# Predicting the distribution of crabeater seals *Lobodon carcinophaga* off east Antarctica during the breeding season

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ABSTRACT: Predictive species–environment models have numerous ecological and management applications, and can provide insight into the functional relationships between a species and its environment. Generalised linear models were used to develop predictive models of crabeater seal *Lobodon carcinophaga* distribution during the breeding season in relation to physical-oceanographic and ice-cover variables. Models were constructed from data collected on shipboard surveys in the pack-ice off east Antarctica between 50 and 115° E from 1985 to 1987, and were tested from surveys in the same region from 1995 to 1997. Models of presence selected ocean depth as the only significant physical-oceanographic predictor variable for both breeding and non-breeding seals. Seals were most likely to be present on the ice at moderate ocean depths of approximately 2500 m. Unlike non-breeding seals, breeding seals were all but absent on the ice associated with depths of >4000 m. The predicted distribution of presence comprised a band delineated by the shelf-break to the south and extending northwards for 1.5 to 5° latitude, with non-breeding seals having a more northerly limit than breeding seals. This band is coincident with the known distribution of the crabeater seals' primary food source (Antarctic krill), and also coincides with frontal features such as the Antarctic slope front and the southern boundary of the Antarctic Circumpolar Current, which are considered to be areas of enhanced primary and secondary productivity. The presence–depth models were improved by the inclusion of ice-cover variables. Breeding seals may avoid areas with a high proportion of all ice as floes <20 m in size, because the chance of successfully weaning a pup in such areas is low.

KEY WORDS:  Crabeater seal · Distribution · Breeding · Generalised linear modelling · Antarctica

## INTRODUCTION

The crabeater seal *Lobodon carcinophaga* is thought to be the most abundant of all seals, with estimates of total abundance in the Antarctic pack-ice varying from 15 to 70 million (Erickson et al. 1971, Gilbert & Erickson 1977). Feeding almost entirely on krill, the high abundance of this large-bodied mammal makes it an important component of the krill-based food chain in the Southern Ocean. This importance is recognised by the Commission for the Conservation of Antarctic Marine Living Resources, which has nominated the crabeater seal as an ecosystem monitoring species (Agnew 1997).

Numerous surveys of crabeater seal distribution and abundance have provided insight into correlations between presence or abundance and features of the environment, but few studies have extended the correlation approach to develop predictive models of crabeater seal presence or abundance. Predictive species–environment models have numerous ecological and management applications, including predicting change in a species' distribution in response to a change in the environment (e.g. climate change,

Leathwick et al. 1996), using the results of biological surveys to optimally locate conservation reserves (Margules & Stein 1989), and improving the efficiency of biological surveys (Nicholls 1989). Although their primary purpose is prediction rather than description, predictive models may also provide insight into the functional relationships between a species and its environment.

The potential to develop predictive models of crabeater seal presence or abundance from existing survey data is limited by the often small environmental domain, relative to the entire species' distribution, over which data have been collected. Crabeater seals require pack-ice as a platform on which to rest, moult and breed. The circumpolar pack-ice covers up to 20 million km$^2$ in late winter to early spring and shrinks to about 4 million km$^2$ in late summer. This vast seasonal change in crabeater seal habitat, combined with the species' mobility (Nordoy et al. 1995, Burns et al. 2004), provides the potential for changes in distribution on a similar scale. Within this large and variable distribution, most crabeater seal surveys have been undertaken in relatively small areas off west Antarctica in summer, when the practical difficulties of surveying in the pack-ice are minimised.

In the present study, crabeater seal surveys were conducted over a broad extent of pack-ice off east Antarctica between longitudes 50 and 115° E during the breeding season (early October to early November; Southwell et al. 2003), when the pack-ice is close to its maximal extent. Here we use the survey data to develop predictive models of crabeater seal presence in relation to a number of physical-oceanographic and ice-cover variables, and discuss insights the models provide on functional relationships between the crabeater seal and its environment.

## MATERIALS AND METHODS

**Data collection.** Shipboard surveys were conducted in the pack-ice between longitudes 50 and 115° E on 9 voyages of the Australian National Antarctic Research Expeditions (ANARE) during the breeding seasons of 1985 to 1987 and 1995 to 1997. Two voyages by the MV 'Nella Dan' in 1985 and 1987 were scheduled specifically to study the breeding biology of crabeater seals *Lobodon carcinophaga* (e.g. Shaughnessy & Kerry 1989). The remaining 7 voyages, 4 by the MV 'Icebird' in 1985 to 1987 and 3 by the RSV 'Aurora Australis' in 1995 to 1997, were early-season re-supply voyages to Australian Antarctic stations. Each voyage made 1 or more north–south traverse across the pack-ice zone during the period early October to early November (Fig. 1). Some of the voyages of the 'Icebird'

and 'Aurora Australis' also traversed between stations near the ice-edge in an east–west direction.

While on survey, a straight-line track was maintained as much as possible to obtain representative sampling of seal distribution in the pack-ice zone. Deviations were frequently required, however, to avoid large or thick floes. Shipboard surveys were conducted from the bridge of each vessel ('Nella Dan': 11 m above sea level [a.s.l.]; 'Icebird': 15 m a.s.l.; 'Aurora Australis': 18 m a.s.l.). Observers searched continuously during the daylight hours on both sides of the vessel. When a group of seals was sighted, the species, group size, group composition (number of adults and pups), perpendicular distance of the group from the ship's track and position of the vessel (from a satellite navigation system) were recorded. Perpendicular distances were measured as unbinned data (Buckland et al. 2001) from the 'Aurora Australis' (see Southwell et al. 2004) and as binned data (0–100, 101–200, 201–300 and >300 m distance bins) from the 'Nella Dan' and 'Icebird'. The position of the ship was also recorded at 30 min intervals during the day on all voyages. In 1985, 1987, 1996 and 1997 ice conditions within 1 km of the ship were visually inspected by an observer on the bridge at 30 min intervals and recorded as cover (in tenths) of floes <20 m, 20 to 100 m and >100 m in size. Finely crushed or broken ice (brash) and newly formed sheets of thin (<10 cm) ice were not considered as an ice floe.

**Accounting for detection and haulout probability.** Sighting histograms indicated that detection probability was relatively constant out to 300 m from the ship's track for each of the 3 ships (see Southwell et al. 2004, for example, for 'Aurora Australis' sightings). Southwell et al. (2004) also showed that the probability of detecting seals on the ice that were close to the track of the 'Aurora Australis' was not significantly different from 1.0. Consequently, to minimise any confounding of presence resulting from variable detection probability, we used only sightings within 300 m strips to either side of the ships' tracks for analysis and modelling.

The probability of crabeater seals being hauled out on the ice varies much less across the daylight hours in the breeding season than at other times of year (Southwell 2005). Nevertheless, prior to analysis we filtered out data collected before 07:00 h and after 17:00 h to reduce confounding of presence by variation in haulout probability. Southwell (2005) estimated mean haulout probability for a sample of crabeater seals to vary between approximately 0.75 and 0.95 within the period 07:00 to 17:00 h during the breeding season.

**Model construction.** We used generalised linear models (GLMs, McCullagh & Nelder 1983) to model the distribution of crabeater seals as a function of physical-oceanographic and ice-cover variables. In GLMs the response variable, here crabeater seal presence, is
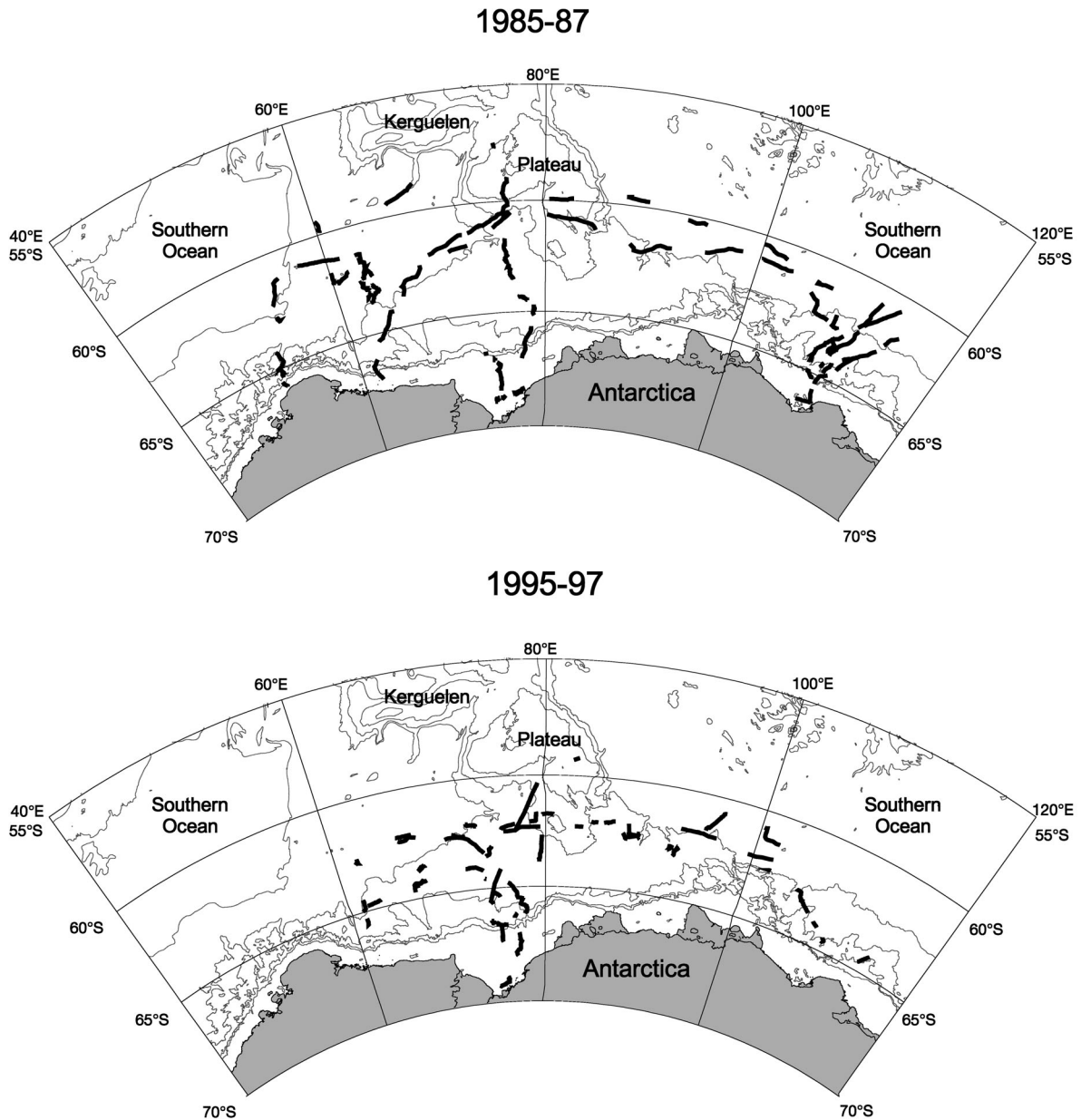
## 1985-87



## 1995-97



Fig. 1. Location of survey tracks off east Antarctica

modelled as the additive sum of linear functions of predictor variables after transformation by a link function. For presence/absence data, a logit link function is used and a logistic regression model is given by:

$$\text{logit}\,(p) = \log\,[p\,/\,(1-p)] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n$$

where $p$ is the probability of presence, $x_1 \ldots x_n$ are predictor variables and $\beta_0 \ldots \beta_n$ are estimated coefficients.

Data from the 1985 to 1987 surveys were used to construct GLMs with the half-latitudinal degree block ($\frac{1}{2}°$ latitude $\times$ 1° longitude) as the unit of analysis. Ship-

board surveys were carried out in 181 such blocks in 1985 to 1987 at varying intensity (transect length: 1.4 to 150.9 km block$^{-1}$; total length: 7200 km). We calculated and modelled the probability of presence separately for groups with pups ('breeding' seals) and groups without pups ('non-breeding' seals) to determine whether breeding status affected distribution. Probability of presence was modelled against 4 physical variables (ocean depth, bottom-relief, distance from the 1000 m isobath [indicative of the top of the continental shelf-break] and distance from the ice-edge)

and 4 ice variables derived from ice-cover data (cover of all ice floes and the proportion of all ice as floes <20 m, 20 to 100 m, or >100 m in size). Ocean depth, bottom-relief and distance from the 1000 m isobath were obtained from GEBCO 1:10 000 000 bathymetric data. Ocean depth was taken as the average of, and bottom-relief as the difference between, maximum and minimum depths in a block. Ice-edge data were obtained from US Navy Joint Ice Centre data derived from NOAA satellite images. Blocks to the north of the 1000 m isobath were given a positive distance, and blocks to the south, a negative distance. Data for the physical variables were available for all 181 blocks surveyed in 1985 to 1987. Ice-cover data, not recorded on 1986 voyages, were available for 122 of these blocks.

Prior to building GLMs, we examined scatterplots of the response variable, and the logit of the response variable, against each predictor variable to check for outlying data and assess the form of possible relationships (linear or curvilinear). To obtain frequency data from the binary response we (1) forced the data into a frequency format by sorting the values for each predictor variable in ascending order, (2) constructed classes that contained approximately equal numbers of samples (blocks), (3) calculated the proportion of blocks where seals were present and (4) calculated the mean value of the predictor variable. With 181 surveyed blocks, we constructed 18 classes, each with approximately 10 sample members, for the variables ocean depth, distance from the shelf-break and distance from the ice-edge. Due to a preponderance of zero values for the ice-cover variables and for bottom-relief due to a relatively flat benthic profile, and because of restricted sampling of ice conditions, it was not possible to construct as many classes, or maintain equal numbers of samples in each class. For these variables, 8 to 10 classes were constructed, with the first class of zero values containing more samples than other classes.

The scatterplots revealed some outlying data to general trends that were associated with blocks over the Kerguelen Plateau. This relatively shallow offshore plateau contrasts with an otherwise uniform increase in ocean depth with northerly distance from the coastline in most of the survey area (Fig. 1). Crabeater seals were absent from all surveyed blocks over the Kerguelen Plateau, whereas blocks from the remainder of the survey area with similar depths to those from the Kerguelen Plateau were very likely to have crabeater seals present. We excluded the 20 surveyed blocks located over the plateau to facilitate modelling of data from most of the survey area.

We considered functions with up to third-order terms to allow for curvilinearity in response–environment relationships. Forward stepwise selection was used to select a set of significant predictor variables by minimising Akaike's information statistic. The selection process was initially applied separately for breeding and non-breeding seals, with the probability of presence as the response variable, a logit link function, and ocean depth, bottom-relief, distance from the shelf-break and distance from the ice-edge as predictor variables. Analysis of deviance was used to test whether the resulting models for breeding and non-breeding seals were different by fitting a minimal set of common predictors and testing the hypothesis that the same relationship applied to both groups. Forward stepwise selection was applied a second time to determine whether any of the ice variables added significantly to the previously developed models using the subset of blocks for which ice-cover data were available. The adequacy of models so developed was assessed by checking for approximate normality of standardised residuals and examining plots of residuals versus fitted values to establish lack of pattern as an indication of model adequacy.

Analysing presence data in relation to environmental variables could be confounded by variable search effort (transect length) between blocks. An effect of transect length on the probability of presence should be evident as a higher mean transect length ($l$) for blocks with seals present ($l_p$) than absent ($l_a$); this expectation was suggested by the data ($l_p = 43.2$ km; $l_a = 37.7$ km). The difference between means was reduced by excluding blocks with small ($l < 10$ km) search effort ($l_p = 44.4$ km; $l_a = 41.5$ km; $t$-test: $t = 0.72$, df = 165, p = 0.2337). Consequently, we excluded blocks with $l < 10$ km in all analyses. In addition to this precaution, transect length was included as a covariate with environmental predictor variables in all analyses, but was never selected as significant. We concluded that transect length did not confound the examination of presence in relation to environmental predictor variables.

Covariance between predictor variables does not constrain the construction of models with high predictive capability, but can make interpretation of functional relationships difficult. To aid interpretation, we examined the interrelationships between the 4 physical and 4 ice-cover variables considered for predictive models by computing Kendall's rank correlation coefficients for pair-wise combinations of the variables. This was carried out using data from the 102 blocks for which physical and ice-cover data were available and which were outside the Kerguelen Plateau region.

**Testing the performance of models.** We tested the performance of presence–physical models, which were constructed from 1985 to 1987 data, in predicting presence during the breeding season at another time (1995 to 1997). Three statistics were computed to assess the performance or accuracy of model predic-

tions: sensitivity (the proportion of blocks for which the model correctly predicted the presence of seals), specificity (the proportion of blocks for which the model correctly predicted the absence of seals) and error rate (the proportion of blocks for which the model made incorrect predictions). These statistics are routinely used to assess the performance of logistic regression models (e.g. Lindenmayer et al. 1991, Pearce et al. 1994). They were calculated by comparing model predictions (probability of presence $p$) with observations from 1995 to 1997 data (binary data: present or absent) after specification of a threshold probability defining presence and absence. Presence is often defined as $p > 0.5$ (and absence as $p < 0.5$), but the decision is somewhat arbitrary. We calculated the statistics for a range of threshold probabilities.

We also assessed whether the predictive performance of presence–physical models improved with inclusion of ice-cover variables by comparing error rates for presence–physical models with error rates for presence–physical–ice models. These models were developed and tested from the subset of blocks in which ice data were recorded (developed from 1985 and 1987 data, tested with 1996 and 1997 data). We again calculated error rate for a range of threshold probabilities.

**Using physical models to predict and map spatial distribution.** Data for the physical variables which contributed significantly to models of distribution were digitised for the 2400 blocks of $\frac{1}{2}°$ in the area bounded by latitudes 55 to 70° S and longitudes 40 to 120° E and stored in a GIS database. Model equations were applied to these data to calculate a predicted probability of presence of breeding and non-breeding seals in each block. Threshold probabilities of presence were chosen to provide a common level of accuracy in model sensitivity for breeding and non-breeding seals, and predicted probabilities of presence were converted to binary presence/ absence data using these threshold probabilities. Distributions were then mapped with the GIS.

## RESULTS

### Correlations between predictor variables

Significant ($p < 0.01$) correlations between 4 of the 6 pair-wise combinations of physical variables (Table 1) reflect a broadly consistent north–south gradient of bottom topography across the survey region, and an approximate paralleling of the ice-edge and the continental shelf-break. The ice-cover variables also exhibit a north–south gradient, with all 4 ice-cover variables significantly correlated with distance from the ice-edge (Table 1).

### Probability of presence in relation to physical variables

Scatterplots of the logit of the proportion of blocks with crabeater seals present against physical variables indicated curvilinear relationships for both breeding and non-breeding seals. Fig. 2 shows that seals were most likely to occur at the approximate mid-range of each physical variable. General concurrence in these presence–physical variable patterns reflects the covariance (discussed above) between the physical variables. In contrast to non-breeding seals, breeding seals were all but absent where ocean depth was >4000 m (the exception being a single group in 1 block) and near the ice-edge. There is an indication of asymmetry in some of the curvilinear responses. Forward stepwise selection using cubic terms for the physical variables and a linear term for transect length selected ocean depth as the only significant variable for both breeding types (breeding seals: deviance = 42.50, df = 2, $p <$ 0.0001; non-breeding seals: deviance = 35.54, df = 2, $p < 0.0001$). Failure of the other 3 physical variables to improve the models is probably more a reflection of the degree of their covariance with ocean depth than a lack of predictive power. Coefficients for the resulting predictive logistic regression equations for breeding and non-breeding seals are given in Table 2. Inspection of normal probability plots of standardised residuals and plots of residuals versus fitted values indicated the model's assumptions had been met. The predicted relationships are shown in Fig. 3. Analysis of deviance found the predictive equations for breeding and non-breeding seals to be significantly different (deviance = 26.21, df = 3, $p <$ 0.0001).

Table 1. *Lobodon carcinophaga*. Kendall's rank correlations between physical and ice-cover variables: D: depth, BR: bottom relief, D1000: distance to 1000 m isobath, DIE: distance to ice-edge, <20: proportion of all ice as floes <20 m, 20–100: proportion of all ice as floes 20 to 100 m, >100: proportion of all ice as floes >100 m and COV: cover of all floes. Asterisks denote correlations with p < 0.01

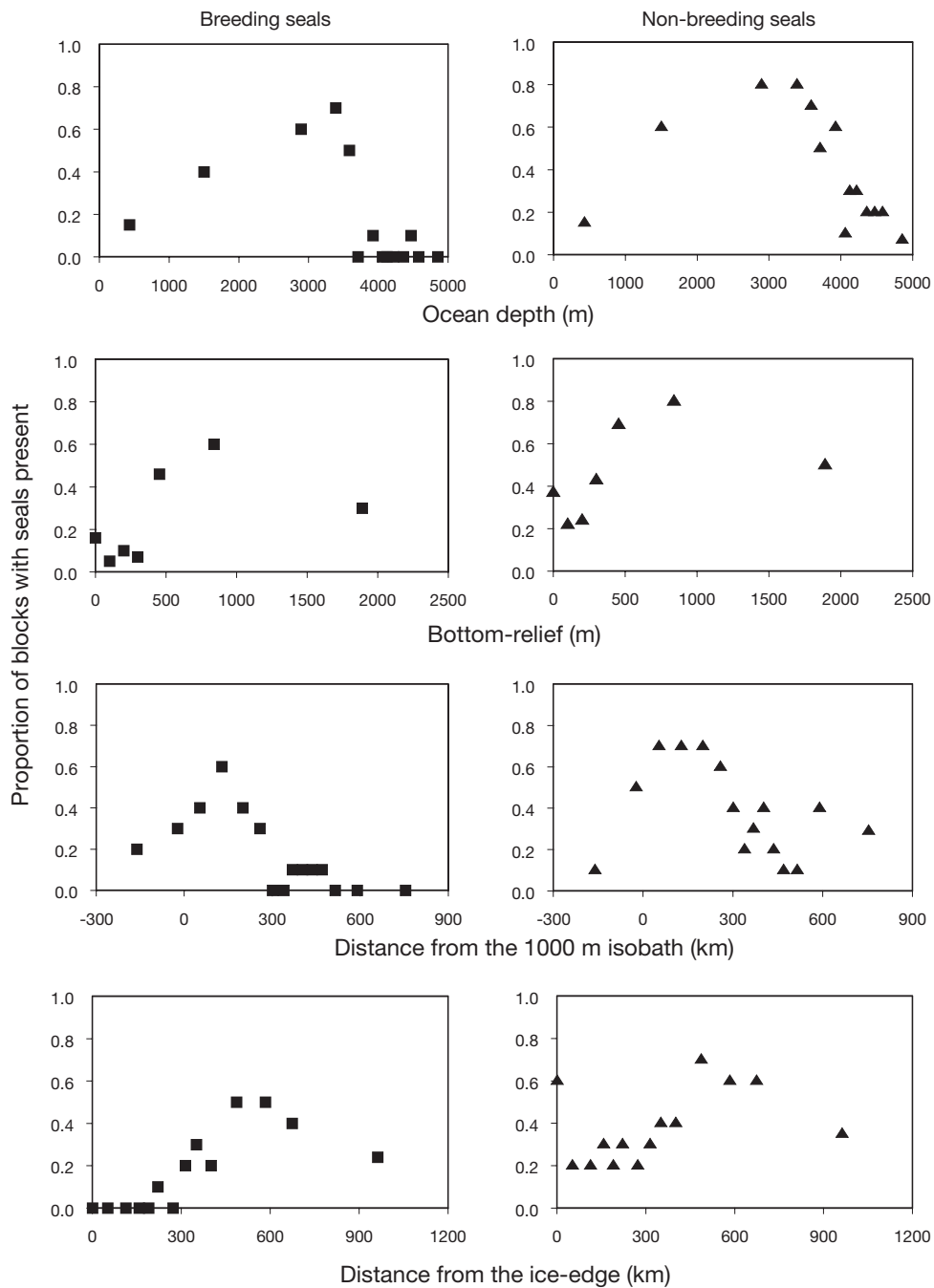|        | BR     | D1000   | DIE     | <20    | 20–100  | >100    | COV     |
|--------|--------|---------|---------|--------|---------|---------|---------|
| D      | −0.109 | 0.706*  | −0.589* | 0.332* | 0.062   | −0.357* | −0.074  |
| BR     |        | −0.827* | 0.159   | −0.069 | 0.031   | 0.069   | 0.052   |
| D1000  |        |         | −0.599* | 0.294* | 0.086   | −0.393* | −0.120  |
| DIE    |        |         |         | −0.230*| −0.186* | 0.476*  | 0.334*  |
| <20    |        |         |         |        | −0.257* | −0.366* | −0.018  |
| 20–100 |        |         |         |        |         | −0.296* | 0.073   |
| >100   |        |         |         |        |         |         | 0.232*  |

Fig. 2. *Lobodon carcinophaga*. Scatterplots of the proportion of blocks with crabeater seals present against physical variables, for blocks off east Antarctica outside the Kerguelen Plateau

## Probability of presence in relation to ice-cover variables

There was no indication of curvilinearity in the logit of responses to ice-cover variables for either breeding or non-breeding seals. Patterns of untransformed presence in relation to ice variables are shown in Fig. 4. Forward stepwise selection using linear terms for the ice-cover variables selected the proportion of all ice as floes <20 m in size for breeding seals and the proportion of all ice as floes 20 to 100 m in size for non-breeding seals (breeding seals: deviance = 11.60, df = 1, p < 0.001; non-breeding seals: deviance = 4.82, df = 1, p < 0.05). Coefficients for the resulting predictive logistic regression equations are given in Table 2. Fig. 4 shows a decreasing trend in the proportion of blocks with

Table 2. *Lobodon carcinophaga*. Coefficients for presence–depth and presence–depth–ice models for breeding and non-breeding seals, where depth is expressed in m

| Model | Breeding seals | | Non-breeding seals | |
|---|---|---|---|---|
| | Term | Coefficient | Term | Coefficient |
| Presence–depth | Intercept | −3.2411 | Intercept | −2.3919 |
| | Depth | $2.5638 \times 10^{-3}$ | Depth | $2.0019 \times 10^{-3}$ |
| | Depth$^3$ | $-1.4615 \times 10^{-10}$ | Depth$^3$ | $-9.1620 \times 10^{-11}$ |
| Presence–depth–ice | Intercept | −2.2070 | Intercept | −2.6317 |
| | Depth | $2.2484 \times 10^{-3}$ | Depth | $2.0914 \times 10^{-3}$ |
| | Depth$^3$ | $-1.2543 \times 10^{-10}$ | Depth$^3$ | $-9.8052 \times 10^{-11}$ |
| | Proportion of ice as floes <20 m | −12.6590 | Proportion of ice as floes 20–100 m | 1.5292 |



Fig. 3. *Lobodon carcinophaga*. Predicted probability of breeding (solid line) and non-breeding (dashed line) crabeater seals being present versus ocean depth

breeding seals present as the proportion of all ice as floes <20 m increases, and an increasing trend in the presence of non-breeding seals as the proportion of all ice as floes 20 to 100 m increases. The predicted relationship between breeding seal presence at locations with an ocean depth of 2500 m and the proportion of ice as floes <20 m (Fig. 5) shows the probability of presence declining rapidly from around 0.8 when there are no floes <20 m to very low probabilities of presence when >0.4 of ice occurs as floes <20 m. A predicted increase in the probability of non-breeding seal presence with an increasing proportion of floes 20 to 100 m in size is less pronounced (Fig. 5).

## Performance of models

The presence–ocean depth model for breeding seals was generally less sensitive (worse at predicting presence), more specific (better at predicting absence) and

less prone to error than the model for non-breeding seals (Fig. 6). Model sensitivity and specificity were highly dependent on the threshold probability for presence/absence, while error rate was less variable. At the threshold probability often used for testing the performance of logistic regression models (p = 0.5), sensitivity for breeding and non-breeding seals was 23 and 67%, specificity 84 and 42% and error rate 34 and 42%, respectively.

Including ice-cover variables improved the predictive power (i.e. lowered the error rate) of the breeding seal model across all but very high threshold probabilities, but no improvement was evident for the non-breeding seal model (Fig. 7). The basis of the test for the non-breeding seal model was probably compromised by the fact that non-breeding seals were present in almost all (95%) of the 63 test blocks (in comparison, breeding seals were present in 65% and absent in 35% of the test blocks).

## Predicted distribution from presence–ocean depth models

To predict the distribution of presence we chose threshold probabilities that reduced and standardised error rates in sensitivity to 20% (or 80% accuracy: p = 0.15 and 0.40 for breeding and non-breeding seals, respectively) at the expense of higher error rates for specificity (60 and 70% for breeding and non-breeding seals). The consequence of this strategy is that the predicted distribution of presence in Fig. 8 would be conservative in that there would be blocks in which seals are incorrectly predicted as absent.

The predicted distributions of presence for breeding and non-breeding seals are broadly overlapping. The main difference is a more northerly limit for non-breeders than breeders. The northerly limits are well south of the average ice-edge for this time of year across all but the eastern end of the survey area.

## DISCUSSION

The ecological forces shaping the distribution of crabeater seals *Lobodon carcinophaga* are likely to be more intense close to and during the breeding season than at other times of the year: (1) breeding seals haul out onto ice floes continuously for 3 to 4 wk (Shaughnessy & Kerry 1989, Southwell 2004) and are thought to fast during this period (Laws
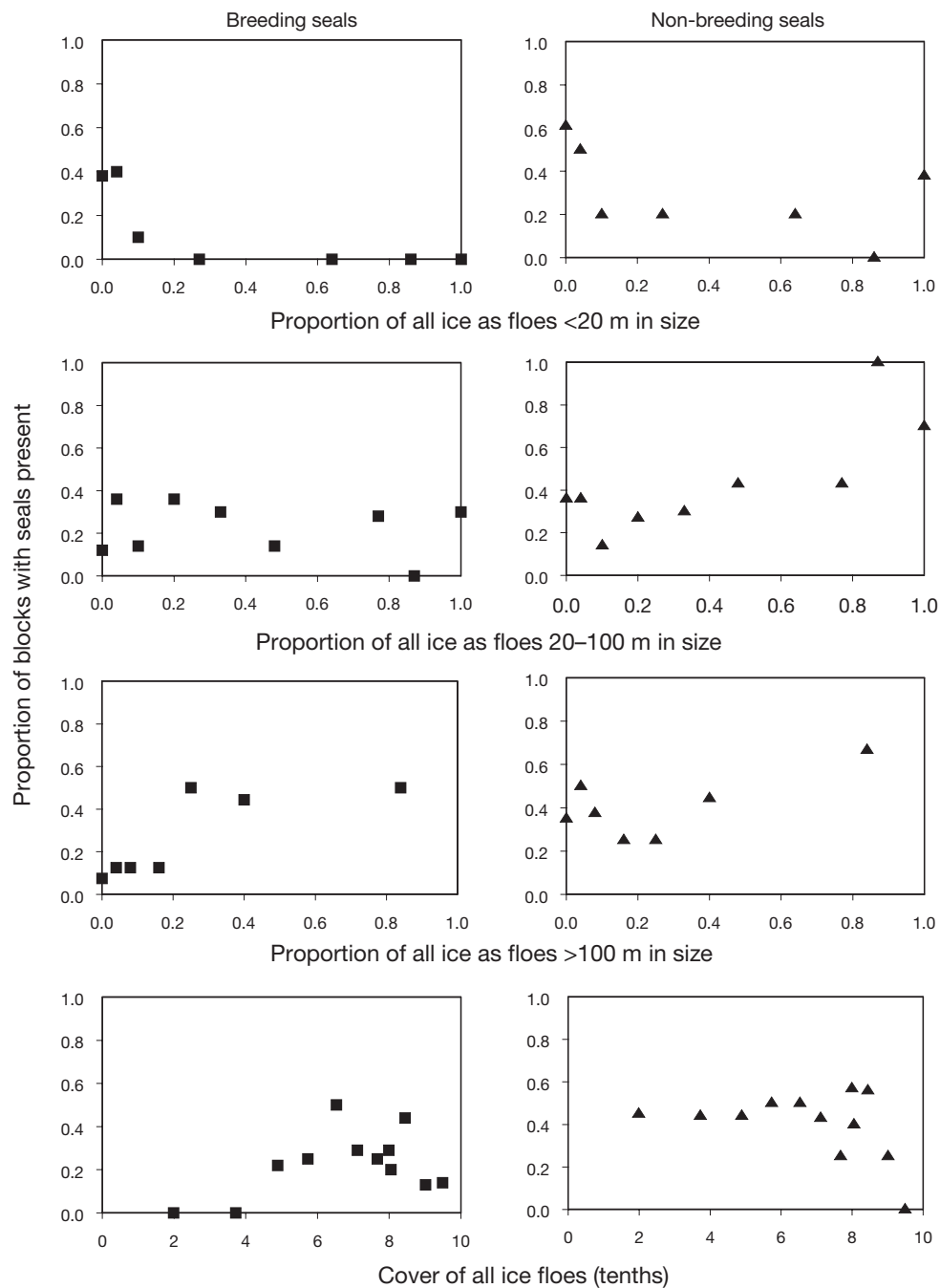
Fig. 4. *Lobodon carcinophaga*. Scatterplots of the proportion of blocks with crabeater seals present against ice-cover variables, for blocks off east Antarctica outside the Kerguelen Plateau

1977); hence, food acquisition would be critical before breeding, when adults need to maximise their fitness prior to the fast, and after, when adults are in poor condition and pups need food to continue growth (Croxall et al. 1985); (2) the quality of protection and shelter offered by ice floes for the relatively long breeding period would be more important than at other times of the year, when seals haul out for shorter periods to rest or moult; and (3) predation pressure is thought to be greatest at the end of the breeding period, when pups enter the water (Siniff et al. 1980, Stone & Meier 1981). As a consequence of these more intense ecological forces, the relationships between crabeater seals and their food resources, shelter sites and predators are likely to be tighter, and hence more amenable to study.
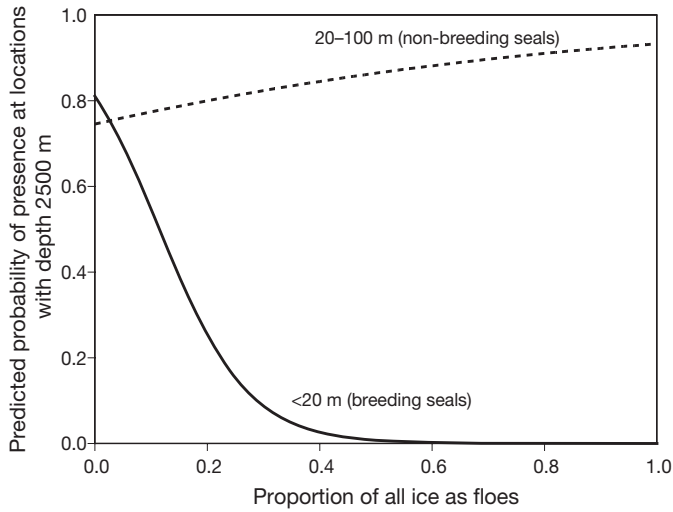
Fig. 5. *Lobodon carcinophaga*. Predicted probability of crabeater seals being present at locations where ocean depth is 2500 m versus the proportion of ice as floes <20 m (breeding seals, solid line) or 20 to 100 m (non-breeding seals, dashed line) in size

Crabeater seals feed primarily on Antarctic krill *Euphausia superba* (Oritsland 1977). The distribution of krill during spring is poorly known, as the presence of ice makes both net and acoustic surveys of krill difficult and the ice is close to its maximum extent at this time. Summer surveys in areas not covered by ice and largely coincident with the area of our study have found krill to be present to northern latitudes of at least 63°S, but to be most abundant in a band where the frontal features of the continental shelf-break, the Antarctic slope front and the southern boundary of the Antarctic Circumpolar Current (ACC) occur (Hosie & Cochran 1994, Pakhomov 1995, Tynan 1998, Hosie et al. 2000, Pauly et al. 2000). The presence–ocean depth models developed in this study predict that crabeater seals are most likely to be present in a band extending northwards by 1.5 to 5.0° latitude from the continental shelf-break, which is broadly coincident with available information on macro-scale distribution of krill and the distribution of frontal features in the survey region. Other regional scale distributional studies of krill predators (the crabeater seal: Ainley 1985, Ackley et al. 2003; seabirds: Ainley & Jacobs 1981, Schneider
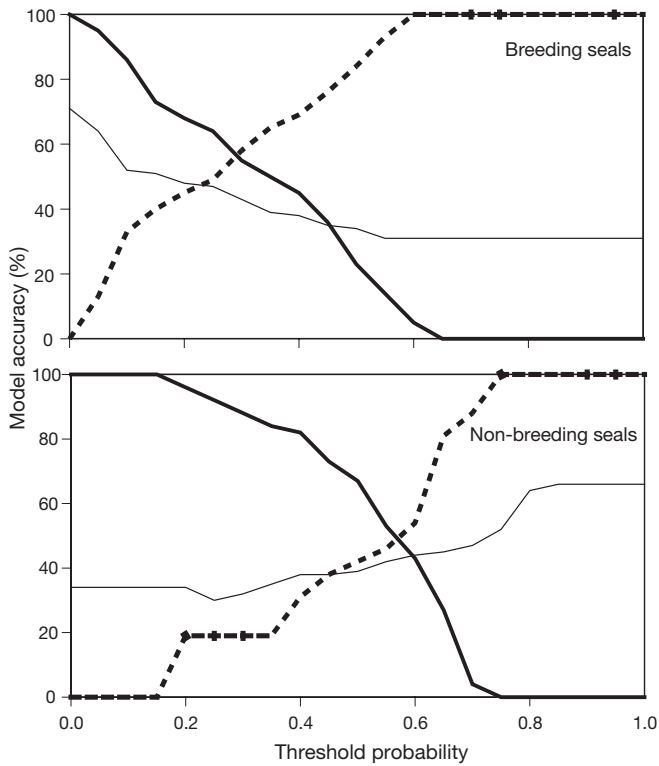


Fig. 6. *Lobodon carcinophaga*. Performance of presence–ocean depth models developed from 1985 to 1987 data when tested with 1995 to 1997 data. Performance is shown for a range of threshold probabilities for presence/absence in relation to sensitivity (thick, solid line), specificity (dashed line) and error rate (thin, solid line)
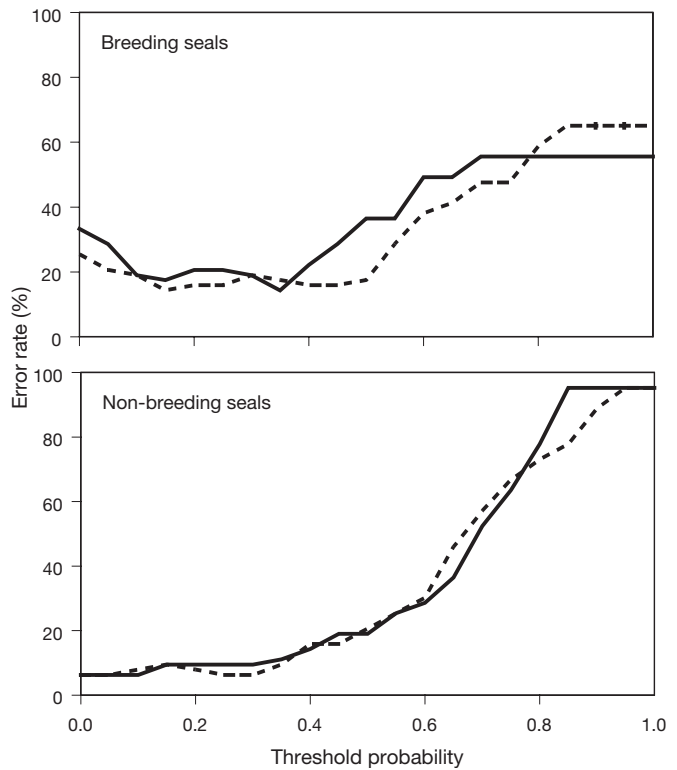


Fig. 7. *Lobodon carcinophaga*. Performance of predictive models which include only ocean depth as a predictive variable (solid line) compared with models which include both ocean depth and ice cover as predictive variables (dashed line). Performance is shown for a range of threshold probabilities for presence/absence in relation to error rate
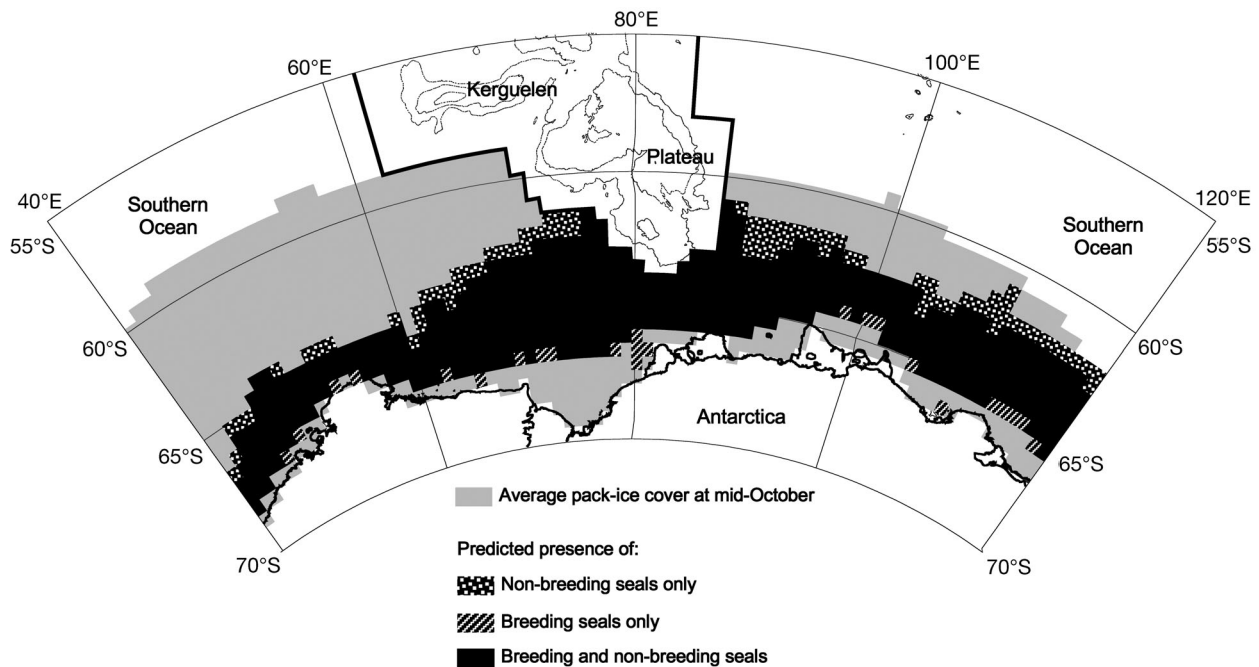
Fig. 8. *Lobodon carcinophaga*. Predicted distribution of presence for breeding and non-breeding crabeater seals in the pack-ice off east Antarctica from presence–ocean depth models. No predictions were made for the Kerguelen Plateau as data from this region were outliers to trends from the remainder of the survey area and were excluded from model construction

1990, Hunt 1991, Pakhomov & McQuaid 1996, Ainley et al. 1998, Raymond & Woehler 2003) have also shown broad spatial coincidence of predator presence or abundance with frontal zones. Further, Tynan (1998) demonstrated a circumpolar coincidence between the southern boundary of the ACC, where the poleward extent of shoaled, nutrient-rich Upper Circumpolar Deep Water occurs, and the distribution of phytoplankton, krill and cetaceans, and predicted this feature would attract not only cetaceans but also other foraging apex predators. Both physical (sluggish currents, shear currents and eddies concentrating krill) and biological (enhanced primary production through nutrient replenishment) processes have been proposed as mechanisms for high biomass or productivity at such zones (Schneider 1990, Hunt 1991, Veit & Hunt 1992, Tynan 1998).

In developing our presence–ocean depth models we excluded data from the Kerguelen Plateau, as these were outliers to different patterns in the remainder of the survey area. Our failure to find crabeater seals in this region contrasts with a finding of high cetacean density in the same area (Tynan 1997), which was attributed to high productivity associated with the southern boundary of the ACC. While such high productivity may also favour the foraging requirements of crabeater seals, the region is at a relatively low latitude and the presence of pack-ice is less predictable than

further south, which may count against a regular presence by crabeater seals.

Our study suggests that the presence of crabeater seals in the breeding season is related to the size of ice floes and that breeding and non-breeding seals differ in their response to floe size. Siniff et al. (1979) observed that breeding crabeater seals tended to seek out larger floes than did non-breeding seals, although their statistical analysis indicated no significant association between breeding status and floe size. Our finding of a significant association between the presence of breeding seals and the proportion of ice as floes <20 m suggests that, rather than seeking out large floes, breeding seals may avoid floes <20 m in size or areas with a high proportion of floes <20 m. Crabeater seals presumably stay on the same floe throughout the weaning period, given the poor mobility of pups and the accumulation of faeces nearby. Given this, and considering that ice floes can easily be broken or sheared into smaller floes by the action of swell, wind and currents (we observed swell from northerly storms penetrating and breaking up the pack-ice as far as 700 km from the ice-edge), small floes may be avoided because they are unlikely to offer a stable platform throughout the weaning period. Floes <20 m in size may also be inadequate in providing protection from predators, such as leopard seals and killer whales, or in offering protection from inclement weather. Avoidance

of areas with a high proportion of floes <20 m may therefore increase the chance of successfully weaning a pup. The more restricted distribution of breeding seals could be partly a consequence of floes <20 m becoming more prevalent as the ice-edge is approached. We cannot offer an obvious biological explanation for the less pronounced relationship between the presence of non-breeding seals and the proportion of ice as floes 20 to 100 m in size.

The models for both breeding and non-breeding seals predict a very low probability of presence near the 'average' ice-edge at this time of year. In reviewing the distribution of pack-ice seals, Laws (1985) and Costa & Crocker (1996) conclude (on the basis of surveys conducted in summer) that crabeater seals are usually found near the outer edge of the pack-ice region. Gilbert & Erickson (1977) argued that this phenomenon was the result of melting sea-ice at the ice-edge inducing a phytoplankton bloom, which led to increased abundance of krill. Laws (1984, p. 626) extended this conclusion to spring in proposing that '...crabeater seals breed in spring wherever there is access for haulout, which in practise restricts it to a zone near the periphery of the pack-ice'. He cautioned, however, that due to the logistical difficulties of working in the pack-ice in spring, the proposal was based on only a few studies from the Antarctic Peninsula and the vicinity of the South Orkney Islands. This proposed association of crabeater seals with the ice-edge in spring is contradicted by the results of our surveys in east Antarctica, and by 2 other studies (Joiris 1991, Van Franeker 1992) conducted in the Weddell Sea in spring subsequent to Laws' (1984) review. The Antarctic Peninsula and South Orkney Island regions differ from the rest of the Antarctic in that the average ice-edge in spring coincides closely with both the continental shelf-break and the southern boundary of the ACC, so the effect of these features could have been confounded in earlier studies.

The high error rates in model predictions when tested against independent data indicate the models are highly simplified representations of reality. This is not unusual when modelling complex ecological relationships, as only a small proportion of the important variables may be measured, and many variables will be subtle, impossible to quantify, or be involved in complex interactions with other variables that have not been identified.

Unexplained variation may be in part a manifestation of looser spatial linkages at meso- and micro-scales. The Antarctic slope front varies spatially in intensity (Jacobs 1986), and, consequently, some variation in biological activity within the frontal zone is to be expected. While the macro-distribution of krill may be reasonably predictable, distribution at meso- and micro-scales is much less so. Several investigators

have attributed temporal variation in the meso-scale distribution of krill to ocean–atmosphere processes, whereby a shift in airflow is believed to cause a disruption of eddie activity and/or water mixing (Priddle et al. 1988, Quetin et al. 1996, Hosie et al. 1997). At a micro-scale, acoustic surveys have found that most krill biomass is found in dense aggregations; for example, Pauly et al.'s (2000) study off east Antarctica found 97% of aggregations were <200 m in length. The unpredictability of krill in space and time may result in a response lag by predators.

Unexplained variation may also be an artefact of the sampling and modelling process. Although we collected data on both ice cover and predator presence, our measurement of only ice cover as an indication of breeding platform quality may oversimplify or fail to adequately represent the role of ice, and the number of sightings of predators was too small for inclusion of predator presence or abundance as a factor in the modelling process. In the absence of data on krill abundance due to the difficulties of both net and acoustic surveys in the ice, we used physical variables such as ocean-depth as likely surrogates for food abundance when modelling seal distribution. Indirect modelling of this 2-step causal chain is likely to increase the amount of unexplained variation (Schneider 1990). Our use of a standard logistic model assumes independence between sampling units (half-latitudinal degree blocks), in contrast to spatial logistic models (e.g. Augustin et al. 1996), which model presence, not only as a function of the environment in the sampling unit, but also in relation to presence in surrounding units. Failure to model spatial correlation, if present, can result in reduced predictive accuracy of the model. Raymond & Woehler (2003) found little difference in the predictive accuracy of standard and spatial logistic models when applied to seabirds in the Southern Ocean using sampling units of 2° latitude × 2° longitude. Given this finding and considering the lower mobility of seals compared with seabirds is likely to result in less spatial correlation for seals at similar scales, we consider it unlikely that our use of standard logistic models would have contributed significantly to error rates when the models were tested against independent data.

LITERATURE CITED

Ackley SF, Bengtson JL, Boveng P, Castellini M and 11 others (2003) A top-down, multidisciplinary study of the structure and function of the pack-ice ecosystem in the eastern Ross

Sea, Antarctica. Polar Rec 39:219–230

Agnew DJ (1997) The CCAMLR Ecosystem Monitoring Program. Antarct Sci 9:235–242

Ainley DG (1985) Biomass of birds and mammals in the Ross Sea. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, p 498–515

Ainley DG, Jacobs SS (1981) Sea-bird affinities for ocean and ice boundaries in the Antarctic. Deep-Sea Res 28A: 1173–1185

Ainley DG, Jacobs SS, Ribic CA, Gaffney I (1998) Seabird distribution and oceanic features of the Amundsen and southern Bellingshausen Seas. Antarct Sci 10:111–123

Augustin NH, Muggleston MA, Buckland ST (1996) An autologistic model for spatial distribution of wildlife. J Appl Ecol 33:339–347

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Burns JM, Costa DP, Fedak MA, Hindell MA and 5 others (2004) Winter habitat use and foraging behavior of crabeater seals along the western Antarctic peninsula. Deep-Sea Res II 51:2279–2303

Costa DP, Crocker DE (1996) Marine mammals of the Southern Ocean. Foundations for ecological research west of the Antarctic peninsula. Antarct Res Ser 70:287–301

Croxall JP, Prince PA, Ricketts C (1985) Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, p 516–533

Erickson AW, Siniff DB, Cline DR, Hofman RJ (1971) Distributional ecology of Antarctic seals. In: Deakin G (ed) Antarctic ice and water masses. Scientific Committee on Antarctic Research, Cambridge, p 55–76

Gilbert JR, Erickson AW (1977) Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. In: Llano L (ed) Adaptations within Antarctic ecosystems. Smithsonian Institute, Washington, DC, p 703–740

Hosie GW, Cochran T (1994) Mesoscale distribution patterns of macrozooplankton communities in Prydz Bay, Antarctica — January to February, 1991. Mar Ecol Prog Ser 106: 21–39

Hosie GW, Cochran TG, Pauly T, Beaumont KL, Wright SW, Kitchener JA (1997) The zooplankton community structure of Prydz Bay, January–February 1993. Proc NIPR Symp Polar Biol 10:90–133

Hosie GW, Schultz MB, Kitchener JA, Cochran TG, Richards K (2000) Macrozooplankton community structure off East Antarctica (80–150° E) during the austral summer of 1995/1996. Deep-Sea Res II 47:2437–2463

Hunt GLJ (1991) Occurrence of polar seabirds at sea in relation to prey concentrations and oceanographic factors. Polar Res 10:553–559

Jacobs S (1986) The Antarctic slope front. Antarct J US 21: 123–124

Joiris CR (1991) Spring distribution and ecological role of seabirds and marine mammals in the Weddell Sea, Antarctica. Polar Biol 11:415–424

Laws RM (1977) Seals and whales of the Southern Ocean. Philos Trans R Soc Lond 279:81–96

Laws RM (1984) Seals. In: Laws RM (ed) Antarctic ecology, Vol 2. Academic Press, London, p 621–715

Laws RM (1985) The ecology of the Southern Ocean. Am Sci 73:26–40

Leathwick JR, Whitehead D, McLeod M (1996) Predicting

changes in the composition of New Zealand's indigenous forests in response to global warming: a modelling approach. Environ Softw 11:81–90

Lindenmayer DB, Cunningham RB, Tanton MT, Nix HA, Smith AP (1991) The conservation of arboreal marsupials of the central highlands of Victoria, south-east Australia. III. The habitat requirements of Leadbeater's possum *Gymnobelideus leadbeateri* and models of the diversity and abundance of arboreal marsupials. Biol Conserv 56: 295–315

Margules CR, Stein JL (1989) Patterns in the distribution of species and the selection of nature reserves: an example from eucalyptus forests in south-eastern New South Wales. Biol Conserv 50:219–238

McCullagh P, Nelder JA (1983) Generalized linear models. Chapman and Hall, New York

Nicholls AO (1989) How to make biological surveys go further with generalised linear models. Biol Conserv 50:51–75

Nordoy ES, Folkow L, Blix AS (1995) Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. Polar Biol 15:261–268

Oritsland T (1977) Food consumption of seals in the Antarctic pack ice. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institute, Washington, DC, p 749–768

Pakhomov EA (1995) Demographic studies of Antarctic krill *Euphasia superba* in the Cooperation and Cosmonaut Seas (Indian sector of the Southern Ocean). Mar Ecol Prog Ser 119:45–61

Pakhomov EA, McQuaid CD (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. Polar Biol 16:271–286

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 Res II 47:2465–2488

Pearce JL, Burgman MA, Franklin DC (1994) Habitat selection by helmeted honeyeaters. Wildl Res 21:53–63

Priddle J, Croxall JP, Everson I, Heywood RB, Murphy EJ, Prince PA, Sear CB (1988) Large-scale fluctuations in distributions and abundance of krill — a discussion of possible causes. In: Sayrhage D (ed) Antarctic Ocean resources and variability. Springer-Verlag, Berlin, p 169–182

Quetin LB, Ross RM, Frazer TK, Haberman KL (1996) Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba*. In: Ross RM (ed) Foundations for ecological research west of the Antarctic peninsula. AGU Antarctic Research Series, American Geophysical Union, Washington, DC, p 357–371

Raymond B, Woehler EJ (2003) Predicting seabirds at sea in the Southern Indian Ocean. Mar Ecol Prog Ser 263: 275–285

Schneider DC (1990) Seabirds and fronts: a brief overview. Polar Res 8:17–21

Shaughnessy PD, Kerry KR (1989) Crabeater seals *Lobodon carcinophagus* during the breeding season: observations on five groups near Enderby Land, Antarctica. Mar Mamm Sci 5:68–77

Siniff DB, Stirling I, Bengtson JL, Reichle RA (1979) Social and reproductive behavior of crabeater seals (*Lobodon carcinophagus*) during the austral spring. Can J Zool 57: 2243–2255

Siniff D, Stone S, Reichle D, Smith T (1980) Aspects of leopard seals (*Hydrurga leptonyx*) in the Antarctic pack ice. Antarct J US 15:160

Southwell CJ (2004) Satellite dive recorders provide insights

into the reproductive strategies of crabeater seals (*Lobodon carcinophagus*). J Zool Lond 264:399–402

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

Southwell C, Kerry K, Ensor P, Woehler E, Rogers T (2003) The timing of pupping by pack-ice seals in East Antarctica. Polar Biol 26:648–652

Southwell C, de la Mare B, Borchers DL, Burt L (2004) Shipboard line transect surveys of crabeater seal abundance in the pack-ice off East Antarctica: evaluation of assumptions. Mar Mamm Sci 20:602–620

Stone S, Meier T (1981) Summer leopard seal ecology along the Antarctic Peninsula. Antarct J US 16:151–152

Tynan CT (1997) Cetacean distributions and oceanographic features near the Kerguelen Plateau. Geophys Res Lett 24: 2793–2796

Tynan CT (1998) Ecological importance of the southern boundary of the Antarctic Circumpolar Current. Nature 392:708–710

Van Franeker JA (1992) Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia Seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). Polar Biol 12: 93–102

Veit RR, Hunt GLJ (1992) The spatial dispersion of seabirds near the South Orkney Island and the Weddell–Scotia confluence. Polar Biol 11:637–641