Estimating the Number of Walruses in Svalbard from Aerial Surveys and Behavioural Data from Satellite Telemetry

CHRISTIAN LYDERSEN,1,2 JON AARS1 and KIT M. KOVACS1

(Received 8 January 2007; accepted in revised form 16 August 2007)

ABSTRACT. All known terrestrial haul-out sites for walruses in Svalbard (n = 79) were surveyed during the period 1–3 August 2006, and sites that were in use (n = 17) were documented using digital photography. A total of 657 walruses were counted on land in the resultant images. An extensive behavioural data set from walruses equipped with satellite relay data loggers, covering August 2002 to August 2005, was used to account for walruses that were in the water. The proportion of walruses at sea during the survey was calculated to be 0.750 on the basis of 28 thirty-day periods from 23 male walruses. Time of day and wind chill did not significantly affect haul-out behaviour. However, a logistic regression model revealed both a correlation among haul-out patterns of individuals within years, and a year effect ($\chi^2 = 6.42, df = 2, p = 0.04$). Because the survey was not flown in a year when satellite tags were deployed, the interannual variance was retained in a model (with no other explanatory variables). The over-dispersion parameter from this model was 2.02 (deviance = 28.33, df = 14). Thus, variance in proportions of time individuals spent at sea was multiplied by this parameter to achieve a corrected SE around the estimate. The 95% CI based on this SE corresponded to a proportion of walruses at sea during the survey between 0.717 and 0.781, resulting in an estimated total number of walruses in Svalbard in August 2006 of 2629 (95% CI: 2318 – 2998).

Key words: walrus, Odobenus rosmarus, aerial survey, digital photography, satellite telemetry, haul-out behaviour, Svalbard

INTRODUCTION

Walruses (Odobenus rosmarus) in Svalbard, Norway, became protected in 1952 (Anonymous, 1952). At that time, these once numerous marine mammals had been exposed to 350 years of unregulated harvest, which had brought them to the brink of extinction (Norderhaug, 1969). Born (1984) summarized observations of walruses in the Svalbard area from 1954 to 1982 and concluded that the summering stock was about 100 animals, and that walrus numbers had increased since 1970. In 1993, a total of 741 walruses were observed in Svalbard, as calculated from maximum numbers of animals counted at various haul-out sites during fixed-wing and ground surveys performed from August to October (Gjertz and Wiig, 1995). As suggested by Born (1984), and later confirmed by satellite tracking (Wiig et al., 1996) and genetic studies (Andersen et al., 1998), the walruses in Svalbard are part of a larger, common Svalbard–Franz Josef Land population, in which most of the males summer in Svalbard and most females...
and calves remain in the Franz Josef Land area. On the basis of this fact, and assuming an equal sex ratio, Gjertz and Wiig (1995) suggested that this shared population consisted of a minimum of 1450 walruses older than two years plus an unknown number of calves. These reports supported the general impression from an increasing number of sightings of walruses at an increasing number of haul-out sites in Svalbard (Norwegian Polar Institute’s (NPI) Fauna and Marine Mammal Sighting Databases) that this population was recovering. No systematic survey has been conducted since the early 1990s, and no attempt has been made in previous surveys to correct the numbers to account for animals in the water.

The purpose of the present study was to estimate the number of walruses in Svalbard during the ice-free summer period by (1) counting walruses on land at all known haul-out sites using aerial digital-photographic images and 2) developing a model based on the analysis of behav- ioural data collected from satellite relay data loggers to account for walruses in the water.

MATERIAL AND METHODS

Aerial Survey

The aerial digital-photographic survey was conducted on 1–3 August 2006. All known terrestrial haul-out sites for walruses were inspected from a helicopter flying at about 300 m (~1000 ft). These included both sites currently in use and historical sites identified by Gjertz and Wiig (1994), unpublished reports held by the Governor of Svalbard’s Environmental Division, NPI’s Fauna Database and Marine Mammal Sighting Database, and extensive coastal boat surveys conducted in 2002–04 (Fig. 1). If walruses were present at a haul-out site, they were easily observed from this altitude, and digital photographs were taken of the hauled-out groups of animals (Nikon D2X and AF Nikkor 80–200 Zoom 1:2.8). Pictures were taken at a shutter speed of 1/500 second or faster to avoid blur induced by helicopter movement. A total of 79 haul-out sites were inspected (Fig. 1). In addition to visiting the known haul-out sites, observers on both sides of the helicopter were constantly watching for hauled-out walruses when flying along the coastline between these sites. The total distance covered during the survey was approximately 4000 km.

Haul-out Behaviour from Satellite Telemetry

Custom-designed satellite relay data loggers (SRDLs), developed specifically for walrus deployments in collaboration with the Sea Mammal Research Unit (SMRU), University of St. Andrews, Scotland, were used to collect data on the time walruses spent in the water versus the time they spent hauled out (Fig. 2). The basic software and hardware in these SRDLs were the same as in previous SRDLs deployed by the SMRU (Fedak et al., 2002) except that they had no speed or temperature sensors. The electronics were embedded in epoxy and encased in a stainless steel housing (a tube 10 cm long × 6 cm in diameter, weighing approximately 0.8 kg, Fig. 2) to give the electronics maximum protection, and then the casings were flooded with polyurethane. At each end of the tag, at the base towards the tusk, there was an extension of the steel housing (2 × 3 cm). Each extension had a hole for a small screw, which went a few millimetres into the tusk to prevent the tag from shifting position; each extension also had a small rim at its terminus that prevented the hose clamps that went over the extensions and held the tag to the tusk from slipping off. A ridge of stainless steel that protruded around the top surface of the tag provided protection for the antennae and sensors (see Fig. 2). Two holes were drilled through this ridge so that sediment, slush or other debris would be flushed away (Fig. 2). Because the protective ridge is only on the front side of the tag and the antennae and the sensors should be pointing upwards, the tag can be deployed on only one side of the animal, in this case the left tusk. Each tag had an identification number welded onto its surface (see Fig. 2, number 7) to enable future recognition if the animal carrying the tag was resightted.

This study used all parts of the tags’ sampling protocols relevant to haul-out behaviour to create correction factors. The SRDLs continually monitor the data their sensors are
collecting (surface sensor, depth sensor, and time interactions) and group the animals’ activities into three different states: diving, hauled out, and at surface. A walrus is identified as **diving** when it is below a preset depth, in this case 6 m. Behaviour is classified as **hauled out** when the tag has been dry for at least 10 minutes, and this state ends when wet-dry sensors indicate wet for more than 40 seconds. A walrus **at surface** is neither diving nor hauled out, i.e., the animal enters this state when it remains above the depth threshold for diving but is not dry long enough to be classified as hauled out.

Summary statistics, with exact start points and duration to the minute of time spent in each of these three states, are constructed for every six-hour time period and transmitted via the Argos satellite system (Toulouse, France). For this study, only the contrast between “not hauled out” (i.e., diving or at surface) and “hauled out” was of interest. Unfortunately, not all of the six-hour summary statistics are received through the Argos system for a variety of reasons, such as satellite availability at the time of transmission, the animal’s surface behaviour, and proximity to other competing Argos devices. For this study, however, behavioural information could be filled in for almost all of the periods for which summary statistics were missing. This was possible because the haul-out events recorded by a SRDL were given consecutive numbers. Thus, unaccounted-for time surrounded by haul-outs with consecutive numbers cannot be time spent hauled out, which means the animal must have been in the water, either at the surface or diving. In addition, in the rare cases for which there are no summary statistics and haul-out events are missing (as revealed by non-consecutive numbers of these events), dive information is often available, and the dive time and extended surface periods between dives can be used to fill in some of the gaps in the record.

During August 2002–04, a total of 23 adult male walruses were equipped with these newly developed walrus SRDLs. The animals were immobilized with an intramuscular injection of etorphine HCl that was reversed with diprenorphine HCl, as described by Griffiths et al. (1993). As soon as a drugged animal showed signs of the influence of the etorphine HCl, the reversal agent was injected. The tag was then mounted to the left tusk using HI-TORQUE™ heavy-duty stainless steel hose clamps (JCS Hi-Torque Ltd., Suffolk, England) and Sicaflex epoxy. Two small holes were drilled in the tusk. A screw with a smaller diameter than the hole was placed into each hole, with its head secured under the hose clamp, to prevent the tag from sliding. The whole deployment process took 2 –3 min. The animal was then rolled onto its belly, and a soft silicon endotracheal tube (20 mm diameter, 90 cm long, Cook Inc. Bloomington, Indiana, USA) was inserted into the trachea and connected to the Zodiac boat pump via a custom-made transition tube. Thus the walrus was kept breathing artificially until the diprenorphine HCl took effect and the animal was breathing again without support. No mortality was experienced when using this intubation technique. All animal handling protocols used were approved by the Norwegian Animal Research Authorities and the Governor (Sysselmannen) on Svalbard.

**Correction Factors**

To create a correction factor that would account for walruses in the water during the survey, we used a data set of haul-out behaviour recorded for each walrus (n = 23) during a 30-day period starting the day after tagging. (The 30 days started 24 h after drugging in order to reduce potential bias in behaviour due to drug effects.) Some of the SRDLs gave haul-out information for more than a year, and for those animals (n = 5) the period 1–30 August in the following year was also included in the analyses. This procedure resulted in 30-day haul-out records for 6 individuals in 2002, 9 in 2003, 11 in 2004, and 2 in 2005 (see Fig. 3).

Our statistical analyses were conducted using the R suite of statistical software (R Development Core Team,
We tested whether there was a diurnal pattern in haul-out behaviour by comparing the time of day (h) for the start and the termination (in two different analyses) of each haul-out period to the expected distribution (uniform, generated by the command "runif" in R with identical sample size) if no time-of-day effect was present. The statistical comparison was performed using the Kolmogorov-Smirnov test in R (command "ks.test"). Haul-out events were sufficiently spread in time to be treated as independent of one another for this analysis.

Weather effects on the proportion of animals hauled out at a particular time were explored using logistic regression models. The haul-out patterns of individuals are autocorrelated by virtue of being a time series. Thus, we explored weather effects on haul-out events that were sufficiently separated in time to avoid time dependence. The length of this period was chosen using the autocorrelation function (acf) in R (Venables and Ripley, 1999:405). Figure 4 shows that, on average, there is no correlation to the previous haul-out state after five days. Thus, all potential effects of weather were explored using data from the first hour every fifth day. Wind chill effects were explored through a logistic regression model run in R, using the binomial proportion of tagged animals as the response variable. For the wind chill analysis, only the nine walruses tagged in 2003 were used. These animals were tagged on Tusenøyane, 90 km W-NW of Hopen Island (Fig. 1), and they generally remained in the vicinity for the first 30 days after tagging. Hopen Island has a meteorological station where data on wind speed (± 0.1 ms⁻¹) and temperature (± 0.1°C) are collected four times per day; we used one record daily, taken at 0100 h. The data on temperature and wind were combined into a wind chill factor (\(T_{wc} = 13.112 + 0.6215T_a - 11.37V^{0.16} + 0.3965T_aV^{0.16}\), 2002 to 2004). For SRDLs that transmitted for more than one year (walruses 1, 2, and 3 in 2004, and 1 and 2 in 2005), we included haul-out information from the first 30 days of deployment, starting 24 h after drugging, in addition to haul-out data from the first 30 days of August the following year. The figure illustrates that within each year, walruses that were tagged at the same time tend to be hauled out (and thus also at sea) at the same time more frequently than would be expected by chance.

FIG. 3. Haul-out chronologies for 28 walrus data sets based on information from satellite relay data loggers (SRDLs) deployed on the tusks of the animals in August 2002 to 2004. For SRDLs that transmitted for more than one year (walruses 1, 2, and 3 in 2004, and 1 and 2 in 2005), we included haul-out information from the first 30 days of deployment, starting 24 h after drugging, in addition to haul-out data from the 30 first days of August the following year. The figure illustrates that within each year, walruses that were tagged at the same time tend to be hauled out (and thus also at sea) at the same time more frequently than would be expected by chance.
where $T_{wc}$ is the wind chill, $V$ is the wind speed in km h$^{-1}$, and $T_a$ is the ambient air temperature in °C, [http://www.nws.noaa.gov/om/windchill/index.shtml](http://www.nws.noaa.gov/om/windchill/index.shtml). The input to this model for behavioural state was based on whether an animal was hauled out or in the water during the first minute of each hour within the data set.

The population-specific haul-out fraction was calculated simply as the average proportion of time spent hauled out across the 30 days of records, and the remainder was the proportion of time spent at sea, which was needed to correct for the number of walruses not hauled out during the survey.

### Estimating the Total Number of Walruses

One digital picture from each haul-out where walruses were present was selected and used to count the number of animals at each site. Counting was performed by three independent readers, and all three counts for each site were identical. Walruses are large animals, and even though they haul out in dense groups, they are easily counted from pictures taken directly above the group, especially given the enlargement possibilities with digital images. Since no diurnal or weather effects were found, the proportion of walruses expected to be in the sea ($p_{Sea}$) during the survey was assumed to be the average for all 28 of the 30-day periods from the tagged walruses. The proportion hauled out would then be $1-p_{Sea}$). The estimated number of animals in the sea is then the number counted on the digital pictures multiplied by $p_{Sea}/(1-p_{Sea})$. But a correction factor that adjusted for the uncertainty due to overdispersion of the data (residual deviance/residual degrees of freedom; Venables and Ripley, 1999) was used to incorporate uncertainty into the estimate. Uncertainty either arose from environmental factors that we tested for, but failed to correlate significantly to haul-out data because of limited statistical power, or was due to other factors not recorded, such as dependence between individuals. Year effects were explored using data from 2002, 2003, and 2004, since data were available from only two individuals in 2005. Again, only data from the first hour each fifth day were used.

### RESULTS

Walruses occupied 17 of the 79 haul-out sites visited during the survey (see Fig. 1). The number of animals at these sites ranged from 1 to 133 individuals (Table 1). A total of 657 walruses were counted on land at the haul-out sites.

Haul-out behaviour data were not complete for the whole 30-day period for all 28 records (Fig. 3). However, the mean fraction of this time for which the SRDLS did achieve data coverage was very high ($0.96 \pm 0.09$; range 0.63–1 of the total time), and for 18 of the 28 records the coverage was 100%. The average duration of haul-out periods was 29.8 h (SD = 14.7 h, range 2–68 h), and the corresponding values for the at-sea periods were 85.6 h (SD = 44.7 h, range 5–236 h). No evidence of diurnal effects on haul-out pattern were found for the tagged walruses during the 30-day period studied when comparing onset ($n = 203$, D-value = 0.059, $p = 0.87$) or termination ($n = 194$, D-value = 0.057, $p = 0.91$) of haul-out.

### TABLE 1. Numbers of walruses counted from digital pictures at the haul-out areas during an aerial survey in Svalbard in August 2006. (Numbers in parentheses refer to the site numbers in Fig. 1).

<table>
<thead>
<tr>
<th>Haul-out Area</th>
<th>Number of Walruses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slettholmen (1)</td>
<td>133</td>
</tr>
<tr>
<td>Havmerra (2)</td>
<td>34</td>
</tr>
<tr>
<td>Halvmåneøya (3)</td>
<td>1</td>
</tr>
<tr>
<td>Andretangen (4)</td>
<td>125</td>
</tr>
<tr>
<td>Kapp Lee (5)</td>
<td>24</td>
</tr>
<tr>
<td>Wahlbergøya (6)</td>
<td>14</td>
</tr>
<tr>
<td>Augustabukta (7)</td>
<td>4</td>
</tr>
<tr>
<td>Svattneset (8)</td>
<td>31</td>
</tr>
<tr>
<td>Palandervågen (9)</td>
<td>13</td>
</tr>
<tr>
<td>Ytre Palanderbuksa (10)</td>
<td>3</td>
</tr>
<tr>
<td>Narkvaløya (11)</td>
<td>9</td>
</tr>
<tr>
<td>Moffen (12)</td>
<td>11</td>
</tr>
<tr>
<td>Lågøya (13)</td>
<td>37</td>
</tr>
<tr>
<td>Isflakbuksa (14)</td>
<td>10</td>
</tr>
<tr>
<td>Kapp Brunøya (15)</td>
<td>31</td>
</tr>
<tr>
<td>Storøya (16)</td>
<td>110</td>
</tr>
<tr>
<td>Krammerpynten (17)</td>
<td>67</td>
</tr>
<tr>
<td>Total</td>
<td>657</td>
</tr>
</tbody>
</table>

![Fig. 4. The average autocorrelation (ACF ± 95% CI) for the 28 thirty-day periods of walrus haul-out behaviour (haul-out is given a value of 0; at sea, a value of 1), with time lags of 1 to 10 days.](attachment:image.png)
DISCUSSION

This walrus survey was conducted in August primarily because this is the period of the year when coastal waters in the Svalbard area are most likely to be ice-free. However, this was also the period for which the most behavioural information was available from satellite tagging records to model the correction factors. Even walruses equipped with SRDLs that had moved out of the Svalbard area for periods of the year (i.e., during the breeding season) had all returned to the archipelago before August (C. Lydersen and K. Kovacs, unpubl. data). In August 2006, the northern pack-ice edge was situated far north of Svalbard, at about 82° N. In this area, the ocean floor at that latitude is located at 4000–5000 m depth, and thus this ice edge is unlikely to serve as a haul-out location for walruses. Walruses are shallow divers (e.g., Gjertz et al., 2001) that feed on benthic invertebrates. In addition, during August 2006 the annual sea ice had all melted or drifted away from the archipelago, giving the walruses no alternatives for hauling out except their terrestrial sites.

One of the basic assumptions for this survey was that all walruses that were hauled out in Svalbard during the time of the survey were counted. Observer biases, which can be a problem during visual aerial surveys, especially for animals like walruses that tend to congregate in large, dense groups (Udevitz et al., 2005), were nonexistent in this survey since counts were made directly from digital photographs. Because of the large size of walruses and the magnification and manipulation options possible when using high-resolution digital pictures, potential reader biases were found not to be a problem. One can never be 100% certain that every hauled-out group of animals was visited during the survey, but our extensive pre-survey ground-truthing and the fidelity generally shown by walruses to traditional haul-out sites make it very likely that the 79 sites visited during the survey represent all of the currently used potential walrus haul-out sites in Svalbard. Additionally, during the 4000 km of survey flying, most of which was along beaches and other types of coastlines with continuous observation from the aircraft, no “new” sites were discovered.

Another factor that can certainly affect the accuracy of a walrus survey is the availability of alternative haul-out platforms (i.e., sea ice) in the survey area. An attempt to perform this survey was made in August 2005, but the survey was aborted because large areas in the southeast of Svalbard contained vast fields of loosely packed annual ice floes. Even though the actual ice cover was low (1–2%), the ice created thousands of potential resting platforms, and the walruses clearly preferred hauling out on the ice to hauling out on land. The area in the southeast of Svalbard where almost all the walruses of Gjertz and Wiig (1995) and about 5% of those in the present study were counted had no animals hauled out on terrestrial sites at all when surveyed in August 2005. It is of course possible to survey walruses when sea ice is present. However, a survey design involving line transects or strip surveys (Borchers et al., 2002) would be required, and the uncertainties in the counts would be much greater.

Haul-out behaviour data in this study include information only for the part of the year pertinent to the aerial survey. During this time interval, the animals spent 75% of
their time at sea and 25% hauled out. Several previously published studies on walrus behavior have documented comparative information on haul-out patterns from either satellite telemetry or time-depth recorders (TDRs) (Born and Knutsen, 1997; Gjertz et al., 2001; Jay et al., 2001; Born et al., 2003, 2005; Acquarone et al., 2006). TDRs provide complete time series of haul-out behavior, while data from satellite tags generally have gaps in the time-string either because the instruments are set to a duty cycle or because not all of the information collected by the tags is received by the Argos system. Unfortunately, few authors quantify the latter data issue in publications. Therefore, only TDR data will be compared here to the current study, in which the SRDLs had close to 100% data coverage (96%). Gjertz et al. (2001) deployed three TDRs on walruses in Svalbard that collected data for 9–19 days. They reported that the average at-sea time was 56 h followed by an average of 20 h hauled out on land, which corresponds to spending 74% of the time in the water. Jay et al. (2001) equipped four Pacific walruses (O. r. divergens) with TDRs that collected data for 29–36 days. These walruses spent 77% of the recorded time in the water. Acquarone et al. (2006), who deployed TDRs that collected data for 5–15 days on six walruses in Greenland, found that these walruses spent 67% of their time in the water, a somewhat smaller percentage than was reported in the two other studies. However, some short records of this small sample could have over-estimated haul-out time if they reported total time of tag deployment, since walruses take some time to recover from drugging. All of these studies were conducted on adult male walruses during late summer (August–September), and all report remarkably consistent proportions of time spent hauled out on land versus time at sea, which are similar to the proportions documented in this study. For whatever reason(s), walruses seem to be quite consistent across their geographic range in spending about 25% of their time out of the water, at least during late summer. Additional information supporting the consistency of this behavior pattern for walruses can be found in a study of sleep in captive walruses, in which four two-year-old walruses were videotaped continuously for 7–17 days in a pool filled with seawater and equipped with a resting platform. The four youngsters spent an average of 75% of their time in the water (Pryaslova and Lyamin, 2006).

Haul-out patterns of the walruses in this study were not significantly affected by ambient temperature or wind speed (or a wind chill factor). But our power to detect a difference is very weak because the sample size for the data subset used in this analysis was small. Additionally, the available weather data are not ideal, in that they were collected from a station about 90 km away from where the instrumented animals were hauled out. This factor is not likely to be a large problem, however: the specific haul-out sites in Tusenøyane where the animals were tagged in 2003 consist of small, flat islands that create little shelter from winds in any direction, so there is no reason to assume that conditions there are very different from those at Hopen, where the meteorological data were measured.

The lack of a wind chill effect was somewhat surprising because temperature and wind speed are often found to affect haul-out behavior in various pinniped species, including the walrus. A study by Born and Knutsen (1997) reported that walruses in their study area abandoned the beach altogether during very bad weather (rain and strong winds up to 20 ms⁻¹). They found a significant correlation between wind chill and numbers of hauled-out animals (1989: -3.0°–8.0°C and 0–4.5 ms⁻¹; 1990: -1.8°–14.3°C and 0–> 20 ms⁻¹) in one of the two study years (1990), but no correlation was found in the less extreme wind year.

There are probably several reasons why weather parameters affect the haul-out behavior of pinnipeds, but the most obvious is their need to maintain thermal balance. Large animals like walruses have a surface-to-volume ratio that is advantageous for heat retention, and their highly gregarious haul-out behavior leads to a reduction of exposed surfaces, which further lessens heat loss in cold weather (Fay and Ray, 1968). If air temperatures fall to levels at which the animals would have to increase circulation to the skin to avoid tissue damage from freezing (Lydersen et al., 1994), they would likely be induced to enter the water, where the temperature would be higher and conditions more stable. However, the range of weather conditions experienced by the walruses in the present study was not dramatic (temperature: -0.4°–8.0°C; wind speed: 0–12.3 ms⁻¹), which is likely the reason that these parameters did not influence the behavior of the animals. These conditions, typical for August in Svalbard, are another reason for conducting surveys at this time of the year, since they mean low variability in haul-out behavior of the animals and provide good flying conditions.

Weather conditions might affect haul-out behavior of walruses not only for purely physiological reasons, but also via increased alertness or nervousness related to the difficulty of detecting terrestrial predators when wind noise is high or visibility is poor. However, the only potential terrestrial predator of walruses in Svalbard is the polar bear (Ursus maritimus), and generally this predator does not attack adult male walruses. In fact, all-male walrus groups on Svalbard seem to ignore polar bears even when they approach quite closely (Gjertz, 1990; personal observation).

No diurnal pattern was found in the haul-out behavior of walruses in Svalbard during August–September. Diurnal patterns in haul-out behavior in pinnipeds are often linked to day versus night variations in temperature, light regimes, or other environmental variables such as tides, which make it more profitable to haul out under certain conditions. In polar regions, higher air temperatures may make hauling out more energetically profitable, and better visibility could increase the chances of detecting a terrestrial predator. Many pinnipeds have diurnal patterns that are influenced by the behavior of their prey; some fish and invertebrates move up or down in the water column diurnally, making
them easier to catch at certain times of the day. During August Svalbard experiences a 24 h sunlight regime, although some resident pinniped species in this area still exhibit diurnal haul-out patterns even under these light conditions (e.g., Reder et al., 2003; Carlens et al., 2006). However, walruses should have no problems with thermoregulation under the conditions experienced in late summer, and their main prey are more or less sessile benthic invertebrates (Fay, 1981; Gjertz and Wiig, 1992) that are probably just as easy to find at any time of day, so diurnal patterns in haul-out behaviour would not be expected for these animals at this time of year. Another point in this context is that most of the haul-out periods registered were longer than 24 h, which suggests a lack of diurnal rhythmicity. Although duration of haul-out periods for the walruses in Svalbard was highly variable, the average length was 29.8 h. Average haul-out periods longer than 24 h were also found for walruses in Greenland (38 h; Born and Knutsen, 1997) and in Alaska (41 h; Jay et al., 2001).

Haul-out behaviour of walruses in Svalbard and elsewhere almost certainly changes with season and with environmental factors over longer time scales, and perhaps diurnal patterns are exhibited at other times of year, but across a few weeks in late summer, no such patterns were seen. Thus a simple population average of time spent at sea could be used to adjust survey numbers to create a total estimate. The uncertainty around the estimate reflects interannual variations in haul-out proportions and the existence of some social synchronicity in haul-out behaviour (also see below). One important factor to note with respect to the correction factor used in this study is that it is based on haul-out behaviour of adult males only. Females and calves might have quite different haul-out patterns; they might have to rest on land more frequently for longer or shorter periods than adult males. Because most of the walruses summering in Svalbard are adult males, the correction factor used here likely provides a quite reasonable correction factor used in this study is that it is based on haul-out behaviour of adult males only. Females and calves might have quite different haul-out patterns; they might have to rest on land more frequently for longer or shorter periods than adult males. Because most of the walruses summering in Svalbard are adult males, the correction factor used here likely provides a quite reasonable estimate for this subpopulation, but it might be inaccurate for regions where female and calf haul-outs are more common.

The temporal pattern seen among individual animals that were marked together in this study suggested some sort of synchronicity in the pattern of haul-out behaviour. Walruses are gregarious mammals that haul out together, and their main prey are more or less sessile benthic invertebrates (Fay, 1981; Gjertz and Wiig, 1992) that are probably just as easy to find at any time of day, so diurnal patterns in haul-out behaviour would not be expected for these animals at this time of year. Another point in this context is that most of the haul-out periods registered were longer than 24 h, which suggests a lack of diurnal rhythmicity. Although duration of haul-out periods for the walruses in Svalbard was highly variable, the average length was 29.8 h. Average haul-out periods longer than 24 h were also found for walruses in Greenland (38 h; Born and Knutsen, 1997) and in Alaska (41 h; Jay et al., 2001).

Haul-out behaviour of walruses in Svalbard and elsewhere almost certainly changes with season and with environmental factors over longer time scales, and perhaps diurnal patterns are exhibited at other times of year, but across a few weeks in late summer, no such patterns were seen. Thus a simple population average of time spent at sea could be used to adjust survey numbers to create a total estimate. The uncertainty around the estimate reflects interannual variations in haul-out proportions and the existence of some social synchronicity in haul-out behaviour (also see below). One important factor to note with respect to the correction factor used in this study is that it is based on haul-out behaviour of adult males only. Females and calves might have quite different haul-out patterns; they might have to rest on land more frequently for longer or shorter periods than adult males. Because most of the walruses summering in Svalbard are adult males, the correction factor used here likely provides a quite reasonable estimate for this subpopulation, but it might be inaccurate for regions where female and calf haul-outs are more common.

The temporal pattern seen among individual animals that were marked together in this study suggested some sort of synchronicity in the pattern of haul-out behaviour. Walruses are gregarious mammals that haul out together, and this was not unexpected. What was surprising, however, was that when spatial information was incorporated into the analyses (Fig. 5), it was found that over the long term, the “groups” marked together hauled out at similar times, but not necessarily at the same place. Thus, the synchronicity was not due to the group’s travelling together at sea when foraging and returning to land together, but reflected a stereotypical pattern that included an at-sea bout of approximately 86 h followed by about 30 h hauled out on land, with groups of animals remaining “in phase.”

The total number of walruses estimated to inhabit Svalbard during August 2006 was 2629 (95% CI: 2318–2998). Born (1984) suggested that there had been an increase in walrus numbers in Svalbard between 1970 and the early 1980s, and there are many recent indications (e.g., more animals observed on terrestrial haul-outs, more haul-out sites being used, more frequent observations of females and calves within the Svalbard area) that they have been increasing steadily since that time. However, it is not straightforward to quantify the rate of this potential increase with the data that are available. The most comprehensive previous survey of walruses in Svalbard, conducted in 1993 (Gjertz and Wiig, 1995), compiled maximum observed numbers near and on haul-out sites, but it did not attempt to correct for animals not counted. Another issue with this earlier survey was that it took place over a period of time long enough for animals from various haul-outs to have moved between sites and perhaps to be counted twice. The time between the surveys of the two largest groups of walruses in 1993 was 12 days. When walruses decide to move, they can cover long distances relatively quickly. Two tracks from walruses equipped with SRDLs in this study were measured to be 849 km during 248 h (10.3 days) and 942 km during 327 h (13.6 days), respectively (C. Lydersen and K. Kovacs, unpubl. data). These measurements correspond to average horizontal surface speeds of 82 km day$^{-1}$ and 69 km day$^{-1}$, suggesting that walruses could swim from the southernmost to the northernmost terrestrial haul-out in Svalbard in about a week. In the 2006 study, the whole of Svalbard was surveyed in less than three days, so this source of error was minimized.

If we take the highest number of walruses observed by Gjertz and Wiig (1995) within a limited time frame to exclude potential double counting, they counted 657
walruses in the period from 23 to 26 August 1993. Of these walruses, an estimated 120 were in the water close to the haul-out sites and 537 were on land. Using this number for comparison with our count, ignoring various uncertainties, the rate of increase in walruses in Svalbard from 1993 to 2006 would be only 1.6% per year (from 537 to 657 in 13 years). Witting and Born (2005) reviewed population parameters for walruses and found a finite growth rate of 7% per year for a population in a phase of growth under favourable environmental conditions with no food limitations. Such conditions are thought to prevail in Svalbard, so we are at a loss to explain the slow estimated growth rate. Our estimate of population growth is incomplete, however, in that we are enumerating only the subpopulation summering in Svalbard, not the whole population living across the northern Barents Sea. A complete survey of the known population range would be useful for management purposes.

In summary, 2629 (95% CI: 2318 – 2998) walruses were estimated to be present in the Svalbard area during August 2006. Since the walruses in this area are predominantly males and are only part of a common Svalbard–Franz Josef Land population, it is reasonable to assume that this population as a whole numbers more than 5000 animals. This population is completely protected from hunting, there are no known interactions with fisheries, and the pollution levels are too low to cause mortality or any impediment to reproduction (Wolkers et al., 2006). The scarce data available for comparisons suggest that the Svalbard–Franz Josef Land walrus population has been increasing over the last two decades, but at a rate that is lower than expected.

ACKNOWLEDGEMENTS

This project was funded by the Norwegian Research Council and the Norwegian Polar Institute. We thank Vidar Bakken, Heinrich Eggenschwiler, Mike Fedak, Dave Griffiths, Andreas Haga, Colin Hunter, Hans Lund, and Sofie van Parijs for help in the field, and Rory Beaton, Mike Fedak, Colin Hunter, and Phil Lovell for help with the development and manufacture of the SRDLs. We also thank Audun Igesund and Jan Roald for help with the figures. We thank Rolf Anker Ims, Audun Stien, and Nigel Yoccoz for statistical advice. Special thanks are extended to the Governor of Svalbard (Sysselmannen) for helicopter support, and to Oddvar Instanes and Alf Torrispllass (Airlift) for their extraordinary efforts in the pilot seats, which allowed us to conduct this survey in a timely fashion.

REFERENCES


LYDERSEN, C., HAMMILL, M.O., and KOVACS, K.M. 1994. Activity of lactating ice-breeding grey seals, Halichoerus grypus,
from the Gulf of St. Lawrence, Canada. Animal Behaviour 48:1417 –1425.