

Estimating Pacific Walrus Abundance and Demographic Rates from Genetic Mark-Recapture



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**US Department of the Interior
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Alaska OCS Region**



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ABOUT THE COVER

Pacific walrus hauled-out on sea ice in the Chukchi Sea. Photo credit U.S. Fish and Wildlife Service.

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1 Introduction

The Pacific walrus (*Odobenus rosmarus divergens*) ranges from the Chukchi Sea to the Bering Sea and utilizes sea ice for multiple life history events, including birthing, breeding, and resting (Fay 1985). Walrus follow the seasonal patterns of ice formation and retreat in the Pacific Arctic and sub-Arctic regions. In winter, Pacific walrus congregate in the Bering Sea and range from Bristol Bay, Alaska to Kamchatka, Russia (Fay 1982). In spring and summer, adult female and juvenile walrus follow the melting sea ice through the Bering Strait into the Chukchi Sea while adult males summer in the Bering Sea (Fay 1982). Adult females and juveniles gradually move south into the Bering Sea as ice forms in autumn and winter.

The northeast Chukchi Sea contains areas with high oil and gas resource potential, which are proximate to areas with high levels of walrus use (Jay et al. 2012). Consequently, the Bureau of Ocean Energy Management (BOEM) requires robust estimates of Pacific walrus abundance, survival, and reproduction to use in planning, management, and mitigation of potential environment impacts from oil and gas activities in the Chukchi Sea. Pacific walrus population abundance estimates have previously been derived from aerial surveys, which have resulted in imprecise estimates (Speckman et al. 2011). For example, an aerial survey conducted in 2006 estimated total population abundance as 129,000 individuals with a 95% confidence interval of 55,000 to 507,000 walrus (Speckman et al. 2011). In addition, demographic information on the walrus population has been limited to modeling of standing age structure data (Taylor and Udevitz 2015, Taylor et al. 2017). Consequently, an alternative approach is necessary to obtain more precise estimates of Pacific walrus abundance and new information on population demographics.

Genetic mark-recapture offers one alternative approach to estimating Pacific walrus abundance. Genetic mark-recapture uses multilocus genotypes to identify unique individuals and create capture histories that can be analyzed with standard mark-recapture methods (Palsbøll et al. 1997). One primary advantage of walrus genetic mark-recapture is that sampling requires only a small biopsy collected remotely with a crossbow. Thus, a large number of animals can be sampled and permanently marked over multiple years, which is not possible with traditional marking techniques that use physical tags.

In 2013, the U.S. Fish and Wildlife Service initiated a genetic mark-recapture project to estimate Pacific walrus abundance, survival, and reproductive rates. Based on a series of simulations, we identified sample size goals that could generate an abundance estimate with a coefficient of variation of 0.25 after the fifth year (i.e. 2017). We conducted successful cruises that met these overall sample size goals from 2013–2016. Consequently, the walrus genetic mark-recapture project was initially developed as a five-year project to evaluate the efficacy of a long-term monitoring program. In addition to the genetic mark-recapture project, the U.S. Fish and Wildlife Service also conducted a Pacific walrus age structure survey in 2016. Data from age structure surveys have been used in numerous peer-reviewed manuscripts (Taylor and Udevitz 2015, Taylor et al. 2017), and age structure surveys currently represent the best available method to collect demographic information on the Pacific walrus. The overall objectives of this study were to (a) estimate walrus population abundance using genetic mark-recapture, (b) estimate walrus survival and reproductive rates. Specifically, the objectives for our sampling in 2017 were (a) collect additional biopsy samples for the walrus genetic mark-recapture project to

increase sample sizes and precision of parameter estimates (b) collect a sample of the standing age structure.

2 Methods

We collected tissue samples from walrus throughout the Bering and Chukchi seas during research cruises in June of each year from 2013–2017 (Figure 1, Figure 2, Figure 3, Figure 4, Figure 5). We navigated the research vessel to areas that were known to be important walrus use areas. Consequently, our sampling throughout the duration of the project was opportunistic.

We approached groups of walrus hauled out on sea ice in small skiffs and collected tissue samples with crossbows and darts outfitted with a removable biopsy tip. We assigned each sampled individual to one of seven age classes (calf, 1 year old, 2 year old, 3 year old, 4 to 5 year old, ≥ 6 years old, unknown) based on the width and/or depth of the snout compared to the length of the tusks (Citta et al. 2014). Tissue samples were processed in the Conservation Genetics Laboratory at the U.S. Fish and Wildlife Service, Region 7. Multilocus genotypes for each sample were constructed with a suite of 114 biallelic single nucleotide polymorphisms, and samples were matched with an approach that accounted for genotyping error (Sethi et al. 2016).

We conducted age structure surveys from the bridge of the ship with at least four observers. Observers classified every member of every group hauled-out on sea ice based on the methods described in Citta et al. (2014). If the group entered the water before all members could be classified, the group was not considered in the final sample. We defined a “group” as one or more animals on ice separated by less than one walrus body length.

2.1 Statistical Analyses

Cormack-Jolly-Seber (CJS) models were developed to estimate survival (ϕ) of wild populations with mark-recapture data (Cormack 1964, Jolly 1965, Seber 1965). Survival estimates from CJS-type models are typically termed “apparent survival” because permanent emigration from the study area and mortality are confounded in a classical CJS model (Williams et al. 2001). However, CJS models also estimate the probability that a previously marked animal is recaptured (i.e. recapture probability). We used the estimated probability of recapture (p) from a CJS model to estimate walrus population abundance with a Horvitz-Thompson-type estimator (Horvitz and Thompson 1952). The Horvitz-Thompson estimator requires capture histories for individual animals and an estimate of (re)capture probability to estimate population abundance (McDonald and Amstrup 2001).

Although walrus were assigned to one of six age classes in the field, previous research has demonstrated that juveniles and adult females have similar survival rates whereas calves have substantially lower survival than juveniles and adult females (Taylor and Udevitz 2015). Thus, we retained calves as a separate age class (calf), but collapsed all juveniles and adult females into one age class (not calf). We removed all adult males and adults of unknown sex from the dataset, and estimated probability of recapture separately for each age class.

We formally estimated abundance of calves, juveniles, and adult females combined (N_I) with the formula (McDonald and Amstrup 2001):

$$N_1 = \sum_{i=1}^n \frac{I_{ik}}{\hat{p}_k}$$

where n is the total number of animals captured throughout the study, I_{ik} is an indicator variable where a 1 represents capture and a 0 represents no capture for individual i in age class k , and \hat{p}_k represents the estimated probability of recapture for age class k .

We used information from vessel based age structure surveys conducted from 2013–2017 (Citta et al. 2014, this study) to estimate the proportion of N_1 that was comprised of adult females (p_F). To estimate total population abundance (including adult males), we assumed a 1:1 ratio of adult females to adult males (Fay 1982) and then multiplied the proportion of the modeled population comprised of adult females (p_F) by the abundance estimate for calves, juveniles, and adult females (N_1). We then summed this quantity with N_1 for a total population estimate:

$$N = N_1 + (p_F N_1)$$

Although previous research indicates the sex ratio of breeding age adults is approximately 1 male to 3 females (Fay 1982), female walruses mature at a much younger age (6 years) (Fay 1982) compared to male walruses (10–15 years) (Fay 1982). Consequently, the overall sex ratio of adult walruses (≥ 6 years old) is likely 1:1 (Fay 1982).

We used a Bayesian state-space formulation of the CJS model due to its flexibility (Royle 2008). We set the proportion of the modeled population comprised of adult females as $p_F \sim \text{Uniform}(0.45, 0.59)$ to incorporate sampling error from age structure surveys. We used uniform priors for probability of recapture [$p_k \sim \text{Uniform}(0, 1)$] and apparent survival [$\phi_k \sim \text{Uniform}(0, 1)$] and ran three chains with a burnin and adaptation of 55000 iterations. We drew 12000 samples from the posterior distribution (3 chains; 100000 MCMC iterations; thinning of 25). We ran all analyses in Just Another Gibbs Sampler (JAGS) (Plummer 2013) with the runjags package (Denwood 2016) in R (R Core Team 2016).

3 Results

We collected 2156 tissue samples comprising 1878 unique walruses for genetic mark-recapture dataset in 2017. In addition, we sampled 3426 individual walruses for the age structure survey in 2017. In 2017, the age structure of the population was as follows: 18% calf, 33% juveniles, and 50% adult females.

In total, we collected 9354 tissue samples on research cruises from 2013–2017. We identified 8303 unique walrus with the sample matching algorithm that identified within and among year recapture events. We observed relatively high within-year recapture rates, ranging from 6% to 9%. Although genotypes and recapture information are available for all samples collected throughout the five-year project, we only report results from 2013–2015 here. The addition of data from 2016–2017 did not substantially improve the precision of the abundance estimate due to the low empirical recapture rates. Consequently, we present a previously published abundance estimate here and an updated abundance estimate with 2016–2017 is not included in this report.

After genotype matching and removing all adult males and adults of unknown sex, 4,313 walrus were sampled from 2013–2015. CJS model results indicated the posterior mean for calf survival was 0.182 (95% Credible Intervals <0.001–0.749), and the posterior mean for calf recapture probability was 0.197 (95% CrI: <0.001–0.785). The posterior mean for juvenile and adult survival was 0.733 (95% Credible Intervals 0.414–1.000), and the posterior mean for juvenile and adult recapture probability was 0.010 (95% CrI: 0.004–0.019). The posterior mean for abundance of calves, juveniles, and adult females was 186,366 individuals (95% CrI: 62,584–316,422; Coefficient of variation = 0.39; Figure 6), and the total estimated population size in 2014 was 283,213 (95% CrI: 93,000–478,975; Coefficient of variation = 0.39; Figure 7).

4 Discussion

Addition of 2017 data did not substantially improve recapture rates. Consequently, we only report preliminary results here from 2013–2015. Modeling mark-recapture data with low empirical recapture rates poses significant challenges. For example, low recapture rates could generate numerically non-identifiable models or numerically identifiable models with high levels of uncertainty in parameter estimates. Specifically, increased uncertainty in recapture probabilities would precipitate large, unrealistic fluctuations in walrus abundance year over year. Indeed, abundance estimates from Horvitz-Thompson estimators are sensitive to annual changes in recapture probability (Regehr et al. 2007).

Our abundance estimates should be interpreted with caution because several CJS model assumptions may be violated in the dataset. First, the model assumes that recapture probability within age classes does not vary (Williams et al. 2001). Although previous research has demonstrated that juveniles and adults exhibit different survival rates (Taylor and Udevitz 2015, Taylor et al. 2017), we collapsed adult and juvenile walrus into one age class due to our low recapture probability rates. Furthermore, additional variation in probability of recapture may exist among individuals, sexes, or age classes.

In addition, the model assumes that emigration from the study area is permanent (Williams et al. 2001), yet preliminary results from the study indicate emigration may be temporary. Survival estimates from this study are relatively low compared to other studies. For example, a recent study estimated annual calf survival as 0.73, juvenile survival as 0.84 (95% CrI: 0.74 to 0.94) and reproductive adult survival as 0.99 (95% CrI: 0.98 to 1.0) (Taylor et al. 2017). Consequently, the low survival estimates from this study may reflect temporary emigration from the study area (i.e. the apparent survival problem) rather than actual mortality. Furthermore, similar to probability of recapture, additional variation in survival may exist among individuals, sexes, and ages. However, the limited number of recaptures precluded accounting for heterogeneity in apparent survival and recapture probability among ages, individuals, and sexes. Consequently, total abundance estimates are likely biased high due to heterogeneity in recapture probability among age classes, temporary emigration from the study area, and other factors such as sampling design (Royle 2008).

In 2006, biologists from the Russian Federation and the U.S. conducted an aerial survey of the Pacific walrus population with thermal imagery. The survey improved on previous designs, and estimated the total walrus population size as 128,806 individuals with 95% confidence intervals of 54,934 to 507,104 (Speckman et al. 2011). The high coefficient of variation for the abundance estimate was attributed to the heterogeneous distribution of walrus

throughout the study area, and a full accounting of the variance associated with estimating the number of animals in water during the survey. Consequently, the estimate from the 2006 aerial survey is biased low (Speckman et al. 2011) whereas our estimated is likely biased high.

Alaska Native walrus hunters joined us on all five research cruises, and one particular hunter from the village of Gambell on St. Lawrence Island participated every year. Alaska Native hunters shared their experience approaching walruses, reading sea ice conditions, interpreting walrus behavior and significantly contributed to the success of the field portion of the project. In addition, Alaska Native hunters facilitated improved communication and collaboration between managers and local villages.

5 Future Directions

The Pacific walrus genetic mark-recapture project was initially designed as a five-year study to evaluate the efficacy of a long-term monitoring program. We did not conduct a research cruise in 2018 or 2019, and we aim to address several questions before conducting the next research cruise to increase efficiency and decrease costs.

The first product that uses all five years of data from the project will address study design and sampling. The manuscript will (1) examine broad-scale walrus genetic structure with both spatially explicit and spatially naïve approaches and (2) evaluate kin structure of walrus groups hauled-out on sea ice. Consequently, the overall goal of the paper is to address the concern that walruses sampled from the same group do not represent independent samples from the perspective of reproductive rates and survival (Figure 8, Figure 9, Figure 10). We anticipate this paper will be published in early 2020.

We are also collaborating with geneticists from the U.S. Geological Survey Alaska Science Center to develop an epigenetic aging tool for Pacific walruses. In the genetic mark-recapture project, field personnel estimated age class of each sampled animal based on the length of the tusks relatively to the wide of the snout (Citta et al. 2014). Preliminary results indicate a high discordance rate in age classes in recaptured animals, indicating a high level of observer error using this method. Furthermore, walruses can live up to 40 years in the wild (Fay 1982), and the tusk aging approach provides limited to no resolution in adult age classes. Consequently, the second product that will come from this project is a Pacific walrus epigenetic aging assay that we anticipate will provide ± 3 years of resolution for adult animals with higher levels of precision for younger animals.

The Pacific walrus epigenetic age assay will be utilized in an integrated population model that uses multiple data sources to estimate survival and abundance. In addition to the mark-recapture dataset, we also have annual samples of the standing age structure from 2013–2017 from shipboard surveys. We are currently developing a maximum likelihood estimator that will combine these two data sources to generate estimates of Pacific walrus abundance, survival, and reproductive rates with increased precision.

In addition to the integrated population model, we are also exploring a new technique called close-kin mark-recapture (CKMR). CKMR incorporates additional information in the form of kinship relationships among individuals in a sample (Bravington et al. 2016a, b). In CKMR all individuals are compared to one another and assigned a kinship category, which could take on one of a discrete set of values such as parent-offspring, unrelated, or self. Thus, a self kinship assignment is a recapture in the traditional mark-recapture framework. In CKMR,

however, parent-offspring is also a type of recapture, and contributes important information to the analysis. Consequently, CKMR has the potential to improve precision of abundance and demographic rate estimates, compared to traditional mark-recapture methods. Age information is essential for precise CKMR estimates because it identifies the time of “marking”, which is the year the sampled animal was born. For example, accurate age information could reduce the number of pairwise comparisons conducted to identify parent-offspring pairs (Jarman et al. 2015). In addition, accurate and precise age information allows CKMR and traditional mark-recapture models to examine additional demographic parameters such as age-at-maturity, age-specific survival, and age-specific reproductive rates (Bravington et al. 2016*a, b*)



Figure 1. Walrus research cruise tracks from 2013

Walrus research cruise tracks from 2013. The cruise was conducted from the *RV Norseman II*.



Figure 2. Walrus cruise tracks 2014

Walrus research cruise tracks from 2014. The cruise was conducted from the *RV Norseman II*.



Figure 3. Walrus cruise tracks 2015

Walrus research cruise tracks from 2015. The cruise was conducted from the *RV Professor Multanovskiy*.



Figure 4. Walrus cruise tracks 2016

Walrus research cruise tracks from 2016. The cruise was conducted from the *RV Professor Multanovskiy*.



Figure 5. Walrus cruise tracks 2017

Walrus research cruise tracks from 2017. The cruise was conducted from the *RV Professor Multanovskiy*.

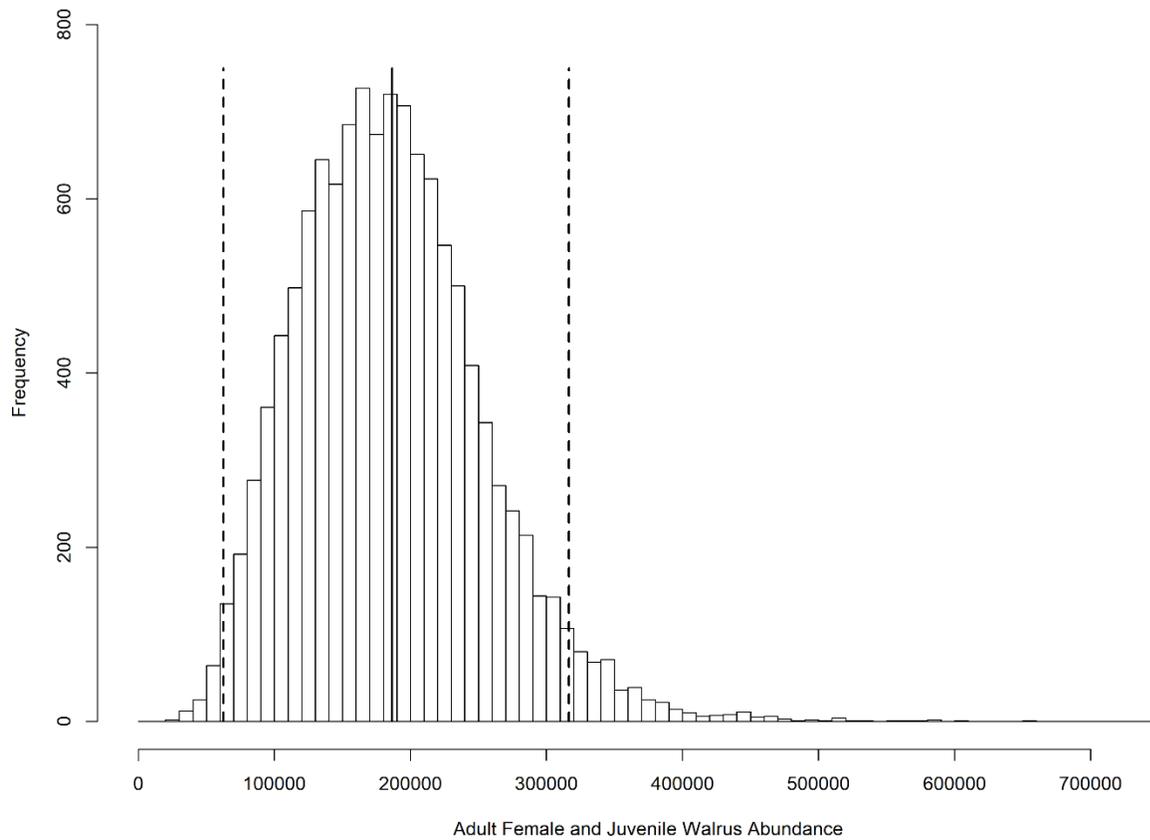


Figure 6. Adult female and juvenile walrus abundance

Posterior distribution for adult female and juvenile walrus abundance. The posterior mean is denoted with a solid line and 95% credible intervals are denoted with dashed lines.

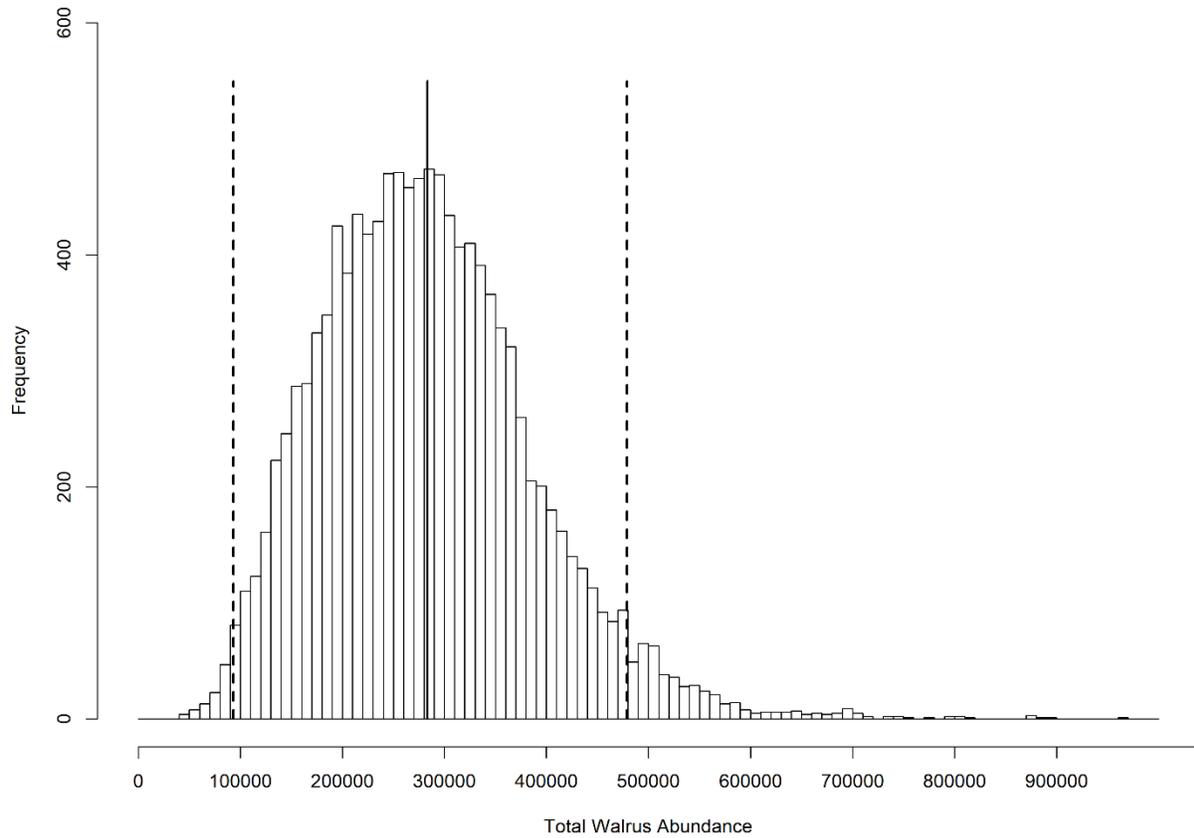


Figure 7. Total walrus abundance

Posterior distribution for total walrus abundance. The posterior mean is denoted with a solid line and 95% credible intervals are denoted with dashed lines.



Figure 8. Several walrus groups on sea ice.
Photo credit: U.S. Fish and Wildlife Service.



Figure 9. Walrus adult female and calf
Photo credit: U.S. Fish and Wildlife Service.

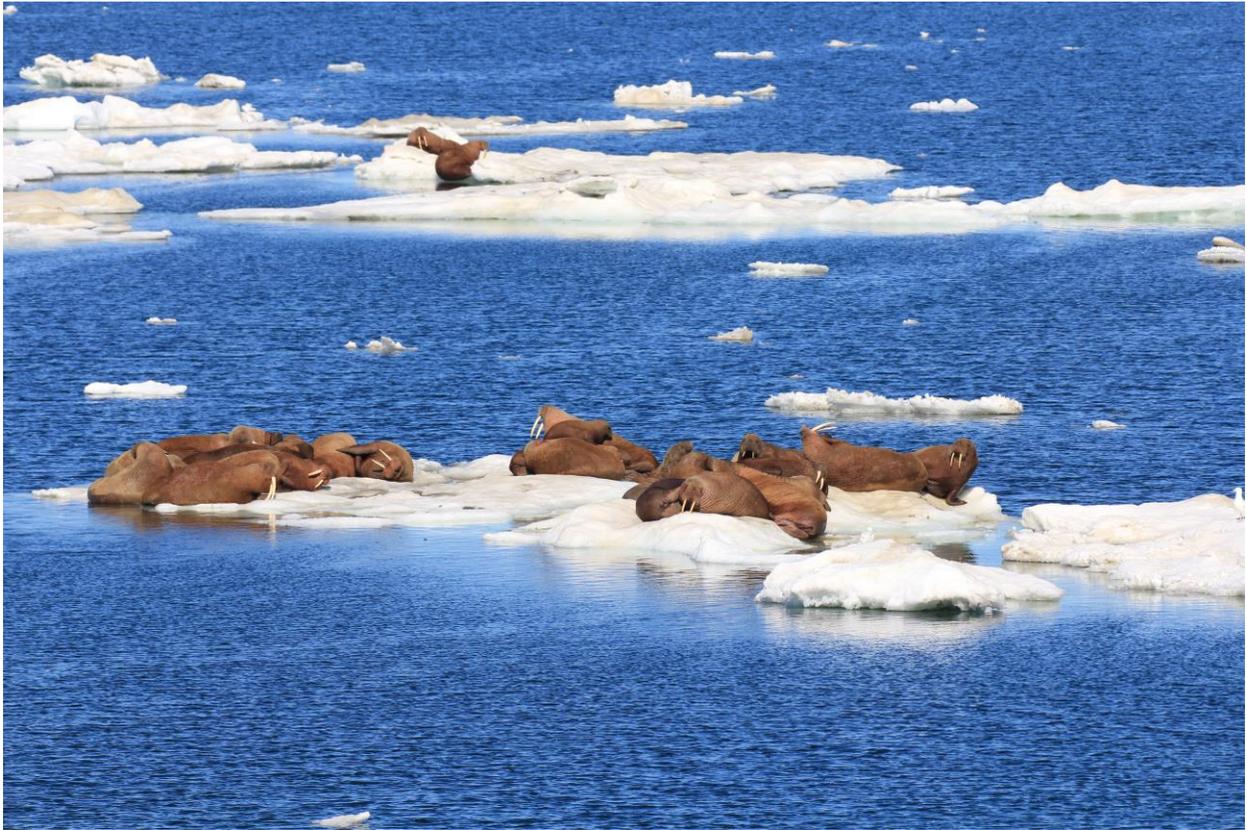


Figure 10. Several walrus groups on sea ice
Photo credit: U.S. Fish and Wildlife Service.

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