

Modelling and characterization of Steller sea lion haulouts and rookeries using oceanographic and shoreline type data

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Abstract

Steller sea lions range across the Pacific rim from Southern California in the east to northern Japan in the west, where they have continuously occupied terrestrial resting sites (haulouts) and breeding sites (rookeries) for hundreds of years, if not longer. Why they choose (and stay) at these locations, and what their preferred habitat is, remains unknown. Thus, two aspects of the Steller sea lion's habitat usage were examined—the oceanographic and the terrestrial. For the oceanographic aspect, spatial models were constructed to determine which oceanographic factors are associated with haulouts and rookeries, and how conditions near sites might differ from conditions elsewhere. The two modelling techniques employed (logistic regression and supervised classification) were evaluated using the kappa statistic (K_{no}), and receiver-operating characteristic (ROC) plots. Supervised classification was found to produce better-fitting models than logistic regression.

In general, Steller sea lions showed preferences for sites associated with waters that were relatively shallow, well-mixed, had higher average tidal speeds and less-steep bottom slopes. Conditions within 1 nautical mile of land were better predictors of haulout and rookery locations than were conditions within 10, 20, and 50 nautical miles. No consistent differences were found in the physical characteristics of waters surrounding sites in the eastern and western populations of Steller sea lions, or between haulouts and rookeries.

Regarding the terrestrial aspect of their habitat, anecdotal accounts describe Steller sea lions as predominantly occupying exposed, rocky shorelines, but this habitat preference has never been quantified. Locations of haulouts and rookeries were compared against a coastline type database to identify the shoreline preferences of Steller sea lions and to look for other spatial trends in site characteristics. Haulouts and rookeries were preferentially located on exposed rocky shorelines and wave-cut platforms. No relationship was found between either latitude or longitude of a site and its average non-pup count.

The results indicate that there are differences in both the oceanographic and terrestrial characteristics of sites used by Steller sea lions versus areas of coastline where they are not found. The models could be used to predict changes in habitat use given changing physical conditions, and could be applied to any central-place forager.

Table of Contents

Abstract.....	ii
Table of Contents.....	iv
List of Figures.....	v
List of Tables.....	vi
List of Plates.....	viii
Acknowledgements.....	ix
Chapter 1 - Introductory Chapter.....	1
Background.....	1
Biogeography of haulouts and rookeries.....	3
Methodology.....	5
Assumptions and limitations.....	7
Hypotheses.....	9
References.....	10
Chapter 2 - Physical oceanographic characteristics associated with Steller sea lion haulouts and rookeries throughout their range in the North Pacific.....	15
Introduction.....	15
Methods.....	16
Results.....	25
Discussion.....	29
Summary.....	40
References.....	42
Chapter 3 - Quantification of Terrestrial Habitat Preferences of Steller Sea Lions.....	48
Introduction.....	48
Methods.....	50
Results.....	55
Discussion.....	57
Summary.....	59
References.....	60
Chapter 4 - Conclusions.....	64
References.....	69
Appendix I - ROC values and K_{no} values for models at varying probability thresholds.....	80
Prediction of Rookery Locations – Mainland & Offshore.....	80
Prediction of Haulout Locations – Mainland & Offshore.....	82
Prediction of Rookery Locations – Offshore Only.....	84
Prediction of Haulout Locations – Offshore Only.....	86
Appendix II - Environmental Sensitivity Index (ESI) shoretypes.....	89

List of Figures

Figure 2.1 Four physical variables used to characterize the waters surrounding Steller sea lion haulouts and rookeries.....	18
Figure 2.2 Example of training area mask, showing application of a 20 nautical mile buffer around Steller sea lion rookeries in the Gulf of Alaska and Eastern Aleutian Islands.....	20
Figure 2.3. Area under curve (AUC) values for models.....	27
Figure 2.4 K_{no} values for classification models, comparing models trained using eastern population sites vs. western population sites.....	28
Figure 2.5 Means and standard errors of habitat and non-habitat areas.....	31
Figure 3.1 Usage of shoreline types by haulouts and rookeries versus available shoreline across entire range.....	56
Figure 3.2 Latitude and longitude vs. average non-pup count of haulouts and rookeries.....	57

List of Tables

Table 3.1. NOAA ESI Shoreline types.....	52
Table 3.2. British Columbia Coastal Response and Oil Spill Atlas	53
Table 3.3. Conversion between BC Shoreline classification and NOAA ESI.....	54
Table A1.1. K_{no} (Kappa) values for predicting rookery locations using rookeries as training areas for classification model.....	81
Table A1.2. ROC values predicting rookeries using rookeries as training areas.	81
Table A1.3. Logistic model performance (K_{no}) predicting rookeries using rookeries as training areas at varying probability thresholds.....	81
Table A1.4 K_{no} (Kappa) values for predicting haulout locations using rookeries as training areas.....	83
Table A1.5 K_{no} (Kappa) values for predicting haulout locations using haulouts as training areas.....	83
Table A1.6 ROC values predicting haulouts using rookeries as training areas...	83
Table A1.7 ROC values predicting haulouts using haulouts as training areas.	83
Table A1.8. Logistic model performance (K_{no}) predicting haulouts using rookeries as training areas.....	84
Table A1.9. Logistic model performance (K_{no}) predicting haulouts using haulouts as training areas.	84
Table A1.10 K_{no} (Kappa) values for predicting rookery locations using rookeries as training areas.	85
Table A1.11 ROC values predicting rookeries using rookeries as training areas.	85
Table A1.12. Logistic model performance (K_{no}) predicting rookeries using rookeries as training areas.....	85
Table A1.13. Classification model performance (K_{no}) predicting haulouts using rookeries as training areas.....	86
Table A1.14. Classification model performance (K_{no}) predicting haulouts using haulouts as training areas.....	87
Table A1.15. ROC values predicting haulouts using rookeries as training areas.	87

Table A1.16. ROC values predicting haulouts using haulouts as training areas. 87

Table A1.17. Logistic model performance (K_{no}) predicting haulouts using rookeries as training areas..... 88

List of Plates

Plate 1. ESI shoreline type 1 – exposed rocky shores.....	89
Plate 2. ESI shoreline type 2 – exposed rocky platforms.....	90
Plate 3. ESI shoreline type 3 – Fine-grained sand beaches.....	90
Plate 4. ESI shoreline type 4 – coarse-grained sand beaches.....	91
Plate 5. ESI shoreline type 5 – mixed sand and gravel beaches.....	91
Plate 6. ESI shoreline type 6a – gravel beaches.....	92
Plate 7. ESI shoreline type 6b – riprap structures.....	92
Plate 8. ESI shoreline type 7 – exposed tidal flats.....	93
Plate 9. ESI shoreline type 8a – sheltered rocky shores.....	93
Plate 10. ESI shoreline type 8b – Sheltered artificial structures.....	94
Plate 11. ESI shoreline type 9 – sheltered tidal flats.....	94

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And this one's for you, Papa.

Chapter 1 - Introductory Chapter

Background

Steller sea lions (*Eumetopias jubatus*, also known as northern sea lions) are the largest members of the Otariid family, and inhabit the northern Pacific Ocean from central California in the east, to northern Japan in the west (Loughlin et al. 1984). Since the late 1970s, there has been a decrease in their overall numbers by over 85% (Loughlin et al. 1992, Trites & Larkin 1996, Calkins et al. 1999). Following these declines, the National Marine Fisheries Service (NMFS) designated the Steller sea lion as a threatened species under the Endangered Species Act in 1990 (55 Fed Reg 12645, Apr 5 & 55 FR 49204, Nov 26). In 1997, two separate populations separated at 144° W longitude were recognized. The western population (Aleutian Islands and Gulf of Alaska), which had suffered a greater decline than the eastern population (SE Alaska, Washington, Oregon, California), was reclassified as endangered (62 FR 24345, May 5).

In accordance with the requirements of the Endangered Species Act, NMFS established protective regulations and began the population recovery process. NMFS appointed a Steller Sea Lion Recovery Team in 1990 and published a Final Recovery Plan in 1992 that recommended management and research actions to aid the species' recovery. The recovery team was reconvened in 2000, and has been charged with drafting a new recovery plan.

An important feature of the Endangered Species Act listing is the designation of the species' critical habitat. Critical habitat is defined as "areas...the loss of which would appreciably decrease the likelihood of the survival and recovery of a listed species or a distinct segment of its population..." (Littell 1992). NMFS designated Steller sea lion critical habitat as all major Steller sea lion rookeries and haulouts in Alaska, as well as terrestrial, air, and aquatic zones surrounding these sites. The terrestrial zone extends 3,000 feet (0.9 km) landward, the air zone extends 3,000 feet (0.9 km) above the terrestrial zone and the aquatic zone extends 20

Introductory Chapter

nm (37 km) seaward in State and Federally managed waters west of 144° W longitude (50 CFR § 226.202). "Major" rookeries and haulouts were defined as those with two hundred or more animals.

In designating critical habitat, NMFS regarded conservation and management of prey resources and foraging areas as essential to the recovery of the Steller sea lion populations (58 Fed Reg 45269, Aug 27, 1993). In proposing the 20 nm aquatic zone, NMFS claimed that aquatic areas surrounding major rookeries and haulouts provided foraging habitats, prey resources and refuges that are not only essential to lactating females and juveniles, but also encompass areas for non-breeding animals year-round and for reproductively active animals during the non-breeding season. Although NMFS admitted that specific foraging sites and their constancy over time have not been well defined, it decided to rely on their ongoing studies using satellite telemetry and their findings of summertime foraging range of postpartum females occurring mainly in relative shallow waters within 20 nm of the rookeries (58 Fed Reg 17181, Apr 1, 1993). Such findings are consistent with the information provided in the Final Recovery Plan, which cited unpublished data of the National Marine Mammal Laboratory (NMFS 1992).

The reasons for Steller sea lion population declines have not been determined (DeMaster & Atkinson 2002, Trites & Donnelly 2003) and population trends show considerable regional variation. Hunter & Trites (2001) identified twelve hypotheses for the Steller sea lion decline: competition with fisheries, juvenile mortality, nutritional stress (junk food and starvation), increased predation, intentional and accidental human kills, migration to other populations, regime shift, disease, pollution, trophic cascade (causing changes in prey availability), and adult mortality. Considerable research effort has focused on the possible effects on Steller sea lions of anthropogenic disruptions such as fishing (Springer 1992, Aydin 2002), incidental and direct mortality (Bigg 1985, Pascual & Adkison 1994, Perlov 1996, Shima et al. 2000), harassment, and disruption of rookery sites. Examining the spatial influence of oceanographic and other environmental factors is a relatively new area of research. To date, relatively little attention has

Introductory Chapter

been given to the relationship between physical and abiotic factors and Steller sea lion distributions, even though this approach is common with other species, both terrestrial and marine.

There is a need to clarify what “critical habitat” is with respect to the Steller sea lion, and perhaps to go beyond protective measures based simply on fixed-radius buffer zones around rookeries. Boundaries of protected areas could instead be based on natural habitat boundaries such as bathymetric contours or other physical or biological oceanographic features.

Biogeography of haulouts and rookeries

Locations of rookeries and haulouts have been very stable historically, with some sites documented to have been in use for more than four centuries (Lyman 1988, Walker et al. 2000). The establishment of truly “new” rookeries (as opposed to recolonizations) appears to be relatively rare (Raum-Suryan 2002).

The stability of site locations presumably indicates that they possess certain favourable characteristics—such as proximity to reliable foraging areas, protection from predators, or some other combination of factors. This in turn implies that the factors that have shaped the selection of haulout and rookery sites must also have been relatively stable over time, and resilient to interannual (or longer) shifts in environmental parameters. Steller sea lions tend to return to their rookeries of birth as adults, but the return rate is not 100% (Milette 1998, Raum-Suryan 2002). This propensity for natal site fidelity is undoubtedly another factor influencing the choice of rookeries, but it may also simply be the product of favourable conditions that have shaped the successful selection of sites, given that haulouts also appear to be as stable over time as rookeries. Furthermore, sea lions have returned to sites that had been previously abandoned or where they were extirpated many years beforehand (Bigg 1985, 1988). Thus, neither natal site fidelity nor conspecific attraction (Stamps 1988) can completely explain the distribution and stability of Steller sea lion rookeries and haulouts.

Introductory Chapter

Although Steller sea lions have been the subject of numerous (and extensive) directed kills and culls, very few, if any, sites have been abandoned, although some have reverted from rookeries to haulouts, and others have changed from haulouts to rookeries (P. Olesiuk, Fisheries and Oceans Canada, Nanaimo, pers. comm, L. Fritz, NMFS, Seattle, pers. comm, K. Pitcher, NMFS, pers. comm). The exceptions are at the extreme edges of the Steller's range, such as the Channel Islands (California) that have been abandoned (K. Ono, University of New England, unpubl. data), and in Japan, where there appears to have been a slight range contraction (V. Burkanov, NMFS, unpubl. data).

Thus, while individual rookery and haulout sites are only occupied relatively briefly from a geological and evolutionary standpoint of the species, the usage and distribution of currently occupied sites—at least in the Bering Sea and Gulf of Alaska region—have been relatively stable and static for a substantial portion of the species' history in this area.

Lyman (1989) quotes several anecdotal 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 rookeries or haulouts are known. Steller sea lions are also noted to 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. They are rarely found in inland waters and are considered a near-shore species. Bigg (1985) noted that year-round haulouts are usually found in places that are directly exposed to oceanic swells, whereas winter-only haulouts are generally not exposed directly to these swells, and are sheltered to some extent by the surrounding topography. Kastelein & Weltz (1991) studied two sites in Prince William Sound, Alaska, and observed that haulout behaviour was probably influenced by the physical geography of a colony site, particularly regarding variations in the number of animals at a site as tidal height changes. 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 believed that they favoured large,

Introductory Chapter

fairly level rock ledges over boulder beaches. Rookeries may be selected according to slightly different criteria from haulouts, since protection of pups from exposure may be an important consideration. Edie (1977) and Fiscus (1970) reported the death of many pups due to wave action from storms—thus suggesting that sites affording some protection from wave exposure may be favoured for rookeries.

Apart from anecdotal descriptions of their habitat preferences, there have been no quantitative studies to date of the factors – biotic or abiotic – that may influence the selection of these sites. My thesis thus has two main objectives: to determine and quantify what terrestrial factors influence Steller sea lion habitat selection, and to determine what physical oceanographic factors might be important in influencing this selection.

Methodology

Logistic regression has frequently been used to model habitat, but typically for terrestrial animals such as songbirds (Dettmers & Bart 1999), muskrats (Nadeau et al. 1995), and wolves (Mladenoff & Sickley 1998). In the aquatic environment, such models are common for fish (Beauchamp et al. 1992, Yu et al. 1995, Parrish et al. 1997, Diller & Wallace 1999, Knapp & Preisler 1999, Guay et al. 2000, Porter et al. 2000, Broad et al. 2001, Oberdorff et al. 2001, Mattingly & Galat 2002, Morita & Yamamoto 2002, Sato et al. 2002). Otherwise, there have been few attempts until very recently to model the habitats of other organisms in the pelagic environment using this approach (Moses & Finn 1997, Gregr & Trites 2001, Hamazaki 2002).

Maintaining the spatial nature of data is central to the concept of a geographic information system (GIS). This allows for methodologies that combine an ecology-based spatial analysis with statistical treatment. A recent review of factors influencing sperm whale distribution emphasized the “absence of consideration of the spatial and temporal scales at which relevant oceanographic

Introductory Chapter

processes occur” and concluded that “multiscale studies . . . are needed” (p.55, Jaquet 1996). Hence, some of the reasons for using a GIS are:

- 1) Retaining the geographic characteristics of the data to produce a meaningful output (e.g. maps correlating oceanographic data with rookery site selection);
- 2) Statistical analysis of a spatial nature is necessary to determine the strength and nature of the relationships between various oceanographic variables such as sea surface (Sydeman & Allen 1999), upwellings (Su & Sheng 1999, Sydeman & Allen 1999), currents, and rookery site selection;
- 3) Ecologically based analysis ensures that any statistically derived relationships make sense within an ecological context.

Oceanographic data such as coastline data and bathymetry have been used in conjunction with observer sightings and satellite data using GIS as a means to develop statistical models for cetaceans (Barber & Chavez 1983, Moses & Finn 1997), but such efforts are often complicated by the three-dimensional (actually, four-dimensional) nature of the marine environment, and by the elusive nature of purely aquatic animals. Due to their life history, pinnipeds present an interesting and useful (from a modeling standpoint) combination of characteristics: their need to breed and rest on land, coupled with their at-sea foraging. Furthermore, observer and telemetry data for Steller sea lions is particularly rich, and much research has gone into trying to understand and model their foraging habits. Consequently, it would be beneficial to both our understanding of Steller sea lions specifically, and of pinnipeds in general, to derive a quantitative method to identify potential habitats (e.g. sea lion rookeries) using the capabilities of a GIS.

The approach described in Chapter 2 combines the use of a GIS to maintain spatial information with a statistical technique (logistic regression) and a technique adopted from remote sensing (supervised classification) to calculate a cell-by-cell prediction probability that relates to the likelihood of waters being near (or being used by) Steller sea lions.

Assumptions and limitations

To effectively model the habitat usage of Steller sea lions, there are some simplifying assumptions that need to be made and justified, and some statistical issues that need to be addressed related to these assumptions.

The primary assumption being made in the models I developed is that the areas chosen for “presence” and “absence” are in fact reflective of the true distributions of Steller sea lions. For the oceanographic model presented in Chapter 2, this is a key distinction, because typically it is the presence or absence of *individual animals* that is being modeled—in my model, presence and absence refer not to individual animals, but to breeding and congregation sites that have proven to be stable over time. Therefore, the model assumptions centre around the use or importance of the waters surrounding a rookery or haulout rather than the presence or absence of individual animals within those waters.

Secondly, the waters surrounding rookeries and haulouts could either be represented as an equally weighted grid within the desired search distance(s), without regard for proximity (i.e., cells close to shore have as much weight as those further away, as long as both are within the specified foraging distance), or they could be weighted based on their distance from shore. I chose to give all cells equal weight, because insufficient telemetry data exists on how Steller sea lions utilize the waters around rookeries and haulouts.

The third assumption I made concerned the size of the rookery or haulout with which waters are associated, and whether this should impart a weight to the areas surrounding each site. Equal weighting was again chosen because the models are intended to reflect long-term habitat decisions that may not be reflected by count data that only includes the past 20-30 years.

The primary difficulty with building a model pertaining to Steller sea lion habitat is that the geographic range is quite large, and crosses the jurisdictional boundaries of four countries (United States, Canada, Japan, and Russia). This made it

Introductory Chapter

difficult to find a consistent data set across the entire study area: quality and scale/resolution may differ depending upon the source of the data. Data that were available for most of the range (excluding Japan and the Commander Islands in Russia) were bathymetry, average tidal speeds, shoreline characterization, and the location of haulout and rookery (breeding) sites.

Bathymetry is an important data set, as the continental shelf is thought to be a key factor in Steller sea lion foraging, and the accessibility of benthic prey may be dictated by the bottom depth. Additionally, features such as seamounts, underwater ridges, and other regions of topographic complexity are typically sites of high biological productivity.

Slope can be derived from the bathymetric data. At large scales, slope often plays a role in determining where regions of upwelling occur, as currents are forced upwards by bottom topography. At finer scales, slope can be a proxy for rugosity (bottom complexity), which typically provides better quality habitat for benthic organisms (Watling & Norse 1998).

Predators often make use of areas of high productivity that are associated with areas of high tidal mixing, fronts, or rips (Schneider et al. 1990, Suryan & Harvey 1998), so both average tidal speed and a calculated stratification parameter (Perry et al. 1983) may be useful in identifying these areas.

All of the data I used were initially provided as point data, spaced as close as ~500 m in near-shore areas and ~1-2 km apart offshore. These data were interpolated using an inverse-distance weighting algorithm, which, although generally considered to be not as accurate as kriging, tends to be less computationally intensive – an important consideration when dealing with data sets of this size. Thus interpolated, the data then formed a contiguous raster grid fully populated with values estimated from the initial data sets.

The problems associated with data interpolation and spatial autocorrelation are acknowledged in the literature (e.g. Gregr & Trites 2001), and remain contentious

among the spatial modeling community. While they may not be fully resolvable, it is important to acknowledge the limitations and possible faults of a technique that has not yet fully matured.

Hypotheses

Site selection likely involves either an optimization or compromise of two factors: proximity to favourable at-sea foraging areas, and availability or accessibility of terrain that allows both ingress and egress during variable tidal heights. If Steller sea lions select sites solely on the criterion that they are close to productive at-sea foraging areas, then the current distribution of sites would be expected to correspond with the available distribution of shoreline types. Conversely, if only terrestrial characteristics of sites are important, the characteristics of waters surrounding rookeries and haulouts would not be expected to differ from waters that are not near Steller sea lion sites.

The two principal chapters of my thesis address these two aspects of the Steller sea lion's habitat usage—the oceanographic and the terrestrial. In the first chapter, my primary hypothesis is that waters near Steller sea lion haulouts and rookeries are different from other coastal waters. Similarly, I expected the waters near rookeries to differ from those near haulouts. Finally, the utility and efficacy of two different techniques for generating habitat models were evaluated.

In the second chapter, I tested two hypotheses concerning the terrestrial habitat needs of Steller sea lions. The first was that the distribution of Steller sea lion haulouts and rookeries is not random with respect to the availability of different shoreline types, and second, that rookeries differ from haulouts in the preferred type of shoreline, presumably because pups and young animals might be less agile than mature animals, and thus less able to access steep or rough sites. Finally, I compared the latitude and longitude, and nature of sites against average non-pup counts to determine whether a relationship existed between either of these factors and the success or popularity of a site.

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Introductory Chapter

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Chapter 2 - Physical oceanographic characteristics associated with Steller sea lion haulouts and rookeries throughout their range in the North Pacific

Introduction

Steller sea lions (*Eumetopias jubatus*) range across the north Pacific from central California in the eastern Pacific to northern Japan in the west. They rest on land at haulouts, and breed on rookeries. There are 88 known rookeries range-wide, and nearly 600 haulouts. Steller sea lions have been divided into two genetically distinct stocks: the eastern stock, which lies east of 144°W, and the western stock, which lies west of this line. The eastern stock has been stable or increasing in numbers over the past several decades, whereas the western stock has experienced a sharp decline since the mid- to late-1970s, and has been listed as an endangered species in Alaska (Trites & Larkin 1996, NMFS 2001a). Locations of rookeries and haulouts have been very stable historically, with some sites documented to have been in use for more than four centuries (Lyman 1988, Walker et al. 2000).

The stability of site locations presumably indicates that they possess certain favourable characteristics—such as proximity to reliable foraging areas, protection from predators, or some other combination of factors. This in turn implies that the factors that have shaped the selection of haulout and rookery sites must also have been relatively stable over time, and resilient to interannual (or longer) shifts in environmental parameters. Steller sea lions tend to return to their rookeries of birth as adults, but the return rate is not 100% (Milette 1998, Raum-Suryan 2002). This propensity for natal site fidelity is undoubtedly another factor influencing the choice of rookeries, but it may also simply be the product of favourable conditions that have shaped the successful selection of sites, given

Characteristics of Steller haulouts and rookeries

that haulouts also appear to be as stable over time as rookeries. Furthermore, sea lions have returned to sites that had been previously abandoned or where they were extirpated many years beforehand (Bigg 1985, 1988). Thus, neither natal site fidelity nor conspecific attraction (Stamps 1988) can completely explain the distribution and stability of Steller sea lion rookeries and haulouts.

The objective of my study was to determine whether stable site usage by Steller sea lions could be driven by correspondingly stable environmental cues, and whether these cues could be used to predict future changes in habitat usage should these cues change.

My approach was to construct spatial models describing the physical characteristics associated with rookeries and haulouts (e.g. bathymetry, tidal speed, etc.). I used two different modelling approaches (logistic regression and supervised classification) to identify locations along the coast that share desirable features associated with sites currently used by Steller sea lions. Comparing selected or preferred sites ("habitat") with non-preferred ("non-habitat") should allow qualitative statements to be made about the habitat preferences of Steller sea lions—from which it might be possible to infer whether these differences represent a life-history strategy in an unpredictable and highly variable environment (Barber & Chavez 1983, Shima et al. 2000).

My primary hypothesis was that waters near Steller sea lion haulouts and rookeries were different from other coastal waters. Similarly, I expected the waters near rookeries to differ from those near haulouts. Finally, the utility and efficacy of two different techniques for generating habitat models was evaluated.

Methods

Models of species-habitat association generally share similar methodologies in terms of input data sets, but differ with regards to how data are used to predict habitat. Most require data about where species have and have not been seen, while some require only presence data (Hirzel et al. 2002, Kery 2002). The most

Characteristics of Steller haulouts and rookeries

common type of habitat models use discriminant analysis, general linear models, decision trees, or artificial neural networks. Where remote sensing data is available, techniques specific to these data sets (supervised/unsupervised classifications) are often applied (e.g. Luoto et al. 2002).

I applied remote sensing multispectral classification techniques to the waters surrounding Steller sea lion rookeries and haulouts. Multispectral image classification can be divided into two broad categories: supervised and unsupervised. In an unsupervised classification, the number of desired output categories (classes) is typically specified. For example, in a satellite image there are typically a number of different layers (called bands), each contributed by a different sensor that is sensitive to a particular portion of the electromagnetic spectrum. When these sensors correspond to red, green, and blue, the combined result is a “true-colour” image, i.e., what we see in a normal colour photograph. Image classification uses algorithms to analyse each component band of a digital image to identify clusters of similar values within each band. In a supervised classification, areas on the image that have a known class membership (e.g. water or trees) can be selected and used as “training areas”. An algorithm would then analyse the remaining pixels in the image to find those that are most similar in value (for each layer or parameter of interest) to the training areas. Both types of analysis (supervised and unsupervised) are aspatial with respect to pixel values (i.e., the spatial location of a pixel does not necessarily reflect which category or class into which it will be placed).

Three main considerations limited my choice of predictor variables. First, the North Pacific study area covered a large geographical range. Second, a fairly high spatial resolution was required to distinguish sites in high-density areas (i.e. areas that had large numbers of rookeries and haulouts). Finally, it was important that factors (e.g. bathymetry and tidal speeds) be temporally invariant (i.e. insensitive to seasonal changes and climatic regime shifts). These considerations effectively narrowed the available data to just four sets: bathymetry, slope, mean tidal speed, and a mixing index (Figure 2.1).

Characteristics of Steller haulouts and rookeries

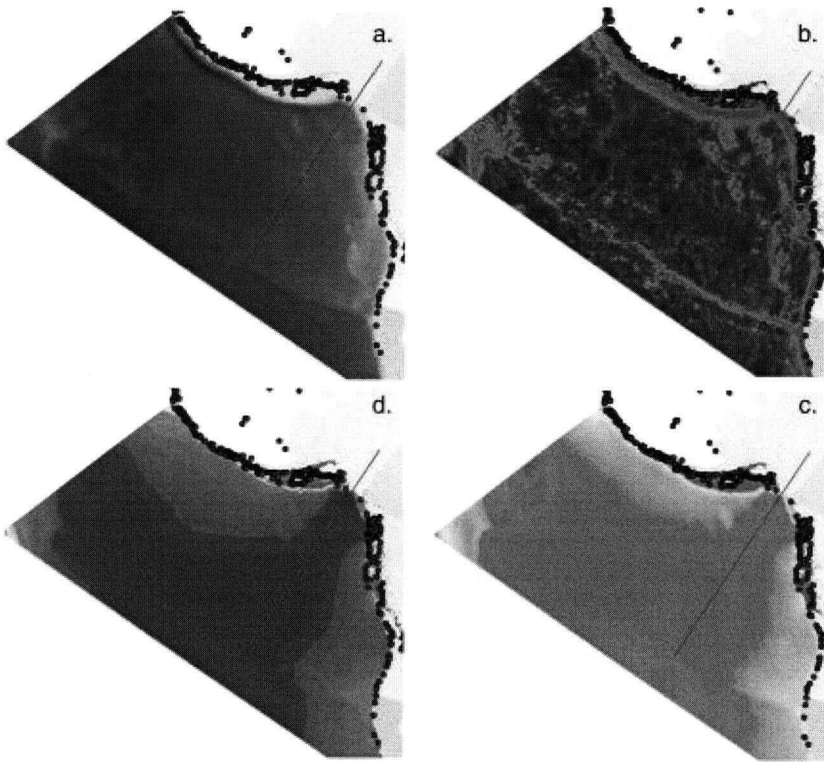


Figure 2.1 Four physical variables used to characterize the waters surrounding Steller sea lion haulouts and rookeries. The diagonal line shows the division between the eastern and western populations of Steller sea lions. a) Bathymetry. Shallow areas are in light grey; deeper areas in dark grey. b) Slope: Areas in light grey have low slope; areas in dark grey have high slope. c) Mixing index: Areas in dark grey are well-mixed; areas in lighter grey are poorly-mixed (stratified). d) RMS tidal speed: Areas in light grey have high tidal speeds; areas in dark grey have low tidal speeds.

Tidal speeds and bathymetry were obtained from M.G.G. Foreman (Institute of Ocean Sciences, Sidney, B.C., pers. comm); slope was derived from bathymetry; and the Simpson-Hunter mixing index (Simpson & Hunter 1974), or stratification parameter was derived from the depth and tidal speed as follows:

$$S = \log_{10} \left[\frac{h}{C_d |\bar{U}|^3} \right]$$

where S is the stratification parameter, h is depth (in cm), U the instantaneous tidal velocity (cm s^{-1}), and C_d the bottom drag coefficient, which was set at 0.0025

Characteristics of Steller haulouts and rookeries

(Perry et al. 1983). This index indicates whether waters are well-mixed ($S < 1.0$), or stratified ($S > 2.0$).

ArcView (ESRI 1992-1999) and ArcGIS (ESRI 1999-2002) were used to perform data input, interpolation, and projection (conversion from degrees of latitude and longitude to metres), while IDRISI32 software (Eastman 2002) was used to perform image analysis and develop the supervised classification models. SPSS (1997) was used to develop the logistic regression models, and to collect summary statistics. Data points were placed on a 600-meter grid and interpolated as necessary using an inverse-distance weighted method. This interpolation was required for three reasons. First, a meaningful slope cannot be calculated from isolated depth data points. Second, the data points from the depth and tidal speed layers do not overlay exactly, which would make calculation of the mixing index (derived from a combination of depth and tidal speed data) impossible unless this interpolation was performed; and third, image classification algorithms require a continuous image, not discrete points, in order to function.

Cell size was based on the minimum distance between sample points in the tidal model, with each point also having an associated depth. The classification algorithm also required that all input data sets have the same resolution. Data were projected from latitude-longitude format to a Lambert projection, which ensured that area measurements remained constant across varying latitudes, since the size of a degree of latitude and longitude varies with position.

Each data set had to be first converted into an 8-bit (256 value) format for input to the classification algorithm, which normally expects satellite images as input. Hence, data were log-transformed, then reclassified into 256 bins (0-255). Thus, all variables received equal weighting in the supervised classification algorithm.

Rookery and haulout locations were obtained from a National Marine Fisheries database (C. Stinchcomb, NMFS, pers. comm.) 52 of 88 rookeries (59%) and 384 of the 594 haulouts (65%) in the database were included for analysis. The

Characteristics of Steller haulouts and rookeries

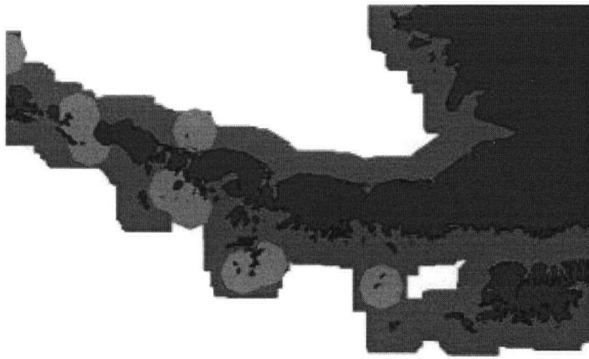


Figure 2.2 Example of training area mask, showing application of a 20 nautical mile buffer around Steller sea lion rookeries in the Gulf of Alaska and Eastern Aleutian Islands. The dark grey area is a 20 nmi coastline buffer.

remaining sites in northern Japan, Russia, and the Bering Sea were excluded because they fell outside of the range of available data.

Training areas—which are used to inform or “train” the model by selecting areas of known classification—were developed for rookeries in both the western and eastern populations using the accepted division line at 144°W longitude. The same procedure was

also applied to haulouts in a separate analysis, and to all “sites” combined (i.e. rookeries and haulouts). Four buffers or search distances of 1, 10, 20, and 50 nautical miles were used to delineate habitat. These varying distances effectively aggregated pixels at different scales, and thus allowed for analysis of scale-dependent effects. The four distances chosen represented typical approximate distances traveled by foraging animals (Merrick & Loughlin 1997), which vary according to sex, season, and age class. Adult males typically travel further than juveniles and adult females, with foraging distances for animals in winter being typically longer than in summer. There are also fishing restrictions within 10 and 20 nmi of certain Steller sites in Alaska (NMFS 2001b) that were implemented by fisheries managers in the belief that they represented important Steller sea lion habitat.

Pixels contained within a given buffer distance of an existing site were considered as habitat, while pixels within the same distance of the coastline, but not within range of any sites were considered to be non-habitat. All other pixels, including land and anything further offshore than the search distance, were masked out and not considered in the analysis (Figure 2.2).

Characteristics of Steller haulouts and rookeries

Sites were not weighted by population size, since the analysis was intended to represent long-term factors influencing habitat selection over time scales long enough to be insensitive to relatively rapid fluctuations in site-to-site animal numbers. Counts at individual sites often vary greatly from year to year (or from survey to survey), to the extent that even an averaged count for a site over the entire survey period would be unlikely to reflect the long-term “suitability” of a site. Additionally, reliable, comprehensive counts of animals only exist for the past 10-15 years, and thus would have skewed the analysis in favour of sites that have only recently had large numbers of animals, without regard for historical counts.

The described training areas were processed by an image classification algorithm in IDRISI called BAYCLASS, or sampled for analysis in a logistic regression model in SPSS.

Supervised classification model

BAYCLASS is a “soft” classifier, meaning that, for each output pixel, the algorithm expresses a degree of probability that the pixel belongs to a particular class (in this case, “habitat” or “non-habitat”). Specifically, each output pixel contains the posterior probability of belonging to the “habitat” class:

$$p(h|e) = \frac{p(e|H) * p(h)}{\sum_i p(e|h_i) * p(h_i)}$$

where: $p(h|e)$ is the probability of the hypothesis being true given the data (posterior probability), $p(e|h)$ is the probability of finding that evidence given the hypothesis being true (this is calculated from the information provided by the training site data), and $p(h)$ is the probability of the hypothesis being true regardless of the data (prior probability).

Prior probabilities were set as 50% each for habitat and non-habitat—in effect, indicating no prior knowledge of how pixels would be allocated. A total of 16

Characteristics of Steller haulouts and rookeries

models were generated (four buffer sizes for all sites in both the western and eastern stocks, plus one each for haulouts and rookeries separately). In order to evaluate the overall success of each habitat model, the resulting output probabilities were input to a "hardening" algorithm called MAXBAY, which produces a hard classification from the probability information. This required setting a probability threshold, below which pixels were considered to be "non-habitat". I initially set threshold values at 95% and lowered them in 5% increments (or raised them to 99%) until the kappa statistic was maximized. Probability thresholds ranged from 60% to 99%.

Logistic Regression Model

Training areas were encoded as 0 (absence: not within buffer distance of a site) or 1 (presence: within buffer distance of a site), and thus used as the dependent variable for the logistic regression model. Each cell containing a value for an oceanographic variable was then associated with a value of the dependent variable. The logistic models were developed using a forward stepwise likelihood ratio procedure in SPSS, which selected the variables with the most explanatory power first. The parameters for these variables were calculated in SPSS, and the values were passed back into ArcView to calculate predicted probabilities according to the logistic model:

$$\text{Pr}(\text{proximity to SSL site}) = \frac{1}{1 + e^x}$$

where:

$$x = a + \sum_i b_i * x_i$$

and a , and b_i represent the regression coefficients calculated for each of the x 's (independent variables) selected during the forward-stepwise selection process. This stepwise procedure was also used to validate the selection of variables

Characteristics of Steller haulouts and rookeries

used in the classification model rather than running a new classification model for each additional variable included.

Validation

The classifications generated by the models were quantitatively evaluated using the IDRISI VALIDATE and ROC functions. VALIDATE generates a series of kappa statistics (Pontius 2000) that assesses model fit. For any kappa statistic, a value of one indicates that a given classification is perfect, with any number above zero indicating that the observed (modelled) classification is better than that expected due to chance. Kappa values less than zero indicate that the model performs worse than a random model.

A standard contingency table compares the number of observed versus expected cells or pixels in each category between a true (or ideal) output and a modelled output. However, standard measures of correlation are aspatial, and thus cannot distinguish between two models with exactly the same number of correctly classified cells in completely different spatial locations. Kappa statistics take into account both location and quantity when evaluating model performance. For my study, I used the K_{no} statistic rather than the $K_{standard}$ because the proportion of classes (habitat to non-habitat) was low. When this is the case, $K_{standard}$ tends to underestimate model performance versus chance. K_{no} is more appropriate in this situation because it rewards accurate estimates of quantity more appropriately than $K_{standard}$ (Pontius 2000).

The performance of each model was thus evaluated in terms of both location and quantity of correctly classified pixels when compared to a theoretical "perfect" classification that was generated by buffering all rookeries (east and west) to the appropriate distance. The variance for each K_{no} value was calculated according to Couto (2003), and used to generate pair-wise (east versus west) z-scores to determine whether the differences in model performance were statistically significant. In the case of haulout predictions, the performance of models trained using rookeries was also evaluated against models trained using haulouts.

Characteristics of Steller haulouts and rookeries

The ROC (Receiver Operating Characteristic) function generates a table with the percentage of true positives (sensitivity) versus false positives (specificity) for each model compared to an ideal reference model. ROC plots were originally used in clinical laboratory settings to determine the diagnostic accuracy and utility of tests and assays (Zweig & Campbell 1993), but have since been found useful for evaluating the success of classification models as well (Fielding & Bell 1997, Pontius & Schneider 2001, Poulin et al. 2002). The sensitivity and specificity were calculated for a number of user-specified thresholds. However, these thresholds were set by ranking pixels according to this percentile threshold (e.g. a 90% threshold means that the pixels with the highest 10% of probability values are selected), rather than by using a set probability value. Thus the thresholds used in VALIDATE and ROC were not directly comparable, although the endpoints (0% and 100% cutoffs) were the same in both cases.

Calculating the area underneath the curve of an ROC plot provided an overall metric of model performance—the area under curve (AUC) statistic. A model with perfect discrimination (ability to distinguish positives from negatives) would have a plot that passes through the upper left corner of the two axes. A model that randomly assigns presence or absence to a pixel has an AUC value of 0.5 by definition, and is represented by a diagonal line from the lower-left to the upper-right of the plot. Thus, models with AUC values >0.5 are said to perform better than a random model.

The AUC statistic is threshold independent, and can be used to get an overall picture of model performance. However, there are instances in which a trivial rule (one that assigns all pixels to one category or another, rather than at random) will outperform all other models according to the K_{no} statistic, but not on the AUC measure. This typically arises when the proportion of habitat to non-habitat pixels is very skewed in one direction or the other, and thus a high proportion of false-positives (or false negatives) can be outweighed by having 100% true positives. The ROC function in IDRISI also calculates K_{no} values at several user-specified thresholds; in cases where a trivial rule (equivalent to setting a threshold of 0% or

Characteristics of Steller haulouts and rookeries

100%) outperformed any other threshold, but the AUC value was over 0.5, the next-highest K_{no} value at a non-zero threshold was selected. If the AUC value was less than 0.5, no further analysis was conducted and the model was rejected. The AUC score was thus used as the initial criterion to select models that warranted further examination with the Kappa statistic.

Prior to calculating the ROC and Kappa statistics, model outputs were first masked to exclude: (1) landmasses, (2) any distance further from shore than the original training data, and (3) areas that contained data that were extrapolated beyond the boundaries of the original input data.

Additionally, a "terrestrial predator exclusion" mask was applied that effectively excluded the mainlands of Alaska and British Columbia, as a proxy for the existence of large terrestrial predators such as grizzly and black bears that may have favoured the selection of sites that were inaccessible to these animals (nearly all of the present sites are offshore). While there are no reports of terrestrial predation on Steller sea lions in the literature, the threat of predation may have been an historical influence on the present location of sites. While some near-shore islands may be within swimming distance of large terrestrial predators, detailed information about presence/absence of bears was not available, so exclusion of the mainland was used as a crude proxy.

Results

Summary of model results

A total of 32 different models were generated (4 buffer distances x 2 populations x 2 site types x 2 methods). Rookery-trained models (both classification and logistic) were evaluated for their ability to predict both rookery locations alone as well as haulouts, while haulout models were only evaluated for their ability to predict haulout locations. All models were also tested both with and without the mainland-exclusion mask.

Characteristics of Steller haulouts and rookeries

Classification models outperformed (or were not significantly different from) logistic models in every instance, with only two of the logistic models performing better than chance (according to ROC plots) at predicting rookery locations (50 nautical miles with eastern training sites, and 20 nautical miles with eastern training sites). Neither of these models performed better than the corresponding supervised classification models ($p < 0.001$). Thus, only K_{no} and ROC scores for the classification models are presented here.

Both classification and logistic models trained using rookery locations were often as successful at predicting haulout locations as models trained using haulouts. Thus, little additional information was gained by including haulouts in the training set. All of the classification models performed better than chance at predicting site locations, as indicated by AUC scores greater than 0.5 and K_{no} scores above 0 (Figures 2.3 and 2.4).

Exclusion of the mainland to simulate avoidance of terrestrial predators did not generally improve model performance in predicting rookery locations. In six of eight cases (50, 20, and 10 nmi, east and western training areas), models that included the mainland outperformed those that excluded it (z -score, $p < 0.001$, except for 10 nmi west, $p < 0.01$). There was no significant difference ($p > 0.05$) between the mainland and offshore models at the 1 nmi distance.

There was no clear trend in model performance between models trained using sites from the western stock versus the eastern stock. In other words, the conditions surrounding sites in the western stock were no more representative of overall conditions than those in the eastern stock.

Characteristics of Steller haulouts and rookeries

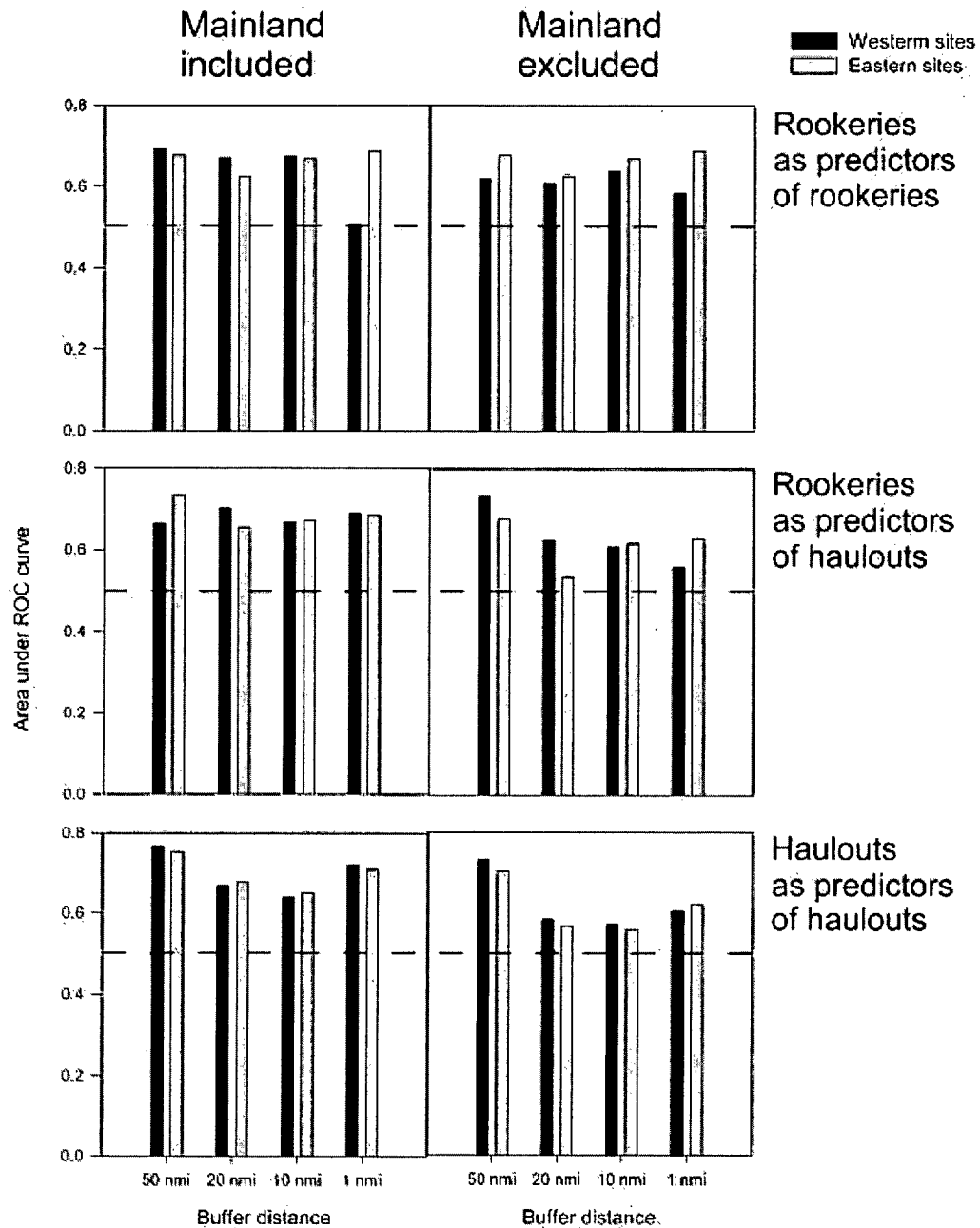


Figure 2.3. Area under curve (AUC) values for models. An AUC value of 0.5 (indicated by the dashed line) or below indicates a model performed worse than chance; higher scores represent better model fit. Scores are for single model runs and are presented for visual reference; refer to figure 2.4 to quantitatively compare model performance.

Characteristics of Steller haulouts and rookeries

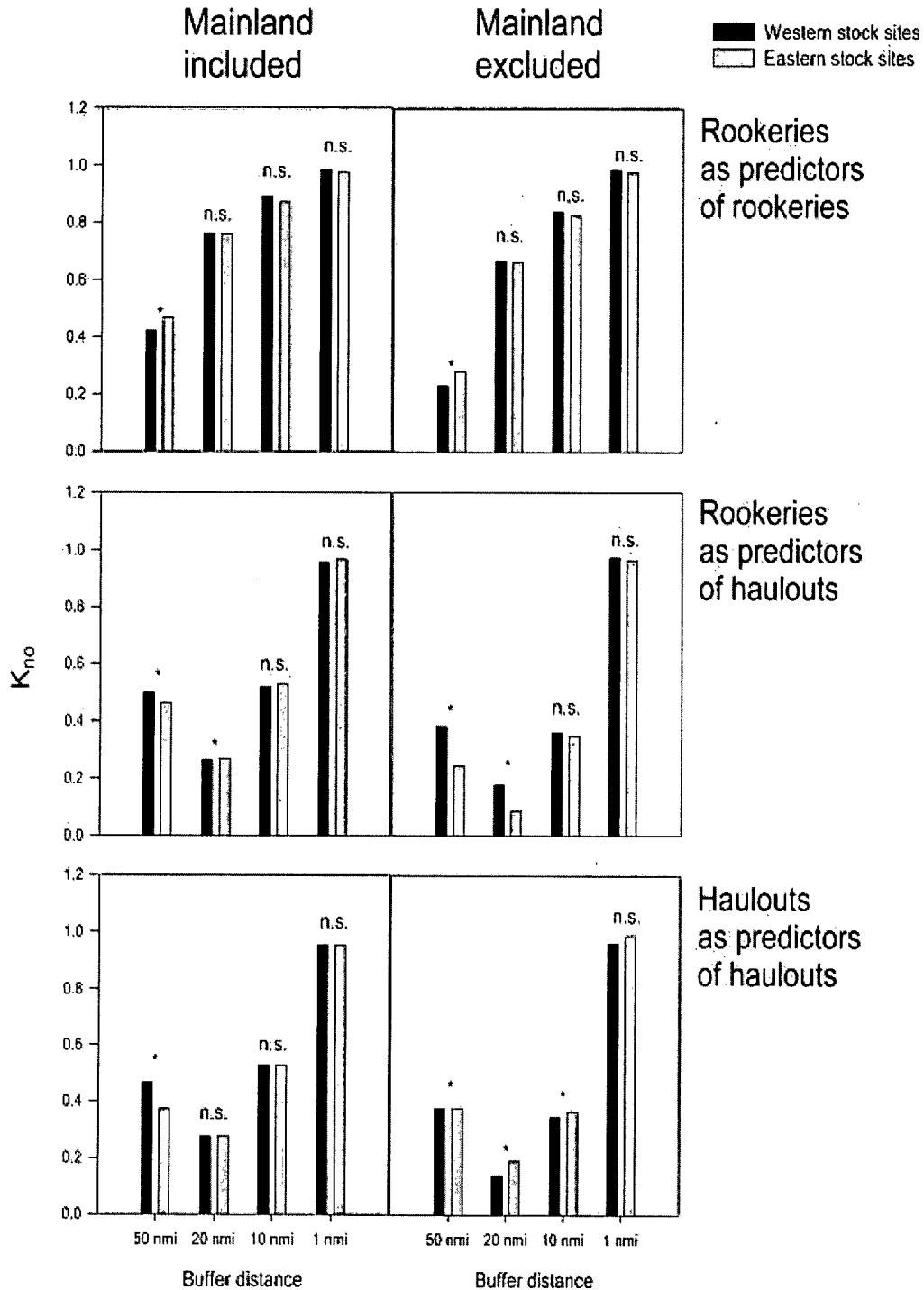


Figure 2.4 K_{no} values for classification models, comparing models trained using eastern population sites vs. western population sites. Higher K_{no} values represent better model fits. K_{no} scores indicated by an asterisk were highly significantly different ($p < 0.001$), while those marked n.s. were not significantly different.

Characteristics of Steller haulouts and rookeries

Oceanographic Conditions Near Rookeries and Haulouts

The training area masks were also used to obtain comparative statistics for habitat and non-habitat areas for each of the input variables. In general, waters near sites (both rookeries and haulouts) were shallower, had less steep slopes and were more well-mixed (as indicated by a lower value of the mixing index). They also had higher average tidal speeds than waters not near sea lion sites. However, there were some exceptions to these overall trends. For example, at the 1 and 10 nmi buffer distances, rookeries in the western stock were surrounded by waters that were slightly deeper than waters elsewhere in the west. Average tidal speeds at 1 nmi around eastern rookeries were also slightly lower than average tidal speeds elsewhere in the east, while the mixing index was the same as non-habitat areas in the east. These results are summarized in Figure 2.5.

Discussion

My study sought to find a relationship between physical oceanographic variables and the locations of terrestrial resting and breeding sites used by Steller sea lions, and to determine whether conditions around sites in the declining western stock differed from those in the stable eastern stock. I also compared the efficacy of two different modelling methods—supervised classification and logistic regression.

There were no consistent differences in the physical conditions associated with rookeries and haulouts used by Steller sea lions in the western and eastern populations. However, waters near sites in both stocks (as defined by the 4 buffer distances) did consistently differ from waters not near sites. Sea lions appear to prefer sites near waters that are more well-mixed, with shallower depths, less steep bottom slopes, and higher average tidal speeds. Conditions within 1 nautical mile of shore also appear to be better predictors of haulout and rookery locations than conditions within 10, 20, or 50 nautical miles. Taken

Characteristics of Steller haulouts and rookeries

together, these parameters may be indicative of areas where prey may be reliably obtained, and may indicate that preferred feeding areas are relatively close to shore.

The present distribution of Steller sea lions is undoubtedly the product of a number of biological and historical factors, including interspecific competition, predation (and predation risk), and interactions with humans. However, physical oceanographic processes may also have had an influence on their distribution. For example, studies of seabirds (Schneider et al. 1990) and tuna (Fiedler & Bernard 1987) have demonstrated the importance of fronts in concentrating prey. Schneider (1990) has also described the existence of a reliable front in the Bering Sea created by bathymetric features. Steller sea lions may well be using similar cues when selecting their terrestrial sites.

This difference between potential habitat (available coastline) and actual habitat (individual sites) may be an example of the difference between fundamental and realized niches (Anderson et al. 2002). A fundamental niche constitutes the autecological requirements of a species—that is, the confluence of physical and biological factors that are necessary for the existence and survival of that species. The realized niche is a subset of the fundamental niche that reflects the influence of competition, predation, and other historical factors. Thus, the location of rookeries and haulouts of Steller sea lions probably reflects their realized niche.

Based on the foregoing, ephemeral factors such as sea surface temperature and salinity would be expected to be less reliably and consistently associated with haulouts and rookeries compared to factors that vary little (if at all) over time, such as bathymetry, slope, and other characteristics that are relatively unaffected by periodic phenomena such as El Niño events. Physiographic features can concentrate prey through various means, such as by inducing upwelling, and have been shown to influence cetacean feeding behaviour (Baumgartner 1997).

Characteristics of Steller haulouts and rookeries

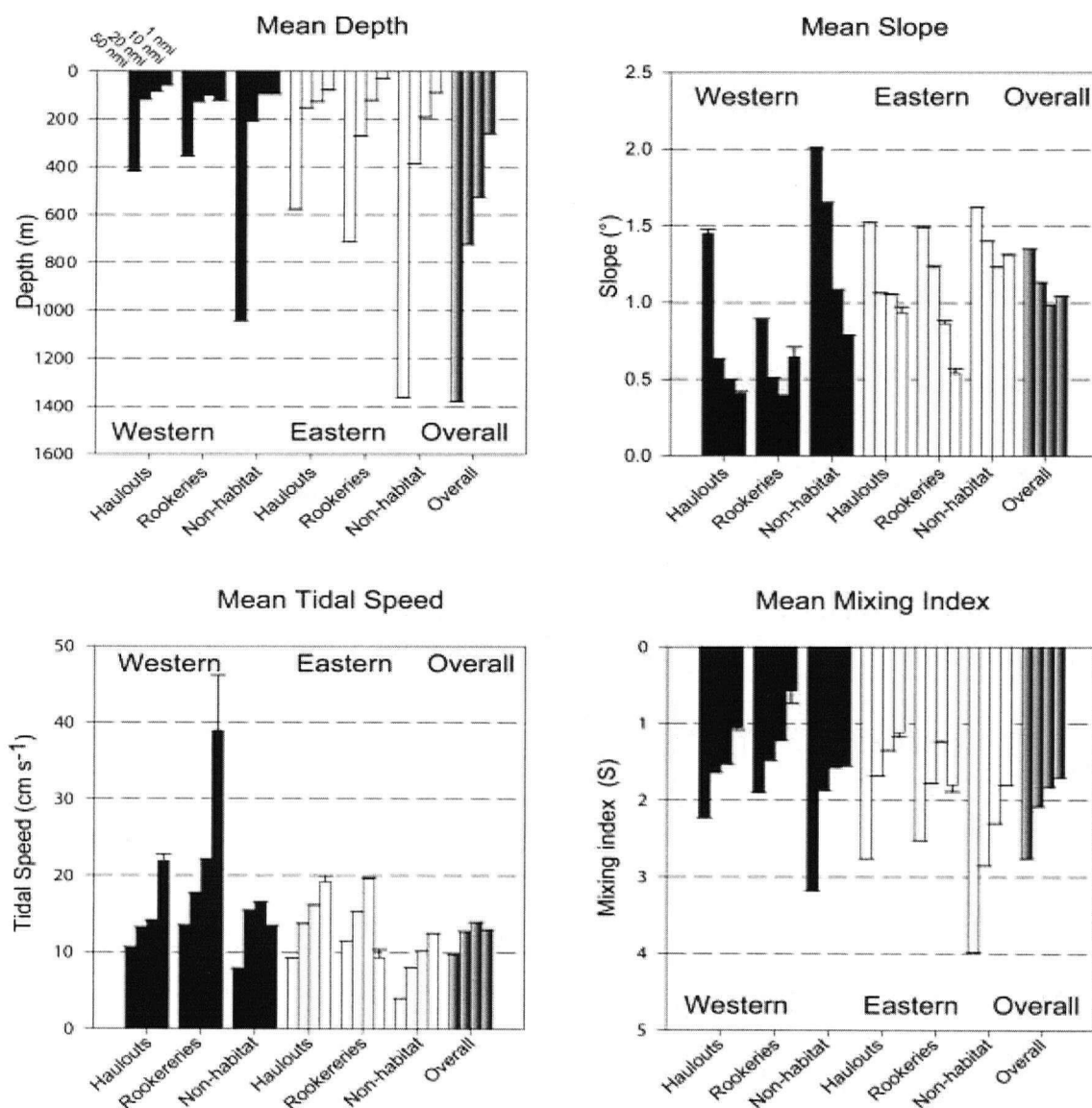


Figure 2.5 Means and standard errors of habitat and non-habitat areas. The overall average includes all areas, both habitat and non-habitat, across both the eastern and western population areas.

Characteristics of Steller haulouts and rookeries

It thus seems reasonable to suggest that sea lions might also take advantage of these persistent features when foraging. The variables used in my study were consistent with this reasoning.

Both supervised and unsupervised classification have become relatively commonplace for habitat modeling in terrestrial environments (e.g. Andries et al. 1994, Mladenoff & Host 1994, Kitron et al. 1996, Osborne et al. 2001, Luoto et al. 2002), but have only recently been applied to aquatic and marine environments (Stanbury & Starr 1999, Mumby & Edwards 2002, Andrefouet et al. 2003). The apparent lag in applying classification techniques to marine systems may reflect a number of differences between terrestrial and marine processes and environments. First, marine environments have an extra spatial dimension as well as a temporal dimension that is more dynamic than that found in most terrestrial ecosystems. The abiotic environment (e.g. nutrient availability) in terrestrial ecosystems also remains functionally static for longer periods than in aquatic systems. Another difference is the boundaries of aquatic ecosystems, which are in constant flux, at least at fine scales. At larger scales, spatial patterns emerge among many aspects of marine ecosystems that are associated with prevailing winds, currents, and more permanent features such as seamounts, shelfbreaks, and other topographic features. Thus organisms have presumably evolved life histories and behaviours that operate at a number of different spatial and temporal scales, and with varying degrees of ability (Levin 1992).

A number of different spatial and temporal considerations need to be addressed when modeling the habitat usage of Steller sea lions. For example, foraging occurs over short temporal and fine spatial scales (measured in minutes to hours and metres to tens of metres), and is influenced by currents and nutrient availability operating at larger scales (i.e. hours to days and hundreds of metres to kilometres). Similarly, reproductive success is simultaneously (and perhaps paradoxically) tied to fine-scale spatial factors such as foraging, beach substrate and wave exposure, as well as to long-term temporal factors such as seasonal changes and larger-scale spatial factors such as overall rookery locations within

Characteristics of Steller haulouts and rookeries

the northern Pacific basin. The scales considered in my analysis ranged from 1-50 nautical miles over long (annual to decadal) time scales.

Hamazaki (2002) used a methodology similar to the one I used, but with a couple of key differences. In his study, the oceanographic data used to generate his model was from a short time period (1990-1996), and the model was tested using an even shorter data set (1997-1998). My model used the longest-term, highest resolution oceanographic data available for this region. Second, Hamazaki's model was dependent upon cetacean sighting data. Such data, as Hamazaki notes, cannot distinguish between when an animal is in its preferred versus its non-preferred habitat. He thus assumed that all areas with sightings of animals represented preferred habitat, whereas all areas with no sightings represented non-preferred habitat. The models I presented do not suffer from these particular assumptions regarding sightings, although other assumptions were made in their place, such as equal (potential) utilization of all waters surrounding a site, and equivalent importance of all selected sites.

Logistic models vs. Supervised Classification Models

Evaluating model performance revealed that all models developed using logistic regression either underperformed or performed no better than models developed using the supervised classification method. This finding indicates that image classification techniques should be considered as an alternative to logistic regression for generating habitat models, particularly when the behaviour and/or range of a species is well-defined.

Logistic regression models have been commonly used for developing habitat models (Morrison et al. 1992), particularly in marine contexts (e.g. Nadeau et al. 1995, Moses & Finn 1997). One of the advantages of logistic regression over supervised classification is their relative ease of interpretation of the results. The use of forward or backward stepwise techniques allows models to be developed using only the variables with the most predictive power. In my analysis, this did not prove to be an important issue because all of the variables were selected for

Characteristics of Steller haulouts and rookeries

inclusion in the logistic regression models. Nonetheless, the coefficients associated with each variable in the logistic regression equation also reflected the relative strength or predictive power of those variables. In the supervised classification method I used, all variables were weighted equally, and there was no straightforward way to determine afterwards which of the variables contributed the most to the final prediction, unless models were generated for each of the variables separately and then cross-compared. It is thus more difficult when using a supervised classification model to assess the relative importance and contributions of the input variables in the final model.

Rookeries vs Haulouts

Models that were first generated by training on rookery sites, and then tested against haulout sites, were as successful or better at predicting where haulouts occur as were the models generated by training on haulout sites, with the exception of the 50 nautical mile distance. This finding indicates that the oceanographic conditions surrounding haulouts were not drastically different from those surrounding rookeries, and that knowing the location of some or all of the rookeries may be sufficient to generate successful haulout prediction models.

Comparing the mean values of the oceanographic parameters associated with habitat and non-habitat areas revealed a number of patterns. First, slope was consistently lower in waters near rookeries and haulouts versus other waters. Second, the mixing index was consistently lower. Third, in the eastern population, and in six of eight instances in the western stock, waters were consistently shallower in habitat areas. Finally, tidal speeds were higher in habitat versus non-habitat areas in 13 of 16 cases. This combination of higher average tidal speeds and lower values of the mixing index (indicating better-mixed waters) is consistent with waters that have higher biological productivities.

The patterns in oceanographic parameters associated with rookeries and haulouts are consistent with the findings of Call and Loughlin (In press), who found that Steller sea lion rookeries were associated with major oceanic currents

Characteristics of Steller haulouts and rookeries

and ecological boundaries (such as oceanic gyres and eddies). They also found that sites with the slowest rate of decline in the eastern population were associated with an area of high tidal flow and mixing (Unimak Pass). Although they also found that rookeries associated with deeper waters had a greater rate of decline, their analysis was confined mainly to rookeries within the western population, and only reflected population trends within that area from 1990-1998. Additionally, they only considered waters within 10 nautical miles of rookeries.

The fact that sites are generally situated near shallower waters may indicate that access to benthic prey is important, and that the diving limitations of Steller sea lions may restrict foraging to relatively shallow waters. Common prey species such as Atka mackerel and walleye pollock (Merrick et al. 1997)—particularly smaller individuals—are often found at shallower depths (Wolotira et al. 1993). Loughlin et al. (2003) reported the maximum observed dive depth of a juvenile Steller sea lion was 328 m, with a mean maximum dive depth for all observed dives (young-of-the-year and juveniles) of 62.42 m. In another study, Merrick & Loughlin (1997), observed that the maximum dive depth among adult females was >250m, although the exact depth reached was not reported. The maximum dive depth of adult males has not been determined, but the diving abilities of adult females and juvenile animals of both sexes are more likely to be limiting factors if access to benthic habitat is a factor in rookery (if not haulout) site selection. Interestingly, Loughlin et al (2003) found that the diving depths of some animals from Washington State (eastern population) were deeper than animals from the Aleutian Islands (western population). This pattern also appeared in the data presented here, with waters around sites in the eastern stock being generally deeper than those waters in the western stock (with the exception of the waters within 1 nmi of rookeries). This raises the question of whether animals in the eastern stock select sites near deeper waters because they are capable of diving to greater depths, or whether the waters near sites in the eastern stock are generally deeper and thus provided an evolutionary impetus to develop (or retain) greater diving abilities. Additional information about the relationship

Characteristics of Steller haulouts and rookeries

between maximum observed dive and maximum available depth is required to resolve this question.

The finding that areas near Steller sea lion terrestrial sites had lower bottom slopes seems contrary to the other trends in physical characteristics of surrounding waters. Areas of higher slope tend to be associated with regions of upwelling, at least at large scales (e.g., the continental shelf/slope). At smaller scales, high-slope areas may aggregate prey or make them easier for predators to find (Sjoberg & Ball 2000). However, these smaller-scale effects are also species-dependent, and some benthic or demersal prey species may be associated with lower-slope areas (Dean et al. 2000). Fine-scale changes in slope would also not be detectable with a 600-m cell size, which means that there may be areas of high slope or surface complexity within a cell that would not be apparent.

There was no consistent difference between the waters surrounding rookeries and haulouts in average depth, slope, tidal speed, or mixing index across all scales (50, 20, 10, and 1 nautical mile radius) and between both stocks (western and eastern). However, in the western rookeries, tidal speeds were consistently higher, and the mixing index was lower (indicating more well-mixed waters) around rookeries compared to haulouts. The same pattern was observed in three out of the four distances examined in the eastern stock (50, 20, and 10 nautical miles) for tidal speed, and two distances (50 and 10 nmi) for the mixing index. No consistent differences were observed for depth or slope, either across all distances or between eastern and western stocks. While all of the differences were statistically significant, the absolute magnitude of the differences was typically quite small, and may not be biologically significant. However, even if using the uninterpolated, isolated datapoints (which would preclude the calculation of the slope and mixing index), the larger question remains as to what an appropriate "sampling" unit is, and whether it even makes sense to be speaking of "sampling" from a "population" of oceanographic data. In other words, how large of an area of ocean (and at what resolution) would we need to

Characteristics of Steller haulouts and rookeries

measure before we are satisfied that we know the characteristics of a given water mass?

Relative success of model predictions

The highest kappa values were obtained for the smallest (1 nmi) buffer distance, which suggests the 1 nmi models performed better. However, the strength of the model fit may be overestimated because the ratio of non-habitat to habitat pixels increases dramatically as the buffer distance decreases. For example, the ratio of habitat to non-habitat pixels in the reference (true) image of 1 nmi buffered rookeries is over 2000 : 1. Thus high K_{no} scores are largely the result of models more accurately predicting the quantity and location of non-habitat pixels. Correctly identifying the few habitat pixels contributes relatively little towards the overall score.

Deciding upon the true "best" model depends on how much weight (or penalty) is given to false negatives (FN) versus false positives (FP). As Fielding & Bell (1997) suggest, models with a higher FP rate may be acceptable for endangered species or other instances where a precautionary approach is desired. On the other hand, if we wish to find only those areas with the highest probability of finding animals, models with a low FP rate would be desirable. Thus, K_{no} measures of agreement were provided to assess model success assuming that FP and FN errors are given equal weighting, as well as ROC plots, which can be used as a threshold-independent means of assessing overall model success. Thus, models with the highest K_{no} score are not necessarily the "best" model because they are also likely to have a high proportion of false positives as the ratio of true positives to true negatives is reduced.

It should be kept in mind that the correct way to interpret the resulting "predictions" of each model is to see each pixel in the map as being indicative of whether there is likely to be a rookery or haulout within x nautical miles of that pixel (where x is the buffer distance used to generate the model). The prediction maps, are, in essence, a prediction of what waters are likely to be near

Characteristics of Steller haulouts and rookeries

haulouts/rookeries, not a precise indication of where the sites themselves are likely to be. This is because it is impossible to locate the specific point from which an area (the buffer distance) could have originated.

Because K_{no} considers both the quantity (number of pixels) and quality (spatial location) of model predictions, a threshold that is too high may result in quantification "penalties" in the kappa statistic due to underestimation of pixel counts, whereas too low a threshold may result in a poor score due to overestimation of quantity. Conversely, a lower threshold may increase the K_{no} score of a given model by increasing the chances of obtaining the right location by virtue of number alone. This is certainly a factor at the smaller buffer distances, where the ratio of non-habitat to habitat pixels is high.

Implications and future directions

Climate change Climate change threatens to alter the structure and function of many ecosystems (Brereton et al. 1995). While my analysis deliberately used oceanographic predictors that were stable over long periods of time, a similar analysis could be conducted using predictors that vary over shorter time scales, or that are otherwise affected by climate change and regime shifts. These variables could include sea surface temperature, salinity, and mean sea level. Forcing the input variables to simulate conditions expected in new climate regimes would allow the models to predict future changes in the sites used by Steller sea lions.

Constraints on range Environmental factors other than those I considered, such as ocean temperature, air temperature, or salinity, might have direct physiological impacts on Steller sea lions and might be more useful in determining the theoretical limits of the sea lion's range. The oceanographic predictors I used did not represent a smooth gradient from one end of the animal's range to the other, and there is no reason to suspect that either the depth, slope, tidal speed, or mixing characteristics were sufficiently different at either extreme of the range to inhibit further expansion. More likely, warmer

Characteristics of Steller haulouts and rookeries

ocean temperatures, availability of favoured prey species, and competition with other species such as California sea lions (*Zalophus californianus*) (Bartholomew & Boolotian 1960) dictate the maximum range extents of Steller sea lions.

Differential weighting of sites If count data were available for sites from a longer time period—such as from archaeological data or historical records—then it would be logical to weight sites in the model according to abundance, to reflect the success or importance of a site. I did not do this because reliable count data were only available for a relatively recent period, and because no count data were available for sites in Washington, Oregon, or California. Additionally, because of the different population trajectories between the eastern and western stocks, it would be difficult to separate the effects of site characteristics from population effects without a reliable baseline count for each site.

Conclusions

My analysis suggests that there are indeed physiographic differences between the waters surrounding Steller sea lion rookeries and haulouts and those areas not occupied by Steller sea lions. These differences indicate that site selection may be driven by proximity to areas of reliable foraging that are generated by persistent tidal mixing, high tidal speeds, and accessible benthic prey (by virtue of depth). Marine mammals have been shown to make use of prey aggregations associated with these features (Brown & Winn 1989, Suryan & Harvey 1998, Keiper 2002), and marine birds have been shown to consistently use tidal rips for foraging (Cairns & Schneider 1990, Hunt & Harrison 1990, Schneider 1991). Haulout sites in other pinnipeds such as harbour seals (Bjorge et al. 2002) and grey seals (McConnell et al. 1999) are also often situated near shallow areas.

There were no consistent differences in the physical characteristics of waters surrounding sites in the eastern and western stocks. Therefore, it is unlikely that the particular physical characteristics examined here are related to the different population trends in the eastern and western stocks, especially since these factors are not subject to change over time. There were also no consistent

Characteristics of Steller haulouts and rookeries

differences between haulouts and rookeries, indicating that there does not appear to be anything special about the waters near breeding sites that would have led to their selection.

Models developed using waters within 1 nautical mile of rookeries and haulouts tended to have higher K_{no} values than those using greater search distances. This may mean that waters closer to these sites are either more important for foraging or more characteristic of preferred habitat than waters further from shore. However, because the ROC values for models across distances did not differ greatly, the higher K_{no} scores may be more indicative of biases in this metric rather than actual differences in model fit, as discussed earlier. Nonetheless, the patterns observed in the average depth, slope, tidal speed, and mixing index (Figure 2.5) also support the interpretation that conditions within 1 nautical mile of rookeries and haulouts are different—and perhaps distinct—habitat.

The techniques I used can be readily applied to other species, but are particularly relevant to central-place foraging species. For species whose range and distributions are not well-known, similar models could be built to predict likely, but unknown, habitat. The technique of supervised classification proved superior in this instance to logistic regression in terms of output accuracy, but provided only limited information about the relative importance of the input variables. This supervised classification technique warrants further exploration and evaluation in other habitat-modelling applications.

Summary

Spatial models were constructed to determine which oceanographic factors are associated with the terrestrial sites used by Steller sea lions to rest (at haulouts) and breed (at rookeries). Predictive models were generated to explain the locations of these sites across the North Pacific rim, and how the waters surrounding sites differ from waters elsewhere. The two modelling techniques employed (logistic regression and supervised classification) were evaluated

Characteristics of Steller haulouts and rookeries

using the kappa statistics (K_{no}), and receiver-operating characteristic (ROC) plots. In general, Steller sea lions showed preferences for terrestrial sites associated with waters that were relatively shallow, well-mixed, had higher average tidal speeds and less-steep bottom slopes. Conditions within 1 nautical mile of land were better predictors of haulout and rookery locations than were conditions within 10, 20, and 50 nautical miles. No consistent differences were found in the physical characteristics of waters surrounding sites in the eastern and western populations of Steller sea lions. It is therefore unlikely that the particular physical oceanographic characteristics associated with the rookeries and haulouts examined are related to the different trends of the two populations, especially since these factors (bathymetry, slope, tidal speed, and mixing) are not subject to significant change across years. There were also no consistent differences between the oceanographic features associated with haulouts and rookeries, indicating that there does not appear to be anything special—at least in terms of the variables examined—about the waters near breeding sites that would have led to their selection. Supervised classification was found to produce better-fitting models than logistic regression, and could be readily applied to address habitat questions associated with other central-place foraging animals in the marine environment.

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Characteristics of Steller haulouts and rookeries

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Chapter 3 - Quantification of Terrestrial Habitat Preferences of Steller Sea Lions

Introduction

Steller sea lions inhabit the north Pacific 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, and rest at nearly 600 non-breeding sites called haulouts. There do not appear to be archaeological records of Steller sea lion breeding or hauling out at sites (at least on the Oregon coast) prior to about 3,000 b.p. (Lyman 1989), although otariids have presumably lived in this region for nearly all of their evolutionary history (~ 3 million years). In the Aleutians, Alaska, and northern British Columbia, the ice edge at the end of the Last Glacial Maximum would have precluded the occupation of present-day sites until at least 20,000 b.p. (Manley & Kaufman 2002). Isolated fossil finds in British Columbia have placed Steller sea lions in this area as early as circa 12,000 b.p. (Harington et al. 2004), when the waters of British Columbia would have been closer in temperature to present-day Cook Inlet or Prince William Sound, Alaska.

A number of people have tried to anecdotally describe characteristics of haulouts and rookeries. For example, Bigg (1985) notes that year-round haulouts are usually found in places that are directly exposed to oceanic swells, whereas winter-only haulouts are generally not exposed directly to these swells, and are sheltered to some extent by the surrounding topography. Lyman (1989) quotes 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. He also noted that they are rarely found in inland waters and considered them to be a near-shore species. Kastelein & Weltz (1991) studied

Terrestrial habitat of Steller sea lions

two sites in Prince William Sound, Alaska, and observed that haulout behaviour was probably influenced by the physical geography of a colony site, particularly regarding variations in the number of animals at a site as tidal height changes. 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 believed that they favoured large, fairly level rock ledges over boulder beaches.

Rookeries may be selected according to slightly different criteria from haulouts, since protection of pups from exposure may be an important consideration. Edie (1977) and Fiscus (1970) reported the death of many pups due to wave action from storms—thereby suggesting that sites affording some protection from wave exposure may be favoured for rookeries.

Considerable research has been undertaken on the haul-out behaviours of phocids (e.g. Pitcher & McAllister 1981, Schneider & Payne 1983, Calambokidis et al. 1987, Brasseur et al. 1996, Watts 1996, Suryan & Harvey 1998, Sjoberg & Ball 2000, Galimberti & Sanvito 2001, Bjorge et al. 2002, Moulton et al. 2002, Nordstrom 2002, Reder et al. 2003). However, research concerning the similar behaviour of otariids in general—and Steller sea lions in particular—with regard to terrestrial factors is sparse and generally qualitative. Apart from anecdotal descriptions of their habitat preferences, there have been no quantitative studies to date of the factors – biotic or abiotic – that may be influencing the selection of Steller sea lion haulouts and rookeries.

Site selection by pinnipeds likely involves either an optimization or compromise of two factors: proximity to favourable at-sea foraging areas, and availability or accessibility of terrain that allows both ingress and egress during variable tidal heights. Protection from wind and waves may also play a role, although observations of sites (Fiscus 1970, Bigg 1985, Lyman 1989, Kastelein & Weltz 1991) indicates that this may not be important, and that favoured sites are actually more exposed than other nearby areas that are more sheltered.

Terrestrial habitat of Steller sea lions

The fact that the same rookery and haulout sites have been consistently used by Steller sea lions 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 also likely to be stable. If sites are being selected solely on the criterion that they are close to productive at-sea foraging areas, then the current distribution of sites would be expected to correspond with the available distribution of shoreline types.

While no clear reason has been found for the precipitous decline in the western stock of Steller sea lions (DeMaster & Atkinson 2002, National Research Council 2003, Trites & Donnelly 2003), differences in the terrestrial physical environment could conceivably affect population trajectories. In particular, low population numbers could be further depressed by such influencing factors as unusual pup mortality (due to exposure or trampling), reduced foraging success, or the inability of males to successfully find and defend territories.

The following tests two principal hypotheses concerning the terrestrial habitat needs of Steller sea lions. The first was that the distribution of Steller sea lion haulouts and rookeries was not random with respect to the availability of different shoreline types—and second, that rookeries differ from haulouts in the preferred type of shoreline, presumably because pups and young animals might be less agile than mature animals, and thus less able to access steep or rough sites. Finally, the latitude and longitude, and nature of sites were compared against average non-pup counts to determine whether a relationship exists between either of these factors and the success or popularity of a site.

Methods

The hypotheses were tested 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

Terrestrial habitat of Steller sea lions

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. Each rank also has subtypes that further characterize the shoreline type (Table 3.1). 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 final data is approximately 1:250 000, with a minimum mapping unit of approximately 100 feet.

In British Columbia, a similar coastline atlas exists with a slightly different classification system (Coastal Resource and Oil Spill Response Atlas, Table 3.2).

At the time my research was conducted, data for the Strait of Georgia was not publicly available. However, this area constitutes a relatively small portion of the overall British Columbia shoreline, and no rookeries or year-round haulouts exist in this area. Since there is no one-to-one correspondence between the NOAA ESI system and British Columbia's system; descriptions (and photos, where applicable) were used to make shore classifications from the British Columbia system compatible with the ESI system (Table 3.3) so that analyses could be performed on the entire shoreline from southern California to the Aleutian Islands as a single unit. One shoreline type from the B.C. system (channels) had no equivalent in the ESI system, so this was left as a separate class.

Steller sea lion rookery and summer haulout locations in Alaska, Washington, Oregon, and California were compiled from the database of Steller sea lion counts conducted by the National Marine Fisheries Service (NMFS), as well as from V. Burkanov (Natural Resources Consultants, Inc, Seattle, Washington, pers. comm), M. Lowry (NMFS, La Jolla, California, pers. comm),

Terrestrial habitat of Steller sea lions

Table 3.1. NOAA ESI Shoreline types.

ESI #	ESTUARINE	LACUSTRINE	RIVERINE (large rivers)
1	Exposed rocky shores with or without wave-cut platform (coastal)		
1A	Exposed rocky shores	Exposed rocky shores	Exposed rocky banks
1B	Exposed, solid man-made structures	Exposed, solid man-made structures	Exposed, solid man-made structures
2	Exposed high-energy shoreline (unidentified cliffs, platforms, and beaches)		
2A	Exposed wave-cut platforms in bedrock, mud, or clay	Shelving bedrock shores	Rocky shoals, bedrock ledges
2B	Exposed scarps and steep slopes in clay		
3	Fine and medium sand, coarse sand, sand and gravel, gravel		
3A	Fine to medium-grained sand beaches	Eroding scarps in unconsolidated sediment	Exposed, eroding banks in unconsolidated sediments
3B	Scarps and steep slopes in sand		
3C	Tundra cliffs		
4	Coarse-grained sand beaches	Sand beaches	Sandy bars and gently sloping banks
5	Mixed sand and gravel beaches	Mixed sand and gravel beaches	Mixed sand and gravel bars and gently sloping banks
6	Gravel beaches and exposed riprap		
6A	Gravel beaches	Gravel beaches	Gravel bars and gently sloping banks
6B	Riprap	Riprap	Riprap
7	Exposed tidal flats	Exposed flats	
8A	Sheltered rocky shores and sheltered scarps in bedrock, mud, or clay	Sheltered scarps in bedrock, mud, or clay	
8B	Sheltered, solid man-made structures	Sheltered, solid man-made structures	Sheltered, solid man-made structures
8C	Sheltered riprap	Sheltered riprap	Sheltered riprap
8D	Vegetated, steeply-sloping bluffs		Vegetated, steeply-sloping bluffs
8E	Peat shorelines		
9A	Sheltered tidal flats	Sheltered sand/mud flats	
9B	Vegetated low banks	Sheltered, vegetated low banks	Vegetated low banks
10A	Salt- and brackish-water marshes		
10B	Freshwater marshes	Freshwater marshes	Freshwater marshes
10C	Swamps	Swamps	Swamps
10D	Scrub-shrub wetlands	Scrub-shrub wetlands	Scrub-shrub wetlands
10E	Inundated Low-lying Tundra		
U	Unranked/Unsurveyed		

Terrestrial habitat of Steller sea lions

Table 3.2. British Columbia Coastal Response and Oil Spill Atlas

Coastal Class	Repetitive Shore Type (#)	Description
2,5	2	Rock Platform
1,3,4	3	Rock Cliff
6-10	4	Rock with Gravel Beach
11-15	5	Rock, Sand and Gravel Beach
16-20	6	Rock with Sand Beach
22	7	Gravel Beach
25	8	Sand and Gravel Beach
27,30	9	Sand Beach
28	10	Sand Flat
29	11	Mud Flat
31	12	Estuary, Marsh or Lagoon
32,33	13	Man-made
24,26	14	Sand and Gravel Flat
21,23	15	Gravel Flat
34	16	Channel

and C. Stinchcomb (NMFS, La Jolla, California, pers. comm). Data for British Columbian sites were obtained from P. Olesiuk (Fisheries and Oceans Canada, Nanaimo, B.C., pers. comm).

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. To allow for slight positional errors and map inaccuracies, only sites within 0.5 nautical miles (approx. 900 metres) of classified shoreline segments were selected for analysis. This yielded 318 haulouts and 38 rookeries out of a total of 594 haulouts and 88 rookeries, or 54% and 43% of all sites across the entire range, respectively. Using a spatial join operation, each site was then assigned to the nearest shoreline segment. In the ESI system, each shoreline segment may 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 shoretypes (which only occurred with 14 of the haulouts and none of the rookeries), two separate analyses were conducted—one using the most landward shoretype, and one using the most seaward type. This allowed for possible changes in exposed shoretype as tidal heights rise and fall.

Terrestrial habitat of Steller sea lions

Table 3.3. Conversion between BC Shoreline classification and NOAA ESI

BC Type	NOAA ESI	BC Shorezone description
3	1. Exposed Rocky Shores	Rock Cliff, narrow
	1A. Exposed Rocky Shores (Estuarine)	
2	2. Exposed Rocky Platforms (High energy shoreline)	Rock ramp, narrow Rock ramp, wide Rock platform, narrow Rock platform, wide
	2A. Rocky shoals, Bedrock Ledges (Estuarine)	
6	3. Fine-grained sand beaches	Sand beach
9		Ramp with sand beach, wide Ramp with sand beach, narrow Platform with sand beach, wide Cliff with sand beach (Rock with sand beach) (Sand beach)
	4. Coarse-grained sand beaches	
5	5. Mixed sand and gravel beaches	Sand & Gravel Beach, narrow
8		Ramp with Gravel & Sand Beach, wide Ramp with Gravel & Sand Beach, narrow Platform with Gravel & Sand Beach, narrow Platform with Gravel & Sand Beach, wide Cliff with Gravel & Sand Beach (Rock with sand & gravel beach) (Sand and gravel beach)
4	6a. Gravel beaches	Gravel beach, narrow
7		Ramp with gravel beach, wide Ramp with gravel beach, narrow Platform with gravel beach, wide Platform with gravel beach, narrow Cliff with gravel beach (Rock with gravel beach) (Gravel beach)
13	6b. Riprap structures	Man-made, Permeable Man-made, Impermeable
10	7. Exposed Tidal flats	Gravel flat, wide
11		Gravel Flat or Fan
14		Sand & Gravel Flat or Fan
15		(Sand Flat) (Mud flat) (Gravel flat) Estuaries
	8a. Sheltered rocky shores	
	8b. Sheltered artificial structures	
17	9. Sheltered tidal flats	High tide lagoon
12	10a. Salt to brackish marshes	Estuaries (Estuary wetland)
	10b. Freshwater marshes	
1	Undefined	Undefined

Terrestrial habitat of Steller sea lions

R (The R Foundation for Statistical Computing 2004) was used to perform statistical analyses. To test whether the usage of shoreline habitat types differed from a random distribution, a Monte Carlo implementation of Fisher's exact test with 10,000 iterations was used to randomly seed sites among shoretypes in proportion to their availability by length. The proportion of rookeries and haulouts in each shoreline type were also compared with Fisher's exact test to determine if habitat usage differed between rookeries and haulouts. Where available, average counts of non-pup animals were compared against the latitudinal and longitudinal position of the site to determine whether there was any correlation between location of sites and population. Population surveys spanned 1979-2002 for Alaskan sites ($n = 316$), and the years 1987, 1992, 1994, and 1998 for British Columbian sites ($n = 30$).

Results

Both haulouts and rookeries had a non-random distribution with respect to available shoreline types ($p < 0.05$, Fisher's exact test, Figure 3.1). Steller sea lions heavily favoured Types 1 and 1A (exposed rocky shores), which accounted for over 70% of rookeries and more than 50% of haulouts. Substrate types 2 and 2A (exposed wave-cut platforms) were the second most frequently used, accounting for more than 13% of rookeries and 27% of haulouts. 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 were found in Types 4, 6B, or 8A. Neither haulouts nor rookeries were found in shoretypes 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.

Terrestrial habitat of Steller sea lions

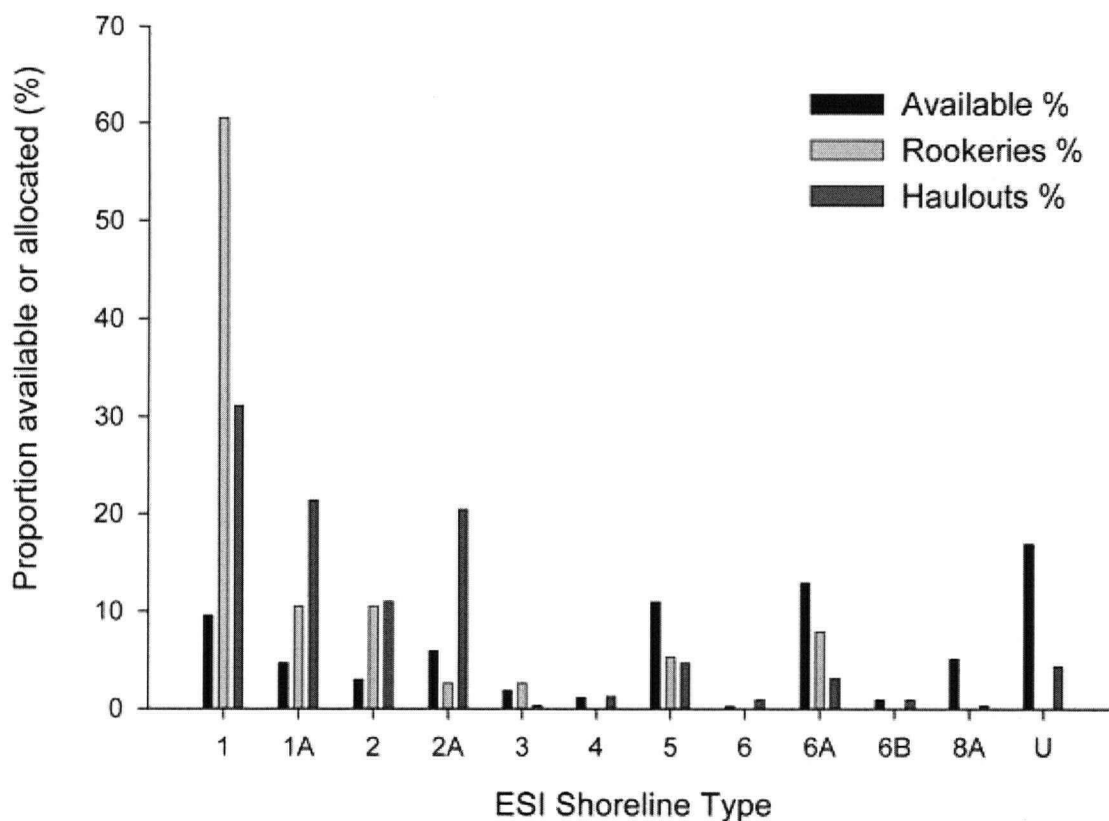


Figure 3.1 Usage of shoreline types by haulouts and rookeries versus available shoreline across entire range. Types 1, 1A, 2, and 2A appear to be heavily favoured, being used in greater proportion than their availability.

Comparison of habitat usage between haulouts and rookeries showed that their distributions were also different ($p < 0.05$, Fisher's exact test). Rookeries were located preferentially in Type 1 (exposed rocky shores with or without wave-cut platform) and 6A (gravel beaches) shoretypes, whereas haulouts were preferentially located in Types 1A (exposed rocky shores) and 2A (exposed wave-cut platforms).

Terrestrial habitat of Steller sea lions

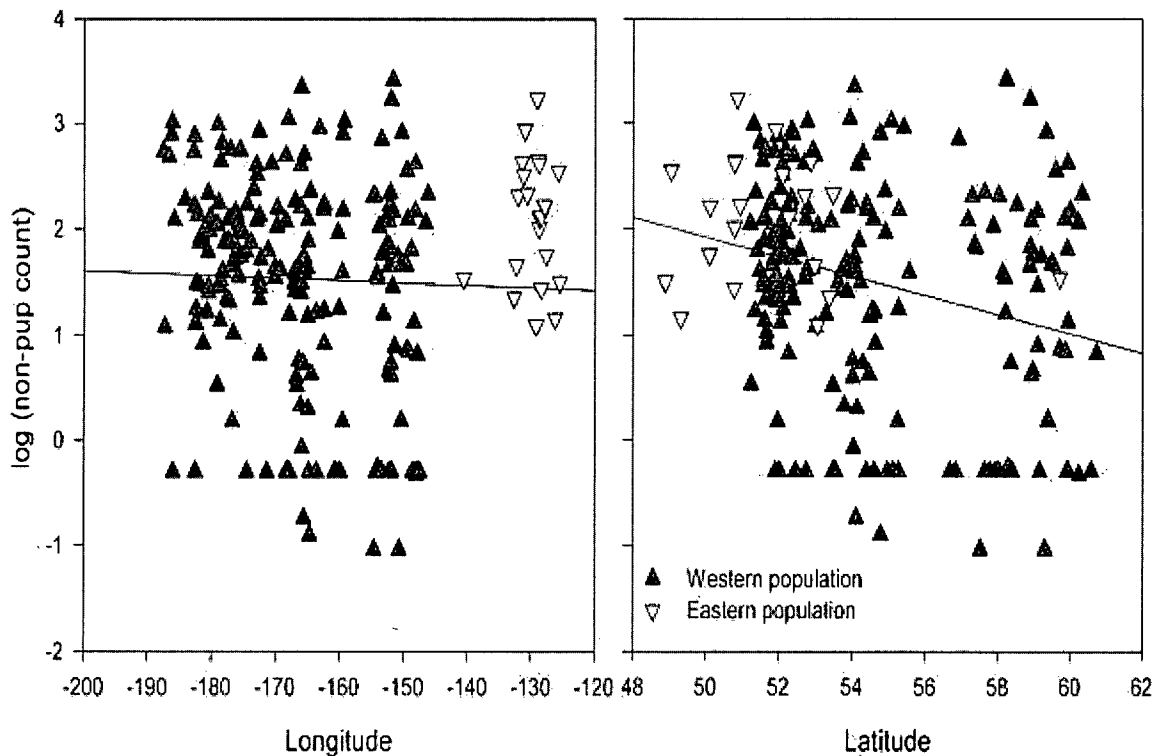


Figure 3.2 Latitude and longitude vs. average non-pup count of haulouts and rookeries. No statistically significant relationship existed between longitude and counts. A weak negative correlation existed between latitude and counts.

No relationship was found between longitude ($r^2=0.003$, $p>0.05$) and the average number of animals found at each site. Latitude was very weakly correlated ($r^2=0.070$, $p<0.001$) with non-pup counts (Figure 3.2).

Discussion

Haulout and rookery sites were 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 consistent with Call & Loughlin (In press), who found that 38 of the 40 rookeries in their study had a rock/slab or cobble beach substrate, while only 2 had a sandy beach substrate.

Terrestrial habitat of Steller sea lions

The lack of relationship between longitude and average non-pup counts is not surprising, given that the physical environment tends to differ less in an east-west direction than it does moving from north to south. Also, the western population is spread out across a large longitudinal gradient (144°W - 144°E), whereas the eastern population is concentrated within a comparatively narrow range of longitudes (144°W - 122°W). Given the differences in population trends between the two populations, this would tend to obscure any overall trend with longitude. There was a very weak relationship between latitude and average non-pup counts (only about 7% of the variance in counts could be explained by latitude), but this is likely an artifact of the fairly large sample size ($n = 215$), and of the generally declining population trend in the western population, which is situated in higher latitudes. Additionally, since data were missing from sites in northern Japan and Russia for the western population, and from California, Oregon, and Washington in the eastern population, the relationship between size of a site and latitude may not be strictly linear or monotonic. Many of the largest sites occur in the Gulf of Alaska and British Columbia, while sites in the southern portion of the eastern and southwestern portion of the western stock are generally smaller. Thus, including all sites would probably produce a bell-shaped curve rather than a strictly linear relationship, with the most populous sites occurring in moderate latitudes towards the northern limit of the eastern stock.

Although there were differences in the distribution of haulouts and rookeries among shoreline types, there did not appear to be a preference for more sheltered shore types among rookeries. This is also consistent with the findings of Call and Loughlin (In press), 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 pup mortality during rough weather due to drowning (Fiscus 1970, Edie 1977, Cunningham & Stanford 1978), sites affording some degree of protection to exposure would be expected to be favoured. However, a number of reports (Kenyon & Rice 1961, Mathisen & Lopp 1963, Cunningham & Stanford 1978) also indicate that Steller sea lions do not associate land with safety during

Terrestrial habitat of Steller sea lions

a storm, and instead raft off-shore during severe weather events. Thus, the degree of shelter from exposure that a site affords may not be a consideration when the site is initially colonized. In addition, there may also be other factors driving the selection of such exposed sites, such as protection from terrestrial predation or proximity to favourable foraging areas.

Higher-resolution terrestrial data detailing information such as the slope, aspect, substrate, and wave exposure of individual sites may reveal differences either between haulouts and rookeries or between western and eastern stocks that were not apparent at this scale of analysis.

Anecdotal reports (Fiscus 1970, Bigg 1985, Lyman 1989, Kastelein & Weltz 1991) have described the preferences of Steller sea lions with regard to haulout and rookery locations, but no studies to date have quantified this preference across a broad geographic range. My findings confirm the anecdotal reports of habitat preferences. Such information about habitat preferences may prove useful in making management decisions that minimize the impacts of human development and disturbance, and forecast responses to climate change that may drive changes in sea lion distribution.

Summary

Steller sea lions range across the Pacific rim from Southern California in the east to northern Japan in the west, where they have continuously occupied terrestrial resting sites (haulouts) and breeding sites (rookeries) for hundreds of years, if not longer. Anecdotal accounts describe Steller sea lions as predominantly occupying exposed, rocky shorelines, but this habitat preference has never been quantified. We compared locations of haulouts and rookeries against a coastline type database to identify and quantify the shoreline preferences of Steller sea lions and to look for other spatial trends in site characteristics. Steller sea lions were found to preferentially locate haulouts and rookeries on exposed rocky shorelines and wave-cut platforms. Shoreline types that were used in lower

Terrestrial habitat of Steller sea lions

proportion than their availability included fine-to-medium-grained sand beaches, mixed sand and gravel beaches, gravel beaches, and sheltered rocky shores). No relationship was found between either latitude or longitude of a site and its average non-pup count.

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Chapter 4 - Conclusions

Chapter 2 investigated the differences in oceanographic conditions around rookeries and haulouts versus other areas of coastline where these sites did not occur. These differences indicate that site selection may be driven by proximity to areas of reliable foraging that are generated by persistent tidal mixing, high tidal speeds, and shallow bottoms (thus making prey more accessible). Marine mammals have been shown to make use of prey aggregations at these features (Brown & Winn 1989, Suryan & Harvey 1998, Keiper 2002), and marine birds have been shown to consistently use tidal rips for foraging (Cairns & Schneider 1990, Hunt & Harrison 1990, Schneider 1991). Haulout sites in other pinnipeds such as harbour seals (Bjorge et al. 2002) and grey seals (McConnell et al. 1999) are also often situated near shallow areas.

Chapter 3 sought to investigate anecdotal reports (Fiscus 1970, Bigg 1985, Lyman 1989, Kastelein & Weltz 1991) that have described the terrestrial preferences of Steller sea lions with regard to haulout and rookery locations. Haulout and rookery sites were located mostly in exposed areas with solid or rocky substrates; sheltered areas and beaches with fine-grained substrates (such as mud and sand) tended to be avoided. This is consistent with (Call & Loughlin In press), who found that 38 of the 40 rookeries in their study had a rock/slab or cobble beach substrate, while only 2 had a sandy beach substrate.

The findings of my research confirm the anecdotal reports of habitat preferences—Steller sea lions appear to prefer exposed, rocky shorelines over sheltered beaches. Although there were differences in the distribution of haulouts and rookeries among shoreline types, surprisingly there did not appear to be a preference for more sheltered shore types among rookeries. This is also consistent with the findings of Call & Loughlin (In press), who found that rookeries tended to be oriented towards the open ocean, rather than on the sheltered sides of islands.

Conclusions

In light of reports of pup mortality during rough weather due to drowning (Fiscus 1970, Edie 1977, Cunningham & Stanford 1978), one would expect that sites affording some degree of protection to exposure would be favoured. However, numerous reports (Kenyon & Rice 1961, Mathisen & Lopp 1963, Cunningham & Stanford 1978) also indicate that Steller sea lions do not associate land with safety during a storm, and instead raft off-shore during severe weather events; thus, the degree of shelter from exposure that a site affords may not be a consideration when the site is initially colonized. Additionally, there may be other factors driving the selection of such exposed sites, such as protection from terrestrial predation or proximity to favourable foraging areas.

There was a weak relationship between latitude and average non-pup counts, but this is likely an artifact of the generally declining population trend in the western population, which is situated in higher latitudes. Additionally, since data were missing from sites in northern Japan and Russia for the western population, and from California, Oregon, and Washington in the eastern population, the relationship between size of a site and latitude may not be strictly linear. Many of the largest sites occur in the Gulf of Alaska and British Columbia, while sites in the southern portion of the eastern and southwestern portion of the western population are generally smaller. Thus, including all sites would probably produce a bell-shaped curve rather than a line, with the most populous sites in moderate latitudes towards the northern limit of the eastern population.

Summary of findings

My analysis suggests that there are indeed physiographic differences between the waters surrounding Steller sea lion rookeries and haulouts and those areas not occupied by Steller sea lions. Steller sea lions also appear to have a strong preferences with regard to the terrestrial characteristics of their breeding and resting sites.

There were no consistent differences in the physical characteristics of waters surrounding sites in the eastern and western populations. Therefore, it is unlikely

Conclusions

that the particular physical characteristics examined here are related to the different population trends in the eastern and western populations, especially since these factors are not subject to change over time. There were also no consistent differences between haulouts and rookeries, indicating that there does not appear to be anything special about the waters near breeding sites that would have led to their selection.

Strengths and weaknesses

Some strengths of the approach used in Chapter 2 are that it: (1) applies a modelling technique (supervised classification) in a novel context, (2) evaluates it against another technique (logistic regression) that is commonly used, and (3) did not require detailed information on the movements of individual animals or groups of animals. Although certain assumptions had to be made about the way in which animals utilized their habitat, the models took advantage of the central foraging strategy to obviate the need for information on individual animal movements. Unlike many other models of species-habitat associations, since the location of every haulout and rookery is known across the range of the animal, there was no need to account for areas that were unsurveyed or had low sighting probabilities, and there was no need to differentiate between "suspected" non-habitat areas (i.e., areas that are actually habitat but are categorized as non-habitat because animals were not sighted there) and actual non-habitat areas

The weaknesses of this approach are, however: (1) Interpreting tests of statistical significance is difficult because the method artificially inflates the apparent sample size by using a cell-based (raster) approach involving millions of grid cells, in which the values of each cell were interpolated from an original data set of hundreds of thousands of points. (2) Issues of spatial autocorrelation (the values in one cell are not independent of the values in adjacent or nearby cells). Another issue is that some of the data themselves were the result of a model; however, since the behaviour of tidal currents is well-described by deterministic physical equations, this may not be as problematic as it first seems, even if the

Conclusions

resulting data is not a perfect or complete description of reality. (3) Other oceanographic factors besides the ones used (depth, slope, average tidal speed, and mixing index) may be more direct indicators of biological productivity and prey accessibility, or have more physiological relevance. Such variables may include chlorophyll concentration, water temperature, or salinity. (4) Data were not available for the entire range of rookeries and haulouts, so sites in the Commander Islands and northern Japan were not included. These areas could be included if similar oceanographic data become available in these regions. (5) Finally, the validation of the models could have been improved. Ideally, a random subset of each of the sites from each of the populations would be used to generate a model. This series of models could then be tested against the ideal model, providing an estimate of the average fit and error of each training set. This was not possible in this analysis due to the amount of processing time required to develop each model combined with the number of putative models to be evaluated.

With regard to the terrestrial (shoreline) data analysis in Chapter 3, the strengths of this approach were: (1) the methods are very straightforward, and can be applied to any other species that occupies the mapped coastline without requiring expensive fieldwork and on-site surveys, as long as the home ranges of the species of interest are well known and/or characterised. (2) it uses a preexisting data set in which the quality of the data were exceptional in terms of both resolution and coverage. This allowed for characterizing nearly half (46%) of all sites according to shoretype.

The weaknesses of this analysis were: (1) the data resolution was still insufficient to identify the shoretypes of sites that were located on very small offshore islands, and did not contain enough information to determine other potentially important factors such as slope, aspect, and degree of wave exposure. This data could only realistically be collected by high-resolution aerial photography or surveying of each site individually. (2) Complete count data were not available for conducting a population-weighted analysis, although historic count data (i.e. prior

Conclusions

to circa 1950) are either unavailable or very sparse for most locations. Ideally, factors with little or no temporal variation (such as latitude, longitude, aspect, etc) should be correlated only with long-term averages of site populations to avoid biases due to recent changes in population status between populations and short-term shifts in population densities. (3) Shoreline type data were not available for sites in Russia and northern Japan, so these sites were not included in the analysis. Nonetheless, clear patterns were apparent with the remaining sites.

If count data were available for sites from a longer time period—such as from archaeological data or historical records—then it would be logical to weight sites in the models according to abundance, to reflect the success or importance of a site. This was not done in this research because reliable count data were only available for a relatively recent period, and because no count data was available for sites in Washington, Oregon, or California. Additionally, because of the different population trajectories between the eastern and western populations, it would be difficult to separate the effects of site characteristics from population effects without a reliable baseline count for each site.

Implications

Climate change threatens to alter the structure and function of many ecosystems (Brereton et al. 1995). While this analysis deliberately used oceanographic predictors that are stable over long periods of time, a similar analysis could be conducted using predictors that varied over shorter time scales, or that are otherwise affected by climate change and regime shifts. These variables could include sea surface temperature, salinity, and mean sea level. Conducting such an analysis would then allow for predictions of changes in range by forcing of the input variables to simulate conditions expected in new climate regimes.

Other environmental factors that have direct physiological impacts, such as ocean temperature, air temperature, or salinity, would be more useful than the factors that were available for this analysis in determining the theoretical limits of

Conclusions

the Steller sea lion's range. The oceanographic predictors used here do not represent a smooth gradient from one end of the animal's range to the other, and there is no reason to suspect that either the depth, slope, tidal speed, or mixing characteristics are sufficiently different at either extreme of the range to inhibit further expansion. More likely, warmer ocean temperatures, availability of favoured prey species, and competition with other species such as *Zalophus californianus* (California sea lions) (Bartholomew & Boolotian 1960) are what dictate the maximum extents of Steller sea lions.

The same techniques used in this analysis could also be applied to other species, but are particularly relevant to central-place foraging species. For species whose range and distributions are not well-known, similar models could be built to predict likely, but unknown, habitat. The technique of supervised classification proved superior in this instance to logistic regression in terms of output accuracy, but provides only limited information about the relative importance of the input variables. This technique warrants further exploration and evaluation in other habitat-modelling applications.

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Appendix I - ROC values and K_{no} values for models at varying probability thresholds

Prediction of Rookery Locations – Mainland & Offshore

Classification models

Using K_{no} as an indicator of overall model success at predicting rookery locations, training the model using the western rookeries using a 1 nautical mile buffer, then applying a 99% cut-off produced the best-fitting model (Table A1.1). Generally – but not in all cases - a higher cut-off threshold resulted in a higher kappa value. Whether the model was trained using the western or eastern set of rookeries did not significantly affect the model fit, with the exception of the 50 nautical mile buffer distance, where training using the eastern set of rookeries yielded a better model fit than training on the western set ($p < 0.001$).

Logistic models

Using the forward stepwise procedure, only the independent variables with the most explanatory power are selected for inclusion in the final model. In all but two of the model runs, all of the variables were selected for inclusion. When using the 1 nautical mile buffer distance, depth was excluded from the final model in both the western and eastern training sets.

However, to facilitate a direct comparison with the supervised classification models, in these two instances, the depth variable was added back in to the logistic models. Interestingly, adding the depth variable back into the models markedly improved their performance versus the models without depth as an explanatory variable. Only three of the logistic models performed better than chance (according to ROC plots – Table A1.2)) at predicting rookery locations, compared with all of the classification models—50 nautical miles (west and east), and 20 nautical miles with eastern training sites (Table A1.3).

Appendix I

Table A1.1. K_{no} (Kappa) values for predicting rookery locations using rookeries as training areas for classification model. Values are given for each training set (west and east), buffer distance (1, 10, 20, or 50 nmi), and probability threshold (60-99%). The highest kappa value for each distance and training set is highlighted in bold.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%		0.4674	0.7611	0.7580	0.8915	0.8712	0.9853	0.9761
95%	0.4084	0.4441	0.7576	0.5169	0.8862	0.6210	0.9791	0.8344
90%	0.4205	0.3873	0.7452	0.2671	0.8758	0.3403	0.9622	0.6157
80%	0.4039		0.6823		0.8452		0.9065	
70%			0.5001		0.7903		0.8454	
60%					0.1837			

Table A1.2. ROC values predicting rookeries using rookeries as training areas. Bold values are above 0.5, and therefore represent models that perform better than a random or trivial model.

ROC	50	50	20	20	10	10	1	1
R-R	nmi	nmi	nmi	nmi	nmi	nmi	nmi	nmi
	W	E	W	E	W	E	W	E
Classification	0.693	0.677	0.672	0.626	0.676	0.668	0.506	0.688
Logistic	0.514	0.663	0.491	0.661	0.448	0.447	0.483	0.478

Table A1.3. Logistic model performance (K_{no}) predicting rookeries using rookeries as training areas at varying probability thresholds. Hatched columns represent models that did not perform better than random in ROC tests, and thus were excluded.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%	0.3152	0.4381		0.7585				
95%	0.1930	0.3651		0.7088				
90%	0.1513	0.3623		0.7055				
80%								
70%								
60%								

The 20 nautical mile logistic model performed slightly better than the corresponding classification model, while the 50 nautical mile logistic models did not perform as well as the corresponding supervised classification models ($p < 0.001$)—compare the highest (bolded) values in Tables A1.1 with A1.3.

Prediction of Haulout Locations – Mainland & Offshore

Classification models

Actual haulout locations were compared against models trained using both haulouts and rookeries separately as training areas to test if conditions near rookery locations alone were sufficient to predict haulouts. Tables A1.4 and A1.5 show the K_{no} values for models generated by training on rookeries and haulouts, respectively.

The same trend in model fits is generally seen, with better fits as the buffer distance decreases, although the model fits for the 20 nmi buffer distances were lower than the 50 nmi buffers. No training set (west or east) was consistently better at predicting haulouts across all distances, although the difference between kappa values was usually negligible. In comparing the best model from each distance, training using rookery sites alone did not produce a significantly better-fitting model ($p > 0.05$) than training on haulout sites, except at the 20 nautical mile distance, where training on rookeries produced a better-fitting model than training on haulouts ($p < 0.001$). At 50 nautical miles, training using haulouts produced a better-fitting model ($p < 0.001$).

Logistic models

Only one of the logistic models trained using haulouts (50 nautical miles east), and two trained on rookeries (50 and 20 nautical miles east) performed better than chance at predicting haulout locations according to ROC plots (Tables A1.6, A1.7).

Neither model outperformed the supervised classification models on the K_{no} score ($p < 0.001$) (Compare Tables A1.4 and A1.5 with Tables A1.8, A1.9).

Appendix I

Table A1.4 K_{no} (Kappa) values for predicting haulout locations using rookeries as training areas. Values are given for each training set (west and east), buffer distance (1, 10, 20, or 50 nmi), and probability threshold (40-99%). The highest kappa value for each distance and training set is highlighted in bold.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%	0.0713	0.1902	0.2765	0.2852	0.5291	0.5242	0.9547	0.9494
95%	0.1510	0.3127	0.2747	0.3023	0.5274	0.4525	0.9481	0.9810
90%	0.2704	0.3727	0.2753	0.2995				0.6108
80%	0.4155	0.3007	0.2773					
70%	0.4604		0.3041					
60%	0.4654		0.3480					
50%	0.4651		0.3489					
40%			0.3409					

Table A1.5 K_{no} (Kappa) values for predicting haulout locations using haulouts as training areas.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%	-0.0734	0.3813	0.2642	0.2663	0.5214	0.5286	0.9562	0.9669
95%	-0.1000	0.4436	0.2647	0.2683	0.5129	0.5257	0.9393	0.9393
90%	0.3872	0.4595	0.2599	0.2816	0.4936	0.4931	0.7553	0.9422
80%	0.4911	0.4644		0.1118				
70%	0.4997	0.4618						
60%	0.4830							

Table A1.6 ROC values predicting haulouts using rookeries as training areas.

ROC	50 nmi	50 nmi	20 nmi	20 nmi	10 nmi	10 nmi	1 nmi	1 nmi
R-H	W	E	W	E	W	E	W	E
Classification	0.664	0.735	0.701	0.655	0.667	0.672	0.688	0.685
Logistic	0.474	0.637	0.484	0.670	0.484	0.481	0.421	0.424

Table A1.7 ROC values predicting haulouts using haulouts as training areas.

ROC	50 nmi	50 nmi	20 nmi	20 nmi	10 nmi	10 nmi	1 nmi	1 nmi
H-H	W	E	W	E	W	E	W	E
Classification	0.769	0.755	0.671	0.681	0.644	0.655	0.724	0.711
Logistic	0.458	0.541	0.495	0.482	0.486	0.488	0.424	0.431

Appendix I

Table A1.8. Logistic model performance (Kno) predicting haulouts using rookeries as training areas. Hatched columns represent models that did not perform better than random in ROC tests, and thus were excluded.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%								
95%		-0.0275						
90%		-0.0206		0.2312				
80%		-0.0052		0.2328				
70%		0.0047		0.2310				
60%		0.0118						

Table A1.9. Logistic model performance (Kno) predicting haulouts using haulouts as training areas.

Threshold (Mainland & Islands)	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%								
95%		-0.1611						
90%		-0.1227						
80%		0.1027						
70%								
60%								

Prediction of Rookery Locations – Offshore Only

Classification Models

Exclusion of the mainland to simulate avoidance of terrestrial predators did not generally improve model performance in predicting rookery locations; in six of eight cases, (50, 20, and 10 nmi, east and western training areas) models that included the mainland outperformed those that excluded it ($p < 0.001$, except for 10 nmi west, $p < 0.01$). There was no significant difference ($p > 0.05$) between the mainland and offshore models at the 1 nmi distance. The same trend in Kno values was apparent with the offshore models: higher values were associated with smaller buffer distances.

With the exception of the 50 nmi distance, where the western-trained model had a better fit than the eastern-trained model ($p < 0.001$), there was no significant difference between models with the mainland mask applied.

Appendix I

Logistic Models

Only two of the logistic models exceeded chance when combined with the mainland exclusion on the ROC plots: 50 nautical miles east and west. In comparison with models that included the mainland, these two models did not show any increase in performance ($p < 0.001$).

Table A1.10 K_{no} (Kappa) values for predicting rookery locations using rookeries as training areas. Values are given for each training set (west and east), buffer distance (1, 10, 20, or 50 nmi), and probability threshold (40-99%). The highest kappa value for each distance and training set is highlighted in bold.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%	0.2112	0.2776	0.6660	0.6611	0.7768	0.8240	0.9844	0.9759
95%	0.2055	0.2522	0.6610	0.3311	0.8382	0.4802	0.9764	0.8026
90%	0.2285	0.1977	0.6471	0.0062	0.8220	0.1041	0.9580	0.5521
80%	0.2135							
70%								

Table A1.11 ROC values predicting rookeries using rookeries as training areas.

	50 nmi W	50 nmi E	20 nmi W	20 nmi E	10 nmi W	10 nmi E	1 nmi W	1 nmi E
Classification	0.619	0.595	0.608	0.538	0.637	0.571	0.583	0.638
Logistic	0.449	0.625	0.436	0.585	0.393	0.393	0.330	0.385

Table A1.12. Logistic model performance (K_{no}) predicting rookeries using rookeries as training areas. Hatched columns represent models that did not perform better than random in ROC tests, and thus were excluded.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%		0.2342		0.6643				
95%		0.2367		0.6514				
90%		0.2417		0.6463				
80%		0.2460						
70%		0.2415						

Prediction of Haulout Locations – Offshore Only

Classification Models

Applying the mainland mask to predictions of haulout locations also did not result in any marked improvement in model performance when using rookeries as training areas; again, in six of eight instances, models that included the mainland outperformed the offshore-only models ($p < 0.001$). At the 1 nautical mile distance, there was no difference between the mainland and offshore models ($p > 0.05$) (Compare Table A1.4 with Table A1.11).

Table A1.13. Classification model performance (K_{no}) predicting haulouts using rookeries as training areas.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%	-0.2210	-0.0472	0.0171	0.0278	0.3338	0.3497	0.9724	0.9647
95%	-0.0979	0.1354	0.0146	0.0519	0.3591	0.2398	0.9645	0.7940
90%	0.0792	0.2427	0.0171	0.0872	0.3526	0.1698	0.9463	0.5487
80%	0.2969	0.2434	0.0339	0.0209				
70%	0.3673	0.2351	0.0947					
60%	0.3787		0.1774					
50%	0.3818							
40%	0.3819							
30%	0.3770							

Similarly, when haulouts were used as training areas to predict haulout sites, models that included the mainland outperformed offshore-only models in six of eight instances ($p < 0.001$, 50, 20, and 10 nautical miles with eastern and western training areas—compare Table A1.5 with Table A1.12). Again, at the 1 nautical mile distances, there was no difference between the models ($p > 0.05$).

When comparing the haulout models on the basis of training area (west vs. east), rookery-trained models outperformed haulout-trained models in three cases ($p < 0.001$, 50 nautical miles west, 20 nautical miles west and east), one haulout-trained model outperformed a rookery-trained model ($p < 0.001$, 50 nautical miles east), and the remaining models showed no significant difference ($p > 0.05$, 10 and 1 nautical miles west and east).

Appendix I

Logistic Models

None of the haulout-trained models, and only two (50 nautical miles and 20 nautical miles, both eastern) of the rookery-trained logistic regression models performed better than chance according to their ROC scores when predicting haulout locations (Tables A1.15 & 16).

The 50 nmi rookery-trained logistic model with the mainland mask outperformed the corresponding model without a mainland mask, while the 20 nmi model did not perform as well as the unmasked model (compare Table Tables A1.8 and A1.17).

Table A1.14. Classification model performance (Kno) predicting haulouts using haulouts as training areas.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%				0.0062		0.3662		0.9874
95%	0.2497	0.1760	0.0126	0.0206	0.3440	0.3628	0.9548	0.9840
90%	0.2659	0.2113	0.0444	0.0237	0.3448	0.2712	0.9604	0.4732
80%	0.3766	0.3737	0.0964	0.1614	0.3231	-0.2330	0.9255	-0.1568
70%	0.3493	0.3786	0.1164	0.1913			0.8078	-0.2800
60%		0.3744	0.1354	0.1552			0.2330	-0.3384
50%			0.1392					
40%			0.1371					

Table A1.15. ROC values predicting haulouts using rookeries as training areas.

	50 nmi W	50 nmi E	20 nmi W	20 nmi E	10 nmi W	10 nmi E	1 nmi W	1 nmi E
Classification	0.733	0.675	0.624	0.534	0.608	0.616	0.558	0.628
Logistic	0.367	0.595	0.411	0.569	0.432	0.444	0.428	0.420

Table A1.16. ROC values predicting haulouts using haulouts as training areas.

	50 nmi W	50 nmi E	20 nmi W	20 nmi E	10 nmi W	10 nmi E	1 nmi W	1 nmi E
Classification	0.734	0.706	0.583	0.567	0.571	0.559	0.605	0.623
Logistic	0.354	0.460	0.392	0.414	0.435	0.447	0.405	0.415

Appendix I

Table A1.17. Logistic model performance (K_{no}) predicting haulouts using rookeries as training areas.

Threshold	50 nmi (W)	50 nmi (E)	20 nmi (W)	20 nmi (E)	10 nmi (W)	10 nmi (E)	1 nmi (W)	1 nmi (E)
99%		-0.2770		0.0172				
95%		-0.2570		0.0104				
90%		-0.2441		0.0130				
80%		-0.2235						
70%		-0.2098						
60%		-0.1999						
50%		-0.1841						
40%		-0.1545						
30%		-0.1438						
20%		-0.0536						
10%		0.0433						

However, the 50 nmi model required a very low threshold (10%) to achieve a positive score, whereas the unmasked model achieved positive scores at all thresholds below 70%, indicating that the unmasked model is more robust overall. This interpretation is also supported by the higher ROC score of the unmasked model (compare Tables A1.6 and A1.15)

Appendix II - Environmental Sensitivity Index (ESI) shoretypes



Plate 1. ESI shoreline type 1 – exposed rocky shores. (Picture courtesy OR&R, NOS, NOAA)

Appendix II



Plate 2. ESI shoreline type 2 – exposed rocky platforms. (Picture courtesy OR&R, NOS, NOAA)



Plate 3. ESI shoreline type 3 – Fine-grained sand beaches. (Picture courtesy OR&R, NOS, NOAA)

Appendix II



Plate 4. ESI shoreline type 4 – coarse-grained sand beaches. (Picture courtesy OR&R, NOS, NOAA)



Plate 5. ESI shoreline type 5 – mixed sand and gravel beaches. (Picture courtesy OR&R, NOS, NOAA)

Appendix II



Plate 6. ESI shoreline type 6a – gravel beaches. (Picture courtesy OR&R, NOS, NOAA)

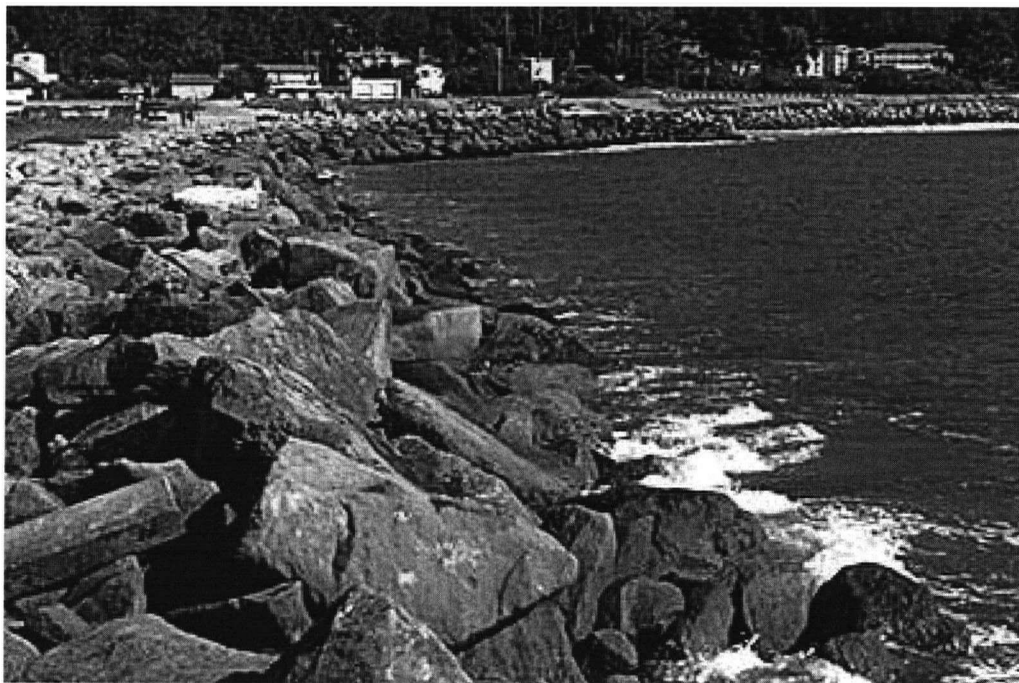


Plate 7. ESI shoreline type 6b – riprap structures. (Picture courtesy OR&R, NOS, NOAA)

Appendix II



Plate 8. ESI shoreline type 7 – exposed tidal flats. (Picture courtesy OR&R, NOS, NOAA)



Plate 9. ESI shoreline type 8a – sheltered rocky shores. (Picture courtesy OR&R, NOS, NOAA)

Appendix II



Plate 10. ESI shoreline type 8b – Sheltered artificial structures. (Picture courtesy OR&R, NOS, NOAA)



Plate 11. ESI shoreline type 9 – sheltered tidal flats. (Picture courtesy OR&R, NOS, NOAA).