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No: 556**

**Determining important marine areas used by European shag breeding on the Isle  
of May that might merit consideration as additional SPAs**

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**NB** This report was originally produced, but not published, in 2012. It uses data and population estimates which were correct at the time.

## Executive summary

- This report presents analyses of locational data collected from adult European shags breeding on the Isle of May, Scotland from 1987-2010 using animal borne instrumentation. Data were available from 16 years, comprising 322 individuals, 1,111 foraging trips and 20,100 foraging locations.
- Data were collected using four different methods: dead-reckoning using VHF telemetry (1987, 1988, 1989, 1990, 1991, 1992, 1994, 1997, 1998), triangulation using VHF telemetry (2001), dead reckoning using compass loggers (2002) and GPS (2003, 2006, 2008, 2009, 2010)
- Shag core distribution, as represented by the 50% kernel, was concentrated in three main foraging areas: around the Isle of May itself, and two areas inshore of the Isle of May, one to the north (near Fife Ness) and one to the west (near the town of Anstruther).
- An overlap analysis across the study split into three periods (1987-1992; 1994-2003; 2006-2010) demonstrated reasonable consistency in distribution across the study, inter-period overlap varying from 54%-68%.
- An assessment of minimum adequate sample size using bootstrapping indicated that approximately 8 years is required to achieve 90% of the long-term population range. Although this was a conservative test, it highlights the value of long term data in understanding population distribution.
- A cumulative utilisation distribution was estimated. A non-linear increase in cumulative proportion was apparent between kernel densities of 20% to 100%. The point of maximum curvature for the best fitting model (a double exponential) was at an area of 156km<sup>2</sup>, representing 93% of the population.
- A habitat preference analysis suggested a strong avoidance of muddy habitats. Within non-muddy habitats, there was evidence that shallower water (<50m) was favoured. No association with particular sea surface temperatures or primary productivities was evident. Additional modelling, beyond the scope of this report, is required to account for individual variation in the distribution data.
- A literature review was conducted on at-sea distribution and associated variables that could determine distribution (diet, depth, habitat association, habitat availability, colony size) of shags around the UK. The findings of this review, together with the data from the Isle of May, were synthesised to inform the potential for identifying important areas for shags at sea across the SPA network.
- The paucity of data across the network, together with inherent differences in habitat availability between the Forth Islands SPA and other SPAs, makes this assessment extremely challenging. However, significant progress could be made when the recently collected tracking data from other colonies is published, enabling the representativeness of the Isle of May to be tested formally.

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# 1 Introduction

## 1.1 Background

Absolute obligations under the EC Birds Directive (EEC 1979) include the creation of a network of Special Protection Areas (SPAs) for those birds on Annex I of the Directive and for regularly occurring migratory birds. In the UK, a programme aimed at establishing such a network has been ongoing since the 1980s. This programme has focussed almost exclusively on the terrestrial and coastal habitats, but since 2001 the focus has broadened to consider important bird concentrations using marine habitats. This work has been undertaken by JNCC, where appropriate on behalf of, and with funding from, the statutory nature conservation agencies.

All species of seabird that occur in the UK, with the exception of the black guillemot, are regarded as migratory and several are on Annex I of the Birds Directive. Most species of duck, grebe and diver that use marine habitats are also migratory and/or on Annex I of the Directive. Consequently, the most suitable territories at sea for these species must be classified as SPAs.

The European shag *Phalacrocorax aristotelis*, a medium-sized member of the cormorant family, breeds around much of the UK. This species, as with others that feed inshore, has not been adequately surveyed in all areas using this method, so alternative approaches are required. It is considered to be migratory and thereby SPAs should be identified for it. To date, 13 breeding colony SPAs have been classified for the species, none of which has a marine component.

## 1.2 Objectives

This report presents analyses of locational data collected from adult European shags breeding on the Isle of May, Scotland (part of the Forth Islands SPA) from 1987-2010 using animal borne instrumentation. This report also aims to investigate distributions in relation to a suite of environmental variables that are available throughout the UK. Together, these data will be interpreted with the aim of informing the identification of possible additional areas at sea that may be suitable for SPA classification for the European shag.

The main output of the report is a series of maps of annual and multi-year European shag distributions determined using kernel density estimations, and overlays and analyses of these distributions in relation to environmental variables (specifically: sea surface temperature, chlorophyll A concentration, benthic substrate and bathymetry). Furthermore, the power of the analyses to detect the importance and persistence of concentrations of shags at sea are explored by investigating the importance of sample size on population foraging range and the degree of inter-annual variation in their location.

The report also provides information that could inform a wider assessment by JNCC and the statutory nature conservation agencies of a possible UK-wide SPA suite for shag towards fulfilment of the obligations of the Birds Directive. In respect of this objective, the report provides a literature review of at-sea distribution of shags across the UK, with special emphasis on the SPA network, and factors relating to distribution (diet, water depth, habitat association, habitat availability and colony size). This synthesis is then integrated with the habitat preference analysis of Isle of May shags to provide the wider assessment.

This work builds on a previous contract by CEH for JNCC (Bogdanova *et al* 2010).

## 2 At-sea distribution of Isle of May shags

### 2.1 Methods

#### 2.1.1 Data collection and processing

Foraging distributions of adults breeding on the Isle of May were obtained using animal borne instrumentation. Four methods were used: dead-reckoning using VHF telemetry (1987, 1988, 1989, 1990, 1991, 1992, 1994, 1997, 1998), triangulation using VHF telemetry (2001), dead reckoning using compass logger (2002) and GPS (2003, 2006, 2008, 2009, 2010). All data were collected during chick-rearing except 2001, when foraging trips during incubation were also recorded. Birds were captured at the nest using a crook at the end of a long pole, and the device attached using tesa tape and/or cable ties. Birds typically carried loggers for short periods (1-2 days) before they were recaptured and the logger retrieved. Sample sizes and logger deployment periods for each year of the study are summarised in Table 1.

Year	Logger type	Deployment period	<i>n</i> birds	<i>n</i> trips	Trips per bird (median; range)	<i>n</i> fixes	Fixes per bird (median; range)
1987	VHF	28 June - 24 July	10	NA	NA	139	15.5 (4-22)
1988	VHF	29 June - 17 July	12	NA	NA	85	7 (2-12)
1989	VHF	10 June - 5 July	7	NA	NA	106	18 (6-23)
1990	VHF	2 July – 8 July	15	23	1 (1-4)	27	1 (1-4)
1991	VHF	12 July – 21 July	24	29	1 (1-2)	43	1.5 (1-5)
1992	VHF	1 June – 18 July	43	100	2 (1-5)	159	3 (1-7)
1994	VHF	9 July – 22 July	9	41	3 (1-10)	60	4 (1-19)
1997	VHF	30 May - 30 July	41	41	1	41	1
1998	VHF	22 June - 31 July	19	19	1	19	1
2001	VHF	17 May - 7 July	41	48	1 (1-3)	48	1 (1-3)
2002	Compass	4 June - 30 June	16	31	2 (1-4)	61	3.5 (1-12)
2003	GPS	1 June - 11 June	10	32	3.5 (2-5)	1181	93.5 (57-241)
2006	GPS	27 June – 28 June	2	5	2.5 (2-3)	197	98.5 (78-119)
2008	GPS	19 June - 24 June	9	21	2 (1-4)	1934	177 (132-414)
2009	GPS	3 June - 23 June	31	202	4 (1-17)	8379	217 (11-857)
2010	GPS	8 June – 24 June	33	260	7 (3-17)	7621	217 (64-552)
TOTAL			322	1111		20100	

**Table 1.** Annual deployment summary over the study period.

##### 2.1.1.1 Dead-reckoning from VHF telemetry (1987, 1988, 1989, 1990, 1991, 1992, 1994, 1997, 1998)

Location was obtained by attaching VHF radio transmitters (CEH; Biotrack Ltd) to adult breeding birds (Wanless *et al* 1991a, 2000; Daunt *et al* 2007). Birds were radiotracked from a station near the highest point on the island (73m a.s.l.). The receiving system consisted of two parallel eight-element Yagi aerials joined by a 2m crosspiece, attached to a vertical 5m mast which allowed the aerials to rotate freely through 360°. The aerials were connected to an ATS R4000 scanning receiver, operating in the 173MHz band. A typical foraging trip consisted of a flight out to the feeding site, a number of dives with periods between dives on the sea surface, and a return flight to

the colony. The method by which information on foraging activity is obtained from radio-tracking is well-established in shags. From the strength and consistency of the signal, it is possible to determine a precise time-activity budget, namely whether the bird is flying (strong, continuous signal), on the water surface (unsteady, continuous signal) or diving (signal disappears, Wanless *et al* 1991a). Locations of foraging birds are then estimated by dead-reckoning, using the bearing of the bird, the flight time to the foraging site, and an average flying speed of  $15.4\text{ms}^{-1}$  (Pennycuick 1997). In 1987 – 1989, the dead reckoning estimates were verified by repeated observations of foraging flocks and independent location estimates obtained by triangulation (Wanless *et al* 1991a, see next section for details on triangulation method).

#### **2.1.1.2 Triangulation from VHF telemetry (2001)**

Location was obtained by attaching radio transmitters (CEH; Biotrack Ltd) to the birds and following the direction and strength of the signal from two tracking positions: the same fixed position on the Isle of May described in the previous section, and one mobile position operating along the strip of the South Fife coast adjacent to where the European shags were foraging (Wanless *et al* 2005). In the majority of cases, triangulation was achieved from more than one point along the coast. Foraging fixes were obtained from the intersection of the two (or more) bearings in the software Tracker.

#### **2.1.1.3 Dead reckoning from compass logger (2002)**

Compass loggers work on the principal of dead reckoning, whereby a foraging track is generated from a series of joined vectors (Peters 2005). The direction of each vector is provided by two perpendicular compass vector sensors, and the length of the vector is derived from published mean flight speeds for the species (Pennycuick 1997). Data are recorded at 1s intervals. Thus, when the bird is not flying, the vector has zero length. Each vector is corrected for wind speed and direction, using hourly weather data from Leuchars weather station, 20km north of the Isle of May, and for the orientation of the logger on the birds' back, estimated from photographs. Thus, the initial step of the process involves identifying sections of flight. Different activities (colony, flight, sea surface and diving) can be readily identified from the output of the logger. The second step of the process is to plot the first compass values against the second compass values. For true bearing to be calculated from the data, this scatter plot must take the form of a ring of data points, from which accurate estimates of maximum values for the first compass (referring to South) and maximum values for the second compass (referring to East) can be made. The coded flights, with associated bearing estimate, are then combined in Multitrace-route (Jensen Software Systems) to produce a foraging track. Each foraging track is then viewed in Excel. A filtering process is carried out to remove those tracks that did not produce a satisfactory output. The criteria for this decision were a) a close association between the start and end point (in reality these are in the same place, i.e. the nest site) and b) a track shape consistent with existing information from VHF telemetry i.e. travelling flights that are relatively direct. This step appears somewhat arbitrary, but in practice it was clear which tracks to retain and which to discard. Among discarded tracks, a second check was made to ensure that the flights had been correctly coded. If no improvements could be made at this point, the track was abandoned. For retained tracks, the vectors were run through an algorithm in Excel to correct for drift. This method brings the end point to the same location as the start point and distributes the drift evenly between all flight vectors. 76% of deployments resulted in foraging tracks that satisfied these conditions.

#### **2.1.1.4 GPS (2003, 2006, 2008, 2009, 2010)**

GPS loggers record latitude and longitude directly. They have revolutionised the quality of data on foraging location, and are the locational logger of choice for summer distributions since they first came on the market at a size sufficiently small to be carried by this species (Wanless *et al* 2005). The data required processing in two steps: 1) locations recorded at the colony were removed; 2) locations recorded during flights to and from foraging areas were removed using a speed threshold of 2 to 5m/s. If travel speed between locations was over the threshold, data were discarded, hence only foraging locations were retained. Sampling intervals of GPS loggers varied among years (range 30-180 sec).

#### **2.1.2 Identification of foraging areas**

Foraging areas around the colony for each year (except 1998 and 2006 when sample size was not sufficient) were identified using kernel density estimation. Fixed kernel analysis was performed in ArcGIS (Hawth's Analysis Tools 3.27), using a smoothing parameter ( $h$ ) identified using the Least-squares cross-validation method (Worton 1989). The smoothing parameter varied between 1.5 and 2km, with the exception of 1992 (3km). Whilst various methods are available to estimate smoothing, LSCV is considered to provide generally unbiased estimates (Seaman & Powell 1996).

We adopted a cell size of 400m. The choice of cell size is usually determined by the trade-off between speed or efficiency of the analysis and its resolution, and should reflect the scale of the data so that the spread in X and Y direction is covered by an adequate number of cells. In this case, the full dataset covers an area of approximately 40x40km, therefore with a cell size of 400m, we have coverage of 100 cells in both directions. This was deemed to provide sufficient resolution. Also, in our experience the kernel outputs are generally fairly insensitive to the choice of cell size with this species.

Kernel maps with 50, 70 and 90% density contours were produced in a Lambert equal-area azimuthal (North Pole) projection for each year. An equal area projection was chosen as it is most appropriate for habitat modelling. Area (in km<sup>2</sup>) of each kernel is presented as well as maps.

Kernel density distributions (as above: 50%, 70% and 90%) were also generated for all years combined (1987-2010, including 1998 and 2006) and all years with GPS data combined (2003-2010, including 2006), using a smoothing parameter of 2km identified, as above, using the Least-squares cross-validation method. The rationale for the latter was the much higher accuracy of fixes that are obtained from GPS compared with other technologies used. To ensure that GPS years did not have additional leverage in the kernel for all years (1987-2010) because of the increased number of fixes obtained (Table 1), the GPS data were sub-sampled by calculating the mean location for each foraging bout. Further sub-sampling to ensure that each individual contributed equally to the data set was not considered necessary, since Kernel density distributions do not require serial independence of data points (De Solla *et al* 1999). Sub-sampling details can be found in Table 2.

Year	Logger type	<i>n</i> birds	<i>n</i> trips	Trips per bird (median; range)	<i>n</i> fixes	Fixes per bird (median; range)
1987	VHF	10	NA	NA	139	15.5 (4-22)
1988	VHF	12	NA	NA	85	7 (2-12)
1989	VHF	7	NA	NA	106	18 (6-23)
1990	VHF	15	23	1 (1-4)	27	1 (1-4)
1991	VHF	24	29	1 (1-2)	43	1.5 (1-5)
1992	VHF	43	100	2 (1-5)	159	3 (1-7)
1994	VHF	9	41	3 (1-10)	60	4 (1-19)
1997	VHF	41	41	1	41	1
1998	VHF	19	19	1	19	1
2001	VHF	41	48	1 (1-3)	48	1 (1-3)
2002	Compass	16	31	2 (1-4)	61	3.5 (1-12)
2003	GPS	10	32	3.5 (2-5)	50	5 (3-8)
2006	GPS	2	5	2.5 (2-3)	5	2.5 (2-3)
2008	GPS	9	21	2 (1-4)	42	5 (2-8)
2009	GPS	31	202	4 (1-17)	469	10 (1-39)
2010	GPS	33	260	7 (3-17)	463	14 (3-28)
TOTAL		322	1111		1817	

**Table 2.** Sample sizes used in kernel distribution analyses after sub-sampling GPS data. A comparison with Table 1 shows the reduction in number of fixes in the GPS years.

### 2.1.3 Consistency in foraging distribution

The importance and persistence of concentrations of shags were examined by quantifying the consistency in the location of foraging areas among years. This was achieved by splitting the study into three time periods that corresponded to patterns of change in key demographic and diet parameters (Newell *et al* 2010) that could potentially impact on foraging distribution:

- 1987-1992: high population size, moderate breeding success, high proportion of sandeels in the diet;
- 1994-2003: low population size, moderate to high breeding success, high proportion of sandeels in the diet;
- 2006-2010: low population size, high breeding success, moderate proportion of sandeels in the diet.

Kernels (50% and 90%) were produced for each time period using the same method as for the annual kernels. The kernels were then converted into grids in ArcGIS and pairwise overlaps (overlap area x2/combined area \*100%) calculated in Matlab.

### 2.1.4 Minimum adequate sample size

To establish whether sufficient data have been collected to adequately represent population at-sea range, the standard approach is to examine the relationship between population range and sample size (i.e. the cumulative population range). The relationship between sample size and population range typically approaches an asymptote smoothly. Two methods are used to determine the relationship. The simple method involves recalculating the population kernel distribution with each addition of a sample. The more complex method is to use bootstrapping, which was chosen here since the error estimations are more representative of the population variation (Ramirez *et al* 2008). However, this method is substantially more conservative since it

estimates cumulative area of individual kernels as the estimate of population range at each step, as opposed to recalculating population kernel with each addition of a sample, the former resulting in a lower rate of increase with increasing sample size and greater variation. However, the latter requires substantial computing time that was beyond the scope of the project.

Minimum adequate sample size was explored at two scales, years and individuals within years. A standard bootstrap procedure was used for each sample size of years ( $n$ ), by choosing years randomly allowing replacement. For each bootstrap sample the total foraging area used was calculated and this was repeated 1,000 times for each  $n$ . The analysis was conducted using the 90% kernels for each year except 1992, which when included produced outputs that could be misinterpreted. Similarly, for the analysis of individuals within years, a standard bootstrap procedure was used for each sample size ( $n$ ), by choosing individuals randomly allowing replacement. The analysis was conducted using the 90% kernels of the 31 birds tracked in 2009, estimated using fixed kernel analysis with a smoothing parameter ( $h$ ) of 100-1000m. In most cases  $h$  was 600-1000m ( $h$  was 100m for a small number of individuals that foraged within a restricted area next to the colony).

### 2.1.5 Cumulative utilisation distribution and maximum curvature

In order to help inform an appropriate SPA boundary, we adopted the approach used by Wilson *et al* (2009) and estimated kernel density distributions of the whole distribution (1987-2010), for the whole distribution excluding 1992 and for the GPS years (2003-2010) at 5% increments from 20%-95% and 1% increments from 95% to 100%. A plot of the relationship between cumulative utilisation distribution and the cumulative proportion of total area ("utilisation curve", Wilson *et al* 2009) was generated.

To identify any discontinuity in the slope of this curve, we estimated the point of maximum curvature following methods used in O'Brien *et al* (in press), based on the following three models for the relationship between cumulative area and cumulative utilisation distribution of the 1987-2010 data set (scaled to lie between 0 and 1):

Single exponential model:

$$y = b(1 - \exp^{-rx})$$

Double exponential model 1:

$$y = b(1 - \exp^{-rx}) + c(1 - \exp^{-sx})$$

Double exponential model 2:

$$b(1 - \exp^{-rx^u})$$

where  $x$  is the cumulative area used;  $y$  is the cumulative utilisation distribution;  $b$  and  $c$  correspond to asymptotes as  $x$  tends to plus or minus infinity, depending on the sign of  $r$  and  $s$ ;  $r$  and  $s$  are rate parameters determining the shape of the curve;  $u$  is a power parameter which changes the shape of the curve away from being that of a standard exponential decay.

Following O'Brien *et al* (in press), maximum curvature was defined by:

$$\frac{\frac{d^2y}{dx^2}}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{3/2}}$$

## 2.1.6 Habitat association

### 2.1.6.1 Habitat overlay

To explore links between shag foraging distributions and environmental conditions, we compared the shag kernel density contours with:

- remotely-sensed sea surface temperature;
- remotely-sensed chlorophyll *a* concentration (chl *a*);
- benthic substrate;
- bathymetry.

SST data (in °C) and chl *a* data (in mg/m<sup>3</sup>) were monthly composites from the study year approximately matching the dates of logger deployment in that year. Where foraging data were collected over a period longer than one month, environmental data were obtained for the month that covered the majority of logger deployments. Data for these two environmental variables were available for shorter periods (daily/weekly); however, these datasets frequently had missing data and were therefore not used.

SST data were obtained from the Advanced Very High Resolution Radiometer (AVHRR) at 0.05° and 0.1° resolution. The higher resolution data were available for all study years except 2009 and 2010; for these years the lower resolution dataset was used. Chl *a* data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) at 0.05° resolution and from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) at 0.1° resolution. No chl *a* data were available for the study area between 1987 and 1997. The higher resolution data from MODIS were available for 2002-2010; for the remaining two years (1998 and 2001) we used lower resolution SeaWiFS data. No data were available for some parts of the study area in some years, most likely due to the imagery being obstructed by cloud cover. All SST and chl *a* datasets were downloaded from:

<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>.

Bathymetry and substrate data were obtained from the British Geological Survey under licence (<http://www.bgs.ac.uk/products/offshore.html>). We only present overlays with SST and Chl A for 2010 (see Bogdanova *et al* (2010) for earlier years).

Bathymetry and benthic substrate data were obtained from the British Geological Survey under licence (<http://www.bgs.ac.uk/products/offshore.html>). Isle of May shags are strongly dependent on the lesser sandeel *Ammodytes marinus* (Harris & Wanless 1991; Daunt *et al* 2008). Lesser sandeels are associated with sandy or gravelly sand substrates (Wanless *et al* 1997a; Wright *et al* 2000; Holland *et al* 2005), and benthic substrate was classified into sandeel-favoured habitat (criteria: sand-to-mud ratio >9:1 containing less than 30% gravel with particle size 625µm–2mm, Wanless *et al* 1997a), sandy gravel habitat (which contains a sandy component but is not considered ideal for sandeels), rocky habitat and muddy habitat.

### 2.1.6.2 Habitat preference

Habitat preference is determined by comparing the habitat used by birds with the habitat potentially available to them. As a measure of habitat use, we quantified the distribution (i.e. proportion of each type) of habitat within the 50% and 90% kernels. As a measure of habitat availability, we quantified the distribution of habitat within a circle with radius equivalent to the maximum range of the respective kernel distribution (11.5km for 50% kernel; 15km for 90% kernel). This latter area represented the birds' potential at-sea distribution based on the assumption that the maximum distance empirically recorded was the distance within which the bird, as a central place forager,

was constrained to forage. Goodness of fit tests were then employed to test for habitat preference (Sutherland *et al* 2004). Because of the low spatial and temporal resolution, gaps in data and lack of evidence of preference from the overlay maps (see also Bogdanova *et al* 2010), this analysis was not carried out for SST or ChlA. For bathymetry and seabed sediment, the analysis was undertaken using the 50% and 90% kernel for the GPS years (2003-2010).

## 2.2 Results

### 2.2.1 Foraging distribution

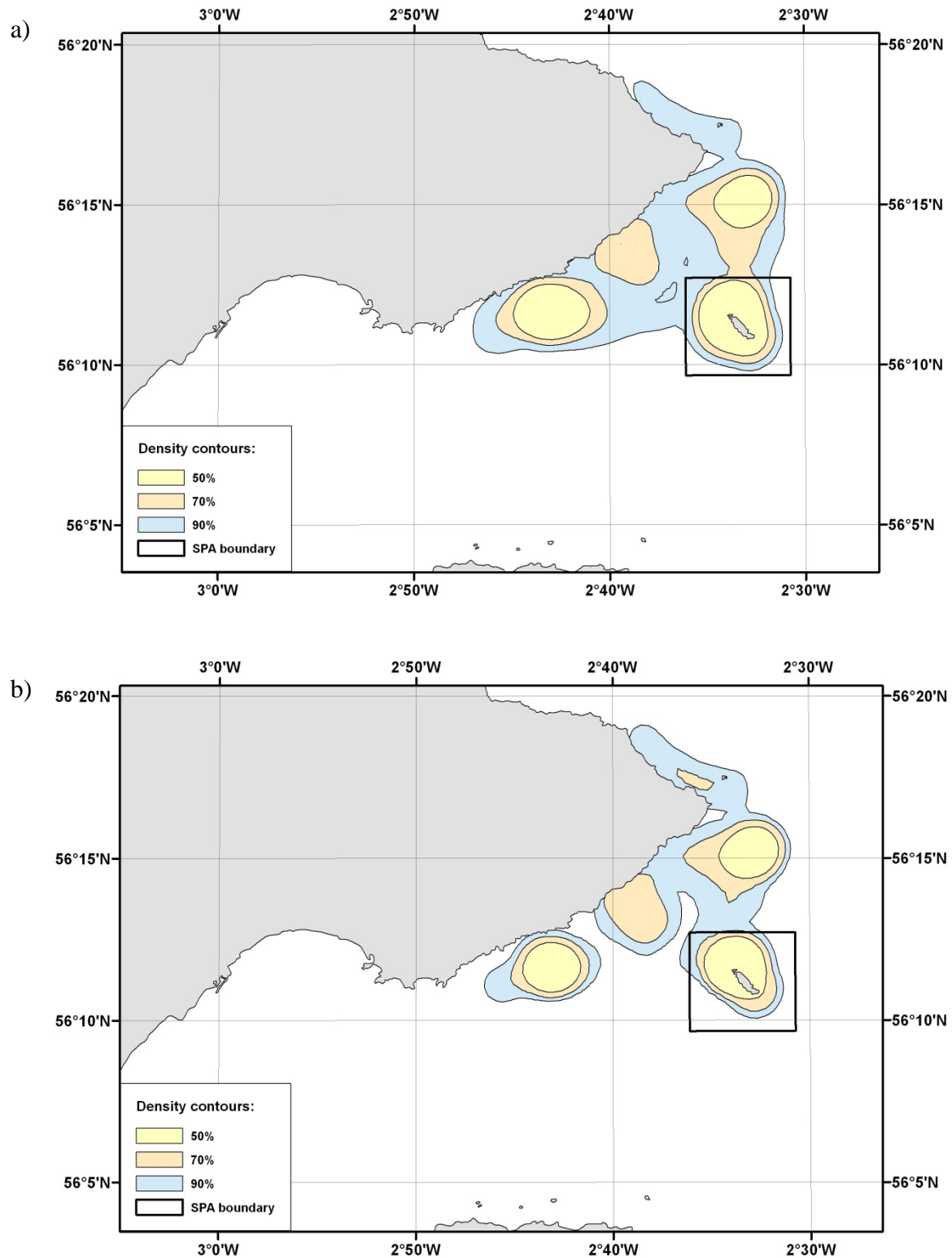
Three core foraging areas were used consistently during the study period: 1) the area surrounding the Isle of May; 2) an inshore area north of the island, near Fife Ness and 3) an inshore area west of the island, along the mainland coast (Fig. 1).

The precise use of the three main foraging areas varied among years as indicated by the kernel density distributions. All three areas were used to a greater or lesser extent in all years except in 1990, 1994 and 2002, where the northern inshore area was not used. The area around the Isle of May was used in all study years, though less intensively in 1990, 2001 and 2002. The northern inshore area was used most intensively in 1987, 2001, 2008, 2009 and 2010. In contrast, the western inshore area was the main focus for foraging in 1988, 1989, 1990, 1991, 1992, 1994, 2001 and 2002 (Fig. 2; data from 1998 and 2006 were not sufficient to estimate kernel density distributions). In one year, 1992, foraging distribution was much more extensive than any other years with birds distributed in particular in a westerly and north-easterly direction.

The average annual area represented by the 50% kernel was 20.0km<sup>2</sup> (range 9.2–86.0km<sup>2</sup>; Table 3). Equivalent values for 70% and 90% kernels were 39.9km<sup>2</sup> (range 17.5–169.7 km<sup>2</sup>) and 84.4km<sup>2</sup> (range 35.2–386.4 km<sup>2</sup>) respectively. The year 1992 had a high impact on these mean values. For the two multi-year maps represented in Figure 1, areas were higher than averages of annual distributions, at 29.9, 64.4 and 133.9km<sup>2</sup> for 1987-2010 and 23.1, 51.4 and 104.8km<sup>2</sup> for 2003-2010.

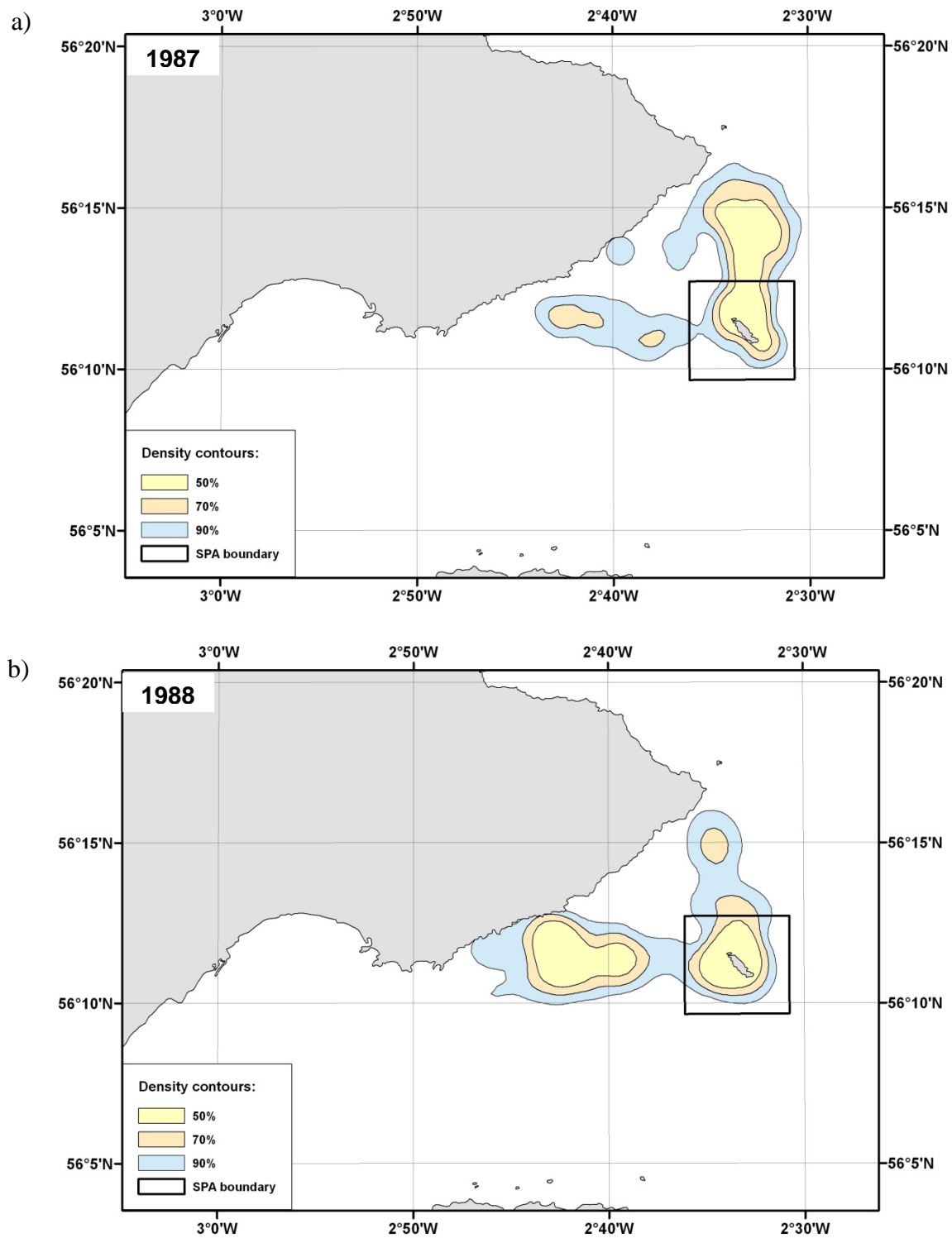


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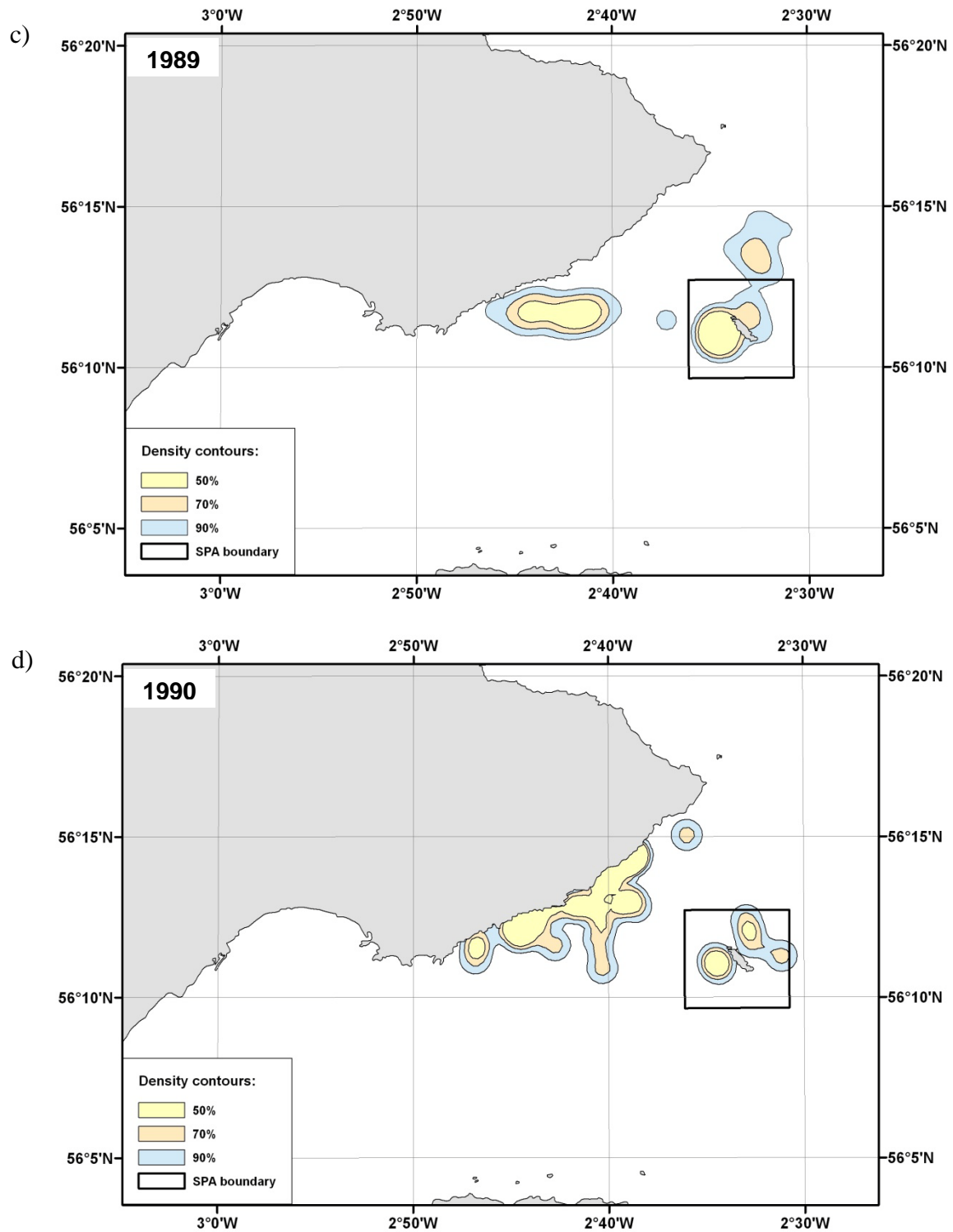
**Figure 1.** Foraging range of shags breeding on the Isle of May a) over the whole study period (1987-2010) and b) in the years where GPS loggers were deployed (2003-2010); 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.

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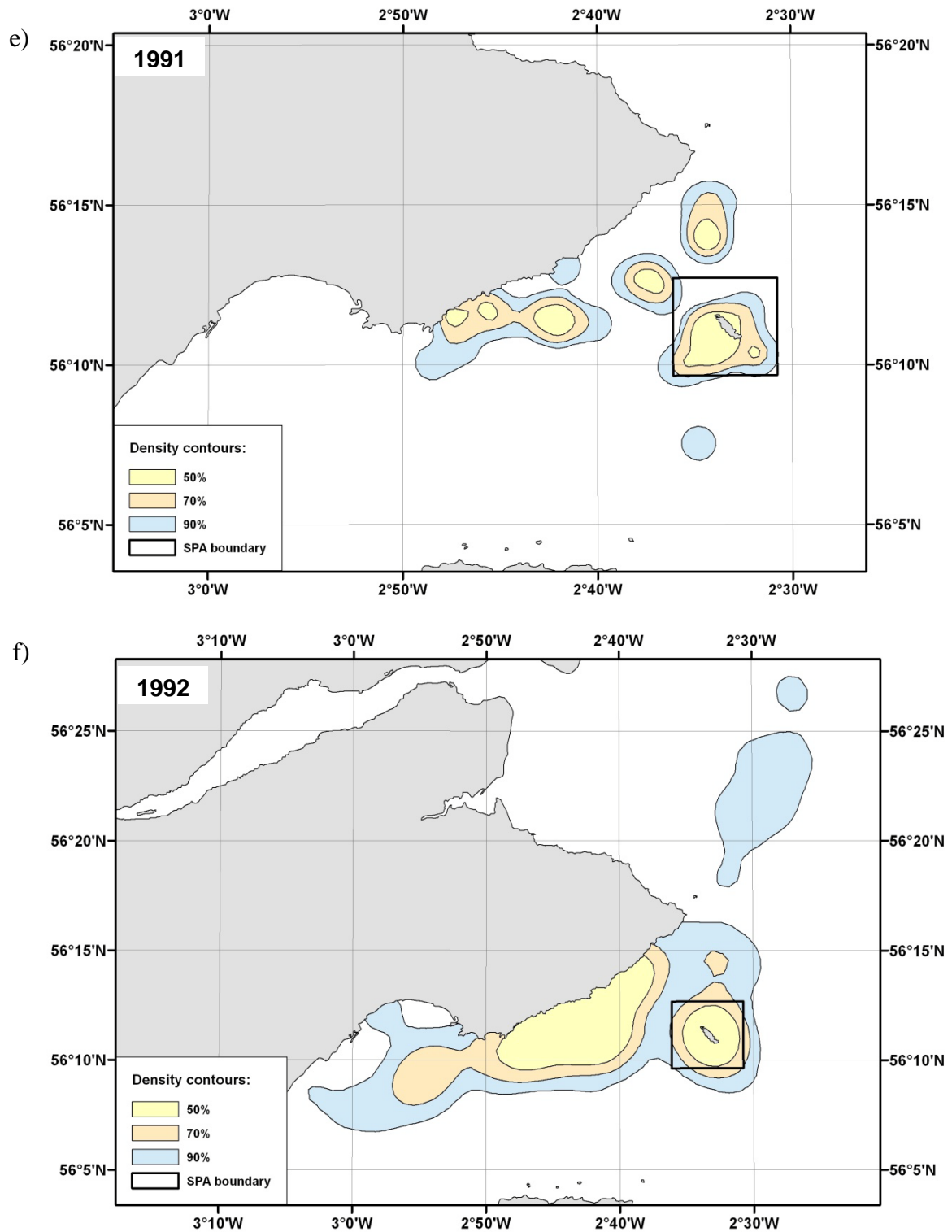
**Figure 2.** Shag population foraging range in a) 1987; b) 1988; 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.

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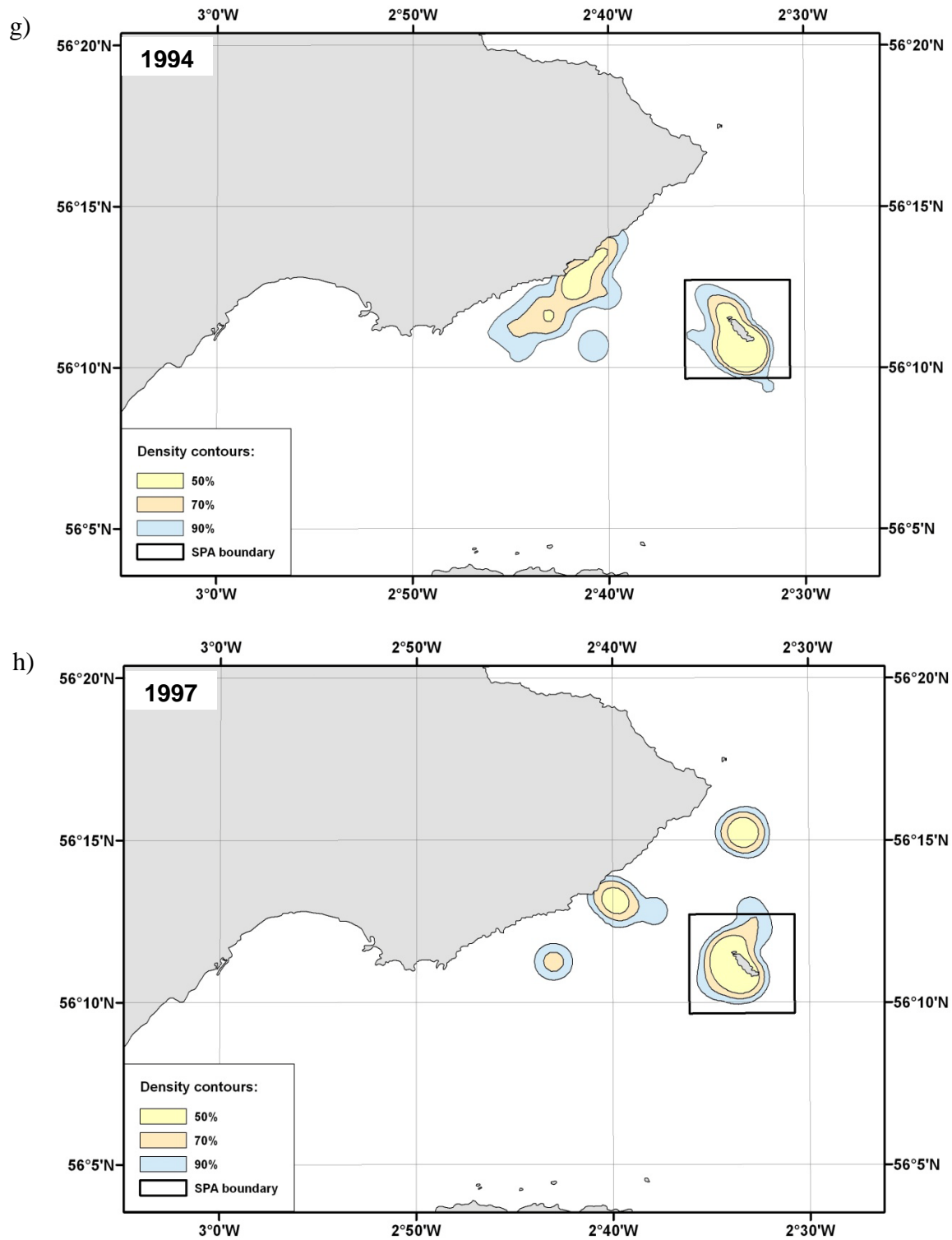
**Figure 2 (cont).** Shag population foraging range in c) 1989; d) 1990; 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.

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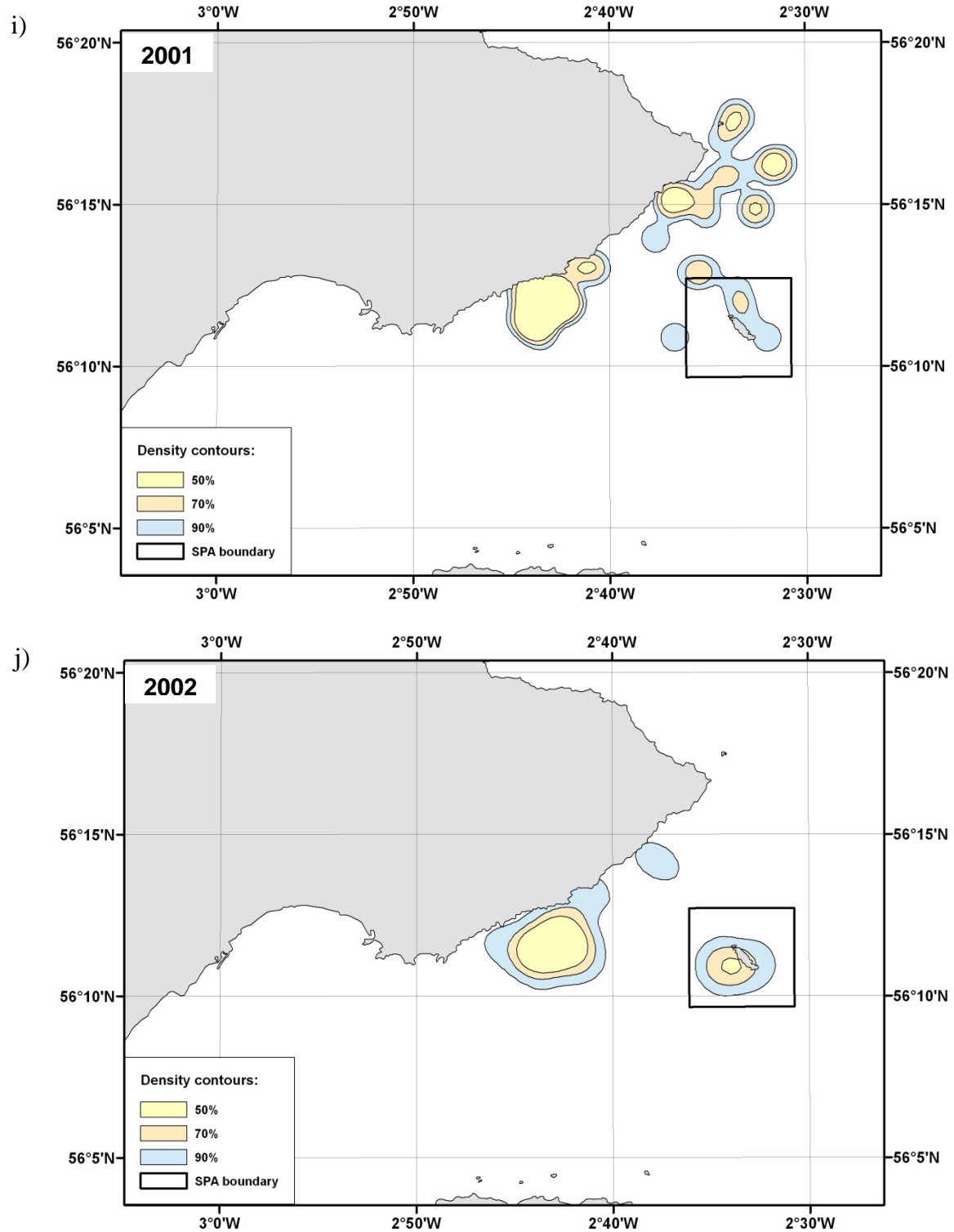
**Figure 2 (cont).** Shag population foraging range in e) 1991; f) 1992; 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.

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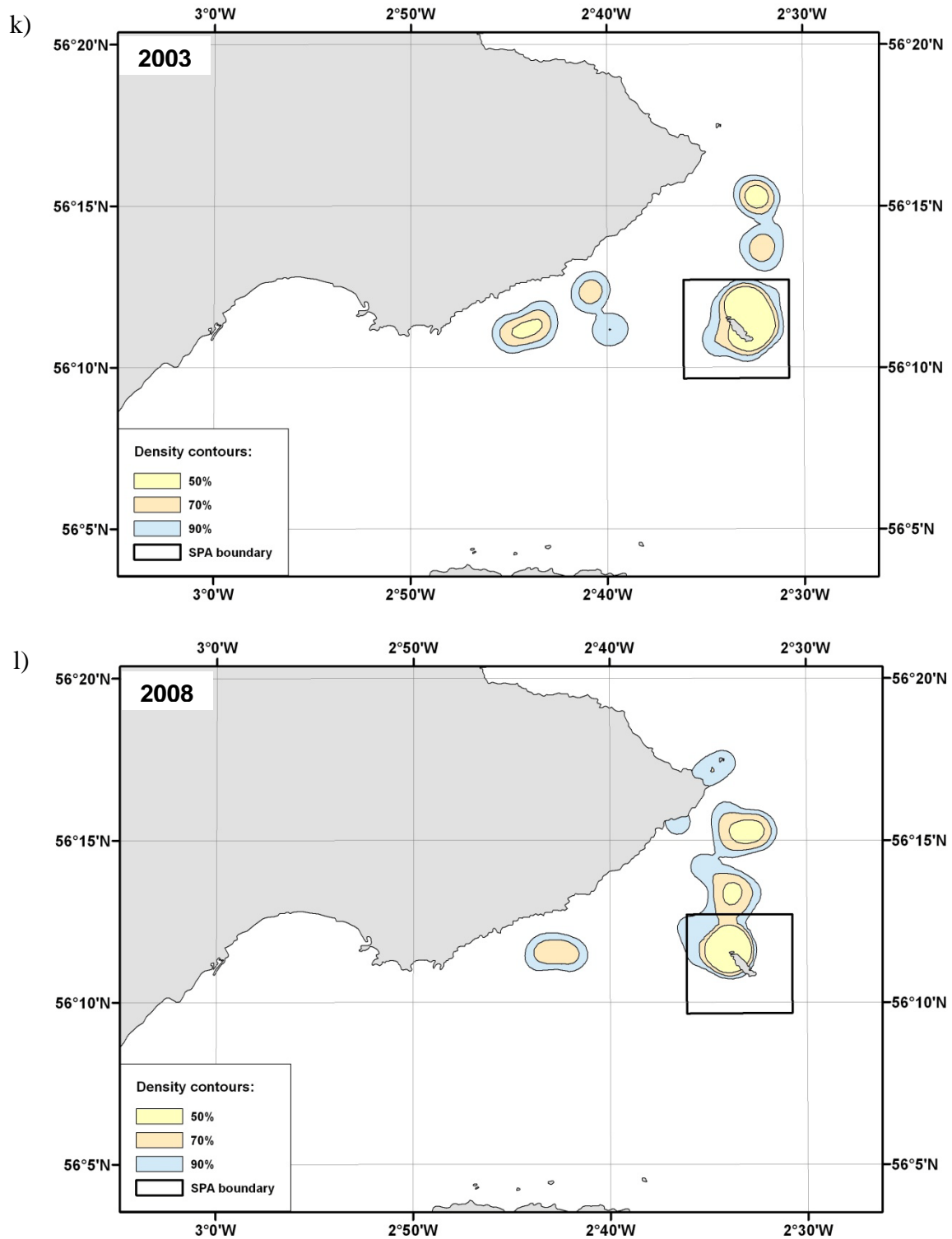
**Figure 2 (cont).** Shag population foraging range in g) 1994; h) 1997; 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.

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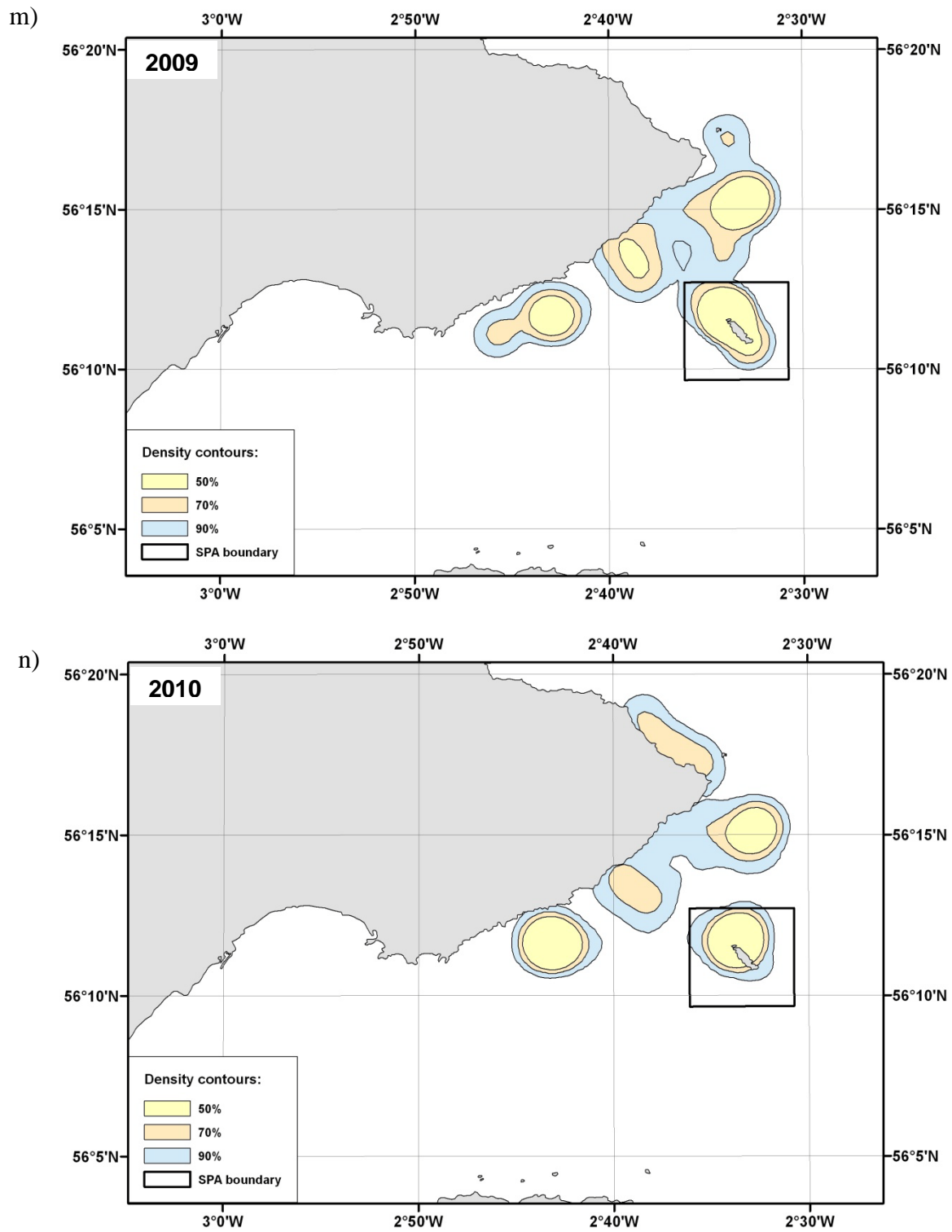
**Figure 2 (cont).** Shag population foraging range in i) 2001; j) 2002; 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.

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**Figure 2 (cont).** Shag population foraging range in k) 2003; l) 2008; 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.

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**Figure 2 (cont).** Shag population foraging range in m) 2009; n) 2010; 50%, 70% and 90% kernel density contours and the current SPA boundary are shown.



**Table 3.** Area (km<sup>2</sup>) of 50%, 70% and 90% kernels in each year and group of years

Year	Area, km <sup>2</sup>		
	50% kernel	70% kernel	90% kernel
1987	18.4	34.1	70.3
1988	22.9	41.4	80.8
1989	10.0	19.9	40.5
1990	19.3	32.1	52.6
1991	15.7	42.1	83.5
1992	86.0	169.7	386.4
1994	10.9	22.8	42.9
1997	10.2	19.7	42.2
2001	14.6	31.0	61.0
2002	9.2	17.5	35.2
2003	13.4	25.1	52.2
2008	14.3	30.2	62.9
2009	19.5	41.8	88.0
2010	14.9	30.9	83.4
1987-2010	29.8	64.4	133.9
2003-2010	23.1	51.4	104.8

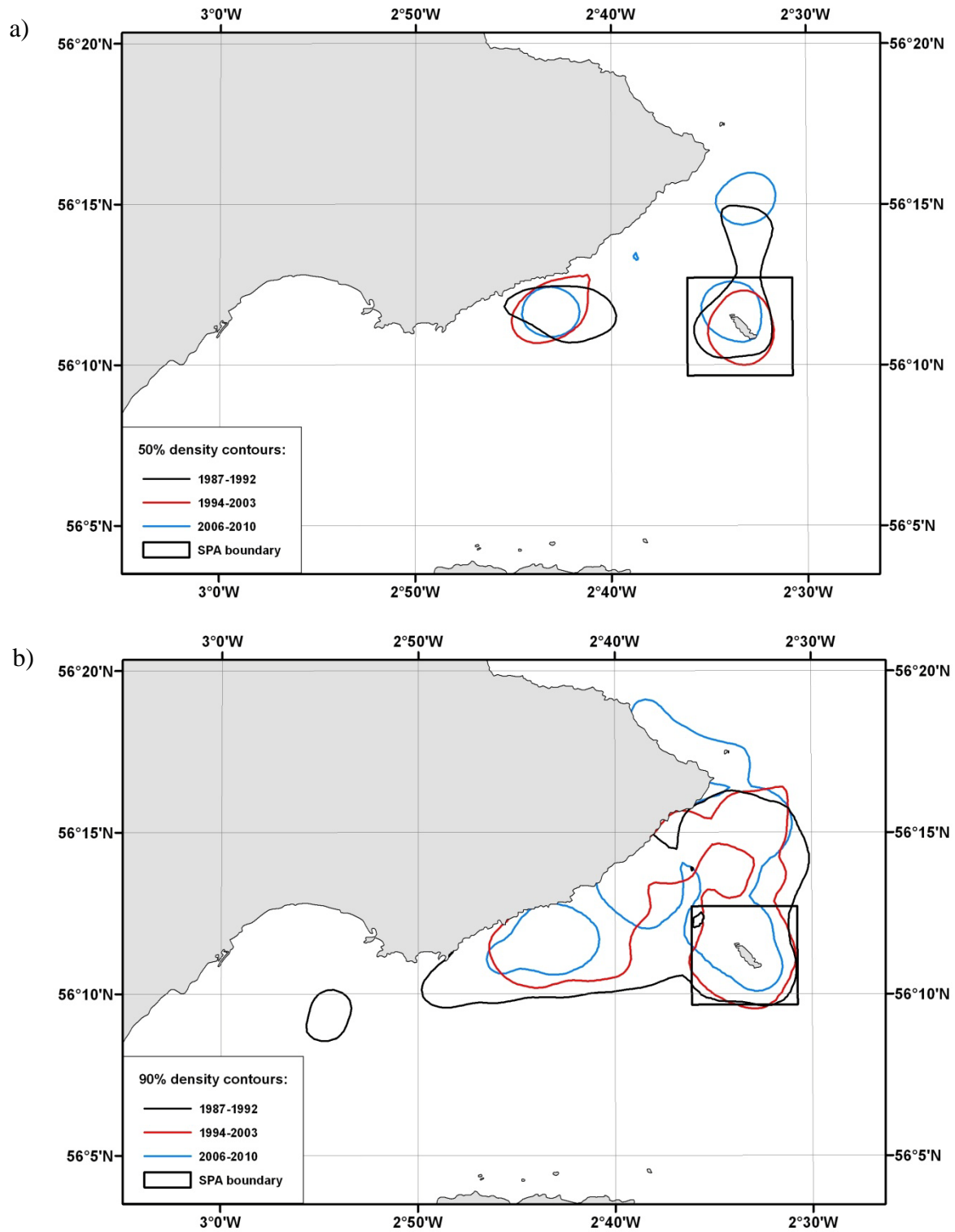
## 2.2.2 Consistency in foraging distribution

Figure 3 illustrates the overlap between the 50% and 90% kernel distributions in the three periods 1987-1992, 1994-2003 and 2006-2010. The percentage overlap estimates are shown in Table 4, and varied from 54%-68%.

<i>50% kernels</i>	1994-2003	2006-2010
1987-1992	64.3	54.3
1994-2003		57.1
<i>90% kernels</i>	1994-2003	2006-2010
1987-1992	74.3	63.0
1994-2003		68.6

**Table 4.** Extent of overlap of 50% and 90% kernels between the three time periods.

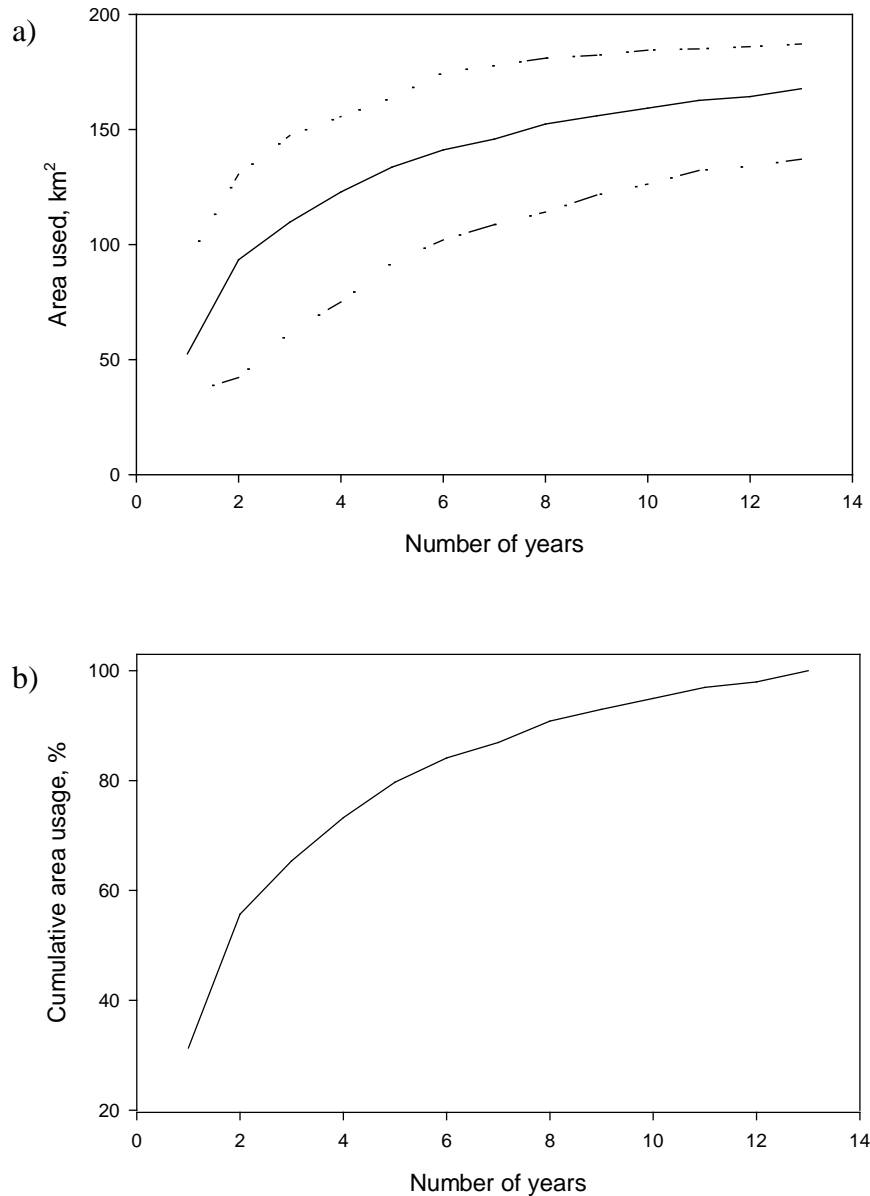
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**Figure 3.** Overlap between a) 50% and b) 90% kernel distributions in the three periods; current SPA boundary also shown.

### 2.2.3 Minimum adequate sample size

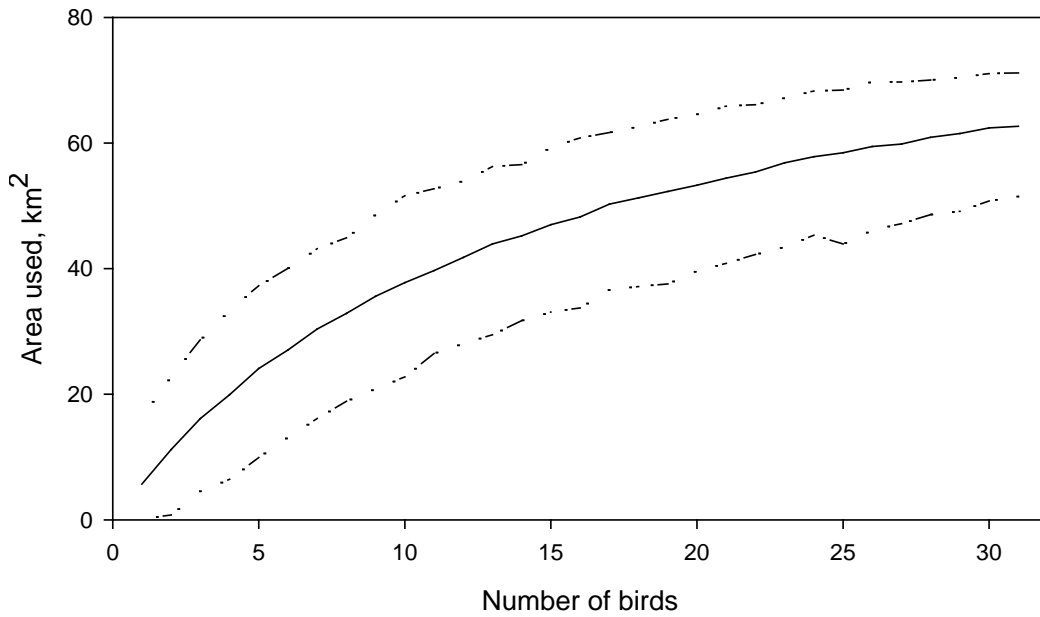
Bootstrap sampling using the 90% kernels from 15 years (excluding 1992) indicated that the cumulative total foraging range showed the expected smooth, non-linear decline in increasing slope, with approximately 8 years required to achieve 90% of the long-term population foraging range (Fig. 4, presented as area used and proportion of the population foraging range).



**Figure 4.** a) area used for each bootstrap sample size (median and 2.5 and 97.5 percentiles); b) as a) but presented as cumulative percentage of the population foraging range.

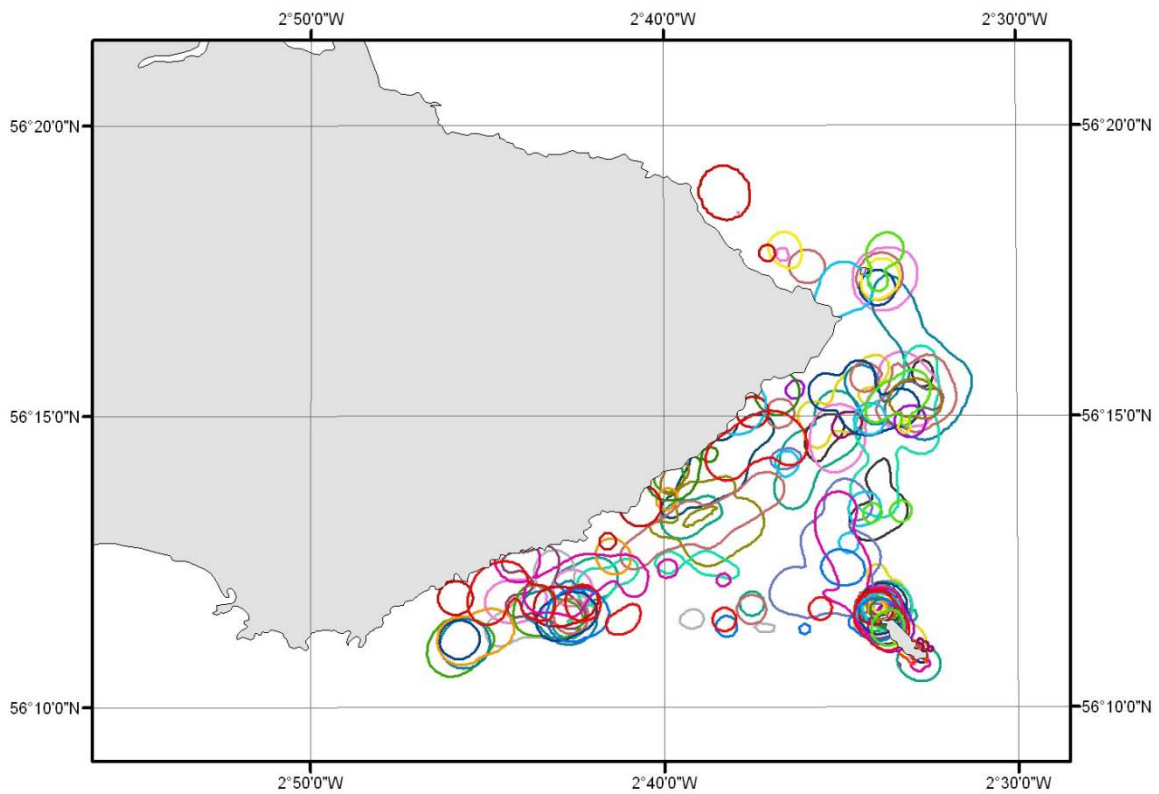
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Bootstrap sampling using the 90% kernels of 31 shags tracked in 2009 indicated that the cumulative total foraging range showed the expected smooth, non-linear decline in increasing slope (Fig. 5).



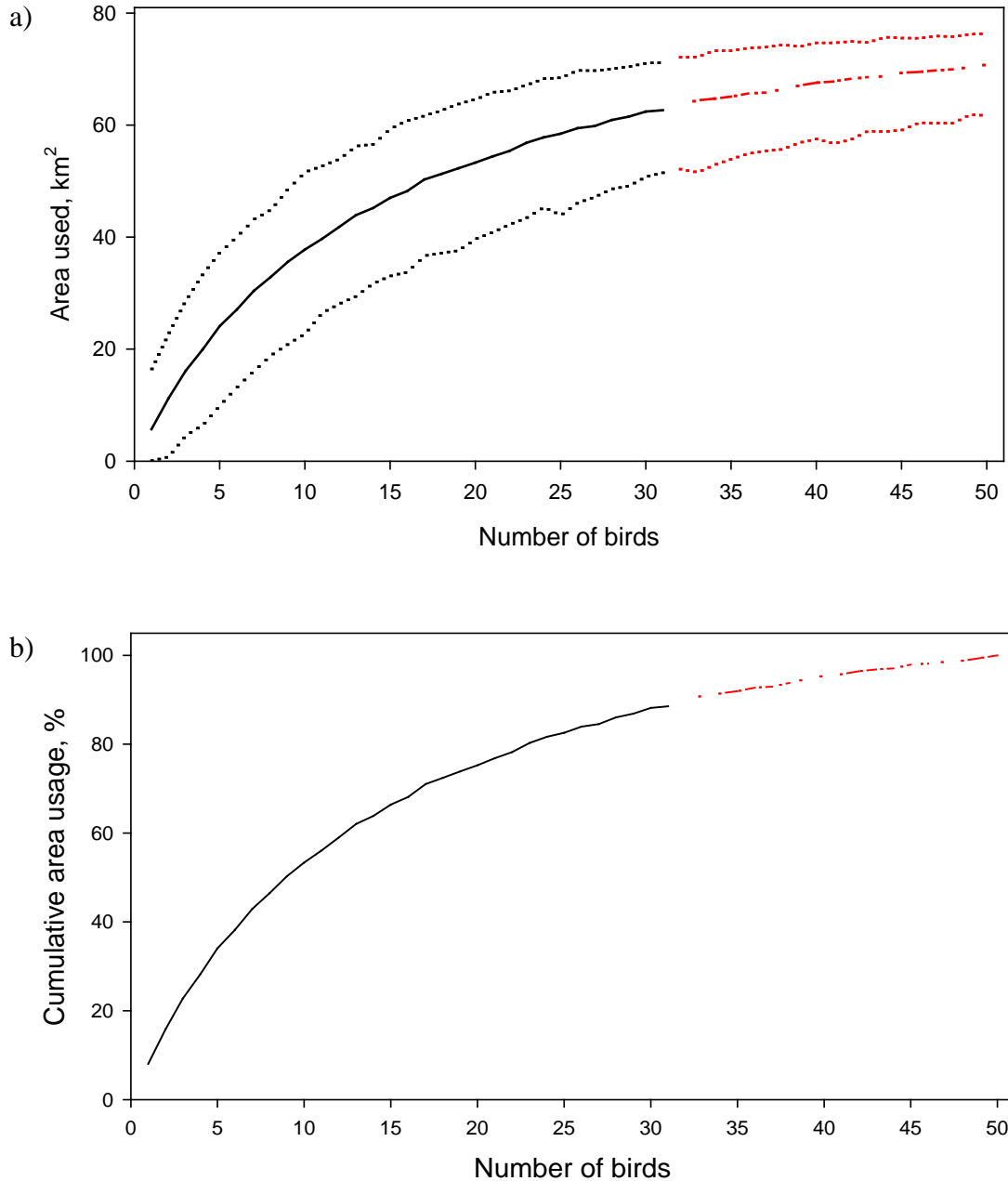
**Figure 5.** Area used (median and 2.5 and 97.5 percentiles) for each bootstrap sample size.

The absence of a clear asymptote in the foraging area estimate reflected the individual variation in shag foraging range which resulted in an incomplete overlap in the foraging area used by different birds (Fig. 6).



**Figure 6.** Individual foraging ranges (90% kernel density contours) of 31 shags tracked in 2009.

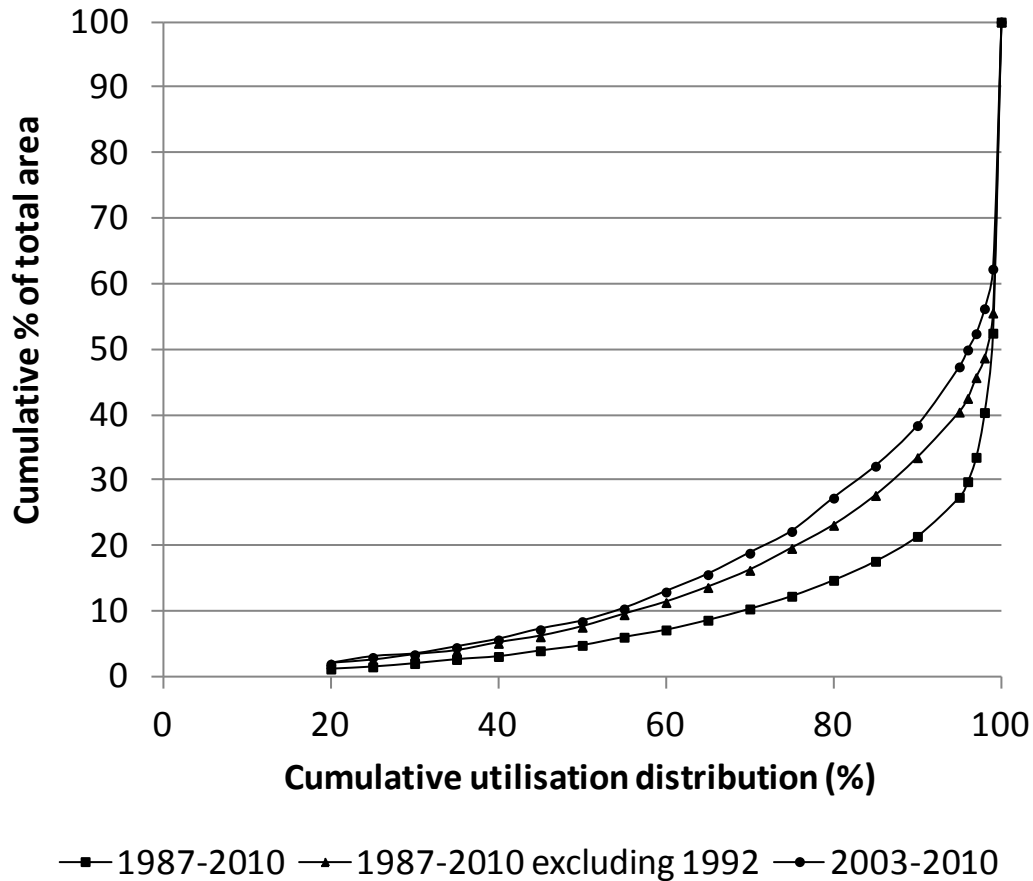
Bootstrap sampling was continued to 50 birds, enabling us to extrapolate the result beyond the actual sample size available. The increase in area used approximately levelled off at a sample size of 45 birds, suggesting that this would be the minimum sample size needed to obtain ~100% the population foraging range in 2009 (Fig. 7a). Converting the area used to proportion of the population foraging range indicated that the sample of 31 birds utilised approximately 90% of the total range over the deployment period in that year (Fig. 7b).



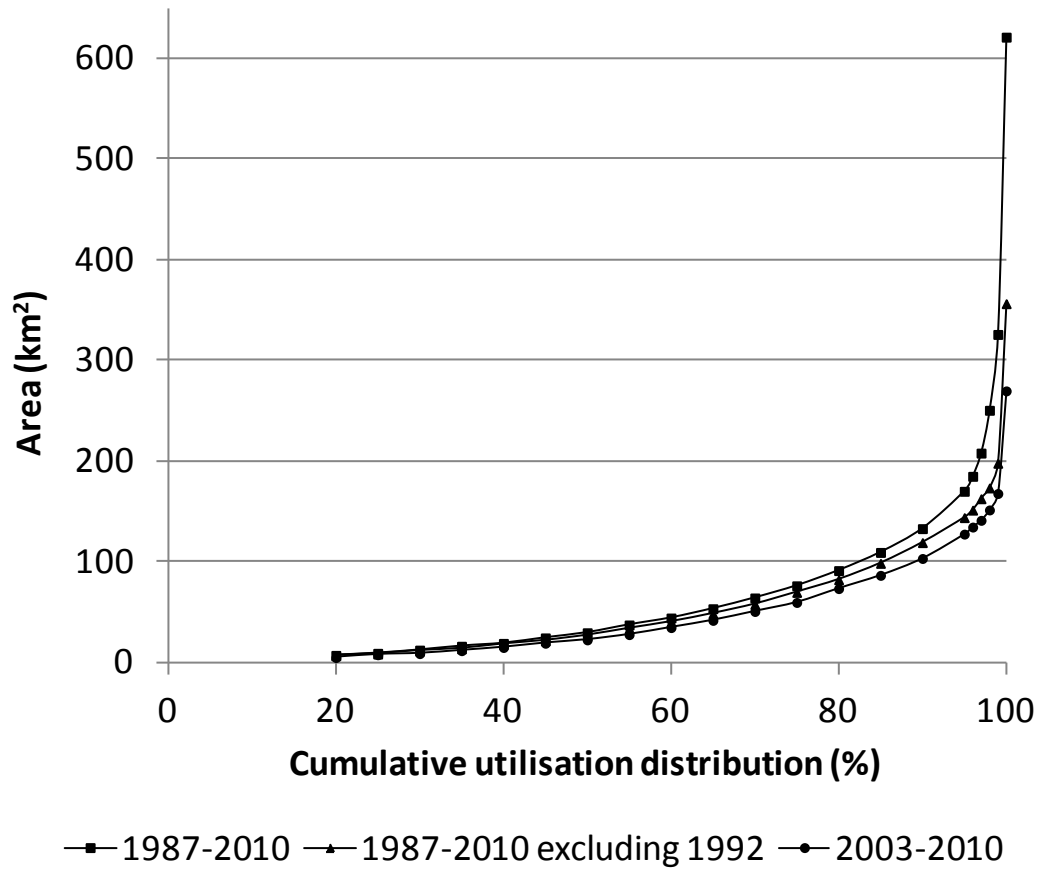
**Figure 7.** a) area used for each bootstrap sample size (median and 2.5 and 97.5 percentiles). Extrapolation beyond the actual sample size of 31 birds is shown with a dashed line; b) as a) but presented as cumulative percentage of the population foraging range (= estimate of area used by 50 birds).

#### 2.2.4 Cumulative utilisation distribution and maximum curvature

The cumulative utilisation distribution curves for the three data sets considered (1987-2010; 1987-2010 excluding 1992; 2003-2010) can be found in Fig 8. A non-linear increase in cumulative proportion is apparent between kernel densities of 20% to 100% which becomes markedly more dramatic between 95% and 99%, and in particular from 99% to 100%. The kernel distributions associated with these plots are shown in Fig 9.

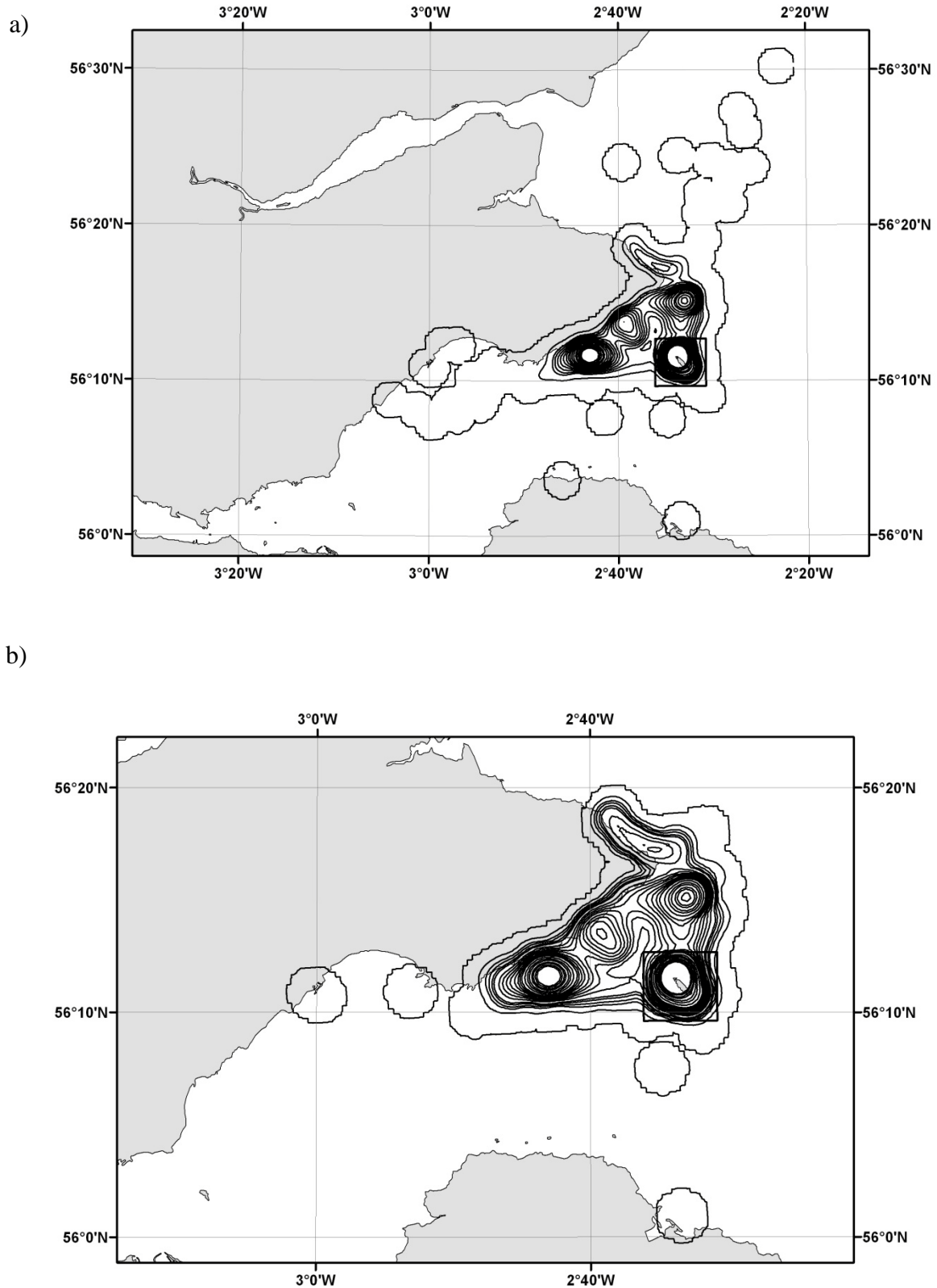


**Figure 8a.** A utilisation plot showing the cumulative % of total area included in each kernel contour at 5% increments from 20% to 95% and 1% increments from 95% to 100% (adapted from Wilson *et al* 2009).



**Figure 8b.** A utilisation plot showing the cumulative area included in each kernel contour at 5% increments from 20% to 95% and 1% increments from 95% to 100% (adapted from Wilson *et al* 2009).

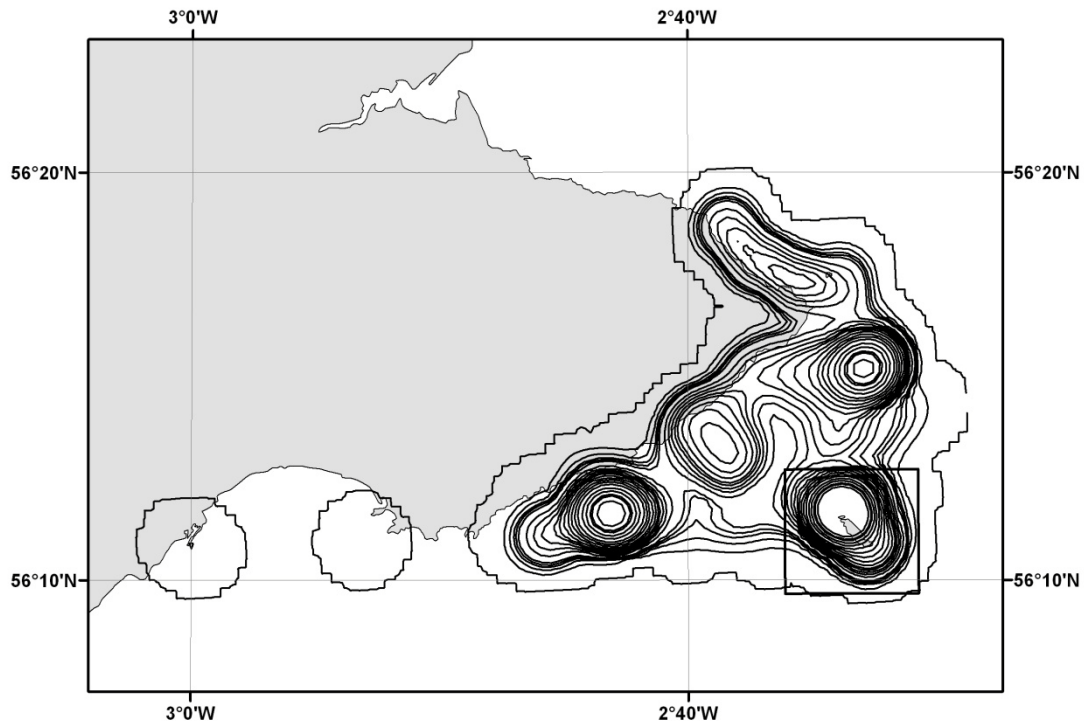
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**Figure 9.** Kernel density distributions (5% increments from 20% to 100% inclusive, following Wilson *et al* 2009) based on data from a) 1987-2010 and b) 1987-2010 excluding 1992.



c)

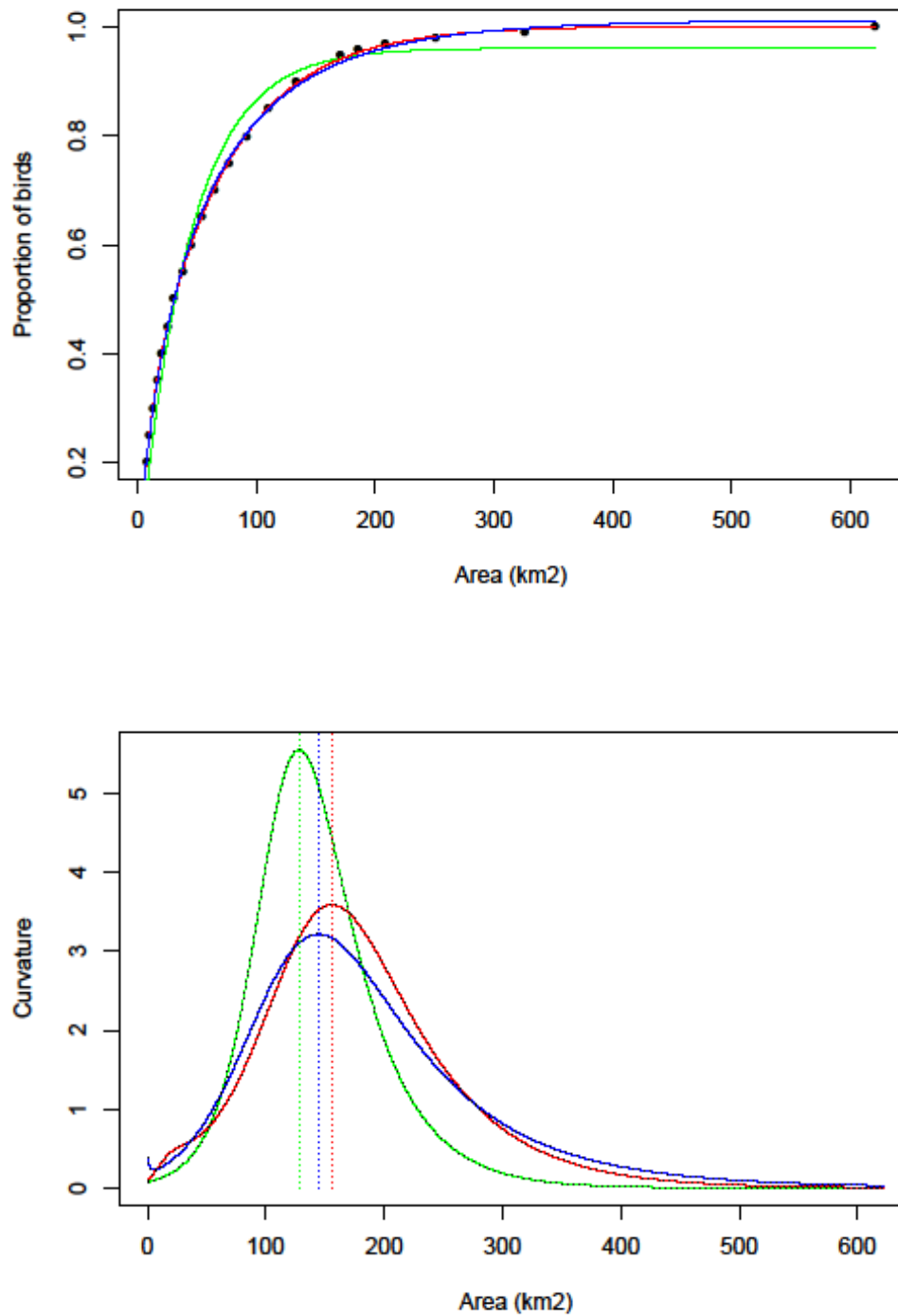


**Figure 9 (cont).** Kernel density distributions (5% increments from 20% to 100% inclusive, following Wilson *et al* 2009) based on data from c) 2003-2010.

All three exponential models that were considered to determine the point of maximum curvature fitted the data well, with double exponential model 1 providing the best fit (Fig. 10a; single exponential model:  $r^2=98.51$ ; double exponential model 1:  $r^2=99.98$ ; double exponential model 2:  $r^2=99.92$ ; though note that  $r$ -squared is not regarded as a particularly meaningful measure of goodness-of-fit for complex non-linear models that do not have an intercept-only model nested within them, and these values should therefore be interpreted with substantial caution; see <https://smtp.biostat.wustl.edu/sympa/biostat/arc/s-news/2007-12/msg00034.html>).

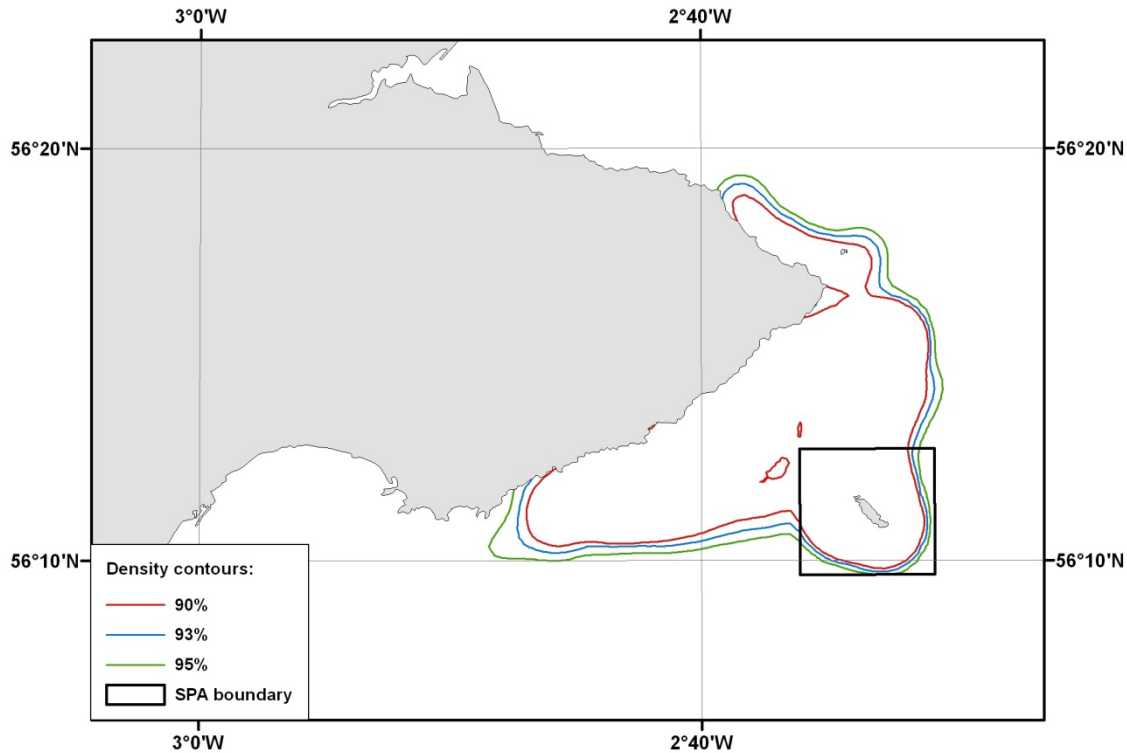
Curvature was at a maximum at an area of  $128\text{km}^2$  and cumulative utilisation distribution of 91% for the single exponential model; equivalent values were  $156\text{km}^2$  and 93% for double exponential model 1 and  $144\text{km}^2$  and 91% for double exponential model 2 (Fig. 10b). The kernel distribution for double exponential model 1 is shown in Fig 11.

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**Figure 10.** Relationship between area used and cumulative utilisation distribution. a) models fitted to the data (green line: single exponential; red line: double exponential 1; blue line: double exponential 2); b) curvature plot for each model with the point of maximum curvature denoted by a vertical line.

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**Figure 11.** Kernel density contours (90%, 93% and 95%) of foraging range of shags breeding on the Isle of May over the whole study period (1987-2010). The intermediate contour of 93% was determined using maximum curvature (see text for details).

## 2.2.5 Habitat association

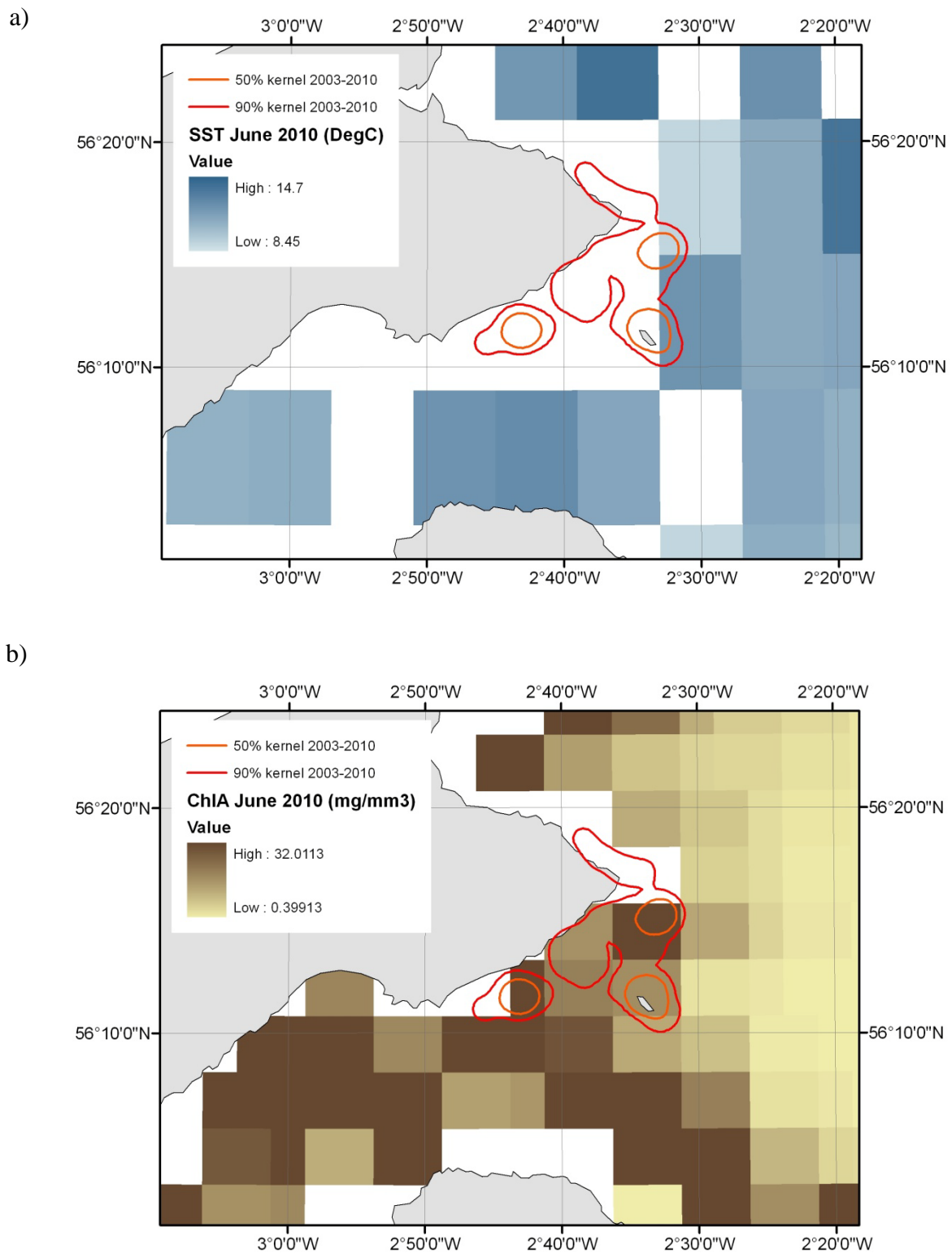
### 2.2.5.1 Habitat overlay

Data for 2010 highlights the difficulty in exploring the relationships between SST or ChlA with shag distributions (Fig 12). Variation is apparent in both variables; however, the low spatial resolution (0.05–0.1°), low temporal resolution (monthly composites) and patchiness of data make comparison with actual and potential foraging range challenging. However, visual examination of these data, and those from earlier years (presented in Bogdanova *et al* 2010) suggest no substantial difference in SST between used and unused areas by shags.

Shags avoided muddy sediments (Fig. 12). This pattern was the strongest habitat association apparent in the data. Sandy sediments are the principal habitat for their main prey species, the lesser sandeel (Wanless *et al* 1997). However, whilst there was evidence that they were selecting sandeel habitats around the island and inshore west of the island, the inshore foraging area north of the Isle of May was primarily located over rocky substrate.

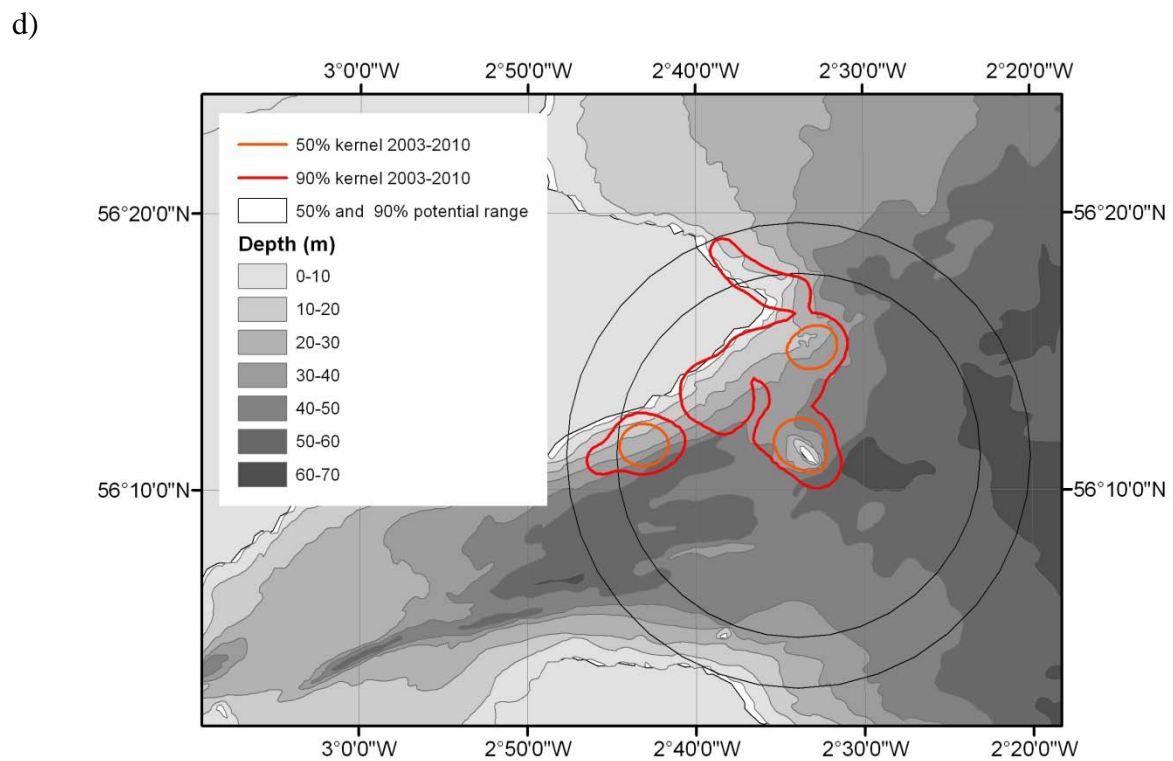
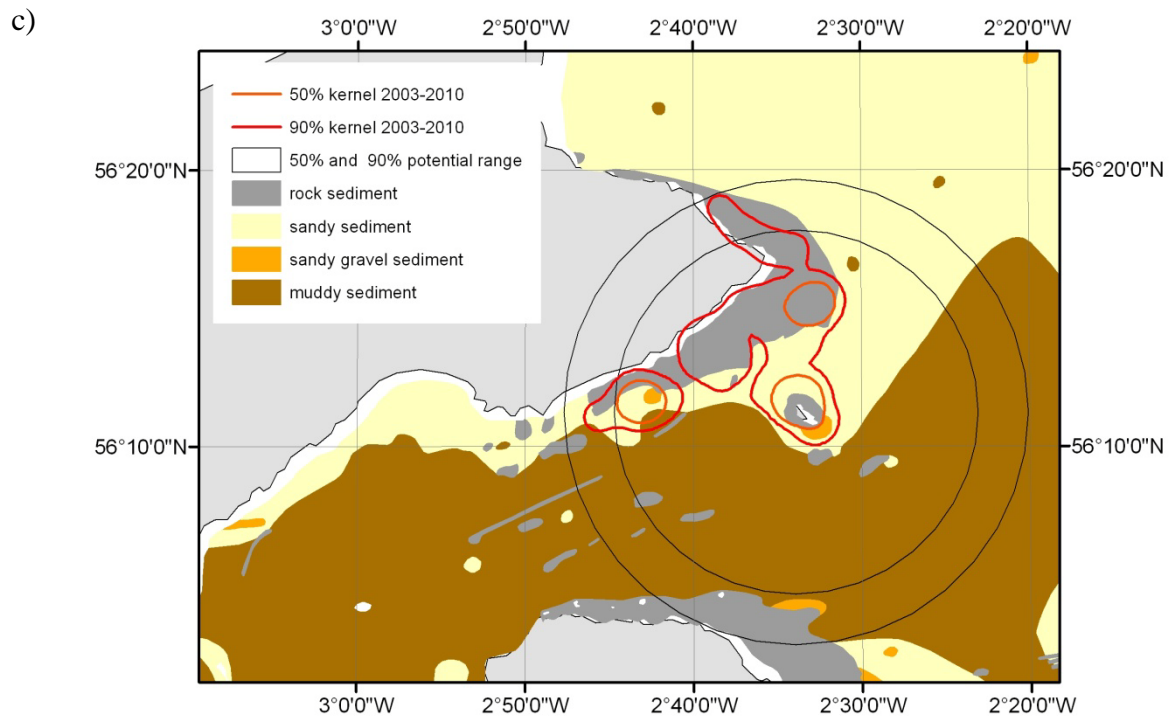
Overall, shags tended to avoid deeper offshore water (>60m). Within the two inshore areas shags foraged primarily at depths of 10-40m, whereas in the area surrounding the Isle of May, particularly south of the island, they also used deeper waters (up to 50m; Fig. 12).

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**Figure 12.** Kernel density distributions (50% and 90% for 2010) in relation to a) June 2010 Sea Surface Temperature and b) June 2010 ChIA concentration.

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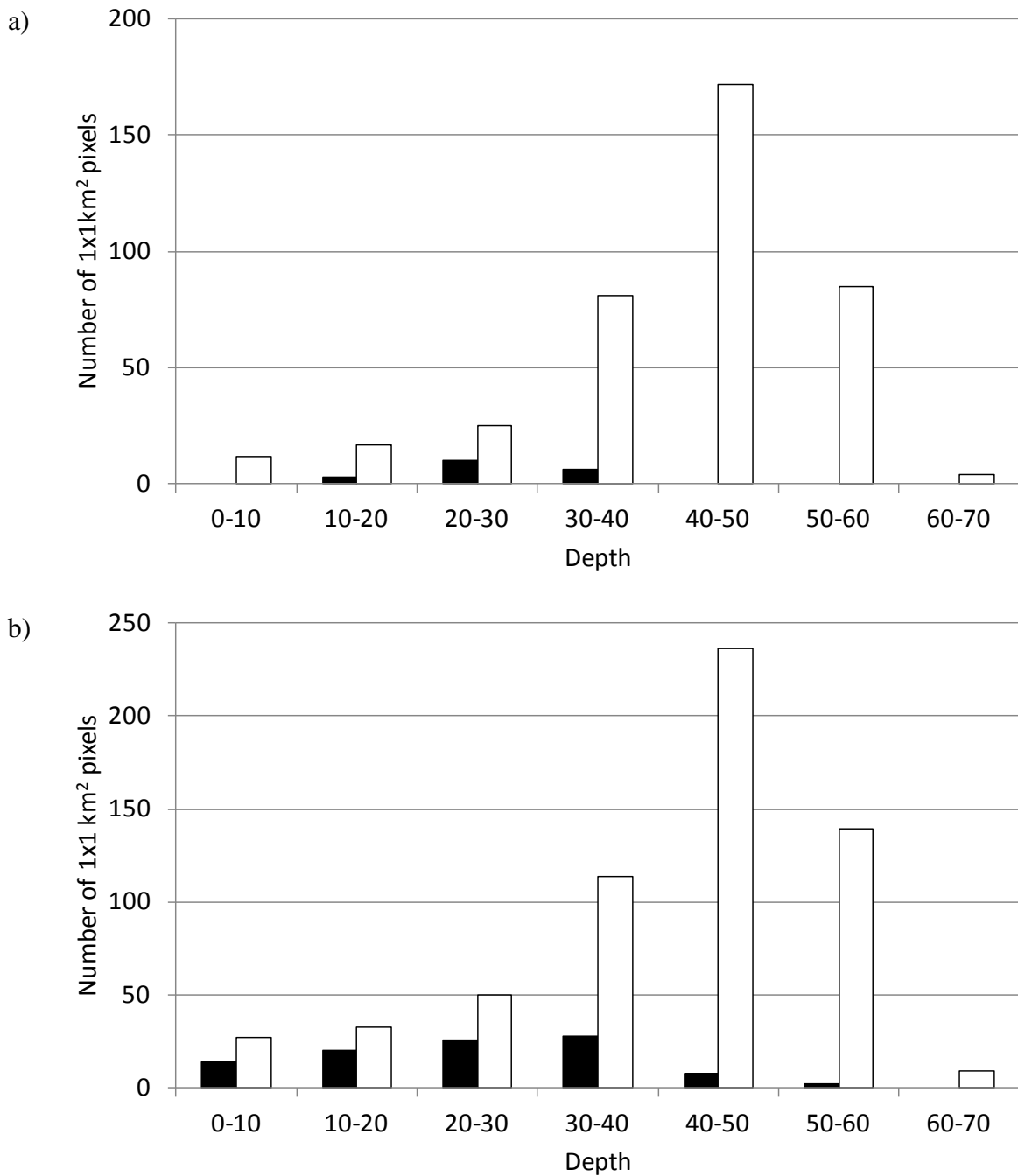
**Figure12 (cont).** Kernel density distributions (50% and 90% for 2003-2010) in relation to c) seabed sediment and d) bathymetry. Potential foraging ranges as set by the 50% and 90% kernels and used in the habitat preference analysis also shown.

### 2.2.5.2 Habitat preference

There was evidence for a preference for shallow water within the potential foraging range (Fig 13; Kolmogorov Smirnov test on distribution across depth bands as depicted in Fig 13; used vs available: 50% kernel:  $\chi^2 = 57.04$ ,  $p < 0.001$ ; 90% kernel:  $\chi^2 = 38.56$ ,  $p < 0.001$ ).

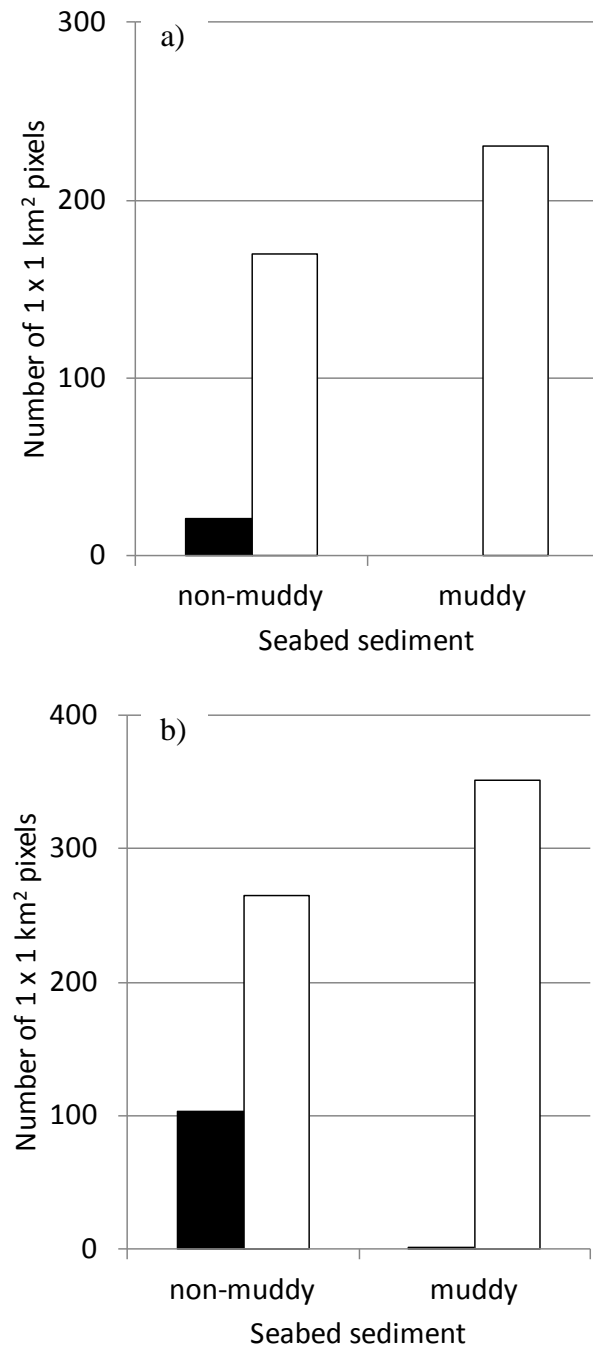
There was strong avoidance (i.e. the opposite of preference) of muddy sediments, with 57% of the potential foraging area comprising muddy habitat but only 1.0% of the area within the 90% kernel comprising this habitat (Fig 14; Fisher's Exact Test on used vs available: 50% kernel:  $p < 0.001$ ; 90% kernel:  $p < 0.001$ ).

These two environmental variables were highly correlated, with muddy sediments found in significantly deeper water than non-muddy sediments (Fig. 15; Kolmogorov Smirnov on distribution across depth bands as depicted in Fig 15 in the two habitats: within potential range as set by 50% kernel:  $\chi^2 = 14.90$ ;  $p < 0.001$ ; within potential range as set by 90% kernel:  $\chi^2 = 10.17$ ;  $p = 0.006$ ). Disentangling correlated variables is challenging. With the avoidance of muddy sediments close to absolute, any additional effect of depth was explored by comparing the distributions of depths used and avoided in non-muddy habitats. In non-muddy areas, shallower depths were preferred (Fig. 16; Kolmogorov Smirnov on distribution across depth bands as depicted in Fig 16; used vs available: 50% kernel:  $\chi^2 = 42.85$ ;  $p < 0.001$ ; 90% kernel:  $\chi^2 = 19.04$ ;  $p < 0.001$ ).



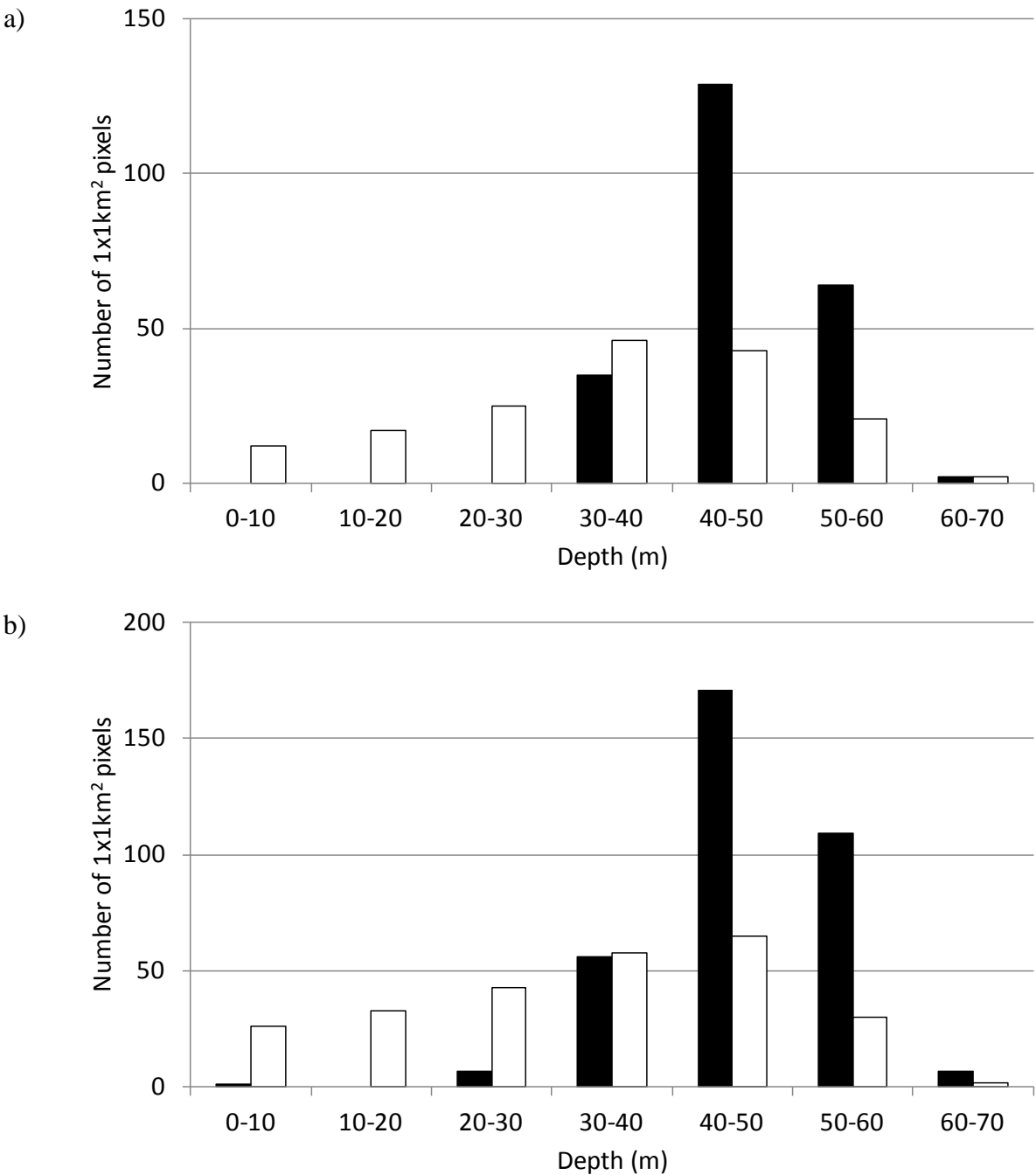
**Figure 13.** Area of each depth class used (closed bars) and available (open bars) for a) the 50% kernel and b) the 90% kernel.

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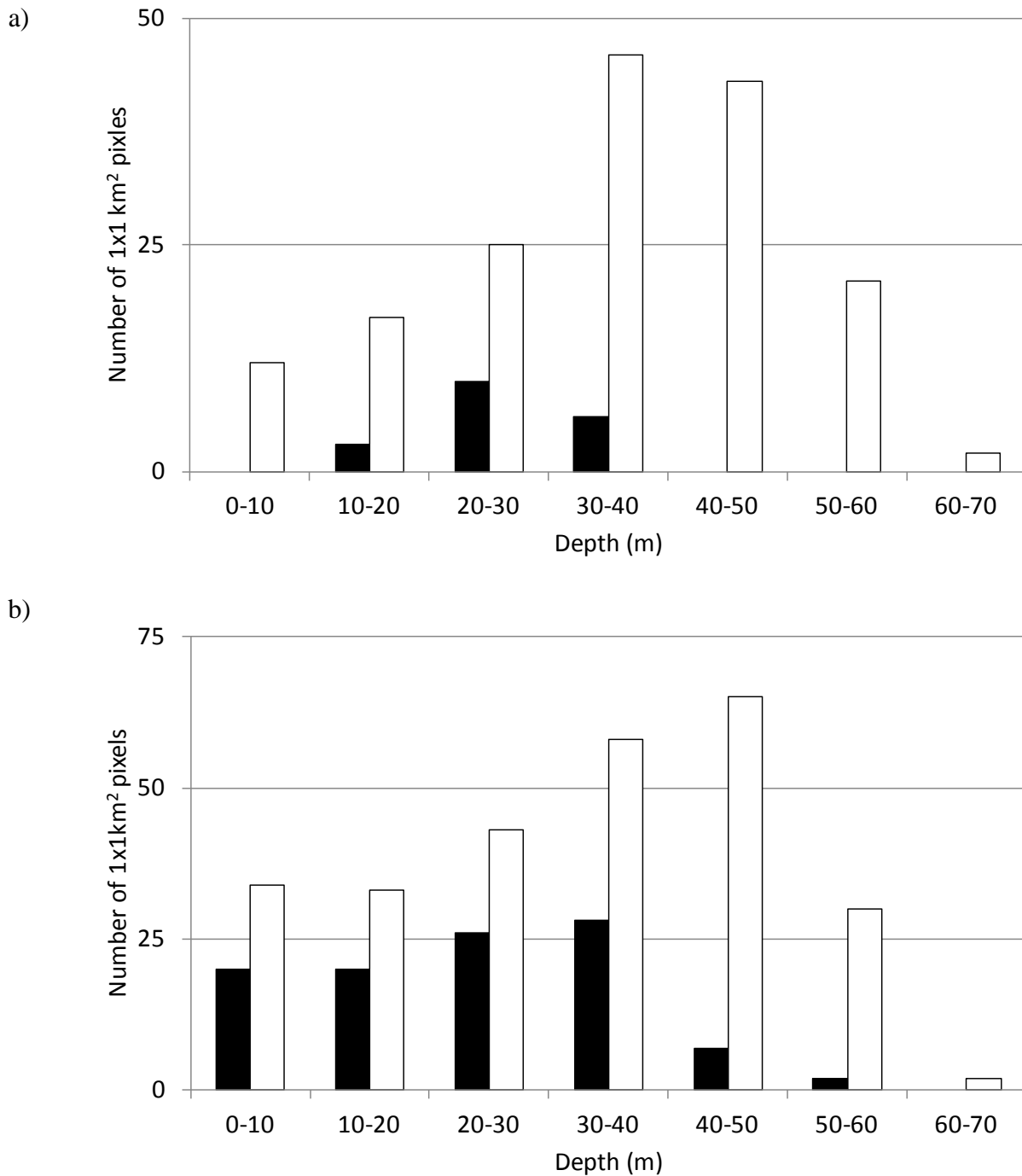


**Figure 14.** Area of non-muddy and muddy sediment used (closed bars) and available (open bars) for a) the 50% kernel and b) the 90% kernel.





**Figure 15.** Area of each depth class comprising muddy sediment (closed bars) and non-muddy sediments (open bars) for a) the 50% kernel and b) the 90% kernel.



**Figure 16.** Area of each depth class comprising non-muddy sediment used (closed bars) and available (open bars) for a) the 50% kernel and b) the 90% kernel.

## 3 Literature review

### 3.1 Introduction

To inform a wider assessment by JNCC and the statutory nature conservation agencies of a possible UK-wide SPA suite for shag towards fulfilment of the obligations of the Birds Directive, a literature review of at-sea area usage by shags in the UK is presented here.

Understanding of at-sea distribution has been reached from two main sources of data: at-sea surveys from ships and animal-borne instrumentation (Wanless *et al* 1993; Stone *et al* 1995). There is a lack of accessible empirical data on precise at-sea locations associated with the SPA network, with the exception of the Isle of May. Because of its coastal distribution, this species has not been adequately surveyed in all areas using at-sea surveys. Furthermore, at-sea surveys are unable to ascertain the origin or status of birds observed, so it is not possible to establish connectivity to the SPA network (Bogdanova *et al* 2010). Animal-borne instrumentation provides an alternative approach that overcomes these two constraints, but has its own limitations: it cannot be undertaken at all colonies, and frequently suffers from small sample sizes resulting in incomplete assessments of population distribution. As a result, few studies have been undertaken using this method, and with the exception of Isle of May, are unpublished and/or only recently collected and therefore not readily available.

Where at-sea distributions are not known in detail, variables linked to at-sea distribution can be explored to provide an indication of likely distribution. Where possible, these can be validated by comparing these variables with known at-sea distributions on the Isle of May.

In this section, we review what is known about at-sea distribution and associated variables for shags in the UK, with special emphasis placed on data associated with the 13 SPAs for this species (Table 5). We then discuss the use of the literature review and Isle of May data to inform potential designations across the SPA network.

**Table 5.** The network of 13 shag SPAs in the UK, and summary of literature on at-sea distribution from ship-based surveys and animal tracking, and diet studies.

SPA	At-sea surveys	Animal tracking	Diet
Buchan Ness to Collieston Coast			
Canna and Sanday			Swann <i>et al.</i> (2008); annual reports to JNCC
East Caithness Cliffs	Kober <i>et al.</i> (2010)		
Fair Isle		RSPB (unpublished)	Harris & Riddiford (1989); annual reports to JNCC
Farne Islands		Richard Bevan (unpublished)	Pearson (1968)
Firth of Forth Islands		Various (reviewed in this report )	Various (reviewed in this report )
Foula			Furness (1982)
Hermaness, Saxa Vord and Valla Field			
Isles of Scilly		RSPB (unpublished)	
Mingulay and Berneray			
Shiant Isles			
St Abb's Head to Fast Castle			
Sule Skerry and Sule Stack			

### 3.2 At-sea distribution and foraging range

Shags are generally found in coastal waters within a few kilometres of land (Wanless & Harris 1993). Ship-based surveys have provided a comprehensive overview of broad scale at-sea distribution, and have demonstrated that this coastal association is apparent throughout the UK (Stone *et al* 1995). Analyses of at-sea survey data have been successful in identifying sufficient concentrations of shags to be considered for

offshore SPA status in the waters off the East Caithness SPA (Kober *et al* 2010). These distributions were found primarily within 2km of colonies (Kober *et al* 2010). Studies off Sumburgh Head identified two important concentrations of shags within 5km of the colony (Wright & Bailey 1993), and studies at North Rona and St Kilda also provided an indication of foraging range of breeders (3km for North Rona, Benn *et al* 1987; 2km for St Kilda, Leaper *et al* 1988). Supporting evidence is available for shags breeding in northern Spain, which foraged within 4km of the breeding colony (Velando *et al* 2005). Overall, these results suggest more restricted foraging ranges at these locations than those recorded on the Isle of May (Wanless *et al* 1991a; Daunt *et al* 2007; Bogdanova *et al* 2010; this report).

Away from the Isle of May, there are no published studies of shag foraging distribution or range using animal-borne instrumentation. A radio-tracking study of shags at North Suter recorded a mean foraging range of 1.5km and maximum of 6.4km (Lynnes 1994). Tracking studies have recently taken place at three SPAs other than the Isle of May: The Farne Islands (Bevan unpublished), Isles of Scillies (RSPB unpublished) and Fair Isle (RSPB unpublished) and at the following colonies that are not SPAs: Muckle Skerry, Orkney; Copinsay, Orkney; Colonsay; Lambay; Puffin Island (RSPB and collaborators, unpublished).

### 3.3 Associated variables

Where data are lacking on at-sea distribution, associated variables can be considered that are informative in assessing the likely distribution of breeding shags around colonies. The following sections review these associated variables. Fundamental amongst these are diet and habitat availability. These two are closely interlinked since prey may be associated with particular habitats; together, they can prove informative of likely foraging distributions in the absence of empirical data on locations.

#### 3.3.1 Diet

The diet of shags in the UK and the rest of northern Europe is dominated by lesser sandeels *Ammodytes marinus* whilst a variety of other species are taken, including Gadidae, Clupeidae and butterfish *Pholis gunnellus* (Wanless & Harris 1997; Velando *et al* 1999). The diet of shags has been studied in detail at three SPAs: The Isle of May, Fair Isle and Canna. The diet of Isle of May shags is dominated by lesser sandeels (Harris & Wanless 1991; Daunt *et al* 2008) but in recent years there has been an increase in species associating with rocky habitats, in particular butterfish (Daunt *et al* 2007; Watanuki *et al* 2008). Diet of shags breeding at Fair Isle is almost completely dominated by lesser sandeels (Harris & Riddiford 1989; Fair Isle annual reports to JNCC, e.g. Shaw *et al* 2007). Lesser sandeels are also important in the diet of shags breeding on Canna (present in 67% of regurgitations, Swann *et al* 2008), but gadoids are also commonly taken (36%). Furness (1982) noted that shags on Foula fed exclusively on sandeels, whereas Pearson (1968) recorded that 99% of total number but only 44% of total weight of prey taken were lesser sandeels.

#### 3.3.2 Dive depth

Foraging depth has been studied in detail using animal-borne instrumentation on the Isle of May (Wanless *et al* 1991b, 1999; Daunt *et al* 2003, 2006; Watanuki *et al* 2005, 2008). These studies show that the majority of shag diving is benthic, to depths typically in the region of 10-40m, though depths of >50m have been recorded. Whilst no dive depth data are published for shags breeding at other SPAs, similar dive distributions have been recorded at Sumburgh Head with a maximum depth of 61m (Wanless *et al* 1997b), and in northern Norway (Barrett & Furness 1990).

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Data from Chausay Islands, northern France, demonstrate that benthic foraging is not universal: Grémillet *et al* (1998) studied depth distribution of shags and found that 44% of trips were pelagic.

### 3.3.3 Habitat association

Away from the Isle of May, there is a paucity of data on habitat association. To our knowledge, the only published example is Wright and Bailey (1993), which reports associations with sandy sediments off the colonies at Sumburgh Head.

### 3.3.4 Habitat availability

In the absence of data on habitat association away from the Isle of May, it is informative to summarise what habitat are available to shags breeding in the SPA network. Following the outcomes of the habitat association modelling in the previous section, we focus on the distribution of seabed sediments and bathymetry within a 15km radius of each SPA (equivalent to the maximum extent of the 90% kernel around the Isle of May).

Table 6 summarises the distribution of seabed sediment around each SPA. Five categories are shown, including one considered suitable for sandeels (sand/gravelly sand); one considered not ideal habitat for sandeels (sandy gravel) and three considered unsuitable for sandeels (gravel, muddy, rock). Table 7 summarises the distribution of bathymetry around each SPA.

**Table 6.** Distribution (%) of seabed sediments in a 15km radius around each SPA.

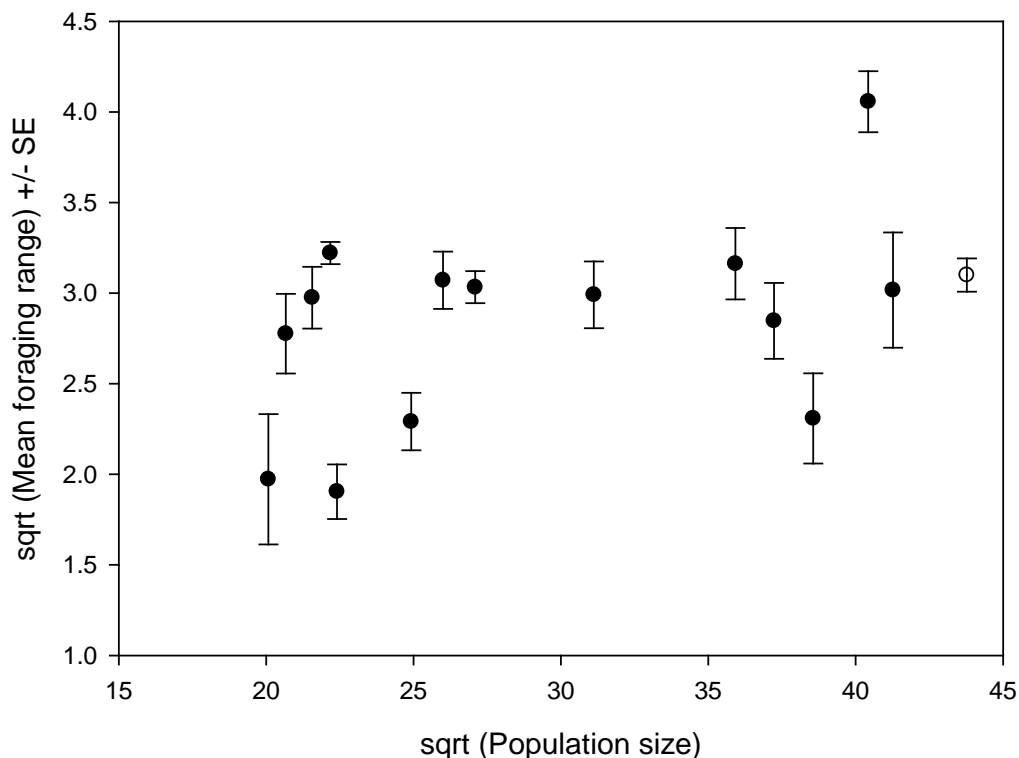
SPA	Sand / gravelly sand	Sandy gravel	Gravel	Muddy	Rock
Buchan Ness to Collieston Coast	98.73	0.00	0.00	1.27	0.00
Canna and Sanday	24.34	8.00	0.00	67.66	0.00
East Caithness Cliffs	71.82	23.16	0.61	0.00	4.41
Fair Isle	31.32	65.83	2.85	0.00	0.00
Farne Islands	33.63	55.22	9.73	0.88	0.53
Firth of Forth Islands	18.37	1.15	0.00	67.67	12.81
Foula	69.38	23.56	0.00	0.00	7.06
Hermaness, Saxa Vord and Valla Field	65.43	33.51	0.71	0.35	0.00
Isles of Scilly	22.24	6.48	0.00	22.24	49.05
Mingulay and Berneray	87.91	11.87	0.00	0.22	0.00
Shiant Isles	22.34	40.15	1.17	36.35	0.00
St Abb's Head to Fast Castle	48.93	4.46	0.00	39.11	7.50
Sule Skerry and Sule Stack	48.59	36.78	0.27	0.00	14.36

**Table 7.** Distribution (%) of bathymetry in a 15km radius around each SPA.

SPA	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	100+
Buchan Ness to Collieston Coast	6.19	7.77	11.08	6.04	7.91	16.69	27.19	14.39	2.73	0.00	0.00
Canna and Sanday	1.33	1.66	7.52	8.08	7.19	5.97	5.86	6.53	13.16	10.51	32.19
East Caithness Cliffs	3.06	4.50	9.42	13.33	22.50	13.92	23.43	9.85	0.00	0.00	0.00
Fair Isle	0.00	0.00	0.00	0.34	1.57	1.91	3.25	11.56	25.59	39.28	16.50
Farne Islands	5.84	10.44	9.38	9.73	14.51	15.75	12.74	16.99	4.60	0.00	0.00
Firth of Forth Islands	16.70	13.62	13.97	18.01	24.69	12.65	0.35	0.00	0.00	0.00	0.00
Foula	0.43	0.22	1.52	3.68	5.74	3.25	5.52	17.64	18.29	24.89	18.83
Hermaness, Saxa Vord and Valla Field	2.75	1.68	2.14	3.06	2.45	3.06	2.75	5.50	10.24	24.92	41.44
Isles of Scilly	2.89	2.19	1.67	1.14	1.05	3.16	8.15	32.87	37.07	9.82	0.00
Mingulay and Berneray	1.90	4.37	13.89	14.89	11.65	9.97	9.85	8.17	5.49	2.02	17.81
Shiant Isles	0.94	1.74	3.08	3.75	6.84	6.97	12.87	14.21	12.06	10.59	26.94
St Abb's Head to Fast Castle	2.00	4.55	6.01	7.65	11.66	23.50	29.51	15.12	0.00	0.00	0.00
Sule Skerry and Sule Stack	0.00	0.00	0.27	1.88	4.17	27.42	17.34	16.53	15.99	14.65	1.75

### 3.3.5 Colony size

It has been demonstrated in northern gannets that there is a positive relationship between colony size and foraging range (Lewis *et al* 2001). Population sizes are known for each of the SPAs in the network. In the absence of colony-specific foraging ranges, the only relationship that can be explored is temporal variation in population size and foraging range on the Isle of May. There was a tendency for foraging range to increase with population size (Fig 17; note data transformations: square root population size to account for area increasing exponentially with range, Lewis *et al* 2001; square root foraging range to ensure model residuals are normally distributed). Thus, the predictive power of population size is low, so there is limited evidence to support the use of colony size to estimate foraging range. However, the possibility cannot be discounted until data from multiple colonies become available.



**Figure 17.** Relationship between square root population size and square root foraging range (not significant,  $p=0.10$ ; see text for details).

### 3.4 Discussion

In summary, there is a paucity of published data on at-sea distributions or associated variables away from the Isle of May. Whilst this is likely to change over the coming years as new animal tracking data are published, there are currently insufficient data to provide concrete recommendations on potential areas of importance at sea for shags breeding at SPAs. The exception to this is the proposed SPA for shags associated with the East Caithness SPA, which has been identified based on concentrations at sea recorded by ship-based surveys (Kober *et al* 2010).

In the absence of direct information on at-sea distributions, indirect measures can be useful in determining areas of likely importance. Typically, the relationship between habitat availability and distribution is then validated where both are available, in this

case the Isle of May. Here, we discuss the potential for using our understanding of shag habitat association and diet at this colony to inform the wider network.

Isle of May shag distributions were most strongly associated with an avoidance of muddy sediments, with birds found primarily in sandy and rocky habitats (Fig 12c; Fig 15). This association ties in closely with their diet, which consists primarily of lesser sandeels and species associated with rocky habitats such as butterfish, and could potentially be used to inform likely important areas for shags at other SPAs. For example, a spatial analysis could be employed to identify all areas within 15km of the SPA which are non-muddy. However, Table 6 shows that only five of the 13 SPAs have >2% muddy habitats within a 15km radius. Thus, this approach could only be taken at these colonies and in the first instance, an examination of the whole Forth Islands SPA would be informative. Fig 18 shows that the amount of potential habitat for shags breeding at Forth Islands other than the Isle of May is quite restricted, since the areas of apparently suitable habitat are smaller than can be found inshore of the Isle of May.

However, diet has not been recorded at these colonies and therefore this approach operates on the assumption that diet is similar to that found on the Isle of May. A study of black-legged kittiwakes *Rissa tridactyla* showed that the diet of those breeding at the inner Forth islands consisted primarily of clupeids, which can be associated with muddy habitats, whereas their counterparts on the Isle of May and Farne Islands were foraging on sandeels (Bull *et al* 2004). This result casts sufficient uncertainty on the assumption of fixed diet across the Forth Islands in shags. It is plausible, given the lack of non-muddy habitats available in the inner Forth islands, that birds from these colonies are foraging on clupeids. Clearly, diet data from these islands would be very informative, but in its absence the approach set out in Fig 18 is unjustified.

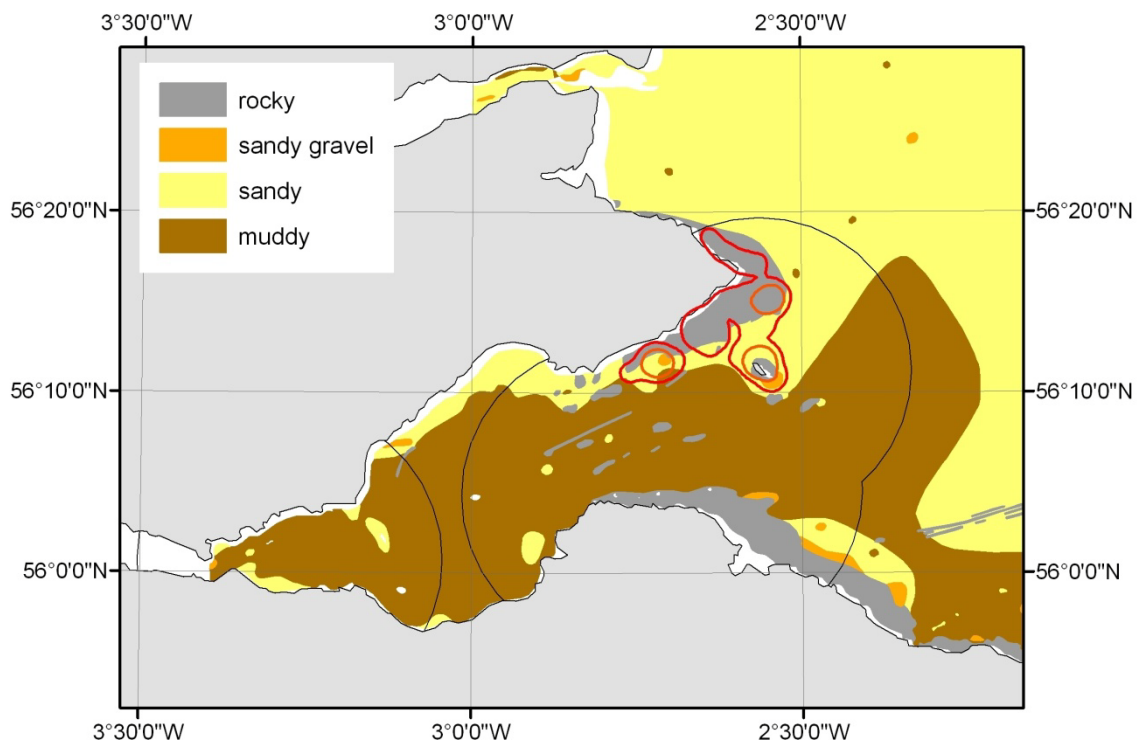
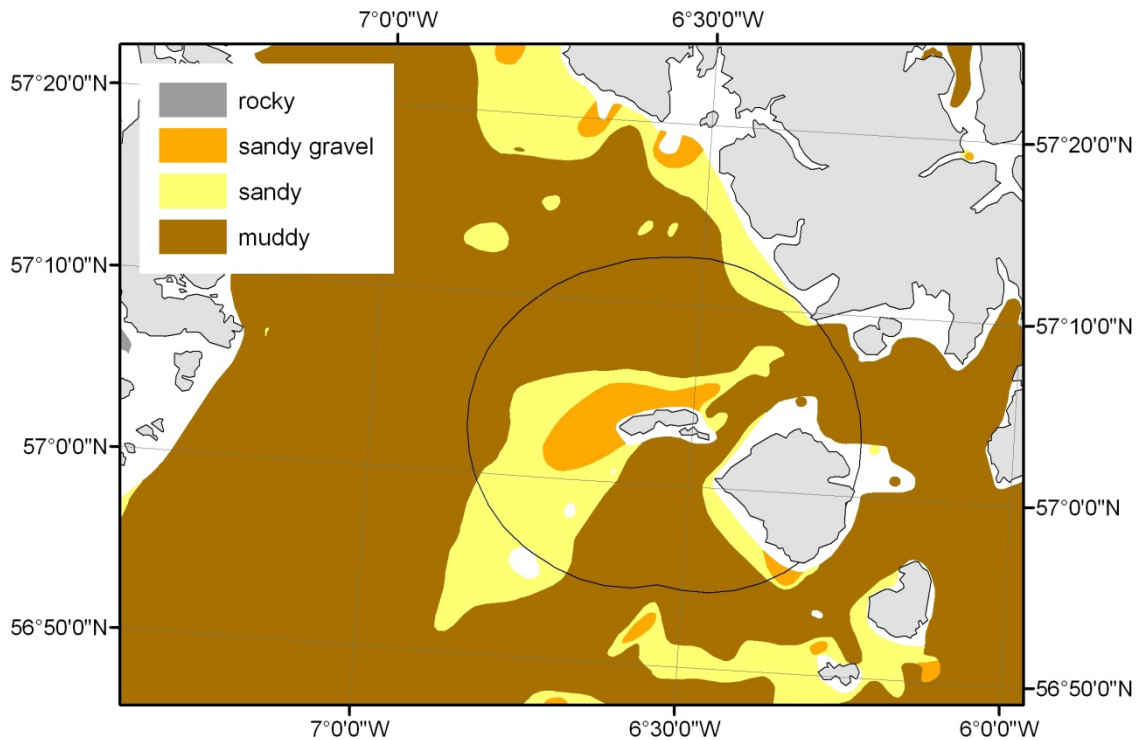


Figure 18. Distribution of seabed sediments around Forth Islands SPA, highlighting the availability of non-muddy habitats within a 15km radius around colonies (shown in black, representing the 90% kernel maximum range). The 2003-2010 50% and 90% kernels for the Isle of May are shown in red.

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A similar assessment can be made for another SPA with significant proportions of muddy habitat within 15km of the colony, Canna and Sanday (Fig 19). At this SPA, diet consists of sandeels and gadoids, and habitat association of all the species within the latter group is not well understood. As such, use of muddy habitats cannot be discounted.

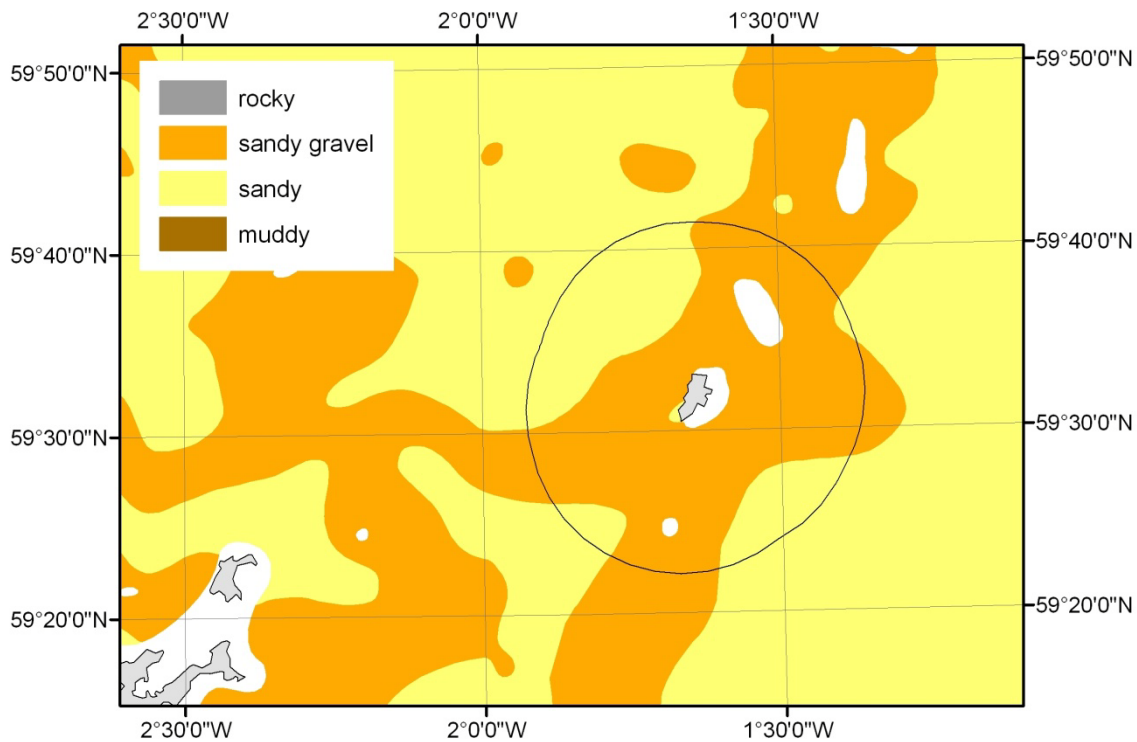


**Figure 19.** Distribution of seabed sediments around Canna and Sanday SPA. 15km radius around colony also shown – see Fig 18 for further details.

The remaining eight SPAs do not contain substantial amounts of muddy habitat within a 15km radius. Thus, the habitat association apparent on the Isle of May cannot readily be used to inform likely distribution. What is commonly found at these colonies is a mosaic of sand/gravelly sand habitat (suitable for sandeels) and sandy gravel (not considered ideal for sandeels). However, it is not possible to be certain that the latter do not contain some sandeels so it would be advisable not to assume that birds were only foraging in the former habitats. A good example to illustrate this is Fair Isle, where the shags are known to specialise on sandeels (Fig 20).



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**Figure 20.** Distribution of seabed sediments around Fair Isle SPA. 15km radius around colony also shown – see Fig 18 for further details.

The same approach could be taken with bathymetry, for which there was evidence for an additional link to shag distribution having accounted for seabed sediment (Fig 16). As is clear from Table 7, the water depths around the SPA network tend to be much deeper than those around the Isle of May. As such, the Forth Islands are somewhat atypical in terms of water depth. It is possible that shags feed benthically at other SPAs. Alternatively, they may feed pelagically, as found in northern France (Grémillet *et al* 1998), and there may be no association with bottom depth. Given these uncertainties, there is little justification to extrapolate from the Isle of May to the SPA network.

There are certain general points that also need to be taken into account when considering habitat association. At the broader scale, the maps will not be completely accurate, and crucially the level of uncertainty is not quantified. In addition, there may be complex fine-scale variation in habitat that these maps do not record. For example, there is some evidence that the rocky habitat frequented by Isle of May shags may have a patchy sediment cover (Thomson 1978) which may explain why it is used even in years where sandeels dominate the diet and species associated with rocky habitats are avoided.

Taken together, the lack of published data from colonies away from the Isle of May and the potential risks of extrapolating from the Isle of May makes assessments of likely distribution of shags across the SPA network extremely challenging. However, important progress can be made when the tacking data from other colonies is published, enabling the representativeness of the Isle of May to be tested formally.

## 4 General discussion

### 4.1 Foraging distribution of shags breeding on the Isle of May

The foraging distribution of European shags breeding on the Isle of May has been studied by CEH using animal borne instrumentation for over two decades, with data available for 16 years over that period. This provides an unrivalled data set for this species. The data show that, over the last two decades, shag core distribution has been concentrated in three main foraging areas: around the Isle of May itself, and two areas inshore of the Isle of May, one to the north (near Fife Ness) and one to the west (near the town of Anstruther). The area around the Isle of May is currently largely protected by the colony extension SPA. The remaining areas are unprotected. Overlap of the 50% and 90% kernel distributions among the three time periods (1987-1992, 1994-2003 and 2006-2010) demonstrated some consistency, with overlaps varying from 54% to 68%. However, it should be noted that there was one year, 1992, which differed markedly from the rest, with a much broader distribution. Although we do not know the reason for the distribution in that year, we have no reason to distrust the data so would advocate its inclusion in analyses.

The multi-year plots that provide an overall distribution across all years (1987-2010) and across the years in which GPS were used (2003-2010) support the above findings. The rationale for a separate multi-year plot for the GPS years was to exclude the lower accuracy fixes obtained from data loggers used prior to the availability of GPS technology. There was little difference between the two plots, largely because although the GPS data were sub-sampled to a frequency equivalent to that obtained from other technologies, a large number of trips were obtained during the GPS years plus foraging range was above average for 2009 and 2010. Alternative analyses are available that incorporate individual and annual effects (e.g. Aarts *et al* 2008) but these were beyond the scope of this report. These analyses would confirm the importance of these three foraging areas used by Isle of May breeding shags; however, the precise location and size of these areas might differ somewhat from those presented here.

With the exception of 2001, all data were collected during chick rearing, hence may not be representative of where the birds forage during other reproductive phases. Typically, foraging range is more extensive during incubation than chick-rearing in seabirds, although there is no evidence for this in shags, with the data from 2001 suggesting no differences in foraging areas used in incubation and chick-rearing. Furthermore, deployment periods were sometimes comparatively short, and in all cases shorter than the typical chick-rearing duration of ca. 50 days (Snow 1960). Foraging range can change dramatically during the breeding season (Wanless *et al* 1988; Daunt *et al* 2007) and short term deployment periods may not capture this variation.

The analyses of minimum adequate sample size of years indicated that approximately 8 years is required to achieve 90% of the long-term population range, which highlights the value of using all available years from this study, not just the GPS years. This finding also has important implications for short-term studies, which typically take place over 1-3 years. The analysis at the individual level for the sample of 31 birds from 2009 indicated that this sample represented ca. 90% of the population range over the deployment period in that year. It is problematic to judge what the implications of this analysis are on the representativeness of years with smaller sample sizes, because one cannot assume that the relationship between sample size and foraging range in 2009 holds in other years. Furthermore, the bootstrapping method is a conservative test (see methods) and had we used the alternative 'simple' approach, or re-calculated population kernel distributions at each step (beyond the scope of this study because of

computing time limitations), a lower sample size would likely have achieved 90% of the population foraging range.

The cumulative utilisation distribution (following Wilson *et al* 2009) showed a non-linear increase in cumulative proportion of total area between kernel densities of 20% to 100%. Maximum curvature from the best fitting double exponential model occurred at an area of 156km<sup>2</sup>, representing 93% of the population. O'Brien *et al* (in press) advocate the use of this metric as an objective criterion for the setting of a boundary of an SPA. We consider that maximum curvature is a useful statistical description of the trade-off between area designated and proportion of the population protected, but that it should not be adopted uncritically as the criterion for boundary setting, for two main reasons. First, we consider it important to establish whether the estimate is sensitive to any issues associated with the underlying data, the level of data smoothing in the kernel analysis (including the effect on the area estimate for 100% of individuals protected, since this approach requires the data to be rescaled to lie between 0 and 1, O'Brien *et al* in press) and the choice of curve. Second, it would be important to establish whether the estimate provides the optimal trade-off that satisfies the conservation goals of the species whilst minimising the area protected. It should not be assumed that this occurs at the point of maximum curvature.

## 4.2 Association with environmental variables

There was no clear evidence that birds were showing a preference for particular sea surface temperatures or primary productivities (see Bogdanova *et al* 2010 for pre-2010 plots). This may result from the low statistical power because of the low resolution of the data. Crucially, however, shags are benthic feeding piscivores (Wanless *et al* 1991b) and will be associating with the distribution of bottom-dwelling fish. There is strong evidence that fish distribution is complex in part because they only spend a proportion of time feeding (when they may associate with e.g. high primary production) and the remainder of the time in other activities such as predator avoidance (where their location may be driven by e.g. benthic habitat, Daunt *et al* 2006). Thus, fish distribution can create a spatial mismatch between oceanography, primary production and the distribution of seabirds (Grémillet *et al* 2008).

Despite these complex, poorly understood factors, the habitat preference analysis suggests a complete avoidance of muddy habitats. The areas used consisted of sandy and rocky habitat. The poor association with sandeel-suitable sediment in the northern inshore area may be because birds do forage in rocky as well as sandy habitats, or because the rocky habitat contains patches of sediment (Thomson 1978) that are suitable for sandeels. Shags fed extensively on species that are found in rocky habitats in 2008 and 2009 (in particular butterfish, Newell *et al* 2008, 2009). However, sandeels predominated in 2003 and 2010 (Wilson *et al* 2003; Newell *et al* 2010), demonstrating that rocky habitats are used even when no species associated with rocky habitats are apparently being taken. Alternative sediment data collected by Marine Scotland (Holland *et al* 2005) suggest that sandeel suitable habitat may be present in the area classed as rocky substrate in the BGS sediment data.

After accounting for association with non-muddy habitats, Isle of May shags showed a preference for shallower water (<50m). This may be due to the costs of foraging in deeper water, or because abundance of prey is higher at shallower depths.

To provide more concrete evidence of an association with particular environmental conditions within their potential foraging range would require spatially referenced mixed models, which was beyond the scope of this report.

### **4.3 Integrating the literature review and Isle of May data to inform the wider SPA network**

A discussion of this can be found in section 3.4. In summary, using findings at one well studied colony to inform other colonies where data are lacking is challenging, since they may differ in a number of different and, crucially, unknown ways. The lack of data from other SPAs and the large differences in habitat availability between the Forth Islands and the wider network make it problematic to provide concrete recommendations on the location of important areas at sea associated with SPAs. Targeted studies (e.g. at the inner Forth Islands) would provide a valuable test of the representativeness of the Isle of May data. In addition, important insights will be gained once the recently collected tracking data from other colonies has been published. Ultimately, an integrated habitat association model using all the available data on shag distributions and associated variables such as diet and habitat availability would provide the most informative outputs for JNCC in their assessment of important areas at sea for this species across the SPA network.

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## 6 References

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. 2008. Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, 31, 140-160
- Barrett, R.T. & Furness, R.W. 1990. The prey and diving depths of seabirds on Hornøy, north Norway, after a decrease in the Barents Sea capelin stocks. *Ornis Scandinavica*, 21, 179-186
- Benn, S., Webb, A., Burton, C.A., Tasker, M.L., Murray, S. & Tharme, A. 1987. Studies of seabirds at North Rona and Sula Sgeir, June 1986. Nature Conservancy Council, CSD Report No 736
- Bogdanova, M., Wanless, S. & Daunt, F. 2010. Pilot analyses of the European shag data in the Firth of Forth SPA. Report to JNCC
- Bull, J., Wanless, S., Elston, D.A., Daunt, F., Lewis, S. & Harris, M.P. 2004. Local-scale variability in the diet of black-legged kittiwakes *Rissa tridactyla*. *Ardea*, 92, 43-52
- Daunt, F., Peters, G., Scott, B., Grémillet, D. & Wanless, S. 2003. Rapid response recorders reveal interplay between marine physics and seabird behaviour. *Marine Ecology Progress Series*, 255, 283-288
- Daunt, F., Wanless, S., Peters, G., Benvenuti, S., Sharples, J., Grémillet, D. & Scott, B. 2006. Impacts of oceanography on the foraging dynamics of seabirds in the North Sea. In: *Top predators in marine ecosystems: their role in monitoring and management*. (eds Boyd, I.L., Wanless, S. & Camphuysen, K.) Cambridge University Press, Cambridge, pp177-190
- Daunt, F., Wanless, S., Harris, M.P., Money, L. & Monaghan, P. 2007. Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology*, 21, 561-567
- Daunt, F., Wanless, S., Greenstreet, S.P.R., Jensen, H., Hamer, K.C. & Harris, M.P. 2008. The impact of the sandeel fishery closure in the northwestern North Sea on seabird food consumption, distribution and productivity. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 362-381
- De Solla, S.R., Bonduriansky, R. & Brooks, R.J. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, 68, 221-234
- Furness, R.W. 1982. Population, breeding biology and diets of seabirds on Foula in 1980. *Seabird*, 6, 5-12
- Grémillet, D., Argentin, G., Schulte, B. & Culik, B.M. 1998. Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? *Ibis*, 140, 113-119
- Grémillet, D., Lewis, S., Drapeau, L., van der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H., Daunt, F., Wanless, S. & Ryan, P.G. 2008. Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and SST to predict marine predator distributions? *Journal of Applied Ecology*, 45, 610-621

Determining important marine areas used by European shag breeding on the Isle of May that might merit consideration as additional SPAs

Harris, M.P. & Riddiford, N.J. 1989. The food of young seabirds on Fair Isle in 1986-88. *Scottish Birds*, 15, 119-125

Harris, M.P. & Wanless, S. 1991. The importance of the lesser sandeel *Ammodytes marinus* in the diet of the Shag *Phalacrocorax aristotelis*. *Ornis Scandinavica*, 22, 375–382

Holland, G.J., Greenstreet, S.P.R., Gibb, I.M., Fraser, H.M. & Robertson, M.R. 2005. Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment. *Marine Ecology Progress Series*, 303, 269-282

Kober, K., Webb, A., Win, I., Lewis, M., O'Brien, S., Wilson, L.J. & Reid, J.B. 2010. An analysis of the numbers and distribution of seabirds within the British Fishery Limit aimed at identifying areas that qualify as possible marine SPAs. JNCC Report No 431. JNCC, Peterborough

Leaper, G.M., Webb, A., Benn, S., Prendergast, H.D.V., Tasker, M.L. & Schofield, R. 1988. Seabird studies around St Kilda, June 1987. Nature Conservancy Council, CSD Report No. 804

Lewis, S., Sherratt, T.N., Hamer, K.C. & Wanless, S. 2001. Evidence for intra-specific competition for food in a pelagic seabird. *Nature*, 412, 816-819

Lynnes, A.S. (1994) Foraging behaviour of the shag *Phalacrocorax aristotelis* in the Moray Firth during chick rearing. Unpublished BSc Honours project, University of Aberdeen

Newell, M., Harris, M.P., Quinn, L., Wanless, S. & Daunt, F. 2008. Isle of May seabird studies in 2008. JNCC Report. JNCC, Peterborough

Newell, M., Harris, M.P., Mackley, E., Wanless, S. & Daunt, F. 2009. Isle of May seabird studies in 2009. JNCC Report. JNCC, Peterborough

Newell, M., Harris, M.P., Skene, A., Wanless, S. & Daunt, F. 2010. Isle of May seabird studies in 2010. JNCC Report. JNCC, Peterborough

Newell, M., Harris, M.P., Skene, A., Wanless, S. & Daunt, F. 2010. Isle of May seabird studies in 2010. JNCC Report. JNCC, Peterborough

O'Brien, S.H., Webb, A., Brewer, M.J. & Reid, J.B. (in press). Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. *Biological Conservation*, doi:10.1016/j.biocon.2011.12.033

Pearson, T.H. 1968. The feeding biology of seabird species breeding on the Farnes Islands. *Journal of Animal Ecology*, 37, 521-552

Pennycuik, C.J. 1997. Actual and 'optimum' flight speeds: field data reassessed. *Journal of Experimental Biology*, 200, 2355-2361

Peters, G. 2005. Data logger deployment. Final report to EU, 'Interactions between the Marine environment, PRedators, and prey: implications for Sustainable Sandeel fisheries (IMPRESS)' (Ed. Camphuysen. C.J.). Appendix 1. 10pp.

Determining important marine areas used by European shag breeding on the Isle of May that might merit consideration as additional SPAs

Ramirez, I., Geraldès, P., Meirinho, A., Amorim, P. & Paiva, V. 2008. Areas importantes para as Aves Marinhas em Portugal. Final report, Project LIFE04NAT/PT/000213. Spea/BirdLife International

Seaman, D.E. & Powell, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075-2085

Shaw, D.N., Davies, S.J. & Breaks, M.T. 2007. Fair Isle seabird studies 2007. JNCC Report. JNCC, Peterborough

Snow, B. 1960. The breeding biology of the shag *Phalacrocorax aristotelis* on the island of Lundy, Bristol Channel. *Ibis*, 102, 554-575

Stone, C.J., Webb, A., Barton, C., Ratcliffe, N., Camphuysen, C.J., Reed, T.C., Tasker, M.L. & Pienkowski, M.W. 1995. An atlas of seabird distribution in North-west European waters. JNCC, Peterborough

Sutherland, W.J., Newton, I. & Green, R. 2004. Bird ecology and conservation: a handbook of techniques. OUP

Swann, R.L., Harris, M.P. & Aiton, D.G. 2008. The diet of European shag *Phalacrocorax aristotelis*, black-legged kittiwake *Rissa tridactyla* and common guillemot *Uria aalge* on Canna during the chick-rearing period 1981-2007. *Seabird*, 21, 44-54

Thomson, M.E. 1978. IGS studies of the geology of the Firth of Forth and its approaches. Institute of Geological Sciences Report 77/17

Velando, A. & Friere, J. 1999. Intercolony and seasonal differences in the breeding diet of European Shag on the Galician coast (NW Spain). *Marine Ecology Progress Series*, 188, 225-236

Velando, A., Munilla, I. & Leyenda, P.M. 2005. Short-term indirect effects of the 'Prestige' oil spill on European shags: changes in availability of shags. *Marine Ecology Progress Series*, 302, 263-274

Wanless, S. & Harris, M.P. 1993. Shag. BWP Update 1: 1-13

Wanless, S., Harris M.P., & Morris J.A. 1991a. Foraging range and feeding locations of shags *Phalacrocorax aristotelis* during chick rearing. *Ibis*, 133, 30-36

Wanless, S., Burger, A.E. & Harris, M.P. 1991b. Diving depth of shags *Phalacrocorax aristotelis* breeding on the Isle of May. *Ibis*, 133, 37-42

Wanless, S., Bacon, P.J., Harris, M.P., Webb, A.D., Greenstreet, S.P.R. & Webb, A. 1997a. Modelling environmental and energetic effects on feeding performance and distribution of shags (*Phalacrocorax aristotelis*): integrating telemetry, geographical information systems, and modelling techniques. *ICES Journal of Marine Science*, 54, 524-544

Wanless, S., Harris, M.P., Burger, M.E. & Buckland, S.T. 1997b. Use of Time-at-depth recorders for estimating depth and diving performance of European Shags. *Journal of Field Ornithology*, 68, 547-561

Wanless, S., Finney, S.K., Harris, M.P. & McCafferty, D.J. 1999. Effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the blue-eyed shag



Determining important marine areas used by European shag breeding on the Isle of May that might merit consideration as additional SPAs

*Phalacrocorax atriceps* and the European shag *P. aristotelis*. Marine Ecology Progress Series, 188, 219-224

Wanless, S., Grémillet, D. & Harris, M.P. 1998. Foraging activity and performance of shags *Phalacrocorax aristotelis* in relation to environmental characteristics. Journal of Avian Biology, 29, 49-54

Wanless, S., Daunt, F., Camphuysen, C.J., Humphreys, E., Scott, B. & Wanless, S. 2005. Setting the scene: seabird foraging behaviour, diet and breeding success. In: Final report to EU, 'Interactions between the Marine environment, PREDators, and prey: implications for Sustainable Sandeel fisheries (IMPRESS)' (Ed. Camphuysen. C.J.) pp88-134

Watanuki, Y., Takahashi, A., Daunt, F., Wanless, S., Harris, M., Sato, K. & Naito, Y. 2005. Regulation of stroke and glide in a foot-propelled avian diver. Journal of Experimental Biology, 208, 2207-2216

Watanuki, Y., Daunt, F., Takahashi, A., Wanless, S. & Sato, K. 2008. Microhabitat use and prey capture of a bottom feeding top predator, the European Shag, shown by camera loggers. Marine Ecology Progress Series, 356, 283-293

Wilson, L.J., Wanless, S., Harris, M.P. & Jones, G. 2003. Isle of May Seabird Studies in 2003. JNCC Report No 362. JNCC, Peterborough

Wilson, L.J., McSorley, C.A., Gray, C.M., Dean, B.J., Dunn, T.E., Webb, A. & Reid, J.B. 2009. Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. Biological Conservation, 142, 1808-1817

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution of home range studies. Ecology, 70, 164-168

Wright, P.J. & Bailey, M.C. 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. SOAFD, Marine Laboratory, Aberdeen. Report No 15/93

Wright, P.J., Jensen, H. & Tuck, I. 2000. The influence of sediment type on the distribution of the lesser sandeel *Ammodytes marinus*. Journal of Sea Research, 44, 243-256