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Regional differences in the spatial and temporal heterogeneity of oceanographic habitat used by Steller sea lions

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Abstract. Over the past three decades, the decline and altered spatial distribution of the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska have been attributed to changes in the distribution or abundance of their prey due to the cumulative effects of fisheries and environmental perturbations. During this period, dietary prey occurrence and diet diversity were related to population decline within metapopulation regions of the western stock of Steller sea lions, suggesting that environmental conditions may be variable among regions. The objective of this study, therefore, was to examine regional differences in the spatial and temporal heterogeneity of oceanographic habitat used by Steller sea lions within the context of recent measures of diet diversity and population trajectories. Habitat use was assessed by deploying satellite-depth recorders and satellite relay data loggers on juvenile Steller sea lions ($n = 45$) over a five-year period (2000–2004) within four regions of the western stock, including the western, central, and eastern Aleutian Islands, and central Gulf of Alaska. Areas used by sea lions during summer months (June, July, and August) were demarcated using satellite telemetry data and characterized by environmental variables (sea surface temperature [SST] and chlorophyll *a* [chl *a*]), which possibly serve as proxies for environmental processes or prey. Spatial patterns of SST diversity and Steller sea lion population trends among regions were fairly consistent with trends reported for diet studies, possibly indicating a link between environmental diversity, prey diversity, and distribution or abundance of Steller sea lions. Overall, maximum spatial heterogeneity coupled with minimal temporal variability of SST appeared to be beneficial for Steller sea lions. In contrast, these patterns were not consistent for chl *a*, and there appeared to be an ecological threshold. Understanding how Steller sea lions respond to measures of environmental heterogeneity will ultimately be useful for implementing ecosystem management approaches and developing additional conservation strategies.

Key words: Aleutian Islands; chlorophyll *a*; composition; diet; diversity; *Eumetopias jubatus*; Gulf of Alaska; heterogeneity; satellite telemetry; sea surface temperature; Steller sea lion.

INTRODUCTION

The ultimate aim of ecological science is to explain and predict properties of living systems (individuals, populations, and communities) as functions of their relationships to various biotic and abiotic environments (DeLaplante 2004). Efforts to assess relationships between these systems and the properties of ecosystems have increased as climate change and the global loss of biodiversity have increased over the past decade (Waide et al. 1999). Across disciplines, however, ecologists are faced with the challenges of understanding how these systems respond to environmental change and heterogeneity. Because population declines of large marine

predators, including Steller sea lions (*Eumetopias jubatus*; see Plate 1), have been attributed to environmental change, many conservation research studies have been dedicated to this topic (Hirons et al. 2001, Stirling 2002, McMahon et al. 2005, Trites et al. 2007b).

Steller sea lions range around the North Pacific Ocean rim from the Kuril Islands and Sea of Okhotsk, through the Aleutian Islands and Gulf of Alaska, and south to Año Nuevo Island, central California (Loughlin et al. 1984). During the early 1970s, there were more than 300 000 Steller sea lions world wide, but index counts of animals present on land at standardized dates and times indicated that an 80% decline occurred over parts of the range since the late 1970s (Loughlin 1998). After this decline became evident in the 1980s, the U.S. population of Steller sea lions was listed as “threatened” under the U.S. Endangered Species Act during 1990 (55 FR 12645). During 1997, the U.S. population of Steller sea

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lions west of 144° W (Cape Suckling, Alaska) was reclassified as “endangered” (62 FR 24345, 62 FR 30772) after molecular and phylogeographic studies suggested there were two distinct population segments (DPS; Bickham et al. 1996, 1998, Loughlin 1997).

To further understand the spatial structure of the western DPS of Steller sea lions, York et al. (1996) used cluster analysis to examine the rates of change in numbers of adult females at rookeries in Alaska during the peak of breeding season from 1975 to 1994 and found consistent groupings of rookeries with common population trends. These data coupled with other studies (e.g., Raum-Suryan et al. 2002) suggest that Steller sea lions conform to a metapopulation, which in this context is a population of populations (Levins 1970) consisting of groups of rookeries with similar demographic trends. Although classical metapopulation theory assumes that space is discrete and patches are homogeneous across the landscape (Hanski and Simberloff 1997), realistically there may be circumstances when local populations have unique demographic responses to local variation in habitat characteristics (Pulliam 1988).

Since the late 1970s, rookeries within the western DPS of Steller sea lions have had different rates of population decline or increase, indicating that conditions may be variable among regions (Pascual and Adkinson 1994, York et al. 1996, Sinclair and Zeppelin 2002, Winship and Trites 2003, Call and Loughlin 2005, Fay and Punt 2006). Nutritional stress, resulting from changes in composition, distribution, abundance, or quality of prey due to changes in environmental conditions, is one of many hypotheses for explaining the decline of the western DPS (Braham et al. 1980, Merrick et al. 1987, Loughlin 1998, Loughlin and York 2000). To examine the nutritional stress hypothesis, Merrick et al. (1997) examined the summer diet of Steller sea lions from six regions in the Aleutian Islands from 1990 to 1993 and found that diet diversity was positively correlated with population trends, supporting the hypothesis that diet was linked to population decline. This hypothesis was further supported by Trites et al. (2007a) who found the diet of Steller sea lions in Southeast Alaska (a region of population increase) was more diverse than that reported for any other region of Alaska. Sinclair and Zeppelin (2002) also evaluated the diet of Steller sea lions across the range of the western DPS and found regional divisions in the diet during summer were closely aligned with patterns described by York et al. (1996). They suggested the implications of diet diversity should be addressed with respect to bottom-up processes and other environmental features that influence the near-shore habitat of rookery regions and ultimately the population stability of Steller sea lions.

The response of fish populations (i.e., prey of Steller sea lions) to environmental variability is most likely mediated through bottom-up processes, which include temperature related changes in the amount or timing of

primary and secondary productivity or the direct effects of temperature on the growth and survival of fish themselves (Hunt 2006). In turn, under the bottom-up concept, patterns in the changes of oceanography and fish populations should be reflected in patterns of sea lion foraging ecology and abundance (Fadely et al. 2005, Gende and Sigler 2006, Womble and Sigler 2006). The objective of this study, therefore, was to investigate these possible linkages by examining the spatial and temporal heterogeneity of sea surface temperature (SST) and chlorophyll *a* (chl *a*) associated with habitat use of Steller sea lions from four regions of the western DPS. Additionally, regional patterns of environmental heterogeneity are discussed relative to concurrent patterns of diet and population trajectories of Steller sea lions. Given the bottom-up scenario outlined above, we expected patterns of SST, chl *a*, diet, and population trajectories of Steller sea lions would consistently coincide across regions.

METHODS

From January 2000 to May 2004, 45 juvenile Steller sea lions (5 months to 35 months of age) were opportunistically captured using hoop nets or SCUBA methodologies (McAllister et al. 2001) at rookeries or haulout sites within four geographic areas of the western DPS, including the western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), and central Gulf of Alaska (CGOA) as outlined in recent literature (Fritz and Stinchcomb 2005, Fay and Punt 2006). To assess the habitat use of Steller sea lions, satellite transmitters were attached to the dorsum of each animal using five-minute epoxy (Devcon Products, Riviera Beach, Florida, USA) while they were manually restrained with valium sedation (1.1–2.0 cc [mL]) or anesthetized following procedures of Heath et al. (1997). Satellite-linked depth recorders (SDR-T16, 13.5 × 4.5 × 3.7 cm, 330 g; Wildlife Computers, Redmond, Washington, USA) were deployed on Steller sea lions from 2000 to 2003, whereas satellite relayed data loggers (SRDL series 9000, 10.5 × 7.0 × 4.0, 370 g, Sea Mammal Research Unit [SMRU], Gatty Marine Laboratory, University of St Andrews, Scotland) were deployed from 2002 to 2004. Both types of instruments were equipped with an ultra-high-frequency radio transmitter.

Daily locations from SDRs and SRDLs were obtained through Service Argos, Inc. (Hyattsville, Maryland, USA), a satellite-based location and data collection system (Fancy et al. 1988). Data collected by SDRs were decoded using Satpak software (Wildlife Computers), whereas data collected by SRDLs were decoded with SMRU's marine mammal behavior visualization system (MAMVIS; Fedak et al. 1996). All data were filtered using a swim speed of 2 m/s with the algorithm described by McConnell et al. (1992).

Analyses for this project were confined to data gathered during summer months (i.e., June, July, and

August) due to the paucity of telemetry, chl *a*, and diet data during the remainder of the year. Satellite positions for the three months were pooled across years for each region and used to delineate four study areas, which were defined as the area representing water within a rectangular polygon superimposed on the telemetry data.

Sea surface temperature data (4.6-km resolution) for the three months from 2000 to 2004 were collected by the moderate-resolution imaging spectroradiometer (MODIS) instrument aboard the Terra satellite and obtained from the Goddard Distribution Center (data available online).⁵ Additionally, chl *a* data, which provide a measure of phytoplankton biomass and are frequently used as a proxy for the standing crop of phytoplankton and ultimate primary productivity (Valiela 1984, Martin 2004), were collected via MODIS aboard the Aqua satellite (4.6 km resolution; 2002 to 2004) and the SeaWiFS instrument aboard the SeaStar spacecraft (9 km resolution; 2000 to 2001) and obtained from the Ocean Color Discipline Processing System (data available online).⁶ All data sets were Level 3 monthly composites (Campbell et al. 1995).

Quality data files, which provided a bin-by-bin designation of whether input pixels were good (level 0), questionable (level 1), cloud (level 2), or bad (level 3), were included with Terra SST data files in order to extract only the best quality estimates (quality level 0 indicates no known problems) using ArcInfo (ESRI, Redlands, California, USA), whereas the chl *a* data files contained only the best quality estimates upon receipt. Windows Image Manager (6.2; Wimsoft, Inc., San Diego, California, USA) was used to cut chl *a* data sets and ENVI (4.0; ITT Visual Information Solutions, Boulder, Colorado, USA) was used to define the datum (i.e., NAD83) to be compatible with other base data (e.g., land cover, telemetry data).

All remotely sensed data were converted to raster grids, which were projected to an Albers equal-area conic projection defined for the State of Alaska using ArcInfo. To create models representing each of the variables, geoprocessing tools (ArcGIS 9.0; ESRI) were used to replace each empty grid cell with the value corresponding to the nearest neighbor cell containing data. For this analysis, Euclidean distances based on the centroids of cells were used to identify the direction to the closest source cell. All grids were then clipped to the study areas demarcated by the telemetry data. Grids representing the three summer months were averaged for each year within each region, forming a "summer" composite. Only July and August chl *a* grids were used to form a summer composite for 2002 because the Aqua sensor was launched that year during June. Annual summer composites were then used to quantify the spatial and temporal heterogeneity of each variable.

Spatial habitat heterogeneity

Measurements of spatial heterogeneity are typically achieved using categorical map analysis, which involves employing a classification scheme to identify homogeneous patches (at a particular scale) that exhibit a relatively abrupt transition to adjacent patches with different characteristics (Kotliar and Wiens 1990, Gustafson 1998). However, unlike terrestrial studies that have landscape covers that can be easily categorized and counted in discrete units, standard classification schemes for oceanographic features such as SST and chl *a* do not exist. Because environmental heterogeneity was the focus of this study, we devised categories to capture the spatial and temporal variation found about the median values of SST and chl *a* concentrations over a five-year period. For each region, the minimum (min) and maximum (max) medians for the five years were used to define core zones of SST and chl *a*. Remaining categories were based on min and max values of the interquartile ranges and extreme values, resulting in a total of five unique data classes for each region (i.e., min min to min first quartile, min first quartile to min median, min median to max median (core), max median to max third quartile, and max third quartile to max max). Hence, each data point in space was assigned to a class that identified its relative variation away from the extreme median values over a five-year period.

Following data classification, patches were defined as a contiguous group of cells of the same mapped category based on an eight-neighbor rule (Forman and Godron 1986, Turner et al. 2001). To quantify heterogeneity of each summer composite, patch density (total number of patches/area), core patch density (number of patches within the core class/area), and diversity indices (diversity, richness, and evenness) were calculated for each region using a pattern analysis computer program (FRAGSTATS 3.3; McGarigal et al. 2002). Simpson's diversity index was calculated using the following metric:

$$SIDI = 1 - \sum_{i=1}^c P_i^2$$

where P_i is the proportion of the landscape occupied by class type i , and c is the number of classes present (Simpson 1949). SIDI represents the probability that any two pixels selected at random would be different patch types. This index equals 0 when the area is dominated by one patch (i.e., 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 (McGarigal and Marks 1995). Although Shannon's diversity index has typically been used to quantify diet diversity for sea lions in the past, we chose to calculate Simpson's diversity index for habitat and diet (below) because it does not depend on sample sizes (Rosenzweig 1995) and it is less sensitive to the presence of rare patch/group types so more weight is placed on common patch/group

⁵ <http://daac.gsfc.nasa.gov>

⁶ <http://oceancolor.gsfc.nasa.gov>

TABLE 1. Summary of sample sizes obtained for this study, including number of tagged Steller sea lions and number of fecal samples collected in the western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), and central Gulf of Alaska (CGOA), USA.

Year	WAI	CAI	EAI	CGOA
Steller sea lions				
2000			1	1
2001		1	3	6
2002	3		7	13
2003			1	1
2004		6	2	
Fecal samples				
2000		22	85	32
2001		33	48	32
2002	60	222	75	21
2003			106	14
2004		71	53	

Note: Blank cells indicate that no effort was made in those regions in those years.

types. Given these characteristics, this index, coupled with the consistency of richness across regions, enabled us to avoid problems associated with having study areas of different sizes.

After testing for normality and homogeneity of variances (SPSS 13.0; SPSS, Chicago, Illinois, USA) for all data sets, individual Kruskal-Wallis tests were used to compare mean SIDI of SST and chl *a* among the four regions and individual Mann-Whitney tests were used to examine all pairwise comparisons (SPSS 13.0). In contrast, individual analyses of variance (ANOVA) were used to compare mean patch density and mean core patch density of SST and chl *a* among the four regions and Tukey tests were used to examine the differences between all possible pairs of means (SPSS 13.0).

Temporal habitat heterogeneity

To compare the interannual variability of SST and chl *a* among regions, a Kolmogorov-Smirnov test (SPSS 13.0) was first used to determine if annual median values within each geographic region were approximately normal. A Bartlett's test was then used to examine homogeneity of variances among regions and a multiple comparison test analogous to a Tukey test was used to examine differences among variances for the four regions (Zar 1999). A significance level of $P \leq 0.05$ was used for all statistical tests.

Diet diversity

To examine the diet diversity of Steller sea lions, fresh fecal samples were collected during summer months at haulout sites and rookeries throughout the Aleutian Islands and Gulf of Alaska from 2000 to 2004. Similar to previous diet studies, it was assumed that fecal samples represented the diet of juvenile and adult female sea lions because adult males fast during the breeding season (Merrick et al. 1997, Sinclair and Zeppelin 2002).

Samples were frozen after collection in the field and later processed at the Alaska Fisheries Science Center's National Marine Mammal Laboratory (Seattle, Washington, USA) following standard procedures (Merrick et al. 1997, Sinclair and Zeppelin 2002). Prey remains (i.e., cephalopod beaks or rostra and fish otoliths, scales, and bones) were identified to family (Pacific Identifications, Victoria, British Columbia, Canada) using the all structures method (Olesiuk et al. 1990). Samples were pooled across years (Merrick et al. 1997, Sinclair and Zeppelin 2002) and cumulative frequency curves (cumulative number of families against number of samples) were plotted for each region to determine if a sufficient number of fecal samples were collected to precisely describe the diet (Pielou 1966, Hurtubia 1973). Percentage frequency of occurrence (FO_i), which is the percentage of fecal samples containing prey category *i*, was calculated for each family within each region and Simpson's diversity index was calculated using the metric presented above; the proportion of the diet comprised by family type *i* was substituted for P_i and the total number of families = *c*. Additionally, diet richness for each region was equal to the number of prey families identified and Simpson's evenness index (SIEI) was calculated using the following metric:

$$SIEI = \frac{1 - \sum_{i=1}^c P_i^2}{1 - \left(\frac{1}{c}\right)}$$

RESULTS

Spatial habitat heterogeneity

After filtering the telemetry data, location data for 45 tagged individuals resulted in 8080 positions ($n = 578$ in the WAI, $n = 2036$ in the CAI, $n = 1412$ in the EAI, and $n = 4054$ in the CGOA), which were used to delineate study areas of habitat use (Table 1, Fig. 1).

Mean SST SIDI from 2000 to 2004 differed significantly among regions ($\chi^2 = 15.782$, $P = 0.001$; Table 2). Post hoc analyses indicated values of SST SIDI for all regions were significantly greater than that for the WAI (Table 3). Additionally, SST SIDI of the EAI was significantly greater than values for the CAI and CGOA (Table 3). Mean patch density of SST from 2000 to 2004 did not differ among regions ($F_{3,16} = 2.616$, $P = 0.087$), whereas mean core density of SST differed significantly among regions ($F_{3,16} = 5.538$, $P = 0.008$), with the EAI being greater than the WAI and CGOA ($P = 0.014$; Table 2).

Mean chl *a* SIDI from 2000 to 2004 differed significantly among regions ($\chi^2 = 15.090$, $P = 0.002$; Table 2). Similar to SST diversity, values of chl *a* SIDI for all regions were significantly greater than that for the WAI (Table 3). Furthermore, chl *a* SIDI of the CGOA was significantly greater than that of the EAI (Table 3). Mean patch density of chl *a* did not differ among regions

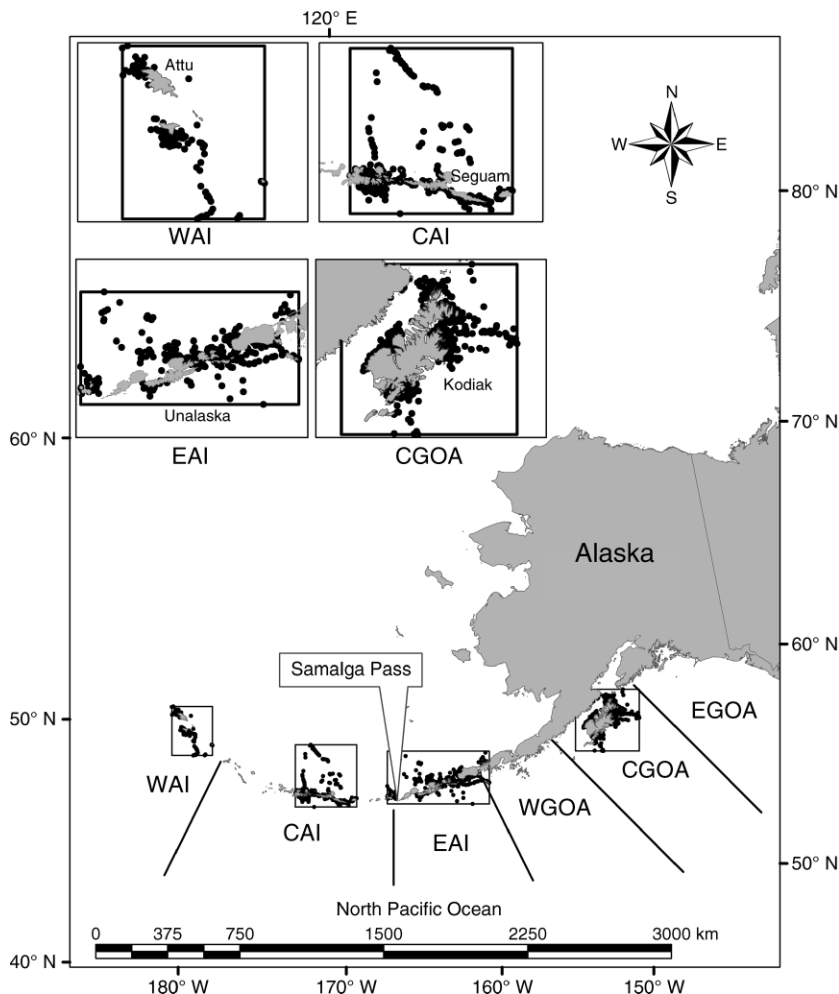


FIG. 1. Telemetry positions ($n = 8080$) of 45 juvenile Steller sea lions with respect to geographical regions in Alaska comprising the western distinct population segment (DPS). Regions include the western Aleutian Islands (WAI), central Aleutian Islands (CAI), Eastern Aleutian Islands (EAI), western Gulf of Alaska (WGOA), central Gulf of Alaska (CGOA), and eastern Gulf of Alaska (EGOA), USA. The study area for each region was defined as a rectangular polygon superimposed on the telemetry data (black dots).

($F_{3,16} = 2.140$, $P = 0.135$), whereas mean core density of chl a differed significantly among regions ($F_{3,16} = 6.113$, $P = 0.006$), with the CAI being greater than the WAI ($P = 0.003$; Table 2).

Temporal habitat heterogeneity

Annual median values of SST and chl a data were normally distributed within each geographic region. A corrected Bartlett's test indicated variances of annual median SST values were heterogeneous for the four regions ($B_c = 13.829$, $P < 0.001$); from year to year, SST was more variable in the WAI than in the EAI ($P < 0.050$; Fig. 2). Although variances of annual, median chl a values were heterogeneous for the four regions ($B_c = 18.539$, $P < 0.001$), post hoc differences were not detected, which may have been a result of a Type II error due to the limited sample size (Zar 1999). Variance of the WAI appeared similar to that of the CAI, whereas

variances for the EAI and CGOA appeared similar (Fig. 2).

Annual median values of both variables illustrated a geographical longitudinal trend, increasing from the WAI to the CGOA (Fig. 2). Linear regression indicated a positive relationship between annual values of median chl a and SST ($F_{1,18} = 27.875$, $P = 0.000$; Fig. 3a) and chl a SIDI and SST SIDI ($F_{1,18} = 6.963$, $P = 0.017$; Fig. 3b).

Diet diversity

Fecal samples ($n = 874$) were collected at rookeries and haulouts in the four regions (Table 1). Similar to previous studies (Merrick et al. 1997, Sinclair and Zeppelin 2002, Call and Loughlin 2005), the majority of fecal samples from the WAI and CAI were composed of hexagrammids, primarily Atka mackerel (*Pleurogrammus monopterygius*; Table 4). Important prey items

TABLE 2. Measures of heterogeneity for sea surface temperature (SST) and chlorophyll *a* (chl *a*), including Simpson's diversity index (SIDI), patch density (number of patches per 100 ha) for the entire study area, and patch density for the core data class.

Region, year, and statistics	SST			Chl <i>a</i>		
	SIDI	Patch density	Patch density (core)	SIDI	Patch density	Patch density (core)
WAI						
2000	0.5	0.0029	0.0005	0.4	0.0008	0.0001
2001	0.6	0.0041	0.0005	0.6	0.0009	0.0001
2002	0.6	0.0036	0.0008	0.6	0.0017	0.0002
2003	0.1	0.0014	0.0000	0.5	0.0014	0.0001
2004	0.5	0.0035	0.0004	0.6	0.0010	0.0001
Mean	0.5	0.0031	0.0004	0.5	0.0012	0.0001
SD	0.21	0.0010	0.0003	0.09	0.0004	0.0000
CV	0.45	0.3000	0.6548	0.17	0.3260	0.3727
CAI						
2000	0.6	0.0017	0.0004	0.8	0.0011	0.0003
2001	0.7	0.0055	0.0010	0.7	0.0014	0.0004
2002	0.7	0.0037	0.0006	0.8	0.0017	0.0006
2003	0.6	0.0043	0.0006	0.7	0.0015	0.0005
2004	0.7	0.0056	0.0008	0.7	0.0017	0.0006
Mean	0.7	0.0042	0.0007	0.7	0.0015	0.0005
SD	0.05	0.0016	0.0002	0.05	0.0002	0.0001
CV	0.08	0.3830	0.3353	0.07	0.1682	0.2716
EAI						
2000	0.7	0.0024	0.0006	0.7	0.0014	0.0002
2001	0.8	0.0032	0.0009	0.7	0.0013	0.0002
2002	0.8	0.0034	0.0011	0.7	0.0017	0.0003
2003	0.8	0.0038	0.0013	0.7	0.0022	0.0005
2004	0.8	0.0034	0.0009	0.7	0.0020	0.0004
Mean	0.8	0.0032	0.0010	0.7	0.0017	0.0003
SD	0.04	0.0005	0.0003	0.00	0.0004	0.0001
CV	0.06	0.1598	0.2716	0.00	0.2229	0.4075
CGOA						
2000	0.7	0.0030	0.0006	0.8	0.0013	0.0003
2001	0.7	0.0017	0.0003	0.8	0.0012	0.0003
2002	0.7	0.0021	0.0005	0.8	0.0015	0.0001
2003	0.7	0.0022	0.0003	0.7	0.0023	0.0006
2004	0.7	0.0028	0.0005	0.8	0.0017	0.0002
Mean	0.7	0.0024	0.0004	0.8	0.0016	0.0003
SD	0.00	0.0005	0.0001	0.04	0.0004	0.0002
CV	0.00	0.2254	0.3049	0.06	0.2724	0.6236

Note: Mean, standard deviation (SD), and coefficient of variation (CV) are provided for each index.

in the WAI also included Pacific cod (*Gadus macrocephalus*), rockfish (*Sebastes* spp.), and salmonids (*Oncorhynchus* spp.). For the CAI, common prey items also included cephalopods, salmonids, and gadids, which were equally represented by Pacific cod and walleye pollock (*Theragra chalcogramma*). Atka mackerel and gadids (walleye pollock and Pacific cod) dominated the diet of sea lions from the EAI, followed by salmonids, sand lance (*Ammodytes hexapterus*), righteye flounder consisting primarily of southern rock sole (*Lepidopsetta biliniata*) and arrowtooth flounder (*Atheresthes stomias*), and Pacific herring (*Clupea harengus*). Walleye pollock, salmonids, and arrowtooth flounder were found most frequently in samples from the CGOA.

After data were pooled across years within each region, cumulative frequency curves indicated sample sizes were sufficient for regional comparisons. The number of prey families (i.e., diet richness) ranged from

TABLE 3. Results of Mann-Whitney *U* pairwise comparisons of sea surface temperature (SST) and chlorophyll *a* (chl *a*) diversity (SIDI) between regions of the western distinct population segment (DPS) of Steller sea lions.

Regional comparison	SST SIDI		Chl <i>a</i> SIDI	
	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>
WAI vs. CAI	2.000	0.021	0.000	0.007*
WAI vs. EAI	0.000	0.007*	0.000	0.005*
WAI vs. CGOA	0.000	0.005*	0.000	0.006*
CAI vs. EAI	1.500	0.014	7.500	0.134
CAI vs. CGOA	7.500	0.134	7.500	0.221
EAI vs. CGOA	2.500	0.014	2.500	0.014

Note: Regions are the western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), and central Gulf of Alaska (CGOA).

* Significant comparisons after *P* values were Bonferroni-corrected to account for the six different tests ($\alpha = 0.05/n$).

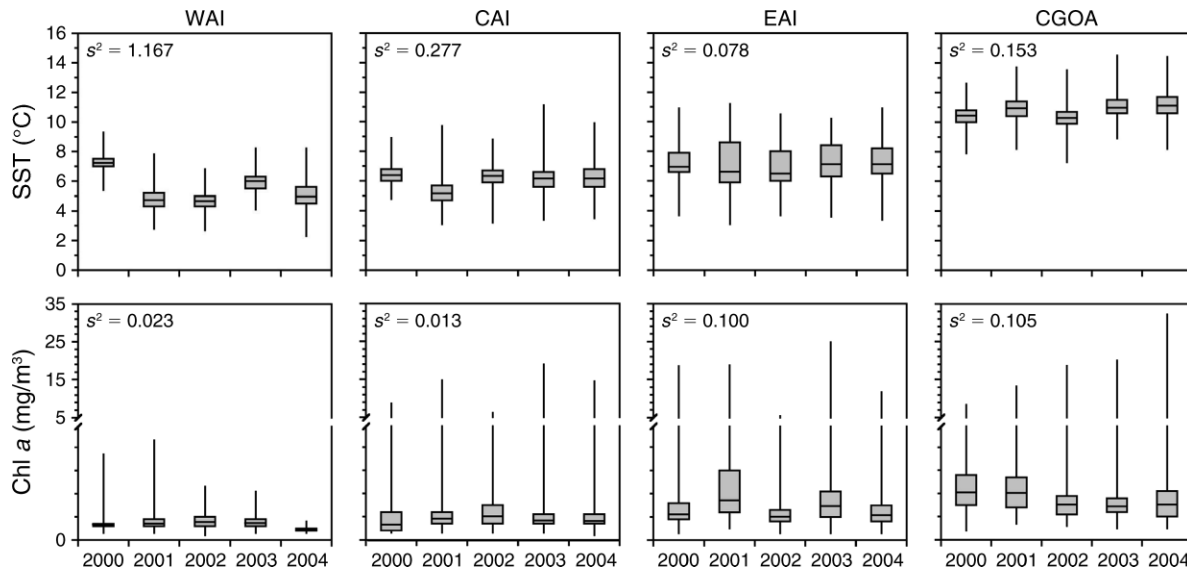


FIG. 2. Box plot parameters used to classify sea surface temperature (SST) and chlorophyll *a* (*chl a*) grids for categorical map analysis. Plots indicate annual median, interquartile range, and extreme values for SST and *chl a* within the western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), and central Gulf of Alaska (CGOA) from 2000 to 2004. Median values were used compare interannual variability of each variable within and among regions. Note the axis break and different scales for *chl a* plots. The variance (s^2) of annual median values is illustrated for each region.

9 to 25 and diet SIDI and SIEI ranged from 0.6 to 0.9 (Table 4).

DISCUSSION

Sea surface temperature heterogeneity

Diet diversity and richness inferred from food habits of opportunistic or generalist apex predators are thought to reflect prey diversity and richness in the environment. In turn, prey (i.e., species) diversity and richness tend to parallel variation in local physical and biological conditions (Ricklefs 1987), typically increasing with habitat heterogeneity or more diverse landscapes (MacArthur 1958, 1964, Rosenzweig 1995, Kerr and Packer 1997, Guégen et al. 1998). During this study, the spatial pattern of environmental heterogeneity as characterized by mean SST diversity over the five years was similar to patterns of diet diversity reported in the literature (Merrick et al. 1997, Sinclair and Zeppelin 2002, Call and Loughlin 2005). Additionally, the regional pattern of SST diversity along with diet richness and diversity patterns found for this study were fairly consistent with regional population trajectories for that same period, possibly indicating a link between environmental diversity, prey diversity, and distribution or abundance of Steller sea lions. SST diversity was greatest in the region of greatest sea lion population increase (EAI), similar for intermediate areas (CAI and CGOA), and lowest in the region of greatest population decline (WAI; Fig. 4). A similar trend was found for diet richness (Table 4), whereas only extreme values of diet diversity coincided with population trends because diet diversity of sea lions from the CAI was less than diet

diversity of sea lions from the WAI and CGOA (Fig. 4). This was unexpected based on previous diet studies and the diet richness observed for the CAI during this study. However, because hexagrammids dominated the diet of sea lions from the CAI, diet diversity in this area was likely confounded by diet evenness.

The habitat heterogeneity hypothesis proposes that species richness and diversity tend to increase with

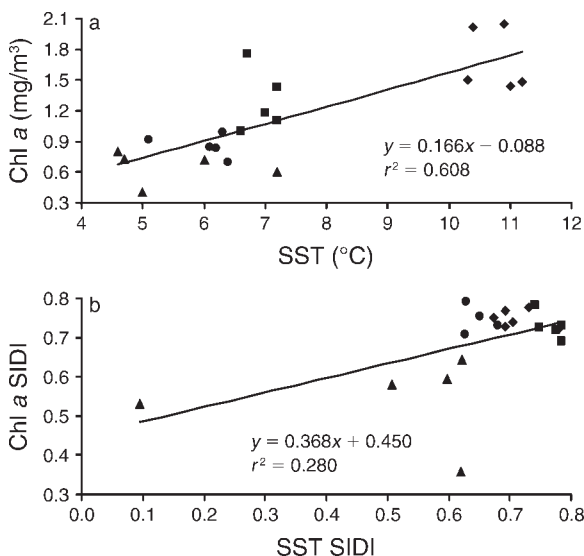


FIG. 3. Positive relationship between annual values of (a) median *chl a* concentration and SST and (b) *chl a* SIDI and SST SIDI within the western Aleutian Islands (WAI; triangles), central Aleutian Islands (CAI; circles), eastern Aleutian Islands (EAI; squares), and central Gulf of Alaska (CGOA; diamonds).

TABLE 4. Percentage frequency of occurrence (% FO) for prey families identified in fecal samples collected from the western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), and central Gulf of Alaska (CGOA) during summer months from 2000 to 2004.

Family	Common name	% FO (<i>n</i>) per region			
		WAI	CAI	EAI	CGOA
Agonidae	poachers		0.4 (2)	1.1 (11)	
Ammodytidae	sandlances	2.1 (2)	0.9 (5)	9.9 (102)	6.4 (14)
Anarhichadidae	wolf-eels			0.1 (1)	
Anoplopomatidae	sablefishes		0.2 (1)		
Bathylagidae	deepsea smelts			0.8 (8)	
Bathymasteridae	ronquils			0.1 (1)	
Cephalopoda	squids/octopus	3.2 (3)	12.2 (66)	3.5 (36)	1.8 (4)
Clupeidae	herrings			8.9 (92)	4.6 (10)
Cottidae	sculpins	2.1 (2)	2.4 (13)	4.3 (44)	
Cyclopteridae	lump/snail fishes			0.1 (1)	
Gadidae	codfishes/whiting	11.7 (11)	6.1 (33)	20.2 (209)	28.4 (62)
Gasterosteidae	sticklebacks			0.7 (7)	
Hemipteridae	sailfin sculpins			0.1 (1)	0.5 (1)
Hexagrammidae	greenlings	58.5 (55)	64.1 (346)	20.4 (211)	0.5 (1)
Liparididae	snailfishes		0.2 (1)	0.3 (3)	
Myctophidae	lanternfishes		2.0 (11)	0.6 (6)	
Osmeridae	smelts			0.7 (7)	5.6 (12)
Petromyzontidae	lampreys			0.4 (4)	
Pholidae	gunnels			0.2 (2)	
Pleuronectidae	righteye flounders	4.3 (4)	1.7 (9)	9.6 (99)	24.3 (53)
Rajidae	skates	2.1 (2)	0.6 (3)	1.1 (11)	
Salmonidae	salmonids	6.4 (6)	8.5 (46)	11.5 (119)	26.1 (57)
Scorpaenidae	rock/scorpion fishes	9.6 (9)	0.7 (4)	1.1 (11)	1.8 (4)
Stichaeidae	pricklebacks			0.1 (1)	
Trichodontidae	sandfishes			3.9 (40)	
Zaproridae	prowfishes			0.7 (7)	
Total number of families (diet richness)		9.0	13.0	25.0	10.0
SIDI		0.6	0.6	0.9	0.8
SIEI		0.7	0.6	0.9	0.9

Notes: Number of samples (*n*) containing each family is indicated in parentheses. Diet richness and Simpson's diversity (SIDI) and evenness (SIEI) are also reported, in the bottom two rows of the table.

habitat heterogeneity because different habitat properties support the specializations of different species (Rosenzweig 1995). Patch metrics for SST corroborated diversity results because greater patch density is indicative of greater spatial heterogeneity (McGarigal and Marks 1995) and mean core density of the EAI was significantly greater than estimates for the WAI and CGOA. Thus, it appears that maximum SST heterogeneity is important for sea lions, especially within the zone of core SST. This may be because greater patch density is associated with greater abundance or diversity of species

(Forman and Godron 1986, Swartzman et al. 1999, Gorresen and Willig 2004), and an increase in patch density increases the patch encounter rate (de Knegt et al. 2007). Our annual composites further suggested that core patches within the EAI were smaller than those in other regions. The composition of patches within the EAI may have been beneficial for sea lions or their prey because small patches offer species a wide array of resources, which can be exploited with a variety of patch use strategies (Kozakiewicz 1995). Additionally, small habitat patches may increase the quality of a given

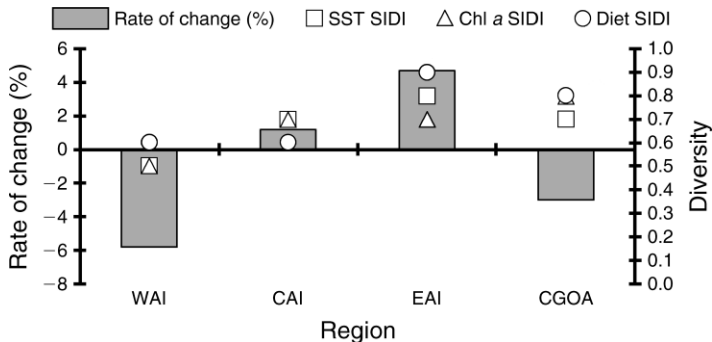


FIG. 4. Rate of Steller sea lion population change (2000–2004) relative to mean diversity (Simpson's diversity, SIDI) of sea surface temperature (SST), chlorophyll *a* (chl *a*), and diet for four regions within Alaska, including the western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), and central Gulf of Alaska (CGOA). Annual rates of population change, which were obtained from Fritz and Stinchcomb (2005), were derived from regression coefficients of log-linear regressions of non-pup counts on three survey years (2000, 2002, and 2004).

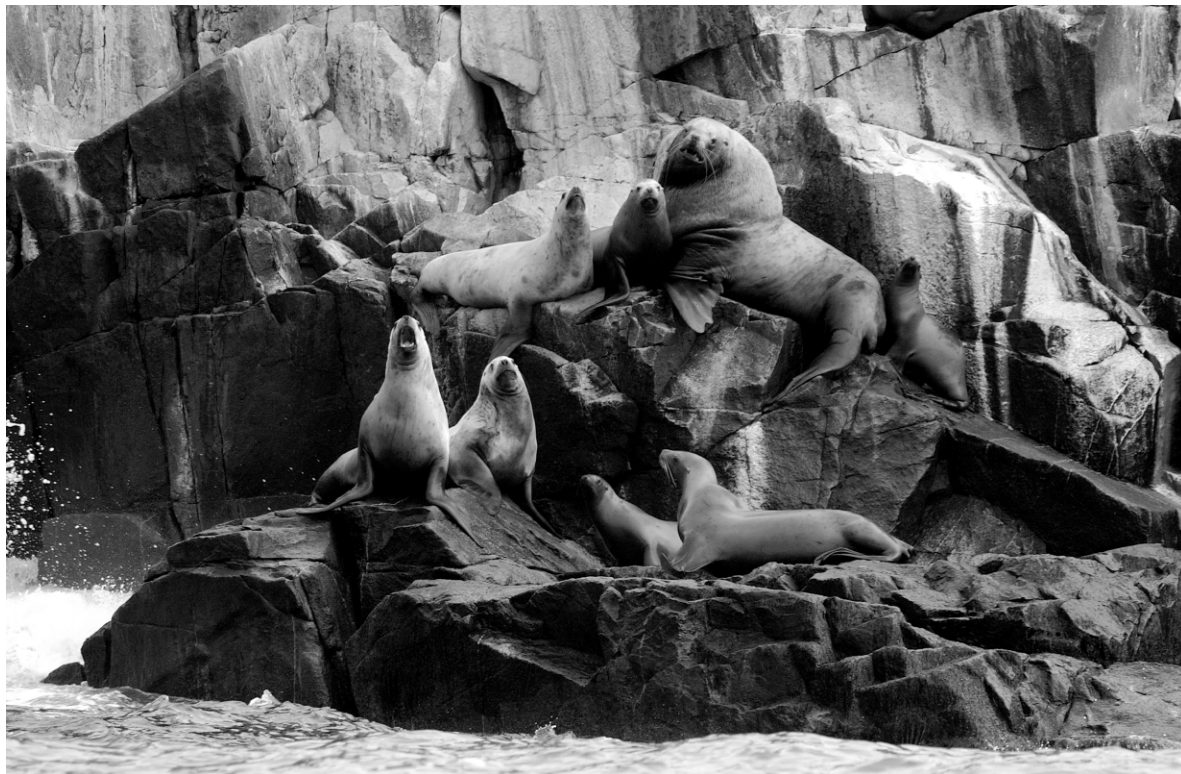


PLATE 1. Steller sea lions (*Eumetopias jubatus*) on Mitrofanía, Alaska (USA). Photo credit: L. W. Fritz.

habitat matrix by supplying complementary resources or predator-free space (Cramer and Willig 2005).

Although the patterns observed during this study provide an initial step for identifying underlying processes influencing spatial patterns of habitat diversity, they do not imply causation and we can only speculate about the mechanisms maintaining diversity within each region. Diversity of SST may have been perpetuated in the EAI because of exposure to more physical forcing than the other three regions. Unlike the other regions, the EAI occurs at the junction of three ecosystems. Rookeries and haulouts within the EAI are not only exposed to local environmental conditions within the North Pacific and eastern Bering Sea, but are also exposed to conditions that originate in the GOA (e.g., eddies) and travel the Aleutian chain (Ladd et al. 2005b). Within areas of the EAI, Steller sea lions are also exposed to four different currents (Alaskan Stream, Alaska Coastal Current, Aleutian North Slope Current, and Bering Slope Current), which aid in the aggregation and transport of nutrients and prey. This area also is associated with high tidal flow and mixing (Ban 2005). Given these features, the EAI including Unimak Pass, have been described as an oceanographically dynamic area with high species richness (Logerwell et al. 2005) and nursery stocks of critical prey (Sinclair and Stabeno 2002).

In addition to being the most diverse area with respect to the spatial composition of SST, our data also indicated interannual SST in the EAI was less variable, and therefore possibly more stable than other areas, especially the WAI. The environmental variability hypothesis proposes that temporally less variable environments permit greater species richness because species are likely to evolve narrow ecological niches, whereas variable environments have less species richness because fewer species are able to tolerate the stressful conditions of a varying environment (Ruggiero and Kitzberger 2004). Because species typically are capable of coexisting in stable environments (May 1973), environmental conditions within the EAI may have been beneficial for Steller sea lions. Organisms in stable ecosystems are faced with fewer or less severe challenges and more energy can be allocated to growth, reproduction, and ultimate population increase (Connell and Oriens 1964). For example, Raum-Suryan et al. (2004) found juvenile Steller sea lions remained close to shore while foraging skills were being developed and suggested the predictability of prey resources adjacent to rookeries and haulouts was critical to survival.

Interannual variability of SST was greater for the WAI than for any other region, possibly resulting in a less stable area for sea lions. In contrast to environmental stability, unpredictable environmental variation may not allow population assemblages to reach equilib-

rium (Owen 1990). Because organisms generally tend to tolerate a narrow range of variation in the environment, extinction rates of rare species also tend to increase in areas with environmental fluctuations (Connell and Orians 1964). Environmental fluctuations may impact individuals or populations directly (physiologically via metabolic and reproductive processes) or indirectly by affecting prey, predators, and competitors (Stenseth et al. 2002). For example, lower SST in the WAI may require an increase in food consumption because a larger subcutaneous lipid store is necessary for thermoregulation in colder habitats (Arnould et al. 1996, Kitts et al. 2004). Water temperature may also influence the spawning, behavior, survival, and availability of forage fish (Bailey et al. 1995). Walleye pollock, Atka mackerel, and Pacific cod, which are common in the diet of Steller sea lions, are either directly affected by temperature or feed on zooplankton or other fish species that respond to temperature changes (Ottersen et al. 1994, Rothschild 1994, Orlov 1997, Yang 1999, Sundby 2000, Shima et al. 2002). These factors, coupled with the need for greater food consumption (Winship and Trites 2003) and the possibility that the prey base is not diverse or rich, may have exacerbated the decline of sea lions in the WAI. Our results were similar to Rodionov et al. (2005) who examined the seasonal changes in surface air temperature (SAT) across the Aleutian Islands and found more variable SAT in the WAI on interannual time scales. Rodionov et al. (2005) hypothesized that increased SAT variability in the WAI may have contributed to the decline of Steller sea lions in the region by impacting them directly (e.g., increased physiological stress) or affecting the production of prey.

Chlorophyll a heterogeneity

The spatial pattern of environmental heterogeneity as characterized by mean chl *a* diversity was inconsistent with patterns of SST diversity, diet diversity, and population trends of Steller sea lions. Chlorophyll *a* diversity was lowest in the WAI and greatest in the CGOA, which were both areas of Steller sea lion decline. These results suggest that resources may be scarce and incapable of sustaining sea lion or prey populations in areas of low productivity or diversity (WAI), whereas there may also be a critical threshold after which the environment may be too productive or diverse for sea lions to utilize efficiently (CGOA). These data support the conceptual idea that some environmental heterogeneity may be advantageous, but too much heterogeneity may lead to reduced encounters between sea lions and their prey. Overall, it appeared that intermediate areas of chl *a* diversity may offer the best combination of food and competitor exclusion. Denslow (1980) suggested that habitats of intermediate productivity tend to be more common (as was the case for our study) and support more individuals because species evolve to deal with the most common habitat conditions.

The extreme values of chl *a* diversity corresponding to the two regions of population decline likely have different effects on Steller sea lions and their prey. The WAI are characterized by a very narrow, steep shelf with limited productivity with respect to the rest of the Aleutian archipelago (Mordy et al. 2005) and it is believed that decreased productivity in this region was responsible for decreases in species richness and walleye pollock abundance (Logerwell et al. 2005). Decreased productivity or diversity in this area may also be disadvantageous for Atka mackerel, which is a planktivorous fish. Because habitat composition appears to be important for the persistence of populations, including those of endangered territorial animals (Gilpin 1987, Lande 1987, Andr n 1994), the abundance of Steller sea lions may have been adversely affected by decreased concentrations of chl *a* coupled with the spatial composition of chl *a*.

Although variations in primary productivity resulting from changes in oceanographic conditions may be the link between climate and animals at higher trophic levels (Strom et al. 2006), this did not appear to be the case for the CGOA. During this study, SST and chl *a* appeared coupled (Fig. 4), but given the amount of variation explained by the analyses and the discordance between the spatial patterns of SST diversity and chl *a* diversity for the EAI and CGOA, it is possible that processes other than those associated with SST contributed to the spatial heterogeneity of chl *a* in the CGOA. Sea surface temperature can also be associated with more than one mechanism (i.e., fronts, upwelling) related to the aggregation or production of phytoplankton and these mechanisms may have differed among regions. Furthermore, the dominant mechanisms responsible for generating the pattern of chl *a* diversity in the CGOA may not have been associated with SST at all. Strom et al. (2006) found a weak relationship between phytoplankton growth rates in the GOA and environmental variables, including temperature, and concluded that no single resource could predict the response of phytoplankton to physical events in this area. It is also believed that local topography such as bathymetric structures contribute to regional differences in mid-trophic assemblages in the GOA and eastern Bering Sea, which is utilized by sea lions from the EAI (Doyle et al. 2002).

Despite the productive conditions of the CGOA during this study, diet richness and diversity were low and the population of Steller sea lions in this region continued to decline over the five years. Although the mechanisms responsible for this pattern are unknown, it has been proposed that disturbance, interspecific density dependence, predation, competitive exclusion, and competition for space can all occur as productivity increases (Tilman 1982, Abrams 1988, Leibold 1999). Our data further suggest that the bottom-up construct we proposed became disjunct at mid-trophic levels. This hypothesis warrants further investigation because the number of intermediate trophic levels has major

consequences for the amount and type of higher predators that can be supported (Strom et al. 2007). Additionally, primary productivity commonly settles out as detritus before it can be used by other trophic levels (Pauly and Christensen 1995). The spatial pattern of chl *a* relative to sea lion population trends may have also been attributed to time lags between the onset of productivity, the response of intermediate-trophic-level biota including fish populations, resource utilization by Steller sea lions, and population growth. Unfortunately, our five-year time series was not sufficient for detecting lagged effects, which have been evident for other studies (Jaquet et al. 1996). This deserves further attention, however, especially in light of the latest Steller sea lion survey, which was conducted during 2007 and indicated numbers are now increasing in the CGOA (area of sea lion decline with greater chl *a* diversity during the time frame of our study), but declining in the CAI (area of sea lion increase with lower chl *a* diversity; Fritz et al. 2008).

The implications described above for the temporal variability of SST may not have been an issue for chl *a* because interannual variability of chl *a* in the CGOA was similar to that in the EAI, where sea lions did not appear to be negatively impacted. Additionally, the interannual variability of chl *a* in the WAI did not coincide with the interannual variability of SST, lending support to the idea that SST may have had direct impacts on the prey of sea lions. It was not surprising to find that chl *a* variability was similar between the eastern regions (CGOA and EAI) and similar between the western regions (WAI and CAI) because an abrupt change in water properties, including chlorophyll fluorescence, occurs between the eastern and central Aleutian Islands near Samalga Pass at $\sim 170^\circ$ W (Fig. 1; Ladd et al. 2005a, Mordy et al. 2005). Despite the reduced concentrations of chlorophyll in the western regions, sea lions from the CAI increased, perhaps a result of the spatial heterogeneity of chl *a* noted above. As for the eastern regions, the cyclical patterns of annual, summer median chl *a* deserve more attention with respect to other physical structures such as eddies, which are seasonally modulated, interannually variable, and have been associated with high chlorophyll concentrations (Okkonen et al. 2003, Ladd et al. 2005b).

Although interannual variability of summer chl *a* was analyzed for each region during this study, intraannual variability and diversity were not examined. However, the marine environment is not static, rather it is in constant flux characterized by disturbance and change. It is well known that the distribution of chl *a* in the GOA varies seasonally (Brickley and Thomas 2004) and our summer composites may not have been a representative sample for the entire year. Although it appeared that sea lion population decline occurred in an area of high productivity and diversity, this pattern may have been an artifact of our sampling design because sea lions are obviously dependent on resources throughout the

year, which may not have been as plentiful beyond the summer months. It is also possible that the patterns we observed were a result of underlying processes operating at different temporal scales within each of the regions. Unfortunately, it is often difficult to infer trophic relations with simple correlation analyses of abundance data because predators typically respond to prey over a wide range of spatial and temporal scales (Russell et al. 1992). For example, the temporal scale of nutrient depletion and zooplankton grazing in the Aleutian Islands may not have corresponded with that of the CGOA. Because we were working with a three-month "snap shot" in time, chl *a* may have appeared lower in the Aleutian Islands as a result of these factors. Given these constraints, the prospect of chl *a* being an appropriate proxy for sea lion prey should be considered further.

Although bottom-up trophic linkages among productivity, diet, and reproductive success or population dynamics of apex predators have been documented for other systems (Hyrenbach and Veit 2003), the mechanistic links between oceanographic features, prey availability, nutritional stress, and changes in sea lion demographics remain a critical research challenge (National Marine Fisheries Service 2008). Our data support the idea that regions of high prey diversity may reflect an environment of high habitat diversity or productivity (Sinclair and Zeppelin 2002). However, the functional relevance of our results is still unclear, especially when examined within the context of sea lion demography. We should also note that our data become even more uncertain if a conservative approach is applied (see Table 3 for an example). Studies in the future should be employed to simultaneously sample the prey environment while examining the fine-scale foraging behaviors of Steller sea lions using GPS technology coupled with in situ measurements of water temperature and fluorescence.

Results should be interpreted with caution because satellite imagery differed among regions due to unequal cloud cover and sea lion sample sizes (including number of tracked individuals used to infer habitat use and number of fecal samples used to characterize diet) were inconsistent among regions and years, possibly biasing our models and results. It is also possible, if not probable, that other mechanisms obscured the patterns we observed among regions. Competition with fisheries (Loughlin 1998, Hennen 2006), fisheries interactions (Loughlin and York 2000), predation (Springer et al. 2003), fisheries management measures (Hennen 2006), the reduction of incidental takes, or a combination of these factors have all been implicated as regulators of sea lion population change. It should also be noted that trends in population abundance data tend to display a gradual response to environmental change (Holmes and York 2003, Holmes et al. 2007); thus, the comparisons made during this study may have only provided a

conservative picture of the possible effects of habitat diversity on population trends of Steller sea lions.

Understanding the links between environmental processes and the regulation of populations is challenging, but necessary for conservation of endangered species and implementation of ecosystem-based fisheries management measures. Overall, the goal of ecosystem-based fisheries management is to maintain ecosystem health and sustainability by recognizing that ecosystems are composed of interconnected organisms that collectively interact with their physical and biological environment and preserving habitat, biodiversity, and predator-prey relationships (Ecosystem Principles Advisory Panel 1999, Livingston et al. 2005). The ecosystem-based management approach also attempts to integrate ecological thresholds and uncertainty into models used to inform management decisions (Mangel et al. 2000). For example, over the past few years, measures of functional (trophic or structural habitat) diversity and environmental factors have been incorporated into some Alaskan fisheries stock assessment models as it has become increasingly evident that ocean temperature and productivity influence the spatial distribution and abundance of many fish species (Boldt 2005, Livingston et al. 2005). However, it is also important for managers to understand how apex predators such as Steller sea lions respond to these measures before implementing ecosystem management approaches and this study provided a basic framework for identifying and defining habitat, quantifying patterns of habitat, detecting natural variability, and formulating conceptual models regarding ecosystem linkages and tolerance thresholds.

Quantitatively characterizing patterns of variation and understanding their correlates and consequences are important steps in investigating the influence of spatial heterogeneity on the structure and function of ecological systems (White and Brown 2003). However, this study represented only a short period within a nearly 30 year decline, during which considerable changes occurred. For example, severe declines first began in the EAI during the early 1970s (Kenyon and Rice 1961, Braham et al. 1980, Loughlin et al. 1992), but this area is now relatively stable with respect to other regions comprising the western DPS (Fritz and Stinchcomb 2005). Unfortunately, understanding the effects of long-term environmental change on the regulation of population structure has been hampered by lack of historical data on the abundance of Steller sea lions prior to the 1970s (Francis et al. 1998), confounding effects of anthropogenic disturbance, three climatic regime shifts (Mantua et al. 1997, Mantua and Hare 2002), and the idea that proximate causes of mortality have changed during the past three decades (York 1994, York et al. 1996, Holmes and York 2003). With the standardization of sea lion surveys, the progression of sea lion research, and the advancement of computer power and software packages, further studies should focus on the impacts of

environmental variability on the spatial structure and population dynamics of Steller sea lions. An understanding of natural variability and the critical habitat of this species will be fundamental for formulating models that can be used to predict behavioral response as habitat composition changes in the future.

Diversity indices are a nonspatial measure of composition without explicit reference to an ecological process (McGarigal and Marks 1995, Gustafson 1998). Although we attempted to interpret the ecological implications of our data, much uncertainty remains regarding the mechanisms underlying the patterns of environmental heterogeneity we observed and their effects on the demographics of sea lions. Additional studies should also incorporate specific hypotheses with respect to specific processes and diversity metrics should be used in concert with spatially explicit metrics of configuration. Understanding the metapopulation dynamics of Steller sea lions will entail having a better understanding of what defines suitable habitat and the spatial arrangement of that habitat (Turner et al. 2001). The integration of environmental heterogeneity with metapopulation models will further our knowledge of the biogeography of this species and will be useful for developing additional conservation strategies.

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