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# Estimating population status under conditions of uncertainty: the Ross seal in East Antarctica

COLIN J. SOUTHWELL[1]*, CHARLES G.M. PAXTON[2], DAVID L. BORCHERS[2], PETER L. BOVENG[3], ERLING S. NORDØY[4], ARNOLDUS SCHYTTE BLIX[4] and WILLIAM K. DE LA MARE[5]

[1]*Department of the Environment and Water Resources, Australian Antarctic Division, Channel Highway, Kingston, TAS 7050, Australia*
[2]*School of Mathematics and Statistics, University of St. Andrews, North Haugh, St Andrews KY16 9SS, UK*
[3]*National Marine Mammal Laboratory, 7600 Sand Point Way NE Seattle, WA 98115, USA*
[4]*Department of Arctic Biology, University of Tromsø, N-9037 Tromsø, Norway*
[5]*CSIRO Marine and Atmospheric Research, Cleveland Laboratories, PO Box 120, Cleveland, QLD 4163, Australia*
**colin.southwell@aad.gov.au*

**Abstract:** The Ross seal (*Ommatophoca rossii*) is the least studied of the Antarctic ice-breeding phocids. In particular, estimating the population status of the Ross seal has proved extremely difficult. The Protocol on Environmental Protection to the Antarctic Treaty currently designates the Ross seal as a 'Specially Protected Species', contrasting with the IUCN's classification of 'Least Concern'. As part of a review of the Ross seal's classification under the Protocol, a survey was undertaken in 1999/2000 to estimate the status of the Ross seal population in the pack ice off East Antarctica between 64–150°E. Shipboard and aerial sighting surveys were carried out along 9476 km of transect to estimate the density of Ross seals hauled out on the ice, and satellite dive recorders deployed on a sample of Ross seals to estimate the proportion of time spent on the ice. The survey design and analysis addressed the many sources of uncertainty in estimating the abundance of this species in an effort to provide a range of best and plausible estimates. Best estimates of abundance in the survey region ranged from 41 300–55 900 seals. Limits on plausible estimates ranged from 20 500 (lower 2.5 percentile) to 226 600 (upper 97.5 percentile).

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**Key words:** abundance, model-based inference, population status

## Introduction

There is increasing recognition that conservation management and policy decisions need to take into account uncertainties associated with supporting information (Williams 2001). Akçakaya *et al.* (2000) recognize three categories of uncertainty: natural variation, which results from naturally occurring changes in species' life histories and environments over time and space; semantic uncertainty, which arises from vagueness in the definition of terms and inconsistency in the use of terms; and measurement error, which arises from imprecise information or estimates of parameters.

There are numerous legislative and administrative mechanisms in place to assess and classify the conservation status and threats to status of species. The scheme for classifying species' conservation status defined by the World Conservation Union (IUCN 2006) has received international acceptance and is one of the most important instruments for decision making in conservation biology. Annex I of the IUCN Red List of Threatened Species discusses the need to take account of uncertainty in estimates of parameters such as distribution, population size, and population trends when classifying conservation status, and recommends that the best estimate for a parameter be qualified with a range of plausible values, or that the best estimate be presented as a range if uncertainty as to what constitutes 'best' exists, rather than relying on a single point estimate.

Administrative mechanisms for conserving and managing species in Antarctica originated with the establishment of the Antarctic Treaty (hereafter the Treaty) in 1959. At the time when the Treaty was established, information on the status of all four ice-dependent phocid species was sparse, but particularly so for the Ross seal (*Ommatophoca rossii* Gray). Maxwell (1967) for example, reported only 50 Ross seal specimens being recorded in the 100 years following its discovery in 1840, and the only estimates of global Ross seal abundance available at the time (Scheffer 1958: 20 000–50 000, Eklund & Atwood 1962: 50 000) were highly speculative and based on a very small number of sightings from extremely limited sampling. Reflecting this lack of information, Scott (1965) regarded the status of the Ross seal as inadequately known and noted that survey data was required to improve knowledge of status. Subsequently, under the Treaty's Agreed Measures for the Conservation of Fauna and Flora, Antarctic Treaty Consultative Parties decided at their fourth meeting in 1966 that Ross seals 'should not be killed or taken except for scientific purposes' and they should be designated 'Specially Protected Species'. Further to this, in 1971 concern that future possible commercial exploitation of Antarctic seals might have a detrimental impact on populations led to the establishment under the Treaty of the Convention for the Conservation of Antarctic Seals (CCAS). Under Annex I of CCAS the Ross seal was designated as a 'Protected Species', which forbids any killing or capturing for commercial exploitation. More recently, in 1991 the Antarctic Treaty Consultative Parties agreed to expand the existing environmental measures into a comprehensive system for the protection of the Antarctic environment through the establishment of the Protocol on Environmental Protection to the Antarctic Treaty (1991) (hereafter the Protocol). Annex II of the Protocol continues the earlier designation of the Ross seal as a 'Specially Protected Species', without taking into account survey efforts in the 1970s and 1980s that provided improved estimates of Ross seal global abundance (Gilbert & Erickson 1977: 222 000, Erickson & Hanson 1990: 130 000).

In contrast to the protected status afforded to the Ross seal by these Antarctic Treaty agreements, in 1996 the IUCN classified the Ross seal as 'Least Concern', which recognizes that there is adequate data to assess that the species is widespread and abundant, and neither threatened nor near threatened (IUCN 2006). At the time of this decision no new information on status had become available since the 1991 designation by the Protocol, but the Scientific Committee on Antarctic Research's (SCAR) Group of Specialists on Seals had just commenced a program to improve understanding of the status of the Ross and other pack ice seal species (the Antarctic Pack Ice Seals (APIS) program: Anon 1994).

Against this background, and given the collection of new data under the APIS program, the XXIII Antarctic Treaty Consultative Meeting requested SCAR to provide a review of the designation of the Ross seal as a Specially Protected Species under the Protocol. In doing so, SCAR had agreed with the Committee for Environmental Protection to employ the most up-to-date IUCN criteria and principles, and hence, accordingly, the issue of uncertainty needs to be considered.

We report here on a survey to estimate the current status of the Ross seal population in the pack ice off East Antarctica between 64–150°E as part of the APIS program. In particular, we address in the survey design and analysis the many sources of uncertainty in estimating the abundance of this species, and provide both a range of best and plausible estimates, as recommended in Annex I of the IUCN Red List.

## Methods

Although this paper focuses only on the Ross seal, the survey effort aimed to provide data for estimating the distribution and abundance of the three seal species that breed in the pack ice (Ross, crabeater (*Lobodon carcinophaga* (Hombron & Jacquinot)) and leopard (*Hydrurga leptonyx* (Blainville)), and to record additional opportunistic data on a fourth species that breeds in the fast ice (Weddell seal *Leptonychotes weddellii* (Lesson)). In designing the survey, priority was given to the crabeater seal as the primary survey species in order to provide information required under another Antarctic Treaty agreement, the Convention for the Conservation of Antarctic Marine Living Resources (Southwell *et al.* 2007b). Consequently, some of the survey design and sampling decisions favoured the crabeater seal over the Ross seal (e.g. deployment of satellite-linked dive recorders, see later). Details of the methodology and results for the crabeater seal are given in Southwell *et al.* (2007b). A condensed outline of the survey region and methodology as it pertains to the Ross seal is provided below.

### *Survey timing and survey region*

As the crabeater seal was the primary survey species, priority was given to it when choosing the time of year to undertake survey work. The optimal time with respect to crabeater haulout behaviour is December–February (Nordøy *et al.* 1995, Bengtson & Cameron 2004, Southwell 2005a). This time is also optimal with regard to ice conditions and the

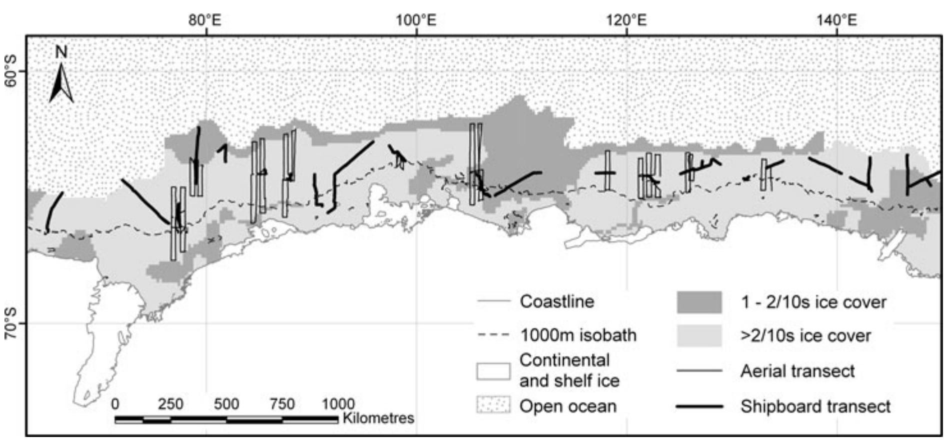


**Fig. 1.** Survey tracklines and distribution of ice at the time of the survey. Note that the short east–west sections joining longer north–south aerial tracklines were not surveyed.

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ability of ships to carry out transects through the pack ice. Ross seals are dependent on pack ice to breed and moult. In East Antarctica Ross seals breed from mid-October to mid-December (Southwell *et al.* 2003), and moulting is thought to occur in January (Skinner & Westlin-van Aarde 1989). The very limited amount of information on movement (Southwell 2005b) suggests that Ross seals stay in the pack ice between these major life history events. Thus within the optimal period for the crabeater seal (discussed above), an optimal period for the Ross seal was considered to be December–January, when all Ross seals, or at least the majority, are thought to inhabit the pack ice and be 'available' for sighting surveys through their haulout behaviour. Survey work was therefore planned to occur during December and January of the summer 1999–2000 (specifically, 4 December 1999–10 January 2000).

The survey region was taken as the area of pack ice between longitudes 64°E and 150°E. At the time of the survey some 1 500 000 $km^2$ had $> 1/10$ ice cover and was considered as suitable habitat for Ross seals.

### *Survey methods*

Double observer line transect sighting surveys of seals hauled out on the ice were conducted from ship and aerial platforms along 9476 km of transect distributed throughout the survey region (Fig. 1). Double observers operated independently from front and back seats in the aircraft and from bridge and above-bridge positions on the ship. Ice and weather conditions placed constraints on the extent to which preferred transect lines could be sampled; the resulting sampling effort was consequently biased away from areas where survey was difficult (e.g. thick ice for ship survey, Southwell *et al.* 2004).

For each seal sighting, observers recorded basic line transect data (distance from the transect line, group size and species), the exact time of the sighting, and a suite of survey and environmental covariates (Southwell *et al.* 2007a) using an automated data logging system (Southwell *et al.* 2002). Sightings by double observers were classified as duplicates (seen by both observers) or singles (seen by one observer) using four criteria (time of sighting, distance from the transect line, species and group size; Southwell *et al.* 2002). After classification, double observer data allowed testing of two critical line transect assumptions (certain detection on the transect line ($g(0) = 1$), and uniformity in the distribution of objects relative to the transect line), and also allowed estimation of $g(0)$ if the former assumption was violated. The $g(0)$ assumption was satisfied in shipboard surveys (Southwell *et al.* 2004) but not in aerial survey (Southwell *et al.* 2007a), and the uniform distribution was violated in shipboard survey for distances $< 40$ m (Southwell *et al.* 2004).

Observers qualified their identification of species as definite or probable, or if identification to species was not possible, recorded the sighting as an unknown species. A decision was made in advance of the survey not to break from the survey track to inspect more closely seals that could not be definitely identified, because this would have reduced the sampling effort. The rationale for this decision was that the increased uncertainty in the abundance estimate that resulted from reduced sampling effort was likely to be greater than the uncertainty resulting from imperfect species identification. It was also thought that most probable or unknown species identifications would occur at moderate to large distances from the transect line, and that the use of line transect analysis would largely account for any bias that could otherwise result from these sightings.

As sighting surveys only provided data to estimate the abundance of seals hauled out on the ice, additional data were required to correct estimates of hauled out seal abundance to total abundance. ARGOS satellite linked dive recorders (SDRs) were deployed on a sample of Ross seals to provide such data. However, because of limited opportunities to capture Ross seals during the survey, the higher priority placed on the crabeater seal as the primary survey species, and the limited number of SDRs available, only two SDRs were deployed on Ross seals during the survey period and within the survey region (Southwell 2003). To increase the sample size for estimation of haulout probability, data from a further nine SDRs deployed on adult and juvenile Ross seals during APIS studies in other regions were also considered (six deployed in the King Haakon VII Sea during 2001–02 (Nordøy & Blix 2005) and three deployed in the Ross Sea during 1999/00 (Ackley *et al.* 2003)). Although the haulout records of these nine seals were not all obtained in the same year as the sighting surveys, all the records overlapped with the month-date range of the survey period. We assumed that variations between individual seals and between dates within the survey period were more important than variations between years and regions of the Southern Ocean. The SDRs measured conductivity at 10 s intervals and summarized the data into 20 min wet/dry periods for transmission. A 20 min period was summarized as wet or dry according to whether the majority of 10 s records for that period were wet or dry, respectively. The 20 min periods were further aggregated into hourly periods and characterized as dry (hauled out) if $\geq 2$ of the three 20 min periods in an hour were recorded as dry.

## Analysis

Estimating Ross seal abundance in the survey region involved three steps: 1) correcting sample counts of hauled out Ross seals for detection probability, 2) correcting sample counts for haulout probability, and 3) inferring density from sampled transects to the entire survey region.

### *Detection probability*

Southwell *et al.* (2007a, 2007b) undertook a comprehensive analysis of detection probability for all seal species sighted from ship and aerial platforms in this survey effort. Prior to their analyses, both shipboard and aerial data were right truncated at 800 m from the transect line to ensure robust estimation of the detection function (Buckland *et al.* 2001), and aerial data were left truncated at 100 m because of reduced visibility directly under the aircraft. Shipboard data were grouped into bins, with the initial bin 0–200 m in width, to negate any bias that might have arisen from the non-uniform distribution of seal groups close to the trackline. Southwell *et al.* analyses considered the effect of a number of animal, survey and environmental covariates on detection probability using conventional multiple covariate line transect models and non-conventional full independence models (Borchers *et al.* 2006). Species, one of the animal covariates considered, was not selected in models for either shipboard or aerial survey, reflecting the generally similar appearance and behaviour, and hence detectability, of the four species. We therefore used the models developed by Southwell *et al.* (2007a, 2007b) from data pooled across all species to estimate the detection probability for Ross seals. Using data pooled across species increased the sample size for estimating detection probability and so minimized the associated variance.

### *Haulout probability*

To estimate the probability of Ross seals being hauled out on the ice at any time of the survey, the hourly values for haulout status obtained from the SDRs were modelled as smooth, non-parametric functions of the temporal variables date and time of day (local solar time) using generalized additive models (GAMs, Hastie & Tibshirani 1990) with a logistic link function and binomial variance. Because the haulout data included many observations (hourly haulout status) for a relatively small number of seals, the individual observations could not be considered truly independent. To account for this 'repeated measures' nature of the data, bootstrap 'replicates' were created by random re-sampling of the entire haulout records for individual seals, with replacement. Thus, a particular seal's haulout record could by chance be included in a bootstrap replicate 0, 1 or more times. A GAM was fit to each of 1000 bootstrap replicates, and the predicted probabilities of haulout as a function of date and time of day were saved for incorporation of the haulout variance into the abundance estimation procedure.

Haulout behaviour was probably influenced by factors additional to date and time of day. For example, weather conditions are known to affect Weddell seal haulout (Sato *et al.* 2003). However, incorporating such additional covariates into the abundance estimation procedure was practically and analytically intractable. It was assumed that the variability in haulout due to such factors would be reflected in the overall uncertainty of the abundance estimate.

### *Combining detection and haulout probabilities to estimate density, and inferring density in the entire survey region from sampled transects by fitting a density surface*

The non-random location of transects undermined the basis for design-based estimates of density and abundance. Consequently, we considered the model-based inference methods of Hedley *et al.* (1999), which involved fitting a density surface as a function of geographic covariates. To apply these methods, ship and aerial transects were divided into approximately 10 km segments and the number ($\hat{N}$) of Ross seals estimated to be present in a given segment was calculated using a Horvitz & Thompson (1952) - like estimator:

$$\hat{N} = \sum_{1}^{g} \frac{n_j}{\hat{d}_j \hat{h}_j} \tag{1}$$

where $g$ is the number of groups sighted in a segment, $\hat{d}_j$ and $\hat{h}_j$ are the estimated overall detection and haulout probabilities respectively for the $j$th sighted group in a segment, and $n_j$ is the number of Ross seals observed in the $j$th group. For the $i$th segment, with known area $A_i$, an estimated density $\hat{D}_i$ was calculated as $\hat{N}_i/A_i$. The segment was subsequently treated as the analytical unit.

A low proportion of segments with Ross seal sightings (definite sightings 3%, definite plus probable sightings 5%) made modelling of a density surface difficult due to the presence of 'excess' zeros. A number of approaches have been proposed for modelling such data. One approach is to separately model presence-absence, and then abundance where present, using an appropriately zero truncated model family. A second approach also involves modelling in two stages, but with the possibility that the present component can still be zero even when the logistic component indicates presence (Zorn 1996, Martin *et al.* 2005). We applied the first approach, which is similar to what Mullahy (1986) calls a hurdle model.

We initially attempted to model presence-absence as a binomial GAM with a logistic link function, and non-zero density as a GAM with a log link function, the GAMs being implemented from the library *mgcv* (Wood 2006) in *v1.8.1.* of the computer package *R* (R Development Core Team 2005). However, after extensive model selection it was eventually decided that the low number of non-zero sightings rendered modelling of these data problematic, and instead non-zero densities were simply modelled as a weighted (by segment area) non-zero mean of the segment densities (i.e. a constant value). To assess whether fitting a flexible density surface improved the precision of the estimates, we decided to model presence-absence in two ways: 1) by fitting a varying surface with the selected model smooths, and 2) by fitting a weighted mean probability surface. The Unbiased Risk Estimator (UBRE, Craven & Wahba 1979, Wood 2006) was used as a model selection criterion in the logistic model in a forward selection procedure. We conservatively included a variable in the model if it lowered the UBRE score, explained a minimum deviance of 4%, and had a significant probability ($P <$ 0.05) associated with it.

Predictive models considered a number of spatial covariates in an effort to produce a robust density surface. Spatial covariates were considered for inclusion in the models as one-dimensional smooths if they were not in a higher interaction. Linear interaction terms were never considered in the absence of a linear main effect. The effective degree of freedom was multiplied by 1.4 in the calculation of UBRE to stop overfitting (Wood 2006). Because the aim of modelling was to predict the distribution of density across the entire survey region on the basis of relationships between density and spatial covariates in sampled areas, only spatial covariates whose values were known with reasonably fine resolution across the entire survey region (i.e. not just along sampled transects) could be considered. Spatial covariates included transformed longitude and latitude and six geographic covariates. The transformations converted longitudes and latitudes onto east–west and north–south nautical mile scales respectively. The geographic covariates included depth, slope, distance to the shelf-break, distance to the ice edge, ice cover and ice width. Depth and slope values for each sampled segment were obtained from satellite altimetry and echo sounding data of sea floor bathymetry (Smith & Sandwell 1997). Taking the shelf-break as the 1000 m isobath which bounds the continental shelf, the shortest distance from each sampled segment to the shelf-break was calculated as a positive value if north of the shelf-break and a negative value if south of the break. Distance to the ice edge was calculated as the shortest distance from each sampled segment to the ice edge. Ice cover for sampled segments was derived from satellite data. Ice width was the north–south distance between the northern and southern edges of the pack ice along the longitude on which the segment was located. Other attributes of ice which have been found to correlate with pack ice seal density, such as floe size and thickness, could not be included as candidate geographic covariates for predictive modelling because there were no data available for these attributes outside of the sampled transect strips. In addition to the six geographic covariates, selected two- and three-way interactions between covariates were considered for inclusion in the model as two- and three-dimensional smooths or as linear interactions, and one non-spatial factor was considered. Interactions of interest were 1) latitude:longitude, 2) distance to shelf-break:distance to ice edge, 3) distance to shelf-break:ice width, 4) distance to ice edge:ice width, and 5) distance to shelf-break:distance to ice edge:ice width. The non-spatial factor (survey platform) was considered to model any difference in segment density associated with the use of the ship or aircraft.

The presence of unaccounted spatial correlation was investigated by plotting semi-variograms of the residuals on the transformed longitude and latitude scales. No immediate increase in variance associated with omnidirectional distance was detected.

After model selection, the value of each selected covariate was calculated for each cell in a 0.25 degree resolution grid between longitudes 64–150°E and latitudes 60–70°S. The predictive presence-absence model was then used to compute the probability of Ross seals being present for each cell in the survey region deemed to be within the pack ice (all cells in the grid except those north of the ice edge or those covered by fast ice, shelf ice, continental ice or ice

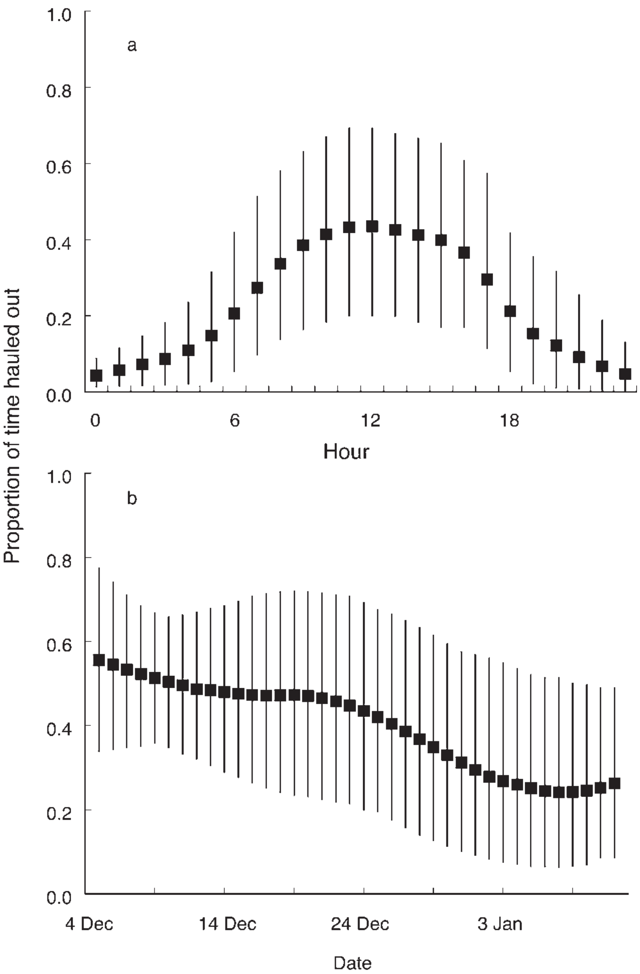


**Fig. 2.** Modelled haulout profile of Ross seals. **a.** By hour within a day, for the mid-point of the survey period (23 December). **b.** Across days within the survey period, for solar midday. Vertical lines are 95 percentile ranges, and closed squares are medians, of the 1000 bootstrap replicates.

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free land; these cells were assumed to have zero or trivial densities compared with cells in the pack ice). Two probabilities were calculated, one from the variable surface presence-absence model and one from the weighted mean probability of presence surface. Probability of presence was estimated for cells within the pack ice zone even though some contained zero or very low ice cover (polynyas). Two point estimates of abundance for the entire survey region were obtained as the product of predicted probability of presence from either the variable surface or the weighted mean surface presence-absence models, the predicted weighted mean non-zero density, and the area of the grid cell.

### *Variance estimation*

Ninety five percent confidence intervals for the abundance estimates derived from the two presence-absence models were constructed by bootstrapping around the entire estimation process (i.e. estimating detection probability, estimating haulout probability, and extrapolating density from sampled to unsampled areas using the predictive model), where day of survey was the bootstrapping unit and 1000 bootstrap replicates were taken. Day was chosen as the sampling unit because it represented a spatially distinct, and therefore probably independent, set of transects.

## Results

A total of 3347 groups of seals were sighted within sampled strips along the 9476 km of ship and aerial transect, of which 115 were identified as definite or probable Ross seals, 2959 as definite or probable crabeater, leopard or Weddell seals, and 273 could not be identified to species. All but three Ross seal sightings were of solitary animals; the three exceptions were pairs.

The presence of a large number of unidentified sightings relative to the number of Ross seal sightings, and of a substantial proportion of sightings considered as probably (40 from 115, or 35%) rather than definitely (65%) Ross seals, leads to some uncertainty in estimating Ross seal abundance related to species identification. Southwell *et al.* (2007b) argued that exclusion of unidentified sightings from estimation of crabeater seal abundance would not have seriously biased abundance estimates because almost all unidentified sightings were located at moderate to large distances away from the transect line, and the use of line transect analysis would largely account for any bias that could otherwise result from exclusion of these sightings. We argue here that the same would be true for Ross seal data. To address uncertainty related to the non-trivial proportion of Ross seal sightings recorded as probable rather than definite, we used definite sightings only to provide a minimum estimate of abundance, and definite plus probable sightings to provide a maximum estimate, for each of the two model-based estimation options.

### *Detection probability*

Detection functions based on data pooled across all seal species sighted in the survey are given in Southwell *et al.* (2007a). Based on these detection functions, estimated mean detectability of Ross seals in the strips sampled from the air was 0.518 for definite sightings and 0.573 for definite plus probable sightings, with corresponding estimates of 0.523 and 0.580 for ship survey. Detectability of individual sightings across both types of survey platform ranged from 0.322–0.596 for definite sightings and from 0.343–0.666 for definite plus probable sightings.

### *Haulout probability*

Ross seals displayed a unimodal pattern of haulout during the survey period, peaking around solar midday (Fig. 2a). The median proportion of time hauled out remained relatively constant across the first half of the survey period, with seals spending approximately half of their time on ice and in the water around solar midday (Fig. 2b), but declined through the second half of the survey period. At the end of the survey the median proportion of time hauled out at solar midday was around 0.3. There was considerable variability in haulout behaviour between individuals, resulting in relatively large 95% percentile ranges around mean or median proportions of time hauled out at any date or time in the survey (e.g. the estimated median proportion at solar midday on 23 December was 0.435, with 95% percentile range of 0.198–0.694).

### *Segment densities*

A total of 1085 segments were used for developing predictive models. The distribution of estimated density by segment

**Table I.** Predictive models of the probability of Ross seals being present, and predicted abundance for the survey region, based on two species identification criteria (definite and definite plus probable) and two modelling approaches (variable surface presence-absence (VSPA) and weighted mean presence-absence (WMPA)). Confidence intervals include variance associated with using the predictive model and in estimating detection probability and haulout probability.

| Species identification | Selected variables | % deviance explained | Model | Estimated abundance | 95% confidence interval |
|---|---|---|---|---|---|
| Definite | s(Longitude) + s(Distance to shelf-break) | 17.1 | VSPA | 42 100 | 26 800–226 600 |
| | | | WMPA | 41 700 | 20 500–131 700 |
| Definite and probable | s(Distance to shelf-break) + s(Distance to ice edge) | 13.9 | VSPA | 41 300 | 24 700–147 400 |
| | | | WMPA | 55 900 | 27 700–187 500 |

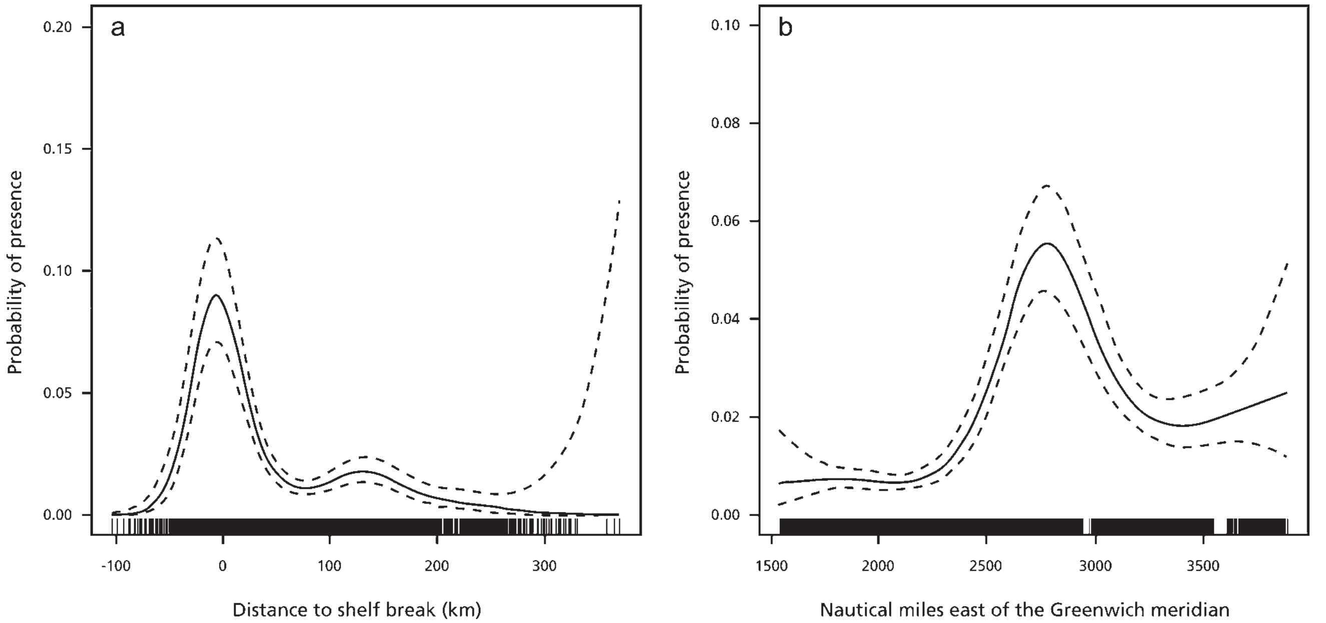


**Fig. 3.** Modelled relationships, based on definite sightings, between the probability of Ross seal presence and spatial covariates. **a.** distance to the shelf-break. **b.** longitude.

was highly skewed, with a large proportion of segments (>95% for definite and definite plus probable sightings) having zero sightings and hence zero estimated density. The mean and range of estimated density per segment was 0.03 (0–2.71) for definite sightings and 0.04 (0–2.47) for definite plus probable sightings.

*Predictive models*

The model for Ross seal presence-absence based on definite sightings contained a smooth of longitude (transformed) and distance to the shelf-break, and explained 17.1% of the deviance (Table I). Figure 3 shows that predicted probability of presence for definite sightings peaked

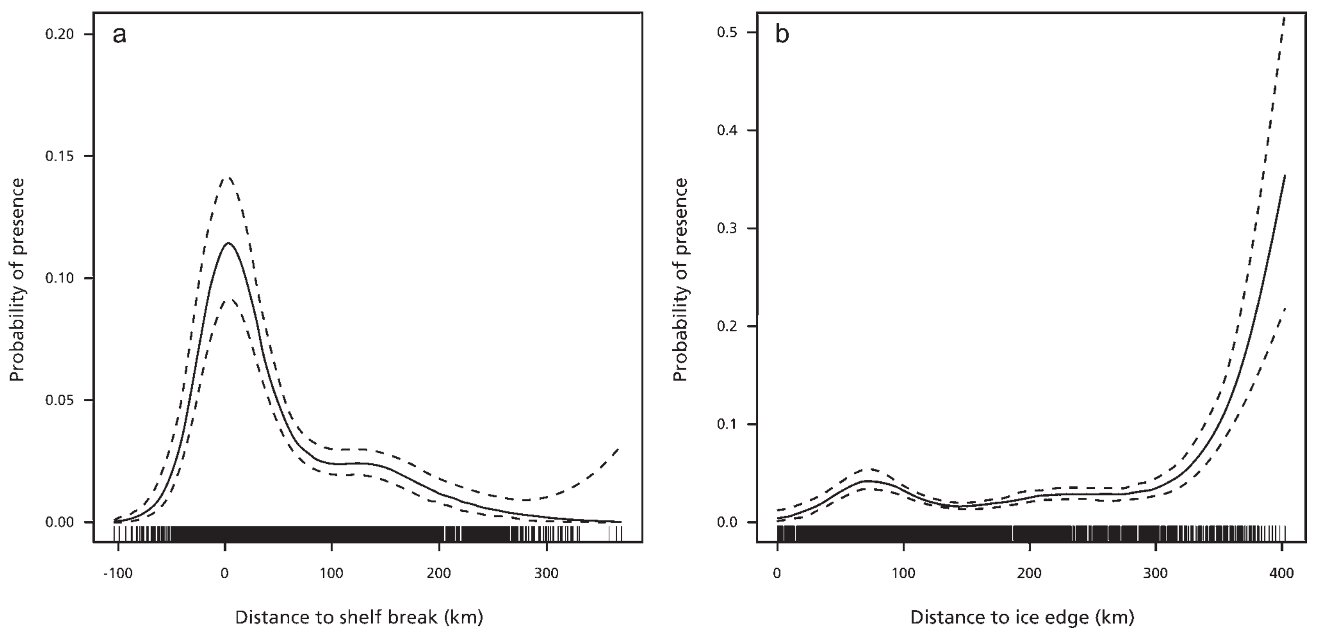


**Fig. 4.** Modelled relationships, based on definite plus probable sightings, between the probability of Ross seal presence and spatial covariates. **a.** distance to the shelf-break. **b.** distance to the ice edge.

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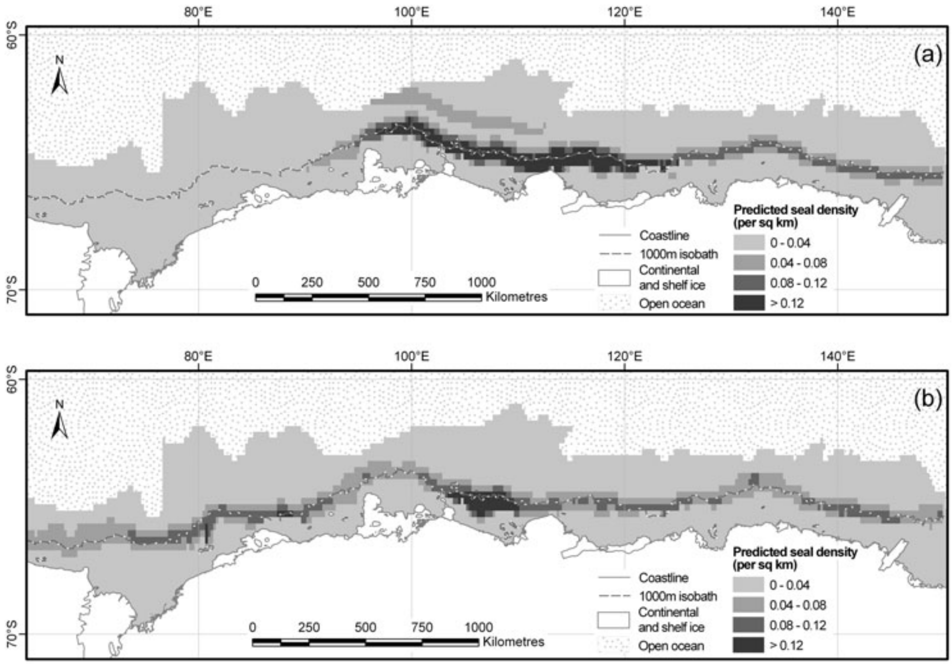


**Fig. 5.** Predicted Ross seal distribution, based on the predictive model. **a.** For definite sightings only. **b.** For definite plus probable sightings.

sharply over the shelf-break and was higher in the middle of the survey region than at the eastern or western edges. The best model for definite plus probable sightings contained a smooth of distance to the shelf-break and distance to the ice edge and explained 13.9% of the deviance. Predicted probability of Ross seal presence based on definite plus probable sightings remained low for 300 km south from the ice edge and thereafter increased sharply, and the relationship with distance to the shelf-break was similar to that for definite sightings (Fig. 4). In accordance with these modelled relationships, the main feature of the predicted density surface maps in Fig. 5 is a band of relatively high density corresponding with the shelf-break region.

### *Estimated abundance in the survey region*

When only definite sightings were considered, point estimates of abundance were slightly over 40 000 for both variable surface and weighted mean presence-absence models (42 100 and 41 700, Table I). When both definite and probable sightings were considered, a similar point estimate was obtained using the variable surface model (41 300) but a higher estimate was obtained using the weighted mean model (55 900). The slightly higher estimate for definite sightings than for definite plus probable sightings for the variable surface presence-absence model (42 100 vs 41 300 respectively) is counterintuitive; this is an artefact of extrapolating over the entire predictive grid with a flexible GAM (mean density for the sampled segments was actually lower for definite than definite plus probable sightings).

### *Uncertainty*

The distributions of the 1000 bootstrap abundance estimates derived from presence-absence models were skewed to the right (see distributions for the variable surface presence-

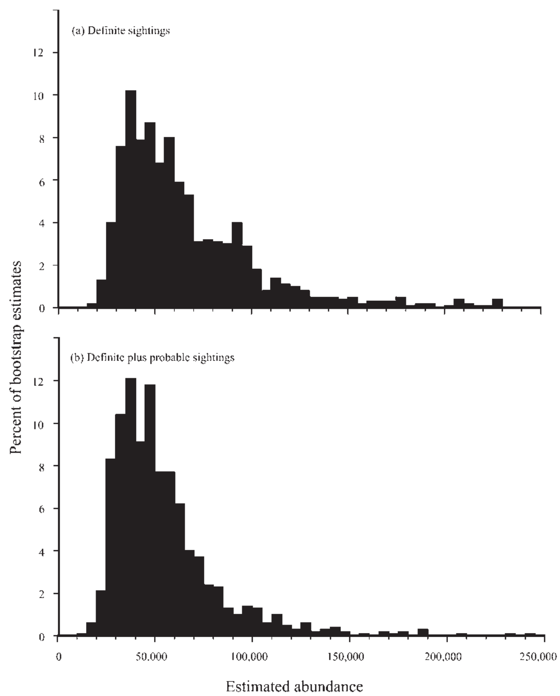


**Fig. 6.** Distribution of 1000 bootstrap abundance estimates derived from variable surface presence-absence models. **a.** For definite sightings only. **b.** For definite plus probable sightings.

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absence model in Fig. 6). The conservative ends of 95% confidence intervals (2.5 percentiles) ranged from 20 500–27 700 animals (Table I). Upper 97.5% percentiles ranged from 131 700–226 600.

## Discussion

Obtaining highly certain estimates of Ross seals abundance is fraught with difficulty. The species inhabits one of the most remote and inaccessible regions on earth where the practical problems of impenetrable ice and frequent poor weather hinder random or pseudo-random sampling, even with the most powerful icebreaking ships or long range aircraft. Furthermore, even though the Ross seal is dependent on the pack ice to breed and moult during the summer when accessibility and survey is easiest, our results show the species spends relatively large amounts of time in the ocean at this time, thus contributing to low sighting rates and infrequent capture opportunities. Added to these practical difficulties are the analytical challenges of attempting to make unbiased inferences for the entire survey region from a survey effort that is invariably non-random and has many zero observations, and of realistically quantifying all of the uncertainties in the estimation procedure.

Previous survey work in East Antarctica in the 1970s and 1980s provided the basis for a regional population estimate of 52 000 Ross seals in a region of similar size and location (90–160°E) to our survey (64–150°E). Our 'best' estimates of Ross seal abundance between 64–150°E in 1999–2000 were of a similar magnitude (41 300–55 900) to Erickson & Hanson's (1990) estimate, but there was considerable uncertainty associated with our estimates, the most conservative (lower 2.5% percentile) being 20 500 and the most optimistic (upper 97.5% percentile) 226 600. In general, previous attempts to estimate pack ice seal abundance have reported point estimates and not quantified the uncertainty around these estimates, or only partially quantified uncertainty, which would have lead to more confidence being placed in those estimates than was justified. Over the last three decades there has been a growing recognition of the many potential sources of uncertainty in wildlife abundance estimation, and the need to quantify all, or at least the major sources, of this uncertainty (Williams *et al.* 2002). We suspect that earlier estimates would have probably had uncertainties of similar magnitude to those encountered in our study.

With uncertainties of this magnitude, it would be possible to detect only very gross changes in abundance from repeated surveys using the same survey design, methods and effort. This raises the question of whether uncertainty in any future surveys might be reduced using the knowledge and experience gained in this survey to allow improved detection of population trends?

The major constraint to reducing uncertainty lies in the low encounter rate. This creates uncertainty in extrapolating to unsurveyed areas due to the small number of sightings available for developing predictive models, and uncertainty in estimating haulout probability due to the limited opportunities for capture and deployment of SDRs. Low encounter rate would also create uncertainty in estimating detection probability, but we circumvented this by pooling data across species. One option for reducing uncertainty might be to undertake surveys at another time of year if encounter rates are higher at other times: Bester *et al.* (1995), for example, observed higher encounter rates of Ross seals in January–early February, when pack ice was less extensive, than in December, in surveys off the Princess Martha coast. This option may only be helpful at very limited times of year however, because 1) encounter rates may be even lower through the winter and spring, even if Ross seals spend more time on the ice in these seasons, as the extent of pack ice is much greater and seals are likely to be more dispersed, and 2) encounter rates are also likely to be low in late summer and autumn because satellite tracking has shown a major proportion of Ross seals migrate north to the open ocean in these seasons (Blix & Nordøy 1998, Nordøy & Blix 2001) where they are completely unavailable to the survey methods used by us (thus creating an additional and more serious problem of bias). The obvious solution of simply increasing the sampling effort in the sighting survey is unlikely to be possible in the future unless alternate, more cost-effective survey platforms become available in the future. Our estimates appear to be relatively robust to uncertainties in species identification given the use of line transect analysis, hence we would not recommend that any future line transect surveys attempt to improve species identification rates by breaking from the transect line if this substantially reduces the sampling effort. In short, we can see little opportunity for improvement unless new technologies provide alternate survey methods or survey platforms.

There is also some uncertainty in assessing past trends in Ross seal populations in East Antarctica related to some differences in data collection and analysis methods between this and previous survey work. Firstly, the earlier survey work discussed above used strip transect methods and as such did not estimate and correct for detection probability, which probably resulted in some negative bias in abundance estimation. Secondly, although earlier counts were corrected for haulout, the correction was only partial, and again this may have resulted in some negative bias. Complete correction is possible with data obtained from SDRs, but this technology was not available to researchers in the 1970s and 1980s, who had to rely on observational data which can only estimate the relative (to time of peak haulout), rather than absolute, probability of being hauled out. Finally, earlier researchers did not use model-based inference to infer from sampled transects to the entire survey regions. If they encountered similar problems as we did in undertaking random transects, their use of design-based inference may have lead to some bias in abundance estimation, but it is not possible to predict the direction that any such bias would have taken.

Two-stage modelling is one solution to the problem of dealing with excess zeros, but this approach can introduce a bias in modelling animal abundance if false zeros are implicit in the data (Borchers unpublished). Given our estimates of Ross seal detectability in the sampled transects, we believe that false zeros would have been inherent in our data, and consequently the abundance estimates provided here would be negatively biased to some extent. A second potential source of negative bias relates to the representativeness of seals sampled (captured) for haulout behaviour. While the sample of seals used to measure haulout should ideally have been random to ensure representativeness, in practise it is only possible to capture seals for deployment of SDRs when they are hauled out on the ice. Due to this practical constraint on sample selection, the capture sample may be biased towards those seals most likely to haul out, thereby over-estimating haulout probability and under-estimating abundance.

The distribution of Ross seal sightings in our survey, and the predictive models developed from those sightings, confirm that the Ross seal has a widespread summer distribution throughout the pack ice in East Antarctica. The tendency for a large proportion of Ross seals to inhabit the most inaccessible regions of our survey region at those limited times of the year when sighting surveys are feasible will continue to present challenges in assessing with high certainty the status of and trends in this species' population in the region.

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