THEME SECTION

Juvenile Steller sea lion dive behavior following temporary captivity

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ABSTRACT: Wild-caught juvenile Steller sea lions *Eumetopias jubatus* (n = 21) were maintained in temporary captivity for up to 12 wk to investigate health, disease, nutrition and behavior. We assessed the effects of captivity on post-release dive behavior and movement of each animal using externally mounted satellite data recorders. Based on a 74.1 ± 9.6 (SE) d tag transmission period, the mean dive depth (26.2 ± 4.0 [SE] m), dive duration (1.4 ± 0.1 [SE] min), dive rate (10.1 ± 0.5 [SE] dives h[1]), trip duration (10.8 ± 0.7 [SE] h), haul-out duration (11.3 ± 0.9 [SE] h) and time wet (46.9 ± 2.6 [SE]%) were within the range of previously published values. Movement (190.0 ± 31.9 [SE] km) between haul-outs and rookeries during the tracking period was also typical of juvenile Steller sea lions in Alaska. This study indicates that temporary captivity has little or no detrimental effect on dive performance or movement in the tracking period following release.

KEY WORDS: Steller sea lion · Dive behavior · Captivity · Satellite data recorder

INTRODUCTION

Steller sea lions *Eumetopias jubatus* (west of 144° W) have declined by over 80% since the 1970s (Loughlin et al. 1992), and the species was listed as 'endangered' in 1997 under the US Endangered Species Act. Low survival of juvenile Steller sea lions (SSLs) has been suggested as a possible contributing factor (Pascual & Adkison 1994, York 1994, Holmes & York 2003). Because this is a life-history phase when diving and foraging abilities are still developing, the dive behavior and movement of juvenile SSLs has received significant research focus: this has resulted in a thorough understanding of typical dive depths, durations, trip distances, inter haul-out movements, and foraging patterns from pup through adult age-classes (Merrick & Loughlin 1997, Loughlin et al. 2003, Raum-Suryan et al. 2004, Fadely et al. 2005, Pitcher et al. 2005).

As part of the extended research effort investigating juvenile (1 to 4 yr) SSL health and behavior, wild-caught individuals (referred to as transient juveniles or TJs) were maintained in temporary captivity at the Alaska SeaLife Center (ASLC), Seward, Alaska, for up to 12 wk to facilitate longer-term study. The primary objective of this study was to assess the effects of temporary captivity on the post-release dive and movement behavior of juvenile SSLs. TJ dive behavior and location data were analyzed and compared to the free-ranging (FR) animals and previously published juvenile SSL dive information.

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MATERIALS AND METHODS

SSLs (n = 26) were captured in Prince William Sound (60° N 148° W) or Resurrection Bay (60° N 149.3° W), Alaska, as part of a larger research project (Fig. 1) (Mellish et al. 2006). Captured animals were transported to a larger support vessel for an initial physiological examination, including blood and tissue sampling under isoflurane gas anesthesia. FR control animals (n = 5), were instrumented with satellite data recorders (SDRs, see below) and immediately released from the support vessel near the capture location. TJs (n = 21), were transported to the ASLC for a period of temporary captivity lasting up to 12 wk. While in captivity, animals were used in various health, disease and nutrition research studies (e.g. Stephens et al. 2005, Mellish et al. 2006, 2007, Thomton & Mellish 2007, Waite et al. 2007). Age was estimated using a combination of body mass, time of year and tooth eruption patterns (King et al. 2007). Prior to release, external SDR-T16 or SPLASH tags (Wildlife Computers) were mounted to the pelage of each animal with 5 min epoxy (Devcon) along the dorsal midline between the foreflippers.

SDR-T16 tags were applied to all FR animals and TJs 1 through 12. These tags were programmed to record dive data in 4 histogram bins: 09:00–14:59 h (mid-day), 15:00–20:59 h (evening), 21:00–02:59 h (mid-night), and 03:00–08:59 h (early morning) Alaska standard time (AST), with the exception of TJ3 and TJ4 which had bins shifted 1 h later for experimental purposes. Dive depths were sampled every 10 s (accuracy ± 2 m) and recorded in the 14 following depth bins: 6–8, 9–16, 17–24, 25–32, 33–40, 41–50, 51–60, 61–70, 71–80, 81–100, 101–120, 121–160, 161–200, and >201 m. Dive duration was determined in 10 s increments and recorded in 1 min duration bins, with the tenth final bin representing all dives >9 min. Time at depth (TAD) was calculated and recorded as the percent time spent in a given depth range within the 6 h periods described above. Time at depth bins for TJs 1 to 8 were 0–8, 9–16, 17–24, 25–32, 33–40, 41–50, 51–60, 61–70, 71–80, and >81 m. Additional bins were added to differentiate between shallow dives (4 to 8 m) and time at the surface (<4 m and wet) for TJs 9 to 12. This additional shallow bin resulted in a modified deepest TAD bin (>62 m). Timeline data reported time wet versus dry for each 20 min increment (%). A daily status message provided maximum daily dive depth.

In 2005, the SDR T-16 model was no longer available and was replaced with the Splash model for TJs 13 to 21. Splash tags were programmed to record dive data in 4 histogram bins: 10:00–15:59 (mid-day), 16:00–21:59 (evening), 22:00–03:59 (mid-night), and 04:00–09:59 (early morning) AST. The 6 h histograms bins were shifted 1 h later so the midnight period spanned the darkest time of day in summer months. Dive depths were sampled every 5 s and recorded in the same depth bins (except for the first: 4–8 as opposed to 6–8 m) as those delimited for SDR-T16 tags with 0.5 m resolution. Dive duration was determined in 5 s increments and recorded in the following 14 duration bins: 0–30, 31–60, 61–90, 91–120, 121–150, 151–180, 181–210, 211–240, 241–270, 271–300, 301–330, 331–360, 361–390 and >391 s. Time at depth bins included 0, 1–4, 5–8, 9–16, 17–24, 25–32, 33–40, 41–50, 51–60, 61–70, 71–80 and >81 m. Timeline data reported time wet versus dry for
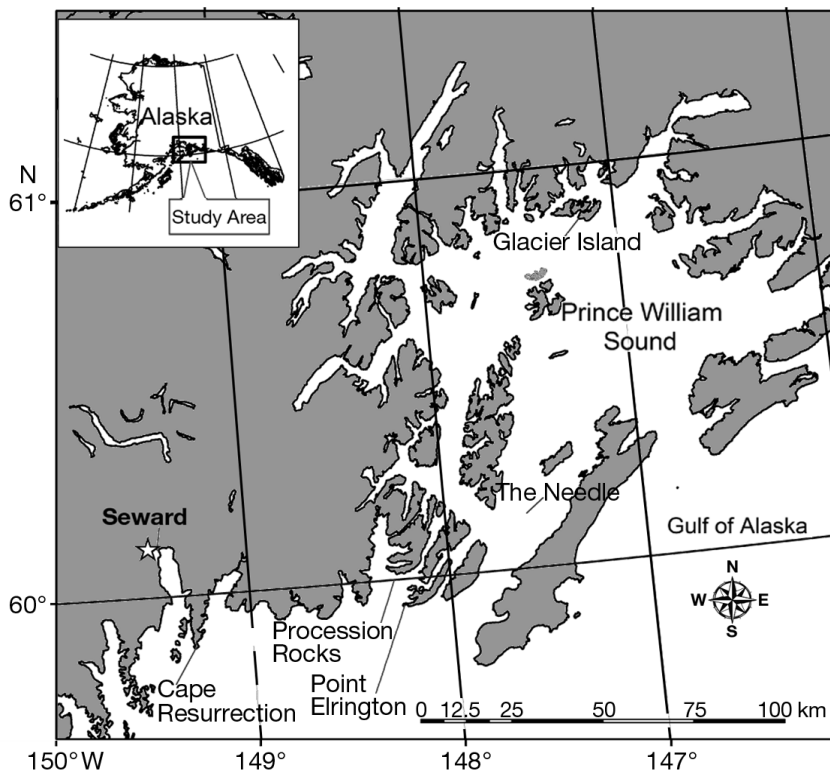

Fig. 1. Study area and capture locations, including Cape Resurrection, Procession Rocks, Point Elrington, Glacier Island, and The Needle. Temporarily captive juvenile Steller sea lions *Eumetopias jubatus* were released either at the capture location or in Resurrection Bay near Seward, Alaska. Asterisk indicates location of the captive facility

each hour (%). Unlike the SDR-T16 tags, the Splash tag daily status messages did not report maximum daily depth; this was therefore determined via histogram depth data, which underestimates depth in each defined bin (especially for dives in the >201 m depth bin).

Summarized dive data were calculated using the range midpoint of each bin for the depth and duration for all dives in each bin and the lower limit of the largest bins. Thus, calculated mean dive behavior values represent each 6 h histogram bin and were subsequently summarized by week post-release or month-of-the-year. Histogram data collection (along with this method of data summary) eliminated the effects of serial auto-correlation inherent in longitudinal dive and tracking data. Trips, defined as time at sea between haul-outs, and haul-out duration (beginning and end) were determined using wet/dry timeline data. An animal was classified as at sea if SDR T-16 tag 20 min timeline status was wet, or SPLASH tag hourly timeline status was ≥50 % wet. The Argos system provides location information for multiple received transmissions, classified by quality and projected accuracy of location (Sorna & Tsutsumi 1986). Maximum distance (shortest water route) from capture haul-out location and release location were measured using ArcMap™ 9.1 software (ESRI®). Trip distances were not calculated for TJs or FRs due to low resolution of location data. After filtering location data (Loughlin et al. 2003) and retaining positions with swim speed ≤3 m s^{-1}, Argos location quality ≥0 and removing locations on land, an average of 3 positions per round-trip remained, which precluded an accurate assessment of trip distances.

All averaged data presented here represent the means with associated standard errors. Weighted linear regression (WLR) was used to test the relationship between natural log (ln)-transformed response variables and time post-release. Responses were weighted by the inverse of each standard deviation (we calculated a mean and standard deviation for all animals in each time unit) to account for varying track lengths and decreasing sample size. One-way repeated measures (RM) ANOVA was used to test for differences in treatments, such as the mean dive duration according to time of day. A mixed-effects general linear model (GLM) was used to test for interactions between response (i.e. mean dive depth) and predictor variables (month-of-the-year, sex, week post-release, age, and their interactions sex × month-of-the-year, and sex × age) and to examine individual variation between animals. The GLM analysis was performed on ln-transformed response variables (dive depth, dive duration and dive rate). Data were analyzed with Sigmastat 3.11 and Systat 11.0 (Systat Software). All procedures were carried out under NMFS permit #881-1668 and ASLC Animal Use Protocols #02-15 and #03-007.

RESULTS

At time of release, TJs ranged in age from 14 to 24 mo (11 male, 10 female) with mean body mass of 124.7 ± 4.7 kg (male: 143.0 ± 8.5 kg; female: 129.4 ± 6.6 kg). FRs ranged from 13 to 25 mo (2 male, 3 female) with mean body mass of 99.4 ± 6.3 kg (male: 109.0 ± 10.0 kg; female: 93.0 ± 7.0 kg). As a result of small FR sample size and restriction to summer months, TJ and FR age and mass differed significantly (t-test, p = 0.044 and 0.005, respectively). A comparison of summer only FRs and TJs (± 2 mo) revealed no significant differences in age but differing mass (t-test, p = 0.082 and 0.014, respectively). TJs were maintained in temporary captivity for 64.7 ± 3.7 d.

The transmission length of satellite tags deployed on TJs (74.1 ± 9.6 d, range 14 to 160 d) was greater than those of FR animals (23.2 ± 7.2 d, range 11 to 50 d). Transmissions likely ceased due to failed attachment or were shed during the annual molt. Individual and summarized dive data are detailed in Table 1 for both TJ and FR individuals.

Dive depth

The mean dive depth displayed a linear increase with time elapsed post-release (WLR: r^2 = 0.892, p < 0.001) (Fig. 2). A mixed-effects GLM was constructed based on the ln-transformed individual mean dive depths per week (as opposed to the WLR of overall mean TJ dive depths per week post-release). The predictor 'week post-release' alone yielded a significant GLM (r^2 = 0.289, p < 0.001); however, an additional interaction (age × sex) improved the predictive power of the model (r^2 = 0.336, Table 2). The mean maximum depth also increased linearly during the tracking period (WLR: r^2 = 0.398, p = 0.002). Summarized time at depth data revealed that both TJs and FRs spent the greatest proportion of time (>0.7) in the shallowest depth bin, regardless of time of day (Fig. 3). Dive depth was deeper in the winter months (Fig. 4). Mean dive depth did not differ between TJs and FRs during the same tracking period (August ± 2 mo, t-test: p = 0.142).

Dive duration

The mean dive duration for TJs was 1.4 ± 0.1 min, with 52.4 % between 0 and 1 min, 23.9 % between 1 and 2 min and less than 4 % longer than 4 min. Similarly, the FR mean dive duration was 1.1 ± 0.1 min, with 52.1 % between 0 and 1 min, 39.4 % between 1 and 2 min and 0.1 % of dives longer than 3 min. Mean dive duration did not differ between FRs and TJs during the same

Table 1. *Eumetopias jubatus*. Summary dive data for temporarily captive transient juvenile (TJ) and free-ranging (FR) Steller sea lions. Age and mass at time of release are reported. Mean maximum (max.) dive depth and mean max. dive duration represent the mean of deepest and longest daily dives. The overall maximum depth and duration recorded are reported as max. depth and max. duration. Mean depth represents the average of all recorded dives (N) for each individual. Mean dive rate data characterize 6 h histogram periods for all animals

ID	Age (mo)	Mass (kg)	Sex	Mean max. dive depth (m)	Number of periods (n)	Max. depth (m)	Mean depth (m)	Number of dives in depth bins (n)	Mean duration (s)	Number of dives in duration bins (N)	Max. duration (s)	Mean max. duration (s)	Dive rate (dives h⁻¹)
TJ01	15	121	M	62	316	162	26	26391	94	26163	455	203	11.0
TJ02	16	104	F	61	9	84	15	2852	64	2919	215	153	9.9
TJ03	18	133	M	157	77	432	37	29665	111	30473	485	247	10.9
TJ04	18	145	F	134	169	256	43	27591	111	27239	335	227	10.2
TJ05	24	129	F	29	40	64	13	7562	57	7213	510	167	11.1
TJ06	24	140	F	21	56	64	13	10805	61	10739	335	158	12.6
TJ07	24	166	F	28	43	70	14	7545	72	7590	485	188	10.6
TJ08	24	176	M	38	23	98	13	4314	70	4219	395	183	9.5
TJ09	17	134	M	134	150	284	70	14805	157	14949	455	271	5.4
TJ10	17	107	F	149	95	244	42	14331	100	14423	455	214	9.8
TJ11	17	114	M	145	92	228	63	20164	148	18910	485	276	7.2
TJ12	17	135	M	117	181	264	56	9404	137	10334	395	229	5.2
TJ13	23	186	M	80	145	201	18	10191	73	10087	361	186	9.2
TJ14	23	144	F	58	150	161	17	12921	74	13169	390	191	12.8
TJ15	23	145	M	72	255	121	20	20706	77	20402	390	190	11.1
TJ16	23	190	M	59	177	161	14	10980	74	11082	390	177	9.0
TJ17	14	128	M	47	189	201	11	12481	40	12431	331	109	9.3
TJ18	14	111	M	44	116	121	11	7455	43	7719	271	124	9.1
TJ19	14	116	F	43	98	61	12	6842	48	6959	331	132	11.6
TJ20	14	105	F	85	242	161	27	20344	73	19768	390	164	11.9
TJ21	17	138	F	70	347	201	16	36434	63	34766	301	151	13.8
Mean		137		126.1		175.2	26.2		83.2		389	188	10.1
SE (TJ 1-21)	1	6		22.2		20.2	4.0		7.2		17	10	0.5
FR10	13	121	M	33	48	112	10	99	49	4978	210	106	5.5
FR11	13	104	F	40	8	72	20	26	73	2275	210	145	9.3
FR13	25	133	F	67	10	100	19	32	70	3093	270	156	9.4
FR14	13	145	F	57	15	108	18	6803	64	6637	210	137	10.6
FR15	13	129	M	24	5	48	12	1590	64	1700	210	125	5.1
Mean	15	99		44.1		88.0	15.5		63.9		222	134	8.0
SE (FR 10-15)	2	6		7.8		12.2	2.0		4.1		12	9	1.1

tracking period (August ± 2 mo, *t*-test: p = 0.424). Mean dive duration increased with time post-release (WLR: r^2 = 0.883, p < 0.001) (Fig. 2) as did mean maximum dive
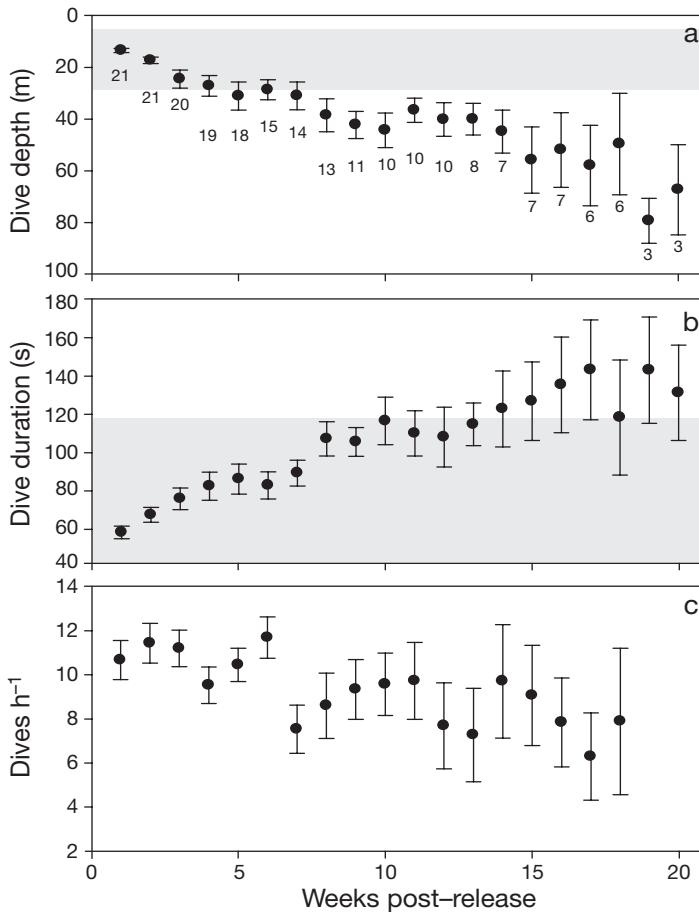

Fig. 2. *Eumetopias jubatus.* (a) Mean dive depth and (b) mean dive duration of Steller sea lions, showing linear increase with weeks post-release. (c) Dives h^{-1}, which decreased with time post-release from temporary captivity. Gray areas: previously reported range of dive depth and duration typical for juveniles of the species (Loughlin et al. 2003, Rehberg 2005). Values in (a) show decreasing sample size week by week (all panels) due to varying individual tracking lengths. Error bars: SE

Table 2. Interactions between mean-dive depth of temporarily captive Steller sea lions (ln-transformed summary by week post-release) and predictor effects, tested using a general mixed-effects model. Model r^2 = 0.336

Effect	df	*F*	p
Retained			
Week post-release	1	24.15	<0.0001
Sex × Age	1	14.69	<0.0001
Removed			
Month-of-year	1	0.729	0.394
Sex	1	1.213	0.272
Sex × Month-of-year	1	0.418	0.519
Age	1	2.011	0.158

duration (WLR: r^2 = 0.185, p = 0.033). A mixed-effects GLM was constructed based on the ln-transformed individual mean dive durations per week (as opposed to the WLR of overall mean TJ dive durations per week post-release). The predictor 'week post-release' alone yielded a significant GLM (r^2 = 0.299, p < 0.001); however, an additional interaction (age × sex) improved the predictive power of the model (r^2 = 0.379, Table 3). Dive duration was also longer in winter months (Fig. 4). In a comparison between the 6 h histogram periods (evening, mid-night, early morning and mid-day) there was no difference in mean or maximum dive duration (One way RM ANOVA on ranks: p = 0.856 and p = 0.269, respectively). Likewise, there was no difference in the maximum dive duration summarized by month of year (1-way ANOVA on ranks: p = 0.151). Dive duration and depth were positively correlated (Pearson's correlation: 0.971).

Time at sea

Trip duration and haul-out visits did not differ between TJ and FR deployments, at 10.8 ± 0.7 h and 11.2 ± 1.5 h (*t*-test: p = 0.837) and 11.3 ± 0.9 h and 10.6 ± 1.0 h (*t*-test: p = 0.701), respectively. The percent time wet (46.6 ± 2.3%) did not differ between TJs and FRs or by sex (*t*-test: p = 0.806 and 0.314, respectively). Time spent at sea differed over months (Fig. 4) (ANOVA p = 0.023), with pairwise comparison showing a difference primarily between the low of 32.5% in April to a high of 68.5% in November (p < 0.001). Mean time at sea did not differ between FRs and TJs during the same tracking period (August ± 2 mo, *t*-test, p = 0.391).

Dive rate

The dive rate for TJs and FRs did not differ (*t*-test: p = 0.075). The TJ dive rate decreased between Weeks 1 and 20 post-release from 10.7 ± 0.9 to 7.8 ± 3.3 dives h^{-1} (WLR: r^2 = 0.678, p < 0.001) as mean dive depth and duration correspondingly increased (Fig. 2). TJ dive rate was significantly higher during the mid-night period (13.2 ± 0.9 dives h^{-1}) and lowest during the mid-day period (7.9 ± 0.9 dives h^{-1}, *t*-test: p < 0.009). The overall dive rate for TJ females was significantly higher (11.0 ± 0.4 dives h^{-1}) than for males (8.3 ± 0.6 dives h^{-1}, *t*-test: p = 0.001). The limited FR sample size precluded assessment of gender differences in dive rate for this group.
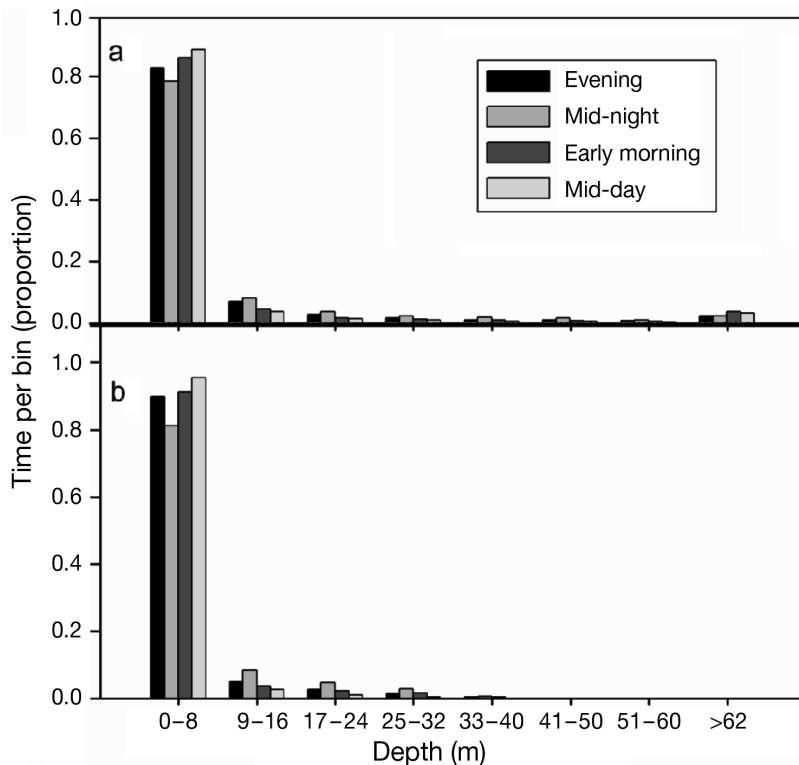
Fig. 3. *Eumetopias jubatus.* Percentage of time spent in various depth bins among (a) temporarily captive (post-release, n = 21) and (b) free-ranging (n = 5) juvenile Steller sea lions

Table 3. Interactions between mean-dive duration of temporarily captive Steller sea lions (ln-transformed summary by week post-release) and predictor effects, tested using a general mixed-effects model. Model $r^2 = 0.379$

Effect	df	F	p
Retained			
Week post-release	1	24.15	<0.0001
Sex × Age	1	14.69	<0.0001
Removed			
Month-of-year	1	0.729	0.394
Sex	1	1.213	0.272
Sex × Month-of-year	1	0.418	0.519
Age	1	2.011	0.158

Movement

The maximum distance TJs traveled from the original capture location during the tracking period averaged 190.0 ± 31.9 km. The first 8 TJs were released at their respective capture haul-outs and traveled a mean maximum distance of 73.6 ± 18.4 km from the release location during the tracking period. TJs 9 to 21 were released in Resurrection Bay; 4 of these returned to their capture location, while 9 traveled between other known SSL haul-outs in southcentral Alaska. For the animals released in Seward, the maximum distance

traveled from Seward (with the exception of TJ 16) averaged 225.8 ± 15.5 km. TJ 16 traveled to haul-outs in Resurrection Bay and Prince William Sound and then ventured outside of the southcentral Alaska region, crossing the 144° longitude which divides the eastern and western SSL stocks. This male aged 23 mo traveled a total of 761 km from the release site (692 km from the capture location at Glacier Island) in 52 d. The final transmission from this individual was near Icy Straits in southeast Alaska (58.447° N, 137.275° W).

DISCUSSION

A concern with temporary captivity of juvenile animals is that development of physiological parameters tied to dive performance may be altered, which could negatively affect post-release growth and survival. Temporary captivity results in confinement and a reduced ability to move, exercise, and dive. Furthermore, incentive to exercise may be reduced because food is provided without work requirement. Effects of long term confinement and de-training on hematology, maximal heart rate, cardiac output and maximum rate of oxygen consumption (VO_{2max}) have been demonstrated in race-horses (von Engelhardt 1977, Eaton et al. 1999, Betros et al. 2002), dogs (Tipton et al. 1974) and lizards (Gleeson 1979). We found no evidence of proximate effects of temporary confinement in our study animals with respect to hematological or clinical chemistry parameters that might suggest impaired diving ability following release (Mellish et al. 2006). Secondary effects of confinement in marine mammals have not been studied, but may include reduced oxygen transport and storage capacity and reduced relative muscle mass. This may lead to reduced exercise and sprint capacity, and endurance. Such effects, if present, may ultimately result in decreased dive and foraging performance, growth rate, and survival.

In the present study, observed dive performance, as measured by mean dive depth and mean duration, is within or exceeds previously published values (Fig. 2), indicating that temporary captivity probably has no detectable effect on dive performance. The sample size and tracking period for FRs (n = 5) was limited due to permit and logistical constraints and does not represent juvenile SSL dive behavior throughout an annual cycle. However, a limited comparison of FRs (n = 5) and
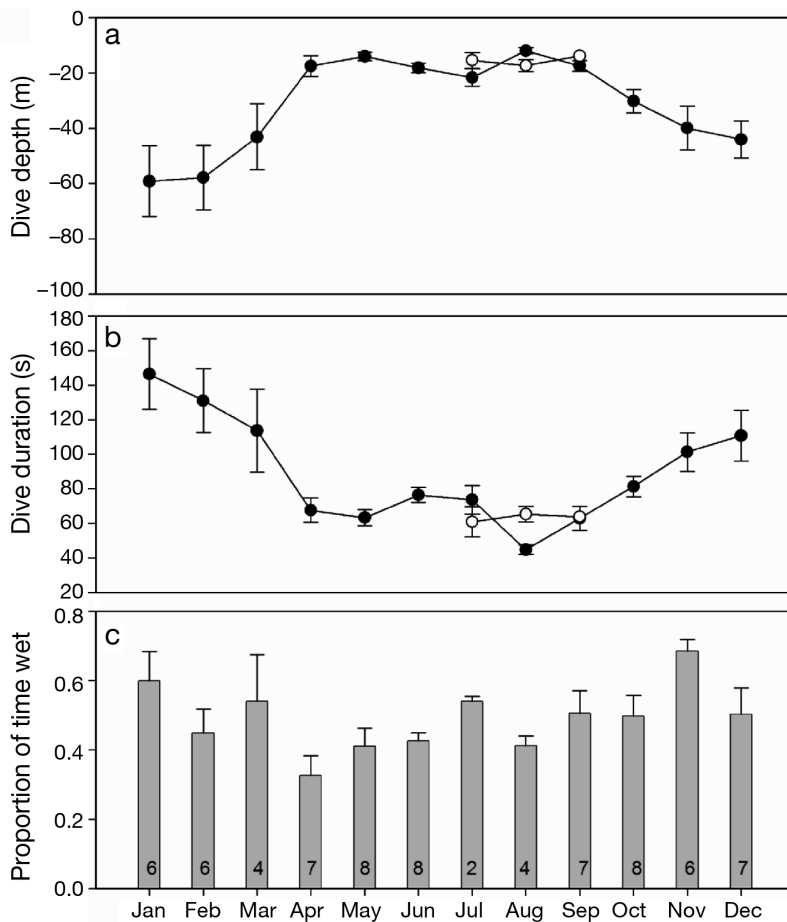
Fig. 4. *Eumetopias jubatus*. Mean (±SE) seasonal (a) dive depth and (b) dive duration for transient juvenile (TJ, black circles) and free-ranging (FR, open circles) Steller sea lions. (c) Time (%) spent in the water after temporary captivity (TJ only); tracking sample sizes per month are indicated within the bars

ued to increase throughout the tracking period. Week 20 values of 67.3 ± 17.4 m and 2.2 ± 0.4 min (n = 6) exceeded previously reported mean values for juvenile SSLs (Loughlin et al. 2003, Rehberg 2005).

As presented in Fig. 2, weekly variation of diving parameters increased over time due to varying tracking lengths and decreasing sample size. To assess the possible influence of tracking the strongest divers longest, we linearly regressed dive depth and duration per week with n ≥ 6 (removing the 2 most heavily weighted data points) and found the same significant relationships.

Exploring possible interactions between our predictor values yielded little interpretive value. Only time since release and the interaction sex × age were not removed from the GLM for each of our response variables. This interaction indicated that older males tended to dive deepest and longest, and that younger females tended to dive shallowest and shortest. This result is not particularly informative, since males in this sample tend to be larger at age than females, and the fact that larger animals dive deeper and longer has been observed previously (Pitcher et al. 2005). We do not believe that any of the interactions we tested are particularly relevant to a discussion of how temporary captivity affects dive performance. The interactions were either dropped from the model because they did not contribute useful information (month, sex, age and sex × month), or they merely described a trait previously known to affect dive behavior in general (sex × age).

The increase in performance (Fig. 2) as a function of increased age (crossed by sex) is likely due to expected mass gain. The relationship between dive abilities and body mass is well documented in multiple otariid species (Kooyman 1989) and during ontogeny (Horning & Trillmich 1997). Maximum dive performance values may be rare performance extremes that are more indicative of an animal's absolute abilities, given age and mass when compared to any other dive behavior parameter (Horning & Trillmich 1997). During ontogeny, mean dive behavior appeared more susceptible to variability in prey accessibility (Horning & Trillmich 1999), whereas maximum values were most related to body mass (Horning & Trillmich 1997, 1999). Thus, an increase in maximum dive depth and duration post-

TJs (n = 9) during the same tracking period (August ± 2 mo) revealed no differences between mean dive depth, mean dive duration and mean time at sea.

When dive data were summarized over the entire tracking period, TJs displayed dive characteristics similar to previously reported values from animals of similar age and geographic region. Alaskan yearling (10 to 22 mo) SSLs dive on average from 16.6 m for 1.1 min (Loughlin et al. 2003) to 22.9 m for 1.7 min (Rehberg 2005) compared to the observed 26.2 ± 4.0 m for 1.4 ± 0.4 min for TJs. TJ dive performance clearly exceeded that previously reported for juvenile SSLs. However, in a temporal analysis of dive performance by week post-release (Fig. 2), TJs (n = 21) dived shallower (mean depth 13.5 ± 0.8 m) for shorter durations (mean duration 1.0 ± 0.1 min) during the first week following release than FR SSLs. By the second week post-release, the mean dive depth (17.4 ± 1.2 m) and duration (1.1 ± 0.1 min) approached those observed by Loughlin et al. (2003). Dive depth and duration contin-

release suggests mass gain and successful diving and foraging behavior.

Similar to the findings of Loughlin et al. (2003), dive depth and duration increased concurrently; in contrast, these parameters were not related to mass at time of release. This may be due to variable individual diving abilities or initial lower foraging motivation due to the abundance of food available during the captive period. The temporal increase in dive duration during the tracking period could be an indication of (1) improved diving ability related to physiological maturation, (2) mass gain and correspondingly increased aerobic dive limits, or (3) behavioral changes in relation to life-history traits of this species (Raum-Suryan et al. 2004). However, mass-specific oxygen carrying capacity reaches a plateau at 18 mo (Richmond et al. 2006), which is younger than the mean TJ age at release (19 ± 1 mo). By the 20th week post-release (TJs aged 24 ± 1 mo), the mean dive depth (26.2 ± 0.4 m) and duration (2.2 ± 0.4 min) were similar to adult females (21 m for 1.3 min, summer; 24 m for 2.0 min, winter: Merrick & Loughlin 1997). Previous studies have found increases in dive rate and time at depth during the first 12 mo and dive depth to 18 mo of age (e.g. Fadely et al. 2005); however, the present study indicates that dive ability may continue to improve until at least 24 mo of age. Another possibility is that physiological maturation (oxygen storage capacity) and/or dive training (such as endurance and breath-hold) is interrupted during the 12 wk captive period. This appears unlikely since normal juvenile SSL diving depth and duration were observed by Week 2 post-release.

The mean percentage times wet for TJs (46.9 ± 2.6%) and FRs (45.4 ± 2.7%) were within the range reported by Rehberg (2005) (female: 39%; male: 50%). SSL dive rate increases during the first 12 mo of age and stabilizes during the second year with dive rates between 5 to 21 dives h^{-1} (Fadely et al. 2005). The dive rate for TJs varied by time of day from roughly 8 (mid-day) to 13 (mid-night) dives h^{-1}. The dive rate decreased over time, likely due to TJs making deeper and longer dives (Fig. 2).

The movement and dispersal of SSLs varies with age. Pups (<1 yr) tend to remain within 500 km of their natal rookery, but begin to travel up to 1785 km as juveniles (1 to 2.9 yr for females and 1 to 4.9 yr for males; Raum-Suryan et al. 2002). Movement then declines to less than 500 km as adults (Raum-Suryan et al. 2002). With one exception, all TJs remained in southcentral Alaska, between Kodiak Island and Prince William Sound, and moved among haul-outs within 312 km of the capture location. Most juvenile SSL round-trip distances are between 15 and 25 km, with durations less than 20 h (Loughlin et al. 2003, Raum-Suryan et al. 2004). Juvenile SSLs in Prince William Sound have typical

trip durations of 8.9 ± 10.2 (SD) h and haul-out for 10.2 ± 8.7 (SD) h (Call et al. 2007), which did not differ from juvenile SSLs in the present study. Trip distances were not calculated for TJs or Frs, due to low resolution of location data; however, these were likely similar, based on observed trip duration.

CONCLUSIONS

Juvenile Steller sea lions held in temporary captivity performed shorter and shallower dives than free-ranging conspecifics in the first week post-release. However, all parameters were within expected ranges for juveniles of the same population by the second week post-release. The overall mean dive depth, dive duration, trip duration, haul-out length, dive rate, percentage of time wet, and movement were equal to or greater than the FR control and published juvenile SSL values. Furthermore, during the 2.7 mo tracking period, TJs appeared to equal adult female diving abilities. The results of the present study indicate that temporary captivity of up to 3 mo probably does not impair dive performance or movement. In addition, dive development may continue until at least 24 mo of age. Further development in longer-term attachment techniques is needed and would greatly improve our ability to understand the complete dive development and transition from the juvenile stage into adulthood.

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