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Biotic and abiotic drivers of harbor seal (*Phoca vitulina*) fine-scale densities in the Salish Sea

Jamie L. Brusa[1] | Scott F. Pearson[2] | Martin G. Raphael[3] | Beth Gardner[1]

[1]School of Environmental and Forest Science, University of Washington, Seattle, Washington

[2]Wildlife Science Division, Washington Department of Fish and Wildlife, Olympia, Washington

[3]U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia, Washington

Correspondence
Jamie L. Brusa, School of Environmental and Forest Science, University of Washington, 107 Anderson Hall, Seattle, WA 98195.
Email: jlbwcc@gmail.com

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Abstract

Understanding relationships between environmental characteristics and variation in species occurrence and density can provide information for managing human activities, protected species, and species of commercial importance in a dynamic system. To identify environmental drivers associated with variation in harbor seal (*Phoca vitulina*) densities in the Salish Sea, Washington, we analyzed 20 years of boat-based survey data and environmental covariates using a hierarchical distance sampling model. We included spatial, temporal, and spatiotemporal environmental covariates in our model and produced fine-scale predictive maps displaying in-water estimated densities from our model results. We found that spatial covariates were the strongest predictors for harbor seal densities in the Salish Sea. Harbor seals were more abundant closer to major river mouths, near shore, in shallower waters, and in areas with more haul-out sites. Additionally, harbor seal density varied with shoreline type. Changes in predicted harbor seal spatial use of the Salish Sea varied but with little difference between breeding/molting and nonbreeding/nonmolting seasons. Our results revealed spatiotemporal variation in harbor seal fine-scale density in the Salish Sea, which are particularly important for conservation planning, as spatiotemporal variation in harbor seal density can exert heterogenous top-down effects on prey species populations, some of which are threatened.

KEYWORDS
habitat, harbor seal, hierarchical distance sampling, *Phoca vitulina*, Salish Sea, spatial distribution

1 | INTRODUCTION

Understanding spatiotemporal variation in marine mammal abundance and density is important because marine mammals can be vulnerable to both environmental change and anthropogenic activities (Kovacs et al., 2012; Read et al., 2006) and often play important ecosystem roles as consumers and sentinels (Moore, 2008; Morissette et al., 2012). For example, marine spatial planning can benefit from information regarding variation in marine mammal density (Jones et al., 2017). Unfortunately, assessing fine-scale patterns in marine mammal spatiotemporal abundances and densities can prove challenging because these analyses tend to require high-quality long-term data (Best et al., 2015; Magera et al., 2013).

Documenting geospatial occurrences of marine meso-predators at the water surface using long-term data can serve as a baseline for environmental changes and assist in managing ecosystems. Pinniped species are long-lived (Brusa et al., 2021; McLaren & Smith, 1985), exert top-down pressure on their ecosystems (Österblom et al., 2007; Parrish, 2009), and have indirect effects in food web dynamics (Connell, 2002; Estes et al., 1998). Therefore, they can reveal valuable ecosystem insights that might not be captured by studying other taxonomic groups.

One of the most well-studied pinniped species, the harbor seal (*Phoca vitulina*), is widely distributed across the Northern Hemisphere and has a highly diverse diet (Eguchi & Harvey, 2005; Howard et al., 2013; Luxa & Acevedo-Gutiérrez, 2013). As a generalist predator, harbor seal diet depends on seasonally available or abundant prey species, such as Pacific herring (*Clupea pallassii*), salmon, Pacific sand lance (*Ammodytes hexapterus*), and squid (Lance et al., 2012; Middlemas et al., 2006; Thomas et al., 2022; Tollit et al., 1998), and prey species abundance can correlate with spatiotemporal patterns of harbor seal occurrence (Grigg et al., 2009, 2012). For example, harbor seals can form large groups (more than 50 individuals) in the water related to spawning events by their prey (Marston et al., 2002). Although measuring prey species abundance is not always possible, environmental variables, such as sea surface temperature, salinity, primary productivity, sediment type, and climate indices, are widely accessible and are known to influence harbor seal prey species availability (Payne & Selzer, 1989; Sobocinski et al., 2020). Environmental variables might serve as useful proxies for predicting harbor seal spatiotemporal occurrences, as they have for other marine mammal species, such as bottlenose dolphins, *Tursiops truncatus* (Torres et al., 2008).

Harbor seals have been described as central place foragers, where animals return to a specific location (i.e., haul-out sites for harbor seals) between foraging trips (Grigg et al., 2009, 2012; Luxa & Acevedo-Gutiérrez, 2013; Sharples et al., 2012). Central-place foragers must contend with tradeoffs associated with distance from their central place and prey availability (Olsson et al., 2008; Schoener, 1979). For example, Grigg et al. (2012) found that harbor seals in San Francisco Bay, California, incurred the tradeoff of using inopportune foraging habitat (i.e., areas with heavy anthropogenic impacts) because of the close proximity to their haul-out site. Harbor seals use haul-out sites to thermoregulate, avoid predators, rest, molt, and nurse pups (Cunningham et al., 2008; Reder et al., 2003; Simpkins et al., 2003; Terhune et al., 2008). Hauling out becomes more important during the life-history events of mating, molting, and nursing pups, which is when harbor seals tend to forage closer to haul-out sites (Boness et al., 1994, 2006; Daniel et al., 2003; Grigg et al., 2009).

The Salish Sea, which encompasses the inshore and nearshore waters of the Strait of Georgia, Strait of Juan de Fuca, and Puget Sound in northwestern Washington state and southwestern British Columbia, serves as a system of cultural, economic, ecological, and research importance (Gaydos et al., 2009; Wilson, 2020). The Salish Sea provides habitat and/or food to a diversity of species including 172 bird and 37 mammal species (Gaydos & Pearson, 2011) and is also home to multiple fish species listed on the United States Endangered Species Act list of threatened and endangered species, including some prey species of harbor seals, such as steelhead trout (*Oncorhynchus mykiss*), chinook salmon (*Oncorhynchus*

tshawytscha), coho salmon (*Oncorhynchus kisutch*), chum salmon (*Oncorhynchus keta*), and rockfish (*Sebastes ruberrimus*) (Lance et al., 2012; Moore & Berejikian, 2017; Wong & Rylko, 2014). Given the cultural and economic value of salmon fisheries in the Salish Sea (Wilson, 2020) and the ecological role of harbor seals as a meso-predator in the Salish Sea ecosystem, we were particularly interested in investigating the spatial dynamics of harbor seals in the Salish Sea.

Here, we take advantage of a monitoring data set with extensive spatiotemporal scale (i.e., nearly 70,000 km of boat-based survey effort from 2001 to 2020) to build predictive surface maps of harbor seal abundance in the United States portion of the Salish Sea. Specifically, we employed hierarchical distance sampling methods to (1) estimate the variation in fine-scale densities of harbor seals (i.e., number of harbor seals within a 4-km^2 grid cell) by season and year and (2) identify environmental covariates associated with variation in fine-scale densities of harbor seals. We expected the relative in-water (observed at the sea surface) abundance and distribution of harbor seals to vary seasonally with changes in the life-history activities of pupping, breeding, and molting. In accordance with central place foraging theory, we also predicted that variation in relative harbor seal abundance would relate to proximity to haul-out sites and environmental factors associated with variation in prey species availability.

2 | MATERIALS & METHODS

2.1 | Study site and harbor seal life history

The Salish Sea encompasses the Strait of Juan de Fuca, Strait of Georgia, and Puget Sound and spans Canadian and United States waters. The major cities of Seattle and Vancouver are located along the shores of the Salish Sea, and about 7,470 km of coastline border the Salish Sea (Gaydos et al., 2009). We defined our study area as the U.S. portion of the Salish Sea (48°N, 123°W; Figure 1). This study area encompasses three harbor seal stocks: Southern Puget Sound, Washington Northern Inland Waters, and Hood Canal (Carretta et al., 2020). In the Salish Sea, harbor seal population sizes have increased from their historically depleted sizes (Newby, 1973) prior to the Marine Mammal Protection Act of 1972 that protected harbor seals from being hunted (Jeffries et al., 2003). The harbor seal population in the U.S. portion of the Salish Sea is now considered stable and at carrying capacity (growth limited by resources) with an estimated abundance of >13,000 individuals (Ashley et al., 2020; Carretta et al., 2023; Jeffries et al., 2003). During the breeding season (mid-June to late August), male harbor seals exhibit aquatic and terrestrial lekking behavior; mating occurs aquatically; and females produce pups and nurse on land (Boness et al., 2006; Coltman et al., 1998; Hayes et al., 2004; Howard et al., 2013). In many areas, including the Salish Sea, harbor seals form colonies on various substrate types including mud flats, sandy, rocky, or cobble beaches, rocky outcroppings, or human-built platforms, such as log rafts and floats (Boness et al., 2006; Boveng et al., 2003; Jeffries et al., 2003).

2.2 | Data collection

Data collection of harbor seal counts and perpendicular distances to the transect line occurred during multispecies vessel-based line transect surveys. The summer surveys, conducted in mid-May to June and again at the end of July, occurred each year from 2001 to 2018 (excluding 2017), and surveys for the remaining months only occurred from 2013 through March of 2020. The survey was designed specifically for monitoring marbled murrelets (*Brachyramphus maromoratus*); however, all marine mammal and bird species, including harbor seals, were recorded during the surveys. Vessels (ranging in size from 5.8 m to 8 m) maintained a speed of 8–12 knots, and survey effort ended if glare obstructed the view of observers or if Beaufort sea state was 3 or greater for more than 25% of a transect. For each survey, two observers constantly scanned 90° arcs (from bow to either port or starboard) recording only harbor seals in the water. For a complete description of field methods, including the rotation of observers, training, and distance testing, see Raphael et al. (2007).

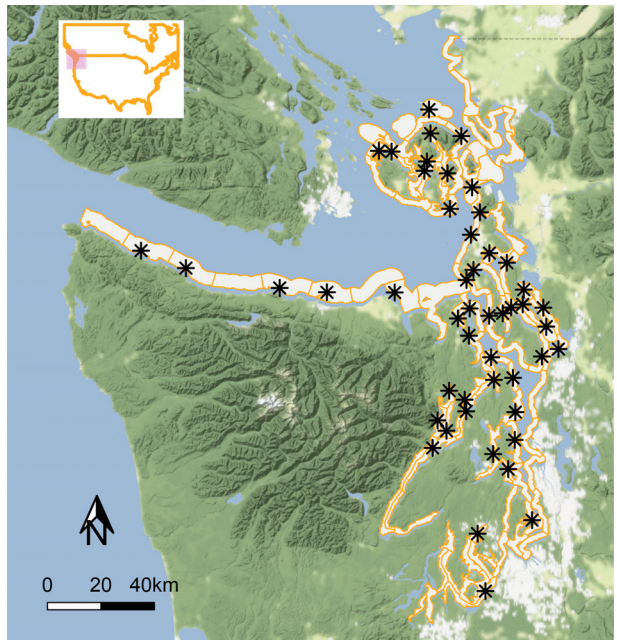

FIGURE 1 Map of study area. The shapes outlined in orange show the primary sampling units, which are composed of four nearshore segments (each approximately 5 km in length) and an offshore zigzag (approximately 20 km in length). A subset of 49 primary sampling units were selected for vessel-based distance sampling and are indicated with an asterisk. The base map was created using the R package "ggmap" (Kahle et al., 2019).

The study area was divided into 98 roughly 20-km-long rectangular areas along the Puget Sound and Strait of Juan de Fuca coastline, defined as primary sampling units (PSUs). Of those 98 PSUs, 30 PSUs were randomly selected (using the random number generator in ArcGIS) for surveys from 2001 through 2020, and an additional 19 PSUs were added for the years 2013–2020. Each PSU was sampled multiple times per year but not in every month. Each PSU consists of one inshore (width of 0–1.5 km from shore) and one offshore (width of 1.5–5 km from shore) subunit. The inshore subunit is divided into four equal-length segments (approximate lengths of 5 km each) forming a transect line parallel to shore (approximately 100 m, 200 m, 300 m, or 400 m from shore); the distance from shore for the inshore segment was randomly selected (using the random number generator in ArcGIS) without replacement for each survey (see Raphael et al. 2007 for details). The offshore transects took a zigzag shape to maximize detection efficiency (zigzags covered the 1.5–5 km distances from shore) and were approximately 15 km in length. Figure 1 shows all 98 PSUs and indicates the 49 PSUs that were sampled; a detailed figure of a PSU is presented by Raphael et al. (2015).

During the spring/summer (May through July), at least two sampling occasions of each of the 30 PSUs occurred (with the order selected at random), and during the fall/winter, additional surveys of all 49 PSUs occurred. For all seasons, consecutive surveys occurred with a minimum of 7 days elapsing before sampling the same PSU again.

2.3 | Covariate data acquisition

We included the following biological/physical covariates: season (breeding/molting or not), chlorophyll-a as a proxy for primary productivity, water depth, spring transition date, fall transition date, the number of harbor seal haul-out sites within 30 km of a PSU segment/zigzag, North Pacific Gyre Oscillation (NPGO)—a type of climate index to

measure variation in ocean currents, categorical shore distance (within 1.5 km or between 1.5 and 5 km from shore), sea surface temperature, salinity, shoreline type (based on substrate composition), nearest distance to river mouth, and upwelling index (Table 1).

We used known haul-out sites for harbor seals (Jeffries et al., 2000, 2003; Figure S1) and created a buffer of 30 km around each haul-out site to capture the influence of hauling out (e.g., resting, social interactions) on in-water harbor seal fine-scale densities. We selected 30 km because harbor seals typically forage within 30 km of their haul-out site (Jones et al., 2017; Tollit et al., 1998) but can vary considerably with some individuals venturing no farther than 5 km away from their haul-out site (Suryan & Harvey, 1998) and others travelling more than 100 km (Peterson et al., 2012). We calculated the number of haul-out site buffers that overlapped the PSU segment/zigzag as a proxy for the relative influence of haul-out sites (maximum proportion of haul-out site in a PSU segment/zigzag was 52% and maximum number was 242 haul-out sites). Given the importance of a central place to a central-place foraging species, we predicted that areas with a greater number of haul-out sites within 30 km would be associated with greater fine-scale densities of harbor seals in the Salish Sea. As most of the haul-out sites were located in nearshore segments, we also predicted that harbor seal fine-scale densities would be greater in the nearshore segments than in offshore zigzags.

We compiled data for sea surface temperature, salinity, and chlorophyll-a using Google Earth Engine (Gorelick et al., 2017). For temperature (NASA JPL/OBPG/RSMAS, 2020) and chlorophyll-a (NASA OB.DAAC, 2018), we used data from the MODerate Resolution Imaging Spectrometer (MODIS) Aqua platform data sets. For salinity, we used data from the Hybrid Coordinate Ocean Model (HYCOM) forecast system at the U.S. Naval Oceanographic Office (Cummings & Smedstad, 2013). We used 30-day averages from the 30 days preceding a survey day using daily estimates and used interpolation from the nearest coordinates and days for any missing data for a specific day at a given PSU segment/zigzag. We extracted daily temperature, salinity, and chlorophyll-a values from 2001 through 2020 using a 26 $\times$ 26 point spatial grid (this grid size balanced data coverage and computing time) to construct a variogram model and kriged values to the midpoint of each PSU segment/zigzag for each given day. We used the R package gstat (Pebesma & Graeler, 2020) to perform the spatiotemporal interpolation, and the R packages "spacetime" (Pebesma et al., 2021), "rgeos" (Bivand et al., 2020), "rgdal" (Bivand et al., 2021), and "sp" (Pebesma et al., 2019) to prepare our data for kriging using R (R Core Team, 2020). We predicted that moderate temperatures, lower salinities, and higher levels of primary productivity, indicated by chlorophyll-a, would be associated with greater fine-scale densities of harbor seals in the Salish Sea because these conditions should be preferred by prey species. Studies in the Salish Sea suggest slightly more foraging activity by harbor seals during the day (Thomas et al., 2011; Wilson et al., 2014); therefore, we can reasonably assume that foraging activity contributed to fine-scale geographic locations of harbor seals during surveys.

During the spring, the winds shift from southerly winter winds to northwesterly summer winds, which also helps drive Pacific currents and results in coastal upwelling in the North Pacific (Mantua et al., 1997; Peterson & Miller, 1975). In the 2–4 months following this upwelling event, the zooplankton community composition shifts to a community dominated by prey items favorable to salmonid fishes (Keister et al., 2011; Liu et al., 2015; Peterson & Keister, 2003; Peterson & Schwing, 2003). The biological spring transition is the approximate date when the zooplankton community composition changes. There is some influence of coastal upwelling on the Strait of Juan de Fuca and, with less influence in the Puget Sound (Deppe et al., 2018). We predicted that fine-scale densities of harbor seals would be associated with the spring transition date, when prey would become more available to Salish Sea harbor seals. Similarly, harbor seal foraging activity can respond to prey pulses, which are often correlated with upwelling, but harbor seals in the Salish Sea, with many prey items from which to choose, do not consistently respond to prey pulses (Wilson et al., 2014). Therefore, including upwelling in the model was purely exploratory.

NPGO has a strong relationship with changes in zooplankton community composition (Di Lorenzo et al., 2008). Typically, negative values for NPGO, indicating a cool phase, are associated with cold-water, lipid-rich copepod species dominance and lower species richness in zooplankton communities (Hooff & Peterson, 2006). NPGO has influenced survival rates and productivity of multiple species of salmon in the North Pacific (Hertz et al., 2016;

TABLE 1 List of covariates included in the harbor seal fine-densities model. For each covariate, there is a short description, if the covariate is spatially, temporally, or spatiotemporally varying, and the location where the data were sourced.

Covariate	Description	Variability	Source
Season – breed/molt	The time of year of the survey – during the breeding/molting season (mid-June through mid-September) or not	Temporal	Huber et al. (2001)
Chlorophyll	Chlorophyll-a concentration from global daily measurements to a resolution of 1 km	Temporal, Spatial	NASA OB.DAAC; https://developers.google.com/earth-engine/datasets/catalog/NASA_OCEANDATA_MODIS-Aqua_L3SMI
Depth	Estimated from satellite altimetry and shipboard soundings at a 15-arc sec spatial resolution	Spatial	Tozer et al. (2019); https://topex.ucsd.edu
Fall transition and Spring transition dates	Annual Julian day of spring or fall transition based on the Pierce and Barth method	Temporal	Compiled by W. T. Peterson; http://www.cbr.washington.edu/status/trans
Haul-out site	Number of haul-out sites that are within 30 km of any part of the segment/zigzag	Fixed	Jeffries et al., (2003); current study
NPGO	North Pacific Gyre Oscillation, monthly measurements	Temporal	Di Lorenzo et al. (2008); http://www.o3d.org/npgo
Offshore or nearshore (shore distance)	We define offshore as >1.5 km and <5 km from shore and nearshore as within 1.5 km of shore	Spatial	Current study
Sea surface temperature	Global daily measurements to a resolution of 1 km	Temporal, Spatial	NASA JPL/OBPG/RSMAS https://developers.google.com/earth-engine/datasets/catalog/NASA_OCEANDATA_MODIS-Aqua_L3SMI
Salinity	Daily surface salinity provided by the hybrid coordinate ocean model	Temporal, Spatial	National Ocean Partnership Program; https://developers.google.com/earth-engine/datasets/catalog/HYCOM_sea_temp_salinity
Shoreline type (based on substrate composition)	Proportion of segment that is each substrate type: sheltered rocky shores, sheltered tidal flats, exposed tidal flats, boulder rubble, gravel beach, mixed sand/gravel beach, coarse-grained sand beach, exposed wave-cut platforms, exposed rocky shore, and human-built sheltered riprap	Spatial	Petersen et al. (2002)
Distance to river mouth	In-water distance from centroid of segment to nearest river mouth	Spatial	Nolan et al. (2003)
Upwelling index	Daily measurements from 48°N, 125°W in metric tons/s/100 m coastline	Temporal	National Marine Fisheries Service, Pacific Fisheries Environmental Laboratory; http://www.cbr.washington.edu/dart/query/upwell_graph_text

Kilduff et al., 2015; Malick et al., 2017), which might affect in-water geospatial occurrences of harbor seals foraging for these species.

Shoreline type has also been used as an indicator for harbor seal distributions (Montgomery et al., 2007); thus, we included it as a predictor variable. We used a subset of shoreline type from the compiled list from Petersen et al. (2002) as modified by Raphael et al. (2015). Shoreline types were categorized based on the wave energy exposure, slope, biological productivity, and substrate, which could include sediment size ranging from fine sand to boulder, vegetation functional group (e.g., marsh grasses, riparian trees/shrubs), and human-made materials (e.g., seawalls). As some segments included more than one shoreline type, we used the most prevalent shoreline type for the nearshore or offshore segment. In Cook Inlet, Alaska, harbor seals selected areas near rocky substrate over other substrate types (Montgomery et al., 2007). Therefore, we predicted that Salish Sea harbor seals might also preferentially select rocky substrates.

We calculated the distance from the PSU segment/zigzag to the nearest major river mouth by assigning a midpoint to each segment/zigzag and measuring the in-water distance between the midpoint and the closest river mouth using the R (R Core Team, 2020) packages "sf" (Pebesma, Bivand, et al., 2021) and "raster" (Hijmans et al., 2023). As moving from freshwater to saltwater is part of the life history of many salmonid species upon which harbor seals prey, river mouths might be focal foraging locations for harbor seals (Wright et al., 2007). Therefore, we hypothesized that the fine-scale density of harbor seals would increase with decreasing distances to river mouths.

We also incorporated two covariates for the detection component of our distance-sampling model, Beaufort sea state as a fixed effect and observer pair as a random effect. We expected that lower Beaufort sea states would facilitate detection of harbor seals because smaller waves would obstruct a sightline to a harbor seal less than larger waves. The data set had limited variability in Beaufort sea state per protocol (see above), as about 93% of observations occurred during a Beaufort sea state of 1 or 2; only about 6% of observations occurred at a Beaufort sea state of 0; and fewer than 1% occurred at a Beaufort sea state of 3 or 4. Observer pair consisted of the unique combination of the two observers collecting data simultaneously on a segment/zigzag.

2.4 | Analytical approach

We used a hierarchical distance sampling model in a Bayesian framework to investigate the spatiotemporal variation in harbor seal in-water fine-scale densities. Distance sampling allows for estimating the state process (abundance) from the detection process by accounting for variation in detection probability with distance from the transect line, and covariates can be incorporated for both the state process and detection components (Buckland et al., 2001; Williams et al., 2002). Hierarchical distance sampling models incorporate information across multiple transects (Royle & Dorazio, 2006) to estimate spatial variation in density. We focused on estimating in-water fine-scale density as the surveys are at sea, but it also is important to note that animals can be diving during the survey and, thus, unavailable for detection. As such, there is a portion of the at-sea population that is not included in our density estimates.

We grouped the observed distances into 27-m bins (to follow a half-normal curve) and truncated the largest 5% distance estimates of all data collected (Buckland et al., 2001), which was 275 m from the transect. We modeled variation in the scale parameter of the half-normal detection function for each repeat visit i to site (segment/zigzag) j, as follows:

$$\log(\sigma_{ij}) = \alpha_0 + \alpha_1 \times \text{Beaufort sea state}_{ij} + \varepsilon_{\text{obs}_{ij}},$$

where α_0 is the intercept, α_1 is the coefficient for the Beaufort sea state covariate, and $\varepsilon_{\text{obs}_{ij}}$ is a random effect of observer such that $\varepsilon_{\text{obs}_{ij}} \sim \text{Normal}(0, \gamma_{\text{obs}})$.

Due to overdispersion in the observed counts, we used a negative binomial for abundance such that:

$$N_{ij} \sim \text{Negative Binomial}(\lambda_{ij}, r),$$

where N_{ij} is the fine-scale density of in-water harbor seals for each repeat visit i to site (segment/zigzag) j, and with a mean and dispersion r. To account for variation in the expected mean abundance, we fit the full model such that:

$$\begin{aligned}\log(\lambda_{ij}) = {} & \beta_0 + \beta_1 \times \text{chlor}_{ij} + \beta_2 \times \text{depth}_{ij} + \beta_3 \times \text{NPGO}_{ij} + \beta_4 \times \text{haulout}_{ij} + \beta_5 \times \text{sst}_{ij} + \beta_6 \times \text{salinity}_{ij} \\ & + \beta_7 \times \text{ST}_{ij} + \beta_8 \times \text{FT}_{ij} + \beta_9 \times \text{substrate}_{ij} + \beta_{10} \times \text{upwell}_{ij} + \beta_{11} \times \text{river}_{ij} + \beta_{12} \times \text{breedmolt}_{ij} \\ & + \beta_{13} \times \text{offshore}_{ij} + \varepsilon_{\text{Year}_{ij}} + \varepsilon_{\text{Segment}_{ij}} + \log(\text{area}_j),\end{aligned}$$

where β_0 is the intercept, $\beta_{1\ldots13}$ represent coefficient values, chlor is chlorophyll-a concentration, haulout is the number of haul-out sites with a 30-km buffer that overlapped a PSU segment/zigzag, sst is sea surface temperature, ST is the spring transition date, FT is the fall transition date, substrate is the substrate composition of the shoreline adjacent to the PSU segment/zigzag, upwell is the upwelling index value, river is the in-water distance to the nearest river mouth from the midpoint of the PSU segment/zigzag, breedmolt indicates if the survey occurred during the breeding/molting season (mid-June through mid-September) or nonbreeding/nonmolting season, offshore indicates if the area sampled was a nearshore segment or offshore zigzag (shore distance covariate from Table 1), $\varepsilon_{\text{Year}}$ is a random effect of year such that $\varepsilon_{\text{Year}} \sim \text{Normal}(0, \gamma_Y)$, and $\varepsilon_{\text{Segment}}$ is a random effect of PSU segment/zigzag such that $\varepsilon_{\text{Segment}} \sim \text{Normal}(0, \gamma_S)$. We included these random effects to account for repeated sampling within years and segments. Finally, $\log(\text{area}_j)$ is an offset for area because each segment/zigzag had a unique length with most segment lengths at 5 km and most zigzag lengths between 15 and 20 km.

We used vague priors for all parameters, $\beta \sim \text{Normal}(0, 10)$ for all abundance parameters (values indicate mean and variance), $\alpha \sim \text{Normal}(o, 100)$ for all detection parameters, and $\gamma \sim \text{Gamma}(1,1)$ for the variance terms of the random effects of year, segment, and observers. We centered all continuous covariates to a mean of zero and scaled all continuous covariates by two standard deviations to better allow comparison of estimated coefficients for continuous covariates with those for categorical covariates (Gelman, 2008). Additionally, we found no evidence of dependence between covariates ($|r| < 0.6$ for all pair-wise covariate comparisons). As correlations between covariates were low and any of the covariates might affect the fine-scale density of harbor seals, we built one exploratory model rather than using a competing model framework (Gelman & Shalizi, 2012). We fit the model using the JAGS language (Plummer, 2003) in R (R Core Team, 2020). We ran a Markov chain Monte Carlo (MCMC) sampler (Casella & George, 1992; Gelfand & Smith, 1990; Geman & Geman, 1993) with three chains for 50,000 iterations after 2,000 iterations of adaptation and 10,000 iterations of burn-in using the "runjags" package (Denwood & Plummer, 2016). Code and data can be accessed at https://github.com/JamieBrusa/Salish-Sea-Harbor-Seals. We visually assessed model convergence for adequate mixing of chains and calculated the Gelman-Rubin $\widehat{R}$ diagnostic (Gelman & Rubin, 1992) for all monitored parameters using the "coda" (Plummer et al., 2006) and "ggmcmc" (Fernández-i-Marín, 2016) packages for R. All $\widehat{R}$ values were below 1.1 (Table S1). We used posterior predictive checks to assess model fit by evaluating the ability of the model to simulate new data from the model that were similar to observed data. We used Bayesian p values to assess goodness of fit for both the abundance and detection components of the model, where we considered values between .1 and .9 to indicate good model fit. We found no evidence of lack of fit (Bayesian p value for abundance = .78, Bayesian p value for detection = .75). For each covariate, we considered it an important predictor if the 95% Bayesian credible interval (BCI) did not include 0, and we considered it a marginally important predictor if the 80% BCI did not include 0.

We used the results of our analysis to predict harbor seal fine-scale densities in the Salish Sea. We used the R packages "fasterize" (Ross et al., 2020), "rgdal" (Bivand et al., 2021), and "sf" (Pebesma et al., 2021) to map harbor seal fine-scale density predictions in areas that were not sampled but that were within 5 km from shore so as to not extrapolate beyond the sampling frame; these predictions were based on modeled relationships between harbor seal fine-scale density and environmental covariates. These predictions are at a resolution of 2 × 2 km pixels.

3 | RESULTS

Total survey effort from 2001 to 2020 (excluding the 2017 and 2019 breeding/molting seasons and only including the first 3 months of 2020) yielded 69,838 km of transect traveled by the survey boat and 19,390 harbor seal sighting events across 1,044 survey days, accounting for 1,257 harbor seal sightings per year (mean raw count per year including all survey years). During the breeding/molting season (June through August), a mean of 204 harbor seals (range = 43–521) were sighted per month per year, and during the nonbreeding/nonmolting season, a mean of 151 harbor seals (range = 4–351) were sighted per month per year. Harbor seals were sighted on 471 of 487 survey days during the breeding/molting season and on 549 of 557 survey days during the nonbreeding/nonmolting season. Observers sighted harbor seals in all areas sampled except for two adjacent segments that were only sampled one day throughout the entire 20-year study period. Group sizes of observed harbor seals ranged from 1 to 54 seals (1 to 34 during the breeding/molting season and 1 to 54 during the nonbreeding/nonmolting season) with a mean of 1.17 seals per group ($SD = 1.11$). However, large groups of 10 or more seals were extremely uncommon and only comprised 0.3% of all harbor seal sightings. The vast majority (93%) of harbor seal sightings were of single seals. The proportion of single seals (i.e., group size = 1) sighted was 94% during the nonbreeding/nonmolting season compared to 91% during the breeding/molting season.

Observer pair affected detection of harbor seals, but Beaufort sea state did not have a strong effect (Figure S2), a likely result given that the vast majority of observations occurred during a Beaufort sea state of 1 or 2 per protocol. A Beaufort sea state of 0 was optimal for detection, and Beaufort sea states of 1, 2, and 3+ all resulted in similar but slightly lower estimates of the scale parameter, σ, resulting in overall lower probabilities of detection. Random effects of observer pair suggested that some observer pairs had much higher detection rates of harbor seals than others (Table S2).

We found that harbor seal fine-scale density was predicted by depth, number of nearby haul-out sites, categorical distance from shore (i.e., within 1.5 km from shore or between 1.5 km and 5 km from shore), distance to river mouth, and shoreline type (Figure 2). The shoreline type and categorical distance from shore had the strongest relationships with spatiotemporal variation in harbor seal fine-scale densities (Table S3). These results suggest that harbor seal fine-scale in-water density was likely highest at a depth between 17 m and 32 m, a distance to river mouth between 9 km and 16 km, and when proximity to haul-out sites increased. Harbor seal fine-scale densities were also greater away from sheltered tidal flats and boulder rubble but were greater near human-built sheltered riprap and sheltered rocky shores and in nearshore (within 1.5 km of shore) waters. None of the temporal covariates were found to be important predictors of harbor seal fine-scale densities, and, similarly, the spatiotemporal covariates were not considered important or only marginally important (Table S3).

The in-water fine-scale density of harbor seals varied between breeding/molting and nonbreeding/nonmolting seasons but had little variation across years (Figure S3). Ninety-five percent of the 4 km^2 pixels on our predictive map had an estimated fine-scale density of 1.49 harbor seals or fewer during the breeding/molting season and 2.00 or fewer during the nonbreeding/nonmolting season. The greatest fine-scale densities of harbor seals occurred around the San Juan Islands and more inland sections of the Strait of Juan de Fuca during the breeding/molting season (Figure 3) where rocky and island associated haul-outs are abundant. During the nonbreeding/nonmolting season, when fewer harbor seals were likely to be hauled out, harbor seal densities ranged from 0.03 seals per km^2 to 2.72 seals per km^2. During the breeding/molting season, seal densities ranged from 0.02 seals per km^2 to 1.92 seals per km^2.

4 | DISCUSSION

Harbor seals play a key role in the Salish Sea as meso-predators that potentially influence commercially important salmonid stocks, some of which are threatened (Allegue et al., 2020; Chasco et al., 2017; Shields et al., 2018; but see

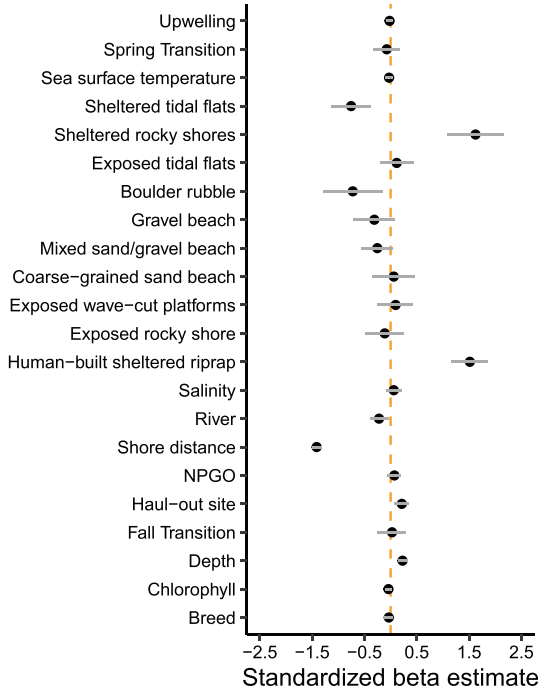

FIGURE 2 Effects of modeled covariates. Important covariates from our model (i.e., those that did not have a 95% credible interval that overlapped 0, depicted by the orange dashed line) included haul-out site, depth, nearshore (defined here as within 1.5 km of shore) versus offshore, boulder rubble shore type, and sheltered tidal flats shoreline type, suggesting a greater density of harbor seals in the water is most likely to occur near haul-out sites, in shallower water (between depths of 7.3 m and 44.5 m), within 1.5 km of the coastline, near river mouths, near sheltered rocky shores and sheltered riprap, and away from boulder rubble and sheltered tidal flats. Note, all continuous covariates were centered and scaled, and depth was recorded with greater negative numbers indicating deeper waters. Gray horizontal lines indicate 95% credible intervals. The values on the *x*-axis represent the centered and scaled parameter estimates.

Nelson et al., 2021), and harbor seals serve as an important prey item for Bigg's killer whales (*Orcinus rectipinnus*[1]) and Steller sea lions (*Eumetopias jubatus*) (Ashley et al., 2020; Gaydos et al., 2005; Steiger et al., 1989). Using a long-term data set of harbor seals observed at the sea surface in the Salish Sea, we found that spatially varying covariates had a stronger relationship with harbor seal in-water fine-scale densities than temporally or spatiotemporally varying covariates. We also found that harbor seal in-water fine-scale densities remained constant across years during our study period from 2001 to 2020. Similarly, S.F.P. (unpublished data) found that abundance estimates of harbor seal stocks based on aerial surveys of hauled out harbor seals were stable during the years that overlapped between their and our study periods (2001–2019).

Harbor seal fine-scale density varied little across years, and none of the temporal covariates we included in our model had a relationship with fine-scale densities of harbor seals. At a smaller temporal scale, our model suggests that harbor seal fine-scale densities differed modestly between the breeding/molting season and nonbreeding/nonmolting season. Despite the 95% BCI for the "breedmolt" covariate overlapping zero, 83% of the posterior values were <0, suggesting that breeding/molting is a marginally important predictor of harbor seal fine-scale density in the Salish Sea. Similarly, (Jones et al., 2017) found that harbor seal geospatial occurrences near Scotland also varied with

[1]In a recent paper by Morin et al. (2024), the authors concluded that eastern North Pacific Bigg's killer whales should be recognized as *Orcinus rectipinnus* and resident killer whales should be recognized as *Orcinus ater*.

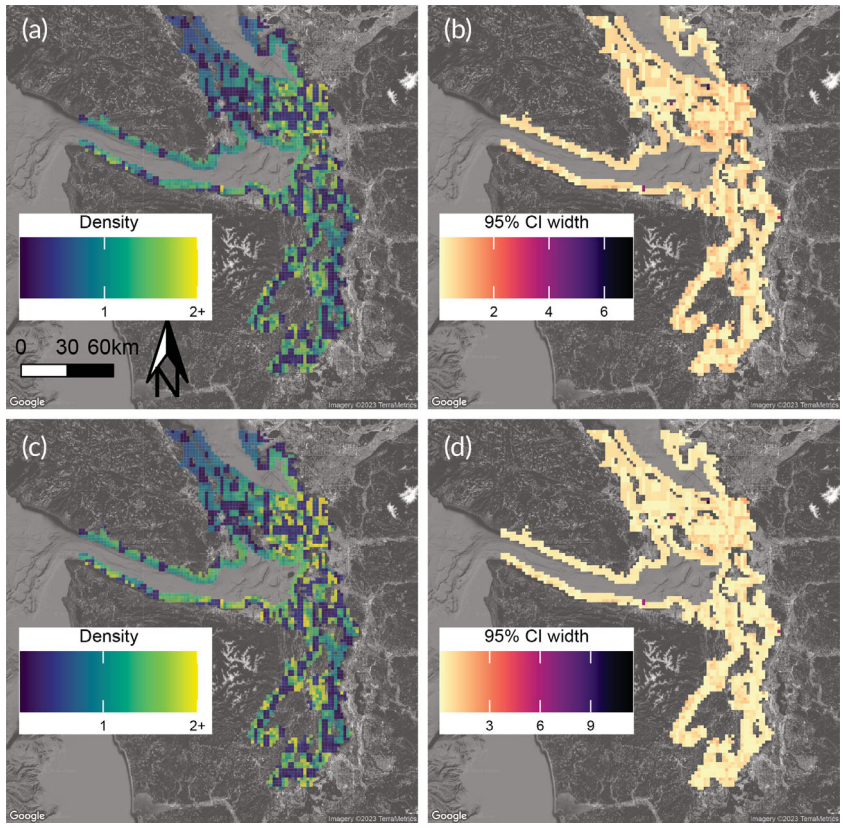

FIGURE 3 Map of harbor seal in-water fine-scale densities. Each pixel represents a 2 × 2 km area. These predictive maps were created using the mean coefficients from our model and environmental data from a representative day during the breeding/molting season (a) and during the nonbreeding/nonmolting season (c). Associated uncertainty maps (b and d) represent the 95% credible interval width using our full model output. The base map was created using the R package "ggmap" (Kahle et al., 2019).

life-history events. Variation in the timing of life-history events across the Salish Sea and behaviors of different demographic groups of harbor seals might have led to our "breedmolt" covariate as only being marginally important. As a capital breeder with limited foraging during the early lactation period (Boness et al., 1994), we would expect lactating females to spend the majority of their time hauled out during the early part of the pupping season. As pupping in the Salish Sea can start as early as June or as late as October (Huber et al., 2001; Temte, 1985), only a portion of lactating females would be in the early lactation period and, thus, less likely to be in the water, at one time. Similarly, because the timing of molting in harbor seals can vary by sex, age class, and geography (Daniel et al., 2003) and because harbor seals tend to make shallower dives during the breeding/molting season (Frost et al., 2001), some age/sex classes might have increased detectability temporally coinciding with decreased detectability of lactating females. The inclusion of PSU segment/zigzag as a random effect in the model might capture spatial variance not accounted for by our covariates, and we assumed to have captured at least some important differences in life-history event timing across PSU segments/zigzags.

The water near the San Juan Islands includes many 2 × 2 km pixels predicted to have high fine-scale densities of harbor seals. This area has many haul-out sites and is the only location in our study area that has sheltered rocky shores, a covariate with one of the strongest positive relationships with harbor seal fine-scale densities. The 2 × 2 km pixels near the San Juan Islands that coincided with high fine-scale densities were also shallower, relatively

near major river mouths (e.g., Skagit River mouth), and tended to have lower salinity than other pixels by the San Juan Islands and most of the rest of the study area. Ward et al. (2012) identified the San Juan Islands as an area of strong predator activity by harbor seals, further supporting that the San Juan Islands are of ecological importance to Salish Sea harbor seals. Interestingly, when estimating density at the stock level in the Salish Sea, Jefferson et al., (2021) found that the Northern Inland Washington Waters stock area, which includes the Strait of Juan de Fuca, part of the Strait of Georgia, and the waters around the San Juan Islands, had the lowest density estimates of the three areas corresponding to the three stocks in the inland waters of Washington. As we did not group densities by stock, our results might reveal a nuance not captured by grouping density estimates by stock; our results of high densities around the San Juan Islands and more inland areas of the Strait of Juan de Fuca but low densities in most of the rest of the waters included in the Northern Inland Washington Waters stock area could also suggest an overall low density estimate for the Northern Inland Washington Waters stock area. Alternatively, as our data set spans more years than the one used by Jefferson et al. (2021), which included 2013–2016, our results might reflect a difference in harbor seal fine-scale densities such that more harbor seals used these waters in the early 2000s or a shift in that more harbor seals started occurring in these waters between 2016 and 2020.

Also coinciding with our model-predicted high fine-scale densities, a large number of harbor seals were detected in Quilcene Bay and in the Admiralty Inlet Area. Multiple large haul-out sites are present in the Admiralty Inlet Area (Jeffries et al., 2000, 2003), and the inlet is an area of strong mixing of waters from tidal action (Moore et al., 2008). Additionally, this area was recognized as a hotspot for resident killer whales, *Orcinus ater* (see Footnote 1; Olson et al., 2018), which feed on prey fish, primarily chinook salmon (Hanson et al., 2010), which harbor seals also consume, potentially indicating that this area is rich in prey items for harbor seals too. The reason for the high fine-scale density in Quilcene Bay is less obvious from the covariate relationships. However, harbor seals haul out on floating oyster and salmon net pens, which are constantly accessible to harbor seals, in Quilcene Bay (London et al., 2012). The high fine-scale densities in Quilcene Bay could also be a result of its proximity to a major river mouth, the Quilcene River, which may serve as a source of abundant prey. Although not exclusive to these two areas, large groups of harbor seals occurred in Quilcene Bay and the San Juan Islands. The large groups could have formed from recreational boats or workers tending to the net pens disturbing the seals, resulting in large numbers of seals entering the water.

Areas with greater concentrations of prey items can often serve as hotspots for marine mammals (Benoit-Bird et al., 2013; Brough et al., 2019; Scott et al., 2010; Torres et al., 2008). Thus, we expected that the spatiotemporal covariates (e.g., chlorophyll-a, sea surface temperature, salinity) included in our analysis would be important predictors of harbor seal fine-scale density, as these variables are often associated with prey abundance. One potential reason that we did not observe the expected relationship is that these environmental variables are crude proxies and may not represent prey species abundance in our study area. Actual measures of prey species abundance would be much more reliable but were not available over the course of the study. We also interpret our results under the assumption that the measurement error of partial availability (i.e., cryptic behavior of an animal, such as diving) across all PSU segment/zigzags on all days is homogenous. However, the estimates of in-water fine-scale densities of harbor seals at the water surface might not correlate with fine-scale densities of submerged harbor seals if this assumption is violated. Alternatively, we might not have observed the expected relationship between spatiotemporally varying covariates and harbor seal density because it is possible that prey abundance may not have a strong driving influence on in-water fine-scale density of harbor seals. Given their generalist feeding habits, harbor seals might buffer themselves against changes in species-specific prey item availability (Hauser et al., 2008; Lance et al., 2012; Luxa & Acevedo-Gutiérrez, 2013). Environmental covariates related to physiological needs of prey species are often not as reliable for predicting spatiotemporal patterns of generalist predators because greater prey species diversity for generalist predators could lead to a broader range of suitable habitat for predators (Casper et al., 2010; Schleimer et al., 2019), and this could be the case in our study.

As central-place foraging theory would imply, the fine-scale densities of harbor seals tended to be lower in areas where there were few or no haul-out sites within 30 km. Large groups (i.e., >10 individuals) of harbor seals were

likely associated with hauling out behavior, which could include returning to or leaving the haul-out site between foraging trips. However, harbor seals in the water near haul-out sites might have entered the water resulting from disturbances from boats (observers did not record any seals entering the water in response to the survey boat). Groups in the water may also be associated with concentrated prey or associated with travel or socializing behavior that can occur throughout the year (Elliser et al., 2022). Haul-out sites, depth, and prey availability are also related to the spatial distributions of harbor seals in other locations and other pinniped species that exhibit central-place foraging (Bedriñana-Romano et al., 2014; Botha et al., 2020; Grigg et al., 2012; Jones et al., 2017). Proximity to haul-out locations and specific shoreline types that provide good substrate for hauling out might also relate to harbor fine-scale densities because they can provide an escape from predators. Bigg's killer whales have been spending more time in the Salish Sea, particularly since 2017 (Houghton et al., 2015; Shields et al., 2018), and estimates suggested they consumed about 1,000 Salish Sea harbor seals in 2017 (Shields et al., 2018), which is likely influencing harbor seal behavior in areas with high predation. Bigg's killer whales might contribute to the highly variable in-water fine-scale densities of harbor seals that our results indicate.

Identifying the relationships between the biotic and abiotic environmental characteristics and fine-scale densities of meso-predators can characterize areas of concern regarding resource extraction and/or species interactions with other species including humans. More specifically, pinpointing areas of very high and very low marine mammal abundances can provide essential information for optimized management of marine and estuarine ecosystems (Harvey et al., 2017). Estimating and mapping habitat associations for highly mobile marine species with dynamic habitat requirements can provide valuable information for marine spatial planning, especially regarding the conservation of marine mammals (Evans, 2018). As harbor seals tend to have dynamic habitat use over space and time, identifying environmental characteristics associated with harbor seal occurrence can be more informative than mapping specific high-use areas, as exemplified by Jones et al. (2017). Our results suggest that Salish Sea harbor seals tend to congregate in shallower and nearshore areas in close proximity to river mouths and haul-out sites. The relationships between environmental covariates and harbor seal in-water densities identified in this study can facilitate efforts to continue protecting harbor seals and their prey species, especially those that have a threatened status.

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AUTHOR CONTRIBUTIONS

Jamie Louise Brusa: Data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Scott Pearson:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; visualization; writing – review and editing. **Martin Raphael:** Investigation; methodology; project administration; visualization; writing – review and editing. **Beth Gardner:** Formal analysis; funding acquisition; investigation; methodology; visualization; writing – review and editing.

ORCID

Jamie L. Brusa https://orcid.org/0000-0003-4787-0460
Scott F. Pearson https://orcid.org/0000-0003-4960-3956

REFERENCES

Allegue, H., Thomas, A. C., Liu, Y., & Trites, A. W. (2020). Harbour seals responded differently to pulses of out-migrating coho and Chinook smolts. *Marine Ecology Progress Series*, *647*, 211–227. https://doi.org/10.3354/meps13389

Ashley, E. A., Olson, J. K., Adler, T. E., Raverty, S., Anderson, E. M., Jeffries, S., & Gaydos, J. K. (2020). Causes of mortality in a harbor seal (*Phoca vitulina*) population at equilibrium. *Frontiers in Marine Science*, *7*(319), 1–11. https://doi.org/10.3389/fmars.2020.00319

Bedriñana-Romano, L., Viddi, F. A., Torres-Florez, J. P., Ruiz, J., Nery, M. F., Haro, D., Montecinos, Y., & Hucke-Gaete, R. (2014). At-sea abundance and spatial distribution of South American sea lion (*Otaria byronia*) in Chilean Northern Patagonia: How many are there? *Mammalian Biology*, *79*(6), 384–392. https://doi.org/10.1016/j.mambio.2014.07.002

Benoit-Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., Kuletz, K. J., Nordstrom, C. A., Paredes, R., Suryan, R. M., Waluk, C. M., & Trites, A. W. (2013). Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS ONE*, *8*(1), e53348. https://doi.org/10.1371/journal.pone.0053348

Best, B., Fox, C., Williams, R., Halpin, P., & Paquet, P. (2015). Updated marine mammal distribution and abundance estimates in British Columbia. *Journal of Cetacean Research and Management*, *15*, 9–26.

Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., Baston, D., Rouault, E., Warmerdam, F., Ooms, J., & Rundel, C. (2021). *rgdal: Bindings for the "Geospatial" Data Abstraction Library* (1.5–23) [Computer software]. https://CRAN.R-project.org/package=rgdal

Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K. O., Giraudoux, P., Davis, M., & Santilli, S. (2020). *rgeos: Interface to Geometry Engine - Open Source ('GEOS')* (Version 0.5–5) [Computer software]. https://CRAN.R-project.org/package=rgeos

Boness, D. J., Bowen, W. D., Buhleier, B. M., & Marshall, G. J. (2006). Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, Phoca vitulina. *Behavioral Ecology and Sociobiology*, *61*(1), 119–130. https://doi.org/10.1007/s00265-006-0242-9

Boness, D. J., Bowen, W. D., & Oftedal, O. T. (1994). Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behavioral Ecology and Sociobiology*, *34*(2), 95–104. https://doi.org/10.1007/BF00164180

Botha, J. A., Kirkman, S. P., Arnould, J. P. Y., Lombard, A. T., Hofmeyr, G. J. G., Meÿer, M. A., Kotze, P. G. H., & Pistorius, P. A. (2020). Geographic variation in at-sea movements, habitat use and diving behaviour of female Cape fur seals. *Marine Ecology Progress Series*, *649*, 201–218. https://doi.org/10.3354/meps13446

Boveng, P. L., Bengtson, J. L., Withrow, D. E., Cesarone, J. C., Simpkins, M. A., Frost, K. J., & Burns, J. J. (2003). The abundance of harbor seals in the Gulf of Alaska. *Marine Mammal Science*, *19*(1), 111–127. https://doi.org/10.1111/j.1748-7692.2003.tb01096.x

Brough, T., Rayment, W., Slooten, E., & Dawson, S. (2019). Fine scale distribution for a population of New Zealand's only endemic dolphin (*Cephalorhynchus hectori*) shows long-term stability of coastal hotspots. *Marine Mammal Science*, *35*(1), 140–163. https://doi.org/10.1111/mms.12528

Brusa, J. L., Rotella, J. J., Banner, K. M., & Hutchins, P. R. (2021). Challenges and opportunities for comparative studies of survival rates: An example with male pinnipeds. *Ecology and Evolution*, *11*(12), 7980–7999. https://doi.org/10.1002/ece3.7627

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford University Press. https://agris.fao.org/agris-search/search.do?recordID=XF2015043142

Carretta, J. V., Forney, K. A., Oleson, E. M., Weller, D. W., Lang, A. R., Baker, J., Muto, M. M., Hanson, B., Orr, A. J., Huber, H., Lowry, M. S., Barlow, J., Moore, J. E., Lynch, D., Carswell, L., & Brownell, R. L., Jr. (2020). *U.S. Pacific marine mammal stock assessments: 2019* (NOAA Technical Memorandum NMFS-SWFSC-629). U.S. Department of Commerce.

Carretta, J. V., Oleson, E. M., Forney, K. A., Weller, D. W., Lang, A. R., Baker, J., Orr, A. J., Barlow, J., Moore, J. E., Wallen, M., & Brownell, R. L., Jr. (2023). *U.S. Pacific marine mammal stock assessments: 2022* (NOAA Technical Memorandum NMFS-SWFSC-684). U.S. Department of Commerce. https://repository.library.noaa.gov/view/noaa/51022

Casella, G., & George, E. I. (1992). Explaining the Gibbs sampler. *The American Statistician*, *46*(3), 167–174. https://doi.org/10.1080/00031305.1992.10475878

Casper, R. M., Sumner, M. D., Hindell, M. A., Gales, N. J., Staniland, I. J., & Goldsworthy, S. D. (2010). The influence of diet on foraging habitat models: A case study using nursing Antarctic fur seals. *Ecography*, *33*(4), 748–759. https://doi.org/10.1111/j.1600-0587.2009.06155.x

Chasco, B., Kaplan, I. C., Thomas, A., Acevedo-Gutiérrez, A., Noren, D., Ford, M. J., Hanson, M. B., Scordino, J., Jeffries, S., Pearson, S., Marshall, K. N., & Ward, E. J. (2017). Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(8), 1173–1194. https://doi.org/10.1139/cjfas-2016-0203

Coltman, D. W., Bowen, W. D., & Wright, J. M. (1998). Male mating success in an aquatically mating pinniped, the harbour seal (*Phoca vitulina*), assessed by microsatellite DNA markers. *Molecular Ecology*, *7*(5), 627–638. https://doi.org/10.1046/j.1365-294x.1998.00373.x

Connell, S. D. (2002). Effects of a predator and prey on a foraging reef fish: Implications for understanding density-dependent growth. *Journal of Fish Biology*, *60*(6), 1551–1561. https://doi.org/10.1111/j.1095-8649.2002.tb02447.x

Cummings, J. A., & Smedstad, O. M. (2013). Variational Data Assimilation for the Global Ocean. In S. K. Park & L. Xu (Eds.), *Data assimilation for atmospheric, oceanic and hydrologic applications* (Vol. II, pp. 303–343). Springer. https://doi.org/10.1007/978-3-642-35088-7_13

Cunningham, L., Baxter, J. M., Boyd, I. L., Duck, C. D., Lonergan, M., Moss, S. E., & McConnell, B. (2008). Harbour seal movements and haul-out patterns: Implications for monitoring and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*(4), 398–407. https://doi.org/10.1002/aqc.983

Daniel, R. G., Jemison, L. A., Pendleton, G. W., & Crowley, S. M. (2003). Molting phenology of harbor seals on Tugidak Island, Alaska. *Marine Mammal Science*, *19*(1), 128–140. https://doi.org/10.1111/j.1748-7692.2003.tb01097.x

Denwood, M., & Plummer, M. (2016). *runjags: Interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS* (Version 2.0.4-2) [Computer software]. https://CRAN.R-project.org/package=runjags

Deppe, R. W., Thomson, J., Polagye, B., & Krembs, C. (2018). Predicting deep water intrusions to Puget Sound, WA (USA), and the seasonal modulation of dissolved oxygen. *Estuaries and Coasts*, *41*(1), 114–127. https://doi.org/10.1007/s12237-017-0274-6

Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., McWilliams, J. C., Bograd, S. J., Arango, H., Curchitser, E., Powell, T. M., & Rivière, P. (2008). North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, *35*(8), L08607. https://doi.org/10.1029/2007GL032838

Eguchi, T., & Harvey, J. T. (2005). Diving behavior of the Pacific harbor seal (*Phoca vitulina richardii*) in Monterey Bay, California. *Marine Mammal Science*, *21*(2), 283–295. https://doi.org/10.1111/j.1748-7692.2005.tb01228.x

Elliser, C. R., Anderson, D., Derie, T., MacIver, K., & Shuster, L. (2022). Open water grouping behaviour in harbour seals (*Phoca vitulina richardii*) of the Salish Sea. *Behaviour*, *159*(13–14), 1375–1386. https://doi.org/10.1163/1568539X-bja10175

Estes, J. A., Tinker, M. T., Williams, T. M., & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, *282*(5388), 473–476. https://doi.org/10.1126/science.282.5388.473

Evans, P. G. H. (2018). Marine Protected Areas and marine spatial planning for the benefit of marine mammals. *Journal of the Marine Biological Association of the United Kingdom*, *98*(5), 973–976. https://doi.org/10.1017/S0025315418000334

Fernández-i-Marín, X. (2016). ggmcmc: Analysis of MCMC samples and Bayesian inference. *Journal of Statistical Software*, *70*(i09), 1–20. https://doi.org/10.18637/jss.v070.i09

Frost, K. J., Simpkins, M. A., & Lowry, L. F. (2001). Diving behavior of subadult and adult harbor seals in Prince William Sound, Alaska. *Marine Mammal Science*, *17*(4), 813–834. https://doi.org/10.1111/j.1748-7692.2001.tb01300.x

Gaydos, J. K., Dierauf, L., Kirby, G., Brosnan, D., Gilardi, K., & Davis, G. E. (2009). Top 10 principles for designing healthy coastal ecosystems like the Salish Sea. *EcoHealth*, *5*(4), Article 460. https://doi.org/10.1007/s10393-009-0209-1

Gaydos, J. K., & Pearson, S. F. (2011). Birds and mammals that depend on the Salish Sea: A compilation. *Northwestern Naturalist*, *92*(2), 79–94. https://doi.org/10.1898/10-04.1

Gaydos, J. K., Raverty, S., Baird, R. W., & Osborne, R. W. (2005). Suspected surplus killing of harbor seal pups (*Phoca vitulina*) by killer whales (*Orcinus orca*). *Northwestern Naturalist*, *86*(3), 150–154. https://doi.org/10.1898/1051-1733(2005)086[0150:SSKOHS]2.0.CO;2

Gelfand, A. E., & Smith, A. F. M. (1990). Sampling-based approaches to calculating marginal densities. *Journal of the American Statistical Association*, *85*(410), 398–409. https://doi.org/10.1080/01621459.1990.10476213

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, *27*(15), 2865–2873. https://doi.org/10.1002/sim.3107

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–472.

Gelman, A., & Shalizi, C. R. (2012). Philosophy and the practice of Bayesian statistics. *British Journal of Mathematical and Statistical Psychology*, *66*(1), 8–38. https://doi.org/10.1111/j.2044-8317.2011.02037.x

Geman, S., & Geman, D. (1993). Stochastic relaxation, Gibbs distributions and the Bayesian restoration of images. *Journal of Applied Statistics*, *20*(5–6), 25–62. https://doi.org/10.1080/02664769300000058

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Grigg, E. K., Allen, S. G., Craven-Green, D. E., Klimley, A. P., Markowitz, H., & Elliott-Fisk, D. L. (2012). Foraging distribution of Pacific harbor seals (*Phoca vitulina richardii*) in a highly impacted estuary. *Journal of Mammalogy*, *93*(1), 282–293. https://doi.org/10.1644/11-MAMM-A-128.1

Grigg, E. K., Klimley, A. P., Allen, S. G., Green, D. E., Elliott-Fisk, D. L., & Markowitz, H. (2009). Spatial and seasonal relationships between Pacific harbor seals (*Phoca vitulina richardii*) and their prey, at multiple scales. *Fishery Bulletin*, *107*(3), Article 3.

Hanson, M. B., Baird, R. W., Ford, J. K. B., Hempelmann-Halos, J., Doornik, D. M. V., Candy, J. R., Emmons, C. K., Schorr, G. S., Gisborne, B., Ayres, K. L., Wasser, S. K., Balcomb, K. C., Balcomb-Bartok, K., Sneva, J. G., & Ford, M. J. (2010). Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. *Endangered Species Research*, *11*(1), 69–82. https://doi.org/10.3354/esr00263

Harvey, G. K. A., Nelson, T. A., Fox, C. H., & Paquet, P. C. (2017). Quantifying marine mammal hotspots in British Columbia, Canada. *Ecosphere*, *8*(7), e01884. https://doi.org/10.1002/ecs2.1884

Hauser, D. D. W., Allen, C. S., Rich, Jr., H. B., & Quinn, T. P. (2008). Resident harbor seals (*Phoca vitulina*) in Iliamna Lake, Alaska: Summer diet and partial consumption of adult sockeye salmon (*Oncorhynchus nerka*). *Aquatic Mammals*, *34*(3), 303–309.

Hayes, S. A., Costa, D. P., Harvey, J. T., & Le Boeuf, B. J. (2004). Aquatic mating strategies of the male Pacific harbor seal (*Phoca vitulina richardii*): Are males defending the hotspot? *Marine Mammal Science*, *20*(3), 639–656. https://doi.org/10.1111/j.1748-7692.2004.tb01184.x

Hertz, E., Trudel, M., Tucker, S., Beacham, T. D., Parken, C., Mackas, D., & Mazumder, A. (2016). Influences of ocean conditions and feeding ecology on the survival of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography*, *25*(4), 407–419. https://doi.org/10.1111/fog.12161

Hijmans, R. J., Etten, J. van, Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., Hingee, K., Ilich, A., Karney, C., … Wueest, R. (2023). *raster: Geographic data analysis and modeling* (Version 3.6–23) [Computer software]. https://cran.r-project.org/web/packages/raster/index.html

Hooff, R. C., & Peterson, W. T. (2006). Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. *Limnology and Oceanography*, *51*(6), 2607–2620. https://doi.org/10.4319/lo.2006.51.6.2607

Houghton, J., Baird, R. W., Emmons, C. K., & Hanson, M. B. (2015). Changes in the occurrence and behavior of mammal-eating killer whales in southern British Columbia and Washington state, 1987–2010. *Northwest Science*, *89*(2), 154–169. https://doi.org/10.3955/046.089.0207

Howard, S., Lance, M., Jeffries, S., & Acevedo-Gutiérrez, A. (2013). Fish consumption by harbor seals (*Phoca vitulina*) in the San Juan Islands, Washington. *Fishery Bulletin*, *111*(1), 27–41.

Huber, H. R., Jeffries, S. J., Brown, R. F., Delong, R. L., & Vanblaricom, G. (2001). Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Marine Mammal Science*, *17*(2), 276–293. https://doi.org/10.1111/j.1748-7692.2001.tb01271.x

Jefferson, T. A., Smultea, M. A., Ward, E. J., & Berejikian, B. (2021). Estimating the stock size of harbor seals (*Phoca vitulina richardii*) in the inland waters of Washington State using line-transect methods. *PLoS ONE*, *16*(6), e0241254. https://doi.org/10.1371/journal.pone.0241254

Jeffries, S., Huber, H., Calambokidis, J., & Laake, J. (2003). Trends and status of harbor seals in Washington state: 1978-1999. *Journal of Wildlife Management*, *67*(1), 207–218. JSTOR. https://doi.org/10.2307/3803076

Jeffries, S. J., Gearin, P. J., Huber, H. R., Saul, D. L., & Pruett, D. A. (2000). *Atlas of seal and sea lion haulout sites in Washington*. Washington Department of Fish and Wildlife, Wildlife Science Division.

Jones, E. L., Sparling, C. E., McConnell, B. J., Morris, C. D., & Smout, S. (2017). Fine-scale harbour seal usage for informed marine spatial planning. *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/s41598-017-11174-4

Kahle, D., Wickham, H., Jackson, S., & Korpela, M. (2019). *ggmap: Spatial visualization with ggplot2* (Version 3.0.0) [Computer software]. https://CRAN.R-project.org/package=ggmap

Keister, J. E., Lorenzo, E. D., Morgan, C. A., Combes, V., & Peterson, W. T. (2011). Zooplankton species composition is linked to ocean transport in the Northern California Current. *Global Change Biology*, *17*(7), 2498–2511. https://doi.org/10.1111/j.1365-2486.2010.02383.x

Kilduff, D. P., Lorenzo, E. D., Botsford, L. W., & Teo, S. L. H. (2015). Changing central Pacific El Niños reduce stability of North American salmon survival rates. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(35), 10962–10966. https://doi.org/10.1073/pnas.1503190112

Kovacs, K. M., Aguilar, A., Aurioles, D., Burkanov, V., Campagna, C., Gales, N., Gelatt, T., Goldsworthy, S. D., Goodman, S. J., Hofmeyr, G. J. G., Härkönen, T., Lowry, L., Lydersen, C., Schipper, J., Sipilä, T., Southwell, C., Stuart, S., Thompson, D., & Trillmich, F. (2012). Global threats to pinnipeds. *Marine Mammal Science*, *28*(2), 414–436. https://doi.org/10.1111/j.1748-7692.2011.00479.x

Lance, M. M., Chang, W.-Y., Jeffries, S. J., Pearson, S. F., & Acevedo-Gutiérrez, A. (2012). Harbor seal diet in northern Puget Sound: Implications for the recovery of depressed fish stocks. *Marine Ecology Progress Series*, *464*, 257–271. https://doi.org/10.3354/meps09880

Liu, H., Bi, H., & Peterson, W. T. (2015). Large-scale forcing of environmental conditions on subarctic copepods in the northern California Current system. *Progress in Oceanography*, *134*, 404–412. https://doi.org/10.1016/j.pocean.2015.04.001

London, J. M., Hoef, J. M. V., Jeffries, S. J., Lance, M. M., & Boveng, P. L. (2012). Haul-out behavior of harbor seals (*Phoca vitulina*) in Hood Canal, Washington. *PLoS ONE*, *7*(6), e38180. https://doi.org/10.1371/journal.pone.0038180

Luxa, K., & Acevedo-Gutiérrez, A. (2013). Food habits of harbor seals (*Phoca vitulina*) in two estuaries in the central Salish Sea. *Aquatic Mammals*, *39*(1), 10–22. http://dx.doi.org/https://doi.org/10.1578/AM.39.1.2013.10

Magera, A. M., Flemming, J. E. M., Kaschner, K., Christensen, L. B., & Lotze, H. K. (2013). Recovery trends in marine mammal populations. *PLoS ONE*, *8*(10), e77908. https://doi.org/10.1371/journal.pone.0077908

Malick, M. J., Cox, S. P., Mueter, F. J., Dorner, B., & Peterman, R. M. (2017). Effects of the North Pacific Current on the productivity of 163 Pacific salmon stocks. *Fisheries Oceanography*, *26*(3), 268–281. https://doi.org/10.1111/fog.12190

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, *78*(6), 1069–1080. https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2

Marston, B. H., Willson, M. F., & Gende, S. M. (2002). Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs. *Marine Ecology Progress Series*, *231*, 229–236. https://doi.org/10.3354/meps231229

McLaren, I. A., & Smith, T. G. (1985). Population ecology of seals: Retrospective and prospective views. *Marine Mammal Science*, *1*(1), 54–83. https://doi.org/10.1111/j.1748-7692.1985.tb00531.x

Middlemas, S. J., Barton, T. R., Armstrong, J. D., & Thompson, P. M. (2006). Functional and aggregative responses of harbour seals to changes in salmonid abundance. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1583), 193–198. https://doi.org/10.1098/rspb.2005.3215

Montgomery, R. A., Hoef, J. M. V., & Boveng, P. L. (2007). Spatial modeling of haul-out site use by harbor seals in Cook Inlet, Alaska. *Marine Ecology Progress Series*, *341*, 257–264. https://doi.org/10.3354/meps341257

Moore, M. E., & Berejikian, B. A. (2017). Population, habitat, and marine location effects on early marine survival and behavior of Puget Sound steelhead smolts. *Ecosphere*, *8*(5), e01834. https://doi.org/10.1002/ecs2.1834

Moore, S. E. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, *89*(3), 534–540. https://doi.org/10.1644/07-MAMM-S-312R1.1

Moore, S. K., Mantua, N. J., Newton, J. A., Kawase, M., Warner, M. J., & Kellogg, J. P. (2008). A descriptive analysis of temporal and spatial patterns of variability in Puget Sound oceanographic properties. *Estuarine, Coastal and Shelf Science*, *80*(4), 545–554. https://doi.org/10.1016/j.ecss.2008.09.016

Morin, P. A., McCarthy, M. L., Fung, C. W., Durban, J. W., Parsons, K. M., Perrin, W. F., Taylor, B. L., Jefferson, T. A., & Archer, F. I. (2024). Revised taxonomy of eastern North Pacific killer whales (*Orcinus orca*): Bigg's and resident ecotypes deserve species status. *Royal Society Open Science*, *11*, Article 231368. https://doi.org/10.1098/rsos.231368

Morissette, L., Christensen, V., & Pauly, D. (2012). Marine mammal impacts in exploited ecosystems: Would large scale culling benefit fisheries? *PLoS ONE*, *7*(9), e43966. https://doi.org/10.1371/journal.pone.0043966

NASA JPL/OBPG/RSMAS. (2020). *MODIS aqua L2P swath SST data set* (Version 2019.0). https://developers.google.com/earth-engine/datasets/catalog/NASA_OCEANDATA_MODIS-Aqua_L3SMI

NASA OB.DAAC. (2018). *Moderate-resolution imaging spectroradiometer (MODIS) aqua chlorophyll data*. NASA Goddard Space Flight Center, Ocan Ecology Laboratory, Ocean Biology Processing Group. https://developers.google.com/earth-engine/datasets/catalog/NASA_OCEANDATA_MODIS-Aqua_L3SMI

Nelson, B. W., Pearson, S. F., Anderson, J. H., Jeffries, S. J., Thomas, A. C., Walker, W. A., Acevedo-Gutiérrez, A., Kemp, I. M., Lance, M. M., Louden, A., & Voelker, M. R. (2021). Variation in predator diet and prey size affects perceived impacts to salmon species of high conservation concern. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(11), 1661–1676. https://doi.org/10.1139/cjfas-2020-0300

Newby, T. C. (1973). Observations on the breeding behavior of the harbor seal in the state of Washington. *Journal of Mammalogy*, *54*(2), 540–543. https://doi.org/10.2307/1379151

Nolan, J. V., Brakebill, J. W., Alexander, R. B., & Schwarz, G. E. (2003). ERF1_2—Enhanced River Reach File 2.0. In *ERF1_2—Enhanced River Reach File 2.0* (USGS Numbered Series 2002–40; Open-File Report, Vols. 2002–40). U.S. Geological Survey. https://doi.org/10.3133/ofr0240

Olson, J. K., Wood, J., Osborne, R. W., Barrett-Lennard, L., & Larson, S. (2018). Sightings of southern resident killer whales in the Salish Sea 1976–2014: The importance of a long-term opportunistic dataset. *Endangered Species Research*, *37*, 105–118. https://doi.org/10.3354/esr00918

Olsson, O., Brown, J. S., & Helf, K. L. (2008). A guide to central place effects in foraging. *Theoretical Population Biology*, *74*(1), 22–33. https://doi.org/10.1016/j.tpb.2008.04.005

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., & Folke, C. (2007). Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems*, *10*(6), 877–889. https://doi.org/10.1007/s10021-007-9069-0

Parrish, F. A. (2009). Do monk seals exert top-down pressure in subphotic ecosystems? *Marine Mammal Science*, *25*(1), 91–106. https://doi.org/10.1111/j.1748-7692.2008.00245.x

Payne, P. M., & Selzer, L. A. (1989). The distribution, abundance and selected prey of the harbor seal, *Phoca vitulina concolor*, in southern New England. *Marine Mammal Science*, *5*(2), 173–192. https://doi.org/10.1111/j.1748-7692.1989.tb00331.x

Pebesma, E., Bivand, R., Racine, E., Sumner, M., Cook, I., Keitt, T., Lovelace, R., Wickham, H., Ooms, J., Müller, K., Pedersen, T. L., Baston, D., & Dunnington, D. (2021). *sf: Simple features for R* (Version 1.0-5) [Computer software]. https://CRAN.R-project.org/package=sf

Pebesma, E., Bivand, R., Rowlingson, B., Gomez-Rubio, V., Hijmans, R., Sumner, M., MacQueen, D., Lemon, J., O'Brien, J., & O'Rourke, J. (2019). *sp: Classes and methods for spatial data* (Version 1.3-2) [Computer software]. https://CRAN.R-project.org/package=sp

Pebesma, E., & Graeler, B. (2020). *gstat: Spatial and spatio-temporal geostatistical modelling, prediction and simulation* (Version 2.0–6) [Computer software]. https://CRAN.R-project.org/package=gstat

Pebesma, E., Graeler, B., Gottfried, T., & Hijmans, R. J. (2021). *spacetime: Classes and methods for spatio-temporal data* (Version 1.2-4) [Computer software]. https://CRAN.R-project.org/package=spacetime

Petersen, J., Michel, J., Zengel, S., White, M., Lord, C., & Plank, C. (2002). *Environmental Sensitivity Index Guidelines, Version 3.0* (NOAA Technical Memorandum NOS ORCA 115). U.S. Department of Commerce.

Peterson, S. H., Lance, M. M., Jeffries, S. J., & Acevedo-Gutiérrez, A. (2012). Long distance movements and disjunct spatial use of harbor seals (*Phoca vitulina*) in the inland waters of the Pacific northwest. *PLoS ONE*, *7*(6), e39046. https://doi.org/10.1371/journal.pone.0039046

Peterson, W. T., & Keister, J. E. (2003). Interannual variability in copepod community composition at a coastal station in the northern California Current: A multivariate approach. *Deep Sea Research Part II: Topical Studies in Oceanography*, *50*(14), 2499–2517. https://doi.org/10.1016/S0967-0645(03)00130-9

Peterson, W. T., & Miller, C. B. (1975). Year-to-year variations in the planktology of the Oregon upwelling zone. *Fishery Bulletin*, *73*, 642–653.

Peterson, W. T., & Schwing, F. B. (2003). A new climate regime in northeast Pacific ecosystems. *Geophysical Research Letters*, *30*(17). https://doi.org/10.1029/2003GL017528

Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. Proceedings of the Third International Workshop on Distributed Statistical Computing (DSC 2003).

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*, 7–11.

R Core Team. (2020). *R: A language and environment for statistical computing* (Version 4.0) [Computer software]. R Foundation for Statistical Computing.

Raphael, M. G., Baldwin, J., Falxa, G. A., Huff, M. H., Lance, M., Miller, S. L., Pearson, S. F., Ralph, C. J., Strong, C., & Thompson, C. (2007). *Regional population monitoring of the marbled murrelet: Field and analytical methods* (General Technical Report PNW-GTR-716). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Raphael, M. G., Shirk, A. J., Falxa, G. A., & Pearson, S. F. (2015). Habitat associations of marbled murrelets during the nesting season in nearshore waters along the Washington to California coast. *Journal of Marine Systems*, *146*, 17–25. https://doi.org/10.1016/j.jmarsys.2014.06.010

Read, A. J., Drinker, P., & Northridge, S. (2006). Bycatch of marine mammals in U.S. and global fisheries. *Conservation Biology*, *20*(1), 163–169. https://doi.org/10.1111/j.1523-1739.2006.00338.x

Reder, S., Lydersen, C., Arnold, W., & Kovacs, K. M. (2003). Haulout behaviour of high Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biology*, *27*(1), 6–16. https://doi.org/10.1007/s00300-003-0557-1

Ross, N., Sumner, M., Alliance, E., & PREDICT, U. (2020). *fasterize: Fast polygon to raster conversion* (1.0.3) [Computer software]. https://CRAN.R-project.org/package=fasterize

Royle, J. A., & Dorazio, R. M. (2006). Hierarchical models of animal abundance and occurrence. *Journal of Agricultural, Biological, and Environmental Statistics*, *11*(3), 249–263. https://doi.org/10.1198/108571106X129153

Schleimer, A., Ramp, C., Plourde, S., Lehoux, C., Sears, R., & Hammond, P. S. (2019). Spatio-temporal patterns in fin whale *Balaenoptera physalus* habitat use in the northern Gulf of St. Lawrence. *Marine Ecology Progress Series*, *623*, 221–234. https://doi.org/10.3354/meps13020

Schoener, T. W. (1979). Generality of the size-distance relation in models of optimal feeding. *The American Naturalist*, *114*(6), 902–914. https://doi.org/10.1086/283537

Scott, B. E., Sharples, J., Ross, O. N., Wang, J., Pierce, G. J., & Camphuysen, C. J. (2010). Sub-surface hotspots in shallow seas: Fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Marine Ecology Progress Series*, *408*, 207–226. https://doi.org/10.3354/meps08552

Sharples, R. J., Moss, S. E., Patterson, T. A., & Hammond, P. S. (2012). Spatial variation in foraging behaviour of a marine top predator (*Phoca vitulina*) determined by a large-scale satellite tagging program. *PLoS ONE*, *7*(5), e37216. https://doi.org/10.1371/journal.pone.0037216

Shields, M. W., Hysong-Shimazu, S., Shields, J. C., & Woodruff, J. (2018). Increased presence of mammal-eating killer whales in the Salish Sea with implications for predator-prey dynamics. *PeerJ*, *6*, e6062. https://doi.org/10.7717/peerj.6062

Simpkins, M. A., Withrow, D. E., Cesarone, J. C., & Boveng, P. L. (2003). Stability in the proportion of harbor seals hauled out under locally ideal conditions. *Marine Mammal Science*, *19*(4), 791–805. https://doi.org/10.1111/j.1748-7692.2003.tb01130.x

Sobocinski, K. L., Kendall, N. W., Greene, C. M., & Schmidt, M. W. (2020). Ecosystem indicators of marine survival in Puget Sound steelhead trout. *Progress in Oceanography*, *188*, 102419. https://doi.org/10.1016/j.pocean.2020.102419

Steiger, G. H., Calambokidis, J., Cubbage, J. C., Skilling, D. E., Smith, A. W., & Gribble, D. H. (1989). Mortality of harbor seal pups at different sites in the inland waters of Washington. *Journal of Wildlife Diseases*, *25*(3), 319–328. https://doi.org/10.7589/0090-3558-25.3.319

Suryan, R. M., & Harvey, J. T. (1998). Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. *Marine Mammal Science*, *14*(2), 361–372. https://doi.org/10.1111/j.1748-7692.1998.tb00728.x

Temte, J. L. (1985). *Photoperiod and the timing of pupping in the Pacific harbor seal* (Phoca vitulina richardsi) *with notes on reproduction in northern fur seals and Dall porpoises* [M.S. thesis]. Oregon State University.

Terhune, J. M., Quin, D., Dell'Apa, A., Mirhaj, M., Plötz, J., Kindermann, L., & Bornemann, H. (2008). Geographic variations in underwater male Weddell seal Trills suggest breeding area fidelity. *Polar Biology*, *31*(6), 671–680. https://doi.org/10.1007/s00300-008-0405-4

Thomas, A. C., Deagle, B., Nordstrom, C., Majewski, S., Nelson, B. W., Acevedo-Gutiérrez, A., Jeffries, S., Moore, J., Louden, A., Allegue, H., Pearson, S., Schmidt, M., & Trites, A. W. (2022). Data on the diets of Salish Sea harbour seals from DNA metabarcoding. *Scientific Data*, *9*(1), Article 1. https://doi.org/10.1038/s41597-022-01152-5

Thomas, A. C., Lance, M. M., Jeffries, S. J., Miner, B. G., & Acevedo-Gutiérrez, A. (2011). Harbor seal foraging response to a seasonal resource pulse, spawning Pacific herring. *Marine Ecology Progress Series*, *441*, 225–239. https://doi.org/10.3354/meps09370

Tollit, D. J., Black, A. D., Thompson, P. M., Mackay, A., Corpe, H. M., Wilson, B., Van Parijs, S. M., Grellier, K., & Parlane, S. (1998). Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology*, *244*(2), 209–222. https://doi.org/10.1111/j.1469-7998.1998.tb00026.x

Torres, L. G., Read, A. J., & Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity. *Ecological Applications*, *18*(7), 1702–1717. https://doi.org/10.1890/07-1455.1

Tozer, B., Sandwell, D. T., Smith, W. H. F., Olson, C., Beale, J. R., & Wessel, P. (2019). Global bathymetry and topography at 15 arc sec: SRTM15+. *Earth and Space Science*, *6*(10), 1847–1864. https://doi.org/10.1029/2019EA000658

Ward, E. J., Levin, P. S., Lance, M. M., Jeffries, S. J., & Acevedo Gutiérrez, A. (2012). Integrating diet and movement data to identify hot spots of predation risk and areas of conservation concern for endangered species. *Conservation Letters*, *5*, 37–47. https://doi.org/10.1111/j.1755-263X.2011.00210.x

Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and management of animal populations*. Academic Press.

Wilson, K. (2020). Governing the Salish Sea. *Hastings Environmental Law Journal*, *26*, 169–182.

Wilson, K., Lance, M., Jeffries, S., & Acevedo-Gutiérrez, A. (2014). Fine-scale variability in harbor seal foraging behavior. *PLoS ONE*, *9*(4), e92838. https://doi.org/10.1371/journal.pone.0092838

Wong, C., & Rylko, M. (2014). Health of the Salish Sea as measured using transboundary ecosystem indicators. *Aquatic Ecosystem Health & Management*, *17*(4), 463–471. https://doi.org/10.1080/14634988.2014.980209

Wright, B. E., Riemer, S. D., Brown, R. F., Ougzin, A. M., & Bucklin, K. A. (2007). Assessment of harbor seal predation on adult salmonids in a Pacific northwest estuary. *Ecological Applications*, *17*(2), 338–351. https://doi.org/10.1890/05-1941

SUPPORTING INFORMATION

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