Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from stable and declining populations in Alaska

Linda L. Milette and Andrew W. Trites

Abstract: Maternal attendance patterns of Alaskan Steller sea lions (*Eumetopias jubatus*) were compared during the summer breeding seasons in 1994 and 1995 at Sugarloaf Island (a declining population) and Lowrie Island (a stable population). Our goal was to determine whether there were differences in maternal attendance between the two populations that were consistent with the hypothesis that lactating Steller sea lions in the area of decline were food-limited during summer. Our a priori expectations were based on well-documented behavioural responses of otariids to reduced prey availability. We found that foraging trips were significantly shorter in the area of population decline, counter to initial predictions. The mean length of foraging trips in the declining area was 19.5 h compared with 24.9 h in the stable area. In contrast, the mean perinatal period (time between parturition and first feeding trip) was significantly longer in the area of decline (9.9 versus 7.9 days), again countering initial predictions. The mean length of shore visits for the declining population was also significantly longer (27.0 h compared with 22.6 h where the population was stable). For both populations, the mean time that mothers foraged increased as pups grew older, whereas the time that they spent on shore with their pups became shorter. Behavioural observations of maternal attendance patterns are inconsistent with the hypothesis that lactating Steller sea lions from the declining population had difficulty obtaining prey during summer.

Résumé : Nous comparons les patterns de présence de la mère auprès des petits chez l'otarie de Steller (*Eumetopias jubatus*) en Alaska durant les saisons de reproduction d'été de 1994 et 1995 à l'île Sugarloaf (une population en déclin) et à l'île Lowrie (une population stable). Le but de notre étude est de déterminer s'il y a des différences dans la présence maternelle entre les deux populations qui s'accordent avec l'hypothèse selon laquelle les otaries de Steller nourricières dans les zones de déclin sont limitées par la nourriture en été. Nos attentes a priori sont fondées sur les réactions comportementales bien connues des otaries à la réduction de la disponibilité des proies. Contrairement à nos prévisions initiales, les sorties de recherche de nourriture sont plus courtes dans les zones de déclin; leur durée moyenne est de 19,5 h, par comparaison à 24,9 h chez la population stable. En revanche, la durée moyenne de la période périnatale (entre la mise bas et la première sortie de quête de nourriture) est significativement plus longue dans la zone de déclin (9,9 jours au lieu de 7,9 jours), encore à l'encontre de nos prévisions. La durée moyenne des visites au littoral chez la population en déclin est aussi significativement plus longue (27,0 h par comparaison à 22,6 h chez la population stable). Chez les deux populations, le temps moyen consacré par les mères à la recherche de la nourriture augmente avec l'âge des petits, alors que le temps passé au littoral en compagnie de leurs petits diminue. Ces observations sur le comportement de présence maternelle ne s'accordent pas avec l'hypothèse selon laquelle les otaries de Steller nourricières dans la population en déclin ont du mal à obtenir des proies durant l'été.

[Traduit par la Rédaction]

Introduction

The world population of Steller sea lions (*Eumetopias jubatus*) declined dramatically through the 1980s and 1990s (Loughlin et al. 1992; National Marine Fisheries Service (NMFS) 1992; Trites and Larkin 1996). Two genetically distinct stocks of Steller sea lions have been identified: an eastern and a western stock divided at 144°W near Cape Suckling, Alaska (NMFS 1995; Bickham et al. 1996; Fig. 1). They were listed as a "threatened" species under the U.S. Endangered Species Act in 1990 and were reclassified in 1997 as "endangered" in the western part of their range (Loughlin 1998). Food limitation because of overfishing is one of the leading hypotheses to explain the overall decline (Hoover 1988; NMFS 1992; Alaska Sea Grant 1993; Merrick 1995; DeMaster and Atkinson 2002), but this hypothesis has been difficult to test (Trites and Donnelly 2003).

Many studies have shown that pinnipeds and other mammals suffering from food shortages typically exhibit reduced body size, reduced productivity, high mortality of pups and juveniles, altered blood chemistry, and specific behavioural modifications (see review by Trites and Donnelly 2003). In terms of behavioural adaptations, pinnipeds appear to increase the time spent at sea and reduce the time spent on shore when faced with food shortages. For example, lactating Antarctic fur seals (*Arctocephalus gazella*) have been shown to adjust the lengths of their trips in response to

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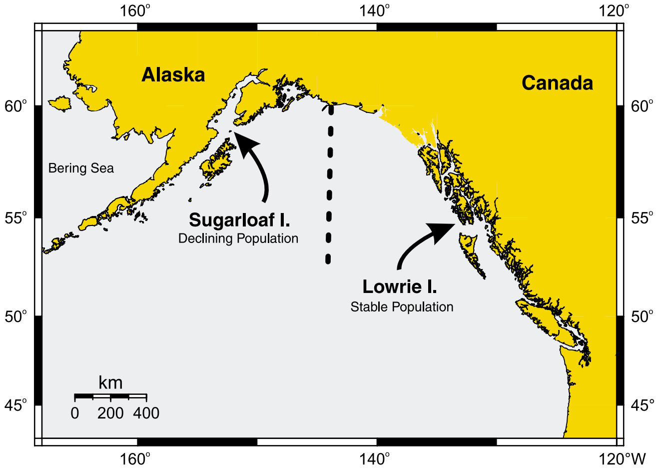
Fig. 1. Study sites in Alaska. The division between the western (declining) and eastern (stable) Steller sea lion (*Eumetopias jubatus*) populations is shown by the broken line.



changes in krill abundance, making longer trips and expending more energy when prey were scarce and making shorter trips and spending more time ashore when prey were abundant (Costa et al. 1989; Boyd et al. 1994; McCafferty et al. 1998; Boyd 1999). During the 1983 El Niño when prey were scarce, female South American fur seals (*Arctocephalus australis*), Galápagos fur seals (*Arctocephalus galapagoensis*), northern fur seals (*Callorhinus ursinus*), and California sea lions (*Zalophus californianus*) also made longer feeding trips than normal (Costa et al. 1985; Trillmich and Limberger 1985; Ono et al. 1987; DeLong and Antonelis 1991; Heath et al. 1991; Majluf 1991; Trillmich and Dellinger 1991). This is also consistent with a more recent study which showed that lactating Steller sea lions at Año Nuevo Island in California spent more time at sea during a moderate 1992 El Niño (Hood and Ono 1997).

We sought to use behavioural observations to determine if one component of the Alaskan Steller sea lion population (lactating females) displayed behaviours that were consistent with the food-limitation hypothesis. We did so by comparing the maternal attendance patterns of lactating Steller sea lions from declining and stable populations during the summer breeding season. The maternal attendance pattern refers to the cycle time that a mother sea lion spends feeding at sea and caring for her pup on shore. This maternal cycle occurs at regular intervals throughout the breeding season.

If the declining population of Steller sea lions was nutritionally stressed as the result of an overall shortage of prey during the summer breeding season, we expected lactating females to spend more time at sea searching for enough prey to meet their metabolic needs compared with females in the stable population. This a priori expectation was based on the well-documented biological effects of the El Niño – Southern Oscillation events in the eastern Pacific Ocean (Barber and Chavez 1983; Cane 1983; Fielder 1984; Arntz et al. 1991; Hood and Ono 1997) and on the effects of changes in krill abundance on pinnipeds in the Antarctic (Boyd et al. 1994; McCafferty et al. 1998; Boyd 1999).

The attendance pattern includes the regular foraging–attendance cycle as well as the perinatal period (the time between the pup's birth and the mother's first feeding trip), during which time the mother suckles her pup and fasts onshore. During the 1983 El Niño event, female California sea lions spent less time onshore during the perinatal period (Ono et al. 1987). Thus, our second a priori expectation was that lactating Steller sea lions in the area of decline should have a shorter perinatal period if they were nutritionally stressed, because they would have less energy reserves at the onset of parturition.

In summary, sea lions and fur seals observed in California, Peru, Antarctica, and the Galápagos Islands responded to reduced prey abundance by increasing the length of their feeding trips and decreasing their perinatal periods. We assumed that lactating Steller sea lions in Alaska would respond in a similar way if they were food-limited during summer in the area of population decline.

Methods

Study sites and materials

We compared maternal attendance patterns and activity budgets for Alaskan Steller sea lions breeding on Sugarloaf Island (58°53′N, 152°02′W), an area of population decline, and on Lowrie Island (54°53′N, 133°30′W), an area where the population has remained abundant (Fig. 1). Sugarloaf Island has four rookeries and an elevation of about 370 m. It is approximately 81 ha with steep grass-covered slopes on all sides. In 1994, 976 adults and 958 pups were counted at all of the Sugarloaf rookeries (Strick et al. 1997). Accounting for animals that were at sea when the census was conducted yields a total population estimate of about 2400 adults (Trites and Larkin 1996). This is significantly lower than the estimated 11 000 adults that were present at their peak in 1979 (Trites and Larkin 1996). The rookery used on Sugarloaf Island was a flat rock outcrop with boulders scattered throughout. Approximately 100 adults used this rookery during the summer breeding season. An observation blind was constructed approximately 20 m above the rookery. However, on sunny days it was possible to get within 10 m of the rookery without the sea lions being aware of the observer.

Lowrie Island is part of the Forrester Island breeding complex and is approximately the same physical size as Sugarloaf Island but is not as steep or as high. In 1994, 4013 adults and 2575 pups were counted at the seven rookeries that make up this complex (Strick et al. 1997). Total number of adults, accounting for animals at sea during the survey, was around 11 000 in 1994 and about 8500 adults in 1979 (Trites and Larkin 1996; Calkins et al. 1999). The rookery used for observations was large and on a steep rock outcrop. About 300 adults occupied it during the summer breeding season. The observation blind was about 60 m above the rookery and was separated from the rookery by a small surge channel.

Field assistants were initially trained in the laboratory to observe sea lions and conduct behavioural scans using videotapes of Steller sea lions recorded during the breeding season and by a protocol manual that we designed. Moreover, at least one field assistant with one or more years of prior experience observing Steller sea lions was assigned to each island in both study years. Binoculars (8 × 35) and spotting scopes were used to observe the animals. Photographs and sketches were used to identify focal animals.

In 1994, we observed Steller sea lion behaviour from 16 May to 11 August on Sugarloaf Island and from 10 May to 1 August on Lowrie Island (Fig. 1). In 1995, observations took place from 10 May to 14 August on Sugarloaf Island and from 16 May to 4 August on Lowrie Island. Observations from both study years covered the entire summer breeding season at each site. Maternal attendance patterns of individually recognizable females with pups were recorded using instantaneous focal scan sampling (Altmann 1974; Martin and Bateson 1986). Attendance was recorded hourly from 0600 to 2000 on most days, but there were a number of days when observations started as late as 0800. Hourly attendance checks were made 2 days/week between 0600 and 0900, 1300 and 1400, and 1700 and 2000. In 1994, logistic difficulties on Lowrie Island prevented the collection of data on five nonconsecutive days. There were also some days on Sugarloaf Island in 1994 where female attendance could only be recorded every 6 h because of poor weather. In 1995, female attendance data were collected hourly and on every day at both sites. Overall, observation efforts for individual focal females ranged from 157 to 554 h depending on their parturition date. Natural markings such as scars or fungal patches were used to identify lactating females. The reliability of using such markings has been verified through annual photographs (1994–1999, L.L. Milette, unpublished data) and acoustic recordings of individual animals (Campbell et al. 2002).

Mean length of trips to sea, visits ashore, and the perinatal period

A feeding cycle was defined as a trip to sea followed by a visit ashore. A trip was assumed to have occurred if the female was absent from the rookery and was not observed floating or swimming near shore. We only included trips in our analysis when the females were observed departing and (or) hauling out with wet pelage after being absent for a period of time. Overnight departures or arrivals were assumed to have occurred at 0100 (the midpoint of nonobservation hours). As a result, the length of feeding trips and visits ashore included in the analysis were accurate to within 12 h (i.e., the maximum error for a single trip or visit was ±6 h). Trips with an accuracy exceeding ±6 h were omitted from analysis. Short trips (0.5–4.0 h) that met the above criteria were included because they were sometimes the only trip observed for a 2-day period. We assumed that females found prey close to the rookery on these short trips. Short disappearances (<30 min) from the rookery were not considered to be trips if females were not wet or were not observed departing or arriving. Under these circumstances, the female could have moved to another location or may have been missed during a scan.

The perinatal period occurred between parturition and the mother's first trip to sea. It was accurate to within 12 h (±6 h). The time of the pup's date of birth was known either exactly or within 12 h if parturition occurred overnight. Overnight births were assumed to have occurred at 0100 (the midpoint of nonobservation hours). For the first trip to sea following parturition, the female had to be observed leaving and (or) arriving on the rookery with wet pelage to be included in the analysis. If the female's first disappearance from the rookery was ambiguous and followed by a regular attendance cycle (~24 h at sea and 24 h ashore), her first trip was omitted and that particular female was not included in the perinatal period analysis. If a female disappeared on or shortly after her pup's birth (i.e., up to 4 days later) and was followed by an unusually long visit of 5–7 days, her second absence was assumed to be the first feeding trip to sea. Furthermore, we only included such a female in the analysis if her departure and (or) arrival from or to the rookery met the criteria previously described. Perinatal periods for individual females at both study sites in 1994 and 1995 were compared using a two-factor analysis of variance.

Length of trips to sea and visits ashore as pups aged

The relationship between pup age and the mean length of trips to sea (or visits ashore) was only determined for mothers with known parturition dates. Some females were omitted from the analysis if the feeding cycle could not be related to the age of the pup. The mean maternal feeding cycle (the length of time at sea and the length of the subsequent shore visit) of all females observed was calculated and plotted at 5-day intervals, where day 0 was the pup's date of birth. We thus plotted the mean feeding cycle of females with pups between the ages of 0 and 4 days, 5 and 9 days, 10 and 14 days, and so on.

We used a repeated-measures ANOVA to test whether the duration of foraging trips or time spent on shore differed between years or populations or with the age of the pup. This analysis was appropriate given that our observations consisted of multiple measurements per animal over time, with data from single individuals often being correlated and exhibiting heterogeneous variability. We assumed the individual sea lions were statistically independent and fit a random coefficient model, which in turn fits a linear trajectory for each animal. This model therefore ensured that equal weights were given to individuals rather than to trips (or visits) and avoided any bias caused by a tendency for individuals that made short trips or visits from being overrepresented (as in the general regression method of repeated-measures ANOVA).

Our data had two fixed effects, each with two levels, location (Lowrie, Sugarloaf) and year (1994, 1995), and one continuous random factor, age of pup at time of trip (or visit). Age of the pup was calculated at the midpoint of the mother's trip (or visit). We excluded the perinatal stay from the "visit length" analysis.

We chose a compound symmetry structure for the variance–covariance matrix, which assumes that all observations for an animal have the same correlation with each other. For example, an animal with a long foraging trip is likely to always have long foraging trips. We used maximum-likelihood methods to estimate all unknown variance–covariance parameters.

Results

Mean length of perinatal period

Sample sizes for perinatal periods ranged from 8 to 41 observations (Tables 1 and 2). Overall, the mean perinatal period for all sites and years combined was 9.1 days ($s_{\bar{x}}$ = 0.29, n = 81). Significant differences in the perinatal period occurred between years ($F_{[1,78]}$ = 22.55, $p < 0.001$) and sites ($F_{[1,78]}$ = 15.96, $p < 0.001$; Fig. 2). Females from the declining population had longer perinatal periods ($\bar{x}$ = 9.9 days, n = 50) than the stable population ($\bar{x}$ = 7.9 days, n = 31), and

Table 1. Numbers of lactating Steller sea lions (*Eumetopias jubatus*) used in the ANOVA to compare duration of perinatal periods, feeding trips, and visits ashore between the two study sites.

	No. of perinatal periods		No. of feeding trips		No. of visits ashore	
Study site	1994	1995	1994	1995	1994	1995
Declining	9	41	26 (210)	40 (381)	26 (215)	38 (350)
Stable	8	23	15 (115)	19 (163)	16 (135)	18 (151)

Note: Mean duration of feeding trips and shore visits were calculated for each female. Total numbers of trips and visits observed from all of the females are shown in parentheses.

Table 2. Maternal attendance patterns of Steller sea lions at both study sites for both years combined (1994 and 1995).

	Perinatal period (days)			Trip lengths (h)			Visit lengths (h)			Total cycle time (h)
Study site	$\bar{x}$	$s_{\bar{x}}$	n	$\bar{x}$	$s_{\bar{x}}$	n	$\bar{x}$	$s_{\bar{x}}$	n	$\bar{x}$
Declining	9.9	0.37	50	19.5	0.78	66	27.0	0.90	64	46.5
Stable	7.9	0.39	31	24.9	1.12	34	22.6	0.96	34	47.5

Note: Total cycle time includes the trip and visit length.

both populations had shorter perinatal periods in 1994 ($\bar{x}$ = 6.7 days, n = 17) than in 1995 ($\bar{x}$ = 9.8 days, n = 64).

Mean length of trips to sea and visits ashore

Depending on the site and the year of observation, the total number of observed trips to sea and visits ashore for 15–40 lactating females ranged from 115 to 381 (Table 1). Overall, mean trips to sea and visits ashore were each about 24 h for all animals combined (Table 2), but individual mean trips and visits ranged widely from 5 to 53 h.

Comparing between sites showed that time spent at sea was shorter overall ($\bar{x}$ = 19.5 vs. 24.9 h; Fig. 2) in the area of population decline than in the stable area ($F_{[1,129]} = 14.93$, $p < 0.001$) and that there were significant differences between years ($F_{[1,602]} = 8.55$, $p < 0.01$). There were also differences in mean times related to the age of the pup ($F_{[1,114]} = 10.58$, $p < 0.01$). Maternal feeding trips increased by an average of 12 min per day for both areas and years as the pups grew older (i.e., the slopes were the same for all four populations, $F_{[1,602]} = 0.06$, $p = 0.81$; Fig. 3, Table 3). This meant that the average length of maternal foraging trips increased by about 7 h between the ages of 10 and 45 days.

Females spent more time ashore with their pups in 1995 than in 1994 at both sites ($F_{[1,117]} = 16.61$, $p < 0.001$; Fig. 2). There was also a significant difference between sites (27.0 h for the declining population and 22.6 h at the stable site, $F_{[1,111]} = 73.94$, $p < 0.001$), as well as a significant linear drop in the average length of visits as the pups grew older ($F_{[1,592]} = 21.11$, $p < 0.001$; Fig. 3, Table 3). Time spent on shore decreased by an average of 30 min per day for both areas and years as the pups grew older (i.e., the slopes were the same for both populations in both years; Fig. 3, Table 3). This meant that the average length of maternal visits decreased by about 17.5 h between the ages of 10 and 45 days.

Discussion

Nutritional stress

Behavioural observations of Steller sea lions showed consistent temporal patterns in the length of feeding trips and in the time that females spent with their pups. However, there were differences between sites in maternal attendance patterns. Furthermore, the differences were not consistent with the food-limitation hypothesis that has been proposed to explain the decline of the western stock of Steller sea lions in Alaska (Trites and Donnelly 2003).

Based on the responses of pinnipeds during periods of prey reduction, the longer perinatal periods, shorter trips to sea, and longer visits ashore at Sugarloaf Island (in the area of population decline) suggest that these lactating Steller sea lions were not food-limited during summer. Instead, the behavioural data suggest that the abundant population at Lowrie Island (in the area of population growth) was nutritionally stressed relative to the Sugarloaf Island population.

During the 1983 El Niño, when prey availability was reduced, nutritionally stressed pinnipeds along the eastern Pacific coast lengthened their foraging trips to meet their metabolic needs (Trillmich and Limberger 1985; Ono et al. 1987; DeLong and Antonelis 1991; Heath et al. 1991; Majluf 1991; Trillmich and Dellinger 1991). In our study, females from the declining area that were hypothesized to be food-limited had shorter foraging trips than females from the stable area. Brandon (2000) and Andrews et al. (2002) also reported shorter maternal foraging trips in the area of decline compared with the stable area based on radio and satellite tracking of lactating Steller sea lions.

On the surface, it would appear that the abundant population in Southeast Alaska was food-limited, not the declining population in the Gulf of Alaska. However, differences in foraging times might merely mean that the much larger population at Lowrie Island required more time to find food because they depleted prey abundance near their rookery at a higher rate over the breeding season than at Sugarloaf Island. Alternatively, the differences in foraging times might also reflect differences in maternal age structure or distances to forage locations rather than an absolute difference in prey abundance.

There is little information to test these alternative explana-

Table 3. Regression equations describing the changes in the duration of female foraging trips and time spent on shore (following the perinatal period) relative to the age of her pup (measured in days) for the declining (Sugarloaf Island) and stable (Lowrie Island) populations in 1994 and 1995.

Study site	Forage-trip length (days)	Shore-visit length (days)
Declining		
1994	0.4911 + 0.00832(pup age)	1.5219 – 0.02076(pup age)
1995	0.6702 + 0.00832(pup age)	1.7748 – 0.02076(pup age)
Stable		
1994	0.7241 + 0.00832(pup age)	1.3040 – 0.02076(pup age)
1995	0.9032 + 0.00832(pup age)	1.5569 – 0.02076(pup age)

Fig. 2. Box plots showing the distribution of mean trips to sea (*n* = 100 females), mean visits ashore (*n* = 98), and mean duration of perinatal periods (*n* = 81) for lactating females from the declining and stable populations. Within each box, the dotted line indicates the mean and the solid line locates the median.

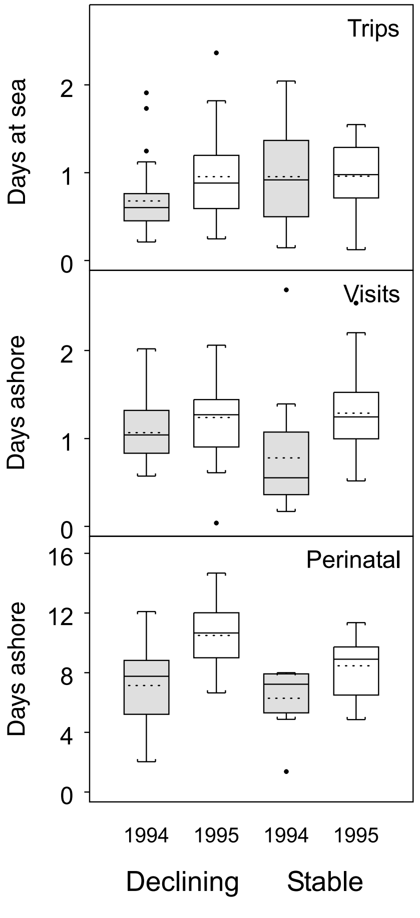
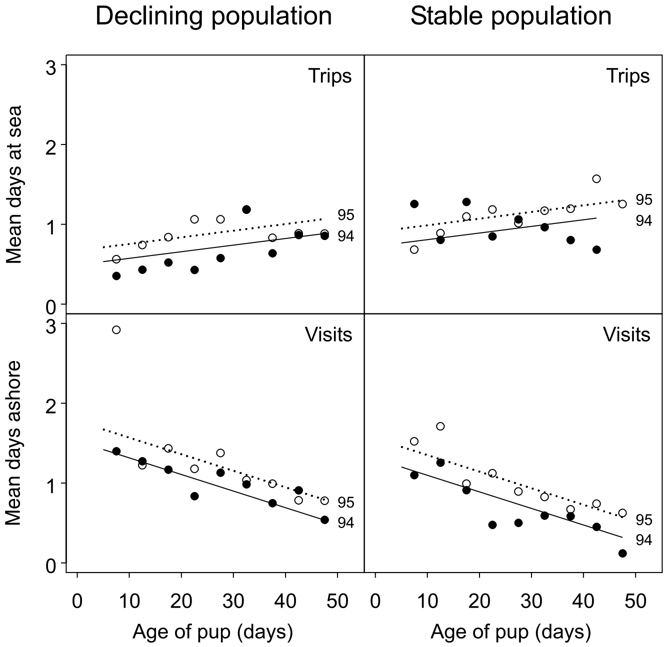


Fig. 3. The relationship between pup age and the mean length of trips to sea and visits ashore for 1994 and 1995. Mean values were calculated per 5-day pup-age period and plotted on the midpoint of each age interval. Sample sizes for each data point ranged from 3 to 77 observations for 3–54 females. Regression equations were calculated using the ungrouped data (Table 3).



tions, but what data are available do not seem to be supportive. For example, it appears that female Steller sea lions begin looking for prey as soon as they leave their rookeries and that they do not capture all of their prey in a single area (Andrews et al. 2002). Females giving birth late in the season should also have had longer first feeding trips than females that gave birth earlier if reduced prey abundance was a significant factor at either site (Gentry and Holt 1986). Although, we were unable to test this (because most of our focal females with known feeding trip lengths gave birth in the early part of the breeding season), the trend appeared to be that early-pupping females had longer foraging trips than the late-pupping females, which does not support the hypothesis that differences in forage times were a function of population density. Boyd et al. (1991) found a similar result when they tested this hypothesis on Antarctic fur seals.

It is debatable whether the foraging behaviours that we documented were influenced by maternal age. Goebel (1988) and Gentry et al. (1986) found that older, larger female northern fur seals that gave birth earlier in the breeding season tended to dive deeper and have shorter foraging trips than the younger, smaller females that tended to give birth later in the season. Given this evidence, it is conceivable that foraging trips of Steller seas lions were shorter in the area of decline because the age structure was older compared with that of the stable population. However, it seems unlikely that age alone could account for all of the observed discrepancy.

Differences in the relative abundance of major prey items may also explain the observed differences in foraging trip lengths between the two study sites. Since the 1980s, the declining population of Steller sea lions in the Gulf of Alaska and Aleutian Islands fed primarily on walleye pollock (*Theragra chalcogramma*) or Atka mackerel (*Pleurogrammus monopterygius*) (Merrick et al. 1997; Sinclair and Zeppelin 2002). In contrast, the eastern Steller sea lion population, which was stable, retained a more diverse diet consisting of a higher proportion of fatty fishes such as Pacific herring (*Clupea pallasi*) and Pacific sandlance (*Ammodytes hexapterus*) (A.W. Trites and D.G. Calkins, unpublished data). The relatively high abundance of pollock in the area of decline compared with other prey species may have resulted in shorter maternal feeding trips. It may also not have been energetically feasible for females to seek out scarce prey. In contrast, the eastern population of Steller sea lions may not have encountered a high abundance of any one type of prey, resulting in longer search periods and a wider variety of prey in their diets.

Dietary differences between the western and eastern Steller sea lions may be a key factor in explaining the population decline. Recent evidence suggests that the declines in the Gulf of Alaska and Aleutian Islands could have been related to the quality and diversity of prey that Steller sea lions consumed (Alverson 1992; Merrick et al. 1997; Trites and Donnelly 2003). The sharpest population declines occurred in areas where diet was the least diverse (Merrick et al. 1997) and contained the lowest net energy content (Winship and Trites 2003).

Alverson (1992) has suggested that the Steller sea lions declined because they ate too much pollock and not enough of the fattier fishes such as herring and sandlance. This has been referred to as the “junk food” hypothesis. The caloric value of pollock is lower than that of fattier fishes and nutritional quality of pollock may adversely affect the health of pinnipeds if consumed in large quantities (Geraci 1975; Thompson et al. 1998; Rosen and Trites 2000). Bioenergetic modelling suggests that young growing sea lions may not be physically capable of meeting their energetic needs if they consume predominately pollock, unlike mature individuals that require proportionally less energy (Winship et al. 2002). The shorter maternal feeding trips in the area of decline suggest that lactating females may have simply been filling up on an abundant but nutritionally inferior prey (pollock) close to shore. Thus, our observations suggest that this age class of Stellers sea lions was likely able to meet its energetic needs by consuming more of the low-energy prey and did not experience an acute nutritional insult.

In addition to the shorter feeding trips, we also observed longer perinatal periods in the area of decline. This suggests that female Steller sea lions had more energy reserves for fasting in the declining area at the onset of parturition than females in the stable area, which is consistent with the finding by Ono et al. (1987) that female California sea lions exhibited shorter perinatal periods during the prey shortage caused by the 1983 El Niño. Physical condition of females during the perinatal period may thus reflect prey availability in winter or spring rather than summer feeding conditions near the rookeries.

Compared with the stable area, females in the area of decline spent more time suckling their pups during daylight observations (Milette 1999). Longer visits in the area of decline suggest that females returned from foraging trips satiated and with sufficient energy reserves to suckle their young and meet their own metabolic needs. Thus, the length of shore visits also suggests that lactating Steller sea lions in the declining population were not nutritionally stressed during the summer breeding season. However, we cannot draw conclusions from our data about other age groups, such as juvenile sea lions.

Contrasting the behavioural ecology of Steller sea lions from the declining population with that of the stable population is a valid means of assessing the potential causes of the population decline. However, the relevant tests and hypotheses that we propose are not necessarily simple and clear-cut. Our main premise that foraging durations should have been greater in declining populations if food limitation was the cause of the decline was heavily influenced by the extreme situations observed during strong El Niño events. In our view, this is parallel to the conditions that overfishing might cause.

An alternative explanation for the population decline is that young Steller sea lions in the Gulf of Alaska and Bering Sea experienced chronic nutritional stress (i.e., 20–30 years duration) rather than an acute nutritional insult (i.e., 1–3 years) that is related to a natural change in the ecosystem that reduced quality of prey rather than decreased quantity of prey consumed (see Benson and Trites 2002; Trites and Donnelly 2003). Such a possibility is consistent with our findings.

Temporal patterns

Maternal attendance patterns at both the declining and stable sites were similar between years. An intriguing observation was that perinatal periods, feeding trips, and visits ashore were shorter in 1994 than in 1995 (Fig. 2). Interannual similarities in Steller sea lion attendance behaviour between the two study sites may reflect large-scale changes in prey availability in the North Pacific Ocean. Longer feeding trips in 1995 suggest that prey were more difficult to obtain in 1995 compared with 1994. However, there was no apparent difference in the relative makeup of species in the summer diets in southeast Alaska during this time (A.W. Trites and D.G. Calkins, unpublished data). The longer perinatal periods in 1995 may reflect better winter feeding conditions such that females would have returned to the summer breeding islands in better physical condition. Such possibilities underline the need to conduct future research on maternal attendance patterns in parallel with prey abundance studies during the winter and summer seasons. This will help to determine potential correlations between prey abundance and the duration of perinatal periods and feeding trips.

Changes in the length of foraging trips

Maternal attendance patterns over the 2-month breeding season appeared to be similar at both sites. We found that the length of maternal foraging trips increased over the breeding season as pups grew older. Increases in foraging trips as pups age have been reported for the Steller sea lion, northern fur seal, Antarctic fur seal, California sea lion, Galápagos sea lion (*Zalophus californianus wollebaeki*), Cape fur seal (*Arctocephalus pucillus*), and South American fur seal (Peterson and Bartholomew 1967; Boness et al. 1985; David and Rand 1986; Doidge et al. 1986; Gentry and Holt 1986;

Trillmich 1986; P. Majluf, personal communication in Oftedal 1987; Higgins et al. 1988; Boyd et al. 1991). Only Melin (1995) failed to find a change in the length of foraging trips of California sea lions over the lactation period. The seasonal increase in foraging trip lengths is probably related to the increasing nutritional demands of the growing pup over time. Milk transfer measurements confirm that both larger and older otariid pups consume more milk than smaller and younger ones (Costa and Gentry 1986; Gentry and Holt 1986; Higgins et al. 1988).

Changes in the length of visits ashore

Our study showed that the duration of shore visits decreased as the pup grew older. This is consistent with results from some studies, but differs with others. For example, Higgins et al. (1988) found that shore visits remained constant as Steller sea lion pups grew older at Año Nuevo Island in California. The constancy of shore visits was also reported for northern fur seals and California sea lions (Gentry and Holt 1986; Melin 1995). In contrast, Antarctic fur seals increased the duration of shore visits over the season (Doidge et al. 1986; Boyd et al. 1991), whereas Cape fur seals decreased their time ashore from the first to second month following parturition (David and Rand 1986). Higgins et al. (1988) speculated that the unvarying duration of shore visits of the Steller sea lions that they observed reflected the time needed for females to rest rather than the increasing nutritional demands of their growing pups. Thus, a mother's resting time may be flexible depending on environmental conditions such as prey availability and location.

If longer foraging trips are insufficient to meet both the mother's metabolic needs and the increased nutritional demands of her pup, mothers may end up resting progressively less during shore visits and forage more frequently to meet nutritional needs. Less time spent on shore should not interfere with the ability of the mother to nurse her pup because pups increase their suckling efficiency as they grow (Higgins et al. 1988) and spend approximately 2 h suckling for each maternal foraging–attendance cycle (trip to sea and subsequent visit ashore; Milette 1999). Therefore, under certain environmental conditions, a decreasing trend in shore visits as pups age may reflect increased suckling efficiency. This speculation is consistent with that posed by David and Rand (1986), who suggested that Cape fur seal mothers might decrease their time on shore as pups age to meet the increasing nutritional demands of their pups. However, Doidge et al. (1986) hypothesized that Antarctic fur seals spent more time on shore as pups aged because wandering pups caused mothers and pups to reunite less quickly over time. Such differences in findings suggest that maternal shore visits are flexible. Increases or decreases in the time spent on shore as pups grow older probably depend on the prey availability, behaviour of the pups, or the terrain of a rookery.

Early shore visits (after the initial feeding trip) when pups were 5–9 days old were significantly longer than subsequent visits in the area of decline and longer than in the stable area. Longer perinatal periods and shore visits when pups are very young may explain why pups in the area of decline were heavier (Merrick et al. 1995) and grew faster (Brandon 2000) than in Southeast Alaska. Shorter foraging trips also mean that pups will fast for shorter intervals between feedings. Good physical condition may also enable mothers to fast longer on shore with their pups after returning from their first feeding trip.

Conclusions

Based on the responses of other pinniped populations during periods of prey reduction, our results suggest that lactating Steller sea lions in the area of population decline were not food-limited during the summer breeding season. Longer perinatal periods, shorter foraging trips, and longer shore visits are inconsistent with the food-limitation hypothesis. Longer perinatal periods in the area of decline may be linked to feeding conditions during the winter or spring rather than summer feeding conditions. Further research is needed to confirm whether the differences in attendance cycles between the stable and declining populations of Alaskan Steller sea lions reflect differences in age structure, distances to forage locations, or differences in the types and relative abundance of prey available.

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