Taking account of dependent species in management of the Southern Ocean krill fishery: estimating crabeater seal abundance off east Antarctica

Colin Southwell
Department of the Environment and Water Resources, Australian Antarctic Division

Charles G. M. Paxton
School of Mathematics and Statistics, University of St Andrews, North Haugh, St Andrews KY16 9SS, Scotland

David Borchers
School of Mathematics and Statistics, University of St Andrews, North Haugh, St Andrews KY16 9SS, Scotland

Peter Boveng
Alaska Fisheries Science Center, NOAA Fisheries

William de la Mare
School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada

Journal of Applied Ecology 2008, **45**, 622–631 doi: 10.1111/j.1365-2664.2007.01399.x

Taking account of dependent species in management of the Southern Ocean krill fishery: estimating crabeater seal abundance off east Antarctica

Colin Southwell[1]*, Charles G. M. Paxton[2], David Borchers[2], Peter Boveng[3] and William de la Mare[4]

[1]*Department of the Environment and Water Resources, Australian Antarctic Division, Channel Highway, Kingston, Tasmania, 7050, Australia;* [2]*School of Mathematics and Statistics, University of St Andrews, North Haugh, St Andrews KY16 9SS, Scotland;* [3]*Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Way Point NE, Seattle, WA 98115, USA; and* [4]*School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada*

Summary

1. The crabeater seal *Lobodon carcinophaga* is considered to be a key species in the krill-based food-web of the Southern Ocean. Reliable estimates of the abundance of this species are necessary to allow the development of multispecies, predator–prey models as a basis for management of the krill fishery in the Southern Ocean.

2. A survey of crabeater seal abundance was undertaken in 1500 000 km^2 of pack-ice off east Antarctica between longitudes 64–150° E during the austral summer of 1999/2000. Sighting surveys, using double observer line transect methods, were conducted from an icebreaker and two helicopters to estimate the density of seals hauled out on the ice in survey strips. Satellite-linked dive recorders were deployed on a sample of seals to estimate the probability of seals being hauled out on the ice at the times of day when sighting surveys were conducted. Model-based inference, involving fitting a density surface, was used to infer densities in the entire survey region from estimates in the surveyed areas.

3. Crabeater seal abundance was estimated to be between 0·7 and 1·4 million animals (with 95% confidence), with the most likely estimate slightly less than 1 million.

4. *Synthesis and applications.* The estimation of crabeater seal abundance in Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) management areas off east Antarctic where krill biomass has also been estimated recently provides the data necessary to begin extending from single-species to multispecies management of the krill fishery. Incorporation of all major sources of uncertainty allows a precautionary interpretation of crabeater abundance and demand for krill in keeping with CCAMLR's precautionary approach to management. While this study focuses on the crabeater seal and management of living resources in the Southern Ocean, it has also led to technical and theoretical developments in survey methodology that have widespread potential application in ecological and resource management studies, and will contribute to a more fundamental understanding of the structure and function of the Southern Ocean ecosystem.

Key-words: aerial survey, dependent species, double observer, line transect, model-based inference, krill harvest management, shipboard survey

Introduction

The living resources of the Southern Ocean have long been exploited by humans. Initially, upper trophic taxa such as fur seals and whales were exploited, but in recent decades exploitation has targeted taxa from lower trophic levels, particularly fish and krill. Exploitation of lower trophic levels has the potential to impact both the harvested species and dependent species from higher trophic levels.

The krill fishery (*Euphausia* spp.) has been the largest fishery in the Southern Ocean since the late 1970s (Croxall & Nicol 2004), with a catch of 100 000–500 000 tonnes per annum

*Correspondence author. E-mail: colin.southwell@aad.gov.au

over the past 25 years. The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), brought into force in 1982, is responsible for managing the harvesting of krill, and was the first convention to apply an 'ecosystem approach' to fisheries management by ensuring specifically that exploitation is sustainable for not only the harvested species but also for dependent species from higher trophic levels (Edwards & Heap 1981). Meeting CCAMLR's objective of managing the krill fishery to take account of dependent species requires better knowledge of the abundance of major krill predators. This information contributes to establishing management objectives for krill escapement from the fishery through calculation of the standing stock of krill required to support predators. In addition, management of the krill fishery is also supported by surveys of krill abundance, but there is considerable uncertainty in these abundance estimates (Nicol, Constable & Pauly 2000). Information on predator abundance helps to define a lower bound for krill abundance by reconciling estimates of krill abundance and natural mortality rate with the amounts of krill consumed by predators. Natural mortality is a key parameter in estimating krill sustainable yields, and precautionary catch limits for krill can be calculated directly from estimates of the quantity of krill consumed by predators (Everson & de la Mare 1996).

As an abundant, widespread, large-bodied predator of krill, the crabeater seal *Lobodon carcinophaga* is considered a key species in the krill-based food-web of the Southern Ocean and a priority in multispecies models for management of the krill fishery. However, existing estimates of crabeater seal abundance vary widely and may not be relevant to current management because they are based on data collected up to three decades ago, and have potential biases and uncertainties that have not been identified or quantified fully. Improved and current estimation of crabeater seal abundance is therefore a priority for multispecies management of the krill-based ecosystem.

This paper reports on a survey of crabeater seal abundance off east Antarctica between longitudes 64–150° E. The region surveyed was broadly similar to the location of an earlier survey of krill biomass and distribution (Pauly *et al.* 2000) and straddled a number of CCAMLR management and reporting areas (Fig. 1a). The survey was also a contribution to the Antarctic Pack-Ice Seals programme (Anon 1995) which aimed to estimate the regional and circumpolar abundance of all pack-ice seal species.

Materials and methods

SURVEY REGION BOUNDARIES AND ESTIMATING THE AREA OF PACK-ICE IN THE SURVEY REGION

The crabeater seal has a circumpolar distribution and is thought to be totally or largely confined to the pack-ice zone. The survey region was taken as the area of pack-ice between longitudes 64–150° E. Pack-ice comprises floes of frozen sea-water drifting with wind and water currents, and is bounded to the north by open ocean and to the south by fast-ice (extensive, unbroken sheets of ice), shelf-ice (floating extensions of continental-ice), the Antarctic continent, or occasionally open water. Because the location of the pack-ice edge varies substantially over both short and long time-scales, definition of the survey region boundary, and hence the size of the survey region, was more complex than in most survey applications.

We used ice maps produced by the National Ice Center (www.natice.noaa.gov) to delineate the location of the pack-ice edge during the survey period. These maps are produced weekly from several sources of remotely sensed and *in situ* information. For each 5° longitudinal span of the survey region, the northern and southern pack-ice edges were taken from the weekly ice map whose date range included the dates of survey effort in that sector.

Within this composite pack-ice edge, the distribution of ice-cover was obtained from sea-ice concentrations derived by Comiso (2003) from passive microwave imagery. The daily grids (*c.* 25×25 km cells) of sea-ice concentration were temporally smoothed by a 3-day moving average to reduce daily variation and eliminate occasional gaps in satellite coverage. Estimates of ice concentration for any date and location were then extracted from the appropriate daily grid as the concentration value in the grid cell containing the location.

SURVEY EFFORT AND TRANSECT PLACEMENT

Sighting surveys were undertaken from an icebreaker (RSV *Aurora Australis*) and two helicopters (Sikorsky S76) based from the ship over the period 4 December 1999–10 January 2000. It was not possible to design a fixed sampling plan in advance of the survey, first because the location of the pack-ice edge was not known prior to the survey and secondly because of the effect of unpredictable ice and weather conditions on the ability to travel along predetermined transect lines. The survey plan was for the ship to undertake a zig-zag pattern of transects across the survey region from east to west and from the northern ice-edge to as far south as possible, and each day when weather allowed, for the helicopters to undertake north–south transects from the ship across the full north–south extent of the pack-ice, or as far as weather and aircraft range allowed. The aim of maximizing the north–south range of flights limited the extent to which flight lines could be separated in an east–west direction to achieve independence; we chose a 10 nm separation in an attempt to optimize this trade-off. During the 24 days when aircraft were available, aerial survey was possible on 10 days, two to six north–south flight lines were undertaken on each of these days, and a total of 37 north–south flight lines were completed (Fig. 1b).

SURVEY METHODS

Shipboard surveys were conducted each day between 0500 h and 2000 h local time while the ship was moving. A two-person observer team operated on each side of the bridge at all times while on effort. Teams searched continuously without optical equipment to the limit of visibility during 55-min sessions, separated by 5-min 'changeover' periods when teams rotated between positions or were replaced by a fresh team. During a subsample of times throughout the survey, additional teams operated from positions above the bridge on each side of the ship (termed 'double observer' mode). These above-bridge teams searched the same area independently and collected the same form of data on sighting a group of crabeater seals, as did bridge teams.

Aerial surveys were conducted at altitude 130 m and speed 90 knots within the time of peak haulout by crabeater seals (approximately 0900–1500 h local time; Southwell (2005a) and Results). Aerial observers operated individually and independently from the front and/or back seats on each side of the aircraft. Flights of up to 2·5 h

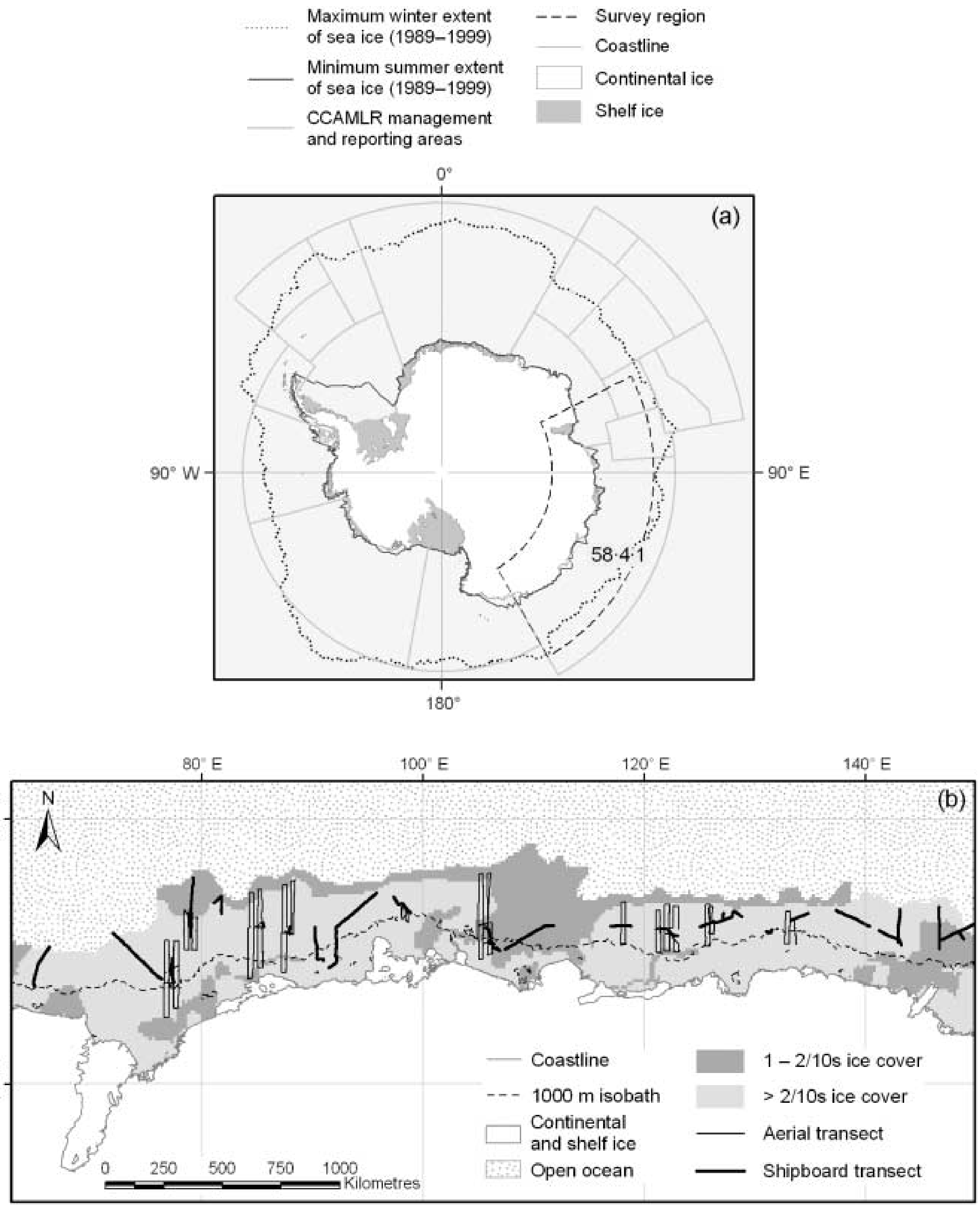

Fig. 1. Location of (a) the survey region in Antarctica and (b) survey tracklines and distribution of ice at the time of the survey. Note that the short east–west sections joining longer north–south aerial tracklines were not surveyed.

duration were broken into 20-min sessions of search effort separated by rest periods of 2–5 min. Double observer mode, with paired observers searching the same area independently from front and back seats on each side of the aircraft, was employed during most flights. Single observer mode (single observer only on each side of the aircraft) was used occasionally to increase north–south range by decreasing the helicopter's payload. Observers searched for seals hauled out on the pack-ice and truncated their search effort to within 1000 m from the flight path.

Crabeater seals needed to be distinguished from a number of other less frequently sighted seal species of similar appearance. Observers recorded data for all species sighted and qualified their identification of species as definite or probable, or if identification to species was not possible, recorded species as unknown. On sighting a seal group, both shipboard and aerial observers recorded basic line transect data (perpendicular distance from the trackline and group size), and the time that the group passed abeam of the survey platform, using an automated data logging system (Southwell *et al.* 2002, 2004). As all species occur in small, tight groups when hauled out on the pack-ice, the seal group was considered as the sighting unit.

In addition to recording these animal-level data, a number of continuous (c) or factor (f) survey-level covariates were recorded for each sighting. For both shipboard and aerial survey these were: side of platform (f: left or right), position in platform (f: bridge or above-bridge, front or back seat) and ice-cover (c). The following covariates were recorded for aerial survey only: observer identity (f), cumulative experience of observer during the survey (c), time since the start of the flight (c), time since start of the session (c), visibility (f: poor, good or excellent), glare (f: present or absent) and shadow (f: present or absent).

Following the survey, sightings of seal groups by paired observers operating in double observer mode were classified as having been seen by only one of the observers ('single sighting') or both observers ('duplicate sighting') using the criteria outlined in Southwell *et al.* (2002). A pair of sightings by double observers, once classified as a duplicate sighting, was considered subsequently to be a single group detected by both observers.

The extent to which conventional line transect (CLT) sampling assumptions were met for shipboard and aerial surveys was investigated by Southwell *et al.* (2004, 2007). Double observer data indicated that the critical assumption of CLT sampling (certain detection on the trackline) was satisfied in shipboard survey but violated in aerial survey. Double observer data also allowed testing the assumption of a uniform distribution of objects in relation to the trackline, potentially violated for shipboard survey because of the need to deviate from a straight-line track to avoid heavy ice. This assumption was violated only at distances of < 40 m from the trackline (Southwell *et al.* 2004). Reactive movement by seals during shipboard survey resulted in lower than expected frequency of sightings close to (< 25 m) the trackline (Southwell *et al.* 2004), but had little effect on aerial sighting frequencies (Southwell 2005b). Obstruction to visibility directly underneath the aircraft by the window configuration resulted in a low frequency of sightings within 75 m of the flight path.

HAULOUT

Satellite-linked dive recorders (SDRs), which transmitted data through the Argos satellite system (Anon 1996), were deployed on 24 adult crabeater seals (Southwell 2005a) within the survey region to estimate the probability of seals being hauled out on the ice. Only one of these SDRs, deployed in December 1999, transmitted haulout data during the sighting surveys. The remaining 23 SDRs were deployed in the survey region during winter and spring (August–November) over 5 years prior to the survey (1994–98). Because these SDRs ceased transmitting data at most 3 months after deployment, they did not provide haulout data during the surveys. However, 12 of the 23 SDRs transmitted data through the period 4 December–10 January of the summer following deployment. In addition, data from a further nine SDRs deployed on crabeater seals outside the survey region (in the eastern Ross Sea) were considered in the analysis. The sample sizes were too small to test for differences in haulout probability among years and regions. We used data from SDRs that transmitted data in the survey period (4 December–10 January), regardless of year and region, to estimate haulout probability for crabeater seals during the survey. 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 aggregated further into hourly periods and characterized as dry (hauled out) if ≥ 2 of the three 20-min periods in an hour were recorded as dry.

ANALYSIS

Estimating detection probability for shipboard survey

Shipboard data were right-truncated at 800 m from the ship's track to ensure robust estimation of the detection function (Buckland *et al.* 2001). Left-truncation was not required. Data were grouped into bins of size 0–200, 201–400, 401–500, 501–600, 601–700 and 701–800 m to negate bias resulting from reactive movement or non-uniform distribution of seal groups within 200 m from the trackline.

As there was evidence that all groups of seals hauled out on the trackline were detected during shipboard survey (Southwell *et al.* 2004), CLT analysis methods were used. The effects of animal- and survey-level variables on detection probability were assessed with a multiple covariate CLT (MCLT) analysis using *Distance 4* (Thomas *et al.* 2002). Variables were selected using a sequential forward stepwise process on the basis of Akaike's information criterion (AIC).

Estimating detection probability for aerial survey

Aerial data were right-truncated at 800 m from the flight path to ensure robust estimation, and left-truncated at 100 m due to obstructed visibility close to the flight path. The trackline for aerial data is hereafter considered to be at 100 m.

Because detection on the trackline may be below one, and Southwell *et al.* (2007) found evidence of correlation in sightings of seal groups by double aerial observers away from the transect line, we used the method of Borchers *et al.* (2006; termed 'point independence': PI) to estimate detection probability. The PI method assumes independence between detections by double observers only on the transect line, and uses MCLT methods to estimate the detection function shape [$g_.(x, \mathbf{z})$] and sight–resight data to estimate the detection function intercept [$\hat{p}_i(0, \mathbf{z})$]. Here x is perpendicular distance and $\mathbf{z}$ is a vector of other covariates in the model.

To estimate $g_.(x, \mathbf{z})$ from double observer data, sightings from double observers are pooled. We use $p(\,)$ to denote detection functions which may be < 1 at distance zero, and $g(\,)$ for those which are 1 at distance zero. The MCLT detection function for observer i [$\hat{g}_i(0, \mathbf{z})$; $i = 1, 2$] is estimated using only data from that observer. An estimate of the combined observer detection function intercept [$\hat{p}_i\,(0, \mathbf{z})$] is obtained from analysis of the sight–resight data generated by the double observers, assuming independent detections at all x, and using a logistic detection function form. This latter estimation process is called a 'full independence' (FI) analysis (Borchers *et al.* 2006). The probability of at least one observer detecting a group at perpendicular distance x with covariates $\mathbf{z}$ [$\hat{p}_i\,(x, \mathbf{z})$] is then estimated by $\hat{p}_.(x, \mathbf{z}) = \hat{p}_.(0, \mathbf{z})\,\hat{g}_.(x, \mathbf{z})$.

We used binary regression with a logistic link and Bernoulli error function to model detection probability. Generalized additive models (GAMs) were used to allow for non-monotonic effect of explanatory variables. The FI detection probability for observer i is then:

$$p_i(x, \mathbf{z}) = \exp\left(\theta_0 + s_x(x) + \sum_k s_k(z_k)\right) \Bigg/ \left(1 + \exp\left(\theta_0 + s_x(x) + \sum_k s_k(z_k)\right)\right) \qquad \text{eqn 1}$$

where θ_0 is a parameter to be estimated and the s_k are one-dimensional smoothing splines (also to be estimated) for each of the k covariates associated with the sightings making up the vector $\mathbf{z}$. Model selection included consideration of linear effects rather than smoothing splines s_x and s_k. Detection functions were fitted using the R library *mgcv* (Wood 2001) and the iterative procedure of Buckland *et al.* (1993). Under the FI assumption the probability of at least one observer detecting a group with variables x and $\mathbf{z}$ is:

$$p_.(x, \mathbf{z}) = p_1(x, \mathbf{z}) + p_2(x, \mathbf{z}) - p_1(x, \mathbf{z})p_2(x, \mathbf{z}). \qquad \text{eqn 2}$$

In the case of the single observer aerial data, the detection function form and parameter estimates obtained for a single observer from the FI analysis were also used to estimate the single observer detection function intercept.

Estimating haulout probability

The hourly values for haulout status of crabeater seals were modelled as smooth functions of date and time of day (local solar time) using GAMs with a logistic link function and binomial variance. Haulout probabilities were assumed not to vary spatially over the survey region, hence no spatial variables were considered in the model. Because the haulout data included many observations (hourly haulout status) for a relatively small number of seals, the individual observations could not be considered independent. To account for this 'repeated-measures' nature of the data, bootstrap 'replicates' were created by random resampling of the entire haulout records for individual seals, with replacement. A GAM was fitted 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 into density estimation.

SPATIAL MODELLING OF DENSITY

A non-random location of transects resulting from unfavourable ice and weather conditions undermined the basis for design-based estimates of density and abundance outside the surveyed transects for shipboard survey (Southwell *et al.* 2004). The same may be true for aerial survey. Consequently, we used the model-based inference methods of Hedley, Buckland & Borchers (1999).

To apply these methods, ship and aerial transects were divided into 5-km segments and the number ($\hat{N}$) of crabeater seals estimated to be present in a given segment was calculated using a Horvitz & Thompson (1952)-like estimator:

$$\hat{N} = \sum_{1}^{j} \frac{n_j}{\hat{d}_j \hat{h}_j}. \qquad \text{eqn 3}$$

where $\hat{d}_j$ and $\hat{h}_j$ are the estimated detection and haulout probabilities for the jth sighted group in a segment, respectively, and n_j is the number of seals in the jth group. For the ith segment, with known area A_i, an estimated density $\hat{D}_i$ was calculated as $\hat{N}_i / A_i$. The segment was treated subsequently as the sample unit, and $\hat{D}_i$ as the response variable, when fitting a density surface. Use of single observer mode on some flights resulted in a bimodal distribution of segment areas even though segment length was constant. To accommodate variation in segment area, weights proportional to segment area were used in fitting the density surface to the $\hat{D}_i$ s.

To model the response density as a function of K spatially referenced covariates contained in the vector **u**, a quasipoisson GAM with square root link function was used:

$$E(\hat{D}_i) = \left(\theta_0 + \sum_{k=1}^{K} s_k(u_{ik})\right)^2, \qquad \text{eqn 4}$$

where θ_0 is the intercept parameter and the s_k are one-dimensional smooth functions (thin plate smoothing splines) of the K spatial covariates. Two- and three-way interactions between the selected spatial covariates (see below) were also considered for inclusion in the model via two- and three-dimensional smooths (using thin plate splines, Wood 2003), or as linear interactions. Variance assumptions were checked by reference to plots of the standardized Pearson residuals against fitted values. Generalized cross-validation was used for model selection, augmented with diagnostic plots, using the principles described in Wood (2001). We included a variable in the model if it lowered the generalized cross-validation score, explained a minimum deviance of 4% and had a significant probability associated with it. All available spatial covariates were considered for inclusion in the model 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.

A variogram showed no evidence of spatial correlation between sampling units over distances < 100 nm. There was a distinct rise in spatial correlation at distances > 100 nm, which we considered an artefact rather than real spatial correlation: it is correlation at short distances that is of importance to statistical independence.

MODELS FOR PREDICTING ABUNDANCE IN THE SURVEY REGION

As the modelling aim here was empirical prediction of density over space rather than explaining what drives distribution, candidate covariates were chosen with regard to their potential predictive capability and availability across the entire survey region rather than their ecological relevance *per se*. Covariance between spatial covariates can lead to spurious interpretation of explanatory models but does not impair the construction and use of empirical prediction models. Consequently, we were not concerned about possible covariance between candidate covariates used for the predictive model. The geographical covariates considered for predictive models were latitude, longitude, 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.

In addition to these geographical 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.

Abundance was estimated by integrating the fitted density surface numerically between 64 and 150° E and 60–70° S, excluding those areas to the north of the ice-edge and those to the south covered by fast-ice, shelf-ice, continental-ice or ice-free land, where crabeater seals were assumed not to occur.

VARIANCE ESTIMATION FOR ABUNDANCE

Variance estimates were obtained by bootstrapping. A non-parametric bootstrap (Efron & Tibshirani 1993) with day as the sampling unit was used for sighting data, and a parametric bootstrap using the fitted haulout model and associated variance–covariance matrix was used for haulout data. Day was chosen as the sampling unit because it represented a spatially distinct, and therefore probably independent, set of transects. There were 29 days of survey effort in total (aerial survey was possible on 10 of the 29 days, shipboard survey on 24 days); 999 bootstrap replicates were taken. The 2·5 and 97·5 percentiles of the bootstrap abundance distribution provided a 95% confidence interval.

Results

DISTRIBUTION AND AREA OF PACK-ICE

The northern edge of the pack-ice was located around 63° S when surveys began in early December at the eastern end of the survey region (Fig. 1b). By the end of the survey in early January to the west of the region, the northern edge was at 65° S. The ice-edge was located north of the 1000-m isobath (taken as indicative of the continental shelf-break) at all times during the survey period. The distance between these features ranged from 120 to 350 km (Fig. 1b). Some large areas with low (≤ 2/10 s) ice-cover occurred at the eastern end and middle of the survey region. During the survey period the total area with > 1/10 ice-cover was calculated to be approximately 1 500 000 km^2.

SURVEY EFFORT

The total survey effort comprised 3172 km of ship transect and 6304 km of aerial transect. Figure 1b shows the distribution of effort in the survey region. Transect segments which were surveyed at times of low (< 0·1) crabeater seal haulout probability (between 20.00 and 01.00 h, Fig. 2) were excluded from spatial analysis for more robust inference (estimated haulout probability is a divisor in equation 3 and when haulout probability is small the estimator can be biased and highly variable). Spatial analyses were based on 1978 5-km transect segments.

NUMBER OF SIGHTINGS

After classification of sightings by double observers as singles or duplicates, right-truncation of both shipboard and aerial sighting histograms and left-truncation of aerial histograms, a total of 2930 sightings of definite or probable crabeater seal groups, 233 sightings of groups of other identified seal species (Ross, leopard and Weddell seals), and 637 sightings of unknown seal groups, were recorded.

As might be expected, at distances close to (< 100 m) the track-line, the ratio of unidentified sightings to definite or probable crabeater sightings was low (aerial: 14 : 564, shipboard: 0 : 242). Given this, and the numerical dominance of crabeater seal sightings compared with other seal species, exclusion of unknowns would not substantially bias an estimate of crabeater seal abundance.

Of the 2930 groups considered definite or probable crabeater seals, 88% were identified as definite and 12% as probable. To address this aspect of uncertainty we used crabeater sightings

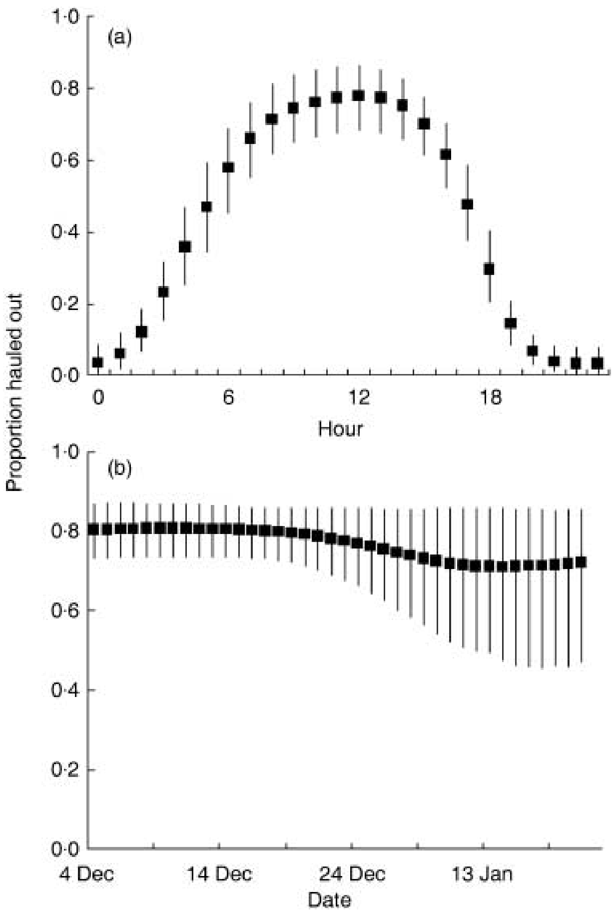

Fig. 2. Modelled haulout profile of crabeater seals (a) by hour within a day, for the mid-point of the survey period (23 December) and (b) across days within the survey period, for solar midday. Vertical lines are 95 percentile ranges, and closed squares are medians, of the 1000 bootstrap replicates.

classified as definite only to provide a minimum estimate of crabeater seal abundance, and definite plus probable sightings to provide a maximum estimate.

DETECTION PROBABILITY

Comparison of AIC values for various models indicated that detection functions could be pooled across species for both shipboard and aerial analyses. Consequently, estimates of detection probability for crabeater seals were based on all sightings of all species. Sighting histograms and estimated detection functions averaged across all other variables apart from distance are given in Fig. 3. Selected detection function models are shown in Table 1.

In addition to distance, side of platform (right-hand-side detected more than left-hand-side) and group size (single seals less detectable than larger groups) were found to affect detectability of seal groups from the ship. For pooled, CLT, aerial double observer data, distance, side of platform (left-hand-side better than right-hand-side) and visibility (good visibility improved detectability) were all found to affect detectability,

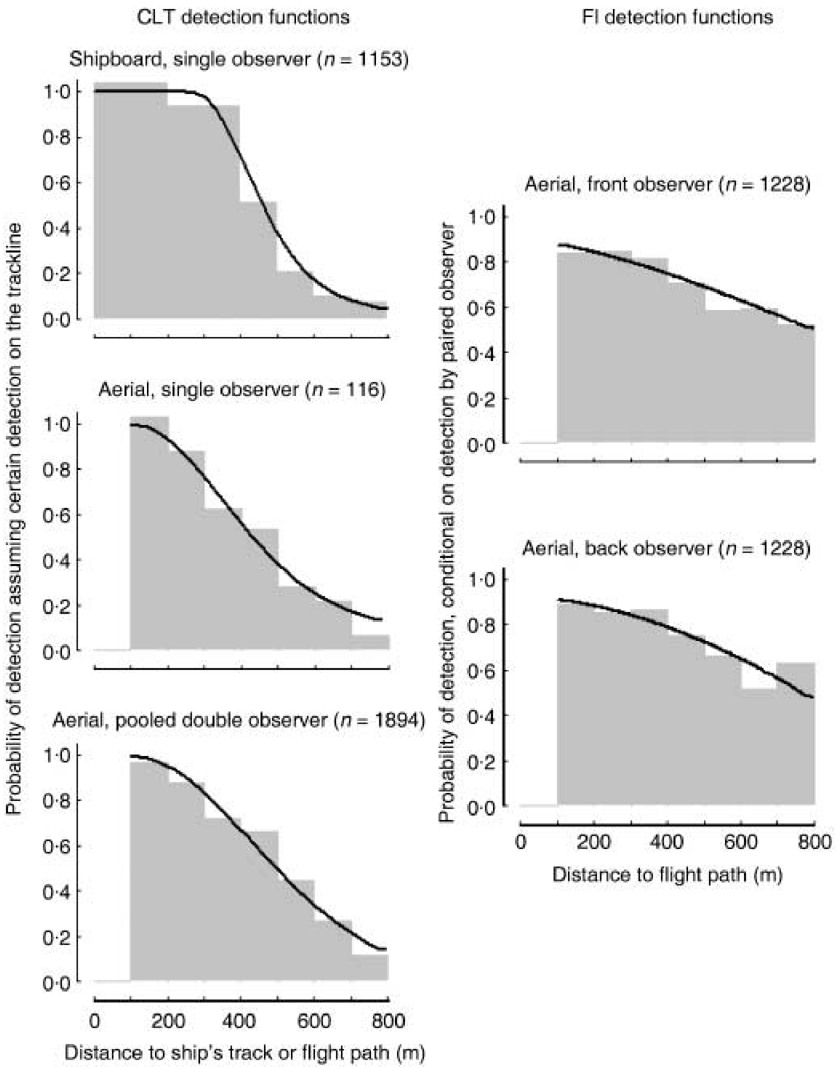

Fig. 3. Detection histograms and detection functions averaged across all other variables apart from distance. Sample sizes are for definite and probable sightings of all known species. CLT: conventional line transect; FI: full independence.

Table 1. Selected detection functions, modelled from sightings with definite and probable species identification (i.e. all sightings except unknown species). Numbers in brackets refer to degrees of freedom (not knots) of smooth. The colons indicate an interaction. MCLT: multiple covariate line transect; FI: full independence

Survey type	Model type	Selected variables
Ship, single observer	MCLT, hazard rate	Distance + side of ship + group size
Aerial, single observer	MCLT, half-normal	Distance + observer
Aerial, double observer	Pooled, MCLT, half-normal	Distance + side of helicopter + visibility
Aerial, double observer	FI, logistic	Distance + side of helicopter + position in helicopter + group size + observer + time since start of flight + visibility + s(ice-cover, 3) + s(experience, 3) + distance:observer + distance:position in helicopter + offset

whereas in the single observer case only distance and observer were important. Several variables were selected in the FI model (Table 1). Southwell *et al.* (2007) provide a discussion of the possible reasons for detection heterogeneity in a previous analysis of similar data (crabeater seals only).

After adjustment for probability of detection on the trackline, estimated detection probabilities ranged from 0·250 to 0·717 for definite sightings and 0·289–0·822 for definite plus probable sightings.

HAULOUT PROBABILITY

Crabeater seals displayed a unimodal pattern of haulout during the survey period, peaking around solar midday (Fig. 2a). At the time of peak haulout, the median proportion of seals hauled out was 78% and the 95% confidence interval 69–86%. The median proportion changed little across the survey period, but variability increased with time into the survey period (Fig. 2b).

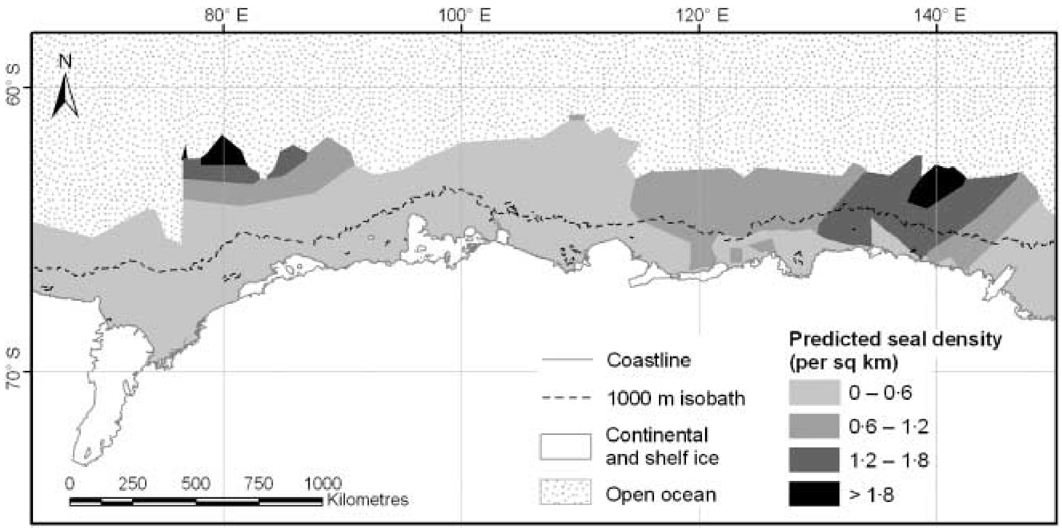

Fig. 4. Crabeater seal density distribution derived from the predictive spatial model, based on all (definite and probable) crabeater sightings.

SEGMENT DENSITIES

The distribution of estimated density by segment was highly skewed, with a large proportion of segments containing no sightings (54·8% for definite sightings, 49·8% for definite plus probable sightings). The mean and range of estimated density per segment was 0·60 (0–16·67) seals/km^2 for definite crabeater seals and 0·62 (0–15·6) seals/km^2 for definite plus probable crabeater seals.

EMPIRICAL PREDICTIVE MODELS OF CRABEATER SEAL DENSITY

The best model for crabeater seal density contained a smooth of latitude and longitude for both definite only and definite plus probable sightings. Both models accounted for just over 20% of observed variability. The models predict density to be relatively high from the ice-edge to the fast ice in the far east of the survey region and at the ice-edge towards the western end of the survey region (Fig. 4).

ESTIMATED ABUNDANCE IN THE SURVEY REGION

Using definite and probable sightings, we estimated the number of crabeater seals in the survey region at the time of the survey to be 946 400 with 95% confidence interval 726 400–1 396 700. The corresponding estimates using only definite crabeater sightings were 914 200 (698 600–1 302 000). Because the longitudinal extent of the survey region stretched across the full breadth of CCAMLR management unit 58.4.1 (80–150° E, Fig. 1a), and the northern extent of pack-ice at the time of the survey was south of the unit's northern boundary, it was also possible to estimate abundance for this unit by integrating the density surface over areas east of longitude 80° E (definite sightings only: 799 500 (597 200–1 118 500); definite and probable sightings: 829 400 (620 800–1 198 800).

Discussion

PAST AND PRESENT ABUNDANCE ESTIMATES

There has been much speculation about the size of, and changes in, crabeater seal populations in the context of its role as a predator of krill in the Southern Ocean. Scheffer (1958) first speculated a circumpolar population of 2–5 million crabeater seals. Shortly after, Eklund & Atwood (1962) proposed a larger population of 5–8 million based on survey work in the Ross Sea and Indian Ocean in 1956/57. Erickson *et al.* (1971) estimated the number of crabeater seals in the Weddell Sea to be around 8–10 million from data collected in 1968/69, and observed that the previous estimates of crabeater populations were 'grossly conservative', and speculated that the circumpolar population may number 50–75 million. This highly speculative estimate was later revised downwards as more areas were surveyed (Erickson & Hofman 1974: 30 million; Gilbert & Erickson 1977: 15 million) and more information on haulout behaviour became available (Erickson & Hanson 1990: 11–12 million). These latter estimates are derived from data collected around the continent between 1972 and 1983.

The circumpolar estimates from the 1950s and 1970–80s, together with data on crabeater seal demographic parameters, have provoked speculation that crabeater seal populations may have increased substantially since the 1950s, along with a change in the structure of the krill-based food-web, in response to a reduction in baleen whale numbers due to exploitation. The hypothesis is that a reduction in baleen whales, which are also consumers of krill, would increase the availability of krill to other predators and allow their populations to increase to some new equilibrium level (Knox 1994). Measurement of trends in crabeater seal demographic parameters (e.g. decreasing age at sexual maturity, Laws 1984) over the period 1940–75 supports this hypothesis. Based on a pre-1950s population of around 5 million, and a subsequent assumed logistic growth with maximal rate of increase of 7·5% per annum (Beddington & Grenfell 1980), Laws (1984) speculated further that crabeater seal populations could reach 50 million by the end of the 20th century. If true, this would represent an order of magnitude increase over 50 years.

Regional estimates of crabeater seal density in Gilbert & Erickson (1977), and summarized in Laws (1984), indicate considerable spatial variation, with regional densities in the period 1968–73 varying by a factor of up to 3·5 (1·86 seals/km^2 in the Oates Coast, Wilkes Land and Queen Maude Land regions compared with 6·56 seals/km^2 in the Halley Bay and Weddell Sea regions). The Wilkes Land region as described in Laws (1984) is largely coincident with the survey region of this study. Laws (1984) reports an estimated 772 000 crabeater seals in this region from surveys in 1972–73. If this estimate were accurate, and if Laws' (1984) speculated increase in crabeater seal populations through to the end of the 20th century were correct, we might expect the current crabeater seal population in this region to number at least a few million.

Our most optimistic estimate of crabeater seal abundance for the slightly larger longitudinal span of 64–150° E in 1999/2000 was 1·4 million, and our best estimate is just under a million. Assuming our estimate is unbiased, this suggests that estimates of population levels in the early 1970s, or estimates of rate of change since then, or both, were over-estimates.

We are confident that our abundance estimate is, at the very least, less biased than previous estimates. The methodology used in previous surveys assumed that detectability in surveyed strips was perfect, that all seals were hauled out at the time of peak haulout, and that seal density in sampled areas was representative of density in the entire pack-ice. Evaluation work showed that none of these assumptions held in our survey, and we would not expect them to have held in previous surveys. However, in our survey the biases resulting from these assumption violations were recognized and corrected for, whereas in previous surveys they may have been recognized but methodologies and technologies that allow these biases to be accounted for were not then available to researchers. The effect of not correcting for incomplete detection and haulout in previous surveys would, by definition, lead to under-estimation of abundance, but the exact magnitude of any such under-estimation is difficult to predict without detailed information on previous survey conditions. Bias resulting from failure to account for non-representative sampling could be either positive or negative, and again the magnitude of any such bias is difficult to determine without detailed information on the location of previous survey effort and re-analysis of those data in a manner consistent with this study.

MANAGEMENT IMPLICATIONS

The estimation of crabeater seal abundance across a large section of east Antarctica provides the basis for estimating the consumption of krill by crabeater seals. This will permit integration of this predator's needs into predicted catch limits, through the estimate of krill mortality. The incorporation of all major sources of uncertainty into our estimation procedure will allow a precautionary interpretation of crabeater abundance and krill consumption estimates, in keeping with CCAMLR's precautionary approach to management.

Undertaking surveys of this kind and scale in Antarctica is extremely challenging and expensive, and in this context any future surveys should take advantage wherever possible of the knowledge gained from this survey effort. In particular, the improved knowledge of crabeater seal distribution may facilitate improvements in survey design, such as stratification and independence of sampling units, which may allow optimal allocation of survey effort and more robust interpretation.

While this study focuses on the crabeater seal and management of living resources in the Southern Ocean, it has also led to technical and theoretical developments in survey methodology that have widespread potential application in ecological and resource management studies. The development of an automated data logging system (Southwell *et al.* 2002) provided a solution to the difficult task of collecting double observer line transect data, as well as multiple covariate data, during aerial survey. This comprehensive data set provided the basis for demonstrating that the central assumption of the theoretically established FI method for analysing double observer line transect data was not met in practice and could not be addressed by modelling detection heterogeneity (Southwell *et al.* 2007). This, in turn, motivated the theoretical development of the PI method (Borchers *et al.* 2006), which is now available to researchers through the latest version of the *Distance* software. Application of the PI method has provided new insights into the detection process (Southwell *et al.* 2007) and will allow improved planning and interpretation of survey data for a variety of ecological and management purposes.

In addition to these directly applied outcomes, improved estimation of crabeater seal distribution and abundance will also contribute to understanding of the structure and function of the Southern Ocean ecosystem. For example, Priddle *et al.* (1998) 'back predicted' a plausible range of primary production estimates for the Southern Ocean by combining population, demographic and physiological parameter estimates for key predators, with a range of plausible food-web efficiency scenarios. Their conclusion that one-third of the total metabolic biomass of all predators in the Southern Ocean was contributed by the crabeater seal demonstrates that accurate estimation of crabeater seal abundance is critical for understanding at this broad, fundamental level.

Acknowledgements

We are grateful to the large number of people who participated or assisted in this survey and the developmental work preceding it: the many observers, the ship captains and crews, helicopter pilots, engineers and voyage management staff on six research voyages from 1994 to 1999, the veterinarians and expeditioners who assisted in capturing seals, and the staff of the Australian Antarctic Division who provided planning, mapping and administrative support. Work within the survey region was carried out under permits of the Commonwealth of Australia Antarctic Seals Conservation Regulations and was approved by the Antarctic Animal Ethics Committee. A portion of the work was supported by the US National Science Foundation under grant OPP-9815961.

References

Anonymous (1995) *Antarctic Pack Ice Seals: An international research program co-ordinated by the SCAR Group of Specialists on Seals*, p. 26. Unpublished report of the 1995 APIS program planning meeting, National Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, USA.

Anonymous (1996) *Argos User's Manual*. Collecte Localisation Satellites, Toulouse, France.

Beddington, J.R. & Grenfell, B. (1980) *The Status of Major Zoological Groups in the Southern Ocean*, 85 pp. International Union for the Conservation of Nature, Gland, Switzerland.

Borchers, D.L., Laake, J.L., Southwell, C. & Paxton, C.G.M. (2006) Accommodating unmodelled heterogeneity in double-observer distance sampling surveys. *Biometrics*, **62**, 372–378.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford.

Buckland, S.T., Breiwick, J.M., Cattanach, K.L. & Laake, J.L. (1993) Estimated population size of the California gray whale. *Marine Mammal Science*, **9**, 235–249.

Comiso, J.C. (2003) *Bootstrap Sea Ice Concentrations for NIMBUS-7 SMMR and DMSP SSM/I, 1970–2003*. National Snow and Ice Data Center, Boulder, CO, USA.

Croxall, J.P. & Nicol, S. (2004) Management of Southern Ocean fisheries: global forces and sustainability. *Antarctic Science*, **16**, 569–584.

Edwards, D.M. & Heap, J.A. (1981) Convention on the Conservation of Antarctic Marine Living Resources: a commentary. *Polar Record*, **20**, 353–362.

Efron, B. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman & Hall, London.

Eklund, C.R. & Atwood, E.L. (1962) A population study of Antarctic seals. *Journal of Mammalogy*, **43**, 229–238.

Erickson, A.W. & Hanson, M.B. (1990) Continental estimates and population trends of Antarctic seals. *Antarctic Ecosystems: Ecological Change and Conservation* (eds K.R. Kerry & G. Hempel), pp. 253–264. Springer-Verlag, Berlin.

Erickson, A.W. & Hofman, R.J. (1974) Antarctic seals. *Antarctic Map Folio Series* (ed. V.C. Bushnell), vol. folio 18. *Antarctic Mammals*. American Geographic Series, New York.

Erickson, A.W., Siniff, D.B., Cline, D.R. & Hofman, R.J. (1971) Distributional ecology of Antarctic seals. *Symposium on Antarctic Ice and Water Masses* (ed. G. Deacon), pp. 55–76. Scientific Committee on Antarctic Research, Cambridge.

Everson, I. & de la Mare, W.K. (1996) Some thoughts on precautionary measures for the krill fishery. *CCAMLR Science*, **3**, 1–12.

Gilbert, J.R. & Erickson, A.W. (1977) Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. *Adaptations Within Antarctic Ecosystems* (ed. L. Llano), pp. 703–740. Smithsonian Institute, Washington, DC.

Hedley, S.L., Buckland, S.T. & Borchers, D.L. (1999) Spatial modelling from line transect data. *Journal of Cetacean Research and Management*, **1**, 255–264.

Horvitz, D.G. & Thompson, D.J. (1952) A generalization of sampling without replacement from a finite universe. *Journal of the American Statistical Association*, **47**, 663–685.

Knox, G.A. (1994) Ecosystem changes resulting from resource exploitation. *Biology of the Southern Ocean*, pp. 349–355. Cambridge University Press, Cambridge.

Laws, R.M. (1984) Seals. *Antarctic Ecology* (ed. R.M. Laws), vol. 2, pp. 621–715. Academic Press, London.

Nicol, S., Constable, A. & Pauly, T. (2000) Estimates of circumpolar abundance of Antarctic krill based on recent acoustic density measurements. *CCAMLR Science*, **7**, 87–99.

Pauly, T., Nicol, S., Higginbottom, I., Hosie, G. & Kitchener, J. (2000) Distribution and abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (80–150° E) during the Austral summer of 1995/1996. *Deep Sea Research*, II, **47**, 2465–2488.

Priddle, J., Boyd, I.L., Whitehouse, M.J., Murphy, E.J. & Croxall, J.P. (1998) Estimates of Southern Ocean primary production – constraints from predator carbon demand and nutrient drawdown. *Journal of Marine Systems*, **17**, 275–288.

Scheffer, V.B. (1958) *Seals, Sea Lions and Walruses. A Review of the Pinnipedia*. Stanford University Press, California.

Smith, W.H.F. & Sandwell, D.T. (1997) Global sea floor topography from satellite altimetry and ship depth soundings. *Science*, **277**, 1956–1962.

Southwell, C. (2005a) Optimising the timing of visual surveys of crabeater seal abundance: haulout behaviour as a consideration. *Wildlife Research*, **32**, 333–338.

Southwell, C.J. (2005b) Response behaviour of seals and penguins to helicopter surveys over the pack-ice off East Antarctica. *Antarctic Science*, **17**, 328–334.

Southwell, C., Borchers, D., Paxton, C.G.M., Burt, L. & de la Mare, W.K. (2007) Estimation of detection probability in aerial surveys of Antarctic pack ice seals. *Journal of Agricultural, Biological and Environmental Statistics*, **12**, 1–14.

Southwell, C., de la Mare, B., Borchers, D.L. & Burt, L. (2004) Shipboard line transect surveys of crabeater seal abundance in the pack-ice off East Antarctica: evaluation of assumptions. *Marine Mammal Science*, **20**, 602–620.

Southwell, C., de la Mare, W., Underwood, M., Quartararo, F. & Cope, K. (2002) An automated system to log and process distance sight–resight aerial survey data. *Wildlife Society Bulletin*, **30**, 394–404.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F., Borchers, D.L., Buckland, S.T., Anderson, D.R., Burnham, K.P., Hedley, S.L. & Pollard, J.H. (2002) *Distance 4.0 User's Guide. Beta 4*. Research Unit for Wildlife Population Assessment, University of St Andrews, St Andrews, UK. Available at: http://www.ruwpa.st-and.ac.uk/distance/.

Wood, S.N. (2001) mgcv: GAMs and generalized ridge regression for R. *R News*, **1**, 20–25.

Wood, S.N. (2003) Thin-plate regression splines. *Journal of the Royal Statistical Society, Series B*, **65**, 95–114.

Received 19 February 2007; accepted 2 August 2007
Handling Editor: Paul Thompson