Distribution and Abundance of California (Zalophus californianus) and Steller (Eumetopias jubatus) Sea Lions in the Inshore Waters of Washington, 2013-2016

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Abstract

Two species of sea lions occur in the inland waters of Washington State: the California sea lion (Zalophus californianus) and the Steller sea lion (Eumetopias jubatus). Both species breed elsewhere, but they typically move into Puget Sound and adjacent waters of the Salish Sea from autumn through spring. There is a need for information on their current abundance and seasonal use patterns as both species prey heavily on threatened/ endangered stocks of salmon and steelhead trout (Oncorhynchus spp.), and empirical abundance estimates of these species are lacking for inland Washington waters. From 2013 to 2016, we conducted 39,399 km of aerial surveys for marine mammals in this area, sighting 255 groups of sea lions. We used a subset of 7,841 km of effort and 165 sea lion sightings made during surveys in good sighting conditions to estimate in-water abundance using line-transect methods. Historical tagging data collected in Pacific Northwest waters were used to evaluate the proportions of time that each species spent on land and conducting dives, and then to develop correction factors to derive total abundance for both sea lion species, providing the first empirical abundance estimates for these waters. We estimated that between 33 and 442 California sea lions were found in Puget Sound/ Hood Canal in different seasons, with nearly 3,000 being found in the broader inland Washington waters in the peak season (spring). Steller sea lions occurred in much smaller numbers, with a peak of 219 animals in Puget Sound/Hood Canal/Strait of Juan de Fuca in autumn (and possibly as many as 600 to 700 in the entire study area). While some estimates suffer from low precision, this study demonstrates that substantial numbers of sea lions use waters of the study area throughout much of the year. Our results provide an important step toward

a better understanding of these two species in the inland waters of Washington, as well as their potential effects on protected salmonid prey species.

Key Words: California sea lion, Steller sea lion, management, Puget Sound, San Juan Islands, Strait of Juan de Fuca, Hood Canal, Washington State, linetransect survey, management, population biology

Introduction

Interest in the biology and ecology of sea lions has increased in recent years for many reasons, not the least of which is concern about the impacts of sea lion predation on fisheries and fish stocks, especially endangered salmonid stocks (see Trites et al., 2006; Trites & Rosen, 2019). The two species of sea lions that inhabit the inland waters of Washington are the California sea lion (Zalophus californianus) and the Steller sea lion (Eumetopias jubatus) (Steiger & Calambokidis, 1986). Both species breed elsewhere (Trites & Rosen, 2019), but portions of the populations of both migrate to inland Washington waters primarily in autumn to spring, outside their summer breeding seasons (Calambokidis & Baird, 1994). These sea lions are primarily males, almost exclusively so for the California sea lion. Numbers present in inland Washington in summer months are much lower, but there are still some California sea lions present in the summer season (Smultea et al., 2022). While both sea lion species feed on a wide variety of prey types, salmon (Oncorhynchus spp.) and steelhead trout (Oncorhynchus mykiss irideus) are among the species consumed in local waters of British Columbia and Washington (Jeffries & Scordino, 1997; Olesiuk, 2018; Trites & Rosen, 2019; Scordino et al., 2022), and there is concern that sea lion predation may be a factor contributing to the decline of salmonid stocks in Pacific Northwest waters.

Pinniped predation on salmonid populations became a serious management problem in the 1980s and 1990s as some individual California sea lions took up residence in inland waters of Washington and British Columbia, where steelhead trout enter freshwater to spawn. The sea lions began taking advantage of the situation to depredate on these fish as they entered narrow waterways at Ballard/Chittenden Locks in Seattle (Scordino, 2010). Various management approaches, including harassment, deterrence, relocation, and even lethal removal, were proposed with mixed results, causing a great deal of controversy (see Gearin et al., 1986; Fraker, 1994; Jeffries & Scordino, 1997).

California sea lions that occur north of the Mexican border are managed by the U.S. National Marine Fisheries Service (NMFS) as a single stock (Carretta et al., 2021). The vast majority of these animals (99.7%) breed on the Channel Islands of southern California (the breeding season is from May through August), but some breeding also occurs in central California (on Año Nuevo Island and the Farallon Islands) (Laake et al., 2018). No California sea lions are known to breed in Washington. Steller sea lions occurring in U.S. waters of the eastern North Pacific are managed as two stocks, with the Eastern U.S. Stock occurring in the waters of California, Oregon, and Washington (Muto et al., 2021). Steller sea lion breeding occurs from late May through August on at least nine rookeries off northern British Columbia (all north of Vancouver Island), as well as on rookeries in Alaskan waters (Wiles, 2015; Olesiuk, 2018). Small numbers of Steller sea lions also give birth in central California and Oregon (Mate, 1973, 1975). Washington State waters have traditionally been outside the breeding range of this species; however, in recent years, some pupping has been documented at sites along the outer coast (Wiles, 2015).

Populations of both sea lion species in the eastern North Pacific have been increasing since being protected in the 1970s under the U.S. Marine Mammal Protection Act and Canadian protective legislation, and their ranges have been expanding (Bigg, 1985; Pitcher et al., 2007). The U.S. California sea lion population had reached apparent carrying capacity at about 275,000 animals by 2014 (Laake et al., 2018). California sea lions have expanded to the north and now move as far as Alaskan waters outside the breeding season (Maniscalco et al., 2004). In the mid-1980s, as many as 3,000 California sea lions may have occurred in the Washington/ British Columbia transboundary area (which also includes the Strait of Georgia and Canadian waters of the Strait of Juan de Fuca and Gulf Islands area) (Everitt et al., 1980; Calambokidis & Baird, 1994). The eastern stock of Steller sea lions has also recovered from past exploitation, numbering approximately 46,000 to 58,000 animals in the early 2000s (Pitcher et al., 2007). Relatively smaller numbers of Steller sea lions occur in the Salish Sea region, but these can still be substantial—up to about 1,000 individuals. For both species, annual fluctuations in occurrence and density are known to happen, and many of the existing Salish Sea abundance estimates and counts are more than 25 y old. Several haul-out sites are used in this area by one or both species, even extending down into southern Puget Sound, south of Tacoma (Everitt et al., 1980; Calambokidis & Baird, 1994; Jeffries et al., 2000).

The fact that most sea lions occurring in the inland waters of Washington are adult males (the largest age/sex class with the highest caloric requirements) suggests that predation on endangered/threatened stocks of salmonids may be substantial (Chasco et al., 2017). This is true even with much lower numbers of animals than for the only year-round resident pinniped in the area, the harbor seal (Phoca vitulina), a much smaller species (see Jefferson et al., 2021). Despite this fact, there has been very little up-to-date information available about total sea lion density and abundance since the 1990s, and seasonal and spatial patterns of variation in inland Washington have not been investigated in any detail. There is a need for a fuller understanding of the impacts of California and Steller sea lion predation on fish stocks of concern within Puget Sound. In nearby British Columbia, Olesiuk stated that "Steller sea lions have emerged as significant predators, and now likely consume more fish and more salmon than any other predator, including humans" (as cited in Trites & Rosen, 2019, p. 42).

Abundance information for pinnipeds comes mostly from haul-out counts at known sites, and numbers of animals in the water (which can be substantial) are generally not counted. Also, haul-out counts are generally only available from regular haul-out sites, despite the fact that both species are broadly distributed throughout the study area (Jeffries et al., 2000). Several tagging studies in the Salish Sea have been conducted in British Columbia (for Steller sea lions: Olesiuk, 2018; Trites & Rosen, 2019) and Washington (for California sea lions: Gearin et al., 2017). These tagging data provide information on pinniped behavior that can be used to facilitate modeling of factors for correcting in-water abundance estimates from aerial line-transect surveys to total abundance, which would include both in-water and on-land components. To our knowledge, linking tagging data with correction factors has not been previously attempted for these species in inland Washington waters.

The present study was conducted to provide updated empirical estimates of density and abundance of both sea lion species in Puget Sound, Washington, using a nontraditional line-transect approach. This involved using line-transect methods from over-water, fixed-wing aircraft surveys supported by the U.S. Navy and NMFS to estimate the number of sea lions in the water, and correcting for animals missed due to being on shore or on a dive (the utility of such an approach for pinnipeds was recently demonstrated by Jefferson et al., 2021). We also provide a preliminary estimate of sea lion numbers in the Strait of Juan de Fuca and San Juan Islands areas (spring and autumn seasons only).

Methods

Study Area

The study area consisted of the inland waters of Washington State, including Puget Sound proper, Hood Canal, the Strait of Juan de Fuca, Haro Strait/San Juan Islands area, and some nearby waters adjacent to the border in British Columbia, Canada (Figure 1). Five geographic survey strata were identified for this study: (1) Strait of Juan de Fuca (U.S. waters only), (2) San Juan Islands (U.S. waters of Haro Strait and the San Juan Islands), (3) Hood Canal, (4) Northern Puget Sound, and (5) Southern Puget Sound. The amount of effort conducted in Canadian waters was relatively small, and analysis of that effort is not included in this article (see Jefferson et al., 2021). The study area and the planned transect lines are shown in Figure 1.

Extensive aerial surveys (39,399 km of observation effort) were conducted over six survey periods in the study area from 2013 to 2016, spanning all four calendar seasons (Table 1). We define the seasons as winter (Dec. to Feb.), spring (March to May), summer (June to Aug.), and autumn (Sept. to Nov.). Most effort was expended in the Puget Sound and Hood Canal areas. However, during April 2015, applying the same field methods, we conducted a 5-d aerial survey (806 km of useable effort) of the Northern Inland Waters region that included adjacent Canadian waters of the southern Strait of Georgia, the San Juan Islands, waters west



Figure 1. Map of the study area, showing survey subareas, planned transect lines, locations of no-fly zones, and California sea lion (*Zalophus californianus*) tagging site. Steller sea lions (*Eumetopias jubatus*) were tagged in the Strait of Georgia, British Columbia, north of the survey study area and of the boundary on this map. The entire inshore region shown on this map is often referred to as the Salish Sea.

Region	Season	# days surveyed	Effort (km)	California sea lion*	Steller sea lion*
Hood Canal	Winter	4	384.7	9	0
	Spring	6	236.3	4	0
	Summer	6	183.8	0	0
	Autumn	8	364.3	1	3
Southern Puget Sound	Winter	4	261.1	0	0
	Spring	6	408.9	2	0
	Summer	6	365.7	1	0
	Autumn	7	516.8	0	0
Northern Puget Sound	Winter	20	663.7	8	0
	Spring	28	1,012.8	20	1
	Summer	27	1,105.8	1	0
	Autumn	40	2,004.1	10	25
NIW – St. Juan de Fuca	Spring	2	114.3	8	0
	Autumn	1	159.2	0	5
NIW – San Juan Islands	Spring	2	59.3	1	0
Transit sightings	All seasons			43	23
	Totals		7,840.8	108	57

Table 1. Number of sightings and effort used in estimating abundance for inland Washington State

*Before truncation

of Whidbey Island, and the Strait of Juan de Fuca. In autumn 2015, we also conducted some systematic survey effort in the Strait of Juan de Fuca.

Aerial Surveys

Aerial line-transect surveys were conducted for marine mammals from a Partenavia P68-C or a Partenavia Observer high-wing, twin-engine airplane. Pre-determined systematic transect lines running east-west were followed, generally oriented perpendicular to water depth contours, following recommended line-transect protocol (Dawson et al., 2008). In all areas except Hood Canal, survey lines were spaced 3.7 km apart; however, in 2016, additional lines were added in the Hood Canal region to increase coverage to address the need for more refined estimates of harbor seals (see Ampela et al., 2021; Jefferson et al., 2021), resulting in 1.8-km line spacing. In the Washington Northern Inland Waters region, survey lines in the San Juan and Gulf Islands closely followed those from a previous 2002-2003 aerial survey for marine mammals; these lines were non-overlapping, oriented 135° from the vertical, and spaced approximately 5.55 km apart. In the Strait of Juan de Fuca portion of the

Northern Inland Waters region, survey lines were spaced about 11.1 km apart and followed an overlapping sawtooth pattern. The different design of the sets of transect lines for the latter two areas (Strait of Juan de Fuca portion of the Northern Inland Waters) had to do with a desire to match transect lines used previously by the NMFS in their historical surveys. Data from our surveys have previously been used to provide estimates of abundance for harbor porpoises (*Phocoena phocoena*; Jefferson et al., 2016) and harbor seals (Jefferson et al., 2021).

One pilot and four professionally trained marine mammal biologists (at least two with over 10 y of related experience) were aboard the aircraft. Two biologists observed from the center seats of the aircraft through bubble windows on each side of the plane. To address line-transect analysis assumptions, the third biologist observed directly below the plane through the belly window (located behind the center seat row) to reduce chances that sightings were missed "on or near" the survey line to align with line-transect protocol (Buckland et al., 2001). A biologist serving as the data recorder sat in the front right co-pilot seat. Surveys were flown at a target speed of 185 km/h and altitude of 234 m. When a sighting was perpendicular to the aircraft, a Suunto inclinometer (Suunto, Vantaa, Finland) was used to record declination angle readings to sightings. Sighting, effort, and environmental data were entered by the data recorder into a laptop computer running *Mysticetus*TM observation software (http://mysticetus.com), which automatically calculated perpendicular distance to the sighting and instantly displayed it on a bathymetric map. Most sightings were recorded in passing mode. Only a small number (< 10%) of sightings were circled (off-effort) to confirm species identifications and group size/composition.

Distribution

Sea lion distribution in the study area was examined by plotting all sightings of each species, regardless of whether or not the sightings were used in the line-transect analysis (i.e., we plotted sightings from the unfiltered dataset). However, it must be cautioned that these plots should not be viewed as providing accurate information on relative densities since the amount of sighting effort by subregion and by season was uneven (Table 1).

Line-Transect Analysis

In total, there were 255 confirmed sea lion sightings plus 30 sightings of unidentified pinnipeds. Of the unidentified pinniped sightings, all were assumed to be harbor seals (which is, by far, the most common pinniped in inland Washington waters), except for two, which were identified as probable sea lions. After filtering (see below), there were 165 sightings of sea lions available for the line-transect analysis.

Separate databases were prepared from the sighting and effort data. Survey data in each database were filtered with the following criteria used to extract relevant data for the line-transect analyses (as part of an approach to ensure meeting assumptions of line-transect theory; see Buckland et al., 2001):

• Only data (e.g., sightings and effort) collected on systematic transect lines were used in density calculations (data from connector effort—shorter perpendicular lines connecting longer systematic survey lines—were excluded). In most cases, connector lines were over land, but even over water, these lines were excluded because the data are often parallel to shore or at a depth contour that leads to violation of line-transect assumptions regarding how representative they are.

- Only data from sea lions observed in the water or on buoys were used (sea lions hauled out on shore or sand bars were excluded).
- Only data collected in "calm" BSS 0 to 2 were used.
- Only data without significant glare issues were used (i.e., "hard" glare through which a marine mammal could not be seen occurring within more than 30% of each of the three observers' fields of view [0 to 90° left and right of the plane's nose and the belly window] for more than 3 min).

Input files for the line-transect analyses were prepared from the filtered data.

We used both conventional line-transect methods (i.e., Conventional Distance Sampling or CDS) and multiple-covariate line-transect methods (i.e., Multiple Covariate Distance Sampling or MCDS) to analyze the aerial survey data for estimating density and abundance of sea lions. The latter approach is generally preferred as it incorporates information on environmental factors that are likely to affect detection probability (e.g., variables describing sighting conditions) and usually (though not always) produces estimates with higher precision (i.e., lower variances). However, datasets with small sample sizes (common in marine mammal studies) can make it difficult or impossible to achieve model "convergence" in some MCDS analyses; it is thus important to always start each analysis with CDS methods (this also helps to determine the appropriate truncation distance and overall modeling approach).

Data were analyzed using the software *DISTANCE*, Version 6.2, Release 1 (Thomas et al., 2010). Estimates of density and abundance (and their associated coefficient of variation) were calculated using the following standard formulae:

$$\begin{split} \widehat{D} &= \frac{n\,\widehat{f}(0)\,\widehat{E}(s)}{2\,L\,\widehat{g}(0)} \\ \widehat{N} &= \frac{n\,\widehat{f}(0)\,\widehat{E}(s)\,A}{2\,L\,\widehat{g}(0)} \\ \widehat{CV} &= \sqrt{\frac{\widehat{var}(n)}{n^2} + \frac{\widehat{var}[\widehat{f}(0)]}{[\widehat{f}(0)]^2} + \frac{\widehat{var}[\widehat{E}(s)]}{[\widehat{E}(s)]^2} + \frac{\widehat{var}[\widehat{g}(0)]}{[\widehat{g}(0)]^2}} \end{split}$$

where $\hat{D} = density$ (of individuals), n = number of on-effort sightings, $\hat{f}(0) =$ probability density function evaluated at zero distance, $\hat{E}(s)$ = expected average group size (using size-bias correction in *DISTANCE*), L = length of transect lines surveyed on effort, $\hat{g}(0) =$ probability of detecting sea lions (in our study, this accounts for both sea lions missed due to being on a dive and those that were hauled out at the time of the survey), \hat{N} = abundance, A = size of the survey area, \widehat{CV} = coefficient of variation, and $v\widehat{a}r$ = variance.

We produced estimates of density and abundance using the entire filtered dataset, stratified by season and by the five survey subareas. To avoid potential overestimation of group size, we used the size-bias-adjusted estimate of average group size available in DISTANCE. To facilitate modeling, the Perpendicular Sighting Distance (PSD) data were truncated to remove outliers. We modeled the data with the Half-Normal (with hermite polynomial and cosine adjustments) and Hazard Rate (with simple polynomial and cosine adjustments) models (Buckland et al., 2001). For each survey subarea, we used a pooled estimate of the probability density function and group size but did not pool sighting rates. The model with the lowest value of Akaike's Information Criterion (AIC) was selected for the final estimates.

We produced two sets of estimates: an uncorrected estimate of only the number of sea lions in the water, and a second estimate that incorporates a $\hat{g}(0)$ correction factor for both missed trackline detections (availability portion only) and sea lions hauled out at the time of the survey (see below). The latter estimate provides an approximation of the total abundance for each species, including both animals in the water and those on land. We used tagging data to model the correction factors (see below).

Sea Lion Tagging and Tracking

In most line-transect studies of pinnipeds, trackline detection probability, $\hat{g}(0)$, is assumed to be unity (1.0). However, $\hat{g}(0)$ is in reality less than 1.0 and ignoring this can cause serious downward bias. Studies that have corrected their estimates for missed detections generally use diving data from tagging studies or double-platform methods. We could not directly estimate trackline detection probability from our aerial survey study because we did not conduct diving experiments nor use independent observers. Instead, we used available tagging data from historical studies performed in the region.

We conducted a thorough search for potential California and Steller sea lion dive and haulout data, and selected datasets considered most appropriate for the objectives of this project. For California sea lions, there was only one set of data available from animals tagged in inland Washington waters (Gearin et al., 2017). In that study, eight adult male sea lions were captured and tagged at Shilshole Bay near Seattle (47.680° N, 122.411° W) during March to June 1995 to 2000. The tags were mounted on the dorsal pelage and contained VHF radio tags and satellite-linked time-depth-recorders (SLTDRs). After release, sea lions spent between < 1 to 30 d in inland Washington waters before departure. After this, they proceeded to migrate south to their breeding grounds. Data collected during the period of time the sea lions were within inland Washington waters are considered representative for this study. Further details on the equipment and methods used in the tagging study are available in Gearin et al. (2017).

For Steller sea lions, 25 animals were captured and tagged during January to March 2004 to 2006 in a floating trap at Norris Rocks off Hornby Island in the central Strait of Georgia, British Columbia (49.484° N, 124.648° W), about 65 km northwest of our study area. Animals were tagged with SPLASH model (or in 6 cases a SPOT4 model) tags and stand-alone Mk9 units (Wildlife Computers, Redmond, WA, USA). The TDRs were mounted on the sea lion's trunk roughly two-thirds of the way down the body from the head. Biologically implausible ARGOS locations were deleted using the travel-speed filter developed by McConnell et al. (1992), as modified by Austin et al. (2003), utilizing a maximum swimming speed of 2 m/s, resulting in several locations per day (mean = 7.2). The Mk9 TDRs were programmed to record both wet/dry sensors and water depth every 10 s. The depth transducer was calibrated based on the zero offset correction algorithm developed by Wildlife Computers in 2009. Sea lions were released at the capture site and were assumed to have remained in the Salish Sea until the hour of the first filtered location outside the Salish Sea. Animals were subsequently assumed to have remained outside the Salish Sea until the hour of the first filtered location within the Salish Sea.

Development of Correction Factors

To calculate the probability of an animal being "available" to the aerial survey, we considered that

$$Pr(available) = [1 - Pr(haulout)] \cdot [1 - Pr(dive)]$$

where Pr(available) = probability of being available for detection on the survey, Pr(haulout) = probability of being hauled out at the time of the survey, and Pr(dive) = probability of being on a dive as the aircraft passed overhead.

For California sea lions, we calculated Pr(haulout) from the wet/dry sensors on the tags, restricting the data to only those locations within Puget Sound and to the hours of 0900 to 1700 h PST (when our aerial surveys were conducted).

For Pr(dive), we used data on dive depths and durations from the TDRs, and considered that sea lions at a depth of ≤ 1.0 m would be visible to the aerial observers. Due to their darker coloration, we assumed that California sea lions at a depth of ≥ 2.0 m would not be visible. Since tagging data were only available for spring months, we assumed that *Pr(available)* for the spring season was also representative of other seasons. Because we did not have access to the full set of raw data from Gearin et al. (2017) and were using only binned data, we were not able to estimate the standard error of Pr(available) for California sea lions. Therefore, the CVs of resulting estimates of density and abundance will underestimate the true variance of the point estimates.

For Steller sea lions, to determine whether animals were in the Salish Sea, we used filtered ARGOS satellite locations as described in Olesiuk (2018). To model the availability of Steller sea lions to detection in aerial surveys, we took a similar approach to that used by Jefferson et al. (2021) for harbor seals, using the raw tagging data in statistical modeling exercises. Due to their larger size and lighter pelage color, we assumed that Steller sea lions at a depth of ≤ 1.5 m would be visible to the aerial observers. We constructed separate models for the probabilities of animals being hauled out and the probabilities of animals diving. To avoid biases with small sample sizes, we restricted data to the time period when transmissions were being received from five or more animals (25 January to 10 March). We used hourly estimates of dive and haul-out probabilities as separate responses; these response distributions are complicated in that they include proportional data, but the majority of observations are 0s and 1s (1s occur in the haul-out data but not in the dive data). Zero- and 1-inflated mixture models exist for analyzing data from these types of distributions (Liu & Kong, 2015), although these existing approaches are limited to a subset of generalized linear mixed (GLM) models. As an alternative approach, we analyzed the data in a beta regression framework with generalized additive models (GAMs), using the 'mgcv' R package (Wood, 2011; R Core Development Team, 2022). Beta regression typically assumes observations do not include 0s or 1s; the 'mgcv' framework allows Os and 1s to be adjusted by small values (e.g., ε). As part of our modeling, we performed a sensitivity to the choice of ε (details in Figure SI; supplemental figures for this article are available on the Aquatic Mammals website).

For the beta regression models of dive and haulout probabilities, we constructed GAMs with hour of day treated as a cyclic penalized spline. We evaluated models that ignored individuals or included individual-level random effects in the intercepts (e.g., certain animals had higher or lower dive or haul-out probabilities). Models treating individuals as factors (or with factor smooths) were not included because our aim was to develop predictions for untagged animals. Similarly, season (day of year) was either ignored as a covariate or modeled as a penalized spline. Following the line-transect modeling, we used AIC to identify the model with the most data support. Since tagging data were only available for the early part of the year, we assumed that Pr(available) was constant for the entire non-breeding season (i.e., autumn through spring). However, as noted in Olesiuk (2018), behavioral patterns change seasonally, with animals (excluding young-of-theyear) spending about twice as much time hauled out during daylight in summer. TDR data were not available for autumn when animals moult, but daytime counts peak in autumn, suggesting a larger proportion are hauled out. We therefore caution the reader that sea lion corrections for the autumn season, in which TDR data were not available, must be considered highly tentative.

Results

Survey Data Collection

A total of 39,399 km of sighting effort was conducted in the study, resulting in a total of 255 sightings of sea lion groups (178 California sea lions and 77 Steller sea lions). After filtering the data (see above), the reduced dataset contained 7,840 km of effort and 165 sea lion sightings (108 California sea lions and 57 Steller sea lions) available for use in line-transect analyses (Table 1).

Correction Factors

Our estimated GAM models for Steller sea lion dive and haul-out probabilities strongly supported the inclusion of the penalized splines on time of day as well as random effects (unique intercepts allowing individual animals to vary). Models including an additional smooth on the day of the year to incorporate seasonal change produced a slightly more parsimonious fit to the data (lower AIC). However, because the marginal effects of seasonality were much smaller in magnitude than time of day effects, and also relatively constant over the duration of this study, we chose to focus interpretation of the models excluding the seasonal term (Figure S1). Our sensitivity analysis across values of the ε parameter in our models highlighted that models of the estimated haul-out probabilities are generally insensitive to the choice of ε (Figure S2); in contrast, the dive probability is more affected by the choice of ε , with larger values resulting in smaller estimated dive probabilities (Figure S3). This latter result is likely

driven by the dive data only being 0-inflated, with no 1s present. Results from these models showed a clear effect of time of day, with dive probabilities highest (and haul-out probabilities lowest) between 0600 and 0800 h. In contrast, dive probabilities were lowest (and haul-out probabilities highest) between 2300 and 0100 h (Figure 2).

For California sea lions, our analysis of the binned tagging data resulted in an estimate of Pr(avail) of 0.2008. This corresponds to a correction factor of 4.98. Due to the unavailability of the raw tagging dataset for California sea lions, it was not possible to calculate a standard error of Pr(avail) for that species. For Steller sea lions, the

results of the GLM modeling yielded an estimate of Pr(avail) of 0.434, with a standard error of 0.0779, corresponding to a correction factor of 2.30.

Distribution

Sightings of California sea lions occurred throughout the study area and in all four seasons, although summer sightings were rare (Figure 3). The animals used greater Puget Sound waters extensively, and sightings extended into the southern portions of the study area (i.e., southern Puget Sound south of the Tacoma Narrows Bridge and the southern portion of Hood Canal). In the Northern Inland Waters region, animals seemed to prefer the



Figure 2. Estimated probabilities of Steller sea lions being hauled out (upper) and diving (lower) as a function of time of day. Solid lines represent predicted means, and gray bands represent ± 2 SEs.

San Juan Islands region over the Strait of Juan de Fuca where only a single sighting occurred (however, there was not much sighting effort in the northern regions).

Steller sea lions showed a broadly similar pattern of occurrence, but with some notable differences. Although they used much of the study area, sightings were uncommon in the San Juan Islands area and did not occur in the southernmost reaches of Puget Sound and Hood Canal (Figure 4). Most sightings were in the autumn, followed by spring, with only one sighting in winter. None were observed during the summer season. In autumn months, they were more likely to be seen in the Strait of Juan de Fuca than in the San Juan Islands area, although it must be noted that there was relatively little effort in those northern regions (see Table 1).

Density and Abundance

We could not achieve convergence with MCDS analysis, thus the estimates make use of CDS. The distribution of perpendicular sighting distances showed an expected pattern in which distance from the transect line was the primary factor affecting detection probability, with the curve showing a very broad "shoulder" (Figure 5). While sightings occurred out to a perpendicular distance of nearly 1.8 km, the best fit was obtained with the data truncated at 520 m. The value of the probability density function ($\hat{f}(0)$) was estimated to be 3.4756, yielding an effective strip width of 288 m.

Estimates of density and abundance for both species by season are shown in Table 2. The high season for the California sea lion was spring, with an estimated total of nearly 2,931 animals occurring in the study area (i.e., Puget Sound, Hood Canal, and the Northern Inland Waters region). Steller sea lion seasonal estimates were much lower, with autumn showing the highest numbers in Puget Sound/Hood Canal/Strait of Juan de Fuca (219 animals, but this estimate did not include the large area of the San Juan Islands, which was not adequately surveyed in autumn and would presumably contain a significant number of Steller sea lions). The area with the highest density for California sea lions



Figure 3. Locations of all sightings of California sea lions made during aerial surveys. This includes sightings that were seen off-effort (not on systematic survey lines) and sightings that were filtered out of the dataset used to produce abundance estimates.



Figure 4. Locations of all sightings of Steller sea lions made during aerial surveys. This includes sightings that were seen offeffort (not on systematic survey lines) and sightings that were filtered out of the dataset used to produce abundance estimates.



Figure 5. Plot of the perpendicular sighting distances and fitted model that uses the Hazard Rate model with a cosine adjustment. The effective strip width is 288 m.

	Season	California sea lion			Steller sea lion			_	
Region		Density	Abundance	95% CI	CV	Density	Abundance	95% CI	CV
	Uncorrect	ted in-water	estimates						
Puget Sound/ Hood Canal	Winter	0.021	54	35-83	21.41	0.000	0	n/a	n/a
	Spring	0.034	89	54-145	24.75	0.001	3	0-25	131.6
	Summer	0.002	7	2-27	79.42	0.000	0	n/a	n/a
	Autumn	0.008	21	9-51	46.74	0.018	47	27-82	28.3
Northern Inland Waters	Spring	0.107	500	51-4,918	82.87	0.000	0	n/a	n/a
Strait of Juan de Fuca	Autumn	0.000	0	n/a	n/a	0.052	48	42-54	6.3
(Corrected esti	mates (inclu	ding in-water	and on-land c	omponents	;)			
Puget Sound/ Hood Canal	Winter	0.102	270	175-415	21.41	0.000	0	n/a	n/a
	Spring	0.168	442	271-723	24.75	0.003	8	1-58	132.8
	Summer	0.012	33	8-135	79.42	0.000	0	n/a	n/a
	Autumn	0.039	104	43-252	46.74	0.041	109	57-208	33.5
Northern Inland Waters	Spring	0.534	2,489	253-24,491	82.87	0.000	0	n/a	n/a
Strait of Juan de Fuca	Autumn	0.000	0	n/a	n/a	0.120	110	76-159	19.0

Table 2. In-water and total density and abundance estimates for sea lions in inland Washington State waters; n/a = not available.

was the Strait of Juan de Fuca (spring season: D = 0.534 animals/km²); however, it must be cautioned that there were only two surveys in that area, with a relatively small number of sightings, and the precision of the estimate is very low (CV = 112.7%). Overall, for Steller sea lions, abundance was much lower compared to that of California sea lions.

Discussion

This study used a relatively new approach to estimating pinniped total abundance, which is in some ways the reverse of what is typically done. We conducted aerial surveys of the study area. This area only covered marine waters and, thus, only allowed us to calculate the in-water portion of the sea lion populations. By developing correction factors (corresponding to trackline detection probability estimates or $\hat{g}(0)$) from tagging studies, we were able to correct for those sea lions missed during our aerial surveys either because they were on shore during the survey or were in the water on a dive deep enough to make them no longer visible to observers in the airplane.

The corresponding correction factors are large and have a major impact on the final estimates of density and abundance. The tagging studies that provided the data for developing the correction factors were conducted previous to our surveys and generally had other goals and objectives (see Gearin et al., 2017; Olesiuk, 2018). Therefore, there were some challenges in using these data to get at the parameters we needed. The main issue was with the seasonal range of the tagging data, which only covered a part of the year (mainly late winter to early summer) and required us to make the assumption that there were no large seasonal deviations in either dive times or amount of time spent hauled out. This is a reasonable assumption for the cooler months (i.e., winter and spring) but may not be for the summer breeding and autumn molting seasons in which animals tend to spend more time on shore. Fortunately, the summer in-water estimates were very low (California sea lions) or nil (Steller sea lions); thus, any bias caused by this factor is not likely to be significant for that season. Autumn estimates may be more affected, however, and this should be kept in mind when interpreting the estimates.

Comparison to Previous Estimates

There are no previous complete empirical estimates of density or abundance available for either species of sea lion in inland Washington waters. This is largely due to the fact that pinniped abundance is traditionally estimated by conducting surveys at rookeries when animals are hauled out during the breeding season (when the highest number of animals is believed to be present), with corrections made for the proportion missed due to being in the water. Because there are no rookeries for either species of sea lion in Washington inshore waters, hard numbers on their abundance in state waters have not been available. This represents a serious problem for management efforts directed both at sea lions and at their prey species and predators. Such information is needed to assess potential impacts from anthropogenic activities, as required by protective legislation, as well as to assess impacts of sea lion predation on declining salmonid populations.

Previously available values are either approximate estimates (i.e., not statistically derived) or only include incomplete numbers of animals hauled out (and generally do not include the inwater component). In the late 1970s, Everitt et al. (1980) counted up to 296 California sea lions and up to 259 Steller sea lions at haulouts in Greater Puget Sound, but these numbers are from when population sizes of both species were much lower. Calambokidis & Baird (1994) suggested that in the early 1990s, there may have been as many as 3,000 California sea lions and more than 1,000 Steller sea lions in the transboundary area between Washington and British Columbia; however, these estimates cover a much larger area than those from the current study and, thus, are not directly comparable. In the late 1990s, Jeffries et al. (2000) stated that there were more than 1,000 California sea lions present in Puget Sound (presumably based on numbers observed at haulouts). In 2015, it was considered that there were about 2,000 to 2,500 Steller sea lions present during their peak season in Washington; however, most of these were seen along the outer Washington coast (Wiles, 2015) and, thus, outside of our study area. In recent years, as many as 100 Stellers have been counted in winter months at the mouth of the Nisqually River, near Tacoma, in inland Washington waters (Wiles, 2015). At Race Rocks in the Strait of Georgia, British Columbia, peak numbers of both sea lion species in recent years have occurred in October and November based on haul-out count studies (Edgell & Demarchi, 2012), which is different from the pattern we observed with California sea lions, which peaked in spring months.

Although none of these estimates is directly comparable to ours, the most recent values are generally in line with what we have estimated. Clearly, the numbers of both species of sea lions in Washington inland waters have increased dramatically since protection was afforded them in the early 1970s; they currently number in the thousands. They have become a significant component of the marine fauna of the Salish Sea and are likely having an important impact on the populations of many of their prey species, including a number of threatened or endangered salmon and trout species (Bigg, 1985; Calambokidis & Baird, 1994). As two of their prey species, the documented increase in sea lion numbers may have also been a factor in recent increased sightings of mammal-eating Bigg's killer whales (*Orcinus orca*) in Salish Sea waters (Houghton et al., 2015; Shields et al., 2018), though this is only speculation at this point.

Caveats and Potential Biases of the Estimates

Line-transect estimates of density and abundance, although generally considered quite robust, can be affected by various factors. These primarily relate to survey design, satisfaction of assumptions of the methodology, and issues affecting detection probability or correction factors. We discuss each of these, in turn, below.

Our aerial surveys were designed to collect high-quality data on all marine mammals in the study area. Although the primary target species of the surveys was the harbor porpoise (Phocoena phocoena; Jefferson et al., 2016), another species of pinniped, the harbor seal, was observed with sample sizes adequate to estimate density and abundance in multiple seasons throughout all of the Washington State portion of the Salish Sea (Ampela et al., 2021; Jefferson et al., 2021). Transect lines in Puget Sound and Hood Canal were designed to provide representative coverage of all marine habitats—both in shallow and deep water areas. Seasonal coverage also occurred in all four seasons, although specific survey windows were also determined by availability of observers and aircraft and, thus, may not always be completely representative of that season. The best example of this is for the autumn surveys, which occurred within the first 21 d of September at the very beginning of that season. We suspect that our autumn estimates may be biased on the low side for this reason (e.g., California sea lions migrate from southern California, and it may take them several weeks or even more than a month to reach Puget Sound; see Gearin et al., 2017).

Our sea lion density and abundance estimates are based on limited datasets and, in particular, the northern part of our study area (i.e., Strait of Juan de Fuca and San Juan Islands) was not surveyed extensively nor in all seasons. Some of the resulting estimates are based on small numbers of on-effort sightings and, therefore, have very low precision (even without accounting for the variance of the correction factors). For these reasons, our estimates should be considered somewhat preliminary, and any estimates with a CV greater than about 40% should not be used for some management purposes (e.g., setting quotas).

One factor that may have compromised even survey coverage is the presence of no-fly zones around large airports and military bases. Because we could not fly over those areas, transect lines had to be planned to avoid them. One of the largest California sea lion haul-out sites in Puget Sound/ Hood Canal is at Naval Base Kitsap at Bangor, where sea lions haul out on port security barriers and even docked submarines (Jeffries et al., 2000). The animals typically spend a good deal of time in the water near haulouts and, because our surveys excluded this area, we may have missed a significant number of sea lions that would otherwise have been seen in the water. This would result in underestimation of density and abundance, potentially affecting both species.

Due to limited sample sizes, we pooled both sea lion species together for estimation of the effective strip width. Although this is not ideal, the two species are of similar size, with similar patterning and behavior at sea. Therefore, we do not think this would cause significant bias. Because many species of smaller marine mammals (including sea lions) can be difficult to detect in poor sighting conditions, we restricted our analyses to only surveys conducted in calm conditions (BSS 0 to 2) and without hard glare issues. The inshore waters of Puget Sound are protected and therefore do not suffer from large swells that can be common in offshore survey areas. These approaches are considered adequate to ensure optimal detection probability.

Management Implications

We provide here the first empirical, quantitatively derived estimates of abundance for California and Steller sea lions in Washington inland waters, which include both on-land and in-water components. The estimates produced in this study, while considered preliminary, have applicability to wildlife managers, as both California and Steller sea lions are important components of the protected Washington State marine fauna. Despite neither species using study area waters to breed (meaning that there are few sea lions of either species present during summer months), both species of sea lions fan out from rookeries at the end of their respective breeding seasons in late August and move into Washington waters, using them extensively from autumn to spring for foraging. There is a tendency for Steller sea lions to move out of an area as California sea lion males move in, possibly due to disturbance or harassment by the smaller species (Mate, 1973, 1975). Steller sea lions of all age classes occur there, but for California sea lions, it is mostly large males that make the long trip up the coast to Washington. Males are the largest members of the

population, with the highest caloric requirements. Investigations over the last several decades have shown that sea lions are major predators of salmonids (including several threatened and endangered species) and thus likely have significant impacts on local fish stocks (Gearin et al., 1986; Fraker, 1994; Jeffries & Scordino, 1997; Olesiuk, 2018; Trites & Rosen, 2019; Scordino et al., 2022).

The ultimate goal for management authorities would be to have improved estimates that are fully up-to-date and include full seasonal and geographic stratification with high levels of precision. Our study demonstrates that it is possible to use historical tagging data to generate correction factors and estimates of sea lion densities. While this approach may be useful to researchers and managers in the region, it is very much a first step toward the ultimate goal of generating up-to-date and precise estimates of densities. Additional monitoring efforts, including aerial surveys and tagging data with large numbers of tagged individuals, are needed in future studies.

Conclusions

Our results indicate that the peak season of California sea lion abundance in the study area is spring when nearly 450 may be present in Puget Sound/Hood Canal and up to 3,000 are found in the whole of the inland waters of Washington State. Abundance of this species in the study area increases from autumn through spring, and then drops dramatically during the summer months. For Steller sea lions, the peak season appears to be autumn when over 200 animals are present in Puget Sound/Hood Canal/ Strait of Juan de Fuca and an unknown number of additional animals are in the northern waters of the San Juan Islands and Haro Strait. Although we cannot empirically estimate total numbers of Steller sea lions in the study area in the peak season of autumn (due to the lack of fall survey data from the San Juan Islands and Haro Strait), if we assume that the density in that area is similar to that in the Strait of Juan de Fuca, this would mean that the study area may contain about 600 to 700 Steller sea lions in the autumn months. The numbers for this species drop to near zero in summer months, however, when almost all of the population is present on their breeding islands further to the north (Bigg, 1985; Olesiuk, 2018; Trites, 2021).

This study represents a first attempt at evaluating sea lion numbers in inland Washington waters using existing data sources. While preliminary with some estimates that suffer from low precision, it has demonstrated that useful estimates of sea lion density and abundance can be garnered from studies that were conducted with other primary goals. One of the advantages of line-transect and other distance sampling survey designs is the ability to collect data on additional species other than those on which the initial study was focused. Such data can provide a meaningful way of evaluating density and abundance for these other species. However, sample sizes of sea lion sightings were relatively small, and some areas were not surveyed adequately in all seasons, preventing us from making estimates for all parts of the study area. More studies are needed on diving behavior of both California and Steller sea lions, especially given newer and more sophisticated tagging technologies. Clearly, to obtain estimates of sea lion numbers in specific portions of inland Washington that are complete, up-to-date, and cover fluctuations during all four seasons, additional dedicated work will be required.

Note: The supplemental figures for this article are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https:// www.aquaticmammalsjournal.org/index. php?option=com_content&view=article&id=10&I temid=147.

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