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**Overwintering Steller sea lion (*Eumetopias jubatus*) pup
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1 Overwintering Steller sea lion (*Eumetopias jubatus*) pup growth and behavior prior to weaning

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16

17 Abstract

18 We measured individual growth, looked for evidence of weaning and examined the
19 interaction of these changes with diving behavior in young-of-year Steller sea lion pups
20 (*Eumetopias jubatus* (Schreber, 1776)) in Alaska during their first winter. Steller sea lions
21 employ an income breeding strategy, in which females provision their young over an
22 individually variable period of months to years. Thus we set out to identify whether these young
23 sea lions showed evidence of weaning during the challenging winter months, describe the nature
24 of their growth during this time, and examine their behaviors in light of these changes. Between
25 2005 and 2008 we captured 71 pups during early winter and recaptured 33 of these pups in early
26 spring. Mark-resight and stable nitrogen isotope ratios in vibrissae indicated most pups remained
27 nutritionally dependent on adult females throughout the winter. All pups increased both mass
28 and lipid mass, with half of growth contributed by lipid mass. Changes in behavior were not
29 correlated with growth excepting a weak but significant effect on rate of vertical travel. This
30 study demonstrated that capture-recapture of Steller sea lion pups is possible, provided seasonal
31 timing, locations and age classes are carefully considered for their likelihood of capture success.

32

33 Key words: Steller sea lion, *Eumetopias jubatus*, capture, recapture, mass, total body fat, lipid,
34 buoyancy, weaning, dive, diving, time-depth recorder, TDR

35 Introduction

36 Swimming and diving behaviors of air-breathing marine predators are shaped by their
37 physical abilities and limitations, by the necessity of the predator to forage or travel underwater,
38 and by the environment they occupy. In the case of young-of-year otariid seals, such as sea lion
39 or fur seal pups, their abilities change over time, along with their need to dive, as they grow and
40 become less dependent on their lactating mothers for nutrition. Compared to phocid seals, which
41 wean weeks after birth, otariid females are income breeders, whose pups benefit from extended
42 lactation periods of months to years, supporting their nutritional needs while they grow and
43 develop their underwater foraging abilities (Costa 1991; Fowler et al. 2006; Lowther and
44 Goldsworthy 2012). The observed behavior of young-of-year pups represents a longer-term
45 trade-off between actively swimming and diving to improve their ability to independently forage
46 after weaning vs. reduced activity to preserve energy for lean and fat tissue growth to enhance
47 their ability to fast post-weaning if needed (Guinet et al. 2005; Gastebois et al. 2011).

48 The physical growth of young pups has a complex relationship with the swimming and
49 diving behaviors we can observe; growth in both total mass and body fat influences the ability of
50 pups to spend time underwater. The ability to store oxygen increases with mass and improves
51 the underwater endurance of these air-breathing predators (Richmond et al. 2006), which is
52 reflected in longer, deeper and more consistent diving (Pitcher et al. 2005). Increasing stores of
53 body fat are a measure of fitness and fasting ability (Noren et al. 2009; Rea et al. 2007), but the
54 reduced tissue density inherent in this increase also alters buoyancy, which can affect diving
55 behavior (Beck et al. 2000; Fahlman et al. 2008a).

Previous work with Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) has described the development of swimming and diving behavior over time (Raum-Suryan et al. 2004; Pitcher et al. 2005) and compared these changes to their environment (Rehberg and Burns 2008). While physical measures have been incorporated in numerous studies of Steller sea lions, sometimes including hundreds of individuals and multiple age classes, this prior work has been cross-sectional in design and has not measured change in individual sea lions over time. The present study is the first to measure this individual growth, look for evidence of weaning in young Steller sea lions and examine the interaction of these changes with swimming and diving behavior observed during the same time period.

Measuring change in behavior in the context of simultaneous change in physical measures is one approach to tease out the influence and benefit of growth on behavior. Longitudinal change in behavior is readily observable by marking or instrumenting pinnipeds in a single handling event. Application of permanent markings, such as numerically coded tags or brands (e.g., Jemison et al. 2013), allows subsequent repeated observation of these known individuals to determine movement patterns, migration patterns, and the onset of maturity. Attachment of electronic location- and dive-recording instruments provides similar longitudinal tracking of movement and migration, with the additional benefit of more frequent location estimates, description of underwater swimming and diving behavior, and the ability to track behavior at times and locations inaccessible to visual observation by researchers. However, it remains a challenge in some pinniped research to collect repeated measurements and samples from the same individual to observe trends in change over time (growth, body fat content) that adequately match the longitudinal repeat measurements possible with visual observations or data-logging instrument data. Such paired study is well-suited to taxa with stereotypic foraging

or migration cycles known to depart and return from predictable capture locations (*e.g.*, adult grey seals, *Halichoerus grypus* (Fabricius, 1791), Beck et al. 2000; adult northern fur seals, *Callorhinus ursinus* (L., 1758), Nordstrom et al. 2013). Longitudinal measures of individual change are more difficult to collect in pinnipeds that have more generalist habits and use multiple-central-place foraging strategies. Steller sea lions are one such otariid; as they move among multiple haulouts, their patterns can be unpredictable and thus limit their availability for recapture (Raum-Suryan et al. 2004).

To conduct this study, we captured and recaptured Steller sea lion pups to monitor their behavior, growth, and to seek evidence of a change in foraging status during five months between captures over their first winter. We looked for changes in their nutritional dependency, from suckling to foraging, by examining the longitudinal trend in stable nitrogen and carbon isotope ratio values along the length of the mystacial vibrissae (whisker) of each sea lion to determine if the trophic level of feeding had changed during the study (Rea et al. 2015; Lowther and Goldsworthy 2016). We also documented suckling behavior observed in the field at the time of recapture of individuals. We simultaneously tracked changes in their diving and swimming performance using dive-behavior recording instruments to determine the influence of physical change on these behaviors that will be necessary for successful independent foraging after weaning.

Materials and Methods

Young-of-year pups (5 months old) were initially live-captured at Perry and Glacier Islands, Prince William Sound, Alaska, during November 2005 and November 2007, using an

underwater capture technique (Raum-Suryan et al. 2004). Captures of pups at this age were non-selective, but some sea lions previously branded as neonate pups (< 2 months of age) were opportunistically captured to provide a longer time-series of repeated sampling for future use. Pups were secured in individual holding boxes, transferred by skiff to a research vessel and weighed using a load cell suspended from a hoist. The on-site attending veterinarian placed pups under isoflurane, which provided anesthesia and analgesia (Heath et al. 1997; Lian et al. (in press)). Researchers identified pup sex, measured lengths and girths, and estimated age of pups according to animal size, canine length (King et al. 2007) and tooth eruption, assuming 1 June as the mean birthdate (Pitcher et al. 2001). Previously un-branded pups were hot-branded on the animal's left side (Hastings et al. 2009) using 0.95 cm diameter stainless steel, forming characters 10.2 cm high by 7.5 cm wide. Branding provided two direct services to this study: identification for future recapture and confirmation of weaning status via future re-sighting. However, the primary purpose of branding was to include these individuals as a cohort in a separate, range-wide long-term program to determine vital rates (*i.e.*, survival, reproduction and dispersal) as recommended by the U.S. National Research Council (2003).

Prior to the start of this study, animal capture, handling, sampling and marking were reviewed and authorized by U.S. National Oceanographic and Atmospheric Administration (NOAA) Fisheries Permits No. 358-1769 and 358-1888 and Alaska Department of Fish and Game (ADF&G) Institutional Animal Care and Use Committee protocol No. 09-28 and earlier. Field research and handling conformed to the ADF&G Division of Wildlife Conservation Animal Welfare Policy, which provides evidence of compliance with the U.S. Animal Welfare Act. Prior to publication, animal handling and marking was reviewed against and found to

123 conform to the Canadian Council on Animal Care guidelines on the care and use of wildlife
124 (CCAC 2003).

125 To determine total body water (TBW) and ultimately the total body fat (TBF) and lean
126 tissue mass of each pup, deuterium oxide (D_2O) was administered intramuscularly at 0.3 – 0.5
127 g/kg sea lion body mass and allowed to equilibrate for ≥ 2 hours (see detailed methods in Rea et
128 al. 2016). Blood (up to 1 mL/kg body mass) for subsequent laboratory analysis was collected
129 into serum separator tubes prior to D_2O injection and twice post-equilibration, approximately 30
130 minutes apart. One mystacial vibrissa (longest on the left side) was collected for stable carbon
131 and nitrogen isotope analysis (Rea et al. 2015). After recovery from anesthesia, pups were
132 released to the water from the research vessel and their return to the capture site was observed.

133 During the initial captures in November 2005, we used 5-minute epoxy (Devcon, Inc.
134 Danvers, Massachusetts) to affix dive-behavior recording instruments (Mk 9 time-depth
135 recorders, TDRs, Wildlife Computers, Inc., Redmond, Washington USA) to the fur along the
136 dorsal midline between the scapulae. Prior to deployment, TDRs were potted in an oval-shaped
137 epoxy disc. To avoid recapturing the same sea lions during a capture effort, pups were marked
138 with fluorescent wax crayon (cattle marker) or a shave mark on top of the head. During the
139 November 2007 initial captures, TDRs were not potted in epoxy, but instead attached squarely to
140 the fur on top of the head using 3 mm mesh (Research Nets, Inc., Bothell, Washington USA) and
141 slower, cooler setting epoxy (10-minute, Devcon, Inc., Danvers, Massachusetts USA). TDRs
142 were programmed to record wet/dry status and depth every 5 seconds and stored these data for
143 download upon retrieval.

During recapture efforts in March-April 2006 and 2008, pups initially captured the previous November were sought at three haulouts in Prince William Sound: Perry Island, Glacier Island, and The Needle. Unlike the initial non-selective November captures, SCUBA divers targeted instrumented pups for recapture. Handling and processing of recaptured pups were similar to the initial November capture, including all measurements, a second set of D₂O injection, equilibration and blood sampling to determine change in fat and lean mass since initial capture, and the longest vibrissa on the right side of the muzzle was collected to determine the stable isotope patterns deposited in vibrissa tissue since the previous capture (Rea et al. 2015). TDR instruments were recovered by either clipping the underlying fur or firmly peeling the instruments from their softened epoxy base. Branding was not repeated, but recaptured sea lions were marked with a fluorescent cattle marker to prevent subsequent recapture during the same effort. Data were downloaded from TDR instruments using *Instrument Helper* software (Wildlife Computers, Inc.) and archived for later analysis. Sea lions were released to the water on their own initiative and subsequent observations verified their return to the haulout.

Weaning status—whether sea lions were still receiving nutrition from their dams during the course of this study—was determined by visually observing suckling behavior of branded individuals during or after the March/April recaptures. We also evaluated whether the pattern of deposition of nitrogen and carbon isotope ratios along the length of the vibrissa collected at time of recapture (10 months of age) had changed since the first vibrissa was collected at 5 months of age when the pup was known to be maternally dependent (see Figure 1 in Rea et al. 2015). In all cases, the profile of isotope values of the recapture vibrissae closely reflected the profile measured along the length of the initial vibrissa (once the effect of abrasion on the tip of the vibrissae was accounted for), thus allowing the profile representing the time period between

capture and recapture to be identified (see Rea et al. 2015). If the pup had weaned at some point between the sampling events at 5 and 10 months of age, we would expect to see a significant decrease in the nitrogen isotope ratio of the new vibrissa tissue growth, representing a change from high trophic level milk diet (as suckling pups are effectively eating their dams) to a lower trophic level fish or invertebrate diet¹ (Newsome et al. 2010; Lowther and Goldsworthy 2016).

To determine TBF and lean tissue mass, serum samples were processed for D₂O content as described by Rea et al. (2016). TBW was calculated from the hydrogen isotope dilution space using the relationship identified by Bowen and Iverson (1998); this measurement was then used to calculate TBF and lean tissue mass following the two-step model of Reilly and Fedak (1990). Buoyancy of each pup at capture and recapture was calculated from the percentage of adipose and lean tissue using an equation developed by Webb et al. (1998), which assumes mass-specific buoyancy of 0.8871 N kg⁻¹ and -0.6689 N kg⁻¹ for each tissue type, respectively, based on study of phocid seal tissue. Finally, changes in all of these point measurements between capture at 5 months and recapture at 10 months of age were calculated.

The series of depth readings collected every 5 seconds by each TDR was processed through the *Instrument Helper* (Wildlife Computers, Inc., Redmond, Washington USA) program to perform zero-offset correction, a method to remove artifacts of the depth-recording pressure transducer drifting over time. Each series of corrected readings was imported to an R (R Core Team 2014) data frame containing the date, time, raw depth and corrected depth value of each

¹ Rea, L.D., Banks, A. R., Farley, S. D., Stricker, C. A., Fadely, B. S., Mellish, J. E., Christ, A. C., and Pitcher, K. W. 2011. Delayed age at weaning in Southeast Alaska Steller sea lions determined using stable isotopes of carbon and nitrogen. *Presented at 19th Biennial Conference on the Biology of Marine Mammals*, Tampa, Florida, 26 November – 2 December 2011.

reading. Wet/dry status was merged into this data frame, and solar elevation² was assigned to each reading to identify whether activity occurred within daylight or darkness. These data were imported to the R package *divemove* (Luque 2007), which identified all individual dives in the series, their maximum depths and dive durations, identified ascent, descent and bottom phases of each dive and their ascent and descent rates. Dive bouts were identified as sets of contiguous diving separated by non-diving intervals of time using a custom R script, which defined bouts as sets of dives less than 10 minutes apart for which the cumulative coefficient of variation in dive depth was less than 25% (Rehberg 2005). Each dive was assigned to a bout, for which the mean depth of dives within each bout, the proportion of bout spent submerged, and the vertical rate of travel within each bout was calculated. Trips-to-sea were identified using a custom R script which examined the series of wet/dry readings and defined trips as contiguous intervals of wet readings terminated by 5 minutes of contiguous dry readings. Each bout was assigned to a trip, for which the mean depth of bouts, the proportion of trip spent submerged, and the vertical rate of travel within the trip were calculated. At the individual sea lion time scale, over the full 5-month deployment duration of each sea lion, the rate of vertical travel (meters · day⁻¹), the proportion of time spent at-sea, and the proportion of time spent submerged was calculated.

The relationship of sea lion growth (change in mass and lipid mass) to sex was determined using ANOVA. One pup was mis-sexed during one of the captures (Table 1) and is excluded from comparisons with a sex effect. The relationship of overall individual sea lion swimming and diving effort measures (rate of vertical travel, proportion of time spent at-sea and proportion of time spent submerged) to growth (change in mass and lipid mass) was assessed

² U.S. Naval Observatory, Astronomical Applications Department. Sun or moon altitude/azimuth table. Available from <http://aa.usno.navy.mil/data/docs/AltAz.php> [accessed 18 November 2016].

using linear regression. The significance of relationships between sea lion diving behavior (mean bout depth, proportion of bout submerged, vertical rate of travel within bout), seasonal influence (month) and daylight (daylight or night) was determined using a linear mixed model having individual sea lion as random effect. All tests were performed using the R system (R Core Team 2014).

Results

We captured 32 and 39 Steller sea lion pups at Perry Island and Glacier Island during November 2005 and 2007, respectively (Figure 1), and branded all previously un-branded pups for future identification. Of these, 2 captured in 2005 were released without time-depth recorders attached because they had not yet molted their brittle lanugo fur. One sea lion captured in 2007 was released without sampling due to a similar un-molted state and large, pre-existing abscesses (treated prior to release). To the remaining 68 sea lions we attached TDRs, took body measurements, collected a vibrissa for stable isotope analysis and assessed total body water. Approximately five months after initial capture, we recaptured 18 and 15 sea lions during March-April 2006 and 2008, respectively, resulting in an overall recapture success of 46%. Functioning TDRs were recovered from 20 sea lions (Table 1), a 29% recovery rate. The epoxy-potted, dorsally-mounted instruments deployed in the 2005-2006 suffered a 46% premature detachment rate; during 2007-2008, detachments were reduced to 13% with the change to non-potted head mounts. One loose TDR was removed from a pup by a capture diver without subsequent recapture, and 1 pup was captured early (February 2006) by another research team when its instrument appeared to be detaching. Initial captures during November required a mean

of 11 minutes dive team effort, while targeted recaptures of marked individuals during March-April required a mean of 117 minutes effort underwater, including successful and unsuccessful recapture attempts.

Sea lion pup total mass was 69.5 ± 7 kg (mean, standard deviation, $n = 20$) at capture and 100.7 ± 19 kg at recapture, and the TBF mass of pups increased from 17.2 ± 3 kg at capture to 34.7 ± 11 kg at recapture (Table 2). The change in TBF contributed 53.8 ± 25 % (range 0-100%) of this growth observed between 5 and 10 months of age (Figure 2, Table 2). Growth in mass and TBF had a significant, positive relationship (Figure 2, linear regression: $R^2 = 0.85$, $F = 112.45$, $P < 0.001$). Male growth in mass (34.6 ± 16 kg, $n=10$) and TBF (19.9 ± 11 kg) was not significantly different from female growth in mass (30.0 ± 15 kg, $n = 9$) and TBF (15.7 ± 10 kg) (Table 2, ANOVA: mass, $F_{(1,17)} = 104.39$, $P = 0.517$; lipid mass, $F_{(1,17)} = 0.392$, $n = 19$). All sea lions were negatively buoyant at capture and remained so at recapture (Figure 3), with five individuals reduced in buoyancy by 10 months of age and 15 increasing over the 5 months between captures. Most sea lions were observed still suckling at or after the conclusion of this study (Table 1). For 19 of the 20 pups, there was no evidence of the significantly lower nitrogen isotope ratio measured in the vibrissae (*e.g.*, Figure 4a). This drop in nitrogen ratio would be expected if they had weaned and thus nutritionally dependent on lower trophic level fish or invertebrate prey at the time of recapture (Figure 4b; Rea et al. 2015; Lowther and Goldsworthy 2016). An initial drop in nitrogen ratio, at birth, is coincident with the switch from trans-placental nutrition to milk feeding. Interestingly, the two sea lions having zero contribution of lipid mass to overall growth during this 5 month study had opposite potential weaning scenarios: SSL2005 622PWS was never observed suckling (Table 1) and had a weak but potential

indication of weaning from stable nitrogen trends (Figure 4b), while SSL2005 630PWS was still observed suckling after the conclusion of this study.

One weak overall effect of sea lion growth was found on the change in sea lion behavior between the first month of monitoring (5 months of age) and the last month (10 month of age). A significant but weak correlation suggests more buoyant sea lions were diving less to depth, with a lower rate of vertical travel (sum of dive depths $\cdot$ day⁻¹) than less buoyant sea lions (Figure 5, linear regression: $R^2 = 0.339$, $F_{(1,17)} = 581.03$, $P = 0.009$). However, we found significant seasonal and diurnal effects on behavior during focused bouts of diving. While the vertical travel rate (the number of meters diving per unit time) had no growth effect, it had a significant, seasonal peak during December – February (Figure 6, GLM: $F_{(4,6801)} = 115.090$, $P < 0.001$) with significantly greater nighttime vertical travel rate during January and February (GLM: $F_{(1,6801)} = 47.505$, $P < 0.001$). The proportion of time spent submerged within bouts had a similar December – February peak (Figure 6, GLM: $F_{(4,6801)} = 24.351$, $P < 0.001$), with a significantly greater proportion of time in nighttime bouts spent submerged during December – February (GLM: $F_{(1,6801)} = 48.184$, $P < 0.001$). Sea lions dove deeper during December – February (GLM: $F_{(1,6801)} = 38.138$, $P < 0.001$) but there was no diurnal effect on dive depth (GLM: $F_{(1,6801)} = 0.627$, $P = 0.429$). This model included duration of daylight, controlling for the effect of day length.

Discussion

We compared the behavior of individual Steller sea lions with their growth over 5 months during their first winter. Our recapture success of less than 50%, and the approximately 2 hours

of dive effort required for each recapture, show that capture/recapture studies of Steller sea lion pups are time consuming, even at favorable locations. Previous to this study, some sea lions were recaptured opportunistically: 57 such live recaptures were made from the 4,705 sea lions branded elsewhere by ADF&G and collaborators during 1992 - 2009. While these recaptures have yielded useful information, they lack consistency in ages, locations, types of information collected and duration of time between repeated measurements. The present study provides this consistency and, thus, ability for robust analysis.

Originally, the main objective of this study was to compare the age-specific changes in behavior and growth of pups that weaned prior to 10 months of age to those sea lions that were still unweaned and maternally dependent at 10 months of age. We hypothesized that different choices by adult females in maternal support would cause different challenges among pups reflected in different growth rates and foraging behaviors among pups driven by different nutritional needs. As it happens, both brand-resight observations and stable isotope trends found in the vibrissae indicated only one of the sea lions in this study had potentially weaned between November and April. Ten years previous to this study, Trites et al. (2006) similarly did not observe any young-of-year Steller sea lions weaning during this winter season in Southeast Alaska. Nonetheless, this project provides valuable information to illustrate the changes in sea lion behavior as they approach weaning and the future demands of independent foraging. This study also complements previous cross-sectional work, as longitudinal study of known individuals allows within-individual patterns to be distinguished from inter-individual variation (Nussey et al. 2008).

Two previous longitudinal studies investigated growth of individual Steller sea lion pups in the wild, but during an earlier life stage—the first 6 weeks of life on their birth rookeries.

296 Similar to our study, Brandon et al. (2005) found no sex difference in growth rate over the first 6
297 weeks of life on Alaska rookeries, although males exhibited overall larger mass than females.
298 The overall greater mass of males evident since birth (Brandon et al. 2005) indicated differential
299 investment during gestation. Higgins et al. (1988), working in California, explained that females
300 calibrated their milk delivery to match the needs of their individual pups during their first 6
301 weeks, preserving the male:female mass difference over time. Because these growth patterns
302 were evident the older pups and longer measurement interval of the present study, it is
303 reasonable to conclude the rate of Steller sea lion pup growth is consistent through their first
304 year. Other investigations of Steller sea lion growth are based on cross-sectional, single-sample
305 data only (*e.g.*, Winship et al. 2001; Rea et al. 2016). On a longer, annual timestep, Baker et al.
306 (1994) studied immature growth of another northern Otariid, the northern fur seal, and found
307 substantial individual variability in growth rates, but overall determined individual mass growth
308 was correlated from year-to-year through the 5th year of age.

309 Earlier work by Brandon et al. (2005) estimated that the proportion of neonate Steller sea
310 lion body fat was $5.6 \pm 2.68\%$ (mean, *s.d.*, $n=116$). By 5 months of age, sea lions in the present
311 study had $24.7 \pm 4\%$ ($n = 20$) of body mass as lipid and, at 10 months, reached $33.9 \pm 6\%$ total
312 body fat. While neonatal lipid mass is unknown in the present study, this suggests young sea
313 lions are continuously increasing their allocation of nutritional resources to body fat. This is
314 supported from a cross-sectional study of young-of-the-year Steller sea lions (that included one
315 capture of these individual pups) that showed the percent TBF increase with age in each area
316 studied (Rea et al. 2016). The rapid increase in this ratio indicates pups are receiving from their
317 mothers an energy surplus above growth and maintenance requirements (Winship et al. 2002).

These stores play key roles in thermoregulation and hydrodynamics, and provide a nutritional buffer during future challenges, such as fasting or limited nutrition coincident with weaning.

This growth observed over 5 months did not have a significant effect on longitudinal changes in behavior, except in the rate of vertical travel per day (Figure 5). And in this case, sea lions that gained more mass and more lipid mass actually dove fewer meters per day at the end of this study than sea lions with smaller gains. For young sea lions that are demonstrably increasing their body size and acquiring the oxygen storage and metabolic advantages that follow this change, this result seems counterintuitive. We suggest this result is not a question of limited ability, but of necessity, and further propose that the ways we are able to measure diving behavioral metrics are not tightly coupled enough with biological process to allow us to infer how immature sea lions meet their life history challenges. Indeed, Fahlman et al. (2008b) and others have demonstrated that behavioral metrics more closely tied to the actual body orientation and limb movement of swimming (e.g., acceleration measured in three dimensions vs. basic dive phase metrics used in the present study) correlate with metabolic costs and the physiological processes supporting Steller sea lion diving.

This is the first study of buoyancy effects upon behavior in a free-ranging otariid. Previously, sea lions were assumed to be negatively buoyant (Crocker et al. 1997). In specialist phocid foragers, such as the northern elephant seal (*Mirounga angustirostris* (Gill, 1866)), that make long-range and deep-diving foraging excursions to capture their prey, buoyancy has been shown to be a significant predictor of diving behavior (Webb et al. 1998). Subsequently, these changes in diving behavior have also been used as a predictor of changes in body composition during long-duration foraging trips (Biuw et al. 2003). A shorter-ranging phocid with foraging

340 more typical of Steller sea lions, the grey seal, showed that more negatively buoyant individuals
341 descended significantly faster (Beck et al. 2000).

342 Similar to previous work on other taxa contrasting buoyancy with behavior (Webb et al.
343 1998; Beck et al. 2000; Biuw et al. 2003), none of the Steller sea lions in this study (Figure 3)
344 and only 1 of 696 other Steller sea lions from age 0 – 3 years (ADFG unpublished data) ever
345 became positively buoyant. For air-breathing marine predators who rely on fat stores for energy,
346 thermoregulation and buoyancy, changes to a more positive buoyancy overall are perhaps better
347 phrased as ‘becoming less negatively buoyant.’ Negatively buoyant sea lions must work harder
348 on ascent from a dive (Sparling and Fedak 2004), which limits their overall foraging time
349 relative to time required for descent and ascent in an oxygen-limited situation. Because the
350 present study found no significant relationship between buoyancy, ascent speed, and descent
351 speed, we could not make this inference. Why should a physical characteristic that intuitively
352 seems central to behavior of an animal in a buoyant environment have no detectable effect on
353 behavior? In controlled trials, Suzuki et al. (2014) recently demonstrated that drag, a function of
354 body shape, has significant effects on Steller sea lion swimming speed, but that buoyancy, a
355 function of body composition, did not. Additionally, evidence for lung collapse has been found
356 in California sea lions (*Zalophus californianus* (Lesson, 1828)), and hypothesized to occur at
357 160-180 m depth (McDonald and Ponganis 2012). Because residual lung air is modeled to cause
358 significant positive bias in buoyancy equal to the effect of lipid mass (Biuw et al. 2003), and sea
359 lions in the present study rarely reached depths which would lead to potential lung collapse
360 (McDonald and Ponganis 2012), any behavioral effects of buoyancy in the present study may be
361 masked. Finally, most sea lions in the present study were not yet weaned. Perhaps they were not
362 exhibiting their physiological limits of diving because they were provisioned by their mothers

and thus foraging behavior was not necessary. The resulting mid-range behavior may not reflect their physiological ability or limitations (Burns 1999). Thus, effects of changes in buoyancy on diving behavior may become more evident after weaning as these individuals transition to an obligate foraging lifestyle and, later, as they begin meeting the energetic demands and foraging time constraints caused by breeding.

Although there was little evidence of change in diving behavior caused by endogenous factors, these growing pups were responding to seasonal cues as reflected in their behavior. This is similar to behavior previous documented in older Steller sea lions (*e.g.*, Pitcher et al. 2005). Mid-winter peaks in diving behaviors, with most nighttime measures significantly higher than those in daylight (Figure 6), are representative of Steller sea lion foraging at any age class. While in the long-term, young sea lions show an increase in the depth, duration and amount of time spent diving (Pitcher et al. 2005), over the winter, seasonal effects are evident for juveniles one year older than the present study (Rehberg and Burns 2005), with juvenile dive frequency and time at sea significantly higher mid-winter than during later months, and lower at night than during daytime. Pups in the present study show a similar seasonal peak, but the diurnal pattern was reversed (Figure 6) with more pup activity at sea during night. Older juveniles swimming at night are similar to the nocturnal foraging of adult females (Rehberg et al. 2009), whereas pups in the present study may be taking advantage of their mother's absence during foraging—and thus unavailability for suckling—to spend time in the water. These observations are consistent with a life history in which early training, while pups are still nutritionally dependent, can provide future benefits after they ultimately wean (Fowler et al. 2007). Future longitudinal studies will be improved by the techniques now available to positively identify weaning and measure behavioral parameters closely tied to the mechanics of swimming and diving.

386

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Figure 1. Study area for capture and recapture of Steller sea lion pups (*Eumetopias jubatus* (Schreber, 1776)) in Prince William Sound, Alaska during November – April 2005-2006 and 2007-2008. Haulouts at which pups were captured are indicated by solid circles; other known haulouts in the area are indicated by open circles. Most initial captures were at seasonally-occupied Perry Island, a haulout used during winter; recaptures during spring were primarily at Glacier Island and The Needle, 45 km and 80 km distant, respectively.

Figure 2. Change in mass compared to change in total body fat (TBF) of individual Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) pups by sex (sex indicated by marker M or F, $n = 19$) between November and April. Pup SSL2007 681PWS was mis-sexed and not included.

Figure 3. Change in buoyancy (N) of Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) pups due to the change in the ratio of adipose to lean tissue between initial sampling at age 5 months and second sampling at age 10 months ($n = 19$). Vertical lines indicate magnitude of change and arrowhead indicates direction.

Figure 4. Example of subjective assessment of weaning using stable nitrogen trends along the vibrissae. Nitrogen (reflecting trophic level) is indicated on y axis, relative age is expressed as distance from the tip of vibrissae as indicated on x axis (increasing age left-to-right, from indicated 'birth' line toward the ages at capture of 5 and 10 months). Black line reflects trend in nitrogen from birth to the first vibrissa pulled at initial capture, with sampling points indicated by dots. Blue line similarly reflects trend in nitrogen from birth to the second vibrissa pulled at recapture. Panel 'a' is SSL2005 614PWS, a sea lion observed continuing to suckle at conclusion of this study and showing no change in trophic level suggesting weaning. Panel 'b' is SSL2005 622PWS, a Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) not observed suckling and

showing a late change in stable nitrogen (highlighted in red) suggestive, but not definitively indicative of, weaning.

Figure 5. Correlation of overall vertical travel rate ($\text{m} \cdot \text{d}^{-1}$) with the change in (a) mass and (b) total body fat (TBF) mass of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) between 5 and 10 months of age. Vertical travel rate is calculated from the first and last 30 days of time-depth recorder diving records to match the point-sample mass and lipid mass measures. Means and confidence intervals are estimated using a linear regression ($n = 20$ sea lions): $\ln(\text{vertical travel rate}) = 174.910 - 17.401(\text{mass})$, $R^2 = 0.257$, $P = 0.007$; $\ln(\text{vertical travel rate}) = 117.312 - 11.989(\text{TBF})$, $R^2 = 0.339$, $P = 0.003$.

Figure 6. Seasonal and diurnal effects on Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) diving behavior – (a) vertical rate of travel within bouts, (b) proportion of time within bouts spent underwater, and (c) mean depth of diving within bouts – between ages 5 months (November) and 10 months (March/April). Night diving is indicated by closed boxes; diving during daylight by open diamonds. Means and confidence intervals are estimated using a general linear model ($n = 20$ sea lions) holding animal as a random effect.

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Table 1. Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) pups captured at age 5 months, and recaptured at age 10 months with successful time-depth recorder recovery (n = 20), at haulouts in Prince William Sound, Alaska.

Animal ID	Brand	<u>Capture</u>		<u>Recapture</u>		Sex	Observed suckling at recapture
		Date	Location	Date	Location		
SSL2005 614PWS	=614	13 Nov 2005	Perry Is	30 Mar 2006	Glacier Is	F	yes
SSL2005 619PWS	J200	14 Nov 2005	Perry Is	01 Apr 2006	Glacier Is	F	no
SSL2005 622PWS	E58	15 Nov 2005	Perry Is	11 Apr 2006	Glacier Is	F	no ¹
SSL2005 628PWS	=628	16 Nov 2005	Perry Is	04 Apr 2006	Glacier Is	F	yes
SSL2005 630PWS	=630	16 Nov 2005	Perry Is	08 Apr 2006	The Needle	F	no
SSL2005 636PWS	J217	17 Nov 2005	Perry Is	30 Mar 2006	Glacier Is	M	yes
SSL2005 638PWS	=638	19 Nov 2005	Perry Is	02 Apr 2006	Glacier Is	M	yes
SSL2007 662PWS	=662	09 Nov 2007	Perry Is	14 Apr 2008	Glacier Is	M	yes
SSL2007 663PWS	E63	09 Nov 2007	Perry Is	14 Apr 2008	Glacier Is	F	yes
SSL2007 667PWS	=668	10 Nov 2007	Perry Is	05 Apr 2008	Glacier Is	M	yes
SSL2007 674PWS	=674	12 Nov 2007	Perry Is	05 Apr 2008	Glacier Is	M	yes
SSL2007 678PWS	=678	14 Nov 2007	Perry Is	15 Apr 2008	Perry Is	M	yes
SSL2007 679PWS	=679	14 Nov 2007	Perry Is	05 Apr 2008	Glacier Is	F	yes
SSL2007 680PWS	=680	14 Nov 2007	Perry Is	07 Apr 2008	Glacier Is	F	no
SSL2007 681PWS	=681	15 Nov 2007	Perry Is	03 Apr 2008	Glacier Is	²	yes
SSL2007 683PWS	=683	15 Nov 2007	Perry Is	11 Apr 2008	The Needle	F	yes
SSL2007 687PWS	=687	16 Nov 2007	Glacier Is	03 Apr 2008	Glacier Is	F	yes
SSL2007 690PWS	=690	16 Nov 2007	Glacier Is	04 Apr 2008	Glacier Is	M	yes
SSL2007 693PWS	=693	17 Nov 2007	Glacier Is	05 Apr 2008	Glacier Is	M	no
SSL2007 696PWS	=696	18 Nov 2007	Perry Is	08 Apr 2008	Perry Is	M	yes

¹ SSL2005 622PWS had inconclusive evidence of weaning from change in stable nitrogen. See Figure 4.

² SSL2007 681PWS was identified as male at capture but female at recapture. Follow up confirmation is unavailable.

Table 2. Mass (kg), total body fat mass (TBF, determined using the deuterium dilution method; Rea et al. 2016), at capture and recapture (ages 5 months and 10 months, respectively), and the fraction of growth due to increased TBF, for Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) in Prince William Sound, Alaska.

Animal ID	Sex	Mass (kg)		TBF Mass (kg)		TBF contribution to growth (%)
		Capture	Recapture	Capture	Recapture	
SSL2005 614PWS	F	64	86.5	15.1	29.2	62
SSL2005 619PWS	F	64	96	14.8	27.0	38
SSL2005 622PWS	F	59	62.5	15.1	12.0	0
SSL2005 628PWS	F	70	76.5	18.9	27.8	100
SSL2005 630PWS	F	73	83	24.6	33.9	92
SSL2005 636PWS	M	70	76.5	19.5	19.3	0
SSL2005 638PWS	M	63	83.5	10.5	25.4	72
SSL2007 663PWS	F	76.5	107	23.1	32.2	30
SSL2007 679PWS	F	64	109	15.1	42.8	62
SSL2007 680PWS	F	68	107.5	16.4	37.3	53
SSL2007 683PWS	F	61	105	16.4	42.0	58
SSL2007 687PWS	F	67	110.5	16.9	42.7	59
SSL2007 681PWS	¹	69.5	101.5	16.5	38.0	67
SSL2007 690PWS	M	84.5	140.5	19.0	53.9	62
SSL2007 667PWS	M	61	103	15.3	43.9	68
SSL2007 662PWS	M	81.5	115.5	21.9	35.9	41
SSL2007 674PWS	M	66	113.5	16.7	43.7	57
SSL2007 678PWS	M	71.5	90	12.3	20.1	42
SSL2007 693PWS	M	82	131	18.4	47.4	59
SSL2007 696PWS	M	73.5	115	17.8	39.6	53

¹ SSL2007 681PWS was identified as male at capture but female at recapture. Follow up confirmation is unavailable.

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(a)

(b)

(a)

(b)

(c)