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Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*)

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ABSTRACT

The harbour porpoise is a highly mobile species and thus represents a considerable challenge in the context of using marine protected areas (MPAs) for conservation. The shelf waters off the west coast of Scotland have been identified as an area of year-round presence, high density in comparison to surrounding areas, and a high young to adult ratio in summer and are thus a suitable area for exploring the location of possible special areas of conservations (SACs) under the EU Habitats Directive. We carried out dedicated surveys over three summers in the southern Inner Hebrides and used generalised additive models (GAMs) to predict areas of high relative density for harbour porpoises for each year. After compensating for survey effects, static bathymetric and persistent hydrographic variables were used in a step-wise model selection procedure. In all years harbour porpoise distribution was best explained by maximum tidal current, with higher densities predicted in areas of low current, and the same high density areas predicted year-on-year. Perimeter-to-area ratio was used to identify which areas should be considered as a basis for designating SACs for harbour porpoise in this area, to form part of the Natura 2000 network. The method used here combines spatial modelling and perimeter-to-area ratio for selecting protected areas, a methodology which is suitable for the protection of other animal species.

1. Introduction

Annex II of the EU Habitats Directive lists species of European Community interest whose conservation requires the designation of special areas of conservation (SACs). An SAC is defined as a ‘site of Community importance where necessary measures are applied to maintain, or restore, to a favourable conservation status, the habitats of populations of the species for which the site is designated’ (EU Habitats Directive 92/43/EEC 1992). SACs and special protection areas (SPAs) designated under the birds directive to protect wild birds, collectively form a network of protected sites across Europe called Natura 2000.

Although the protected area is increasingly the tool of choice for conservation, the identification, management and monitoring of protected areas in the marine environment is challenging, especially for highly mobile species such as cetaceans. A good example of a problematic species is the harbour porpoise, listed on Annex II of the Habitats Directive, for which it is difficult to identify sites ‘essential to the life and reproduction’, as specified under the Directive. For harbour porpoises, identification of sites important to the species is especially difficult because their small size and shy nature make them difficult to observe at sea except in calm conditions, also because they are highly mobile and wide ranging. Also, unlike bottlenose dolphins (*Tursiops truncatus*) for which SACs have been more easily identified (Wilson et al., 1997, 1999; Ingram and Rogan, 2002), they have no clearly identifiable markings and are difficult to approach, making it difficult to study individual ranging patterns and area use, which are possible using photo-ID methods. These difficulties have contributed to the very low number of proposed protected areas for harbour porpoises and to date none have been selected in UK waters, which hold a high proportion of the species in Europe (SCANS-II, 2008). An

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ad hoc meeting convened in 2000 by the European Commission (EC (2001) Habitats Committee, Hab. 01/05) concluded that 'it is possible to identify areas representing crucial factors for the life cycle of this species' identifiable by:

- the continuous or regular presence of the species (although subject to seasonal variations),
- good population density (in relation to neighbouring areas),
- high ratios of young to adults during certain periods of the year.

The shelf waters around the Hebrides Islands west of Scotland hold one of the highest densities of harbour porpoises in Europe (SCANS-II, 2008; Evans and Wang, 2008), thus meeting the criterion of 'good population density'. An aerial survey of the Inner Hebrides area in July 2006 also found this area to have a high calf:adult ratio – 10% of all animals sighted in good/moderate sea conditions were calves (SCANS-II, unpublished data). Although year-round data are sparse from this area, harbour porpoises have been recorded in every month of the year (Reid et al., 2003) meeting the 'continuous or regular presence' criterion. Thus, the sea area off the Inner Hebrides is an appropriate region for exploring the location of possible special areas of conservation (SACs) for harbour porpoise according to the *ad hoc* meeting.

The main threat to harbour porpoises within European waters is by-catch in bottom-set gill and tangle net fisheries (ICES, 2008), but there is little by-catch in Hebridean waters (Northridge and Hammond, 1999). However, fish farms are significant sources of anthropogenic pollution in coastal waters of northwest Scotland, both through chemical and faecal pollution and through the noise disturbance caused by the use of acoustic deterrent devices (ADDs) which are deployed to scare seals away from fish farm cages (Parsons et al., 2000b). These devices have been shown to exclude porpoises from areas of potentially important habitat (Johnston, 2002; Olesiuk et al., 2002), and are used extensively on salmon farms throughout the west coast of Scotland (Gordon and Northridge, 2002; Quick et al., 2002).

Other sources of noise may also cause porpoises to be displaced from preferred habitat. Much of the coastal and offshore waters of the west coast of Scotland are used for military training exercises. Every year since 1946, NATO has conducted joint maritime course (JMC) training exercises three times a year (Parsons et al., 2000a). These activities introduce several potential sources of disturbance including increased boat traffic, submarine activity, military jets, and the use of active sonar. There is some evidence for a correlation between decreases in harbour porpoise sightings and the onset of these training exercises which suggests that porpoises may be displaced from the area (Parsons et al., 2000a).

Identifying which particular areas should be protected for a particular species is a major challenge. An approach that is increasingly being used to identify areas that are important to cetaceans and therefore suitable for protection is spatial modelling (Hooker et al., 1999; Cañadas et al., 2005; Notarbartolo-di-Sciara, 2008; Panigada et al., 2008). This technique is already widely used in conservation of terrestrial animals, from vertebrates (Loyn et al., 2001; Suárez-Seoane et al., 2002; Gibson et al., 2004; Rondinini et al., 2005; Dayton and Fitzgerald, 2006; Moilanen and Wintle, 2007; Jensen et al., 2008; Goldberg and Waits, 2009) to invertebrates (Smith et al., 1996; Cabeza et al., 2004; Matern et al., 2007; Steck et al., 2007). Protected areas, including MPAs typically have fixed geographical boundaries (Agardy, 1994; Hooker et al., 1999; Hyrenbach et al., 2000); the results of spatial models based on fixed environmental features are therefore easiest to interpret to inform traditional protected area design. In this context for MPAs, environmental features in the marine environment can be divided into three main categories: (i) static bathymetric; (ii) persistent hydrographic; and (iii) ephemeral hydrographic (Hyrenbach et al., 2000). Optimal protected area design also requires consideration of its size, compactness and cost (Possingham et al., 2000; Leslie et al., 2003; Parnell et al., 2006). These considerations have been shown to be important to the conservation of both marine (Airimé et al., 2003; Leslie et al., 2003; Roberts et al., 2003) and terrestrial animals (Helzer and Jelinski, 1999; Moilanen and Wintle, 2007; Hamaide et al., 2009). One method of optimising protected area design is through minimising the perimeter length to area ratio, both minimising the cost of the reserve in terms of enforcement (Possingham et al., 2000), and resulting in compact reserves with high connectivity (Helzer and Jelinski, 1999; Airimé et al., 2003; Leslie et al., 2003; Roberts et al., 2003; Moilanen and Wintle, 2007; Hamaide et al., 2009).

In this study, we use spatial modelling to predict high-use areas for harbour porpoises that are consistent in time over 3 years of survey in waters around the southern Inner Hebrides based on static bathymetric and persistent hydrographic features with the intention that the results are used to inform the selection of the first SACs for the protection of harbour porpoises in UK waters. Such methodology also has wide applicability to the definition of protected areas for the conservation of other animal species, whether marine or terrestrial.

2. Materials and methods

2.1. Study area

The survey area encompassed the southern Inner Hebrides off the west coast of Scotland (55°18–56°51 N, 5°26′–7°25′W) including all of the coastal islands and water between the Scottish mainland and Skye to the north, Tiree to the west, and Islay to the south (Fig. 1).

2.2. Survey data

Systematic cetacean surveys were carried out on a monthly basis from the Hebridean Whale and Dolphin Trust (HWDT) motor–sailor research vessel, *Silurian,* over three consecutive summers from 2003 to 2005. At least once a month between May and September the study area was surveyed according to a zig-zag type design. Surveys were not designed to achieve strictly equal coverage but aimed to cover the area as evenly as possible over a period of 10 days within the constraints of weather conditions and location of ports (Fig. 2).

The surveys were carried out at an average speed of 6 knots, under motor when winds were low and under sail when winds were sufficiently high. Visual observations were made from the front deck (2 m above sea level) in Beaufort sea state $\leqslant 3$, by teams of trained volunteers under the supervision of an experienced cetacean observer. Two observers positioned on the front deck searched a sector from $-5°$ to $90°$ of the transect line on either side of the vessel by eye or with 7×50 binoculars (Marine Opticron). When any cetaceans were spotted, the species and group size was recorded directly into a computer running the International Fund for Animal Welfare (IFAW) software Logger 2000. Observers switched sides after 30 min, and the watch was changed every hour to avoid observer fatigue.

All survey data were recorded via Logger 2000 to an Access database, automatically recording GPS location every 10 s along with depth, wind speed and direction and boat speed from the vessel's NMEA compatible instruments. Environmental conditions (sea state, swell, visibility, sun glare, and weather conditions) were recorded every 15 min or whenever they changed. Survey effort and engine status, whether it was on or off, were noted whenever they changed.

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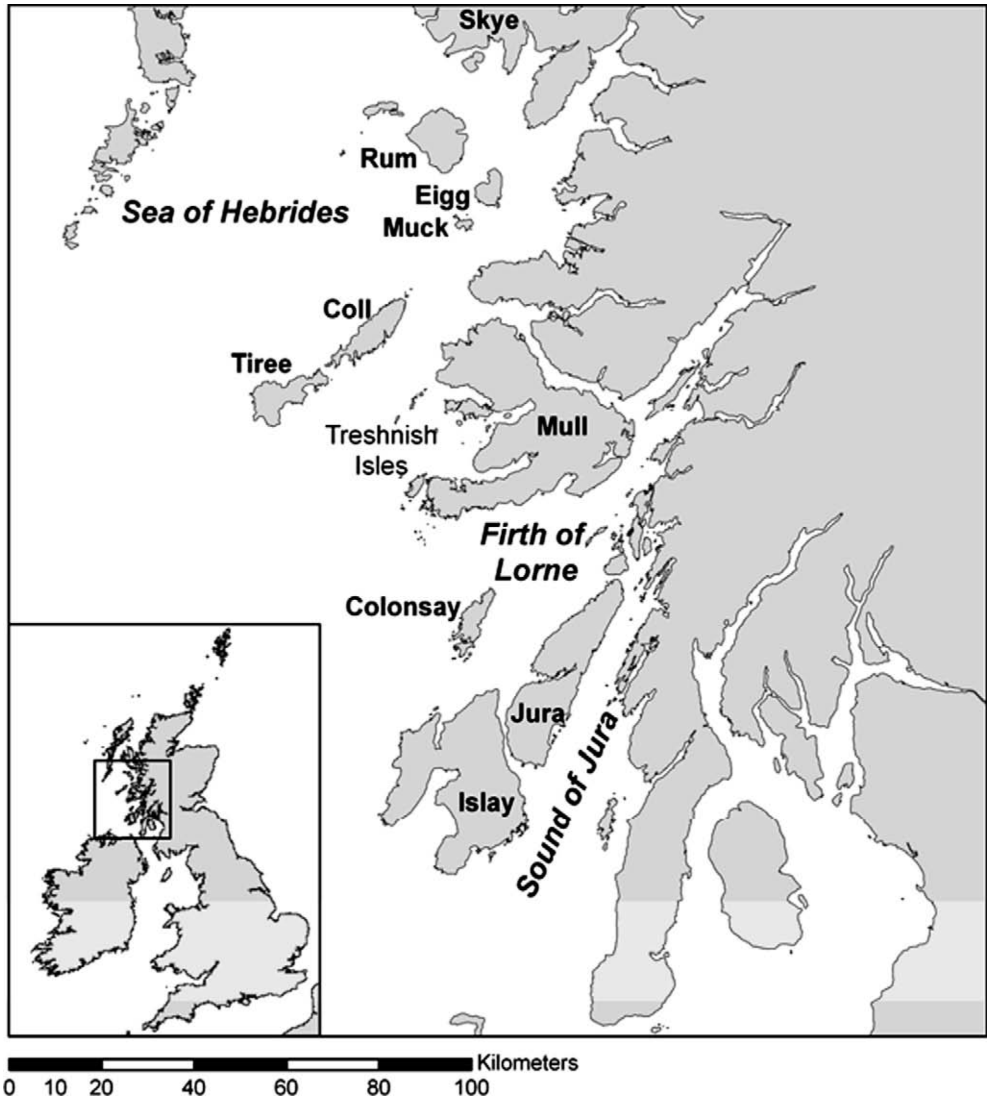

Fig. 1. Map of the survey area in the southern Inner Hebrides, west coast of Scotland, UK.

2.3. Survey variables

Harbour porpoise sighting rates were investigated with respect to three survey variables: sea state, boat speed and engine status. Sea state has previously been shown to have a significant effect on sightings rates of harbour porpoises (Palka, 1996; Barlow et al., 2001; Teilmann, 2003). Boat speed is important to include because bias resulting from random movement of animals increases as the ratio of boat speed to animal speed decreases (Buckland et al., 2001). Harbour porpoises have been shown to respond to survey vessels by moving away from them (Palka and Hammond, 2001). Engine noise is likely to increase this response, so ‘engine on’ was included as a factor variable as a proxy for noise levels resulting from engine noise.

2.4. Environmental variables

A range of environmental predictor variables were available for inclusion in the models including temporal/tidal variables and physical seabed variables. These are described below and listed in Table 1.

Harbour porpoises have been shown to change their surfacing behaviour (Westgate et al., 1995; Otani et al., 1998) and vocalisation behaviour with time of day (Carlström, 2006); time of day was measured as a ratio between the time elapsed since sunrise to the time between sunrise and sunset. Sunrise and sunset times were based on Tobermory (the starting point of all surveys: 56°37′N, 6°4′W) sourced from POLTIPS (version 3.2.4, Proudman Oceanographic Laboratory). This method of calculation compensated for the varying length of day during the survey season.

Tidal variables, such as tidal state, tidal speed or tide height, have an important influence on both the distribution (Marubini et al., 2009), and behaviour (Calderan, 2003; Johnston et al., 2005) of harbour porpoises. Several tidal variables were thus included in the models: temporally varying tidal variables (relative time in the tidal cycle and position in the spring-neap cycle); and spatially varying tidal variables (spring tidal amplitude and maximum tidal current speed). For the temporally varying tidal variables, it was first necessary to determine the closest port to each data point on which to base the tidal data (calculated using ESRI ArcGIS 9.0, based on tidal ports from POLTIPS). To calculate the position of each data point within the spring-neaps tidal cycle (NeapSpring) a ratio was calculated between the actual tidal amplitude (based on the survey date and tidal amplitude for the closest port) and the spring water tidal amplitude in metres for the same port. Tidal state was converted into a continuous index ‘relative time

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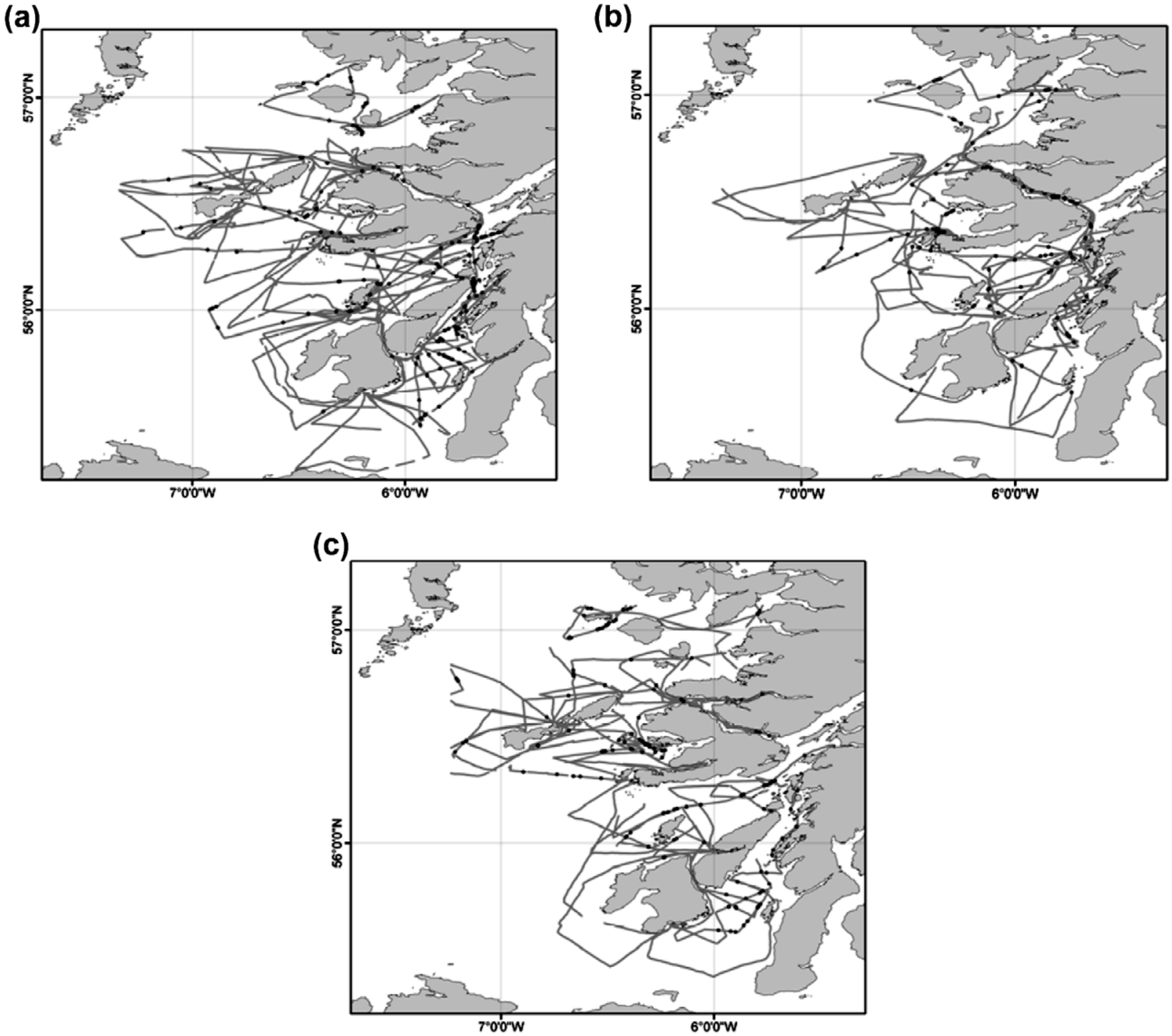

Fig. 2. Survey effort (grey) and harbour porpoise sightings (black dots) for (a) 2003, (b) 2004, and (c) 2005 in the southern Inner Hebrides, Scotland from the HWDT vessel *Silurian*.

in the tidal cycle' from 0 to 1 (TideState), calculated as a ratio between the time elapsed since the last low water to the total time between two low tides. To translate this index into approximate tidal states: 0–0.1 is half of the first low water slack tide; 0.1–0.3 is flood tide; 0.3–0.6 is high water slack tide; 0.6–0.9 is ebb tide; and 0.9–1.0 is the second half of the low water slack tide. For the spatially varying tidal variables, spring water tidal amplitude (STideAmp) and maximum tidal current speed (MaxTideCur) were sourced from the Proudman Oceanographic Laboratory high resolution CS20 model which had a resolution of approximately 1.8 km (see Holt and Proctor, 2008).

Depth and slope have also been shown to be significant predictors of harbour porpoise distributions (Watts and Gaskin, 1985; Read and Westgate, 1997; Raum-Suryan and Harvey, 1998), with porpoises generally found in the deeper water of their range, especially in steep sided canyons (Watts and Gaskin, 1985). In this study, depth and slope were sourced for each data point from the Digibath 250 m resolution bathymetry (version 1.0, BGS), extracted from TINS format using an ArcGIS 9.0 data extraction tool. Sediment type is a good proxy for the distribution of harbour porpoise prey fish such as sandeels and herring (Maravelias, 1999, 2001; Wright et al., 2004). It has been used previously as a proxy for prey distribution in Scottish waters for both grey seals (*Halichoerus grypus*, Aarts et al., 2008) and minke whales (*Balaenoptera acutorostrata*, Macleod et al., 2004). Sediment type was available as categorical data (RSDB codes) describing the different sediments types from the UK Hydrographic Office (2005). These classes were transformed to values for the percentages of mud, gravel and sand in the sediment using the Folk-classification (Folk, 1980).

A lack of available environmental data for inshore areas such as the Sound of Mull, the upper Firth of Lorne and the upper Sound of Jura meant that survey data from these areas could not be included in the analyses.

The coarsest scale for the available environmental data was 1.8 km, so all survey tracks were divided into 2 km segments. Where data were stored within the survey Access database (survey variables), the mean of each variable was determined for each segment, or the most recent value determined (e.g. last recorded sea state) using Access macros. For all environmental variables, values were determined for the mid point of each segment using the STJG GIS extraction tool version 1.0.1 (S. Gontarek, pers. comm.) in ArcGIS 9.0 (ESRI Inc.).

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Table 1
Summary statistics for the environmental variables for the three survey years. Significance of a Mann–Whitney test between 2003 and 2005 (2003 annotated), 2003 and 2004 (2004 annotated), and 2004 and 2005 (2005 annotated), shown as $^{*}p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$. Mean and standard deviation are given where the variables are normally distributed, median and inter quartile range (IQR) are given where the variables are not normally distributed.

	2003	2004	2005
Distance surveyed (km)	2634	1742	1754
Number of 2 km segments analysed	954	607	689
Groups per segment	0.082	0.092	0.125
Boat speed (knots)			
Range	0.5–10.3***	1.2–10.0*	0.8–9.8***
Mean (sd)	5.9 (1.2)	6.0 (1.2)	6.5 (1.0)
Sea state			
Range	0–3	0–3	0–3**
% $\leqslant$1	32%	23%	15%
Engine on/off			
Mean	N/A	0.88	0.89
TimeOfDay			
Range	0.06–0.95	0.10–0.92**	0.12–0.81
Mean (sd)	0.48 (0.20)	0.50 (0.17)	0.48 (0.15)
NeapSpring			
Range	0–2.3***	0–1.2***	0.3–1.4***
Mean (sd)	0.84 (0.36)	0.56 (0.24)	0.76 (0.24)
TideState			
Range	0–1**	0–1	0–1***
Median (IQR)	0.51 (0.25–0.75)	0.46 (0.26–0.72)	0.58 (0.34–0.79)
Depth (m)			
Range	2–208*	7–214	10–182
Mean (sd)	60 (34)	60 (33)	63 (35)
Slope (°)			
Range	0–14	0–22	0–19
Median (IQR)	0.35 (0–0.92)	0.30 (0–0.96)	0.37 (0–1.08)
% Sand			
Range	0–94	0–94***	0–94***
Median (IQR)	63 (43–76)	69 (43–94)	69 (30–76)
% Mud			
Range	0–100**	0–100***	0–100
Median (IQR)	5 (2–30)	5 (4–30)	5 (4–30)
% Gravel			
Range	0–100*	0–100***	0–100*
Median (IQR)	1 (1–55)	1 (1–20)	1 (1–20)
STideAmp (m)			
Range	0.3–2.4***	0.6–2.4***	0.5–2.4
Median (IQR)	1.90 (0.86–2.03)	1.96 (1.85–2.05)	1.96 (1.74–2.15)
MaxTideCur (m/s)			
Range	0–3.1	0–2.6	0–3.1
Median (IQR)	0.45 (0.24–0.66)	0.45 (0.22–0.62)	0.44 (0.26–0.71)

2.5. Modelling

Prior to modelling, a Spearman's rank correlation test was carried out to test for correlations between environmental variables. If there was a significant ($p < 0.05$) moderate correlation ($r > 0.3$) between variables, the first of the variables selected by the stepwise model selection was retained and any variables with which it was correlated were discarded.

Generalised additive models (GAMs) were used to relate the number of groups of porpoises detected per 2 km segment to the survey and environmental variables for each year of survey data. GAMs relate predictor variables to data responses that can be non-normally distributed with non-linear smooth functions, with the general form (as given by Hastie and Tibshirani, 1990):

$$E[y] = g^{-1}\left(\beta_0 + \sum_k S_k(x_k)\right) \tag{1}$$

where $E[y]$ is the expected value of the response variable y (here the number of harbour porpoise groups per 2 km segment), $g()$ is the link function linking the response to the non-linear smooths S of the k predictor variables x_k and the intercept term β_0. The response variable (count) was found not to be overdispersed, so a Poisson distribution was assumed and a log link function used (Wood, 2006a).

The GAMs were fitted in R version 2.3.0 (The R Foundation for Statistical Computing 2006) using the MGCV library (Wood, 2006b), in which the degree of smoothness (or degrees of freedom) of the smooth functions of the predictor variables is determined as part of the model fitting process (Wood, 2006a). The default smoothing spline used in MGCV is a thin plate regression spline (TPRS), which allows a smooth function to be estimated with multiple predictor variables in noisy data, without knowledge of the knot locations (where the different splines join) being required (Wood, 2006a). This method removes the subjectivity that is introduced by estimating knot locations, which is required for other smoothing methods.

In MGCV, the default *dimension* (k = equivalent to setting the maximum number of degrees of freedom for each smooth function) is 10 for single covariate smooth functions. To reduce potential overfitting of smooth functions to the data, two approaches were used. Firstly, as suggested by Kim and Gu (2004), the estimated degrees of freedom in a smooth function were forced to count for 1.4 degrees of freedom in the UnBiased Risk Estimator (UBRE) score (Wood, 2006a, see below), thus penalising the GAM function for using too many degrees of freedom. Secondly, the smooth functions for each of the variables except for time of day, relative time in the tidal cycle, latitude and longitude, were limited to 4 or less estimated degrees of freedom. Responses to time of day and relative time in the tidal cycle could vary sinusoidally; to allow this type of response the degrees of freedom were not restricted to below the default value of 10.

Stepwise addition of survey and environmental variables to the null model (no predictor variables) was carried out (forward stepwise selection), and models compared based on minimising the UBRE score. The UBRE score is the Poisson GAM equivalent of the AIC value, and balances fit with the number of parameters used to describe the model (Wood, 2006a). In selecting the best model, predictor variables were only added if they reduced the AIC equivalent of the UBRE score (multiplying UBRE by sample size, n) by 2 or more, as recommended by Burnham and Anderson (2002). Survey variables (sea state, boat speed, and engine on/off) were added to the model first, to account for changes in detection probability, before adding environmental variables. Latitude and longitude were only considered if the remaining environmental variables were neither significant nor reduced the UBRE score. Longitude can be considered a proxy for distance to mainland.

The final models were used to predict harbour porpoise distribution over a 4 × 4 km grid, set to twice the segment size as recommended by Hedley (2000) for visual comparison between the outputs of the models corresponding to different years and the actual survey data.

2.6. Selecting suitable areas for protection

When considering which areas are suitable for protection, there is a trade-off between maximising the amount of protection for habitat that is important for a species, whilst minimising the cost required to manage a protected area (Possingham et al., 2000). In this study, we used the ratio of perimeter length to area to inform how much area might be protected; the smaller the ratio the greater the clumping and connectivity of selected areas (Leslie et al., 2003; Roberts et al., 2003).

Accordingly, the areas encompassed by the top 1%, 5%, 10%, 25% and 50% of predicted harbour porpoise relative density were calculated and compared over the 3 years. Only areas with

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predicted relative densities above each threshold in all 3 years were included. For each threshold, the perimeter-to-area ratio was calculated and plotted against the corresponding threshold. To obtain confidence intervals around the curve, the survey data was resampled randomly 1000 times, and the GAMs and perimeter-to-area ratio recalculated for each iteration. The threshold at which the perimeter-to-area ratio confidence interval was low, and the ratio levelled off to a relative plateau, thus maximising connectivity whilst minimising area, was used to select those areas suitable for protection.

3. Results

3.1. Survey and area characteristics

A total of 12,094 km was surveyed in the Inner Hebrides off the west coast of Scotland during the summers of 2003, 2004 and 2005; 6130 km were surveyed in Beaufort ⩽3 during which 220 groups of a total of 399 harbour porpoises were detected (Fig. 2). Harbour porpoise detections were distributed fairly evenly over the survey area but were concentrated mainly within coastal areas, with fewer detections in more offshore areas to the west of Islay, Mull, Coll and Tiree (Fig. 2).

There were strong correlations ($r > 0.5$) between spring tidal amplitude and latitude, and between maximum tidal current and the proportion of mud in the sediment. Spring tidal amplitude increased with latitude from virtually nothing (0.25 m) around Islay to a maximum around Skye (2.38 m). The negative correlation between maximum tidal current and the amount of mud in the sediment showed a tendency for more mud in areas of low tidal current. There were several significant moderate correlations ($r > 0.3$) as shown in Table 2. The correlations suggested that high tidal current speeds were associated with a high proportion of gravel in the sediment. Sediment was also correlated with depth, deeper water being associated with a high proportion of mud but a low proportion of gravel in the sediment. In addition, the proportion of mud in the sediment showed a moderate longitudinal gradient, with areas close to the mainland being associated with a higher proportion of mud in the sediment.

3.2. Models

Of the survey variables, sea state was the most important predictor of harbour porpoise detection rate in all models, explaining between 3.2% (2003) and 18.2% (2005) of the deviance (Table 3). Detection rate decreased significantly above sea state 1 (Fig. 3a). Boat speed had an effect on detection rate only in 2003 when it was the most important survey variable explaining 3.7% of the deviance. In this case, detection rate decreased with increasing boat speed (Fig. 3b). Whether the engine was on or off during the survey had not been recorded in 2003, but was a significant predictor of detection rate in 2004, explaining 2.3% of the deviance (Table 3). Unexpectedly, detection rate was higher when the engine was on than when it was off; however the engine was mainly used in low sea states when there was insufficient wind to sail.

Maximum tidal current was the most significant environmental predictor of harbour porpoise detection rate in all 3 years,

Table 2

Spearman's rank correlation coefficient for all significant ($p < 0.05$) correlations between environmental variables, where $^{\dagger}p < 0.05$; $^{\ddagger}p < 0.01$; and $^{*}p < 0.001$. Values shown in bold show strong correlations ($r > 0.5$) and values shown in italics are moderate correlations ($0.5 > r > 0.3$). Abbreviations: Mon = month; Yr = year; Lat = latitude; lon = longitude; Spd = speed; SS = sea state; *T* = time of day; NpSp = position in the spring-neap cycle; TS = relative position in the tidal cycle; Dpt = depth; Slp = slope; San = % sand; Mud = % mud; Gra = % gravel; MTC = maximum tidal current; TA = spring tidal amplitude.

	Mon	Yr	Lat	Lon	Spd	SS	*T*	NpSp	TS	Dpt	Slp	San	Mud	Gra	MTC
Yr	0.14^{*}														
Lat	0.26^{*}	0.13^{*}													
Lon	NS	NS	*-0.33^{*}*												
Spd	NS	0.22^{*}	$-0.06^{\ddagger}$	NS											
SS	-0.13^{*}	NS	NS	$0.07^{\ddagger}$	$-0.05^{\dagger}$										
T	-0.10^{*}	NS	NS	$-0.07^{\ddagger}$	0.07^{*}	-0.10^{*}									
NpSp	*0.38^{*}*	-0.14^{*}	NS	NS	NS	$0.06^{\ddagger}$	NS								
TS	$0.06^{\ddagger}$	$0.05^{\dagger}$	NS	NS	NS	NS	-0.17^{*}	$-0.07^{\ddagger}$							
Dpt	NS	$0.04^{\dagger}$	$0.07^{\ddagger}$	$0.06^{\ddagger}$	NS	NS	NS	-0.09^{*}	$0.06^{\ddagger}$						
Slp	$0.05^{\dagger}$	NS	0.14^{*}	0.12^{*}	NS	NS	NS	NS	NS	0.14^{*}					
San	NS	NS	-0.12^{*}	NS	NS	NS	NS	NS	$0.05^{\dagger}$	-0.08^{*}	-0.10^{*}				
Mud	0.08^{*}	0.08^{*}	0.21^{*}	*0.35^{*}*	$-0.06^{\ddagger}$	NS	0.07^{*}	NS	NS	*0.43^{*}*	0.14^{*}	$-0.05^{\dagger}$			
Gra	$-0.07^{\ddagger}$	$-0.06^{\ddagger}$	-0.11^{*}	-0.25^{*}	$0.06^{\ddagger}$	NS	$-0.07^{\ddagger}$	$-0.05^{\dagger}$	$-0.06^{\ddagger}$	-0.35^{*}	NS	*-0.35^{*}*	**-0.86^{*}**		
MTC	-0.14^{*}	NS	-0.22^{*}	*-0.47^{*}*	$0.07^{\ddagger}$	NS	NS	NS	NS	-0.16^{*}	-0.18^{*}	NS	**-0.52^{*}**	*0.35^{*}*	
TA	0.25^{*}	0.13^{*}	**0.93^{*}**	-0.11^{*}	$-0.04^{\dagger}$	NS	NS	NS	NS	NS	0.15^{*}	-0.07^{*}	0.26^{*}	-0.16^{*}	-0.28^{*}

Table 3

Results of forward GAM model selection of the number of harbour porpoise groups per 2 km segment for 2003–2005. Variables are shown in order of importance, first compensating for survey effects (sea state, boat speed and engine on/off). Smooths are shown with the number of degrees of freedom in parentheses. UBRE_{Δ} is the reduction in UBRE score caused by the addition of the variable to the model, with the first UBRE score in bold showing the starting UBRE score. AIC_{eq} is the equivalent reduction in AIC, calculated by multiplying UBRE by the sample size *n*. *n* is 714 for 2003, 455 for 2004, and 516 for 2005.

Order	2003				2004				2005			
	Smooth (d.f.)	% Dev	UBRE_{Δ}	AIC_{eq}	Smooth (d.f.)	% Dev	UBRE_{Δ}	AIC_{eq}	Smooth (d.f.)	% Dev	UBRE_{Δ}	AIC_{eq}
1	s(Speed, 2.6)	3.7	**−0.5472**		s(SeaState, 1)	9.9	**−0.5346**		s(SeaState, 3.6)	18.2	**−0.5596**	
2	s(SeaState, 1)	+3.2	−0.0108	−8.0	factor(EngOn)	+2.3	−0.0054	−2.5	s(MTidCur, 1)	+2.7	−0.0092	−4.7
3	s(MTidCur, 1)	+9.0	−0.0361	−25.8	s(MTidCur, 1.6)	+7.9	−0.0298	−13.6				
4	s(NeapSpr, 1)	+6.3	−0.0210	−15.0	s(NeapSpr, 1)	+5.6	−0.0157	−7.2				
5	s(TideSt, 5.5)	+8.9	−0.0166	−11.9								
6	s(Lon, 1)	+1.0	−0.0033	−2.3								
Total		32.1				25.7				20.9		

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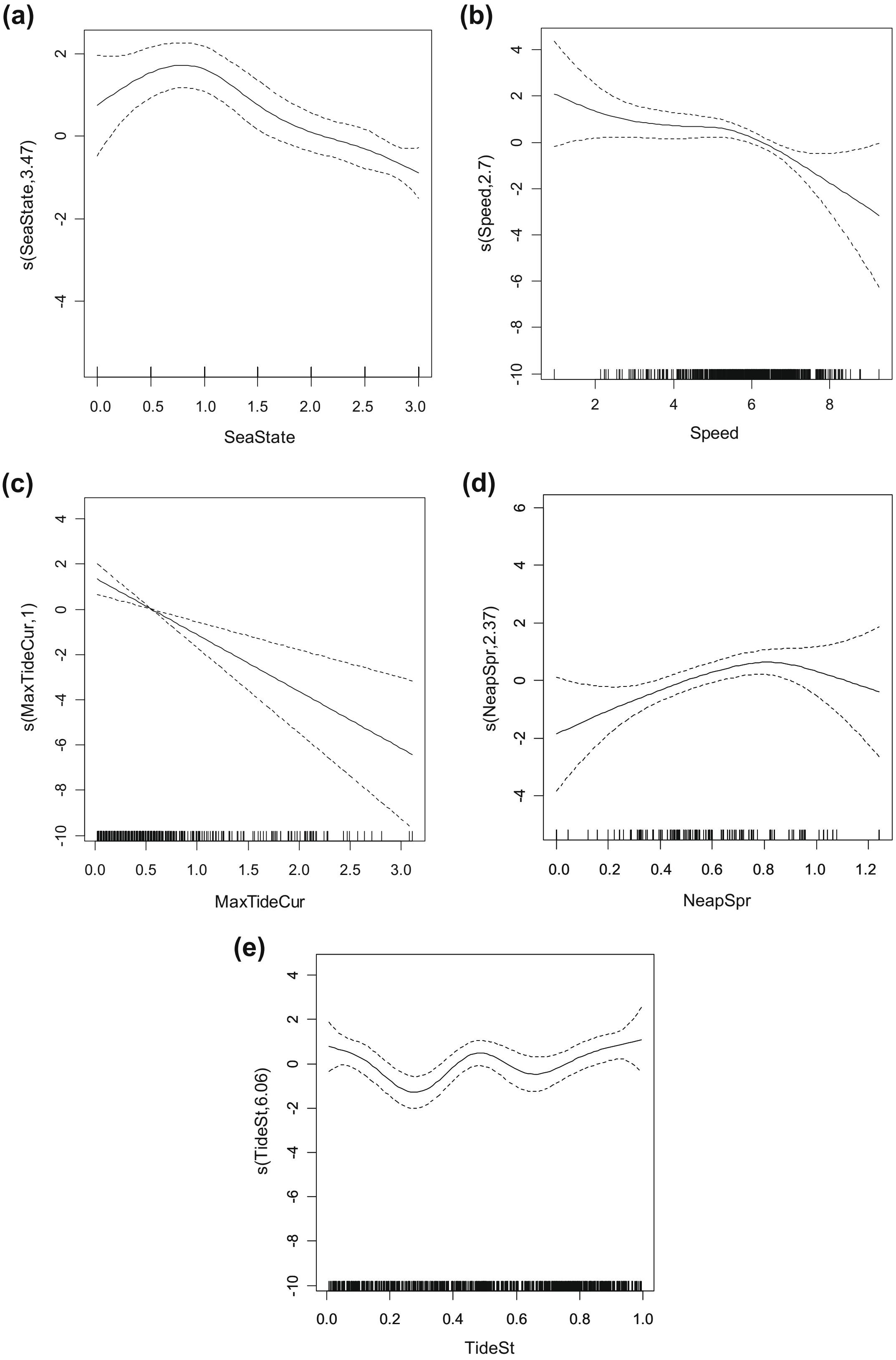

Fig. 3. Relationships between visual detections of harbour porpoise groups and (a) sea state in 2005 (d.f. = 3.5), (b) boat speed in 2003 (d.f. = 2.7), (c) maximum tidal current in 2003 (d.f. = 1), (d) position in the spring-neap cycle in 2004 (d.f. = 2.4), and (e) position in the tidal cycle in 2003 (d.f. = 6.1) for all 2 km segments ($n_{2003} = 713$, $n_{2004} = 455$, and $n_{2005} = 516$). The estimated 95% confidence intervals are shown by the dotted lines around the smooths.

explaining between 2.7% (2005) and 9.0% (2003) of the deviance. Detection rate decreased linearly with increasing tidal speed (Fig. 3c). Position in the spring-neap tidal cycle was the next most significant predictor except in 2005, explaining 5.6% (2004) and 6.3% (2003) of the deviance (Table 3), with higher detection rates during spring than neap tides (Fig. 3d).

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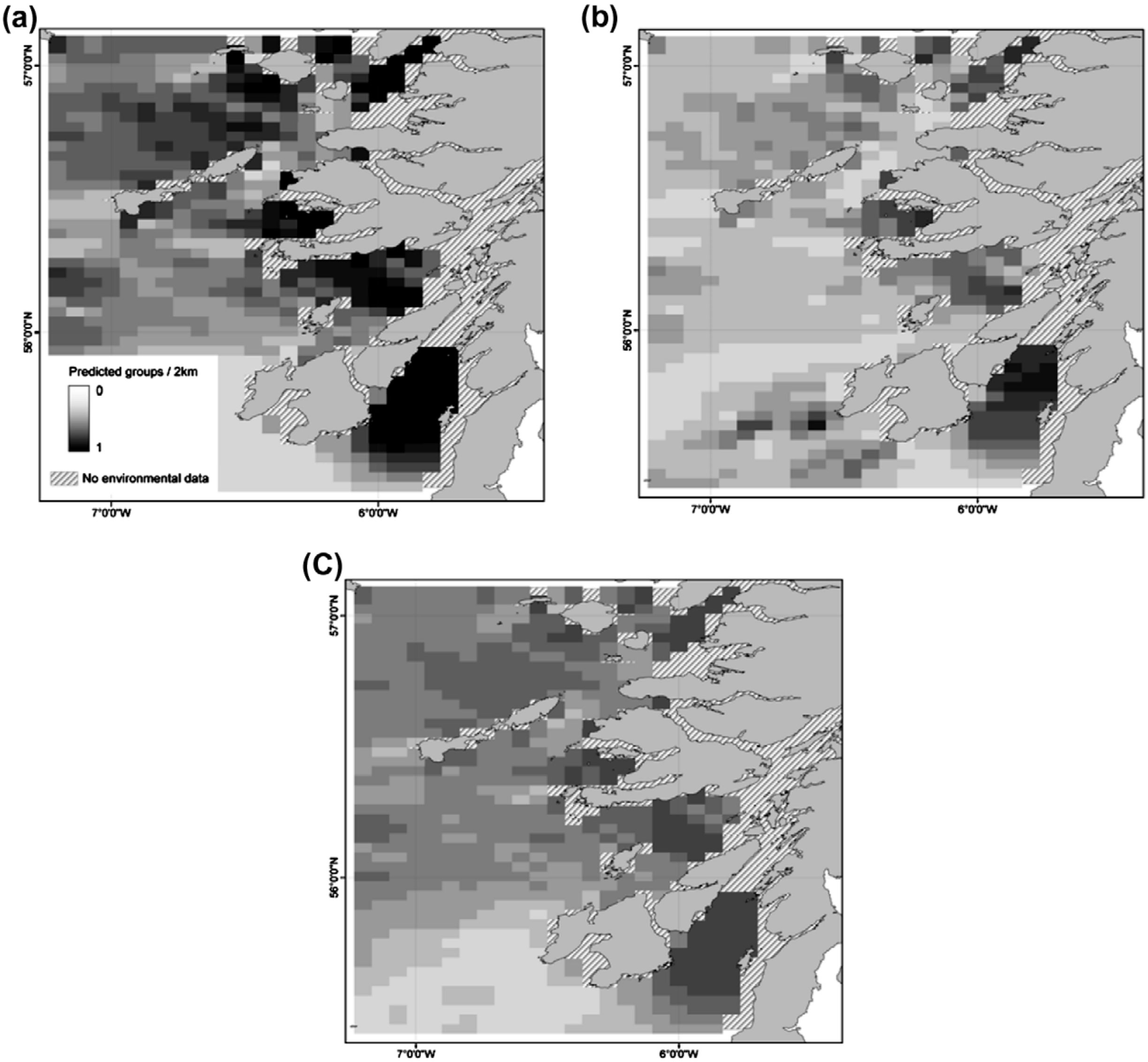

Fig. 4. Spatial prediction of harbour porpoise density (groups/2 km) for (a) 2003, (b) 2004, and (c) 2005.

Only in 2003 were any additional variables significant in explaining the distribution of harbour porpoises. Relative time in the tidal cycle explained 8.9% of the model deviance (Table 3), with harbour porpoises being detected at a higher rate during slack tides than during flood or ebb (Fig. 3e). Longitude was significant in explaining detection rates in 2003, but only explained 1.0% of the model deviance. Higher densities of harbour porpoises were predicted in the east (towards the mainland) of the survey area, than in the west.

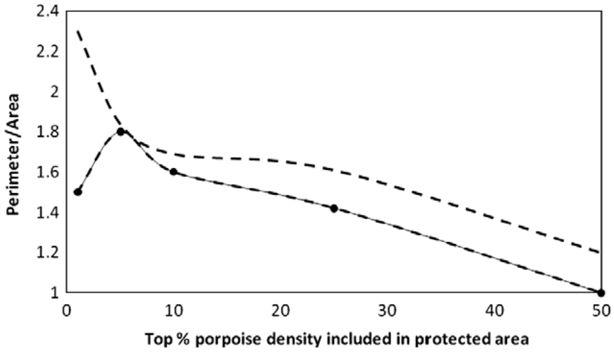

Fig. 5. Perimeter-to-area ratio for the areas encompassed by the top 1%, 5%, 10%, 25%, and 50% of predicted harbour porpoise relative density for all 3 years. The solid line shows the mean, and the dotted line shows the upper and lower confidence intervals. Mean areas encompassed approximate to 256 km^2, 672 km^2, 1200 km^2, 3088 km^2 and 6096 km^2, respectively.

3.3. Model predictions of distribution

To make predictions over the entire area, it was necessary to select values for the survey variables and temporally varying covariates; these were selected based on providing the highest density of harbour porpoises at the time of prediction and on the precision of the fitted smooth function. Using different values of these covariates would not change the location of the high density areas, only the actual densities predicted. Sea state = 1 was selected because sea states lower than this were infrequently encountered and the smooth had wide confidence intervals at lower values of sea state. A typical boat speed of 6 knots was assumed, again because this had the tightest confidence interval, with the engine on. Position in the spring-neap cycle was selected to be close to spring tides (NeapSpr = 1), and position in the tidal cycle was chosen close to

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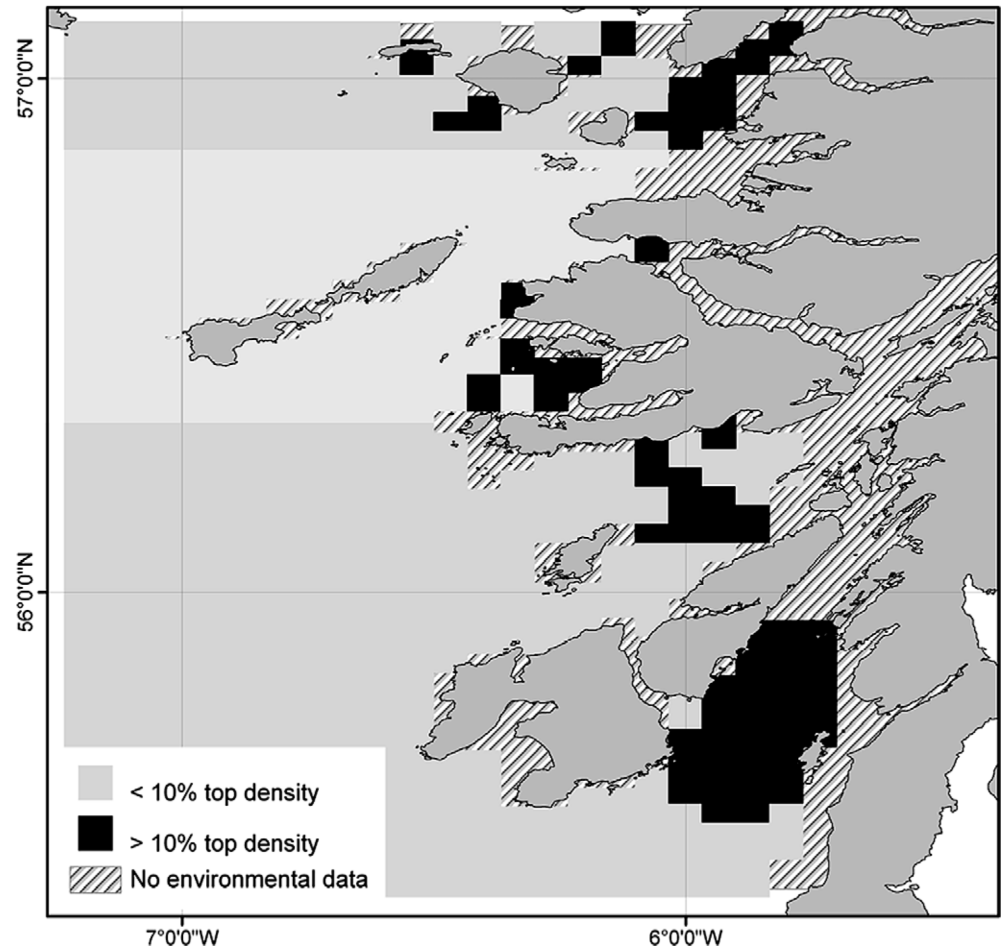

Fig. 6. High use areas of 10% highest predicted harbour porpoise density (groups/2 km) in all 3 years.

high water slack (TideSt = 0.8), because more porpoises were observed at these times.

There were differences in the distribution of harbour porpoise density predicted by the three independent yearly models (Fig. 4) but the same general areas were consistently predicted as high-use areas. Highest densities were predicted in the Sound of Jura, the Firth of Lorne, between Mull and the Treshnish Islands, in patches around the Small Isles (Rum, Eigg and Muck) and the Sound of Sleat (between Skye and the mainland).

3.4. Areas suitable for protection

The perimeter-to-area ratio had highest variability around the mean when the highest 1% of predicted density was included (Fig. 5). The highest perimeter–area ratio was obtained when the highest 5% of predicted density was included (Fig. 5). At 10%, the perimeter–area ratio confidence interval was narrow (1.6–1.69), suggesting there was little variation in the areas selected, while having relatively low perimeter–area ratio. Therefore, areas with the highest 10% of predicted density (0.6–1.1 porpoises/km), were selected as areas suitable for potential protection (Fig. 6). These high density areas had slightly higher encounter rates than the inshore areas for which environmental data were lacking (0.15 sightings per 2 km vs. 0.11 sightings per 2 km).

4. Discussion

Our study shows that the same high-use areas for harbour porpoises in the southern Inner Hebrides were predicted over 3 years. This allows us to propose areas suitable for consideration as potential SACs in accordance with EU Habitats Directive criteria, within a region of high relative density in a European context.

We used spatial models to determine suitable areas for protection for harbour porpoises, an approach previously used to define important areas of other marine species distributions (Hooker et al., 1999; Cañadas et al., 2005; Wilson et al., 2005; Louzao et al., 2006; Parnell et al., 2006), as well as terrestrial mammals (Gibson et al., 2004; Rondinini et al., 2005; Greaves et al., 2006; Moilanen and Wintle, 2007), birds (Loyn et al., 2001; Suárez-Seoane et al., 2002; Grand et al., 2004; Moilanen and Wintle, 2007; Jensen et al., 2008), amphibians (Rondinini et al., 2005; Dayton and Fitzgerald, 2006; Goldberg and Waits, 2009), and invertebrates (Smith et al., 1996; Cabeza et al., 2004; Grand et al. 2004; Matern et al., 2007; Steck et al., 2007). Information on species–habitat relationships is clearly important when designing and implementing protected areas (Hooker et al., 1999; Hyrenbach et al., 2000; Loyn et al., 2001; Cabeza et al., 2004; Rondinini et al., 2005; Louzao et al., 2006; Moilanen and Wintle, 2007; Hamaide et al., 2009). It is well understood that MPAs based on static or persistent environmental features are easier to implement (Hyrenbach et al., 2000), and there are examples of the use of both static (Hooker et al., 1999), and persistent oceanographic (Louzao et al., 2006; Notarbartolo-di-Sciara et al., 2008) features being used to define the boundary of MPAs for mobile marine species. In our study, we used both static features (depth, slope and sediment type) and persistent hydrographic features (maximum tidal current and maximum tidal amplitude) to predict harbour porpoise relative density. Maximum tidal current was shown to be the most

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significant environmental variable explaining the relative abundance of harbour porpoises in all 3 years of study (Table 3). The tidal regime is a dominant and persistent feature of the environment in the southern Inner Hebrides, and thus provides a useful metric on which to base SACs for harbour porpoises in this area.

Sea state explained only 3.2% of the deviance in 2003, but increased to 18.2% in 2005 (Table 3). The effect of this was to reduce the ability of the models to explain the distribution of harbour porpoises with environmental variables from 25.2% in 2003 to only 2.7% in 2005 (Table 3). However, unlike the study of Dall's porpoises by Forney (2000), the most important environmental predictor remained the same despite the increase in sea state, which gives us added confidence in the importance of maximum tidal current as an important feature of the environment for harbour porpoises in the Hebrides.

The higher relative densities of harbour porpoises detected during low maximum tidal currents is not reflected in other studies of the species. Previous studies of harbour porpoises based on land observation in known harbour porpoise "hotspots" have suggested that within these areas harbour porpoises are at highest densities at maximum tidal speeds (Calderan, 2003; Johnston et al., 2005; Pierpoint, 2008). In boat-based surveys carried out in the Inner Hebrides to the north of our study area, harbour porpoises were detected at higher rates during high tidal currents (Marubini et al., 2009). However, in all of these studies tidal current was included as a temporally varying measure. Our study is the first to use a spatial measure of tidal current, with temporal variations considered separately as 'relative time in the tidal cycle'. Also, the tidal regime of the southern Inner Hebrides is unique, with tidal speeds in excess of those reported in the other studies. For example, the maximum current recorded in the analysis of harbour porpoise distribution in the northern Inner Hebrides was only 2 knots (Marubini et al., 2009), significantly less than the 8 knots recorded in the southern Inner Hebrides.

The high tides in the southern Inner Hebrides are due to the unusual tidal regime in the area, dominated by the M_2 constituent. An amphidromatic point to the south of Islay (Proctor and Davies, 1996) results in a small tidal amplitude but strong semi-diurnal currents in the North Channel region (the narrow channel between Scotland and Ireland just to the south-west of Islay). Tidal amplitude increases northwards along the coastline, but current strength is largely dependent on seabed topography, with strongest currents found in the channels and sounds between the islands of the Inner Hebrides. The phase of the tide, rather than the amplitude, is critical here in setting up sea surface gradients that drive strong currents and "tidal races". A well-known example is the Gulf of Corrywrecken tidal race, where currents reach $4\ \mathrm{m\ s^{-1}}$ (around 8 knots), and which is driven by the large phase lag of the M_2 tide between the Sound of Jura and the Firth of Lorne. Away from the sounds and channels, tidal currents are typically of the order of $1\ \mathrm{m\ s^{-1}}$ (around 2 knots), but can be substantially less in sheltered inshore waters.

We selected areas for potential protection that consistently had >10% of the highest density of harbour porpoises over the 3 years of the study (Fig. 6). This was chosen to maximise the clumping and connectivity of the selected area. From a conservation perspective it is clear that protecting as large an area as possible is the ideal (Parnell et al., 2006), but social and economic considerations inevitably constrain the size of protected areas (Possingham et al., 2000; Leslie et al., 2003). Protected areas need to be of an appropriate size to provide adequate protection of habitat for the species whilst being feasible to be managed with available resources. By optimising the size of the area based on the perimeter length to area ratio, we obtain an efficient design that should allow movement of harbour porpoises, their prey or the zooplankton that determine the location of their prey, whilst at the same time reducing enforcement and management costs (Airimé et al., 2003; Leslie et al., 2003; Roberts et al., 2003). There was little variation around the perimeter–area ratio at this threshold, suggesting that the areas selected using our methods are relatively robust.

The inclusion of temporal variables in the models illustrates some of the short term fluctuations in harbour porpoise densities using the core areas. The temporal variables that were significant in explaining the density of porpoises were position in the spring-neap cycle (2003 and 2004), and relative time in the tidal cycle (2003). These non-spatial variables did not change the location of the high density areas, only the actual densities predicted. Thus, higher densities of harbour porpoises are predicted during spring tides, and at the slack phases of the tidal cycle (Fig. 3d and e). This increase may be due to changes in harbour porpoise behaviour with more visible feeding cues at such times, or due to changes in their sightability, perhaps because sea state is lower. It is also possible that harbour porpoise foraging distribution is more concentrated in restricted locations at these times, mirroring the change in behaviour of their prey, and more dispersed at other times. This suggests that at spring and slack tides, the high density areas are more important to the porpoises than at other times, which could help inform a more temporally managed protected area.

It is clear that harbour porpoises in the southern Inner Hebrides use the entire area, not just the identified core areas (Fig. 2). This may explain why we were only able to explain a relatively low amount of variation of harbour porpoise distribution with environmental variables: as little as 2.7% in 2005 but as much as 25.2% in 2003 (Table 3). The sightings of harbour porpoises over a wide area of the Inner Hebrides likely include animals travelling between foraging locations. The fitted relationships between detection rate and environmental variables may thus reflect more than the use of foraging habitat (Ballance et al., 2006). Our results showed that environmental variables explained a higher amount of model deviance in years when sea states were good, increasing from 2.7% in 2005 when sea state explained 18.2% of the deviance, to 25.2% in 2003 when sea state explained only 3.7% of the variation (Table 3). Thus it appears that the lower sightings rates that result during poor sea state make it more difficult to determine habitat preferences of porpoises, a result also found by Forney (2000). However, that the same environmental variables were selected in the same order in all 3 years, generating the same predicted high-use areas, gives us confidence in the robustness of our results and, in particular, that maximum tidal current is the main spatial predictor of harbour porpoise habitat.

Although our 3 year study provides valuable information for the summer months, it tells us nothing about winter distribution or habitat use of harbour porpoises. Even for summer, a 3 year period is insufficient to account for all environmental variation, including any major climate shifts that might occur over longer periods of time (Airimé et al., 2003). In 2005, there was a clear change in the ecosystem of the southern Inner Hebrides: minke whales virtually disappeared from the area, basking sharks significantly increased in abundance, and some seabird populations failed to fledge chicks (Stevick et al., 2007). However, despite this difference in the ecosystem in 2005, the same high-use areas were predicted (Fig. 4), which again provides us with additional confidence in the robustness of our results.

Our results are the first step towards consideration of SACs for harbour porpoise in the Hebrides. The next step is to decide which, if any, of the areas identified as important habitat should become proposed SACs, and what should be their boundaries. There are a number of non-scientific considerations that are beyond the scope of this paper. Most important is the involvement of the local communities and other stakeholders in the area. In this area of the southern Inner Hebrides, the main users of the sea include fishermen deploying crab/lobster pots or dredging for scallops; aquaculture for salmon, mussels and oysters; tourism in the form of whale-watching trips and recreational boat traffic; and navy for military exercises. As described above, salmon farming and naval exercises are likely to be the main focus of measures to protect porpoise habitat as part of SAC management plans.

Scientific aspects of SAC area definition include whether or not to include a wider area, or buffer zone, around identified high-use areas (Kelleher, 1999; Allison et al., 2003). Such a buffer could reduce the effect of pollution or noise in the adjacent areas (Sobel, 1995; Hooker et al., 1999). For example, Hooker et al. (1999) defined a 10 km buffer around the core protected area based on the distance over which seismic or tanker traffic noise source levels were reduced to acceptable levels. Acoustic deterrent devices (ADDs) deployed to protect salmon farms from seals have been shown to displace harbour porpoises from their habitat within a 3.5 km radius of the source (Olesiuk et al., 2002). Thus, for harbour porpoises on the west coast of Scotland, a 3.5 km buffer zone might be considered. Military sonar has a much larger range and the impacts of this on harbour porpoises would need to be taken into consideration.

Which areas of those identified in Fig. 6 should be proposed as SACs? There appear to be four clear clusters of predicted high use: the Sound of Jura, the Firth of Lorne, the area between Mull and the Treshnish Islands, and Sound of Sleat (see Fig. 1 for locations). We recommend that these four areas be considered as potential SACs for harbour porpoises. These areas have been well surveyed and consistently generated sightings, which is not the case in the north of the study area in the waters around the Islands of Rum, Eigg, and Muck (Fig. 2).

A further consideration, arising from a lack of environmental data, is whether some of the unmodelled coastal areas should be included (Fig. 6). Detection rates within these coastal areas were only slightly lower on average than in the identified high-use areas. Much of these coastal waters are also clearly important for harbour porpoises.

The southern Inner Hebrides currently includes 34 SACs and 18 SPAs for birds (JNCC, 2009a). Most of the SACs are land-based protected areas, although a few contain a marine component. Within the high use and coastal areas important to harbour porpoises there are two SACs for harbour seals (*Phoca vitulina*), one for grey seals (*H. grypus*), one for otters (*Lutra lutra*), and the upper Firth of Lorne is an SAC for its reefs (JNCC, 2009b). In addition, the area encompassing Rum, Eigg, Muck, Coll, Tiree, and Mull (Fig. 1) has been nominated as the UK's first National Marine Park (Scottish Executive, 2006). If this is established, the management of harbour porpoise SACs could thus be integrated with the management of the new Marine Park.

We have shown that a habitat-based modelling approach for identifying areas to be protected in an MPA based on a species needs (Agardy, 1997; Airimé et al., 2003) is an effective and practical method for harbour porpoise in the southern Inner Hebrides. The identification of maximum tidal current as a robust predictor of harbour porpoise relative density shows that the approach also helps us to understand the processes that influence distribution and habitat use. We recommend that these results are used as the basis for designation of SACs for harbour porpoises in the southern Inner Hebrides.

Habitat-based modelling has become widely used for defining areas for marine (Hooker et al., 1999; Cañadas et al., 2005; Wilson et al., 2005; Louzao et al., 2006; Parnell et al., 2006) and terrestrial species (Loyn et al., 2001; Cabeza et al., 2004; Rondinini et al., 2005; Moilanen and Wintle, 2007; Hamaide et al., 2009). However, habitat-based modelling combined with protected area design techniques, such as minimising the perimeter-to-area ratio, are relatively rare in the literature (Cabeza et al., 2004; Jensen et al., 2008). Although the direct applicability of our results is limited to harbour porpoises off the west coast of Scotland, we demonstrate that even in a complex environment this method is easy to implement, works well and could thus have wide applicability in protected area design.

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