

Immature Steller sea lion (*Eumetopias jubatus*) dive activity in relation to habitat features of the eastern Aleutian Islands

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ABSTRACT

Current flow and bathymetry in the Aleutian Islands define unique habitats that influence prey distribution and foraging behavior of top-level predators. We explored whether oceanographic features and bathymetry influenced the diving activity of 30 immature sea lions (ages 5-21 months) equipped with satellite-linked depth recorders in the Eastern Aleutian Islands during 2000-2002. Sea surface temperature (SST) and chlorophyll *a* concentrations were obtained from remote sensing satellite imagery and associated with locations where sea lion diving was recorded. Most locations associated with diving to > 4 m were within 10 nautical miles (nm) of shore and associated with onshelf waters < 100 m deep. Use of offshore and deeper waters in the Bering Sea increased during May, as did trip durations. General movements at that time were generally northwesterly from the North Pacific Ocean to the Bering Sea. Diving activity varied coincidentally with increases in SST and chlorophyll *a* concentrations, but also with sea lion age. Associations with habitat features did not consistently explain variability in dive count, time-at-depth, dive focus or focal depth. Nearshore diving tended to be influenced by distance from shore or seafloor depth, whereas increased SST coincided with activity of sea lions diving > 30 nm offshore. Immature sea lions developing into independent foragers in the relatively shallow pass areas of the Eastern Aleutian Islands do so at a time of rapid changes in oceanography and prey availability.

Key words: Alaska, foraging behavior, geographic information system, oceanography, otariid, pinniped, remote sensing, satellite telemetry, satellite tracking

INTRODUCTION

The ocean surrounding the Aleutian Island archipelago is spatially and temporally dynamic with distinct habitats characterized by current flow and bathymetry (Ladd *et al.*, 2005a; Stabeno and Reed, 1994; Stabeno *et al.*, 1999; Stabeno *et al.*, 2002). The Alaska Coastal Current, characterized by relatively warm, fresh waters and low nutrient levels, dominates the eastern passes, whereas the cooler, saltier waters of the Alaska Stream carry higher nutrient concentrations to deeper passes west of Samalga Pass (Fig. 1; Ladd *et al.*, 2005a). Productivity of the relatively shallow eastern passes (e.g., Unimak Pass) is limited by complete mixing within the water column, but nutrient mixing through the deeper passes contributes to seasonally increased productivity northward in the Bering Sea (Ladd *et al.*, 2005a). Distributions of many pelagic and demersal fish species along the Aleutian Island chain are subsequently influenced by these features, with less species richness west of Samalga Pass but also pockets of higher biomass within several passes (Logerwell *et al.*, 2005; Sinclair and Stabeno, 2002). Distributions and foraging behavior of top-level predators are likewise effected (Hunt *et al.*, 1998; Ladd *et al.*, 2005b; Springer *et al.*, 1996). Steller sea lion population trends (Loughlin and York, 2000; York *et al.*, 1996), diet (Merrick *et al.*, 1997; Sinclair and Zeppelin, 2002), and ecological associations of rookeries and haulouts (Call and Loughlin, 2005) also vary along the Aleutian Island chain. In this diverse region, oceanographic variability may influence Steller sea lion foraging behavior, and consequently the growth and survival of naive sea lions as they develop foraging skills during the transition from maternal dependence.

Steller sea lions give birth from late May through July (Merrick *et al.*, 1995; Pitcher *et al.*, 2001). Precise weaning dates have not been determined, but weaning is

thought to occur when pups reach about 10-12 months of age (Pitcher and Calkins, 1981; Porter, 1997) though suckling may occur in juveniles up to three years old (Pitcher and Calkins, 1981). By 10-12 months of age juvenile sea lions dive on average to 17 m, but maximum dive depths range between 63-288 m (Loughlin *et al.*, 2003). Diving ability develops throughout the first year of life due to ontogenetic changes in diving ability, weaning, learned behavior, or in response to seasonal environmental fluctuations (Loughlin *et al.*, 2003; Merrick and Loughlin, 1997; Richmond, 2004). Previous analyses of Steller sea lion dive and travel behavior have not specifically examined links between diving activity and detailed habitat characteristics, and the relationship between diving behavior and oceanographic and bathymetric features has not been quantified. All studies of otariids published to date reporting significant relationships between dive behavior and habitat have been conducted on lactating southern hemisphere fur seals during pup rearing (Georges *et al.*, 2000; Guinet *et al.*, 2001; Lea and Dubroca, 2003; McCafferty *et al.*, 1998) or adult northern fur seals during winter migration (Ream *et al.*, 2005). In this context, a critical gap exists in our knowledge of how environmental variability may affect naive pinniped foragers as they transition to nutritional independence.

Steller sea lion populations in parts of Alaska declined by 80% since 1959 (Loughlin *et al.*, 1992), prompting a threatened listing in 1991 under the U.S. Endangered Species Act for the species as a whole and an endangered listing in 1997 for the genetically distinct stock west of 144° W longitude (Bickham *et al.*, 1996; Loughlin, 1997). The western stock declined at about 4% per year during 1991-2002, though since 2000 the decline may have abated in the Central (CAI) and Eastern Aleutian Islands (EAI, Sease and Gudmundson, 2002). Models suggesting decreased survival of ages 1-4 years during

the early 1980s (York, 1994; York and Holmes, 2003) generated hypotheses for the decline that include chronic nutritional stress of juveniles due to inadequate prey availability or quality that could arise from indirect commercial fishery effects, environmental change (Alverson, 1992; Loughlin and Merrick, 1989) or both factors. Because of their endangered status and concern over prey availability, management measures were enacted to reduce spatial overlap of fisheries with presumed foraging areas of Steller sea lions. This analysis explores the relationship between immature Steller sea lion diving activity and habitat features in the Aleutian Islands to better characterize potential foraging habitats.

METHODS

Captures and Instrument Deployment

Thirty immature sea lions were captured at or near haul-out sites in the northern Gulf of Alaska and Aleutian Islands during 2000-2002 (Table 1, Fig. 1) using land or scuba capture techniques (Loughlin *et al.*, 2003; McAllister *et al.*, 2001). Captures occurred during February or March of each year and during November of 2001. Dive data from sea lions captured in 2000 were included in diving analyses conducted by Loughlin *et al.* (2003).

Animals captured on land were physically restrained or given an intramuscular injection of diazepam ($\sim 1.5 \text{ mg kg}^{-1}$). All sea lions captured at sea were anesthetized with inhalable isoflurane delivered with oxygen via a facemask or endotracheal tube from a field portable anesthesia machine (Heath *et al.*, 1996). Once a sea lion was restrained, morphometric measurements were taken and instruments attached. Mass was measured to $\pm 0.1 \text{ kg}$ with an electronic load cell, and dorsal standard length was measured to $\pm 1 \text{ cm}$. Instruments were attached to the dorsal pelage near the shoulders using quick-setting epoxy. Age was estimated assuming a mid-June birth date (Pitcher *et al.*, 2001) and was based on capture date, tooth eruption, and sea lion size (Calkins and Pitcher 1982). However, due to the size overlap between 9 and 21 month olds during March, some may have been misclassified. Sea lions were monitored while recovering from the effect of anesthesia whether on land or on a research vessel, then allowed to voluntarily return to the water.

Dive Activity and Location

We used two types of 0.25-watt satellite dive recorders (SDRs) packaged by Wildlife Computers, Redmond, WA (ST10 in 2000, SDR-T16 in 2001 and 2002) and programmed to record and transmit data as described in Loughlin *et al.* (2003). Briefly, both models transmitted data on transmitter status (wet or dry), maximum dive depth, and time at depth (TAD) summarized within four 6-h periods (2100-0259 h; 0300-0859 h; 0900-1459 h; 1500-2059 h). Depths were sampled every 10 seconds with a resolution of 2 m, and the maximum depth reached for each dive was recorded into one of 14 data bins: ≤ 4 m, $> 4-6$ m, $> 6-10$ m, $> 10-20$ m, $> 20-34$ m, $> 34-50$ m, $> 50-74$ m, $> 74-100$ m, $> 100-124$ m, $> 124-150$ m, $> 150-174$ m, $> 174-200$ m, $> 200-250$ m, and > 250 m. Thus, dives were recorded once the sea lion was > 4 m below the surface. Time-at-depth recorded the proportion of time spent diving in a depth bin for the time at sea during a 6-h period. We calculated TAD as the total proportion of time spent diving within a 6-h period to > 4 m (e.g., if a sea lion spent half of a 6-h period at sea, and spent half its dive time at ≤ 4 m, one quarter at $> 4-6$ m and one quarter at $> 6-10$ m, the TAD would be 25%).

Diving activity was described directly by the number of dives to each depth bin (dive count) and the TAD from SDR bin data, and by indices derived from bin data: dive rate (number of dives per time spent at sea within a 6-h period), mean dive depth (Loughlin *et al.*, 2003; Merrick and Loughlin, 1997), dive focus and focal depth bin (Frost *et al.*, 2001). To calculate dive focus and focal depth, histogram dive count data were condensed into six bins of 4-10 m, $> 10-20$ m, $> 20-34$ m, $> 34-50$ m, $> 50-100$ m, and $> 100-174$ m. Dive focus (DF) is based on Simpson's Diversity Index and reflects diving variability by quantifying dive dispersion among the six bins (Frost *et al.*, 2001; Hastings *et al.*, 2004).

Diving occurred to mainly one bin if $DF > 0.5$, and equally among all bins if $DF = 0.167$ (Frost *et al.*, 2001). Focal depth indicates the dominant depth bin ($DF > 0.5$) to which dives were made.

Sea lion locations were calculated by Service-Argos, Inc. from satellite-derived position fixes based on the Doppler shift of uplinks between the SDR and polar orbiting satellites (Fancy *et al.*, 1988). A hierarchical location class (LC) reflecting position accuracy for each fix was assigned by Service-Argos, with LC3 being the most accurate. By comparing satellite fixes to GPS ship locations during pre-deployment trials, we estimated mean ($\pm SD$) accuracies of 0.4 km (± 0.3 km) for LC3, 0.7 km (± 0.6 km) for LC2, 1.5 km (± 1.5 km) for LC1, 4.9 km (± 5.3 km) for LC0, 2.9 km (± 5.2 km) for LCA and 17.4 km (± 26.2 km) for LCB. Because locations are not sent by the transmitter, locations calculated by Service-Argos may not coincide exactly with dive data, and not all dive data types may be received during a 6-h sampling interval. Thus, additional processing was required to match dive histogram data with location data. Locations were iteratively sorted based on maximum swim speed and the Keating Index, a geometric measure of location accuracy (Keating, 1994). If swim speeds between two successive locations exceeded 3 m s^{-1} (Loughlin *et al.*, 2003; Merrick and Loughlin, 1997), the poorer quality (based on LC) location was removed. If location qualities were equivalent, the location with the lower Keating index was retained. LCA and LC0 locations were considered equivalent when filtering based on location quality, and ranked higher than LCB. Locations received from land that had no associated dive data were eliminated, and dive data for which no location could be assigned were likewise removed. Locations received during dry periods (based on surface-timeline data) were summarized as a single

location based on the highest quality location during a dry period. Gross outliers were removed during the last stage of the filtering process by rejecting locations with a Keating index > 20 km. One location was then selected from each 6-h binned dive data-sampling period based on LC. This final filtering stage provided representative temporal coverage across sampling periods (i.e., bias associated with obtaining more locations during optimal uplink periods was diminished), and reduced autocorrelation among locations used to quantify sea lion diving behavior with respect to location. However, if sea lions were more likely to be at the surface near haul-outs than offshore (with a higher probability of obtaining a better LC), locations assigned to diving activity may have been slightly biased shoreward. For analyses associating dive activity with spatially specific environmental variables (bathymetry, sea surface temperature (SST) and chlorophyll concentration), only dive data linked to at-sea locations (transmissions received while SDR was wet) were used.

Habitat Data

Habitat was characterized using bathymetric and oceanographic features. Bathymetry was calculated from National Imaging and Mapping Agency (NIMA) digital data of all soundings found on National Oceanic and Atmospheric Administration (NOAA) nautical charts in the area. Each sea lion location was spatially matched to the closest sounding and assigned that bathymetry value. Distances to nearest soundings were relatively short (88% of locations were < 1 km from a sounding, 95% were < 5.5 km from a sounding), except around Amlia Island where there were almost no soundings from a depth of 80 m to the shoreline. The minimum distance from each location to the nearest shoreline (not instrument deployment site or point of departure for a trip) was calculated in ArcMAPTM 8.2 (ESRI, CA). Locations were classified as being on either the Bering Sea or North

Pacific Ocean side of the Aleutian Island chain. The SST (daytime 11 & m sensor) and chlorophyll *a* (SeaWiFS analog) data were obtained from the Moderate Resolution Imaging Spectrophotometer (MODIS) carried aboard the Terra satellite. Monthly averages of 4.89 km² grids (MODIS Level 3 mapped product) were obtained corresponding to periods of telemetry coverage during 2000-2002 for 161-177°W longitude and 51-57°N latitude. Though some ability to detect frontal structures was lost, monthly resolution was chosen because it maximized the resultant number of data cells, which were limited on shorter time scales due to cloud cover. MODIS data were filtered for the best data quality (class 0) based on accompanying data quality files. Data in 2000 and after March 2002 were classified as provisional (partially validated), and data for 2001 through March 2002 were validated.

All data were combined in an ArcGIS® geographic information system (ESRI, CA) software. Each location with accompanying dive data was linked with data on SST, chlorophyll *a* concentration, seafloor depth, and distance to shore through the ArcGIS spatial analyst module. Associations between habitat variables and locations of sea lion diving activity were examined using Statistical Package for Social Sciences (SPSS, version 11) software. Mean monthly sea lion movement bearings and distances were determined from average monthly locations for individual sea lions using at-sea locations only, and following statistical techniques for circular data (Zar, 1984).

Of the 30 instrumented animals, effects of habitat type on dive activity were explored in more detail for sea lions that provided continuous telemetry data during March-June in any of the three years of study. Of the nine meeting that criterion, one was excluded because of a lack of SST data associated with calculated locations. All eight sea

lions were estimated to be 9-12 months old during this period (Table 1). Dive count, TAD, dive focus and focal depth distributions were normalized by applying a square-root transformation, then standardized by subtracting the mean from each value and dividing by the standard deviation (normal deviate Z score; Zar, 1984). Normal deviates were input as dependent variables in a stepwise multiple regression model with time period, month, distance to shore, seafloor depth, region (Bering Sea or North Pacific Ocean), and SST as independent variables. Variables were included in the model if significance of $F < 0.05$, and rejected if $F > 0.1$. The model was run independently for each sea lion to explore individual behavioral differences.

RESULTS

Captured sea lions (11 males, 19 females; Table 1) weighed 72-152 kg. Duration of data collection was between 29-181 days (Table 1), with a median duration of 71 days. Most sea lions (25 of 30) were captured in the EAI, though one sea lion captured near Kodiak Island entered the area during the study period. The common period of data coverage among years was between March and June (Table 2).

Removing duplicate dry locations reduced an initial sample size from 13,796 to 7,582 locations. When filters for swim speed and location quality were applied and duplicate at-sea locations removed, 3,263 locations remained associated with dive data. When locations not exhibiting evidence of diving to > 4 m were removed, the sample size was 2,626 locations, or about 19% of the initial Argos position fixes. This contained 143,149 dives and 1,991.5 hours of diving to > 4 m. Selecting locations when the SDR was wet (removing dive data transmitted from a haul-out location) reduced the available sample to 1,151 with either dive count or TAD data, and 820 locations with both dive data types during 763 trips. Of these locations, 38 (3.3%) were obtained from two sea lions 5 months old at capture, 1,013 (88.0%) from 24 sea lions 8-9 month old at capture, and 100 (8.8%) from four sea lions 17-21 month old at capture. These data were utilized for comparisons of dive location and activity with bathymetric and oceanographic features.

Diving Locations and Trip Durations

Habitat use indexed by proportion of locations associated with diving to > 4 m (Table 3) varied significantly with distance to shore (ANOVA on angular-transformed data, $F_{(2,229)} = 702.2, P < 0.001$) and bathymetry ($F_{(3,151)} = 52.2, P < 0.001$). There was a significant interaction effect between season and distance to shore ($F_{(4,229)} = 0.148$,

$P < 0.001$) but not between season and bathymetry ($F_{(6,151)} = 0.865$, $P = 0.522$). Most locations associated with diving to > 4 m were within a 5-10 nautical mile (nm, 1 km = 0.540 nm) straight-line distance of shore and in waters less than 100 m deep (Table 3). All locations were within 15 nm of shore during November-January, but only three sea lions were tracked during that period. During May-July, the proportion of locations within 5 nm decreased (to about 85%), and 13% were greater than 10 nm from shore (Table 3). Summary proportions were likely slightly biased nearshore because the filter selected higher quality locations when making a choice between a set of mixed LCs. Poor quality LC A and B locations comprised 27.3% of locations < 5 nm, but 61.5% of locations between 5-10 nm.

Locations greater than 30 nm offshore were located in the Bering Sea and included waters > 200 m off the continental shelf (Fig. 2), whereas the most distant offshore locations into the North Pacific Ocean were < 30 nm offshore and associated with shelf waters < 200 m deep south of Unimak Island and Unimak Pass (Fig. 2). The longest duration trips and greatest distances offshore during the May-July period (Fig. 2) occurred during May. Mean maximum trip distances to shore of locations associated with diving to > 4 m varied by trimester (ANOVA on log-transformed distances, $F_{(2,760)} = 16.478$, $P < 0.0001$), and were significantly smaller during February-April (0.3 nm, 95% CI 0.3-0.4 nm, $n = 478$) than during May-July (0.7 nm, 95% CI 0.5-0.8 nm, $n = 231$) (Bonferroni $P < 0.05$), but did not differ from November-January (0.6 nm, 95% CI 0.4-0.9 nm, $n = 54$). Of the 30 instruments deployed, 17 were operational during May when most offshore (> 20 nm) diving locations were recorded (Fig. 2). Of those active in May, about 23% (CI = 5-67% assuming a binomial distribution) of the instrumented sea lions indicated offshore

diving behavior (1 of 2 in 2000, 1 of 4 in 2001, and 1 of 8 in 2002). Mean trip durations also varied by trimester (ANOVA on log-transformed durations, $F_{(2,760)} = 17.348$, $P < 0.0001$). Mean trip duration during February-April (0.37 d, 95% CI 0.35 -0.39 d, $n = 478$) was significantly shorter than during May-July (0.52 d, 95% CI 0.47-0.58 d, $n = 231$; Bonferroni $P < 0.05$), but did not differ with durations during November-January (0.42 d, 95% CI 0.34-0.52 d, $n = 54$).

General movements among areas indicated by the compass direction between mean monthly locations for sea lions east of Samalga Pass (calculated as the mean monthly latitude and longitude for an individual) did not indicate a significant orientation during Feb-Apr (Table 4). However, movements were significantly oriented towards a bearing of 293° during May-June (Table 4). Direction bearings of Feb-Apr and Apr-May travel for sea lions relocating > 10 nm between months tended to orient N-NE (though not statistically significant, $P = 0.100$). May to June movements were associated with travel towards Unimak Pass, or from Unimak Pass area north and west through the Krenitzen Islands. This directed movement was shown by sea lions regardless of their initial location, and was coincidental with seasonally changing environmental conditions. Distances between monthly mean locations varied by month. May-June displacements were significantly greater than Feb-Mar distances (Table 4).

Effects of Age on Diving Activity

Most dives (as a proportion of total dives) were made to depths less than 20 m, though some were to as deep as 100-124 m (Fig. 3). Diving activity, as indexed by dive rate, TAD, mean depth of dives and dive focus changed with sea lion age (Fig. 4). Dive rate and TAD both increased throughout the first 12 months of age, while mean dive depths

became deeper up to 18 months of age (Fig. 4). Dive rate and TAD declined after 17 months of age. Dive focus varied inversely with TAD, and as TAD increased through the first 14 months, dives became spread over more depth bins (indicated by focus values of < 0.5 , Fig. 4). When translated to time of year, age differences in diving activity become particularly evident during winter months of November-January (corresponding to ages 5-7 months and 17-19 months), when juveniles dove more frequently, deeper, and spent more time at depth than did pups.

Diving Activity and Oceanography

Monthly averages of SST associated with diving locations indicated substantial changes in regional thermal structure in the study area (Fig. 5). Sea surface temperatures associated with diving locations cooled during November-March, then warmed progressively each month during March-June (ANOVA, $F_{(8,716)} = 172.8$, $P < 0.0001$). By May, increased chlorophyll *a* concentrations were evident over the study area (Fig. 5), with significant differences in concentrations among December, March ($0.49 \pm 0.02 \text{ mg m}^{-3}$, $n = 19$) through April ($0.55 \pm 0.03 \text{ mg m}^{-3}$, $n = 29$), and May ($2.20 \pm 0.24 \text{ mg m}^{-3}$, $n = 58$) through June ($1.51 \pm 0.39 \text{ mg m}^{-3}$, $n = 16$; $P < 0.05$, Tamhane multiple comparison test for unequal variances).

Diving activity did not vary with chlorophyll *a* concentration (ANOVA for dive rate, median depth, and dive focus all $P > 0.10$), likely due to limited sample sizes in 2.0-4.0 mg m^{-3} ($n = 7$) and $> 4.0 \text{ mg m}^{-3}$ ($n = 10$) categories. Dive activity did vary with SST (ANOVA, dive rate $F_{(5,613)} = 2.61$, $P = 0.024$; median depth $F_{(5,716)} = 2.277$, $P < 0.045$; dive focus $F_{(5,831)} = 2.275$, $P < 0.0001$; Fig. 6). As temperatures increased dive rate and median

depth of dive increased, and maximum depths were more dispersed through the water column (as indicated by decreased dive focus; Fig. 6).

Association of habitat variables and diving activity

Up to three variables accounted for 6-89% of variability in dive activity (Tables 5-6), though no variable was common as an explanatory factor in all sea lions. Only two sea lions (6308 and 7485) had variability accounted for in all four dive-activity indices by the environmental variables considered (Tables 5-6). Dive count and TAD were greatest during two periods, 2100-0259 h and 1500-2059 h (ANOVA, Bonferroni $P < 0.05$), and focal depths tended to be deeper in daylight hours. Dive focus was relatively unaffected by time of day. Time of day was a common influence for dive count and TAD, and somewhat less for focal depth and dive focus. Month in which diving occurred was a significant positive factor for two sea lions, but had a negative influence on TAD for one animal. Sea lions diving on the North Pacific Ocean side of the Aleutian Islands tended to make fewer dives than when on the Bering Sea side, though there was an effect on TAD for only one individual (as indicated by the “region” factor, Table 5). Seafloor depth influenced TAD in three of seven sea lions, the number of dives for one sea lion, but was not of a consistent sign of effect. Sea surface temperature also influenced proportion of time spent at depth for two sea lions, but did not appear to affect the number of dives performed.

Dive locations of five sea lions whose dive count or TAD was influenced by distance from shore or seafloor depth were clustered among the nearshore areas of the Krenitzen Islands, Unalaska Island and Bogoslof Island. Median dive depths did not vary during March-June, though one individual (#6310) showed tendencies for deeper diving

after May, while another (#6300) made fewer deeper dives. In contrast, the three sea lions whose diving was influenced by month or SST ranged widely throughout the eastern Aleutian Islands, and undertook offshore trips (distinguishable in Fig. 2, May-July north of the Aleutian Islands). All three exhibited relationships between date and median depth of dives, though one (#7483) was opposite to that of the others such that the deeper dives were made during March while in the northern Pacific Ocean.

DISCUSSION

In the eastern Aleutian Islands, juvenile Steller sea lions developed foraging skills mostly within nearshore habitats 5-10 nm from shore in waters ≤ 100 m deep. This is similar to findings of Raum-Suryan *et al.* (2004) that 90% of juvenile sea lion trips in Prince William Sound and Southeast Alaska were within 15 km (8 nm) round trip distance from a haulout, and Loughlin *et al.* (2003) that measured a mean trip distance (for round or between haulout trips) of 17 km (9.1 nm). Trip distance in both of those studies, however, was the distance actually traveled by the sea lion from a haulout, rather than the distance from shore of locations associated with diving determined in our study. Distance from shore of diving locations provides a somewhat different perspective of habitat use and one way of evaluating the utility of managed protection areas. That is, while juvenile Steller sea lions made trips of up to 447 km (241 nm; Loughlin *et al.*, 2003) or round trips from haulouts of up to 111 km (60 nm; Raum-Suryan *et al.*, 2004), we found that most diving locations during November-April in the eastern Aleutian Island region were less than 5-10 nm offshore. Diving in more distant waters off the Bering Sea shelf increased during May-June, and May locations tended to be northwest of April locations, indicative of general movements downstream of the Alaska Coastal Current or up into the Bering Sea (Fig. 2, Table 4). These general patterns of juvenile Steller sea lion distributions and diving activity may have been related to changes in development with ontogeny, or to seasonal changes in physical habitats or prey availability.

Evaluation of the influence of ontogenetic versus environmental effects depends largely upon assumptions regarding juvenile nutritional status. Otariids have adopted strategies of extended lactation periods (Oftedahl *et al.*, 1987), and weaning in pinnipeds

generally begins when maternal input cannot meet maintenance and growth needs of the pup (Lee *et al.*, 1991). Because of their relatively large body mass, Steller sea lions require close proximity to abundant prey resources to maintain a positive energy balance of mother and pup (Boyd, 1998), and pups accompany mothers to multiple haul-out sites after leaving rookeries in late summer. Gradual weaning provides opportunities for pups to develop swimming, diving and foraging skills while receiving nutrition from maternal milk, buffering changes in prey availability (Trillmich, 1996). While pups may begin ingesting solid food as early as 3 months of age (Raum-Suryan *et al.*, 2004), mean trip durations of < 0.75 days during November-May were consistent with maternal dependency, being within a range of trip durations measured for adult females presumed to be supporting pups during winter (0.75 d [Merrick and Loughlin, 1997] to about 2.5 d [Trites and Porter, 2002]). By May, trips of many immature sea lions exceeded this duration and were farther offshore, a possible indication of nutritional independence (Loughlin *et al.* (2003), Raum-Suryan *et al.*, 2004).

Previous studies found that diving ability of young-of-the-year Steller sea lions, expressed as increased dive rates and deeper dive depths, progressively developed between winter and summer (Merrick and Loughlin, 1997; Loughlin *et al.*, 2003). Our findings confirm development in diving ability through 12 months of age, and found that in winter juveniles dove more, spent more time underwater, and utilized more of the water column than pups in the same areas. Between 1-2 years of age, however, there was an apparent leveling of diving ability as measured by dive rate and TAD. This may be related to developmental changes in mass-specific oxygen storage capacity, which were shown by Richmond (2004) to plateau between 9-17 months of age in Steller sea lions, or could have

been due to environmental interactions. Changes in diving activity may result from increased knowledge of prey locations (Merrick and Loughlin, 1997), changes or differences in foraging habitat (Loughlin *et al.*, 2003), or changes in prey distribution and availability.

Seasonal and spatial variability of prey may play an important role in foraging success and survival of immature sea lions developing foraging skills during the transition to nutritional dependence. Successful foraging of immature sea lions could lead to earlier and more rapid development of their physiological capacity to increase diving ability (Richmond, 2004). The greater diet diversity of sea lions in the EAI area is presumed to reflect local prey abundance and concentrating features of the habitat (Sinclair and Zeppelin, 2002), and thus extensive use of demersal habitats < 100 m in the eastern pass areas may provide access to this prey diversity. Winter (December-April) diets of sea lions in the EAI are dominated by pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*), but also include a number of forage fish species (Sinclair and Zeppelin, 2002). Summer (May-September) diets are dominated by pollock, Pacific salmon (*Onchorhynchus* spp.), herring (*Clupea pallasii*), and Atka mackerel, but also include squid and octopus (class Cephalopoda). Large aggregations of pollock are found throughout the eastern Bering Sea and in the Unimak Pass and Unalaska areas during summer (Logerwell *et al.*, 2005; Yanagimoto *et al.*, 2002), and salmon seasonally migrate along the Aleutian Islands and through passes (Pearcy, 1992). Pacific herring migrate from winter grounds offshore over the eastern Bering Sea slope inshore to coastal spawning areas (including the Alaska Peninsula and Unimak Pass area), where they remain to feed during summer (Wespestad, 1991).

These prey species occupy depths shown to be exploited by juvenile sea lions in our study. Juvenile pollock inhabit depths of 30-110 m in the daytime and move within 40 m of the surface at night (Brodeur *et al.*, 1999; Schabetsberger *et al.*, 2000). Capelin (*Mallotus villosus*) spawn along shore at night in the eastern Bering Sea during mid-May through late July, and during the rest of the year are found at depths of 20-90 m over seafloor depths of 90-125 m (Brodeur *et al.*, 1999; Naumenko 1996). Most dives by sea lions measured in our study were to < 50 m, but deeper diving also occurred (Fig. 3).

Unfortunately, data on seasonal, geographic and depth distributions of sea lion prey are not available for direct comparison with dive locations of our instrumented animals. However, it may be reasonable to assume that the distributions of some fish prey respond to changes in the physical environment. Associations with frontal features or specific oceanographic habitats have been identified for adult lactating sub-Antarctic fur seals (Georges *et al.*, 2000) and Antarctic fur seals (Guinet *et al.*, 2001; McCafferty *et al.*, 1998). Oceanographic features associated with Steller sea lion diving locations tracked seasonal changes in SST and primary productivity (Fig. 5). Use of Bering Sea off-shelf waters by juvenile Steller sea lions, and the tendency for immature sea lions to move with a northwesterly bearing during May was concurrent with a period of rapid changes in SST and chlorophyll *a* concentrations (Ladd *et al.*, 2005a). These movements could thus have been as a response of the juvenile (or its mother) to prey shifting in response to this greater productivity north of the Aleutian Islands. Though we found diving activity to vary with SST, temperature may have been less influential than physiological development. Sea surface temperatures increased rapidly during March-July (Fig. 5), a period corresponding to rapid increases in dive rate and TAD of 9-13 month olds (Fig. 4). There was not a

similarly strong relationship between SST and dive activity (Fig. 6). However, diving activity during offshore trips of three sea lions into the Bering Sea diving was related to SST (Tables 5 and 6), and off-shelf trips may be more appropriate for examining associations with oceanographic features at the spatial and temporal scales used in this study.

Off-shore trips may also be potentially associated with eddies that propagate from the Aleutian passes and are important frontal features of the Bering Sea basin and outer shelf (Stabeno *et al.*, 1999), with consequences for nutrient and biota mixing (Okkonen, 2001) and prey concentration (Springer *et al.*, 1996). Winter migrating adult male (Loughlin *et al.*, 1999) and adult female (Ream *et al.*, 2005) northern fur seals utilized surface currents in the North Pacific and Gulf of Alaska to facilitate travel, but also foraged in areas associated with eddies (Ream *et al.*, 2005).

Beyond associations with broad seasonal changes and some individual results, we did not detect strong environmental associations with changes in diving activity. The explanatory power of environmental variables on diving activity was high for some sea lions but not others in the regression analysis, and there were not consistent relationships between oceanographic features and diving activity among individuals. Similar to our study, McCafferty *et al.* (1998) found significant individual variation in accounting for dive activity, and Guinet *et al.* (2001) found more variation in diving activity was accounted for by environmental variables when examined on larger spatial scales (incorporating spatial trends that smoothed local variability). Sampling limitations and ecological factors may have independently or collectively contributed to this result in our study.

Associations could have been obscured due to disparate measurement scales of satellite imagery data and telemetry data, or to animal behavior. Because each location represented dive activity within a 6-h period to minimize pseudoreplication in testing for habitat associations, precise diving locations could not be resolved with this instrumentation. We found location accuracies varied, but were generally within 0.4-4.9 km. Using a single location to represent activity within a 6-h period could potentially represent diving activity within a maximum diameter of 13-45 km (7-24 nm) because surface swimming velocities for otariids range from 0.6-2.1 m s⁻¹ (Ponganis *et al.*, 1990; Rosen and Trites, 2002). If dive rate is inversely related to surface swimming speeds (Crocker *et al.*, 2001), the error radius was likely less than or at the lower end of that range. Satellite imagery of SST and chlorophyll concentration was resolved to 4.89 km² and averaged monthly. Thus, activity associated with a single location may have only broadly represented dive behavior associated with a spatial location and habitat feature. This combination of techniques did not provide the resolution to detect finer-scale associations such as might exist with tidally generated fronts, shown to be an important habitat feature for foraging seabirds in the Aleutian Islands (Hunt *et al.*, 1998; Ladd *et al.*, 2005b). Because of persistent cloud cover and extent of water column mixing in Aleutian passes (Ladd *et al.*, 2005a), satellite imagery was not optimal for detecting associations among diving activity and habitat type for nearshore divers, but was likely more appropriate for sea lions diving farther offshore.

Behavioral variability might also obscure otherwise significant relationships when pooled for analyses, and naive foragers may not have well-defined responses that vary significantly with habitat features. Similarly, associations would be obscured if diving

activity were not related to foraging, but rather in response to changing storm directions (suggested by Sease and York [2003] to explain changes in haul-out use) or predator avoidance. Satellite depth recorders deployed on immature sea lions thus provide data for foraging trips, relocations, and activity while a pup is awaiting mother's return. Without other data that determine foraging activity directly, foraging must be inferred or assumed from behavioral data and it is difficult to interpret whether movements and habitat use reflect maternal or juvenile responses to prey availability or other factors. The approach used in this study was thus adequate to examine general associations between diving location or activity and bathymetric and oceanographic features. Additional modeling could be undertaken to examine habitat selection, presuming appropriate assumptions are made regarding accessibility of habitats. Relationships with nearshore oceanographic features that may be related to prey abundance will require sampling at finer scales than were available for this study.

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LITERATURE CITED

- Alverson, D.L. (1992) A review of commercial fisheries and the Steller sea lion *Eumetopias jubatus*: the conflict arena. *Rev. Aquat. Sci.* **63**: 203-256.
- Bickham, J.W., Patton, J.C. and Loughlin, T.R. (1996) High variability for control-region sequences in a marine mammal: implications for conservation and biogeography of Steller sea lions (*Eumetopias jubatus*). *J. Mammal.* **77**: 95-108.
- Boyd, I.L. (1998) Time and energy constraints in pinniped lactation. *Am. Nat.* **152**: 717-728.
- Brodeur, R.D., Wilson, M.T. and Walters, G.E. (1999) Forage fishes in the Bering Sea: distribution, species associations, and biomass trends. In: *Dynamics of the Bering Sea*. T.R. Loughlin and K. Ohtani (eds) Fairbanks, AK: Univ. Alaska Sea Grant Program, Rep. 99-06, pp. 509-536.
- Calkins, D.G. and Pitcher, K.W. (1982) Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. In: *Environmental Assessment of the Alaskan Continental Shelf. Final Reports* **19**: 455-546.
- Call, K.A. and Loughlin, T.R. (2005) An ecological classification of Alaskan Steller sea lion (*Eumetopias jubatus*) rookeries. *Fish. Oceanogr.*: this issue.
- Crocker, D.E., Gales, N.J. and Costa, D.P. (2001) Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *J. Zool.* **254**: 267-277.

Fancy, S.G., Pank, L.F., Douglas, D.C., Curby, C.H., Garner, G.W., Amstrup, S.C. and Regelin, W.L. (1988) Satellite telemetry: a new tool for wildlife research and management. *U.S. Fish and Wildl. Serv. Resour. Publ.* **172**: 154pp.

Frost, K.J., Simpkins, M.A. and Lowry, L.F. (2001) Diving behavior of subadult and adult harbor seals in Prince William Sound, Alaska. *Mar. Mammal Sci.* **17**: 813-834.

Georges, J., Bonadonna, F. and Guinet, C. (2000) Foraging habitat and diving activity of lactating Subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Mar. Ecol. Prog. Ser.* **196**: 291-304.

Guinet, C., Dubroca, L., Lea, M.A., Goldsworthy, S., Cherel, Y., Duhamel, G., Bonadonna, F. and Donnay, J. (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach to using geographic information systems. *Mar. Ecol. Prog. Ser.* **219**: 251-264.

Hastings, K.K., Frost, K.J., Simpkins, M.A., Pendleton, G.W., Swain, U.G. and Small, R.J. (2004) Regional differences in diving behavior of harbor seals in the Gulf of Alaska. *Can. J. Zool.* **82**: 1755-1773.

Heath, R.B., Calkins, D., McAllister, D., Taylor, W. and Spraker, T. (1996) Telazol and isoflurane field anesthesia in free-ranging Steller's sea lions (*Eumetopias jubatus*). *J. Zoo Wildl. Med.* **27**: 35-43.

Hunt, Jr., G.L., Russell, R.W., Coyle, K.O., and Weingartner, T. (1998) Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Mar. Ecol. Prog. Ser.* **167**: 241-259.

Keating, K.A. (1994) An alternative index of satellite telemetry location error. *J. Wildl. Manage.* **58**: 414-421.

Ladd, C., Hunt Jr., G., Mordy, C., Salo, S. and Stabeno, P. (2005a) Marine environment of the central and eastern Aleutian Islands: physical mechanisms, nutrient availability and primary production. *Fish. Oceanogr.*: this issue.

Ladd, C., Jahncke, J., Hunt, Jr., G.L., Coyle, K.O. and Stabeno, P.J. (2005b) Frontal structure and its relationships to biology and seabirds. *Fish. Oceanogr.*: this issue.

Lea, M.-A. and Dubroca, L. (2003) Fine-scale linkages between the diving behavior of Antarctic fur seals and oceanographic features in the southern Indian Ocean. *ICES J. Mar. Sci.* **60**: 990-1002.

Lee, P.C., Majluf, P. and Gordon, I.J. (1991) Growth, weaning and maternal investment from a comparative perspective. *J. Zool.* **225**: 99-114.

Logerwell, E.A., Aydin, K., Barbeaux, S., Brown, E., Connors, M.E., Lowe, S., Orr, J., Ortiz, I., Reuter, R., Schaufler, L. and Spencer, P. (2005) Geographic patterns in the demersal ichthyofauna of the Aleutian Islands shelf. *Fish. Oceanogr.*: this issue.

Loughlin, T. R. (1997) Using the phylogeographic method to identify Steller sea lion stocks. In: *Molecular Genetics of Marine Mammals*. A. Dizon, S.J. Chivers, and W. F. Perrin (eds) Lawrence, KS: Soc. Mar. Mammal. Spec. Publ. 3, pp. 159-171.

Loughlin, T.R. and Merrick, R.L. (1989) Comparison of commercial harvest of walleye pollock and northern sea lion abundance in the Bering Sea and Gulf of Alaska. In:

Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. Fairbanks, AK: Alaska Sea Grant Program, Rep. 89-01, pp. 679-700.

Loughlin, T.R. and York, A.E. (2000) An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. *Mar. Fish. Rev.* **62**: 40-45.

Loughlin, T.R., Perlov, A.S. and Vladirimov, V.A. (1992) Range-wide survey and estimation of total abundance of Steller sea lions in 1989. *Mar. Mammal Sci.* **8**: 220-239.

Loughlin, T.R., Ingraham Jr., W.J., Baba, N. and B.W. Robson. (1999) Use of a surface-current model and satellite telemetry to assess marine mammal movements in the Bering Sea. In: *Dynamics of the Bering Sea*. T.R. Loughlin and K. Ohtani (eds) Fairbanks, AK: Univ. Alaska Sea Grant Program, Rep. 99-03, pp. 615-630.

Loughlin, T.R., Sterling, J.T., Merrick, R.L., Sease, J.L. and York, A.E. (2003) Immature Steller sea lion diving behavior. *Fish. Bull.* **101**: 566-582.

McCafferty, D.J., Boyd, I.L., Walker, T.R. and Taylor, R.I. (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. *Mar. Ecol. Prog. Ser.* **166**: 285-299.

McAllister, D.C., Calkins, D.G. and Pitcher, K.W. (2001) Underwater capture of juvenile Steller sea lions with SCUBA: a narrated video presentation. In: *Cold Water Diving for Science*. S.J. Jewett (ed.) Fairbanks: Univ. Alaska Sea Grant Program, Rep. 01-06, pp. 53-55.

Merrick, R.L., Brown, R., Calkins, D.G. and Loughlin, T.R. (1995) A comparison of Steller sea lion, *Eumetopias jubatus*, pup masses between rookeries with increasing and decreasing populations. *Fish. Bull.* **93**: 753-758.

Merrick, R.L., Chumbley, M.K. and Byrd, G.V. (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. *Can. J. Fish. Aquat. Sci.* **54**: 1342-1348.

Merrick, R.L. and Loughlin, T.R. (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Can. J. Zool.* **75**: 776-786.

Naumenko, E.A. (1996) Distribution, biological condition, and abundance of capelin (*Mallotus villosus socialis*) in the Bering Sea. In: *Ecology of the Bering Sea: A Review of Russian Literature*. O.A. Mathisen and K.O. Coyle (eds) Fairbanks: Univ. Alaska Sea Grant Program, Rep. 96-01, pp. 237-256.

Oftedal, O.T., Boness, D.J. and Tedman, R.A. (1987) The behavior, physiology, and anatomy of lactation in the Pinnipedia. *Curr. Mammal.* **1**: 175-245.

Okkonen, S.R. (2001) Altimeter observations of the Bering Slope Current eddy field. *J. Geophys. Res.* **106**: 2465-2746.

Pearcy, W.G. (1992) *Ocean Ecology of North Pacific Salmonids*. Seattle: University of Washington Press, 179pp.

Pitcher, K.W. and Calkins, D. (1981) Reproductive biology of Steller sea lions in the Gulf of Alaska. *J. Mammal.* **62**: 599-605.

Pitcher K.W., Burkanov V.N., Calkins D.G., Le Boeuf B.J., Mamaev E.G., Merrick R.L. and Pendleton G.W. (2001) Spatial and temporal variation in the timing of births of Steller sea lions. *J. Mammal.* **82**: 1047-1053.

Ponganis, P.J., Ponganis, E.P., Ponganis, K.V., Kooyman, G.L., Gentry, R.L. and Trillmich, F. (1990) Swimming velocities in otariids. *Can. J. Zool.* **68**: 2105-2112.

Porter, B. (1997) Winter ecology of Steller sea lions (*Eumetopias jubatus*) in Alaska. MS thesis, University of British Columbia, 84pp.

Raum-Suryan, K.L., Rehberg, M.J., Pendleton, G.W., Pitcher, K.W. and Gelatt, T.S. (2004) Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska. *Mar. Mammal Sci.* **20**: 823-850.

Ream, R.R., Sterling, J.T. and Loughlin, T.R. (2005) Oceanographic features related to northern fur seal migratory movements. *Deep-Sea Res. Pt. II.* **52**: 823-843.

Richmond, J.P. (2004) Ontogeny of total body oxygen stores and aerobic dive potential in the Steller sea lion (*Eumetopias jubatus*). MS thesis, University of Alaska, 114pp.

Rosen, D.A.S. and Trites, A.W. (2002) Cost of transport in Steller sea lions, *Eumetopias jubatus*. *Mar. Mammal Sci.* **18**: 513-524.

Schabetsberger, R., Brodeur, R.D., Cianelli, L., Napp, J.M. and Swartzman, G.L. (2000) Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea. *ICES J. Mar. Sci.* **57**: 1283-1295.

Sease, J.L. and Gudmundson, C.J. (2002) Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) from the western stock in Alaska, June and July 2001 and 2002.

NOAA Tech. Memo. NMFS-AFSC-131: 45pp.

Sease, J.L. and York, A.E. (2003) Seasonal distribution of Steller's sea lions at rookeries and haul-out sites in Alaska. *Mar. Mammal Sci.* **19**: 745-763.

Sinclair, E.H. and Stabeno, P.J. (2002) Mesopelagic nekton and associated physics of the southeastern Bering Sea. *Deep-Sea Res. Pt. II* **49**: 6127-6145.

Sinclair, E.H. and Zeppelin, T.K. (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *J. Mammal.* **83**: 973-990.

Springer, A.M., McRoy, C.P. and Flint, M.V. (1996) The Bering Sea green belt: shelf-edge processes and ecosystem production. *Fish. Oceanogr.* **5**: 250-223.

Stabeno, P.J. and Reed, R.K. (1994) Circulation in the Bering Sea basin observed by satellite-tracked drifters: 1986-1993. *J. Phys. Oceanogr.* **24**: 848-854.

Stabeno, P.J., Schumacher, J.D. and Ohtani, K. (1999) The physical oceanography of the Bering Sea. In: *Dynamics of the Bering Sea*. T.R. Loughlin and K. Ohtani (eds) Fairbanks, AK: Univ. Alaska Sea Grant Program, Rep. 99-06, pp. 1-28.

Stabeno, P.J., Reed, R.K. and Napp, J.M. (2002) Transport through Unimak Pass, Alaska. *Deep-Sea Res. Pt. II* **49**: 5919-5930.

- Trillmich, F. (1996) Parental investment in pinnipeds. In: *Parental Care: Evolution, Mechanisms, and Adaptive Significance. A Volume in Advances in the Study of Behavior, Vol. 25.* J.S. Rosenblatt and C.T. Snowdon (eds) San Diego Academic Press, pp. 533-577.
- Trites, A.W. and Porter, B.T. (2002) Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. *J. Zool.* **256**: 547-556.
- Wespestad, V.G. (1991) Pacific herring population dynamics, early life history, and recruitment variation relative to eastern Bering Sea oceanographic factors. PhD thesis, University of Washington, 237pp.
- Yanagimoto, T., Nishimura, A., Mito, K., Takao, Y. and Williamson, N.J. (2002) Interannual changes of biological properties of walleye pollock *Theragra chalcogramma* in the central Bering Sea. *Prog. Oceanogr.* **55**: 195-208.
- York, A.E. (1994) The population dynamics of northern sea lions, 1975-1985. *Mar. Mammal Sci.* **10**: 38-51.
- York, A.E. and Holmes, E.E. (2003) Using age structure to detect impacts on threatened populations: a case study using Steller sea lions. *Conserv. Biol.* **17**: 1794-1806.
- York, A.E., Merrick, R.L. and Loughlin, T.R. (1996) An analysis of the Steller sea lion metapopulation in Alaska. In: *Metapopulations and Wildlife Conservation.* D.R. McCullough (ed.) Covelo: Island Press, pp. 259-292.
- Zar, J.H. (1984) *Biostatistical Analysis.* Englewood Cliffs: Prentice Hall, 718pp.

Table 1. Capture and deployment data for 30 immature Steller sea lions transmitting from the Aleutian Island archipelago west of 162° W longitude during 2000-2002.

ID	Sex	Mass (kg)	Age coverage (months)	Capture location	Region ¹	Capture date	Date of last transmission	Deployment period (days)
6295	f	87.0	9-11	Seguam	CAI	29-Feb-00	29-Apr-00	60
6296	f	85.8	9-11	Seguam	CAI	29-Feb-00	21-Apr-00	52
6297	f	76.2	9-11	Seguam	CAI	29-Feb-00	23-Apr-00	54
6298 ²	m	109.0	9-12	Seguam	CAI	29-Feb-00	11-Jun-00	103
6299	f	100.2	9-10	Aiktak	EAI	9-Mar-00	7-Apr-00	29
6300 ²	m	79.6	9-12	Aiktak	EAI	9-Mar-00	14-Jun-00	98
6303	m	132.0	21-23	Akutan	EAI	26-Feb-01	7-May-01	70
6304	f	101.2	9-11	Aiktak	EAI	1-Mar-01	28-Apr-01	58
6305	f	105.8	9-12	Ugamak	EAI	1-Mar-01	1-Jun-01	92
6306	f	102.8	21-22	Tigalda	EAI	3-Mar-01	24-Apr-01	52
6307	m	86.6	9-10	Tigalda	EAI	3-Mar-01	6-Apr-01	34
6308 ²	f	87.0	9-13	Aiktak	EAI	3-Mar-01	29-Jul-01	148
6309	f	107.0	9-11	Aiktak	EAI	3-Mar-01	19-May-01	77
6310 ²	f	99.4	9-12	Aiktak	EAI	3-Mar-01	1-Jul-01	120
6311	f	152.0	21-23	Akun	EAI	4-Mar-01	6-May-01	63
6312	f	116.0	9-11	Akun	EAI	4-Mar-01	30-Apr-01	57
6466	f	85.8	5-6	Ugamak	EAI	13-Nov-01	4-Jan-02	52
8238	f	83.8	5-7	Ugamak	EAI	13-Nov-01	24-Jan-02	72

8239	f	107.6	17-23	Aiktak	EAI	14-Nov-01	14-May-02	181
6475 ²	m	124.0	9-12	Aiktak	EAI	12-Mar-02	7-Jul-02	117
7469	m	94.6	9-12	Long Is.	CGOA	2-Mar-02	16-Jun-02	106
7481	f	102.0	9-10	Basalt	EAI	10-Mar-02	15-Apr-02	36
7482	f	71.8	9-11	Aiktak	EAI	11-Mar-02	10-May-02	60
7483 ²	m	81.8	9-12	Aiktak	EAI	11-Mar-02	4-Jul-02	115
7484	m	114.6	9-11	Aiktak	EAI	11-Mar-02	4-Jun-02	85
7485 ²	m	122.8	9-13	Aiktak	EAI	11-Mar-02	5-Aug-02	147
7486	m	127.8	9-11	Aiktak	EAI	11-Mar-02	3-May-02	53
7487 ²	f	85.6	9-12	Aiktak	EAI	11-Mar-02	14-Jun-02	95
7488	m	135.0	9-11	Aiktak	EAI	12-Mar-02	31-May-02	80
7489	f	118.6	9-10	Aiktak	EAI	12-Mar-02	7-May-02	56

¹ CAI: central Aleutian Islands; EAI: eastern Aleutian Islands; CGOA: central Gulf of

Alaska.

² Sea lions included in stepwise multiple regression model.

Table 2. Monthly coverage (number of sea lions transmitting during at least half of month) of 30 immature Steller sea lions within the Aleutian Islands during 2000-2002.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2000			6	4	2	2						
2001			10	9	4	2	1				3	3
2002	2	1	12	12	7	5	1					
Total	2	1	28	25	15	9	2	0	0	0	3	3

Table 3. Percentages of locations (associated with diving to > 4m) stratified by distance to shore and seafloor depth in the Eastern and Central Aleutian Islands combined. Values are means ($\pm 1 SE$) of individually stratified proportions for 3 sea lions during November-January, 26 during February-April, and 9 during May-July.

Season	Seafloor depth (m)	Distance to shore (nm)			<i>Pooled</i>
		< 5	5-10	> 10	
<i>Nov-Jan</i>	< 50	63.4 (1.6)	0.9 (0.9)	0.0 (0.0)	<i>64.3 (1.3)</i>
	50-100	32.3 (3.6)	1.7 (1.7)	0.9 (0.9)	<i>34.9 (1.5)</i>
	100-150	0.9 (0.9)	0.0 (0.0)	0.0 (0.0)	<i>0.9 (0.9)</i>
	> 150	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	<i>0.0 (0.0)</i>
	<i>Pooled</i>	<i>96.6 (3.4)</i>	<i>2.6 (2.6)</i>	<i>0.9 (0.9)</i>	
<i>Feb-Apr</i>	< 50	68.7 (5.2)	0.7 (0.4)	0.0 (0.0)	<i>69.5 (5.3)</i>
	50-100	21.2 (3.7)	2.7 (1.0)	0.3 (0.2)	<i>24.3 (3.8)</i>
	100-150	4.8 (3.6)	1.0 (0.5)	0.0 (0.0)	<i>5.8 (3.6)</i>
	> 150	0.1 (0.1)	0.3 (0.3)	0.0 (0.0)	<i>0.4 (0.3)</i>
	<i>Pooled</i>	<i>94.9 (1.5)</i>	<i>4.8 (1.4)</i>	<i>0.3 (0.2)</i>	
<i>May-Jul</i>	< 50	63.3 (8.6)	0.2 (0.2)	0.0 (0.0)	<i>63.5 (8.6)</i>
	50-100	20.5 (6.5)	1.5 (0.6)	1.2 (1.2)	<i>23.2 (6.0)</i>
	100-150	0.5 (0.3)	0.7 (0.5)	1.0 (1.0)	<i>2.1 (1.4)</i>

	> 150	0.2 (0.2)	0.2 (0.2)	10.8 (8.2)	11.2 (8.2)
	<i>Pooled</i>	84.5 (8.4)	2.6 (1.0)	12.9 (8.3)	
<i>All seasons</i>		92.5 (2.3)	4.1 (1.0)	0.8 (0.5)	
	< 50				67.7 (4.1)
	50-100				24.8 (3.0)
	100-150				4.6 (2.5)
	> 150				2.9 (2.0)

Table 4. Bearing and distance of general movements between monthly mean locations for immature Steller sea lions tracked in the Eastern Aleutian Islands during 2000-2002^a.

Length of mean vector (r) and Rayleigh test for significance calculated following Zar (1984). CI for non-significant bearings is $\pm 90\%$.

	Bearing (\pm CI)	r	P	Distance (nm)	n
<i>All distances</i>					
Feb/Mar	47°	0.198	ns	8.4 (3.5) ^c	24
Apr	328°	0.115	ns	10.0 (3.0)	21
May	293° (33°) ^b	0.617	0.002	13.1 (4.6)	15
Jun/Jul	219°	0.393	ns	27.4 (9.4) ^c	12
<i>Distances > 10 nm</i>					
Feb/Mar	19°	0.567	ns		3
Apr	23°	0.425	ns		6
May	273° (20°) ^b	0.969	< 0.005		5
Jun/Jul	224°	0.504	ns		7

^a Sea lion #7469 was excluded because it had previously undertaken a westward movement from near Kodiak Island to Unimak Pass in May and stayed near that area in June.

^b CI approximated using methods of Zar (1984).

^c Significant difference among months (ANOVA $P=0.036$) owing to the Feb/Mar and Jun/Jul contrast (Bonferroni $P<0.05$).

Table 5. Results of stepwise multiple regression between number of dives or TAD to > 4 m (as z-score of square-root transformed number) with temporal and environmental variables for 8 immature Steller sea lions during March-June of 2000 ($n = 2$), 2001 ($n = 2$) and 2002 ($n = 4$). Significant independent factors, sign of the relationship, sample size, and adjusted R^2 and significance of model are presented by individual sea lion.

Animal ID	Significant factors	n	R^2	P
<i>Dive count</i>				
6298	Period (-), region (-)	17	0.456	0.006
6300		35	-	<i>ns</i>
6308	Period (-), region (-)	57	0.337	< 0.001
6310	Seafloor depth (+)	59	0.057	0.039
6475	Month (+), shore distance (-)	26	0.498	< 0.001
7483	Period (-), region (-)	95	0.131	0.001
7485	Period (-)	16	0.639	< 0.001
7487		17	-	<i>ns</i>
<i>Time at depth</i>				
6298	Period (-), month (+)	22	0.344	0.007
6300		37	-	<i>ns</i>
6308	Period (-), SST (+)	57	0.250	< 0.001
6310	Region (+), seafloor depth (+)	60	0.165	0.002
6475	Month (+), shore distance (-)	26	0.480	< 0.001
7483	Month (-), SST (+)	92	0.132	0.001
7485	Period (-), seafloor depth (-)	19	0.889	< 0.001

7487	Seafloor depth (+)	15	0.218	0.045
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Table 6. Results of stepwise multiple regression between dive focus or focal depth bin (as normal deviates) and temporal and environmental variables for 8 immature Steller sea lions during March-June of 2000 ($n = 2$), 2001 ($n = 2$) and 2002 ($n = 4$). Significant independent factors, sign of the relationship, sample size, and adjusted R^2 and significance of model are presented by individual sea lion.

Animal ID	Significant factors	n	R^2	P
<i>Dive focus</i>				
6298		25	-	<i>ns</i>
6300	SST (-), shore distance (-)	40	0.471	< 0.001
6308	Shore distance (-)	70	0.167	< 0.001
6310		68	-	<i>ns</i>
6475		30	-	<i>ns</i>
7483	Month (+), SST (-), shore distance (-)	104	0.244	< 0.001
7485	Period (+)	19	0.203	0.030
7487		18	-	<i>ns</i>
<i>Focal depth bin</i>				
6298	Month (-)	17	0.252	0.023
6300		35		
6308	Month (+), SST (-)	57	0.167	0.003
6310	Period (+), month (+), SST (-)	59	0.258	< 0.001
6475		26		
7483		95		
7485	Period (+), region (+)	16	0.520	0.003

7487		17		
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Figure 1. General map showing Aleutian Islands study area west of 162°W longitude, identifying capture locations (underscored), island landmarks and ocean currents (ACC: Alaska Coastal Current), and regions referred to in the text (CAI: Central Aleutian Islands; EAI: Eastern Aleutian Islands; WGOA: Western Gulf of Alaska; CGOA: Central Gulf of Alaska). Bathymetric contours indicate 100 m (light dashed) and 500 m (dark). Most tagging in the EAI occurred within the Krenitzen Island group, forming the western boundary of Unimak Pass.

Figure 2. Filtered locations (dots) of diving to > 4 m by 30 immature Steller sea lions west of 162°W longitude during 2000-2002 ($n = 1,151$ locations), grouped by season (November-January, February to April, and May-July). Isobaths are 100 m (light) and 500 m (dark). Dive locations in November-January are represented by the following animals: 6466, 8238, and 8239; in February-April by: 6295-6300, 6303, 6304-6312, 8239, 6475, 7469, and 7481-7489; and in May-July by: 6298, 6300, 6303, 6305, 6309, 6310, 6311, 8239, 6475, 7469, 7482, 7483, 7484, 7485, 7486, 7487, 7488, and 7489.

Figure 3. Mean ($\pm SD$) proportion of dives to > 4 m by depth bin for 30 immature Steller sea lions west of 162°W longitude during 2000-2002. Dive count data ($n = 143,139$) from both wet and dry satellite telemeter transmissions are included.

Figure 4. Relationships between mean ($\pm SE$) dive rate, TAD, mean dive depth, and dive focus by estimated age for 30 Steller sea lions diving to > 4 m west of

162°W longitude during 2000-2002. Sample sizes vary from $n = 5$ dives for 7-month olds to $n = 331$ dives for 8 and 9-month olds. Results are based on dives performed by the number of sea lions within each age category as shown in Table 2.

Figure 5. Mean ($\pm SE$) sea surface temperatures (top; $n = 29$ sea lions) and chlorophyll a concentrations (bottom; $n = 18$ sea lions) associated with locations of diving to > 4 m by juvenile Steller sea lions in the Aleutian Islands during 2000-2002. Sea surface temperatures and chlorophyll a concentrations were estimated from satellite imagery data.

Figure 6. Mean ($\pm SE$) dive activity indices (dive rate, median dive depth, dive focus and focal depth bin) associated with sea surface temperature ($n = 27$ sea lions) associated with locations of diving to > 4 m by juvenile Steller sea lions ≤ 8 months old in the Aleutian Islands during 2000-2002. Sea surface temperatures and chlorophyll a concentrations were estimated from satellite imagery data.