Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey

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Summary

1. Understanding the ecological processes that underpin species distribution patterns is a fundamental goal in spatial ecology. However, developing predictive models of habitat use is challenging for species that forage in marine environments, as both predators and prey are often highly mobile and difficult to monitor. Consequently, few studies have developed resource selection functions for marine predators based directly on the abundance and distribution of their prey.

2. We analysed contemporaneous data on the diving locations of two seabird species, the shallow-diving Peruvian Booby (*Sula variegata*) and deeper diving Guanay Cormorant (*Phalacrocorax bougainvilliorum*), and the abundance and depth distribution of their main prey, Peruvian anchoveta (*Engraulis ringens*). Based on this unique data set, we developed resource selection functions to test the hypothesis that the probability of seabird diving behaviour at a given location is a function of the relative abundance of prey in the upper water column.

3. For both species, we show that the probability of diving behaviour is mostly explained by the distribution of prey at shallow depths. While the probability of diving behaviour increases sharply with prey abundance at relatively low levels of abundance, support for including abundance in addition to the depth distribution of prey is weak, suggesting that prey abundance was not a major factor determining the location of diving behaviour during the study period.

4. The study thus highlights the importance of the depth distribution of prey for two species of seabird with different diving capabilities. The results complement previous research that points towards the importance of oceanographic processes that enhance the accessibility of prey to seabirds. The implications are that locations where prey is predictably found at accessible depths may be more important for surface foragers, such as seabirds, than locations where prey is predictably abundant.

5. Analysis of the relative importance of abundance and accessibility is essential for the design and evaluation of effective management responses to reduced prey availability for seabirds and other top predators in marine systems.

Key-words: central place foragers, foraging ecology, habitat use, Humboldt Current System, predator–prey interactions, spatial distribution

Introduction

Understanding the ecological processes that underpin species' distribution patterns is a fundamental goal in ecology (Levin 1992). A current challenge in marine spatial ecology is to move beyond existing methods for mapping and modelling species distributions and movement patterns to develop more mechanistic models of habitat selection (Robinson *et al.* 2011). In marine systems, there are growing concerns about the effects of fisheries on prey availability to top predators (Duffy 1983a; Becker & Beissinger 2006; Crawford *et al.* 2006; Cury *et al.* 2011;

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Bertrand *et al.* 2012), and hence a need to identify and predict important foraging areas for marine predators so that strategies can be developed to safeguard prey availability in these areas.

In previous studies, data on marine predators have been mapped against remote-sensing data on environmental covariates and used to define foraging areas in terms of sea-surface temperature (SST), chlorophyll concentration (Chl *a*) and other environmental variables (Redfern *et al.* 2006; Tremblay *et al.* 2009; Wakefield, Phillips & Matthiopoulos 2009), with the idea that these variables are proxies for the distribution of prey. However, environmental variables are not always good predictors of prey distribution (Grémillet *et al.* 2008) and, thus, habitat models based on environmental covariates may not adequately predict the spatial responses of predators to changes in prey distributions that are not effectively signalled by changes in covariates. In contrast, resource selection functions that predict the probability of a species' occurrence at a particular location as a function of resource attributes (Boyce *et al.* 2002) provide a powerful mechanistic tool for investigating how seabirds might adjust foraging patterns in response to management actions or variation in environmental conditions.

However, developing resource selection functions is challenging for marine species foraging on pelagic prey, as both predators and prey are often highly mobile and difficult to monitor (Redfern *et al.* 2006). A few studies have explored the relationship between seabird abundance, prey densities and environmental variables, using concurrent vessel-based survey data (e.g. Ainley *et al.* 2009; Santora, Ralston & Sydeman 2011; Renner, Arimitsu & Piatt 2012; Cox, Scott & Camphuysen 2013; Goyert 2014). Integrating analysis of seabird telemetry data with data on prey densities and environmental variables collected from a separate platform presents a number of additional challenges. Bertrand and colleagues used vessel tracking data to explore correlations between the movement patterns of fishing vessels and the spatial distribution of targeted fish stocks (Bertrand, Diaz & Lengaigne 2008). Yet, to our knowledge, no previous studies have used tracking data to develop resource selection functions for marine predators in terms of their prey. Our objective was to investigate foraging site selection by seabirds using seabird tracking data and contemporaneous vessel-based survey data on the abundance and distribution of their prey. This approach is expected to be especially valuable for marine species that are more easily tracked than observed in vessel-based surveys, including less common seabird species, as well as pinnipeds and sea turtles, or where the costs of vessel-based surveys are prohibitive.

It is well-established that prey availability is a function of accessibility, as well as abundance (Cairns 1987; Hunt, Harrison & Cooney 1990; Piatt 1990; Boyd 1999). We defined accessibility in terms of the probability that prey biomass falls within a specific habitat envelope accessible to the predator. For air-breathing foragers, such as

seabirds, the depth distribution of prey can be a key factor determining its availability. Diving is energetically costly for both plunge-diving and pursuit-diving seabirds (Ellis & Gabrielsen 2002; Green *et al.* 2010) and is unlikely to occur at random. We therefore tested the hypothesis that the probability that a seabird dives at a given location is a function of the relative abundance of prey through the water column and the probability that this prey is found in the upper water column. We developed a series of resource selection functions to assess the relative importance of the abundance and depth distribution of prey in foraging site selection for surface foragers.

We present analysis of the foraging patterns of two species of seabird, the Peruvian Booby (*Sula variegata* [Tschudi, 1843]) and Guanay Cormorant (*Phalacrocorax bougainvilliorum* [Lesson, 1837]). The Peruvian Booby and Guanay Cormorant are both endemic to the northern Humboldt Current System, where both species forage primarily on the small pelagic Peruvian anchoveta (*Engraulis ringens* [Jenyns, 1842]). The two seabird species often forage together in large flocks but have different foraging modes (Murphy 1936; Duffy 1983b). Peruvian Boobies are plunge divers, foraging in the upper water column (up to 9 m depth, Zavalaga *et al.* 2010), whereas Guanay Cormorants are pursuit divers, capable of foraging at much greater depths (up to 74 m depth, Zavalaga & Paredes 1999).

The general decline in seabird populations in the northern Humboldt Current System since the mid-1960s has been attributed to the development of the industrial anchoveta fishery (e.g. Jahncke, Checkley & Hunt 2004). Guanay Cormorants have exhibited a substantial decline from around 21 million to 2 million birds since 1955, while populations of Peruvian Boobies have been more stable at around 2 million birds (Jahncke 1998; Goya 2000; Weimerskirch *et al.* 2010). The Humboldt Current System is characterized by environmental variability at multiple temporal and spatial scales, leading to variation in the abundance and distribution of anchoveta (Chavez *et al.* 2008). In particular, the depth distribution of anchoveta is limited by the oxycline, which is relatively shallow in the Humboldt Current System, but subject to environmental forcing (Bertrand *et al.* 2008). Both seabird species have evolved in the context of this variability, but, nevertheless, suffer population declines during severe oceanographic anomalies (Nelson 1978; Duffy 1983a).

Materials and methods

DATA

Patterns of foraging site selection by Peruvian Boobies and Guanay Cormorants were analysed by overlaying the locations of diving behaviour for each species on representations of the prey field (Boyd *et al.* 2015a). Seabird tracking data and acoustic survey data were collected at the island group of Pescadores (*c.* 11·77°S, 77·27°W), Peru (Fig. 1), in the first week of December 2008. The study site supports colonies of both Peruvian Boobies
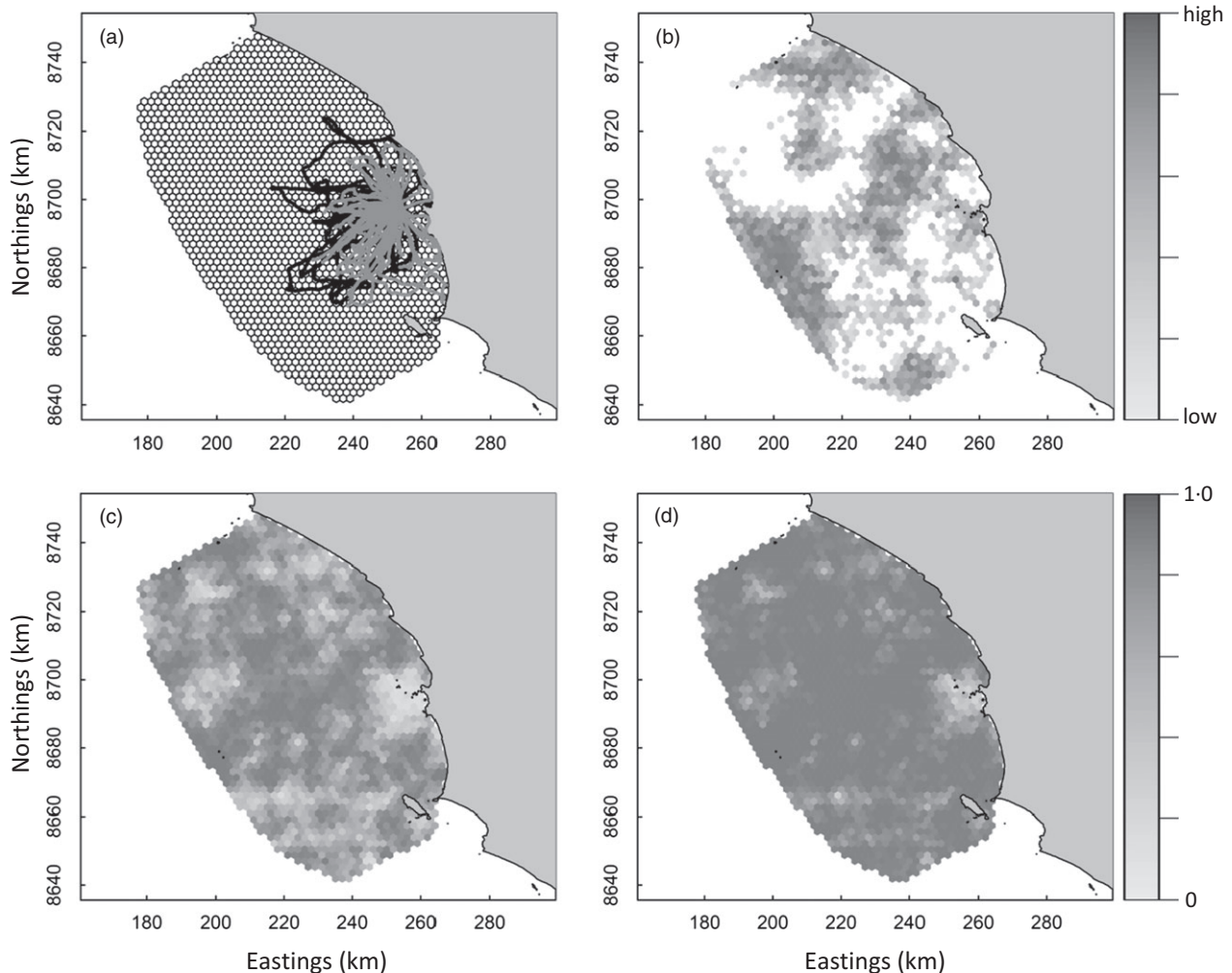
Fig. 1. The study region showing (a) observed tracks for Peruvian Boobies and Guanay Cormorants in December 2008 overlaid on 2-km-hexagonal grid cells; (b) a single Bayesian posterior prediction of the relative acoustic densities of anchoveta; and (c and d) a single Bayesian posterior prediction of the probability that the upper depth limit of aggregations is <7·5 m (c) or 10 m (d) below the echosounder. Black and grey lines in (a) indicate tracks for Peruvian Boobies and Guanay Cormorants, respectively. Land is shown in pale grey.

and Guanay Cormorants. Approximately 15 000 boobies and 190 000 cormorants were breeding at the colony during the study period (Weimerskirch *et al.* 2010). Diving locations were identified using a combination of global positioning system (GPS) and time-depth recorder (TDR) data (see Weimerskirch *et al.* 2012). The prey field was represented by Bayesian posterior predictions of the three-dimensional spatial distribution of prey based on contemporaneous acoustic survey data (Boyd *et al.* 2015b, and Appendix S1, Supporting Information).

Analysis of resource selection based on animal movement patterns faces two associated methodological challenges. Firstly, for any animal track, movement observations are inherently spatially-clustered, leading to uneven sampling effort. Secondly, behavioural observations within trips are likely to be characterized by serial autocorrelation. Treating autocorrelated observations as independent may lead to spurious significance tests and exaggerate resource preferences (Aebischer, Robertson & Kenward 1993; Aarts *et al.* 2008). Here, both issues were addressed by generating a set of regular hexagonal grid cells encompassing the seabird tracking data (Fig. 1a), and treating behaviour in each cell visited on each trip as the sampling unit rather than

each observation. Individuals sampled in this study did not follow the same route or return to the same location on subsequent trips, so trips could be treated as independent.

Data collection protocols for the two seabird species differed. For the Guanay Cormorants, 11 trips by 5 individuals during the period 1–5 December 2008 were recorded by GPS (MiniGPSlog, Earth and Ocean GPS, Kiel, Germany, 30 g) at minimum intervals of 30 seconds, and by time-depth recorders (TDRs; G5, CEFAS Technology, Lowestoft, UK, 3 g) at 1-s intervals. All sampled individuals were breeding, with two or three chicks aged 1–2 weeks. The sex of Guanay Cormorants is not easily determined in the field and could not be ascertained for several individuals. The mean mass at recovery for Guanay Cormorants was 2000 g (range: 1750–2350 g; $n = 5$). TDR observations were georeferenced by interpolating the GPS data and matching the resulting track with the TDR record. For each trip, grid cells were identified as including diving behaviour if at least one observation greater than 1 dbar occurred in a cell. The 1 dbar threshold (indicating a depth of 1 m below the sea surface) was applied to remove superficial bathing activity from the analysis and reduce measurement error.

For the Peruvian Boobies, 13 trips by six individuals were recorded by high-resolution GPS (Gipsy GPS, Technosmart, Rome, Italy, 25–30 g) at 1-s intervals during the period 2–5 December 2008. All sampled individuals were breeding, with one or two chicks aged 2–3 weeks. The sample included three male and three females. Peruvian Boobies are sexually dimorphic, with females larger than males. Mass at recovery was collected for three individuals: one male weighed 1420 g, while two females weighed 1650 and 1850 g. GPS units do not receive a satellite signal while the bird is submerged (Wilson & Vandenabeele 2012), and so the tracking data for Peruvian Boobies were characterized by occasional brief gaps in the regular 1-s sequence of GPS observations. Prior analysis of pilot data collected for Peruvian Boobies at Isla Guañape Sur in northern Peru in 2007 showed that such gaps corresponded to diving behaviour (Boyd 2012; see also Wanless *et al.* 1993; Weimerskirch *et al.* 2012). Gaps in the GPS data were geo-referenced by interpolating between locations immediately before and after the gap. For each trip, grid cells were identified as including diving behaviour if at least one gap in the GPS data occurred in a cell.

The Instituto del Mar del Péru (IMARPE) conducted an acoustic survey on the RV 'Olaya' off Grupo Pescadores during 2–5 December 2008. The survey design was systematic, based on parallel, equally spaced, onshore–offshore transects approximately 10 km apart. For the purposes of this analysis, the study region was restricted to the on-shelf area covered by the survey. This region encompasses the movement patterns of all seabirds tracked as part of this study.

Acoustic backscattering data were collected using a calibrated Simrad scientific echosounder (EK60) operating at 120 kHz and processed by IMARPE using ECHOVIEW acoustic post-processing software (Myriax Software, Hobart, Tas., Australia). Acoustic backscatter was identified to species based on known backscattering characteristics, ground-truthed using biological samples taken from mid-water trawls during the survey (Castillo *et al.* 2009; Simmonds *et al.* 2009). The proportion of anchoveta in the diets of Peruvian Boobies and Guanay Cormorants is characterized by latitudinal variation as well as seasonal and interannual variation. For Isla Mazorca (*c.* 25 miles north of Grupo Pescadores), Jahncke & Goya (1998) estimated that anchoveta represented *c.* 70% of the diet of Guanay Cormorants and 90% of the diet of Peruvian Boobies in December based on data collected from 1995 to 1997. Only backscatter attributed to anchoveta was used in the analysis presented here.

The acoustic backscattering data were processed in two ways. First, the nautical area scattering coefficient (NASC) attributable to anchoveta was computed from the mean volume backscattering strength over 1-nm-transect segments (elementary distance sampling units, EDSUs). This output was used as the basis for modelling relative abundance (see Boyd *et al.* 2015b). Secondly, relatively homogeneous regions of acoustic backscatter were identified using the school detection algorithm in Echoview. This output was used as the basis for modelling the depth distribution of aggregations of anchoveta (see Appendix S1). For each identified aggregation, the height and mean depth were estimated by the school detection algorithm and used to calculate the depth of the upper limit of the aggregation. All depths refer to depths below the echosounder (i.e. depths are measured from 3·4 m below the sea surface).

Seabird tracking data are spatially continuous, whereas the acoustic data were derived from discrete transects. Integrated analysis of continuous and discrete data was achieved by evaluating seabird behaviour in grid cells and using Bayesian geostatistical analysis (Diggle & Ribeiro 2007) to generate 100 posterior predictions of the acoustic densities and upper depth limits of anchoveta aggregations to a set of grid cells encompassing the seabird tracking data (Fig. 1). Bayesian geostatistical posterior prediction reproduced the spatial patterns and statistical properties of the acoustic densities and depth distributions of anchoveta (Boyd *et al.* 2015b; and Appendix S1). Predicted acoustic densities were transformed to fish densities using constant values taken from the literature (Appendix S1 in Boyd *et al.* 2015b).

RESOURCE SELECTION FUNCTIONS

For both seabird species, the probability that diving behaviour occurred in a cell was modelled as a Bernoulli process. Surveys based on visual observations generate presence/absence data, enabling direct comparison of locations where the target species was observed and not observed, but seabird tracking data provide information on presence only. A methodological issue in many presence-only studies is the need to generate pseudo-absence data as a contrast to the observed presence data. A widely used approach is to compare presence locations with a hypothetical set of available locations (Boyce *et al.* 2002; Zavalaga, Halls & Dell'Omo 2010), but the definition of available locations is open to question. The model structure developed here avoids this issue by only using data for cells visited by seabirds, and therefore known to be available. Prey attributes in cells identified as the location of diving behaviour were contrasted with prey attributes in cells visited by seabirds but not identified as locations of diving behaviour. Each sample (i.e. set of seabird observations belonging to the same trip within a grid cell) was treated as a single Bernoulli trial. No adjustment was made for the amount of time a seabird was in a grid cell because this is a function of the decision to forage in a cell. To test the hypothesis that seabird diving behaviour is a response to the relative abundance of prey in the upper water column, the observed diving behaviour was linked to prey availability via a logit link function:

$$\text{logit}\,(y_{i,j}) = \eta_{i,j}. \qquad \text{eqn 1}$$

where $y_{i,j}$ is the observed binary response variable indicating whether or not the bird dived at location i on the jth trip. The predictor, $\eta_{i,j}$, was assumed to be a multiplicative function of the relative abundance of prey and the probability that the prey occurs in the upper water column, as in:

$$\eta_{i,j} = \beta_0 + \beta_1 * \rho_i * P(d_i < \delta) + u_j, \qquad \text{eqn 2}$$

where β_0 is an intercept, β_1 is a coefficient on the fixed effects, ρ_i refers to the relative abundance of prey, d_i refers to the upper depth limit of prey aggregations, δ is a scaling parameter, and u_j accounts for the random effects on trip j. With a multiplicative structure, prey that is inaccessible because it is deep in the water column is discounted, even if relative abundance is high. In contrast, an additive model structure, in which the predictor is a function of the relative abundance of prey plus the depth of prey, would allow for a high probability of selecting a location where prey was relatively abundant even if it was deep in the water

column. We did not use generalized additive models (Hastie & Tibshirani 1990) for this reason.

Relationships between seabird responses and the relative abundance and distribution of their prey are expected to be nonlinear (Cairns 1987; Piatt 1990; Piatt *et al.* 2007). Nonlinearities were incorporated by using the logistic function to model the relationship between the probability of diving behaviour and the predictor (eqn 1). This model structure allows for a wide range of functional forms. The contribution of prey abundance to the predictor was modelled in three ways (Table 1): using a binary indicator for the presence/absence of prey at a location (e.g. Model 2), as a linear function of prey abundance at a location (e.g. Model 3), and as a power function of prey abundance with an estimated exponent (e.g. Model 4). The presence/absence model allows for a sharp threshold at a point consistent with the detection threshold in the acoustic survey, while the power function allows for greater flexibility in the shape of the response. The model for the depth component incorporates an estimated scaling parameter, δ (eqn 2), which allows for nonlinearities in the response to the depth distribution of prey. Models were estimated for the abundance component and the depth component separately, and both combined (models 6, 7, 8). A null model was also estimated for comparison (Model 1).

The seabird data were derived from multiple individuals, with one or more trips per individual. Pooling data across individuals or trips is only appropriate if individuals or trips do not differ (Aebischer, Robertson & Kenward 1993). Here, variation at the trip level was incorporated by treating trips as random effects. The random effects (u_j in Table 1) were added to the linear predictors, implying that the expected probability of diving behaviour was inherently higher or lower for some trips. The random effects were assumed to follow a normal distribution with zero mean and variance σ^2.

MODEL LIKELIHOOD

The exogenous variables for the abundance and depth distribution of anchoveta in each grid cell were derived from Bayesian geostatistical analysis of the acoustic data. Uncertainty in these variables was taken into account by using 100 Bayesian posterior predictions of the relative abundance and depth distribution of anchoveta (Boyd *et al.* 2015a). For each model, parameters were estimated using the following objective function:

$$\text{NLL}\left(Y, X \middle| \psi\right) = -\frac{1}{N}\sum_{n=1}^{N} \log\left\{\text{L}\left(Y, X_n \middle| \psi\right)\right\}, \qquad \text{eqn 3}$$

where NLL is the negative log likelihood, ψ represents all model parameters and X represents the posterior predictions of the prey field $\{n = 1, \ldots N\}$. This objective function treats each posterior prediction as an independent data set rather than as an alternative representation of the distribution of anchoveta. An alternative configuration,

$$\text{NLL}\left(Y, X \middle| \underline{\psi}\right) = -\log\left\{\frac{1}{N}\sum_{n=1}^{N} \text{L}\left(Y, X_n \middle| \underline{\psi}\right)\right\}, \qquad \text{eqn 4}$$

would better reflect the fact that the set of posterior predictions represents multiple possible realizations of a single true distribution. However, using this configuration (eqn 4), the NLL tends to be minimized by fitting a few posterior predictions well but many posterior predictions poorly. In contrast, under the configuration used here (eqn 3), the NLL is minimized by fitting all the posterior predictions reasonably well, with greater weight effectively given to areas that are similar across the posterior predictions, which represent areas of relative certainty.

MODEL IMPLEMENTATION

Bayesian methods were also used to account for parameter uncertainty. All models were estimated using the random effects module of AD Model Builder (ADMB, Fournier *et al.* 2012). Prior distributions were incorporated into relevant models as follows: $\beta_0 \sim N(0, 10)$, $\beta_1 \sim N(0, 10)$, $\beta_2 \sim U(0.001, 1)$, $\delta \sim U(0.1, 30)$, $\sigma \sim U(0.001, 3)$. It was necessary to convert zero prey abundances to the minimum nonzero prey abundance (*c.* 0.0002 fish per m²) to fit models 4 and 8 in ADMB. All models were therefore fitted using this amended data set. A single chain was generated, with a thinning rate of 100 to 500. After discarding the first 250 parameter sets, 500 parameters sets were saved from each chain. Convergence was evaluated using the Brooks–Gelman multivariate statistic (Gelman & Rubin 1992; Brooks & Gelman 1998), among other diagnostics.

MODEL COMPARISON

For each species, models were compared using the deviance information criterion (DIC):

$$\text{DIC} = \overline{D} + pV, \qquad \text{eqn 5}$$

where D is the deviance, $\overline{D}$ is the posterior mean of the deviance and $pV = \text{var}(D)/2$ (Gelman *et al.* 2003). The two species data sets were not combined into a single multispecies model because information on diving behaviour was derived from different sources (i.e. gaps in the GPS record for Peruvian Boobies and TDR data for Guanay Cormorants).

Results

MODEL COMPARISON

For both species, Bayesian analysis indicated that the model with greatest support from the data was the depth-only model (Model 5, Table 1), closely followed by the full model (Model 8). The difference in DIC (delta-DIC) between these two models was low (< 2) for both species, indicating similar levels of support. For Peruvian Boobies, models that included the relative abundance of prey but not depth (models 2–4) received similar support to the null model (Model 1), whereas the presence/absence model (Model 2) and the abundance power function model (Model 4) received greater support than the null model when applied to data for Guanay Cormorants.

Comparison of the observed and predicted probabilities of diving behaviour (Fig. 2) indicates that the observed data were well reproduced for Peruvian Boobies in the depth-only model (Model 5), with limited improvement in model fit in the full model (Model 8). The improvement

Table 1. Model comparison by delta-DIC for foraging site selection models for Peruvian Boobies and Guanay Cormorants. I refers to the indicator function for the presence or absence of simulated anchoveta; ρ refers to predicted densities of anchoveta; z refers to the probability that the upper depth limit of simulated aggregations is less than an estimated scaling parameter, δ; and u_j refers to the random effect for the jth trip. The number of parameters includes δ where appropriate

			Brooks–Gelman statistic	$\overline{D}$	pV	DIC	delta-DIC
Peruvian Boobies:							
1	$\eta_i = \beta_0 + u_j$	2	1·00	279·5	11·7	291·2	18·1
2	$\eta_i = \beta_0 + \beta_1{*}I_i + u_j$	3	1·03	275·9	14·9	290·8	17·7
3	$\eta_i = \beta_0 + \beta_1{*}\rho_i + u_j$	3	1·02	279·7	13·6	293·2	20·1
4	$\eta_i = \beta_0 + \beta_1{*}\rho_i^{\beta_2} + u_j$	4	1·01	276·0	15·6	291·6	18·5
5	$\eta_i = \beta_0 + \beta_1{*}z_i + u_j$	4	1·00	256·9	16·3	273·1	0·0
6	$\eta_i = \beta_0 + \beta_1{*}I_i{*}z_i + u_j$	4	1·02	263·9	16·5	280·4	7·3
7	$\eta_i = \beta_0 + \beta_1{*}\rho_i{*}z_i + u_j$	4	1·02	279·6	12·4	292·0	18·9
8	$\eta_i = \beta_0 + \beta_1{*}\rho_i^{\beta_2}{*}z_i + u_j$	5	1·01	254·4	20·1	274·5	1·4
Guanay Cormorants:							
1	$\eta_i = \beta_0 + u_j$	2	1·00	218·7	8·4	227·1	10·1
2	$\eta_i = \beta_0 + \beta_1{*}I_i + u_j$	3	1·01	217·2	7·5	224·7	7·8
3	$\eta_i = \beta_0 + \beta_1{*}\rho_i + u_j$	3	1·01	218·4	8·9	227·4	10·4
4	$\eta_i = \beta_0 + \beta_1{*}\rho_i^{\beta_2} + u_j$	4	1·01	215·9	7·7	223·6	6·7
5	$\eta_i = \beta_0 + \beta_1{*}z_i + u_j$	4	1·01	201·3	15·7	217·0	0·0
6	$\eta_i = \beta_0 + \beta_1{*}I_i{*}z_i + u_j$	4	1·05	211·3	13·8	225·1	8·1
7	$\eta_i = \beta_0 + \beta_1{*}\rho_i{*}z_i + u_j$	4	1·02	218·4	8·8	227·2	10·2
8	$\eta_i = \beta_0 + \beta_1{*}\rho_i^{\beta_2}{*}z_i + u_j$	5	1·05	200·4	17·6	218·0	1·0

in fit with the addition of abundance in the full model is more apparent for Guanay Cormorants.

PARAMETERS

The overall probability of diving per cell was similar for the two species, 0·17 for Peruvian Boobies (number of cells visited in 13 trips = 315) and 0·17 for Guanay Cormorants (number of cells visited in 11 trips = 243). For both species, posterior distributions for the scaling parameter, δ, in the depth-only model (Model 5) indicate that birds were more likely to dive when prey is fairly shallow (Fig. 3a, b). The posterior median was 7·76 m (90% probability interval: 5·86–10·58 m) for Peruvian Boobies and 9·57 m (90% probability interval: 7·45–12·10 m) for Guanay Cormorants. This is consistent with observed mean maximum dive depths of 1·8 m ± 1·4 m for Peruvian Boobies (n = 593) and 6·3 m ± 4·9 m for Guanay Cormorants (n = 2492) (Weimerskirch *et al.* 2012). The predicted probability of diving increased steeply at shallow depths for Peruvian Boobies, and more slowly for Guanay Cormorants (Fig. 4a). Thus, Guanay Cormorants were more

likely to dive when prey was at moderate depths than Peruvian Boobies (Fig. 5a). The relationships between diving probabilities and the depth distribution of prey were very similar in the full model (Model 8, Fig. 3).

The full model (Model 8) also provides information on the relationship between the probability of diving and the relative abundance of prey. For both species, the probability of diving increased sharply at relatively low levels of abundance followed by a levelling off (Fig. 4b). Posterior distributions for the power parameter, β_2, were similar for the two species (Fig. 3c, d). The main difference between the two species in the modelled relationship to abundance is that Peruvian Boobies were more likely than Guanay Cormorants to dive at all levels of abundance if anchoveta were close to the surface (Fig. 5b).

SPATIAL APPLICATION

Diving behaviour is also influenced by the structure of foraging trips. Observed diving behaviour and predicted dive probabilities based on the full model (Model 8) are shown for specific trips by Peruvian Boobies and Guanay
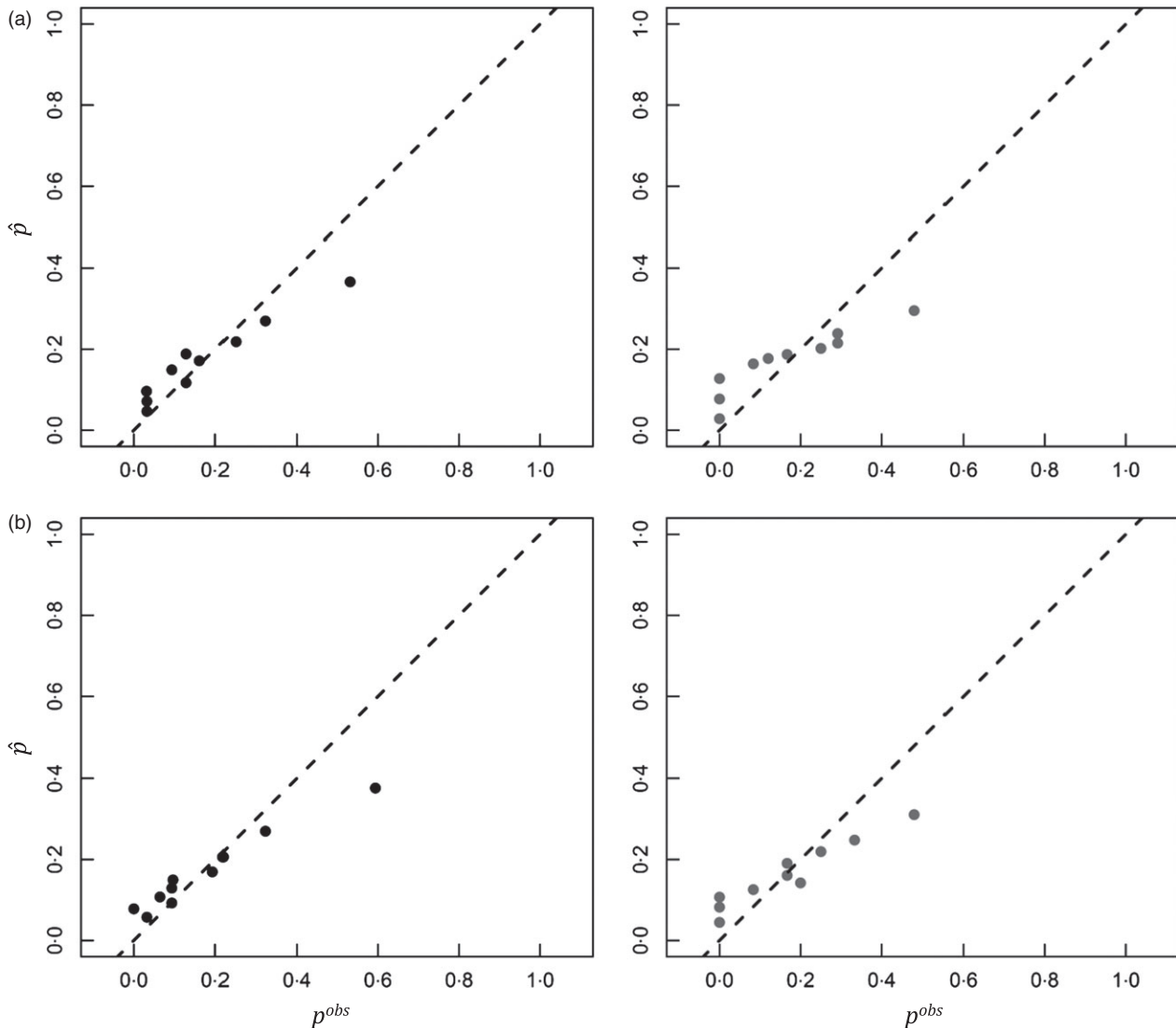
Fig. 2. Observed versus predicted probabilities that diving behaviour occurs in a cell for Peruvian Boobies (black) and Guanay Cormorants (grey) based on (a) the depth-only model (Model 5) and (b) the full model (Model 8). Median predicted probabilities were computed for each observation over 100 Bayesian posterior predictions of the spatial distribution of anchoveta and 500 saved parameter sets. The observed response variable is binary, so predicted probabilities were grouped by quantile, and the mean of predicted probabilities ($\cap p$) was compared to the mean of the associated observed values (p^{obs}) for each quantile group. Each point shown here thus represents the mean of *c.* 31 values for Peruvian Boobies and 24 values for Guanay Cormorants.

Cormorants in Fig. 6. As expected, the figure indicates that individuals flew over cells with relatively low predicted dive probabilities near the colony to reach areas with higher predicted probabilities. The figure also indicates that individuals flew over some cells with relatively high predicted dive probabilities on their return to the colony. Birds that have fed sufficiently to meet their own energy requirements and provision their young are expected to return directly to the nest, as stopping *en route* might increase digestion and degrade the value of food provided to chicks (Boersma *et al.* 2009).

Discussion

In this study, a series of resource selection functions was developed to assess seabird foraging site selection in terms

of the abundance and distribution of their prey. Previously, Zavalaga, Halls & Dell'Omo (2010) analysed foraging site selection by Peruvian Boobies at Isla Lobos de Tierra and Isla Lobos de Afuera in northern Peru, in terms of bathymetry, SST and Chl *a* concentrations, as proxies for ocean productivity. They found that Peruvian Boobies foraged over the continental shelf or shelf break, and that Chl *a* concentrations were significantly higher in foraging areas than expected from a random distribution, but that the SST of foraging areas was similar to that of available areas.

Here, we developed resource selection functions for seabirds directly in terms of the abundance and distribution of their prey. For both Peruvian Boobies and Guanay Cormorants, the models with greatest support were consistent with the hypothesis that foraging behaviour is a
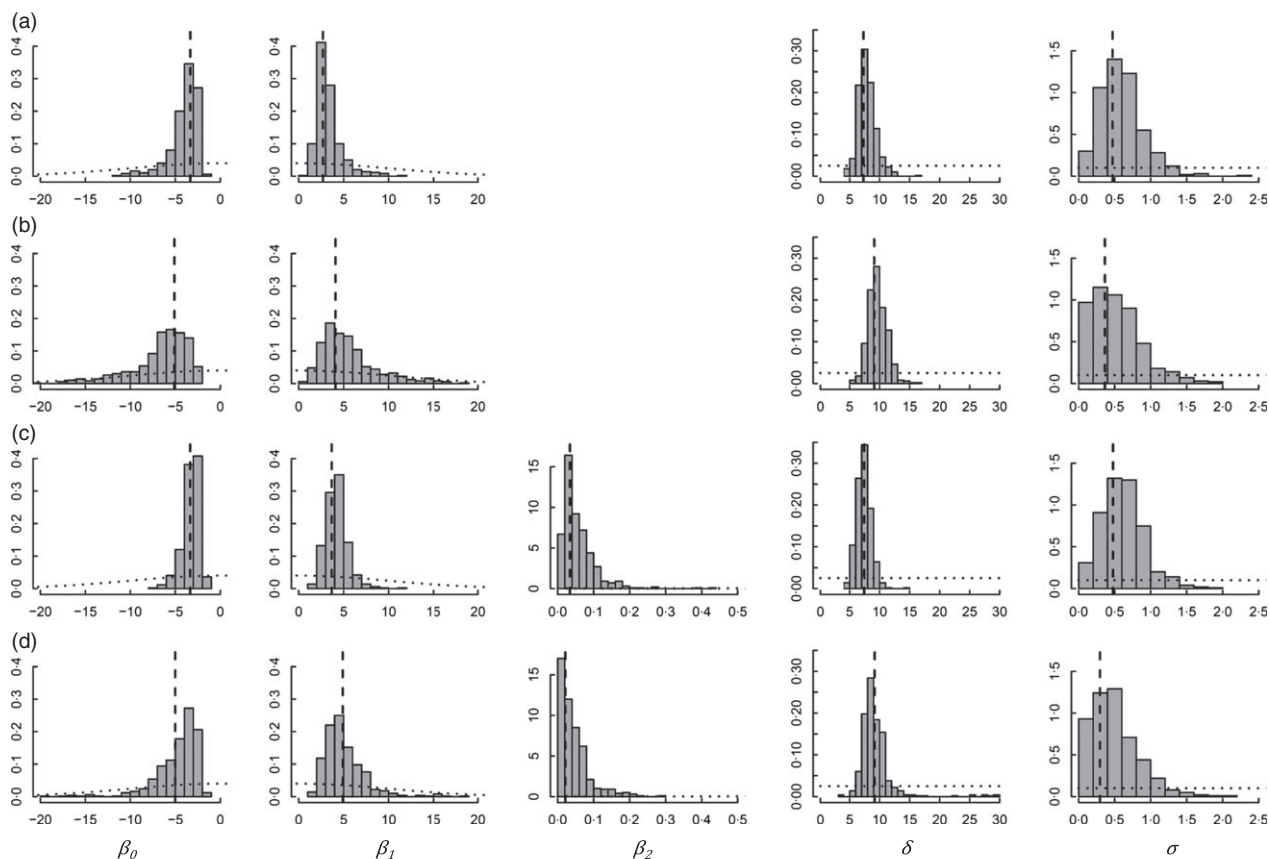
Fig. 3. Posterior parameter distributions for ((a) and (b)) the depth-only model (Model 5) and ((c) and (d)) full model (Model 8), for Peruvian Boobies ((a) and (c)) and Guanay Cormorants ((b) and (d)). Dotted lines indicate the prior distributions; dashed lines indicate the maximum-likelihood estimates.

response to the availability of prey in the upper water column. In particular, the results highlight the importance of the depth distribution of prey in foraging site selection. This finding holds for both species, despite well-established differences in their diving capabilities (Zavalaga & Paredes 1999; Zavalaga *et al.* 2010; Weimerskirch *et al.* 2012). Even though the Guanay Cormorant is capable of diving more deeply, our analysis indicates that they foraged on prey aggregations at relatively shallow depths during the study period (Weimerskirch *et al.* 2012). Bayesian model comparison indicated weak support for the addition of abundance to the depth-only model and suggested that Guanay Cormorants may be more sensitive to the abundance of prey than Peruvian Boobies. Remaining differences between observed and predicted probabilities may reflect factors that are not revealed in the acoustic survey data, such as conspecific attraction. Guanay Cormorants, in particular, are social foragers, generally aggregating to forage in large flocks (Duffy 1983b), and previous research has shown that conspecific attraction plays an important role in foraging site selection for Guanay Cormorants (Weimerskirch *et al.* 2010, 2012).

Previous research has highlighted predictable spatial associations between seabirds and static or dynamic habitat features that serve to enhance prey accessibility (e.g.

Yen, Sydeman & Hyrenbach 2004; Renner, Arimitsu & Piatt 2012). Hunt *et al.* (1998), for example, found that Least Auklets (*Aethia pusilla* [Pallas, 1811]) and Crested Auklets (*A. cristatella* [Pallas, 1769]) in the Aleutian Islands foraged in areas where physical processes, such as tidally driven upwelling and convergence, concentrated copepods near the surface and euphausiids high on the slope of a sill (see also Hunt, Harrison & Cooney 1990; Coyle *et al.* 1992). Hunt, Harrison & Cooney (1990) and Vilchis, Ballance & Fiedler (2006) identified thermocline topography as a key feature influencing the abundance and distribution of seabirds, probably because of its effect on prey availability. In the Humboldt Current System, Bertrand *et al.* (2014) showed that physical structures, such as internal waves, induce local deformations in the vertical location of the oxycline, where zooplankton, fish, Peruvian Boobies and Guanay Cormorants aggregate.

In this study, for both Peruvian Boobies and Guanay Cormorants, there was a sharp increase in the probability of diving behaviour at relatively low levels of abundance followed by a levelling off, suggestive of a saturation effect (Fig. 5b). This pattern is very similar to the type II functional response found by Cox, Scott & Camphuysen (2013) based on the analysis of concurrent survey data for
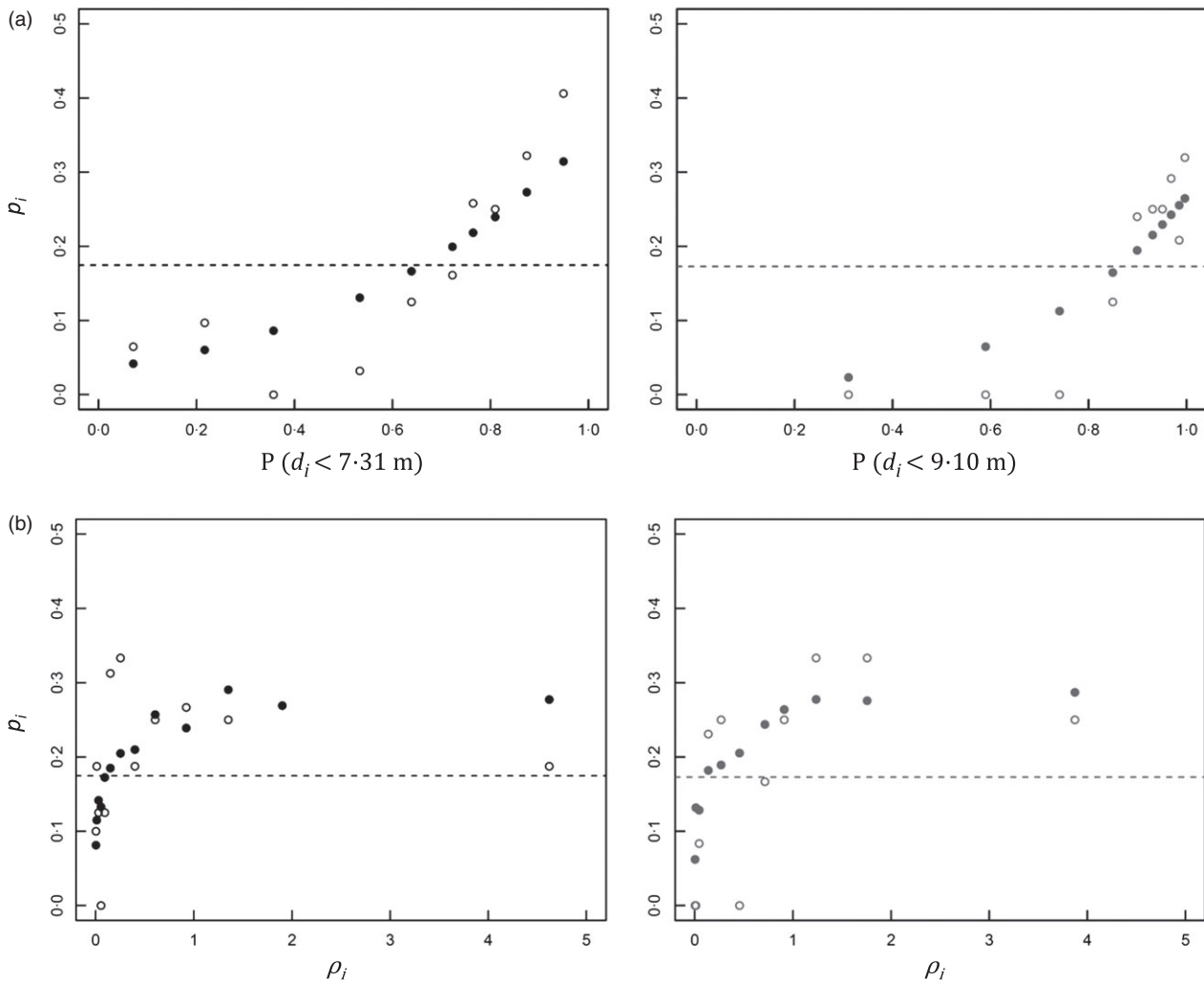
Fig. 4. Comparison of observed probabilities (circles) and predicted probabilities (points) of diving behaviour for Peruvian Boobies (black) and Guanay Cormorants (grey). Panel (a) shows diving probabilities per grid cell as a function of the probability that the upper depth limit of aggregations is less than the estimated scaling parameter for the depth-only model (Model 5). Panel (b) shows diving probabilities per grid cell as a function of abundance measured in terms of numbers of fish per m^2 for the full model (Model 8). For display purposes, a single parameter set (the maximum-likelihood estimates) was used in each plot. In each panel, the values on the horizontal axis were grouped by quantile, and the mean of associated observed values and mean of predicted probabilities were computed for each quantile group. Dashed lines indicate the observed mean probability of diving behaviour per grid cell for each species.

Common Guillemots or Murres (*Uria aalge* [Pontopiddan, 1763]), Black-legged Kittiwakes (*Rissa tridactyla* [Linnaeus, 1758]), and various prey species (see also Piatt 1990; Enstipp, Grémillet & Jones 2007). The weak support for abundance-based models may reflect the specific foraging conditions in 2008 in which prey was relatively abundant at shallow depths (Weimerskirch *et al.* 2012) such that abundance may not have been a limiting constraint. Resource selection patterns may vary with foraging conditions. Central place foraging theory predicts that individuals should become more selective in terms of prey items or increase load sizes in response to reduced prey availability (Orians & Pearson 1979). Burke & Montevecchi (2009) found that single prey-loading Common Murres were more selective in terms of prey size when foraging conditions were unfavourable (but also see Piatt 1990). The association between predators and prey may be stronger when prey availability is low or when prey is more patchily distributed. Vlietstra (2005) found that the spatial associations between Rhinoceros Auklets (*Cerorhinca monocerata* [Pallas, 1811]) and Pacific Loons (*Gavia pacifica* [Lawrence, 1858]) and prey biomass were stronger on days when regional prey abundance was relatively low. Logerwell, Hewitt & Demer (1998) also found that the association between Thick-billed Murres (*Uria lomvia* [Linnaeus, 1758]) and their prey was poor when the spatial variance of prey was relatively low, suggesting that there is limited advantage to aggregating at slightly more profitable locations if prey distribution is fairly uniform. Continuation of research on foraging site selection by Peruvian Boobies and Guanay Cormorants, encompassing a wide range of foraging conditions, would strengthen understanding of how the two species adapt their resource selection patterns in response to reduced prey availability.
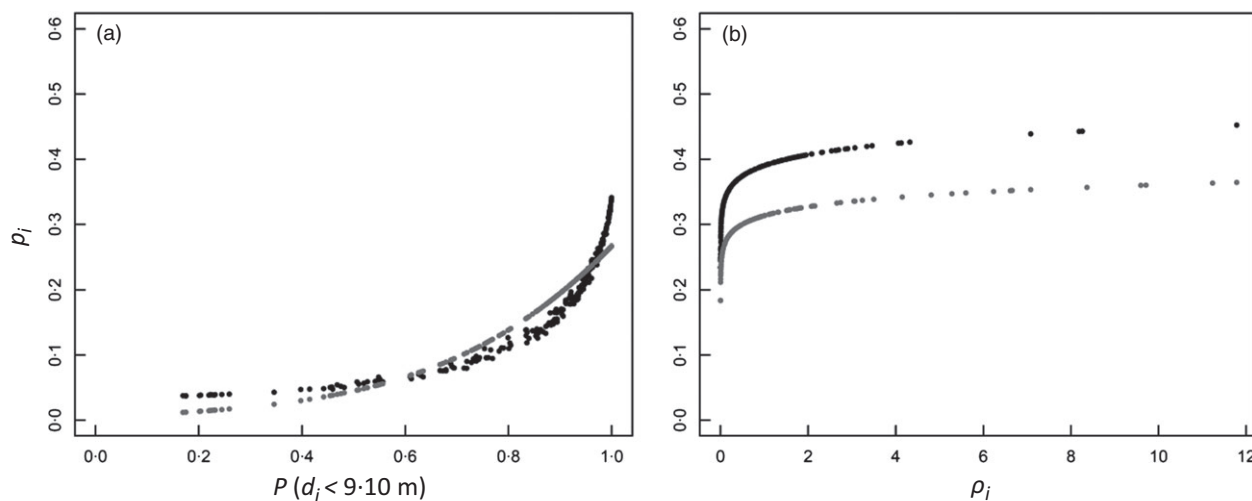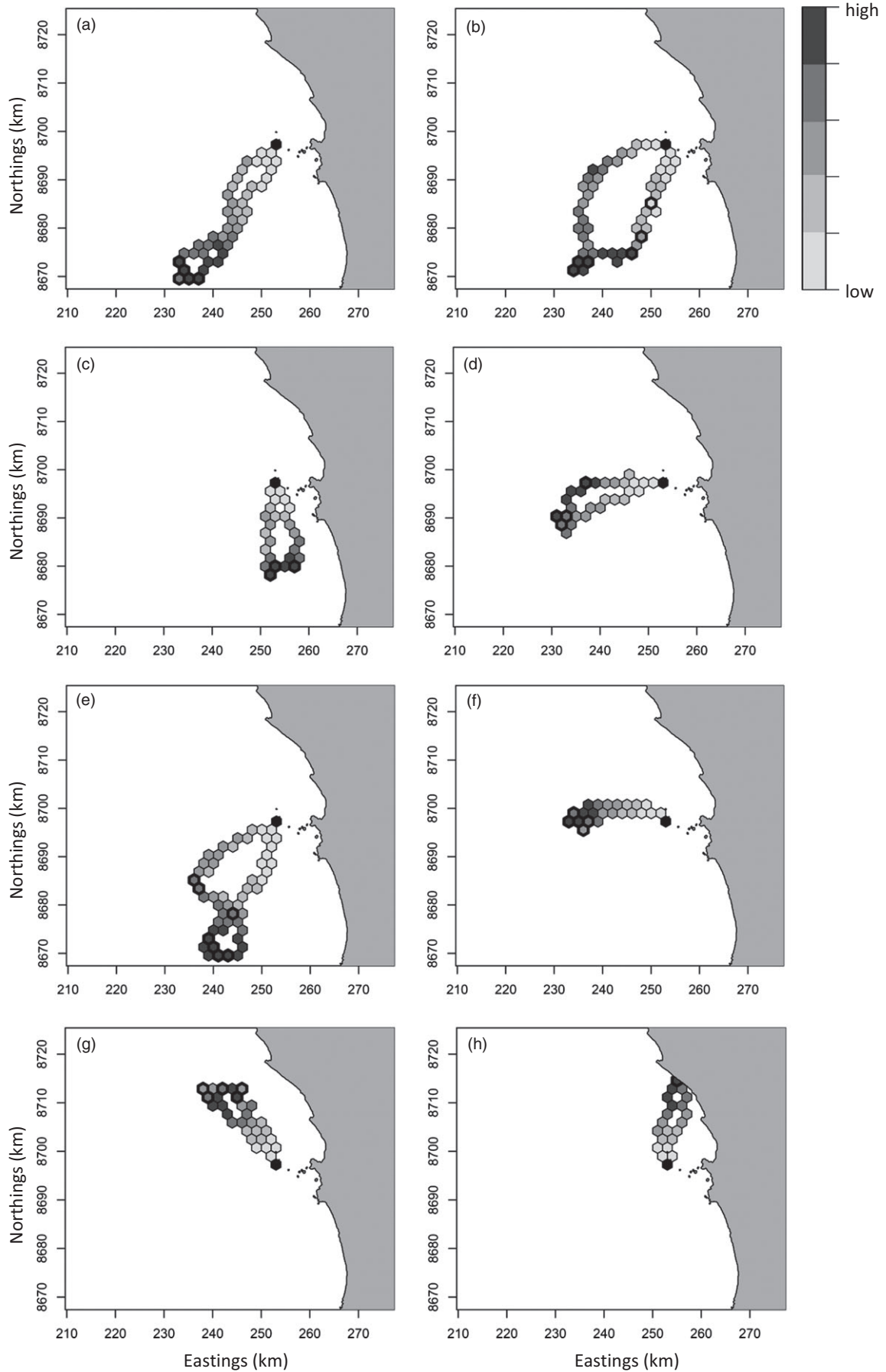
Fig. 5. Comparison of predicted probabilities of diving behaviour for Peruvian Boobies (black) and Guanay Cormorants (grey). For display purposes, a single parameter set (the maximum-likelihood estimates) was used for each set of points. Panel (a) shows predicted diving probabilities per grid cell for various depth distributions based on the depth-only model (Model 5). Predicted diving probabilities were estimated based on the depth distributions of anchoveta in the same set of cells for both species. The horizontal axis refers to the probability that the upper depth limit of aggregations is less than the estimated scaling parameter for Guanay Cormorants, but predictions for Peruvian Boobies are based on the estimated scaling parameter for Peruvian Boobies. Each point on the horizontal axis is therefore associated with a range of values on the vertical axis for Peruvian Boobies because of variation in the distribution of anchoveta through the water column. Panel (b) shows predicted diving probabilities per grid cell for various levels of abundance assuming that all prey is accessible based on the full model (Model 8).

Several authors have emphasized the importance of scale in analysing relationships between predators and prey (Hunt & Schneider 1987; Piatt 1990; Logerwell & Hargreaves 1996; Swartzman & Hunt 2000; Wakefield, Phillips & Matthiopoulos 2009). Differences in the temporal and spatial resolutions of data can undermine efforts to match foraging behaviour to available prey (see Torres, Read & Halpin 2008). The strength of association may be scale-dependent. In some cases, a close association has been detected at broad spatial scales reflecting physical oceanographic structures such as water masses, but not at the finer scales corresponding to biological structures (Hunt, Heinemann & Everson 1992; Russell *et al.* 1992). In contrast, Benoit-Bird *et al.* (2013) found that the spatial distributions of Black-legged Kittiwakes and Thick-billed Murres were associated with fine-scale prey patch characteristics, such as depth and the interior density of prey aggregations, rather than prey densities integrated over broader scales. In this study, the spatial and temporal resolutions were set by the acoustic survey, which was based on systematic transects *c.* 10 km apart (processed at a resolution of 1 nm) and took place over a 4-day period. Uncertainty in the relative abundance and distribution of anchoveta was taken into account by using 100 Bayesian posterior predictions of the abundance and depth distribution of anchoveta to construct the independent variables representing prey availability. The results suggest that the spatial and temporal resolutions were adequate to capture features of the spatial distribution of anchoveta that were sufficiently consistent over the period of the survey to support a relationship with the foraging patterns of seabirds, at least in terms of the depth distribution.

There are growing concerns about the effects of fisheries on prey availability to top predators in marine systems (Duffy 1983a; Becker & Beissinger 2006; Crawford *et al.* 2006; Cury *et al.* 2011; Bertrand *et al.* 2012). Effective management responses will be based on an understanding of the defining attributes of prey availability, the processes that enhance prey accessibility and underpin foraging patterns, and the susceptibility of these processes to management (Hyrenbach, Forney & Dayton 2000; Hooker *et al.* 2011). Analysis of the relative contributions of processes that increase the abundance of prey versus those that increase their accessibility is essential for designing effective management strategies for species threatened by reduced prey availability. The resource selection functions developed here provide the link between predators and

Fig. 6. Observed and predicted probabilities of diving per grid cell in specific trips by Peruvian Boobies (a to d) and Guanay Cormorants (e to h). Grid cells where diving behaviour occurred are indicated with bold outlines. For each grid cell, median predicted probabilities, computed over 100 Bayesian posterior predictions of the spatial distribution of anchoveta and 500 saved parameter sets, are indicated by graduated shading. The direction of each track is indicated by an arrow. The colony is indicated by the black grid cell. Land is shown in grey.

prey in a mechanistic individual-based foraging model designed to assess the effects of changes in abundance and depth distribution of prey on seabird foraging success (Boyd 2012).

The results of the present study highlight the importance of the depth distribution of prey for surface-foraging seabirds, such as Peruvian Boobies and Guanay Cormorants, indicating that processes that concentrate prey close to the surface, such as the depth of the oxycline, need to be considered alongside those that enhance abundance. This does not imply that efforts to safeguard prey biomass for top predators (Furness 2006; Cury *et al.* 2011) are unimportant. In most cases, abundance is both more directly impacted by anthropogenic forces and more amenable to management. Rather, the implication is that accessibility also needs to be taken into consideration (see Taylor *et al.* 2008). In terms of spatial prioritization, management may be best focused on identifying areas where prey is predictably accessible to species of concern, for example through the action of localized processes that enhance accessibility, and then safeguarding the abundance of prey in these areas through the creation of marine protected areas and/or broader scale marine spatial planning and fisheries management.

Acknowledgements

Data accessibility

ADMB template and data files are archived in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.m498n (Boyd *et al.* 2015a).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Bayesian geostatistical posterior prediction of the depth distribution of aggregations of small pelagic fish.

Figure S1. Proportional representation of acoustic backscatter (m^2 per nautical mile^2) in December 2008. Elementary distance sampling units (EDSUs) are marked by crosses (zero values for anchoveta) and circles (positive values, diameter of the circles proportional to the logarithm of relative anchoveta abundance). The shelf break (200 m isobaths) is indicated by the dashed line.

Figure S2. Prior distributions (dashed lines) and samples from the posterior densities (histograms) for the spatial parameters.

Figure S3. The distribution of the observed log-transformed upper depth limit of aggregations (histogram); and the mean (solid line) and 2.5th and 97.5th percentiles (dashed lines) of samples from the corresponding posterior densities.

Figure S4. Quantitative summaries of the spatial pattern of observed data and posterior predictions. Box plots represent empirical variograms computed from posterior predictions. The dashed line represents the empirical variogram for the observed data. The dotted line represents the mean of the theoretical variograms computed from 100 samples from the posterior distributions of the spatial parameters.

Figure S5. Four Bayesian posterior predictions of the probability that the upper depth limit of aggregations is less than 7.5 m below the echosounder. Land is shown in pale grey.