MARINE MAMMAL SCIENCE, 10(3):311–324 (July 1994)

THE INFLUENCE OF CLIMATIC SEASONALITY ON THE LIFE CYCLE OF THE PRIBILOF NORTHERN FUR SEAL

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ABSTRACT

Weather conditions recorded from 1956 to 1986 on St. Paul Island, Alaska, were probed to establish their influence upon the northern fur seal's life cycle (*Callorhinus ursinus*). Air temperatures, wind speeds, and relative humidity levels were seasonally decomposed and compared with the timing of pupping and migration. Most pups are born in early July when air temperatures and relative humidity approach their highest annual levels and wind speeds are at their lowest. Weather conditions favor growth and survival of pups from July to September but are unfavorable in June. A rapid deterioration in weather through October and November corresponds with the fall migration of pups and lactating females. The data suggest the pivotal event in the fur seal's life cycle is the timing of birth and survival of nursing pups. As such, the ultimate determinant of the precisely timed fur seal life cycle appears to be climatic seasonality during the breeding season.

Key words: northern fur seals, *Callorhinus ursinus,* Pribilof Islands, life cycle, weather conditions, air temperature, wind speed, relative humidity, seasonal decomposition.

Northern fur seals (*Callorhinus ursinus*) exhibit an annual life cycle that is highly synchronized and predictable (Bartholomew and Hoel 1953; Peterson 1965, 1968; Lander and Kajimura 1982; Bigg 1986; Trites 1992). For example, on the Pribilof Islands, Alaska, mature males will begin arriving on the breeding beaches in May (Fig. 1). The mature females (5–6 yr and older) will arrive later, during June and July, and give birth to a single pup within an average 0.8 d of arriving ashore (Peterson 1965, Bigg 1984, Gentry and Holt 1986). Over 75% of the births will occur during the first three weeks of July (Bartholomew and Hoel 1953, Peterson 1968, Trites 1992). By late July–early August the rigidness of the breeding structure will break down as the territorial

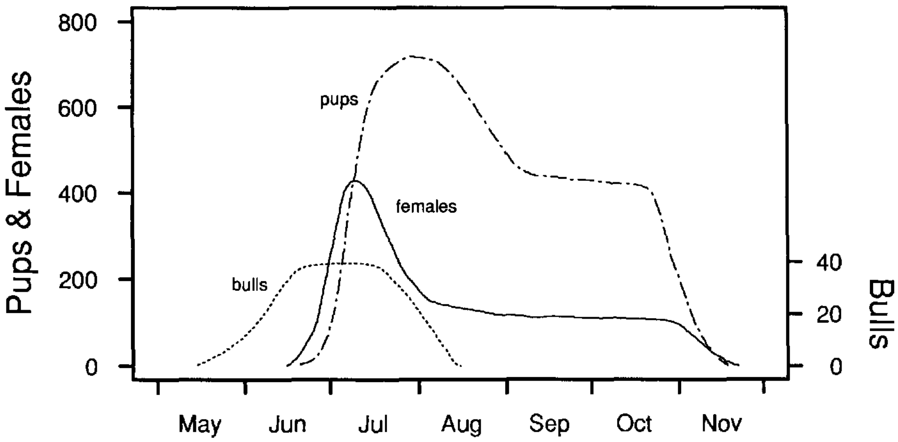

Figure 1. Smoothed counts of territorial bulls, nursing females, and pups made by Peterson (1965) at Kitovi study site in 1962 and 1963. The data are representative of the annual cycle of fur seals on the Pribilof Islands. Ticks on the x-axis mark the first of each month.

bulls begin leaving. Females and pups, however, will not leave until late October through early December after the pups have been weaned (Bartholomew and Hoel 1953, Peterson 1968, Ragen 1990). At this time the adult females will begin a winter migration that may extend as far south as California before returning to their rookeries again in the summer (Townsend 1899, Ognev 1935, Taylor *et al.* 1955, Bigg 1990). Weaned pups usually return to their rookeries after one to three years at sea. The cycle will repeat itself each year with little or no variability in its timing.

The precise timing of arrival and departure from the breeding islands, the timing of pupping and molting, and the consistency of annual migration patterns of northern fur seals have long intrigued biologists and naturalists. Such synchronization is clearly the product of a long evolutionary process of adaptation to many factors such as climate, incidence of disease and parasites, availability of prey, voracity of predators, *etc.* It is unlikely however that all of these determinants have equally defined the fur seal's life cycle. Furthermore, the timing for the series of stages the population passes each year (*i.e.*, pupping, molting, migration, *etc.*) may not be equally critical to individual fitness. In other words, it is possible that the life cycle has evolved about a pivotal event (*e.g.*, the timing of birth), which in turn could be a function of one or more environmental determinants (*e.g.*, prey abundance and climatic seasonality).

Peterson (1965) felt that the precise timing of the annual life cycle was determined by a single event or fixed point and suggested it was the timing of molting or departure of the pups. He further noted that the optimal time for birth was July because air temperatures were tolerable by pups and adults, and because pups had enough time to grow before being forced by storms to leave in November (Peterson 1968). Thus, Peterson speculated that climatic seasonality during the breeding season ultimately determined the precise timing of the fur seal's life cycle.

There has never been a thorough examination of weather patterns and their relation to the reproductive cycle of the northern fur seal. The following, therefore, examines Peterson's hypothesis to determine if weather patterns in the Bering Sea are consistent with the annual synchronization of arrival, birth, and departure of Pribilof fur seals. The analysis summarizes 30 yr of weather data recorded on an hourly basis at St. Paul Island (1956–1986). Mean monthly air temperatures, wind speeds, and relative humidities are contrasted with the timing of arrival and departure of fur seals to and from the Pribilof Islands as recorded by Peterson (1965). Results of the study, while correlational, are compelling and are discussed in terms of proximate and ultimate environmental determinants of seasonal breeding.

Methods

Weather data were collected by the Coast Guard Station on St. Paul Island and transcribed on magnetic tape. The weather was recorded every hour from 1956 to 1963 and from 1982 to 1986, and once every three hours from 1964 to 1981 (NOAA, National Climatic Center, Asheville, N.C.). Air temperature, wind speed, and relative humidity were selected for analysis because they are believed to have a major influence upon pup mortality (Bartholomew and Wilke 1956, Irving *et al.* 1962, Keyes 1965, Ohata and Miller 1976, Blix *et al.* 1979, Trites 1990). Monthly means and variances were calculated for the weather data and compared to the timing of pupping and migration. The time-series data were further seasonally decomposed to separate inclement weather conditions from seasonal effects, using the method of Cleveland and Terpenning (1982) to interpret the complex patterns of weather. Seasonal weather patterns were analyzed and yearly trends and irregular weather conditions that might affect fur seals were noted.

Results

Mean Monthly Conditions

Average weather conditions (air temperatures, wind speeds, and relative humidities) are summarized by month in Table 1 and Figure 2. The Pribilofs are consistently wet and windy, with mean monthly wind speeds varying between 7.1 and 8.5 m sec^{-1}, and humidity levels between 82% and 89%. The highest wind speeds are recorded from January to April when the fur seals are absent from the breeding islands. The arrival of territorial bulls in May corresponds to a sudden drop in average wind speeds and an increase in average air temperatures from 0.2° C in April to 3.8° C in May. Wind speeds drop to their lowest values in July when the pups are born. At the same time air temperatures rise, peaking in July and August.

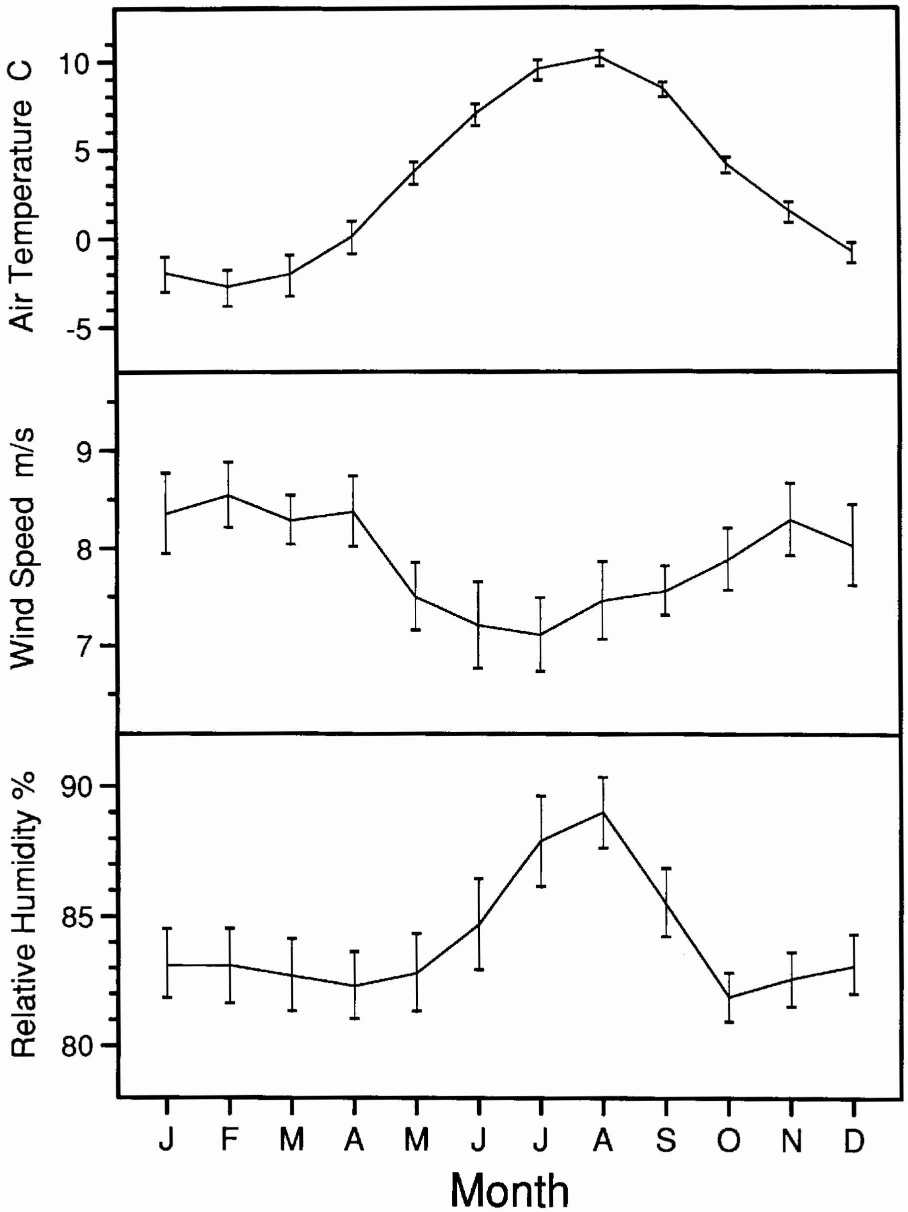

Figure 2. Mean weather conditions (air temperature, wind speed, and relative humidity) recorded by month at St. Paul Island for the period 1956–1986. Vertical bars indicate 95% confidence limits.

Seasonal Decomposition

Monthly time series of air temperatures, wind speeds, and relative humidities are seasonally decomposed in Figures 3, 4, and 5. The top panel in each figure shows the monthly averages of the raw data sets. The data are decomposed into

Table 1. Average weather conditions of the Bering Sea and Pribilof Islands by month. The mean sea surface temperatures were calculated from available data spanning the period 1953–1982 (Ingraham 1983) for the continental shelf area surrounding the Pribilof Islands. Mean wind speeds, air temperatures, and relative humidities were calculated from hourly weather records from St. Paul Island from 1956 to 1986.

Month	Sea surface temperature (°C)	Wind speed (m sec^{-1})	Air temperature (°C)	Relative humidity (%)
January	2.13	8.353	−1.905	83.1
February	1.46	8.544	−2.691	83.1
March	1.43	8.286	−1.994	82.7
April	2.09	8.375	0.163	82.3
May	3.32	7.496	3.767	82.8
June	5.65	7.202	7.035	84.7
July	8.20	7.106	9.572	87.9
August	9.41	7.454	10.241	89.0
September	8.90	7.554	8.447	85.5
October	7.38	7.878	4.202	81.9
November	5.45	8.290	1.545	82.6
December	3.54	8.024	−0.726	83.1

a trend component that describes the long-term variation in the series, a yearly seasonal component that describes variation that more or less repeats itself every year, and an irregular component that describes the remaining variation not explained by the trend or the season (Cleveland and Terpenning 1982). The sum of the three components (trend, seasonal and irregular) equals the original time series.

Removal of the periodic oscillations in weather conditions results in the seasonally adjusted time series (trend). The most notable alteration in weather trends was a decrease in humidity levels from 1956 to 1970, followed by a sudden increase in 1971. In general, air temperatures are much more stable and predictable than either wind speeds or relative humidity levels. Wind speeds appear to have fluctuated randomly since 1956. The only apparent trend is a general decline in wind speed since 1974.

Weather on the Pribilof Islands is dominated by a very strong seasonal component (Fig. 6). The highest air temperatures and relative humidities were recorded during the summer months of July and August, the same time that pups are born. The lowest monthly wind speeds were recorded during the months of June and July. It is equally apparent, from the year-to-year evolution of the seasonal component (shown by the vertical bars in Fig. 6), that air temperature is much more stable than relative humidity and wind speed. This is also illustrated in the irregular plots (Fig. 7). From 1956 to 1986 there was virtually no within-monthly variation in mean air temperatures while fur seals were ashore (May–October). This is unlike the irregular variation in mean wind speed and relative humidity which is consistently large throughout all months of the year (Fig. 7).

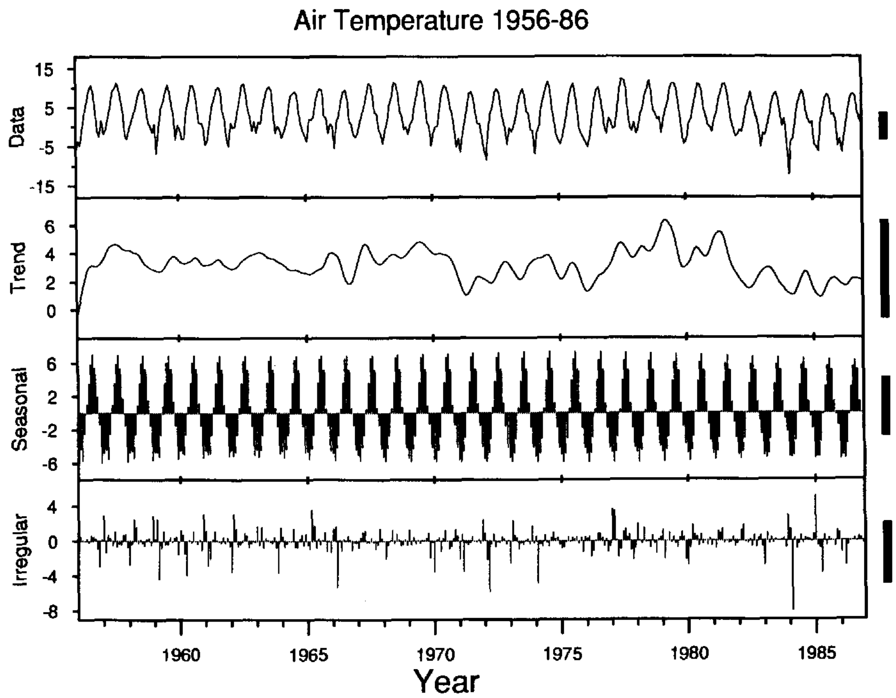

Figure 3. Monthly air temperatures (°C) recorded on St. Paul Island from 1956 to 1986. The data are decomposed into a trend, seasonal effect, and irregular component (residual); the sum of which equals the original data set. Vertical bars at the right of each panel show the relative variation in scaling among the four plots.

Discussion

Changes in climate at St. Paul Island (Fig. 2–7) correspond to the annual synchronization of arrival, birth, and departure of northern fur seals from the Pribilof Islands (Fig. 1). However, it is not so easily concluded that climatic seasonality is the ultimate determinant of the fur seal's life cycle. An ultimate factor must be one that has a direct consequence on survival and reproduction (Baker 1938, Gwinner 1981), as opposed to a proximate factor which controls physiological processes but does not by itself directly alter vital rates. Thus, photoperiod and female nutrition in the fall might be considered proximate factors that entrain the individual's physiology to implant the blastocyst and ensure that the young are born when conditions are optimal for survival (Boyd 1991). Conditions that directly affect the survival of neonates could act as ultimate factors.

Climate and Neonatal Survival

Of the many factors that might affect the survival of pups during their first few days of life, none may be more critical than the prevailing weather. Rain

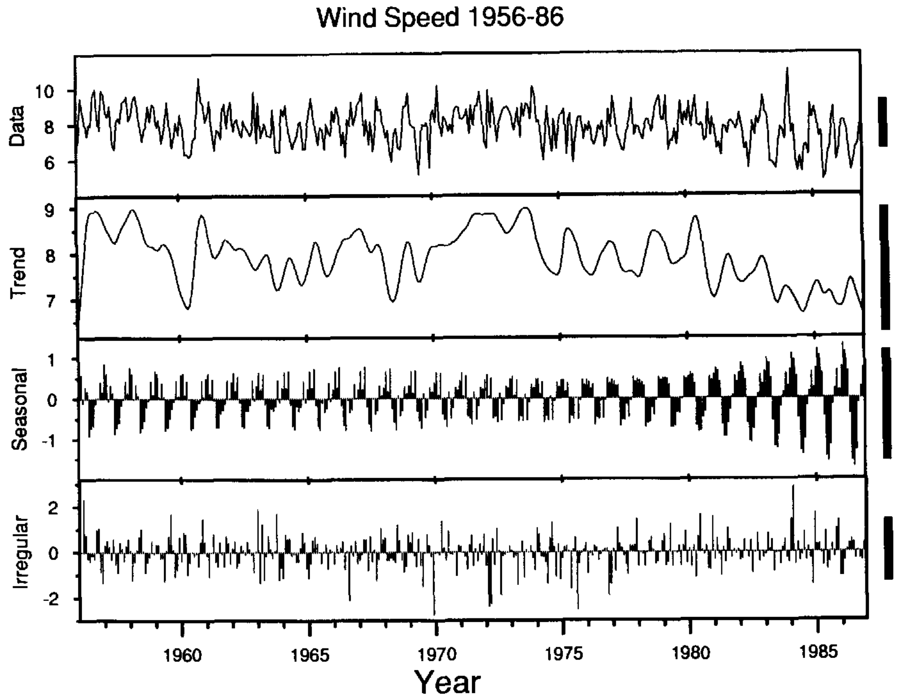

Figure 4. Monthly wind speeds (m sec^{-1}) recorded on St. Paul Island. The data are decomposed into a trend, seasonal effect, and irregular component (residual). Vertical bars at the right of each panel show the relative variation in scaling among the four plots.

in combination with wind and low air temperatures can bring northern fur seal pups to their lower limit of tolerance (Irving *et al.* 1962, Keyes 1965, Ohata and Miller 1976, Blix *et al.* 1979) and cause high pup mortality (Roppel *et al.* 1963, Vladimirov 1974). This is because the pup is small (5.4-kg mean birth weight) and is poorly insulated by fat, skin, and fur (Irving *et al.* 1962). The fat layer at birth is thin (2–4 mm), increasing little over the first two weeks of life (Blix *et al.* 1979), and the insulating layer of air trapped in the short (7.7 mm) dense underfur is easily destroyed by wind and rain (Scheffer 1962, Webb and King 1984). Adult type underfur, with its superior insulating qualities, does not appear on the pups until the young have molted (mid-August through end of September, Scheffer 1962).

The ability of northern fur seal pups to cope with diverse climatic conditions on land was recently explored using a thermal-energetic model (Trites 1990). The study identified the combination of environmental extremes that pups can withstand during their first week of life and concluded that healthy, average-sized pups born during July on the Pribilofs could tolerate any combination of air temperature, wind speed, and level of humidity recorded during July since the mid-1950s. However, the model predicted pups born earlier in the year, or pups born with low birth weights, could succumb to hypothermia during periods of cold, wet, and windy weather. These predictions are consistent with the

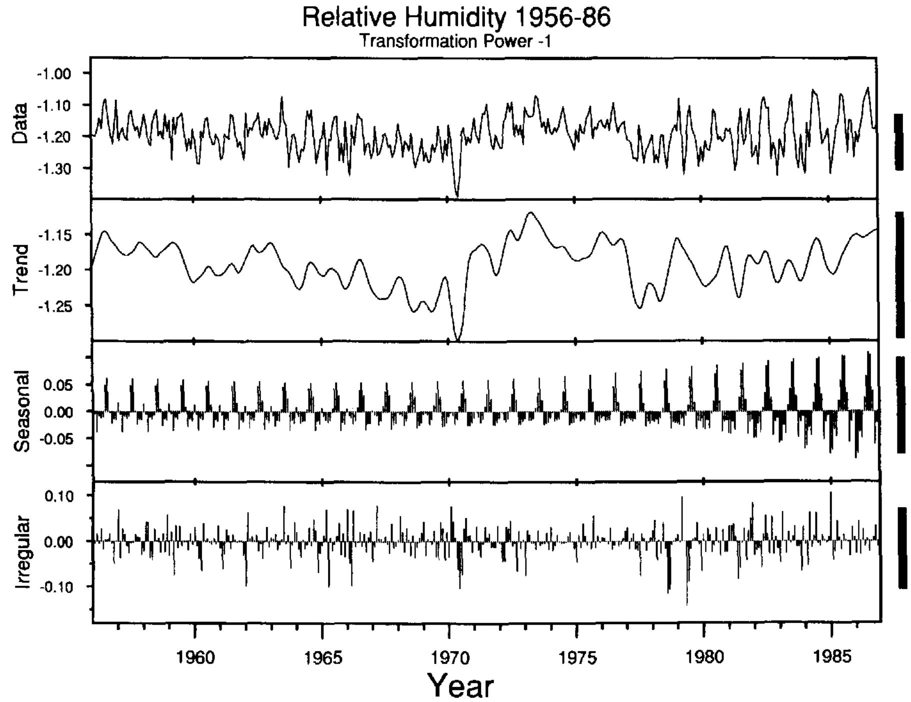

Figure 5. Monthly levels of relative humidity recorded on St. Paul Island from 1956 to 1986. The data are transformed according to $x' = -x^{-1}$ and are decomposed into a trend, seasonal effect, and irregular component (residual). Vertical bars at the right of each panel show the relative variation in scaling among the four plots.

positive relationship demonstrated between the weight of pups and their future survivorships (Calambokidis and Gentry 1985, Baker and Fowler 1992). They are also consistent with positive correlations reported between air temperatures and estimates of pup survival on land (York, in press).

Pups are more vulnerable to inclement weather and climate change during the early postnatal period than at later stages of physical development. Thus, the small, poorly insulated neonates would have difficulty coping with the combination of environmental conditions that occur in June (Trites 1990). However, in July, when most pups are born, there is a significant rise in air temperature (from 7.0° C in June to 9.6° C in July), and wind speeds are at their lowest annual level (7.1 m sec^{-1}; see Fig. 2, 6). Wind speeds in July, August, and September are relatively low (7.1, 7.5, and 7.6 m sec^{-1}, respectively) and air temperatures are their warmest (9.6°, 10.2°, and 8.4° C respectively), thereby ensuring the pup three months of favorable weather (see Trites 1990). Thus, pupping in early July allows sufficient time for most pups to grow before weaning and should facilitate high pup survival.

Weather conditions deteriorate drastically from September to November subsequent to the pup molting and the development of adult-type pelage. Air temperatures, for example, drop (from 8.4° to 1.5° C) and winds increase (from

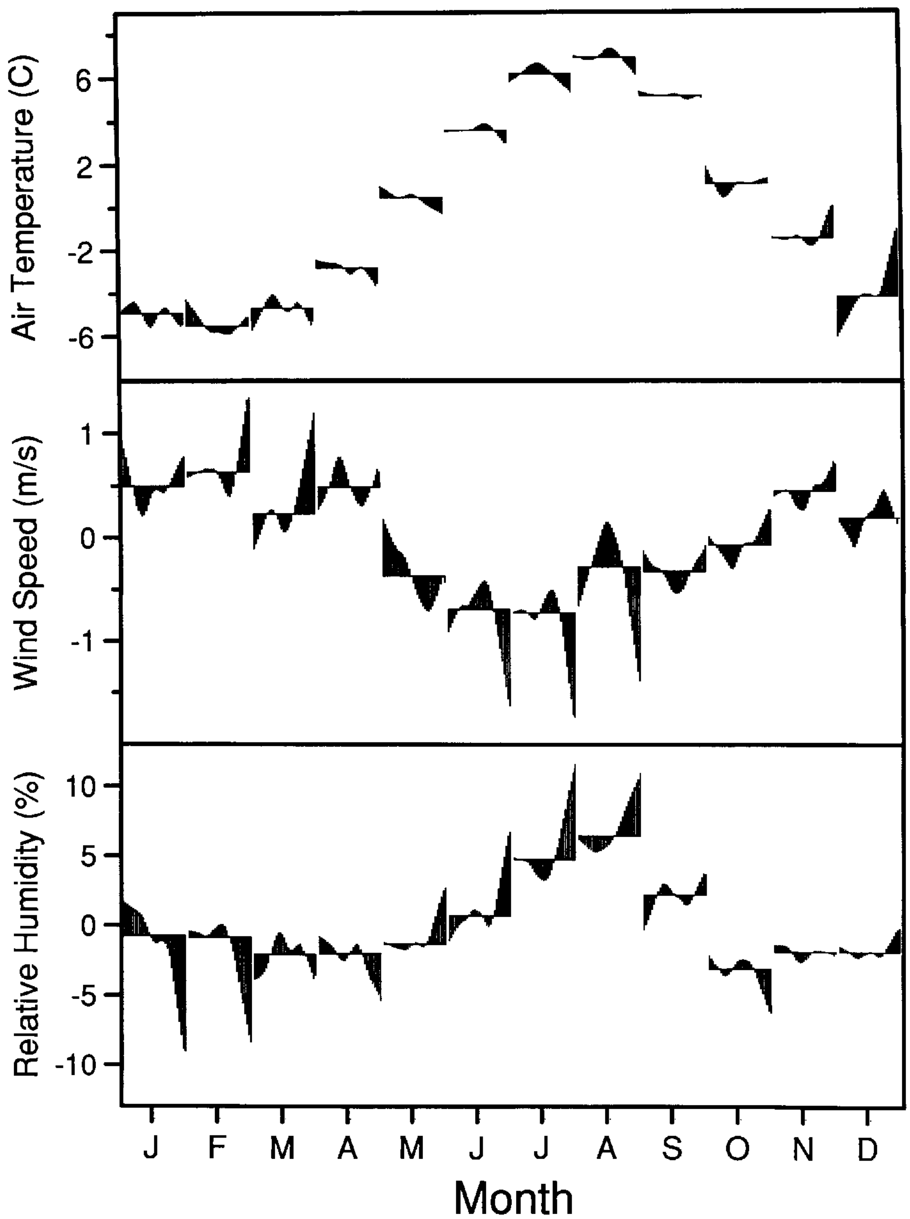

Figure 6. Seasonal component of air temperature, wind speeds, and relative humidity levels from 1956 to 1986. Horizontal lines are at the mid-mean of the seasonal component for each month; vertical lines show year-to-year evolution of the seasonal component. Note the relative humidity is transformed according to $x' = -x^{-1}$.

7.6 to 8.3 m sec^{-1}). The severity of November weather may influence the time of weaning and limit the length of stay of mothers and pups on the Pribilof Islands (Peterson 1965). Furthermore, sea temperatures in the Bering Sea drop rapidly from October to December (Table 1) and may be too low for swimming

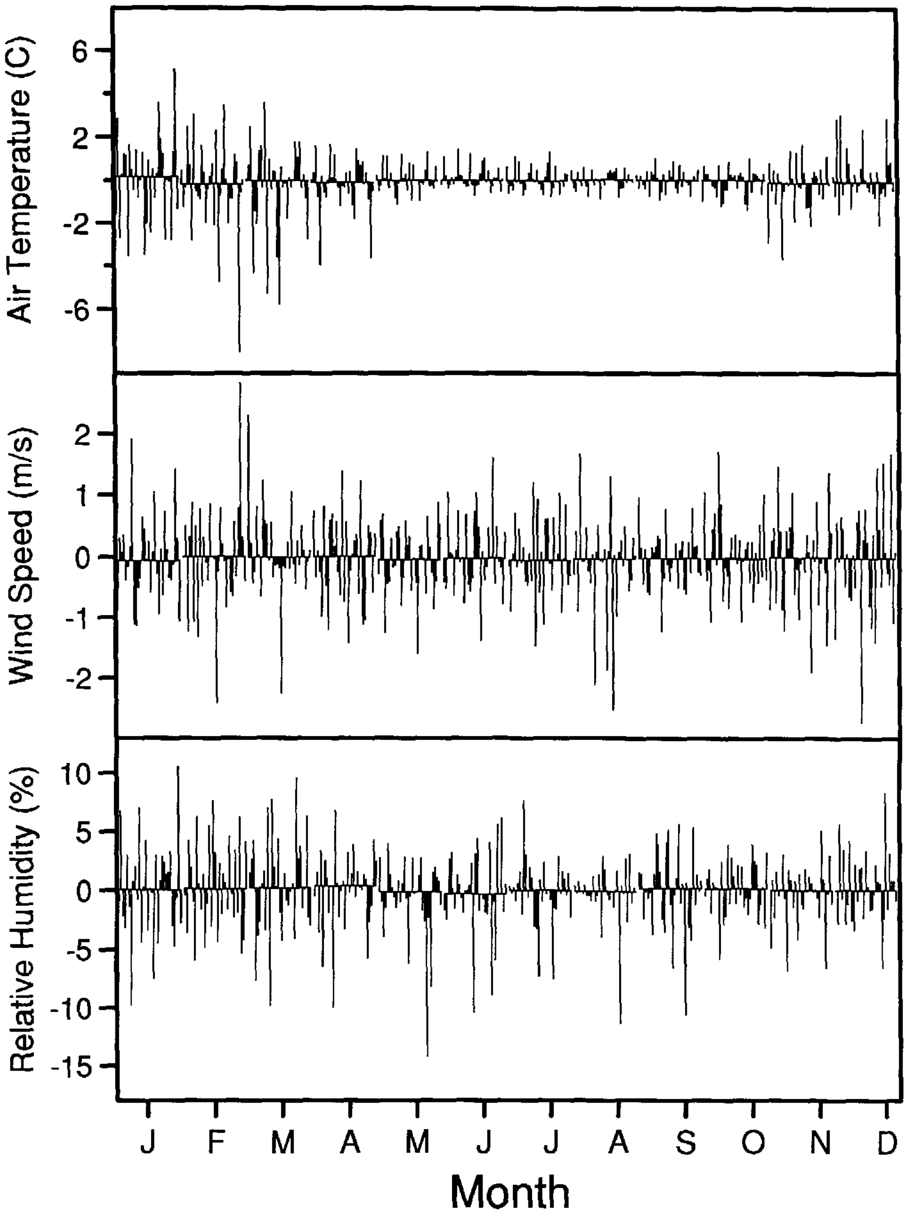

Figure 7. The irregular component of air temperatures, wind speeds, and relative humidity levels from 1956 to 1986. Horizontal lines are at the mid-mean of the irregular component for each month; vertical lines show year-to-year evolution of the irregular component. Note that relative humidity is transformed according to $x' = -x^{-1}$.

pups to maintain their core body temperatures (see Trites 1990). Such speculations are consistent with field observations indicating most pups and females begin leaving just prior to November 1 and are entirely absent from the islands by mid-December (Fig. 1; Peterson 1965, 1968).

Climatic Seasonality and the Life Cycle

The small amount of annual variation in mean birth dates of northern fur seal pups (Trites 1992) suggests that accurate timing of reproduction is important to the survival of pups (Boyd 1991). In terms of weather, the accurate timing of reproduction ensures that pups are born at the most appropriate time of the year to ensure optimal survival. However, the timing of birth may also reflect prey availability. Unlike most phocids that can meet the energy demands of lactation from stored resources, otariids must alternate between foraging at sea and nursing their pups on shore (Boyd 1991). Thus, it is conceivable that food, or some other factor besides weather, might ultimately determine the precise timing of the fur seal's life cycle.

Data on the seasonal abundance of fur seal prey species near the Pribilof Islands is scant. However, there are indications that food abundance can be inferred from the influence of water temperature upon fish distributions (Alton 1974, Walsh and McRoy 1978, Mclain and Favorite 1976, Fritz *et al.* 1993). Thus, it might be inferred from the high correlation between Bering Sea water temperatures (Table 1) and monthly air temperatures on the Pribilof Islands ($r^2 = 0.80$, $t_{10} = 6.76$, $P < 0.001$) that weather conditions and prey abundance are linked by climatic seasonality.

The successful bearing and raising of young is ensured by an interplay of different factors. Most notably, an abundance of prey must be readily available to replenish the lipid-rich milk reserves of the mother while foraging at sea. At the same time the newborn pup must be able to contend with prevailing environmental conditions while ashore.

Lactating females could probably forage just as successfully in June near the Pribilof Islands as they appear to do in July. Such is the case for piscivorous sea birds raising chicks in nests and burrows on the Pribilof Islands. Similarly, Steller sea lion pups (which are about four times larger than fur seal pups at birth) are born on the Pribilofs in late May through June. Thus it is doubtful that prey availability in June, unlike prevailing weather conditions, would compromise the growth and survival of the small and poorly insulated northern fur seal pups.

Synthesis

The highly synchronized and consistent pattern of reproduction observed in northern fur seals from one year to the next appears to reflect climatic seasonality as suggested by Peterson (1965, 1968) and is likely a strategy that maximizes reproductive success (Bronson 1988, Ims 1990). However, the pivotal event that maximizes the survival of young fur seals appears to be the timing of birth, rather than the timing of molt and departure of the pups. Individual physiologies have presumably been entrained by proximate environmental factors to ensure the breeding season is predictable and precisely timed. As such, day length appears to cue the timing of embryonic implantation in mid-November leading to synchronous pupping eight months later (Craig 1964, Daniel 1981, Temte

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Received: 1 March 1991
Accepted: 8 February 1994