

WINTER ECOLOGY OF STELLER SEA LIONS
(*Eumetopias jubatus*) IN ALASKA

by

BOYD PORTER

Associates of Arts, University of Alaska Anchorage

B.A. Biological Sciences, University of Alaska Anchorage

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Department of Zoology
The University of British Columbia
Vancouver, Canada

Date 12/15/97

ABSTRACT

The goal of this study was to describe aspects of the winter ecology of Steller sea lions (*Eumetopias jubatus*) from behavioural observations made at a winter haulout between January and April 1996 in Southeast Alaska (Timbered Island, 133° 48' W, 55° 41' 45" N). My major hypotheses were: 1) Mothers suckle male offspring more than female offspring, and spend less time on shore to provide for the higher metabolic needs of males. 2) Mothers with yearlings have higher demands than those with pups and should spend more time nursing and more time at sea foraging. Another important goal was to describe the weaning process.

Mature females and their dependent young (pups age < 1 y and yearlings 1-2 y) predominated on the winter haulout while numbers of mature male and sub-adult males remained low. There was considerable variability in numbers of animals on shore from one day to the next. A Drop-one Stepwise regression showed numbers on shore were correlated with weather and sea conditions. The ranked order of important variables included: wave height, air temperature, wind speed, wind direction, sky cover, barometric pressure, ocean swell, and tide height. Haul-out patterns were negatively correlated with poor weather and rough sea conditions. No diurnal haul-out pattern was detected.

Two measures of maternal investment were made: the time spent suckling by different sex and age class (pups and yearlings), and the time their mothers spent on land and at sea foraging.

Differences between the average length of male pup-suckling bouts ($\bar{x} = 37.2 \pm 2.8$ min. SE, $n=12$) were not significantly longer than female suckling time ($\bar{x} = 35.9 \pm 2.3$ min., $n=12$). However, yearlings suckled significantly longer ($\bar{x} = 44.0 \pm 2.8$ min. SE, $n=5$) than pups ($\bar{x} = 36.5 \pm 1.8$ min., $n=24$). Males spent an average of 33.9% (± 1.1 SE) of the time they were with their mothers onshore suckling compared to 29.9% (± 4.4) by female offspring, but the difference was not statistically significant, and the proportions did not change during the 3 month study period.

Average trips to sea by mothers with yearlings lasted 2.3 d ($\bar{x} = 59.7 \pm 4.7$ h SE, $n=6$) and were significantly longer than the 1.9 d average trips of mothers with pups ($\bar{x} = 48.0 \pm 6.3$ h, $n=18$). Mothers with male pups (< 1 y) were away for an average of 2.2 d ($\bar{x} = 52.5 \pm 15.2$ h SE, $n=12$) compared to 1.8 d ($\bar{x} = 43.5 \pm 12.6$ h, $n=12$) for those with female pups. Mothers spent an average of 35.2 h (± 7.0) on land with male offspring and 34.5 h (± 6.0) with females before departing on foraging trips. Mature females ($n=30$) showed little seasonal variation in trip duration. Shore visits averaged 19.4 h between trips to sea ($n=30$, SE=0.90, range 11.2-29.2h). Differences in time spent on shore between offspring genders and age classes were not statistically significant. Lactating females spent an average of $14.2 \pm 1.1\%$ SE ($n=30$) of their time on shore while immature animals spent three times as long ($40.2 \pm 2.1\%$).

Average rotation time (feeding/resting cycle) from sea to the haulout by mature females was 3.0 days and was consistent through the season. Weaning of pups and juveniles was not observed between January and April. Haul-out patterns during the winter were influenced more by disturbance, sea and weather conditions than by endogenous rhythms.

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Dedication

I would like to dedicate this thesis to my loving wife Diana for her undivided support throughout this process, and for never losing sight of the common goal.

Chapter I: Introduction, Status of the Population, and Theories for the Decline

Introduction

Steller sea lions (*Eumetopias jubatus*) are large eared seals that range from California to the Kamchatcka Peninsula in Russia. In 1980 the world population was estimated to be between 245,000 and 290,000 (Loughlin *et al.* 1992). Since then the population has declined dramatically leading to them being listed as "threatened" in 1990 under the U.S. Endangered Species Act. They were reclassified as "endangered" in parts of their range in 1997 (U.S. Federal Register 62:2434355). Two genetically distinct stocks of Steller sea lions have been identified: an eastern and western stock divided at Cape Suckling, Alaska 144° west longitude (NMFS 1995, Bickham *et al.* 1996). The eastern stock remains threatened, and the western stock has been upgraded to endangered.

My study sought to document the winter ecology of Steller sea lions from each of the two stocks, one that is declining, the other which has increased in recent times. The immature animals (<3 yrs.) are of special interest because little is known about them, and it has been suggested that a high mortality of this age class may be key to explaining the population decline. A more specific hypothesis, not tested here, is that juvenile sea lions may not be obtaining enough food to meet their metabolic requirements (NMFS 1992).

Work was completed at three sites, Cape St. Elias (1995), Marmot Island (1996), and Timbered Island (1996). Only data from Timbered Island are presented in this thesis because disturbances affected the reliability of data from the other two sites.

My study describes haul-out patterns and activities of sea lions during winter, the harshest time of the year. I sought to contrast the maternal investment by mothers of male and female offspring. I also attempted to document the weaning process and noted

behaviours that might indicate nutritional stress. Finally, I recorded weather and sea conditions to determine their influence on the numbers of animals on shore.

I begin with an overview of the status and trends of sea lion populations in California, British Columbia, Alaska, and Russia. This is followed by a discussion of current theories for the decline, a description of the study site and general methods. Chapter II describes the amount of time all age classes spend on shore (hauled out) using hourly counts. It evaluates environmental variables and their effect on haul-out time, details factors causing disturbance, and tests for diurnal patterns. This chapter is aimed at understanding the winter haul-out behaviour and the factors influencing it to provide predictions and a baseline for future surveys and capture work. Chapter III describes attendance patterns of immatures and mature females with dependent offspring. Females with different sex offspring were compared to test the hypothesis that those providing for male pups would require the female to spend more time at sea. Mean trip times for the group were evaluated for trends or patterns. Chapter IV describes immature suckling patterns, compares male and female on-teat times and proportions of time spent suckling. It also evaluates group and individual suckling behaviour to look for patterns or trends from January to April. Major findings and an overview of some of the lessons I learned are outlined in Chapter V.

Steller Sea Lion Biology

The Steller sea lion ranges from the Channel Islands, off southern California, around the Pacific Rim to northern Japan, with most of the world population breeding between the central Gulf of Alaska and the western Aleutians (Scheffer 1958, Schusterman 1981, King 1983, Loughlin *et al.* 1984). They are polygynous and are gregarious on land. Males arrive at breeding rookeries in mid-May, and remain on land until mid July (Gisiner 1985). Males have no active role in rearing pups. Mature females arrive at rookeries and give birth to a single precocial pup during June and early July, with the peak of pupping in mid June.

Parturition and nursing occur exclusively on land. Mature females enter a brief postpartum estrus after giving birth and copulate 10-14 days later (Sandegren 1970, Gentry 1970). After a delay of 3-4 months, the fertilized zygote implants on the uterine wall and embryonic development lasts for 9 months (Calkins and Pitcher 1982). Female Steller sea lions reach sexual maturity at age 3 and may potentially produce a single offspring each year. They nurse only their own pup and are aggressive toward non-filial pups attempting to suckle. Immature animals spend much of their time swimming, playing, and resting while mother is away, and in close proximity resting or suckling when she is present. By August and September most rookery sites are abandoned and pups and their mothers disperse to haulout sites.

If rearing of the pup lasts longer than a year, a second pup may be born while the first one is still nursing, which results in competition for mother's milk. Immature sea lions may continue to suckle for up to 3 years while also foraging opportunistically, although the majority wean within one year (Calkins and Pitcher 1981; Merrick *et al.* 1988). Young sea lions (1-3 years) are often seen suckling from adult females at rookery and haulout sites (Gentry 1970, Sandegren 1970, Calkins and Pitcher 1982). Calkins and Pitcher (1982) reported that 61% of adult females were still lactating in April-May. The weaning process and transition to independent feeding are not well documented, although most pups wean by the end of their first year (Pitcher and Calkins 1982). Most adults and dependent young disperse from rookeries to haulouts by September for the remainder of the year.

Status and Trends of the Population

The center of the world distribution of Steller sea lions occurs in the Aleutian Islands and Gulf of Alaska, from the most western point of the Aleutian Peninsula east to Prince William Sound. This region has experienced the most dramatic declines (Loughlin *et al.* 1992, Merrick *et al.* 1987) from a high of 225,000 in the late 1970s to fewer than 85,000 in the late 1980s (Trites and Larkin 1996). South of this point, from the Kenai Peninsula east to Cape St. Elias, counts of adults and juvenile sea lions indicate the

population began declining sometime after 1980. However, counts of pups at Seal Rocks, the only major rookery in the area, have ranged from 491 to 799 during 1978-1991, with no detectable trend (ADF&G unpubl. data). The only area in Alaska that appears to support a healthy population of sea lions is Southeast, from Cape Saint Elias south to the Canadian border. The estimated number of sea lions in this region increased from less than 100 in the 1920s (Rowley 1929) to 350 in 1945 (Imler and Sarber 1947), 2500 in 1957 (Mathisen and Lopp 1963), and leveled off at about 9000 in the early 1970s. This population now appears stable or slightly increasing.

Further details on the status of Steller sea lions by region are contained in Appendix 1.

Theories on the Decline in Alaska

The population decline of Steller sea lions coincided with the rapid growth of groundfish fisheries in Alaska and the reduction of other Alaskan pinniped species: harbor seals, *Phoca vitulina richardsi* (Pitcher 1990), and northern fur seals, *Callorhinus ursinus* (Trites 1992). Similar declines have been reported in some seabird breeding colonies. The decline of these northern pinnipeds may be causally connected with similar large scale changes occurring concurrently in a number of commercial fisheries and may impact the economic development of commercial fisheries throughout Alaska. For example, the North Pacific Fisheries Management Council, which regulates fisheries in the Bering Sea and Gulf of Alaska has recently found itself considering the energetic and nutritional requirements of Steller sea lions when allocating commercial harvests of pollock and other fish species.

Other possible causes of the sea lion decline include changes in distribution, disease, pollution, harvest and increased predation. However, available data suggest that these explanations are unlikely (NMFS 1992). Sea lions collected in 1985 and 1986 from the Gulf of Alaska, showed signs of nutritional stress which were correlated with the decline in Gulf of Alaska pollock stocks (Calkins and Goodwin 1988, Lowry 1990). While a cause-effect mechanism for the decline has not been identified, nutritional stress is

a leading hypothesis (Calkins and Goodwin 1988, Merrick 1995, NMFS 1995). Calkins *et al.* (1997) found reduced growth of sea lions in the Gulf of Alaska during the 1980s in support of the nutritional stress hypothesis. Changes in prey abundance due to ground fish fisheries or natural changes in the ecosystem are more likely to be at the root of the decline.

Pollock make up over 50% of the prey consumed by sea lions in both Southeast and northern populations (Calkins and Goodwin 1988). It seems likely that the removal of large quantities of ground fish, particularly pollock, could have some impact on local availability of food for sea lions, especially in winter months. For example, in the same study by Calkins and Goodwin, the size of the fish consumed declined from 1975-76 to 1985-86 judging from otolith samples obtained from sea lion stomachs.

If prey species are less abundant and more difficult to capture, inexperienced juveniles should be affected more than older individuals. Competition for these lower fish stocks could place the juveniles (who may have more difficulty capturing larger prey) at a disadvantage and may result in less than adequate nutrition for metabolic needs and growth.

The period immediately after the end of parental care is critical in the development of mammals. Compared to juvenile Steller sea lions, older animals swim faster (Ragen 1990) and can presumably sustain themselves for longer when faced with temporary food shortages. Eberhardt and Siniff (1977) have shown how the survival over the first two years of life can account for changes in the abundance of four different pinniped species. Using mathematical models and age structure data from field samples to gain insight into the changes that have occurred, York (1994) found the simplest explanation for the observed changes in Steller sea lions was a 20% decline in juvenile survivorship (age 0-3 yrs) between 1975 and 1985, with no change in the adult survival or fecundity. Possible causes of the population decline and the change in age structure were examined by writing a Leslie matrix population equation in terms of changes in juvenile and adult survival rates and fecundity, and examining the short-term behaviour of the trajectories of the average

age of adult females, total number of females, and total number of pups with respect to those changes in the vital parameters.

Study Area

Steller sea lions were observed from 20 January to 1 April 1996, on Timbered Island ($133^{\circ} 48' W$, $55^{\circ} 41' 45'' N$) in Southeast, Alaska (Fig. 1.1). This island is the most westerly of six islands located in the Maurelle Islands Wilderness Area. It is round, 1.0 ha, 150 m wide, and has a maximum elevation of 38 m. Three sides of the island are exposed to the Gulf of Alaska; the other faces Prince of Wales Island. The sea lions haul out along the edges of the main island and on two low, exposed rocks 30 m offshore that are awash during stormy weather and high tides. Observations were performed from blinds situated at opposite ends of the island each with clear, unobstructed views of the two main haulout sites.

Timbered Island was selected as a typical winter haulout site based on historical accounts and annual aerial count data which indicated a high number of animals present during past winters (ADF&G unpubl.census data). The site was selected for the high proportion of juveniles and for convenience of observations during a winter study.

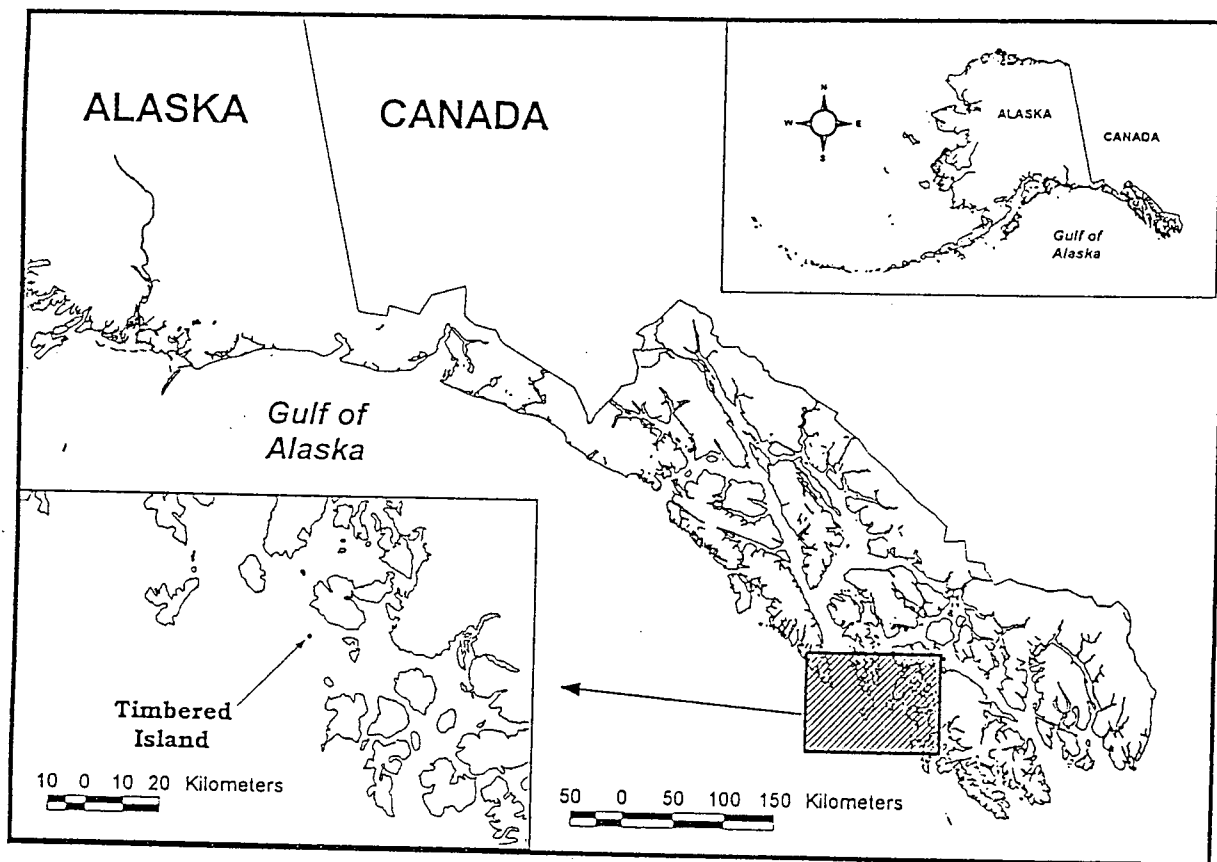


Figure 1.1 Map of the Gulf of Alaska showing the Timbered Island study site ($133^{\circ} 48' \text{ W}$, $55^{\circ} 41' 45'' \text{ N}$).

Chapter II: Environmental Correlates of Winter Haul-out Patterns of Steller Sea Lions

Introduction

Little is known about Steller sea lion haul-out patterns during the winter months when many mature females are providing for dependent young and the juveniles are beginning to forage independently. Environmental conditions are usually harshest during winter and may compound any difficulties that young experience as they move from milk to solid food. Many feel that a high mortality of young during this time of the year may contribute to explain the recent decline in sea lion numbers (Merrick 1995, NMFS 1995). Understanding the response of sea lions to environmental conditions may provide new insights into the juvenile mortality hypothesis and will help predict when the majority of animals are likely to be on land. This is important for continued population monitoring (*i.e.* aerial and land survey counts) and may help guide future attempts to capture Steller sea lions at winter haulouts.

The following chapter describes the age and sex composition of Steller sea lions using a winter haulout in Southeast Alaska from January to April. Counts and environmental data are used to assess numbers of animals ashore, their variability and to explore diurnal patterns. Additional sources of disturbances are also documented.

Methods

Data Collection

Sea lions were counted hourly during daylight hours from 20 January to 1 April 1996. A few counts were also made after dark using night vision equipment. Counts included: total animals on land by sex and age, total numbers in the water, and

miscellaneous behavioural observations (*e.g.*, response of sea lions to eagles and other disturbance). Additional information recorded hourly included: weather (wind direction and speed, cloud cover, temperature), and sea conditions (swell and wave conditions, tide stage). Categories for each weather variable are listed in Appendix 3.

Binoculars (8x30) and variable power spotting scopes (15x - 60x) increased the accuracy of counts and observations, and Night Vision Goggles (Generation II) were used for night counts. Counts were made using hand tally counters and recorded on field data forms. A programmed stopwatch maintained consistent on-the-hour start times. Observations were performed from blinds situated 35 m from the animals.

Typically the animals used one main haulout. However, periodic shifting of haulout groups were caused by poor weather or other disturbances. When sea lions hauled out on more than one site per day, an attempt was made to count each area at least three times per day (morning, midday and evening) while maintaining hourly counts at the main haulout. This provided a more accurate estimate of total numbers during times of disturbance.

Some animals observed had been previously branded by Alaska Department of Fish and Game. A total of 799 sea lions were branded during two summers at the Forrester Island rookery in southeast Alaska. Branded animals were < 1 year and < 2 years during this study. For methods see Merrick *et al.* (1996). Brand numbers observed during this study and sex and ages are listed in Appendix 2.

Age Criteria

Because age structure may affect overall growth and stability of the haulout population, the ability to identify sex and age groups in the field is critical to monitoring seasonal composition changes. Most studies of sea lions have tended to lump all immature age classes into one category. In my study, an effort was made to distinguish age classes according to:

Pups: Animals less than one year old. Smaller body size and distinct shape of the head. No visible canine tooth eruption.

Juveniles: Animals older than one year, but less than three. Clearly smaller than adults with fully erupted canine teeth. No accurate criteria were established to separate two and three year old animals within this group.

Mature Females: Four years or older. Slender head and neck, visibly larger than juveniles, but front shoulders not developed as in SAMS.

Sub Adult Males (SAMS): Between 4-6 years of age. Heads broader than those of mature females, neck and shoulders developed enough to distinguish them from adult females, but much less developed than those of adult males.

Mature Males: Animals at least 7 years old. May reach over twice the body size of the adult females; massive head, neck and shoulders.

Some immature animals at the study site had previously been part of a sample of 799 pups branded during summer by the Alaska Department of Fish and Game in 1994-1995 at Forrester Island 150 km south of Timbered Island. Pups were branded on the left shoulder with the letter "F" followed by three digits. Sex and weight of each individual were recorded at the time of branding (ADF&G unpubl. data). These brands confirm the age of branded individuals and served as a standard to compare with and more accurately classify unmarked animals.

A Drop-one stepwise linear regression (Neter *et al.* 1986) showed numbers on shore were correlated with environmental conditions. This tested the importance of weather and sea conditions, with total numbers of animals present on land as the dependent variable. All independent variables were included in the "full equation". The least significant variable was then dropped and the significance of the remaining variables recalculated. This was repeated until only one significant variable remained.

Variables included in the full equation were: month, time of day, tide height, wind speed, barometric pressure, swell height, sky cover, wind direction, temperature, wave height. Weather categories are listed in Appendix 3. Wave height and wind speed were estimated near the haulout using a modified Beaufort Scale. Sea state was defined as condition of the ocean surface compared to flat calm, and was a relative measure similar to wave and swell. Temperature, and barometric pressure were measured at the blind 35 m from the animals. Sky cover was measured as a proportion of cloud cover overhead.

Results

Counts and Trends

The number of animals present varied greatly from day to day (Fig. 2.1). Some fluctuation in numbers can be explained by females leaving to feed while other more drastic changes in numbers were related to weather, sea-state, or disturbance. High numbers of mature females and their dependent young predominated. Numbers of mature males and sub-adult males remained low throughout the winter.

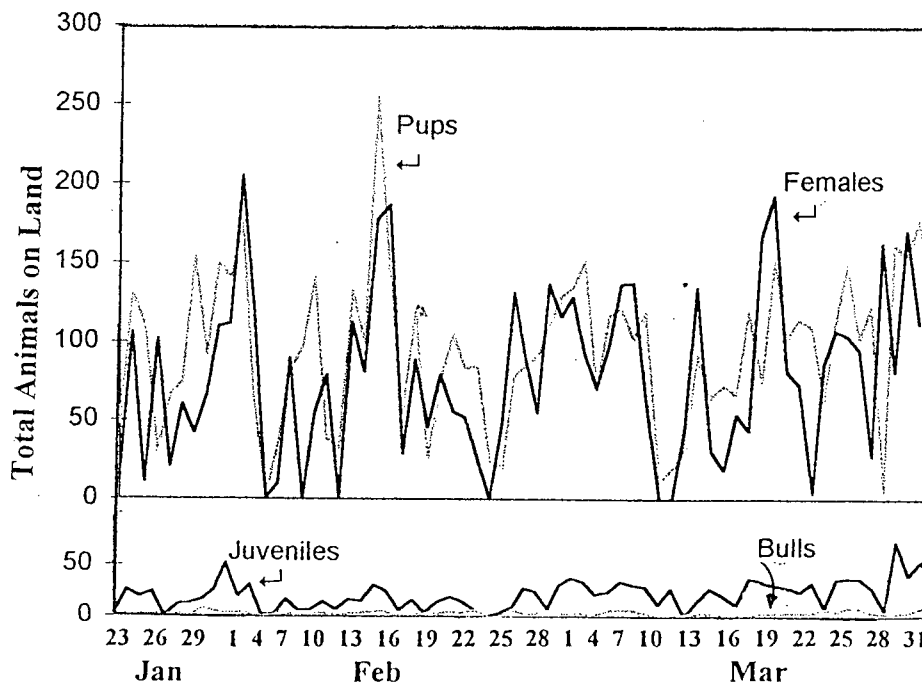


Figure 2.1 Mean daily count of animals on land by sex and age class. 1996.

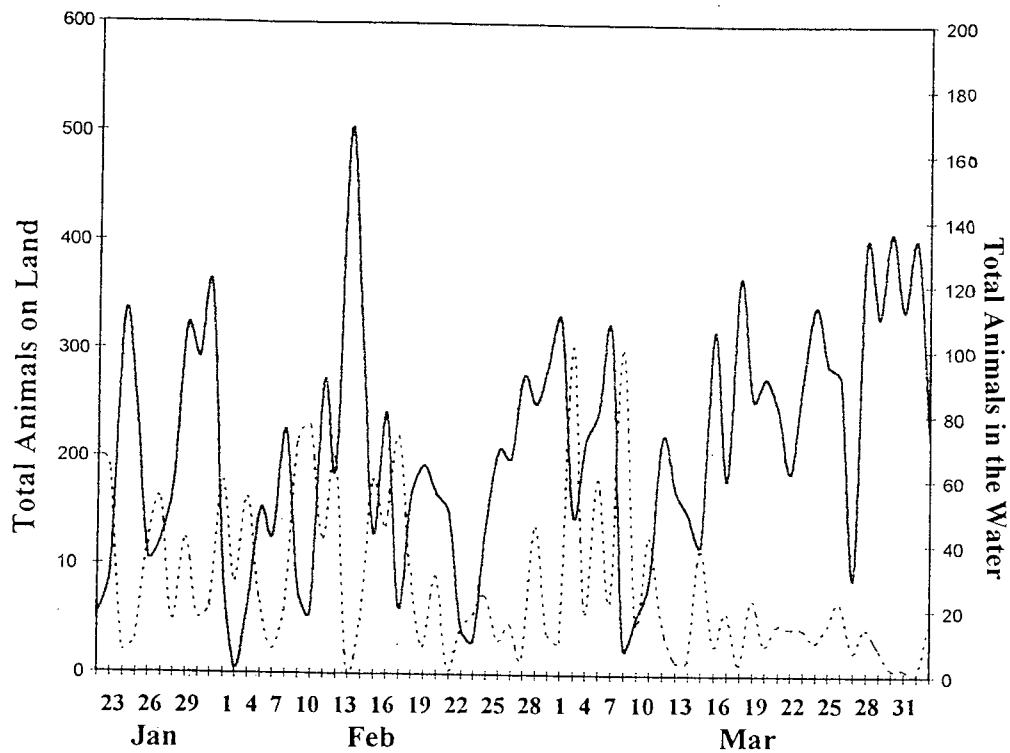


Figure 2.2 Mean daily total animals on shore and in the water.

Diurnal and Nocturnal Haul-out Patterns

A Linear regression fit to the hourly counts of sea lions showed no significant trend through the day, ($F_{1,518} = 1.63$, $P = 0.20$), nor was there any diurnal pattern observed using locally weighted regression (Fig. 2.3).

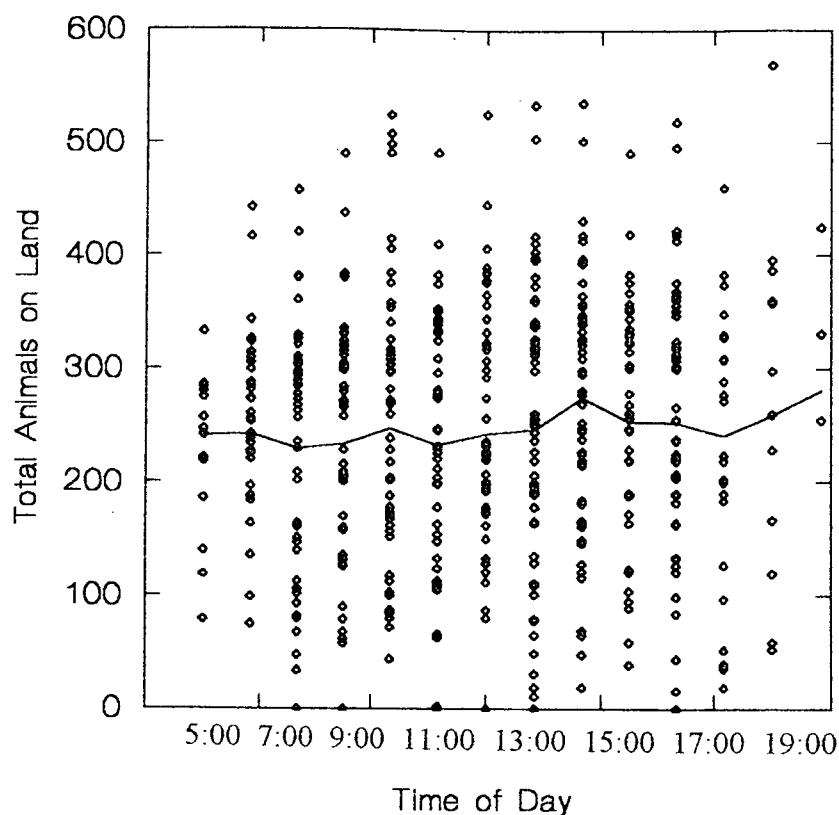


Figure 2.3 Total animals on shore during January to April by hour of day (all data pooled). A robust locally weighted regression shows no diurnal pattern (Loess $f=0.2$).

A small sample of counts on 4 nights (2100-0500 hrs) indicated the animals remained active and continued to arrive and depart as they did during the day.

Weather and Sea State

Weather had the strongest influence on numbers of animals hauled out. Correlates were ranked using the counts and codes for each hour to better understand the relationship of environmental variables and numbers of animals on shore. Using the Drop-one stepwise regression, all weather and sea conditions were ranked by the order of their significance to total animals hauled out on land. Month and time-of-day were found to be non-significant variables and were subsequently dropped. The remaining environmental factors (final equation) were ranked by declining importance in their ability to explain total numbers of animals on shore at any time (Table 2.1).

Table 2.1 Summary statistics for stepwise regression equation (partial F-test).
Correlates ranked from most to least significant.

Variable	<i>RSS</i>	<i>SSM</i>	<i>DF</i>	<i>MSM</i>	<i>F</i>	<i>P value</i>
Wave	18101.60	1518.9	4	379.7	8.3	< 0.001
Temp	17596.59	1013.8	1	1013.84	22.3	< 0.001
WindS	18081.90	1499.2	6	249.86	5.5	< 0.001
Sky	17524.02	941.3	3	313.76	6.9	< 0.001
Barom	17131.72	548.96	1	548.96	12.0	< 0.001
Swell	17120.50	537.8	1	537.76	11.8	< 0.001
WindD	17230.14	647.4	3	215.79	4.7	0.003
Tide	16806.10	223.3	1	223.34	4.9	0.027

Wave intensity was the primary correlate to numbers of animals on land (Fig. 2.4a). As wave height increased, numbers of animals decreased on shore (Fig. 2.5a). Waves were driven by a combination of tide, wind, and wind direction, and produced a pounding surf on shore. Its intensity appeared to be related to low numbers of animals on shore.

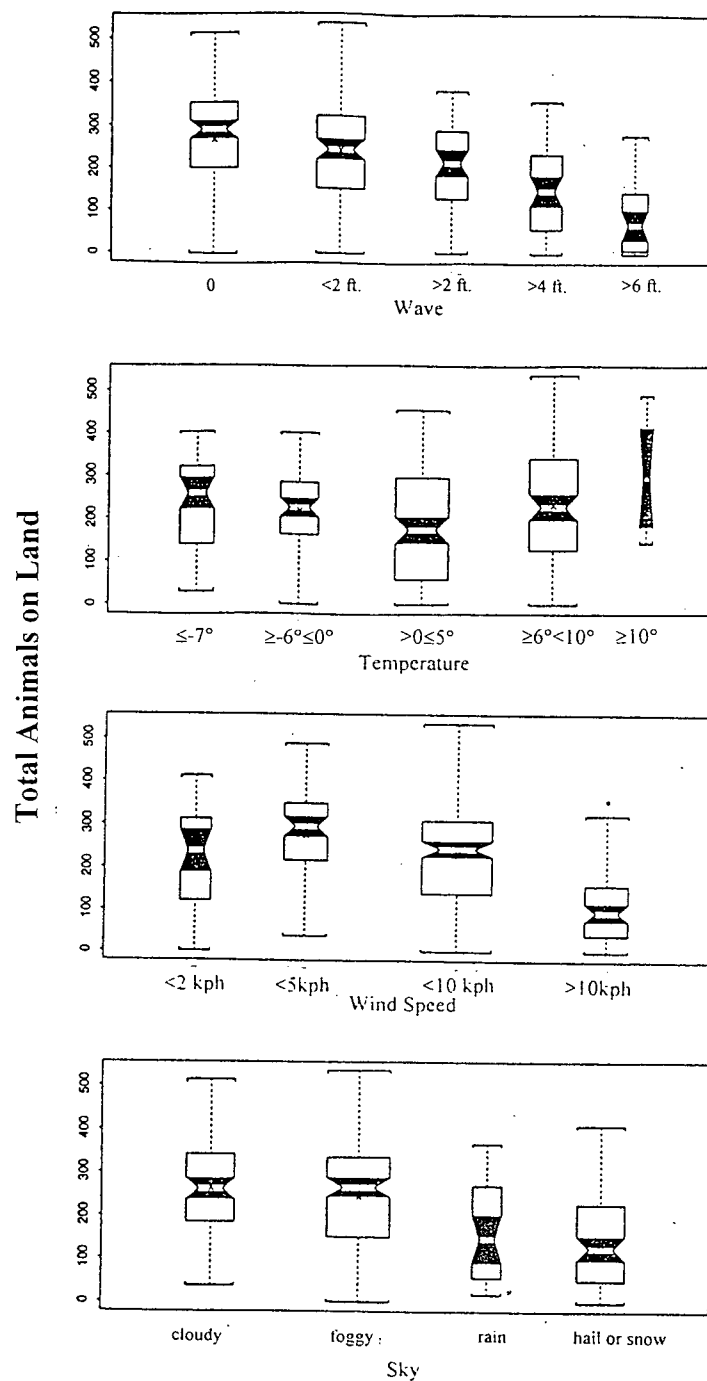


Figure 2.4 Box plot distributions of numbers of animals on shore showing the relationship between haul-out numbers and the intensity of environmental conditions. Environmental correlates are ranked by order of importance. The median is shown with a horizontal line, and vertical bars show the range. Notches are 95% confidence limits on the median. Box widths are proportional to sample size. Total numbers of observations were based on 562 hours of hourly counts.

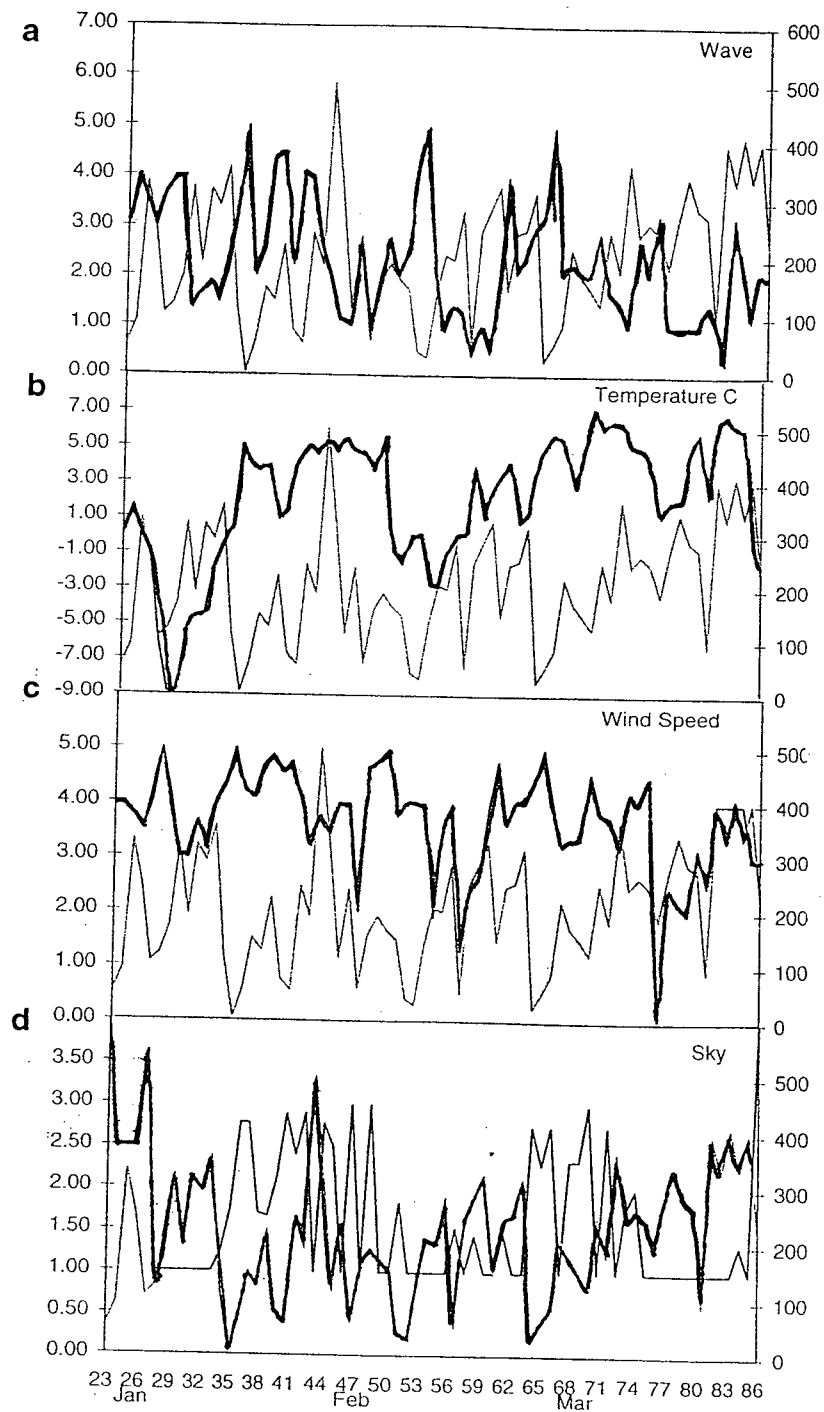


Figure 2.5 Mean daily environmental conditions (black) plotted overtop of mean daily counts of sea lions on shore (gray).

Ambient temperatures were typically low ($\bar{x} = 1.9^{\circ}$ SD = 4.2° C, range -16.7° to 11.1° C) and had a significant affect on sea lion numbers on shore (Fig. 2.4b). In combination with wave and swell, sea spray carried along the surface at extreme high wind speeds often created a disturbance effect that was similar to that of precipitation. Wind speeds ranged from 0 - 160 kph. Winds less than 10 kph had little effect on total numbers (Fig. 2.4c), but fewer animals remained on shore beyond that intensity. Wind measured on the intensity scale (modified Beaufort scale) (Append. 2) averaged 3.7 (SD= 0.9). Overall animals hauled out were affected by a combination of wind chill (ambient air temperature, wind, humidity) and sea state.

Disturbance

Sea lions enter the water more readily during winter than those on rookeries in summer. Causes of disturbance included: heavy snow or rain, birds, low flying aircraft, sea lions with unusual marks or entangled in nets, or California sea lions.

Eagles, crows, magpies, gulls and ravens are common scavengers at sea lion haulouts. Eagles and ravens disturbed the sea lions when they flew low or flared their wings over the animals in what appeared to be a deliberate attempt to disturb them to get access to scat material or aborted foetuses. Eagles may pose a threat of injury during confrontations as they become bold in repeated attempts to reach fresh foetuses. In January this resulted in the entire haulout stampeding into the water. As winter progressed, the sea lions became more habituated to the eagles and ravens. They were less likely to stampede at the first site of them, and even lunged at them as they flew overhead. Small birds (crows, magpies, gulls) often moved about near the animals with little disturbance.

The sound of low flying aircraft, even obscured in clouds, was sufficient to send most animals into the water. The distance to the aircraft did not seem to matter as much as how well sound traveled on any particular day. Animals appeared to be more likely to react to aircraft on calm days with little sea and wind noise.

Several animals came ashore with unusual marks on their hair or entangled in pieces of net or webbing. This was noticed by nearby animals and several times disturbed the entire haulout. Similarly, on several occasions California sea lions hauled out nearby and caused disturbance. Most adult animals simply moved to another site on shore away from the general area where the California sea lions hauled out. Juvenile Steller sea lions were more curious of the anomaly and treated the strangers as play objects. Consequently, the California sea lions observed swimming near the haulout often had a number of juvenile Steller sea lions in tow. But the most dramatic disturbances were caused by the California vocalizations which are very different and distinct from those of Steller sea lions.

Discussion

Sea lions spend time both in the water and on land. The sea is usually more uniformly stable while terrestrial conditions are more variable. A homeotherm that inhabits both land and sea must possess thermoregulatory versatility. Pinnipeds do this by physiological means (primarily vasoconstriction and blubber layer) and by extensive behavioural adjustments (Fay and Ray 1968). Water has twenty times the thermal conductivity of air. This means that for most of the time, and for most pinniped species, the problem is to conserve heat in the water and to dissipate it when out (Renouf 1990). In my study, numbers of animals on shore changed with temperature, which was the second most important environmental correlate explaining variation in haulout numbers (Fig. 2.4b).

Most past research has focused on summer rookery sites where there is a strong site fidelity in the form of dependent pups or a breeding territory. Animal haul-out patterns at these summer sites are predictable and well documented (Gentry 1970; Withrow 1982; Merrick 1985; Sandegren 1970; Kastelein and Weltz 1990; Gisiner 1985; Smith 1988). This is not the case for winter sites. Winter haul-out patterns likely reflect traditional and seasonal access to an available prey base and a weaker more flexible tie associated with their dependent offspring.

During the winter, sea lions haul-out in variable sized groups with fluctuating sex and age compositions. They are sociable and gregarious and appear to search out places providing optimal social stimulation both in and out of the water. With the exception of sick animals or an occasional male, they are rarely observed alone on land (Sandegren 1970). This herd formation may serve as an antipredator behaviour against predation. Studies on birds and mammals have found that individuals in groups spend less time in surveillance than they do when alone (Powell 1974; Berger 1978).

Much recent Steller sea lion work has relied on satellite and VHF telemetry, and on time-depth recorders to provide information about the haul-out behaviour of individual animals. While these data generate valuable insight into the habits of small numbers of animals, and even on specific subclasses such as lactating females (e.g., Swain 1996, Merrick *et al.* 1994), individual behaviour is variable. The variation with small samples using these methods likely masks the general trends seen more clearly in groups. For example, Yochem *et al.* (1987) reported that 7 of 17 radio-tagged harbour seals at San Miguel Island (California) preferentially hauled-out during darkness, although the colony as a whole showed a midday peak on shore. The group method used in my study allowed large numbers of animals to be observed to evaluate overall group patterns.

Patterns and Trends

In contrast to summer behaviour, where sea lions follow a predictable diurnal cycle of arriving at the rookery in early morning hours and departing in the evening (Higgins 1984, Sandegren 1970, Merrick 1985, Gisiner 1985, Smith 1988), no diurnal patterns in numbers of individuals hauled out were identified in this study (Fig. 2.3). It is possible however, for a diurnal pattern to be masked by the arrival of females concurrent with those leaving to feed. Similarly, it is possible for an inherent diurnal pattern to be lost due to disturbance or severe weather conditions. Such effects might deform or obscure an inherent pattern. Another possibility is that the lack of pattern observed is part of a diel trend which would be obvious using a 24 hour count.

Little is known about sea lion haul-out patterns during the night. A small random sample of counts using night vision optics indicated that animals remained active and continued to arrive and depart in no predictable pattern. Continuous counts after dark using night vision optics, however are needed.

Among pinnipeds, diurnal haul-out patterns, during summer, have been reported for Weddell seals (*Leptonychotes weddelli*; Siniff *et al.* 1977), ringed seals (*Phoca hispida*; Smith 1973, Finley 1979), harbor seals (*Phoca vitulina*; Wilson 1978, Boulva and McLaren 1979, Hoover 1981, Stewart 1981,1984), Steller sea lions (Withrow 1982, Sandegren 1970, Gentry 1970), and California sea lions (Mate 1975).

During the winter Steller sea lions did not exhibit the diurnal pattern seen in summer. The high variability in numbers ashore each day suggests that factors other than day length were important. In summer, numbers of hauled out sea lions are generally low in the early morning (0600 hrs.) with an increase as animals return from feeding, rising to a peak in mid-afternoon (1500 hrs.); A reversal occurs through the evening as animals return to the sea to forage (1800 to 2300) (Sandegren 1970, Gentry 1970, Merrick 1987, Withrow 1982).

During summer, sea lions feed mainly at night when foraging payoffs are thought to be greatest, *i.e.* there is a nocturnal peak in prey availability as these preferred prey make a vertical migration to the surface (Beamish 1966; Harden Jones 1968; Hansen 1979). Sullivan (1980) suggested that diurnal haul-out in sea lions was probably due to nocturnal or crepuscular feeding schedules rather than to promote thermoregulation. More energy would be expended to reach those same prey after they retreated to deeper water during daylight. The prey base in winter may also be different than summer and consequently lack the nocturnal predictability and availability. Foraging effort (more dives per unit effort) is also greater during the winter suggesting that sea lions are working harder to obtain prey (Swain 1996, Merrick and Loughlin 1997).

Weather

Weather conditions can have a marked effect on hauling out behaviour (Table 2.2). For example, Withrow (1982) found summer Steller sea lion numbers were most predictable using three variables ranked by order of importance: date, visibility and time of day. Sandegren (1970) found summer storms and strong rain or hail drove most sea lions into the water.

Table 2.2
Published environmental correlates of hauling-out in pinnipeds

References	Visibility	Wind	Tide	Temp	Solar	Storms	Precipitation	Snow /Ice	Time
Bartholomew and Wilke 1956				X		X			
Boulva and McLaren 1979		X		X					
Fay unpubl.				X		X			
Fay and Ray 1968							X		
Godsell							X		
Hansen <i>et al.</i> 1995		X		X					
Hoover 1981 ¹									X
Kastelcin and Weltz 1990 ¹			X	X					
Kenyon and Rice 1959									
Kenyon and Rice 1961 ¹								X	
Laws 1956 ¹				X					
Mate 1975 ¹									X
Paulian 1964				X					
Pierotti and Pierotti 1980				X					
Porter 1997 ¹	X	X	X	X		X	X	X	
Ray and Smith 1968		X		X	X				
Sandegren 1970 ¹			X			X	X	X	X
Smith 1965		X		X	X				
Stewart 1981, 1984, 1987		X		X	X				X
Sullivan ¹ ???									X
van Wijngaarden 1962				X					
Vaz-Ferreira and Palerm 1961 ¹				X					
Waters 1965								X	
Wartzok 1991		X		X	X				
Watts 1992		X		X			X		
Wilson 1978			X						X
Withrow 1982 ¹	X		X						X

¹ Sea lion studies

He also found the pattern was diurnal, although numbers of animals ashore during the summer varied considerably with weather and tide conditions. They tended to avoid snow-covered surfaces and often remained in the water until the snow either melted or washed away from the rocks (Kenyon and Rice 1961; Sandegren 1970). Hooker's and Australian sea lions occupy dune areas during winter where heat losses to the substrate are less than on damp sand (Ling and Walker 1979, Beentjes 1989). South American sea lions (*Otaria byronia*) may escape the heat altogether by remaining in the water during periods of high air temperatures (Laws 1956). Harbor seals can extend their thermal comfort zone by escaping into the water when the comfort zone limits have been exceeded (Watts 1991).

Precipitation

Heavy rain, snow, and hail all affected haul-out numbers during this study, while light precipitation had no marked effect. Sandegren (1970) also found that animals departed from the haulout during periods of intense hail or rain. Heavy precipitation also reduces the numbers of harbor seals (Godsell 1988; Watts 1992), and walrus on shore (Fay and Ray 1968, Jemmison ADF&G Juneau Ak. pers.comm). Marlow (1975) reported that Hooker's sea lions (*Phocarcos hookeri*) leave the beach during heavy rainstorms, then return when the rain eased. In contrast, Beentjes (1989) found an all male group of the same species did not react to heavy precipitation.

Sea lions became active during periods of heavy precipitation and often returned to the sea. They rafted nearby and did not haul-out again until visibility improved. A possible explanation for this reluctance to remain on land, while visibility was impaired, may be the potential risk of predation. However, sea have few terrestrial predators aside from man, and they are seldom at risk from land predation.

Withrow (1982) noted that sunlight breaking through the clouds, in an area where there was almost constant cloud cover, was enough to cause entire haulouts to stampede into the water. Heavy precipitation may simply be a similar strange occurrence and cause for alarm in an otherwise predictable environment.

Wind and Sea State

Strong winds and rough sea state are seldom independent of one another and, in most cases, are linked to general poor weather conditions. Wind direction had a significant effect when it blew directly toward the haulout as it tended to magnify the already rough sea state. East and southeast winds were the strongest at the Timbered site in winter and were normally associated with the most severe weather patterns. The main haulout was sheltered from NW winds, and even extremely high winds from that direction had little effect on numbers on land. High wind and rough seas often caused large numbers to enter the water. During these conditions, animals moved out to sea away from the rocks and rafted nearby, or dispersed to feeding areas.

Many times there appeared to be safe areas for sea lions to remain ashore during violent weather, but they did not. They may have perceived the increased risk of injury or death. This is consistent with other studies, where sufficient space was available yet animals departed the haulout during poor weather (Withrow 1982; Fiscus pers.comm.). Haulout patterns have been observed in harbor seals where abundant alternative rocks are available for haul-out yet animals congregate together (Kreiber and Barrette 1984; Terhune 1985). On two occasions animals were injured when rapidly changing sea conditions caught them unaware on shore and violently tumbled them across the rocks. Sea lions may perceive the risk and choose to leave to avoid surf conditions that pose a potential risk of injury.

Temperature

In winter, sea lions may enter the water (the more stable of the two environments) to maintain body heat during low ambient air temperatures and icing conditions. Whether alone or in combination, wind-chill factor¹, ambient temperature, and ice on the rocks may

¹ Wind chill is a combination of ambient air temperature, wind, and humidity.

make it more thermodynamically expensive to be exposed on the rocks than to enter the water.

Tide

There was a negative relationship between numbers of Steller sea lions on shore and stage of the tide. Several studies have report that the haul-out cycle of Steller sea lions is strongly influenced by tide (Kastelein and Weltz 1990). Calkins *et al.* (1997) also found that tide was a significant predictor at 10 of their 13 sites. Withrow (1982) found no effect from tide and thought that date and time were more important during summer.

The main Timbered Island haulout is a semi-flat, offshore rock. It is awash when high tides are accompanied by > 6 foot swells. Sea lion haulouts are seldom submerged during high tides as are many typical harbor seal haulouts; although at some sites such as Timbered Island, space becomes limited during high tide cycles as animals compete for dry space. The effect of tide is site-specific, since the space available for haul-out at high tide levels varies between sites and may be further compounded by different densities of sea lions.

Conclusions

These findings have obvious ramifications for census work. Contrary to the endogenous rhythms of summer animals, Steller sea lion haul-out patterns in winter are influenced by weather patterns, sea conditions and frequent disturbances. Once the winter haulout is cleared, the pattern may be altered for one or several days. This is in sharp contrast to summer animals that quickly recover and resume haul-out. This means that an aerial survey at midday would not include the high proportion of the population as it would during summer. Weather and, to a lesser degree, tide appear to be more important than time of day when counting numbers of sea lions on land during winter, and should be considered when absolute numbers are important. Observers should also be alert for large groups in the water, or high numbers of wet animals on shore indicating a past disturbance. Counts during these times would underestimate actual numbers. These

findings may also be useful for scheduling when best to visit winter haulout sites for capture work.

Summary

Haul-out patterns of Steller sea lions were observed at Timbered Island, Alaska during winter (Jan-Apr). Mature females and their dependent young predominated while numbers of mature male and sub-adult males remained low. There was considerable variability in numbers of animals on shore from one day to the next. A Drop-one Stepwise regression showed numbers on shore were correlated with weather and sea conditions. The ranked order of importance included: wave height, air temperature, wind speed, wind direction, sky cover, barometric pressure, swell height, and tide height. No diurnal pattern was detected. Additional sources of disturbance included: precipitation, birds, aircraft, entangled sea lions, and California sea lions. A small sample of night counts indicate high activity and a lack of predictable haul-out patterns.

Chapter III: Winter Attendance Patterns of Female Steller Sea Lions

Introduction

Unlike most phocids, lactating otariid females must make intermittent trips to sea to feed (Trillmich and Lechner 1986, Gentry 1970, Sandegren 1970, Merrick 1987). This constant shift between time on shore with the pup and time spent at sea foraging is repeated throughout lactation and is referred to as the maternal attendance pattern. It is an important part of the otariid rearing strategy. Pinniped neonates must attain sufficient body weight and energy reserves prior to weaning to survive the first year of life. Pups are mostly dependent upon the milk produced by their mother, although some may begin to supplement milk with solid food late in their first year.

Foraging theory predicts that the amount of time an animal devotes to capturing prey is related to individual metabolic needs and the availability of prey (Stephens and Krebs 1986). Temporal patterning, duration of foraging at sea and the time spent onshore nursing should be related to food availability, female body mass and distance to the foraging grounds (Gentry and Holt 1986). For example, the amount of milk consumed by Antarctic fur seal pups (Arnould *et al.* 1996) and the growth of offspring during maternal attendance correlate with the length of maternal foraging trips (Goldsworthy 1995). Central Place Foraging Theory states that when foraging a long distance from the haul-out, a mother should make fewer trips but return with a greater quantity of energy per trip. Similarly, those foraging nearby should make many short trips, returning with lower energy per trip (Orians and Pearson 1977). Increased home ranges in the winter further suggest that prey densities are reduced, because home-range area is a positive function of metabolic requirements and productivity of the foraging area (McNab 1963, Harestad and Bunnell 1979, Lindstedt *et al.* 1986). Mature females providing for male pups during this period should spend longer at sea to provide for their larger offspring.

The first winter following birth is believed to be a critical stage in the life history of young Steller sea lions and may contribute to understanding the population decline that has occurred in most parts of Alaska (York 1994, Merrick 1996, Trites and Larkin 1996). With these considerations in mind, I evaluated maternal investment relative to age and sex of offspring. My goal was to measure the amount of time mothers and young spent on shore and at sea, and to compare their winter (Jan - Apr) haul-out patterns with similar data available from summer (May - Aug). Foraging trip duration and time on shore was used as a measure of maternal investment to test two hypotheses: 1) that mothers of male offspring spend more time at sea than do mothers of female offspring to provide for the greater nutritional needs of the larger males, and 2) that mothers of yearlings (age 1-2 y) take longer foraging trips than females with pups (age 6-9 mo.). Both of these strategies, if they were utilized, would offset the cost of rearing larger and more demanding immature animals.

Methods

Data Collection

Time ashore and at sea were based on the presence or absence of females at the haulout during daily behavioural observations. Since most females could not be identified individually, they were counted as present only when seen with identifiable dependent branded offspring. Mature females were scored as away if they were not observed on the haulout during daily observations. The proportion of time spent away equalled the amount of time the female was absent divided by the total period of observation days. The behaviour and association of branded immature sea lions (yearlings and pups) were noted every 15 minutes using focal sampling (Martin and Bateson 1986). Behavioural observations were restricted to daylight hours (0600-1900) and include 562 hours of observation time. Females missing in the evening or discovered in the morning were assumed to have departed or arrived during the middle of the night.

Females present at dusk and dawn were assumed to have spent the night on the haul-out. Similarly, females absent at dusk and the following dawn were assumed to have

been away all night. When females were present only at the beginning or end of observations, the mid point during the night was calculated as the departure or arrival time. It was not possible to exclude the chance that individuals were hauled out at other sites, although previous work done with satellite telemetry has shown females rarely haul-out on multiple sites during foraging trips (Merrick 1996, ADF&G unpubl.data).

The average duration of trips was calculated for each female. The means from each female were then averaged to determine the average duration of foraging trips at my study site.

To determine if duration of time mature females were at sea was a good measure of foraging duration, it was necessary to define "foraging trip". Behavioural observations of short trips often consisted of animals rafting or swimming near shore for short periods (pers. obs.). Several summer studies, using VHF telemetry, found gaps in the frequency distributions of the signal record suggesting non-foraging activity during short trips (Boyd 1991, Brandon 1996). Higgins (1984) found no foraging trips lasting less than 8 hours. Based on the distribution of forage trips I recorded, I assume that animals with trips > 200 hrs made an unrecorded visit to the haul-out, or had moved their offspring to another site for an extended period. I also assumed that those with trips ≤ 2.5 hours were obscured for a short period and inaccurately noted as "absent" when they were actually present on land. Hence, only those trips greater than 2.5 hours and less than 200 hours were counted as foraging trips.

Results

Daily attendance of mature females and their dependent offspring are shown in Figure 3.1. Additional immature sex and age information is listed in Appendix 2.

Individual foraging trip durations showed distinct upper and lower cut-off points with very few data points at either extreme (Figure 3.2).

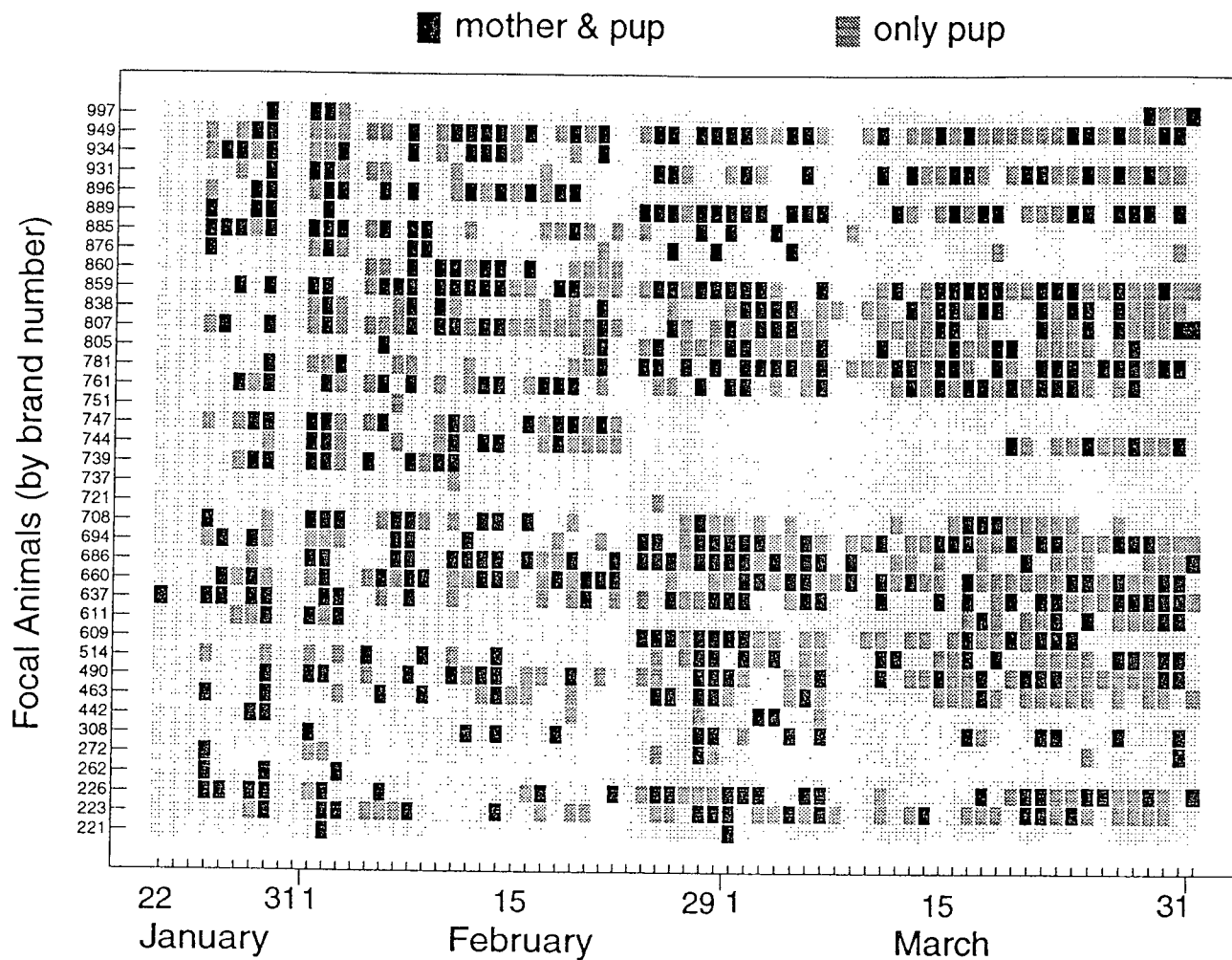


Figure 3.1 Daily attendance of mature females and their dependent offspring. The Y axis corresponds to individual brand numbers. Animals sighted at least once during the day were scored as present. Gray boxes indicate the immature was present. Black boxes indicate both the immature/mother pair was present. Timbered Island, Alaska 1996.

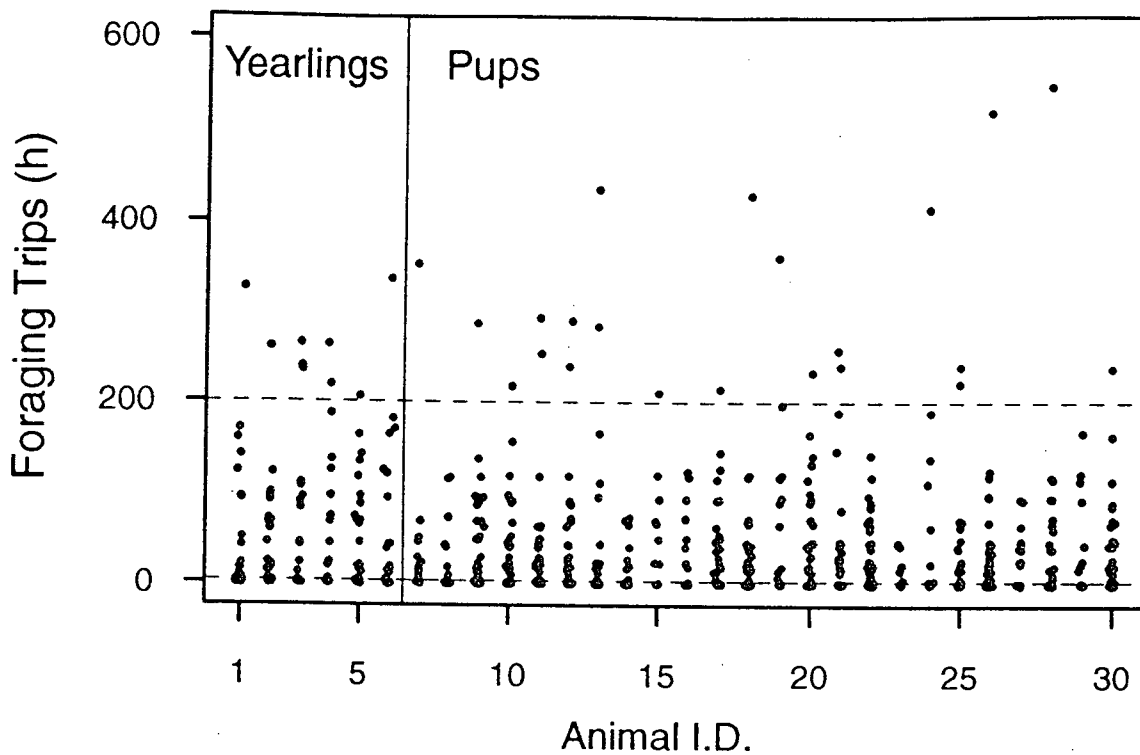


Figure 3.2 Individual foraging trips for 30 mature females with pup (<1 y) and yearling (<2 y) offspring. All recorded foraging trips by individuals are shown including those above and below the cut-off points. Additional information about the sex, age, and brand numbers of the offspring of mothers 1-30 is contained in Appendix 2.

Average trips by mothers with yearlings lasted 2.3 d ($\bar{x} = 59.7 \pm 4.7$ h SE, $n=6$) and were significantly longer than the 1.9 d average trips of mothers with pups ($\bar{x} = 48.0 \pm 6.3$ h, $n=18$) [$t_{28}=1.74$, $P=0.047$; Fig. 3.3]. Mothers with male pups (< 1 y) were away for an average of 2.2 d ($\bar{x} = 52.5 \pm 15.2$ h SE, $n=12$) compared to 1.8 d ($\bar{x} = 43.5 \pm 12.6$ h, $n=12$) for those with female pups. Mature females ($n=30$) showed little seasonal variation in trip duration (Fig. 3.4): They spent an average of 19.4 h on shore between trips to sea ($n=30$, SE=0.90, range 11.2-29.2h). Differences between offspring genders and age classes were not statistically significant (Fig. 3.5). Lactating females spent an average of $14.2 \pm 1.1\%$ SE ($n=30$) of their time on shore while immature animals spent $40.2 \pm 2.1\%$ (Fig.3.5).

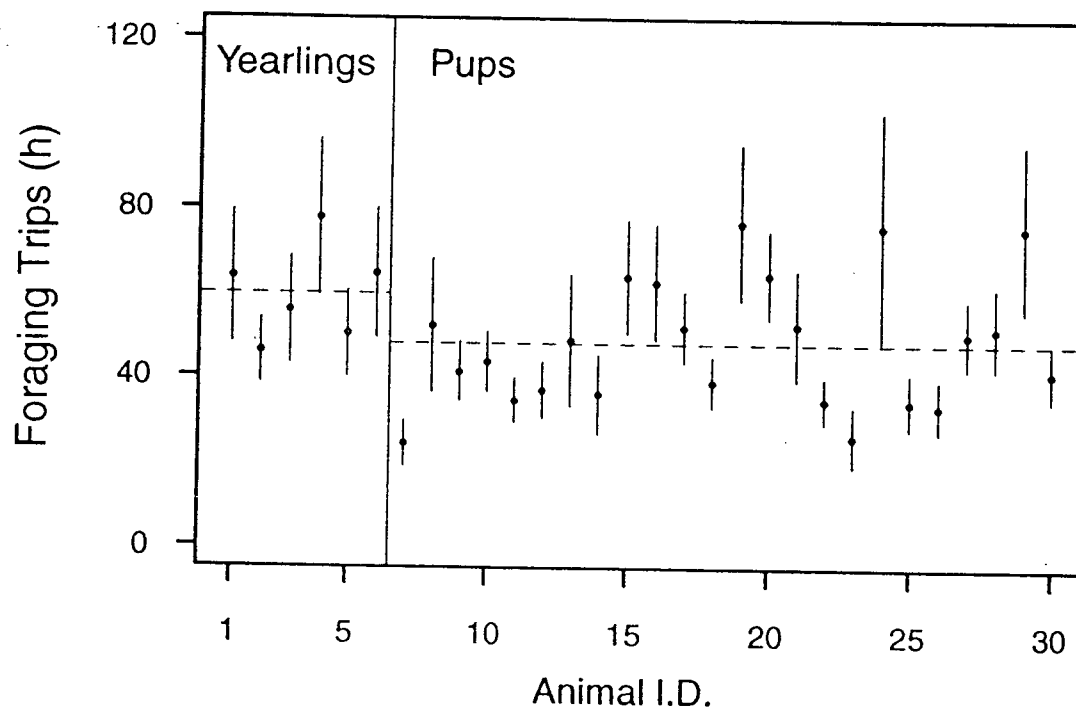


Figure 3.3 Mean trip duration for individual mature females. Means are shown ± 1 standard error. Dotted lines show the mean length of trips for all females with yearlings (left) and pups (right).

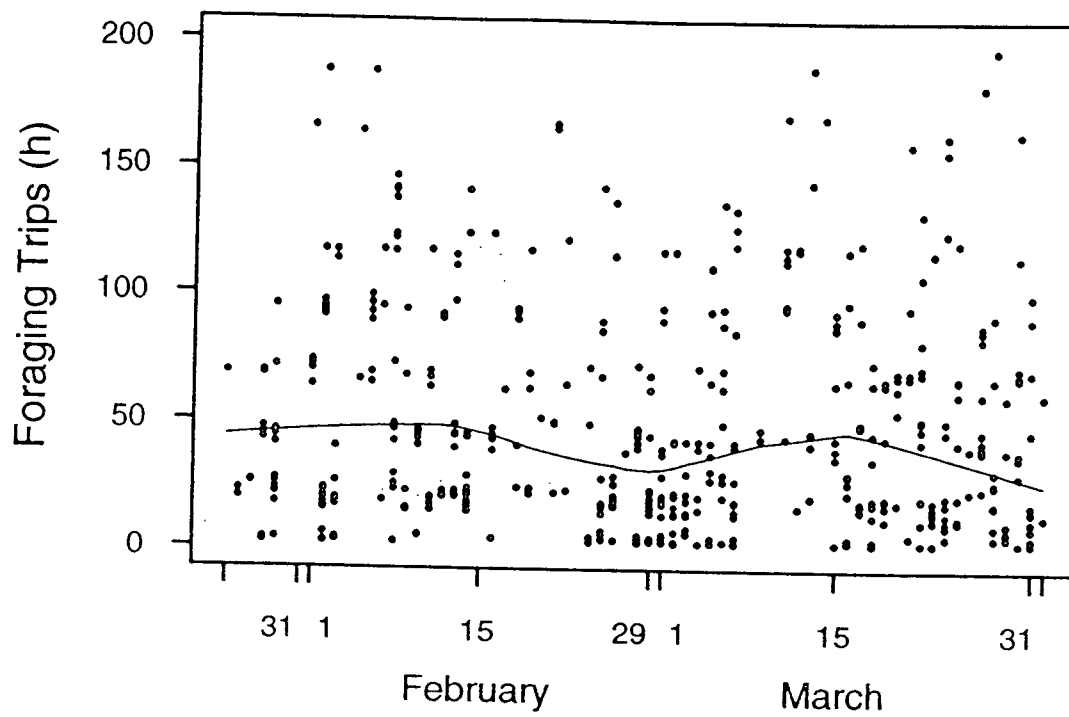


Figure 3.4 Durations of all trips 3 - 200 h ($n=552$) by time of year for 30 mature females with dependent offspring. The data were fit with a locally weighted regression (loess, $f = 0.5$).

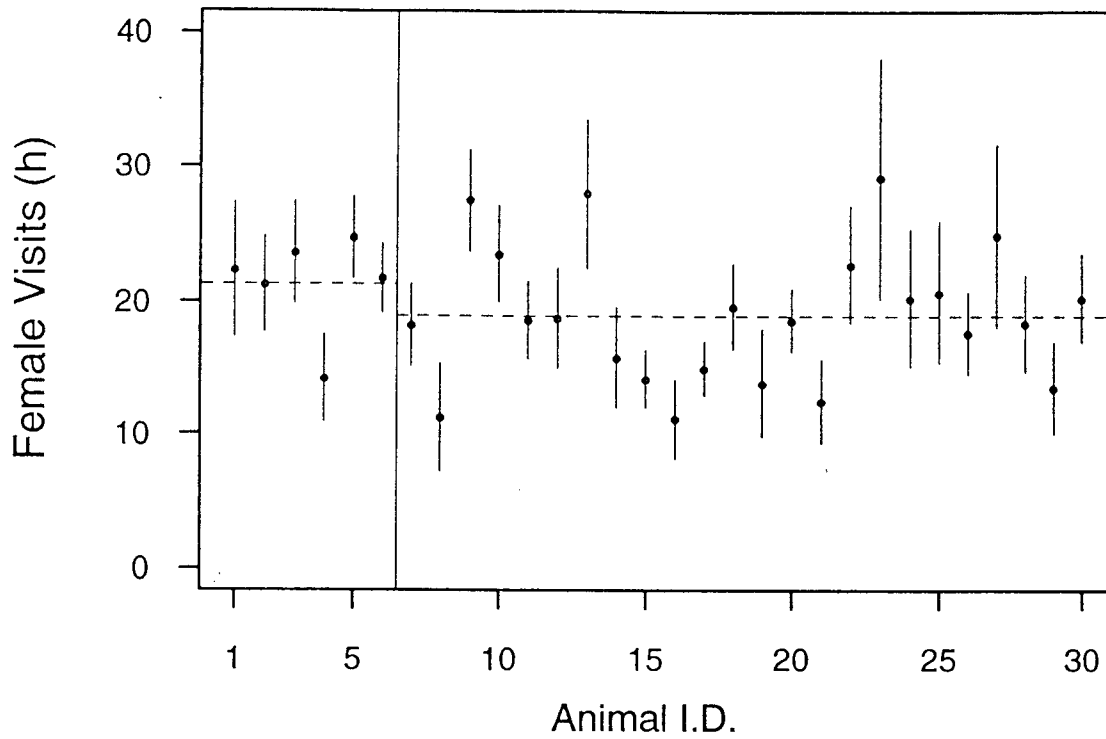


Figure 3.5 Mean shore visit (h) for individual mature females. Means are shown ± 1 standard error. Dotted lines show the mean length of trips for all females with yearlings (left) and pups (right).

Discussion

In summer sea lions typically depart rookeries in the late evening and return around dawn (Withrow 1982; Higgins 1984; Merrick 1995; Swain 1996). They presumably feed most at night because the species of fish that move up the water column each night in search of food (Beamish 1966; Harden Jones 1968; Hansen 1979) would require less time and energy to pursue near the surface than at depth during the day. Incidental bycatch of sea lions during fishing operations is greatest from 2300 to 0300 hours in summer (Loughlin and Nelson 1986). However, this may be typical only for sea lions searching for prey which migrate vertically with diel light patterns. Although vertical migrating fish (herring, pollock) comprise much of their diet, they eat a range of fishes and invertebrates including many non-vertical migrating prey such as: cephalopods, rockfishes, and flatfishes (Calkins and Trites unpubl. data).

The considerable variability in the duration of trips between and within individuals (Figs. 3.1-3.2) may reflect flexible foraging strategies. For example, the differences may reflect age and experience of the mature female at locating and capturing prey. However, if trip duration is simply an indication of prey availability, it seems reasonable that changes should have been consistent between individuals.

Sex and Age Differences

In theory, the higher energetic demands of rearing male pups compared to female pups should be reflected in the amount of time mothers spent at sea, and on shore. But, there was no correlation between mature females trip durations and the sex of their dependent young. Similar results have been reported from studies of other species, such as Australian sea lions (Higgins 1990), Galapagos sea lions (Trillmich 1986b) and northern fur seals.

Winter Pattern

During the summer while tending neonates on rookeries, foraging trips by females average between 1.0 and 1.9 d (Gentry 1970; Sandegren 1970; Higgins 1988, Swain 1995, Merrick 1987, Merrick and Loughlin 1997) compared to my finding of 2.3 d in winter. Foraging effort appears to be greater during winter as sea lions travel further and dive more frequently (Swain 1996, Merrick and Loughlin 1997). Data from satellite telemetry shows adult females do not forage as close to haul-out sites in winter as in summer (Merrick 1995; ADF&G unpubl.). This suggests that either prey availability is reduced near the winter sites, or that a richer prey supply is available beyond the typical summer foraging range. Some prey ordinarily consumed in summer (e.g., capelin, *Mallotus villosus*, and salmon, *Oncorhynchus spp.*) are more commonly found nearer shore in summer than in winter (Merrick and Loughlin 1997). Several of these preferred prey spawn near shore or do so anadromously during the summer. Consequently, they are likely to be more accessible to sea lions at that time. The increased frequency of shorter and shallower dives in late spring suggests sea lions are foraging on spawning fish such as herring (Swain 1997).

There was no apparent change in the duration of female foraging trips from Jan 20 to Apr 1 (Fig. 3.4). Merrick and Loughlin (1996) found a similar result using satellite and VHF telemetry to measure winter foraging trips of mature Steller females with and without dependent offspring. Melin (1995) also reported a lack of seasonality in the foraging trips of female California sea lions during the winter period. These results differ from reports of increasing foraging trip durations over the lactation period in several species of fur seals (David and Rand 1986, Gentry and Holt 1986, McCann and Croxall 1986) and reports of a seasonal decrease in foraging trip lengths in Australian sea lions (Higgins and Cass 1993). This lack of seasonal pattern in Steller sea lions may reflect a consistent abundance of prey, the plasticity of foraging behaviour responding to changes in prey abundance and distribution or physiological or behavioural limitations.

Proportion of time at Sea

Foraging theory predicts that the amount of time an animal devotes to capturing prey is related to individual metabolic needs. This functional relationship is well documented for otariids (Costa *et al.* 1989, Trillmich and Ono 1991, Boyd and Arnborn 1991, Boyd *et al.* 1994). Thus, females should spend more time at sea if prey are less abundant, or more patchy during the winter to meet their metabolic needs and those of their dependent offspring.

Lactating females at Timbered Island spent an average of 86% of their time at sea based on behavioural observations. Immature animals spent significantly shorter periods of their daily activity budget at sea averaging 60% during winter (based on behavioural observations in this study) and 37.5% during summer (based on satellite telemetry, Merrick and Loughlin 1996). These results are similar to those reported by Melin (1995) for California sea lions (March - May: lactating females 75%, dependent pups 33%).

Steller females spend a similar proportion of their time at sea during winter and summer. Higgins (1988) found lactating Steller females spent an average of 70% of their time at sea during summer observations and more time at sea as the pup aged². The difference between the amount of time spent at sea by lactating and non-lactating females suggests that females that are not providing for dependent offspring have different foraging strategies.

Non-lactating California sea lions (Melin 1995) and northern fur seals (Gentry and Holt 1986) appear to be more mobile, to travel further, and to forage in more productive areas than those with dependent offspring. Females with dependent offspring in the winter may not only have greater energy demands but may also be limited in the distance they can travel away from the haul-out. Therefore, lactation status of the female must be considered when comparing the foraging strategies of individual females. Comparisons between satellite estimates and behavioural methods must be made with caution because of the lack of coverage during the dark hours. Behavioural methods could slightly over-

² No reference was made to indicate the time frame in which data was collected.

estimate trip length if females return during the night, and underestimate it if they depart during darkness. A similar amount of error exists using telemetry data due to gaps in the satellite coverage (± 6 h) and due to more chance of a satellite hit while on land.

Foraging by Immatures

Recent population declines of Steller sea lions point toward reduced juvenile survival (Merrick *et al.* 1988; Loughlin and Merrick 1989; York 1994). Juvenile sea lions would be especially susceptible to increased mortality brought on by reduced food availability because young animals, especially newly weaned pups, are inexperienced foragers with limited ranges (Merrick 1995). Young of the year Steller sea lions, with satellite recorders attached, had home ranges smaller than mature females (Merrick and Loughlin 1993). Body size may preclude pups from exploiting the deep foraging areas successfully until they are older, or perhaps there is a learning component to foraging that takes time to develop. Young animals may thus be limited in what food is available to them (Merrick and Loughlin 1997).

Immature Steller sea lions likely make a gradual transition from mother's milk to independent foraging. However, exactly when they begin to forage independently is not known (See Ch. II and IV). Most weaning is thought to occur between April and May, but young animals may begin to forage while they are still suckling. It was unclear from observations whether immature animals accompanied their mothers on foraging trips, or if they foraged independently during her absence. Young sea lions may supplement their milk diet with solid food, during the winter, once they are old enough to forage on their own. Dependent juveniles have shallow dive depths and short foraging trips, which may reflect their weaning status (Calkins 1997, Swain 1997). In contrast, independent juveniles have high indices of foraging effort (Swain 1997). Although no studies have investigated the onset of solid food ingestion, Oftedal (1987) reported California sea lion pups had ingested solid food at 7 months and Steller sea lions are thought to be similar. There appears to be a nutritional or developmental necessity for Steller sea lion pups to remain dependent on their mothers to various degrees until near the end of their first year.

Melin (1995), using VHF telemetry, found California sea lion young of the year took short trips (1 day) while their mothers were away, but she suggested they do not accompany them on foraging trips.

On several occasions, immature animals were observed near the Timbered Island haul-out with prey items on the surface, although it was unclear whether they had caught the live prey themselves, or if they had scavenged them. Most incidents involved thrashing at the surface and were similar to adult foraging behaviour in which large prey are brought to the surface and torn apart before being swallowed. The identifiable prey include: octopus (*Octopus* spp.), lingcod (*Ophiodon elongatus*), and rock fish (*Sebastes* spp.).

The net benefit of shifting to an alternative resource must be the difference between the value of the resource and the cost of obtaining it. Thus, the timing of independence should be a function of the individual offspring's stage of development and the availability of alternative resources for replacing parental care. In this case it is the availability of prey and the young animal's ability to locate and catch it. Maternal foraging activities may be hindered by the offspring if females must spend more time being vigilant, or consume food of lower quality in areas of reduced danger from predators (Sadler 1969; Carl and Robbins 1988). Females are also restricted in their foraging range by the fasting ability of the offspring and the amount of resources they can carry (Broekhuizen and Maaskamp 1980; Gittleman 1988; Gittleman and Thompson 1988). It may therefore be more energetically efficient for the pup to remain at the haulout rather than accompanying its mother on foraging trips. Most available data suggests that females with dependent offspring are tied to a specific location where the offspring is waiting and have limited range from that location until the young are fully weaned.

Conclusion

The duration of foraging trips did not increase as expected over the winter months to meet the rising energetic demands of the growing pups (Fig. 3.4). There are a number of possible explanations. One is that the females adjusted the quality of their milk rather than trip length. Lipid and energy content of milk of some otariid species has been found

to increase with trip duration (Trillmich 1990, Trillmich and Lechner 1986, Reidman and Ortiz 1979), although this has yet to be investigated for Steller sea lions. Offspring may also obtain an increasing proportion of energy on their own as they begin to forage independently. If prey are patchy or less abundant during the winter, females may adjust their foraging effort rather than the duration of their foraging trip. California sea lions for example, have been shown to increase the duration and depth of dives and decrease the time spent swimming under poor food conditions (Feldkamp *et al.* 1991).

Adult female Steller sea lions foraged over larger areas in winter compared to summer (Swain 1996). Merrick and Loughlin (1997) found that, although winter trips were longer, Steller sea lion females foraged approximately the same amount of time per day while at sea during both summer and winter. These observations suggest that food was not any more difficult to obtain, or less abundant during the winter. They also suggest that trip length may indicate distance to the prey source and that foraging effort (diving for prey) may be more indicative of prey abundance.

Prey movements and availability may shift erratically during the winter, and lead to a wide range of foraging trip durations both within the group and within individuals. This could mask any seasonal pattern in the changing metabolic needs of the offspring.

Mothers with yearling offspring spend significantly more time at sea compared to those with pups. This may reflect their need to bring back more resources, or alternatively, may be part of the weaning process whereby they spend progressively more time away from the offspring as the young approach independence.

Summary

I studied the winter foraging patterns of lactating Steller sea lions (*Eumetopias jubatus*) during the late stages of nursing when the young are moving from milk to independent foraging. Trip duration and nursing visits to shore by female Steller sea lions with pups (<1 y) and yearlings (<2 y) were noted during 545 hours of behavioural observations from (Jan to Apr), 1996 at a non-breeding haul-out site in Alaska. Trips by females with yearling offspring ($\bar{x} = 59.7 \pm 4.7$ h) were significantly longer than by

females with pups ($\bar{x} = 48.0 \pm 6.3$ h; $t_{28} = 1.74$, $P=0.047$). The duration of foraging trips by mothers of male pups ($\bar{x} = 52.5 \pm 4.9$ h) and female offspring ($\bar{x} = 43.5 \pm 3.6$ h) were not significantly different. There was no evidence of diurnal or seasonal patterns.

Mothers of yearlings ($\bar{x} 21.3 \pm 1.5$ h) and pups ($\bar{x} = 18.9 \pm 1.0$ h) spent similar time on shore during visits. Mothers of male pups ($\bar{x} = 18.8 \pm 1.6$ h) and female pups ($\bar{x} = 19.0 \pm 1.5$ h) were also similar. Mature lactating females were absent from the Timbered haul-out 66% of the time compared to 56.2% for immature animals.

Chapter IV: Winter Suckling Behaviour of Immature Steller Sea Lions

Introduction

Steller sea lions (*Eumetopias jubatus*), like all otariids, are sexually dimorphic with adult males often exceeding the mass of females by a factor of three. Male sea lions are, on average, bigger than females at birth and grow faster during the nursing period. This has also been documented in other otariids such as: South African fur seals (Rand 1956), New Zealand fur seals (Crawley 1975), Antarctic fur seals (Croxall *et al.* 1988), northern fur seals (Trites 1991), Galapagos fur seals (Trillmich 1986c), and California sea lions (Oftedal *et al.* 1987).

Adults should invest more heavily in offspring of one sex where additional investment has greater fitness returns (Clutton-Brock 1982, Trivers and Willard 1973, Maynard Smith 1980). In mammals, in which body size and early growth affect the fitness of males more than females, mothers should invest more heavily in sons (Clutton-Brock *et al.* 1991).

Many studies of growth in sexually dimorphic pinnipeds have pointed to increased maternal investment in male pups as the primary factor responsible for larger male size at birth and during early ontogeny (Trillmich 1986, Costa *et al.* 1988, Boyd and McCann 1989, Cappozzo *et al.* 1991). But offspring are not passive recipients of parental resources (Kretzmann *et al.* 1993). The suckling behaviour of males may be the proximate mechanism rather than any conscious effort on the part of the mother (Clutton-Brock *et al.* 1985).

Steller sea lions are polygynous, and large mature bulls able to defend breeding territories will copulate with many females each season, resulting in high fitness returns. Large body size, and aggressiveness are the two most important characteristics governing

successful territoriality in male sea lions during competition for breeding opportunities. Large body size is important for both fighting with rivals and to fast for long periods (2-3 months) since bulls do not feed during their territorial tenure. Few studies have directly investigated male body size in relation to the ability to obtain or hold territories in otariids (Peterson 1967, Gentry 1970), although studies of other size dimorphic species indicate that body size is a key ingredient for access to mating (Epsmark 1964, Clutton-Brock *et al.* 1982, Clinton 1990, Haley 1994, Haley *et al.* 1994).

In theory, male pups should consume more milk than females and require mothers to invest more energy to support their greater growth rates and higher total metabolic costs associated with larger body size (Kerley 1985, Costa and Gentry 1986). Male California (Oftedal *et al.* 1987a) and Steller (Higgins 1984) sea lion pups consume more milk than female pups. California sea lion mean growth rates were significantly greater for male pups regardless of their initial birth size (Ono and Boness 1996). Male Elephant seals are born heavier, grow faster, are weaned later, and tend to be more persistent in their attempts to obtain milk after weaning (Reiter *et al.* 1978). Other strategies, such as sneak suckling, are utilized by the immature animals to obtain additional nutrition (pers. obs). The suckling duration, frequency, and control over when suckling occurs should reflect behavioural differences in the way that mothers distribute their resources.

My primary objective was to use differences in suckling frequency and duration in Steller sea lion pups to test for differential maternal investment. I also sought to determine whether the frequency of suckling declined during the winter months as many of the young animals approach independence and begin to supplement their diet with solid food.

Two hypotheses were tested: first, mothers spend more time nursing male offspring than female offspring; and second, pups or young of the year suckle for shorter periods than the larger yearling offspring. Both hypothesized strategies could offset the cost of rearing a larger and more energetically demanding immature animal.

Methods

During the summers of 1994 and 1995 newborn Steller sea lion (SSL) pups were branded at breeding sites in Southeast Alaska by ADF&G. 30 of these branded and easily followed animals were observed at Timbered Island. Sex and age of individuals at branding are listed in Appendix 2. The activity of these branded animals, which were between the ages of 8-10 months (pups) and 20-22 months (yearlings), was noted every 15 minutes during daylight hours using instantaneous focal sampling (Martin and Bateson 1986). Observations were made during daylight hours each day and were constrained only by day length and 3 days of extreme weather conditions. Total daily observation time increased during the study because of the longer days as the season progressed. The sex of the branded animals was recorded at the time of branding (D. Calkins, ADF&G, unpubl. data), but was not known to the observers during this study. This presented an ideal blind experiment. Once the behavioural data were compiled and entered into the data base the corresponding individual sex and age information was then used to test for differences.

Visual aids included 7x35 binoculars and 15 - 60 variable power spotting scopes to increase the accuracy observations. A programmed stopwatch was used to maintain consistent 15 minute scan times. Daily behavioural information was collected with minimal observer disturbance to the sea lions from blinds 35 m from the animals.

All activities of focal animals were recorded instantaneously at 15 minute intervals. Suckling bouts³ less than 15 minutes would, in theory, be included in the 15 minute category. Individuals were not followed between observations. Animals therefore, could have started suckling after one instantaneous scan and stopped prior to or after the next, resulting in missed suckling time. However, scan sampling data is assumed to measure average suckling time accurately for each of the branded animals if a sufficient number of observations are made and the observation interval is short relative to the average duration of the behaviour pattern (Martin and Bateson 1986).

³ Bout - Period of time animal is engaged in an activity including short breaks.

Analyses

The initial sample consisted of 30 focal animals later determined from branding records to consist of 16 males and 14 females. Numbers of focal animals present varied considerably from day to day and resulted in an uneven number of observations for each animal. The number of 15 minute suckling bouts recorded per animal ranged from 8 to 155 ($\bar{x} = 69.3$ 42.8 SD) with a total of 774 bouts used for the analysis. A total of 562 hours of scan sampling was performed during 70 days, with approximately 15 immatures observed at any one time. Observation hours averaged 8.4 h per day (range 1-14.5 h per day). Suckling sessions, or bouts, included on-teat times and short breaks in-between. Every effort was made to score animals as suckling only when they were actually on teat, as indicated by subtle head and body movements and position relative to the mature female. Neither milk intake nor changes in milk composition were measured. Animals observed suckling less than 7 times ($n=1$, female yearling) were excluded from the analyses. This resulted in a final sample of 29 focal animals.

Two approaches were taken to test whether males suckled significantly longer than females. The first compared the absolute time spent suckling, *i.e.* the number of minutes. The second compared the relative amount of time spent suckling, *i.e.* the proportion of time males and females spent engaged in suckling while with their mothers.

All statistical and graphical analysis were performed using SYSTAT/SYGRAPH software, release 5.03 (Wilkinson 1990), and Microsoft EXCEL 5.0 for windows 5.0 (1993). Proportions were transformed (arcsine square-root) to satisfy assumptions of normality and homogeneity of variance (Zar 1984). Suckling bouts were skewed. Therefore the individual means, which were normally distributed were used to test for differences.

Results

Age and Sex Differences

The frequency of suckling bouts by immatures were exponentially distributed with a positive skew to the right (Fig. 4.1). It was not possible to normalize the data. Sample size (n) was equal to the number of subjects, not the number of observations. Comparing the individual means, which were normally distributed, showed mean suckling time for males pups ($\bar{x} = 37.2 \pm 2.8$ min. per bout, $n=12$) was slightly but not significantly longer than female suckling time ($\bar{x} = 35.9 \pm 2.3$ min., $n=12$, $t_{22} = 1.59$, $P = 0.37$). Because there was no significant difference between sex of pups, the mean suckling times of pups and yearlings were pooled to test for age differences. Average suckling bouts for yearlings ($\bar{x} = 44.0 \pm 2.8$ min.SE, $n=5$) were longer than for pups ($\bar{x} = 36.5 \pm 1.8$ min., $n=24$) ($t_{27}=1.85$, $P= 0.038$).

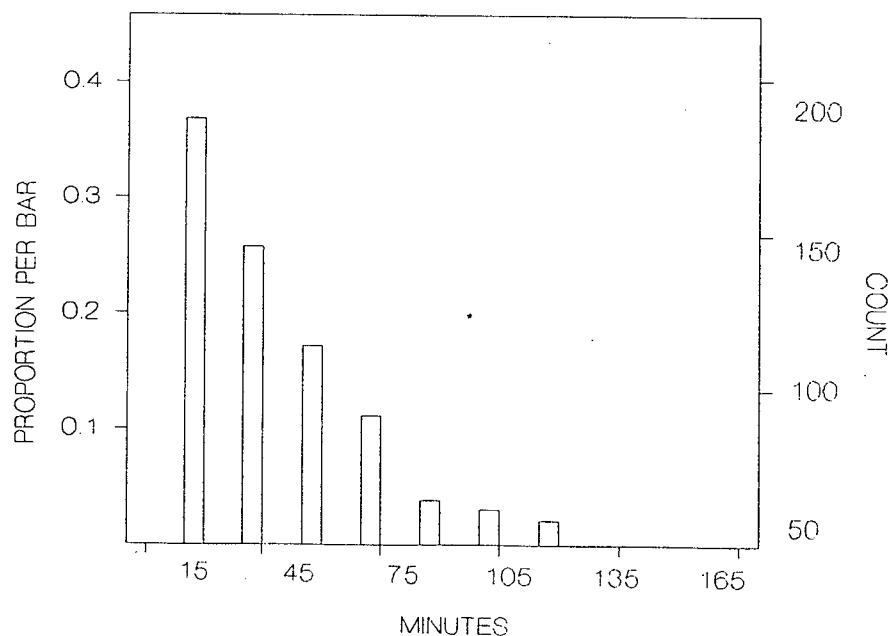


Figure 4.1 Histogram of 774 suckling bouts by 29 male and female immature Steller sea lions.

Suckling by Proportion

The proportion of time that yearlings spent suckling while their mothers were observed on the haulout was significantly longer than pups (yearlings $\bar{x} = 40.2 \pm 3.9\%$ SE, pups $\bar{x} = 32.3 \pm 4.1\%$) [$t_{27}=1.76$, $P = 0.044$]. But there was no significant difference between the proportion of time that males ($32.8 \pm 2.7\%$) and females ($31.7 \pm 2.8\%$) spent with their mothers suckling. Expressing suckling as a proportion of total hours of observations (instead of only the time the mother was available) also showed a significant difference between yearlings ($\bar{x} = 33.3 \pm 1.3\%$) and pups ($\bar{x} = 21.3 \pm 3.3\%$) [$t_{27}=3.43$, $P=0.001$]. Similarly suckling as a proportion of total time observed did not differ significantly between female ($\bar{x} = 22.3 \pm 2.1\%$) and male pups ($\bar{x} = 20.4 \pm 2.2\%$) [$t_{22} = 0.60$, $P = 0.28$]. Observations indicated that immature animals were responsible for the termination of the majority of the suckling bouts, suggesting that suckling time was not constrained by the availability of the mother, nor by the female's willingness to suckle their offspring.

Seasonal Changes

Daily proportion of time spent suckling was plotted for the two gender groups to test for change over time using locally weighted regression (loess). The proportion of time immatures suckled on any given day did not change over the course of the study and did not indicate an overall weaning trend ($\bar{x} = 26.1\%$, $SD = 27.2$, range 0 - 100 %).

A significant correlation between the numbers of immature and mature females on shore ($r = 0.86$, $P < 0.05$) also suggests a high proportion of young were not fully behaviourally or metabolically weaned during the winter.

Discussion

Many factors affect the quantity of milk consumed, although field data generally preclude quantifying many of these. In most cases milk consumption is generally accepted

as being equal to duration of suckling multiplied by the suckling rate. Consequently, assuming constant suckling rates, animals that suckle more frequently and for longer durations consume more milk. This interpretation has been widely accepted (Brown 1959, 1964; Graham and Searle 1970; Munro 1962). Higgins *et al.* (1988) found that average bout duration for Steller pup increased from 11.2 min. the first week to 21 min. by the fifth week with a maximum bout of 61 minutes, suggesting an increase in milk intake. Milk transfer measurements, using tritiated water, have shown that larger pups ingest more milk than smaller ones (Higgins *et al.* 1984). Suckling time is a reliable indicator of the amount of milk consumed by young dairy cattle (Wettemann *et al.* 1978), and the Galapagos fur seal (Trillmich 1986a), but this may not be true for all species.

It seems unlikely that milk yield increases linearly with suckling time over long periods. Presumably, the rate of milk yield declines with the time the mother is present so that much of the late suckling activity, or after long bouts, is non-nutritive (Trillmich 1990). Much of the late suckling by Steller sea lions may also be for the pup's psychological comfort.

Gender and Age Differences

In many mammal species, male offspring grow faster than females and demand greater investment from their mothers (McClure 1981, Clutton-Brock 1981, Neumann 1979). Though this may not always be the case for all species (Neumann 1979), it was consistent for Steller sea lions where male pups suckled slightly but, not significantly longer per bout (37.2 ± 2.8 min.SE) than female pups (35.9 ± 2.3 min.). Yearling animals were physically much larger than pups and also suckled longer than pups, although the differences were not statistically different. A larger sample size is needed to test for age differences. This difference is consistent with my hypothesis that larger offspring consume more milk to gain a larger size.

Mothers invested similar time suckling (on teat time) in male offspring as female offspring. Males did not have more access to their mothers for suckling, nor did adult

females with dependent male offspring spend longer at sea during foraging trips than mothers of female young (Chapter 3). Pups of both gender suckled for similar proportions of time when the adult female was present, and their suckling bouts on shore between foraging trips were of similar length.

Several studies have compared the suckling behaviour of otariids by sex and age. For example, Higgins *et al.* (1988) did not find a difference between the time 28 male and female Steller sea lion pups suckled during bouts over the first months of life, nor an increase in the overall time they suckled as they grew older (5 - 11 months). Sandegren (1970) found that Steller pups between the ages of 6-14 weeks suckled for longer periods as they grew older. Suckling averaged 11 minutes for pups less than 2 days old, 19 minutes for pups between 10 and 20 days old, and 23 minutes for juveniles, showing a gradual increase with age. This compares to suckling bout times in this study of 36.5 ± 1.8 min. for pups (6-10 months), and 44.0 ± 2.8 min. for yearlings aged (9-20 months).

Steller yearlings ($33.3 \pm 1.3\%$ SE, $n=5$) suckled more as a proportion of their overall activity budget than pups ($21.3 \pm 3.3\%$ $n=24$). In the Galapagos fur seal, male yearlings and 2 year olds suckled more than equal-aged females (Trillmich 1986a). Differences between the proportions of time that Steller pups suckled were not statistically significant. This contrasts with a study by Ono *et al.* (1987) who found that the larger and faster growing male California sea lion pups (< 2 mo. old) spent a greater proportion of their time suckling (14.6%) than female pups (10.7%). Oftedal *et al.* (1987a) found male California sea lion pups received more milk per day than females.

Male northern fur seal pups, (*Callorhinus ursinus*, a sexually dimorphic species) consume over 61% more milk than females, but ingest less relative to their body mass (Trillmich 1986; Costa and Gentry 1986). In contrast, Macy (1982) found that the same species suckled pups of either gender for the same duration and with the same frequency. In the less dimorphic grey seal (*Halichoerus grypus*), the energetic cost of rearing males was around 10% higher than for females (Anderson and Fedak 1987). However, in the highly dimorphic southern elephant seal (*Mirounga leonina*), there appeared to be no difference in maternal expenditure on males or females during lactation, although males

were born heavier (McCann *et al.* 1989). Oftedal *et al.* (1983) estimated that milk intake for male California sea lion pups was 27% greater than for female pups, and that lactating females therefore invested a greater amount of milk energy and nutrients into male pups. Goldsworthy (1995) found male Antarctic fur seal pups gained significantly more body mass compared with daughters during maternal attendance, suggesting that sons consumed more milk.

Kovacs (1986) studied Grey seals at several sites on the Isle of May and found that male pups suckled significantly longer than the slower growing female pups. Male Atlantic harbor seal (*Phoca vitulina concolor*) pups suckled for the same amount of time per bout, but suckled for a greater proportion of time than females (Rosen and Renouf 1993). Sex differences in suckling frequency and/or in the duration of suckling bouts have also been found in red deer, goats, American bison, and African elephants (Clutton-Brock *et al.* 1981; Pickering 1983; Lee and Moss 1986), though they are apparently absent in a number of ungulates that show unusually fast juvenile growth rates, including pronghorn, *Antilocapra americana* (Byers and Moodie 1990).

Male immature Steller sea lions eventually reach a mature body mass nearly three times that of females and the visible sexual dimorphism is evident quite early in life. Male pups are significantly larger than their female counterparts soon after birth, and are heavier during all years measured (Merrick *et al.* 1995). Male offspring may consequently have different metabolic requirements, which could be met with longer suckling bouts.

Nutrition

Other studies have shown milk delivery is directly correlated with suckling time in populations with poor nutrition, since weaker or less well-developed young may take longer to exhaust the mother's milk supply, or may be prepared to suck longer for lower levels of delivery (Mendl and Paul 1989). The condition of the mother is important and is related to the time spent nursing. The offspring of malnourished rats, for example, suckle more than those of well-fed mothers (Hall *et al.* 1979). In ungulates confined to poor pasture, milk yields do not exhibit the normal postpartum rise but rather begin to decline

shortly after birth (Oftedal 1985). Heavier otariid mothers may also be able to suckle their pups longer than lighter ones. Future studies should consider if differences in food availability and quality, between study sites and years, contribute to variability in suckling.

In mammals, females undergo physiological changes during lactation which coincide with offspring development (Hanwell and Peaker 1977). Female mice produce more milk for larger litters (Blaxter 1961), and increase milk production when new pups are added from other litters (Enzmann 1933). Milk quality also changes during lactation. In California sea lions, fat increases from 32% at 0-2 months to 44% by the fourth month postpartum, while dry matter increases from 41% to 54% (Oftedal *et al.* 1983). It seems reasonable that milk quality would change during the late stages of lactation to provide for growing sea lion offspring, however no data exists to test this.

In theory, there should be much variation in milk quality and quantity during the time a female sea lion spends on shore feeding her offspring, but there is no reason to believe that feeding would vary between ages or the genders of their dependent offspring. It would be useful to measure the actual milk delivery per bout, and to measure milk composition in mothers of both genders and age classes.

Suckling by Proportion

The proportion of time spent suckling by male and female pups was not significantly different, but differences in the proportions for yearlings and pups were significant. Personal observations suggest that immature animals in both age classes and genders were also responsible for the termination of the majority of the suckling bouts. This implies that suckling time was not constrained by the availability of the mother, nor by the female's willingness to suckle her offspring.

Weaning

The termination of parental care has been especially emphasized as a time of conflict. The parent, offspring, and environment will ultimately all interact to determine when independence will occur. Offspring are expected to attempt to gain additional

parental investment beyond what parents are willing to provide (Trivers 1972). Contrary to Trivers' (1974) expectation that parent offspring conflict over weaning would be the rule, it was the exception in Steller sea lions. Natural selection on the parent will select for the amount of care that will allow the offspring to become independent and allow the parent to subsequently reproduce successfully. Natural selection on the offspring will presumably select for development at a rate which coincides with decreasing parental care and an increasing ability to obtain resources from the environment (Case 1978).

The initial sample of yearlings observed included animals which were not used in the suckling analysis because they rarely if ever suckled. Three female immatures appeared to be nutritionally independent. No independent pups were observed. Of five California sea lions seen suckling beyond 15 months of age, two were known to be male. However, there is some evidence that California sea lion mothers may tend to nurse their female yearlings for a longer period of time, probably because females tend to stay near the natal islands while male yearlings migrate north (Francis and Heath 1991). Similarly, in elephant seals and zebu cattle the female juveniles are weaned earlier than males (LeBoeuf and Briggs 1977; Reinhardt and Reinhardt 1981).

Despite differential growth of Steller sea lions in relation to sex (Calkins and Pitcher 1982; Calkins *et al.* 1997), adult size may be directly related to female investment during offspring care. Larger size benefits male reproductive success more than females. A larger sample is needed to determine if Steller sea lions are more likely to wean female offspring earlier than males. It may be possible to show, with additional data, that male offspring prolong weaning by demanding milk more persistently. If so, male immatures may remain with their mothers for longer and benefit from both milk reserves and additional skills while accompanying their mothers on foraging trips. The larger yearling male offspring appeared to be more successful at acquiring milk and succeeded more often than the smaller yearling females in acquiring it. Similarly, Atlantic harbour seal mothers did not reject attempts to nurse by pups of either sex, although males suckled proportionately more because they initiated more suckling bouts than female pups (Rosen and Renouf 1993).

Along with the advantages of learning, even a small amount of milk suckled may provide significant fat, proteins, or vitamins which are not yet readily available from alternative resources. Thus, offspring may obtain very small, yet important units of parental investment, even though they are mostly independent.

The high proportion of young animals at my site that were still dependent on their mothers for milk (98%) may not be indicative of the entire population. It is possible that independent young are more mobile, and have less site fidelity to any one haulout. To more clearly understand this distribution it would be useful to examine more winter haul-out sites during March through April (the most likely transition period) to determine the proportion of immature animals still actively suckling. As a contrast, it would also be interesting to visit more of the summer non-breeding haul-outs during the breeding period to gather sex and age composition counts, and extended suckling information from animals which have otherwise been missed during the majority of the past research. A high proportion of the sea lion population remains on haulouts year round (Loughlin *et al.* 1992, Trites and Larkin 1996) with approximately 45% of the adults and juveniles not returning to rookeries during the summer (Loughlin *et al.* 1992).

Weaning occurs when mammalian mothers stop producing milk, or refuse to suckle their pups, and consequently offspring must feed themselves. The transition in Steller sea lions is most likely a gradual one. Eventually, at some stage the young may not be dependent on their mother for food (metabolic weaning), but still maintain a behavioural attachment (behavioural weaning).

On many occasions mature females attempted to deter their young from suckling by turning away or lying flat on their ventral surface when the offspring attempted to suckle. The response of the immature was to climb on and over the mother and bite at her flippers in an attempt to move her into suckling position. The young were allowed to stay close, and even to lay their head on the mother's back, but were rebuffed when attempting to go near the teats to suckle. When this conflict arose between mother and offspring, male offspring were more successful at eventually obtaining milk.

I pose one hypothesis to explain the variation in weaning of different genders. During observations it appeared that the male immature animals were much more persistent in their attempts to obtain milk. It may be that the slightly larger male pups are more driven by the need for additional food during a critical time of transition, and are consequently more persistent when rebuffed by their mothers. The mature females appear to be more overwhelmed by the larger male offspring during their efforts to obtain access to the teats. Clutton-Brock *et al.* (1985) similarly postulated that the proximate mechanism is probably the behaviour of larger male immatures rather than any conscious effort on the part of the mother.

I expected that immature animals would suckle less late in lactation as animals approached weaning, but there was no apparent pattern. Merrick (1988) and Higgins *et al.* (1988) also failed to find a seasonal trend during summer. An increasing trend has been reported in northern fur seals (Costa and Gentry 1986) and an increase in milk consumption typically occurs from early to mid lactation in most terrestrial mammals (Ofstedal 1984). Seasonal changes in suckling frequency did not give a good indication of weaning, or of impending independence of young Steller sea lions during late lactation. It is not clear whether suckling and milk production were keeping pace with the increased needs of the growing pups.

Milk Stealing

Suckling attempts on non-filial mothers by two pups were observed in this study. Reidman and LeBoeuf (1982) consider three situations resulting in pups obtaining milk from other mothers: (1) fostering - where a mother accepts and cares for a non-filial pup (with no mother) in addition to her own, with maternal care lasting from a nursing bout of several minutes to many days; (2) adoption - where a female exclusively cares for an alien pup after losing her own; and (3) allomaternal care - where a mother provides milk to an alien pup while that alien pup is still with its own mother.

The first case involved sneak suckling by a branded female pup which was never seen with its own mother and was considered to be a starveling⁴ because of its poor and deteriorating condition. It made several successful milk stealing attempts on sleeping mother-pup pairs. By stretching its neck so as to not wake either of the sleepers, and keeping a low profile, it could often suckle for short periods before being discovered. Typically, when a mature female discovered the alien attempting to suckle she immediately reacted aggressively, often nipping the stranger as it retreated. However, even after being attacked by a mature female the starveling pup persisted in its repeated attempt to obtain milk. Females became more and more vicious in their attacks as it continued to approach several of the same pairs many times. As this animal became severely emaciated the entire group became less tolerant of its presence and in the last days of starvation it was forced into isolation at the periphery of the haulout. After a severe storm lasting two days it died.

The second case (allomaternal care) involved an animal which was identifiable by natural markings, appeared healthy, and on other occasions was observed suckling from its own mother. This pup was observed stealing milk from the same resident mother-pup pair on several occasions, but suckling was allowed to continue without incident. This pair continuously allowed the strange pup to suckle many times with no sign of aggression. The non-filial pup was able to suckle while one or both of the pair were awake as well as during active periods. In several instances, both the resident and the non-filial were observed suckling together without incident. The mother-pup pair remained together throughout the study.

Stealing milk is an indication that offspring are under-fed, and strongly suggests that pups need more milk than their mothers are providing. Milk stealing is uncommon among pinnipeds and mothers are aggressive toward nonfilial pups attempting to suckle. Females returning to the rookery must locate their own pup among many others. It is generally agreed that among otariids, mother-pup recognition is by auditory and olfactory cues (Bartholomew 1959; Sterling 1970; Trillmich 1981; Roux and Jouventin 1987).

⁴ Starveling - An immature animal visibly in poor or deteriorating condition and never observed with its mother. Most animals in similar condition do not survive (pers. obs).

Initially the mother finds the general location of her young with a pup attraction call, then, as she approaches the immature, they will touch noses for confirmation, recognizing its unique odor. Mothers normally nurse only their pup and can inflict serious injuries on nonfilial pups attempting to suckle.

Adult female Steller sea lions seldom allow strange pups near their teats, much less allow them to suckle. Both mothers and pups were aggressive toward intruding conspecifics and were very protective of their mother's teats. Ono and Boness (1996) observed only 10 attempts by California sea lions in 3 years at one site, and noted that male pups were no more likely to attempt non-filial suckling. Higgins (1984) observed only a single case which lasted for 30 seconds before the pup was chased away.

There was a range of individual variation in the tolerance of both mature females and their offspring to the distance they would allow strange pups near the teats. Other studies of otariids have shown that the incidence of milk stealing and fostering behaviour are more frequent during nutritional stress. Milk stealing is occasionally common in Antarctic fur seals and may be more prevalent when pups are nutritionally stressed (Lunn 1992). It may be advantageous for nutritionally stressed pups to attempt to steal milk, compared with the alternative, starvation. Macy (1982) found female northern fur seal pups sneak-suckled slightly more during their mothers absence and that male offspring avoided sneaking and that pups sneak suckled more during the early stages of dependence than late.

In the northern elephant seal, pups are successful at stealing milk from females other than their mothers, and may have evolved delayed dental eruption and moulting to facilitate their behaviour (Reiter *et al.* 1978). This may give them an edge in avoiding detection and is more commonly the male pups that are successful. Approximately 10% of weaned elephant seal pups obtained additional milk by surreptitiously suckling alien females. This occurred even though young animals caught stealing or entering the harem were severely bitten and chased from the area, often resulting in serious wounds (Reiter *et al.* 1978).

In winter, when many immature sea lions are being weaned, animals in different stages of independence may be more prone to resort to drastic measures to obtain food for survival. If food abundance is low, it may be in the best interest of the female to either place all investment into last years offspring, or the new pup, but not both.

Conclusion

The principal behavioural differences in maternal investment for Steller sea lions appear to be a greater length of the dependent period, longer suckling bouts, and a higher proportion of time suckling by yearlings.

Sneak suckling is not common among Steller sea lions as an alternative to maternal care. The potential for injury may out-weigh any gain in resources and deter most young from attempting to approach strange females.

Pinnipeds are good subjects for the study of differential growth and maternal investment since neonates are born on land and are removed from the primary source of food, consuming only milk. This investment becomes much more difficult to measure during the late stages of development as the young animals are beginning to forage independently while still obtaining milk from their mothers. Future research could combine both behavior observations and telemetry locations to determine the degree of maternal investment by mothers of known sex and age pups.

Summary

Suckling by pup (<1 y) and yearling (<2 y) Steller sea lions was observed from (January - April 1996) at a non breeding haulout site in Alaska. The primary goal was to determine whether the larger and faster growing males suckled more than females. A secondary goal was to characterize the weaning process. Group mean suckling bouts for male pups were similar (37.2 ± 2.8 min. SE) to female suckling times (35.9 ± 2.3 min). However, the daily proportion of time spent suckling by male ($22.2 \pm 2.1\%$ SE) and females ($20.4 \pm 2.2\%$), was not different and did not change during the 3 month study period. There was no seasonal change in the proportion of time spent suckling during the

winter. A significant correlation between the numbers of immatures and mature females on shore ($r = 0.862$, $P < 0.05$) suggests a high proportion of young are not fully behaviourally or physiologically weaned during the winter period.

Chapter V: General Discussion

There has been considerable speculation that poor juvenile survival during the winter has driven the population decline of Steller sea lions. This was the impetus for me to study the winter ecology of Steller sea lions. Winter is believed to be a difficult transition period for young animals because of the harsh environmental conditions that occur at this time of year.

A number of tools can be used to study their winter ecology, such as time-depth recorders, satellite tags, radio telemetry, and behavioural observations. I chose to use behavioural techniques due to their low cost and because behavioural observations allow larger sample sizes than remote-sensing methods. Consequently, I could better describe the patterns of time spent by Steller sea lions on shore and at sea, as well as activities on shore. I also avoided some of the biases associated with small samples and variability related to age and individual experiences.

Major Findings

Sitting day after day watching and recording the numbers, behaviour, and weather conditions revealed a lot about the Steller sea lion. I learned, for example, that endogenous rhythms do not appear to be the driving force behind numbers of animals on land at any given time during the winter. Instead, weather and disturbance, not time of day, influence their haul-out patterns most. I also found the most important variables influencing numbers on shore by order of importance were: wave height, temperature, wind speed, sky cover, barometric pressure, swell height, wind direction, and tide stage. Counts and environmental data can be used as a correction factor for population monitoring and should allow some predictive ability for researchers wanting to know when best to visit these sites in winter.

Recording attendance patterns revealed that mature female Steller sea lions providing for dependent offspring spent an average of 19.3 h on land with their young and an average of 53.85 h at sea. Most young did not accompany their mothers on foraging trips. These data also showed differential investment in male/female offspring, and yearling/pup age classes. Differential investment appears to be subtle in Steller sea lions, yet it could have long lasting effects. Quality of neonatal care, for example, can significantly impact the ultimate adult size, even when resources obtained later in life are abundant (Neumann 1979). This might be particularly important for male reproductive success (Macy 1982).

Major Lessons

In addition to the major findings, I learned a considerable amount about the *do's* and *dont's* of behavioural studies of Steller sea lions. Most of my thesis deals with the *do's*; the things that worked out. However, it may be useful for others who might want to carry out a similar study to consider some lessons I learned about the counting, marking and aging of animals, the causes and effects of disturbance, the recording of suckling patterns, and the construction and placement of observation blinds. My insights follow:

Blind

The blind must be close enough to the animals to properly perform observations and not too close to disturb the sea lions. Unfortunately there are often few choice locations with clear unobstructed views due to the configuration of most haulouts. Prevailing winds may determine or limit the possible sites because Steller sea lions are easily disturbed by human scent. Observers may therefore, be forced to forgo data collection during days when there may be a high risk of disturbance. The uneven haulout terrain also makes it hard to keep individuals in sight as they are often obscured behind boulders or other animals. It is also important to build a proper blind to allow observers a safe, protected, comfortable work platform. Without the advantages of a blind, long hours in inclement winter weather could have a marked affect on data quality and quantity.

The shelter prevents much of the precipitation from fogging or clouding the optics and becomes a solid base to support a spotting scope, binoculars and dry data forms.

Marking

Because of the importance of identifying and following known individuals I tested several marking techniques: wrist-rockets were used to launch paint pellets and dye filled eggs and balloons, Cap-tur tranquilizer dart guns with syringes filled with hair dye, and hand launched eggs filled with dye were thrown. All these attempts at marking were unsuccessful. The smell of dye and projectiles bouncing on the rocks caused disturbance. The distance to the animals was beyond the accurate range for most methods and stalking closer was limited by terrain and tide levels. Freezing temperatures also made the use of dye difficult or ineffective. In contrast to summer time, the winter aggregations of Steller sea lions were much more prone to enter the water and remain there for longer periods. This made the marking attempts ineffective in terms of the amount of time they took up and their lasting effect on the animals. Once the animals went into the water, they did not resume haul-out patterns for several days.

Sex and Age Determination

A great deal of time was devoted to developing criteria for estimating ages determination of immature animals, but this was unsuccessful beyond the two age classifications (pups < 1 y and juveniles > 1 y). The subtle sexual dimorphisms and individual variation made sexing the young animals difficult. The only reliable means was to look for genitalia when animals rolled onto their backs, but this proved to be marginally successful because young animals seldom rolled onto their backs. It was also limited by small sample size. I felt it was possible to re-identify an animal if it had sufficient natural marks and scars (≥ 3). However, young animals had few obvious scars or marks compared to adults to be readily identified.

Disturbance

An attempt was made at two other study sites to combine behavioural work with capture and satellite attachments, but this caused a great deal of disturbance. Steller sea lions are difficult to approach. Even after an animal is darted and tranquilized, researchers cannot approach the drugged animal without disturbing the entire group. The impact of human scent and activity on the haulout caused animals to avoid the site for long periods; sometimes weeks. Human disturbance was only one of many factors that caused animals to abandon their haulout. This is in sharp contrast to the effects of disturbance during summer when recovery is a matter of hours. New methods are now being explored for scuba divers to capture Steller sea lions underwater. This should create little or no disturbance to animals on shore and enable larger numbers of sea lions to be captured and fitted with satellite telemetry transmitters. Combining behavioural observations with telemetry transmitters will provide a clearer understanding of Steller sea lion movements and activity.

The winter animals spooked more than summer animals due, in part, to the high numbers of young animals present in winter relative to the other age groups. Juveniles seemed to start most stampedes into the water and were frightened by everything: birds, odd sounds from the surf, a flipper slapped on the rocks, floating material, each other, or several times nothing that I could see. What might start as play often ended with a group running into the water. When groups went into the water the remaining animals often followed, clearing the haulout. This reflex to enter the water seemed to be lessened if there were bulls present, making the group more cohesive. The group seemed to look to the bulls for reassurance and would usually stay if the bulls remained on shore. However, overall numbers of mature bulls at winter sites are low.

Suckling

Alternatives to suckling observations include doubly-labeled (H_3O_{18}) water techniques for measures of milk intake, which require multiple recaptures of individuals and complete disturbance of the haulouts. Recapturing pups during summer, seldom

proved to be successful, and re-capturing winter juveniles is even less feasible, confirming the need for alternative methods of studying and quantifying suckling. It was not always clear whether immature animals were suckling or were simply poised in the suckling position.

It is important to have clearly defined definitions of what is considered on-teat. The protocol I designed allowed for only those animals with head and neck movements and appropriate body position in relation to their mother's teats to be noted as suckling. Young animals could otherwise be easily mistaken for suckling while sleeping nearby. This is where the use of a powerful spotting scope is helpful. With terms clearly defined the method is at least consistent and comparable. Although my on-teat time is not an actual measure of milk intake, it is comparable for investment purposes. Scan sampling is a consistent method to collect suckling data as a measure of time on teat.

Additional work will involve a comparison between the declining and increasing populations. Work is now being completed in the declining area and will be compared to my data set to check for signs that animals are suffering nutritional stress. These differences in maternal attendance (foraging trips) and maternal investment (suckling) will be compared to look for subtle signs that mothers of young sea lions in the declining population are partitioning their resources differently than those in the stable area.

Individual Variability

Variability reflects individual adaptations for survival in a complex and unstable environment. However, individual variability poses problems for researchers dependent on satellite-linked transmitters to determine average group trip time at sea or critical foraging habitat. It also poses problems for behaviour work because it is difficult to discern whether differences in attendance patterns reflect changes in the abundance or distribution of prey, or some other factor. Differences in time away might reflect travel time or foraging efforts (more dives per unit effort). Are the animals spending more time at sea to go further, or more time pursuing widely scattered prey? This is where the two methods, behaviour and telemetry, must be combined to approach such questions.

Final Thoughts

Sea lions are an important part of a complex food web and the alarming decline in Steller sea lion numbers in past years indicates the problem is serious, wide spread, and has gone on for a long time. Understanding what is happening to the Steller sea lion population may not only save the sea lion from extinction, but may help to understand the intricacies of an ecosystem. Since we depend on that same ecosystem for a great deal of our food, it is in our best interest to diagnose the problem before it is too late. Picking away at the small pieces is the only way we can hope to discover the answer. Understanding the winter ecology of Steller sea lions is a key piece in unravelling the puzzle.

Appendix 1: World Population Trends

Aleutian Islands and Gulf of Alaska

This region is the center of the world distribution of sea lions. It has also experienced the highest declines (Loughlin *et al.* 1992, Merrick *et al.* 1987) where sea lions have dropped from 225,000 in the late 1970s to fewer than 85,000 in the late 1980s (Trites and Larkin 1996). Aerial and ground surveys have shown the decline began in the eastern Aleutian Islands in the mid 1970s (Braham *et al.* 1980). It appears to have spread eastward to the Kodiak Island area during the late 1970s and early 1980s, and westward to the central and western Aleutian Islands during the early and mid 1980s (Merrick *et al.* 1987, Byrd 1989). The greatest declines were observed in the eastern Aleutian Islands and western Gulf of Alaska, but also occurred in the central Gulf of Alaska and central Aleutian Islands.

Kenai Peninsula East to Cape St. Elias

In the region from Kenai Peninsula east to Cape St. Elias, counts of adults and juvenile sea lions began to decline sometime after 1980. The 1991 count at Seal Rocks was 59% lower than the peak number counted in 1979. At both Seal Rocks and Cape St. Elias the decline appears to have been rapid during 1989-1991. Counts of pups at Seal Rocks, the only major rookery in the area, have ranged from 491 to 799 during 1978-1991, with no detectable trend (ADF&G unpublished data).

Southeast Alaska

In southeast Alaska, sea lion populations appear stable or slightly increasing. The largest Steller sea lion rookery in the world (1989-1991), is currently Forrester Island located in the southernmost portion of southeastern Alaska. An increase in pup production has occurred at Forrester with 3,261 pups counted there in 1991, up from

2,187 in 1979 (ADF&G, unpublished data). The two other rookeries, White Sisters and Hazy Island, classified as haulouts until the late 1970s, now have females using them to give birth. Since then, there has been a steady increase in pup numbers on these former haulouts (Trites and Larkin 1996).

The estimated number of sea lions in southeast Alaska (assuming that Forrester Island has always been the major rookery) increased from under a 100 in the 1920s (Rowley 1929) to 350 in 1945 (Imler and Sarber 1947), 2,500 in 1957 (Mathisen and Lopp 1963), and leveled off at about 9,000 in the early 1970s. The population increased from 4,500 animals in 1956 to 17,000 in 1991 at an average rate of about 4% per year. The population appeared to remain relatively stable through the 1970s and early 1980s, but has been increasing since about 1986. However, since 1985 the population appears to be growing faster than can be accounted for by intrinsic growth alone (roughly 8% per year), suggesting the possibility that some emigration of sea lions has occurred from either British Columbia or from other regions of Alaska (Trites and Larkin 1992).

California to British Columbia

Numbers in California have declined, especially in southern California. Currently the southernmost breeding site is Año Nuevo Island, where historically, peak counts ranged between 1500 and 2500. Since 1984 numbers have consistently been below 1200. During the breeding season counts in 1988 and 1990 were under 600 adults and juveniles (LeBoeuf and Morris 1990, Gisiner pers. comm.). Año Nuevo Island produces more pups than any other rookery in California. Pup production from 1980-1985 was about 300 pups per year (M. Pearson pers. comm.); with a minimum of only 139 pups born in 1990 (LeBoeuf and Morris 1990). Similar declining trends can be seen on other rookeries along the California coast. Statewide counts between 1927 and 1947 ranged between 5000 and 7000 non-pups with no apparent trend, but have subsequently declined by over 50%, remaining at about 2000 to 2500 non-pups between 1980 and 1990. These data, together with a limited number of counts made during other times of year by Bonnell *et al.* (1983) and Bonnot Ripley (1948), suggest the species' distribution in California may have shifted

northward. Changes in breeding season numbers have been less pronounced and slower than changes in distribution outside the breeding season, perhaps due to breeding site fidelity. Tagging, satellite telemetry, and coordinated counts with other parts of the species' range are needed to determine the relative contributions of emigration and reduced productivity to the decline in numbers of Steller sea lions in California (NMFS 1992).

The population of Steller sea lion in Oregon have been relatively stable since 1981 at about 2,000-3,000 animals. There are no sea lion rookeries in Washington State, although animals do occur there occasionally during the year. At this time, however, there are no data available that can be used to evaluate trends in numbers of Steller sea lions in Washington (NMFS 1992).

Extensive sea lion reduction programs were conducted at many locations in British Columbia from 1912 through 1966. In 1913, 10,000-12,000 animals (including pups) were counted; in 1965 the number was about 4,000 (Bigg 1985). Today there are about 7400 animals.

The Canadian Department of Fisheries reduced sea lion numbers through the 1940s, 50s and 60s by culling and encouraging killing for mink or pet food. A census taken during the summer of 1961 (Fisheries Research Board of Canada, Unpubl. Data), indicated there were approximately 1500 pups and 4500 resident adults in British Columbia waters. During the summer months approximately 70% of the 1956-57 population, or 3100 adults, were found to be concentrated on the two rookeries off Cape St. James and the Scott Islands (Pike and Maxwell 1958). Pup counts in the 1970s and 1980s have ranged from about 1,000 to 1,400 with no identifiable trend. The most recent census was in 1987 when 1,084 pups and 6,109 non-pups were counted (P. Olesiuk, pers. comm.). Bigg (1988) speculated that a northward shift in distribution may have occurred from rookeries in British Columbia, which could partly explain the increase in sea lion numbers in southeast Alaska (NMFS 1992).

Russia

A comparison of recent and historic counts of Steller sea lions in the Russian Federation indicates that the number of animals is about one-third of historic levels. In some instances, the decrease in numbers has been accompanied by complete disappearance of rookeries (Perlov 1991). Numbers of adult and juvenile sea lions at major rookeries and haulouts in the Kuril Islands have declined 74%, from 14,076 in 1969 to 3,615 in 1989 (Merrick *et al.* 1990). Most of the decline occurred between 1969 and 1974. The numbers appear to have remained stable since 1974. Pup numbers have declined 60%, from 3,673 in 1963 to 1,476 in 1989. Based on 1989 counts, Burkanov *et al.* (1991) estimated that the total number of sea lions, including those on haulouts, rookeries and those observed swimming in the water near the site at the time of the survey, along the Kamchatka Peninsula and the Commander Islands was 3500-3800. This was 1.6 to 3.5 times lower than counts in 1982-1985 similar to what has occurred in the U.S. portion of the Bering Sea, and may continue. There are about 2000 sea lions on a few islands in the Sea of Okhotsk, where numbers are reduced from previous levels, but remain stable (Perlov 1991).

Appendix 2: Branded Animals Sighted

Brand numbers 201- 399 were yearlings. Those 401-998 were pups.

<u>Assigned #</u>	<u>Brand #</u>	<u>Sex</u>	<u>Assigned #</u>	<u>Brand #</u>	<u>Sex</u>	<u>Assigned #</u>	<u>Brand #</u>	<u>Sex</u>
	<u>221</u>	<u>F</u>		<u>721</u>	<u>F</u>	<u>28</u>	<u>931</u>	<u>M</u>
<u>1</u>	<u>223</u>	<u>M</u>		<u>737</u>	<u>M</u>	<u>29</u>	<u>934</u>	<u>M</u>
<u>2</u>	<u>226</u>	<u>M</u>	<u>14</u>	<u>739</u>	<u>F</u>	<u>30</u>	<u>949</u>	<u>M</u>
	<u>262</u>	<u>F</u>	<u>15</u>	<u>744</u>	<u>F</u>		<u>997</u>	<u>F</u>
	<u>272</u>	<u>F</u>	<u>16</u>	<u>747</u>	<u>M</u>			
<u>3</u>	<u>308</u>	<u>M</u>		<u>751</u>	<u>F</u>			
	<u>442</u>	<u>F</u>	<u>17</u>	<u>761</u>	<u>F</u>			
<u>4</u>	<u>463</u>	<u>F</u>	<u>18</u>	<u>781</u>	<u>F</u>			
<u>5</u>	<u>490</u>	<u>M</u>	<u>19</u>	<u>805</u>	<u>M</u>			
<u>6</u>	<u>514</u>	<u>F</u>	<u>20</u>	<u>807</u>	<u>F</u>			
<u>7</u>	<u>609</u>	<u>M</u>	<u>21</u>	<u>838</u>	<u>F</u>			
<u>8</u>	<u>611</u>	<u>M</u>	<u>22</u>	<u>859</u>	<u>M</u>			
<u>9</u>	<u>637</u>	<u>M</u>	<u>23</u>	<u>860</u>	<u>F</u>			
<u>10</u>	<u>660</u>	<u>M</u>	<u>24</u>	<u>876</u>	<u>M</u>			
<u>11</u>	<u>686</u>	<u>F</u>	<u>25</u>	<u>885</u>	<u>F</u>			
<u>12</u>	<u>694</u>	<u>F</u>	<u>26</u>	<u>889</u>	<u>F</u>			
<u>13</u>	<u>708</u>	<u>F</u>	<u>27</u>	<u>896</u>	<u>M</u>			

Appendix 3: Weather Codes

SKY

- 1 Cloudy
- 2 Foggy
- 3 Rain
- 4 Hail or Snow

WIND

- 0 Calm
- 1 Slight breeze < 2 kph
- 2 Breeze < 5 kph
- 3 Wind < 10 kph
- 4 High wind > 10 kph
- 5 Gale wind > 30 kph

WAVE

- 1 No white cap
- 2 White cap (small/infrequent) < 2 ft.
- 3 White cap > 2 ft.
- 4 White cap > 4 ft.
- 5 White cap > 6 ft.

SWELL

- 1 Flat calm
- 2 > 4 ft.
- 3 > 6 ft.
- 4 > 10 ft.

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