Research Article



Estimation of In-Water Density and Abundance of Harbor Seals

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ABSTRACT Ecologists and managers require accurate population estimates of marine mammals to assess potential anthropogenic threats to these animals. We present estimates of in-water density and abundance of a distinct stock of harbor seals (*Phoca vitulina richardii*) in Hood Canal, Washington, USA. We used aerial line-transect survey data collected from 2013 to 2016 to directly estimate harbor seal density and abundance in the waters of Hood Canal, a deep-water fjord in the Salish Sea. We estimated a correction factor for trackline detection probability from dive and surface time data gathered from regional seal tagging studies, and applied this factor to correct for seals missed on the trackline during surveys. We applied conventional and multiple covariate line-transect approaches in the analysis. The resulting best estimate of in-water density of harbor seals in the Hood Canal study region was 5.80 seals/km², with an estimated abundance of 2,009 seals. We did not derive a correction factor to account for the number of seals on land (i.e., hauled out). Therefore, these estimates do not reflect total stock size but provide a starting point to evaluate potential influences of anthropogenic activities, particularly those involving underwater noise, on this marine mammal stock. © 2021 The Wildlife Society.

KEY WORDS abundance, density, harbor seal, Hood Canal, line-transect, marine mammals, underwater sound, Washington.

Noise-related disturbance of protected marine species is a concern for government agencies, industry representatives, scientists, and regulators, and is the subject of increasing regulatory attention. In Washington, USA, Hood Canal and adjacent Dabob Bay are important training and testing areas for the United States Navy (USN; Department of the Navy 2015). Training and testing activities produce impulsive sounds via impact pile driving, in-water explosives, and air guns, and non-impulsive sounds, including naval sonars and vibratory pile driving. To characterize the potential effects of underwater sounds on marine mammals, it is first necessary to estimate the abundance (i.e., number) and individual density (i.e., number/km²) of these animals in ensonified areas (Department of the Navy 2015). Several marine mammal species occur in Hood Canal. Of these, the harbor seal (Phoca vitulina richardii), is the most abundant, and the only resident marine mammal (London et al. 2012). Based on genetic analyses (Huber et al. 2010, 2012), the National Marine Fisheries Service (NMFS) considers harbor seals inhabiting Hood Canal to be a separate stock from other harbor seals in inland Washington waters (Carretta et al. 2015, 2018).

Harbor seals, like all pinnipeds, are amphibious, spending time on land (i.e., hauled out) and in the water. Therefore,

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only a subset of the population is on land at any given time. Seal abundance is usually estimated by counting the number of hauled-out animals, typically at tidal states when maximum numbers of animals are expected to be on land, and then correcting for the proportion of animals at sea using available haul-out data (e.g., % wet/dry) from tagged seals (Huber et al. 2001, Hammill et al. 2007, Palka et al. 2017).

We were interested in in-water abundance estimates, excluding hauled-out seals because in-water abundance values provide a more direct way to estimate effects of underwater sound on seals, and hauled-out animals are not directly exposed to underwater noise. The objective of this study was to estimate in-water density and abundance of harbor seals in Hood Canal to better understand their potential exposure to underwater sound generated by USN training, testing, and in-water construction activities.

STUDY AREA

Hood Canal (47.6040°N, 122.9488°W) is located in the western part of the Salish Sea, approximately 45 km due west of Seattle, Washington, with an area of approximately 385 km^2 (Fig. 1). Hood Canal is a deep-water fjord with complex bathymetry, including relatively deep waters in the main channel and considerable slope adjacent to shorelines (\bar{x} depth ~54 m below \bar{x} high water; max. depth = 183 m). Hood Canal is situated on the Olympic Peninsula, which is characterized by a temperate oceanic climate and few



Figure 1. Inland waters of Washington, USA, the Hood Canal study area, and 6 sub-regions used to estimate density of harbor seals, August 2013–January 2016. Aerial survey lines were spaced 3.7 km apart (indicated by solid lines), excepting a reduction in line spacing to 1.8 km in Hood Canal during 1 survey in 2016 to increase sample size robustness and resolution in this area (indicated by dashed lines). 1 = Hood Canal Bridge to navigation marker 8 and 9, 2 = Area 1 to Hazel Point to Marker 11, 3 = Area 2 to Oak Harbor (marker 12) to Misery Point (marker 15), 4 = Area 3 to Trident Head (green marker 9 to Teku Point), 5 = Area 4 to Lilliwaup Bay to Duwato Bay, and 6 = Area 5 around the Great Bend to Belfair. Navigational markers correspond to those of National Oceanic and Atmospheric Administration Chart 18476.

temperature extremes. Naval Base Kitsap-Bangor is located on the eastern shore of Hood Canal. Including Naval Station Bremerton, the 2 comprise the third-largest naval base in the United States. Hood Canal has several internal bays, the largest of which is Dabob Bay, which is also a naval restricted area. In addition to USN use, Hood Canal is used for recreational and subsistence fishing and shellfish aquaculture. The dominant marine mammal species in Hood Canal are harbor seals, California sea lions (Zalophus californianus), Steller sea lions (Eumetopias jubatus), and killer whales (Orcinus orca). There are 5 major harbor seal haul-out sites in Hood Canal: Quilcene Bay, Dosewallips, Duckabush, Hamma Hamma, and Skokomish (London et al. 2012, Jeffries 2014; Fig. 1). For study purposes we divided Hood Canal into 6 pre-defined geographic subregions (Fig. 1). These sub-regions were established with input from NMFS scientists to designate regions of nearuniform seal density and consistent levels of human activity. The sub-regions extended from the Hood Canal Bridge through the Great Bend at the southern extent of the Canal and were designated into 6 sub-regions (navigational marker locations correspond to those of National Oceanic and Atmospheric Administration [NOAA] Chart 18476): 1=Hood Canal Bridge to navigation marker 8 and 9, 2=Area 1 to Hazel Point to Marker 11, 3=Area 2 to Oak Harbor (marker 12) to Misery Point (marker 15), 4=Area 3 to Trident Head (green marker 9 to Teku Point), 5 = Area 4 to Lilliwaup Bay to Duwato Bay, and 6=Area 5 around the Great Bend to Belfair. We conducted 6 aerial surveys from summer 2013 through winter 2016. Seasons were defined as winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug), and fall (Sep-Nov).

METHODS

Aerial Surveys and Data Treatment

We analyzed data collected during 6 aerial surveys conducted by Smultea Sciences throughout the Salish Sea from 2013-2016. Surveys occurred in 6 discrete periods (each spanning 6 to 10 days, depending on weather) across 4 seasons: 2 in winter (Jan 2015 and 2016), 1 in spring (Apr 2015), 1 in summer (Jul 2014), and 2 in fall (late Aug-Sep 2013 and Sep 2014). This dataset provided the best temporal and spatial resolution available for the study area. The Hood Canal study area was one of a number survey blocks in the study. Smultea et al. (2017) describe the aerial survey methods we used in this study. Surveys followed line-transect survey protocol (Buckland et al. 2001; Marques and Buckland 2003, 2004) and were flown at speeds of approximately 185 km/hour (100 knots) and at a target altitude of 229 m, as approved and permitted under NMFS research permits 14451, 15569, 1425-03, and 19829. Parallel transect lines followed an east-west orientation, generally perpendicular to the bathymetric contours, to avoid biasing surveys by following depth contours. Aerial survey lines were spaced 3.7 km apart, excepting a reduction in line spacing to 1.8 km in Hood Canal during 1 survey in 2016 to increase sample size robustness and resolution in this area (Fig. 1). We conducted aerial surveys in 6 discrete 6-10-day periods from summer 2013 through winter 2016, irrespective of tidal state. The survey data used to support this study are openly available at the Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) data repository: http://seamap.env.duke.edu/dataset/1966 (dataset reference 1966), accessed 3 April 2020; and

http://seamap.env.duke.edu/dataset/1398 (dataset reference 1398), accessed 3 April 2020. Queries about use of the dataset should be directed to the corresponding author.

We included in the analysis only confirmed sightings of harbor seals collected on systematic transect lines in calm seas (Beaufort sea states [BSS] of 0–2). We excluded sightings made in BSS > 2 because harbor seals were difficult to detect in water when whitecaps were present. Harbor seals were readily distinguishable from the 2 other common pinniped species in the project area (California sea lion and Steller sea lion) based on differences in size, pelage patterns and body shape (Jefferson et al. 2015). We used conventional distance sampling and multiple covariate distance sampling (MCDS) methods to analyze the aerial survey data and estimate density and abundance of harbor seals observed in the water (Buckland et al. 2001; Marques and Buckland 2003, 2004).

Harbor seal habitat includes the shallow-water sand and mud flats of the intertidal zone, making the distinction between animals in the water and those hauled out sometimes unclear. Therefore, we assumed that all seals encountered during aerial surveys were in 1 of 3 categories: in-water seals were largely submerged in the water (only head sticking out occasionally), out-of-water seals were high and dry on haul-out areas (e.g., islands, rocks, piers, submarines), and wet-belly seals were lying on mud or sand flats partially submerged or with wet bellies. We excluded seal sightings in the out-of-water and wet-belly categories from our density estimation of in-water animals. According to NMFS and Washington Department of Fish and Wildlife haul-out count survey methodology, wet-belly seals are considered to be on land (Jeffries 2014). Therefore, we excluded this category in our analysis to avoid potentially double counting these animals because the in-water estimates may eventually be integrated and compared with haul-out count data collected by these agencies to estimate the total size of the Hood Canal stock.

Density and Abundance Estimation

We analyzed the filtered data using the software DISTANCE 6.2, release 1 (Thomas et al. 2010). We calculated estimates of density and abundance (and their associated CV) using the following standard line-transect formula:

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

where D = density (of individuals), n = number of on-effort sightings, f(0) = detection function evaluated at zero distance, E(s) = expected average group size (using size-bias correction in DISTANCE), L = length of transect lines surveyed on effort (in km), $\hat{g}(0) = \text{trackline}$ detection probability, A = size of the survey area (km²), and var = variance.

We produced estimates of density and abundance using the entire filtered dataset (i.e., all surveys and seasons) stratified by survey sub-region, and also produced overall pooled estimates (with the 6 sub-regions pooled). Several surveys began on 30 or 31 August, and we treated these as reflective of the fall season because they were part of a survey effort that occurred predominately in fall (Sep). Although there were 6 sub-regions of interest (Fig. 1), we combined sub-regions 1 and 2 because of low sample sizes, resulting in only 5 sub-regions for the final analysis. We obtained 530 sightings for analysis in the 5 sub-regions (Table 1).

To avoid potential overestimation of group size, we used the size-bias-adjusted estimate of average group size available in DISTANCE, and we calculated the variance using the O2 method available in DISTANCE. To facilitate modeling, we truncated the perpendicular sighting distance data to remove outliers and obtain the best model fit (i.e., fitting the shape criterion of Buckland et al. 2001, and with lowest CV). The optimal truncation distance was 0.30 km. We modeled the data with the half-normal (with Hermite polynomial and cosine adjustments) and hazard rate (with simple polynomial and cosine adjustments) models. We selected the model with the lowest value of Akaike's Information Criterion for the final estimates.

We could not directly estimate trackline detection probability from the data collected in this study because we did not collect seal dive data or use independent observers. Instead, we used data from time-depth recorders deployed on harbor seals in the San Juan Islands, approximately 120 km north of the study area (National Marine Mammal Laboratory, unpublished data; Wilson et al. 2014). We estimated g(0), availability bias portion only, as:

$$\hat{g}(0) = \frac{s+t}{s+d},$$

where s = average length of time spent at or near the surface, t = window of time in which aerial observers could detect the animals (10 sec), and d = average dive duration.

We compiled dive and surface times from the Wilson et al. (2014) dataset. We filtered tag data to exclude periods >10 minutes because dive durations >10 minutes were rare, and surface times >10 minutes may be indicative of hauledout seals (Suryan and Harvey 1998). There are some potential biases in the Wilson et al. (2014) data. For example, dives <5 m were not recorded as dives. This dataset, however, provided the most relevant available data for calculating $\hat{g}(0)$ for harbor seals in Hood Canal.

RESULTS

The estimate of $\hat{g}(0)$ based on data from time-depth recorders reported in Wilson et al. (2014) for harbor seals was 0.204 ± 0.242 (SE). Because of variability in dive and surface times, this parameter had a large associated variance (CV = 118.6%). We present 2 coefficients of variation in our density and abundance estimates: one that incorporates this variance factor (CV), and another that does not (CV') (Table 1). The former was obtained from a study that was not part of this aerial survey project. Previous studies of pinnipeds using line-transect methods did not include a $\hat{g}(0)$ estimate (therefore assuming that trackline detection is unity) or did not include its variance in the final coefficient of variation for their abundance estimates (Buckland et al. 1993, Herr et al. 2009, Bengtson et al. 2011). Therefore, providing both the CV and CV' in our results facilitates direct comparisons to previous studies of pinnipeds using line-transect methods.

After conducting experimental analyses using conventional line-transect methods, and the use of several different covariates, we obtained the best model from an MCDS approach using the covariates BSS and percentage of cloud cover. The chosen model was the half-normal model with a cosine adjustment (Fig. 2). The effective strip width was 0.209 km (CV = 2.58%). We derived estimates of density and abundance for the 5 analyzed sub-regions and the overall study area, along with their relevant components (Table 1). Estimated abundance within the 5 analyzed subregions ranged from 85 to 1,142 seals (Table 1). The inwater density of harbor seals for the entire Hood Canal

Table 1. In-water density and abundance estimates from aerial surveys for harbor seals in Hood Canal, Washington, 2013–2016.

Sub-region	Number of sightings ^a	Effort ^b (km)	x group size	Trackline detection probability g(0)	Individual density (number/km ²) ^b	95% CI (density)	Abundance ^c	95% CI (abundance)	% CV ^d	% CV' ^e
1,2	13	133.8	1.2	0.204	1.16	0.75-1.78	85	55-131	120.3	21.3
3	38	73.7	1.2	0.204	5.93	3.62-9.71	120	73-196	120.6	23.4
4	308	433.1	1.2	0.204	8.77	7.22-10.67	1,142	939–1,389	118.8	9.4
5	71	168.1	1.2	0.204	5.45	3.77-7.89	235	162-340	119.6	17.2
6	100	238.3	1.2	0.204	5.38	4.24-6.84	427	336-542	118.9	11.3
Overall pooled	530	1,047.0	1.2	0.204	5.80	5.05-6.66	2,009	1,750–2,308	118.6	6.9

^a Before truncation.

^b On-effort survey status only.

^c In-water seals only; does not include hauled-out (i.e., out-of-water and wet-belly) animals.

 $^{\rm d}$ Coefficient of variation with large g(0) variance factor.

^e Coefficient of variation without large g(0) variance factor.



Figure 2. Perpendicular distance histogram and fitted detection function for harbor seal sightings using multiple covariate distance sampling, with the covariates Beaufort sea state and percentage cloud cover. The chosen model was the half-normal model with a cosine adjustment. Data were collected in Hood Canal, Washington, USA, between August 2013 and January 2016.

study region was 5.80 seals/km², and the pooled overall (in-water) abundance estimate was 2,009 seals (CV = 118.6%; CV' = 6.9%).

DISCUSSION

Most previous attempts to use line-transect methods with pinnipeds have surveyed for seals only on solid substrates (e.g., land, sea ice) and therefore do not use line-transect methods to explicitly estimate in-water densities (Mizuno et al. 2002, Southwell et al. 2004, Chambellant and Ferguson 2009, Bengtson et al. 2011, Ver Hoef et al. 2013). Only a few studies have used line-transect methods to directly estimate in-water pinniped densities, and many of these simply assume that detection on the trackline is certain (i.e., g(0) = 1.0; Buckland et al. 1993) or incorporate g(0) but do not include the associated variance component in their overall coefficient of variation for density and abundance (Herr et al. 2009). We used line-transect methods for estimating in-water density of seals, and included a correction for availability bias and its variance component in the final estimates produced. Previous work by Reay (2005) made use of a line-transect approach to study gray seals (Halichoerus grypus) in the United Kingdom, but that work was focused more on evaluating different estimates of g(0) than on producing useable estimates of density and abundance. Lowry and Forney (2005) were able to apply a unique approach in which they conducted coordinated haul-out counts and aerial line-transect surveys to separately develop estimates of the on-land and at-sea components, which were then combined to produce an overall estimate of California sea lion abundance in central and northern California, USA. The latter approach was not possible for our study, which relied on available datasets.

Line-transect methods for estimating in-water density are more commonly applied to cetaceans, which cannot be counted on land, and certain issues specific to pinnipeds did present challenges in our analysis, for example, how to handle wet-belly seals that were not clearly in water, or truly hauled out, and the paucity of studies on g(0) values for pinnipeds. Our study helps demonstrate the use of line-transect and other distance sampling methods for estimating in-water density of pinnipeds, and thereby encourages and facilitates their use and further development.

Our results represent an average for all 4 seasons and for different times of day (excluding nighttime hours). The overall estimate of 2,009 seals (CV' = 6.9%), however, should not be considered a stock size estimate because it does not include a correction coefficient for the number of seals hauled out during the aerial surveys (the development of which was beyond the scope of this work). Harbor seal stocks in Washington have generally increased since hunting bounties ended in 1960 and the Marine Mammal Protection Act came into effect after 1972 (Jeffries et al. 2003). The current size of the Hood Canal stock (i.e., in-water and hauled-out animals) has not been presented by NMFS because there are no official stock size estimates available from the last 14 years (Carretta et al. 2018). The last reported stock size estimate was 1,088 seals in 1999 (Carretta et al. 2015) and was thought to be relatively stable at 1,068 seals in 2002 (London 2006).

For the purposes of this analysis, it was necessary to pool data from sub-regions 1 and 2 because of small numbers of seal observations in those areas (especially sub-region 2, where a no-fly zone is located; Fig. 1). It may be possible to develop separate estimates for these sub-regions in the future. The best option for doing so would be to collect additional data in the areas where there are few data available at present to increase sample sizes and evaluate potential trends. It would also be worthwhile to develop more precise estimates of trackline g(0) for harbor seals, if appropriate

survey data can be identified. Additional work is also needed to better integrate in-water surveys, which are usually performed randomly with respect to tide, with on-land pinniped haul-out surveys, which are usually timed with a particular tide level, to coincide with maximum numbers onshore. Additionally, for management purposes, it would be desirable to have seasonal estimates of density and abundance, stratified by survey sub-regions.

The estimates presented here provide a starting point to better understand anthropogenic effects on harbor seals in Hood Canal, which are managed by NMFS as a separate stock. Our estimates could eventually be integrated and compared with regional seal haul-out census data to produce an updated stock size estimate. Any such effort should be undertaken with caution; aerial surveys focusing on in-water animals are usually performed randomly with respect to tide, and pinniped haul-out surveys are typically timed to occur at low or high tide. We also note that haul-out patterns for harbor seals in Hood Canal differ from those elsewhere in the Salish Sea; specifically, seals in this region are most likely to haul out several hours after high tide, versus at low tide (London et al. 2012). These different methodologies affect the proportion of seals hauled out, and therefore available for observation. Further, in practice, determining the number of seals hauled out at any given time is difficult; harbor seal haul-out behavior in Hood Canal is complex, not wellcorrelated with environmental cycles, and often affected by unpredictable human disturbance factors (London et al. 2012). Despite these limitations and challenges, we believe that line-transect methods have been underused with pinnipeds, and have the potential to provide valuable in-water density and abundance data for future projects.

MANAGEMENT IMPLICATIONS

Estimates of in-water abundance are necessary components of future estimates for harbor seals in Hood Canal, and therefore important for the effective management of this stock. Information about the distribution and abundance of marine protected species is required to estimate the number of animals that might be affected by a specific activity, including activities that generate underwater noise.

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LITERATURE CITED

- Bengtson, J. L., J. L. Laake, P. L. Boveng, M. F. Cameron, M. B. Hanson, and B. S. Stewart. 2011. Distribution, density, and abundance of packice seals in the Amundsen and Ross Seas, Antarctica. Deep Sea Research Part II: Topical Studies in Oceanography 58:1261–1276.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.
- Buckland, S. T., K. L. Cattanach, and R. C. Hobbs. 1993. Abundance estimates of Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise and northern fur seal in the North Pacific, 1987–1990. International North Pacific Fisheries Commission Bulletin 53:387–407.
- Carretta, J. V., K. A. Forney, E. M. Oleson, D. W. Weller, A. R. Lang, J. Baker, M. M. Muto, B. Hanson, A. J. Orr, H. Huber, et al. 2018. U.S. Pacific marine mammal stock assessments: 2017. NOAA-TM-NMFS-SWFSC-602. U.S. Department of Commerce, Washington, D.C., USA.
- Carretta, J. V., E. M. Oleson, D. W. Weller, A. R. Lang, K. A. Forney, J. Baker, M. M. Muto, B. Hanson, A. J. Orr, H. Huber, et al. 2015. U.S. Pacific marine mammal stock assessments: 2014. NOAA-TM-NMFS-SWFSC-549. U.S. Department of Commerce, Washington, D.C., USA.
- Chambellant, M., and S. H. Ferguson. 2009. Comparison of strip- and line-transect sampling to estimate density and abundance of ringed seals (*Phoca hispida*) in western Hudson Bay, 2007 and 2008. Canadian Science Advisory Secretariat Research Document 2009/002, Ottawa, Ontario, Canada.
- Department of the Navy. 2015. Northwest Training and Testing FEIS/ OEIS. <https://www.nwtteis.com/>. Accessed 5 Jun 2019.
- Hammill, M. O., J. F. Gosselin, and G. B. Stenson. 2007. Abundance of Northwest Atlantic grey seals in Canadian waters. NAMMCO Scientific Publications 6:99–115.
- Herr, H., M. Scheidat, K. Lehnert, and U. Siebert. 2009. Seals at sea: modelling seal distribution in the German Bight based on aerial survey data. Marine Biology 156:811–820.
- Huber, H. R., B. R. Dickerson, S. J. Jeffries, and D. M. Lambourn. 2012. Genetic analysis of Washington State harbor seals (*Phoca vitulina richardii*) using microsatellites. Canadian Journal of Zoology 90:1361–1369.
- Huber, H. R., S. J. Jeffries, R. F. Brown, R. L. Delong, and G. Vanblaricom. 2001. Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. Marine Mammal Science 17:276–293.
- Huber, H. R., S. J. Jeffries, D. M. Lambourn, and B. R. Dickerson. 2010. Population substructure of harbor seals (*Phoca vitulina richardsi*) in Washington State using mtDNA. Canadian Journal of Zoology 88: 280–288.
- Jefferson, T. A., M. A. Webber, and R. L. Pitman. 2015. Marine mammals of the world: a comprehensive guide to their identification. Second edition. Elsevier/Academic Press, New York, New York, USA.
- Jeffries, S., H. Huber, J. Calambokidis, and J. Laake. 2003. Trends and status of harbor seals in Washington State: 1978–1999. Journal of Wildlife Management 67:208–219.
- Jeffries, S. J. 2014. Aerial surveys of pinniped haulout sites in Pacific Northwest inland waters. Prepared for Commander, U.S. Pacific Fleet, Pearl Harbor, Hawaii. https://www.navymarinespeciesmonitoring.us/ files/1915/0099/5952/Jeffries_2014_JP02_Aerial_Surveys_of_Pinniped_ Haulout_Sites_June_2014.pdf>. Accessed 5 Jun 2019.
- London, J. M. 2006. Harbor seals in Hood Canal: predators and prey. Dissertation, University of Washington, Seattle, USA.
- London, J. M., J. M. Ver Hoef, S. J. Jeffries, M. M. Lance, and P. L. Boveng. 2012. Haul-out behavior of harbor seals (*Phoca vitulina*) in Hood Canal, Washington. PLoS ONE 7(6):e38180.
- Lowry, M. S., and K. A. Forney. 2005. Abundance and distribution of California sea lions (*Zalophus californianus*) in central and northern California during 1998 and summer 1999. Fishery Bulletin 103:331–343.
- Marques, F. F. C., and S. T. Buckland. 2003. Incorporating covariates into standard line transect analyses. Biometrics 59:924–935.
- Marques, F. F. C., and S. T. Buckland. 2004. Covariate models for the detection function. Pages 31–47 in S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, editors. Advanced distance sampling. Oxford University Press, New York, New York, USA.

- Mizuno, A. W., A. Wada, T. Ishinazaka, K. Hattori, Y. Watanabe, and N. Ohtaishi. 2002. Distribution and abundance of spotted seals *Phoca largha* and ribbon seals *Phoca fasciata* in the southern Sea of Okhotsk. Ecological Research 17:79–96.
- Palka, D. L., S. Chavez-Rosales, E. Josephson, D. Cholewiak, H. L. Haas, L. Garrison, M. Jones, D. Sigourney, G. Waring, M. Jech, et al. 2017. Atlantic Marine Assessment Program for Protected Species: 2010–2014. OCS Study BOEM 2017-071. Bureau of Ocean Energy Management, Washington, D.C., USA.
- Reay, N. 2005. Estimation of g(0) for bottlenose dolphin, grey seal, and harbour porpoise in Cardigan Bay, SAC. Thesis, University of Wales, Bangor, United Kingdom.
- Smultea, M. A., K. Lomac-MacNair, G. Campbell, S. S. Courbis, and T. A. Jefferson. 2017. Aerial survey of marine mammals conducted in the inland Puget Sound waters of Washington, summer 2013–winter 2016. Final Report. Prepared for Commander, U.S. Pacific Fleet and Naval Sea Systems Command. https://www.navymarinespeciesmonitoring.us/ files/3614/9935/7314/Smultea_et_al_2017_Puget_Sound_Aerial_Surveys_2013-2016_June2017.pdf>. Accessed 5 Jun 2019.
- Southwell, C. J., B. De La Mare, D. Borchers, and L. Burt. 2004. Shipboard line transect surveys of crabeater seal abundance in the

pack-ice off east Antarctica: evaluation of assumptions. Marine Mammal Science 20:602–620.

- Suryan, R. M., and J. T. Harvey. 1998. Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. Marine Mammal Science 14:361–372.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.
- Ver Hoef, J. M., M. F. Cameron, P. L. Boveng, J. M. London, and E. E. Moreland. 2013. A spatial hierarchical model for abundance of three iceassociated seal species in the eastern Bering Sea. Statistical Methodology 17:46–66.
- Wilson, K., M. Lance, S. Jeffries, and A. Acevedo-Gutiérrez. 2014. Fine-scale variability in harbor seal foraging behavior. PLoS ONE 9:e92838.

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