

DEVELOPMENT OF DISPERSAL, MOVEMENT
PATTERNS, AND HAUL-OUT USE BY PUP
AND JUVENILE STELLER SEA LIONS
(*EUMETOPIAS JUBATUS*) IN ALASKA

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ABSTRACT

Population declines of Steller sea lions (*Eumetopias jubatus*) in western Alaska (west of 144°W) may be a result of reduced juvenile survival. We used satellite telemetry to study the at-sea distribution and movement patterns of pup (1.6–11.9 mo) and juvenile (12.0–35.1 mo) Steller sea lions. We studied trip distance, duration, and interhaul-out movements of sea lions in relation to age, sex, and month of year in the decreasing western population (WP; Prince William Sound, Kodiak, Aleutian Islands, Alaska) and the increasing eastern population (EP; Southeast Alaska). We deployed 103 satellite transmitters (29 WP; 74 EP) on sea lions between 1998 and 2001. Round trip distance and duration increased with age, trip distance was greater in the WP than the EP, trip duration was greater for females than males, and haul-out use was clustered. Changes in round trip distance and duration occurred from April to June for all age classes studied indicating that the annual timing of weaning may be less variable than the age of weaning. Overall, 90% of round trips were ≤ 15 km from haul-outs and 84% were <20 h, indicating nearshore areas adjacent to haul-outs are critical to the developing juvenile.

Key words: Steller sea lion, *Eumetopias jubatus*, satellite telemetry, dispersal, distribution, animal movements, Alaska, endangered.

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Studies of dispersal, at-sea distribution, and movement patterns of juveniles can play a critical role in understanding pinniped behavior (Merrick and Loughlin 1997, Burns and Castellini 1998, Burns *et al.* 1999, McConnell *et al.* 2002). Knowledge of pinniped behavior ultimately leads to information regarding survival and its affect on the population growth of the species (Eberhardt and Siniff 1977, York 1994, Craig and Ragen 1999, Hastings *et al.* 1999). Whereas the primary focus of juvenile pinniped studies has been on dive behavior (Burns and Testa 1997, Horning and Trillmich 1997, Bowen *et al.* 1999, Burns *et al.* 1999, Baker and Donohue 2000), information regarding at-sea distribution and movements, particularly for otariids, is lacking.

Post-breeding dispersal patterns of pinniped pups may reveal important information regarding localized prey resources and predators. In most species juveniles are more prone to dispersal than adults (Greenwood 1980). For example, the rapid, directed dispersal of weaned southern elephant seal (*Mirounga leonina*) pups from their natal site was attributed to insufficient local prey density and avoidance of predation by killer whales, *Orcinus orca* (Guinet *et al.* 1992, McConnell *et al.* 2002). Similarly, weaned Weddell seal (*Leptonychotes weddellii*) pups moved away from breeding areas earlier than adult females, suggesting they avoided areas of low prey abundance surrounding breeding areas where adults congregate (Testa *et al.* 1985, Castellini *et al.* 1992, Burns *et al.* 1999).

The development of movement patterns with age is important in understanding individual foraging patterns and how those patterns may be influenced by the availability of prey resources. In a non-migratory species, the availability and predictability of prey patches is crucial to survival. Significant reductions in prey availability during events such as El Niño Southern Oscillations can have overwhelming effects on pinniped survival (DeLong and Antonelis 1991, Trillmich and Dellinger 1991). If localized prey resources are depleted, young pinnipeds, who may be more food-limited by changes in prey distribution (Merrick and Loughlin 1997), may not have the knowledge or diving capacity to forage successfully. For example, in juvenile Hawaiian monk seals, *Monachus schauinslandi*, the proximate cause of low survival may not be the lack of suitable prey, but rather inadequate foraging skills resulting in starvation (Craig and Ragen 1999).

Understanding the geographical relationships between pinniped terrestrial and aquatic phases of life is essential in assessing the distribution and intensity of foraging (McConnell *et al.* 1999). As central place foragers (Orians and Pearson 1979), pinnipeds must develop foraging skills within a range limited by their swimming ability and their access to terrestrial breeding and resting sites. One potential strategy is to minimize travel time between foraging areas and haul-out sites. The use of several central place haul-out sites, or a multiple central place foraging strategy (McLaughlin and Montgomerie 1989) reduces overall travel costs while still providing access to foraging areas. The use of these sites may depend upon seasonal resource availability, conspecific competition, fisheries competition, and predators. Ultimately, these areas may be critical to the survival of the developing juvenile.

Steller sea lions, *Eumetopias jubatus*, in the North Pacific exemplify the case of a long-lived species in which dramatic population declines are thought to result from reduced juvenile survival (Pascual and Adkison 1994, York 1994). Extremely low sightings of branded Steller sea lion (SSL) pups in the WP during the mid-1980s also support these findings (Chumbley *et al.* 1997, Raum-Suryan *et al.* 2002). SSL pups are born from late May to early July, with the peak

of pupping occurring in June (Pike and Maxwell 1958, Mathisen *et al.* 1962, Gentry 1970, Pitcher and Calkins 1981, Pitcher *et al.* 2002). Pups first enter the water 2–4 wk after birth (Sandegren 1970) and once 2–3 mo old, begin to disperse from the rookery (Calkins and Pitcher 1982, Merrick *et al.* 1988). As juveniles, they tend to disperse widely, but when they reach adulthood, generally remain within about 500 km of their natal rookery (Raum-Suryan *et al.* 2002). Since the 1970s, the genetically distinct western population (WP) (pups born west of Cape Suckling, Alaska, 144°W; Prince William Sound west to Russia) has declined by over 80% (Loughlin *et al.* 1992, Trites and Larkin 1996, Sease *et al.* 2001) resulting in its status as “endangered.” While causes of the decline are unknown, one prominent hypothesis is that of reduced prey availability (either by environmental changes, commercial fishing activities, or both) resulting in nutritional stress (Loughlin and Merrick 1989, Merrick 1995). In contrast to the declining WP, the Southeast Alaska portion of the eastern population (EP) (pups born east of Cape Suckling; Southeast Alaska to California) (Bickham *et al.* 1996, 1998; Loughlin 1997) has increased to near historic levels (Calkins *et al.* 1999, Sease *et al.* 2001). Due to the low interchange of breeding adults between stocks (Bickham *et al.* 1996, Raum-Suryan *et al.* 2002), it is unlikely that SSLs from the EP could repopulate the WP.

Factors affecting the at-sea distribution of young sea lions are important in evaluating the potential competitive interaction that has been suggested between commercial fisheries and SSLs (Alverson 1992, Fritz and Ferrero 1998). Without information on at-sea behavior, it is difficult to evaluate whether prey limitation is a factor in the recent decline of the SSL. Confounding our understanding of juvenile movements is the variability in lactation length; juveniles may wean from one to three years of age (Gentry 1970, Sandegren 1970, Calkins and Pitcher 1982). Until recently very little information existed on SSL pup and juvenile age classes once they left the rookery (Merrick and Loughlin 1997, Baba *et al.* 2000, Loughlin *et al.* 2003). Using satellite telemetry, Merrick and Loughlin (1997) concluded that the foraging ability of five juvenile SSLs developed throughout the first year of life, with animals making relatively short at-sea trips. Baba *et al.* (2000) provided location information for one yearling that traveled within the coastal waters of the Okhotsk Sea and the Sea of Japan during winter. A study conducted by Loughlin *et al.* (2003) on 13 young-of-the-year and 12 yearling SSLs revealed that by the time young SSLs had reached one year of age, they appeared to be as capable as adults in their movement and dive behavior. These studies provided an important preliminary understanding of juvenile SSL foraging behavior, but were based on small sample sizes, ages ≥ 5 mo, and did not include any pups or juveniles from the increasing Southeast Alaska population.

An improved understanding of pup and juvenile SSL natal rookery dispersal, at-sea movements, and haul-out use is critical in determining ecological factors affecting the success of these age classes. We studied movements of pup (1.6–11.9 mo) and juvenile (12.0–35.1 mo) SSLs in an increasing and decreasing population to determine if behavioral differences might help explain the divergent trends of these two populations. We compare trips of sea lions in this study with the results of previous SSL studies (Merrick and Loughlin 1997, Loughlin *et al.* 2003). Our specific objectives were to describe pup dispersal from natal rookeries, determine if round trip distance and duration varied significantly with age, sex, month, or population, and to determine the source of variability in interhaul-out movements and haul-out use.

Table 1. Deployment of SDRs on male (M) and female (F) Steller sea lion pups (1.6–11.9 mo) and juveniles (12.0–35.1 mo) in the western and eastern populations (SEA indicates Southeast Alaska) in Alaska.

Region	Capture	Number SDRs				Deployment duration (d)
		Pups		Juveniles		
		M	F	M	F	mean (range)
Western Population						
Prince William Sound	April 2000	4	4	0	2	46.9 (10–77)
Prince William Sound	Aug. 2000	0	0	1	3	67.8 (51–103)
Kodiak Island	March 2001	1	2	0	0	87.7 (59–106)
E. Aleutian Islands	Sept. 2001	0	2	0	0	29.0 (29)
Prince William Sound	Nov. 2001	1	4	3	2	110.8 (36–144) ^a
Eastern Population						
Central SEA	March 1998	7	5	0	0	81.8 (30–143)
Southern SEA	July 1998	3	7	0	0	21.3 (11–34)
Northern SEA	Nov. 1998	5	5	0	0	44.7 (12–119)
Central SEA	Aug. 1999	4	6	0	0	5.7 (3–13)
Northern SEA	Jan. 2000	2	5	2	1	101.1 (60–181)
Central SEA	Sept. 2000	0	0	3	2	143.6 (82–190)
Central & Northern SEA	May 2001	4	4	4	2	59.5 (25–91)
Central SEA	Aug. 2001	0	0	2	1	109.3 (68–184)

^a Five SDRs were still transmitting at time of analysis, therefore, average and maximum durations were based upon a cutoff date of March 2002.

METHODS

Captures

We captured SSL pups (1.6–11.9 mo) and juveniles (12.0–35.1 mo) at six locations in the WP (Prince William Sound, Kodiak Island, Eastern Aleutian Islands) and 10 locations in the EP (Southeast Alaska; Table 1, Fig. 1). Age was estimated using tooth eruption patterns, mass, standard length, girth (Alaska Dept. Fish and Game, unpublished data) and a mean calendar birthdate of 155.4 d (95% CI: 154.6, 156.2) for the EP of Southeast Alaska and 165.6 d (95% CI: 163.7, 167.6) for the WP (Pitcher *et al.* 2001).

SSLs were captured near or on a haul-out using either SCUBA divers and an underwater noosing technique² or hoop nets on land. The divers used a pole baited with herring (*Clupea harengus*) to entice the animal to stretch through a noose, suspended on a second pole, which was then cinched around the neck. The sea lion was then secured and placed into an aluminum capture box in a 6.1- or 6.7-m skiff.

When sea conditions prevented underwater captures, sea lions were captured on shore with hoop nets (17% of all captures). All captured sea lions were transported to the research vessel, immobilized with gas anesthesia (Heath *et al.* 1997), weighed to the nearest 0.1 kg, length measured to the nearest 0.5 cm, and telemetry devices attached. Satellite tags (Type ST-6, ST-10, and SDR-T16; Wildlife Computers,

² Unpublished report. D. McAllister. 1998. An operational dive plan for in-the-water Steller sea lion captures. Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Rd., Anchorage, AK 99518.

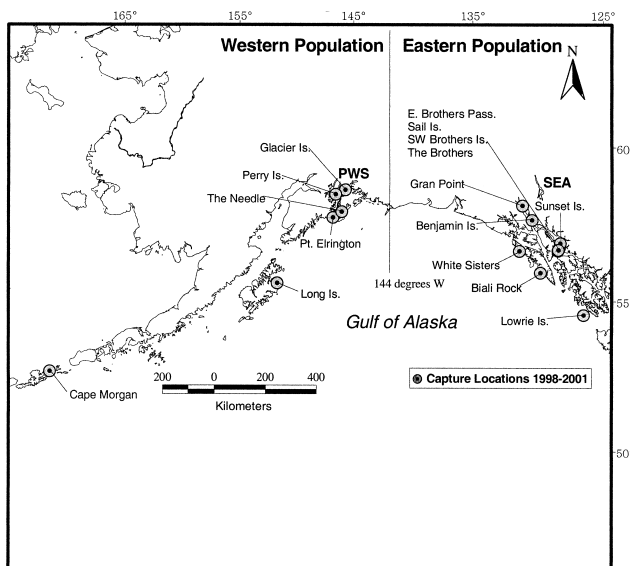


Figure 1. Locations of haul-outs and rookeries where pup and juvenile Steller sea lions were captured in the western population ($n=6$) and eastern population ($n=10$) between March 1998 and November 2001. PWS refers to Prince William Sound and SEA to Southeast Alaska.

Redmond, WA), were glued to the pelage with fast-setting epoxy (TitanTM epoxy #332, DevconTM 5-min, or 10-min epoxy) along the midline of the back with the leading edge of the SDR even with the leading edge of the front flipper. All sea lions were released near the capture site after recovery from anesthesia (2–6 h after initial capture).

Satellite Telemetry

SDRs relayed time on-land/at-sea, position, and diving behavior. SDRs were duty cycled one day on/one day off ($n = 14$, 1998; $n = 29$, 2000) or not duty cycled ($n = 18$, 1998; $n = 10$, 1999; $n = 32$, 2001). To distribute transmissions throughout the day and limit transmissions to hours when satellites were most likely in view we programmed SDRs prior to each capture trip to transmit during “best” (variable from 1998 to 2001 as new satellites became available) hours of transmission coverage. Although no location positions were received during “off” days, timeline data continued to be stored and was available to calculate trip duration for all animals.

Location Error

SDR transmissions and position at the time of transmission were received by the Argos satellite system. We tested for location errors by obtaining simultaneous global positioning system (GPS) locations and Argos locations. Our location error estimates were greater than those reported by Argos (Table 2), however we found that the mean error for class A (mean = 1,454, SE = 369) was less than that of class

Table 2. Estimated accuracy of Argos location class qualities compared to those we estimated from SDRs ($n = 10$) transmitting while docked using ship's global positioning system (GPS) receiver.

Location Class (Quality)	Argos predicted accuracy (m)	Test accuracy (m)			
		n	Mean	SE	Range
3	<150	7	254	39	100–393
2	150–350	13	634	277	21–3851
1	350–1000	17	1393	285	200–4447
0	>1000	7	1728	389	395–2684
A	No estimate	20	1454	369	100–6382

0 (mean = 1,728, SE = 389), and therefore retained class A locations in our analyses. Other investigators (Brothers *et al.* 1998, Britten *et al.* 1999, Vincent *et al.* 2002) also reported location class A errors to be less than location class 0.

To remove poor quality locations, we filtered our data using a three-step process. First, we used SATPAK software (Wildlife Computers, Inc. 2000) to decode and format the data provided by Service Argos and then deleted location class Z (invalid locations) and location class B (unacceptable error) from the data. Second, we imposed a swim speed filter of ≤ 10 km/h (based on Merrick and Loughlin 1997) on all at-sea locations to ensure that the distances between sequential locations were possible given a sea lion's swim speed. Lastly, to delete locations that passed through the swim speed filter due to a large time interval between location fixes, we computed the Keating error index (Keating 1994) for at-sea locations and deleted those with an index value of >25 . This index value was previously used for harbor seals (*Phoca vitulina*) in Prince William Sound, Alaska (Lowry *et al.* 2001).

Data Analysis

We determined whether animals were on land or at sea during each location estimate by using the wet/dry state indicator present within the several transmissions used to make up each Argos location. We analyzed round trips (to and from the same haul-out site) with at least three at-sea locations per trip. Straight-line maximum round-trip distance from the haul-out was computed using the Great Circle Distance calculation (Bowditch 1995). Additionally, for long-distance movements where trips intersected land, nearest over-water distance was measured interactively using ArcView software (ESRI, Inc. Redlands, CA) with data on the local Universal Transverse Mercator projection to minimize distance measurement error. Timeline data were stored continuously for all individuals even while transmissions that would relay a position fix were absent. Therefore, sample size for trip duration was greater than that for distance data.

We used mixed effects linear models (Littell *et al.* 1996) to investigate the relationships between the response variables (round trip distance and duration, and interhaul-out distance) and predictor variables age, sex, population, and month. In these analyses, we used the natural logarithm of the response and the natural logarithm of age. This ln-ln analysis assumes an underlying nonlinear relationship of the form $y = \beta_0 * x_1^\beta$ where y is the response variable, x is the predictor, and the β s are the regression coefficients. Analyzing the ln-response also has the effect that we are predicting the geometric mean response rather than predicting the

arithmetic mean response as would occur with analysis on the original scale; the transformation also yields more symmetric residuals than would occur with the skewed distribution of the untransformed data. Ln-age, sex, population, month, and their interactions were included in the models as fixed effects; no interactions that included both ln-age and month were included because of the confounding of these variables within animals. To account for the potential lack of independence of the observations caused by using repeated responses from individual animals, the individual animal was included as a random effect in the analyses (*i.e.*, variation among animals, rather than among observations, was used in computing standard errors of estimates) (Littell *et al.* 1996). Autocorrelation of responses within animals was modeled as a spatial process with the "distance" between observations a function of elapsed time (Littell *et al.* 1996). In some analyses, the autocorrelation was estimated to be 0; we then only included the animal random effect. Initially, we included all predictor variables in the models and eliminated predictors one-at-a-time based on Wald F statistics. We continued this process until only important (Wald *p*-value < ~ 0.05) predictors remained. Lower order effects with large *p*-values were retained in final models when they were contained in higher order interactions that had small *p*-values. Marginal means (*i.e.*, SAS least-squares means; Littell *et al.* 1996) were estimated for categorical effects retained in final models and for ln-differences (*i.e.*, effect sizes) between these means. Estimated means and effect sizes, and their confidence intervals, were transformed back to the original response scale; the transformed means are geometric means, and the effect sizes are ratios of the mean responses. We used a similar analysis to examine the relationship between round trip distance and duration.

We tested whether the number of haul-outs used by pup and juvenile sea lions varied by age, sex, and population using a generalized linear model (Poisson error, log link; Littell *et al.* 1996). To account for differing sampling intensities, the length of time a transmitter was attached and functioning also was used as an explanatory variable.

We used nearest neighbor (*i.e.*, single linkage) clustering, which defines the distance between clusters as the shortest distance between any points in the two clusters (Kaufman and Rousseeuw 1990) to group haul-outs used by at least one SDR equipped sea lion based on the shortest distance over water between them. This method is related to construction of minimal spanning trees and is appropriate for the movement of sea lions from one haul-out to the next in a chain manner. We examined the usage-distance relationship in PWS and SEA by plotting the distance between pairs of haul-outs and the number of sea lions using both sites. Additionally, we used nearest neighbor cluster analysis with the "distance" between haul-outs defined as the number of SDR equipped sea lions using both haul-outs. We did this to determine if haul-out use patterns were affected by factors other than the distance between the two sites (*e.g.*, haul-out size, sea lion capture location).

RESULTS

Deployments

We deployed 103 SDRs (74 EP, 29 WP) on pup (1.6–11.9 mo; $n = 75$) and juvenile (12.0–35.1 mo; $n = 28$) SSLs (46 male, 57 female) between March 1998 and November 2001 (Table 1). Length of deployment per SDR averaged $66 \text{ d} \pm 4.6$ overall, $75 \text{ d} \pm 7.9$ in the WP and $62 \text{ d} \pm 5.6$ in the EP for a total of 6,761

deployment days. Five SDRs were still transmitting at time of analysis; therefore, average and maximum deployment durations were based upon a cutoff date of 31 March 2002. Sea lions were tracked during most months of the year from March 1998 through March 2002 (excluding September–October 1998 and April–July 1999). Data from pups <5 mo-of-age and juveniles 14–17 mo-of-age were limited because of short retention of instruments during the annual molting period of August through November.

Of the 29,375 locations received from Argos, 9,751 were at-sea locations that fell within the trips determined from the timeline and wet/dry state data. Of these, we retained 68% ($n = 6632$, Fig. 2, 3) for analyses after filtering. The percentages of each Argos at-sea location quality category after filtering were: class 3, 4%, class 2, 10%, class 1, 30%, class 0, 33%, and class A, 23%. We received an average of 3.0 ± 0.13 at-sea locations/animal/day pre-edit (classes A, 0–3) and 2.3 ± 0.09 at-sea locations/animal/day post-edit (classes A, 0–3).

Dispersal

Of the ten SDRs we deployed on molting pups at White Sisters rookery (EP) in August of 1999, two pups dispersed (presumably with their mothers) within 2.5 mo after birth (the other eight transmitters molted off within a week of deployment). One pup dispersed 76 km north to Graves Rocks rookery and another pup dispersed 120 km southeast to Biali Rocks haul-out (Fig. 3).

In addition to the interhaul-out movements of animals within populations, a 19-mo-old male moved between the breeding range of the eastern and western populations. This individual was tagged in January at Benjamin Island and remained at two haul-out sites (within 67 km of each other) for 3.5 mo before traveling from the EP to the WP, a trip of approximately 1,300 km in 48 d with stops at a minimum of five haul-outs along the way. Another individual (a 9-mo-old male) tagged in March near Kodiak Island (WP) traveled 500 km toward the EP before the transmitter failed in early June. Besides these long-range, east-west movements, a 9-mo-old male traveled south from Frederick Sound in May to the northern Queen Charlotte Islands, British Columbia, before traveling north to Lowrie Island rookery in June, a total interhaul-out trip length of approximately 840 km. These movements may represent postweaning dispersal.

Round trips

Overall, 90% of pup and juvenile round trips (departure and return to the same haul-out, $n = 857$) were ≤ 15 km and 84% were ≤ 20 h (Fig. 4a, b), indicating that pups and juveniles did not travel far nor spend long periods of time at sea when using a particular haul-out site. SSL at-sea locations were primarily concentrated adjacent to haul-outs and nearshore in the WP (Fig. 2) and EP (Fig. 3). Round trips >15 km and >20 h were completed only by animals 9 mo and older. Maximum ($n = 77$) trip distance ranged from 1.2 to 111.0 km. Trip distance increased significantly with trip duration ($F_{1,802} = 402.9$, $P < 0.0001$), but at different rates in each population. Distance increased faster with increasing duration in the EP than in the WP ($F_{1,294} = 18.6$, $P < 0.0001$). Sex had no effect on the relationship between distance and duration and was therefore removed from the final model. There was no obvious pattern (*i.e.*, long trips preceded by short trips, repeated long or short trips) in the temporal distribution of movement types nor between males and females.

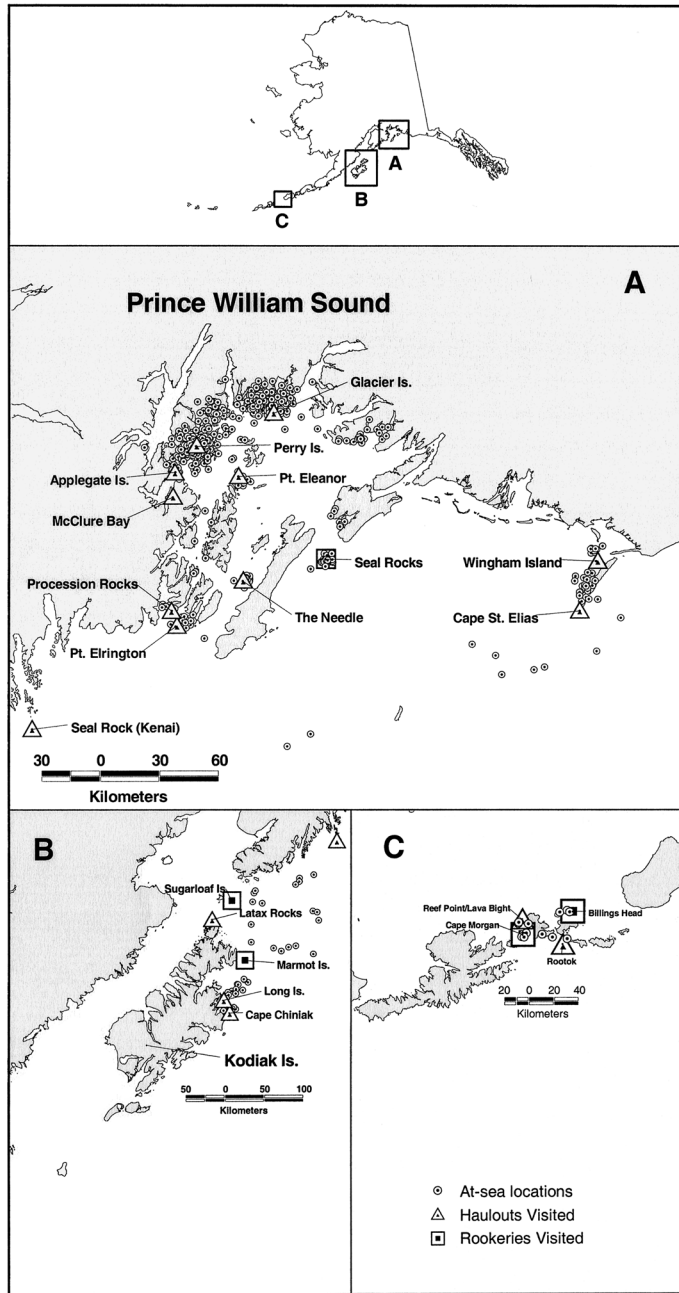


Figure 2. Filtered at-sea locations, rookeries, and additional haul-outs visited by pup and juvenile Steller sea lions (April 2000–March 2002) in the western population regions of a) Prince William Sound, b) Kodiak, and c) eastern Aleutian Islands.

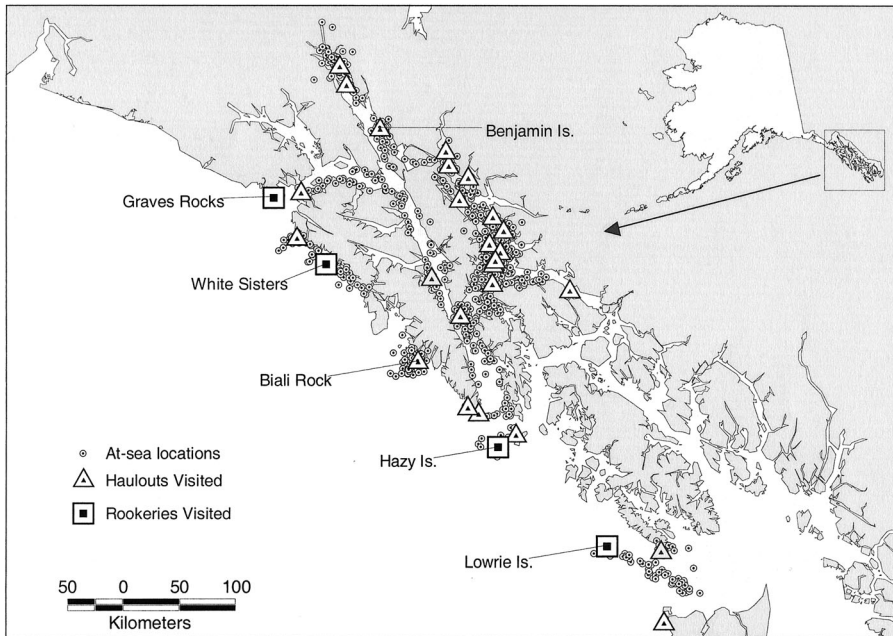


Figure 3. Filtered at-sea locations, rookeries, and additional haul-outs visited by pup and juvenile Steller sea lions in the eastern population region of Southeast Alaska (March 1998–February 2002).

There was a slight significant geometric mean trip distance increase with age ($F_{1,70} = 3.67$, $P = 0.059$). Moreover, there appeared to be a marked increase in trip distance once animals reached about 10-mo-of-age (Fig. 5). Geometric mean trip distance was significantly greater in the WP (mean = 6.5 km, 95% CI: 5.08, 8.26) than in the EP (mean = 4.7 km, 95% CI: 3.92, 5.53) ($F_{1,69} = 4.89$, $P < 0.030$; Fig. 5) and was influenced by month with greater trip distances from April to June and again in October than during other months of the year ($F_{11,213} = 2.62$, $P < 0.004$; Fig. 6). Sex did not appear to have a significant effect on trip distance and was therefore removed from the final model.

Trip duration also increased with age ($F_{1,157} = 52.5$, $P < 0.0001$; Table 3). Again, there was a noticeable increase in trip duration once animals reached about 10 mo-of-age (Fig. 7). Females had a significantly greater geometric mean trip duration (mean = 2.7 h, 95% CI: 2.37, 3.03) than males (mean = 2.2 h, 95% CI: 1.91, 2.52) ($F_{1,91} = 4.71$, $P = 0.0326$; Table 3, Fig. 7) but the effects of sex and population on trip duration varied by month of year (Table 3, Fig. 8a, b).

Interhaul-out Movements

Month was the only factor that influenced interhaul-out distance ($F_{11,124} = 3.29$, $P = 0.0005$) with a noticeable increase in distance moved during July and less so in August (Fig. 9). Some spring and summer movement can be attributed to dependent juveniles traveling from haul-outs back to rookeries in the late spring

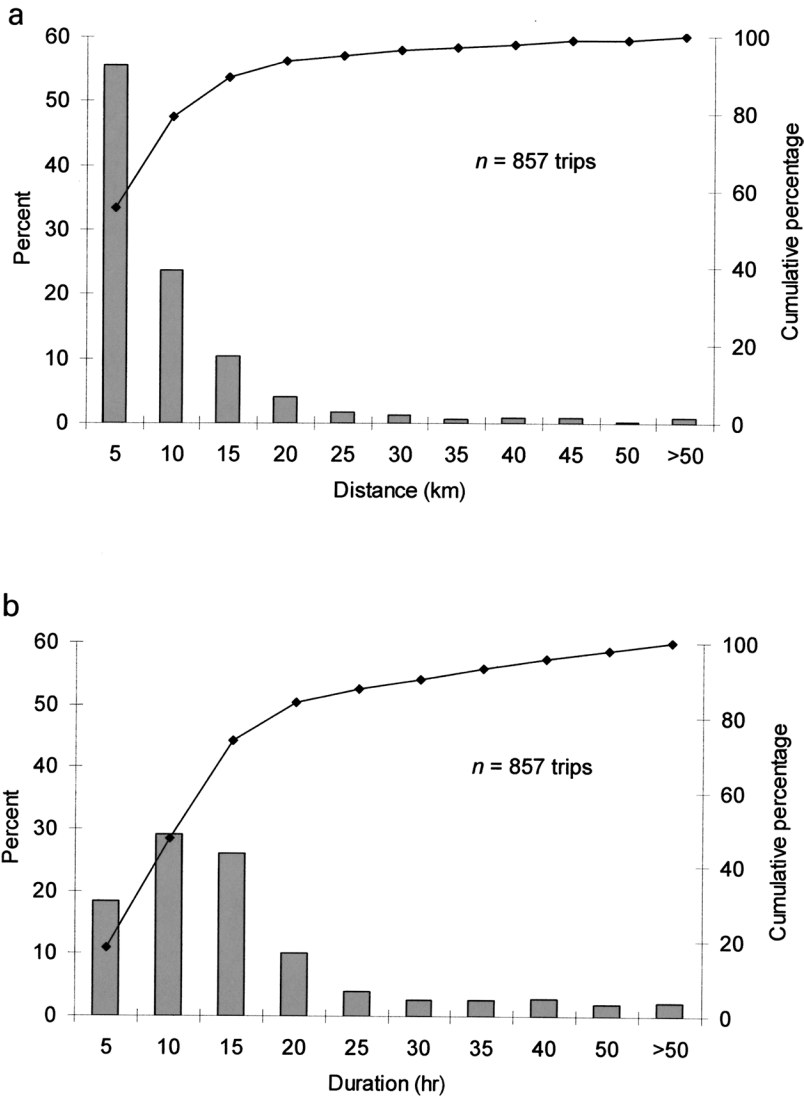


Figure 4. Percent of overall pup and juvenile Steller sea lion round trips ($n = 857$) in relation to a) distance (km) from haul-out and b) duration (h) of trip.

and early summer. For example, of the 14 sea lions captured during May 2001, six (46%) moved 170 km from haul-outs in Frederick Sound to Hazy Island rookery. Four other juveniles also returned to rookeries during April–June. The average interhaul-out distance per sea lion for individuals using >2 haul-outs ($n = 53$) was $79.3 \text{ km} \pm 7.73$. Based on sea lion ($n = 27$) trip duration between haul-outs, interhaul-out swim speed was estimated at $2.82 \text{ km/h} \pm 0.31$ (range: 0.4–6.05 km/h) and sea lions ($n = 27$) traveled a maximum interhaul-out distance of 127 km within a 24-h period.

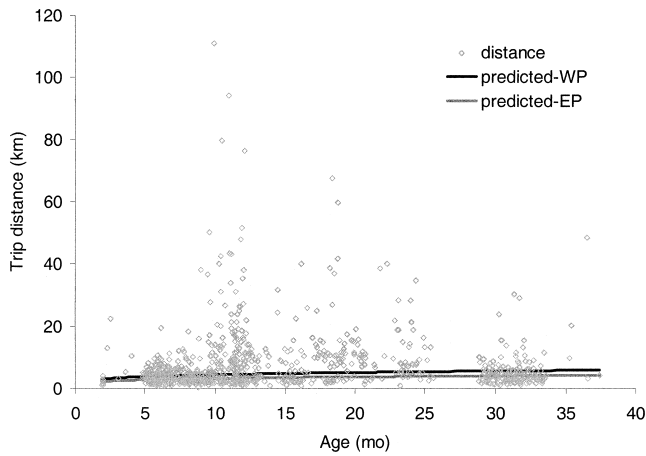


Figure 5. Round trip distance (km) from haul-out in relation to age (mo) for pup and juvenile Steller sea lions from the western population (WP) and eastern population (EP).

Haul-out Use

Fifty-one different haul-out and rookery sites (hereafter referred to as haul-outs) were used during this study, 30 in the EP and 21 in the WP (Fig. 2, 3). In the EP, the number of haul-outs used by a sea lion was a function of the length of time the transmitter was attached, which was not the case for the WP. After correcting for transmitter attachment duration, sea lions in the EP used 28.6% more haul-outs on average (mean = 2.1 haul-outs, 95% CI: 1.9, 2.4) than sea lions in the WP (mean = 1.6 haul-outs, 95% CI: 1.3, 2.1) ($F_{1,99} = 8.02$, $P = 0.0056$). Sex had no effect on number of haul-outs used.

On an individual basis, 48% ($n = 49$) of sea lions used one haul-out during their entire deployment period (mean = 46.7 d, SE = 6.1), whereas 52% ($n = 54$) used

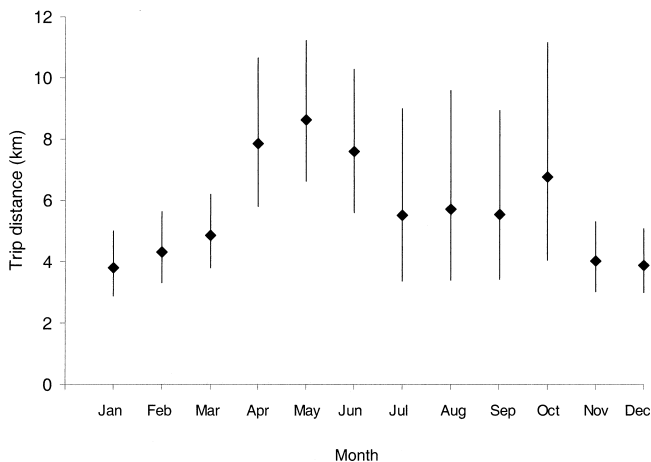


Figure 6. Geometric mean round trip distance (km) for pup and juvenile Steller sea lions by month of year. Error bars indicate confidence intervals.

Table 3. Summary of mixed effects linear model to investigate the relationship of sea lion ($n = 103$) trip duration with age (ln transformed), sex, population, and month. Presented are main effects retained in and those removed from the final model.

	df	F	P
<u>Effects retained</u>			
age	1,157	52.50	<0.0001
sex	1,91	4.71	0.0326
population	1,104	0.83	0.3643
month	11,1264	3.31	0.0002
sex*month	11,2397	3.14	0.0003
population*month	10,1282	2.75	0.0023
<u>Effects removed</u>			
age*sex	1,153	0.49	0.4838
age*population	1,125	0.80	0.3719
age*sex*population	1,108	1.65	0.2022
sex*population	1,97	2.32	0.1310
sex*population*month	10,1051	1.13	0.3344

two or more (SE = 0.2, range: 2–9) during their deployment period (mean = 82.8 d, SE = 5.9). Sea lions sometimes traveled among the same haul-outs multiple times. For example, one 3-yr-old male moved 16 times among six haul-outs in 91 d and a 2-yr-old female moved 12 times among four haul-outs in 82 d.

In Prince William Sound, the distance-based cluster analysis of haul-out use revealed that nine haul-outs clustered into two groups and one outlying site (Fig. 10). In general, most haul-outs used by the same individual sea lion were relatively close together (<70 km apart). However, individual sea lions did not necessarily use haul-outs that were the closest together. For example, no instrumented sea lion used both the Pt. Elrington and Procession Rocks haul-outs even though these were the closest pair of haul-outs in the sample (Fig. 10).

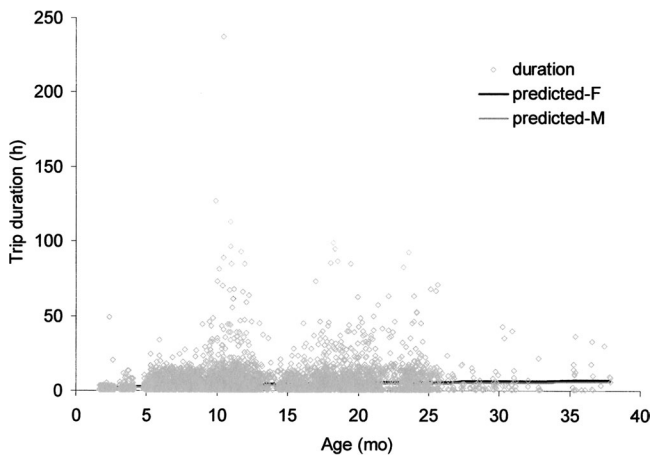


Figure 7. Round trip duration (km) in relation to age (mo) for female (F) and male (M) pup and juvenile Steller sea lions.

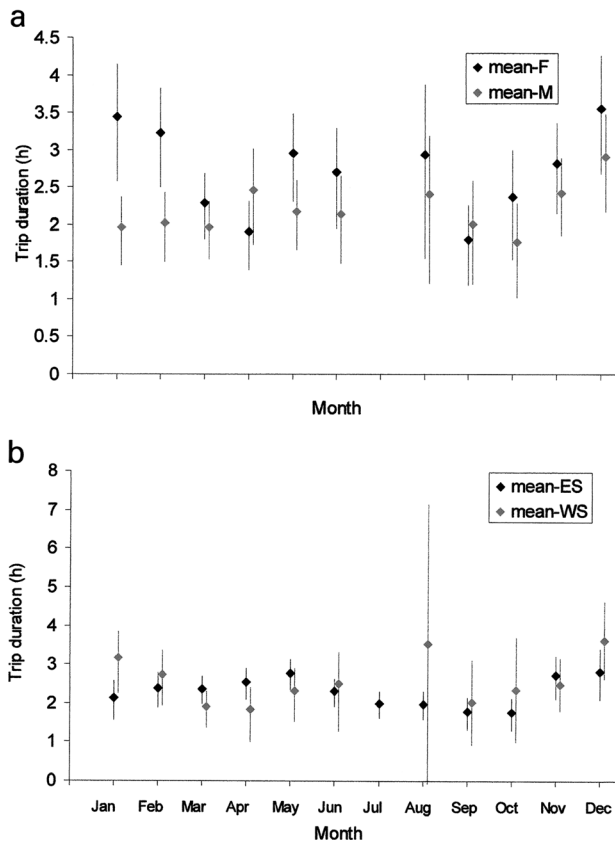


Figure 8. Geometric mean round trip duration (h) for pup and juvenile Steller sea lions by a) sex, and b) population (eastern population, EP; western population, WP) by month of year. Error bars indicate confidence intervals.

In Southeast Alaska, a larger sample of sea lions ($n = 74$) and haul-outs used ($n = 30$), indicated a more complex pattern of haul-out usage. Based on between haul-out distances, we identified six clusters of haul-outs and a number of isolated sites (Fig. 11a). The clusters were Frederick Sound (8–9 sites), Stephens Passage (3 sites), Lynn Canal (3 sites), Central Outer Coast (5 sites), Northern Outer Coast (4 sites), and Southern Outer Coast (3 sites) (Fig. 11a). The Frederick Sound and Stephens Passage clusters combined at a higher level with several of the isolated sites to form a Southern Inside Waters “meta-haul-out” (Fig. 11a). Similar to the PWS distance-usage results, there was a general pattern of decline in the likelihood of sea lions using two haul-outs as the distance between those haul-outs increases. The maximum distance between haul-outs with >1 SDR equipped sea lion in common was 450 km, but most sharing >1 sea lion were <250 km apart. However, the usage pattern in Southeast Alaska was again similar to Prince William Sound in that the closest pairs of haul-outs did not always have the greatest common usage (Fig. 11a). Haul-outs in the Central Outer Coast cluster shared few sea lions within

Dispersal

Dispersal of mother-pup SSL pairs from natal rookeries from August-October has been long known from land-based rookery studies (Calkins and Pitcher 1982, Merrick *et al.* 1988) and brand resight studies (Raum-Suryan *et al.* 2002). However, the use of satellite telemetry provided us with the opportunity to discover pup (and presumably mother) postbreeding movements and the capabilities of pups to swim any significant distance. This study provides an earlier stage in the progression of movement behavior with the result that 2-mo-old pups were capable of traveling up to 120 km from the rookery. Resights of pups branded at birth have previously indicated that they were able to move over 400 km from natal rookeries by 5 mo-of-age (Raum-Suryan *et al.* 2002). Dispersal from rookeries may allow lactating females and their pups the ability to exploit more productive foraging areas. For example, Weddell seal pups were thought to improve foraging success by avoiding regions of low prey abundance and conspecific competition near breeding areas where adults congregated (Testa *et al.* 1985, Castellini *et al.* 1992). New Zealand sea lion (*Phocarctos hookeri*)³ and Australian sea lion (*Neophoca cinerea*; Gales *et al.* 1992) mothers with their 4–5-mo-old pups also employ a strategy of rookery dispersal. Chase (1998) suggested that prey patch depletion of central-place foragers should be strongest directly adjacent to the central place (*i.e.*, rookery), diminishing with distance. For example, scuba diver surveys indicated prey were less abundant where double-crested cormorants (*Phalacrocorax auritus*) foraged near the colony than where cormorants did not forage (Birt *et al.* 1987). Antarctic fur seals (*Arctocephalus gazella*) migrate away from breeding areas in winter to forage in other locations (Boyd *et al.* 2002). Many SSL rookery sites are virtually abandoned during winter while numbers of animals on haul-out sites increase dramatically (Sease and York 2003) suggesting prey resources near rookeries may be only seasonally available. Although moving a pup between haul-out sites may pose increased risk of predation, moving closer to available prey resources reduces energy demands of adult females providing better potential survival of their pups.

Similar to brand-resighting studies (Raum-Suryan *et al.* 2002), all long distance movements (>500 km) of juveniles in this study were conducted by males. The general pattern of more extensive movements by male than female otariids has been reported for Antarctic fur seals (Boyd *et al.* 1998), northern fur seals, *Callorhinus ursinus* (Kajimura 1984, Loughlin *et al.* 1987, Kajimura and Loughlin 1988) and California sea lions, *Zalophus californianus* (Antonelis and Fiscus 1980). Brand-resights of SSL males at locations farther from natal rookeries and at a later age than females may reflect the later age at first reproduction for males (Raum-Suryan *et al.* 2002).

Near the completion of this project two satellite transmitters were attached to 10-mo-old male pups in the central Aleutian Islands. This sample was too small to be included in the quantitative analysis for this manuscript. However, it is notable that both pups traveled greater distances (~950 km) than any pup of similar age in our study and suggests that additional work should focus on comparing sea lion movements in the far western stock with those in the areas described here.

³ Personal communication from Ian Wilkinson, Department of Conservation, Science and Technical Centre, 65 Victoria St., Wellington, New Zealand, October, 2002.

Round Trips

Pup and juvenile round trips to sea were primarily short in distance (≤ 15 km) and duration (< 20 h) and were similar to results of young SSLs in western Alaska and Washington in which 88% of trips were < 15 km and < 20 h (Loughlin *et al.* 2003). Gray seals (*Halichoerus grypus*) are also known to make short, small scale, return trips from haul-out sites to sea and back (McConnell *et al.* 1999). At-sea locations of harbor seals in Prince William Sound are generally close to capture haul-outs (Gotthardt 2001, Lowry *et al.* 2001), site fidelity being common for harbor seals (Brown and Mate 1983, Suryan and Harvey 1998). Short round trips performed by SSL pups and juveniles may indicate SSLs are foraging close to the haul-out while their mothers are traveling farther offshore. The presence of lungworm (*Filaroides sp.*) L1 larvae in the feces of SSL pups indicates that some animals as young as 3 mo-of-age are supplementing their diet with fish as they contract this parasite by ingesting fish with L3 larvae encysted in the gut wall.⁴ California sea lions are known to ingest solid food by 7–10 mo-of-age and wean from 6 to 11 mo-of-age (Oftedal *et al.* 1987, Melin 1995). Trites and Porter (2002) used behavioral observations to suggest that SSL pups and yearlings make independent trips away from haul-outs while their mothers forage (*e.g.*, pup and yearling trips averaged 43% less time than those of lactating females). Similarly, California sea lion pups, which do not accompany their mothers on foraging trips, also spend time away from the rookery while their mothers are away (Melin *et al.* 2000). Although “significant” supplemental feeding prior to weaning is unlikely in SSLs (Alaska Dept. Fish and Game, unpublished data), areas adjacent to haul-outs may be used by dependent SSLs as they learn how to forage and weaned young as they increase their foraging skills.

Regional divisions in summer SSL diet are closely aligned with patterns in declines of populations of SSL females and their pups (York *et al.* 1996) suggesting diet and decline of SSLs are linked (Sinclair and Zeppelin 2002). The area adjacent to a haul-out or rookery could be critical not only for the development of juvenile foraging skills, but in the availability and accessibility of localized prey. SSLs appear to tailor their foraging behavior to the predictable patterns of their prey, targeting prey when they are nearshore and densely schooled in spawning or migratory aggregations (Sinclair and Zeppelin 2002). For example, harbor seal blubber fatty acid signatures were different at haul-outs only 9–15 km apart in PWS, suggesting seals may depend on a very localized prey base adjacent to haul-outs (Iverson *et al.* 1997). Despite the presence of suitable haul-outs SSLs occasionally raft together in the water near a concentration of prey such as eulachon (Gende *et al.* 2001, Marston *et al.* 2002), Pacific herring (Gende *et al.* 2001) or salmon.⁵ Walleye pollock (*Theragra chalcogramma*), nearshore throughout the year, is one of the most dominant prey items by frequency of occurrence in SSL diets in Alaskan waters (Pitcher 1981, Calkins and Goodwin 1988, Calkins 1998, Sinclair and Zeppelin 2002). The temporal and spatial distribution of nearshore spawning aggregations of Pacific herring and Pacific cod (*Gadus macrocephalus*) and migratory movements of Pacific sand lance (*Ammodytes hexapterus*) and Pacific salmon (*Oncorhynchus* spp.) coincide with the highest SSL seasonal and frequency consumption of these prey (Sinclair and Zeppelin 2002). Low abundance of prey species (flatfish and gadids)

⁴ Personal communication from Kimberlee Beckmen, Alaska Department of Fish and Game, 1300 College Rd., Fairbanks, AK 99701, March 2002.

⁵ Personal communication from Shane Moore, P.O. Box 2980, Jackson, WY 83001, April 2002.

adjacent to some SSL rookeries coincided with the area of the highest observed declines in WP SSLs (Mueter and Norcross 2000). Given that young SSLs remain very close to shore while foraging skills are being developed, availability and predictability of prey resources adjacent to rookeries and haul-outs appears to be critical to survival.

Seasonal changes in the distribution of dependent pups and juveniles presumably reflect increased movements of their mothers. Increased movements in the spring may be a result of nutritionally dependent older young traveling from winter haul-outs back to the rookeries with their mothers. Our location data indicated that ten individuals traveled from haul-outs to rookeries during the months of April through July. Two of these individuals were later observed on the rookeries suckling. Although it is not uncommon to observe adult females nursing yearlings on the rookery, this is the first direct evidence we have of instrumented individuals traveling back to rookeries with their mothers.

Another possible reason for increased movements in spring may be the result of movements of sea lions to areas of spawning aggregations of prey. A female nursing a pup in the spring is estimated to consume twice as much energy as a female of the same age without a pup (Winship *et al.* 2002) requiring a possible expansion in foraging range. Seasonal movement of prey may be more important in determining California sea lion attendance patterns late in the lactation period (*i.e.*, spring) than increasing energy demands of the pup (Melin *et al.* 2000). In spring and early summer in PWS, schools of herring, capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), and salmon return to nearshore areas to spawn (Barraclough 1964, Anthony *et al.* 2000, Norcross *et al.* 2001), and during summer, when they are highest in energy content, sand lance are readily available as they swim above the sand in dense schools (Robards *et al.* 1999). Frederick Sound, Southeast Alaska, is a major migratory corridor for pink salmon (*Oncorhynchus gorbuscha*) that return to spawn in Stephens Passage and Frederick Sound in July and August (Heard 1991) where >12 haul-outs are located (Fig. 11).

The noticeable increase in round trip distance and duration around 10 mo-of-age may indicate that newly weaned individuals are foraging independently, and being less experienced than their older conspecifics, travel farther from haul-outs to either locate or consume prey. The age of weaning is highly variable in SSLs, occurring anywhere from 1 to 3 yr-of-age (Gentry 1970, Sandegren 1970, Calkins and Pitcher 1982). Based on changes in movements and dive characteristics, Loughlin *et al.* (2003) assumed weaning occurred after 9 mo-of-age for SSLs in Washington and western Alaska. Trites and Porter (2002) suggest that weaning does not occur during winter, but later in the spring (*i.e.*, April–June). We found that a similar change in movement distance and duration occurs at approximately the same time of year (*i.e.*, April–June) for young of the year and older juveniles. This may indicate that the annual timing of weaning is less variable than the age of the offspring.

An increase in trip duration and distance coupled with increased foraging effort is predicted if prey availability is reduced (Merrick and Loughlin 1997). Previous studies comparing SSL eastern and western populations in recent decades found little evidence for nutritional stress in adult females and pups from the WP. Pup growth rates and masses were found to be greater in the WP than the EP (Merrick *et al.* 1995, Rea *et al.* 1998, Brandon 2000). Adult female mass was greater in the WP (Adams 2000), perinatal period was longer and time spent nursing was greater in the WP (Milette and Trites 2003), and adult female foraging effort (trip length and time spent ashore) was less in the WP than the EP (Brandon 2000, Milette and

Trites 2003). In contrast, we found round trip distance was greater for pups and juveniles in the WP than the EP (effects of population on trip duration were difficult to discern due to the variability of trip duration by month of year). One possible explanation may be that juveniles are weaning or supplementing their feeding earlier in the west than in the east. Another possibility may be that juveniles are having greater difficulty locating sufficient prey in the WP. Independently foraging juveniles are confronted with greater nutrition-related challenges during food shortages than older, more experienced individuals (Trites and Donnelly 2003). The temporal, spatial, and seasonal unpredictability of sea lion prey requires flexibility in sea lion foraging strategies. However, juveniles are usually inexperienced foragers and may not be able to increase their foraging effort through behavioral adaptations (Merrick 1995). Merrick *et al.* (1997) reported that SSL populations in the Aleutian Islands and Gulf of Alaska (WP) with the lowest diversity of prey experienced the highest rates of decline. Consistent with these results, the summer diet of the increasing population of SSLs in Southeast Alaska was more diverse than that reported for any other region in Alaska.⁶ The advantages of consuming several species of prey is one of foraging efficiency in that diverse prey is easier to find (more prey patches), capture (patch densities are increased), and handle (prey size is correct) (Merrick *et al.* 1997), thus requiring less foraging time during trips to sea.

Differences in male and female foraging behavior between sexually dimorphic pinnipeds has been reported for dive depth (Boyd and Croxall 1996, Boyd *et al.* 1998), dive duration (Beck *et al.* 2003), and geographic distribution (Hindell *et al.* 1991, LeBoeuf *et al.* 1993, Stewart and DeLong 1993, Boyd *et al.* 1998). Although our study did not address dive behavior, and we found no pattern of geographic separation between the sexes, we found that female SSL pups and juveniles had longer trip durations than males. It is possible that females may have longer trip durations than males because they may be more selective than males when searching for prey (Beck *et al.* 2003) or that males are able to dive deeper than females (Boyd and Croxall 1996, Boyd *et al.* 1998) and thus able to exploit additional prey resources in a shorter period of time. The additional examination of male and female SSL dive depth and duration (Alaska Dept. Fish and Game, unpublished data), dive focus (Frost *et al.* 2001), and time spent at sea could provide additional possible reasons why pup and juvenile females have greater trip distances and possibly duration than males.

Haul-out Use

Optimal foraging theory (Orians and Pearson 1979) suggests that foraging animals should not travel farther than necessary from the central place, or alternatively should choose a central place that minimizes travel distance. We found mothers and pups travel together to different haul-out sites, thus conforming to a multiple central place foraging strategy by females. In contrast to a classic central-place forager (Orians and Pearson 1979, Schoener 1979, Stephens and Krebs 1986) a multiple central place forager is an individual that is not restricted to a single central place but travels between a limited number of central places (McLaughlin

⁶ Presentation 15th Biennial conference on the biology of marine mammals. A. Trites, D. G. Calkins, A. J. Winship. 2003. Diet and decline of Steller sea lions in Alaska. Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, BC, Canada, V6T 1Z4.

and Montgomerie 1989, Chapman *et al.* 1989). One strategy to reduce energy costs of central place foraging for adult female SSLs with dependent young is to minimize travel time between foraging areas and the haul-out site. Foraging decisions of young sea lions are presumably dependent upon their mother's choice of a particular haul-out and thus reflect her decisions perhaps more than her offspring. Travel time to foraging locations could be reduced by using haul-out sites closest to a sea lion's current foraging area. We observed four nutritionally dependent (three observed suckling) EP yearlings (between 1 and 2 yr-of-age) with their mothers at locations other than their capture site. Moreover, we have similar observations of permanently marked pup and juvenile SSLs ($n = 33$) suckling from their mothers at more than one haul-out (Alaska Dept. Fish and Game, unpublished data). South American sea lions (*Otaria flavescens*), New Zealand sea lions (*Phocartos bookeri*), and Australian sea lion females and their young also are known to travel from natal rookeries to other locations during winter (Vaz-Ferreira 1981, Gales and Fletcher 1999).^{3,7} In contrast California sea lions pups remain dependent throughout the winter and into the spring, but pups do not travel with their mothers away from the rookery to other haul-out sites (Melin *et al.* 2000).

Where neighboring colonies (or haul-outs) overlap in potential foraging range, feeding habitat use in the area between colonies should also reach an equilibrium defined by the need to minimize travel cost between the feeding site and the colony (Cairns 1989). For SSLs, we found a pattern of clustered haul-out use in that sea lions used haul-outs in close proximity to one another more frequently than distant sites. As haul-out use is defined by availability of prey resources adjacent to haul-outs, SSLs appear to exhibit colony-specific foraging areas as has been shown for Antarctic fur seals (Boyd *et al.* 2002), northern fur seals, shy albatross (*Thalassarche cauta*) (Brothers *et al.* 1998), and black-legged kittiwakes (*Rissa tridactyla*) (Ainley *et al.* 2003). Individual foraging decisions result in the distribution of a predator population (*e.g.*, SSLs) at equilibrium that is proportional to the distribution of resources in the environment (Fretwell 1972). Thus, we believe there is a limit to available prey resources within a given distance of haul-outs and, when the cost (time and travel distance) outweigh the benefits (available prey resources and resting sites), the geographic haul-out cluster structure is no longer maintained.

With the increasing SSL population near the highest in recorded history in Southeast Alaska (Calkins *et al.* 1999), the geographic rookery structure in Southeast Alaska also has changed dramatically. Forrester Is. rookery, the largest, has existed for many years, followed by the establishment (or possibly reestablishment) of Hazy Is. rookery during the 1980s, White Sisters rookery during the 1990s (Calkins *et al.* 1999), and Graves Rocks and Biali Rocks rookeries in the early 2000s (Alaska Dept. Fish and Game, unpublished data). Brand resighting data suggest that Hazy Is. may be the birthplace of many of the sea lions observed in Frederick Sound during this study (Alaska Dept. Fish and Game, unpublished data), hence the strong connection between these two areas. Similarly, brand resighting data in Southeast Alaska suggests a pattern of geographic partitioning such that pups tend to be resighted at haul-outs closer to their natal rookeries than at more distant rookeries (Alaska Dept. Fish and Game, unpublished data). Prey availability being equal, it is more cost-effective to forage closer to the natal rookery or a nearby haul-out than it is to travel to a distant rookery.

⁷ Personal communication from Dan Costa, Center for Ocean Health, 100 Shaffer Rd., University of California, Santa Cruz, CA 95060, October 2002.

We found that SSL females and pups disperse from the natal rookery at an early age and that foraging strategies differed among individuals, some conforming to central-place and others to a multiple central-place foraging strategy. At-sea round trip distance and duration increased with age, yet, in general, pup and juvenile sea lions remained relatively close to haul-out sites. Our findings support previous studies indicating that patterns in trip distance, duration, and interhaul-out movements suggest young sea lions are weaning sometime between April and June. Although the question of nutritional stress could not be answered within the scope of this study, evidence suggests that nearshore areas adjacent to haul-outs and rookeries continue to be crucial to the survival of young Steller sea lions.

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