



Foraging effort of juvenile Steller sea lions *Eumetopias jubatus* with respect to heterogeneity of sea surface temperature

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ABSTRACT: Among many other factors, the decline of the western distinct population segment of Steller sea lions *Eumetopias jubatus* in Alaska (USA) has been attributed to changes in the distribution or abundance of prey due to the cumulative effects of fisheries and large-scale climate change. However, the depletion of localized prey resources due to small-scale environmental variability and perturbations may be impeding recovery, resulting in the need to understand how the environment currently affects this species on smaller spatial and temporal scales. The objective of this study, therefore, was to assess how Steller sea lions respond to changes in localized environmental features. Satellite-relayed data loggers were deployed on juvenile Steller sea lions ($n = 24$) from July 2002 to May 2004 in the Aleutian Islands and Gulf of Alaska. Weekly indices of foraging effort (mean and maximum trip duration, diving activity) of Steller sea lions were examined with respect to corresponding patterns of sea surface temperature (SST) data obtained from the moderate resolution imaging spectroradiometer. An assortment of landscape metrics was used to characterize the heterogeneity of frontal features derived from SST gradients because it has been suggested that Steller sea lions depend on prey patches associated with these features. Multivariate analyses indicated that fractal dimension and patch density of frontal features were significant factors for predicting different aspects of foraging effort ($p < 0.05$; $n = 6$ models). Overall, results suggested that aggregated frontal features associated with small-scale temperature gradients were probably conducive to foraging effort of Steller sea lions, but additional mechanisms should be investigated further.

KEY WORDS: *Eumetopias jubatus* · Environmental heterogeneity · Foraging effort · Fractal dimension · Frontal features · Gradients · Sea surface temperature · Steller sea lion

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INTRODUCTION

Over the past 30 yr, populations of Steller sea lions *Eumetopias jubatus* in western Alaska (USA) have declined by 80% (Braham et al. 1980, Loughlin 1998, Fritz et al. 2008). Decreased juvenile survival and reproductive rates have been implicated as proximate factors for the decline of the endangered, western distinct population segment (wDPS) of Steller sea lions

(York 1994, Merrick 1995, York et al. 1996, Holmes & York 2003, Holmes et al. 2007). Nutritional stress resulting from changes in distribution, abundance, or quality of prey due to commercial fisheries and large-scale oceanographic changes is among the ultimate factors proposed for explaining the decline (Merrick 1995, Loughlin 1998, Loughlin & York 2000, DeMaster & Atkinson 2002). Short-term environmental variability and local environmental perturbations have also

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been suggested as hypotheses for population decline (Pascual & Adkinson 1994, Merrick 1995, Benson & Trites 2002) or lack of recovery (Fritz & Hinckley 2005, Atkinson et al. 2008, NMFS 2008), resulting in the need to understand how the environment currently affects Steller sea lions at finer scales in local coastal areas (Trites et al. 2007).

Steller sea lions heavily utilize nearshore habitats (Merrick & Loughlin 1997, Loughlin et al. 2003, Raum-Suryan et al. 2004) by adopting a strategy of central place and multiple central place foraging to cope with the spatial and temporal distribution of localized prey resources (Raum-Suryan et al. 2004). Although the foraging behavior of juvenile Steller sea lions has been fairly well detailed (Merrick & Loughlin 1997, Loughlin et al. 2003, Raum-Suryan et al. 2004, Fadely et al. 2005, Pitcher et al. 2005, Call et al. 2007), few studies have assessed the effects of environmental features on foraging effort. Loughlin et al. (2003) satellite-tagged 25 juvenile Steller sea lions from 1994 to 2000 in Alaska and Washington and concluded that Steller sea lions have the foraging flexibility to take advantage of predictable behavioral traits of prey species and localized oceanographic conditions that enhance prey concentrations. Others have suggested that Steller sea lions are constrained by prey persistence (Gende & Sigler 2006) and changes in prey availability resulting from seasonal variability (Merrick & Loughlin 1997, Womble & Sigler 2006), and that they depend on the presence of large, dense prey patches associated with nearshore temperature gradients (Sinclair & Zeppelin 2002). Hence, further analyses of telemetry data are needed to understand relationships of foraging behaviors with environmental variability and spatial patterns of oceanographic structure, which ultimately affect the distribution or abundance of prey (Loughlin et al. 2003). For example, the oceanographic structure of water temperature likely influences prey distribution, which in turn affects foraging behavior and possibly fecundity or mortality of Steller sea lions (Pascual & Adkinson 1994).

Spatial and temporal heterogeneity of the environment have been empirically and conceptually challenging to ecologists because complex environments are difficult to describe quantitatively. Furthermore, ecologists have become increasingly aware of the importance of examining ecological processes at scales relevant to the organism and process under study (Turner et al. 1989, Wiens 1989). This is especially important in the marine environment, which is a highly dynamic system. However, with advances in geographic information systems (GIS) and remote sensing techniques, the spatial heterogeneity of the marine environment can be characterized over time by an assortment of patches and gradients (White & Brown

2003), which are considered the structural and functional components of landscapes (Cadenasso et al. 2003). Spatial patterns of ocean structure and heterogeneity can be quantified through time using an assortment of landscape metrics, which focus on the abundance (i.e. composition) and spatial arrangement or complexity (i.e. configuration) of patches (Gustafson 1998, McGarigal et al. 2002). The quantification of environmental heterogeneity using these metrics has become a common practice in the advancing field of landscape ecology, which is the study of landscape patterns, ecological processes that influence patterns, and effects of patterns on population persistence and animal movement (Hargis et al. 1997, Fahrig & Nuttle 2003, Lovett et al. 2003). Although landscape ecology has traditionally focused on ecological processes and spatial patterns in terrestrial ecosystems, the principles of this discipline can also be applied to aquatic systems (Wiens 2002).

If environmental heterogeneity is in part responsible for changing the abundance or distribution of prey for Steller sea lions on a localized scale, then changes in environmental features should be reflected in patterns of sea lion foraging behavior. The objective of this study, therefore, was to assess how Steller sea lions respond to changes in heterogeneity of the environment at spatial scales relevant to individual sea lion perception. More specifically, the foraging effort of Steller sea lions was examined with respect to an assortment of landscape metrics that were used to characterize spatial patterns of sea surface temperature (SST) gradients. We chose to work with SST as an environmental indicator because it has been hypothesized to affect Steller sea lions on multiple scales (Sinclair & Zeppelin 2002, Trites et al. 2007) and has been linked to food habits and population dynamics at regional scales (Call & Loughlin 2005, Lander et al. 2009). Additionally, SST allows for differentiating water mass structure (Boyd et al. 2001) and can be used to derive oceanographic frontal features, which we elaborate on in the methods.

MATERIALS AND METHODS

Juvenile Steller sea lions were opportunistically captured at rookeries or haulout sites within the Gulf of Alaska and Aleutian Islands using hoop nets or dive captures (McAllister et al. 2001; Table 1, Fig. 1). Animals were either sedated with valium (1.1 to 2.0 ml) and manually restrained or anesthetized (Heath et al. 1997). Sea lions were weighed to the nearest 0.5 kg, and standard length and axial girth were measured to the nearest 1.0 cm. Measurements of tooth size (upper canine), body size, and time of

Table 1. *Eumetopias jubatus*. Capture location, including latitude, longitude (decimal degrees), region, and date of capture, date of last transmission for satellite transmitters, number of days tracked, sex, age at capture, and study area for juvenile Steller sea lions, as indicated by their identification (ID) number. WAI: western Aleutian Islands, CGA: central Gulf of Alaska, EAI: eastern Aleutian Islands, CAI: central Aleutian Islands, M: male, F: female. Dates given as mo/d/yr. Data for 3 individuals were discarded because of sensor failure (nos. 8245 and 9928) or limited data (no. 9929)

ID	Location	Latitude (°N)	Longitude (°E)	Region	Date of capture	Date of last transmission	No. of days tracked	Sex	Age (mo)	Study area (km ²)
7820	Buldir	52.340	175.900	WAI	07/03/02	08/13/02	41	M	12	35248.2
7821	Attu	52.918	172.461	WAI	07/05/02	08/24/02	50	F	12	10834.2
7822	Attu	52.918	172.461	WAI	07/05/02	07/20/02	15	F	12	14400.8
8245	Long Island	57.778	-152.416	CGA	02/27/03	03/06/03	7	F	9	–
8250	Aiktak	54.183	-164.852	EAI	03/05/03	04/19/03	45	F	21	2869.6
8252	Aiktak	54.183	-164.852	EAI	03/07/03	03/26/03	19	F	21	2452.2
9922	Tigalda Rocks	54.139	-164.978	EAI	11/10/03	12/14/03	34	F	5	4130.6
9923	Tigalda Rocks	54.139	-164.978	EAI	11/10/03	11/22/03	12	F	5	3744.3
9924	Tigalda Rocks	54.139	-164.978	EAI	11/10/03	01/03/04	54	F	5	1808.4
9925	Two Headed Isl.	56.897	-153.569	CGA	11/16/03	02/12/04	88	M	5	2869.6
9926	Two Headed Isl.	56.897	-153.569	CGA	11/16/03	12/26/03	40	F	5	2452.2
9927	Two Headed Isl.	56.897	-153.569	CGA	11/16/03	01/11/04	56	M	17	4130.6
9928	Two Headed Isl.	56.897	-153.569	CGA	11/16/03	12/22/03	36	M	5	–
9929	Two Headed Isl.	56.897	-153.569	CGA	11/16/03	11/22/03	6	M	5	–
10006 ^a	Two Headed Isl.	56.897	-153.569	CGA	11/17/03	01/02/04	46	M	5	2154.8
9930	Long Island	57.781	-152.278	CGA	11/18/03	05/17/04	181	F	29	24891.5
10007	Kagalaska	51.866	-176.340	CAI	05/06/04	07/07/04	62	M	11	12260.9
10008	Kagalaska	51.865	-176.340	CAI	05/07/04	07/20/04	74	M	11	5492.6
10009	Silak Island	51.865	-176.340	CAI	05/07/04	07/23/04	77	M	11	4634.8
10010	Silak Island	51.865	-176.340	CAI	05/07/04	07/31/04	85	M	11	154125.8
10011	Silak Island	51.865	-176.340	CAI	05/07/04	08/02/04	87	M	11	9178.5
10012	Little Tanaga Isl.	51.823	-176.340	CAI	05/16/04	06/22/04	37	F	23	7957.7
10013	Billingshead	54.290	-165.580	EAI	05/19/04	07/01/04	43	M	11	32665.1
10014	Akun Island	54.290	-165.580	EAI	05/19/04	06/27/04	39	M	35	44530.7

^aThe other 2 study areas for this individual are described in the text (see 'Results')

year were used to infer ages of all sea lions (King et al. 2007). Satellite relayed data loggers (SRDLs; Sea Mammal Research Unit [SMRU], Gatty Marine Laboratory, University of St. Andrews, Scotland) were attached to the dorsal pelage of each sea lion using Five Minute Epoxy (Devcon).

In addition to providing location data, the SRDLs were programmed to maintain a 3-state model of animal activity, determined from time interactions and surface and depth sensors. Information on behavior was processed and compressed into records of behavioral states including time spent on shore (i.e. hauled out), extended surface periods, and dive cycles. Sea lions were considered hauled out when on shore (dry) for more than 6 min, whereas surface periods were defined as the time at sea (wet) above a defined dive threshold (<6 m) for more than 6 min. Dives were defined as being >6 m in depth and >8 s in duration. Due to bandwidth restrictions, dives were sampled at intervals of 4 s, stored in memory, randomly sampled, and transmitted in bouts of 2 or 7 to ensure they were a representative sample of the time spent at sea (Fedak et al. 2002). Each day, temperature profiles were also collected every 2 h during the deepest dive.

Haulout, surface, and dive records reported by the SRDLs contained the start and end times of unbroken periods spent in each state of activity. SRDLs also collated summary statistics on the proportion of time spent in each of the 3 states for six 4 h periods d⁻¹ (period 1 = 0:00–3:59 h, period 2 = 4:00–7:59 h, period 3 = 8:00–11:59 h, period 4 = 12:00–15:59 h, period 5 = 16:00–19:59 h, period 6 = 20:00–23:59 h Greenwich Mean Time, GMT). Daily locations and behavioral data from SRDLs were obtained through the Service Argos system (Argos 1996) and decoded in a marine mammal behavior visualization system (MAMVIS; Fedak et al. 1996) by the SMRU. All data were filtered using a swim speed of 2 m s⁻¹ with the algorithm described by McConnell et al. (1992), and time was used as a means to interpolate the position of dives along a direct line between successive locations.

Standard mapped images of SST (level 3, weekly composites, 4.6 km resolution) collected by the moderate resolution imaging spectroradiometer (MODIS) instrument aboard NASA's Aqua satellite were obtained from the Ocean Color Discipline Processing System (Campbell et al. 1995). Windows Image Manager (6.2; Wimsoft) was used to clip a northern sub-

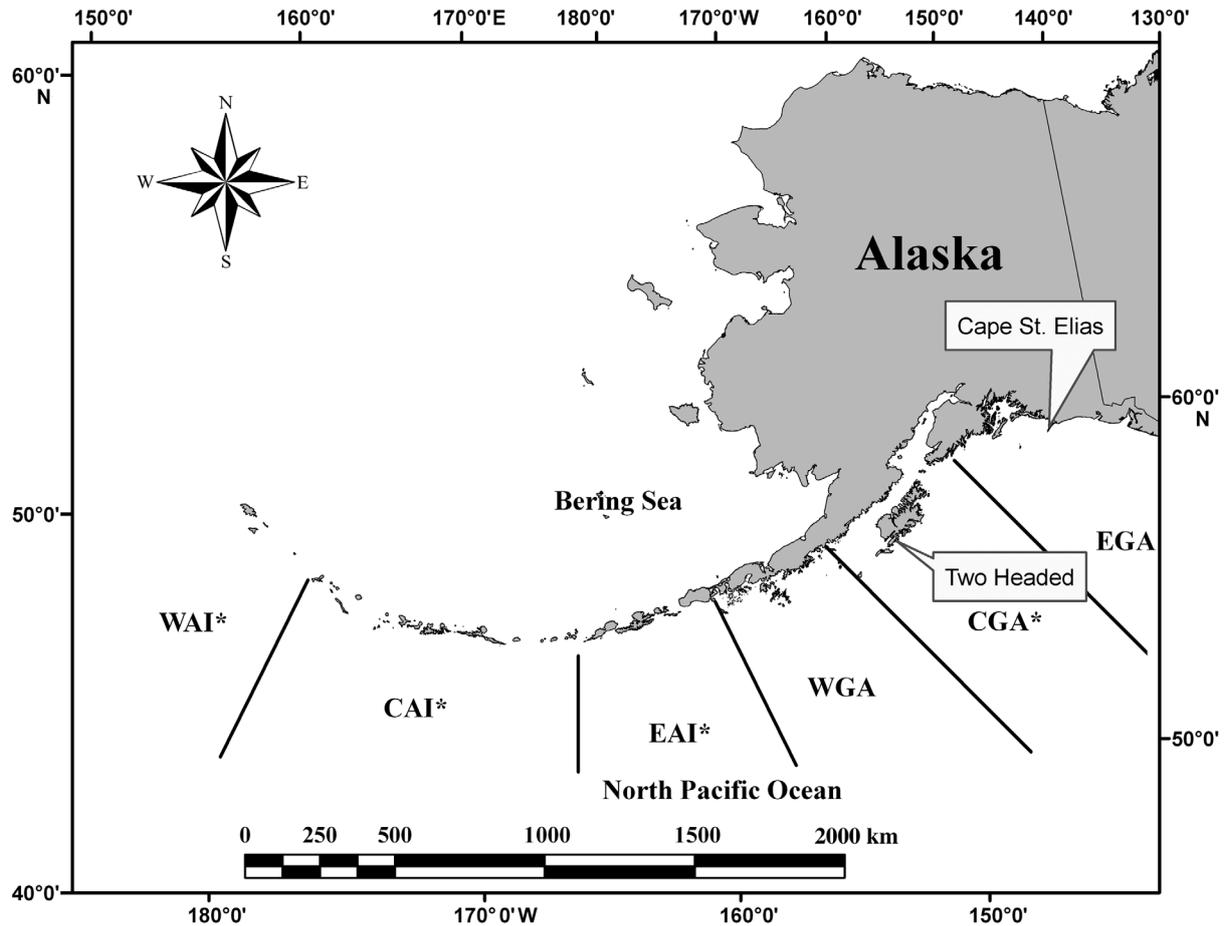


Fig. 1. *Eumetopias jubatus*. Geographical regions in Alaska comprising the western distinct population segment (wDPS) of Steller sea lions. Asterisks (*) indicate regions where sea lions ($n = 24$) were captured. Regions include the western Aleutian Islands (WAI), central Aleutian Islands (CAI), Eastern Aleutian Islands (EAI), western Gulf of Alaska (WGA), central Gulf of Alaska (CGA), and eastern Gulf of Alaska (EGA)

polar region (including Alaska) from all global remote sensing images, and ENVI (4.0; ITT Visual Information Solutions) was used to define the datum (i.e. NAD83). ArcInfo was used to convert all remote sensing data to raster grids and project them to an Albers equal-area conic projection defined for the state of Alaska, USA (ArcGIS 9.0, ESRI). SST data for the week of 28 July to 4 August 2002 were not available for analyses.

With the exception of 1 individual (no. 10006), 1 study area was devised for each individual by plotting all data collected for the duration of instrument deployment. A minimum convex polygon (MCP) constituting a simple home range was superimposed on the telemetry data (Hawths Analysis tools extension, ArcGIS) for each individual and buffered by 15 km to alleviate edge effects and to account for error of satellite telemetry positions, which ranges from 0.4 to 17.4 km in areas of Alaska (Fadely et al. 2005). Each buffered MCP was then enclosed by a rectangular area that totally covered the geometry of the polygon (Fig. 2). Study areas

were deemed the 'area of influence' for each individual assuming these represented individual perception. Weekly SST grids were then clipped to each individual study area. The same methods were used to devise 3 study areas representing habitat use before, during, and after a trip conducted by sea lion no. 10006, a 5 mo old pup that dispersed ~615 km from Two Headed Island to Cape St. Elias 11 d after being tagged (Table 1, Fig. 1). The methods were modified for this individual because we assumed it followed its mother on that excursion and the entire Gulf of Alaska was not influencing its foraging effort.

Data classification. To examine environmental heterogeneity for this study, weekly categorical maps comprising SST patches and gradients were derived for categorical map analysis. Frontal features, which are hydrographic features generally defined as an interface between 2 dissimilar water masses and often characterized by a steep temperature gradient (Etnoyer et al. 2006), were defined as cells where the

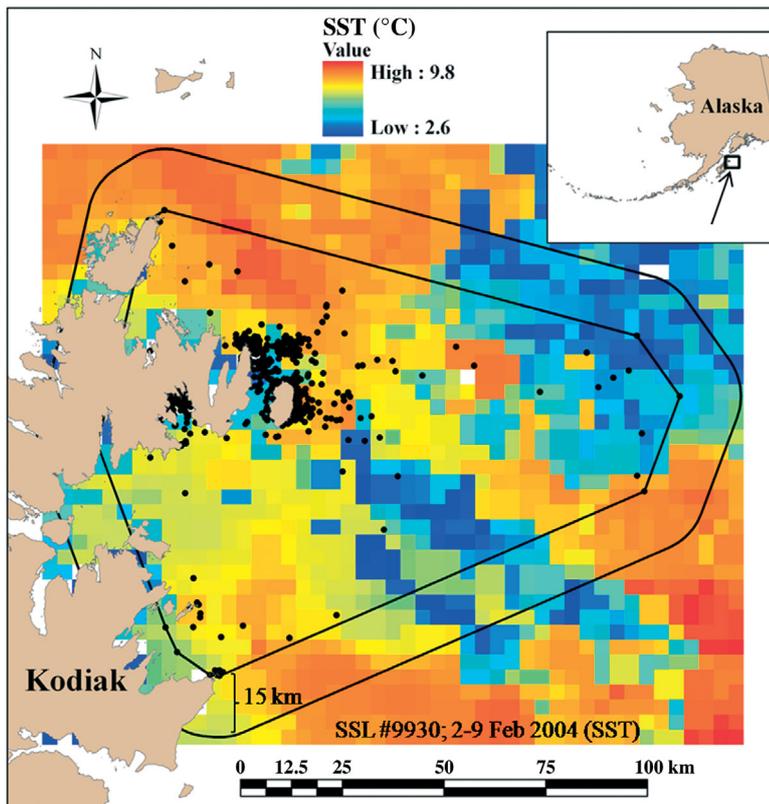


Fig. 2. *Eumetopias jubatus*. An example illustrating how study areas were devised for 21 juvenile Steller sea lions. A minimum convex polygon was superimposed on pooled, filtered telemetry data for each individual, buffered by 15 km, and then enclosed by a rectangular area that totally covered the geometry of the polygon. Weekly sea surface temperature grids were then clipped to each individual study area

SST gradient was greater or less than 1 SD from the mean gradient of the study area for each individual (Moore et al. 2002); hence, this classification scheme resulted in 3 data classes (Fig. 3). To create gradients, defined as a change in a property across a defined spatial extent representing a pattern of continuous variation of a single focal variable (Lovett et al. 2003, White & Brown 2003), the slope function (Spatial Analyst extension, ArcGIS 9.1) was used to calculate the rate (degrees) of maximum change in SST from each data cell and its 8 neighbors for each weekly grid per individual.

After data classification, FRAGSTATS 3.3 (McGarigal & Marks 1995) was used to determine the number of patches corresponding to each data class, where a patch was defined as a contiguous group of cells of the same mapped category using an 8-neighbor rule (i.e. 2 grid cells of the same cover type are considered part of the same patch if they are adjacent or diagonal neighbors; Forman & Godron 1986, Turner et al. 2001). Three landscape metrics, which measure the aggregate properties of the entire grid mosaic, were used to characterize heterogeneity of SST for each remote sensing week, including patch density (PD), Simpson's diversity index (SIDI), and area-weighted mean

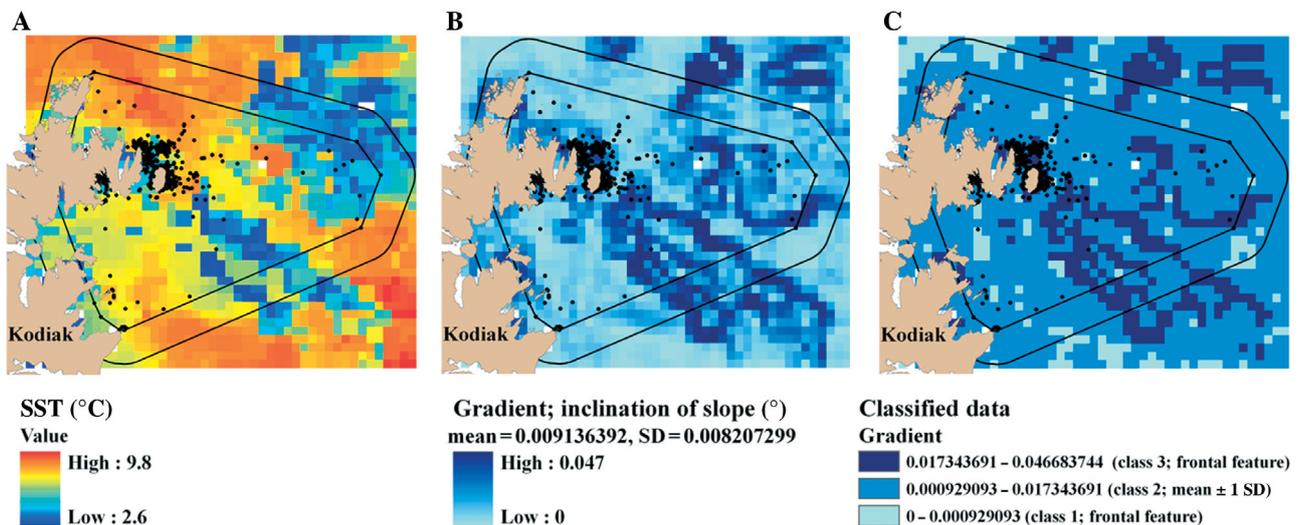


Fig. 3. *Eumetopias jubatus*. The methodology used for classifying (A) weekly sea surface temperature (SST) data entailed (B) deriving SST gradients by calculating the rate of maximum change in SST from each data cell and its 8 neighbors. (C) Frontal features were then defined as cells where the SST gradient was greater (class 3) or less than (class 1) 1 SD from the mean gradient of the study area for each individual

fractal dimension (AMFD). We chose to examine PD and SIDI of SST because Lander et al. (2009) found that these covariates may be linked to regional population trends of Steller sea lions, whereas AMFD provides a measure of complexity.

PD (total number of patches area⁻¹) was computed for individual study areas and reported as number of patches per 100 ha. The AMFD was calculated using the following metric:

$$\text{AMFD} = \sum_{i=1}^n \left\{ \left[\frac{2 \ln(0.25 p_i)}{\ln a_i} \right] \left(\frac{a_i}{\sum_{i=1}^n a_i} \right) \right\} \quad (1)$$

where n = total number of patches, p_i = perimeter (m) of patch i , and a_i = area (m²) of patch i . This metric increases as shape complexity of patches within the landscape mosaic increases and is advantageous because it represents complexity (or departure from Euclidean geometry) across a range of spatial scales (i.e. patches). This metric was weighted because small maps are more prone to effects caused by map borders; a greater proportion of patches are truncated at the edges of the map (Hargis et al. 1997). Additionally, SIDI was calculated for each week using the following metric:

$$\text{SIDI} = 1 - \sum_{i=1}^c P_i^2 \quad (2)$$

where P_i = the proportion of the landscape occupied by class type i , and c = the number of classes present. SIDI represents the probability that any 2 pixels selected at random would be different patch types (McGarigal et al. 2002), and SIDI = 0 when the area is dominated by 1 patch (no diversity) and approaches 1 as the number of different patch types increases and the proportional distribution of area among patch types becomes more even. Relative to other diversity indices (e.g. Shannon's diversity index), SIDI is less sensitive to the presence of rare patch/group types, so more weight is placed on common patch/group types. This characteristic coupled with a fairly consistent number of map classes (i.e. richness) across regions enabled us to avoid problems associated with having study areas of different sizes.

Four class metrics were computed only for patches corresponding to map classes representing frontal features to further elucidate how these specific patches influenced the foraging effort of sea lions. In addition to PD and AMFD, area-weighted mean class area (AMCA) was calculated using the following metric:

$$\text{AMCA} = \frac{\sum_{j=1}^n a_{ij} \left(\frac{a_{ij}}{\sum_{j=1}^n a_{ij}} \right)}{10000} \quad (3)$$

where a_{ij} = area (m²) of patch ij and n = number of patches corresponding to frontal features. The metric is divided by 10 000 to convert to ha. Additionally, the percentage of landscape (PLAND) comprising these classes was also calculated (Σ area of each designated class patch/area \times 100). This estimate approaches 100 as the entire image becomes composed of a single patch (McGarigal et al. 2002).

Statistical analysis. Trip durations for individual sea lions were calculated using the departure and arrival times for trips at sea provided in the haulout records. Mean trip duration and percentage of time spent diving for each sea lion were calculated for each remote sensing week. Trips that straddled 2 weeks were assigned to the week containing the greater proportion of the trip. Maximum trip duration wk⁻¹ was also examined for each individual. All partial weeks were used in analyses.

Mean and maximum trip duration wk⁻¹ were log-transformed after conducting Kolmogorov-Smirnov tests for normality (SPSS 13.0) and examining histograms and q-q plots of the response variables (R 2.4.1, R Foundation for Statistical Computing). Generalized linear models (GLMs) with a Gaussian error, identity link, and first-order autoregressive correlation structure were used to examine mean and maximum trip duration wk⁻¹, and percentage of time spent diving wk⁻¹ with respect to the covariates region, age (at capture), and environmental metrics described above (geepack 1.0-10, R 2.4.1; Liang & Zeger 1986, Zeger & Liang 1986). Individual sea lion was used as the grouping variable, and the central Aleutian Islands (CAI) region was used as the control. These models accounted for longitudinal data, repeated measures, and correlated responses within each sea lion for the response variables, and possible time-dependent covariates. This approach is advantageous because it accounts for serial correlation in the response, is robust to deviations from normality, and employs a quasi-likelihood approach to provide generalized estimating equations (GEE; Yan & Fine 2004, Halekoh et al. 2006).

Sex was not examined as a predictor variable because preliminary data analyses indicated that the response variables did not differ between males and females. Year or season also were not examined due to paucity of data and because previous studies indicated that year was not an important factor for predicting trip duration for Steller sea lions (Call et al. 2007). Optimal models were developed by using a backward stepwise elimination procedure to remove non-significant terms one at a time based on the significance levels of Wald test statistics ($p \leq 0.15$ for model retention, $p \leq 0.05$ for significance). Separate

analyses were conducted for each response variable for the 2 different groups of metrics (i.e. landscape and class metrics; $n = 6$ models). Lastly, to assess the appropriateness of final models, q-q plots and residual plots were examined (R 2.4.1).

RESULTS

From 3 July 2002 to 19 May 2004, 24 juvenile Steller sea lions (5 to 35 mo old) were captured at rookeries or haulout sites within the western ($n = 3$), central ($n = 6$), and eastern ($n = 7$) Aleutian Islands, and the central Gulf of Alaska ($n = 8$; Fig. 1, Table 1). Data for 3 individuals were discarded because of sensor failure (nos. 8245 and 9928) or limited data (no. 9929). Instrument deployment for the remaining 21 sea lions lasted from 12 to 181 d. Study areas for individual sea lions ranged from 1808.4 to 154 125.8 km² (Table 1). The 3 study areas representing habitat use before, during, and after the trip conducted by sea lion no. 10006 were 2154.8 km², 216 828.9 km², and 5039.4 km², respectively.

Trip durations

Overall, the duration of trips ($n = 1475$) for all individuals ($n = 21$) ranged from 0.1 to 177.1 h (mean \pm SD = 8.6 ± 14.8 h). Average trip duration ind.⁻¹ ranged from 3.0 to 28.6 h, whereas maximum trip duration ranged from 14.1 to 177.1 h (68.4 ± 47.8 h; Table 2). Mean trip duration wk⁻¹ ranged from 0.9 to 117.6 h (12.3 ± 14.5 h, $n = 151$ wk, range = 2–23 wk ind.⁻¹).

Activity patterns

Summary statistics for the 3 behavioral states were obtained for 896 complete records (full 24 h periods; range = 7–124 records ind.⁻¹, $n = 21$ ind.). On a weekly basis, sea lions spent an average \pm SD of $55.7 \pm 18.3\%$ (range = 0.0–98.3%) of their time on shore, whereas $44.3 \pm 18.3\%$ was spent at sea (range = 1.7–100.0%; $n = 145$ wk, range = 2–23 wk ind.⁻¹). While at sea, sea lions spent an average of $11.2 \pm 6.8\%$ (range = 0.0–28.4%) of their time diving and $33.1 \pm 14.2\%$ (range = 1.5–83.1%) of their time at the surface. However, these activities varied considerably within and among individuals (Table 3).

Time of day during which most diving activity occurred varied among individuals, but on average, sea lions spent a greater proportion of time diving at night during period 3 (Table 4), followed by crepuscular periods (periods 2 and 4; Table 4). A greater propor-

Table 2. *Eumetopias jubatus*. Steller sea lion identification (ID), sample size (number of trips at sea), and mean \pm SD and range (minimum and maximum) of trip duration (h) for individual deployment periods

ID	No. of trips	Trip duration (h)			
		Mean	SD	Min.	Max.
7820	51	8.4	15.5	0.1	105.8
7821	52	14.1	13.2	0.1	48.3
7822	29	4.2	10.2	0.1	51.0
8250	81	4.6	4.5	0.1	23.6
8252	28	4.6	3.8	0.1	14.1
9922	73	3.0	6.6	0.1	50.6
9923	14	11.2	25.5	0.1	98.2
9924	71	5.7	8.0	0.1	53.7
9925	90	3.4	3.9	0.1	20.8
9926	48	5.3	5.1	0.2	29.0
9927	29	28.6	42.5	0.1	177.1
10006	90	3.7	11.5	0.1	109.7
9930	145	19.4	25.3	0.1	151.7
10007	84	6.0	6.2	0.1	31.5
10008	108	7.5	6.5	0.1	36.5
10009	95	8.7	7.4	0.1	46.5
10010	123	8.1	17.7	0.1	156.3
10011	87	13.0	9.7	0.1	47.3
10012	62	6.0	6.0	0.1	35.0
10013	60	8.5	11.0	0.1	54.3
10014	55	8.4	14.8	0.1	94.6

tion of time spent diving consistently occurred at night for sea lions captured in the CAI and eastern Aleutian Islands (EAI) during May 2004.

From a regional perspective, sea lions from the western Aleutian Islands (WAI) spent an average \pm SD of $47.1 \pm 17.9\%$ of the day on shore, $7.3 \pm 3.4\%$ diving, and $45.6 \pm 16.9\%$ at the surface (traveling, resting, or diving to depths < 6 m). Sea lions from the CAI spent an average of $57.0 \pm 13.0\%$ of the day on shore, $13.0 \pm 5.4\%$ diving, and $30.0 \pm 9.0\%$ at the surface. Sea lions from the EAI spent an average of $64.4 \pm 16.0\%$ of the day on shore, $8.3 \pm 5.7\%$ diving, and $27.3 \pm 13.0\%$ at the surface. Sea lions from the central Gulf of Alaska (CGA) spent an average of $49.9 \pm 22.2\%$ of the day on shore, $12.3 \pm 8.4\%$ diving, and $37.8 \pm 15.9\%$ at the surface.

GLMs

Predictors of weekly mean and maximum trip durations, and percentage of time spent diving varied among models (Table 5). Foraging effort as indicated by all response variables increased with age for all models (Table 5). Mean trip duration did not differ significantly among regions, whereas maximum trip duration was greatest in the WAI and differed significantly from the CAI (Table 5). Additionally, sea lions from the WAI and the EAI spent less time diving wk⁻¹

Table 3. *Eumetopias jubatus*. Steller sea lion identification (ID), number of days of data (number of records), and summary statistics for activity patterns, including mean \pm SD percentage of time spent diving, at the surface, and hauled out on shore for the duration of the deployment period

ID	No. of days	Diving	Range	At surface	Range	Hauled out	Range
7820	23	6.9 \pm 6.9	0.0–28.8	35.9 \pm 23.5	0.3–89.5	57.2 \pm 28.5	0.0–99.7
7821	34	7.8 \pm 4.2	0.0–17.7	51.8 \pm 26.1	6.1–99.2	40.4 \pm 27.6	0.0–93.9
7822	9	4.7 \pm 3.8	0.0–8.9	36.7 \pm 32.7	2.4–91.3	58.6 \pm 35.8	0.0–97.6
8250	39	9.7 \pm 6.8	0.0–23.3	24.8 \pm 15.0	0.0–72.6	65.6 \pm 19.6	11.1–100.0
8252	15	8.2 \pm 7.6	0.0–22.7	20.9 \pm 17.9	0.0–63.6	71.0 \pm 23.5	27.8–100.0
9922	31	3.9 \pm 4.2	0.0–16.4	25.1 \pm 20.9	0.0–99.8	70.9 \pm 23.0	0.0–100.0
9923	7	2.3 \pm 2.7	0.0–5.8	35.5 \pm 31.2	0.0–99.8	62.2 \pm 30.9	0.0–100.0
9924	49	3.4 \pm 3.7	0.0–18.0	21.4 \pm 18.4	0.0–61.4	75.3 \pm 20.8	20.6–100.0
9925	33	4.1 \pm 5.0	0.0–17.2	24.2 \pm 14.7	0.0–54.8	71.7 \pm 17.8	34.6–100.0
9926	36	3.0 \pm 4.1	0.0–16.6	23.6 \pm 18.8	0.0–78.1	73.5 \pm 20.9	5.3–100.0
9927	48	18.7 \pm 12.3	0.0–39.4	41.6 \pm 28.1	0.0–88.9	39.7 \pm 38.3	0.0–100.0
10006	41	1.3 \pm 2.5	0.0–11.3	29.9 \pm 25.3	0.0–99.0	68.8 \pm 26.6	0.0–100.0
9930	124	17.5 \pm 7.9	0.0–39.9	44.9 \pm 23.8	0.0–86.0	37.5 \pm 28.8	0.0–100.0
10007	56	8.6 \pm 7.7	0.0–26.4	21.3 \pm 12.8	0.0–69.1	70.1 \pm 17.7	29.9–100.0
10008	62	12.0 \pm 5.5	0.0–31.4	31.4 \pm 13.5	0.0–59.3	56.6 \pm 17.4	12.2–100.0
10009	68	12.4 \pm 6.2	0.0–27.7	32.4 \pm 16.0	0.0–75.2	55.2 \pm 21.0	0.0–100.0
10010	61	11.5 \pm 7.7	0.0–35.9	31.4 \pm 21.0	0.0–86.6	57.1 \pm 26.5	0.0–100.0
10011	64	19.1 \pm 6.7	0.0–35.9	31.6 \pm 14.4	0.0–63.8	49.3 \pm 19.4	6.3–100.0
10012	31	12.6 \pm 3.0	7.7–22.7	24.9 \pm 12.6	9.8–64.6	62.4 \pm 13.9	25.1–80.9
10013	34	14.3 \pm 7.2	0.0–29.3	28.8 \pm 19.0	1.6–77.8	56.9 \pm 23.9	0.0–98.4
10014	31	11.5 \pm 5.6	2.6–28.8	32.6 \pm 21.3	6.4–83.1	55.9 \pm 25.5	0.0–91.0

Table 4. *Eumetopias jubatus*. Mean percentage of time spent diving within 6 periods of the day for 21 juvenile Steller sea lions, as indicated by their identification number (ID). Time of day refers to Greenwich Mean Time (GMT). Overall mean \pm SD are provided for each period

ID	1 (00:00–3:59 h)	2 (04:00–7:59 h)	3 (08:00–11:59 h)	4 (12:00–15:59 h)	5 (16:00–19:59 h)	6 (20:00–23:59 h)
7820	3.4	2.6	15.2	10.9	4.2	5.3
7821	9.9	5.4	1.4	1.6	13.2	15.1
7822	5.5	1.6	7.7	9.0	1.4	3.0
8250	0.2	8.1	20.1	25.9	2.5	1.2
8252	0.5	6.9	9.9	16.0	12.5	3.2
9922	1.2	6.9	3.8	6.4	3.6	1.8
9923	0.4	7.9	2.7	2.2	0.7	0.0
9924	2.0	5.4	4.1	3.9	2.8	1.9
9925	2.7	1.3	1.8	4.0	6.9	4.0
9926	4.0	2.0	2.7	4.1	1.7	3.2
9927	10.8	24.5	30.2	30.1	13.0	3.4
10006	1.9	1.4	0.9	1.3	1.5	1.0
9930	9.1	28.3	33.9	23.1	5.6	5.3
10007	0.6	2.2	23.2	19.0	5.9	1.0
10008	0.9	2.6	34.7	26.6	4.1	3.1
10009	2.0	4.7	29.5	25.4	7.9	4.8
10010	4.8	6.5	27.5	17.5	6.5	6.5
10011	4.7	5.2	44.6	38.4	14.6	7.0
10012	0.0	4.0	48.5	21.8	0.9	0.5
10013	3.4	15.3	40.8	12.2	6.4	7.9
10014	4.9	7.6	37.5	10.4	4.6	3.9
Mean \pm SD	3.5 \pm 3.2	7.2 \pm 7.2	20.0 \pm 16.2	14.8 \pm 10.8	5.7 \pm 4.3	4.0 \pm 3.4

than did sea lions from the CAI and presumably the CGA (Table 5). Percentage of time spent diving wk^{-1} increased with an increase in fractal dimension at both the landscape (mean \pm SD AMFD = 1.097 \pm 0.036, range = 1.026–1.182) and class (i.e. localized frontal

features) scales (mean \pm SD, AMFD = 1.059 \pm 0.024, range = 1.010–1.128; Table 5). Weekly mean trip durations were inversely related to PD of frontal features (mean \pm SD PD = 0.0035 \pm 0.003 patches 100 ha^{-1} , range = 0.0002–0.0096; Table 5).

Table 5. *Eumetopias jubatus*. Results of 6 stepwise generalized estimating equations used to examine 3 predictor variables (weekly, mean and maximum trip duration, and percentage of time spent diving by 21 juvenile Steller sea lions) with respect to age, region, and metrics (landscape and class) of sea surface temperature heterogeneity. All models were significant. * $p \leq 0.05$. EAI: eastern Aleutian Islands, WAI: western Aleutian Islands, SIDI: Simpson's diversity index, AMFD: area-weighted mean fractal dimension, PD: patch density, PLAND: percentage of landscape, CGA: central Gulf of Alaska

Response variable Variables retained	Coefficient estimate	SE	Wald	p	Model p
Landscape					
Mean trip duration wk ⁻¹					
Intercept*	2.510	0.112	498.484	0.000	4.172 × 10 ⁻⁸
Age*	0.004	0.002	6.378	0.012	
Region (EAI)	-0.214	0.121	3.136	0.077	
Max. trip duration wk ⁻¹					
Intercept	2.860	0.091	996.593	0.000	4.649 × 10 ⁻¹⁰
Age*	0.004	0.002	5.465	0.019	
Region (WAI)*	0.289	0.055	27.619	1.477 × 10 ⁻⁷	
% time diving wk ⁻¹					
Intercept*	-32.569	19.945	2.666	0.001	1.547 × 10 ⁻⁷
Age*	0.098	0.021	21.465	3.603 × 10 ⁻⁶	
Region (EAI)*	-4.194	2.157	3.782	0.052	
Region (WAI)*	-4.223	1.648	6.568	0.010	
SIDI	-6.549	3.936	2.769	0.096	
AMFD*	37.819	18.315	4.264	0.039	
Class					
Mean trip duration wk ⁻¹					
Intercept*	2.481	0.163	231.250	0.000	1.468 × 10 ⁻⁷
Age*	0.004	0.002	6.067	0.014	
Region (EAI)	-0.209	0.119	3.083	0.079	
PD*	-33.014	16.229	4.138	0.042	
PLAND	0.006	0.004	2.984	0.084	
Max. trip duration wk ⁻¹					
Intercept*	3.028	0.114	704.327	0.000	2.721 × 10 ⁻⁸
Age*	0.004	0.001	8.934	0.003	
Region (EAI)	-0.161	0.102	2.491	0.114	
Region (WAI)*	0.196	0.055	12.920	0.000	
PD	-21.547	11.220	3.688	0.055	
% time diving wk ⁻¹					
Intercept	-24.666	16.752	2.168	0.141	4.864 × 10 ⁻⁷
Age*	0.110	0.021	28.274	1.053 × 10 ⁻⁷	
Region (CGA)	-3.486	2.303	2.292	0.130	
Region (EAI)*	-5.712	2.090	7.472	0.006	
Region (WAI)*	-5.510	1.763	9.768	0.002	
AMFD*	30.284	15.732	3.706	0.054	

DISCUSSION

Similar to other studies of otariids (McCafferty et al. 1998, Baker & Donohue 2000, Baylis et al. 2005), including Steller sea lions (Raum-Suryan et al. 2004, Fadely et al. 2005, Pitcher et al. 2005, Call et al. 2007, Rehberg & Burns 2008), age was a significant factor for predicting the amount of time spent at sea and diving. These results were not surprising, as an increase in experience coupled with the development of physiological abilities (muscle and blood oxygen stores and thermal tolerance) occur with age and growth (Rich-

mond et al. 2005, 2006), enabling sea lions to remain at sea for longer periods of time. Summary statistics of activity patterns were also similar to findings of other researchers who found that on average, Steller sea lions spent 44% of their time at sea (Rehberg 2005, Call et al. 2007). Our results also corroborated other studies (Loughlin et al. 2003, Fadely et al. 2005, Call et al. 2007) indicating that most diving activity of pups and juveniles occurred during the night when sea lions may have been foraging on shallow vertically migrating prey such as walleye pollock *Theragra chalcogramma*. Pollock tend to school at depth during daytime hours and disperse as they rise in the water column at night (Sinclair et al. 1994). These results imply that sea lions spent the remainder of time at sea conducting other activities (unless foraging activities occurred within 6 m of the surface).

Sea lions from the WAI spent less time diving while at sea, yet maximum trip durations were greatest for this group of animals. These results coupled with the proportion of time spent at the surface possibly indicate that more time was allocated to traveling and less to resource utilization. Relative to the other 2 regions, sea lions from the EAI also spent less time diving during the week, but their diving behavior constituted a greater proportion of their overall time at sea (Table 3). Assuming that foraging indices are indicators of variability in marine resources (Boyd 1999) and reflect differences in the cost of prey acquisition (Costa et al. 1989, Merrick

& Loughlin 1997), these data suggest that sea lions from the EAI were either more efficient foragers than those from the WAI or resources were more attainable in the EAI than the WAI. Results of Lander et al. (2009), which indicated that diet diversity and habitat diversity were greater for the EAI than the WAI, support the latter notion if in fact diet and habitat diversity reflect prey diversity and abundance in the environment. Results should be interpreted with caution, however, because regional differences in diving effort may have been hampered by foraging behavior, age, season, or interaction effects (which were not examined due to

lack of degrees of freedom). Various foraging tactics are used by Steller sea lions to feed on different types of prey as a result of differences in prey characteristics such as size, age, and behavior. Because dominant prey types vary among regions (Sinclair & Zeppelin 2002, Lander et al. 2009), it is possible that foraging effort among regions was influenced by different strategies used for the pursuit, capture, and consumption of disparate prey. Furthermore, sample sizes were limited and all age classes of sea lions were not equally represented among regions. The weaning status of sea lions captured for this study was unknown, and individuals that were still nursing may have influenced our interpretation of the results if they were less motivated to find food resources affected by environmental heterogeneity (McIntyre & Wiens 1999). Unfortunately, lack of long-term data for most animals prevented us from examining how these behaviors changed over longer periods of time.

Other studies have indicated that the amount and spatial arrangement of resources and habitat constrain the location, movement, and foraging dynamics of other species (Crist et al. 1992, Ferguson et al. 1998, With et al. 1999). Our results indicated that diving activity of Steller sea lions increased as the shape complexity of localized frontal features within the study areas increased, whereas average weekly trip duration was inversely related to PD of those features. Assuming that increases in foraging effort and trip durations are predicted if prey availability is reduced (Trillmich & Ono 1991, Lunn et al. 1993, Hood & Ono 1997, Merrick & Loughlin 1997, McCafferty et al. 1998, Georges et al. 2000, Melin 2002, Weimerskirch et al. 2003), this combination of results suggests that sea lions had a more difficult time obtaining resources as the structure of SST frontal features became more complex, but may have attained resources more quickly as the number of patches comprising frontal features increased. Thus, aggregated, dense frontal features were probably conducive to foraging effort as opposed to time periods when these features were forming or dissipating. The lack of significance for AMCA and PLAND further suggests that complexity, rather than size, of frontal features influenced diving behavior.

Frontal zones, including thermal fronts, tend to be regions of enhanced primary productivity relative to surrounding areas (Graham et al. 2001, Okkonen et al. 2003, Bradshaw et al. 2004) and are important to other marine mammals (Hindell et al. 1991, Sinclair et al. 1994, Moore et al. 2002, Etnoyer et al. 2006, Doniol-Valcroze et al. 2007), seabirds (Hunt et al. 1999), sea turtles (Etnoyer et al. 2006), pelagic fishes (Royer et al. 2004), and other marine fauna (Graham et al. 2001). These predators likely concentrate at fronts due to food availability or thermal constraints, which may be evo-

lutionary, ecological, or physiological (Brandt 1993). For example, metabolic rates and gut passage rates of some fish species are affected by water temperature (Gillooly et al. 2001). It is also believed that water temperature influences the availability, behavior, spawning, and survival of forage fish (Bailey et al. 1995), which are important prey species of Steller sea lions. Additionally, frontal features may be beneficial because they have more thermal habitats per unit area than surrounding waters and have a greater probability of encompassing a preferred range of temperature (Brandt et al. 1980), thereby meeting energetic demands and other requirements needed for survival.

Unlike diving activity, trip duration did not increase as fractal dimension of frontal features increased, despite the idea that the 2 variables generally coincide or that it may take longer to navigate around irregular patches. However, assuming frontal features at the scales examined were used by Steller sea lions, other factors such as permeability of features, proximity among features, or location of features relative to haulouts or rookeries may have affected the results. For example, the spatial arrangement and shape of features presumably reflect their connectivity, but not necessarily their boundary characteristics. Although diving activity appeared to be more efficient during times when study areas contained connected, aggregated features, the configuration of features may not have affected trip durations if the features themselves did not pose a barrier to sea lions. Additionally, if sea lions tend to target frontal features of a specific configuration, which may be indicative of the strength of an underlying process or the concentration of a prey field, then trip durations may not have been related to measures of AMFD or the amount of diving activity because those features can potentially occur anywhere within a given study area mosaic.

In contrast to results reported by Lander et al. (2009), which indicated that regional patterns of SST diversity were fairly consistent with regional population trajectories of Steller sea lions, indices of foraging effort examined for this study were not related to SST diversity. Although this was unexpected, our results and those of Lander et al. (2009) appear to conform to the theory that landscape composition (e.g. habitat diversity) has large, direct effects on population dynamics and persistence (possibly through direct effects on reproduction and mortality), whereas landscape configuration (e.g. fractal dimension) affects population dynamics indirectly through its effects on among-patch movements (Fahrig & Nuttle 2003). Although an interesting observation, additional empirical evidence is needed to assess this hypothesis, which differs slightly from classical metapopulation theory, an approach that predicts that survival of endangered

populations is dominated by stochastic events and the spatial arrangement of suitable habitat (Hanski 1998).

The National Marine Fisheries Service (NMFS) Recovery Plan for Steller sea lions (NMFS 2008) suggests that critical habitat should be enhanced to incorporate the spatial and temporal variation of essential oceanographic features that potentially influence the distribution and abundance of prey and ultimate conservation of Steller sea lions. It is therefore necessary to determine which features constitute essential habitat, how those features persist over time, and how sea lions (and their prey) exploit those features. For this study, we described how the foraging effort of Steller sea lions was related to the heterogeneity of small-scale surface temperature gradients. However, we have an incomplete understanding of how exactly those features were truly perceived or used by sea lions because the distributions of sea lion locations (or dives) were not analyzed with respect to the exact locality of defined features due to the spatial resolution of the telemetry and remote sensing data. Furthermore, the environmental patterns demarcated for this exercise may have been sensitive to changes in scale and decision rules used to classify the data (e.g. patch definitions and parameter inputs; Turner et al. 1989). Similar studies in the future will undoubtedly benefit from simultaneously sampling the prey environment, the sophistication of ocean observing satellites, and the advancement of GPS technology.

Linking underlying processes to observed environmental patterns is essential for understanding the functional relevance of our results. Tidal advection, weather conditions, wind-forcing, and bottom topography can all contribute to the formation of frontal features and create patterned heterogeneity in the marine environment. At larger meso-scales, these gradients and/or fronts can represent the boundaries between different water masses or they may be indicative of other meso-scale features such as transient eddies (Ladd et al. 2005). It has been suggested that northern fur seals *Callorhinus ursinus*, and possibly Steller sea lions on longer pelagic excursions, are attracted to these features (Sinclair et al. 1994, Fadely et al. 2005, Ream et al. 2005), which likely concentrate productivity and prey, facilitate movement, and increase foraging opportunities (Ream et al. 2005). At smaller spatial scales, such as headlands and islands where Steller sea lions tend to congregate more often, currents may interact with topography to produce complex 3-dimensional secondary flows that result in physical and biological fronts that can influence the distribution of many organisms (Wolanski & Hamner 1988). Other 2-dimensional horizontal features such as coastal fronts are also associated with vertical motion and heterogeneity (Abbott 1993) and may be surface expressions of greater

subsurface gradients (Roughan et al. 2005). Although there were cases when plotted temperature profiles within or near the border of classified features supported this idea, the majority of temperature profiles collected during this study indicated that sea lions were foraging within the mixed layer. Hence, small-scale surface gradients, which typically result from surface wind stress (Langmuir circulation) or internal tides and are often marked by an entrainment of surface debris, buoyant particulates, and plankton (Wolanski & Hamner 1988, The Open University 2001), should be investigated further. Thin layers, which occur in coastal areas, contain high concentrations of living organisms, and possibly result from similar processes (Franks 1995, Johnston et al. 2009), also warrant future attention.

Typing small-scale features used by juvenile Steller sea lions inevitably will entail the use of additional sensors to collect precise *in situ* measurements of oceanographic variables in coastal waters unavailable to satellite remote sensing platforms. Recent advances in biologging instruments, including the development of a conductivity-temperature-depth SRDL (CTD-SRDL), are promising and have allowed examination of the behaviors of larger marine mammals in the context of a 3-dimensional environment (Biuw et al. 2007), mapping major fronts (Charrassin et al. 2008), and analyzing data in innovative ways (Weise et al. in press).

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