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At-sea distribution of female southern elephant seals relative to variation in ocean surface properties

Corey J. A. Bradshaw, Jane Higgins, Kelvin J. Michael,
Simon J. Wotherspoon, and Mark A. Hindell

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We examined the relationships between physical oceanography (sea surface temperature − SST, sea surface height anomaly − SSH, ocean colour − OC, bathymetry − BA, sea-ice concentration − SI, and their associated gradients) and the foraging distribution (time at sea) of female southern elephant seals using generalized linear and generalized additive models (GLM and GAM). Using data from 28 separate foraging trips (22 unique individuals) over two years, we found that during the post-lactation trips (summer), the best GLM demonstrated a negative relationship between time at sea and SST and BA, but a positive relationship with SST gradient and SSH. During the post-moult (winter) trips, there was a negative relationship with OC gradient, SSH, and BA. The best post-lactation GAM identified a positive relationship with OC gradient, negative relationships with OC and SST gradient, and a non-linear relationship with SST. For the post-moult trip there was a negative relationship with OC, SST, BA and BA gradient, and a positive relationship with SST gradient. The relationship between the predicted time and observed time at sea was significant only for the post-lactation GAM, although predictability was low. That SST and its gradient predicted a small, but significant proportion of the variation in time at sea is indicative of the frontal zones within this area that are generally more biologically productive than surrounding regions. It appears that coarse-scale oceanographic configuration influences foraging behaviour in southern elephant seals only subtly. Nonetheless, some of the mechanisms influencing predator foraging are congruent with expectations of distribution of marine food resources at coarse spatial scales.

C. J. A. Bradshaw and M. A. Hindell: Antarctic Wildlife Research Unit, School of Zoology, University of Tasmania, Private Bag 05, Hobart, Tasmania 7001, Australia. J. Higgins and K. J. Michael: Antarctic Cooperative Research Centre and Institute of Antarctic and Southern Ocean Studies, University of Tasmania, Private Bag 77, Hobart, Tasmania 7001, Australia. S. J. Wotherspoon: School of Mathematics and Physics, University of Tasmania, Private Bag 37, Hobart, Tasmania 7001, Australia. Correspondence to C. J. A. Bradshaw: Current address: Key Centre for Tropical Wildlife Management, Charles Darwin University, Darwin, Northern Territory 0909, Australia; tel.: +61(0)8 8946 6713; fax: +61(0)8 8946 7088; e-mail: corey.bradshaw@cdu.edu.au.

Introduction

Within ocean ecosystems, biological resources are heterogeneous in distribution and abundance and depend to some degree on the physical characteristics of the water column (Lutjeharms *et al.*, 1985; Mann and Lazier, 1996; Guinet *et al.*, 2001). Physical parameters such as temperature, salinity, water chemistry, currents, wind action, and sea ice can correlate well with primary production (Denman and Abbott, 1994; Knox, 1994; Loeb *et al.*, 1997; Kögeler and Rey, 1999; Rutherford *et al.*, 1999). However, organisms in higher trophic levels that depend directly or indirectly on the distribution and abundance of primary or first-order secondary production may not always demonstrate clear relationships to the physical parameters. Although some correlations between apex predator (e.g., seals, whales, seabirds) foraging patterns and physical characteristics of the marine environment have been found (Hindell *et al.*, 1991; McConnell *et al.*, 1992; Jaquet *et al.*, 1996; Pakhomov and McQuaid, 1996; Guinet *et al.*, 1997, 2001; Tynan, 1997, 1998; Georges *et al.*, 2000), the degree to which models can be used to predict predator performance is highly variable. Factors such as the spatial and temporal scales of investigation (Mehlum *et al.*, 1999; Fauchald

et al., 2000; Guinet *et al.*, 2001), "downstream" effects that re-distribute plankton beyond the conditions responsible for their production and growth (Guinet *et al.*, 2001), and dilution effects through the foodweb may all act to restrict the predictive ability of these models (El-Sayed, 1988; Guinet *et al.*, 2001).

With the increasing availability of broad-scale satellite imagery, measurements of various physical attributes of the oceanscape have been used as covariates in models examining variation in marine predator behaviour and distribution including sea surface temperature (Hindell *et al.*, 1991; Sydeman and Allen, 1999; Georges *et al.*, 2000; Lea and Dubroca, 2003), ocean colour (from which phytoplankton concentration can be estimated — Ainley *et al.*, 1991; Jaquet and Whitehead, 1996; Jaquet *et al.*, 1996), sea-ice extent and concentration (Trathan *et al.*, 1996; Barbraud *et al.*, 2000; Bornemann *et al.*, 2000), bathymetry (Rodhouse *et al.*, 1996; Gentry *et al.*, 1998; Bonadonna *et al.*, 2001; Hooker *et al.*, 2002; Lea and Dubroca, 2003), and sea surface height anomalies (Nel *et al.*, 2001). However, the predictive ability of derived models appears to be limited by the often patchy distribution of physical data in space and time (Sumner *et al.*, 2003), the various spatial scales of investigation (Jaquet, 1996; Boyd *et al.*, 2001; Bradshaw *et al.*, 2002), and the expected non-linear association between predator foraging and physical variables (e.g. Burns *et al.*, in press).

Previous models examining these relationships have generally used simple multi-variate linear approaches with standard parametric assumptions (Guisan and Zimmermann, 2000; Guinet *et al.*, 2001). The low predictive capacity of the resulting models may be due to subtle or weak influences of coarse-scale oceanographic patterns on predator foraging behaviour, or a result of the complex relationships that may exist but yet remain poorly modelled with the standard approaches such as multiple linear regression. Generalized linear models (GLM) have an advantage over these techniques because they do not force data into unnatural scales and allow for non-linearity and non-normal responses (i.e., one can choose the underlying distributions to avoid uninterpretable data transformations — Hastie and Tibshirani, 1990; Guisan *et al.*, 2002). However, in some cases the use of more empirically based techniques such as the semi-parametric extension of GLM, generalized additive models (GAM), can provide better predictions because of their ability to deal with highly non-linear and non-monotonic relationships between the response and explanatory variables (Guisan and Zimmermann, 2000; Guisan *et al.*, 2002).

The expectation of a spatial relationship between the distributions of a predator and its prey is contingent on two general assumptions: (1) the predator has knowledge of or can predict the distribution of its prey, and (2) the prey are accessible (Matthiopoulos, 2003). One apex marine predator that may lend itself well to the investigation of oceanographic influence on foraging behaviour is the southern elephant seal (*Mirounga leonina*). This species is a high-level consumer in the Southern Ocean (Clarke, 1983; Boyd *et al.*, 1994; Hindell *et al.*, 2003) that ranges widely (millions of km^2) during its annual foraging trips (McConnell and Fedak, 1996; Bradshaw *et al.*, 2003, in press; Hindell *et al.*, 2003).

Elephant seals are also amenable to data collection given their tendency to return to the breeding colony to breed and moult; therefore, the collection of foraging distribution and behaviour through archival and satellite-relayed tags has provided substantial data over the last 15 years. The impressive annual foraging routes take individuals through extensive variation in the properties of the oceanscape in which they feed. Indeed, during a foraging trip temperature ranges can exceed 15°C (Campagna *et al.*, 2000; Bradshaw *et al.*, 2002), sea ice can be present or absent (Bornemann *et al.*, 2000), the depth of water in which foraging occurs can range from hundreds to thousands of metres, and the individuals can traverse many different frontal and oceanographic zones (Field *et al.*, 2001; Hindell *et al.*, 2003). Thus, this extensive variation may provide sufficient scope to predict foraging performance from physical information.

The objectives of this study were therefore to examine the relationships between physical oceanography and the foraging distribution of female southern elephant seals. Specifically, we examined the potential linear and non-linear relationships between the time spent by elephant seals in particular regions of the Southern Ocean and sea surface temperature, ocean colour, bathymetry, ice concentration, sea surface height anomaly, and their associated spatial gradients. Relationships were examined during the middle of the post-lactation (summer) and post-moult (winter) foraging trips separately using a series of generalized linear and additive models (GLM and GAM). Foraging trips were separated on the basis of potential different underlying relationships between surrogate measures of prey dispersion (i.e., oceanographic variables) for summer vs. winter months (Bradshaw *et al.*, 2003; Hindell *et al.*, 2003).

Material and methods

Animal capture and foraging data

Adult female southern elephant seals from Macquarie Island (54°30′S 158°50′E) were captured, sedated, weighed, and equipped with Time-Depth Recorder archival tags (TDRs, Wildlife Computers, Redmond, Washington, USA) from 1999 to 2002 prior to departure for the post-lactation (PL — Oct–Jan) or post-moult (PM — Feb–Sep) foraging trips following the procedures outlined in Hindell and Slip (1997) and Field *et al.* (2002). All animal handling procedures were reviewed and approved by the Antarctic Science Advisory Committee (ASAC 1171). All sampled females were of known age (born in 1993) to minimize the

potentially confounding effects of age and cohort in the analyses. The TDRs sampled time, depth, light level, and temperature every 30 s for the duration of each foraging trip (Bradshaw et al., 2002). At-sea locations were derived from light data and geo-location software (Multi-trace, Jensen Software, Germany). The resulting locations were processed using a Kalman filter (analogous to a coarse velocity filter that uses a maximum travel velocity threshold to remove locations requiring unrealistic swim speeds − McConnell and Fedak, 1996; Bradshaw et al., 2002) developed to smooth the geo-location-estimated trajectories of marine vertebrates (Sibert et al., 2003). Once filtered the tracks for each seal and for each foraging trip were summarized by time per unit area to incorporate the remaining uncertainty in foraging trajectories. This was done by creating a raster latitude/longitude grid centred on the track and estimating the time spent per cell by all individuals combined (Figure 1A). The time-spent value assumed a constant rate of travel between successive locations. Raster grids were defined for each month of the foraging trip (calendar month); however, we chose to analyse only the middle period of each foraging trip (PL: Nov−Dec; PM: June−Aug) to avoid incorporating major transit phases (leaving and arriving to Macquarie Island) into the analysis (Figure 2). Hence, we isolated the most-probable main periods of prey ingestion and assimilation during each foraging trip.

Spatial resolution

The spatial resolution of the grid cells was determined from a previous analysis estimating the combined inherent spatial error in geo-location estimates and oceanographic data (Bradshaw et al., 2002). Geo-location estimates often result in position accuracy of greater than $\pm 1°$ of latitude depending on the region in question and time of year (Hill, 1994; Le Boeuf et al., 2000; Bradshaw et al., 2002; van den Hoff et al., 2002). Additionally, remotely sensed oceanographic data, such as sea surface temperatures (SST), have errors arising from temperature interpolation in regions where the number of valid observations is reduced due to excessive cloud cover and the poor polar light regime in winter months (McClain et al., 1985; Sumner et al., 2003).

Therefore, to determine the optimal spatial scale incorporating the errors inherent in the geo-location method and the least-accurate oceanographic data set, sea surface temperature (see below), we repeated the methods outlined in Bradshaw et al. (2002). Briefly, this involved defining 10 different spatial scales from 50×50 km (2500 km^2) to 500×500 km (250 000 km^2), at incrementing intervals of 50×50 km. We assumed a linear, constant rate of movement between successive daily positions, and constructed grid cells from these trajectories at the same spatial scale. Thus, we were able to determine the seal's putative times of entry and exit for each cell along the trajectory based on the limits of the grid cell at each spatial scale.

TDR-recorded temperatures were then summarized for each grid cell between these entry and exit times. Next, the SST interpolated grids were averaged over each monthly interval based on a time fraction-weighted mean for the files overlapping the time period in question. The number of interpolated SST values falling within the limits of each grid cell comprised the basis of all summary parameters for the SST data. For each scale, individual seal, time period, and grid cell we calculated the percentage of interpolated SST values lying between the upper and lower 95% confidence limits of the mean TDR temperature. Based on this methodology, we determined that the highest agreement between TDR-recorded temperatures and remotely sensed SST data occurred at a spatial resolution of 300×300 km (Bradshaw et al., 2002, in press). This spatial scale was used for all subsequent analyses.

Oceanographic data

Sea surface temperature
We used the Advanced Very High-Resolution Radiometer (AVHRR) Pathfinder Sea Surface Temperature monthly data set available in Hierarchical Data Format (HDF) from the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center (JPL PO.DAAC). The equal angle, eight-day "best SST" data for both ascending and descending passes at 18-km spatial resolution were used (Vazquez et al., 1998).

Ocean colour
Monthly averaged ocean colour data were derived from the SeaWiFS Level-3 data to determine regions of high phytoplankton concentration (an indication of higher primary productivity). Data sets are available in HDF from the NASA Goddard Space Flight Center Distributed Active Archive Center (GSFC DAAC). Level-3 data consist of 9×9-km bins of average chlorophyll α concentration (mg cm^{-3}).

Sea-ice concentration
We used monthly images of sea-ice concentration from The National Snow and Ice Data Center (NSIDC) to determine the ice cover of the ocean where elephant seals forage (Cavalieri et al., 1990). The combined Scanning Multi-channel Microwave Radiometer (SMMR) and Special Sensor Microwave/Imager (SSM/I) sea-ice concentration time series is produced from brightness temperatures (TBs) obtained from GSFC. Data are gridded at a resolution of 25×25 km and represent sea-ice concentrations ranging from 0% to 100% ($<15\%$ classified as open water).

Bathymetry
Data were abstracted from the ETOPO5 digital data set (NOAA National Geophysical Data Center, 1988) to determine ocean depth. Data were generated from a digital
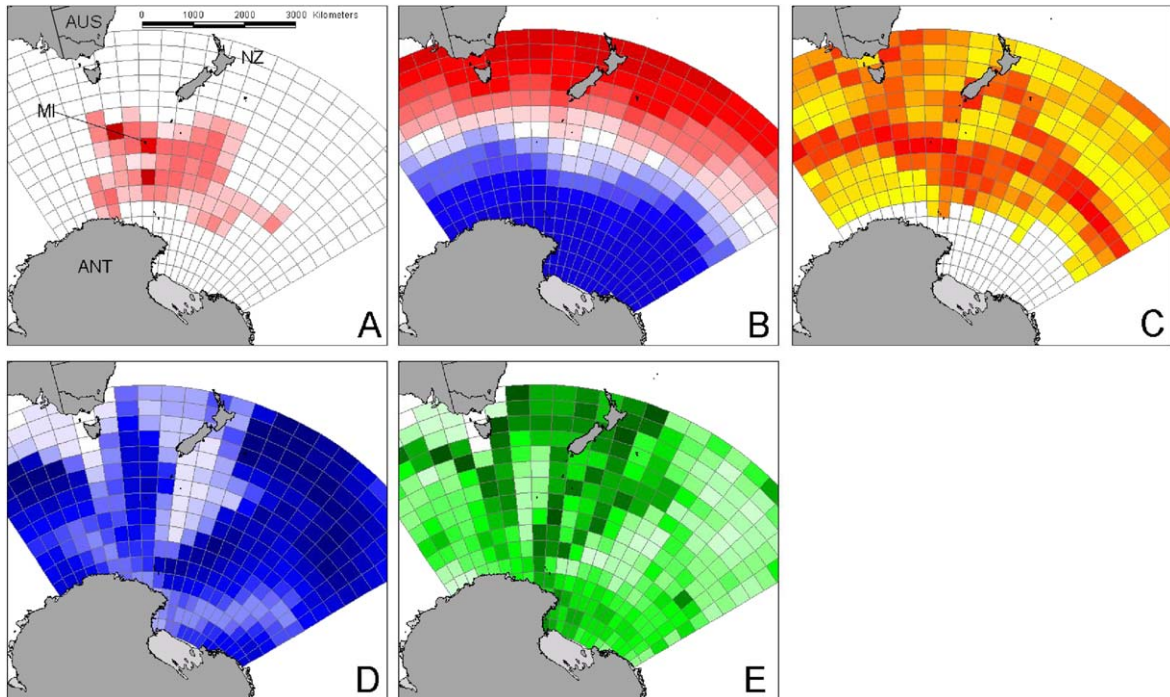
Figure 1. An example of post-lactation (November 1999) response (seal use) and explanatory (oceanographic) variables displayed in the 300 × 300-km grid resolution. Darker grid cells indicate higher values. A. Time spent by adult female southern elephant seals, B. Sea surface temperature, C. Sea surface temperature gradient, D. Bathymetry, and E. Bathymetric gradient.

database of land and sea floor elevations on a 5-min latitude/longitude grid. Data values are in whole metres, representing the elevation of the centre of each cell. Data points within the ocean therefore are assigned a negative number of metres.

Sea surface height anomaly

Satellite altimetry is a practical way of measuring global sea level variation (Church *et al.*, 2001). The height of the sea surface relative to a gravitational equipotential surface is determined by the mass of water at a given location and by the water density (a function of temperature, salinity, and pressure). A radar altimeter measures changes in sea surface height due to both of these factors − re-distribution of mass and changes in density (Roemmich *et al.*, 2001). Maps of Sea Level Anomalies (MSLA) data products were obtained from the final combined processing of TOPEX/ POSEIDON and ERS-1/2 data. The MSLA values provide an indication of fluctuation in both current strength and direction around long-term averages. The MSLA grids contain the data for global mapping of ocean variability, i.e., both the sea level anomalies signal (in millimetres) and the errors as a percentage of the signal variance. These are available every 10 days and plotted with a 0.25 × 0.25° resolution. Altimeter measurements are corrected for instrumental errors, environmental perturbations (wet tropospheric, dry tropospheric, and ionospheric effects), ocean wave influence (sea state bias), tide influence (ocean

tide, earth tide, and pole tide), and inverse barometer effect (AVISO, 2000).

Analysis

Oceanographic gradients

A gradient measure was derived from the data describing bathymetry, ocean colour and sea surface temperature (Guinet *et al.*, 2001). Using IDL software, a Sobel operator was applied to each of the arrays in turn to create three new spatial variables. The IDL Sobel operator calculates a gradient by applying two 3 × 3 matrix operators. One matrix is sensitive to E−W gradients, and the other to N−S gradients. The numbers derived from applying the two matrices are squared and added, and the square root taken to provide a non-directional measure of the oceanographic data.

Data selection for model construction

There was a possibility of temporal autocorrelation of foraging behaviour and oceanographic variables between the different months; here, the position and time spent per grid cell may have depended on the distribution of time per grid cell in the previous month. To avoid the problems associated with temporal autocorrelation, we randomly selected 50% of the grid cells to construct the models. The remaining 50% of the data describing each grid cell were used to validate the fitted values from each best-fit model selected (see following sections).
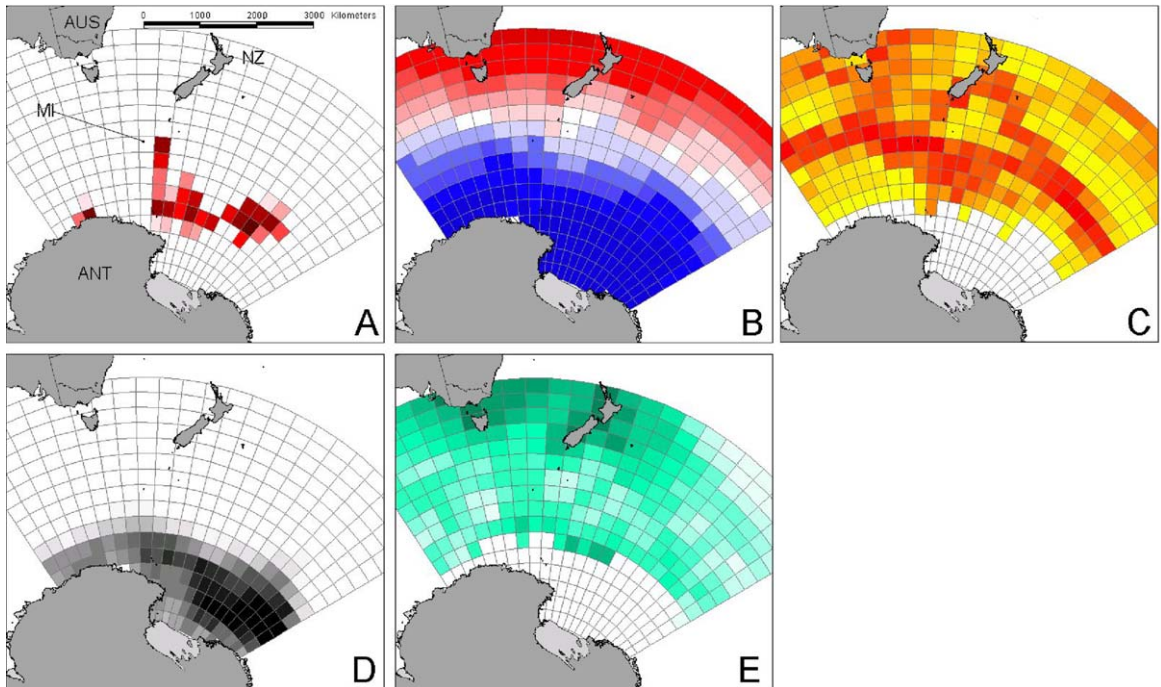
Figure 2. An example of post-moult (August 2001) response (seal use) and explanatory (oceanographic) variables displayed in the 300×300-km grid resolution. Darker grid cells indicate higher values. A. Time spent by adult female southern elephant seals, B. Sea surface temperature, C. Sea surface temperature gradient, D. Sea-ice concentration, and E. Ocean colour.

Distribution of oceanographic variables

An inspection of boxplots and histograms for each variable considered demonstrated that ocean colour, ocean colour gradient, and sea-ice concentration were strongly right skewed due to the high frequency of zero values. Despite attempting to account for the skewed distributions using a log-transformation on the response variable (time) or a monotonic link function (see below), residuals remained highly skewed and heteroscedastic.

Therefore, we adopted a transformation strategy of these variables based on biological grounds. We believed that the presence or absence of sea ice to elephant seal foraging was more important than estimated cover itself, so we reduced sea-ice concentration to a binary variable (i.e., "ice" vs. "no ice"). Similarly, the distribution of mean ocean colour in summer indicated several extreme outliers $> 1.0 \text{ mg cm}^{-3}$ chlorophyll α. These extreme values could be highly influential to model fits, and large ocean colour can result from satellite error; therefore, we used 1.0 mg cm^{-3} chlorophyll α as the productivity threshold (see Nixon and Thomas, 2001), and truncated the distribution so that all values $> 1.0 \text{ mg cm}^{-3}$ chlorophyll α were set to 1.0. A similar distribution was observed for the gradient in chlorophyll α during summer, so all gradient values > 1.0 were truncated to 1.0 mg cm^{-3}. The distribution of colour values in winter was similarly right skewed, although the mean concentration of chlorophyll α was much lower ($\bar{x}_{sum} = 0.40$, s.e. $= 0.05 \text{ mg cm}^{-3}$;

$\bar{x}_{win} = 0.17$, s.e. $= 0.01 \text{ mg cm}^{-3}$). Therefore, we truncated the winter colour values to $\leq 0.25 \text{ mg cm}^{-3}$ and the gradient of these values to 0.05 to avoid extensive outlying values.

Generalized linear models (GLM)

We used the generalized linear model (GLM) function in R (Ver. 1.7.1) to fit a series of linear models to the data. GLMs extend the standard regression model in two ways: (1) the response y may be distributed about its expected value μ according to any distribution F from the exponential family (including the Normal, Gamma, Binomial, Poisson, and Negative Binomial distributions),

$$y_i \sim F(\mu_i)$$

and (2) the predictors $x_1, x_2, \ldots, x_m$ enter the model through the linear predictor η, which is related to the expected response μ by a monotonic link function $\eta_i = \eta(\mu_i)$,

$$\eta(\mu_i) = \eta_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \ldots + \beta_m x_{mi}.$$

These features relax the restrictions imposed by the standard regression model on both the distribution of the response, and the functional relation between the response and predictors.

Inference for a GLM is based on the theory of maximum likelihood estimation, and likelihood ratio tests and analysis

of deviance replace the classical F-tests and analysis of variance of the standard regression model (McCullagh and Nelder, 1989). A useful measure of comparative model fit is the Akaike Information Criterion (AIC − Akaike, 1973). The use of the AIC parallels the use of Mallow's C_p for model selection in the standard regression model (Venables and Ripley, 1999), with smaller values of the AIC being preferred. A major advantage of the AIC is that it is valid for the comparison of non-tested models, allowing models with different link and distributional assumptions to be compared.

Both Gamma and Normal response models were considered, with identity-, log- and inverse-link functions. A stepwise procedure based on the AIC was used to select amongst candidate models incorporating both untransformed and log-transformed predictors. Only the top model based on Akaike's Information Criterion (AIC) was considered. The best model was constructed from the first randomly chosen 50% of the data for both PL and PM foraging trips, and the remaining data were used to validate the model predictions. Significance of best-fit model terms was tested using analysis of deviance. The per cent change in deviance between the final model and the null model was calculated as a measure of the amount of variation explained by the final model.

Generalized additive models (GAM)

We also used the generalized additive model (GAM) function in S-Plus (Ver. 6.1) to fit a series of linear and non-linear models to the data. GAMs extend GLMs by assuming the linear predictor is of the form:

$$\eta(\mu_i) = \eta_i = f_1(x_{1i}) + f_2(x_{2i}) + \ldots + f_n(x_{mi})$$

where f_i are arbitrary smooth functions that are to be estimated (Hastie and Tibshirani, 1990). That is, where a GLM estimates regression coefficients β_0, β_1, …, β_m, a GAM estimates the smooth functions f_1, f_2, …, f_m, and where the results of a GLM are typically presented as tables of coefficients, the results of a GAM are presented as scatter plots of the estimated f_1, f_2, …,f_m. There is no requirement that all the f_i are to be estimated − it is possible for the functional form of some of the f_i to be specified *a priori*. When the form of every f_i is specified, the model reverts to a GLM. The level of smoothing imposed on the estimated f_i is arbitrary and is controlled by a number of smoothing parameters. These parameters are in essence arbitrary but are typically chosen according to a data-driven automatic selection rule (Simonoff, 1996).

Inference for the GAM is again based on the theory of maximum likelihood, but is conditional on the choice of smoothing parameters. That is, test p-values account for the uncertainty due to the distribution of the response about its expected value, but do not account for uncertainty in the choice of smoothing parameters. Thus, p-values in GAMS are conditional on the choice of smoothing parameters, and these may be somewhat arbitrary.

For this reason, test p-values should only be taken as an approximate guide. The advantage of GAMs is that they automatically transform each predictor to give the best model fit, relieving the user of the burden of selecting the form in which predictor variables should enter the model. Although GAMs provide flexibility, their key disadvantage is that they are purely additive − it is not possible in standard GAMs to represent interactions amongst predictors.

As for the GLM procedure, the occupancy time per grid cell was modelled using both Gamma and Normal responses, with identity-, log- and inverse-link functions. A stepwise procedure based on the AIC was used to select amongst candidate models incorporating untransformed, log-transformed and smoothed predictors. Additionally, we examined the results of the AIC stepwise selection using several different starting models because selection could be influenced by the choice of starting model. Terms that were consistently selected were used to construct the final model for both the PL and PM trips separately. As for the best-fit GLM, the best-fit GAM was constructed from the first randomly chosen 50% of the data for both PL and PM foraging trips, and the remaining data were used to validate the model predictions.

Results

We collected 28 separate foraging records during the 1999 (n = 17) and 2000 (n = 11) post-lactation foraging trips (22 unique individuals), and 19 separate foraging records during the 2000 (n = 10) and 2001 (n = 9) post-moult foraging trips (16 unique individuals). Adult females travelled a maximum distance of 1491 ± 105 km (mean ± standard error) from Macquarie Island during the post-lactation trip, and 2761 ± 156 km from the island during the post-moult foraging trip.

Generalized linear model selection

Both the AIC and an examination of residuals from the fitted model showed that a Gamma GLM with a log-link function was the most appropriate model for occupancy time per grid cell as a function of the oceanographic response variables and their gradients. The Gamma distribution captured the strong right skew of the response variable (i.e., many grid cells with low use and few with high use). The choice of a log-link function induces a multiplicative relation between response and predictor variables.

Model selection identified two separate best-fit models to explain the variation in the PL and PM foraging trip test data sets. During the PL trip, the best model included sea surface temperature, its gradient, sea surface height anomaly, and bathymetry. This model explained 18.2% of the deviance from the null model (100[132.39 − 108.27]/ 132.39). In general, there was a negative relationship

between seal use and bathymetry and sea surface temperature, but a positive relationship with sea surface temperature gradient and sea surface height anomaly (Figure 3). Analysis of deviance indicated strong support for the effects of sea surface temperature (Dev = −9.44; $F_{1,107}$ = 12.25; p < 0.001), sea surface temperature gradient (Dev = −20.66; $F_{1,107}$ = 26.81; p < 0.001), and bathymetry (Dev = −5.06; $F_{1,107}$ = 6.56; p = 0.012) on seal use. There was little support for the effect of sea surface height anomaly on seal use (Dev = −2.09; $F_{1,107}$ = 2.71; p = 0.103). The relationship between the predicted time and observed time for the validation data set was not significant (least-squares regression: r^2 = 0.002, $F_{1,107}$ = 0.21, p = 0.65; Figure 4).

During the post-moult trip, the best-fit model included ocean colour gradient, sea surface height anomaly, and bathymetry. This model explained 24.2% of the deviance from the null model (100[33.09 − 25.07]/33.09). In general, there was a negative relationship between seal use and all three terms (Figure 5). Analysis of deviance revealed that sea surface height anomaly and bathymetry contributed significantly to the model (sea surface height anomaly: Dev = −4.63; $F_{1,13}$ = 4.62; p = 0.051; bathymetry:

Dev = −7.70; $F_{1,13}$ = 7.67; p = 0.016). However, there was no support for the effect of ocean colour gradient on seal use (Dev = −2.45; $F_{1,13}$ = 2.44; p = 0.142). There was no significant relationship between the predicted and observed values for the validation set, possibly due to the low degrees of freedom (d.f. = 31).

Even though the best-fit models explained a significant amount of variation in seal use, model validation revealed little predictive power of the defined models. The predicted line between the observed and predicted data sets does not pass through the origin as a consequence of the best-fit model not explaining a large proportion of the overall variance in the data.

Generalized additive model selection

As for the GLM procedure, the occupancy time per grid cell was modelled as a function of the oceanographic response variables and their gradients using a Gamma distribution GAM with a log link. Model selection identified two separate best-fit models to explain the variation in the PL and PM foraging trip test data sets, but these differed somewhat from those identified using GLM. During the PL
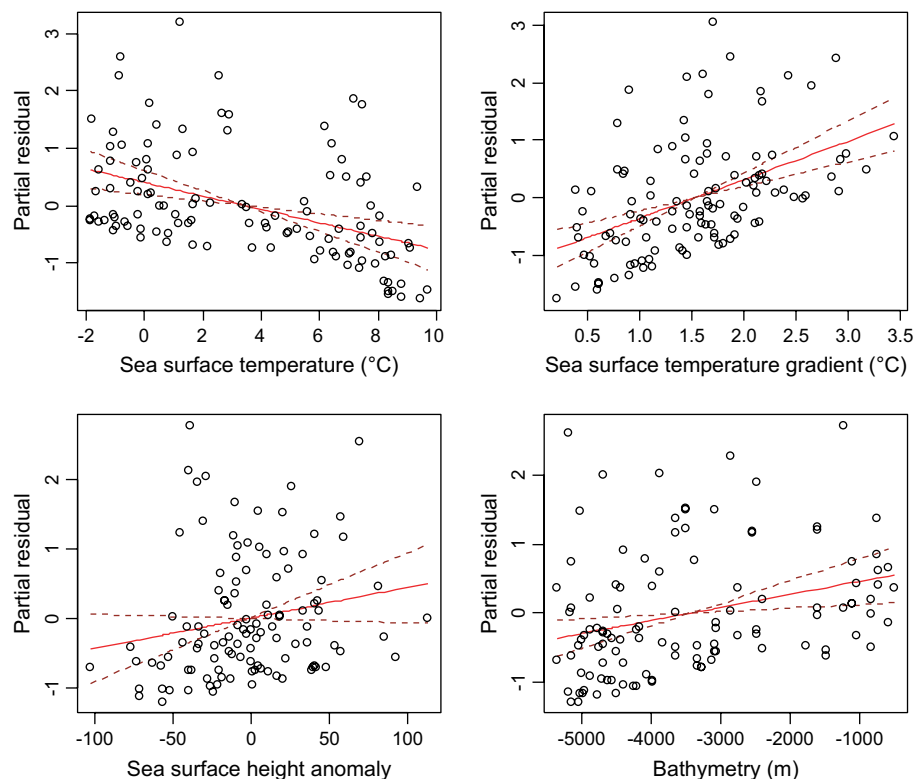

Figure 3. Partial residual plots generated from the most-parsimonious generalized linear model relating post-lactation seal use to oceanographic variables: sea surface temperature (negative), sea surface temperature gradient (positive), sea surface height anomaly (positive), and bathymetry (negative). Solid lines are the fitted linear models. Dashed lines are approximate 95% point-wise confidence intervals.
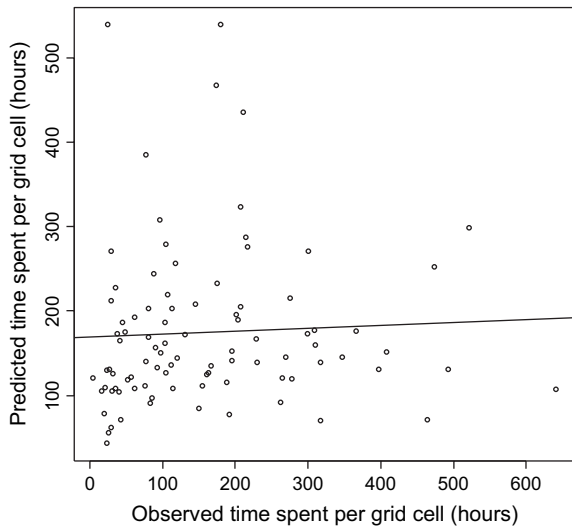
Figure 4. Relationship between the amount of time spent per grid cell predicted from the best generalized linear model and the observed time spent per grid cell. The solid line represents the least-squares regression.

trip, the best-fit GAM included ocean colour, its gradient, sea surface temperature and its gradient. In general, there was a negative relationship between seal use and ocean colour gradient and sea surface temperature gradient, and a positive relationship with ocean colour (Figure 6). There was a non-linear relationship between seal use and sea surface temperature, with maximum use occurring between 4 and 5°C (Figure 6). The relationship between the predicted time and observed time for the validation data set was significant (least-squares regression: $r^2 = 0.04$, $F_{1,110} = 4.15$, $p = 0.044$; Figure 7).

During the post-moult trip, the best-fit model included mean ocean colour, sea surface temperature and its gradient, bathymetry and its gradient. There was a negative relationship between seal use and ocean colour, bathymetry gradient and sea surface temperature (the latter being a negative log-linear relationship), and a positive relationship between sea surface temperature gradient and bathymetry (Figure 8). However, there was no significant relationship between the predicted and observed values for the validation set (least-squares regression: $r^2 < 0.01$, $F_{1,15} = 0.07$, $p = 0.79$).

Discussion

The foraging behaviour and distribution of marine predators will be influenced largely by the distribution of their prey, the latter being influenced to various degrees by the physical and biological properties of the ocean (Charrassin and Bost, 2001). Although simple covariates describing ocean surface properties have been useful in explaining

some of the variation in the foraging behaviour of apex predators (Georges *et al.*, 2000; Guinet *et al.*, 2001; Nel *et al.*, 2001), the predictive capacity of simple models is variable. In contrast to other studies (e.g., Guinet *et al.*, 2001; Nel *et al.*, 2001), our results suggest that even more complex, non-linear models still fail to provide a strong predictive framework for apex predator foraging at coarse spatial scales. Much of this reduced predictive capacity may result from the relatively sparse data collected from remote satellite instruments, especially during the heavily clouded winter months (Sumner *et al.*, 2003). Additionally, measurement of surface properties may not necessarily capture the oceanographic patterns at depth to which deep-diving species such as elephant seals may respond more strongly (sub-surface information based on climatological mean fields is limited). Furthermore, the data used to describe predator foraging were basic spatial occupancy (time per unit area), and this parameter may still have included transit and non-foraging behaviour even though the major transiting periods were removed from the analysis.

An important potential limitation of the models' pre-dictive capacity may reside in the choice of the spatial scale of investigation. The large grid cell size (300 × 300 km) determined from optimal temperature agreement (Bradshaw *et al.*, 2002, in press) provided a high degree of spatial averaging in oceanographic conditions. Improvements in the estimates of foraging tracks (satellite telemetry or improved geo-location algorithms) and better spatial resolution in surface oceanographic data would likely result in a different selection field for GLM and GAM approaches. Of course, subtler effects of oceanographic configuration on elephant seal foraging behaviour at finer spatial scales are likely to exist, but the coarse spatial scale of investigation used in our analysis was incapable of describing these. However, a greater spatial resolution would necessarily result in a higher sample size (i.e., greater number of grid cells) that may further complicate the problem of temporal autocorrelation in animal behaviour. With relatively few spatial blocks used to derive the models, randomization of the data prevented the problems associated with high temporal autocorrelation in our analyses.

Although there was some consistency in the results of the best-fit GLM and GAM for each foraging trip (sea surface temperature for the PL model; bathymetry for the PM model), strong differences were found. Because GAMs are more flexible than similarly constructed GLMs, GAMs can over-fit models more frequently. The collective information from the two approaches indicates that prediction may still be difficult because the *mechanisms* influencing seal behaviour may not be identified; rather, our modelling only indicates which factors impact behaviour. The application of the concept of parsimony in model selection results in the fewest number of terms that result in the best predictions. Additionally, because GLM and GAM effec-tively model ecological niches (those that include biotic
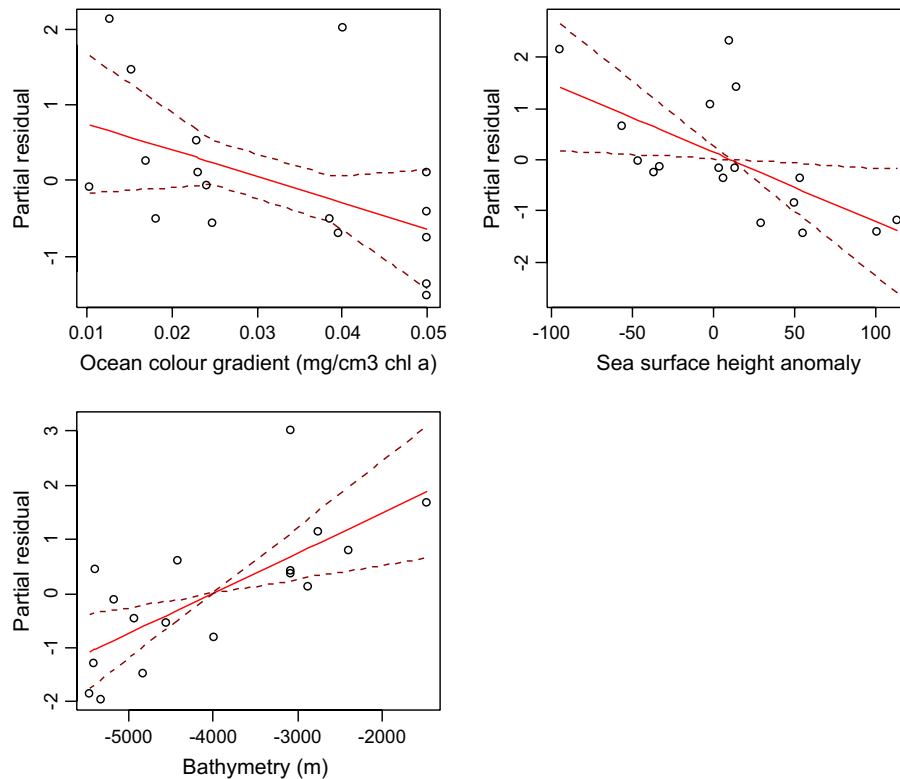
Figure 5. Partial residual plots generated from the most-parsimonious generalized linear model relating post-moult seal use to oceanographic variables: ocean colour gradient (negative), sea surface height anomaly (negative), and bathymetry (negative). Solid lines are the fitted linear models. Dashed lines are approximate 95% point-wise confidence intervals.

interactions and competitive exclusion) rather than fundamental niches (primarily a function of physiological performance and ecosystem restraints), their predictive capacity from region to region is expected to be low (Roloff and Kernohan, 1999; Guisan *et al.*, 2002).

The ability to predict foraging behaviour of wide-ranging predators may be severely restricted by other factors not directly related to the physical properties of the environment. First, the physical configurations of the local marine environment may not directly influence the structure and composition of elephant seal prey communities because of dilution and downstream effects (El-Sayed, 1988; Guinet *et al.*, 2001). Second, there is still a limited understanding of how physical properties may influence or relate to plankton abundance and distribution within the upper layers of the Southern Ocean. Finally, accessibility and predator knowledge of the foraging environment are also central components of any relationship between animal behaviour and oceanographic configuration (Matthiopoulos, 2003). Although elephant seals from Macquarie Island have the ability to access areas within 3000−5000 km of the island itself (Hindell and McMahon, 2000; McConnell *et al.*, 2002; Hindell *et al.*, 2003), they do demonstrate strong preference for individual foraging regions (Field *et al.*, 2001; Bradshaw *et al.*, in press) that may have evolved due

to the higher costs of compensating for local reductions in food availability (Bradshaw *et al.*, in press). This strong tendency to return to known foraging regions may therefore over-ride local events that could lead to higher prey availability in regions adjacent to the foraging routes chosen by adult individuals.

Nonetheless, one of the most consistent properties describing a small, but significant component in the variation of spatial occupancy was sea surface temperature and its spatial gradient. In general, seals spent more time in areas of colder water; however, the non-linear relationship during the PL indicates that surface waters around 4°C were most often selected. The prominent frontal zones within this region (Rintoul *et al.*, 1997, 2001; Budillon and Rintoul, 2003) have been identified as a potentially important features for vertebrate marine species originating from Macquarie Island (Hull *et al.*, 1997; Hull, 1999; Field *et al.*, 2001; Hindell *et al.*, 2003). Higher temperature gradients associated with these and other frontal features may be indicative of higher relative productivity than surrounding areas (Rintoul *et al.*, 1997, 2001; Tynan, 1998; Guinet *et al.*, 2001; Moore and Abbott, 2002). An examination of sub-surface temperature, salinity, and oxygen values from the Java OceanAtlas (http://odf.ucsd.edu/joa/index.html) at depths of 300−700 m (average
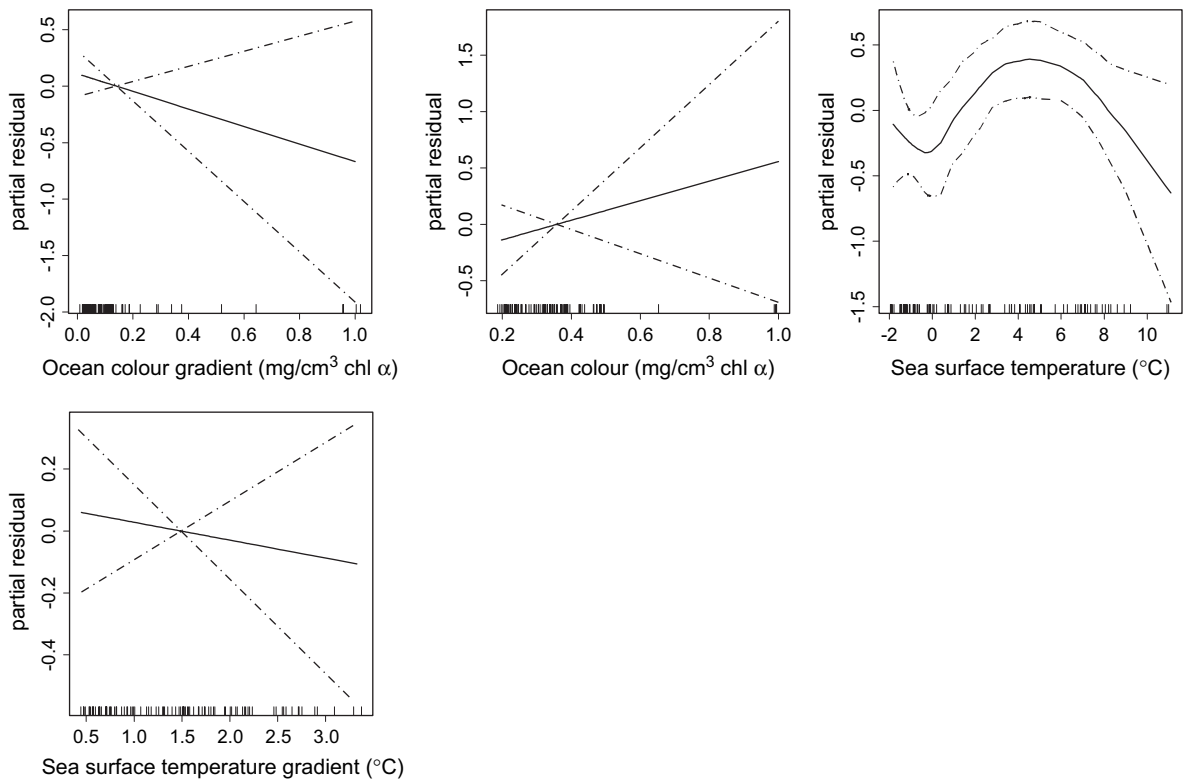
Figure 6. Partial residual plots generated from the most-parsimonious generalized additive model relating post-lactation seal use to oceanographic variables: ocean colour gradient (negative), ocean colour (positive), sea surface temperature (non-linear), and sea surface temperature gradient (negative). Solid lines are the fitted linear models. Dashed lines are approximate 95% point-wise confidence intervals. Tick marks on the x-axis show the locations of the observations on that variable.

foraging depth range for southern elephant seals − Field *et al.*, 2001) supported the results using surface data alone. Within the frontal zone areas where surface temperature gradients were highest, sub-surface temperatures ranged
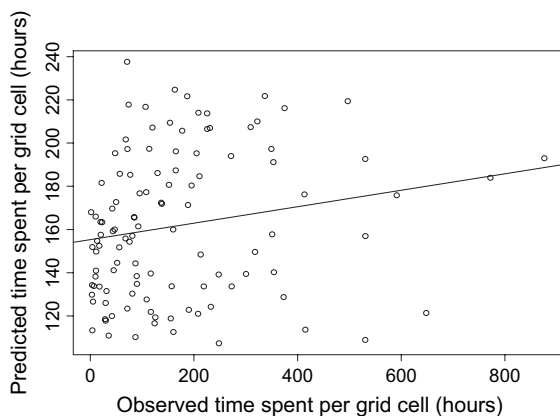

Figure 7. Relationship between the amount of time spent per grid cell predicted from the best generalized additive model and the observed time per grid. The solid line represents the least-squares regression.

between 2 and 4 degrees. However, there was a noticeable reduction in sub-surface oxygen content in these areas (~ 4 ml l^{-1}). Sub-surface salinity measures demonstrated relatively low variability at these depths (34.6−34.7 psu). The identification of bathymetry and its gradient as potential explanatory terms may be indicative of the effect of the Macquarie ridge on the southern deflection of the frontal zones and associated eddies south of Macquarie Island (Gordon, 1972; Rintoul *et al.*, 2001).

Understanding the often subtle influence of the coarse-scale physical properties of vast ocean systems on marine biological communities on which they depend is limited ultimately by the quantity and quality of the data collected. The paucity of oceanographic data during winter remains one of the largest obstacles to understanding these processes, especially for large, wide-ranging marine predators that extend well into the pack-ice zones surrounding Antarctica. Increased resolution of location, behaviour and remotely sensed data, in addition to more advanced methods of spatial summary (i.e. non-raster) may also improve model performance. More complex, non-linear modelling approaches may also provide more insight (see Guisan and Zimmermann, 2000 for review), although the underlying mechanisms of foraging pattern may be
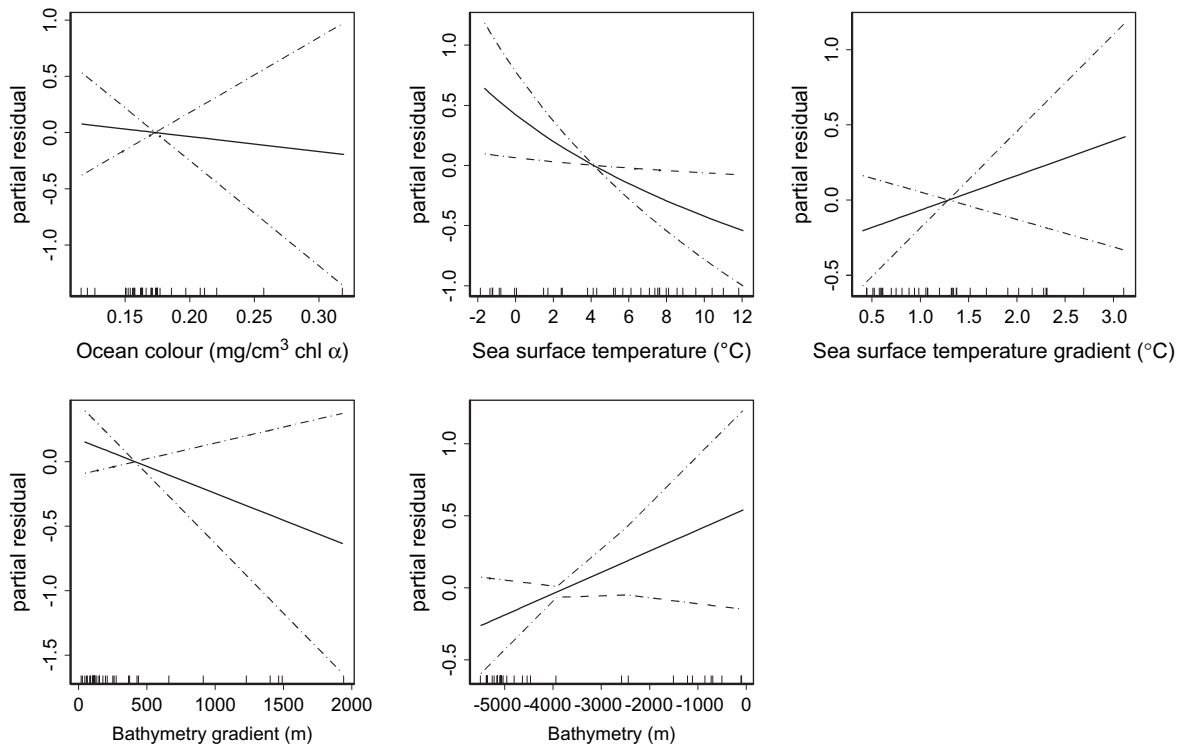
Figure 8. Partial residual plots generated from the most-parsimonious generalized additive model relating post-moult seal use to oceanographic variables: ocean colour (negative), sea surface temperature (log-linearly negative), sea surface temperature gradient (positive), bathymetry gradient (negative) and bathymetry (negative). Solid lines are the fitted linear models. Dashed lines are approximate 95% point-wise confidence intervals. Tick marks on the x-axis show the locations of the observations on that variable.

driven more by long-term evolutionary processes rather than contemporaneous oceanographic configuration (Bradshaw *et al.*, in press). As well, more specific estimates of foraging itself, such as foraging "effort" determined by diving behaviour (Boyd *et al.*, 1997; Bowen *et al.*, 2001; Field *et al.*, 2001; Charrassin *et al.*, 2002), changes in travel rate (McConnell and Fedak, 1996; Campagna *et al.*, 1999; Le Boeuf *et al.*, 2000; McConnell *et al.*, 2002), and estimates of relative lipid changes (Biuw *et al.*, 2003) may identify closer associations between specific oceanographic variables and foraging distribution. Finally, both the strength and direction of correlations with certain oceanographic features that act as surrogate measures of productivity can depend on the spatial scale of investigation (Jaquet and Whitehead, 1996; Guinet *et al.*, 2001). The use of coarse-scale methods to obtain at-sea locations (geolocation) does not provide information on the fine-scale foraging behaviour of southern elephant seals. Therefore, our ability to detect scale dependencies in the models constructed was not possible. Despite the poor predictive capacity of the models examined in this study, some of the mechanisms influencing predator foraging are congruent with expectations of distribution of marine food resources at coarse spatial scales.

Acknowledgements

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