

Insights into the Timing of Weaning and the Attendance Patterns of Lactating Steller Sea Lions (*Eumetopias jubatus*) in Alaska During Winter, Spring, and Summer

Andrew W. Trites,¹ Boyd P. Porter,² Volker B. Deecke,¹ Andrea P. Coombs,¹ Michelle L. Marcotte,¹ and David A.S. Rosen¹

¹Marine Mammal Research Unit, Fisheries Centre, University of British Columbia,
Room 247, AERL, 2202 Main Mall, Vancouver, BC, V6T 1Z4

²Alaska Department of Fish and Game, Ketchikan, AK 99901, USA

Abstract

Behavioral observations of lactating Steller sea lions (*Eumetopias jubatus*) and their offspring were recorded at four haulout sites in Alaska to determine (1) whether sea lions wean during winter while they are 7 to 9 mo old and (2) whether sea lions using sites in the Gulf of Alaska (the declining endangered population) made longer foraging trips than sea lions in southeast Alaska (where the population appeared larger and healthier). Longer foraging trips are commonly thought to be an indicator of nutritional stress. Eight sets of behavioral observations were made using focal and scan-sampling techniques at haulouts from 1995 to 1998 during three seasons (winter, spring, and summer). Counter to expectations, we found no significant differences between haulout populations in the time that lactating Steller sea lions spent at sea or on shore. This suggests that lactating sea lions did not have more difficulty capturing prey from winter through summer in the area of decline compared to where sea lion numbers increased. Lactating Steller sea lions in both regions did make longer foraging trips in winter than they did in spring and summer. These changes in foraging patterns among seasons were consistent among all years and sites. The proportion of time that immature Steller sea lions suckled declined through the spring to early summer, suggesting that sea lions began supplementing their milk diet with solid food in the spring. We did not observe any sea lions weaning during winter; rather, most appeared to wean at the start of the breeding season when they were 1 or 2 y old. Sea lions observed in southeast Alaska during the late 1990s while population growth was slowing suggest that most males weaned at 2 y and that about 50% of females weaned at 1 y and the remainder at 2 y.

Key Words: Steller sea lion, *Eumetopias jubatus*, wean, forage, nutrition stress, Alaska

Introduction

Steller sea lions (*Eumetopias jubatus*) consist of two genetically distinct populations (Bickham et al., 1996). The eastern population (east of Cape St. Elias, Alaska) increased through the 1980s and 1990s, while the western population declined and was declared endangered in 1997 (Trites & Larkin, 1996; Loughlin, 1998; Figure 1). For much of the 1990s, the leading hypothesis for the decline of the western population of Steller sea lions was food stress, with the most dire consequence thought to be the starvation of immature animals following weaning (Calkins & Goodwin, 1988; Alaska Sea Grant, 1993; York, 1994; DeMaster & Atkinson, 2002; Trites & Donnelly, 2003). Proposed shortages of food (either reduced total consumption of all principal sea lion prey or reduced consumption of higher quality—high-energy—species) may have been caused by commercial fisheries and/or by natural changes in the ecosystem (Trites & Donnelly, 2003; Trites et al., 2006).

The primary objective of our study was to fill an important gap in our understanding of the life history of Steller sea lions—specifically, to determine when Steller sea lions wean and are most susceptible to prey shortages. Empirical evidence to date can only ascertain that the majority of Steller sea lions wean sometime before their first birthday (June) (Pitcher & Calkins, 1981), although some may nurse for 2 y or longer (Gentry, 1970; Sandegren, 1970; Perlov, 1980; Calkins & Pitcher, 1982). Weaning may occur during late gestation (April to May) (Pitcher et al., 1998) or it may occur much earlier (November to March) (Merrick, 1995; Merrick & Loughlin, 1997). The timing of weaning is uncertain and may hold the key to understanding the decline of the western sea lion population if the apparent absence of young animals (York, 1994) can be related to a critical time of year such as winter when young animals may have greater difficulty in finding food.

In addition to weaning behavior, we also sought to document seasonal patterns in attendance behaviors (time on shore nursing and time at sea feeding) of mature females with pups (0 to 12 mo) and yearlings (13 to 24 mo). We particularly wanted to know how foraging times changed over the course of a year and whether there was any indication of sea lions having greater difficulty procuring prey during the winter than during summer. We also wanted to test for differences in maternal attendance patterns between animals in the regions of population increase and population decline of Alaska. If the decline of Steller sea lions was related to a shortage of prey, the *a priori* expectation was that animals in this region would make longer feeding trips and would spend less time with their young than those in stable populations (Costa et al., 1989; Trillmich & Ono, 1991; Boyd et al., 1994; Boyd, 1999; Campagna et al., 2001; Soto et al., 2006).

Behavioral research provides a means for determining the timing of weaning and assessing the nutritional status of Steller sea lions. To date, most behavioral studies of Steller sea lions have concentrated on summer breeding areas (rookeries) (see Gentry, 1970; Sandegren, 1970; Gisiner, 1985; Milette & Trites, 2003) and have overlooked the nonbreeding sites (haulouts); yet, roughly 45% of the Steller sea lion population use haulouts during the summer rather than return to the rookeries (Trites & Larkin, 1996). Thus, we documented the attendance patterns and suckling behaviors of sea lions using haulouts comprised of juveniles, nonbreeding immature animals, and mature females with and without dependent young.

Materials and Methods

Study Areas

Eight sets of behavioral observations were made over 4 y (1995 to 1998) from a total of four different haulout sites (Table 1). Winter observations were made at Cape St. Elias (1995) and Marmot Island (1996, 1997) in the Gulf of Alaska (declining populations), and at Timbered Island (1996) in southeastern Alaska (a stable or increasing population; Figure 1). Spring observations were made at only one site (Timbered Island in 1998), while summer observations were made at Timbered Island (1996, 1997) and Sea Otter Island (1997, declining population). Our most consistently observed site was Timbered Island (winter 1996 to spring 1998).

Observations were performed from blinds with clear, unobstructed views of each haulout. All four sites were selected as typical Steller sea lion winter haulouts based on historical accounts and annual aerial count data, which indicated that high numbers of mature and immature animals were present during previous years (Alaska Department of Fish and Game [ADF&G] unpubl. census data). The sites were also selected for their ease of observation as well as for observer safety and logistical considerations.

Data Collection

Time spent ashore and at sea by pups, yearlings, and mature females with dependants was determined by the presence or absence of recognizable individuals at the haulout during daily observations. Many mature females observed at haulout sites in the Gulf of Alaska could be readily identified from distinct natural fungal patches; however, females from the increasing population (at Timbered Island) had fewer natural markings, making it difficult

Table 1. Dates and locations of behavioral observations of Steller sea lions on haulout sites in southeast Alaska and the Gulf of Alaska; total number of days and hours of observation are noted, as well as the number of individual mature females and immature sea lions (pups and yearlings) that were recognized by brands (branded) or natural markings (focal). Mature females were recognized by natural markings.

Location	Year	Season	Observation period		Immature		Mature females	Total days	Total hours
			Start	End	Branded	Focal			
Cape St. Elias	1995	Winter	28 Jan.	23 March	0	13	5	54	339
Marmot Island	1996	Winter	19 Jan.	15 Feb.	0	10	9	27	78
		Winter	23 Jan.	14 March	3	29	26	50	285
Timbered Island	1996	Winter	22 Jan.	31 March	38	8	10	69	353
		Spring	6 April	6 June	24	29	34	61	596
		Summer	15 June	6 Aug.	37	7	7	52	602
Sea Otter Island	1997	Summer	20 May	7 Aug.	36	11	20	79	875
		Summer	21 May	6 Aug.	0	19	18	77	747
All Sites					138	126	129	469	3,875

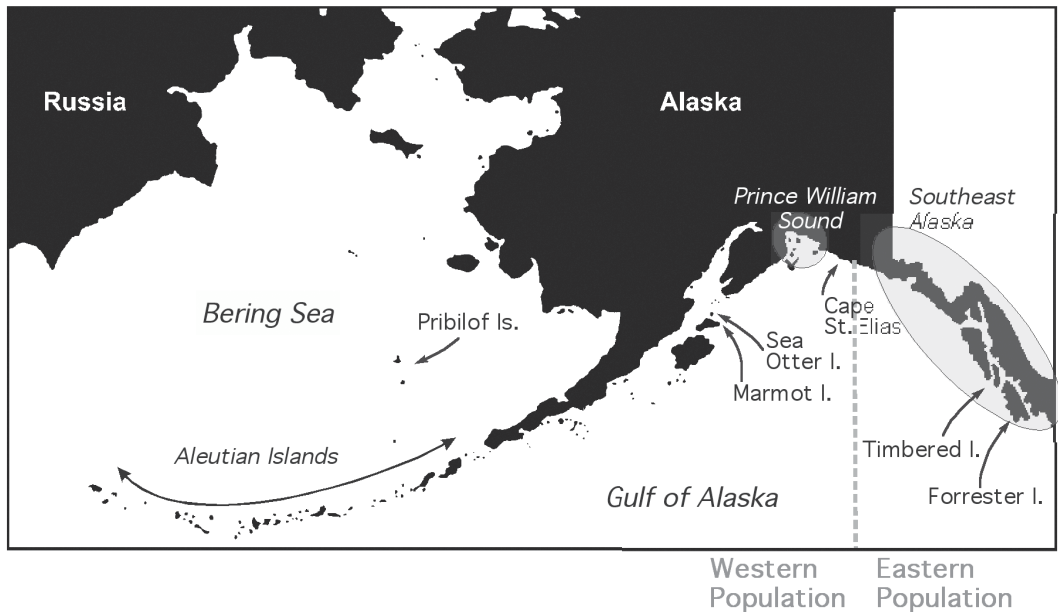


Figure 1. Locations of the four Steller sea lion behavioral study sites; Forrester Island, shown for reference, is where many of the immature sea lions we observed were branded as pups in 1994 and 1995.

to reliably identify individuals. Instead, we only counted them as present when seen with recognizable dependent offspring. A number of the pups and yearlings present at this site were previously branded in 1994 and 1995 (with a letter and three digits) by the ADF&G (1996) on Forrester Island (one of three major breeding sites in southeast Alaska; Figure 1, Table 1) when they were 1 mo old. Mature females were scored as away if they were not observed on the haulout with their dependent pup or yearling during daily observations.

The behavior and association of mothers and immature sea lions (pups and yearlings) were noted every 15 min using focal sampling (Martin & Bateson, 1993). Behavioral observations were restricted to daylight hours (maximum 0600-1900 h; average 0800-1630 h) and included more than 3,800 h of observations over 469 d (Table 1).

Data Analysis

Data from all sites and years were analyzed in the same manner to compare sites and seasons. Steller sea lions present at both dusk and dawn were assumed to have spent the night on the haulout. Similarly, animals absent at dusk and the following dawn were assumed to have been away all night. We also assumed that dry animals noted within the first 3 h of daily observations had spent the night on the haulout. When focal animals were first seen at the start of observations in the morning (but not the previous dusk), or last seen at the end of the day (but not the following morning), the midpoint during the

night (between the end and start of observations) 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 showed adult females rarely haul out on multiple sites during foraging trips (ADF&G unpubl. data; Merrick & Loughlin, 1997). It was nevertheless possible for adult females to return to their haulouts and not reunite immediately with their pups and yearlings.

We defined trips (time spent away from the haulout) to be > 2.5 h and < 200 h as per Trites & Porter (2002). Short absences (≤ 2.5 h) often consisted of animals rafting or swimming near-shore for short periods (Trites, pers. obs.). This is consistent with summer studies at other sites in Alaska that used VHF telemetry and noted gaps in the frequency distributions of the signal record that were indicative of nonforaging activity (Brandon, 2000). Higgins et al. (1988) studied Steller sea lions in California and found no foraging trips lasting < 8 h. We examined the distribution of recorded trips and assumed those animals with trips > 200 h made an unrecorded visit to the haulout or had moved to another site for an extended period. We also assumed that those with absences ≤ 2.5 h were obscured for a short period and incorrectly noted as "absent" when they were actually present on land or in the water adjacent to the haulout. Hence, only absences > 2.5 h and < 200 h were included in our analyses. Average trip duration was calculated for each mother, pup,

and yearling such that each animal contributed only a single value (their mean) to the appropriate grand mean estimate of trip duration (for all females or all immature animals combined).

Lengths of feeding trips from different field seasons were compared with both parametric (ANOVA) and nonparametric models (median test and Kruskal-Wallis test; Zar, 1996). Median lengths of feeding trips were broken down by week for the most extensive data sets (Timbered Island) and examined for directional changes over the field seasons.

Site fidelity was examined by calculating the percent of observation time that immature sea lions and their mothers were seen at a particular haulout. Percent of time present equaled the total number of hours that focal animals were on any given haulout divided by the total number of hours observers spent at any given site in any given season. We determined the percent of time young animals were with their mothers by dividing total time mothers were present by the number of hours we observed their young on the haulouts. This implicitly assumes that mothers were not on the haulout without their offspring. Percentages were arcsine-transformed for statistical analysis. An ANOVA model was used to test for geographic and seasonal differences in site fidelity of mothers and immature sea lions, as well as to test for differences in maternal attendance.

The proportion of time that young sea lions suckled was calculated as (1) a function of the total time they were on shore and (2) a function of the total time that their mothers were present. Percentages were arcsine-transformed and analyzed separately for yearlings and pups. To exclude weaned juveniles, only animals observed suckling at least once were included in the analysis. ANOVA was applied to the mean percentages, and Tukey tests were conducted to determine when and where suckling times differed significantly (Zar, 1996).

The proportion of the observed immature animals in the population that were observed to still be suckling during a particular week was also calculated in two ways. The first method calculated the proportion of branded immature sea

lions (known to be < 24 mo) seen suckling during each week of observation. Only animals observed at least ten times per week were included in this analysis to ensure that we did not misclassify an animal as weaned due to insufficient observations. In general, a dependent offspring should suckle for about 10% of the time it is present (see "Results") and would likely be classified as weaned if rarely observed. Our second method to determine the timing of weaning used data from immature animals of unknown ages (i.e., focal animals that were not branded). Of this group, we assumed that animals were not fully weaned if they were seen suckling at least once each day.

Results

Suckling and Weaning

During winter, pups suckled for an average of 26% of the time they were on shore; however the percent of time varied from an average of 15% at Timbered Island ($n = 23$ focal animals) to 34% at Cape St. Elias ($n = 5$), and 20 and 36% at Marmot Island ($n = 8$ and 3). Standardizing suckling behavior—by calculating it as a portion of the time that mothers were present—showed that pups spent an average of 44% of their time with their mothers actively suckling (Table 2). There were no significant differences among the winter and spring sites ($F_{4,39} = 0.53$, $p = 0.72$). Thus, although there was considerable variability in the time that pups spent on shore in each area and between years waiting for their mothers to return, the pups appeared to spend a relatively uniform proportion of the time they had with their mothers engaged in suckling during the winter.

During the spring, pups at Timbered Island suckled an average of 45% of the time they were with their mothers ($n = 5$ pups), which corresponded to 44% of the time they were observed on shore; during winter, however, pups at Timbered Island suckled an average of 41% of the time they were with their mothers ($n = 23$ pups), which corresponded to 15% of the time they were observed on shore. Comparing these two sets of numbers suggests that the attendance patterns of mothers and pups were more synchronized during spring than during winter.

Table 2. Percent of time that branded Steller sea lion pups ($n = 44$) and yearlings ($n = 70$) were observed suckling with their mothers

Season	Pups suckling			Yearlings suckling			Age class comparison	
	% time	SE	n	% time	SE	n		
Winter	44.2	3.79	39	43.6	3.20	38	$t_{75} = 0.12$	$p = 0.90$
Spring	44.6	14.73	5	27.6	3.49	13	$t_{16} = 1.64$	$p = 0.12$
Summer	--	--	--	17.7	2.30	19	--	--

Yearlings (observed between the ages of 1.5 to 2.0 y old) suckled an average of 44% of the time they were with their mothers during winter (average of three sites: St. Elias, 1995; Timbered, 1996; Marmot, 1996 and 1997). Time spent suckling dropped significantly to 28% in spring (Timbered, 1998) and to 18% in summer (Timbered, 1996 and

1997; and Sea Otter, 1997) ($F_{7,62} = 5.23, p < 0.001$; Table 2).

An average of 87.6% of the branded pups observed at Timbered Island suckled through the winter months (at 31-41 w of age, based on a mean birth date at Forrester Island of 4 June; Pitcher et al., 2001a). Resuming observations

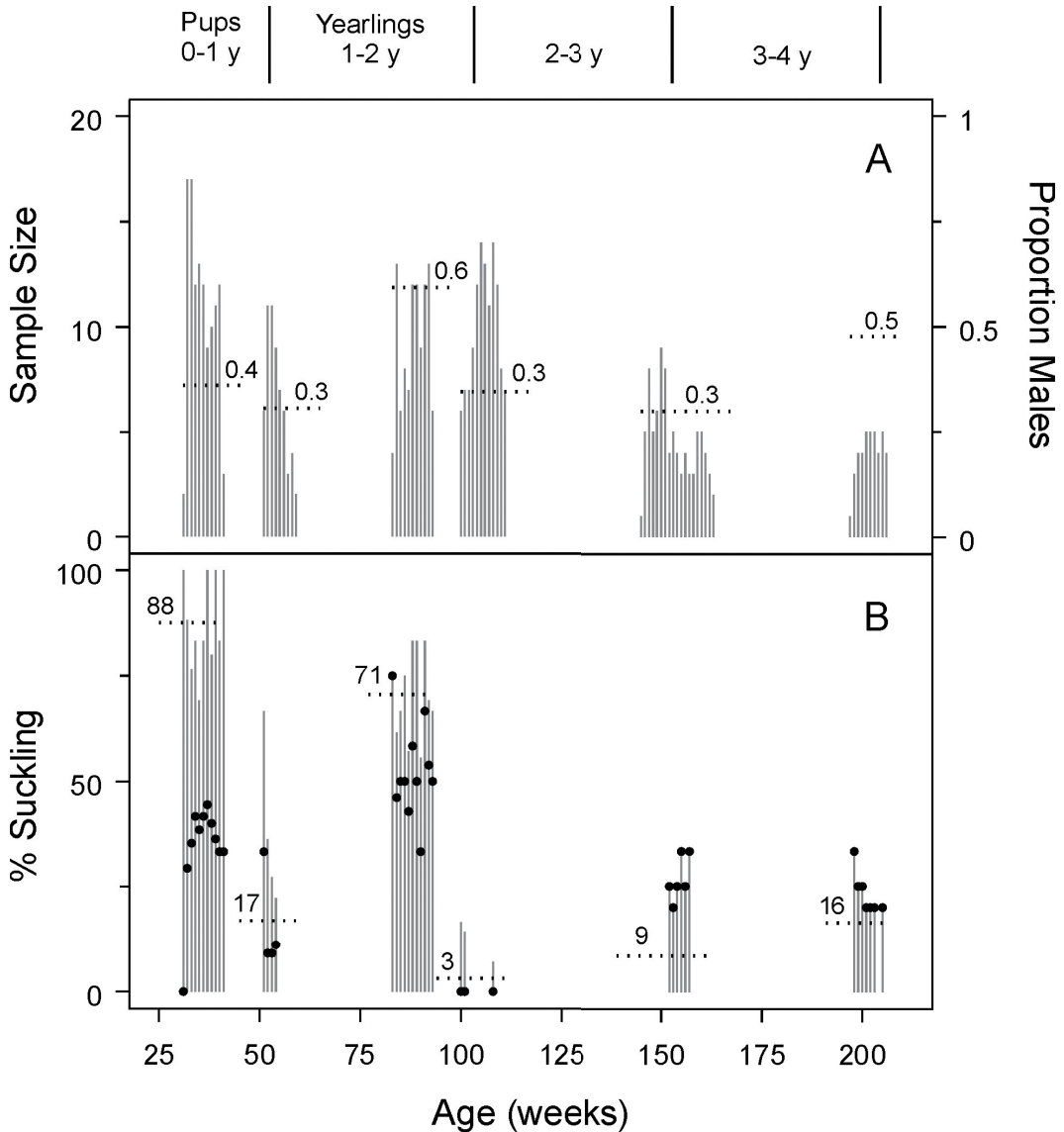


Figure 2. A. Number of branded Steller sea lions hauled out at Timbered Island by age in weeks and B. percent of branded pups and juveniles observed suckling by age in weeks. Sea lions were only observed during the periods denoted by the vertical bars in A. The dotted horizontal lines in A (right y-axis) indicate the proportion of branded pups and juveniles present on the haulout that were males. The dotted horizontal lines in B denote the mean percent of branded sea lion pups observed suckling during each study interval. Data points indicate the percentage of marked male pups observed suckling. Note that the individuals were branded in 1994 and 1995 at Forrester Island and have an assumed birth date of 4 June. Also note that the estimated percentage of sea lion pups continuing to suckle at age 3 and 4 y was the result of a repeated observation of a single male pup (brand no. F490).

during summer showed a significant drop in the percentage suckling at ages 51 to 54 w (Figure 2B). Most of the branded pups that remained at our study sites were females, and none were observed suckling through the remainder of the summer (ages 55 to 59 w). We also observed an average of 70.6% of the branded yearlings suckling at Timbered Island during the winter months (at 83 to 93 w of age), but only 15% during the first 2 w of summer observations (Figure 2B).

The ratio of male to female pups observed suckling was approximately equal from January to June; however, significantly more males than females were observed suckling a year later at 1.5 to 2 y of age (Figure 2B). A shift was also observed in the proportion of male pups observed at Timbered Island, which fell from 46% in January to 29% in June, and rose to 56% by the following January (Table 3). These data suggest that a greater proportion of female pups weaned in their first year, while a greater proportion of males stayed with their mothers for a second year.

We were able to determine the exact date of weaning for three focal animals. These three weaned on 2 June 1997 and 1 July 1999 at Timbered Island (both females, brand nos. F781 and F674, respectively) and on 20 June 1997 at Sea Otter Island (animal identified by natural markings, but sex unknown). These individuals suckled consistently until these dates and were not seen with their mothers thereafter. Thus, they were between the ages of 1 y and 13 mo when weaned based on an assumed mean date of birth of June 4 (Pitcher et al., 2001b).

Overall, most Steller sea lions appeared to wean at the start of the breeding season when 1 or 2 y old. In general, most males observed in southeast Alaska during the late 1990s appeared to wean at about 2 y of age, while females were weaning at 1 and 2 y (Figure 2, Table 3). This is based on the high proportion of males (~90%) and females (~50%) still suckling towards the end of their second year, and the rarity of animals observed suckling at > 2 y. Our data further indicated that a few immature sea lions maintained a bond with their mothers for longer. In this regard, one of our male focal animals (brand no. F490) was observed suckling in all periods of observation at Timbered Island—and was still suckling on our last day of observations when he was 4 y old and larger than his mother.

Attendance Patterns and Site Fidelity

Mean trip lengths of lactating females averaged 54 h in winter (3 sites over 3 y, eastern and western populations combined, $n = 68$ females), 30.4 h in spring (1 site, $n = 39$), and 39.5 h in summer (2 sites over 2 y, $n = 63$) (Table 4). The parametric model and nonparametric tests detected significant differences in mean time spent away from the haulouts ($F_{7,162} = 3.39$, $p = 0.002$). A Tukey test on mean time away indicated differences among all three seasons, but not for different sites for the same time of year. Thus, we concluded that time spent away by lactating sea lions was longer on average in winter than in spring and summer (Table 4, Figure 3).

Time spent away from the haulouts in the region by pups and yearlings during winter were pooled

Table 3. Proportion of marked Steller sea lions observed suckling by age, sex, and time of year, and proportion of all marked individuals that were male at Timbered Island

Age (months)	Month of observation	Males			Females			Total N	% males
		Mean	SE	<i>n</i>	Mean	SE	<i>n</i>		
7	January	0.67	0.21	6	0.71	0.18	7	13	46
8	February	1.00	0.00	8	1.00	0.00	11	19	42
9	March	1.00	0.00	5	0.89	0.11	9	14	36
12	June	0.50	0.29	4	0.40	0.16	10	14	29
13	July	0.25	0.25	4	0.00	0.00	5	9	44
19	January	0.80	0.20	5	0.25	0.25	4	9	56
20	February	1.00	0.00	8	0.50	0.22	6	14	57
21	March	1.00	0.00	8	0.67	0.21	6	14	57
34	April	0.00	0.00	2	0.00	0.00	6	8	25
35	May	0.00	0.00	4	0.08	0.08	13	17	24
36	June	0.00	0.00	5	0.09	0.09	11	16	31
37	July	0.00	0.00	5	0.08	0.08	13	18	28
46	April	0.50	0.50	2	0.00	0.00	4	6	33
47	May	0.50	0.29	4	0.00	0.00	4	8	50
48	June	0.50	0.50	2	0.00	0.00	2	4	50
49	July	0.00	--	1	0.00	0.00	5	6	17

Table 4. The mean duration of trips made by immature and lactating Steller sea lions observed using haulouts in the western and eastern populations from winter to summer

Age class	Season	Western population			Eastern population			Regional comparison	
		Trip (h)	SE	<i>n</i>	Trip (h)	SE	<i>n</i>		
Immature	Winter	39.0	4.47	33	40.0	2.91	37	$t_{68} = -0.19$	$p = 0.85$
	Spring	--	--	--	35.8	3.83	38	--	--
	Summer	38.6	8.56	14	32.5	3.13	66	$t_{78} = 0.78$	$p = 0.44$
Lactating	Winter	59.7	5.91	32	49.0	3.47	36	$t_{66} = 1.60$	$p = 0.11$
	Spring	--	--	--	30.4	2.90	39	--	--
	Summer	32.1	4.26	6	46.6	4.61	57	$t_{61} = -1.01$	$p = 0.32$

(after finding no significant differences between the two age groups) and averaged 39.5 h (3 sites over 3 y, $n = 70$ immatures; Table 4). Mean trip lengths of yearlings were 36 h in spring (1 site, $n = 38$) and 35.5 h in summer (2 sites over 2 y, $n = 80$; Table 4). Sample sizes were insufficient to calculate mean trip lengths of pups in spring and summer. No significant seasonal change was noted in time spent at sea by immature sea lions when data from the two regions were pooled ($F_{2,185}$

$= 1.12$, $p = 0.33$; Table 5); however, there was a significant difference within the eastern population in the mean duration of time spent away (40 h winter, 36 h spring, and 33 h summer; $F_{2,138} = 5.36$, $p = 0.002$; Table 4). Comparing age classes revealed that time spent away by immature sea lions was significantly shorter than lactating females during winter ($t_{136} = -3.43$, $p < 0.001$) and summer ($t_{141} = -2.31$, $p = 0.02$), but not during spring ($t_{75} = 1.11$, $p = 0.27$) (Table 5, Figure 3). The longest average

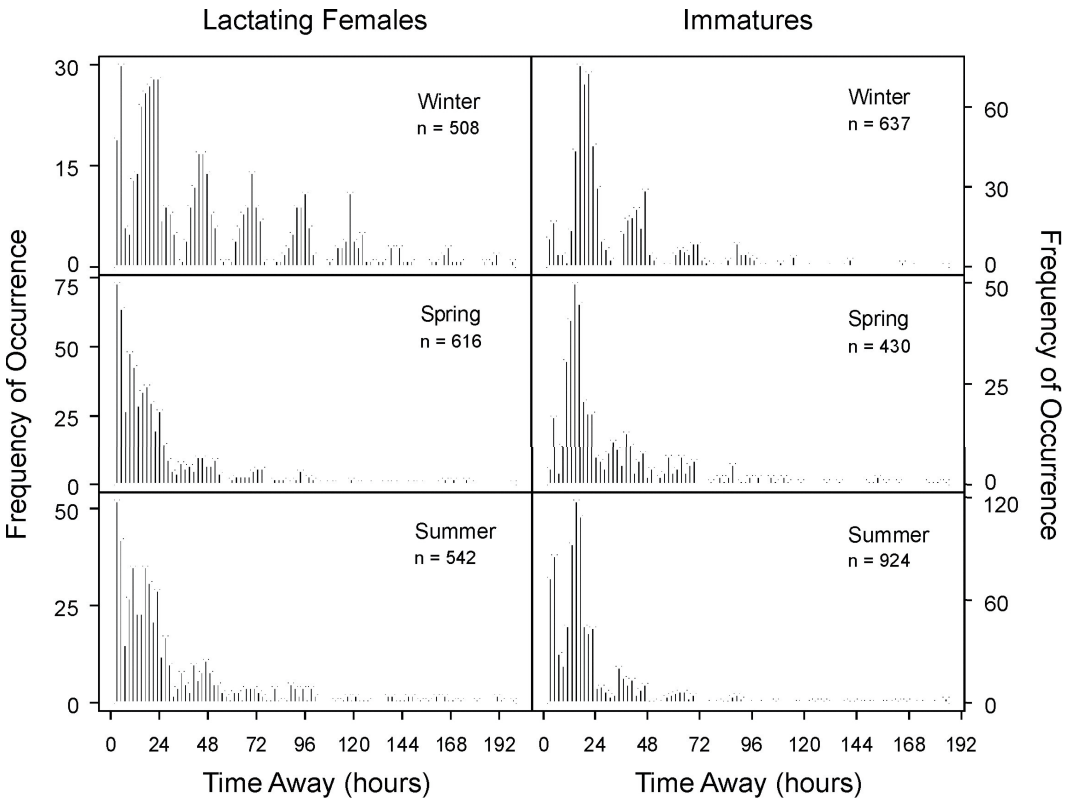


Figure 3. Time spent away from Timbered Island by all identifiable lactating and immature Steller sea lions in winter (January to March), spring (April to May), and summer (June to July); immature sea lions include pups and yearlings, and time away shows intervals > 3 h and < 200 h. Time away likely reflects individual trips, but it may also include some multiple trips if animals were missed when they returned to the haulout or if they used an alternative haulout between visits to our study sites.

Table 5. The mean duration of trips made by immature and lactating Steller sea lions observed using haulouts during winter, spring, and summer

Season	Immatures			Mature females			Age class comparison	
	Trip (h)	SE	<i>n</i>	Trip (h)	SE	<i>n</i>		
Winter	39.5	2.59	70	54.0	3.37	68	$t_{136} = -3.43$	$p < 0.001$
Spring	35.8	3.83	38	30.4	2.90	39	$t_{75} = 1.11$	$p = 0.270$
Summer	33.6	2.97	80	45.2	4.22	63	$t_{141} = -2.31$	$p = 0.022$

times away occurred during winter for both mature and immature age categories (Table 5).

Known mother-immature pairs had identical trip durations for 81 recorded trips. Such "paired" trips occurred at three sites (Sea Otter, Marmot, and Timbered Islands) over 2 y (1997 to 1998) and all three seasons. The majority of these trips (63%) were observed during spring observations at Timbered Island in 1998. One interpretation is that mothers and their young were traveling together; however, it is more likely that mothers (identified by their association with their offspring) had returned to the haulout to await their pup following a relatively short feeding trip and were not recognized until their branded offspring had appeared.

Pooling site fidelity data from pups and yearlings (after finding no significant differences between the two age groups) revealed significant differences between sites and seasons in the percent of time that immature sea lions spent on shore ($F_{7,134} = 11.35$, $p < 0.001$) and with their mothers ($F_{7,134} = 6.98$, $p < 0.001$) (Table 6). Seasonally, immature Steller sea lions spent more time on haulouts during winter than they did during summer. We did not detect any significant variations between different sites within the same season, and we found the same results for their mothers. This correlation between attendance patterns of mothers and young is not surprising given the bond and dependence that exists between mothers and their young.

Some of the immature sea lions consistently used the Timbered Island haulout (where we observed sea lions for the greatest number of years and seasons, and where we knew the ages and sexes of many immature sea lions from their brand numbers). Other sea lions used this site for weeks at a time, while some were only seen for a few days. For these infrequent visitors, Timbered Island was likely one of a number of haulout sites used by some mature females and their dependent young. Thus, it is difficult to generalize about site fidelity other than to say that some sea lions showed high site fidelity to a single site while others were likely regular users of a number of different sites.

The proportion of branded Steller sea lions at Timbered Island shifted from roughly equal

numbers of males and females at age 7 mo (54% females) to a preponderance of females by age 12 mo (71%); however, the proportion switched to predominately males at ages 19 to 21 mo (57% males) before falling in April to June (to 25%; Table 3). The proportion of males remained low for the next 12 mo. The differences likely reflect sex-specific behavioral differences in the timing of weaning and dispersal of young sea lions.

Table 6. Proportion of time that immature Steller sea lions ($n = 143$) were seen on shore (as a function of total number of h observed) or were observed with their mothers (as a function of the total number of h their mothers were present)

Season	Time on shore			Time with mother		
	%	SE	<i>n</i>	%	SE	<i>n</i>
Winter	24.1	2.12	52	45.0	3.15	52
Spring	13.9	1.96	34	41.0	5.30	34
Summer	12.2	0.94	57	21.2	3.24	57

Discussion

Our study evolved from a series of exploratory investigations and would have been strengthened by choosing to continuously follow two sites from winter to spring. Unfortunately, we did not anticipate the difficulties of observing Steller sea lions in winter and did not realize at the time that the majority of weaning did not occur during winter. Our findings are thus pieced together from different sites, years, and seasons. While we are confident about our overall findings, they are not as clear and precise as we would have liked. Future behavioral studies would therefore be well advised to focus on following one or more haulout sites for an entire year or longer with no break in observations.

Suckling and Weaning

Weaning is ultimately a resolution of an inherent conflict between the length of time it is beneficial for a mother to continue to invest in a current offspring and the longer period that it is beneficial for an offspring to have its parent continue that investment (Trivers, 1974; Mock &

Forbes, 1992; Godfray, 1995). Initially, the cost of nursing is relatively small for the female while conferring a comparatively large benefit to the pup; however, the potential cost of continued nursing to the female increases as the pup grows in size and increases its energetic demand. There is also an incurred cost if continued nursing jeopardizes the mother's future reproductive success.

The polygynous mating system of Steller sea lions means that mothers will be more closely related to their offspring than pups will be to their siblings. This results in a discrepancy in the cost of future reproduction and optimal time of weaning from the mothers' and pups' perspectives. The point in time when weaning occurs should therefore primarily reflect the females' interest given that she ultimately has control in providing milk to her pup (Godfray, 1995). Nevertheless, some pups may wean themselves and depart prior to a mother terminating nursing (e.g., northern fur seals; Gentry, 1998). The exact timing of weaning is likely dependent on a number of variables, including maternal condition, future maternal reproductive potential, gender and age of offspring, and environmental conditions. Hence, weaning is probably a gradual process that occurs on different schedules by mother/pup pairs within the same population.

We detected a drop in the proportion of time that yearlings (observed between 1.5 to 2.0 y) spent suckling from winter to spring and summer (Table 2). This presumably reflects a gradual process of weaning during which the yearlings likely supplement their milk diet with solid food. We did not note a similar change for pups, however, due perhaps to insufficient sample sizes of this age group during spring and summer (Table 2). We found no indication that weaning started in winter (January to March). Rather, it appears to start during spring (April to May). This conclusion is consistent with the observation of Pitcher & Calkins (1981) that fewer multiparous females in the Gulf of Alaska during the 1970s were lactating between April and May (61%) than between June and March (when 82% were lactating). It is also consistent with our observation that pups and yearlings spent a greater proportion of their time in the water during spring compared to winter (Table 6).

An average of 88% of the pups we observed at Timbered Island during winter (January to March) were suckling (Figure 2B). The remaining 12% of the pups were not seen long enough to confirm whether they were weaned. We suspect that these individuals were still dependent, however, and were either simply in transit to other haulouts with their mothers when seen or had made short, independent trips to our study sites from their principal haulouts while their mothers were

foraging. Extending this logic to the yearlings observed in winter suggests that our estimated proportion of dependent yearlings is also underestimated.

Our data suggest that most Steller sea lions weaned shortly before their first or second birthdays, although we did observe a single individual nursing at 3 and 4 y of age (Figure 2B). Our data further suggest that significant numbers of dependent young left the haulouts in the summer with their mothers and returned with them in the fall and winter (based on the dip and rise in proportion of branded sea lions observed suckling between spring and winter from ages 6 mo to 1.5 y; Figure 2B). Observations during the breeding season have noted that significant numbers of pregnant sea lions arrive on rookeries with suckling subadults (ages 1+ y) in late May and early June (Gentry, 1970; Perlov, 1970; Sandegren, 1970). Following birth, a mother may show increased antagonism towards her dependent subadult until it has weaned, or she may reject her newborn pup and renew her bond with the persistent subadult.

Observations from Timbered Island showed that yearling males (observed at ages 1.5 to 2 y) returned with their mothers to the haulout in significantly greater numbers than females (Figure 2). This may reflect yearling males being more persistent at driving off a newborn pup, which, in turn, might be related to the higher energetic needs of young males compared to females (Winship et al., 2001, 2002). The higher proportion of females observed at 2.5 to 3 y is consistent with young males tending to travel further from their haulouts and rookeries of birth (Raum-Suryan et al., 2004).

Our observations indicated that the proportion of time immature Steller sea lions suckled declined through the spring to early summer, suggesting that most sea lions weaned before the start of the following breeding season when 1 or 2 y old. Our conclusion that sea lions wean shortly before their first or second birthdays is consistent with that drawn by Raum-Suryan et al. (2004) and Rehberg (2005) using telemetry data. Rehberg (2005) found that the diving patterns of pups changed near the end of their first year (11 to 12 mo) to resemble those of adults. Pitcher et al. (2005) also noted changes in mean-dive-duration and maximum-daily-depth around first and second birthdays, while Raum-Suryan et al. (2004) noted that the annual timing of weaning appeared to be less variable than the age of the offspring at weaning.

The declining proportion of time spent suckling suggests that sea lions began supplementing their milk diet with solid food beginning in the spring when the reduced lengths of trips by lactating females (Figure 3) suggest that prey were more easily obtained. In retrospect, it is perhaps not

too surprising that Steller sea lions should begin to wean during spring and complete weaning by early summer. Each pup represents a major investment to the female both in terms of absolute energy input (Winship et al., 2002) and in terms of lifetime reproductive success (given they produce a maximum of one pup per year). It would therefore not make evolutionary sense for a mother to wean her pup at a time of the year that is not optimal for its survival. Weaning shortly before the start of the next breeding season also allows a female to return to a rookery to give birth and mate.

One interpretation of our data from southeast Alaska is that about 50% of females observed in the 1990s weaned at 1 y, and the remainder weaned at 2 y (Figure 2, Table 3). In contrast, it appears that most males weaned at 2 y. While it might be argued that weaned male pups would have left our study area and would therefore not have been observed as yearlings, the disproportionately high numbers of male yearlings compared to females using our study haulouts suggests otherwise (Table 3). Our conclusions are based on observations made in southeast Alaska during the late 1990s while the Forrester Island breeding population (the largest rookery and closest to Timbered Island) had stabilized and the overall growth of the southeast Alaska population had slowed (Calkins et al., 1999; Sease & Loughlin, 1999).

The apparent plasticity in timing of weaning (ranging from 1 to 3 y) suggests that populations incurring nutritional stress may nurse their pups for a second year to enhance the pups' chances of survival. Females appear to wean sooner than males. The higher proportion of males we observed suckling at 1.5 y may be indicative of a population approaching carrying capacity. Thus, it is possible that mean age of weaning in populations that are at or near carrying capacity is 2 y—as opposed to 1 y in an increasing population—and that the sex ratio of suckling young in a food stressed population may be equal for 2 y olds and biased towards males at 3 y. Such a shift in weaning dates would effectively cut the birth rates of Steller sea lion populations by more than half, thereby stabilizing population growth or contributing to population decline. Such a mechanism is mathematically equivalent to maintaining birth rates and reducing juvenile survival and may account for a large part of the decline of sea lions in western Alaska.

Attendance Patterns and Site Fidelity

The sex ratio of branded Steller sea lions at Timbered Island showed that pups were present in roughly equal numbers during winter and spring, but that females predominated in the summer (Figure 2A). This suggests that a greater proportion of males did not wean in their first year and, therefore,

followed their mothers to the rookeries. The dependence of many of the older males at ages 1.5 to 1.8 y is shown by their higher numbers at the haulout (Figure 2B). By age 3 y (when most sea lions were weaned), we observed primarily females (of the branded cohort). The absence of 3-y-old branded males suggests either a high mortality of males following weaning or, more likely, that males had a higher tendency to disperse further from haulouts near natal sites than did the females. The dispersal theory is supported by reports of larger numbers of young branded males appearing at sites further away from Forrester Island (where they were born) compared to females (Raum-Suryan et al., 2002).

Our eight sets of field studies (spanning 4 y, 3 seasons, and 4 different haulout sites) showed significant differences in sea lion attendance behavior among seasons (winter, spring, and summer), but not among haulout sites in the declining Gulf of Alaska region and the increasing southeast Alaska region. This suggests that the lactating sea lions we observed using the haulout sites in the declining area were not having any more difficulty procuring prey than sea lions at haulout sites in the growing population. We cannot comment on what type of prey they were obtaining, however, and can only draw conclusions about the time that they were away and the time that they spent on shore with their offspring.

Diets of the endangered Steller sea lions in the Gulf of Alaska have been dominated by walleye pollock (Merrick et al., 1997; Sinclair & Zeppelin, 2002), while animals in the growing southeast Alaska population consumed a more diverse diet that includes pollock, salmon, herring, sand lance, and rockfish (Trites et al., unpubl. data). Our behavioral observations suggest that prey may be equally available to sea lions in both areas; however, the energy content and nutritional quality of the diets consumed in each region are quite different (Trites & Donnelly, 2003; Winship & Trites, 2003). Recent feeding experiments with captive Steller sea lions suggest that young sea lions may not have the stomach capacity to physically process enough low-energy fish to meet their daily energy requirements. Even with a diet of high-energy fish, young sea lions appear to have very little excess stomach capacity to process more fish (Rosen & Trites, 2004). Older sea lions do not appear to be similarly constrained. This apparent physiological limit combined with relatively high energetic needs may explain why Steller sea lions wean at such a relatively old age compared to other species of pinnipeds.

Porter & Trites (2004) observed pups in the water during winter with fish in their mouths but did not see any of the pups swallow the fish they held. They also noted two cases of suckling by nonfilial pups (an extremely rare event among

Steller sea lions). The persistence of the pups' attempts to steal milk was surprising in light of the risks of being bitten by lactating females and the apparent ability of pups to capture fish. These observations add further credence to the view that pups are physiologically unable to subsist independently on a mixed diet of solid foods and require high lipid milk to meet their daily energy needs.

Our data indicated that lactating sea lions were away for longer periods in winter than in spring and summer (Figure 3). They also indicated that mothers and their young spent more time on shore during winter than in the summer. These findings are generally consistent with a model of greater maternal investment in winter. The behavioral data also suggested that pups spent a higher proportion of their time on shore and were not with their mothers during foraging bouts (Trites & Porter, 2002).

Conclusions

Our study reports the first behavioral observations of Steller sea lions using haulouts through the winter, spring, and summer months and fills an important gap in understanding their life history. Counter to our expectations, we did not observe any significant differences between the declining and increasing populations in time spent by lactating females at sea or on shore. Rather, lactating females showed seasonal changes that were consistent among all areas and years studied. This, in turn, is consistent with the view that lactating Steller sea lions make a greater maternal investment during the winter than during the spring or summer. Equally important is the discovery that weaning does not occur during winter as some have speculated, but, rather, it occurs just prior to the start of the next breeding season when conditions are likely optimal for the survival of the newly weaned offspring.

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