

DISPERSAL, ROOKERY FIDELITY, AND
METAPOPOPULATION STRUCTURE OF STELLER
SEA LIONS (*EUMETOPIAS JUBATUS*) IN AN
INCREASING AND A DECREASING
POPULATION IN ALASKA

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ABSTRACT

Over the past 24 yr, 8,596 Steller sea lion (*Eumetopias jubatus*) pups were branded on their natal rookeries throughout Alaska with the objectives of determining survival rates, recruitment, movements, and site fidelity. Our objectives here were to examine the extent of dispersal of Steller sea lions away from their natal rookeries, movements between stocks, and degree of natal rookery fidelity. Pups (<1 yr old) usually remained within 500 km of their natal rookery. Branded juveniles dispersed widely and were resighted at distances up to 1,785 km from their natal rookeries. Adults generally remained within 500 km of their natal rookeries. No interchange of breeding animals between the ES (eastern stock) and WS (western stock) was observed. Although natal rookery fidelity was prevalent, 33% of the 12 observations of females branded in the WS during 1987–1988 and 19% of the 29 observations of females branded in the ES during 1994–1995 were observed with newly born pups at sites other than their natal rookeries. Steller sea lions generally conformed to the metapopulation concept as depicted by Hanski and Simberloff (1997), with local breeding populations (rookeries) and movements among these local populations having the potential of affecting local dynamics.

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Key words: Steller sea lion, *Eumetopias jubatus*, dispersal, rookery fidelity, brand, Alaska, endangered, metapopulation.

Steller sea lions are a gregarious species that congregate throughout the year at traditional terrestrial haul-out sites between bouts of feeding at sea. During the breeding season, adult sea lions further concentrate on specific haul-outs known as rookeries, where males establish territories within which mating and parturition occur (Sandegren 1970, Calkins and Pitcher 1982, Loughlin *et al.* 1984). Both sexes reach sexual maturity at a similar age, females from three to six years and males from three to seven years. However, whereas most females begin breeding at maturity, breeding for most males is delayed until 9–11 yr-of-age, when males are capable of maintaining a breeding territory (Thorsteinson and Lensink 1962, Perlov 1971, Pitcher and Calkins 1981). Males establish territories on rookeries in early May and remain until mid-July (Thorsteinson and Lensink 1962, Gentry 1970, Gisiner 1985). Adult females come to shore soon after males and give birth to a single pup between mid-May and mid-July, with a peak in pupping occurring during June (Pike and Maxwell 1958, Mathisen *et al.* 1962, Pitcher *et al.* 2002). Pups are generally weaned within a year although some juveniles continue suckling up to three yr-of-age (Gentry 1970, Sandegren 1970, Pitcher and Calkins 1981).

Steller sea lions breed and range throughout the coastal waters of the North Pacific Ocean, occurring from central California along the Pacific Rim, through the Gulf of Alaska, Bering Sea, and Aleutian Islands to Japan (Kenyon and Rice 1961, Loughlin *et al.* 1984). The population has been divided into two stocks based primarily on genetic evidence (Bickham *et al.* 1996, Loughlin 1997). This division occurs at Cape Suckling, Alaska (144°W), creating an eastern and western stock (Fig. 1). Over the past 30 yr these two stocks have exhibited opposing population trends. Overall, the western stock (WS) in Alaska has declined by over 80% (Loughlin *et al.* 1992, Trites and Larkin 1996, Sease *et al.* 2001), whereas the eastern stock (ES) in Alaska has increased substantially (Calkins *et al.* 1999, Sease *et al.* 2001). The WS is classified as “endangered” and the ES as “threatened” under the U.S. Endangered Species Act.

As populations in the WS continued to decline, it became increasingly important to determine survival rates, the amount of interchange between stocks, dispersal, and natal rookery fidelity (philopatry) of Steller sea lions. Genetic studies using mitochondrial DNA indicated there was little interchange of breeding adult females between stocks (Bickham *et al.* 1996). However, Bickham *et al.* (1996) were unable to provide information regarding movements of sea lions within stocks and, because mitochondrial DNA is maternally inherited, they could not determine breeding interchange of males between stocks. Other methods such as radio telemetry (Merrick *et al.* 1994) and flipper tagging (*e.g.*, Gilmartin *et al.* 1993, Thompson *et al.* 1994) can provide information on movement patterns, however these individual markers are temporary, often lasting no more than a few years. Branding (*e.g.*, Calkins

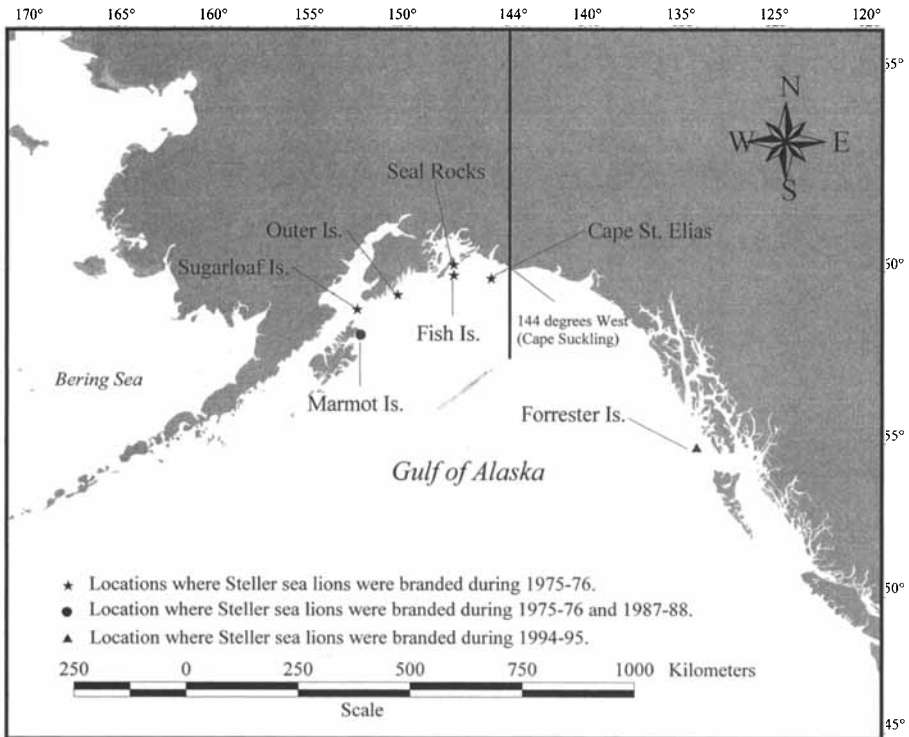


Figure 1. Locations where Steller sea lions were branded in western stock 1975–1976 (★), both 1975–1976 and 1987–1988 (●) and in the eastern stock during 1994–1995 (▲). Cape Suckling (144°W) divides eastern and western stocks.

and Pitcher 1982, Merrick *et al.* 1996, Pomeroy *et al.* 2000, Schwarz and Stobo 2000) provides a permanent means to uniquely identify an individual.

Between both populations (WS and ES), sea lions have traditionally used up to about 50 rookeries and over 250 haul-out sites in Alaska along a coastline extending approximately 2,600 km from Dixon Entrance in Southeast Alaska to Attu Island, the westernmost Aleutian Island (Loughlin *et al.* 1984, Loughlin *et al.* 1987a, Sease *et al.* 2001). Steller sea lions, with multiple breeding rookeries within each stock, appear to conform to a metapopulation structure as portrayed by Hanski and Simberloff (1997) *e.g.*, spatially segregated into assemblages of local breeding populations with movement or migrations among local populations with the potential of having some effect on local dynamics, including the possibility of population reestablishment following extinction. One of the most important aspects of metapopulation dynamics is the flow of individuals between populations (Gilpin 1987). Information regarding relative habitat (rookery) quality can be gained by cueing on the presence or absence of conspecifics or “conspecific attraction” (Kiestler and Slatkin 1974; Stamps 1987, 1988; Shields *et al.* 1988). The breeding habits and dispersal patterns of the permanently marked Steller sea lions may provide further information to evaluate the applicability of the metapopulation concept

to Steller sea lions. Previous studies have not been able to fully evaluate the metapopulation dynamics within stocks because the methods used lacked the required resolution (*e.g.*, genetics) or longevity (*e.g.*, radio telemetry and flipper tags).

In this study we analyzed resighting observations, collected during a 25-yr period, of Steller sea lions branded in both the ES and WS. Objectives of branding studies included determining rates of survival, fecundity, movements, and site fidelity. Our objectives in this paper were to determine: (1) extent of dispersal of Steller sea lions away from natal rookeries, (2) movements of Steller sea lions within metapopulations and between stocks; (3) degree of natal rookery fidelity, and (4) mechanisms that may be responsible for the dispersal and natal rookery fidelity of Steller sea lions.

All research was conducted under the authorization of U.S. Marine Mammal Protection Act and U.S. Endangered Species Act permits issued by the Office of Protected Resources within the National Marine Fisheries Service.

METHODS

Steller sea lion pups were hot-branded with brief (2–4 sec per character) applications of a hot iron to destroy hair follicles and pigment-producing cells for a permanently bald brand (Merrick *et al.* 1996). All brands were approximately 5 cm wide by 8 cm high. It usually required no more than one minute to apply a three or four-character brand and the animal was released immediately afterward.

We branded 8,596 Steller sea lion pups during the 21-yr period from 1975 to 1995. Pups were branded in the WS during 1975–1976 and 1987–1988 and in the ES during 1994–1995 (Fig. 1). Pups ($n = 7,046$) were branded at two sites in July 1975 and six sites in June 1976 (Fig. 1) with brands unique as to year and branding location (Table 1). This initial branding pattern provided a means to determine Steller sea lion dispersal and site fidelity. However, because individuals were not uniquely identifiable, it was difficult to quantify these parameters. Therefore, during further branding studies, sea lions were branded with numeric digits unique to each individual. During June–July 1987 and 1988, we branded and tagged 751 pups at Marmot Island in the WS (Fig. 1, Table 1). Three-digit sequential numbers were branded on the right shoulder of each pup in 1987 (numbered 51–401) and on the left shoulder of each pup in 1988 (numbered 401–800). The number 401 was used in both years but on different shoulders. During June 1994 and 1995 we branded 799 pups at Forrester Island in the ES (Fig. 1, Table 1). Four-character brands with three sequential numbers were applied on the left shoulder of each pup in 1994 (F201–F599) and 1995 (F600–F999). Plastic Allflex[™] cattle ear tags embossed with the same number as the brand were applied to the rear margins of both foreflippers of each pup during the 1987–1988 and 1994 branding events.

Brand resighting effort varied from year to year after each branding event in the WS. Dedicated resighting effort was conducted primarily one to four

Table 1. Description of date, location, brand, and number of male and female Steller sea lions branded as pups during each branding event. Also presented are number of individuals resighted, percent of individuals resighted, and number of resighting locations. Several pups branded at Forrester Island have unclear brands and were not identifiable to cohort or sex. In these cases, cohort or sex was combined (94-95).

Year	Location	Brand	Number branded		Number resighted			Percent total resightings	Total # resighting locations
			Male	Female	Male	Female	Unid		
1975	Marmot	O	319	279	a	a		13	
1975 ^b	Sugarloaf	X	373	346	a	a		13	
1976	C. St. Elias	L	10	13	a	a		4	
1976	Marmot	T	1,879	1,790	a	a		16	
1976	Outer	V	125	121	a	a		8	
1976	Seal Rocks	J	165	151	a	a		5	
1976 ^b	Sugarloaf	X	737	706	a	a		16	
1976	Fish	E	16	13	a	a		4	
TOTAL			3,623 ^c	3,419 ^c	104	104	59%	22	
1987	Marmot	50-401	165	186	41	43	21%	16	
1988	Marmot	401-800	196	204	145	147	39%		
TOTAL			361	390	76	84	50%	45	
1994	Forrester	F201-F599	216	183	84	92	53%	38	
1995	Forrester	F600-F999	221	179	84	37			
94-95	Forrester		437	362	160	176	55%	102 ^d	

^a Sea lions were cohort-branded and number and percent of individuals resighted unknown.

^b Sea lions were branded with "X" on left shoulder 1975 and right shoulder 1976.

^c Three individuals branded during 1975-1976 were unidentified as to sex.

^d Includes 26 individuals not identifiable as to cohort.

years following the 1975–1976 branding period. This effort included observations at Sugarloaf Island rookery from April to July 1978–1980 and Marmot Island rookery from May to July 1979–1980 and June to July 1983–1985, 1987. Observations also were conducted at Cape St. Elias haul-out from March to June 1977 and March to July 1978. Additional resightings were made opportunistically during research cruises throughout the Gulf of Alaska from 1975 to 1978, 1985 to 1986, and 1989 to 1990. Dedicated resighting effort of pups at Marmot Island was focused primarily through the winter (November 1987–March 1988) following the 1987 branding event. After this initial resighting effort, observations were conducted at Marmot Island during the breeding season (June to July) 1988–1999 (excluding 1989, 1990, and 1997). At Sugarloaf Island observations were conducted from May through August 1994–1999 in conjunction with collection of daily population counts and behavioral data. Branded animals were also resighted at Sea Otter Island haul-out (May–August 1997) and Fish Island rookery (June–July 1995–1998) in conjunction with daily population counts.

In the ES, dedicated resighting effort (July 1994–February 1995) was conducted at Forrester Island following the 1994 branding event. We conducted additional resighting effort at Forrester Island (May–August 1995, June–July 1996–1998, and 2000) in conjunction with population counts and behavioral studies. We visited most rookery and haul-out sites in Southeast Alaska ($n = 21$) during June–July 1999 and Southeast Alaska and northern British Columbia, Canada ($n = 42$) during June–July 2000. Opportunistic resighting observations took place after all branding events at a wide variety of locations and at all times of the year during the past 25 yr by a variety of biologists and members of the public working along the coast.

During June–July 2000, we digitally photographed resighted branded sea lions. This proved to be a successful tool for identifying brands that were difficult to read in the field. Images also were archived for future match comparisons.

A major difficulty in analysis of these data was the variable and unquantified resighting effort among years and geographic areas. This rendered some potential quantitative analyses invalid and resulted in largely descriptive results.

Analysis

We used the log-likelihood ratio for contingency tables (*G*-test; Zar 1984) to compare the number of sea lions resighted (by age group, sex, and distance) that were branded at Marmot *vs.* Forrester. For purposes of analyses, we classified Steller sea lions <1 yr as pups, 1–2.9 yr as juvenile females, 1–4.9 yr as juvenile males, ≥ 3 yr as adult females, and ≥ 5 yr as adult males. Some brands from Forrester Island were unrecognizable as to individual. We used these individuals in overall comparisons between Marmot and Forrester. However, because the sex and/or cohort of these individuals were unknown, they were not included in male *vs.* male or female *vs.* female comparisons. We determined distance traveled from natal rookeries using the Great Circle Dis-

tance calculation (American Practical Navigator 1995). Actual distances of travel were probably much greater than the minimum, straight-line distances reported here.

RESULTS

Resightings of Branded Animals

Steller sea lions branded during 1975–1976 were resighted many times ($n = 5,746$) throughout the years (1975–1998, Fig. 2). However, because these animals were not uniquely identifiable, we cannot determine how many “individuals” were resighted. The proportion of individual branded animals resighted from Forrester Island (55%) during six years of resighting effort was significantly ($G = 39.03$, $df = 1$, $P < 0.001$) higher than from Marmot Island (39%) during 13 yr of resighting effort. Moreover, the relative number of branded sea lions resighted from Forrester Island was higher and remained stable over time in contrast to the lower and declining relative number from Marmot Island (Fig. 3).

Our resighting effort was substantially greater during the five months following the 1987 branding event at Marmot Island than after either the 1988 branding event at Marmot Island or the 1994–1995 branding events at Forrester Island. To remove the potential bias of greater resighting effort at Marmot Island before age one, we compared the proportion of resighted sea lions ≥ 1 -yr-of-age. This comparison indicated an even greater difference in resighting rates between Forrester Island (42%) and Marmot Island (17%) branded sea lions ($G = 126.95$, $df = 1$, $P < 0.001$). For the Marmot Island animals similar percentages of females (16%) and males (17%) were observed ($G = 0.32$, $df = 1$, $P > 0.05$), whereas for the Forrester Island animals a higher percentage of females (40%) than males (31%) was observed ($G = 7.29$, $df = 1$, $P < 0.01$). This may change as males mature and become more visible as territorial bulls (higher sighting probability).

Fewer female sea lions branded at Marmot Island were resighted as adults compared to Forrester Island ($G = 68.76$, $df = 1$, $P < 0.001$). Only 7.4% ($n = 29$) of females branded at Marmot Island were observed as adults (≥ 3 yr) whereas at Forrester Island 30% ($n = 110$) of females branded were observed as adults. There was no significant difference ($G = 0.70$, $df = 1$, $P > 0.05$) between the 10% ($n = 37$) of males branded at Marmot Island that were observed as adults (≥ 5 yr) compared to 12% ($n = 53$) of males branded at Forrester Island observed as adults. However, males branded at Forrester Island in 1994 and 1995 were only five or six yr-of-age during the last resighting effort and number of resightings will likely increase as they begin breeding.

Dispersal

Steller sea lions branded during all decades dispersed widely from their natal rookeries (Fig. 2) with a maximum observed dispersal distance of 1,785

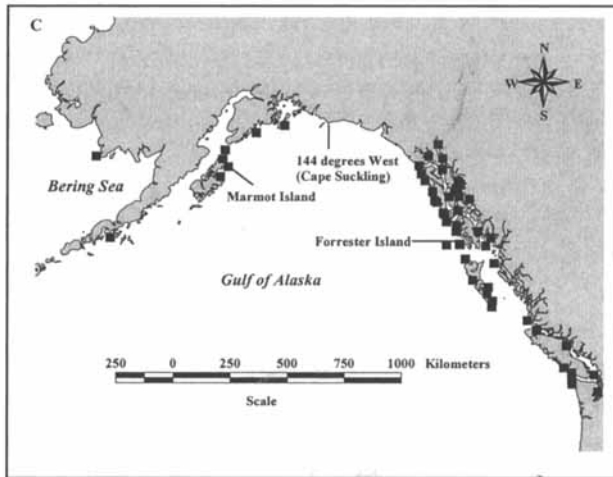
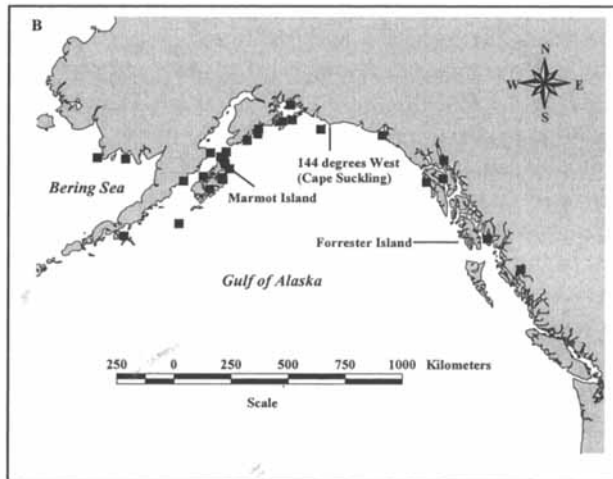
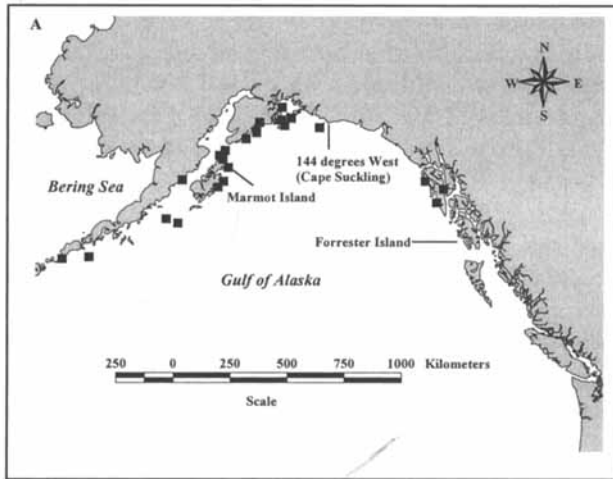
km. Dispersal distance from the natal rookery varied greatly with age. Pups (<1 yr) generally remained within 500 km of their natal rookeries. Sea lion pups were observed alive at distances up to 356 km from their natal rookery at Marmot Island and 492 km from their natal rookery at Forrester Island. Only one pup was reported >500 km from its natal rookery. This was a male, 0.9 yr-of-age, branded at Marmot Island in 1987 that was found dead in a gillnet near Yakutat, 708 km away. Juveniles (females: 1–2.9 yr, males: 1–4.9 yr) dispersed much greater distances, up to a maximum distance of 1,785 km from their natal rookeries. Juvenile Steller sea lions branded at Marmot Island were observed at maximum distances of 1,251 km (Annette Island, Southeast Alaska) and 1,503 km (Lorreta Island, British Columbia). The most distant locations where Forrester Island juveniles were observed included the Bering Sea (Cape Newenham, 1,785 km), the western Gulf of Alaska (Jude Island, 1,746 km), and Washington State (1,100 km).

Adult males (≥ 5 yr) and adult females (≥ 3 yr) branded in the 1970s, 1980s, and 1990s tended to remain within 500 km of their natal rookeries. Of sea lions branded during 1975 and 1976, exceptions included 3% of observations (3–11 yr) observed at distances of approximately 900–1,000 km in Southeast Alaska (ES) and 940 km in the Aleutian Islands (WS) from their natal rookeries. Of resighted adult males ($n = 37$) branded at Marmot Island as pups during 1987 and 1988, two individuals (5.0 and 6.4 yr-of-age) were observed at distances of 605 km in the Bering Sea (WS) and 982 km in Southeast Alaska (ES). All adult females ($n = 29$) were resighted within 450 km of Marmot Island in the WS. Of resighted adult males ($n = 53$) branded as pups at Forrester Island, two individuals (5.4 and 5.1 yr-of-age) were observed at distances of 1,100 at Chiswell Island and 1,179 km at Marmot Island in the northern Gulf of Alaska (WS). Other than one 3.3-yr-old adult female observed at Carmanah Point, British Columbia, 913 km from Forrester Island, all other adult females ($n = 109$) branded as pups at Forrester Island during 1994 and 1995 were observed within 500 km of Forrester Island.

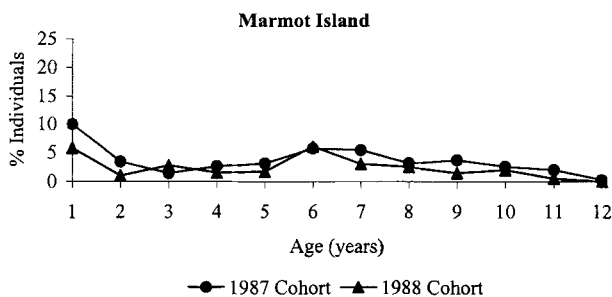
Males tended to utilize more haul-outs and rookeries and to disperse greater distances than females. Males branded at Marmot Island during 1987–1988 were resighted at 26 different locations, whereas females were resighted at 17 locations. Forrester Island males were resighted at 47 different locations and females at 32 different locations. Few ($n = 2$ males) sea lions branded at Marmot Island were observed at distances greater than 1,000 km from their natal rookery. In contrast, more males ($n = 24$) than females ($n = 5$) branded at Forrester Island were observed at locations greater than 1000 km from Forrester Island ($G = 16.78$, $df = 1$, $P < 0.001$).

Movement Between Stocks

There was little interchange of sea lions between eastern and western stocks. From 1979 to 1987, sea lions branded during 1975–1976 in the WS were observed 23 times (0.4% of 5,746 total resightings) at three different locations in the ES up to 1,000 km away (Table 2). At least four different individuals



A)



B)

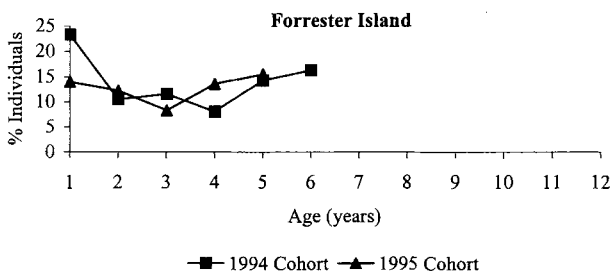


Figure 3. Percentage of Steller sea lion individuals resighted per year of age (excluding age category 0–1 yr) after branding at Marmot Island, WS (A) and Forrester Island, ES, (B).

were resighted. Additionally, 17 of the 23 resightings were of adult (≥ 5 yr) animals. Only 1.4% ($n = 5$) of males and 0.3% ($n = 1$) of females branded at Marmot Island during 1987–1988 were observed in the ES (Table 2). Similarly, a small proportion (4.6% of males, $n = 20$; 1.4% of females, $n = 5$) of sea lions branded at Forrester Island during 1994–1995 were observed in the WS (Table 2).

Males continued to move between stocks at an older age than females. One female (2.4 yr-of-age) and five males (0.9–6.4 yr-of-age) from Marmot Island were resighted in the ES (Table 2). Females from Forrester Island were re-

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Figure 2. Resighting locations of Steller sea lions branded in western stock (A) 1975–1976 (■, $n = 23$ unique locations), and (B) 1987–1988 (■, $n = 30$ unique locations), and in eastern stock (C) 1994–1995 (■, $n = 56$ unique locations). Cape Suckling (144°W) divides eastern and western stocks.

Table 2. Comparisons of individuals branded in either western stock (WS) or eastern stock (ES) and resighted in breeding range of opposite stock. Age (yr) range, (ES, WS), and sex (M—Male, F—Female, U—Unknown) of individuals and number of resight locations in opposite stock and distance range from natal rookery are presented.

Natal rookery	Stock	Year branded	Sex	Number branded	Number resightings		Number individuals ES	Number resightings WS	Number individuals WS	Age (yr)	Number of locations	Distance (km)
					ES	WS						
Marmot	WS	1975	U	598	3		^a			6.8–6.9	1	1,010
Marmot	WS	1976	U ^b	3,669	10		^a			3.1–11.1	4	918–1,010
Sugarloaf	WS	1976	U	1,443	8		^a			3.1–6.1	3	932–1,024
Outer	WS	1976	U	249	2		^a			5.9	1	936
Marmot	WS	1987	M	165	5	4				0.9–6.4	5	708–1,281
Marmot	WS	1987	F	186	1	1				2.4	1	991
Marmot	WS	1988	M	196	1	1				3.9	1	1,503
Marmot	WS	1988	F	204	0	0						
Forrester	ES	1994	M	216				26	10	1.1–5.4	5	1,000–1,207
Forrester	ES	1994	F	183				8	3	1.1–2.1	2	1,000–1,210
Forrester	ES	1994 ^c	U	399				11	4	1.1–3.0	2	1,000–1,079
Forrester	ES	1995	M	221				21	10	1.0–4.4	5	1,000–1,785
Forrester	ES	1995	F	179				6	2	1.0–1.1	1	1,000
Forrester	ES	1995 ^c	U	400				4	2	1.1	2	1,000–1,179
Forrester	ES	94–95 ^d	U	799				8	3	U	2	1,000–1,179

^a Number of individuals the number of resightings includes is unknown.

^b One individual was identified as male.

^c This represents all individuals branded during that cohort year (399 branded during 1994, 400 branded during 1995).

^d Brands are unreadable as to cohort, therefore number branded includes all individuals branded during 1994 and 1995.

sighted in the WS from 1.0 to 2.1 yr-of-age and males from 1.0 to 5.4 yr-of-age (Table 2).

Although no adult Steller sea lions were observed breeding in the opposite stock, some adults of breeding age did move between stocks. Of those sea lions branded in the WS during 1975–1976, individuals with three unique cohort brands representing three or more individuals from 5.9 to 6.9 yr-of-age were observed in the ES during April and July of 1992. Additionally, one adult male (11 yr), branded at Marmot Island in 1976, was observed in the ES during July 1987. This individual would have been both reproductively and physically mature enough to hold a territory and breed.

Natal Rookery Fidelity

Of females branded during 1975 and 1976, there were 211 resightings of females observed with newly born pups (females observed with pups from May through July) (Table 3). These sea lions were not marked with uniquely numbered brands, therefore only total resightings, and not number of individuals, were ascertained. Females observed with pups ranged in age from 3 yr (observed in 1979) to 22 yr (observed in 1998). Slightly more females with pups were resighted at their natal rookery (112 resightings, 53%) than at other rookeries (99 resightings, 47%).

Of the 390 females branded in 1987 and 1988, only twelve females (3%) were resighted with newly born pups (Table 3). Eight females were observed on Marmot Island (natal rookery) and four on Sugarloaf Island (78 km away). Another female was observed with a pup at Cape St. Elias during February 1995, but the birth site was unknown.

One female branded in 1987 was observed at Outer Island (150 km from Marmot Island) with a pup during October 1990. She would have been 3 yr old when she gave birth. Birth by a female at three yr-of-age was previously reported by Pitcher and Calkins (1981), but appears to be unusual.

Unlike Marmot Island, significantly ($\chi^2 = 11.64$, $n = 31$, $P < 0.001$) more females from Forrester Island gave birth at their natal rookery ($n = 25$) than at a non-natal rookery ($n = 6$) (Table 3). The first branded adult female from Forrester Island observed with a newly born pup was four yr-of-age. The mean age at which females were first observed with a pup at Forrester Island was 5.8 yr-of-age ($n = 31$); however since some Forrester Island females may have still been sexually immature this estimate is probably low.

Although adult males branded as pups in 1975–1976 were observed, no records were kept about their status as territorial bulls. Few males ($n = 37$) branded at Marmot Island during 1987 and 1988 were resighted as adults (≥ 5 yr), and of those observed, even fewer ($n = 9$) were observed as territorial bulls. Of the 361 males branded in 1987 and 1988, eight territorial bulls were resighted at Marmot Island and one territorial bull was resighted at Sugarloaf Island (78 km away). Territorial bulls that were branded in 1987 were first observed holding territories at age 11 whereas those branded in 1988 were first observed holding territories at age 10. No territorial bulls or

Table 3. Steller sea lion females banded at natal rookery (band site) and resighted with newly born pups (May–July) at natal or non-natal rookeries. Resightings (not individuals) presented for those females banded 1975–1976 because number of individuals could not be determined. Locations of non-natal rookeries and distance (km) to each non-natal rookery where females were observed with newly born pups is presented.

Brand site	Year	# Females banded	# w/pup natal	# w/pup non-natal	Res. w/pup natal ^a	Res. w/pup non-natal ^a	Location	Distance
Marmot	1975	279	—	—	24	3	Sugarloaf	78 km
							Fish	315 km
Sugarloaf	1975	346	—	—	0 ^b	5	Marmot	78 km
Cape St. Elias	1976	13	—	—	— ^c	1	Marmot	448 km
Marmot	1976	1,790	—	—	65	0	—	—
Outer	1976	121	—	—	— ^c	45	Marmot	150 km
Seal Rocks	1976	151	—	—	— ^c	5	Marmot	357 km
Sugarloaf	1976	706	—	—	23 ^b	40	Marmot	78 km
							Fish	288 km
Fish	1976	13	—	—	0	0	—	—
Marmot	1987	186	4	2	—	—	Sugarloaf	78 km
Marmot	1988	204	4	2	—	—	Sugarloaf	78 km
Forrester	1994	183	13	4	—	—	Hazy	137 km
							White Sisters	357 km
Forrester	1995	179	11	1	—	—	Cape St. James	360 km
Forrester ^c	94–95	362	1	1	—	—	Hazy	137 km
							White Sisters	357 km

^a Same individual may have been observed multiple times.

^b No resighting effort at Sugarloaf between 1981 and 1993.

^c No resighting effort at Cape St. Elias, Outer Island, or Seal Rocks during pupping season.

adult females have been observed switching to a different rookery once breeding had been established.²

DISCUSSION

Resightings and Movement Between Stocks

Resightings of branded Steller sea lions showed wide dispersal from natal rookeries, particularly of juvenile animals, occasionally travelling over 1,500 km to other rookeries and haul-outs and crossing stock boundaries. Yet individuals returned to breed at either their natal rookery or a non-natal rookery within their respective stocks.

York *et al.* (1996) suggested that the declining population trend in the WS could be stabilized or reversed with sufficient immigration of females from the ES. However, current evidence indicates this is unlikely. Bickham *et al.* (1996) concluded there was a low rate of exchange (9.5 migrants per generation) of breeding females between stocks as determined with mitochondrial DNA analysis. Our observations of stock fidelity by breeding females support these findings. We detected no breeding females and only one potentially breeding male in their non-natal stock.

York *et al.* (1996) estimated that if the WS decline continued for another 30 yr, rookeries would begin to disappear in the WS and the probability of extinction would increase rapidly. The low interchange of breeding females indicates this decline probably resulted from reduced survival and/or fecundity within the WS and not emigration to the ES. The lower proportion of resighted individuals in the WS *vs.* the ES suggests lower survival rates in the WS. Although it is highly probable that differences in survival do exist between eastern and western stocks, we are cautious about drawing conclusions from our data without accounting for differences in resighting probability. Future analyses will include mark-recapture models to determine survival rates, which in turn could be used to test the role of demographic parameters in explaining opposing population trends in the eastern and western stocks.

Dispersal

Steller sea lion pups first enter the water 2–4 wk after birth (Sandegren 1970) and, with their mothers, begin to disperse from rookeries to haul-outs between 2 and 3 mo of age (Calkins and Pitcher 1982, Merrick *et al.* 1988). Even at a young age, pups are able to travel hundreds of kilometers. Merrick *et al.* (1994) reported Steller sea lion pups ranging more than 250 km by their sixth month. Similarly, during our study we observed five-month-old pups at

² After submission of this manuscript, a branded adult female observed with a newly born pup at Cape St. James rookery during June 2000 was observed with a newly born pup at Forrester Island rookery during June 2001. This is the first record we have of a breeding adult giving birth at two different rookeries (Alaska Department of Fish and Game, unpublished data).

haul-outs over 400 km from the natal rookery. Because pups are maternally dependent through most of the first year (Pitcher and Calkins 1981), their distribution probably reflects the distribution of foraging resources available to their mothers. Once weaned, pups may disperse more extensively due to competition with adults for limited resources (Baker 1978) or to assess future alternative breeding locations.

In many mammalian species natal dispersal (juveniles undergoing a permanent movement from birth site to first breeding site) is more extensive than breeding dispersal (movement of individuals, which have reproduced, between successive breeding sites) (Greenwood 1980) and this seemed to be the case with Steller sea lions. The purpose of juvenile dispersal may be to investigate potential new breeding sites, and finding conspecifics at these sites may increase the potential for future breeding. During this study dispersal of juvenile Steller sea lions was similar during all decades and between stocks. Pups left their natal rookeries within the year after their birth, dispersed widely in all directions as juveniles and, as adults, generally remained within 500 km of their natal rookery.

Differences between dispersal, migration, and movement patterns of males and females has been reported for many pinniped species, including Antarctic fur seals, *Arctocephalus gazella* (Boyd *et al.* 1998); northern fur seals, *Callorhinus ursinus* (Kajimura 1984, Loughlin *et al.* 1987b, Kajimura and Loughlin 1988), and California sea lions, *Zalophus californianus* (Antonelis and Fiscus 1980); with a general pattern of more extensive and variable movements by males. Steller sea lion males continued to be resighted at locations farther from the natal rookery, and at a later age, than females, perhaps reflecting the later age at first reproduction for males. This trend was more pronounced in the branded males from the ES than from the WS, again perhaps reflecting higher survival in the ES. These observations also support conjecture that high levels of dispersal may be a result of increasing population densities (Myers and Krebs 1971, Baker 1978).

Steller sea lions are capable of travelling hundreds of kilometers and visiting many rookeries and haul-outs. The dispersal of sea lions to various haul-outs or rookeries may be guided by the presence or absence of conspecifics (conspecific attraction) as generally suggested for other highly mobile species (Stamps 1988, Smith and Peacock 1990). The presence or absence of conspecifics may yield information on the relative quality of a habitat patch (in this case a haul-out, rookery, or nearby foraging areas) (Kiestler and Slatkin 1974; Stamps 1987, 1988; Shields *et al.* 1988).

Natal Rookery Fidelity

We found that natal rookery fidelity (philopatry) was only moderately strong for Steller sea lions in the Gulf of Alaska (67%), and in Southeast Alaska (81%). Natal and breeding site fidelity are commonly reported among polygynous pinnipeds such as elephant seals, *Mirounga angustirostris* (Huber 1987, Le Boeuf and Reiter 1988), and northern fur seals (Bartholomew and Hoel

1953, Baker *et al.* 1995). Baker *et al.* (1995) suggested there was a selective advantage of returning to the natal site.

The dispersal of breeding females from their natal rookeries to other rookeries within their parent stock supports the metapopulation concept as envisioned by Hanski and Simberloff (1997). We observed movements of females born on one rookery to another rookery where they subsequently produced young within both stocks. In the ES we saw the establishment (reestablishment?) of new rookeries and were able to determine through observations of branded animals that females born at an established rookery moved to these new breeding sites. The ES in Southeast Alaska has nearly doubled over the past 25 yr (Calkins *et al.* 1999), therefore the dispersal of females to new rookeries may have been a density-dependent response. The parent rookery, Forrester Island, has remained stable in size over the past 10 yr, while the overall population has continued to increase through growth at the newly established rookeries. In a similar manner, an expanding colony of gray seals (*Halichoerus grypus*) increased their total breeding range rather than more densely occupying the existing breeding area (Pomeroy *et al.* 2000).

Our results provide additional evidence that Steller sea lions in the Gulf of Alaska occupy two distinct stocks, with little interchange of breeding adults. Although Steller sea lions are commonly reported as having a high degree of natal rookery fidelity, we demonstrated that dispersal to non-natal breeding sites was not uncommon. From a metapopulation perspective, such dispersal to non-natal sites is an important strategy for colonizing new and previously occupied habitat or locating potentially higher quality breeding habitats than their natal sites, both of which are necessary for long-term population survival (Hanski 1999).

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