Demographic consequences and characteristics of recent population mixing and colonization in Steller sea lions, *Eumetopias jubatus*

KELLY K. HASTINGS,* MICHAEL J. REHBERG, GREGORY M. O'CORRY-CROWE, GREY W. PENDLETON, LAURI A. JEMISON, AND THOMAS S. GELATT

Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Road, Anchorage, AK 99518, USA (KKH, MJR, GWP, LAJ)
Harbor Branch Oceanographic Institute, Florida Atlantic University, 5600 US 1 North, Fort Pierce, FL 34946, USA (GMO)
National Marine Fisheries Service, Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115, USA (TSG)

* Correspondent: kelly.hastings@alaska.gov

Steller sea lions (*Eumetopias jubatus*) are composed of two genetically distinct metapopulations (an increasing "eastern" and a reduced and endangered "western" population, or stock for management purposes in U.S. waters) that are only recently mixing at new rookeries in northern Southeast Alaska, east of the current stock boundary. We used mark-recapture models and 18 years of resighting data of over 3,500 individuals marked at the new rookeries and at neighboring long-established rookeries in both populations to examine morphology, survival, and movement patterns of pups born at new rookeries based on whether they had mitochondrial DNA haplotypes from the western or eastern population (*mtW* or *mtE*); examine survival effects of dispersal to the Eastern Stock region for animals born in the Western Stock region; and estimate minimum proportions of animals with western genetic material in regions within Southeast Alaska. Pups born at new rookeries with *mtW* had similar mass, but reduced body condition and first-year survival (approximately −10%) compared to pups with *mtE*. *mtE* pups ranged more widely than *mtW* pups, including more to the sheltered waters of Southeast Alaska's Inside Passage. Fitness benefits for western-born females that dispersed to Southeast Alaska were observed as higher female survival (+0.127, +0.099, and +0.032 at ages 1, 2, and 3+) and higher survival of their female offspring to breeding age (+0.15) compared to females that remained west of the boundary. We estimated that a minimum of 38% and 13% of animals in the North Outer Coast–Glacier Bay and Lynn Canal–Frederick Sound regions in Southeast Alaska, respectively, carry genetic information unique to the western population. Despite fitness benefits to western females that dispersed east, asymmetric dispersal costs or other genetic or maternal effects may limit the growth of the western genetic lineage at the new rookeries, and these factors require further study.

Key words: dispersal, *Eumetopias jubatus*, genetics, mark-recapture, mtDNA, population dynamics, Southeast Alaska, Steller sea lion, survival

Spatial dynamics driven by demography and long-distance dispersal are important processes determining population responses (e.g., range shifts or adaptation to changing local conditions) to rapid environmental change (Neubert and Caswell 2000), such as due to global climate change (Travis et al. 2013) or abrupt regime shifts (Scheffer et al. 2001). The importance of dispersal to the stability and persistence of metapopulations inhabiting heterogeneous environments is well established (Hanski 1999). Dispersal is the relocation of the home range

of animals in response to environmental or social conditions that potentially leads to gene flow (Ronce 2007). Dispersal patterns are influenced by numerous factors, including density of competitors, resource availability, inbreeding avoidance, lack of breeding partners, and needs for escape from predators or pathogens (Courchamp et al. 1999; Bonte et al. 2012).

Dispersal strategies are most often condition-dependent (Clobert et al. 2009), allowing animals to track favorable conditions and reduce environmental uncertainty (Travis et al. 2013;

Ponchon et al. 2015). For example, prospecting visits can inform animals about good-quality habitat, such as through conspecific density and breeding performance (Danchin et al. 1998; Reed et al. 1999; Ponchon et al. 2013, 2017). Dispersal may also lead to range expansions and colonization of new breeding habitat (Munilla et al. 2016). The relationship between density and dispersal patterns can be complex when habitat patches with high densities also have high resource abundance. In such cases, a positive relationship between settlement probability and population density (Fernández-Chacón et al. 2013) and a negative relationship between dispersal probability and density (Baguette et al. 2011) may result. Demographic consequences and drivers of dispersal patterns are most often context-specific, and studies of demographic characteristics related to genetic makeup of colonizers in their new environments are particularly lacking.

Steller sea lions (*Eumetopias jubatus*) are composed of two genetically distinct populations in U.S. waters ("eastern" and "western"; Fig. 1) as determined by a formerly distinct break in mitochondrial DNA (mtDNA) lineage distributions (hereafter, *mtHap* with two groups: *mtW* for the western population and *mtE* for the eastern population), despite high genetic diversity throughout the range (Bickham et al. 1996; O'Corry-Crowe et al. 2006). The breeding distributions of the two populations, until the late 1970s, were separated by a distance of ~1,000 km (between Forrester Islands, Southeast Alaska [eastern population], and Seal Rocks, Gulf of Alaska [western population]; Fig. 1; Pitcher et al. 2007). This population break is likely ancient and is consistent with a pattern of geographic isolation in one or more glacial refugia in the northern Pacific (Harlin-Cognato et al. 2006), allowing morphometric differences to develop (Phillips et al. 2009). Specifically, large ice-free regions existed in Beringia and south of the ice sheets ranging down to Eurasia and North America, during the Wisconsin glaciation 65,000–18,000 BP, and these served as insular refugia during the last glacial maximum (Harlin-Cognato et al. 2006). Genetic
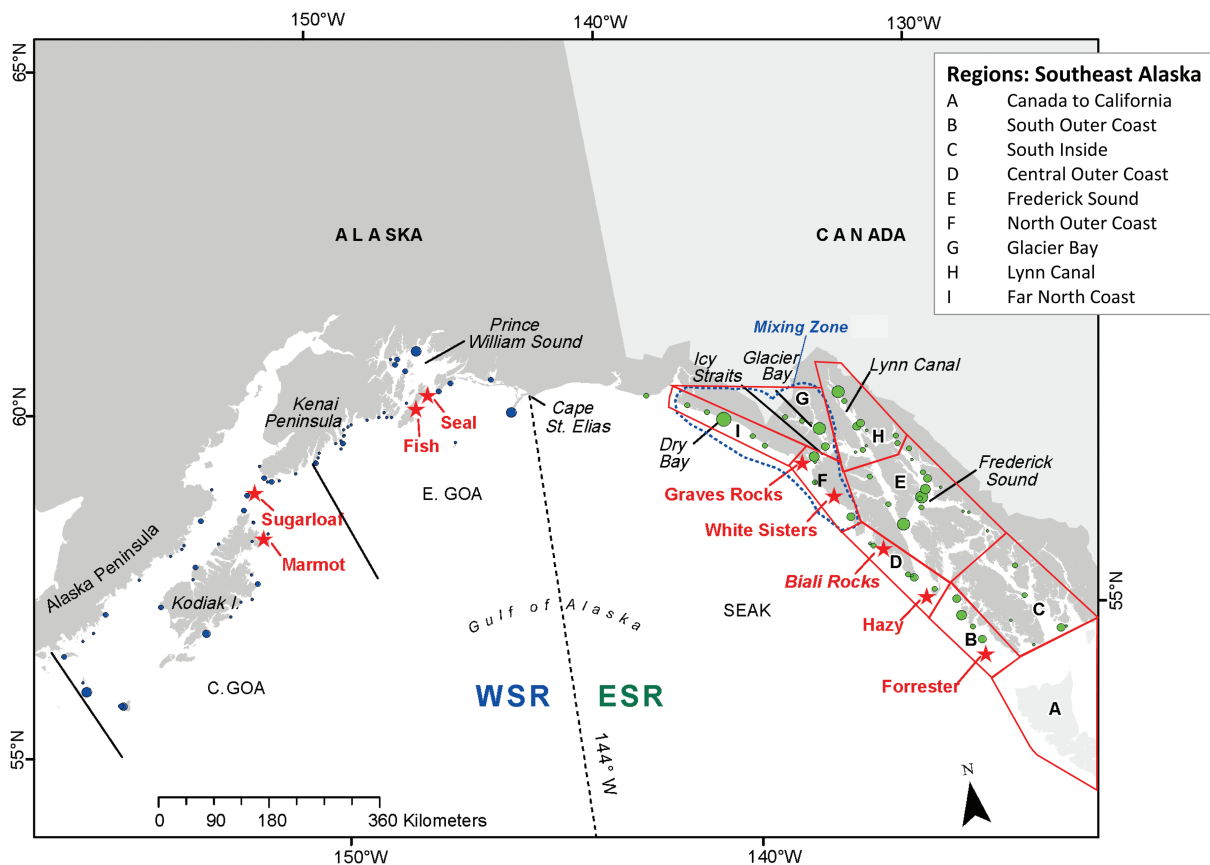
Fig. 1.—Map of the study area where Steller sea lions (*Eumetopias jubatus*) were branded and resighted from 2000 to 2018. Pups were marked at eight rookeries in red stars: Marmot Island, Sugarloaf Island, Fish Island, Seal Rocks, Graves Rocks, White Sisters, Hazy Islands, and Forrester Islands. Sea lions were resighted but not marked at a fifth small rookery in Southeast Alaska (SEAK), Biali Rocks. 144°W marks the stock boundary between the Western (WSR) and Eastern Stock regions (ESR). Regions A–I in Southeast Alaska are from Jemison et al. (2018); we present names for these regions in the legend. Four large areas grouped these regions for some analyses: Main Study Area (I, F, G), South Area (D, E, H—not including Hazy Islands), Far South Area (A, B, C, and Hazy Islands), and West Area (the Western Stock region). The core Mixing Zone in the Eastern Stock region is delineated by the blue dashed line and is a zone with significant mixing of animals born in both the Western and the Eastern Stock regions. E. GOA and C. GOA are large management areas: eastern and central Gulf of Alaska (Fritz et al. 2016). Dots are other sites used by at least 20 nonpups (blue dots for the Western Stock region and green dots for the Eastern Stock region). The sizes of the dots indicate maximum numbers of nonpups counted during aerial or brand–resight surveys from 2000 to 2015 (ranges are: 20–200, 201–500, 501–1,000, 1,001–1,500, 1,501–2,500, 2,501–3,500, > 3,500).

variation in Steller sea lions is consistent with the presence of four insular refugia during or before this glacial maximum: the Pacific Northwest (currently the eastern population), the Gulf of Alaska, the Aleutian Islands (together composing the current western population), and Russia (currently the Asian population—Harlin-Cognato et al. 2006). The current genetic pattern is also consistent with a linear recolonization of the range between historical refugia, also influenced by isolation-by-distance due to female philopatry, where females usually breed within < 500 km of their natal rookery (Harlin-Cognato et al. 2006; O'Corry-Crowe et al. 2006; Hastings et al. 2017).

In addition to genetic differences, the dynamics of the two populations have differed dramatically in recent times. A severe (> 80%) population decline of the western population beginning in the 1970s (Merrick et al. 1987) led to a listing of this population as "endangered" under the U.S. Endangered Species Act (U.S. Federal Register 1997). Although increasing population trends have been observed for portions of the western metapopulation since 2003 (Fritz et al. 2014, 2016), the western population remains much smaller than its historical size (Fritz et al. 2015b). By contrast, steady population growth of the eastern population over the same time period (Pitcher et al. 2007) led to removal of a U.S. Endangered Species Act listing of "threatened" for this population in 2013 (U.S. Federal Register 2013). The two populations are also considered stocks for management purposes under the U.S. Marine Mammal Protection Act with the stock boundary placed at 144°W, which separates the Eastern and Western Stock regions (Southeast Alaska is the northernmost area of the Eastern Stock region; Fig. 1). Two previous haul-outs in northern Southeast Alaska have transitioned to rookeries since 1990 ("new rookeries": White Sisters and Graves Rocks; Fig. 1), in what was once part of the hiatus in breeding distributions between the two populations. Growth in numbers of nonpups using these and nearby sites was high at 8.2% per year from 1970 to 2009 (Mathews et al. 2011).

This "Mixing Zone" (dotted area in Fig. 1 showing the core Mixing Zone; the extended Mixing Zone also includes regions Frederick Sound [E] and Lynn Canal [H]), within the Eastern Stock region, is used by significant numbers of Western Stock region-born animals (Jemison et al. 2018). At the new rookeries in the Mixing Zone, pups with maternal genetic origins in the eastern and western populations are produced and adults from both populations are interbreeding (Jemison et al. 2013; O'Corry-Crowe et al. 2014). An additional small (~200 pups in 2015—Fritz et al. 2015a), recently formed (since at least 2002) rookery, Biali Rocks, to the south of White Sisters (Fig. 1), has not been sampled for genetic composition. Growth of the two new rookeries was fueled by a steady dispersal of eastern-lineage females northward from the densely populated Forrester Islands rookery with a stable trend (to Hazy Islands rookery established ~1979, to White Sisters established ~1990, and to Graves Rocks established late 1990s—Pitcher et al. 2007; Fig. 1) and from western-lineage females eastward from severely declining rookeries in the Western Stock region (Jemison et al. 2013; O'Corry-Crowe et al. 2014). Dispersal

of Western Stock region-born females was influenced by dispersal distance: the less distant Prince William Sound rookeries (eastern Gulf of Alaska) contributed more females (Seal Rocks and possibly Fish Island; Fig. 1) than the more distant rookeries in the central Gulf of Alaska (Marmot Island and Sugarloaf Island; Fig 1; Jemison et al. 2013).

The mixing of these genetic lineages is both very recent and unprecedented in the last 20,000+ years, and is likely a function of the gradual reduction in the size of the historical gap between the breeding distributions of the two populations, likely poor conditions in the Western Stock region, and a particularly productive environment, and positive feedback from conspecific attraction, at their new mixing point (O'Corry-Crowe et al. 2014). High productivity likely resulted in part from exposure of new marine habitat following deglaciation, especially in Glacier Bay (reviewed by Mathews et al. 2011; Rehberg et al. 2018).

The demographic consequences of dispersal and mixing on these lineages are currently unknown. Recent work indicated that only Western Stock region-born females cross the stock boundary (Jemison et al. 2013). Virtually no branded, Eastern Stock region-born females have been observed in the Western Stock region in contrast to 6.7% of branded, Western Stock region-born females in the Eastern Stock region at age 5 years (Jemison et al. 2013). In contrast, males from both populations regularly cross the stock boundary, at least temporarily, especially males born in Prince William Sound and in southern Southeast Alaska, and males ≤ 5 years of age (Jemison et al. 2013). The use of the Mixing Zone improved survival of males and females born in southern Southeast Alaska (Hastings et al. 2011), but demographic consequences of dispersing across the stock boundary have not been evaluated for animals born in the Western Stock region. Also unknown is the role of genetics in demographic processes of the two populations; however, mark-recapture modeling to estimate early pup survival (i.e., marking to 1 year of age) of a very small sample of animals from Graves Rocks (n = 46) found little evidence of an *mtHap* effect (Pendleton et al. 2016). Potential genetic factors determining dispersal patterns, morphologies, and behavior of the two lineages in their common and new environment are also of interest. For example, undetermined genetic factors possibly contributed to the growth of the eastern population, rather than environmental factors alone (Bickham et al. 1996).

The occurrence of western-lineage Steller sea lions in the Eastern Stock region is of interest to managers, particularly for consideration of continued recognition of the current stock boundary and appropriate protection measures for endangered western Steller sea lions in Southeast Alaska (Jemison et al. 2018). Although the Mixing Zone has been identified as important habitat for western Steller sea lions (Jemison et al. 2018), quantification of the proportions of animals related to the western population in regions of Southeast Alaska, including Western Stock region-born animals and animals with *mtW* born at new rookeries, is needed to fully understand the degree of genetic mixing occurring throughout Southeast Alaska and to provide for assessment of stock-specific impacts

from anthropogenic activities. The objectives of this study were: 1) to determine how body morphology, 2) survival, and 3) large-scale movement patterns differed between Steller sea lions born at the new rookeries based on *mtHap*; 4–5) to describe fine-scale site use in regions of Southeast Alaska by birth region and *mtHap* to provide plausible theoretical values for the proportions of Steller sea lions related to the western population in regions of Southeast Alaska; and 6) to estimate fitness effects (survival and offspring survival) of dispersal of Western Stock region-born Steller sea lions to the Mixing Zone.

MATERIALS AND METHODS

Steller sea lion pups were captured, anesthetized, and hot-branded with unique alpha numeric combinations at 2–4 weeks of age at the new rookeries, Graves Rocks (*n* = 163) and White Sisters (*n* = 368, total = 531), over 4 years (2002, 2004, 2005, and 2016; Table 1). Maximum pup counts during summer aerial surveys in 2002 and 2015, respectively, were 99 and 506 at Graves Rocks and 403 and 915 at White Sisters (Fritz et al. 2015a). For nearly all pups marked, we collected a skin sample (flipper punch from the webbing of a hind flipper; for all but four pups captured) and measured dorsal standard length (±0.5 cm, from the tip of the tail to the tip of the nose), axillary girth (±0.5 cm, girth at the pit of the foreflippers), and body mass (±0.5 kg; Table 1). DNA was extracted from skin samples and a segment of the mtDNA control region consisting of 531 base pairs was amplified and sequenced as in O'Corry-Crowe et al. (2006).

Haplotype was determined for animals born in 2002–2005 by O'Corry-Crowe et al. (2014) and for animals born in 2016 in this study. The program WHICHRUN (v. 4.1—Banks and Eichert 2000) was used to determine if an animal's haplotype through the maternal line (*mtHap*) was of an eastern or western lineage (*mtE* or *mtW*), or was not in the baseline or of low power (occurred in similar frequencies in the eastern and western populations, or just found once in one populations' baseline—O'Corry-Crowe et al. 2014). The baseline consisted of equal numbers of individuals (*n* = 270) from each population sampled outside the Mixing Zone. We assigned a *mtHap* to 408 of the 527 pups with a sample collected from the new rookeries; the remaining 119 were not assigned a *mtHap* because the sample was not analyzed (26%, *n* = 31) or due to low power or too little sample (35%, *n* = 42), or because the

haplotype was in neither baseline (39%, *n* = 46). Some level of unassignment was expected given the baseline was limited to 270 mtDNA haplotypes for each population and the observed level of unassignment is not expected to affect results (O'Corry-Crowe et al. 2014). Resightings and photographs of branded animals were collected annually from May to August throughout their range since 2000, during standardized surveys and from miscellaneous sightings that covered the entire geographic range of the species from California through Russia and into the Bering Sea (Hastings et al. 2011; Fritz et al. 2014; Wright et al. 2017; Jemison et al. 2018). Research on live animals followed American Society of Mammalogists guidelines (Sikes et al. 2016) and was approved by institutional animal care and use committees and by permits granted by the U.S. National Marine Fisheries Service.

Objective 1: Morphometric differences by mtHap for pups born at the new colonies.—We fit generalized linear models for two response variables: body mass (kg) and condition index (no units) for all pups assigned an *mtHap* that were sampled from 2002 to 2016 (*n* = 408). The condition index was calculated as (axillary girth in cm/dorsal standard length in cm) * 100, following Rea et al. (2016). Explanatory variables included in models were based on results from Hastings et al. (2011), which used these data from White Sisters and Graves Rocks, 2002–2005: sex, birth year, natal rookery, and *mtHap*. Predictor variables were included as main effects for all models, and all interactions of birth year * natal rookery * *mtHap* were included in condition index models. Models were fit using *glm* in R (R Core Team 2018) and the best model was chosen based on Akaike's information criterion (AIC—Burnham and Anderson 2002).

Objective 2: Survival differences by mtHap for animals born at new rookeries.—We first fit Cormack–Jolly–Seber (CJS) models (Cormack 1964; Seber 2002) to determine the best models for survival (*S*) and resighting (*p*) probabilities for animals marked at the new rookeries from 2002 to 2005 with known *mtHap* (*n* = 350). We excluded data from the 2016 cohort because only two years of resighting data for this cohort were available. Capture histories consisted of annual summer resight occasions from 2002 to 2018 (17 occasions), where 0 indicated the animal was not seen with certainty that summer (May–August) and 1 indicated the animal was photographed that summer and the photograph was used to confirm the animal's identity with a master photograph library. The base

Table 1.—Numbers of Steller sea lion (*Eumetopias jubatus*) pups born at the new rookeries that were branded, sampled for DNA, and assigned to a maternal genetic lineage (*mtHap*: *mtE* or *mtW*) from 2002 to 2016 by birth year. New rookeries were White Sisters and Graves Rocks (see Fig. 1). #*mtHap* assigned differed from number samples for DNA due to samples not analyzed, low power of some samples, or results of some samples not in the baseline data. %*mtW** is the proportion *mtW* of those assigned (2002–2005 data from O'Corry-Crowe et al. 2014).

Year	White Sisters				Graves Rocks			
	#Branded	#DNA	#*mtHap* assigned	%*mtW**	#Branded	#DNA	#*mtHap* assigned	%*mtW**
2002	127	127	102	0.314	50	50	44	0.705
2004	94	94	73	0.370				
2005	147	146	95	0.263	43	42	36	0.639
2016					70	68	58	0.517
All	368	367	270	0.311	163	160	138	0.609

S and *p* model were from the best model from Hastings et al. (2011, 2018), where *S* for females varied for ages 0, 1, 2, and 3+, and *S* for males varied for ages 0, 1, 2, 3–8, and 9+, with an additive effect of natal rookery. The base *p* model included ages 1, 2, 3, 4+ for females and 1, 2, 3, 4, 5, 6, 7, 8+ for males, with an additive effect of year. We verified that there was little indication that *p* varied with natal rookery for this subset of the data and then included *p* models with an additive effect of *mtHap* for all ages, at ages 1 and 2, and at age 1 only. For *S*, we included models with mass or *mtHap* effect for all ages, for ages 0 (i.e., first-year survival) and 1 (i.e., second-year survival), and for age 0 only (16 models fit). For all mark-recapture models (CJS and multistate, see below) we used programs MARK (White and Burnham 1999) and RMark (Laake 2013) to fit models and estimate parameters; best models were chosen based on AIC corrected for small sample size (AICc—Burnham and Anderson 2002).

Objective 3: Coarse-scale movements by mtHap for animals born at new rookeries.—For the same data set (*n* = 350 animals) and based on the best model from objective 2, we fit multistate models (Nichols et al. 1992) to examine movement patterns based on *mtHap*. We condensed "regions" from Jemison et al. (2018) to four broader "areas" (Fig. 1): a Main Study Area (regions I, F, and G), an area just south of the Main Study Area (South Area: regions H, E, and D—not including Hazy Islands), an area far south of the Main Study Area (Far South Area: regions A, B, and C, and Hazy Islands in D), and an area north and west of the Main Study Area (West Area = Western Stock region). This coarser scale was used because sample sizes of these 350 animals seen per region were too small to estimate movement probabilities among all regions. We altered capture histories such that the 1's of the CJS models' capture histories were replaced with four alphabetic codes for areas to indicate where animals were photographed. If an animal was seen in multiple areas per summer, we chose the area with the least number of resightings for capture histories, to provide the largest sample possible for areas outside of the Main Study Area. The priorities were Far South Area > West Area > South Area > Main Study Area, because sample sizes of resightings of

nonpups grouped by animal * year * area were 1,100 (72%) in the Main Study Area, 365 in the South Area, 32 in the West Area, and 24 in the Far South Area. We included an additive effect of area on *p* in all models and fit models for movement probabilities between areas (*ψ*) that included all combinations of sex, age-class (juveniles 0–3 years versus animals 4+ years [adult females and subadult or adult males]), natal rookery, and *mtHap* effects (16 models fit).

Objective 4: Fine-scale site use by birth region and mtHap for all animals marked from Kodiak through Southeast Alaska.—For the remaining three objectives, we required a larger data set to produce region-specific estimates for Southeast Alaska, particularly regional *p*, and to estimate parameters for Steller sea lions born to the north and south of the new rookeries. We used a data set (hereafter, "full data set") of 3,164 animals marked at eight rookeries from Marmot Island through Southeast Alaska from 2000 to 2010 by the U.S. National Marine Fisheries Service, Marine Mammal Laboratory and by the Alaska Department of Fish and Game (as in Jemison et al. 2013, 2018; Table 2; Fig. 1). Although several smaller rookeries exist in the eastern and central Gulf of Alaska, together the four rookeries where pups were marked in the Western Stock region are the four largest rookeries, producing ~85% of the pups in the eastern and central Gulf of Alaska in recent years (Fritz et al. 2015a). We included the same data as Jemison et al. (2013, 2018) except for animals born on White Sisters and Graves Rocks, only those of known *mtHap* were included (350 rather than 461 pups from these rookeries), and resightings of all animals from 2000 through 2018, rather than through 2012 or 2014, were used.

The purpose of objective four was to produce estimates based on age-class, sex, birth region, and *mtHap* of *ψ* (regional movement probabilities) and *S* for modeling proportions in objective 5. Three birth regions indicated if the animal was born in the Western Stock region (all *mtW*), the Mixing Zone (Eastern Stock region: either *mtW* or *mtE*), or southern Southeast Alaska (Eastern Stock region: all *mtE*). We altered the coding of the capture histories for the full data set and fit multistate models in five modeling exercises to produce estimates for five regions:

Table 2.—Numbers of Steller sea lion (*Eumetopias jubatus*) pups marked from 2000 to 2010 from Kodiak Island through Southeast Alaska and resighted to 2018 included in multistate models to examine fine-scale site use by birth region and maternal genetic lineage (*mtHap*: *mtE* or *mtW*) in Southeast Alaska. Groups were WSR (born in the Western Stock region, all with *mtW*), MZ (born in new rookeries in the Mixing Zone of the Eastern Stock region: Graves Rocks and White Sisters, with either *mtW* or *mtE*), or South (born in the southern Southeast Alaska, Eastern Stock region: Forrester and Hazy rookeries, all with *mtE*). PWS = Prince William Sound. See Fig. 1 for locations of rookeries.

Group	Natal rookery	Birth year								Total
		2000	2001	2002	2003	2004	2005	2008	2010	
South	Forrester Islands		286	141	291	277				995
South	Hazy Islands		213		101		225			539
MZ–*mtE*	Graves Rocks			13			13			26
MZ–*mtE*	White Sisters			70		46	70			186
MZ–*mtW*	Graves Rocks			31			23			54
MZ–*mtW*	White Sisters			32		27	25			84
WSR	Fish Island, PWS		32							32
WSR	Seal Rocks, PWS		75		100		80			255
WSR	Sugarloaf Island	151		105		110		93	100	559
WSR	Marmot Island	107		89		75		85	78	434

Central Outer Coast (D), Frederick Sound (E), North Outer Coast (F), Glacier Bay (G), and Lynn Canal (H; Fig. 1). The Far North Coast region (I) had only 10 resightings in summer months and so was pooled with the North Outer Coast (F). The Canada through California region (A), South Outer Coast region (B), and South Inside region (C) were not analyzed, but instead were considered composed of ~100% animals born in southern Southeast Alaska, as only 12 branded White Sisters-born animals, no branded Graves Rocks-born animals, and three Western Stock region-born branded animals were ever observed there. To create these capture histories, the "1" was replaced with "A" if in the region of interest and "N" if the animal was not in the region of interest.

For the single S model we fit, we based the structure for Mixing Zone-born animals on the best resulting model from objective 2, and the structure for southern Southeast Alaska-born animals on results of Hastings et al. (2011, 2018). We based the structure of S for Western Stock region-born animals on the best model from Fritz et al. (2014), but all natal rookeries were pooled (Marmot, Sugarloaf, Fish, and Seal) and no additive effects were shared between Western Stock region- and Eastern Stock region-born animals. We fit the same p model as in objective 2 but allowed p to differ inside versus outside the region, and allowed this difference to vary among years, for regions with adequate sample size of resightings (> 10/year/region; North Outer Coast [F], Glacier Bay [G], and Lynn Canal [H] regions only). We fit a ψ model that estimated probabilities of moving into and out of the region by age-class (juveniles 0–3 years versus animals 4+) and group. The four groups were 1) Western Stock region-born, 2) Mixing Zone-born with mtW, 3) Mixing Zone-born with mtE, and 4) southern Southeast Alaska-born. We also fit a ψ model where movement patterns varied with natal rookery (Southeast Alaska animals only), age-class, and group, for regions with adequate sample sizes of animals using the region per group * natal rookery ($n > 10$ animals; North Outer Coast [F] and Glacier Bay [G] regions only).

Objective 5: Proportions of western-population-related Steller sea lions in regions of Southeast Alaska.—We calculated plausible theoretical values for the minimum proportions of western-population-related Steller sea lions using regions of Southeast Alaska using three types of information that were collected over disparate time periods. The first information type was age-, sex-, and group-specific estimates of S and ψ from the best models produced from objective 4 (seven groups were animals born at [1] Forrester, [2] Hazy, [3] White Sisters with mtE, [4] White Sisters with mtW, [5] Graves Rocks with mtE, [6] Graves Rocks with mtW, and [7] in the Western Stock region). The second information type was relative pup production for the same seven groups, using average maximum pup counts from aerial surveys in 2013 and 2015 (Fritz et al. 2015a). The third information type was the proportion mtE and mtW for White Sisters and Graves Rocks, based on averages from 2002 to 2005 and 2016 (Table 1). For Eastern Stock region-born animals, pups at age 0 were 3,568 at Forrester Islands, 1,912 at Hazy Islands, 914 at White Sisters (also assumed 30% mtW; Table 1), and 523 at Graves Rocks (also assumed 60%

mtW; Table 1). For Western Stock region-born animals, we used the total number of pups produced from Kodiak Island through Cape St. Elias (3,025 pups, including Marmot Island, Latax Rocks, Two-headed Island, Sugarloaf Island, Ushagat Island, Shakun Rocks, Outer Island, Chiswell Island, Fish Island, Seal Rocks, The Needle, Glacier Island, Cape St. Elias; ~85% of pups were born at the four largest rookeries: Marmot, Sugarloaf, Fish, and Seal).

For each sex–age (where ages, i, were 1–30 years) in the seven groups, we estimated the number of animals alive and inside ($N_{\bar{I}}$) versus outside ($N_{\tilde{O}}$) the region of interest using:

$$N_{\bar{I},i} = (N_{\bar{I},i-1} * S_{i-1 \text{ to } i} * \psi_{\bar{I},i-1 \text{ to } \bar{I},i})$$
$$+ (N_{\tilde{O},i-1} * S_{i-1 \text{ to } i} * \psi_{\tilde{O},i-1 \text{ to } \tilde{I},i}), \text{ and}$$
$$N_{\tilde{O},i} = (N_{\tilde{O},i-1} * S_{i-1 \text{ to } i} * \psi_{\tilde{O},i-1 \text{ to } \tilde{o},i})$$
$$+ (N_{\bar{I},i-1} * S_{i-1 \text{ to } i} * \psi_{\bar{I},i-1 \text{ to } \tilde{o},i}).$$

Using the resulting $N_{\bar{I},i}$, numbers of males and females were summed for each age, and the seven groups were reduced to four, by summing numbers for Forrester + Hazy (group 1 = born in southern Southeast Alaska); White Sisters with mtE + Graves Rocks with mtE (group 2 = born in the Mixing Zone with mtE); White Sisters with mtW + Graves Rocks with mtW (group 3 = born in the Mixing Zone with mtW); and born in the Western Stock region (group 4 = Western Stock region). For each of the four groups, we then summed $N_{\bar{I},i}$ for three age ranges (ages 1–3, ages 4–30, and ages 1–30 for juveniles, adults, and all ages totals, respectively), resulting in 12 group * age-range totals. After summing the group totals for each age range (resulting in three age-range totals), we divided the group * age-range totals by the age-range totals to obtain the group composition in the region for the three age ranges.

This procedure produced theoretical values of the proportions of western-related animals that would use regions of Southeast Alaska 30 years into the future, assuming as constant over time: pup production at the level of 2013–2015 values; age-, sex-, and group-specific S and ψ values at the level of 2000–2018 values; and proportions of mtE and mtW pups produced at new rookeries at the level of 2002–2005 and 2016 values. The calculated proportions are not actual estimates of current proportions because of known changes over time in pup production and potential, but unknown, changes in age-specific survival. Because only mtDNA was used, the contribution of male genetic data was ignored, and mtE pups produced at the new rookeries could have carried western genetic material through the paternal line. Therefore, proportions of animals with mtW were minimum proportions of animals carrying western genetic material. However, only two Western Stock region-born males (T22 and T25 from Marmot Island) have been observed as territorial bulls in Southeast Alaska, suggesting any bias in estimated proportion would be very small.

Objective 6: Survival effect for Western Stock region-born animals in the Eastern Stock region.—We used the full data set used for objectives 4–5 but recoded "1" as location in capture histories using "A" if animals were in the Eastern Stock region

(any region of Southeast Alaska and through California) and "N" if in the Western Stock region (the entire Western Stock region through the Bering Sea). We fit five *S* models which, for Western Stock region-born animals, included models with and without survival differences based on location (Eastern Stock region versus Western Stock region), and models with and without sex-specific effects of location on survival.

RESULTS

The proportion of *mtW* pups at Graves Rocks declined in recent samples from 0.705 in 2002, to 0.639 in 2005, and 0.517 in 2016 (Table 1). The proportion of *mtW* pups at White Sisters from 2002 to 2005 varied annually a maximum of 0.11 among years versus 0.19 among years at Graves Rocks (Table 1). We found no support for a linear (on the logit scale) trend in the proportions of *mtW* at Graves Rocks over these few data points (AICc weight < 0.05).

Objective 1: Morphometric differences by mtHap for pups born at the new colonies.—Morphometrics varied little with *mtHap* for pups born at the new rookeries. A slightly larger body mass for *mtW* (+0.5 kg) than *mtE* animals was not statistically supported (Supplementary Data SD1), and variation in pup body mass between the two new rookeries or with birth year was also not supported for this subset of the data (Supplementary Data SD1; but see Hastings et al. 2011). Expected masses (from model 2 for mass; Supplementary Data SD1) were 30.6 and 31.1 kg for *mtE* and *mtW* male pups, and 25.2 and 25.7 kg for *mtE* and *mtW* female pups, respectively. Condition index varied with natal rookery * birth year as in Hastings et al. (2011) and with *mtHap* (model 1 versus 3; Supplementary Data SD1). *MtW* pups were in poorer condition than *mtE* pups, although effect sizes were very small: expected values for condition index (based on model 1 for condition index; Supplementary Data SD1) varied only from 69.0 to 71.6 among groups, were 1.0–1.5 higher for Graves Rocks than White Sisters pups in 2002–2005, consistent with Hastings et al. (2011), and were 0.77 higher in *mtE* compared to *mtW* pups.

Objective 2: Survival differences by mtHap for animals born at new rookeries.—First-year survival was higher for *mtE* than for *mtW* pups born at the new rookeries. The best CJS model included an effect of *mtHap* on *S* and *p* only for the first year for *S*, and at age 1 for *p* (Supplementary Data SD2a). First-year survival was 0.11–0.13 lower (Table 3) and resighting rate at age 1 was 0.16–0.18 lower for *mtW* than *mtE* pups.

Objective 3: Coarse-scale movements by mtHap for animals born at new rookeries.—The best multistate model included effects of age-class and *mtHap* on ψ (Supplementary Data SD2b). Greater movements for juveniles than animals 4+ years old (Table 4) was expected (Jemison et al. 2013, 2018). The *mtHap* effect was driven by greater use of the South Area by *mtE* than *mtW* animals, and *mtW* animals were more likely to remain in the Main Study Area, especially as juveniles. For juveniles, 0.194 more *mtW* than *mtE* remained in the Main Study Area (for individuals 4+ years old, 0.030 more *mtW* than *mtE*

Table 3.—Estimates of first-year survival probabilities (*S*) of Steller sea lions (*Eumetopias jubatus*) by sex, natal rookery, and maternal genetic lineage (*mtHap*: *mtE* or *mtW*), for animals born at the new rookeries (with 95% CI). Two natal rookeries were Graves Rocks and White Sisters (see Fig. 1).

| | First-year survival probabilities (*S*) | |
	mtE	*mtW*
Females, Graves Rocks	0.785 (0.680–0.862)	0.677 (0.552–0.780)
Females, White Sisters	0.707 (0.606–0.790)	0.580 (0.454–0.696)
Males, Graves Rocks	0.749 (0.647–0.830)	0.632 (0.514–0.735)
Males, White Sisters	0.664 (0.571–0.746)	0.531 (0.416–0.643)

remained in the Main Study Area; Table 4). Similarly, 0.191 more *mtE* than *mtW* used the South Area (for individuals 4+ years old, 0.047 more *mtE* than *mtW* used this area; Table 4). Differences in use of the West Area and Far South Area with *mtHap* and age-class were not obvious from multistate model results (Table 4). Instead, the raw data suggested similar use of the West Area regardless of *mtHap* or natal rookery, although use of the West Area was male-dominated, as expected (Jemison et al. 2013): 21 animals were seen in the West Area (11 *mtE* and 10 *mtW*, 19 males and two females, with one *mtE* and one *mtW* female); 15 of those were born at White Sisters and six born at Graves Rocks. Sample sizes were also too small for analyses for the Far South Area, but the raw data suggested a potentially greater use of the Far South Area by *mtE* and White Sisters-born animals. Twelve animals were seen in the Far South Area, 10 *mtE* and two *mtW*, and all 12 were from White Sisters, but equally represented by sex (seven males and five females).

Objectives 4–5: Fine-scale site use by birth region and mtHap for all animals marked from Kodiak through Southeast Alaska, and proportions of western-population-related Steller sea lions in regions of Southeast Alaska.—Western Stock region-born animals occurred principally in the North Outer Coast (F) and Glacier Bay (G) regions in the summer, as previously reported for these data (Jemison et al. 2018): 7–8% of nonpups in those regions are estimated to be Western Stock region-born animals (Table 5). However, *mtW* animals (summing proportions of Western Stock region-born and Mixing Zone-born with *mtW* in Table 5) make up 37–38% of animals in those regions. *MtW* animals also occur in significant numbers in Lynn Canal (H) and Frederick Sound (E), making up 13–18% of animals in those regions in summer (Table 5). Very few *mtW* animals move south along the outer coast to Central Outer Coast (D) but instead the fine-scale site-use pattern suggests their movement into inside waters of Southeast Alaska to Lynn Canal and Frederick Sound may be via Icy Straits (Table 5; see Fig. 1). The Central Outer Coast (D) is populated by *mtE* animals instead. Although southern Southeast Alaska-born Steller sea lions have low rates of movements to most of the five regions during summer (Supplementary Data SD3) and lower survival rates than Steller sea lions born at the new rookeries (Hastings et al. 2011), their high pup production (79% of pups produced in Southeast Alaska were born there) resulted in > 0.20 of southern Southeast Alaska-born Steller sea lions in all regions (Table 5).

Table 4.—Estimates of movement probabilities (ψ) of Steller sea lions among geographic areas by age-class and maternal genetic lineage (*mtHap*: *mtE* or *mtW*, from model 6; Supplementary Data SD2b), for animals born at the new rookeries. See Fig. 1 for area descriptions. The probability of remaining in an area from one occasion to the next is indicated by *. Age-classes were juveniles (0–3 years old) versus animals 4+ years old (adults for females, subadults + adults for males). Estimates (with 95% *CI*) are shown only for the Main Study Area and other areas that animals used considerably (> 0.05 of a group moved to).

	Movement probabilities (ψ)	
	mtE	*mtW*
Juveniles (0–3 years old)		
Main to West	0.025 (0.011–0.058)	0.034 (0.013–0.082)
Main to Main*	0.691 (0.632–0.743)	0.885 (0.835–0.922)
Main to South	0.261 (0.211–0.318)	0.070 (0.043–0.111)
Main to Far South	0.023 (0.009–0.061)	0.011 (0.002–0.071)
South to West	0.026 (0.006–0.105)	0.029 (0.001–0.441)
South to Main	0.252 (0.172–0.355)	0.186 (0.071–0.405)
South to South*	0.690 (0.580–0.782)	0.785 (0.557–0.914)
South to Far South	0.032 (0.008–0.125)	0 (0–0)
Animals 4± years old		
Main to West	0 (0–0)	0.017 (0.006–0.044)
Main to Main*	0.918 (0.886–0.942)	0.948 (0.916–0.968)
Main to South	0.082 (0.058–0.114)	0.035 (0.020–0.061)
Main to Far South	0 (0–0)	0 (0–0)
South to West	0.010 (0.001–0.066)	
South to Main	0.240 (0.176–0.317)	
South to South*	0.675 (0.582–0.756)	
South to Far South	0.075 (0.035–0.155)	
Far South to West	0 (0–0)	
Far South to Main	0 (0–0)	
Far South to South	0.362 (0.083–0.779)	
Far South to Far South*	0.638 (0.221–0.917)	

Objective 6: Survival effect for Western Stock region-born animals in the Eastern Stock region.—A survival benefit for sea lions being in the Eastern Stock region was observed for Western Stock region-born females. Western Stock region-born females in the Eastern Stock region had higher annual survival than Western Stock region-born females that were in the Western Stock region (+0.127, +0.099, and +0.032 at ages 1, 2, and 3+ years old, respectively; Supplementary Data SD2c, model 2). This resulted in survival to breeding age (i.e., 4 years old for females) significantly higher for *mtW* females born at the new rookeries (0.55) than for females born in the Western Stock region (0.41). Model results suggested a benefit for males as well but only when the effect of being in the Eastern Stock region on survival was set equal for males and females (Supplementary Data SD2c: additive effect, model 5); a survival benefit for males was not supported from data on males alone (Supplementary Data SD2c, model 3). The model with equal effect for females and males (Supplementary Data SD2c, model 5) produced survival differences of females (+0.089, +0.067, +0.03 for ages 1, 2, and 3–8 years old, respectively) and males (+0.107, +0.086, +0.045 for the same ages). Survival estimates at ages 1+ years old were similar (±0.05) for

Western Stock region-born females in the Eastern Stock region compared to estimates for females born at Graves Rocks from Hastings et al. (2011).

DISCUSSION

Adult female Steller sea lions that successfully dispersed from the depleted western population to northern Southeast Alaska where new rookeries have developed and which was characterized by high population growth had increased survival and greater reproductive success in terms of pup survival to breeding age than those who remained west of the stock boundary. However, pups born in this recently colonized area that had maternal origins from the depleted western population had slightly poorer body condition and lower first-year survival, and had more restricted movements than their counterparts from the growing eastern population. Together, these findings have provided a uniquely detailed insight into the dispersal strategies of a large marine mammal and the consequences of these strategies in terms of realized fitness cost-benefit. They also indicate that inherent genetic factors as well as environmental factors may contribute to increased fitness in a recently colonized area.

For Steller sea lions, the frequent use of the North Outer Coast and Glacier Bay (regions I, F, and G) by Western Stock region-born females, and also Frederick Sound [E] and Lynn Canal [H] for Western Stock region-born males, has been reported previously, and a southeastward shift in the current stock boundary to promote recovery and greater protection for endangered western Steller sea lions has been suggested (Jemison et al. 2018). Even greater protection may be required by consideration of the maternal genetic origin of animals, as a minimum of 13–38% of the animals aged 1+ years in the Extended–Core Mixing Zone are expected to be of the western genetic lineage (Table 5). The U.S. Endangered Species Act treats Distinct Population Segments as species, and its goal is not only the long-term survival of species but also protection of the biological diversity of protected species (Kelly 2010). Consequently, evaluation of the location of the stock boundary, including consideration of the dynamic Mixing Zone's unique status, or clarification of critical habitat of western Steller sea lions in Southeast Alaska may be warranted based on the genetic makeup of animals regardless of geographic location of residence or birth. Our results and those of previous studies (O'Corry-Crowe et al. 2014; Jemison et al. 2018; Rehberg et al. 2018) may guide precedent-forming management policy under the Endangered Species Act that deals with recently colonized areas whose spatial, demographic, and reproductive relationships with source populations are still in flux.

Increased survival for Western Stock region-born females that had successfully crossed the historical gap between breeding ranges of these populations was similar to recent findings of increased survival for southern Southeast Alaska-born females colonizing the same range hiatus (Hastings et al. 2011). This lends further support that range convergence was

Table 5.—Proportions of Steller sea lion (*Eumetopias jubatus*) nonpups using regions in the population mixing zone (northern–central Southeast Alaska) by birth region, age-class, and maternal genetic lineage (*mtW* or *mtE*: western or eastern maternal haplotype). Birth regions were WSR (born in the Western Stock region, all with *mtW*), MZ (born in the new rookeries in the Mixing Zone of the Eastern Stock region: Graves Rocks and White Sisters, with *mtW* or *mtE*), or South (born in southern Southeast Alaska, Eastern Stock region: Forrester and Hazy rookeries, all with *mtE*). Regions of Southeast Alaska were: F, northern Outer Coast (OC); G, Glacier Bay; H, Lynn Canal; E, Frederick Sound; and D, central Outer Coast (Fig. 1). *mtW* Total* = sum of WSR and MZ-*mtW*.

Group	Region of Southeast Alaska				
	F	G	H	E	D
	North OC	Glacier Bay	Lynn Canal	Fred Sound	Central OC
Juveniles (1–3 years old)					
South	0.298	0.208	0.282	0.522	0.461
MZ–*mtE*	0.326	0.449	0.421	0.302	0.523
MZ–*mtW*	0.258	0.272	0.288	0.166	0.004
WSR	0.118	0.071	0.009	0.010	0.012
mtW Total*	0.376	0.343	0.297	0.176	0.016
Animals 4+ years old					
South	0.203	0.207	0.510	0.765	0.665
MZ–*mtE*	0.411	0.396	0.375	0.170	0.290
MZ–*mtW*	0.314	0.322	0.098	0.053	0.014
WSR	0.072	0.075	0.017	0.012	0.031
mtW Total*	0.386	0.397	0.115	0.065	0.045
All nonpups (1+ years old)					
South	0.223	0.208	0.427	0.630	0.566
MZ–*mtE*	0.393	0.420	0.392	0.243	0.403
MZ–*mtW*	0.302	0.299	0.167	0.115	0.009
WSR	0.082	0.073	0.014	0.012	0.022
mtW Total*	0.384	0.372	0.181	0.127	0.031

most likely due, at least in part, to favorable conditions near the new rookeries, such as potentially high productivity compared to their natal sites (Mathews et al. 2011; Rehberg et al. 2018). High productivity near the new rookeries as a primary driver of these patterns was also potentially suggested by heavier pups produced in the Mixing Zone than in southern Southeast Alaska (Hastings et al. 2011). Successful Western Stock region-born female dispersers also had similar survival to Mixing Zone-born females, including some of the highest survival probabilities observed for Steller sea lions across their range (see figure 7 in Wright et al. 2017), perhaps due to a common environmental cause. However, more study is required to determine the role of environmental conditions versus potential inherent factors in shaping these patterns, particularly, 1) if a higher quality of individual, with higher survival capacity, successfully dispersed; and 2) if interbreeding among eastern and western Steller sea lions resulted in larger pups, with higher survival and fitness, than pups with parents from the same stock (Acevedo-Whitehouse et al. 2003).

Emigration patterns can be caused solely by natal environmental conditions irrespective of conditions in the new environment (Baines and McCauley 2018). Western Stock region-born females moved farther (the outer coastline distance from Graves Rocks to Forrester Islands is shorter [~400 km] than to Marmot Island or Seal Rocks [~1,000 and 600 km, respectively]), against the primary direction of the Alaska Coastal Current (north and west—Stabeno et al. 2016), and through an area with fewer established Steller sea lion haul-outs (Fig. 1) than southern Southeast Alaska-born females to utilize the productive Mixing Zone. This difference suggests particularly low

productivity in the west may also have been the impetus for the riskier dispersal undertaken by Western Stock region-born females. Whether release from predation pressure, pollutants, or pathogens were factors in the movement of Western Stock region-born females east remains unknown. Susceptibility to pathogens due to reduced heterozygosity may be greater following severe population decline and in threatened populations (Acevedo-Whitehouse et al. 2003; Spielman et al. 2004). Predation, such as by transient killer whales (*Orcinus orca*), salmon sharks (*Lamna ditropis*), and Pacific sleeper sharks (*Somniosus pacificus*), may be a significant source of mortality for juvenile Steller sea lions in Prince William Sound and around the Kenai Peninsula (Horning and Mellish 2012), where many emigrant females originated (Jemison et al. 2013). However, transient killer whales occur in significant numbers and are known predators on Steller sea lions in Southeast Alaska as well (Dahlheim and White 2010).

If the benefits of leaving a poor patch are greater than the costs of dispersal, individuals should leave poor-quality habitat patches for high-quality patches (Clobert et al. 2012). Reduced survival of Western Stock region-born Steller sea lions using Southeast Alaska (successful dispersers) compared to those that remained in the Western Stock region due to the dispersal movement was not addressed by our study due to model limitations in determining survival effects for both the areas of origin and destination; instead, only the effect of the origin on survival was estimated. Sample sizes were inadequate to address this question because few animals were observed crossing the stock boundary (Jemison et al. 2013). For example, the highest annual movement rate observed for animals crossing the boundary

was only 0.039 (Western Stock region-born juveniles moving to North Outer Coast [F]; Supplementary Data SD3). Transfer costs of dispersal often observed for vertebrates include increased mortality due to higher risk of predation and wounding (Soulsbury et al. 2008; Johnson et al. 2009), and physiological costs due to increased energy expenditure for movement (Gustine et al. 2006). Postsettlement costs for vertebrates once in a new environment include loss of social rank and higher levels of intraspecific aggression (Cant et al. 2001), and decreased survival and reproductive success due to unfamiliarity with the new environment (Pärt 1991; Brown et al. 2008).

Postsettlement costs in terms of survival for western females that had successfully dispersed to the Eastern Stock region were not obvious in our study; instead, their survival was higher than those that were in the Western Stock region. However, ~10% lower first-year survival for *mtW* pups compared to *mtE* pups born in the same productive area may reflect a potential greater cost to western mothers from dispersal through reduced offspring survival. If a transfer cost occurred for dispersing Western Stock region-born females, it likely occurred during their juvenile years up to age 3, as most females dispersed before breeding age (Jemison et al. 2013, 2018), such that conditions during juvenile years potentially affected their future reproductive success at 4–5+ years of age. Despite this potential cost, survival to breeding age (i.e., 4 years of age for females) was significantly higher for *mtW* females born at the new rookeries (0.55) than for females born in the Western Stock region (0.41), suggesting a fitness benefit of higher survival of female offspring, in addition to their own survival, for dispersing western mothers.

Although genetic factors have yet to be addressed, if dispersal costs to mothers account for differences in pup survival based on *mtHap*, these costs must have been greater for Western Stock region-born than southern Southeast Alaska-born dispersers. Possible transfer costs of dispersal affecting offspring survival include reduced body condition of dispersers, especially western dispersers, which made longer-range and potentially riskier movements to the new rookeries than southern Southeast Alaska-born dispersers. Southern Southeast Alaska-born, dispersing females also probably had local knowledge of foraging and resting areas which are numerous between the natal site (Forrester Islands) and the new rookeries. For Western stock region-born, dispersing females, however, only a few significant haul-outs exist on the long, exposed coastline between Prince William Sound and the new rookeries: the two largest are Cape St. Elias and Dry Bay, an ephemeral but very large, early spring haul-out associated with a seasonal eulachon (*Thaleichthys pacificus*) aggregation (Jemison et al. 2018; Fig. 1). Given that the average maximum observed distance of females away from their natal rookeries in Alaska in summer was 1,000 km (Jemison et al. 2018), female immigrants from Marmot Island may have displayed the longest-range dispersal for average members of this group. However, we observed a single branded female born at Rogue Reef, Oregon (Eastern Stock region—Wright et al. 2017) that produced pups in the new rookeries from ≥ 5 to 15 years of age, nearly 2,000 km from her natal site.

The northward travel by southern Southeast Alaska-born females to the new rookeries may be assisted by the Alaska Coastal Current, which flows northward until Prince William Sound and then westward, especially when it is strongest during fall and winter, whereas Western Stock region-born females must travel counter to this current to the new rookeries (Stabeno et al. 2016). However, the coastal current is complex and noncontinuous in Southeast Alaska (Stabeno et al. 2016) and its influence on movements of Steller sea lions is unknown. These factors suggest energy expenditure for movement may have been greater for western than eastern dispersers.

The similar body size of pups regardless of *mtHap* and only slight reduction in body condition of *mtW* compared to *mtE* pups born at the new rookeries suggests that if body condition was reduced for Western Stock region-born mothers due to higher dispersal costs likely incurred during juvenile ages, this did not obviously compromise pup birth weight or neonatal growth. However, unaccounted-for effects of mixed-stock lineage and of male lineage on growth patterns and size of offspring may confound results based on *mtHap* alone. If body size has a genetic basis based on maternal contribution in Steller sea lions, *mtW* pups born at the new rookeries would be heavier than *mtE* pups because western Steller sea lions are heavier or larger than eastern Steller sea lions as neonates, during their first year, and as juveniles and adults (Merrick et al. 1995; Sweeney et al. 2015; Rea et al. 2016). If the similar size of pups born at the new rookeries, regardless of *mtHap*, is due in part to maternal contribution, this suggests reduced offspring size for *mtW* mothers or that maternal characteristics differ between western and eastern dispersers. It is unknown if maternal effects contributed to this pattern, such as if Western Stock region-born dispersers were younger, smaller, or leaner than southern Southeast Alaska-born dispersers, suggesting riskier and particularly longer-range movements were undertaken by only significantly compromised females. Dispersal propensity is often related to body size or condition, but may be positively or negatively associated with these factors depending on the context (Bowler and Benton 2005). A younger age structure of mothers from the western versus eastern population at the new rookeries, as would result if the sites were first colonized by eastern animals and later by western animals, may also produce this result. Maternal effects on offspring size are largely unstudied in Steller sea lions, but neonatal survival and attendance were reduced for younger or primiparous mothers compared to older or multiparous mothers (Maniscalco et al. 2006; Burkanov et al. 2011; Hastings 2017). If offspring size was reduced for Western Stock region-born mothers who dispersed, this may also suggest that female Steller sea lions are capable of pursuing different reproductive strategies in different areas, such as producing few, large pups in poor environments where offspring survival may be compromised, versus more, smaller pups capable of surviving in productive environments.

If dispersing females experienced increased intraspecific aggression or reduced protection from a social network due to their loss of or their low social rank, then postsettlement costs

may also have compromised pup body condition and survival. A lack of local knowledge of foraging, resting, or predator-free areas leading to reduced offspring survival could also contribute to postsettlement cost. Reduced local knowledge or a compromised social network for western-population-related mothers may be indicated by the reduced movements of *mtW* pups compared to *mtE* pups. Steller sea lion pups remain dependent on their mothers for at least ~1 year and commonly for 2+ years (Trites et al. 2006), accompanying her to foraging patches and resting areas and presumably learning from their mother about their environment. Knowledge of the local environment may be particularly important for Steller sea lions in Southeast Alaska, which depend on ephemeral and geographically patchy prey, especially in winter and spring, which also occur at relatively persistent and predictable prey hot spots (Womble et al. 2005; Gende and Sigler 2006). Social network dynamics coupled with ecological factors may shape foraging behaviors (Allen et al. 2013), and be critical to information transmission in social animals (Kurvers et al. 2014).

Whether *mtW* pups remaining near their natal sites were exposed to greater hazards such as storms, predators, pollutants, and fisheries interactions is unknown. Steller sea lions in Southeast Alaska generally move from outside waters in summer to inside waters in winter, perhaps for protection from storms or following food resources (Sease and York 2003). Although prevalences of antibodies to various diseases were similar in both the eastern and western populations (Burek et al. 2005), serological studies based on *mtHap* for pups from the new colonies are needed to determine if lower first-year survival of *mtW* compared to *mtE* pups was due in part to lower immunity of *mtW* pups to novel disease strains in their new environment.

Finally, personality traits may be relevant to the observed patterns. The "behavioral dispersal syndrome" is a group of traits that link variation in morphology and behavior to dispersal patterns (Spiegel et al. 2017). Often higher levels of aggressiveness, boldness, and exploratory behavior, also correlated with reduced levels of sociality, are associated with higher dispersal tendency (Sih et al. 2004, 2012; Wolf and Weissing 2012; Spiegel et al. 2017). Boldness and exploration may assist dispersers in quickly learning about their new environment (Korsten et al. 2013 and references therein), but greater aggressiveness of dispersers may lead to lower reproductive success, such as due to poor parenting (Price and Sol 2008). Genetics at least partially underlie some personality traits (Hansson et al. 2003), such as exploratory behavior and novelty seeking, which have been linked to the dopamine D4 receptor in vertebrates across diverse taxa (Ebstein 2006; Fidler et al. 2007). Foraging behavior may also differ between dispersers and nondispersers; high foraging activity has been linked to the "for" gene, which is coupled with a greater tendency toward long-distance dispersal and higher metabolic rates (Edelsparre et al. 2014; Spiegel et al. 2017). Whether differing dispersal cues, such as if western dispersers are highly dispersive individuals responding to rapid and severe population decline compared to eastern dispersers making less risky movements from environments

gradually reaching carrying capacity, results in differences in personality traits, foraging behaviors, and other genetic factors of western versus eastern dispersers requires more study.

Monitoring of the genetic composition and growth of the new rookeries is required to verify if the proportion of *mtW* animals produced at these rookeries may be declining in recent years. This may be due to reduced dispersal pressure on western females due to favorable environmental changes in their natal areas (Fritz et al. 2014, 2016) coupled with asymmetric costs for dispersal for western versus eastern females (this study). This study has shown fitness benefits for dispersing females from a severely declining population through higher female survival and higher offspring survival for successful dispersers. Reduced survival of pups based on maternal genetic origin may have been due to asymmetric costs of dispersal, maternal effects, or genetic factors possibly linked to personality traits of females that may differ with the magnitude of dispersal drive. The potential role of these more subtle but intriguing factors in the observed patterns requires further study.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Results of generalized linear models for examining effects of sex, natal rookery, birth year, and maternal genetic lineage (*mtHap*) on body mass or body condition index of Steller sea lion (*Eumetopias jubatus*) pups

born at the new rookeries. Natal rookeries were White Sisters or Graves Rocks; birth years were 2002, 2004, 2005, and 2016.

Supplementary Data SD2.—Model selection results for Cormack–Jolly–Seber (CJS) models and multistate models for examining effects of age, sex, natal rookery, body mass of pups, and maternal genetic lineage (*mtHap*) on probabilities of survival (*S*), resighting (*p*), and movement between geographic regions (*ψ*) for Steller sea lions (*Eumetopias jubatus*) born at the new rookeries (a–b), and survival effects for being east of the stock boundary for western-born sea lions (c). Time = year, natal rookeries (nr) were White Sisters or Graves Rocks. For female and males, respectively, four and five age-classes were used for *S* and four and eight age-classes for *p*. *MtHap* and body mass of pups at capture were included as additive effects across age (*mtHap* or mass), at age 0 only (first-year survival, *mtHap*-0 or mass0), at age 0 and 1 only (*mtHap*-01 or mass01, effect equal across these ages), and for *p*: age 1 only (*mtHap*1) or age 1 and 2 only (*mtHap*12, effect equal across these ages). Regions in multistate models were Main Study Area, South Area, Far South Area, and West Area (see text). Npar = number of parameters in the model, ΔAICc = based on Akaike's information criterion corrected for small sample size, the difference in values from the top model, Weight = weight of the model in the model set (based on AICc).

Supplementary Data SD3.—Estimates of movement probabilities (*ψ*) into and out of geographic regions for Steller sea lions (*Eumetopias jubatus*) within northern and central Southeast Alaska by birth region, age-class, and maternal genetic lineage (*mtE* or *mtW*: eastern or western maternal haplotype). Birth regions were WSR (born in the Western Stock region, all *mtW*), MZ (born in the new rookeries in the Mixing Zone of the Eastern Stock region: Graves Rocks and White Sisters, *mtW* or *mtE*), or South (born in the southern Southeast Alaska, Eastern Stock region: Forrester and Hazy rookeries, all *mtE*). Regions of Southeast Alaska were: F, north Outer Coast (OC); G, Glacier Bay; H, Lynn Canal; E: Frederick Sound; and D: central Outer Coast (see Fig. 1). Movement probabilities were estimates of *ψ* for a) not in region *to* in region and b) in region *to* in region, from multistate mark-recapture models. * in b) indicate estimates for regions * groups which had very low probabilities of movement to the region in a). Two values for Region F, north Outer Coast, are for natal rookeries: Forrester, Hazy and White Sisters, Graves Rocks.

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