Wanted dead or alive: characterizing likelihood of juvenile Steller sea lion predation from diving and space use patterns

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ABSTRACT: Understanding linkages between behaviors and mortality risk is critical for managing populations. Juveniles constitute a particularly vulnerable life stage, with growing evidence that within stages, individual strategies may be associated with greater predation risk and mortality. These forms of predator–prey dynamics are rarely explored in marine environments due to difficulties in confirming vital status of individuals, and the lack of data sets that link mortality to behavior. We analyzed 2 concurrently collected data sets for juvenile Steller sea lions *Eumetopias jubatus* in the Gulf of Alaska to examine associations between mortality and specific behavioral patterns. Forty-five juvenile Steller sea lions were instrumented with external satellite tags and internally implanted vital rate transmitters (LHX tags). From 2005 through 2018, 25 juveniles remained alive and 20 died (18 confirmed predation). Using a binomial generalized linear mixed-effects model, we tested whether the probability of individual mortality was associated with seasonally specific dive patterns (time wet, dive depth) or horizontal movement patterns (home range size, average trip distance). Additionally, in 3 cases, external tags were transmitting until death. To examine links between fine-scale ante-mortem behavioral patterns and predation susceptibility, we compared dive patterns recorded during the last 3 d of data transmissions (both for animals which survived and for those which died) to dive patterns recorded during other periods at sea. Results suggest individuals that spent more time dry or dove shallower had a greater mortality probability, which could reflect foraging tactics of predators. This study highlights the effectiveness of combining multiple telemetry systems for exploring the vulnerability of individuals to the consumptive effects of predators.

KEY WORDS: Predation · Bio-logging · Diving behavior · *Eumetopias jubatus* · Risk · Marine mammal

1. INTRODUCTION

Predator–prey dynamics include a suite of ecological interactions that, along with resource distribution, underpin animal movements and space use (Lima & Dill 1990). These dynamics manifest through non-consumptive or consumptive effects of predators. Non-consumptive effects are changes in the behaviors of individual prey as a result of perceived risk or 'fear', and can include increased vigilance (Laundré et al. 2001, Ciuti et al. 2012), decreased time spent foraging (Hamilton & Heithaus 2001, Ciuti et al. 2012), foraging in sub-optimal habitats (Wirsing et al. 2008), and/or broad

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changes in space use (Tolon et al. 2009, Breed et al. 2017, Kohl et al. 2018). Alternatively, the consequence of consumptive effects is the mortality of an individual.

Both forms of predator effects have associated fitness consequences. Fear or risk-induced changes to behavior and space use may impact fitness, but there is debate as to the extent to which these effects scale to populations or ecosystems (Kauffman et al. 2010). Alternatively, predation mortality can directly shape populations and ecosystems through trophic cascades, altered sex ratios, or predator-induced selective pressures (Réale & Festa-Bianchet 2003, Ripple et al. 2016). Therefore, susceptibility to predation has significant management implications for endangered species (Blumstein et al. 2001, Iribarren & Kotler 2012), especially for populations that have limited ability to absorb mortalities due to low numbers and/or low reproductive rates, or if predation on juveniles constrains recruitment.

Increased susceptibility to predation is well established for certain life-history stages, conditions, and habitats. Old and juvenile animals are typically at a greater risk of predation relative to other life-history stages (Byström et al. 1998, Lundvall et al. 1999, Réale & Festa-Bianchet 2003, Frid et al. 2009, Walsh & Reznick 2009, Choh et al. 2012). The use of habitat with a greater probability of encountering predators can also increase the risk of predation (Lone et al. 2014). However, it is becoming increasingly apparent that behavioral traits can also be associated with individuals' susceptibility to predation (Jones & Godin 2010, Krams et al. 2013). For example, in years with high predation rates, there was moderate selection for survival of female bighorn sheep *Ovis canadensis* with bold behavioral types and increased predation of docile animals (Réale & Festa-Bianchet 2003).

The links between individuals' behaviors and mortality have been explored in laboratory and terrestrial settings (Jones & Godin 2010, Réale & Festa-Bianchet 2003), but there is a considerable lack of empirical studies in marine ecosystems (Hays et al. 2016). While the fate of individuals in marine environments is commonly tracked via mark-recapture efforts (Shuert et al. 2015), observations of predation events have been labeled as 'empirically intractable' (Williams et al. 2004) for marine vertebrates. Due to this absence of observed mortalities, most of our understanding of the predator–prey dynamics in marine ecosystems focuses on non-consumptive effects through theoretical models of resource and risk trade-offs (Frid et al. 2006, 2007, 2009, Wirsing et

al. 2008) and behavioral assessments of how risk shapes animals' movements and space use (Hammerschlag et al. 2015, Breed et al. 2017). Here, we explore how advances in biotelemetry provide a novel opportunity to investigate the susceptibility to predation *in situ* for a marine meso-predator by combining observations of mortality and individual behaviors.

After an 80% population decline, Steller sea lions *Eumetopias jubatus* were listed as endangered in 1997 throughout the western extent of their distribution (western distinct population segment [wDPS], west of 144°W) (62 Federal Register 24345). At the height of the decline, juvenile survival appeared to be depressed (Pascual & Adkison 1994, York 1994, Holmes & York 2003). Presently, some regions of the wDPS such as the Gulf of Alaska are stable or slightly increasing (NMFS 2010), but data from telemetry studies show that in these regions, 91.7% of juvenile mortalities (95% CI: 78–100%) can be attributed to predation (Horning & Mellish 2009, 2012). Contemporary levels of predation pressure have thus been suggested as one potential driver behind the lack of the recovery of the wDPS as a whole. Since 2003, new biotelemetry methods have been developed and applied to explore survival of and predation on juvenile Steller sea lions in the Gulf of Alaska (Horning & Hill 2005, Mellish et al. 2007, Horning et al. 2008, Horning & Mellish 2009). The implantable Life History Transmitter (LHX tag) records sensor data over the course of an animal's life (Horning & Hill 2005). Following the death of an animal, the positively buoyant LHX tags emerge from the dismembered, digested, or decomposing carcass and begin transmitting data to ARGOS satellites, including temperature profiles and the date and time of death (Horning & Mellish 2009, 2014). *Post hoc*, the temperature data can be used to characterize whether the mortality event was due to predation or other natural causes, with some additional differentiation of the type of possible predator (Horning & Mellish 2009, 2014).

By pairing 'observations' of predation from LHX tags with data from traditional, externally attached telemetry devices for tracking animal movement and behavior, this bio-logging system provides a unique opportunity to gain a better understanding of the vulnerability of juveniles in an endangered marine species to the consumptive effects of predators. The objective for this study was to assess whether individual juvenile Steller sea lions' behavioral patterns (horizontal/vertical movements) are associated with

greater probability of predation at coarse and fine temporal scales.

2. MATERIALS AND METHODS

2.1. Study area and animals

Juvenile Steller sea lions, between 12 and 26 mo of age (age determined as per Raum-Suryan et al. 2004, King et al. 2007), were captured from the Prince William Sound (60.77° N, 147.61° W) and Kenai Fjords region of the Gulf of Alaska (59.87° N, 149.31° W), as described in Mellish et al. (2006, 2007), Thomton et al. (2008) and Bishop et al. (2018). Briefly, between 2005 and 2014, 45 animals (17 females, 28 males) were captured in the field and transported to the Alaska Sea-Life Center for a period of temporary captivity lasting up to 3 mo (Table 1). During this time, animals were monitored through a range of health assessments; additional details on holding, husbandry and transport can be found in Mellish et al. (2006, 2007).

2.2. Instrumentation

During temporary captivity, animals underwent surgery for the implantation of 1 (n = 2) or 2 (n = 43) life-history tags (LHX1 and LHX2 tags, Wildlife Computers) into the peritoneal cavity using a standard aseptic technique and anesthesia (Horning et al. 2008). All animals underwent postoperative monitoring for a minimum of 1 wk (up to 6 wk) (Mellish et al. 2007), after which they were released at Lowell Point, Alaska (60.08 N, 149.43 W). Prior to release, 44 animals were instrumented with external satellite data recorders (SDRs: either SDR-T16, SPOT 5, or SPLASH, Wildlife Computers) mounted to their dorsal pelage as described in Mellish et al. (2007) and Thomton et al. (2008). SDRs were programmed with continuous duty cycles and recorded dive data (dive depth, dive duration, and time at depth) in 4 and 6 h histogram bins (Thomton et al. 2008). Dive data were redundantly transmitted through the Argos satellite system, but reception is subject to satellite coverage. Most dive data were received when animals were hauled out. Location estimates were provided by the Argos service provider (Woods Hole Group), and are based on the Doppler shift detected in multiple sequential transmissions being received during 1 pass of low polar orbiting satellites. Data and location estimates were obtained until the SDRs were shed, or until the tag's batteries were exhausted and the tags

no longer transmitted. The average SDR transmission duration was 77.23 d (Bishop et al. 2018). Control studies found no evidence of an effect of temporary captivity, surgery, or telemetry implants on the post-release diving, horizontal movements, or survival of animals in this study (Mellish et al. 2007, Thomton et al. 2008, Shuert et al. 2015, Bishop et al. 2018).

2.3. Horizontal movement behaviors

This study applied the utilization distributions (UDs) previously derived for each animal in Bishop et al. (2018). In brief, filtered locations were interpolated using a continuous time-correlated random walk state-space model (crawl package in R). From the resulting pseudolocations, seasonal kernel density grids were generated using fixed likelihood cross-validation bandwidth (Geospatial Modeling Environment, GME v0.7.2.0). Seasons were defined as spring–summer (March–August) and fall–winter (September–February). Isopleths were calculated in GME, and the 95% UD area (km^2) was defined as the seasonal home range for each individual. Two animals did not meet the minimum sample size requirement for kernel density analysis (Seaman et al. 1999), resulting in a final data set of 50 UDs across 42 animals (some individuals may have a UD in more than one seasonal period; Table S1 in the Supplement at www.int-res.com/articles/suppl/n040p357_supp.pdf).

The average horizontal distance traveled per foraging trip, defined as the locations at sea between 2 subsequent haul-out events, was calculated for each animal seasonally. To identify trips within an animal's track, each pseudolocation derived from the state-space model was classified as 'wet' or 'dry' based on dive histogram data for that date and time. For SDR-T16 and SPOT 5 tags, the wet/dry status was recorded every 20 min. For SPLASH tags, time-line data reported percentage of time dry per hour, and hours where >50% of the time was dry were considered hauled out (Thomton et al. 2008). All wet locations between known dry states were considered a single trip, and were given a unique trip ID. Overall, the location and dive data sets lined up 75.6% of the time. In cases where a series of pseudolocations were wet, but were followed by positional data with no corresponding wet/dry information, the trip or haul-out ID was reset to indicate a new trip, providing a conservative estimate of trip distance in these cases. Distance traveled (m) for each trip was calculated as the Euclidean distance of the entire path in ArcGIS 10.6 (Table S1).

Table 1. Descriptions of tagged animals in the study: sex, age at release, release date, season(s) (SS: spring–summer; FW: fall–winter) for which there are tracking and diving data available, and vital status (alive/dead). For animals that died, information on the season in which the animal died, date of mortality event, and cause of death (Horning & Mellish 2009, 2014) are provided. Whether the horizontal and vertical data from each individual were included in the 2 binomial models is indicated. A mortality date followed by [+] indicates the individual died while wearing its external tag

ID	Sex	Age at release (mo)	Release date (mm/dd/yy)	Tracking data season(s)	Vital status	Season died	Mortality date (mm/dd/yy)	Cause of death	Horizontal binomial model	Vertical binomial model
LHX2_07	F	22	5/14/14	SS	Dead	SS	6/28/15	Predation	Y	N
LHX2_08	F	12	5/14/14	SS	Dead	SS	4/19/15	Predation	Y	N
LHX2_11	F	26	8/28/14	FW	Dead	FW	1/25/16	Predation	Y	N
TJ27	M	22	4/16/06	SS	Dead	SS	3/19/07	Inconclusive	Y	N
TJ32	M	15	10/10/07	FW	Dead	FW	2/25/08	Predation	Y	Y
TJ33	M	15	10/10/07	FW	Dead	FW	2/11/08[+]	Predation	Y	Y
TJ35	M	15	10/9/07	FW	Dead	SS	5/18/08	Predation	N	N
TJ43	F	16	11/12/08	FW, SS	Dead	FW	2/4/12	Inconclusive	Y	Y
TJ44	M	16	11/11/08	FW	Dead	FW	11/7/09	Predation	Y	Y
TJ46	M	16	11/11/08	FW	Dead	FW	1/6/10	Predation	Y	Y
TJ47	F	16	11/11/08	FW	Dead	FW	1/17/09[+]	Predation	Y	Y
TJ51	F	13	7/21/09	SS	Dead	FW	10/21/09	Predation	N	N
TJ52	M	25	7/29/09	SS, FW	Dead	SS	8/6/11	Predation	Y	Y
TJ54	M	13	7/21/09	SS	Dead	SS	5/12/10	Predation	Y	Y
TJ57	M	17	11/24/10	FW, SS	Dead	FW	9/27/11	Predation	Y	Y
TJ58	M	17	11/23/10	FW	Dead	FW	2/12/11[+]	Predation	Y	Y
TJ59	M	17	11/23/10	FW, SS	Dead	FW	1/29/12	Predation	Y	Y
TJ62	F	12	6/29/11	SS	Dead	SS	3/14/13	Predation	Y	Y
TJ63	M	12	6/22/11	SS	Dead	FW	12/2/11	Predation	N	N
TJ64	F	12	6/22/11	SS	Dead	FW	12/4/11	Predation	N	N
LHX2_03	F	22	5/14/14	SS	Alive				Y	Y
LHX2_04	F	22	5/14/14	SS	Alive				Y	Y
LHX2_05	F	22	5/14/14	SS	Alive				Y	N
LHX2_09	F	14	8/28/14	FW	Alive				Y	N
LHX2_10	F	26	8/28/14	FW	Alive				Y	Y
LHX2_12	F	26	8/28/14	FW	Alive				Y	N
TJ22	F	17	11/22/05	SS, FW	Alive				Y	N
TJ23	M	17	11/22/05	FW	Alive				Y	N
TJ24	M	22	4/17/06	SS	Alive				Y	N
TJ25	M	22	4/17/06	SS	Alive				Y	N
TJ26	M	22	4/17/06	SS	Alive				Y	N
TJ34	M	15	10/9/07	FW, SS	Alive				Y	Y
TJ36	M	15	10/9/07	FW	Alive				Y	Y
TJ38	M	22	4/29/08	SS	Alive				Y	Y
TJ39	M	22	4/29/08	SS	Alive				Y	Y
TJ40	F	22	4/29/08	SS	Alive				Y	Y
TJ41	M	22	4/29/08	SS	Alive				Y	Y
TJ45	M	16	11/12/08	FW	Alive				Y	Y
TJ48	M	16	11/11/08	SS, FW	Alive				Y	Y
TJ50	M	13	7/29/09	SS	Alive				N	Y
TJ53	M	14	9/10/09	FW	Alive				N	N
TJ55	M	13	7/29/09	FW, SS	Alive				Y	Y
TJ56	M	17	11/24/10	FW	Alive				Y	Y
TJ60	F	18	12/20/10	FW	Alive				Y	Y
TJ61	M	12	6/29/11	SS	Alive				N	Y

2.4. Diving behaviors

Data transmissions received via Argos were decoded in the program DAP (Wildlife Computers). For some individuals (n = 7), the raw diving data could not be correctly decoded by DAP and data from these individuals were not used. Clean data were processed in R version 3.5.1 using R Studio. Diving data consisted of binned dive depth (m), dive duration (min), and time at depth (TAD; %). TAD is the percentage of time spent in any given depth bin (m) for each 6 h recording period. Data processing

followed the methods of Thornton et al. (2008). Briefly, dive depths were 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. For SPLASH tags, dive duration was recorded in 30 s duration bins, with the 14th bin representing all dives >390 s. For SPOT-5 and SDR-T16 tags, dive duration was recorded in 1 min duration bins, with the 10th bin representing all dives >9 min. TAD for SPLASH tags was recorded in the following bins: 0–4, 9–16, 17–24, 25–32, 33–40, 41–50, 51–60, 61–70, 71–80, and >80 m. For SPOT-5 and SDR-T16 tags, TAD was recorded in the following bins: 0–4, 9–16, 17–24, 25–32, 33–40, 41–48, 49–56, 57–62, 63–70, 71–78, 79–86, and >86 m. Overall and daily means for dive depth (m), dive duration (min), and time wet (%) were calculated for all individuals (Table S1). As the 0–4 m depth bin in the TAD data represents an animal hauled out, time wet was calculated as the percent of time spent in all other bins combined. TAD data were not available for SPLASH tag animals (n = 6); therefore, they were removed from the analysis. Although average dive duration was calculated, it was not included in subsequent analysis due to collinearity with dive depth.

2.5. Analysis: general horizontal and diving behaviors associated with predation events

As previously described, between 2005 and 2014, 45 weaned SSL between the ages of 12 and 24 mo were released with LHX tags (Horning & Mellish 2014, Horning et al. 2017). Through 2016, 20 mortalities had been detected (Horning & Mellish 2014, Horning et al. 2017). Two of 20 returned insufficient data to determine causa mortis, and the remaining 18 were classified as predation events (Table 1) (Horning & Mellish 2014, Horning et al. 2017). All animals that died, including the 2 inconclusive events, were initially considered for this analysis unless otherwise excluded (see next paragraph), as predation could not be ruled out as a cause of death.

Juvenile Steller sea lions exhibit seasonal differences in horizontal movement patterns (Bishop et al. 2018) and in diving behaviors (Fig. 1) (Mellish et al. 2007, Thornton et al. 2008). Therefore, in cases where SDR-derived behavioral data were collected in a season that did not match the season in which the mortality event occurred (n = 4; Table 1), the animal was removed from further analyses. Similarly, for animals that died, if there were behavioral data available for both seasons (n = 4; Table 1), we only used the data from the season that temporally matched their mortality event. Including data limitations previously discussed during horizontal and diving data processing, this resulted in final data sets for 38 animals with horizontal data (22 alive, 16 dead) and 28 animals with diving data (16 alive, 12 dead; Table 1).

Two binomial generalized linear mixed-effects models (GLMMs) were run in R version 3.5.0 to assess the probability of mortality (0 = alive, 1 = dead) relative to (1) horizontal predictor variables and (2) vertical-diving predictor variables. For the horizontal behavior model, home range area (km^2), average distance traveled per trip (m), sex, and interactions between season and home range area, and season and average trip distance were included as predictor variables to account for seasonal behavioral differences (Fig. 1). For the vertical-diving behavior model, average dive depth (m), percentage of time spent wet, sex, and interactions between season and average dive depth, and season and percentage of time wet were included as predictor variables. In both GLMMs, animal ID was included as a random effect to account for effects of individual heterogeneity introduced by pseudo-replication of live animals for which we included both seasons for which we had data (n = 42 from n = 38 IDs for the horizontal GLMM; n = 31 from n = 28 IDs for the vertical GLMM). Model selection was based on criteria established by Richards (2008). AICc values were calculated for the models described above, and for all simpler versions of both global models, including an intercept-only (null) model. The best models were identified as those with the lowest AICc. Additionally, we retained any models with a ΔAICc ≤ 6, excluding those that were more complicated versions of models with lower AICc scores (Richards 2008). We used the R package DHARMa to conduct validation of the residuals for the best models (Fig. S1).

2.6. Analysis: ante-mortem behaviors at a fine temporal scale

Three animals in our study died with their SDR still attached and transmitting on the day of their confirmed predation event (TJ33, TJ47, and TJ58), whereas for most animals, the SDR stopped transmitting due to other reasons. The most common cause for end-of-record (EOR) is likely either exhaustion of the primary batteries powering the device, or the device falling off due to weakened attachment or being shed during the annual molt (Kooyman et al. 2015). Other possible causes may include technical device failures
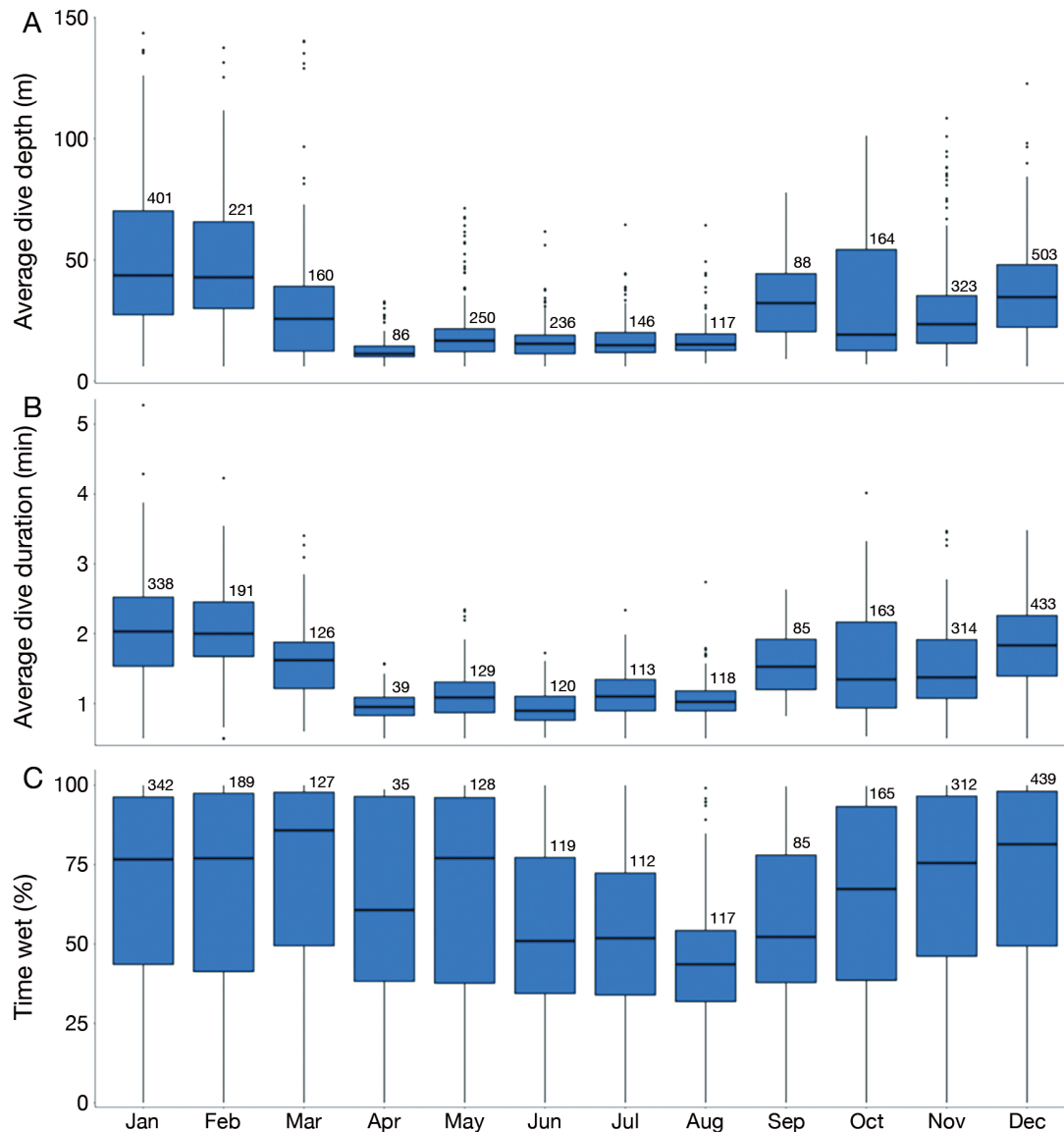
Fig. 1. Seasonal variations in diving behavior of juvenile Steller sea lions (n = 28) including individuals' (A) average daily dive depth (m), (B) average daily dive duration (min), and (C) average percent time wet per day. Boxes represent the interquartile range around the median (dark line). Whiskers represent the 75th and 25th percentiles, and circles outside of whiskers represent possible outliers. Numbers above boxplots indicate the total number of samples in each month

(e.g. software lockup, antenna broken off) or mortality of the host animal. The 3 predation events concurrent with the end of the telemetry record provided an additional opportunity to investigate fine-scale differences in behavior associated with predation events. Specifically, we explored if the difference between behaviors at the end of a tracking data set and the average behavior of an individual varied based on whether the end of track represented a mortality. To do this, we first selected all animals that had greater than 50 d of dive data in the season in which their SDR record ended (n = 16 for dive depth; n = 11 for percent time wet). For each animal, the mean dive depth and

mean percent time wet were calculated across the last 3 d of tracking data. We then selected a day at random from the same season as when their track ended, and starting with that date, calculated the mean dive depth and percent time wet across a window of the next 3 d for each individual. The difference in mean dive depth (D_{depth}) and mean percent time wet (D_{wet}) between the last 3 d and the random window was then calculated for each animal. Negative values for D indicated that an animal dove shallower or spent less time wet at the end of its track, and positive values indicated that an animal dove deeper or spent more time wet at the end of its track. We then performed a

non-parametric Wilcoxon signed-rank test to compare D_{depth} between animals with end of track mortality (n = 3) and EOR (n = 13), and to compare D_{wet} between animals with end of track mortality (n = 3) and EOR (n = 8). Due to the small sample size of animals with mortality at the end of their tracking data, we repeated this process 50 times, and we considered the differences between groups significant if >5% of the replicate trials resulted in a p-value <0.05.

3. RESULTS

3.1. Horizontal and vertical behaviors associated with mortality

Exploratory analysis revealed that there was considerable seasonal variation apparent in both dive depth and dive duration (Fig. 1). When looking at seasonal behavioral patterns as predictors of mortality, there was no evidence to support a relationship between individuals' horizontal movement patterns and vital status; the intercept-only null model was the best model (Table 2A). When considering vertical movement and haul-out patterns, percentage of time spent wet and an interaction between percentage of time wet and season were retained in the best model for predicting mortality; however, this model only accounted for 30% of overall model weight (Table 2B). Probability of mortality increased as the percentage of time wet decreased, but this pattern was only apparent in the summer (Fig. 2). The second-best model from our selection criteria, and the only other model with a ΔAICc < 6 that was not a nested version of a simpler model, was the null model (Table 2B).

Table 2. Binomial generalized mixed-effects linear models predicting juvenile Steller sea lion vital status (alive = 0, dead = 1) from seasonal (A) horizontal movement patterns and (B) vertical movement patterns. All models that met our selection criteria (Richards 2008) are shown above the dashed lines and include the coefficient estimate for any fixed effects retained in the model. Models that had a ΔAICc ≤ 6 but were a more complicated version of a model that had a lower AICc score are shown with the variables included indicated by an 'x'

(A) Horizontal distance model	Trip distance	Home range	Trip distance × season	Home range × season	Sex	df	AICc	ΔAIC	Weight
1						2	59.8	0	0.300
2	x					3	61.5	1.66	0.131
3		x				3	61.8	1.99	0.111
4					x	3	61.9	2.06	0.107
5		x		x		4	62.7	2.93	0.069
6	x		x			4	63.0	3.24	0.059
7	x				x	4	63.7	3.86	0.043
8	x	x				4	63.9	4.11	0.038
9		x			x	4	64.1	4.28	0.035
10		x		x	x	5	65.1	5.27	0.022
11	x	x		x		5	65.2	5.40	0.020
12	x		x		x	5	65.4	5.62	0.018
13	x	x	x			5	65.6	5.79	0.017

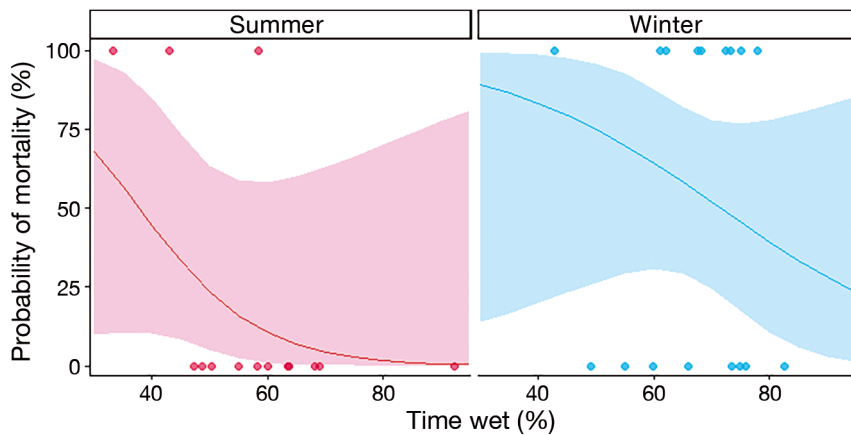| (B) Vertical distance model	Dive depth	Time wet	Dive depth × season	Time wet × season	Sex	df	AICc	ΔAIC	Weight
1		−0.096		0.045		4	44.1	0.00	0.309
2						2	45.6	1.44	0.150
3	x	x		x		5	46.6	2.46	0.090
4	x					3	46.6	2.50	0.088
5		x		x	x	5	47.0	2.84	0.075
6		x				3	47.7	3.59	0.051
7					x	3	48.0	3.87	0.044
8	x	x	x	x		6	48.1	3.98	0.042
9	x	x				4	48.8	4.72	0.029
10	x		x			4	48.9	4.78	0.028
11	x				x	4	49.3	5.15	0.024
12	x	x		x	x	6	49.7	5.56	0.019

Fig. 2. Logistic regression from the best model for predicting the probability of mortality, relative to vertical behaviors for juvenile Steller sea lions. The percentage of time spent wet had a negative association with probability of mortality, with evidence of a stronger effect in spring–summer (n = 14) than in fall–winter (n = 17). Residual distributions are shown in Fig. S1

3.2. Fine-scale ante-mortem behavior

For animals in which the end of track was associated with a predation event (n = 3), dives prior to mortality were generally shallower (median D_{depth} = −10.5 m). This pattern was significantly different (12/50 randomized Wilcoxon tests, p < 0.05; Table S2) when compared to the D_{depth} for animals where the end of their tracks were not associated with a predation event but represented cessation of successful tag uplinks for unknown reasons (median = 4.6 m). No significant difference was observed when comparing D_{wet} between animals with and without mortalities at the end of their tracks (1/50 randomized Wilcoxon tests, p < 0.05; Table S3).

4. DISCUSSION

This data set from an endangered meso-predator, while small, represents a unique opportunity to characterize the diving, movement and haul-out behavior of juveniles that died — most from predation — and compare them with those of juveniles that survived for a longer period of time. Within our limited data set, we found no evidence that horizontal movement patterns shortly after release — including trip distance or home range size — were associated with the probability of predation later in the juvenile's life (but during a comparable season). Findings regarding the diving behavior were mixed. There was some evidence that time spent wet during post-release tracking had a weak, negative relationship with predation

probability later in the juvenile's life, when seasonal effects were considered. Also, 3 juveniles appeared to conduct shallower dives in the days preceding their death by predation than during other periods at sea within the same season.

Overall, our results suggest that the likelihood of predation for the individuals in this study may be affected by variables that were not directly tested here, but that may be indirectly linked to our observed parameters. For example, we found some evidence suggesting individuals that spent less time wet, and more time hauled out, had a greater probability of mortality. Individuals that are more temporally and spatially associated with haul-outs may also spend more time in the water near haul-outs. Such a pattern, particularly in the summer, when our observed effect was stronger, might expose these individuals to greater predation risk by specialist predators known to target sea lion rookeries, such as transient killer whales *Orcinus orca* (Heise et al. 2003, Maniscalco et al. 2007). The finding of shallower diving by the 3 animals tracked until just before death is also consistent with observed evasion patterns exhibited by harbor seals *Phoca vitulina* when being actively pursued by killer whales (Womble et al. 2007).

Opportunistic and generalist predators, such as sharks, are also known to predate on Steller sea lions (Sigler et al. 2006, Frid et al. 2009). Data collected from some predation events associated with the present study specifically suggest Pacific sleeper sharks *Somniosus pacificus* as a likely predator in at least 5 mortalities (see Horning & Mellish 2014). While our understanding of Pacific sleeper shark ecology is limited, one study found that Pacific sleeper sharks spent 75% of the time at depths greater than 50 m (Hulbert et al. 2006). Our data indicated that juvenile Steller sea lions in the same region, the Gulf of Alaska, typically only dive to depths >50 m in the winter, thus predation by sharks would most likely occur at the upper limit of Pacific sleeper shark vertical movements, and more likely in winter than summer. While our results did not indicate that individuals' average dive depth was associated with probability of mortality, 65% of the mortalities in our study were observed in fall/winter.

While the resolution of our data in conjunction with small sample sizes poses challenges for the predic-

tive potential of our results at the population level, together, our findings support the hypothesis by Frid et al. (2009) that posits a combination of opportunist and specialist predators affecting Steller sea lions in the region. Disentangling the behavioral patterns and risk of predation in a multi-predator system is challenging (Willems & Hill 2009), and it is at present unclear how the differential effects of multiple predator types may be reflected in assessments of individual sea lion behavior. We were unable to include predator type as an interactive term in our analysis as there are only 5 mortalities likely to be associated with sleeper shark predation, whereas the nature of the predator could not be determined in the remaining 13 mortalities clearly identified as predation events. Future work that includes information on the relative incidence of events attributable to one predator or another — the actual amount of predation pressure from killer whales and sharks seasonally — would enable a better understanding of the drivers associated with consumptive effects of predation in this system. Identifying the predator species can be challenging in both terrestrial and marine environments, particularly if carcasses cannot be recovered for visual or molecular evaluation (Mumma et al. 2014). This can have implications for using predator control measures as a management tool (Ripple et al. 2019). The development of advanced signal processing algorithms to integrate information from multiple sensors (e.g. temperature, motion, depth), including novel sensors (e.g. ingestion), could improve the ability to identify predators, and represents an important area of future tag development.

Though not directly assessed in the present study, it is also important to consider how the behaviors we observed in our data might be influenced by risk, as perceived by juvenile sea lions (non-consumptive effects). An expanding body of literature suggests that interactions between resource availability and predators can influence foraging decisions and have associated fitness consequences (Heithaus et al. 2008, Frid et al. 2009). Behavioral patterns observed in juveniles, if responsive to perceived risk or possibly a risk–reward trade-off, might therefore change during late ontogeny as individual foraging strategies emerge. In our data set, the majority of mortality events occurred within 1.5 yr of the behavioral data, an age where the animals were still considered juveniles when predation occurred. In a single case, the mortality event occurred approximately 3.5 yr later. Like many pinnipeds, Steller sea lions exhibit physiological and behavioral ontogeny of diving patterns within their first year (Pitcher et al. 2005, Richmond

et al. 2006, Rehberg & Burns 2008). However, currently there is very little known about the development of individual behavioral strategies among Steller sea lions beyond this period, i.e. from juvenile to adult stages. Our data set was limited in assessing these differences due to both the relatively short duration of external tracking and the influence that seasonal behavioral changes have in masking individual patterns (Fig. 1). However, for other marine meso-predators, fidelity to an adult foraging strategy relatively earlier in life is associated with increased longevity across individuals (Authier et al. 2012). Thus, further investigations into how the long-term behavioral profiles of individuals relate to the tradeoffs between resource acquisition and the likelihood of predation could provide insights into the vulnerability of individuals within endangered populations.

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