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Winter movements and long-term dispersal of Steller sea lions in the Glacier Bay region of Southeast Alaska

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ABSTRACT: Steller sea lions *Eumetopias jubatus* in the Glacier Bay region of northern Southeast Alaska experience greater survival and more rapid population growth than sea lions elsewhere in this region. To better understand demographics of sea lions in the region, and to describe the origins and behavior of sea lions and relate these descriptions to previous studies, we studied genetic origins, residency, foraging range, diving behavior, and dispersal of immature sea lions (≤24 mo of age) captured in Glacier Bay. Fifty-two percent of individuals had maternal origins in the distant (550 km) endangered western population rather than in the local recovered eastern population. During winter, 5 mo old pups, dependent on their dams for nutrition, remained within Glacier Bay, diving to shallow depths (≤108 m) mainly during daylight, whereas older (17 mo old) juveniles ranged more widely to areas of known seasonal prey aggregations, performing deep (≥241 m) nocturnal dives. Both pups and juveniles remained within the northern portion of Southeast Alaska, in contrast to farther-ranging pup and juvenile sea lions captured elsewhere in Southeast Alaska. Over the long term, females from Glacier Bay remained within this northern area through maturity and were sighted breeding in this area only. Restricted ranging patterns and natal and breeding philopatry by Steller sea lions of both eastern and western distinct population segment origin in the Glacier Bay region reveal that optimal foraging and breeding conditions likely prevail and help explain the recent colonization, increased survival, and rapid population growth of this species in the region.

KEY WORDS: Steller sea lions · Alaska · Glacier Bay · Foraging · Eastern distinct population segment · eDPS · Western distinct population segment · wDPS · Prey availability

INTRODUCTION

Steller sea lions *Eumetopias jubatus* are distributed along the North Pacific rim from northern Japan to California (Loughlin et al. 1984, Burkanov & Loughlin 2005) in 2 distinct population segments with a boundary at longitude 144° W (Fig. 1): the endangered western distinct population segment (wDPS), north and west of Glacier Bay, and the recently delisted eastern distinct population segment (eDPS), to the south and east (Hoffman et al. 2006, O’Corry-Crowe et al. 2006, National Marine Fisheries Service 2013, Allen & Angliss 2015). However, genetic analysis of Steller sea lion pups from recently colonized rookeries in northern Southeast Alaska revealed that this region, which includes Glacier Bay, represents a mixing zone between these 2 evolutionarily distinct population segments (O’Corry-Crowe et al. 2014). Thus, the distinct population segment (DPS) of origin for sea lions in this area is not always clear. The non-

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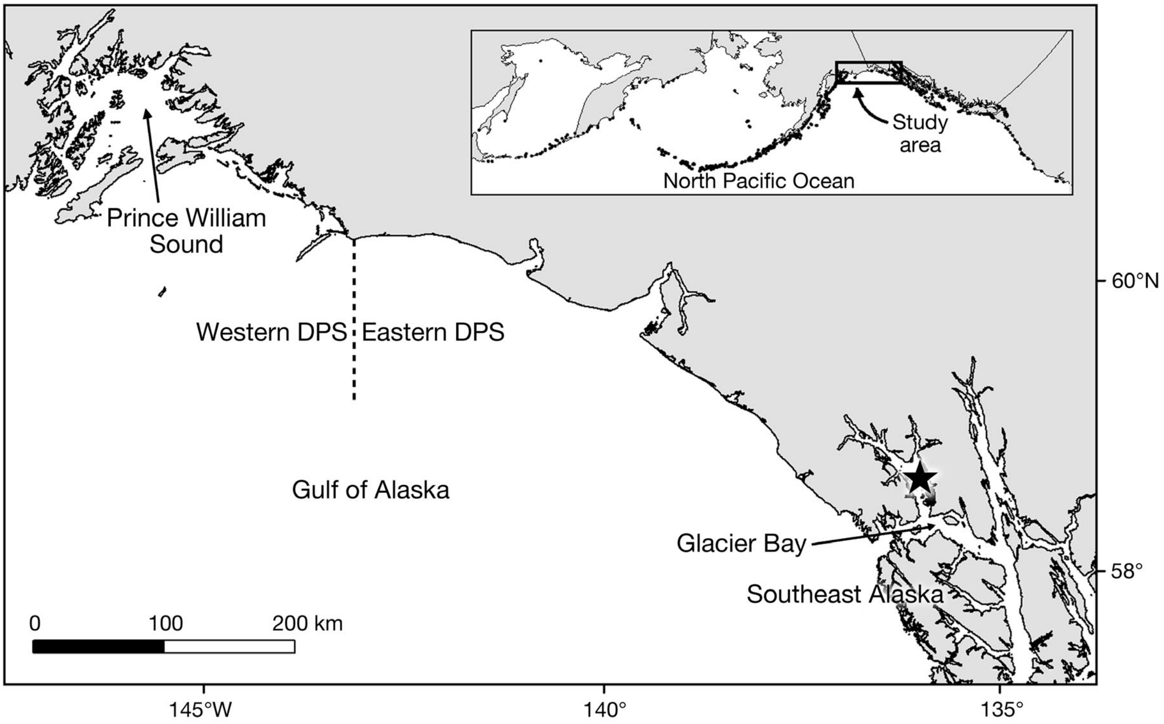

Fig. 1. Study area within which Steller sea lions captured at South Marble Island (indicated by dark star) were tracked by satellite telemetry and by brand-resight observations. Dashed line indicates the geographic boundary between the eastern distinct population segment (DPS) and western DPS. Inset map locates the study area within the range of Steller sea lions (haulouts indicated by dark dots) along the North Pacific rim

neonate Steller sea lions of the Glacier Bay, Icy Strait, and Cross Sound region (hereinafter the Glacier Bay region) have not previously been captured, marked, satellite tracked, or genotyped. The primary objective of this study was to investigate the foraging behavior and dispersal patterns of this relatively unknown subgroup and understand these behaviors in the context of the larger population.

Understanding the movement patterns of Steller sea lions in the Glacier Bay region is important for several reasons. First, unlike sea lions born farther north and south, the Steller sea lions born on and colonizing rookeries in this area near the population boundary are drawn from both the eDPS and wDPS (O'Corry-Crowe et al. 2014), with females born in Prince William Sound having particularly high probabilities of being within this region (Jemison et al. 2013). Second, the sea lion pups in this region have significantly greater survival rates than sea lions elsewhere in Alaska (Hastings et al. 2011, Fritz et al. 2014, Pendleton et al. 2016). Third, the number of sea lions in the Glacier Bay region has increased rapidly compared to elsewhere across the range of Steller sea lions (composite growth of 8.28% yr^{-1}, 1970–2009; Mathews et al. 2011, Fritz et al. 2014). Fourth, Steller sea lions within the eDPS, previously listed as threatened under the US Endangered Species Act, were delisted in 2013 (National Marine Fisheries Service 2013); however, the adjacent wDPS remains listed as endangered. Given the occurrence of both eDPS and wDPS sea lions in the Glacier Bay region and the high survival rates recorded for pups in northern Southeast Alaska, investigating the residency patterns, individual movements, diving behavior, and natal dispersal of non-neonate and juvenile Steller sea lions in the Glacier Bay region could provide critical insights into the factors that influence sea lion behavioral ecology, survival, and reproductive success in this transition zone between 2 DPSs with very different population trajectories.

Throughout Southeast Alaska, including the Glacier Bay region, the eDPS of Steller sea lions has grown steadily over the past 30 yr (Pitcher et al. 2007, Mathews et al. 2011). In contrast, over the same time span, the wDPS north and west of Glacier Bay declined by approximately 80%, followed by a geographically uneven recovery in survival and population size since 2003 (Fritz et al. 2014, 2016). The Glacier Bay region contains haulouts (including South Marble Island, established 1985) and breeding rookeries (White Sisters, established early 1990s; Graves

Rocks, established 1999) colonized more recently than those colonized north of Glacier Bay by the wDPS and south of Glacier Bay by the eDPS (Womble et al. 2009, Mathews et al. 2011, O'Corry-Crowe et al. 2014). The rapid growth in the number of sea lions in the Glacier Bay region is in contrast to the sympatric harbor seal *Phoca vitulina* which declined precipitously in Glacier Bay from 1992 to 2008 (Mathews & Pendleton 2006, Womble et al. 2010).

Unlike Steller sea lions studied in other regions of Alaska, non-neonate and yearling Steller sea lions of the Glacier Bay region have not been tracked using satellite telemetry. The objective of this study was to place these relatively unstudied subgroups of sea lions in the context of the larger population. We accomplished this by comparing the behavior of immature Steller sea lions in the Glacier Bay region during the winter of 2009 to 2010 to the behavior of immature sea lions previously studied in other regions of Alaska (Raum-Suryan et al. 2004, Pitcher et al. 2005) and to prey availability in this region. We also compared their age-specific mass with that of Steller sea lions of similar age from other regions. The population origins of these sea lions were identified using analysis of mitochondrial DNA (mtDNA) and placed in context with the genetic origins of Steller sea lions in adjacent areas (O'Corry-Crowe et al. 2014). Finally, natal dispersal movements of captured sea lions were examined to determine where Steller sea lions marked in Glacier Bay settled to breed at maturity.

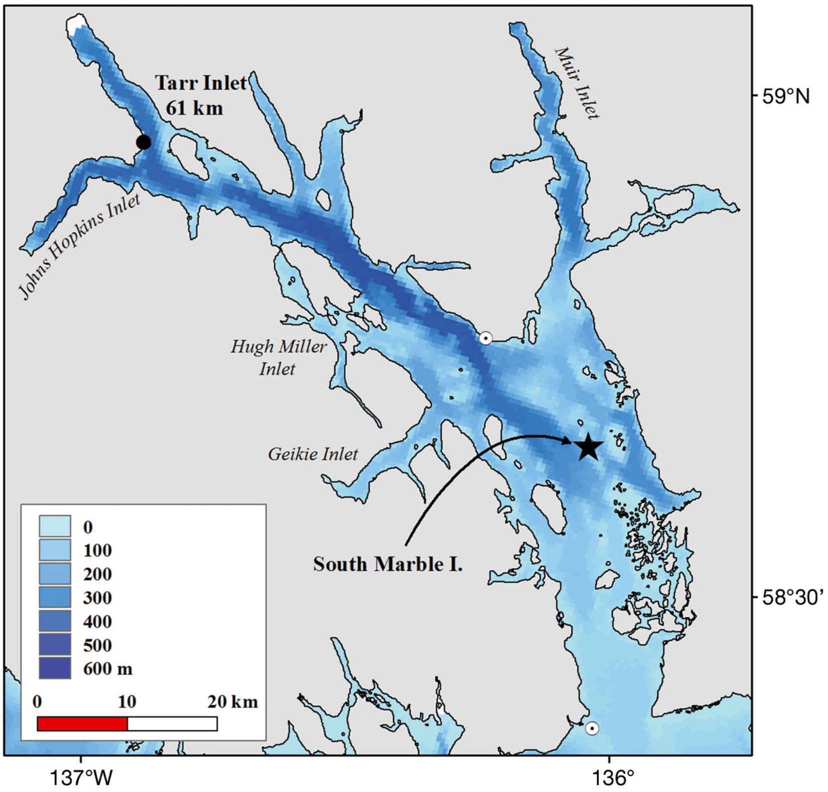

Fig. 2. Range of 5 Steller sea lion pups and 3 juveniles captured and tagged at South Marble Island (indicated by dark star) and moving and diving within Glacier Bay during winter 2009 to 2010. Dark circles indicate haulouts occupied by pups; dotted circles indicate other haulouts available. Shortest path movement distances from the point of capture to each haulout used are indicated adjacent to haulout names. Seafloor depth is indicated by shading and provides context to Table 4 and text

MATERIALS AND METHODS

Glacier Bay (58° 40' N, 136° 05' W) is a subarctic tidewater glacial fjord in northern Southeast Alaska that has undergone rapid deglaciation over the last 225 yr (Field 1947, Hall et al. 1995; our Fig. 1). Glacier Bay is a marine protected area (MPA) that constitutes part of Glacier Bay National Park, a Biosphere Reserve and World Heritage Site, and includes over 240 000 ha of marine waters (National Research Council 2001; our Fig. 2).

Young-of-year Steller sea lion pups (5 mo old) and juveniles (17 mo old) were captured during late autumn, November 2009 (Table 1), at the South Marble Island haulout in central Glacier Bay (Fig. 2), using the underwater dive capture technique (Raum-Suryan et al. 2004). Sea lions were then transferred by skiff to a research vessel and placed under isoflurane anesthesia (Heath et al. 1997). Researchers weighed the sea lions using a load cell (IQ Plus 590-DC, Rice Lake Weighing Systems) and aged them using canine length (King et al. 2007) assuming 1 June as birthdate (Pitcher et al. 2001). Tissue samples were taken from the hind flippers using a stainless steel ear-notching tool and preserved in 90% ethanol for genetic analysis. Total DNA was extracted and amplified, and 531 bp of the mtDNA control region were sequenced (O'Corry-Crowe et al. 2006). Likelihood-based assignment tests (to either the eDPS or wDPS) based on mtDNA haplotype for these newly sampled animals were conducted against previous population baselines calculated for the eDPS

Table 1. Steller sea lion pups (5 mo old) and juveniles (17 mo old) live captured, marked, sampled, and released at South Marble Island, Glacier Bay, Alaska, during November 2009. Animal identifiers used in this paper are the brand markings applied to each individual. Individual assignments to the eastern or western distinct population segment (DPS) based on mitochondrial DNA (mtDNA) frequencies are indicated; LP indicates statistical power too low to determine, n/a indicates assignment was not possible. Sea lions observed occupying a rookery between 2009 and 2015 are identified by rookery location; sea lions observed breeding at the rookery and year of first reproduction are indicated. Blank entries indicate sea lions were not observed at a rookery and/or breeding. F: female; M: male

Animal identifier	Sex	Age (mo)	Mass (kg)	mtDNA DPS assignment	Dispersal to rookery	Observed breeding (yr)
=716	F	5	67.0	Western		
=717	F	5	54.5	Western	Graves Rocks	Yes (2014)
=718	F	5	68.0	Western		
=723	F	5	55.5	Eastern		
=728	F	5	73.5	Western	Graves Rocks	Yes (2015)
=730	F	5	64.5	Eastern	Graves Rocks	Yes (2015)
=732	F	5	52.5	Western	Graves Rocks	Yes (2014)
=733	F	5	59.0	Eastern	White Sisters	Yes (2015)
=734	F	5	72.5	n/a	Graves Rocks	
=735	F	5	75.0	Western	Graves Rocks/ White Sisters	Yes (2014)
=737	F	5	65.0	Wastern	White Sisters	Yes (2014)
=739	F	5	52.0	LP	Graves Rocks	Yes (2014)
=740	F	5	66.0	Western	Graves Rocks	Yes (2015)
=741	F	5	71.0	Western	Graves Rocks	
=743	F	5	62.5	Eastern		
=746	F	5	59.0	n/a	White Sisters	Yes (2014)
=721	M	5	89.5	Western		
=726	M	5	68.5	Eastern		
=729	M	5	63.0	Eastern	Graves Rocks	
=731	M	5	73.5	Eastern		
=736	M	5	73.5	LP		
=738	M	5	87.0	Western		
=744	M	5	87.0	Western	Graves Rocks	
=745	M	5	75.5	Western		
=7521	F	17	112.0	Eastern	White Sisters	Yes (2012)
=727	F	17	116.0	LP	White Sisters	
=719	M	17	169.0	Western	Graves Rocks	
=720	M	17	112.5	Eastern		
=722	M	17	141.5	Eastern		
=4=	M	17	156.0	Eastern	Graves Rocks	
=742	M	17	96.0	n/a		

and wDPS (O'Corry-Crowe et al. 2014; see Table 4). To facilitate long-term tracking of movement, survival, and reproduction estimates, sea lions were hot branded on the left shoulder (Hastings et al. 2009) using 0.95 cm diameter stainless steel irons, forming characters 10.2 cm high by 7.5 cm wide.

A subset of pups and juveniles was tracked using satellite-relay dive- and location-reporting instruments (SPLASH Model 201C, Wildlife Computers) attached to the fur using 10 min epoxy (Devcon). Tags were attached to the top of the head of all juveniles and 1 pup; all other pups had tags attached along the dorsal midline between the scapulae (Table 1). Tags were programmed to achieve 8 mo endurance (November through July) at 250 transmissions d^{-1}.

Long-term (multi-year) movements and reproduction were identified by visually resighting branded sea lions during annual dedicated surveys between November 2009 and July 2015. Most surveys were conducted by observing haulouts and rookeries from nearby skiffs, with land-based observation possible at some rookeries. Most observations were collected during dedicated brand-resight cruises visiting Southeast Alaska and Gulf of Alaska haulouts and rookeries in June and July each year. More intensive land-based surveys were conducted annually at the Lowrie Island rookery mid-May through mid-July. The summer breeding season observations were augmented by aerial surveys (primarily during spring at the seasonal Dry Bay/Alsek River haulout; Fig. 3) and both periodic (e.g. Benjamin Island, Gran Point; Fig. 3) and opportunistic (e.g. Inian Islands, South Marble Island; Figs. 2 & 3) skiff-based visits during other months (Jemison et al. 2013). Survey effort was variable across the study area, with extra effort (repeat visits over 2–3 d) made at breeding rookeries and larger-sized haulouts. Individual marked sea lions were observed using binoculars, and all identities were confirmed by making digital photographs of brands for comparison to a photographic catalog of known branded sea lions. Pupping of females was determined by observing marked adult females and recording behaviors, using standardized behavior codes, suggesting presence of a dependent pup (i.e. nursing, nuzzling, following, and reuniting; Hastings & Jemison 2016). Breeding of males was identified by observing territorial behavior (i.e. males appeared to defend space with females) on the rookeries and photo-confirming their identities.

Telemetry data processing and analysis

The SPLASH tags were programmed to provide Argos system location estimates at irregular time

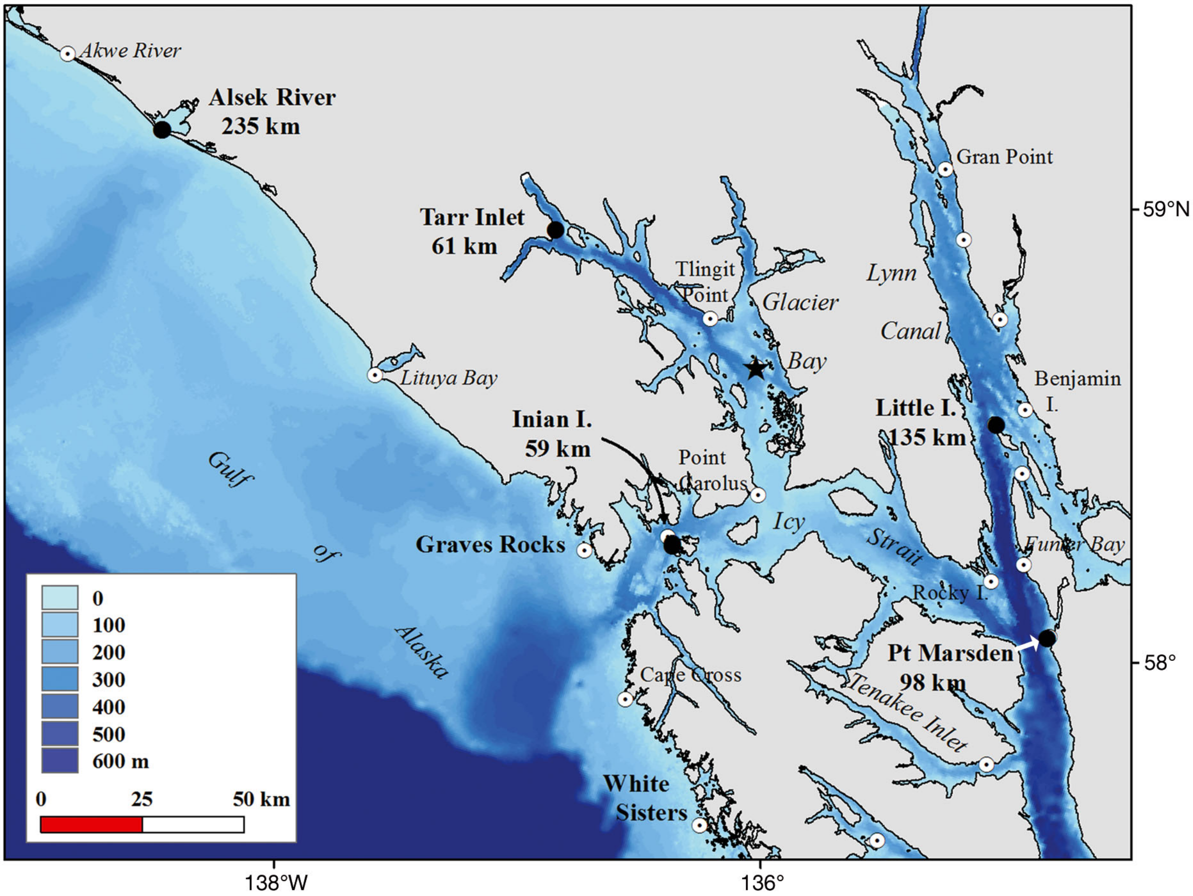

Fig. 3. Glacier Bay region, indicating range of 7 Steller sea lion juveniles captured at South Marble Island (indicated by dark star) and moving throughout northern Southeast Alaska during winter 2009 to 2010. Dark circles indicate haulouts occupied by juveniles; dotted circles indicate other haulouts available. Shortest path movement distances from the point of capture to each haulout used are indicated adjacent to haulout names. Seafloor depth is indicated by shading and provides context to Table 4 and text

intervals. Tags were also programmed to summarize dive depth (the count of dives within fourteen 50 m depth ranges during 4 daily 6 h periods) and the proportion of time at depth (the proportion of time spent in each of 14 depth ranges, including a surface category, during 4 daily 6 h periods) and to report the depth of the deepest dive per 24 h period (accurate to 2 m). Tags also reported a continuous haulout timeline indicating whether each of seventy-two 20 min intervals d^{-1} were majority wet or majority dry and also provided a sporadic indicator of whether the tag was in wet or dry mode. Time-at-depth summaries were trimmed using the haulout timeline data such that only the time spent off the haulout was used for analysis. Location estimates and data provided via the Argos system were extracted using DAP 2.0 software (Wildlife Computers 2009) into a Microsoft Access database and queried for analysis.

A haulout residency calendar was constructed to identify when particular haulouts were used by individual sea lions. Argos locations coded wet or dry were plotted (ArcMap 10.2, ESRI) against a map of known haulout locations and manually reviewed in sequence to determine the start date and end date of each sea lion's residency at a particular haulout. From this information, inter-haulout movements were identified and minimum haulout-to-haulout movement distances measured.

For each central-place haulout used by each individual, we summarized characteristics of diving and swimming behavior relevant to potential prey as determined from previous studies (Abookire et al. 2002, Robards et al. 2003, Arimitsu et al. 2008, Womble et al. 2014). Maximum dive depths made by individual sea lions while resident at the haulout were summarized (mean ± SD) for each 6 h dive period. Maximum dive depths for each 6 h dive period were also linked to the Argos location estimate(s) which occurred during the same period. We compared these depth-linked locations to an underlying model of seafloor depth (Rehberg & Gelatt 2003) to determine the proximity of an individual Steller sea lion's diving to the seafloor, an indicator of mid-water vs. benthic diving. To determine the relative focus on diving during daylight vs. darkness, an indicator of foraging effort on vertically migrating prey vs. light-insensitive prey, we calculated a ratio of the proportion of time spent submerged during daylight vs. the proportion of time spent submerged during darkness. Time submerged was calculated as the fraction of time spent deeper than the surface category within the trimmed time-at-depth summaries. Daylight hours were bounded by civil twilight as calculated by the US Naval Observatory sunrise/sunset calculator for Gustavus, Alaska (http://aa.usno.navy.mil/data/docs/RS_OneYear.php, accessed on 29 October 2010). Values >0 indicated that a greater proportion of daylight hours were spent diving, values <0 indicated a greater proportion of night hours were spent diving, and values centered about 0 indicated no difference. The single maximum depth readings recorded each day (accurate to 2 m) were presented in descriptive form because sample sizes were too small to allow inferences of population effects after accounting for age class and location (Rehberg et al. 2009).

Mass of captured sea lions was compared among 3 areas (Glacier Bay [present study], elsewhere within Southeast Alaska, and Prince William Sound [Rea et al. 2016]; Fig. 1), age class (5 mo old pup and 17 mo old juvenile), and sex using an ANOVA (R Core Team 2014), and post hoc comparisons were performed using the Tukey's HSD test. Fitted values were plotted against residuals and quantile–quantile plots made to assess whether model assumptions were met.

RESULTS

We captured twenty-four 5 mo old Steller sea lion pups (16 female, 8 male) and seven 17 mo old juveniles (2 female, 5 male; Table 1) at the South Marble Island haulout in central Glacier Bay, Alaska (Fig. 2). A subset of 5 pups (3 female, 2 male) and all 7 juveniles were instrumented with SPLASH tags (Table 2). Pups were tracked for 77 d (median; range 44–139) and juveniles for 75 d (median; range 36–79), far short of the intended tag endurance (240 d), with 6 of the 8 head-mounted SPLASH tags failing prematurely within 7 d of each other. Subsequent observation of 4 head-mounted tags revealed their antennae had been sheared off at the base.

Winter movement, diving, and foraging behavior

All but 3 pups (1 female and 2 males, all non-tagged) were visually observed alive after the end of their first winter at Glacier Bay. The 5 pups tracked by satellite from November through January remained within Glacier Bay for the duration of tag deployments (Fig. 2). Two pups (female =740, male =745) moved 61 km northward from South Marble Island to Tarr Inlet in the upper West Arm of Glacier Bay on 23 December 2009, whereas the remaining 3 pups used the South Marble Island haulout for the duration of their tag deployments. Pups at South Marble Island dove to maximum daily depths of 82 ± 24 m (mean ± SD, n = 3), whereas pups at Tarr Inlet increased their diving depths to 158 ± 34 m (n = 2). Pups at South Marble Island were tracked diving in waters 96 ± 56 m deep (maximum depth 383 m; Fig. 2). The maximum dive depths made by pups in this area reached 70 ± 6% (mean ± SD) of the water depth available to them. Two pups at Tarr Inlet swam in deeper waters, 204 ± 101 m (maximum depth 412 m, Fig. 2), but their diving used a shallower fraction of the water column available to them, coming within 60 ± 5% of water depth. Pups in all regions of Glacier Bay favored daytime diving, with a day:night proportion of time diving ratio of 0.20 ± 0.06 (mean ± SD, n = 5 pups)

All juveniles except 1 male were visually observed alive by late March, the end of the 2009–2010 winter.

Table 2. SPLASH tags deployed on 5 pup (5 mo old) and 7 juvenile (17 mo old) Steller sea lions at South Marble Island, Glacier Bay. Tracking duration and geographic range of movement from the initial capture site are indicated. Except for =740, all tags suffered premature failure; despite greater longevity of tracking, behavior of this sea lion was unremarkable and retained within summaries. F: female; M: male

Animal identifier	Sex	Capture date	Age (mo)	Deployment duration (d)	Range
=740	F	13 Nov 09	5	139	Glacier Bay
=741	F	13 Nov 09	5	62	Glacier Bay
=743	F	13 Nov 09	5	93	Glacier Bay
=744	M	13 Nov 09	5	44	Glacier Bay
=745	M	13 Nov 09	5	36	Glacier Bay
=7521	F	7 Nov 09	17	74	Glacier Bay
=727	F	8 Nov 09	17	78	Outer coast
=719	M	6 Nov 09	17	75	Icy Strait
=720	M	6 Nov 09	17	79	Outer coast
=722	M	7 Nov 09	17	73	Icy Strait
=4=	M	7 Nov 09	17	77	Glacier Bay
=742	M	13 Nov 09	17	44	Lynn Canal

Juveniles were satellite tracked from November through January, with both females and 1 male remaining within Glacier Bay throughout the period (Fig. 2). Juvenile Steller sea lions in Glacier Bay alternated time foraging in areas between South Marble Island and fjords within Glacier Bay (Fig. 2), diving to maximum daily depths of 152 ± 84 m (n = 7) and reaching 75 ± 4 % of the seafloor depths available to them (see Table 4). By December, 2 juvenile males moved out of Glacier Bay to the Inian Islands (59 km southward; Fig. 3) in Cross Sound, making dives 198 ± 49 m deep and reaching 57 ± 9 % of seafloor depth. One male travelled west through Icy Strait and Cross Sound and eventually northward 235 km to the outer coast near the Yakutat Forelands on 7 December and remained in the vicinity of the Alsek River and the Fairweather Grounds through 24 January, making dives of 88 ± 47 m and using 91 % of water depth available. One male travelled eastward 145 km to Point Marsden in Chatham Strait and to Little Island, an ephemeral haulout site, in Lynn Canal, making dives of 316 ± 32 m within average water depths of 406 m and using 73 % of seafloor depth.

Unlike pups, juveniles exhibited variability in diving behavior across individuals and regions. Juveniles resident at South Marble Island spent similar time diving in both daylight and darkness, with a day:night ratio of 0.03 ± 0.07 (resident for 255 animal-days; Fig. 4). Two juveniles travelling just outside Glacier Bay to the Inian Islands shared a remarkably similar preference for daylight diving (ratio of 0.28 ± 0.0007, resident for 80 animal-days; Fig. 4). Daylight preference was similarly observed for single individuals on the outer coast and at Tarr Inlet, and 2 juveniles showed a darkness preference at Hugh Miller Inlet in the West Arm of Glacier Bay and Little Island (Fig. 4), but these residencies were shorter than others.

Body condition

Male pups captured at South Marble Island in Glacier Bay were heavier than females (77.4 ± 6.5 vs. 64.7 ± 7.5 kg), and male juveniles were heavier than females (135.0 ± 30.0 vs. 114.0 ± 2.8 kg). The mass of pups captured at South Marble Island was not significantly different from same-age mass of pups of the wDPS in Prince William Sound ($F_{1,2}$ = 14.2, p = 0.67), but Glacier Bay pups were significantly heavier than same-age pups from elsewhere in Southeast Alaska (males 14.2 kg heavier, females 9.1 kg heavier; Table 3). In contrast, the juvenile male sea lions had no significant overall geographic difference in mass ($F_{1,2}$ = 10.8, p = 0.69), but female juveniles from Glacier Bay were significantly heavier than those from elsewhere in Southeast Alaska (females 13.1 kg heavier; Table 3).

Demographic origins

Of 24 pups and 7 juveniles captured in Glacier Bay, genetic analysis was successful for 20 and 5, respectively (Table 1); 6 individuals were not assigned to a DPS due to missing samples or low statistical power. This revealed that 60 % of the pups were assigned to the wDPS and 40 % to the eDPS based on mtDNA frequencies. By contrast, most juveniles (4 of the 5

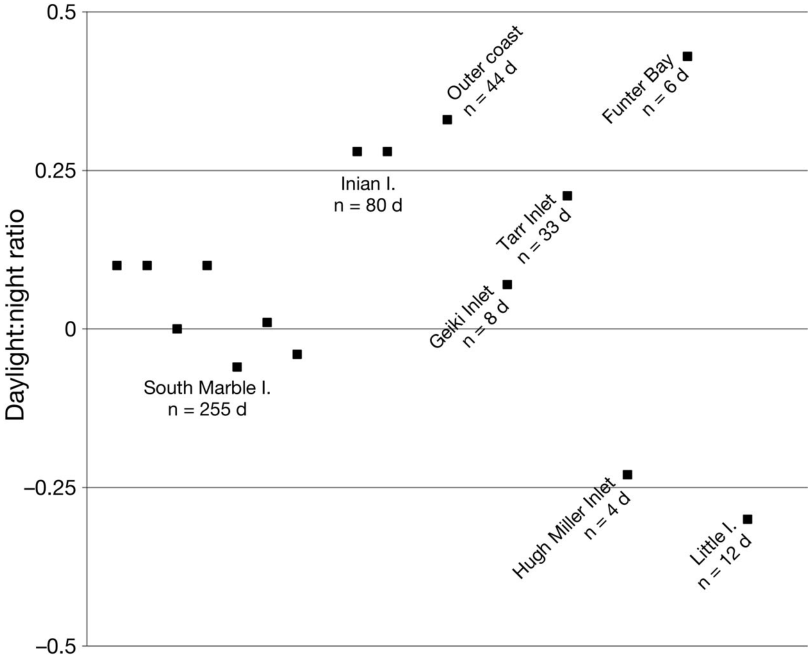

Fig. 4. Relative diurnal focus of diving behavior at the 8 central-place haulouts utilized by 7 Steller sea lion juveniles during November 2009 to January 2010. Day:night ratio values >1 indicate greater proportion of daylight hours were spent diving than the proportion of darkness hours spent diving, values <1 indicate the opposite, and values near zero indicate similar diving focus during daylight and darkness. Points represent the ratio for 1 individual during its residency at a central-place haulout indicated by name. South Marble Island was visited by 7 sea lions, Inian Islands were visited by 2 sea lions, and the remaining haulouts were used by 1 individual only. The number of days sea lions were resident at each location is indicated

Table 3. Mass of 17 pup (5 mo) and 7 juvenile (17 mo) Steller sea lions captured during this study in Glacier Bay (South Marble Island, 2009), contrasted with sea lions previously captured elsewhere in Southeast Alaska (Benjamin, Hazy, and Brothers islands, 1998–2002) and sea lions captured in Prince William Sound (Perry and Glacier islands, 2001–2007). Numbers in parentheses indicate number of individuals. Similar superscripts indicate no significant difference. F: female; M: male

Age (mo)	Sex	Mass (mean ± SD) Glacier Bay	Southeast Alaska	Prince William Sound
5	F	64.7 ± 7.5 (13)^{a}	55.6 ± 9.7 (13)	64.2 ± 7.6 (44)^{a}
5	M	77.4 ± 6.5 (4)^{b,c}	63.2 ± 10.0 (1)1^{b}	76.2 ± 10.0 (37)^{c}
17	F	114.0 ± 2.8 (2)	100.9 ± 6.2 (4)	124.7 ± 11.2 (12)
17	M	135.0 ± 30.3 (5)	123.0 ± 17.6 (9)	141.2 ± 19.5 (9)

having stock assignments available) were assigned to the eDPS. Long-term brand-resight observations through summer 2015 indicated that most Steller sea lions in this study remained within the same area they occupied during the brief 3 mo period they were tracked with the SPLASH tags immediately after capture, with a few seasonal and individual exceptions. Of 13 sea lions (10 female, 3 male) observed through 2015, 8 were observed at the seasonal ephemeral haulout at the Alsek River (235 km swimming distance; Fig. 3). Only 2 male sea lions travelled away from northern Southeast Alaska into Prince William Sound between 2009 and 2015 (Fig. 1).

By the summer 2015 breeding season, 14 of the 18 surviving female pups and juveniles (now at age 6–7 yr) were observed during brand-resight work at either Graves Rocks (n = 8) or White Sisters (n = 6), the nearest breeding rookeries to Glacier Bay (84 km and 142 km swimming distance, respectively; Fig. 3). Strong evidence indicated 11 of these females produced pups: 8 females were observed nursing and 3 were interacting extensively with adjacent pups (mutual nuzzling, pups following females, and pups reuniting with females). No sea lions captured in Glacier Bay were observed at other rookeries besides Graves Rocks or White Sisters prior to breeding. Over a similar timespan, no males were observed holding territories on the breeding rookeries, as the oldest males were 7 yr of age, too young to defend and maintain a breeding territory. Five of these males were observed at the Graves Rocks and White Sisters rookeries through 2015, and 1 travelled to the wDPS rookery at Seal Rocks (717 km distant) near Prince William Sound in the central Gulf of Alaska (Fig. 1). One male was observed with a fishing lure at the edge of its mouth in October 2014 at Port Frederick, 75 km southeast of South Marble Island, and harvested at that site the same day by a subsistence hunter.

DISCUSSION

The 16.6% annual growth in abundance of Steller sea lions at South Marble Island over the 18 yr (1991–2009) prior to this study (Mathews et al. 2011), the 0.569 survival rate of females born at nearby Graves Rocks to maturity (Hastings et al. 2011), and documentation of wDPS females permanently emigrating to and breeding at Graves Rocks (Jemison et al. 2013, O'Corry-Crowe et al. 2014) suggest that favorable conditions occur in the Glacier Bay region for Steller sea lions.

There are several factors that may make the Glacier Bay region favorable for Steller sea lions and may contribute to increased survival, decreased mortality, and/or increases in immigration rates of sea lions from other areas. Glacier Bay is a recently deglaciated fjord that has undergone rapid advances and retreats of tidewater glaciers over the last 225 yr and is a highly dynamic and productive marine environment. Previous studies have documented high levels of primary productivity, sustained levels of mixing (Etherington et al. 2007), high concentrations of zooplankton and forage fish (Robards et al. 2003, Arimitsu et al. 2008), and the relatively recent colonization of Glacier Bay by Pacific salmon *Oncorhynchus* sp. (Milner & Bailey 1989), an important seasonal prey resource for Steller sea lions (Sigler et al. 2009). Large aggregations of marine mammals including humpback whales *Megaptera novaeangliae*, harbor seals, sea otters *Enhydra lutris*, and sea lions (Mathews & Pendleton 2006, Womble et al. 2010, Mathews et al. 2011, Saracco et al. 2013, Williams et al. 2017) occur in Glacier Bay, and collectively these studies suggest that the Glacier Bay region provides productive foraging areas and a rich prey environment for top predators in the nearshore marine environment. Glacier Bay proper and adjacent coastal waters within Glacier Bay National Park also comprise a marine protected area (MPA) with regulations to minimize threats to Steller sea lions and other marine mammals via approach regulations and closures (Womble & Gende 2013). Subsistence hunting of sea lions is prohibited in Glacier Bay, and commercial fishing within the MPA boundary is currently being phased out (Mackovjack 2010); these protections could result in decreased sea lion harassment and/or mortality (Mathews et al. 2011). Herein we discuss the results from this study focused on sea lion diving behavior and movement in the context of prey availability in the region, which has been quantified from previous studies.

Sea lions tracked in this study remained in the Glacier Bay region during winter (November–March), a time that demands the highest predicted daily food requirements for sea lions (Winship et al. 2002), providing support for the premise of a rich prey environment. Similarly, the choice of females to remain in the Glacier Bay region, or at the nearest rookery (White Sisters) to breed, indicates they find prey resources locally for reproduction. Finally, sea lions moved to locations having known prey abundance in the region (Robards et al. 2003, Womble et al. 2005, 2009, Womble & Sigler 2006, Sigler & Csepp 2007). Collectively, these findings suggest that adequate prey resources are available to support sea lions in this region and thus reduce the need for them to emigrate elsewhere.

Haulout selection is important to this generalist, opportunistic predator (Trites et al. 2007), which periodically moves to different locations within its range to exploit seasonally abundant and accessible prey (Womble & Sigler 2006, Sigler et al. 2009). Income breeders (Boyd 1998) such as Steller sea lion females, rely on foraging throughout a prolonged lactation period to provision their young and, thus, depend on prey near the haulouts where their dependent pups are waiting. This foraging strategy is readily observed visually and by remote satellite tracking, because Steller sea lions reside at central-place haulouts adjacent to seasonal prey hot spots for weeks to months (observed in Southeast Alaska by Gende & Sigler 2006). This strategy reduces predation risk and energy expenditure by allowing short-distance and -duration foraging trips (Raum-Suryan et al. 2004, Fadely et al. 2005, Rehberg et al. 2009) interspersed with terrestrial rest and suckling bouts (McLaughlin & Montgomerie 1989). The Steller sea lions captured in Glacier Bay remained within the Glacier Bay region throughout the winter (Fig. 3), sharing common usage of the White Sisters and Graves Rocks rookeries and Inian Islands haulout (Fig. 3). This is similar to observations in previous work by Raum-Suryan et al. (2004, their Fig. 11, the northern outer coast cluster), which demonstrated that sea lions tracked in this region formed a smaller, isolated grouping of sea lions, centered among Glacier Bay, Graves Rocks, and White Sisters, relative to the wider-ranging groupings of sea lions tracked elsewhere in Southeast Alaska.

Examination of the known aggregations of prey available may, in part, explain why sea lions exhibit high fidelity to the Glacier Bay region during winter. Generally throughout Southeast Alaska, winter sea lion diet consists mainly of gadids (50%), forage fish (14%), cephalopods (8%), flatfish (8%), and some Pacific salmon (1%; Winship & Trites 2003). However, focal studies of sea lion diet in Lynn Canal and Frederick Sound (regions east and south of the present study) suggest there is regional and seasonal variation in the prey species consumed by sea lions. In both regions, seasonally available prey species such as eulachon, capelin *Mallotus villosus*, and northern lampfish *Stenobrachius leucopsarus* were important during spring (Womble & Sigler 2006, Sigler et al. 2009).

Specific to the Glacier Bay region, the prey assemblage includes dense forage fish schools including Pacific herring *Clupea pallasii*, capelin, and northern lampfish (Arimitsu et al. 2007, 2008), which are rich in lipid content (Van Pelt et al. 1997) and in some regions occur in shallower waters during daylight than other forage fish consumed by Steller sea lions (Abookire et al. 2002). Likewise, sea lions in this area showed a daylight preference in foraging behavior (Fig. 4) and foraged at shallower depths relative to other locations (Fig. 3). Although food habits have not been examined for sea lions in this area, capelin have been documented in Steller sea lion scats during autumn, winter, and spring in other regions of Southeast Alaska. Previous studies have shown that capelin are abundant in Glacier Bay and likely serve as an important prey resource for sea lions and other marine predators. In addition, during summer months, prey were found higher in density and shallower in the water column (<100 m depth) in the Beardslee Entrance (near South Marble Island haulout) compared to Johns Hopkins Inlet (near Tarr Inlet haulout; our Fig. 2; Womble et al. 2014). Similarly, sea lions in this study dove deeper near Tarr Inlet, a deeper habitat, than at South Marble Island, a shallower habitat. Shallower prey depths in lower Glacier Bay likely provide opportunities for more efficient foraging by Steller sea lions given other marine predators including harbor seals, sea lions, and humpback whales have been observed foraging in this region regularly (Womble et al. 2014). Dense aggregations of walleye pollock, sand lance, salmon, and capelin have also been documented in the lower bay (Robards et al. 2003, Arimitsu et al. 2008).

Steller sea lions occupy an ephemeral spring haulout at Tarr Inlet in upper Glacier Bay, and sea lions have been observed actively foraging in the upper reaches of Tarr Inlet (Fig. 2; Womble et al. 2005, 2009, J. N. Womble pers. obs.), likely taking advantage of seasonally available prey. Pacific sand lance

Ammodytes hexapterus, and herring are present in the warmer mid-bay waters near South Marble Island haulout, whereas walleye pollock and capelin are found in the cooler waters to the north at Tarr Inlet (Arimitsu et al. 2007). Any benefit gained by the longer-distance movements juveniles are making to distant foraging areas outside Glacier Bay (Fig. 3) does not appear to be required by adult females tending the pups tracked in this study (Fig. 2), who apparently find sufficient quantities of local prey despite the additional demands of nursing their pups. Remaining in Glacier Bay may also reduce predator exposure for the younger pups, a less important consideration for the older, longer-ranging juveniles.

In Cross Sound, west of Glacier Bay, several juveniles spent time foraging in the tide rips adjacent to the Inian Islands (Fig. 3), behavior also observed during monthly aerial surveys of Steller sea lions (Womble et al. 2009) and skiff-based surveys during summer (Alaska Department of Fish and Game [ADF&G] unpubl. data). North Inian Pass is a dynamic area comprised of a narrow channel with strong tidal currents that links the inside waters of Icy Strait with the Gulf of Alaska. It is also a primary migratory corridor for Pacific salmon, a seasonally important prey species for sea lions, entering inside waters from spring through autumn. These tide rips also aggregate other important prey, as Steller sea lions have been photo-documented feeding on rockfish, flatfish, and gadids here (ADF&G unpubl. data, J. N. Womble pers. obs.)

Farther afield, during December, 1 juvenile made a long-distance move north along the outer coast to reside at the mouth of the Alsek River (235 km; Fig. 3). Large numbers of sea lions gather here during late winter and spring (February–May) to feed on pre-spawn and spawning eulachon *Thaleichthys pacificus* (Womble et al. 2005). The Alsek and nearby Akwe rivers support the largest known seasonal aggregation of Steller sea lions in Alaska outside the breeding season (ADF&G and US Forest Service unpubl. data). Between 2012 and 2015, 8 sea lions branded in this study were also photo-documented at this location at least once during the spring eulachon run (ADF&G unpubl. data). Eulachon are one of the most energy-rich prey species consumed by sea lions and likely important for sea lions prior to the energetically demanding reproductive season (Womble et al. 2005). The earlier arrival of this individual at the Alsek River possibly indicates the sea lion was targeting additional prey species. The Alsek River is at the head of a submarine canyon leading inward from deeper waters, and, unlike other locations used by juvenile sea lions from Glacier Bay, the shelf break is accessible from this location (Fig. 3). Piatt et al. (2006) suggested these northern Gulf of Alaska canyons induce upwelling and enhance vertical mixing over the shallow waters of the continental shelf, concentrating short-tailed albatross *Phoebastria albatrus* feeding behavior over localized, predictable hot spots of prey in similar fashion suggested for Steller sea lions by Sigler et al. (2009). Indeed, the sea lion tracked over winter here performed the shortest trips and shallowest diving observed in this study (Figs. 3 & 4), relative to sea lions foraging at more inland locations. Individual female harbor seals captured in Glacier Bay also use this region of the Gulf of Alaska extensively, during autumn, winter, and spring, suggesting this area may be an important foraging region for pinnipeds in general (Womble & Gende 2013).

One male juvenile (=724) appeared to use a predictable, dense food supply by moving 135 km eastward to Little Island haulout in Lynn Canal, which is typically occupied late summer through early autumn (Fig. 3; Womble et al. 2009). At nearby Benjamin Island, Pacific herring was the most common species found in sea lion diets and comprised >80% of pelagic prey biomass available to them (Womble & Sigler 2006). Peak seasonal herring biomass coincided with this male's visit (Sigler & Csepp 2007), during the winter season when herring energy content is highest (Vollenweider et al. 2011). Womble et al. (2009) identified overwintering herring aggregations such as this as primary hot spots correlated with large numbers of nearby hauled-out sea lions. Walleye pollock (a gadid, *Gadus chalcogrammus*) was also important throughout the year for sea lions but was much lower in available biomass (Womble & Sigler 2006). While this sea lion's movement and diving reflect a response to this prey hot spot, more dispersed and less energy-dense prey were also available throughout Southeast Alaska. Walleye pollock was the most abundant and widely distributed forage species during summer, found in 2 locations occupied by juvenile Steller sea lions in this study (Fig. 3): Glacier Bay and the Inian Islands (Arimitsu et al. 2007, McGowan et al. 2016). Both walleye pollock and North Pacific hake *Merluccius productus* were available year round and consumed throughout Southeast Alaska (Womble & Sigler 2006, Womble et al. 2009), with hake occurring at deeper depths than pollock (Csepp et al. 2011). These 3 mesopelagic fish taxa were not found at the seafloor, with peak energy density of both pollock and herring found shallower than 150 m during December (Sigler et al. 2009), a good match to the less-than-benthic diving performed by juveniles in this study in all locations (Table 4).

Foraging Steller sea lions share this region of Southeast Alaska with other piscivores during winter. Harbor seals, bald eagles *Haliaeetus leucocephalus*, and humpback whales are observed in high prey density locations along with Steller sea lions in Lynn Canal (Fig. 3; Martson et al. 2002, Sigler & Csepp 2007). Harbor seals consume similar prey to sea lions in Glacier Bay (Herreman et al. 2009, Blundell et al. 2011), including capelin, herring, and pollock, but the seal population has undergone a precipitous decline (Mathews & Pendleton 2006, Womble et al. 2010), in contrast to the rapidly increasing sea lion numbers (Mathews et al. 2011). Like sea lions, harbor seals in areas associated with floating glacial ice habitat in Glacier Bay have available to them great depths (Johns Hopkins Inlet, approximately 370 m), but 95% of seal dives are made to <100 m (Womble et al. 2014) as they pursue epipelagic prey. In contrast, the Steller sea lions occupying similar deep glacial habitat in this study (Tarr Inlet, Geike Inlet; Table 4) are reaching 83 to 90% of the available bottom depth. While this difference might allow sea lions to acquire more abundant prey at depth, the difference in diving may not indicate competitive exclusion of harbor seals by sea lions. Instead, Womble et al. (2014) suggest that harbor seals are using these deeper sites, with their less abundant prey, because the floating ice provides stable resting platforms and refuge from predation.

Foraging behavior, or lack thereof, of pups spending the winter in Glacier Bay met our expectations from previous studies: pup diving was shallower, less frequent, and did not show a nighttime focus or seasonal response in the same way as older juvenile behavior, which seems to more closely respond to prey habits (Raum-Suryan et al. 2004, Pitcher et al. 2005, Rehberg & Burns 2008). Pups in this study remained in Glacier Bay (Fig. 2), were observed suckling, and were likely dependent on adult females for nutrition. This area likely protected pups from winter storms relative to the more exposed habitat used by juveniles (Fig. 3). Because the unweaned pups were able to remain at the South Marble Island and Tarr Inlet haulouts through the winter, and the typical attendance cycle of dams and their dependent pups during winter in Southeast Alaska is 2 d (Trites & Porter 2002), adult female sea lions clearly had sufficient access to prey resources in or near Glacier Bay to support their pups through the winter months. Furthermore, 5 of the 7 juveniles were observed still suckling after the tracking portion of this study concluded, at 17 mo of age and older. Stable isotope

Table 4. Proportion of seafloor depth (mean ± SD) reached by the maximum diving depth of 7 Steller sea lion juveniles (17–19 mo of age) at 8 central-place haulouts during November 2009 to January 2010. The number of days sea lions were resident at each location is indicated in parentheses. Blank entries indicate an individual was not present at a given haulout. See Figs. 2 & 3 for haulout locations

Animal identifier	Proportion of seafloor depth used per haulout (mean ±SD)							
	South Marble Island	Inian Islands	Outer coast	Geike Inlet	Tarr Inlet	Hugh Miller Inlet	Funter Bay	Little Island
=719	0.78 ± 0.25 (54)	0.50 ± 0.29 (21)						
=720	0.73 ± 0.28 (30)		0.91 ± 0.29 (44)					
=722	0.75 ± 0.20 (5)	0.63 ± 0.32 (59)						
=4=	0.80 ± 0.28 (55)			0.90 ± 0.24 (8)				
=7521	0.77 ± 0.28 (72)							
=727	0.72 ± 0.25 (21)				0.83 ± 0.28 (33)	0.86 ± 0.31 (4)		
=742	0.68 ± 0.31 (18)						0.73 ± 0.31 (6)	0.82 ± 0.25 (12)

trends along the vibrissae of sea lions captured in this study (ADF&G unpubl. data, L. Rea pers. comm.) provided another indication of whether or not individuals were weaned by demonstrating whether the trophic level of their diet had changed at time of capture (i.e. from higher level based on milk to lower level based on direct fish consumption). These stable isotope results corroborated the suckling observations well: except for 1 juvenile with a weak weaning signal (=742, also never observed suckling; L. Rea pers. comm.), juveniles and pups in this study were still nutritionally dependent on their dams.

As in previous tracking studies (Raum-Suryan et al. 2004) and brand-resight movement studies (Raum-Suryan et al. 2002, Jemison et al. 2013), the longest-range movements tracked by satellite telemetry (in the short term) and brand-resight observations (over the long term) were accomplished by males. During this study (2009–2015), these males had not yet reached maturity (9–13 yr; Pitcher et al. 2001) and had not been observed holding territories on breeding rookeries (Table 1). The longest movements documented during this study were based on brand-resight data collected through 2015: 2 males moved westward into the wDPS. One male (=744) moved between Prince William Sound (Fig. 1) in July 2012, 2013, and 2014 and the Alsek River in spring 2013 and 2014. A second male (=720) was observed at Glacier Island in Prince William Sound (Fig. 1) at age 4 and thereafter observed at Graves Rocks, Inian Islands (specifically, Northwest Inian Island and Middle Pass Rock), South Marble Island, and the Alsek River. Given that males have been documented moving >3500 km from natal rookeries in summer to remote haulouts in winter (Jemison et al. 2013), the longest movements in this study were small by comparison, supporting the idea that adequate prey resources are available in the Glacier Bay region. A study examining sex- and rookery-specific patterns of movement indicated that sea lions born in the Glacier Bay region were less likely to travel west into the wDPS than animals born in Prince William Sound to move east into the eDPS (Jemison et al. 2013). Because there is strong genetic division between the eDPS and the wDPS (O'Corry-Crowe et al. 2014) and microsatellite analysis demonstrates little male-mediated gene flow between the populations (Hoffman et al. 2006), males captured in Glacier Bay are unlikely to move away from the Glacier Bay region and westward into the wDPS at maturity. Indeed, Hastings et al. (2011) found males born in this area that did disperse west into the wDPS had lower survival to age 7 than males who remained in this area.

The sea lions captured in Glacier Bay during winter have a similar blend of mtDNA-derived (maternal) genetic stock origins (Table 1) to those observed at the nearby newly colonized Graves Rocks rookery (Gelatt et al. 2007, O'Corry-Crowe et al. 2014), where the newborn cohorts consist of roughly half eDPS- and half wDPS-origin individuals. Because this area is situated on the interface of genetically and demographically distinct population segments, the growth in sea lion numbers here (Mathews et al. 2011) would seem most naturally to be an expansion of the thriving eastern population on its northern fringe. Hoffman et al. (2006) speculated as much, indicating that the declining wDPS was not being replenished by the expanding eDPS despite their close demographic proximity. Instead, growth in this area is more likely related to colonization of the growing eDPS by individuals emigrating from the wDPS (O'Corry-Crowe et al. 2014). This study corroborates these observations by demonstrating the short-term tendency of sea lions captured at South Marble Island to remain within a limited foraging radius (Figs. 1 & 2). In the longer term, young females captured here remained in this area to breed, years later (Table 1), at the Graves Rocks rookery. Regardless of whether these females are eDPS or wDPS in genetic origin, if current survival trends continue, their offspring will be twice as likely to survive through age 7 than pups born at other Southeast Alaska rookeries (Hastings et al. 2011). Survival trends imply that this area provides sufficient resources to support Steller sea lions, in robust condition, throughout their life cycle. Several lines of evidence from our study and others suggested that the Glacier Bay region, a site of rapid population growth and colonization (Mathews et al. 2011), appears to provide the resources and conditions for sea lions captured here to remain here into their reproductive years and continue the growth of this genetically mixed population on the interface of the eDPS and wDPS.

The Glacier Bay region is dynamic in terms of productivity, prey availability, and the concentrations of upper trophic level marine predators that occur here (harbor seals, Steller sea lions, humpback whales; Womble et al. 2010, Mathews et al. 2011, Saracco et al. 2013, Williams et al. 2017); thus, future interdisciplinary studies aimed at elucidating the linkages between primary productivity, prey availability, and the diving and foraging behavior of sea lions and other species will be important. A follow-up study, to mark a new cohort of pups born at rookeries adjacent to Glacier Bay and update our understanding of the genetic composition of Steller sea lions in this area, is in progress.

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