

Differences in diving and swimming behavior of pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska

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Abstract: Reduced juvenile survival caused by prey depletion is one hypothesis for the decline in the western Alaska population of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)). To understand the exposure of young sea lions to these depletions, the swimming and diving behavior of pups, juveniles, and subadults was evaluated relative to prey behavior. Pups made shorter and shallower dives (13 m, 0.9 min) than juveniles or subadults, as expected based on physiological limitations, but juveniles and subadults dived to similar depths and durations (29 m, 1.7 min and 38 m, 2.0 min, respectively). Activity patterns of juveniles and subadults reflected diurnal prey migrations, while pup activity did not. Longitudinal trends in pup dive behavior reflected both physiological and behavioral development, while juvenile dive behaviors reflected seasonal changes in prey availability. Results suggest that adult females must continue to provide nutritional support to pups during winter because of the limited diving ability of these young animals. For this reason, the flexible lactation strategies that allow for longer nursing periods during periods of low prey availability and reduce female fecundity may improve juvenile survival.

Résumé : La réduction de la survie des jeunes à cause d'une diminution des proies est l'une des hypothèses avancées pour expliquer le déclin de la population des lions de mer de Steller (*Eumetopias jubatus* (Schreber, 1776)) dans l'ouest de l'Alaska. Afin de comprendre l'exposition des lions de mer immatures à ces déplétions, nous avons évalué le comportement de nage et de plongée chez les petits, les jeunes et les subadultes en fonction du comportement des proies. Comme on peut s'y attendre à cause de leurs restrictions physiologiques, les petits font des plongées plus courtes et moins profondes (13 m, 0,9 min) que les jeunes et les subadultes, alors que les jeunes et les subadultes plongent à des profondeurs et pour des durées semblables (respectivement 29 m, 1,7 min et 38 m, 2,0 min). Les patrons d'activité des jeunes et des subadultes, mais pas ceux des petits, correspondent aux migrations journalières des proies. Les tendances longitudinales du comportement de plongée des petits reflètent leur développement tant physiologique que comportemental, alors que les comportements de plongée des jeunes correspondent aux changements saisonniers de disponibilité des proies. Nos résultats laissent croire que les femelles adultes doivent continuer à fournir un support alimentaire aux petits pendant l'hiver à cause des capacités restreintes de plongée de ces animaux de bas âge. C'est pourquoi les stratégies flexibles d'allaitement qui permettent des périodes prolongées d'alimentation lactée durant les moments de faible disponibilité des proies et qui réduisent la fécondité des femelles peuvent augmenter la survie des jeunes.

[Traduit par la Rédaction]

Introduction

Because swimming and diving are necessary for prey capture by pinnipeds, characteristics of these behaviors can shed light on the foraging environment faced by the animal. Differences in diet and prey availability alter behavioral patterns in many air-breathing marine predators (Croxdall et al. 1988; Bost et al. 2002; Bowen et al. 2002; Harcourt et al. 2002; Ropert-Coudert et al. 2002; Watanabe et al. 2003). Within a species, differences in diving patterns among individuals or age classes reflect relative foraging ability and (or) different foraging requirements. For example, in phocid mother-pup pairs monitored simultaneously, lactating adult

females dove deeper, longer, and with greater regularity than their nutritionally dependent offspring (Bowen et al. 1999; Sato et al. 2003). Such behavioral differences have important ecological consequences, because individuals with different foraging abilities and requirements may respond differently to changes in prey abundance or availability. In particular, younger divers have been shown to be more susceptible than older, experienced foragers to changes in prey availability (Horning and Trillmich 1999) due, in part, to their lower aerobic thresholds and smaller body size (Burns 1999; Richmond et al. 2006). These observations suggest there should be observable differences in dive patterns among individuals in different age classes and that behav-

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ioral differences should become apparent when prey type or availability changes.

The challenge in interpreting changes in diving behavior as indicative of shifts in foraging behavior results from the fact that not all aquatic activity is targeted at prey nor are all foraging dives successful. For central place foragers (Raum-Suryan et al. 2004) such as the Steller sea lion (hereinafter SSL; *Eumetopias jubatus* (Schreber, 1776)), diving patterns can be examined at three levels of increasing complexity. At the broadest scale, the proportion of time an air-breathing, land-based underwater predator spends at sea off the haulout is the fundamental measure of effort. Within these trips to sea, the proportion of time spent underwater is a measure of effort more directly reflective of foraging activity, because diving mammals should maximize their energetically expensive time underwater only if prey are actively being sought (Thompson and Fedak 2001). Finally, the depth and duration of individual dives describe how time spent underwater is allocated (among many, short dives or a few, long dives) and is useful for understanding foraging strategy (Croxall et al. 1988; Horning and Trillmich 1999; Harcourt et al. 2002). These measures, combined with knowledge of potential prey and compared among animals of different life stages, can provide a basis for inferring whether SSL at different ages are actually foraging.

This study applies the above three metrics of diving effort to the analysis of immature SSL diving behavior to understand whether young animals are foraging, which is important when attempting to understand the effect of prey availability upon population dynamics. A 10%–20% reduction in juvenile survival has been strongly implicated in the marked decline of the western Alaska SSL stock (hereinafter WS; York 1994; Loughlin 1997), and one hypothesized mechanism for this reduced survival is the inability of juvenile sea lions to acquire sufficient prey in the months past weaning in areas of reduced prey availability (Ferrero and Fritz 2002). However, understanding the influence of prey abundance and distribution on juvenile SSL survivorship is complicated because juveniles enjoy an extended lactation period of 1–3 years (Bonner 1984; Trillmich 1990; Pitcher et al. 2001). During this time, swimming and diving alternate with onshore nursing bouts (Trites and Porter 2002), and there is no reliable way to determine if an individual is completely independent from maternal investment. While preweaning diving may permit development of the foraging behaviors required for survival postweaning (Kovacs and Lavigne 1992; Horning and Trillmich 1997; Sato et al. 2003), because the offspring is subsidized by energy from the mother, preweaning diving behavior may not vary in response to the same factors that influence postweaning diving. Therefore, studies of young SSL swimming and diving patterns must make inferences about the amount of energetic support received and the potential impact this might have on foraging patterns based on dive metrics alone.

To better understand the exposure of young sea lions to prey depletions, this study monitored the diving and swimming behavior of SSL pups (young of the year) within the WS and compared it with the behavior of older animals (yearlings and subadults). We hypothesized that pups would be less-capable divers than older SSL, as reflected by dive

depth and duration, and thus would have a more limited ability to respond to changes in prey availability. We further hypothesized that younger sea lions would spend less time at sea and underwater than older sea lions within the same season, reflecting less reliance on independent foraging. Finally, we hypothesized that longitudinal trends in pup behavior would reflect physiological development as well as the onset of independent foraging, whereas temporal trends in diving behavior of older sea lions would primarily reflect responses to foraging conditions. We concluded by commenting on the potential contribution the limited diving ability of young sea lions may have on population trends in the WS given local foraging conditions.

Materials and methods

To study the development of diving behavior and activity budgets, 11 pup (9–12 months old), 18 juvenile (17–24 months old), and 4 subadult (≥ 30 months old) SSLs were monitored using external dive-recording satellite tags between November 2001 and July 2005 (Table 1). Sea lions were captured at six haulouts within the Gulf of Alaska (hereinafter GOA, Prince William Sound and Kodiak Island) and the central Aleutian Islands (hereinafter CAI; Fig. 1) using either the underwater dive-capture technique (Raum-Suryan et al. 2004) or on-land capture using handheld nets. Animals were transferred by skiff to a research vessel for processing under isoflurane anesthesia (Heath et al. 1997). The age class (pup, juvenile, or subadult) of each animal was determined by examining canine length (King et al. 2007), tooth eruption, and animal size. Within each age class, age in months was estimated by date using an assumed birth date of 1 June (Pitcher et al. 2001).

Satellite-relay data loggers (hereinafter SRDL; Model 7000, Sea Mammal Research Unit, St. Andrews, Scotland) were attached to the fur of each animal using cool-setting epoxy (10-Minute Epoxy No. 14255, ITW Devcon, Danvers, Massachusetts) and 3 mm nylon mesh (Research Nets, Inc., Bothell, Washington). To maximize the number of transmissions received, SRDLs were typically affixed to the top of the head ($n = 25$ animals), antenna rearward. For the eight animals with insufficient head size to permit SRDLs to be affixed squarely, SRDLs were affixed dorsally between the scapulae, antenna forward. SRDLs weighed approximately 300 g in air, 0.3% of the mass of the smallest sea lion monitored. A pressure transducer and conductivity sensor monitored instrument depth and immersion status (wet or dry) every 4 s. These data were aggregated into measures of diving behavior and activity budget as described in detail by Fedak et al. (2001) and stored in onboard memory prior to transmission to the Argos satellite data-relay system (Argos/CLS 2000).

SRDLs were programmed to report the date, time, maximum depth, and duration of individual dives. Dives were identified as intervals during which sea lions remained below a threshold depth for longer than a threshold time. Because of uplink bandwidth constraints, only a subset of dives were successfully relayed by the Argos satellite system. As experience was gained with SRDL performance, these thresholds were altered to increase data throughput: the initial threshold of 4 m and 8 s ($n = 2$ sea lions) was increased

Table 1. Steller sea lions (*Eumetopias jubatus*) captured for this study and satellite-relay data logger (SRDL) deployment durations (release of tagged sea lion to apparent tag failure) in ascending order of age class and deployment date.

Animal identifier	Capture haulout	Region	Sex	Mass (kg)	Age class	Age at SRDL deployment start (months)	SRDL deployment start date	SRDL deployment duration (days)
W594 ^a	Long Island	GOA	M	87	Pup	9	2 March 2002	13
W596 ^b	Long Island	GOA	M	126	Pup	9	3 March 2002	50
W599 ^b	Long Island	GOA	M	99	Pup	9	4 March 2002	86
W685 ^b	Two-Headed Island	GOA	F	88	Pup	9	5 March 2002	63
W688 ^b	Two-Headed Island	GOA	M	114	Pup	9	5 March 2002	81
406AL	Yunaska Island	CAI	M	133	Pup	10	29 March 2003	86
407AL	Yunaska Island	CAI	F	90	Pup	10	29 March 2003	80
408AL	Kagalaska Island	CAI	F	109	Pup	10	1 April 2003	90
409AL	Kagalaska Island	CAI	F	120	Pup	10	1 April 2003	43
411AL	Kagalaska Island	CAI	F	107	Pup	10	2 April 2003	80
412AL	Kagalaska Island	CAI	M	124	Pup	10	3 April 2003	113
280PW ^b	Perry Island	GOA	M	142	Juvenile	17	11 November 2001	121
286PW ^b	Perry Island	GOA	F	123	Juvenile	17	12 November 2001	95
404AL	Yunaska Island	CAI	F	146	Juvenile	22	29 March 2003	88
410AL	Kagalaska Island	CAI	F	148	Juvenile	22	1 April 2003	120
437PW	Perry Island	GOA	F	127	Juvenile	17	14 November 2003	156
435PW	Perry Island	GOA	F	128	Juvenile	17	14 November 2003	160
X252	Perry Island	GOA	M	138	Juvenile	17	15 November 2003	151
X196	Perry Island	GOA	F	128	Juvenile	17	15 November 2003	147
443PW	Glacier Island	GOA	F	125	Juvenile	17	16 November 2003	66
445PW	Glacier Island	GOA	M	121	Juvenile	17	17 November 2003	141
446PW	Glacier Island	GOA	F	120	Juvenile	17	17 November 2003	149
449PW	Glacier Island	GOA	M	128	Juvenile	17	18 November 2003	122
564PW	Glacier Island	GOA	F	116	Juvenile	20	27 January 2005	122
565PW	Glacier Island	GOA	F	130	Juvenile	20	27 January 2005	151
587PW	Perry Island	GOA	M	177	Juvenile	21	27 February 2005	134
590PW	Glacier Island	GOA	M	134	Juvenile	21	1 March 2005	126
592PW	Perry Island	GOA	M	141	Juvenile	21	2 March 2005	100
444PW	Glacier Island	GOA	M	230	Subadult	30	17 November 2003	116
563PW	Glacier Island	GOA	F	170	Subadult	32	27 January 2005	151
574PW	Glacier Island	GOA	M	156	Subadult	32	30 January 2005	134
328PW	Glacier Island	GOA	M	233	Subadult	45	1 March 2005	151

Note: CAI, central Aleutian Islands; and GOA, Gulf of Alaska.

^aExcluded from all analyses because of early SRDL failure.

^bExcluded from proportion of time spent at sea (TAS), proportion of time at sea spent diving (TASD), and dive frequency analysis because of SRDL programming differences.

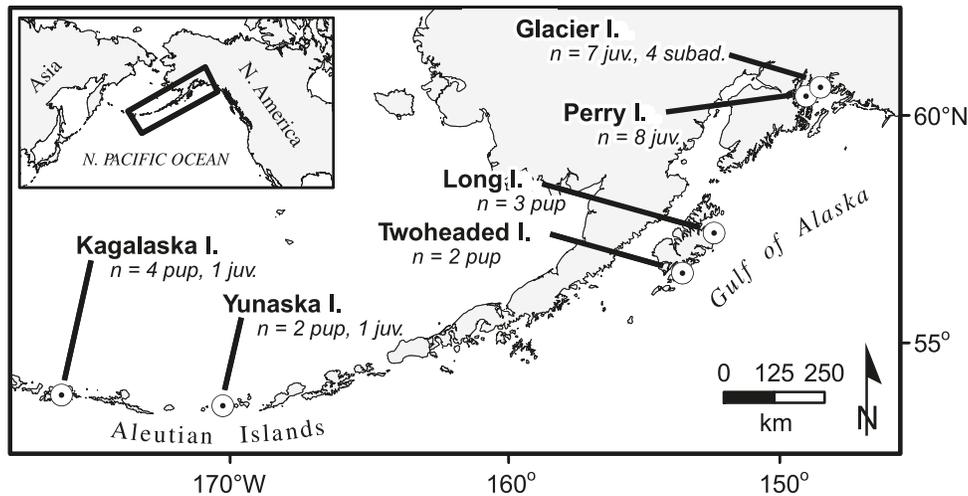
to 6 m and 8 s ($n = 5$ sea lions) and finally to 8 m and 8 s ($n = 26$ sea lions). To permit comparisons, data collected by all 33 SRDLs were standardized such that only dives reaching the 8 m and 8 s threshold were retained for analysis. Resolution of dive depth and duration decreased with increasing values, with dives of up to 2 min and 170 m having 4–8 s duration resolution and 3–6 m depth resolution.

SRDLs also reported the proportion of time individuals spent hauled out on land, swimming near the surface, and diving below the threshold depth and duration. These activity budgets were reported for each of six 4 h summary periods within each day. The proportion of time spent at sea (TAS) was calculated as the inverse of the proportion of time hauled out, and the proportion of time at sea spent diving (TASD) was calculated as the proportion of TAS spent below the threshold depth and duration. Because TASD was sensitive to the dive threshold, it was only computed for the

26 SRDLs programmed with the 8 m and 8 s thresholds. To evaluate the relative proportion of data received from the tags, the number of dives made (as reported by the 4 h summary data) was compared with the number of individual dive records successfully received via satellite, and the number of activity budget records expected (by deployment length) was compared with the number of activity budget records actually received.

The start and end time of day (sunrise \leq day $<$ sunset) and night (sunset \leq night $<$ sunrise) at the midpoint of all sea lion activity within each region (GOA and CAI) was determined for each day using United States Naval Observatory Astronomical Applications Department (Washington, District of Columbia) data. Sunset and sunrise were defined as the limit of civil twilight: solar elevation 6° below the horizon. Individual dives were grouped by 24 h day (midnight-to-midnight Coordinated Universal Time, UTC) and then

Fig. 1. Number of Steller sea lion (*Eumetopias jubatus*) pups, juveniles, and subadults captured and instrumented at each haul out location within the central Aleutian Islands and the Gulf of Alaska.



assigned to day or night categories based on the time at which they occurred. The average depth and duration of dives made by each individual was calculated for each week of instrument deployment, using those day and night periods having at least six dives. Each 4 h activity budget (TAS, TASD, and dive frequency) was also categorized as day or night, based on whether the majority of the period occurred during day or night. Only days in which data from all six summary periods in the 24 h period were received were retained for analysis of activity patterns. From these grouped data, weekly mean TAS, TASD, and dive frequency (dives \times (h at sea)⁻¹) were calculated if at least 3 days of activity budget data were available for that week. The correlation between individual dive depth and duration was calculated for each age class.

To understand the influence of age, season, sex, and time of day on sea lion diving and swimming, behavior was analyzed at two temporal scales. At both scales, response variables were mean dive depth (m), mean dive duration (min), dive frequency, TAS, and TASD. First, a broad-scale comparison among the pup, juvenile, and subadult age classes was performed on behavior observed during the spring season (March–June). The effects of age class, time of day (day or night), sex, and their interactions were tested using a separate model for each response variable. Only behavior observed during spring was included in this comparison because data were available for all age classes during this time ($n = 5$ male and $n = 5$ female for pups, $n = 5$ male and $n = 5$ female for juveniles, and $n = 3$ male and $n = 1$ female for subadults). Next, a second set of finer scale models examined the longitudinal (month to month) trend in behavior within the pup ($n = 10$, March–June) and juvenile ($n = 18$, November–June) age classes. Separate models for each response variable tested the effects of month of age, time of day, sex, and their interactions within each age class. Subadults were omitted from this fine-scale analysis. Effect of study year was not included because of limited sample size. Regional effects were excluded from the models owing to confounding with age class, as most juveniles and all subadults were captured within the GOA. To quantify this possible confounding influence, we tested for a

regional main effect on the pup sample, the only age class having similar sample size in each region. Previous studies of SSL juvenile diving (Loughlin et al. 2003; Pitcher et al. 2005) similarly pooled samples across years and regions.

To make these comparisons, linear mixed-effects models (SPSS version 12, SPSS Inc., 2003) were employed, because they avoided pseudoreplication by accounting for the unbalanced sampling design, the influence of individual animals, and the serial autocorrelation among dives made by each sea lion. Within all models, individual sea lion was included as a random effect, to prevent individual animals from unduly influencing the analysis. An autoregressive covariance structure, which accounted for the lack of independence of sequential observations within each animal, was selected using the method of Singer (1998). The type III sum of squares accounted for the unbalanced sampling design. Response normality was examined using quantile–quantile plots, skewness, and kurtosis. Data were transformed using the \log_e (dive depth and duration), arcsine-root (TAS and TASD), and square root (dive frequency). Significance was preset at $P < 0.05$ and Bonferroni post hoc tests identified pairwise differences within and between fixed effects.

Results

Of the 33 SRDL tags deployed on sea lions, one failed shortly after deployment and was excluded from analysis. The remaining 32 SRDLs operated for 112 ± 34 days (mean of individual animals ± 1 SD, Table 1). On average, tags successfully relayed depth and duration for $48\% \pm 16\%$ of the 180 830 dives made by sea lions and $93\% \pm 10\%$ of possible TAS, TASD, and dive frequency data. Data relay became more successful as dive thresholds were increased from 4 m and 8 s to 8 m and 8 s: individual dive reporting improved from $36\% \pm 15\%$ to $51\% \pm 15\%$ of dives, and activity reporting from $81\% \pm 14\%$ to $95\% \pm 9\%$ of possible recording periods. Because older sea lions proved difficult to capture in the CAI, most juveniles and all subadults were monitored within the GOA region (Table 1, Fig. 1) during this 4 year project. Examination of possible confounding by region showed that geography had little effect upon the be-

Table 2. Effects of age class on mean (95% confidence interval) responses for pup ($n = 5$ males and $n = 5$ females), juvenile ($n = 5$ males and $n = 5$ females), and subadult ($n = 3$ males and $n = 1$ female) Steller sea lion (*Eumetopias jubatus*) diving during spring (March–June) with statistically similar means indicated by similar letters.

Response	Age class		
	Pup	Juvenile	Subadult
Depth (m)	13 (10.2–16.5)	29a (23.9–34.0)	38a (25.8–56.5)
Duration (min)	0.9 (0.8–1.1)	1.7b (1.5–1.9)	2.0b (1.5–2.7)
TAS (%)	41 (33–50)	56c (50–62)	69c (55–80)
TASD (%)	10 (5–17)	27d (20–34)	32d (16–50)
Frequency (no. of dives \times (h at sea) ⁻¹)	3.1 (1.8–4.8)	4.6e (3.4–6.0)	6.0e (3.1–10.0)

Note: TAS, proportion of time spent at sea; and TASD, proportion of time at sea spent diving.

havior of pups: dive depth and duration did not differ by region ($F_{[1,7.760]} = 1.000$, $P = 0.347$; $F_{[1,7.739]} = 3.662$, $P = 0.093$, respectively). Whether this lack of regional effect existed for juveniles or subadults was unknown and untestable. Mass at capture was similar by sex for pups and juveniles (two-sample Student's t : $t_{[9]} = -1.172$, $P = 0.272$; $t_{[9]} = -1.471$, $P = 0.175$, respectively); subadult mass differences by sex could not be tested.

Overall, dives were shallow (31 ± 17 m, mean of individual animals ± 1 SD) and short (1.7 ± 0.6 min), and sea lions spent $48\% \pm 12\%$ of their time at sea, with $27\% \pm 10\%$ of this time at sea spent diving. The deepest dives by age group were 325 m by a 10-month-old pup, >361 m by a 33-month-old juvenile, and >361 m by a subadult (361 m is the recording limit of SRDL programs). The longest dives were 4.9 min by a 10-month-old pup and 13.2 min by a 19-month-old juvenile. The largest subadult made a few 32.9 min dives; other subadults dived for a maximum of 18 min. Individual dive depth and duration were significantly, positively correlated for pups (linear regression: $R^2 = 0.649$, $n = 37310$, $P < 0.001$), juveniles ($R^2 = 0.726$, $n = 116201$, $P < 0.001$), and subadults ($R^2 = 0.703$, $n = 27319$, $P < 0.001$).

Age class comparisons

The broad-scale models comparing pup, juvenile, and subadult diving patterns during spring found significant differences in behavior due to age class and time of day. Mean values for comparisons are shown in Tables 2 and 3. Overall, juvenile sea lions dove 11 m deeper and 0.6 min longer than pups (depth: $F_{[2,29.6]} = 18.257$, $P < 0.001$; duration: $F_{[2,29.5]} = 18.607$, $P < 0.001$), but dive frequency did not differ significantly. Juveniles spent 26% more TAS and 12.5% more TASD than pups (TAS: $F_{[2,26.2]} = 7.377$, $P = 0.003$; TASD: $F_{[2,28.4]} = 6.516$, $P = 0.005$). Subadult diving and activity patterns were not significantly different from those of juveniles, but were greater than pups for all main effects (F tests above; Table 2). There was a small but significant effect of sex on dive duration (males dove 24 s longer than females: $F_{[1,28.3]} = 6.075$, $P = 0.020$), but sex did not significantly influence any other dive metric and there were no sex by age class interactions.

There were significant interactions between age class and time of day for all parameters measured, but this effect was less evident in dive performance than activity patterns (Table 3). While the day/night contrast was significant for

both pup and juvenile dive depth and duration ($F_{[2,707.0]} = 27.488$, $P = 0.002$; $F_{[2,665.0]} = 24.001$, $P = 0.009$, respectively), effect sizes were small (pups, 2.2 m and 0.1 min; juveniles, 7 m and 0.2 min; Table 3). Subadult diurnal contrasts were larger (14 m and 0.5 min; Table 3).

In contrast, diel differences in activity patterns were more pronounced, with animals of all age classes less aquatically active during the day than during the night. In general, the magnitude of the difference between day and night activity patterns decreased with age as daytime activity increased. For example, pups spent 48% less TAS, 7% less TASD, and dove 6.6 times less frequently during the day than during the night (Table 3; TAS: $F_{[2,766.6]} = 259.704$, $P < 0.001$; TASD: $F_{[2,724.8]} = 73.352$, $P < 0.001$; dive frequency: $F_{[2,744.2]} = 274.659$, $P < 0.001$). Juveniles were also less aquatically active during the day, but because diel differences were small (Table 3), juvenile activity patterns differed from those of pups only during daylight hours, when juveniles were much more active than pups. Similarly, subadults were less aquatically active during the day, but daytime activity levels did not differ from those of juveniles. In contrast to age-related differences in daytime activity patterns, TASD and dive frequency did not differ by age during the night, although confidence intervals were wide.

Developmental and seasonal changes

The second set of analyses was designed to identify longitudinal changes in behavioral patterns owing to ontogeny, season, and (or) time of day. Models were run for pups and juveniles separately, in part because of their dissimilar record lengths, and subadults were excluded. Pups were monitored during 4 months in the spring (March–June) when they were between 9 and 12 months of age. Over this period the average depth of dives made by pups increased by 6 m ($F_{[3,57.0]} = 9.508$, $P < 0.001$; Fig. 2A), but duration did not change ($F_{[3,89.4]} = 0.760$, $P = 0.519$; Fig. 3A). In addition, as pups got older (and the season progressed), a diurnal pattern emerged as the dives made at night became deeper and longer than those made during daylight (significant month of age \times time of day interaction: $F_{[3,137.4]} = 6.910$, $P < 0.001$; $F_{[3,124.5]} = 5.642$, $P = 0.001$, respectively; Figs. 2A, 3A). By June, pup dive depth and duration became similar to juvenile diving ($F_{[1,22.676]} = 12.147$, $P = 0.002$; $F_{[1,24.976]} = 10.987$, $P = 0.003$, respectively; Figs. 2, 3). Dive frequency also increased significantly from 1.8 to 4.3 dives \times (h at sea)⁻¹ between April and June ($F_{[2,67.7]} = 5.949$, $P = 0.004$).

Table 3. First-order interactive effects of age class and time of day on mean (95% confidence interval) responses for pup ($n = 5$ males and $n = 5$ females), juvenile ($n = 5$ males and $n = 5$ females), and subadult ($n = 3$ males and $n = 1$ female) Steller sea lion (*Eumetopias jubatus*) diving during spring (March–June) with statistically similar means indicated by similar letters.

Response	Age class					
	Pup		Juvenile		Subadult	
	Day	Night	Day	Night	Day	Night
Depth (m)	12 (10–16)	14 (11–17)	32a (27–38)	25b (21–30)	46a (31–68)	32b (21–47)
Duration (min)	0.9 (0.7–1.0)	1.0 (0.8–1.1)	1.8a (1.6–2.0)	1.6b (1.4–1.8)	2.3a (1.7–3.0)	1.8b (1.3–2.4)
TAS (%)	19 (12–26)	67c (58–75)	57a,b (50–63)	56a,c (50–62)	62b (48–75)	75 (62–86)
TASD (%)	6 (2–12)	15c (8–24)	27a,b (20–34)	27a,c (20–34)	29b (14–47)	34c (18–53)
Frequency (no. of dives \times (h at sea) ⁻¹)	1.0 (0.3–2.0)	6.6c (4.5–9.0)	4.2a (3.0–5.6)	5.0c (3.7–6.6)	4.3a (1.8–7.8)	8.1c (4.5–12.7)

Note: TAS, proportion of time spent at sea; and TASD, proportion of time at sea spent diving.

Overall, dives were more frequent at night (Fig. 4A), but there was no significant month of age \times time of day interaction. Sex \times month of age interactions were not significant for dive depth, dive duration, or dive frequency.

Pup activity patterns also changed with age and season. Pup TAS increased from 31% to 53% between April and June ($F_{[2,243,5]} = 10.187$, $P < 0.001$). There was a significant month of age \times time of day interaction as the increase in TAS was driven by the marked increase in the amount of time pups spent at sea during the night in May and June ($F_{[4,65,311]} = 22.823$, $P < 0.001$; Fig. 5A), but a smaller increase during the day ($F_{[4,76,3]} = 5.028$, $P = 0.001$). In contrast, overall TASD did not increase significantly with age for pups ($F_{[4,59,564]} = 2.104$, $P = 0.092$), but did vary by time of day ($F_{[1,118,0]} = 78.420$, $P < 0.001$). Pups of all ages spent significantly more TASD during night than during day (Fig. 6A), and TASD significantly increased with month of age only during the night ($F_{[4,76,4]} = 3.303$, $P = 0.015$), indicating this diurnal pattern was always present and became more pronounced with age. Because overall TASD remained constant over time, increased underwater activity by pups was driven solely by changes in TAS.

Unlike the relatively short dive record for pups, information on the diving behavior and activity budgets of juveniles was collected over an 8 month period from November to June, when sea lions were between 17 and 24 months of age. Juvenile dive depth and duration declined progressively with increasing month of age (by 19 m and 52 s; $F_{[7,138,8]} = 2.949$, $P = 0.007$; $F_{[7,118,0]} = 4.095$, $P < 0.001$, respectively). Juvenile dive depth and duration also had significant time of day ($F_{[1,420,2]} = 42.772$, $P < 0.001$; $F_{[1,397,8]} = 25.9$, $P < 0.001$, respectively) and month of age \times time of day effects ($F_{[7,425,6]} = 3.9$, $P < 0.001$; $F_{[7,405,3]} = 2.5$, $P = 0.015$, respectively). From November to February, juvenile dives were significantly deeper and longer at night than during daylight, but this pattern was absent between March and June (Figs. 2B, 3B). Whereas overall dive frequency did change with month of age ($F_{[7,123,3]} = 2.306$, $P = 0.030$), there were no significant differences between individual months. Instead, there was a complex month \times time of day interaction ($F_{[7,394,9]} = 37.978$, $P < 0.001$) as juveniles dove more frequently during daylight from December to February, but more frequently at night from April through June (Fig. 4B). As a result, the frequency of daytime dives declined as animals aged and spring advanced. There were no significant month of age \times sex interactions for dive depth, duration, or frequency.

Unlike dive behavior, there was no significant variation in overall juvenile activity patterns owing to month of age. However, as with dive frequency, this apparent lack of trend masked a complex interaction between time of day and month, with juveniles spending significantly more TAS during daytime from November to February, but more TAS at night between April and June ($F_{[7,421,0]} = 35.627$, $P < 0.001$; Figs. 5B, 6B). Similarly, juveniles spent progressively less TASD during daylight as the season progressed, but TASD at night did not change ($F_{[7,423,6]} = 15.423$, $P < 0.001$; Fig. 6B). As a result, most diving activity took place during daylight in winter, but at night in spring. Sex \times month of age interactions were not significant for TAS or TASD.

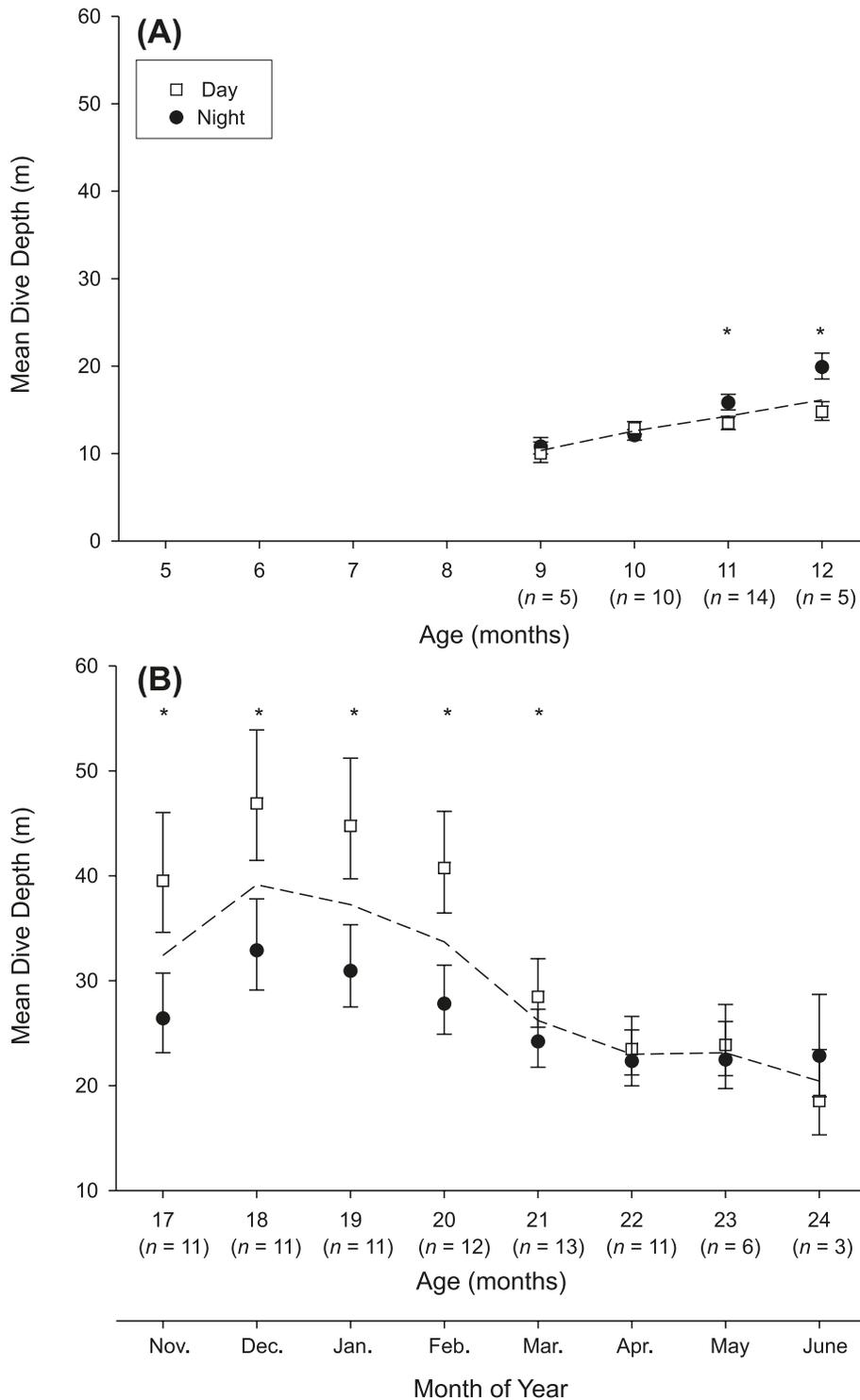
Discussion

This study examined metrics of diving behavior in young sea lions to determine how animal age influenced foraging ability and, by extension, the degree to which juveniles might be at greater risk because of reduced prey availability. We found that pups were less aquatically active than older sea lions, as expected for individuals dependent on lactating females, but this difference disappeared by late spring, coincident with their expected weaning (Pitcher et al. 2001). The effects of age on diving and activity patterns likely integrate physiological development and foraging choices: the dives of young pups were both shorter and shallower than those of older animals because of their reduced breath-hold ability, whereas the more frequent diving by older animals likely reflects their increased reliance on independent foraging and need to target prey during periods when they were most accessible. In combination, the possible vulnerability of pups to prey depletions caused by reduced diving ability relative to older SSLs may explain the extended lactation strategy of SSL females.

Diving and activity differs by age class

The significant differences between the diving behavior and activity patterns of pups, juveniles and subadults during spring suggest that pups are less-capable divers than older sea lions. The shorter, shallower, and less-frequent dives of younger animals likely reflects their smaller body mass, lower mass-specific oxygen stores, and higher diving metabolic rates, all of which contribute to a calculated aerobic dive limit (cADL) that is 0.5 min shorter for pups than juveniles (Richmond et al. 2006). In other pinnipeds, reduced

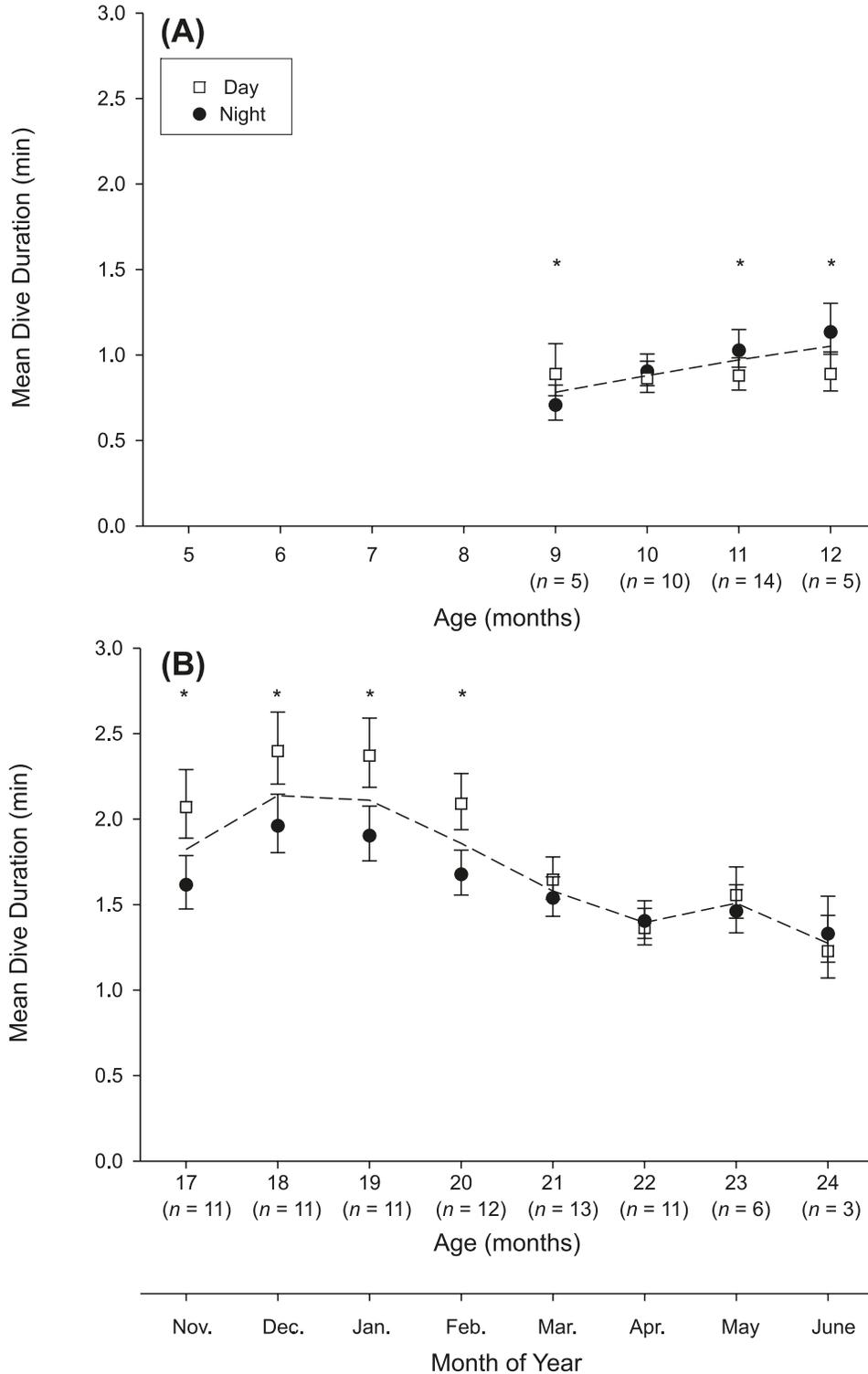
Fig. 2. Comparison of trend in mean (95% confidence interval) dive depth (m) during daylight (□) and night (●) for Steller sea lion (*Eumetopias jubatus*) pups (A) and juveniles (B). Significant ($P < 0.05$) differences between daylight and night values are indicated by asterisks. Broken line indicates overall mean by month. The x axes of plots are aligned by month of year.



aerobic dive capacity has been shown to limit the ability of younger animals to make lengthy dives (Horning and Trillmich 1997; Burns 1999; Loughlin et al. 2003; Pitcher et al. 2005). Interestingly, the larger subadult sea lions did not significantly outperform juveniles, suggesting that the impact of any physiological constraint had eased by the time ani-

mals were in their second year of life. In these comparisons, there was some indication that males made longer dives than females. This difference cannot be attributed to differences in physiological capacity (Richmond et al. 2006), but may reflect the fact three of the four oldest animals were male, as were the two largest animals (Table 1). However, any

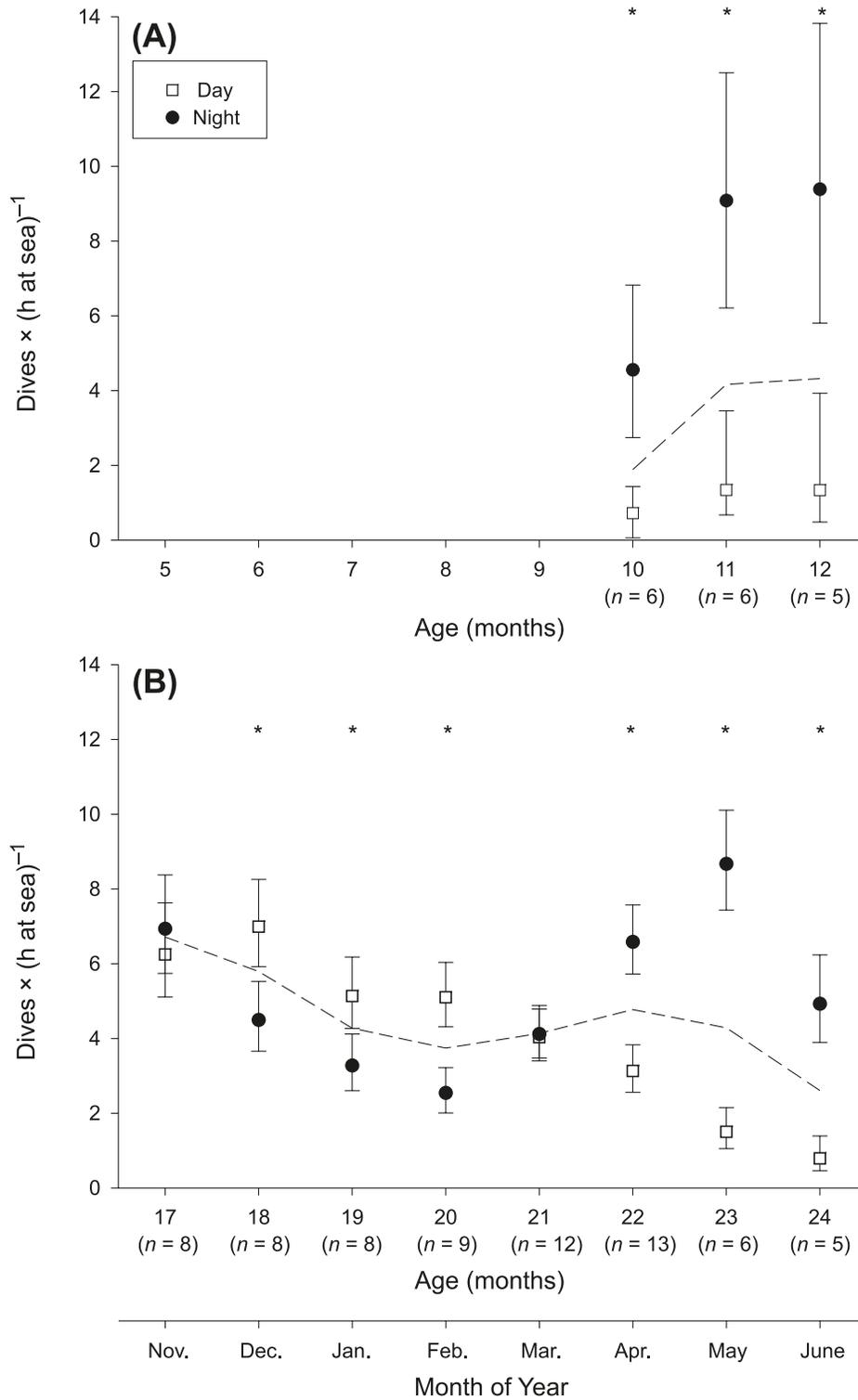
Fig. 3. Comparison of trend in mean (95% confidence interval) dive duration (min) during daylight (□) and night (●) for Steller sea lion (*Eumetopias jubatus*) pups (A) and juveniles (B). Axes and other markings as in Fig. 2.



interpretation based on mass is tenuous because sea lions were weighed only at time of capture. It is also possible that behavioral differences attributed to age may instead reflect regional or interannual effects. Unfortunately, capture difficulties produced an unbalanced sample that precluded direct testing of such effects.

After the first year of life, potential influence of prey selection upon behavior become more apparent, as shown by differences in activity patterns between pups, juveniles, and subadults. Pups spent less TAS and T ASD than juveniles or subadults. Because these activities are independent of physiological breath-holding ability, and TAS and T ASD are

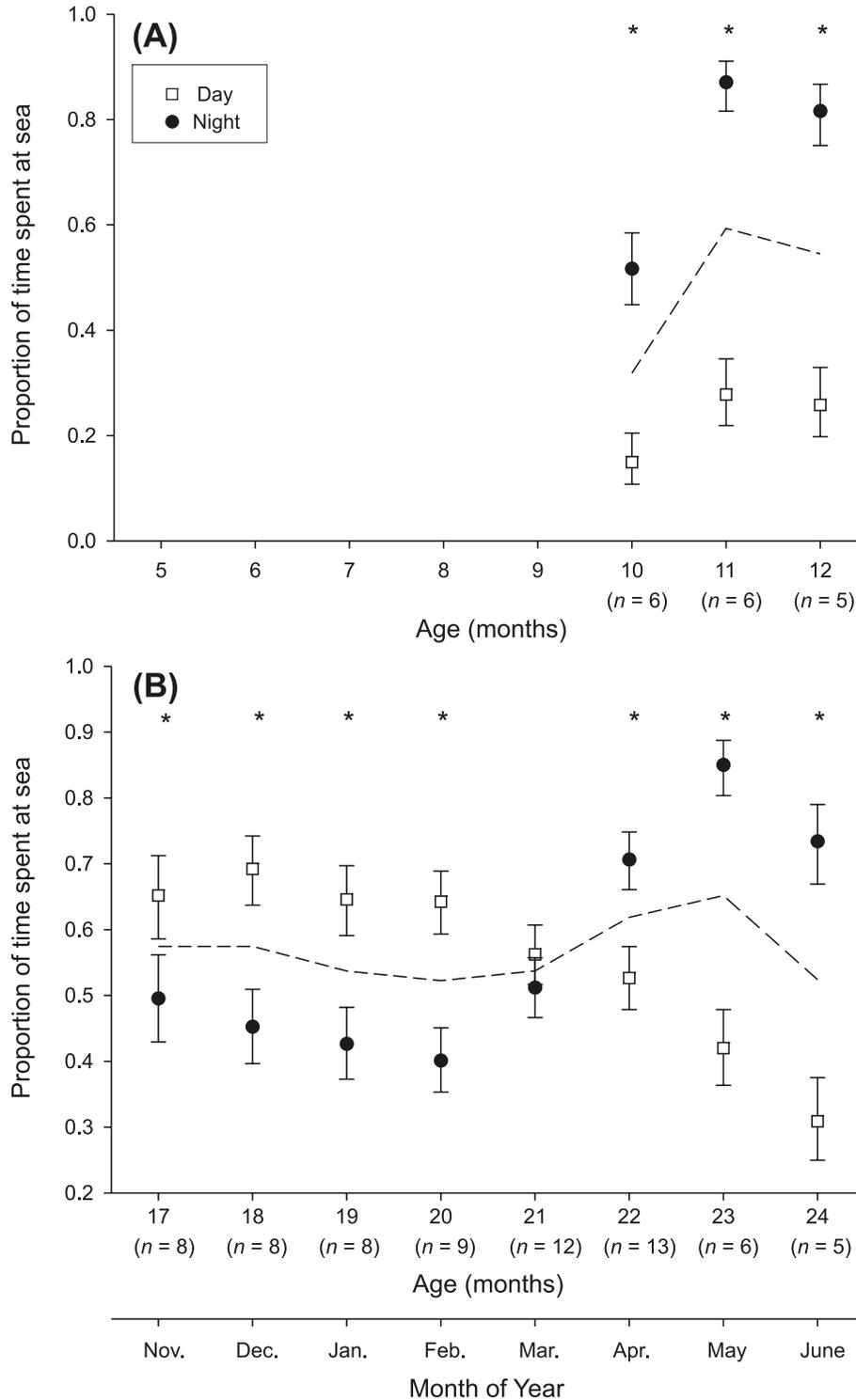
Fig. 4. Comparison of trend in mean (95% confidence interval) dive frequency (dives \times (h at sea)⁻¹) during daylight (□) and night (●) for Steller sea lion (*Eumetopias jubatus*) pups (A) and juveniles (B). Axes and other markings as in Fig. 2.



measures of how animals remain submerged in potential pursuit of prey, these are likely better indices of the degree to which different age classes rely on foraging to meet their nutritional needs. Pups in this study were 10–12 months old and likely still dependent on maternal resources for some of their nutrition, as the earliest weaning opportunity is thought

to be just prior to their dams giving birth in June (Trites and Porter 2002). However, sea lion pups, like most otariids, begin diving and ingesting prey well before weaning (Raum-Suryan et al. 2004; Pitcher et al. 2005), and Williams et al. (2007) found that lactating California sea lion (*Zalophus californianus* (Lesson, 1828)) females are unable to meet

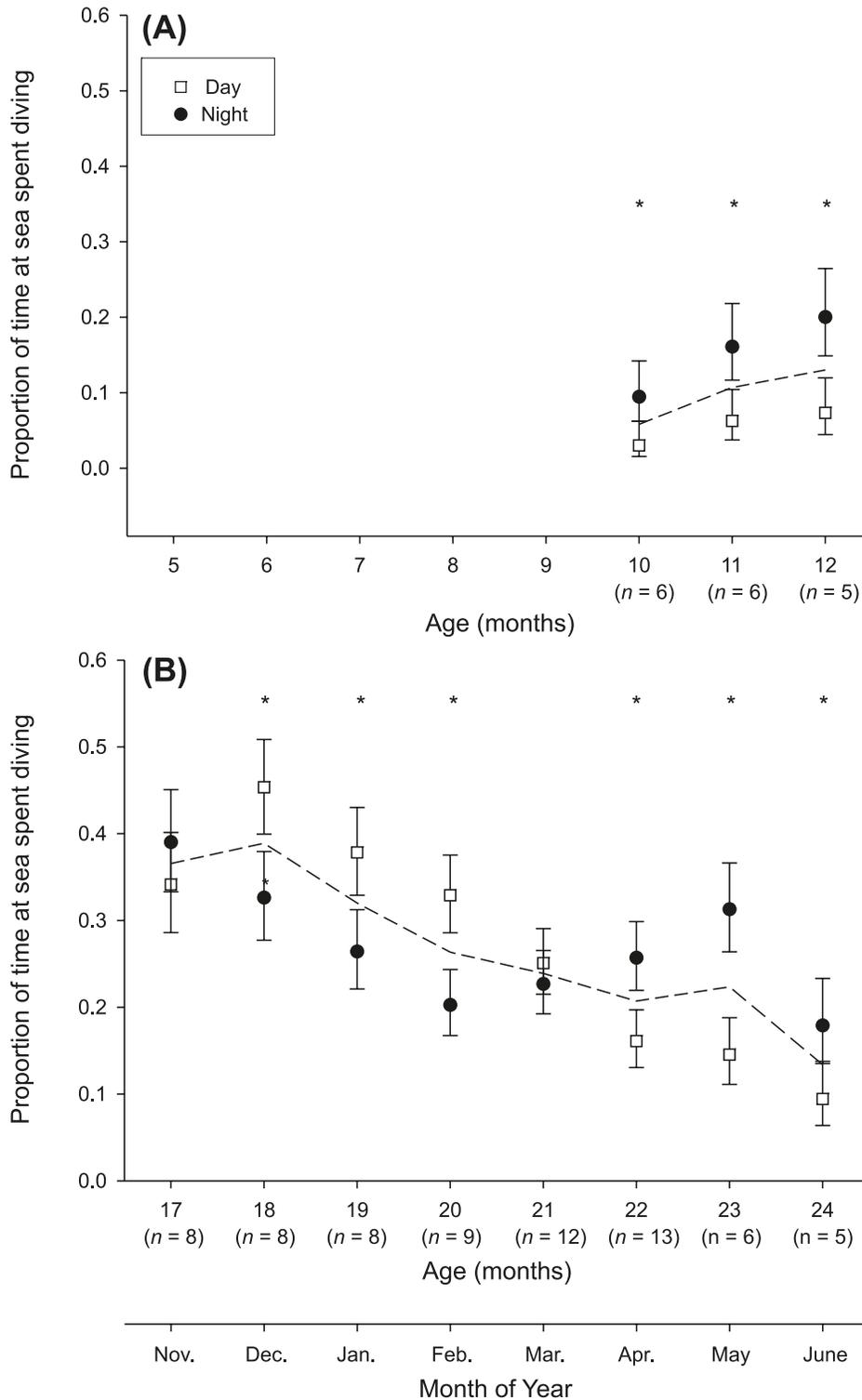
Fig. 5. Comparison of trend in mean (95% confidence interval) proportion of time spent at sea (TAS) during daylight (□) and night (●) for Steller sea lion (*Eumetopias jubatus*) pups (A) and juveniles (B). Axes and other markings as in Fig. 2.



100% of pup nutritional demands by 6 months of age. Thus, some spring season pup diving activity likely represents foraging. Still, the much older and larger juveniles (22–24 months of age) and subadults (≥30 months) must forage to much greater extent. This is reflected in the threefold greater proportion of time at sea older animals spent diving (10% vs. 27% and 32% TASD).

In addition to differences in the magnitude and extent of diving activity, there was also a marked difference in the impact of time of day on the behavior of pups and older sea lions. While pups spent similar TAS during night as the older juveniles, pups were far more likely to be resting on land during the day than older animals. Because lactating adult females are more frequently onshore during the day

Fig. 6. Comparison of trend in mean (95% confidence interval) proportion of time spent at sea spent diving (TASD) during daylight (□) and night (●) for Steller sea lion (*Eumetopias jubatus*) pups (A) and juveniles (B). Axes and other markings as in Fig. 2.



(Loughlin et al. 1998), pups may reduce their daytime aquatic activity to “forage” by suckling their dams. Indeed, when their dams are present on the haul out, pups spend approximately 20% of their time suckling (Higgins et al. 1988). The importance of aquatic activity at night is high-

lighted by the fact that pups, juveniles, and subadults all had similar TASD and dive frequency during this period. The early emergence of a diel pattern similar to that seen among marine vertebrates that forage on vertically migrating species (Croll et al. 1992; Burns and Testa 1997; Horning

and Trillmich 1997; McCafferty et al. 1998; Baker and Donohue 2000; Baird et al. 2005) suggests that sea lions are foraging when venturing out at night, even at a young age.

Longitudinal trends describe foraging

The patterns observed in the comparison between age classes were also evident within each age class, but developmental shifts were confounded by seasonal changes. For example, the average depth and duration of juvenile dives declined progressively from November to June, even as the cADL increased with age (Richmond et al. 2006). Since TAS and T ASD remained relatively constant over this period, changes in dive metrics likely reflect seasonal changes in prey behavior, and therefore strongly suggest that SSLs 17 months and older are foraging to meet some of their energetic needs. Because most juveniles were captured within the GOA, it is possible this trend is more reflective of juvenile behavior in the GOA than in the CAI.

During winter, the most common SSL prey in the study area are walleye pollock (*Theragra chalcogramma* (Pallas, 1814)), Pacific cod (*Gadus macrocephalus* Tilesius, 1810), Pacific herring (*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847), and Atka mackerel (*Pleurogrammus monopterygius* (Pallas, 1810)) (Sinclair and Zeppelin 2002). Of these, pollock, herring, and mackerel vertically migrate and are more accessible near the surface at night (Schabetsberger et al. 2000; Thomas and Thorne 2001; Nichol and Somerton 2002). Juvenile diving behavior during winter appears to track these changes: dives are deeper, longer, and more frequent during daylight, and sea lions spend more of their time at sea submerged during daylight than at night. Why juvenile sea lions target prey at depth during the few daylight hours in winter, rather than foraging more extensively when prey are more accessible during the long winter night, is not known. It may be that sea lions are targeting prey when they are more densely aggregated near the seafloor, rather than when dispersed throughout the water column. Such benthic foraging has been suggested to be a more efficient foraging strategy than pelagic foraging for crabeater seals (*Lodobon carcinophagus* (Hombron and Jacquinot, 1842)) diving in winter (Burns et al. 2004), and for Australian sea lions (*Neophoca cinerea* (Péron, 1816)) foraging in an environment where resources are patchily distributed and of generally low availability (Costa and Gales 2003).

There was a marked shift in the diving patterns of juveniles during early spring, coincident with the return of Pacific salmon (genus *Oncorhynchus* Suckley, 1861) aggregations in the nearshore environment. Returning salmon become a dominant SSL prey item (Sinclair and Zeppelin 2002) and, like other preferred prey, are known to vertically migrate (Friedland et al. 2001). Thus, the increase in proportion of short shallow dives and the frequency of diving activity (reflected in TAS and T ASD) during the short spring nights suggests that sea lions were actively targeting prey at night. Night-time foraging would also allow sea lions to target surface-active herring schools, pollock, and (or) salmon during periods when visual predators such as orca (*Orcinus orca* (L., 1758)) are less likely to be hunting (Frid et al. 2007). Night foraging would also allow juveniles to remain on the rookery during daylight for social interactions or

suckling opportunities, if still receiving maternal support. In combination, these findings suggest that juvenile SSL diving behavior is shaped by a complex interaction between physiological ability, prey availability, and inter- and intra-specific relationships.

Seasonal or ontogenetic shifts in the diving patterns of pups were much less evident, largely because the data represented a shorter period of time. However, pups did appear to be developing their foraging ability in the spring, as dive depth, duration, and frequency, TAS, and T ASD increased slightly with age. Because this increase in performance coincided with a minimal increase in physiological capacity (the cADL increased by ~18 s, Richmond et al. 2006), changes in behavior more likely reflected increasing reliance on prey rather than response to increased breath-hold capacity. While our hypothesis that pups rely more heavily on foraging to meet their energetic needs in spring was supported by the strong similarities in the pattern of behavior between pups and older sea lions (discussed earlier), and by observations that feces from pups as young as 3 months contained evidence of prey ingestion (Raum-Suryan et al. 2004), there was no direct evidence for increased prey intake in older pups. Similarly, the emergence of a diurnal pattern in diving and swimming activity has been correlated with the onset of foraging activity in Galapagos fur seal pups (*Arctocephalus galapagoensis* Heller, 1904) (Horning and Trillmich 1997) and northern fur seals (*Callorhinus ursinus* (L., 1758)) (unpublished manuscript cited by Baker and Donohue 2000).

The possibility that pups forage during spring on vertically migrating prey resources clarifies several otherwise unexplained day–night contrasts. In this study, the largest differences between pup and juvenile activity patterns occurred during daylight, whereas the largest age-related increases in pup performance and activity patterns occurred at night. In combination with cADL estimates, these findings suggest that during the spring pups are restricted to foraging at night when vertically migrating prey are near the surface, while older sea lions can also forage during daylight and upon demersal species. That reduced aerobic capacity can restrict the foraging choices of young animals to species and times when prey are near the surface has previously been noted in other otariids and phocids (Horning and Trillmich 1997; Burns 1999; Horning and Trillmich 1999).

Broader impacts

In contrast to other high-latitude otariids, young SSLs have a remarkably long period of nutritional dependency upon their dams. For example, northern fur seals, which occur at the same latitudes, nurse their pups for only 4 months (Gentry et al. 1986), and the lengthy dependent period of species such as the Australian sea lion (Higgins and Gass 1993) and Galapagos fur seals (reviewed by Kovacs and Lavigne 1992) are typically attributed to the relatively resource-poor environments in which they are found (Gentry et al. 1986). In these species with longer dependent periods, pups are known to begin diving prior to weaning, with dive performance increasing with age (Horning and Trillmich 1997). The links between prey behavior, physiological capacity, and diving patterns observed in this study suggest why it might benefit SSL females to extend lactation through the winter months, despite the relatively high

productivity of Alaskan coastal waters. As we have seen, juvenile foraging dives during winter are both long and deep, and young pups (at 5 months) would likely be unable to sustain this activity given their limited breath-hold ability. Indeed, the average duration of juvenile dives during winter is nearly twice the cADL of pups in winter (Richmond et al. 2006). By supporting their pups into spring, females can wean them at a time when foraging dives are less demanding as prey resources become more prevalent in shallower waters, thus increasing the likelihood of pup survival. That pups do begin to rely more heavily on prey during spring is suggested by the increase in diving activity and the alignment of their diurnal activity patterns with those of older animals.

The longer lactation period observed in SSLs may also provide time for social transfer of foraging skills and information, as has been suggested for other pinnipeds (McCafferty et al. 1998). SSLs are social foragers (Gende et al. 2001) that target seasonally abundant prey resources by moving between multiple central place haul-out locations (Raum-Suryan et al. 2004; Womble and Sigler 2006). Observations that SSL depart haulouts en masse (Higgins et al. 1988; C.A. Clark, Alaska Department of Fish and Game, personal communication, 2007) and with similar bearings (M.J. Rehberg, unpublished data) suggest that they may use an information center foraging strategy (Bonadonna et al. 2001). Thus, early training may (or may not, see Fowler et al. 2007) provide an additional benefit to the pup during the period of extended maternal care.

However, the benefit to the adult female of extending maternal care beyond the first year is less clear, as it will effectively decrease her fecundity. Still, during years of poor forage availability, lactating SSL females can evince high abortion rates (to 45% during the years of greatest population decline, Pitcher et al. 1998), and extend the suckling period of their existing pup (Bonner 1984; Trillmich 1990; Pitcher et al. 2001). If such behavior improves juvenile survival by partially compensating for nutritional deficits incurred because of their limited foraging ability, it could improve the female's lifetime reproductive success. In addition, because reduced juvenile survival causes greater population loss than reduced fecundity for SSL (Pascual and Adkinson 1994), extended and flexible lactation durations may buffer sea lion stocks from large swings in population size during periods of reduced prey availability.

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Committee and United States Marine Mammal Protection Act permits 782-1532 and 358-1564.

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