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## A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern gannets breeding in the North East Atlantic

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### ABSTRACT

Seabirds are well monitored and protected at their breeding grounds but spend most of their life at sea, where they are less well monitored and afforded little protection. In an attempt to address this dichotomy, attention has been directed toward establishing a network of marine reserves for seabirds, based largely on information from at-sea surveys and/or biotelemetry studies. Nevertheless, these approaches are costly, are typically only available for a limited number of locations, and not suitable for species that have either poor at-sea detectability or are unable to carry tracking devices. Here we develop a technique to identify important areas for breeding seabirds based on at-sea projections from colonies. Synthesising data from colony surveys with detailed information on population dynamics, foraging ecology and near-colony behaviour, we project colony-specific foraging distributions of the Northern gannet (*Morus bassanus*) at colonies in the UK, Ireland and France. We test the ability of our models to identify at-sea hotspots through comparison with existing data from biotelemetry studies and at-sea visual surveys. These models show a positive spatial correlation with one of the most intensive at-sea seabird survey datasets. While there are limitations to estimating at-sea distributions of seabirds, implemented appropriately, we propose they could prove useful in identifying potential Marine Protected Areas for seabirds. Moreover, these models could be developed to suit a range of species or whole communities and provide a theoretical framework for the study of factors such as colony size regulation.

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### 1. Introduction

Changes are occurring in the marine environment and, as wide-ranging apex predators acting as bio-indicators of marine systems (Furness and Camphuysen, 1997), seabirds require protection from the deleterious effects of climate change (Grémillet and Boulinier, 2009), fisheries (Lewison et al., 2004; Pauly et al., 1998; Votier et al., 2004), pollution (Votier et al., 2005), and offshore development (Grecian et al., 2010; Inger et al., 2009; Langton et al., 2011; Witt et al., 2012). One of the key tools to alleviate these pressures could be the designation of Marine Protected Areas (MPAs) for seabirds, although this approach has limitations related with the scale of marine systems, the dynamic nature of the oceans, and thus the ephemeral nature of many species. Furthermore,

the high costs associated with implementing wide-scale protection will likely force MPAs to be small and targeted for particular species assemblages (Game et al., 2010). This proves problematic for the conservation of species, such as seabirds, that require protection of disparate breeding and foraging grounds (Guilford et al., 2008). Thus, these areas have very different selection criteria for protection and require separate consideration.

Seabird research has historically focused on colony-based studies because, as central-place foragers, seabirds are easily accessed during the breeding season (e.g. Mitchell et al., 2004). Systematic at-sea visual surveys began to address this imbalance in the 1970s (Haney, 1985; Stone et al., 1995), and have provided vital information on the wide-scale distributions of seabirds (e.g. Piatt et al., 2006). However, there are limitations to at-sea surveys, and while they yield large sample sizes, they are usually unable to distinguish colony of origin, age, or the reproductive status of individual birds. Inferring colony level changes from observations in the marine environment is therefore problematic.

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The advent of individual-based tracking technology (reviewed by Ropert-Coudert and Wilson (2005)) has shed light on the ecology of seabirds when away from the colony (Burger and Shaffer, 2008; Wilson et al., 2002). Nevertheless, limitations in device size have until recently confined deployments to large species (Phillips et al., 2003), and there may be deleterious effects of both device attachment and handling (Barron et al., 2010). Tracking studies provide detailed ecological information at the individual level, but this is typically available for only a restricted number of locations, and a consensus on the most appropriate method for data analysis is lacking (Wakefield et al., 2009). For a comparison of the predictive performance of different modelling techniques see Opper et al. (this issue). Consequently, a mismatch exists between colony-based and at-sea studies, a dilemma that greatly inhibits our ability to make decisions on the conservation and management of seabird populations.

In addressing this mismatch, studies have linked both vessel-based visual counts and satellite tracking data to environmental variables in order to aid the delineation of marine Important Bird Areas (IBAs) for pelagic foraging seabirds (Amorim et al., 2009; Louzao et al., 2009). In the UK, the Joint Nature Conservation Committee (JNCC) has begun to identify Special Protection Areas (SPAs) offshore using the European Seabirds At Sea database (ESAS), which provides long-term, year-round, distribution data on UK seabird populations (Kober et al., 2010). Collaborative marine IBA projects in Spain and Portugal have used these techniques to produce the first complete marine IBA network at a national level, incorporating 59 marine IBAs and gazetting 57,135 km<sup>2</sup> (Arcos et al., 2009, this issue; Ramirez et al., 2008; SEO/BirdLife, 2009). These highlight the importance of productive areas, which due to their small to medium-scale repeatability, association with physical features, and established appeal to marine top predators (Fauchald, 2009; Hyrenbach et al., 2000; Louzao et al., 2006; Paiva et al., 2010; Weimerskirch, 2007) makes them ideal candidates for conservation (Piatt et al., 2006).

An alternative approach for designating protected areas at-sea would be to collate information collected through colony-based counts and project at-sea distributions based on known foraging ranges (BirdLife, 2010). While this technique lacks the rigour of at-sea surveys or bio-logging studies, it has the advantage of being simple, inexpensive and quick to implement. Moreover, it can be applied to species for which at-sea detectability is low, or attachment of tracking devices impossible (*i.e.* for small species). In addition, if foraging projection models were integrated with fundamental ecological principles, it may be possible to create more sophisticated and accurate model predictions that represent realistic estimates of at-sea density distributions. Using simple methods to designate seabird MPAs may also make the process more transparent to stakeholders (O'Brien et al., this issue).

Here, we develop a model that predicts the at-sea distribution of a central-place forager, the Northern gannet (*Morus bassanus*, hereafter gannet) a large and well-studied piscivorous apex predator. Colony-based studies of this species have demonstrated that: (1) foraging range is positively correlated with colony size both across multiple colonies and within a single colony over time (Lewis et al., 2001); (2) population densities are elevated around colonies (McSorley et al., 2003); and (3) foraging behaviour is linked to resource availability (Garthe et al., 2007; Hamer et al., 2007; Votier et al., 2010). We combine this ecological information with data collected on the size and distribution of colonies (Mitchell et al., 2004; Nelson, 2002), building a model that predicts distributions for all UK, Irish, Channel Island and French colonies. We validate these spatial predictions using data from at-sea visual surveys and tracking data. The development of a technique that can accurately predict the spatial distribution of seabirds will be vital in identifying both areas in need of protection, and areas of

potential conflict with anthropogenic threats. We consider the utility of this approach for other seabird species and multiple species, enabling a community level approach to seabird conservation.

## 2. Materials and methods

### 2.1. Step 1: Collating information on colony demographics

The gannet is a key species for European conservation as ca. 70% of the world population breed around UK, Irish and French shores (Mitchell et al., 2004). Long-term monitoring at a number of colonies have provided breeding population estimates, along with detailed ecological information. Gannet colony locations and colony sizes were taken from Mitchell et al. (2004) and combined with recent information on Channel Island (Ortac and Les Etacs) and northern French (Rouzic) colonies (Grémillet et al., 2006; Nelson, 2002) (see Table 1). We use Apparently Occupied Nests (AONs) as our measure of colony size, which is equivalent to the number of breeding pairs (Mitchell et al., 2004). We build a model in seven steps that first projects a foraging radius around each colony, and then add constraints to the projections through application of current ecological understanding of the species (Fig. 1).

### 2.2. Step 2: Constraining foraging ranges by population size

Intra-specific competition for resources during the breeding season is believed to be an important factor in regulating colony size for seabirds in general (Furness and Birkhead, 1984), and gannets in particular (Lewis et al., 2001). This within-population competition is typified by the strong positive relationship between colony size and foraging trip duration, and so when projecting foraging ranges we must account for this effect. Information on colony size and location was used to derive a colony specific estimate of foraging distance (*fd*) using the density dependent relationship described by Lewis et al. (2001), where observations at a number of gannetries indicate foraging trip duration, and thus foraging distance (based on Hamer et al., 2000) to be positively related to colony size (Eq. (1)). This estimated the foraging distance (*fd*) of colonies based on the square root of colony size in number of pairs (*p*) (Table 1).

Eq. (1) (Lewis et al., 2001):

$$fd = 0.344\sqrt{p} + 40.062 \quad (1)$$

### 2.3. Step 3: Projection of foraging radius from the colony

We combined the colony-specific foraging distances with information on colony location (Table 1), to construct a colony-centred foraging radius. This was overlaid upon a high resolution digital elevation model (TerrainBase, National Geophysical Data Centre) to derive the total available area of marine habitat, and exclude any areas of land within range of the colony. The density of breeding gannets was calculated from the colony size (*p*) and area of available marine habitat, to give an estimate of colony-specific foraging effort (pairs km<sup>-2</sup>). This process was repeated for each colony and summed to give a total population distribution estimate for all colonies (Fig. 2a). Pairs were assumed to be uniformly distributed across the foraging radius, and so high gannet densities occurred only at the overlap between two or more colonies, or when the foraging range was constrained by local topography.

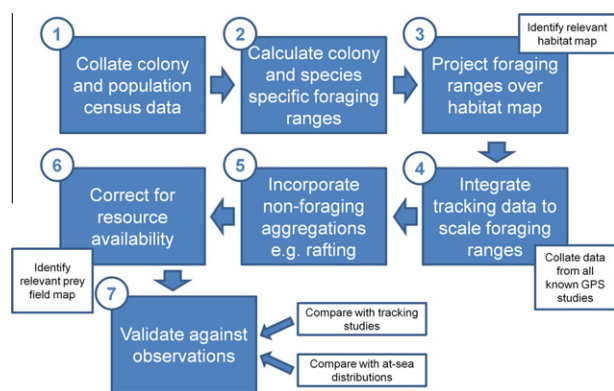
### 2.4. Step 4: Integration of tracking data

Comparison of our initial foraging distance estimates with mean distances calculated from gannet Global Positioning System

**Table 1**

Details of gannet colonies included in the model; consisting of all UK, Irish, Channel Island and French colonies, the most recent population estimate for that colony (Apparently Occupied Nests), the predicted foraging range derived from Lewis et al. (2001) and the maximum range estimated by multiplying the foraging range by a scale parameter (3.4) derived from existing tracking data.

Colony	Longitude	Latitude	AON (Year)	Foraging range (km)	Maximum foraging range (km)
St Kilda, Outer Hebrides, Scotland	−8.547	57.871	59,622 (2004)	124.0	421.9
Bass Rock, East Lothian, Scotland	−2.631	56.076	48,065 (2004)	115.4	392.7
Grassholm, Pembrokeshire, Wales	−5.486	51.730	39,292 (2009)	108.2	368.1
Little Skellig, Kerry, Ireland	−10.510	51.782	29,683 (2004)	99.3	337.8
Ailsa Craig, Ayrshire, Scotland	−5.122	55.252	27,130 (2004)	96.7	329.0
Hermaness, Shetland, Scotland	−0.926	60.808	24,353 (2008)	93.7	318.8
Rouzig, Brittany, France	−3.436	48.900	17,507 (2005)	85.5	291.1
Sula Sgeir, Outer Hebrides, Scotland	−6.169	59.095	9225 (2004)	73.1	248.7
Noss, Shetland, Scotland	−1.018	60.146	8652 (2003)	72.0	245.1
Bempton, Yorkshire, England	−0.161	54.148	6487 (2008)	67.7	230.5
Les Etacs, Channel Islands	−2.240	49.704	4862 (2005)	64.0	217.9
Sule Stack, Outer Hebrides, Scotland	−4.407	59.085	4618 (2004)	63.4	215.8
Bull Rock, Cork, Ireland	−10.298	51.589	3694 (2004)	60.9	207.4
Roareim (Flannans), Outer Hebrides, Scotland	−7.678	58.284	2760 (2004)	58.1	197.8
Ortac, Alderney, Channel Islands	−2.291	49.723	2547 (2005)	57.4	195.4
Scar Rocks, Wigtownshire, Scotland	−4.705	54.665	2500 (2005)	57.2	194.8
Fair Isle, Shetland, Scotland	−1.629	59.534	2488 (2008)	57.2	194.7
Great Saltee, Wexford, Ireland	−6.613	52.117	2446 (2004)	57.1	194.2
Troup Head, Aberdeenshire, Scotland	−2.310	57.694	1810 (2007)	54.7	186.1
Foula, Shetland, Scotland	−2.112	60.133	919 (2004)	50.5	171.8
Sule Skerry, Outer Hebrides, Scotland	−4.505	59.024	400 (2007)	46.9	159.7
Ireland's Eye, Dublin, Ireland	−6.056	53.408	375 (2007)	46.7	159.0
Lambay, Dublin, Ireland	−6.003	53.497	83 (2007)	43.2	147.0
Clare Island, Mayo, Ireland	−10.048	53.802	3 (2004)	40.7	138.4
St Margaret's Island, Pembrokeshire, Wales	−4.719	51.642	1 (2004)	40.4	137.5



**Fig. 1.** Flow chart representing the steps involved in at-sea projection model development. This simple seven-step framework is adaptable to incorporate other data sources, allowing application of this method to different seabird species.

(GPS) tracking data suggest the ranges produced using Eq. (1) underestimate the total distances travelled. The mean predicted foraging distance across all colonies derived from Lewis et al. (2001) was 69.4 km (range = 40.4–124.0 km) (Table 1, Fig. 2a), while gannets tracked from UK and French colonies between 1998 and 2006 travelled on average up to 150.9 km from the colony (range = 100–223 km) (Table 2). To account for this disparity we use the mean of the ratio of tracked/predicted calculated from the three colonies for which we have GPS tracking data, multiplying the estimated foraging distance by 1.4. This difference most likely reflects inter-annual differences in resources, and allows the incorporation of environmental conditions *i.e.* the relationship with colony size prevalent in 2000 (Lewis et al., 2001), while also including the accuracy of GPS data to identify foraging locations.

Foraging events tend to occur at the distal part of the track (Hamer et al., 2009), and so we also adjust our foraging ranges

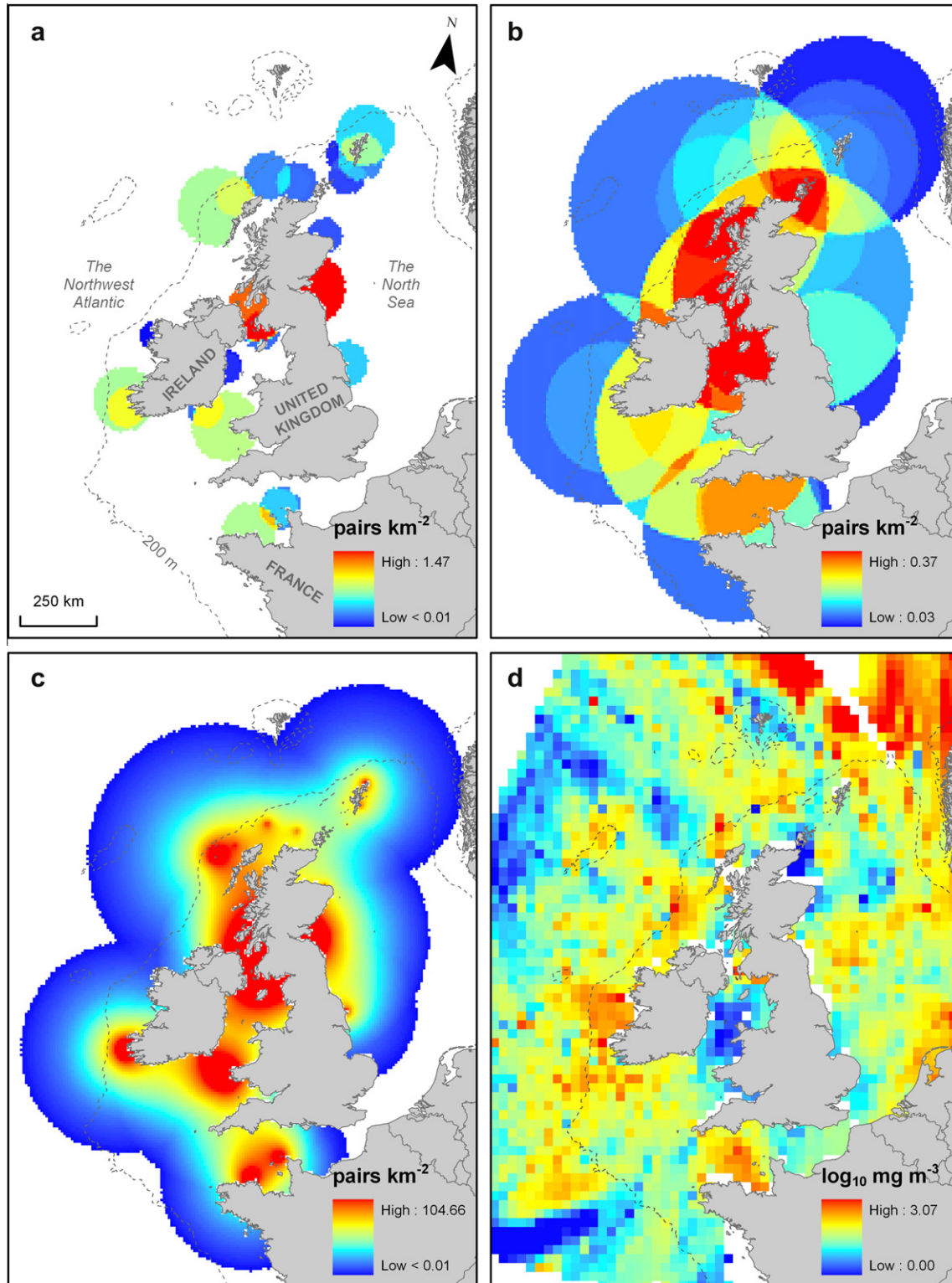
by converting mean foraging ranges to maximum foraging ranges to incorporate these behaviours. We corrected our foraging distances to provide estimates of maximum foraging range using the ratio of the mean displacement from the colony, to the maximum displacement from the colony *i.e.* max/mean (Table 2). We used the mean of these ratios, 2.4, to convert the transformed foraging distances into maximum foraging distance, giving a final scale parameter of 3.4 (*i.e.*  $1.4 \times 2.4$ ). After adjustment the mean maximum foraging distance across all colonies was 236.1 km (range 137.5–421.9 km) (Table 1, Fig. 2b).

### 2.5. Step 5: Incorporation of near-colony maintenance and transiting behaviours

Near-colony areas are important for maintenance behaviours (Wilson et al., 2009), and central-place foragers also spend large proportions of time transiting between the colony and diffuse foraging sites; therefore bird density decreases with increasing distance from the colony, and for gannets this decline takes a log or exponential form (Camphuysen et al., this issue; Garthe et al., 2011; McSorley et al., 2003). To incorporate this behaviour, we multiplied the number of pairs within a given cell (calculated in Eq. (1)) by the inverse scaled log distance from the focal colony (Fig. 2c). This weighted the waters in close proximity to the colony to be of relatively higher importance due to transiting and maintenance behaviours, thus creating hotspots for gannet densities around a colony (see Fig. 2c). However it is unlikely in all cases that these are also important foraging locations (Grémillet et al., 2006).

### 2.6. Step 6: Correction of distributions for resource availability

Food availability has been demonstrated to be a good proxy for the at-sea distribution of seabirds (Furness and Tasker, 2000; Kaiser et al., 2006; Votier et al., 2010), and so in order to make inferences about the importance of certain areas for foraging, our



**Fig. 2.** Predicted distributions of the Northern gannet (*Morus bassanus*) around the UK, Ireland, Channel Islands and northern France. (a) Information on colony size and location (Grémillet et al., 2006; Mitchell et al., 2004; Nelson, 2002) generated foraging radii (Lewis et al., 2001) forming colony-specific foraging areas. Density (pairs  $\text{km}^{-2}$ ) was calculated using the area of ocean circumscribed by the radial foraging arc and the estimated colony size. (b) Estimation of maximal foraging ranges derived from tracking studies (see Table 2) were used to extend the initial predictions. (c) Distributions weighted by a log-linear density decay function. (d) The average June abundance of calanoid copepods ( $\log_{10} \text{mg m}^{-3}$ ) around the UK and Ireland (1953–2002) taken from the SAHFOS continuous plankton recorder.

at-sea projections of seabird abundance were also weighted by resource availability.

While fine-scale information on the distribution of forage fish is unavailable, other environmental variables can act as a proxy for

food availability (Grémillet et al., 2008a; Votier et al., 2010). For gannets, changes in foraging behaviours such as at-sea path tortuosity and derived ground speed are correlated with north-east Atlantic copepod abundance in the month of June (Votier et al.,

**Table 2**

Comparison of predicted and observed foraging ranges that and mean and maximum foraging ranges that informed Step 4 of the modelling process.

Colony	Predicted range (km)	Year tracked	Observed range (km)	Ratio observed/predicted	Max range (km)	Ratio max/mean
Bass Rock	115.4	1998 <sup>a</sup>	223	1.9	540	2.4
		2002 <sup>b</sup>	320	2.8	590	1.8
		2003 <sup>c</sup>	155	1.3	276	1.8
Bass Rock year average			232.7	2.0	468.7	2.0
Grassholm	108.2	2006 <sup>d</sup>	120	1.1	404	3.4
Rouzic	85.5	2006 <sup>e</sup>	100	1.2	176	1.8
Colony average			150.9	1.4	349.6	2.4

<sup>a</sup> Hamer et al. (2001).<sup>b</sup> Hamer et al. (2007).<sup>c</sup> Hamer et al. (2009).<sup>d</sup> Votier et al. (2010).<sup>e</sup> Grémillet et al. (2006).

2010). We constructed a resource field (Fig. 2d) using long-term data on calanoid copepod abundance (1953–2002) (CA) taken from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS), Continuous Plankton Recorder (CPR) survey (Johns, 2008), the largest multi-decadal near-surface phyto- and zooplankton monitoring programme in the world (Richardson et al., 2006). Although a regime shift occurred in the North Sea during this time altering the composition of copepod species (Beaugrand, 2004), seabird distributions were not overly affected (Grandgeorge et al., 2008). We use a long timescale in order to provide adequate spatial coverage. The resource field was then used to estimate the amount of time a gannet would spend in a specific cell, using parameters taken from Votier et al. (2010).

Predicted gannet distributions were interpolated (triangle-based linear interpolation) to match the spatial structure of the CPR data (37 km<sup>2</sup>) (Sims et al., 2006). The speed a gannet would fly through the cell based on copepod abundance was then derived from the relationship described by Votier et al. (2010) (see Eq. (2)). To calculate the time a gannet spent within each grid cell, the cell size was divided by the speed estimate and scaled to be between 0 and 1. We then multiplied the projected gannet distributions (Fig. 2c) by the scaled time estimate, to correct for the availability of resources.

Eq. (2) (Votier et al., 2010):

$$\text{Derived ground speed (kph)} \\ = -35.710(\log_{10} \text{Copepod Abundance}) + 39.761 \quad (2)$$

For species, such as gannets, reliant on fisheries discards for at least part of their diet (Grémillet et al., 2008b; Votier et al., 2010) data on the location of fisheries taken from the Vessel Monitoring System (VMS) may be important. However at present the spatial and temporal scale of available data means we are unable to model gannet distributions at the scale of this study (Witt and Godley, 2007).

Overall these six steps produced a map of predicted breeding gannet distributions that incorporated: (1) the effect of intra-specific competition, (2) the importance of distant areas for foraging behaviour, (3) near-colony maintenance and transiting behaviours, and (4) the availability of resources within those areas. As we are predicting the distribution of breeding birds, we represent our model as relative abundance of gannet pairs km<sup>-2</sup>.

### 2.7. Step 7: Validation of predicted at-sea distributions

For comparison with our at-sea projections we used gannet distribution data taken from two sources: data from all known gannet tracking studies in this region, and extraction of interpolated at-sea gannet distributions from the ESAS database managed by the JNCC (Kober et al., 2010).

Gannet tracking data consists of tracks from four colonies: Bass Rock ( $n = 13$  individuals,  $n = 13$  trips), Grassholm ( $n = 21$  individuals,  $n = 21$  trips), Rouzic ( $n = 20$  individuals,  $n = 20$  trips), and Great Saltee ( $n = 5$  individuals,  $n = 27$  trips), three using GPS loggers (Grémillet et al., 2006; Hamer et al., 2009; Votier et al., 2010) and one using satellite telemetry (Hamer et al., 2001). These provide a comprehensive insight into the movements of individual birds at sea, allowing a useful comparison with our predicted distributions (Fig. 3b). However, the tracking data are used to parameterise the model and so formal validation is not appropriate.

We used ESAS data incorporating observations of gannets made from at-sea ship transects between May and September (1980–2005) to best represent the breeding season, although these data include observations of all age classes. These were interpolated using Poisson kriging to account for unequal sampling effort and the inflated number of zero counts (Monestiez et al., 2006), giving an estimate of individual birds per km<sup>2</sup> for the UK fisheries limit (Kober et al., 2010) (Fig. 3c). While this does not provide an exact match to the spatial extent, or age structure, of our predictions, it does represent the most accurate available record of the spatial extent of gannets in UK waters.

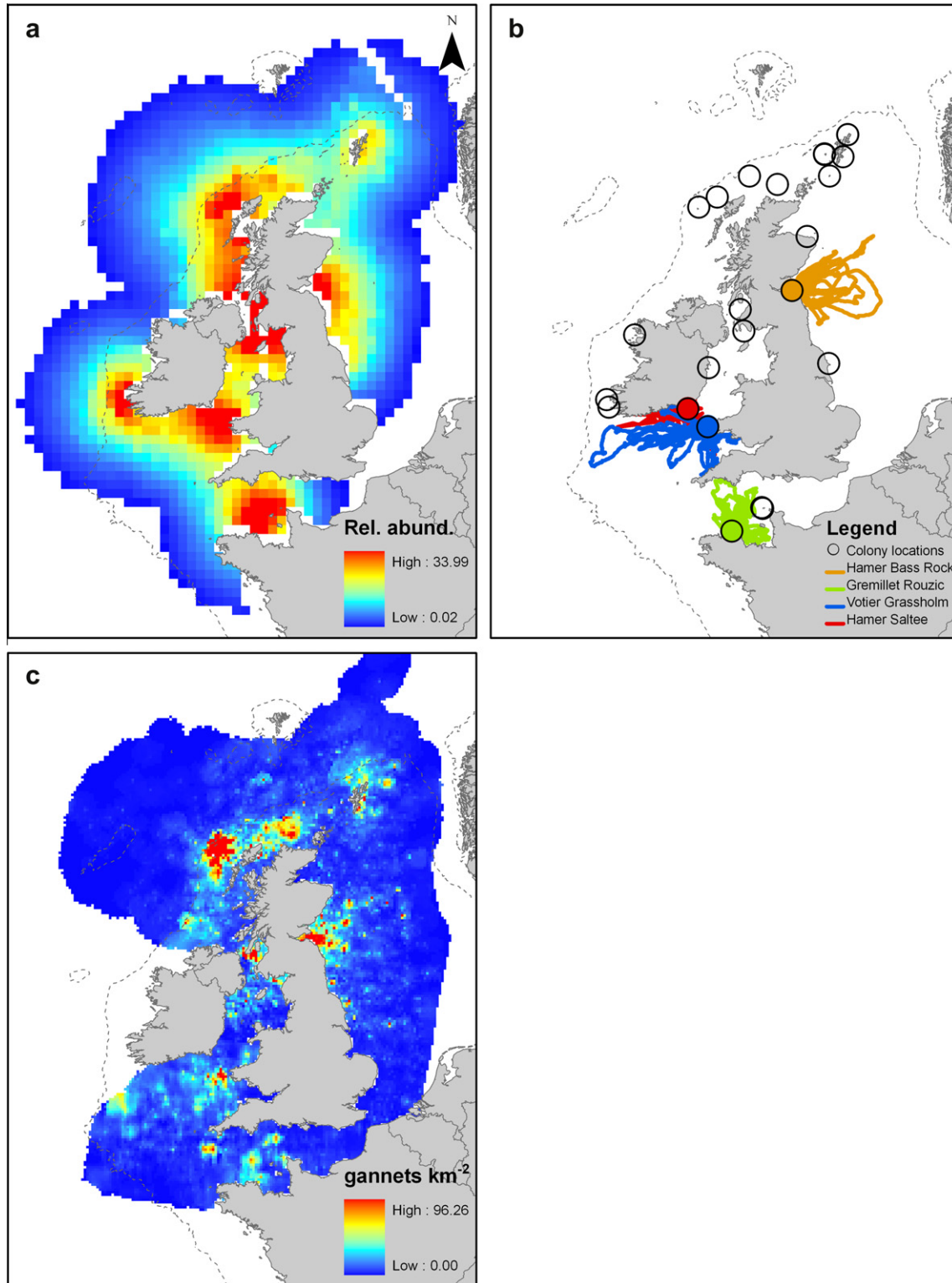
We quantitatively compared the ESAS database and our predictive models of density with a Spearman's rank correlation, using only cells where an observed and predicted value were available, including zero counts. ESAS data were interpolated to match 37 km<sup>2</sup> spatial resolution of model outputs. Seabird distributions are likely to be spatially auto-correlated and so we bootstrapped the test by sampling a random 10% of the dataset for the correlation, and then iterated this process 10,000 times. Results are therefore presented as mean  $p$  and  $r_s$  ( $\pm$ std.). All analyses were carried out in MATLAB (R2009b, Mathworks) and ArcGIS 9.3 (ESRI, USA).

## 3. Results

The final output of our model estimates the at-sea distribution of all gannets breeding at colonies in the UK, Ireland, Channel Island and France (Fig. 3a). Distributions are weighted by near colony attendance and resources, so that high densities occur around gannetries and at areas of high copepod abundance.

### 3.1. Comparison of predicted distributions with tracking data

Gannets tracked in 2006 from Grassholm foraged exclusively to the south and west of the colony but did not venture north of the Celtic Sea Front into the Irish Sea. Gannets tracked from the southern Irish colony of Great Saltee also foraged predominantly to the west of the colony and within 100 km of the southern Irish coast, but did not overlap with birds tracked from Grassholm (Fig. 3b).



**Fig. 3.** Comparison of predicted distributions with collated tracking and ESAS distributional data. (a) Relative abundance of breeding gannets as predicted by the at-sea projection model developed in this study. (b) Location of ganneries around the UK, Ireland and northern France overlaid with tracking data taken from four colonies (Grémillet et al., 2006; Hamer et al., 2009, 2001; Votier et al., 2010). (c) The at-sea breeding season distribution of Northern gannets (*Morus bassanus*) using data taken from the JNCC European seabirds at sea database for the last 25 years, and interpolated to give density of individuals per km<sup>2</sup> (Kober et al., 2010).

Our projected distributions show a similar pattern; the paucity of copepods lowering gannet densities in the Irish Sea, and the productive zone around the Celtic Sea Front elevating densities (Fig. 3a).

Grémillet et al. (2006) demonstrated a preference in gannets for productive/mixing zones by linking GPS tracks with the tidal front

between eastern and western Channel waters. Our predicted distributions for the Channel centre around the Rouzic colony, but are skewed east by the presence of the Channel Island colonies of Ortac and Les Etacs which together represent 7409 breeding pairs (Table 1). Hamer et al. (2009) found strong associations between foraging behaviour and the tidal mixing front to the east of Bass

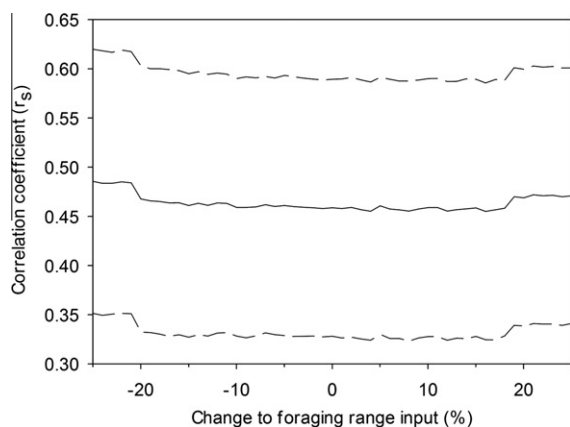
Rock. The copepod data show a latitudinal gradient in a similar area to this front (Fig. 2d), that lower gannet densities in the region north east of the colony compared with predictions from earlier model steps (see Fig. 2).

### 3.2. Comparison of predicted distributions with ESAS data

Our predictions of habitat use by breeding gannets developed using an integrated modelling approach show a statistically significant correlation with the ESAS dataset (Spearman rank order correlation,  $r_s = 0.459 \pm 0.130$ ,  $p < 0.001 \pm 0.002$ , Fig. 3a and c). To investigate the relevance of the different development steps in the model we also compared outputs from the other model steps with the ESAS data. There were weak correlations between the ESAS data and both Step 3 ( $r_s = 0.137 \pm 0.051$ ,  $p = 0.033 \pm 0.067$ , Fig. 2a) and Step 4 ( $r_s = 0.126 \pm 0.051$ ,  $p = 0.003 \pm 0.015$ , Fig. 2b). The output from Step 5, the model not corrected for copepod availability (Fig. 2c), also showed a statistically significant correlation with the ESAS dataset (Spearman rank order correlation,  $r_s = 0.326 \pm 0.084$ ,  $p < 0.001 \pm <0.001$ ), but did not produce a better fit than the final model.

To test the importance of adjusting foraging ranges in Step 4 we carried out a sensitivity analysis. The foraging ranges input into the model were varied by  $\pm 25\%$  and the final model outputs tested against the ESAS data (Fig. 4). Varying the foraging range of each colony had very little influence on the final output, which still showed a statistically significant correlation with the ESAS dataset ( $r_s = 0.455\text{--}0.486$ ,  $p < 0.001$ ).

During ESAS surveys more gannets are seen due to transiting and maintenance behaviours around colonies, and gannet distributions around colonies are elevated using the log-linear decay function. The data also highlight some important offshore areas; the Hebridean shelf break appears to aggregate gannets in both the ESAS data and our predictions, but this could be due to the occurrence of a number of colonies in the area. Broadly, both techniques suggest similar areas of low gannet density in areas such as the Rockall plateau, Orkney, north-east North Sea, the eastern English Channel, the Celtic Sea and the South West approaches. These areas have few or no gannetries, and visual comparison with data on copepod abundance (Fig. 2d), suggests they may be poor foraging areas. Nevertheless, the Celtic Sea and South West approaches support large fisheries for pelagic and demersal fish (Witt and Godley, 2007) which may provide a food resource to gannets and other seabirds (Votier et al., 2004).



**Fig. 4.** The correlation between model outputs and the ESAS gannet distributional data was not sensitive to changes in foraging ranges; the mean  $r_s$  (solid line) and s.d. (dashed line) showed little variation when adjusting the foraging ranges input into the model by  $\pm 25\%$  and still showed a statistically significant correlation (mean  $r_s = 0.455\text{--}0.486$ ,  $p < 0.001$ ).

## 4. Discussion

We present a method that, based on our current understanding of gannet foraging behaviour, quickly and effectively highlights important at-sea regions. Data collected from at-sea visual surveys has been vital in estimating habitat use on broad temporal and spatial scales, and while tracking data provides fine scale spatial information, sample sizes are comparatively small and it is improbable that data will ever be collected from all seabird colonies. In contrast, our approach predicted distributions for 25 gannetries, totalling 299,522 pairs of breeding birds and representing ca. 70% of the global breeding population (Mitchell et al., 2004). Moreover, adaptation of these models for other central-place foragers, as well as multiple species, could provide an integrated framework to guide both the siting of future MPAs for seabirds, and the mitigation of offshore construction activities, fisheries management and oil pollution events through marine spatial planning.

There are few other syntheses of tracking and colony-based studies, but our results suggest that the models are robust and comparable to the observed distributions of gannets at sea. Differences in distribution between the ESAS data and our predictions may be due to our exclusion of the German, Norwegian and Faroese colonies. Birds from these are all capable of foraging within UK and Irish waters, although the colonies are much smaller. Our models also exclude immature birds which may comprise  $>50\%$  of the population and are highly vagile (Votier et al., 2011). Nevertheless, the efficiency of this technique also allows modelling of species traditionally hard to study at sea, and offers obvious benefits as a technique when compared to at-sea studies and tracking studies (Louzao et al., 2009). By emphasising the importance of near colony areas, and including distributional changes due to resource availability, our models highlight important areas at the colony level both in the near-shore and offshore. Nevertheless, the distributions predicted by models with and without resource characterisation are very similar suggesting that other proxies may be more appropriate, or that calanoid copepod and fish abundances are not correlated spatially. The importance of this step will be highly species specific. This technique integrates all at-sea activities and so any MPA that would arise from this approach would protect transiting and foraging activities. Areas of importance specific to foraging could be identified through, for example, Area Restricted Search analysis of individual GPS data (Fauchald and Tveraa, 2003).

There are limitations to projecting at-sea distributions of seabirds in this way. The decay and resource weighting techniques may not capture seabird movements adequately, but do provide a framework for the future development of this technique. Furthermore, gannets are known to alter foraging behaviour relative to prey abundance and distribution (Garthe et al., 2007; Montevecchi, 2007; Montevecchi et al., 2009), and so foraging distance and trip duration are not always correlated (Garthe et al., 2011). Resources also move throughout the breeding season, potentially altering small-scale distributional patterns. Information from tracking studies could be used to inform near-colony distributions *i.e.* through kernel analysis or a lattice-based approach (Barry and McIntyre, 2011), but these are highly species and colony specific (McSorley et al., 2003, 2008; Wilson et al., 2009), and not available for species unable to carry devices. Furthermore, there is no direct trophic link between gannets and copepods, and as copepod and fish abundances may be poorly correlated spatially it may be inappropriate to use a planktonic resource map to infer the distribution of a piscivorous plunge-diving seabird (Grémillet et al., 2008a). While gannets are known to feed on a range of prey including mackerel, garfish, herring, sandeel and fisheries discards (Garthe et al., 2011; Nelson, 2002; Votier et al., 2010) at present spatially

resolved fish abundance data are not widely available at this scale, but there is scope to combine log book and VMS data to provide such information (Bertrand et al., 2008).

In the absence of *in situ* estimates of prey availability remote-sensing data can be employed as a proxy to define important foraging habitats for seabirds, but should be used cautiously (Grémillet et al., 2008a). The flexibility of our model permits the incorporation of more appropriate resource maps in the future. Previous identification of pelagic IBAs for seabirds has collated a range of information on seabird distributions and proxies for foraging habitats, including; bathymetry, distance to features such as the coast, shelf-break and colonies, remotely sensed chlorophyll-a, and sea surface temperature, and identification of both large-scale and local fronts (SEO/BirdLife, 2009). Nevertheless, our model was not sensitive to changes in foraging range estimates; the results of a sensitivity analysis (Fig. 4) varying foraging ranges by  $\pm 25\%$  produced a model statistically comparable with the ESAS data set.

When implementing protection for wide ranging and pelagic seabirds, it will be important to protect features of known importance to the targeted species. Thermal fronts, upwellings, mixing zones, and other tidal features (Tew Kai et al., 2009) are known to provide food resources and exhibit a high degree of spatial and temporal predictability (Game et al., 2009). Recent developments in composite front maps could allow the tracking of marine animals through dynamic systems in virtual real-time (Miller, 2009), allowing detailed analysis of an animal's response to these systems. Indeed, relating biology to consistent marine features would allow MPA design to be linked to bathymetry, aiding implementation and enforcement (Hyrenbach et al., 2006).

Seabird conservation requires a multi-faceted approach, involving not only protection at the nest site, but also consideration of near-colony rafting aggregations, safeguarding of foraging stock through protection of pelagic foraging zones, and consideration of the wintering grounds. Indeed the protection of over-wintering areas is important for both winter foraging and staging (Guilford et al., 2009), and population mixing (González-Solis et al., 2007). The wintering grounds of gannets breeding in the UK and France, and many other key populations of European seabirds are mainly outside the EU. Therefore, while similar tools (biotelemetry, at-sea surveys and modelling) can be utilised to define the winter habitats of these species, protecting these areas will require international cooperation (Lascelles et al., this issue). For wide-ranging species, international cooperation has aided the protection of breeding season foraging grounds (e.g. the Agreement on the Conservation of Albatrosses and Petrels), and tracking could prove vital in quantifying the utilisation of marine sanctuaries by target species, and enforcing vessel compliance (Hyrenbach et al., 2006; Pichegru et al., 2010).

The development of precise distributional models provides a framework for testing population level processes. Perturbations such as environmental change, pollution events, or offshore construction could be simulated to investigate demographic responses at specific colonies. The projection of accurate colony-specific distributions could also allow investigation of the potentially regulatory effect that the near-colony marine environment has on colony-level processes (Ashmole, 1963), or the density dependence due to the proximity of other colonies (Furness and Birkhead, 1984), and could be applied to a number of other centrally-placed marine predators.

A network of protected areas is required to mitigate the threats facing seabirds, and this approach not only offers a timely method to draw attention to potentially important ocean habitats for seabird conservation, but also provides a theoretical framework to advance our understanding of the intrinsic and extrinsic factors that influence colony demographics.

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