping period to molting period ratio would be lower.

We suggest that changes in pupping phenology and the sex/age structure of seals on shore may reflect environmental changes and, when monitored in conjunction with population counts, may help us better interpret annual changes in seal numbers. The fairly constant sex/age ratios observed during 1995–1998, the low rate of pup abandonment, and the increasing population trend on Tugidak Island since 1994 (Jemison and Pendleton unpublished) suggest that oceanic conditions around Tugidak Island were favorable in those years.

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