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Results and evaluation of a survey to estimate Pacific walrus population size, 2006[1]

SUZANN G. SPECKMAN
U.S. Fish and Wildlife Service,
Marine Mammals Management,
1011 E. Tudor Road,
Anchorage, Alaska 99503, U.S.A.
E-mail: suzann_speckman@fws.gov

VLADIMIR I. CHERNOOK
Giprorybflot, Research and Engineering Institute for
the Development and Operation of Fisheries,
18-20 Malaya Morskaya Street,
St. Petersburg 190000, Russia

DOUGLAS M. BURN
U.S. Fish and Wildlife Service,
Marine Mammals Management,
1011 E. Tudor Road,
Anchorage, Alaska 99503, U.S.A.

MARK S. UDEVITZ
U.S. Geological Survey,
Alaska Science Center,
4210 University Drive,
Anchorage, Alaska 99508, U.S.A.

ANATOLY A. KOCHNEV
ChukotTINRO, Pacific Research Institute of Fisheries
and Oceanography, Laboratory of Marine Mammals Study,
P. O. Box 29, Anadyr, Chukotka 689000, Russia

ALEXANDER VASILEV
Giprorybflot, Research and Engineering Institute
for the Development and Operation of Fisheries,
18-20 Malaya Morskaya Street,
St. Petersburg 190000, Russia

CHADWICK V. JAY
U.S. Geological Survey,
Alaska Science Center,
4210 University Drive,
Anchorage, Alaska 99508, U.S.A.

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ALEXANDER LISOVSKY
Giprorybflot, Research and Engineering Institute
for the Development and Operation of Fisheries,
18-20 Malaya Morskaya Street,
St. Petersburg 190000, Russia

ANTHONY S. FISCHBACH
U.S. Geological Survey,
Alaska Science Center,
4210 University Drive,
Anchorage, Alaska 99508, U.S.A.

R. BRADLEY BENTER
U.S. Fish and Wildlife Service,
Marine Mammals Management,
1011 E. Tudor Road,
Anchorage, Alaska 99503, U.S.A.

ABSTRACT

In spring 2006, we conducted a collaborative U.S.–Russia survey to estimate abundance of the Pacific walrus (*Odobenus rosmarus divergens*). The Bering Sea was partitioned into survey blocks, and a systematic random sample of transects within a subset of the blocks was surveyed with airborne thermal scanners using standard strip-transect methodology. Counts of walruses in photographed groups were used to model the relation between thermal signatures and the number of walruses in groups, which was used to estimate the number of walruses in groups that were detected by the scanner but not photographed. We also modeled the probability of thermally detecting various-sized walrus groups to estimate the number of walruses in groups undetected by the scanner. We used data from radio-tagged walruses to adjust on-ice estimates to account for walruses in the water during the survey. The estimated area of available habitat averaged 668,000 km^2 and the area of surveyed blocks was 318,204 km^2. The number of Pacific walruses within the surveyed area was estimated at 129,000 with 95% confidence limits of 55,000–507,000 individuals. Poor weather conditions precluded surveying in other areas; therefore, this value represents the number of Pacific walruses within about half of potential walrus habitat.

Key words: Pacific walrus, *Odobenus rosmarus divergens*, thermal imagery, population estimate, abundance, distribution, aerial survey.

The Pacific walrus (*Odobenus rosmarus divergens*) is an important ecological component of the Bering and Chukchi seas, and an irreplaceable cultural and economic resource for the Native peoples who reside in this region (Fay *et al*. 1997). Pacific walruses inhabit sea ice habitats and terrestrial haul-outs in the Russian Federation (Russia) and the United States of America (U.S.), and management of this species is therefore an international responsibility. In both countries, regulations governing the conservation and management of marine mammals recognize the important role that marine mammals play in marine ecosystems, and provide for subsistence harvest for the needs of Native peoples. With Russian and U.S. management mandates as framework for decision-making, the U.S. Fish and Wildlife Service (USFWS), U.S. Geological Survey (USGS), and the Russian institutes Research and Engineering Institute for the Development and Operation of the Fishing Fleet (Giprorybflot) and Pacific Research Center for Fisheries Management, Chukotka branch (Chukot-TINRO), collaborated to complete a survey of the Pacific walrus in spring 2006. The goal of the 2006 Pacific walrus survey was to estimate population size with enough precision to track future trends in abundance.

Historical trends in Pacific walrus abundance can only be conjectured due to incomplete data and lack of precision of population estimates from previous surveys. Based on large, sustained harvests in the 19th and 20th centuries (Fay 1957), Fay (1982) speculated that a minimum of 200,000 walruses were present prior to commercial hunting. Since that time, population size is believed to have fluctuated markedly in response to varying levels of human exploitation (Fay *et al.* 1989). Large-scale commercial harvests reduced the population to an estimated 50,000 to 100,000 animals in the mid-1950s (Fedoseev 1962, Fay *et al.* 1997). The population is believed to have increased rapidly in size from the 1950s to the early 1970s in response to reductions in commercial hunting pressure (Gol'tsev 1976, Fay *et al.* 1989). Evidence to support a population increase included range expansion back into areas with traditional haul-outs that had been unoccupied for many decades (Gol'tsev 1972, Pinigin and Prianishnikov 1975, Fedoseev 1982, Estes and Gol'tsev 1984, Fay *et al.* 1986). Researchers concluded that the Pacific walrus population approached or exceeded the carrying capacity of its environment in the late 1970s or early 1980s, based on changes in physical condition of walruses (Fay and Kelly 1980, Sease 1986, Fay *et al.* 1989) and decreased productivity (Sease 1986, Fay *et al.* 1989, Fay *et al.* 1997, Garlich-Miller *et al.* 2006).

In the 1980s, researchers began predicting that Pacific walrus abundance would decline in the future because of the density-dependent negative impacts of exceeding carrying capacity (Fay and Stoker 1982*b*, Fay *et al.* 1986, Sease 1986, Fay *et al.* 1989). However, no time series of estimates of Pacific walrus population size exists that could be used to assess trends in walrus abundance during this time period. Between 1975 and 1990, cooperative contemporaneous visual aerial surveys were carried out by the U.S. and the former Soviet Union to estimate Pacific walrus population size across its range. Fall surveys were conducted at 5 yr intervals, producing population estimates ranging from about 200,000 to 300,000 individuals (see reviews: Hills and Gilbert 1994, Gilbert 1999). Observers used visual methods to count or estimate numbers of walruses hauled out on pack ice and counts from photographs to estimate numbers on land, but could not accurately detect or enumerate walruses that were swimming in the water. Surveyed areas included all known terrestrial haul-out sites, but were limited to an unknown but very small percentage of available sea ice habitats. The proportion of the targeted ice habitat sampled in any one day did not exceed approximately 7% (Gilbert 1999). Efforts to survey the Pacific walrus population were suspended by both countries after 1990 due to unresolved problems with survey methods that produced population estimates with unknown bias and unknown, but presumably large, variances that severely limited their utility (Gilbert *et al.* 1992, Gilbert 1999, Udevitz *et al.* 2001). In Russia, fall aerial surveys of walruses at terrestrial haul-outs and on ice in the Chukchi Sea were suspended after 1990 for political and economic reasons as well. The population estimates generated from these surveys are considered minimum values that cannot be used for detecting trends in population size (Gilbert *et al.* 1992, Hills and Gilbert 1994).

Growing need for information on Pacific walrus population size prompted the USFWS and USGS to host an international workshop on walrus survey methods in the year 2000. Participants concluded that it would not be possible to obtain a population estimate with adequate precision for tracking trends using the existing visual methodology and any feasible amount of survey effort (Garlich-Miller and Jay 2000). They recommended investing in research on walrus distribution and haul-out patterns, and exploring new survey tools, including remote sensing systems and development of satellite transmitters, prior to conducting another aerial survey. Remote sensing systems were viewed as having great potential to address many of the shortcomings of visual aerial surveys by sampling larger areas per unit of time (Garlich-Miller and Jay 2000), objectively detecting and quantifying walruses (Udevitz *et al*. 2008), and reducing observer error (Burn *et al*. 2006). Design of new satellite transmitters and attachment techniques was recommended as a way to develop a correction factor to adjust an on-ice estimate for walruses in the water and unavailable for detection during an aerial survey (Garlich-Miller and Jay 2000).

Five years of cooperative research and development in both the U.S. and Russia led to improvement of existing remote sensing technology, culminating in construction of thermal detector arrays in both countries with high spatial resolution and thermal sensitivity. Burn *et al*. (2006) successfully demonstrated that walrus groups can be detected at a variety of spatial resolutions and Udevitz *et al*. (2008) demonstrated that thermal imagery can be used to estimate numbers of walruses hauled out on ice within a specific region. Additional pilot surveys of walruses in 2005 made it clear that technology and expertise existed in both countries to make a range-wide survey of the Pacific walrus population using airborne thermal imagery practicable (Chernook *et al*. 2006*a*). Improvements in satellite transmitter design, functionality, and attachment methods from 2002 to 2006 resulted in the ability to measure haul-out status of tagged walruses and obtain data for estimating the proportion of the population hauled out during an aerial survey (Jay *et al*. 2006, Udevitz *et al*. 2009).

We conducted a bilateral Pacific walrus survey in spring 2006 using jointly developed study design and methods (Burn *et al*. 2006, Chernook *et al*. 2006*b*, Udevitz *et al*. 2008, Burn *et al*. 2009) to estimate the number of walruses hauled out on ice in the Bering Sea. We also used satellite-linked radio transmitters to collect information on haul-out status of individual walruses (Jay *et al*. 2006), which we used to develop a model of walrus haul-out behavior. We applied the model to aerial survey results to adjust for the estimated number of walruses in the water, yielding an estimate of the total number of Pacific walruses within the surveyed area in spring 2006. Finally, we assessed the results of our survey and made recommendations for future work.

Methods

Study Area

In late winter and early spring, Pacific walruses are found in the Bering Sea pack ice where open leads, polynyas, or thin ice allow access to water (Fay 1982, Fedoseev 1982). During this time of year, walruses do not generally use terrestrial haul-outs (Fay 1982). Pack ice in the Bering Sea is almost exclusively single-year ice that forms and melts annually (Fay 1974). Walruses use floating ice floes as substrate for birthing and nursing calves, resting, and for passive transport to new feeding areas. Although capable of diving to deeper depths, walruses usually feed in shallow waters of 100 m or less (Fay 1982, Fay and Burns 1988, Jay *et al*. 2001).

In April 2006, we sought to survey the extent of potential walrus habitat in the Bering Sea. For survey design purposes we defined this as the area covered by sea ice with water depth less than 200 m. To measure the size of the study area after the survey was completed, we refined this definition using two criteria: sea ice of sufficient thickness (30 cm or more) to support hauled out walruses, and water depth <200 m. The 200 m isobath was derived from a bathymetric map with horizontal resolution of 1–12 km (Smith and Sandwell 1997). Extent of sea ice was estimated from weekly sea ice charts available from the National Ice Center (NIC; (http://www.natice.noaa.gov/), which are produced from all available *in situ*, remote sensing and model data sources (NIC 2006). The charts identify sea ice forms and stages not evident through standardized processing of remote sensing sources, and are available as GIS polygons coded with World Meteorological Organization SIGRID ice classification codes specifying ice type, concentration, and stage of development (WMO 1989). We included any areas with ice of thickness greater than 30 cm (all SIGRID stage codes except 81, 82, and 84), and excluded ice-free areas (SIGRID concentration code 00) as well as areas with non-zero concentrations of thinner ice formation.

The study area extended south into regions of open water where ice coverage may have been very low, because walruses are known to haul-out on sparse ice if the floes can support their weight (USFWS and USGS unpublished data). Sea ice extent is dynamic, fluctuating with winds, currents, temperature, and other environmental conditions, and no sea ice habitat utilization model is currently available for the Pacific walrus. Estimates of the extent of potential walrus habitat and hence, extent of the study area, are therefore approximate. To the north, the study area extended to the Bering Strait (Fig. 1). In Russia, the southern boundary was just north of Karaginskiy Island. In the U.S., the study area extended southward to St. Matthew Island and into Bristol Bay, depending on ice conditions.

Survey Design

The estimation method used for the 2006 Pacific walrus population estimate is based on survey blocks (strata), which we defined as the contiguous area covered by one crew in a single day of surveying (Udevitz *et al.* 2008). Initial intent was that each block would be surveyed once. Before data collection began, north–south boundaries of blocks were defined by lines of latitude across ice-covered areas of the Bering Sea. East–west boundaries of blocks were determined after the survey was completed, based on the area covered each day.

Within each block, a systematic random sample of transects was surveyed with airborne thermal scanners using standard strip-transect survey methodology. Thermal (infrared) imagery of walruses hauled out on pack ice was the primary type of data collected. Walruses are generally warmer than the background environment of ice and snow, and groups of walruses hauled out on ice are therefore detectable with thermal imagery, whereas walruses in water cannot be detected (Chernook *et al.* 1995, 1999; Burn *et al.* 2006). The amount of heat produced, or thermal signature, was determined for each walrus group that was detected by a thermal scanner. Infrared radiation cannot penetrate cloud cover or fog, and therefore thermal scanning could only take place during periods when skies were clear between the ice and the scanner aircraft. Pilot studies indicated that walrus groups are less likely to be thermally detected under very cold conditions (Burn *et al.* 2009). Therefore, we planned to conduct surveys only when the ambient air temperature was above −12°C (10°F),

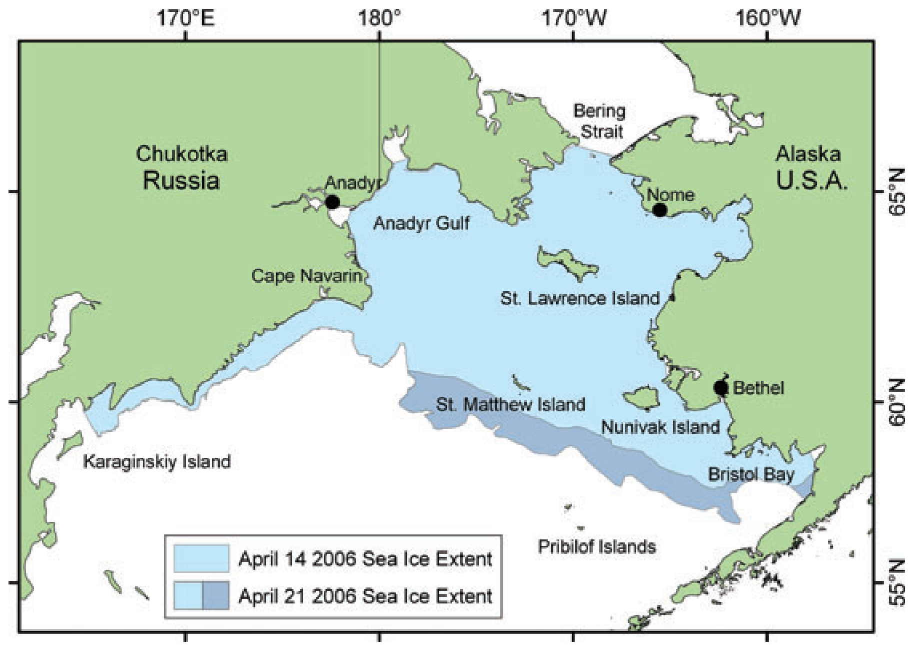

Figure 1. Important place names and targeted study area during the 2006 walrus survey, defined as sea ice of sufficient thickness (30 cm or more) to support hauled out walruses, and water depth <200 m. Approximate size of the study area was 676,000 km^2 on 14 April 2006 and 708,000 km^2 on 21 April 2006.

and the wind chill factor was above −18°C (0°F). If temperatures were cold, we planned to decrease the altitude to increase spatial resolution of the thermal imagery.

An independent set of walrus groups within thermally scanned areas was aerially photographed with high-resolution digital cameras. Counts of walruses in photographed groups were used to estimate the probability of thermally detecting walrus groups on the ice and to model the relationship between thermal signatures and the number of walruses in a group. Before the aerial survey began, 45 walruses to the south and southwest of St. Lawrence Island were tagged with satellite transmitters containing conductivity sensors, which recorded wet and dry intervals as a proxy for haul-out status. We combined the 2006 data on haul-out status with similar data from 2004 and 2005 to adjust the estimate of walrus numbers hauled out on ice to account for the proportion of walruses in the water and unavailable for detection by a thermal scanner. Together, these data provided a basis for estimating Pacific walrus population size within the surveyed area.

U.S. Data Collection

U.S. thermal imagery was collected from an Aero Commander 690B turbine twin-engine aircraft, which accommodated two pilots and two scientists. This aircraft was fitted with a thermal infrared (8.5–12.5 μm) scanner with a 0.625 milliradian instantaneous field of view. The system, built by Argon ST (Ann Arbor, MI) was equipped with a 3,000 pixel detector array and had 12-bit radiometric resolution, a 90° angle of view, and absolute sensitivity of 0.12°C. The system also included a position and orientation system to georeference the thermal imagery into the Universal Transverse Mercator (UTM) coordinate system (Applanix Corp., Richmond Hill, Ontario, Canada).

Thermal imagery data were viewed in real-time during survey flights and continuously written to a storage disk as the aircraft flew along transect lines within a survey block. Survey transects were oriented north–south and ranged in length from 60 to 225 km in length. Scanning of a transect produced a single "thermal image." Initial survey operations for the scanner aircraft were conducted at 6,400 m above ground level (AGL), producing imagery with 4 m pixel size. On 19 April, surveys were conducted at both 6,400 m and 3,200 m AGL to collect imagery with both 4 m and 2 m pixel sizes, which correspond to 12 km and 6 km wide strip widths, respectively. Survey operations on 21 and 22 April were also conducted at 3,200 m AGL. Transects were spaced with 24 km between strips in the 6,400 m surveys and with 12 km between strips in the 3,200 m surveys.

We photographed as many walrus groups as possible within the area covered by the thermal scanner within 1 h of scanning, to minimize the effect of changes in group size over time. Aerial photographs of walrus groups were taken from a second aircraft, an Aero Commander 680 twin-engine piston aircraft equipped with a vertical camera port, which accommodated two pilots and two scientists. When possible, the photography plane was directed to general areas with walrus groups by the thermal scanning aircraft crew, which reduced search time. All walrus groups seen were photographed in high-resolution with a digital single lens reflex Nikon D2X 12.4 megapixel camera, producing images with dimensions of 4,288 × 2,848 pixels. Photographs were taken from a nominal altitude of 700 m AGL using an image-stabilized 200 mm f2.8 Nikon camera lens and 1.4 × Nikon teleconverter, giving an overall focal length of 280 mm. Walruses very rarely reacted to the aircraft at this flight altitude.

Aerial photographs were georeferenced with a Global Positioning System (GPS) unit, and aircraft position, altitude, and time were recorded as metadata for each photograph. The camera was connected to a notebook computer equipped with Nikon Capture software. The ability to review photos within seconds after collection greatly improved our efficiency, as we could quickly determine if a photo pass was successful and repeat the pass only if necessary. To increase the sample size for calibration and detection models, while transiting to and from survey transects, we opportunistically photographed and scanned supplemental walrus groups in "off-transect" areas, *i.e.*, areas outside of the 6 km or 12 km wide thermally scanned strips used for estimating population size per the survey design.

The final data set was comprised of walrus groups that were either thermally detected or photographed, or both. Some groups were thermally detected but not photographed because the photography plane flew relatively slowly and simply could not reach all thermally scanned areas. Groups that were photographed but not thermally detected were too small for detection under the existing conditions. Some walrus groups were both thermally detected and photographed.

Russian Data Collection

All Russian thermal imagery and photographic data were collected simultaneously from a single aircraft, a twin-engine Let L-410 specially equipped for scientific surveys. This aircraft accommodated two pilots and four scientists. Thermal imagery was collected with a Malakhit-M thermal scanner, which had an angle of view of 120°, radiometric resolution of 12 bits, and sensitivity of 0.1°C. The system had a 1.3 milliradian instantaneous field of view providing a resolution of 1.3 m at 1,000 m AGL, with a strip width of 3.4 km. Surveys were conducted below cloud cover at altitudes from 500 to 1,000 m AGL, yielding strip widths ranging from 1.7 to 3.4 km and resolution that ranged from 0.65 to 1.3 m. Transects were oriented from north to south and were usually spaced with 15.6 km between transect lines. On 18 and 24 April, when high walrus densities were encountered, we reduced the distance between transects to 7.8 km.

As the aircraft flew along transect lines within a survey block, thermal images were viewed in real-time by the scanner operator and data were temporarily stored in a buffer. When walruses were identified and verified by the scientific crew using thermal and/or visual observations, thermal data were written from the buffer to the storage disk. Unlike the U.S. thermal imagery that consisted of a single file for each transect, Russian data were collected as multiple sequential files for each transect. If we did not see any walruses, then thermal data for that area were not saved, which may have resulted in the loss of imagery that may have contained some small walrus groups.

Three high-resolution digital Nikon D70s cameras with focal length of 50 mm, producing images with dimensions of 3,008 × 2,000 pixels, were used to photograph walrus groups within the scanned area. Each camera had an angle of observation of 27° × 18°. Cameras were mounted on the aircraft so that one photographed directly below the aircraft, along the transect line, and the other two photographed the areas to either side, giving total coverage of about 80°. When walruses were detected, the thermal scanner operator began recording thermal scanner data and all three cameras began operating simultaneously. Each thermal image file and digital photograph included information on time, flight altitude, and location determined by a GPS. A fourth camera, a Nikon D70s with focal length of 18–200 mm, was used to manually photograph broader areas ($F = 18$ mm) when walrus groups were abundant, to record orientation among groups in relation to one another. We used this camera with the long focal-length lens ($F = 200$ mm) to obtain more detailed photos of walrus groups. Thermal images, photographs, and visual observations were collected synchronously, which provided accurate registration of all data. This synchronous collection of imagery and photographs did not provide the level of independence achieved for the U.S. data, but this independence was not required here because we did not use the Russian data for estimating detection probabilities. Collection of thermal imagery and photography was automated using custom-designed computer software. Data collection was coordinated by providing the entire scientific team with radio communication, which was recorded so that visual observations could be integrated with other data types. We collected supplemental thermal images and photographs of off-transect walrus groups to increase sample size for calibration.

Data Processing

Thermal imagery—Although the U.S. and Russian teams processed their data using different software tools, the processing techniques themselves were parallel, yielding comparable results. U.S. thermal infrared imagery was imported using a custom software application developed by Argon ST (Ann Arbor, MI). This program integrated the thermal data and position information to create georeferenced thermal images in the UTM coordinate system. ERDAS Imagine (Leica Geosystems, Atlanta, GA) software was used for initial data visualization and export to ASCII format. Sensor artifacts (*i.e.*, temperature values that were impossibly high or low) were recoded to missing values before the data were processed (Burn *et al.* 2006, Burn *et al.* 2009). The same procedures were used for processing both the 2 and 4 m resolution thermal images (Burn *et al.* 2009), which were then used to identify walrus groups (Burn *et al.* 2006). A walrus group was considered distinct from other groups if its corresponding thermal signature was separated by one or more pixels (2–4 m, depending on resolution) from thermal signatures of other groups. Geo-referencing made it possible to overlay each photograph on its corresponding thermal image so that each walrus group could be matched with its thermal signature (see Burn *et al.* 2006, Burn *et al.* 2009 for examples). The unique patterns and features of the ice in the background, visible in both the photographs and thermal images, assisted in making final matches.

Russian thermal imagery was processed by a multifunctional program that was developed specifically for viewing and processing thermal imagery data files (Giprorybflot, St. Petersburg, Russia). This program allowed for the correction of geometric and temperature distortion of thermal images, and enabled selection and attachment of positional coordinates to groups of walruses and subsequent export of corrected data to the software package Surfer (Golden Software, Golden, CO), which was used to calculate the thermal index. Data were processed separately for each group of walruses and exported into Surfer as a GRID file in ASCII format with absolute temperature units. Walrus groups were considered separate from neighboring groups if they were separated by a distance of more than 3–4 m.

Counting walruses in photographed groups in U.S. and Russian data—The number of walruses in each photographed group was counted using ERDAS Imagine software. Each photographed walrus group was counted three times by the same analyst (U.S. data) or three different analysts (Russian data), who marked each walrus with a uniquely colored symbol. If the three counts were not identical, the symbols for all three counts were simultaneously displayed and a fourth count was made to rectify differences. To ensure that groups of walruses in photographs reflected the same groups that were recorded by the thermal scanner, only walruses hauled out completely on the surface of an ice floe were counted. Counting error for photographs was assumed to be unbiased and small relative to other sources of variation.

Detecting walrus groups in U.S. data—The procedure for detecting walrus groups in U.S. thermal imagery data is summarized here and reported in more detail in Burn *et al.* (2009). Each thermal image (one transect line) was subdivided into a series of 200×200 pixel "tiles," which covered an area 800 m on a side in 4 m imagery, and 400 m on a side in 2 m imagery. The temperature value for each pixel was rounded to the nearest 0.1°C to create a temperature histogram for the pixels in each tile.

We calculated three statistics to represent characteristics of walrus signatures from the temperature histogram for each tile. Tiles that exhibited extreme values for one or more of these characteristics were examined further to determine if walrus signatures were present: (1) maximum temperature; (2) length of right-hand tail, calculated as the difference between the maximum temperature and the warmest histogram bin with a frequency of 10 or more pixels; and (3) maximum gap between histogram values (Burn *et al.* 2009). Temperatures near maximum for a tile are characteristic of thermal signatures of walrus groups because walruses are typically the warmest objects in their immediate environment. Long right-hand tails and large gaps in the temperature histograms are also characteristics of walrus thermal signatures because walruses are relatively rare features, typically present in less than 0.1% of the pixels in a tile (Burn *et al.* 2009). Lower threshold values for each of these three parameters were determined based on tiles that contained photographed walrus groups.

Tiles with no parameters that exceeded their threshold values were eliminated from further consideration at this point. Data for remaining tiles were examined in detail for the spatial arrangement of the warmest pixels and their degree of contrast with adjacent pixels. Tiles with "false positive" signatures that corresponded to features such as open leads and rock faces along the shoreline could be eliminated easily based on visual inspection of the images. Walrus groups are typically located on thicker ice floes that register colder temperatures and therefore tend to be represented by pixels that have a high degree of contrast with adjacent pixels. These characteristics were used to identify which of the remaining tiles contained pixels that corresponded to walrus groups (Burn *et al.* 2009).

Detecting walrus groups in Russian data—Initial recognition of walrus groups in Russian thermal imagery was done in real-time aboard the survey aircraft. The low survey altitude allowed simultaneous thermal and photographic surveying, supplemented by visual observations. The high-resolution (1.3 m) of the thermal scanner made visual recognition of walrus thermal signatures possible during the flight. Only sections of the transect lines with thermal signatures were recorded. These recorded thermal images were later examined more closely using a method similar to that described in Burn *et al.* (2006) for final detection of walrus groups. We constructed temperature histograms for each section of a thermal image as described earlier. The point at which the bars of the temperature histogram rapidly decreased from thousands of elements to less than ten elements defined the threshold temperature value. Any pixels with a temperature higher than the threshold value were considered occupied by walruses.

Calculating walrus thermal index values—Once a walrus group was identified in the U.S. data, the appropriate pixels needed to be assigned to the group. Edges of walrus groups were not always distinct, given the averaging of temperatures over 2–4 m intervals in these data. Determination of which pixels belonged to each detected walrus group was accomplished with a disjoint cluster analysis relative to pixel locations within the tile (row and column coordinates) and temperatures (Burn *et al.* 2009). This procedure assigned each pixel to one of 10 clusters by minimizing Euclidian distances, relative to these three normalized variables, among pixels in the same cluster (Anderberg 1973). By definition, the warmest cluster in a tile was always included as part of a group. However, in some cases, walrus groups consisted of more than one contiguous cluster. Clusters were ranked by their mean temperatures. Additional clusters were added to walrus groups until a cluster was more similar to the next coldest cluster (background) than it was to the next warmest cluster (previously designated as a walrus group). The temperature value for each pixel in a walrus group was standardized by subtracting the modal temperature for all non-walrus pixels in the tile. A thermal index was then calculated for each walrus group in the U.S. data as the sum of these standardized temperatures. Using the modal temperature of each tile to standardize relative to the local ambient temperature reduced overall variability of the relation between the index and the number of walruses counted in a photographed group.

Calculating thermal index values for the Russian data was more straightforward, because the higher resolution of these data combined with real-time identification of groups allowed pixels to be assigned to each group directly from the temperature histograms. The thermal index for each walrus group was estimated as the average of three different thermal volume calculations using Surfer.

Estimating weather conditions—Walrus haul-out behavior varies with weather (Nikulin 1947, Fay and Ray 1968, Udevitz *et al*. 2009). Therefore, data on weather within each survey block at the time it was surveyed were required for the model used to estimate the proportion of the walrus population that was hauled out on ice during the survey. Estimates of air temperature at 2 m above sea level, and wind speed at 10 m above sea level, were obtained from the North American Regional Reanalysis (NARR) data set produced by the National Center for Environmental Prediction (Mesinger *et al*. 2006). This data set contained estimates at 3-h intervals (0300, 0600, . . . , 2400 Alaska Standard Time [AST]) for each point in an approximately 20 × 20 km grid covering the Bering Sea. The average weather conditions in each survey block were estimated for the day it was surveyed by taking the average of the values for all NARR points located within the block during the 12 h period from 0900 to 2100 AST on that day. Block R-900T/R-1000T/A-217T/A-219T did not contain any NARR points, so for this block, we took the average of all NARR points within 10 km of the block boundaries (seven NARR points).

Statistical Analysis

Estimating group detection probabilities—Logistic regression models (Hosmer and Lemeshow 2000) developed by Burn *et al*. (2009) were used to estimate probabilities of detecting walrus groups in the U.S. thermal imagery (Fig. 2). These models had the form

$$Y_i \sim \text{Bernoulli}(p_i),$$

where

$$\text{logit}(p_i) = \beta_0 + \beta_1 X_i,$$

Y_i is a binary variable indicating whether group i was detected or not, and X_i is the size of group i. Models were fit with maximum likelihood, using data for all photographed groups, including those photographed off-transect. Separate models were developed for 2 and 4 m resolution data (Fig. 2; Burn *et al*. 2009).

The Russian data included only one photograph of an undetected group, which was not sufficient for formally estimating a detection function. However, the undetected group consisted of just a single walrus. There was one additional photograph of a single walrus that was detected and there were six photographed groups of two walruses that were all detected. Thus, it is likely that almost all groups containing more than one walrus, as well as some individual walruses, were detected. Based on this, we assumed that the number of walruses undetected in the Russian thermal imagery was a negligible proportion of the population and did not attempt to account for them.

Calibrating thermal index values—Calibration models were developed to estimate the number of walruses in each group detected in thermal imagery based on its thermal index value. Models used for the U.S. data were negative binomial regression models (McCullagh and Nelder 1999) developed by Burn *et al*. (2009). These models

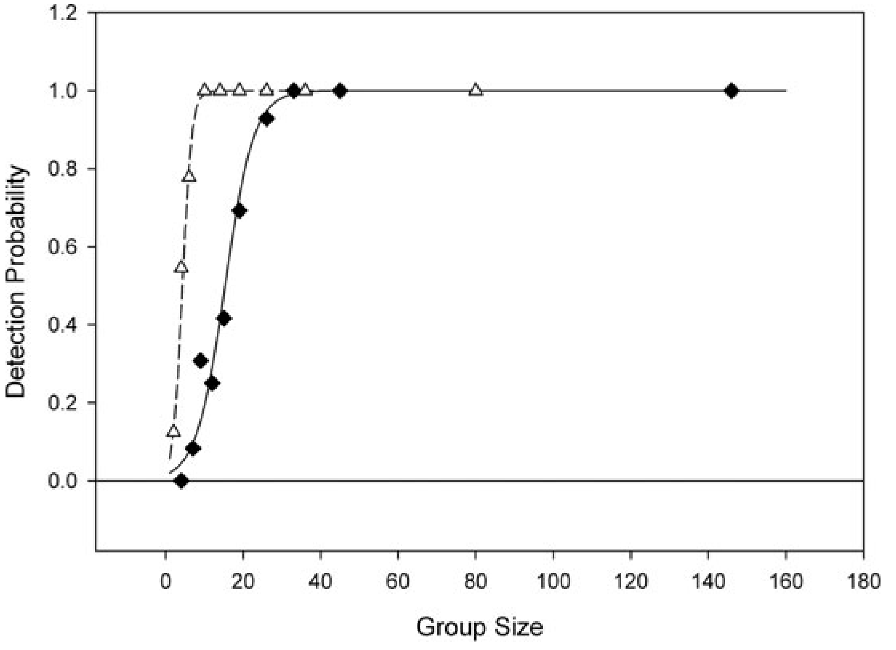

Figure 2. Estimated probabilities for detecting walrus groups in 2 m (dashed line) and 4 m (solid line) U.S. thermal imagery. Observed proportions of photographed groups detected are indicated by triangles (2 m imagery) and diamonds (4 m imagery). Adapted from Burn *et al.* (2009).

had the form

$$Y_i \sim \text{Negative Binomial}\,(\mu_i, k),$$

where Y_i is the size of group i,

$$\mu_i = E(Y_i) = \beta_0 + \beta_1 X_i,$$

X_i is the thermal index value for group i, and

$$\text{var}(Y_i) = \mu_i + k\mu_i^2.$$

Models were fit with maximum likelihood, using all observations of groups that were detected in thermal imagery, including those that were detected off transect. Separate models were developed for 2 and 4 m resolution data (Fig. 3B, C; Burn *et al.* 2009).

The same methodology was used to develop calibration models for the Russian data, using photographs of walrus groups that were detected in the Russian thermal imagery (Fig. 3A). As with the U.S. data, only observations of groups that were detected in thermal imagery were used because these models were conditional on groups being detected. Data for all thermally detected and photographed groups,

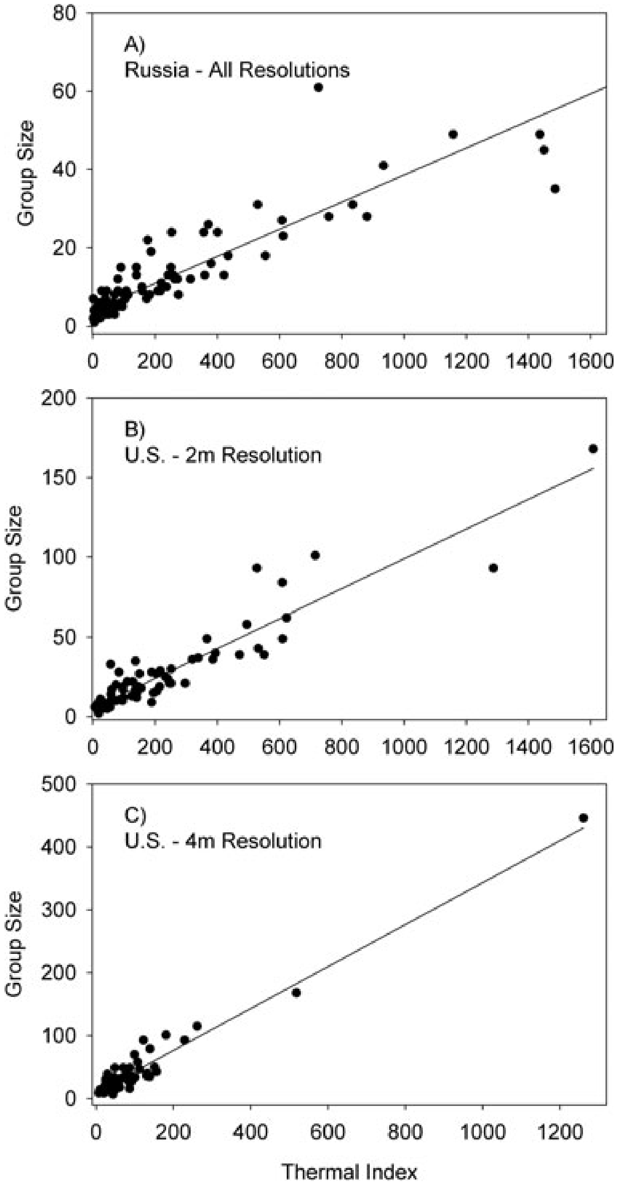

Figure 3. Final calibration models for walrus group size and thermal index values. (A) Russian data, all resolutions; (B) U.S. data at 2 m resolution; and (C) U.S. data at 4 m resolution. Panels B and C adapted from Burn *et al*. (2009).

including those photographed off transect, were used. Calibration functions were estimated using generalized linear models (McCullagh and Nelder 1999), with an identity link function and the same linear predictor as for the U.S. data (*i.e.*, the linear function of the thermal index, μ_i). Normal, Poisson, negative binomial, and gamma distributions were considered for fitting the error distribution. Models were fit with maximum likelihood. AIC (Burnham and Anderson 2002) was used to select the final calibration model and deviance and deviance residuals were used to assess the fit of this model to the data (McCullagh and Nelder 1999).

Estimating haul-out probabilities—We used data described in Udevitz *et al*. (2009) to develop a model for estimating the proportion of walruses in each block that was hauled out on the ice and therefore available to be detected by a thermal scanner during the survey. Udevitz *et al*. (2009) used satellite-linked transmitters to obtain sequential information about location and haul-out state for Pacific walruses in the Bering Sea during April of 2004, 2005, and 2006 ($n = 43$ walruses). The transmitters contained conductivity sensors that provided nearly continuous records of haul-out state for each tagged walrus (*i.e.*, whether the walrus was in water or hauled out on ice). Geographic locations associated with the observations of haul-out state were estimated, when possible, by the Argos location and data collection system (Argos 2007). Udevitz *et al*. (2009) used these data along with NARR weather data to develop a hierarchical Bayesian model that estimated the probability of a walrus being hauled out on the ice as a function of temperature, wind speed, and time of day (Fig. 4). Their approach required estimates of weather conditions associated with each individual observation of haul-out state, so they used imputation to estimate weather conditions associated with observations that could not be linked directly to NARR points based on an Argos determined location.

Here, we did not require estimates of haul-out probabilities for individual walruses, but rather, we required only estimates of the proportion of walruses hauled out in each block when it was surveyed. Therefore, we used a slightly different approach that modeled these proportions directly and did not require imputation. We used the same data on haul-out state of 43 walruses as Udevitz *et al*. (2009), except we only used observations corresponding to NARR time points with data for at least five walruses. This resulted in data for 496 time points, with observations of haul-out state from 5 to 26 walruses at each time point. We determined the proportion of the radio-tagged walruses that were hauled out on the ice at each of these time points. For each observation of haul-out state with an associated Argos location, the corresponding weather conditions were estimated from the NARR time point at the NARR grid point closest to the Argos location. Average weather conditions were estimated for each time point by taking the average of the values for all the NARR points associated with tagged walruses during the 12 h period centered on that time point. This 12 h period corresponded with the 12 h period used to estimate average weather conditions for survey blocks, and was also the shortest period that contained at least one Argos location for every time point.

These data were used in a hierarchical Bayesian model (Gelman *et al*. 1997) to estimate walrus haul-out proportions. The likelihood for this model was

$$Y_t \sim \text{Binomial}(p_t, n_t),$$

where

$$\text{logit}(p_t) = \beta_0 + \beta_1 X_{1t} + \beta_2 X_{2t} + \beta_3 X_{3t} + \beta_4 X_{4t} + \beta_5 p_{t-1} + \tau_t,$$

Y_t is the number of radio-tagged walruses hauled out on the ice at time t, n_t is the total number of tagged walruses at time t, X_{1t} and X_{2t} are indicator variables for time-of-day (corresponding to NARR time points with $X_{1t} = 1$ for 1800 AST,

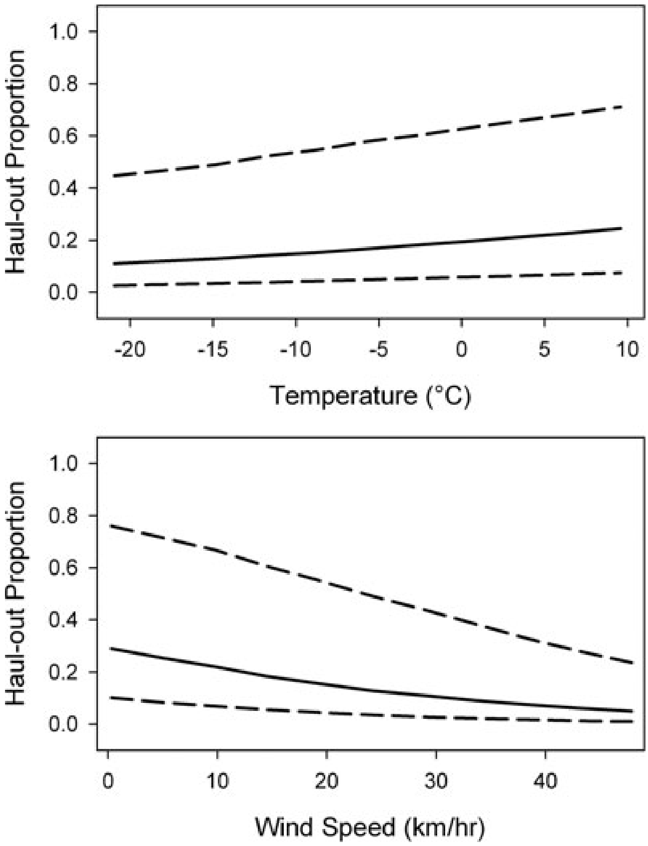

Figure 4. Estimated proportions of Pacific walruses hauled out on sea ice in April, as functions of temperature and wind speed. Plotted values are posterior means with 95% credibility intervals, at 1500 AST and the mean value of the other weather variable.

$X_{2t} = 1$ for 0900 or 1200 AST), X_{3t} is air temperature (°C at 2 m above sea level), and X_{4t} is wind speed (km/h at 10 m above sea level). These time-of-day and weather variables are the same as those included in the final haul-out probability model developed by Udevitz *et al.* (2009). τ_t is a random effect for time, with

$$\tau_i \sim \text{Normal}\left(0, \sigma_\tau^2\right).$$

p_{t-1} is analogous to the lag variable used by Udevitz *et al*. (2009) to account for serial autocorrelation in the data. Standard, non-informative prior distributions were used for all parameters.

Markov Chain Monte Carlo (MCMC) methods, implemented with WinBUGS software (Spiegelhalter *et al*. 2003), were used for estimation. To estimate haul-out proportions associated with survey blocks, data on tagged walruses were augmented by adding observations corresponding to the average weather conditions associated with those blocks and a time-of-day value of 1500 AST, which was the mid-point of the time period used to estimate average weather conditions. Values for p_{t-1} and

τ_t were randomly drawn from their distributions in the data at each iteration, so that the posterior predictive distributions (Gelman *et al*. 1997) of the proportions for each block reflected the variability associated with random rather than average time points with the given conditions. We used three separate MCMC chains, initialized with different starting values. Discarding the first 4,000 iterations from each chain, we used the last 4,000 for estimation. We assessed convergence by examining the trace for each parameter over the iterations within chains (Spiegelhalter *et al*. 2003), Gelman-Rubin statistics for comparisons among chains (Brooks and Gelman 1998), and the ratio of MCMC error to the posterior standard error for each parameter (Spiegelhalter *et al*. 2003). The final 4,000 iterations from each chain were combined to give 12,000 iterations for estimating posterior distributions of parameters and haul-out probabilities.

For comparison to the model-based estimates of haul-out probabilities, we also estimated the overall proportion of time walruses spent hauled out, based directly on the observed proportions for tagged walruses during the survey period. For this estimate, we used data from the same tagged walruses used in the model, except we only included data from walruses during the survey period of 3–23 April 2006 ($n = 26$ walruses) and only considered observations between 0900 and 2100 AST, corresponding to the daily time period used for estimating block haul-out proportions. Also, because these calculations did not require linkage to NARR time points, we used the complete, continuous haul-out record for each walrus, with an observation of haul-out state for each 30 min interval, rather than restricting consideration to the haul-out state at the NARR time points. We estimated the mean haul-out proportion with a ratio estimator (Thompson 2002), obtained by taking the total number of hauled out 30 min intervals (summed over walruses) divided by the total number of intervals being considered (also summed over walruses). We used a bootstrap procedure (Manly 1991) to estimate confidence limits for the mean proportion. A bootstrap sample estimate was obtained by sampling with replacement from the set of walruses under consideration to match the original sample size and then calculating a new ratio estimate of the mean from the haul-out records of the selected walruses. This was repeated to obtain 1,000 bootstrap sample estimates. Ninety-five percent confidence limits were then estimated by taking the 2.5 and 97.5 percentiles of the bootstrap sample estimates.

Estimating numbers of walruses—The basic approach developed for the pilot survey conducted by Udevitz *et al*. (2008) was used to estimate the total numbers of walruses on sea ice for both U.S. and Russian data. However, survey conditions encountered by Udevitz *et al*. (2008) likely resulted in a negligible number of undetected walruses hauled out on surveyed transects, and no attempt was made to account for them in that study. Also, Udevitz *et al*. (2008) only estimated numbers of walruses hauled out on the sea ice and made no attempt to account for walruses that were in the water and therefore not available to be detected during the survey. Here, we extended their approach to incorporate detection functions to account for hauled out walruses that were not detected on surveyed transects and to incorporate estimates of haul-out probabilities to account for walruses not available to be detected because they were in the water during the survey.

The calibration models were used to estimate the number of walruses in each group that was thermally detected on a survey transect, but not photographed. For thermally detected groups that were photographed, the group size was determined directly from the photographic count. The detection models were used to estimate the probability of thermally detecting a group as a function of its size. We used these estimated detection probabilities in Horvitz-Thompson estimators (Thompson 2002) of the number of hauled out walruses on each surveyed transect:

$$\hat{Y}_{tb} = \sum_{g=1}^{G_{tb}} \left(\frac{\hat{Y}_{gtb}}{\hat{d}_{gtb}} \right),$$

where $\hat{Y}_{gtb}$ is the group size and $\hat{d}_{gtb}$ is the estimated detection probability for the gth detected group, $g = 1, \ldots, G_{tb}$, on transect t in block b. For Russian transects, we assumed $\hat{d}_{gtb}$ 7 = 1.

The total number of walruses hauled out on sea ice in the surveyed blocks was estimated as a sum of separate ratio estimators (Thompson 2002) of the totals for each block:

$$\hat{N}^* = \sum_{b=1}^{B} \left(\hat{R}_b \sum_{t=1}^{T_b} A_{tb} \right) = \sum_{b=1}^{B} \hat{N}_b^*,$$

where

$$\hat{R}_b = \frac{\sum_{t=1}^{t_b} \hat{Y}_{tb}}{\sum_{t=1}^{t_b} A_{tb}}.$$

A_{tb} is the area of transect t in block b, T_b is the number of transects in block b, t_b is the number of surveyed transects in block b, and B is the number of blocks. To estimate the total number of walruses in the surveyed blocks, including those that were in the water during the survey, we used another Horvitz-Thompson type (Thompson 2002) extension to incorporate the estimated haul-out probabilities in this estimator, as

$$\hat{N} = \sum_{b=1}^{B} \frac{\hat{N}_b^*}{\hat{p}_b} = \sum_{b=1}^{B} \hat{N}_b,$$

where $\hat{p}_b$ is the estimated mean haul-out proportion for block b. For blocks that were surveyed more than once, the average of the estimated totals from the replicates was used in place of $\hat{N}_b^*$ or $\hat{N}_b$.

Udevitz *et al*. (2008) estimated variances and confidence intervals with a bootstrap procedure based on the general approach of Booth *et al*. (1994) for finite populations. The procedure involved generating a series of simulated populations, estimating statistics of interest by resampling from each simulated population, and then averaging these statistics over the simulated populations. We extended this approach to account for the additional components of variation due to estimation of the detection functions and the haul-out probabilities.

We generated simulated populations of transects (with associated walrus observations) for each block by first replicating the complete set of surveyed transects in the block as many times as possible without exceeding the total number of potential transects in the block. A random sample without replacement was then added from the surveyed transects to complete the population of potential transects. Bootstrap survey samples were obtained by drawing random samples without replacement from the simulated populations to give the same number of transects as in the original survey.

For each bootstrap survey sample, we also obtained a bootstrap sample of photographic counts for fitting the calibration and detection models. A bootstrap sample of photographed groups included all of the photographed groups in the bootstrap sample of surveyed transects if the number of those groups was less than or equal to the number on surveyed transects in the original sample. Otherwise, we sampled without replacement from the photographed groups in the bootstrap sample of transects to obtain the same number as in the original survey. We then completed the bootstrap sample of photographed groups by sampling with replacement from the original sample of groups photographed off survey transects to obtain the same total sample size (*i.e.*, number of groups photographed on transects plus number of groups photographed off transects) as in the original survey. This resampling strategy was designed to approximate the survey protocol which supplemented data from walrus groups photographed on survey transects with additional off-transect photographs. Finally, for each bootstrap survey sample, we also sampled with replacement from the posterior distributions of the mean haul-out probabilities for each block to obtain estimates of the block haul-out probabilities to use with that bootstrap sample.

Estimation for each bootstrap sample followed the same procedure as for the original sample. We obtained 100 bootstrap samples and associated estimates of population size for each simulated population and then calculated the standard error and 2.5 and 97.5 percentiles of those estimates. We repeated this process for 1,000 simulated populations and took the average of the standard errors and 2.5 and 97.5 percentiles as our estimates of standard errors and 95% confidence limits (Manly 1991) for the estimates from the original survey. We checked for convergence of estimates to ensure the numbers of bootstrap samples and simulated populations were sufficient.

The relative contributions of variance components were assessed by repeating the bootstrap procedure, without accounting for one or more of the components. First, we excluded the components due to uncertainty in the calibration and detection functions by repeating the full bootstrap procedure, using the originally estimated calibration and detection functions rather than resampling from the photographic counts and re-estimating the functions for each replicate. Next we excluded the component due to sampling variation by again repeating the full bootstrap procedure, using the original sample of transects from each block rather than resampling from simulated populations of transects. Finally, we excluded the component due to uncertainty in the haul-out probabilities by repeating the full bootstrap procedure, using the estimated mean haul-out probability for each block rather than sampling from the posterior distributions of these means. The components of variation due to these three sets of factors are not additive, and the portion of the total variance accounted for by their inclusion depends on what other factors are also included. However, we assessed relative contributions by comparing the estimated variances from the corresponding partial bootstrap procedure to the variance estimates obtained from the full bootstrap procedure.

Results

Airborne thermal infrared surveys of the Pacific walrus in the Bering Sea were conducted from 4 to 22 April 2006 in the U.S. and from 3 to 23 April 2006 in Russia, AST, with U.S. and Russian scientific crews coordinating survey efforts on their respective sides of the border. Exceptionally cold temperatures and abundant fog across the Bering Sea in 2006 reduced the number of days suitable for surveying to 9 d in the U.S. and 10 d in Russia. For most of the survey period, temperatures were 2.8°C–8.3°C colder than 10 yr averages in Nome and Gambell, Alaska (National Weather Service, Nome, AK).

During the survey, the size of the study area, *i.e.*, the portion of the Bering Sea <200 m deep and with sea ice ≥30 cm thick, fluctuated around a mean of 668,000 km^2 (±8%). Weekly estimates of study area extent based on NIC ice charts ranged from 676,000 km^2 on 7 April, to 620,000 km^2 on 14 April, to 708,000 km^2 on 21 April 2009. Southerly winds in late March pushed the pack ice to the north, reducing the size of the ice field, and cold temperatures throughout April resulted in additional freezing and expansion of ice along the southern edge of the ice pack. All surveys were conducted over pack ice concentrations ranging from about 50%–100% total concentration. In the U.S., the surveyed area extended from the Bering Strait to north of Nunivak Island (Fig. 5). In Russia, the surveyed area extended from the Bering Strait to Cape Navarin (Fig. 5).

During the survey, a total of 63 thermal images at 4 m resolution were collected in the U.S, covering 61,582 km^2. When cold weather conditions persisted, flight altitude in the U.S. was reduced to 3,200 m AGL, yielding a resolution of 2 m, and an additional 21 images were collected, covering 12,996 km^2. A total of 91 transects were thermally scanned in Russia with resolutions ranging from 0.65 to 1.3 m,

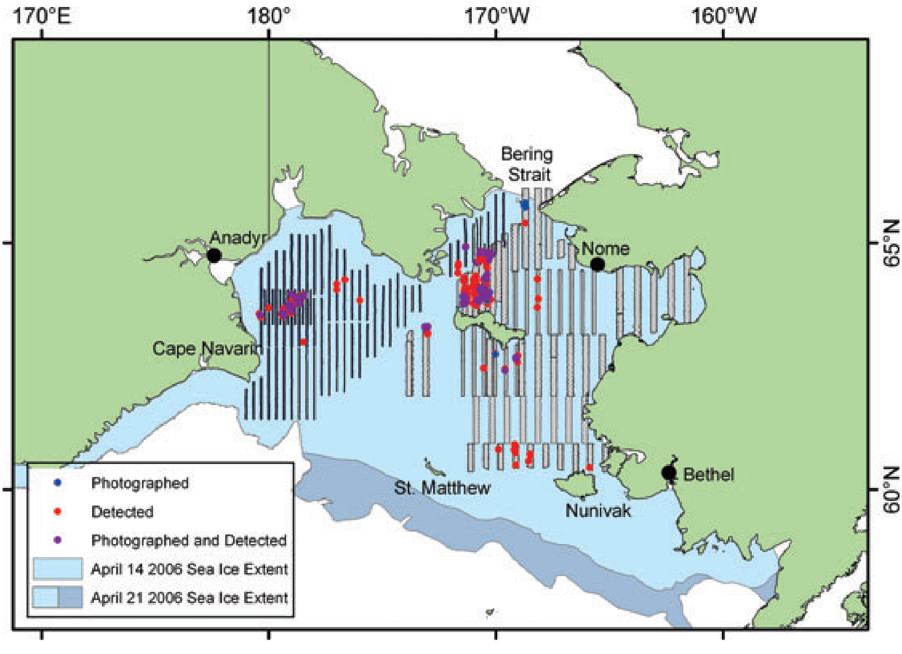

Figure 5. All surveyed transects and walrus locations on those transects (*i.e.*, not including locations of off-transect walrus groups). Width of transect indicates strip width during survey, 1.4–3.3 km for Russia and 6 km or 12 km for the U.S. For account of daily survey effort and walrus sightings see Speckman *et al*. (2009).

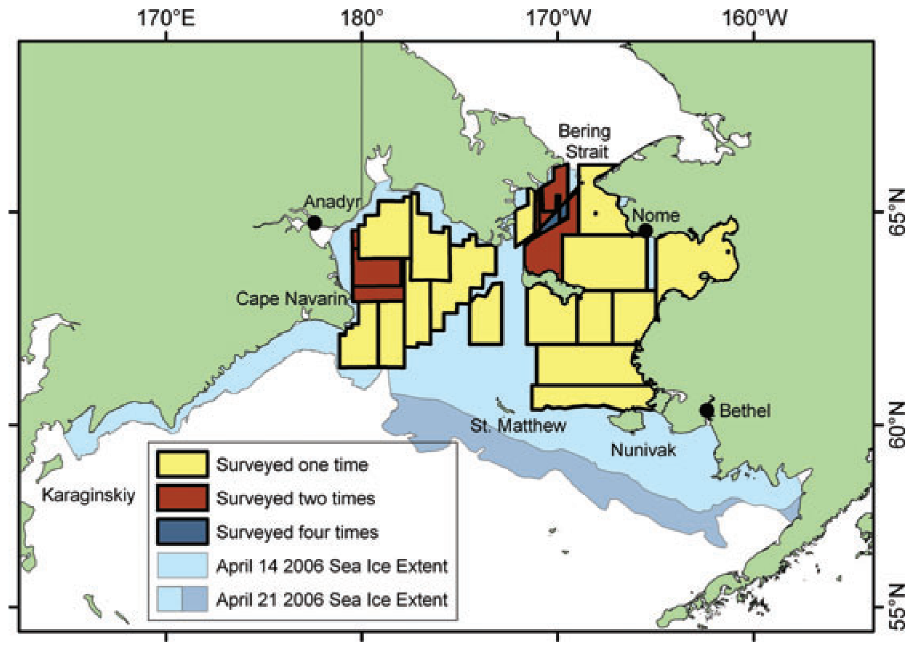

Figure 6. Final block structure and extent of surveyed area for 2006 walrus survey.

covering 21,845 km^2. The area represented by the surveyed transects (surveyed blocks) did not include the entire study area as defined earlier (Fig. 5). We defined surveyed blocks as the minimum area that included the transect strips covered by a crew in a single day plus a distance equal to half the transect spacing on either side (Fig. 6). The area of these surveyed blocks, combined for both Russia and the U.S., was 318,204 km^2, representing 48% of the study area based on an average study area size of about 668,000 km^2.

Transects covering a total of 96,423 km^2 of sea ice were surveyed, representing from 9% to 45% of the area in 26 survey blocks (Table 1). However, this total includes transects in six blocks that substantially overlapped previously surveyed blocks (Fig. 6). Survey blocks were originally defined as the contiguous area covered by one crew in single day of surveying and the intent of the original design was to survey each block once. However, three areas were surveyed twice and one small area was surveyed four times (Fig. 6). The U.S. team successfully surveyed Block A-217, on the north side of St. Lawrence Island, on 17 April at 4 m resolution. On 19 April, the U.S. team intended to survey south of St. Lawrence Island but was unable to do so due to low cloud cover. Satellite imagery showed an opening in the cloud cover on the north side of St. Lawrence Island, and the U.S. team returned to that area to scan a different systematic sample of transects and to obtain additional scanner calibration data (block A-219). The uppermost corner of A-217 and A-219 (A-217T and A-219T) was also scanned twice by the Russian survey team (R-900T and R-1000T; Fig. 6), resulting in four samples for this area. Blocks R-100 and R-1100, and R-900 and R-1000 also overlapped on the Russian side. These repeated surveys occurred when weather conditions or equipment malfunctions prevented surveying in new

Table 1. Area covered and number of walrus groups hauled out on sea ice that were detected on surveyed transects in Bering Sea, April 2006.

Block[a]	Pixel size (m)[b]	April 2006 date	Scanned area (km^2)	Block area (km^2)	Sampling intensity[c]	Detected groups
R-200	1	3	2,741	16,292	0.17	0
R-300	1	5	2,650	14,817	0.18	4
R-400	1	18	3,003	20,344	0.15	0
R-500	1	11	1,470	12,551	0.12	0
R-600	1	12	1,113	12,077	0.09	0
R-700	1	13	2,457	14,321	0.17	0
R-800	1	23	703	4,638	0.15	7
R-100	1	4	2,838	15,498	0.18	61
R-1100	1	17	3,196	11,555	0.28	81
R-900	1	23	296	1,610	0.18	2
R-1000	1	19	954	7,287	0.13	26
A-100	4	15	6,734	15,006	0.45	1
A-304	4	4	4,824	14,272	0.34	0
A-313	4	13	3,616	11,403	0.32	10
A-314	4	14	5,224	12,826	0.41	0
A-400	4	4	11,235	31,616	0.36	0
A-500	4	10	7,775	21,506	0.36	12
A-800	4	12	8,973	29,823	0.30	0
A-221	2	21	7,812	28,985	0.27	4
A-321	2	21	5,184	18,200	0.28	33
A-217	4	17	6,542	15,042	0.43	0
A-219	4	19	5,097	15,042	0.34	94
R-900T[d]	1	23	229	1,188	0.19	37
R-1000T[d]	1	19	195	1,632	0.12	0
A-217T[d]	4	17	1,116	2,212	0.50	0
A-219T[d]	4	19	446	2,212	0.20	0

[a]Prefix R indicates block surveyed by Russian crew. Prefix A indicates block surveyed by U.S. crew.

[b]Size of pixels on the infrared image produced by the scanner (*i.e.*, image resolution).

[c]Sampling intensity is the proportion of the block covered by the scanner (=scanned area/block area).

[d]T indicates the block that was surveyed four times (see Fig. 6 for location).

areas. Previously scanned areas were then re-surveyed in an effort to supplement data for areas that did currently have suitable conditions. More detailed figures showing surveyed areas and results for each date are available in Speckman *et al*. (2009).

In most of these cases, the later blocks did not completely overlap the earlier blocks. However, based on the areas that did overlap and the distribution of detected walruses within these blocks, we assumed they constituted replicate surveys of the same portions of the population. This resulted in a partition of a 318,204 km^2 survey area into 20 blocks, redefined based on area covered, without reference to the time of coverage. For blocks that were surveyed on more than one occasion, we estimated totals by averaging the estimated number of walruses from each occasion.

In the U.S., 124 unique walrus groups (91 on survey transects + 33 off-transect) were photographed in areas that were scanned at 4 m resolution and 85 unique

Table 2. Summary of photographed walrus groups detected in U.S. and Russian thermal imagery.

Region	Image resolution (m)	Number of photographed groups	Number of photographed groups detected/not detected	Size of smallest detected group	Size of largest undetected group
U.S.	2	85	71/14	2	6
	4	124	67/57	7	24
Russian	0.65–1.3	90	89/1	1	1

walrus groups (33 on survey transects + 55 off transect) were photographed in areas that were scanned at 2 m resolution (Fig. 5, Table 2). Sizes of the U.S. photographed groups ranged from 2 to 446 walruses (mean = 27) for the 4 m imagery and from 1 to 168 walruses (mean = 22) for the 2 m imagery (Fig. 7). There were 57 photographed groups that could not be detected at 4 m resolution and 14 photographed walrus groups that could not be detected in the 2 m imagery. A total of 154 walrus groups were detected in U.S. thermal imagery on survey transects.

In Russia, photographs were obtained of 90 walrus groups (50 on survey transects + 40 off transect) in areas that were scanned (Fig. 5, Table 2), with sizes ranging from

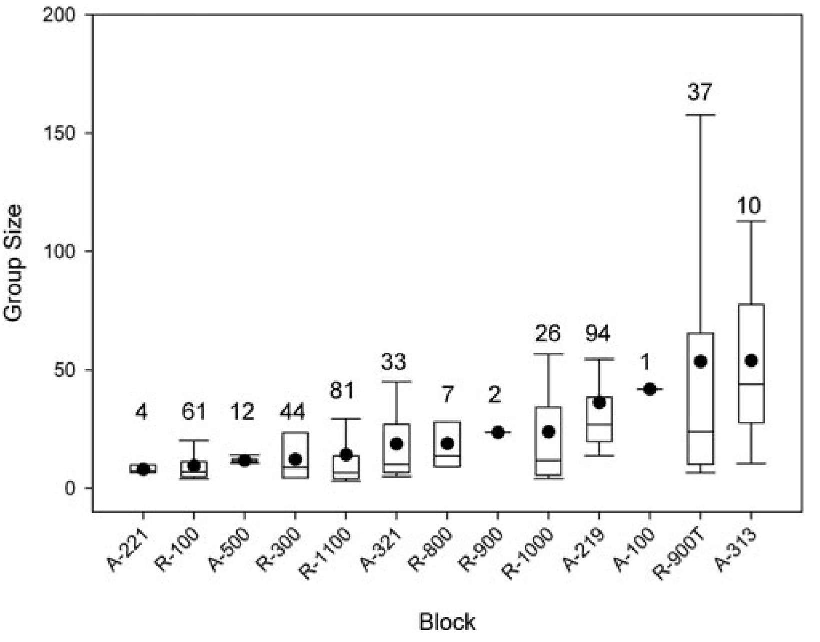

Figure 7. Estimated sizes of walrus groups detected on survey transects in the Bering Sea, April 2006. The line within the box indicates the median, and the lower and upper box boundaries indicate the 25th and 75th percentiles. Whiskers (error bars) above and below the box indicate the 10th and 90th percentiles, and circles indicate means. Numeric values indicate numbers of groups.

1 to 150 walruses (mean = 20; Fig. 7). All but one of these groups was detected in the corresponding thermal imagery. On Russian survey transects, 218 groups of walruses were detected in thermal imagery. To detect walrus groups in thermal imagery, we used the program Surfer. We selected −0.9°C as the threshold value to separate walrus groups from their background of snow, ice, and water (range −6°C to −23°C). This threshold value was warmer than the freezing point of water (−2°C) yet colder than any walrus groups detected (range 1°C–29°C).

In total, 372 walrus groups were detected using thermal imagery from surveyed transects in 11 blocks (Table 1). The largest aggregations of walruses hauled out on sea ice were encountered in central Anadyr Gulf and to the north of St. Lawrence Island (Fig. 5). Smaller aggregations were found to the south and west of St. Lawrence Island, between St. Matthew and Nunivak islands, and along the Russia–U.S. international border in the northern Bering Sea.

Detection Probabilities

Larger walrus groups were more likely to be detected using thermal imagery than smaller groups when resolution was coarser than the approximate scale of walrus body size (about 2–4 m). The detection models developed by Burn *et al*. (2009) indicated that groups were always detected in the 2 m imagery if they contained more than about 10 walruses and in the 4 m imagery if they contained more than about 34 walruses (Fig. 2). For smaller groups, detection probabilities decreased with group size to a value of 0.06 for single walruses in the 2 m imagery and 0.02 for single walruses in the 4 m imagery (Fig. 2).

In U.S. blocks with detected walruses, estimated detection probabilities averaged ≥0.83 except in block A-500, where the average detection probability was 0.28 (Fig. 8). Average detection probabilities were lower in this block because it was surveyed at 4 m resolution and all of the detected groups were relatively small (maximum group size = 14, Fig. 7). As noted earlier, it was apparent that essentially all walrus groups were detected on Russian surveyed transects and we did not attempt to account for any undetected groups on Russian transects.

Thermal Index Calibration and Estimated Group Sizes

For the Russian data (Fig. 3A), as with the U.S. data (Fig. 3B, C), the thermal index had a strong linear relation to group size and variation increased with values of the thermal index. The negative binomial model fit this variance structure substantially better than models with other error distributions (ΔAIC ≥ 5). Therefore, the negative binomial model was selected for calibrating the Russian thermal index. This model had the same structure as the final calibration models selected by Burn *et al*. (2009) for the U.S. data. For the final Russian calibration model, using data with about 1 m resolution, the estimated intercept (β_0) was 3.97 (SE = 0.44), the estimated thermal index coefficient (β_1) was 0.03 (SE = 0.002), and the dispersion parameter (k) was 0.04 (SE = 0.02). Examination of deviance and deviance residuals did not indicate any lack of fit for this final model.

Based on these calibration models (or photographs, when available), estimated sizes of groups detected on surveyed transects ranged from 1 to 446 walruses. Mean estimated group sizes within individual blocks ranged from 8 to 54 walruses (Fig. 7). Four groups each contained more than 200 individuals.

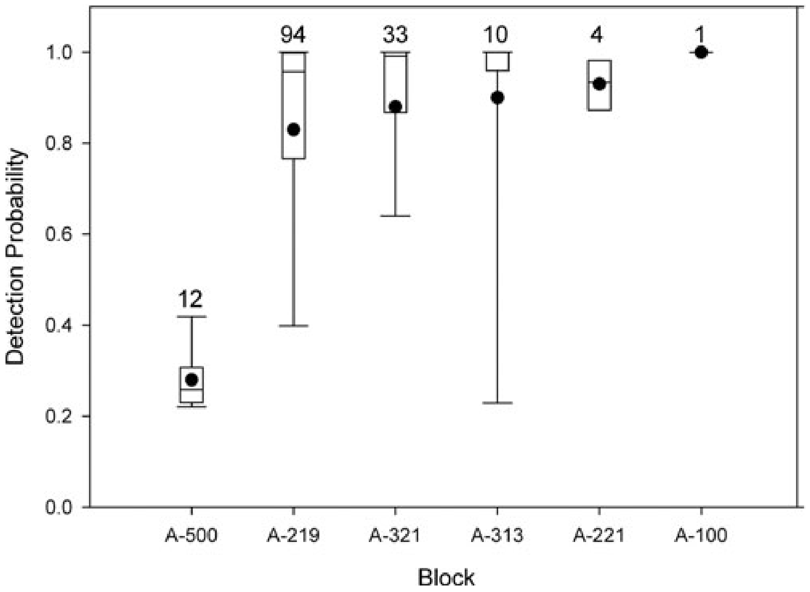

Figure 8. Estimated probabilities of thermally detecting walrus groups hauled out on U.S. survey transects in the Bering Sea, April 2006. The line within the box indicates the median, and the lower and upper box boundaries indicate the 25th and 75th percentiles. Whiskers (error bars) above and below the box indicate the 10th and 90th percentiles, and circles indicate means. Numeric values indicate numbers of groups.

Haul-out Probabilities

The model for estimating the proportion of the walrus population hauled out in surveyed blocks indicated that these proportions increased with increasing temperatures and decreasing wind speeds (Fig. 4). Parameter estimates are given in Table 3.

Table 3. Parameter estimates for model of walrus haul-out proportions in the Bering Sea, April 2004–2006.

Parameter[a]	Mean[b]	95% Credibility interval	
		Lower limit	Upper limit
β_0	−2.75	−2.90	−2.60
β_1	0.21	0.00	0.42
β_2	−0.24	−0.42	−0.07
β_3	0.18	0.08	0.27
β_4	−0.40	−0.51	−0.29
β_5	4.98	4.54	5.44
σ_τ^2	280	13	1878

[a]See text for descriptions of parameters.
[b]Median for = 70. Posterior distributions for other parameters were approximately symmetric so medians were essentially the same as the means.

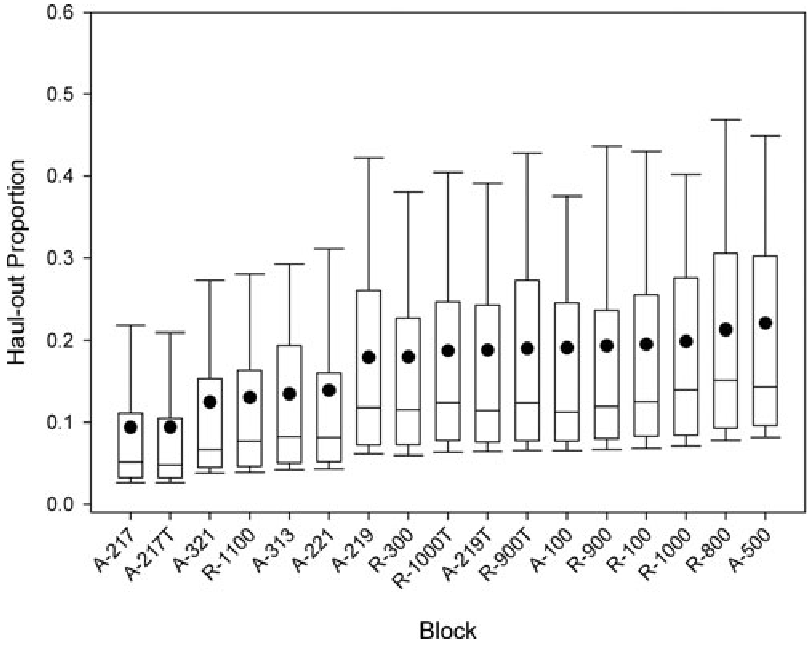

Figure 9. Box plots summarizing posterior distributions of estimated proportions of walruses hauled out on sea ice in Bering Sea survey blocks while the blocks were being surveyed, April 2006. The line within the box indicates the median, and the lower and upper box boundaries indicate the 25th and 75th percentiles. Whiskers (error bars) above and below the box indicate the 10th and 90th percentiles, and circles indicate means.

Examination of parameter traces, Gelman-Rubin statistics, and ratios of MCMC to posterior errors indicated convergence of the MCMC chains.

Estimated mean haul-out proportions ranged from 0.09 to 0.22 for blocks in which walruses were detected during the survey (Fig. 9). In the six blocks with the lowest mean haul-out proportions (blocks A-217, A-217T, A-321, R-1100, A-313, and A-221; Fig. 9), mean wind speeds were highest, ranging from 19 to 29 km/h. Mean wind speeds in all other blocks were 12 km/h or less. Mean temperatures were -7°C or less in all blocks except A-500, where the mean temperature was -2°C and the estimated mean haul-out proportion was correspondingly high (Fig. 9). Posterior distributions for the block haul-out proportions tended to be very broad and highly skewed (Fig. 9).

Estimated Numbers of Walruses

No walruses were detected in nine survey blocks (Table 1). For three of the four blocks that were surveyed multiple times, estimated numbers of hauled out walruses differed substantially between replicates (Table 4). Lower estimated numbers of hauled out walruses (Table 4) coincided with lower mean haul-out proportions (Fig. 9) in replicate surveys of block R-900/R-1000, block A-217/A-219, and block R-900T/R-1000T/A-217T/A-219T. In the latter two cases, no walruses were detected in the block on the day with the lowest mean haul-out proportion. For block

Table 4. Estimated numbers of walruses hauled out on sea ice and estimated total numbers of walruses (hauled out on sea ice and in the water) during repeated surveys of blocks in the Bering Sea, April 2006.

			Walruses on ice			Total walruses		
		April 2006		95% Confidence limits			95% Confidence limits	
Block	Replicate	date	Number	Lower	Upper	Number	Lower	Upper
R-100	1	4	3,159	727	6,457	16,173	2,811	78,210
R-1100	2	17	4,170	502	8,957	31,888	3,061	184,406
R-100,1100	All		3,665[a]	611	8,191	24,031[a]	2,726	158,879
R-1000	1	19	4,741	0	16,553	23,819	0	174,859
R-900	2	23	257	0	999	1,325	0	10,663
R-900,1000	All		2,499[a]	0	13,947	12,572[a]	0	142,452
A-217	1	17	0	–	–	0	–	–
A-219	2	19	11,802	4,340	18,824	65,736	14,983	277,343
A-217,219	All		5,901[a]	0	17,750	32,868[a]	0	245,077
A-217T	1	17	0	–	–	0	–	–
A-219T	2	19	0	–	–	0	–	–
R-1000T	3	19	0	–	–	0	–	–
R-900T	4	23	10,268	396	26,405	53,938	2,099	321,889
R-900T,1000T, A-217T,219T	All		2,567[a]	0	20,244	13,485[a]	0	214,156

[a] Average of estimates for the indicated blocks.

R-100/R-1100, differences in estimated numbers of hauled out walruses did not correspond with differences in mean haul-out proportions (Table 4, Fig. 9). Even after accounting for differences in haul-out proportions, estimates of total numbers of hauled out walruses still differed substantially between replicates.

Combining totals from all blocks, we estimated there were approximately 129,000 walruses (95% confidence limits = 55,000–507,000) in the surveyed area (Table 5). This includes an estimated 22,000 walruses (95% confidence limits = 8,453–45,439) that were hauled out on the sea ice when the blocks were surveyed (Table 5).

The average proportion of the time that tagged walruses were hauled out over the entire survey period (3–23 April) was 0.15 (95% confidence limits 0.14–0.17). This is similar to the overall model-based estimate of 0.17 obtained as the ratio of the estimated numbers of hauled out walruses over total walruses (22,000/129,000).

The precisions of estimated block and combined totals were all relatively low (Table 5), with a standard error for the overall total of 120,000 (CV = 0.93). The largest portion of the variance was due to the spatial variation associated with surveying only a sample of transects within each block and the temporal variation associated with replicate surveys. Removing these sampling components from the variance estimate for the total reduced the variance estimate by 84%. However, almost the same portion of the variance was due to uncertainty associated with estimating haul-out proportions. Removing this component reduced the variance estimate by 78%. The uncertainty associated with estimation of calibration and detection functions contributed relatively little to the total variances, and removal of this component resulted in less than a 1% reduction. The estimated total for just the number of walruses hauled out on ice (Table 5) had a standard error of 10,000 (CV = 0.46).

Discussion

This study is the first to attempt to use thermal imagery to estimate the number of Pacific walruses hauled out on ice across their spring range, the ice-covered continental shelf of the Bering Sea. It is also the first time that a model of walrus haul-out behavior has been applied to survey data to estimate the proportion of the population in the water during a survey. Our approach was designed to address key shortcomings of earlier Pacific walrus surveys (Estes and Gilbert 1978, Gilbert *et al*. 1992, Gilbert 1999) by (1) enabling coverage of a much larger area than was previously possible, (2) enabling more accurate estimation of the numbers of walruses in groups, (3) accounting for the probability of detection of groups based on group size, (4) accounting for the proportion of the population that was in the water during the survey, and (5) fully quantifying the uncertainty associated with the estimation process.

Sampling Intensity

The relatively high CV for the estimated number of walruses on ice is indicative of the extraordinary spatial and temporal variability in walrus distribution. Increasing sampling intensity (area sampled) is recognized as a general way to reduce high survey variances, including surveys for walruses (Estes and Gilbert 1978, Wade and DeMaster 1999). However, Gilbert (1999), in a summary of efforts to understand

Table 5. Estimated total numbers of walruses and numbers of walruses hauled out on sea ice in surveyed blocks in the Bering Sea, April 2006. The average of the replicate estimates (Table 4) is presented for blocks with repeated surveys.

	Walruses on ice			Total walruses		
		95% Confidence limits			95% Confidence limits	
Block	Number	Lower	Upper	Number	Lower	Upper
R-200	0	–	–	0	–	–
R-300	274	56	554	1,519	228	7,468
R-400	0	–	–	0	–	–
R-500	0	–	–	0	–	–
R-600	0	–	–	0	–	–
R-700	0	–	–	0	–	–
R-800	871	155	1,805	4,093	368	19,390
R-100,1100	3,665	611	8,191	24,031	2,726	158,879
R-900,1000	2,499	0	13,947	12,572	0	142,452
A-100	93	0	196	488	0	2,479
A-304	0	–	–	0	–	–
A-313	1,865	0	3,487	13,815	0	75,079
A-314	0	–	–	0	–	–
A-400	0	–	–	0	–	–
A-500	1,430	359	2,846	6,484	1,246	28,702
A-800	0	–	–	0	–	–
A-221	126	0	330	905	0	6,445
A-321	2,319	1,975	6,726	18,546	585	131,211
A-217,219	5,901	0	17,750	32,868	0	245,077
R-900T,1000T, A-217T,219T	2,567	0	20,244	13,485	0	214,156
Total	21,610	8453	45,439	128,806	54,934	507,104

the relationship between increased sampling intensity and coefficient of variation for aerial walrus surveys, cautioned that "the only effect of increasing sampling effort has been increasing the chance of sampling an area with a large group." Gilbert (1999) noted that for past walrus surveys, coefficients of variation seem unrelated to improvements in survey design or attempts to increase sampling effort. His warning was unfortunately prescient; in the 2006 walrus survey, sampling intensity (9%–45%; mean 27%) was far greater than that achieved in earlier survey efforts (<7% per day), yet still was insufficient to substantially reduce coefficients of variation. The CV for our on-ice estimate, 0.46, was similar to CVs for past on-ice surveys (0.24–0.59; Udevitz *et al*. 2001).

The CVs for survey blocks reported here are larger than those in the trial survey conducted in 2003 by Udevitz *et al*. (2008). This is likely because the 2003 survey used smaller blocks confined to a region around St. Lawrence Island, where walrus distribution may have been more uniform. Two of the three lowest coefficients of variation for U.S. blocks in our survey were for blocks in this region. Temporal variation was not assessed in the trial survey (Udevitz *et al*. 2008), but was a substantial component of variation in our blocks with replicate surveys.

Walrus densities on sea ice during the 2006 survey were highly variable at several spatial scales, which may reflect heterogeneity in habitat conditions, including ice type and prey availability (Fay 1982, Simpkins *et al*. 2003, Ray *et al*. 2006). Effects of spatial variability in walrus distribution might be reduced by stratification or adaptive sampling (Estes and Gilbert 1978, Thompson and Seber 1996), but these techniques may be difficult to implement (Gilbert 1999). Data from the 2006 survey, with its extensive coverage of spring walrus habitat, could serve as the foundation for improvements in future survey design.

Replicate Surveys

Replicate surveys of the same block also illustrate the extraordinary temporal and spatial variability in estimates of walrus numbers, which may have been caused by several factors. First, differences in walrus distribution may have resulted in the presence of very few walruses on survey transects on some days but large numbers on others (Estes and Gilbert 1978, Gilbert 1989*a*, Hills and Gilbert 1994). This type of variability is reflected in the large confidence intervals for numbers hauled out on ice, most of which is attributable to sampling variation. Second, the proportion of walruses in the block that was hauled out on the ice and available to be detected may have varied between replicates (Udevitz *et al*. 2009). This was accounted for by incorporating estimates of the proportion of the walrus population hauled out in each block when it was surveyed. However, there was a large amount of uncertainty associated with estimated haul-out proportions and this is reflected in the large confidence intervals for the estimated totals. Finally, walruses may have moved in or out of the block between replicates. However, examination of data on movements of radio-tagged walruses (USGS, unpublished data) did not indicate any net movements of walruses into or out of blocks during the survey period. The replicate surveys obtained for some blocks provide estimates of the average number of walruses in those blocks over the period of time spanned by the replicates. The associated confidence intervals account for the temporal as well as spatial components of sampling variation.

Time of Year and Type of Survey

We conducted the 2006 aerial survey in spring, when virtually the entire Pacific walrus population is utilizing sea ice habitats. The idea of surveying in spring rather than fall was also supported by Gilbert (1999). A spring survey allowed us to focus on developing improvements to methods for one habitat type, sea ice, and avoid complications of developing and carrying out contemporaneous surveys at terrestrial haul-outs. Previous fall survey efforts relied on aerial estimates of numbers hauled out on both ice and land, which necessitated the use of two different strategies for enumerating walruses. An additional advantage to spring surveys is that spring weather is generally more stable, with fewer days of clouds and fog, than weather in autumn (Gilbert 1999). A disadvantage of spring surveys is the larger area that must be surveyed, but the likelihood of more favorable weather in spring may at least partially compensate for that (Gilbert 1999).

Detection Probability

Differences in remote sensing equipment and survey methods accounted for differing probabilities of detecting small walrus groups in Russian and U.S. thermal imagery. With an integrated thermal scanning and photography system that operated from a single aircraft, the Russian team flew at an altitude low enough to acquire high-resolution digital photographs in which individual walruses could be discriminated. The low altitude limited the strip width of the thermally scanned area, and hence the total area that could be scanned, but resulted in high-resolution thermal imagery in which even single walruses could routinely be detected. With the option of using a second aircraft for photography, and with a larger area to survey, the U.S. team chose to maximize strip width of the thermally scanned area and the total area that could be scanned by flying at a higher altitude. This reduced resolution of the thermal images and the likelihood of detecting small groups, which had been shown to comprise a small proportion of the total number of walruses (Estes and Gilbert 1978; Burn *et al.* 2006, 2009).

"False positives" were unlikely to have impacted our results. Adult female walruses reach 3 m in length and weigh from 580 to 1,039 kg; males reach 3.6 m and weigh as much as 1,560 kg (Jefferson *et al.* 2008). The largest seals within the study area, bearded seals (*Erignathus barbatus*), are substantially smaller than adult walruses, ranging up to 2.5 m in length and weighing up to 360 kg (Jefferson *et al.* 2008). Bearded seals typically haul out alone, rather than in groups or dense concentrations. Our detection models indicated that the probability of detecting a single walrus with the U.S. scanner was extremely low; it is therefore unlikely that seals on ice were incorrectly counted as walrus groups in the U.S. imagery.

At about 1.3 m, Russian thermal imagery was of much higher resolution, making it more likely that individual walruses could be detected. However, surveys dedicated to harp seals (*Phoca groenlandicus*) using the same thermal scanner used in this study are conducted at much lower altitudes (200 m) than the 2006 walrus survey (1,000 m) specifically to increase resolution of thermal imagery and increase detection probability of this much smaller species (Chernook *et al.* 1999). Detection of small species such as individual seals from 1,000 m is very unlikely. Furthermore, walruses and bearded seals tend to be segregated in their distributions across suitable habitat due to competition for prey or predation interactions (Burns 1970, Lowry and Fay 1984, Simpkins *et al.* 2003). Using visual observations, Russian crews occasionally identified bearded seals and seals of other species. However, none of the observed seals was detected in thermal imagery. Although the detection of bearded seals in thermal imagery from Russia cannot be ruled out completely, it is highly unlikely that bearded seals contributed significantly to our estimate of the total number of walruses.

Detection probability during aerial surveys generally decreases as a function of distance from the flight line (Buckland *et al.* 1993). This may have been the case for the 2006 walrus survey, although we did not explicitly investigate whether detection of walrus groups in thermal imagery depended on distance from the flight line. However, both the detection and calibration functions were estimated based on photographed groups located at a range of distances from the flight lines, so that the estimated functions effectively averaged over any distance effects. Therefore, we do not expect there would be any appreciable distance-related bias in those estimates. If there were a distance effect, it would probably improve precision to account for this, but it likely would not have a large impact on the precision of the overall estimate of population size.

Weather

Although we used an improved detection method (Burn *et al.* 2009), colder temperatures resulted in lower detection probabilities for walrus groups in U.S. thermal imagery than for similarly sized groups in the pilot survey conducted by Udevitz *et al.* (2008). Estimates of detection probabilities were therefore incorporated to account for undetected groups on surveyed transects. The proportion of the variance associated with estimation of the detection function contributed relatively little to the overall variance of the estimates. High-resolution data collected by the Russian team were minimally affected by the cold temperatures, as virtually all walruses were detected in the Russian thermal imagery.

Unseasonably cold temperatures and abundant fog across the Bering Sea in 2006 limited the number of days during which surveys could successfully be conducted. Reducing the altitude at which the U.S. thermal imagery was collected increased the resolution of the data to 2 m, thereby increasing the probability of detecting smaller walrus groups (Burn *et al.* 2009), but this also decreased the sampling intensity and correspondingly increased the variance of the estimated totals for these blocks.

The area sampled by the 2006 survey included only about 48% of the estimated available ice habitat of the Pacific walrus population at the time of the survey. Persistent fog and cloud cover prevented us from surveying an area southwest of St. Lawrence Island, the area south of Nunivak Island, and the nearshore area south of Cape Navarin. Large aggregations of walruses have been documented to the southwest of St. Lawrence Island during April surveys in other years (Fedoseev 1979, Fay 1982, Braham *et al.* 1984, Fedoseev *et al.* 1988, Burn *et al.* 2006). Large aggregations of walruses are intermittently present in April to the south of Nunivak Island (USFWS, unpublished data; Fay 1982, Braham *et al.* 1984) and smaller numbers have been documented to the south of Cape Navarin (Fay 1957, Fedoseev 1979, Fedoseev *et al.* 1988). Given the high variability in walrus distribution, it is not known how many walruses were present in areas not covered by the 2006 survey.

Haul-out Behavior

This is the first Pacific walrus survey to account for the proportion of the population in the water during the survey. Walruses spend most of their time in the water (Lydersen *et al*. 2008, Udevitz *et al*. 2009), and spend more time in the water on cold and windy days than on warmer days (Nikulin 1947, Fay and Ray 1968, Udevitz *et al*. 2009). Even on days when numbers of walruses on ice are largest, there is still a substantial proportion of the population in the water (Udevitz *et al*. 2009). Our empirical estimate of the average proportion of tagged walruses hauled out on ice during the survey period and our model-based estimate of this average are similar to the average proportions (0.30–0.13) estimated by Born *et al*. (2005) for an Atlantic walrus in sea ice habitat, and are within the range of values (0.35–0.15) that have been estimated for walruses at terrestrial haul-out sites (Born and Knutsen 1997, Gjertz *et al*. 2001, Jay *et al*. 2001, Born *et al*. 2005, Acquarone *et al*. 2006, Lydersen *et al*. 2008). Although these longer-term averages appear to be relatively consistent, the proportion of the population hauled out at any given point in time is quite variable (this study, Udevitz *et al*. 2009). Part of this variation can be attributed to the time-of-day and weather effects that were accounted for by our haul-out model. However, a substantial portion of this variation is due to apparently random factors, resulting in low precision for the estimated proportion of the population hauled out in a given region on any given day. The precisions of our estimated total numbers of walruses are extremely low, in part because they fully account for the variance associated with estimating these proportions for specific blocks on specific days rather than averaging these proportions over the entire survey period.

Our data indicate that the majority of the Pacific walrus population will likely be in the water during an April survey. On average, regardless of the technology used, it will not be possible to directly enumerate more than about 15% of the population by counting individuals hauled out on ice during this time period. Adjusting the population estimate for the high proportion of walruses in the water contributed substantially to the variance estimate, raising the CV for the on-ice estimate from 0.44 to 0.93 for the adjusted estimate. Future studies involving the use of tagging data to adjust for animals in the water, including studies based at terrestrial haul-outs, should consider ways to reduce this source of variability. Researchers might also consider development of technologies that would allow detection and enumeration of walruses in the water rather than on refinement of technologies that are only applicable to the much smaller proportion of the population expected to be hauled out.

Historical Context of the 2006 Pacific Walrus Survey

The 2006 estimate is lower than other estimates of Pacific walrus population size to date (Table 6). However, estimates of population size from 1975 to 2006 (Table 6) are highly variable and not directly comparable among years (Fay *et al*. 1997, Gilbert 1999) because of differences in survey methodologies, timing of surveys, and segments of the population surveyed, as well as incomplete coverage of areas where walruses may have been present. Therefore, these estimates do not provide a definitive basis for inference with respect to population trends.

A decline in Pacific walrus population size from its peak in the late 1970s and 1980s would not be unexpected, however. Walrus researchers in the 1970s and 1980s were concerned that the population had reached or exceeded carrying capacity, and

Table 6. Population estimates of the Pacific walrus from simultaneous or cooperative Soviet–U.S. or Russia–U.S. surveys attempting to estimate total population size. Estimates are not directly comparable among years because of different survey methodologies, incomplete coverage of areas where walruses may have been present, different segments of the population surveyed, and different timing of surveys (see text).

Year	Season	Estimated population size	Sources
1975	Fall	220,000–248,000	Fay *et al*. 1997 from Gol'tsev 1976, Estes and Gilbert 1978, Estes and Gol'tsev 1984
1976	Spring	328,000	Gilbert 1999 from Krogman *et al*. 1979, Braham *et al*. 1984
1980	Fall	291,000–311,000	Fay *et al*. 1997 from Taggart and Zabel 1980, Johnson *et al*. 1982, Fedoseev 1984
1985	Fall	244,000	Fay *et al*. 1997 from Sherburne 1985; Fedoseev and Razlivalov 1986; Gilbert 1986, 1989*a*, *b*; Mazzone 1987
1987	Spring	208,000	Fedoseev *et al*. 1988
1990	Fall	201,000	Gilbert *et al*. 1992, Hessing and Sheffield 1990
2006	Spring	129,000	This study

predicted that density-dependent mechanisms would begin to cause a decrease in population size (Fay and Stoker 1982*b*, Fay *et al*. 1986, Sease 1986, Fay *et al*. 1989). Estimates of demographic parameters from the late 1970s and 1980s support the idea that population growth was slowing (Fay and Stoker 1982*a*, Fay *et al*. 1986, Fay *et al*. 1989).

We know that the overall estimate for 2006 of about 130,000 walruses is biased low, because we were unable to survey some areas known to be important to walruses. We could not survey south of Nunivak Island, an area where walruses are known to aggregate (Krogman *et al*. 1979), and where several thousand walruses were sighted after the 2006 survey was completed (USFWS, unpublished data). We were also unable to survey areas to the southwest of St. Lawrence Island and to the south of Cape Navarin, where aggregations of walruses have been documented during April in other years (Fay 1957, Fedoseev 1979, Fay 1982, Braham *et al*. 1984, Fedoseev *et al*. 1988, Burn *et al*. 2006, Burn *et al*. 2009). However, earlier estimates of walrus population size are also likely to be negatively biased, since they did not adjust for walruses in the water, a proportion of the population that may be as high as 0.65–0.87 (Born and Knutsen 1997, Gjertz *et al*. 2001, Jay *et al*. 2001, Born *et al*. 2005, Acquarone *et al*. 2006, Lydersen *et al*. 2008, Udevitz *et al*. 2009). Although a precursory comparison of estimated numbers of observed or detected walruses might suggest that walrus population size in 2006 was lower than it was 20–30 yr ago (Table 6), more surveys will be required to verify any trends in population size and to quantify such changes.

Management Implications

Our efforts to create a more accurate survey methodology for Pacific walruses have resulted in a tool that can support international management of this species. Although legislation governing the management of marine mammals in the U.S. and Russia differs between the two countries, both rely on sound assessments of population status. For example, the U.S. manages walrus under the authority of the MMPA, which frames its regulatory actions around the concept of Optimum Sustainable Population level (OSP; Gerodette and DeMaster 1990), typically estimated to be between 50% and 80% of carrying capacity for marine mammals (DeMaster 1984, Taylor and DeMaster 1993). In the U.S., therefore, a population size below carrying capacity would not necessarily be a cause for concern from a management perspective. Under the MMPA, the Secretary of Interior may prescribe regulations for subsistence harvest only after a species or stock has been determined to be depleted. It cannot be determined from our 2006 estimate whether walrus population size is below OSP and meets the definition of a depleted stock. In Russia, management of marine mammals, including walruses, occurs under the federal law "On Fisheries and Conservation of Aquatic Biological Resources." The State Fisheries Committee sets and allocates annual quotas for walrus take, including subsistence harvest, based on data from at least two population surveys and observations at coastal haul-outs. By itself, the single 2006 estimate of Pacific walrus population size does not meet the management standards for either country, and additional population estimates are needed to determine the status of the population relative to OSP in the U.S. and for re-evaluation of quotas in Russia.

Future Pacific Walrus Surveys

The spring 2006 walrus survey was the result of unprecedented U.S.–Russia collaboration and innovations in technology. We have entered a new era of cooperation and shared technical sophistication between the U.S. and Russia. Ease of movement between countries and ability to attend international scientific and technical meetings facilitates communication, and fosters professional relationships that allow us to work together jointly to address the sometimes controversial issues that are inherent to wildlife management, especially of harvested species like the walrus. New technology was jointly developed to address issues that have long plagued attempts to estimate the size of the Pacific walrus population. We reported here on development and performance of thermal imagery as a tool for surveying large areas of sea ice for walruses quickly and accurately, without the biases that have accompanied past visual survey efforts. This technique worked well, successfully detecting small groups at higher resolutions, and resulting in the most accurate enumeration of Pacific walruses and the largest surveyed area to date. Our study is also the first population estimate of Pacific walruses to account for numbers in the water, and include an estimate of precision that fully accounts for all sources of uncertainty.

Other long-standing issues remained problematic, however. The extreme spatial and temporal aggregation of this species on ice, combined with the vast ice-covered area it inhabits and the severity of the weather (Estes and Gilbert 1978, Hills and Gilbert 1994), continue to make survey design and execution a challenge. Because the uncertainty associated with estimation of calibration and detection functions contributed relatively little to the total variances, we recommend that future aerial thermal scanning surveys for walruses be conducted at altitudes up to 6,400 m AGL, as weather allows, to maximize the area surveyed. The decision to survey sea ice in spring was made before summer sea ice in the Chukchi Sea was retreating regularly over deep water, forcing much of the walrus population to haul out on terrestrial haul-outs in Chukotka and Alaska in late summer and fall. Given the low precision of the Pacific walrus population estimate for spring 2006, any decision to estimate walrus population size from surveys of spring sea ice should be weighed against the potential benefits of other survey methods.

Time series of accurate abundance estimates are valuable for management purposes, but by themselves, provide no information about factors causing identified population trends. An understanding of how demographic parameters (survival, reproduction, movement) vary in space and time, and in relation to environmental influences, is fundamental to the management of animal populations (Eberhardt and Siniff 1977), especially for species that are harvested by humans (Fay *et al*. 1989). Increased emphasis on estimating demographic rates (Gerodette and DeMaster 1990, Chivers 1999), as well as a reassessment of methods for estimating population size, would benefit future management of the Pacific walrus.

If summer sea ice in the Chukchi Sea continues to retreat as predicted (Maslanik *et al*. 2007, Meier *et al*. 2007, Serreze *et al*. 2007), essentially all Pacific walruses may regularly use terrestrial haul-outs in fall in the near future. This would allow development of methods for coastal aerial photographic surveys with replicated counts from each haul-out, which could result in much lower variance estimates than surveys of walruses on ice (Taylor *et al*. 2007). Existing technology and satellite-linked transmitters could be used to adjust numbers on terrestrial haul-outs for the proportion of the population in the water. Future efforts to estimate Pacific walrus population size should consider development of methods for coastal aerial photographic surveys. Regardless of the methods used, close collaboration between U.S. and Russian specialists will be necessary.

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