

QUANTIFICATION OF TERRESTRIAL HAUL-OUT AND ROOKERY CHARACTERISTICS OF STELLER SEA LIONS

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ABSTRACT

Steller sea lions (*Eumetopias jubatus*) are known to have occupied the same terrestrial haul-out and rookery sites across the North Pacific Rim for centuries, but it is not known why they choose and stay at these locations, or what defines their preferred habitat. Classifying and comparing the shoreline type of haul-outs and rookeries against sites not used by Steller sea lions showed that they preferentially locate their haul-outs and rookeries on exposed rocky shorelines and wave-cut platforms. However, no preference was found for selecting rookeries on sheltered shore types. Shoreline types used less frequently by sea lions included fine-to-medium-grained sand beaches, mixed sand and gravel beaches, gravel beaches, and sheltered rocky shores. Quantifying the shoreline types used by sea lions confirms anecdotal reports of habitat preferences and may prove useful in identifying and protecting sea lion terrestrial habitat, or in forecasting how climate change might affect the distribution of sea lions.

Key words: Steller sea lion, *Eumetopias jubatus*, haul-out, rookery, terrestrial habitat.

Steller sea lions (*Eumetopias jubatus*) inhabit the North Pacific Ocean from central California in the eastern Pacific to northern Japan in the west, where they haul-out on land to breed at 88 known rookeries (breeding sites), and rest at nearly 600 haul-outs (non-breeding sites) (Loughlin *et al.* 1984, 1992). The sites used by Steller sea lions are generally described as rocky areas that are exposed to oceanic swells, with limited shelter by the surrounding topography (Fiscus 1970, Bigg 1985, Lyman 1989, Kastelein and Weltz 1991). Sea lions may select rookeries according to slightly different criteria than they would use to choose haul-outs because protection of pups from exposure to inclement climate may be an important consideration. Pup deaths due to wave action are not uncommon (Fiscus 1970, Edie 1977), thereby suggesting that sites affording some protection from wave exposure may be favored for rookeries.

Specific choice of sites within an island or beach may also be influenced by the presence of marine predators, currents, and undersea topography (Stirling 1983). A number of studies have identified factors affecting haul-out site selection of phocids (*e.g.*, Pitcher and McAllister 1981, Schneider and Payne 1983, Calambokidis *et al.* 1987, Brasseur *et al.* 1996, Watts 1996, Suryan and Harvey 1998, Sjoberg and Ball 2000, Galimberti and Sanvito 2001, Bjorge *et al.* 2002, Moulton *et al.* 2002, Nordstrom 2002, Reder *et al.* 2003). However, research concerning the similar behavior of otariids, and Steller sea lions in particular, is sparse and generally qualitative. Apart from anecdotal descriptions of their habitat preferences, there have been no quantitative studies of the factors that may influence the choice of sites used by Steller sea lions for haul-outs and rookeries. Quantifying habitat preferences may thus prove useful in the conservation and management of Steller sea lions by identifying potential habitat, and may have bearing on understanding the decline of the western population if their terrestrial habitat needs differ from those of the increasing eastern population. We tested two principal hypotheses concerning the terrestrial habitat needs of Steller sea lions. The first was that the distribution of Steller sea lion haul-outs and rookeries is not random with respect to the availability of different shoreline types. Our second hypothesis was that the preferred type of shoreline for rookeries differs from that of haul-outs, presumably because pups and young animals might be less agile than mature animals and thus less able to access steep or rough sites.

METHODS

We tested the hypotheses using shoreline classification data from the National Oceanographic and Atmospheric Administration (NOAA) and the British Columbia Ministry of Sustainable Resource Management (MSRM). To aid in oil-spill response, NOAA has produced maps of shoreline types for most of the coastal United States (National Oceanic and Atmospheric Administration (NOAA) Office of Response Restoration (OR&R) Hazardous Materials Response Division 1997). Shorelines are characterized using a ranking system that considers characteristics such as substrate grain size, permeability, slope, exposure, and ease of cleanup, among others. The ranks range from 1–10, where Type 1 shorelines are judged least susceptible to oil damage and 10 are the most vulnerable to oil damage (Appendix 1). Each rank also has subtypes that further characterize the shoreline type. Depending upon whether a shoreline is estuarine, lacustrine, or riverine, the same ESI number may designate a slightly different habitat type with the same approximate oil spill vulnerability. The scale/accuracy of the shoreline classification data is approximately 1:250,000, with a minimum mapping unit of approximately 100 ft. In British Columbia, a similar coastline atlas exists with a slightly different classification system (Coastal Resource and Oil Spill Response Atlas). Data for the Strait of Georgia were not publicly available—an area that constitutes a relatively small portion of the overall British Columbia shoreline where no rookeries or year-round haul-outs exist. Because there is no one-to-one correspondence between the NOAA ESI system and the British Columbia system, descriptions (and photographs where applicable) were used to make shore classifications from the British Columbia system compatible with the ESI system so that analyses could be performed on the entire shoreline from southern California through the Aleutian Islands as a single unit. One shoreline type from the British Columbia system (channels) had no equivalent in the ESI system and thus was left as an additional shoreline class. Rookery and summer haul-out locations for

Steller sea lions in Alaska, Washington, Oregon, and California (Appendix 2, 3) were compiled from the database of sea lion counts conducted by the Alaska Department of Fish and Game (ADF&G), the National Marine Fisheries Service (NMFS), as well as from M. Lowry¹ and C. Stinchcomb.² Data for sites in British Columbia were obtained from Olesiuk (2003). ESRI ArcView 3.2 (ESRI 1992–1999) and ArcGIS 8.3 (ESRI 1999–2002) were used to spatially analyze, display, and export data. Site locations and the coastline data were converted from latitude–longitude format to a common projection system to ensure that measurements of length were accurate. Only sites within 0.5 nautical miles (~900 m) of classified shoreline segments were selected for analysis to allow for slight positional errors and map inaccuracies. This yielded 294 haul-outs (99 in the Eastern population, 195 Western population) and 38 rookeries (14 in the Eastern population, 24 Western population) out of a total of 594 haul-outs and 88 rookeries, or 50% of all the haul-outs and 43% of all the rookeries across the entire range (California to Japan). Excluded sites tended to be those on very small offshore islets, where shoreline data were not available. Using a spatial join operation, each site was assigned to the nearest shoreline segment. In the ESI system, each shoreline segment could have multiple habitat types assigned to it, with numbers ordered from the most landward to the most seaward type. In cases where a site was assigned to a shoreline segment with multiple shoreline types (which only occurred for fourteen of the haul-outs and none of the rookeries), two separate analyses were conducted—one using the most landward shoreline type and one using the most seaward type. This allowed for possible changes to occur in exposed shoreline type as tidal heights rise and fall. Statistical analyses were performed using R (The R Foundation for Statistical Computing 2004), and a Monte Carlo implementation of Fisher's exact test (using 10,000 iterations to randomly seed sites among shore types in proportion to their availability by length) was used to test whether the usage of shoreline habitat types differed from a random distribution. The proportions of rookeries and haul-outs in each shoreline type were also compared with Fisher's exact test to determine if habitat usage differed between rookeries and haul-outs. This ratio of habitat usage to habitat availability is also known as a Habitat Suitability Index (HSI) (Rettie and Messier 2000, McLoughlin *et al.* 2002, Mahoney and Virgl 2003).

RESULTS

Haul-outs and rookeries both had nonrandom distributions with respect to available shoreline types ($P < 0.05$, Fisher's exact test, Fig. 1). Steller sea lions heavily favored shoreline Types 1 and 1A (exposed rocky shores), which accounted for over 70% of rookeries and more than 50% of haul-outs. Substrate Types 2 and 2A (exposed wave-cut platforms) were the second most frequently used shoreline types, accounting for more than 13% of rookeries and 27% of haul-outs. Shoreline types that were used in lower proportion than their availability included Types 3 (fine to medium-grained sand beaches), 5 (mixed sand and gravel beaches), 6A (gravel beaches), and 8A (sheltered rocky shores). Types used in approximate proportion to their availability were 4 (coarse-grained sand beaches), 6 (gravel beaches and exposed riprap), and 6B (riprap). No rookeries occurred in Types 4, 6B, or 8A, and neither

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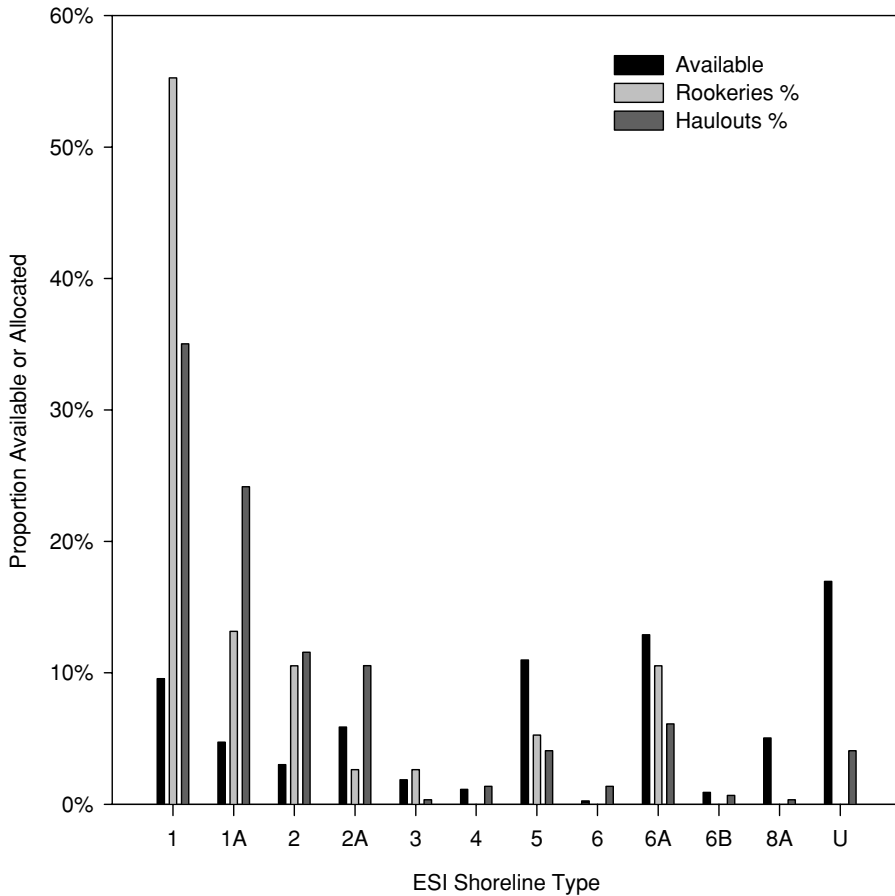


Figure 1. Allocation of shoreline types among rookeries and haul-outs relative to availability. Shoreline Type "U" is undetermined or unknown.

haul-outs nor rookeries were found in shoreline Types 10, 10D, 10E, 11, 1B, 1C, 2B, 3A, 3B, 3C, 6C, 7, 8, 8B, 8C, 8D, 8E, 9, 9A, or 9B, although most of these types (with the exception of 7, 10A, and 9A) represented less than 5% of the available shoreline. The availability of different shoreline types was similar between coastlines in the eastern and western population areas, whether grouped by supertype (Fig. 2A) or broken into subtypes (Fig. 2B). However, Type 6 shorelines tended to be more common in the eastern population area and Type 5 shorelines more common in the western population area. Use of Type 2 shorelines by sea lions (relative to availability) was slightly higher (35% relative to availability) in the western population than in the eastern population (Fig. 3), whereas utilization of Type 1 shorelines was proportionately more than twice as high as in the eastern population. Substrate Types 3, 5, and 6 were all used in rough proportion to their availability in both populations, and Type 4 was used in proportion to its availability in the western population. There was one site each in Types 8 and 10 in the western and eastern populations, respectively. Comparison of habitat usage between haul-outs and rookeries showed that

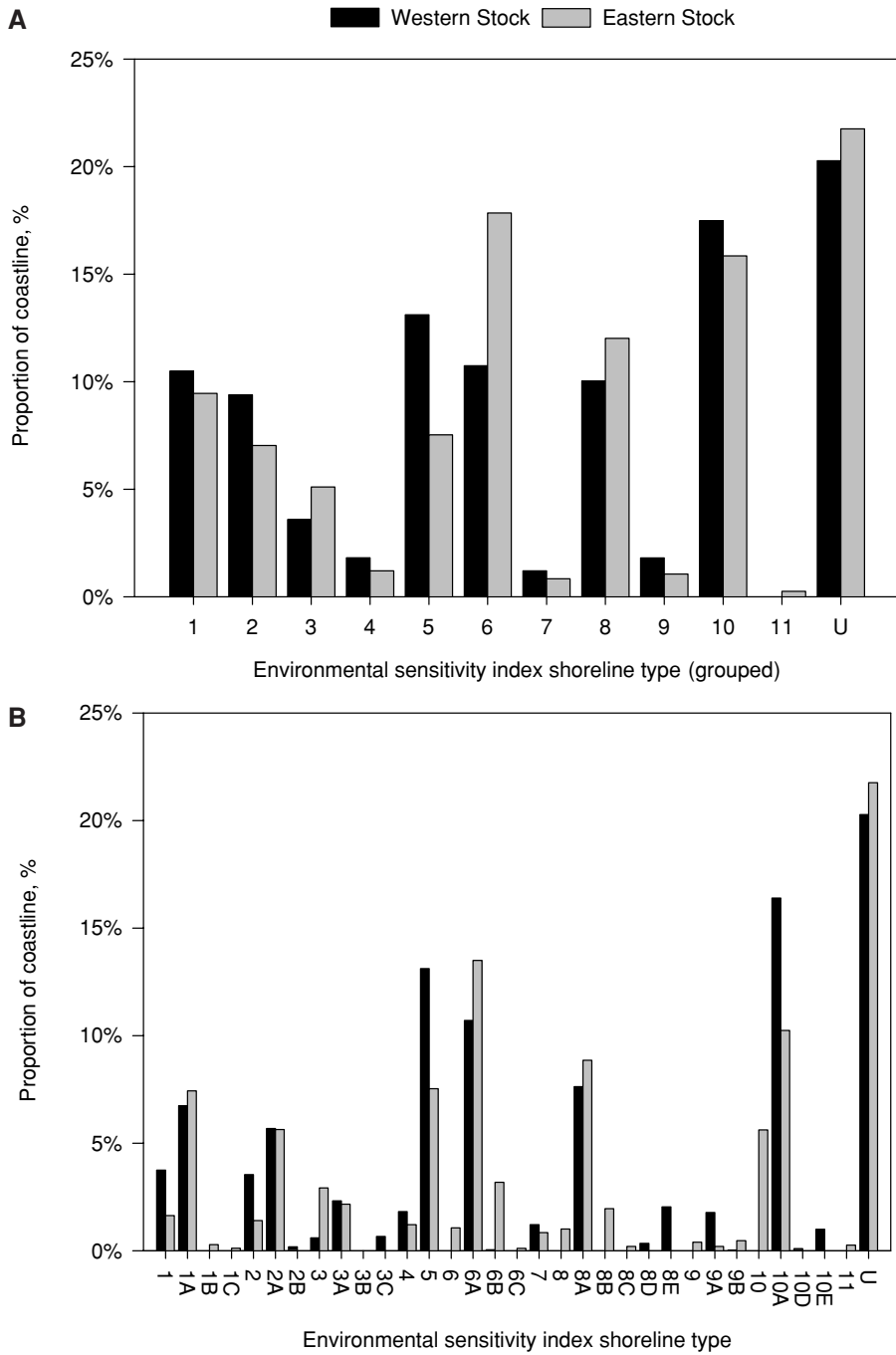


Figure 2. The proportion of coastline available to sea lions in the eastern and western population grouped by (A) shoreline supertype and (B) shoreline subtype.

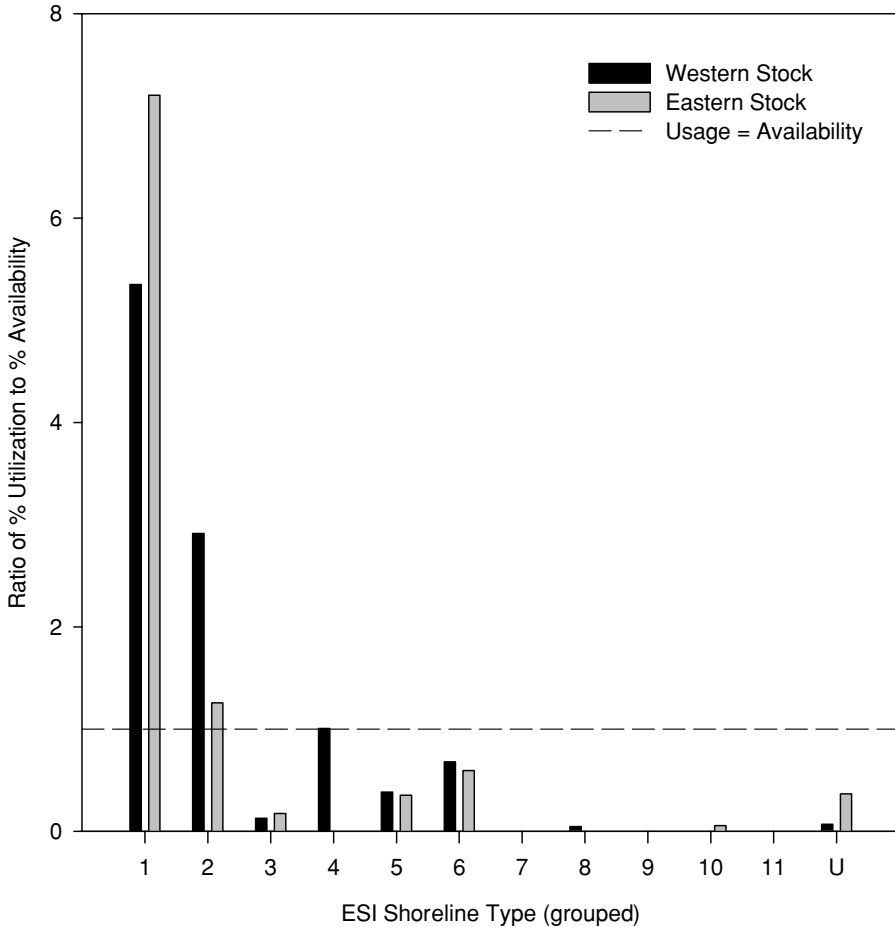


Figure 3. Comparison of overall (rookery and haul-out) usage of shoreline types, by population. The dashed line represents usage in proportion to availability.

their distributions differed ($P < 0.05$, Fisher's exact test). Rookeries were located preferentially in Type 1 (exposed rocky shores with or without wave-cut platform) and 6A (gravel beaches) shore types, whereas haul-outs were preferentially located in Types 1A (exposed rocky shores) and 2A (exposed wave-cut platforms).

DISCUSSION

The terrestrial habitats used today by Steller sea lions across their Pacific Rim range presumably share characteristics that have been selected through evolutionary processes to optimize survival and reproduction. Archaeological records of Steller sea lions breeding or hauling-out on the Oregon coast do not exist prior to about 3000 B.P. (Lyman 1989), although otariids have presumably lived in this region for nearly

all of their evolutionary history (~3 million yr). Occupation of present-day sites in Alaska and northern British Columbia is presumed to have been precluded until at least 20,000 B.P. due to the extent of the ice edge at the end of the Last Glacial Maximum (Manley and Kaufman 2002).

The genetic delineation between the eastern and western populations of Steller sea lions (and the recently delineated Asian population) is likely a result of populations being isolated in refugia off the coast of British Columbia and in the Gulf of Alaska during the Pleistocene (Bickham *et al.* 1998, Harlin-Cognato *et al.* 2006). Present-day rookeries in northern Japan, the Kamchatka peninsula, and the Aleutian Islands may be remnants of these refugia (Harlin-Cognato *et al.* 2006). Isolated fossil finds have placed Steller sea lions in British Columbia as early as *circa* 12,000 B.P. (Harington *et al.* 2004) when the waters of British Columbia were closer in temperature to present-day Cook Inlet or Prince William Sound, Alaska. Despite the decline in the western population, there has been no observed decrease in the occupied range nor have any rookery or haul-out sites been fully abandoned.^{3,4} Thus, the sites in use today are still reflective of those being used prior to the beginning of the population decline.

The fact that Steller sea lions have consistently used the same rookery and haul-out sites historically, with some sites documented to have been in use for more than four centuries (Lyman 1988, Walker *et al.* 2000), indicates that the factors driving site selection are likely to be stable. If sites are being selected solely on the criterion that they are close to productive foraging areas—and this certainly appears to be an important reason (Antonelis 2002)—then the current distribution of sites should correspond with the available distribution of shoreline types (so long as areas of oceanographic productivity are not consistently associated with certain shoreline types, which may not be true of offshore islets). In other words, if the terrestrial characteristics of haul-outs are unimportant or secondary to proximity of foraging areas, the locations of haul-outs among shoreline types should be randomly distributed.

A number of biologists have described anecdotally the characteristics of haul-outs and rookeries used by Steller sea lions. For example, Bigg (1985) noted that year-round haul-outs are usually found in places that are directly exposed to oceanic swells, whereas winter-only haul-outs are generally not exposed directly to these swells and are sheltered to some extent by the surrounding topography. Lyman (1989) quoted several accounts of the habitat preferences of Steller sea lions, noting that they breed almost exclusively on rocky areas of offshore islands and that few mainland rookery or hauling areas are known. He also noted that Steller sea lions breed only on offshore islets and rocks, and do not habitually enter bays, estuaries, or river mouths—showing a preference for outer reefs and large offshore rocks. Other observations include that they are rarely found in inland waters and are a near-shore species (Lyman 1989), and that their haul-out behavior is influenced by the physical geography of a colony site, particularly variations in the number of animals at a site as tidal height changes (Kastelein and Wetz 1991). Fiscus (1970) also reported that sea lions preferred rookery beaches composed of sand, clay, and small cobblestones or gravel over sections composed of boulders and large rocks. He also felt that they favor large, fairly level

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rock ledges over boulder beaches, although Stirling (1983) noted that the availability of space may be important, even when available land is abundant.

Our quantitative analysis of shoreline types showed that haul-out and rookery sites were indeed located mostly in exposed areas with solid or rocky substrates. Steller sea lions tended to avoid using sheltered areas and beaches with fine-grained substrates (such as mud and sand). This is also consistent with Call and Loughlin (2005) who found that thirty-eight of the forty rookeries in their study had a rock/slab or cobble beach substrate, although two had a sandy beach substrate.

We found the availability of shoreline types were largely similar between the eastern and western populations. Utilization of shoreline types was also similar between sites in the eastern and western populations although a higher proportion of sites in the western population favored substrate Type 2 (exposed wave-cut platforms), whereas substrate Type 1 (exposed rocky shores) was moderately more favored in the region of the eastern population. Both Type 1 and 2 sites have similar exposure characteristics (both are very exposed) but differ mainly in their topography. Type 1 sites have a steep ($>30^\circ$) intertidal zone, whereas Type 2 sites have a flat or gently sloping intertidal zone. Thus, Type 2 sites would tend to have available hauling-out area rapidly reduced by rising tide (once a threshold height was reached), whereas Type 1 sites would tend to have a gradual decrease in available area as the tide rises. As tide appears to have a strong influence on Steller hauling-out behavior (Kastelein and Weltz 1990, Kucey 2005), and tends to induce crowding (Kastelein and Weltz 1991), differences in how sites are affected by tidal patterns could have varying energy implications for animals occupying those sites.

Although there were differences in the distribution of haul-outs and rookeries among shoreline types, there did not appear to be a preference for rookeries to occur on sheltered sites. This agrees with the findings of Call and Loughlin (2005) who found that rookeries tended to be oriented towards the open ocean, rather than on the sheltered sides of islands.

In light of reports of pups dying during rough weather due to drowning (Fiscus 1970, Edie 1977, Cunningham and Stanford 1978), sites affording some degree of protection to exposure were expected to be favored. However, a number of reports (Kenyon and Rice 1961, Mathisen and Lopp 1963, Cunningham and Stanford 1978) also indicate that Steller sea lions do not associate land with safety during a storm and instead raft offshore during severe weather events. Thus, the degree of shelter from exposure that a site affords does not appear to be a consideration when the site is initially colonized. Instead, other factors driving the selection of such exposed sites might be protection from terrestrial predation (*e.g.*, bears and wolves) or proximity to favorable foraging areas. Higher-resolution terrestrial data detailing information such as the slope, aspect, substrate, and wave exposure of individual sites may yet reveal such differences either between haul-outs and rookeries or between western and eastern populations that were not apparent at our scale of analysis.

Overall, site selection by pinnipeds likely involves either an optimization or compromise of two factors: proximity to favorable foraging areas and availability or accessibility of terrain that allows both ingress and egress during variable tidal heights (Bartholomew 1970). Neonates stand the best chance of survival in sites offering protection from high tides and favorable thermal protection (Trites 1990, Antonelis 2002), but significant neonate mortality may result from unusual fluctuations in tidal height and storm surges. Thus, protection from wind and waves may also play a role in site selection, although observations of sites (Fiscus 1970, Bigg 1985, Lyman

1989, Kastelein and Weltz 1991) indicates that this may not be important and that favored sites are more exposed than other nearby areas that are more sheltered.

Anecdotal reports (Fiscus 1970, Bigg 1985, Lyman 1989, Kastelein and Weltz 1991) have described the preferences of Steller sea lions with regard to haul-out and rookery locations, but no studies have quantified this preference across a broad geographic range. Our findings confirm the anecdotal reports of habitat preferences. Such information about habitat preferences may prove useful in the conservation and management of Steller sea lions. Although no clear reason has been accepted for the precipitous decline in the western population of Steller sea lions (Loughlin and York 2000, NMFS 2001, National Research Council 2003, Trites and Donnelly 2003, DeMaster *et al.* 2006), differences in the terrestrial physical environment could conceivably affect population trajectories. For example, the site fidelity of Steller sea lions (Milette 1998, Raum-Suryan *et al.* 2002) could result in a spatial version of the "predator pit" (Krebs 1996) if sea lions occupy a wide range of habitat when populations are large but are later displaced from their optimal rookeries and haul-outs by hunting or other forces. Under such a scenario, the smaller local populations using the lower-quality habitat could be prevented from increasing because of unusual pup mortality (due to exposure or trampling), reduced foraging success, or the inability of males to successfully establish and defend territories. The quantification of terrestrial habitat needs of Steller sea lions may also help to identify sites that might be colonized as sea lions continue to recover from the effects of past human hunting and culling. It may also assist in making management decisions that minimize the impacts of human development and disturbance, and may help to forecast the response of sea lion distribution to climate change.

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LITERATURE CITED

- ANTONELIS, G. A. 2002. Rookeries. Pages 1051–1052 in W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. Academic Press, San Diego, CA.
- BARTHOLOMEW, G. A. 1970. A model for the evolution of pinniped phylogeny. *Evolution* 24:546–559.
- BICKHAM, J. W., T. R. LOUGHLIN, J. K. WICKLIFFE AND V. N. BURKANOV. 1998. Geographic variation in the mitochondrial DNA of Steller sea lions: Haplotype diversity and endemism in the Kuril Islands. *Biosphere Conservation* 1:107–117.
- BIGG, M. A. 1985. Status of the Steller sea lion *Eumetopias jubatus* and California sea lion *Zalophus californianus* in British Columbia Canada. *Canadian Special Publication of Fisheries and Aquatic Sciences* 77:1–20.
- BJORGE, A., T. BEKKBY AND E. B. BRYANT. 2002. Summer home range and habitat selection of harbor seal (*Phoca vitulina*) pups. *Marine Mammal Science* 18:438–454.
- BRASSEUR, S., J. CREUWELS, B. V D WERF AND P. REIJNDERS. 1996. Deprivation indicates necessity for haul-out in harbor seals. *Marine Mammal Science* 12:619–624.
- CALAMBOKIDIS, J., B. L. TAYLOR, S. D. CATER, G. H. STEIGER, P. K. DAWSON AND L. D. ANTRIM. 1987. Distribution and haul-out behaviour of harbor seals in Glacier Bay, Alaska. *Canadian Journal of Zoology* 65:1391–1396.

- CALL, K. A., AND T. R. LOUGHLIN. 2005. An ecological classification of Alaskan Steller sea lion (*Eumetopias jubatus*) rookeries: A tool for conservation/management. *Fisheries Oceanography* 14:243–258.
- CUNNINGHAM, W., AND S. STANFORD. 1978. Steller sea lion investigations at Cape St. Elias, March 22 through July 5, 1978. Alaska Department of Fish and Game, Anchorage, AK.
- DEMASTER, D., A. W. TRITES, P. CLAPHAM, S. MIZROCH, P. WADE, R. J. SMALL AND J. M. VER HOEF. 2006. The sequential megafaunal collapse hypothesis: Testing with existing data. *Progress in Oceanography* 68:329–342.
- EDIE, A. G. 1977. Distribution and movements of Steller sea lion cows (*Eumetopias jubata*) on a pupping colony. M.Sc. thesis, University of British Columbia, Vancouver, BC. 97 pp.
- ESRI. 1992–1999. ArcView. Environmental Systems Research Institute, Redlands, CA.
- ESRI. 1999–2002. ArcGIS. Environmental Systems Research Institute, Redlands, CA.
- FISCUS, C. H. 1970. Steller sea lions at Ugamak Island, Aleutian Islands, Alaska. Department of the Interior, United States Fish and Wildlife Service, Bureau of Commercial Fisheries, National Marine Mammal Laboratory, Seattle, WA. 80 pp.
- GALIMBERTI, F., AND S. SANVITO. 2001. Modeling female haul-out in southern elephant seals (*Mirounga leonina*). *Aquatic Mammals* 27:92–104.
- HARINGTON, C. R., R. L. M. ROSS, R. W. MATHEWES, K. M. STEWART AND O. BEATTIE. 2004. A late Pleistocene Steller sea lion (*Eumetopias jubatus*) from Courtenay, British Columbia: Its death, associated biota, and paleoenvironment. *Canadian Journal of Earth Sciences* 41:1285–1297.
- HARLIN-COGNATO, A., J. W. BICKHAM, T. R. LOUGHLIN AND R. L. HONEYCUTT. 2006. Glacial refugia and the phylogeography of Steller's sea lion (*Eumetopias jubatus*) in the North Pacific. *Journal of Evolutionary Biology* 19:955–969.
- KASTELEIN, R. A., AND F. C. WELTZ. 1990. Distribution abundance reproduction and behavior of Steller sea lions *Eumetopias jubatus* in Prince William Sound, Alaska, USA. *Aquatic Mammals* 15:145–157.
- KASTELEIN, R. A., AND F. C. WELTZ. 1991. Distribution and behaviour of Steller sea lions (*Eumetopias jubatus*) in Prince William Sound, Alaska, June 1989. *Aquatic Mammals* 17:91–97.
- KENYON, K. W., AND D. W. RICE. 1961. Abundance and distribution of the Steller sea lion. *Journal of Mammalogy* 42:223–234.
- KREBS, C. J. 1996. Population cycles revisited. *Journal of Mammalogy* 77:8–24.
- KUCEY, L. 2005. Human disturbance and the hauling out behaviour of Steller sea lions (*Eumetopias jubatus*). M.Sc. thesis, University of British Columbia, Vancouver, BC. 75 pp.
- LOUGHLIN, T. R., AND A. E. YORK. 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. *Marine Fisheries Review* 62:40–45.
- LOUGHLIN, T. R., D. J. RUSH AND C. H. FISCUS. 1984. Northern sea lion distribution and abundance: 1956–80. *Journal of Wildlife Management* 48:729–740.
- LOUGHLIN, T. R., A. S. PERLOV AND V. A. VLADIMIROV. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. *Marine Mammal Science* 8:220–239.
- LYMAN, R. L. 1988. Zoogeography of Oregon coast marine mammals: The last 3,000 years. *Marine Mammal Science* 4:247–264.
- LYMAN, R. L. 1989. Seal and sea lion hunting: A zooarchaeological study from the southern northwest coast of North America. *Journal of Anthropological Archaeology* 8:68–99.
- MAHONEY, S. P., AND J. A. VIRGL. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. *Canadian Journal of Zoology* 81:321–334.
- MANLEY, W. F., AND D. S. KAUFMAN. 2002. Alaska paleoglacier atlas. Institute of Arctic and Alpine Research (INSTAAR), University of Colorado, Boulder, CO.
- MATHISEN, O. A., AND R. J. LOPP. 1963. Photographic census of the Steller sea lion herds in Alaska, 1956–58. Special Scientific Report on Fisheries 424. U.S. Fish and Wildlife Service, 20 pp.

- McLOUGHLIN, P. D., R. L. CASE, R. J. GAU, H. D. CLUFF, R. MULDER AND F. MESSIER. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132:102–108.
- MILETTE, L. L. 1998. Reproductive life history, survival, and site fidelity of Steller sea lions (*Eumetopias jubatus*) in Alaska. Alaska Department of Fish and Game, Wildlife Conservation Division, Juneau, AK.
- MOULTON, V. D., W. J. RICHARDSON, T. L. McDONALD, R. E. ELLIOT AND M. T. WILLIAMS. 2002. Factors influencing local abundance and haulout behaviour of ringed seals (*Phoca hispida*) on landfast ice of the Alaskan Beaufort. *Canadian Journal of Zoology* 80:1900–1917.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA) OFFICE OF RESPONSE & RESTORATION (OR&R) HAZARDOUS MATERIALS RESPONSE DIVISION. 1997. Kodiak Island and Shelikof Strait, Alaska; Bristol Bay, Alaska; Southern California; San Francisco Bay, California; Northern California; Western Alaska (Volume 1 and 2); Kodiak, Alaska; Southeast Alaska (Volume 1 and 2); Cook Inlet, Alaska; North Slope, Alaska; Aleutian Islands, Alaska; NW Arctic, Alaska (Volume 1 and 2); Prince William Sound, Alaska (Volume 1 and 2); Oregon and Washington Environmentally Sensitive Areas. ESI Maps, CD-ROM. NOAA OR&R, Seattle, WA.
- NATIONAL RESEARCH COUNCIL. 2003. The decline of the Steller sea lion in Alaskan waters: Untangling food webs and fishing nets. National Academies Press, Washington, DC.
- NMFS. 2001. Endangered Species Act. Section 7 Consultation—Biological opinion on authorization of Gulf of Alaska and Bering Sea/Aleutian Islands groundfish fisheries based on the Fishery Management Plan for the Gulf of Alaska and Bering Sea/Aleutian Islands groundfish as modified by amendments 61 and 70. Appendix A to the Draft SEIS for Steller Sea Lion Protection Measures, August 2001. NMFS—Alaska Region, Protected Resources Division, Silver Spring, MD.
- NORDSTROM, C. A. 2002. Haul-out selection by Pacific harbor seals (*Phoca vitulina richardii*): Isolation and perceived predation risk. *Marine Mammal Science* 18:194–205.
- OLESIU, P. F. 2003. Recent trends in the abundance of Steller sea lions (*Eumetopias jubatus*) in British Columbia. Working Paper 2003-11. DFO National Marine Mammal Review Committee (Available from the author at Pacific Biological Station, Nanaimo V9T 6N7, BC), 9 pp.
- PITCHER, K. W., AND D. C. McALLISTER. 1981. Movements and haulout behavior of radio-tagged harbor seals, *Phoca vitulina*. *Canadian Field-Naturalist* 95:292–297.
- RAUM-SURYAN, K. L., K. PITCHER, D. G. CALKINS, J. L. SEASE AND T. R. LOUGHLIN. 2002. Dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumetopias jubatus*) in an increasing and a decreasing population in Alaska. *Marine Mammal Science* 18:746–764.
- REDER, S., C. LYDERSEN, W. ARNOLD AND K. M. KOVACS. 2003. Haulout behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biology* 27:6–16.
- RETTIE, W. J., AND F. MESSIER. 2000. Hierarchical habitat selection by woodland caribou: Its relationship to limiting factors. *Ecography* 23:466–478.
- SCHNEIDER, D. C., AND P. M. PAYNE. 1983. Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. *Journal of Mammalogy* 64:518–520.
- SJOBERG, M., AND J. P. BALL. 2000. Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: Bathymetry or central-place foraging? *Canadian Journal of Zoology* 78:1661–1667.
- STIRLING, I. 1983. The evolution of mating systems in pinnipeds. Pages 489–527 in J. F. EISENBERG AND D. G. KLEIMAN, eds. *Advances in the study of mammalian behavior*. American Society of Mammalogists, Shippensburg, PA.
- SURYAN, R. M., AND J. T. HARVEY. 1998. Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. *Marine Mammal Science* 14:361–372.

- THE R FOUNDATION FOR STATISTICAL COMPUTING. 2004. R: A language and environment for statistical computing. R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria.
- TRITES, A. W. 1990. Thermal budgets and climate spaces: The impact of weather on the survival of Galapagos (*Arctocephalus galapagoensis* Heller) and northern fur seal pups (*Callorhinus ursinus* L.). *Functional Ecology* 4:753–768.
- TRITES, A. W., AND L. P. DONNELLY. 2003. The decline of Steller sea lions in Alaska: A review of the nutritional stress hypothesis. *Mammal Review* 33:3–28.
- WALKER, P. L., D. J. KENNETT, T. L. JONES AND R. DELONG. 2000. Archaeological investigations at the Point Bennett pinniped rookery on San Miguel Island. Pages 628–632 in D. BROWNE, K. MITCHELL AND H. CHANEY, eds. U.S. Department of the Interior, Minerals Management Service, Pacific OCS Region, Camarillo CA.
- WATTS, P. 1996. The diel hauling-out cycle of harbour seals in an open marine environment: Correlates and constraints. *Journal of Zoological Society London* 240:175–200.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:
Supplementary Appendix 1
Supplementary Appendix 2
Supplementary Appendix 3