

Estimating spatial, temporal and individual variability in dolphin cumulative exposure to boat traffic using spatially explicit capture–recapture methods

E. Pirotta¹, P. M. Thompson², B. Cheney², C. R. Donovan³ & D. Lusseau¹

¹ Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, UK

² Lighthouse Field Station, Institute of Biological and Environmental Sciences, University of Aberdeen, Cromarty, UK

³ Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, UK

Keywords

Bayesian modelling; capture–recapture; disturbance; dolphin; exposure rate; home range; marine traffic; *Tursiops truncatus*.

Correspondence

Enrico Pirotta, Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK. Tel: 01224 274106
Email: enrico.pirotta@abdn.ac.uk

Editor: Trevor Branch

Associate Editor: Mads Heide-Jorgensen

Received 13 January 2014; accepted 31 March 2014

doi:10.1111/acv.12132

Abstract

Appropriate management of the effects of human activities on animal populations requires quantification of the rate at which animals encounter stressors. Such activities are heterogeneously distributed in space, as are the individual animals in a population. This will result in a heterogeneous exposure rate, which is also likely to vary over time. A spatially explicit analysis of individual exposure is therefore required. We applied Bayesian spatially explicit capture–recapture models to photo-identification data to estimate the home range of well-marked individuals in a protected coastal population of bottlenose dolphins. Model results were combined with the estimated distribution of boat traffic to quantify how exposure to this disturbance varied in time and space. Variability in exposure between individuals was also investigated using a mixed-effects model. The cumulative individual exposure to boat traffic varied between summers, depending both on the overall area usage and the degree of individual movement around the activity centres. Despite this variability, regions of higher risk could be identified. There were marked inter-individual differences in the predicted amount of time dolphins spent in the presence of boats, and individuals tended to be consistently over- or underexposed across summers. Our study offers a framework to describe the temporal, spatial and individual variation in exposure to anthropogenic stressors when individuals can be repeatedly identified over time. It provides opportunities to map exposure risk and understand how this evolves in time at both individual and population levels. The outcome of such modelling can be used as a robust evidence base to support management decisions.

Introduction

Human pressure on the natural environment is increasing, particularly in the marine environment where new industries targeting offshore areas are growing alongside traditional activities such as fishing and shipping (Halpern *et al.*, 2008). Animal interactions with some anthropogenic activities can lead to their direct death (e.g. by-catch) (Read, Drinker & Northridge, 2006). Repeated exposure to other activities also has the potential to cause long-term effects on animal populations. These indirect population-level effects are mediated by the repeated non-lethal disruption of individuals' behaviour and the consequent changes in individual vital rates (New *et al.*, 2013). The management of such effects requires a detailed understanding of the rate at which individual animals encounter the stressors. Human activities are not homogeneously distributed in space (Halpern *et al.*, 2008). For example, in the marine environment, ship traffic tends to concentrate along specific routes and in specific

periods of the year (Schreier *et al.*, 2007). Energy exploitation, renewable or non-renewable, is also directed where extraction is the most efficient and profitable (Pelc & Fujita, 2002). Moreover, different animals in a population are expected to use their habitat in different ways as a result of their sex, life stage, condition and social interactions with conspecifics (Bixler & Gittleman, 2000; van Beest *et al.*, 2011; Campioni *et al.*, 2013; Mattisson *et al.*, 2013). Population density and the heterogeneous distribution of resources in the environment can also affect individual habitat selection (Schoener & Schoener, 1982; Schradin *et al.*, 2010; Naidoo *et al.*, 2012). In addition, changes in local conditions may influence the size and location of individual home ranges through time (Wang & Grimm, 2007). Consequently, individuals in a population are likely to be heterogeneously exposed to human disturbance. Exposure rate may also vary if the entire population changes the use of its range in response to variability of the biotic and abiotic environment (Schofield *et al.*, 2010). We thus need to

understand how exposure rates evolve in time and space, both for the overall population and between different individuals. Such information would support tailored management plans to minimize the risk that cumulative exposure to disturbances will affect the conservation status of animal populations while preventing over-precautious regulation. The idea of a spatially explicit analysis of exposure has been widely implemented in the management of chemical contamination (Hope, 2000; Linkov *et al.*, 2002; Crocker, 2005; Wickwire *et al.*, 2011), but there are relatively few examples addressing other anthropogenic stressors (Williams & O'Hara, 2010; Bauduin *et al.*, 2013; Redfern *et al.*, 2013; Vaes & Druon, 2013), and none of them carries out the analysis at an individual level. Many studies have now shown that boat traffic can affect the activity budget of exposed marine mammals, through both the noise introduced in the environment (e.g. Aguilar Soto *et al.*, 2006) and the physical interactions between the vessels and the animals (e.g. Lusseau, 2003). Because of its heterogeneous distribution in space, it offers a useful test-bed to develop analytical tools to quantify spatio-temporal variability in individual exposure rates.

Capture–recapture techniques can be used to monitor individual animals in a population over time. Spatially explicit capture–recapture models have been developed to combine individual capture histories with spatial information of where captures have occurred (Borchers & Efford, 2008; Royle *et al.*, 2009a,b). This approach generates robust density estimates by accounting for the varying probability of capturing an individual depending on its distance from the sampling unit. Each individual in the population is assumed to have an activity centre where it shows the maximum probability of being encountered. Encounter probability declines with distance from the centre following a specified detection function (Efford, 2004). As a result, these methods can be used to estimate the probability of observing each animal across the study area which, effectively, provides information on how individuals use space. Therefore, this novel application of spatially explicit capture–recapture techniques offers a means to investigate individual-level processes and characterize the home ranges of specific animals. The overlap between the estimate of an individual's range and the predictions of the spatial and temporal distribution of a stressor can then be used to describe the exposure of that individual to the stressor. Although management tends to address the status of targeted populations, the performance of individuals has relevant consequences on population dynamics (Coulson *et al.*, 2006), especially in small populations of long-lived species (Vindenes, Engen & Saether, 2008). It is therefore critical to characterize individual heterogeneity and understand how this is integrated at a population level.

In this study, we focus on the coastal population of bottlenose dolphins, *Tursiops truncatus*, (hereafter 'dolphins' or 'bottlenose dolphins') that uses the Moray Firth (Scotland) (Cheney *et al.*, 2013). This is a Special Area of Conservation (SAC) for the species under the European Habitats Directive (92/43/EEC) and supports a mix of traditional and

emerging marine industries (Thompson *et al.*, 2010). These industries require adequate management to address the European mandate of maintaining a 'favourable conservation status' for the population. We use a spatially explicit capture–recapture framework to estimate the probability of observing each individual dolphin across the study area based on a long-term photo-identification dataset. We then quantify dolphin exposure to disturbance from boat traffic and its heterogeneity in time, in space and across individuals.

Materials and methods

Data collection

Regular boat surveys were conducted between May and September 2006–2011 as part of the long-term bottlenose dolphin SAC monitoring programme (Cheney *et al.*, 2013) (Table 1). Photo-identification was carried out on the encountered dolphins following the methods described in Cheney *et al.* (2013) and Cheney *et al.* (2012). For the purpose of this study, we only considered well-marked individuals with nicks in their dorsal fins. Moreover, in order to standardize the area covered within each year, we excluded some exploratory trips made in 3 years outside the usual study area (Supporting Information Fig. S1).

Boat model

We used an existing model for the spatial and temporal distribution of boat traffic in the Moray Firth (Lusseau *et al.*, 2011; New *et al.*, 2013). The model builds on several sources of data (land-based observations, GPS tracks, large vessels' AIS data and boat deployment rates from the harbours around the Firth) and predicts the behaviour of different types of boats departing from specific ports, as well as simulating commercial traffic routes from the North Sea. Layers of various types of vessel activity are then combined to generate aggregate boat densities across the area. This is expressed as the number of vessel-hours per day over a year that boats occupy each 1 km by 1 km cell of a grid overlaid to the study area. While accounting for seasonal variability in boat traffic, the model does not include inter-annual changes. For more details about the boat model, the reader should refer to Lusseau *et al.* (2011) and New *et al.* (2013).

Table 1 Summary of the photo-identification surveys by year, number of marked individuals identified and number of independent spatial captures per individual (mean and range)

Year	No. of surveys	No. of marked individuals identified	No. of spatial captures per individual
2006	33	45	5 (1–15)
2007	27	46	7 (1–18)
2008	27	33	7 (1–17)
2009	35	52	9 (1–19)
2010	25	60	8 (1–17)
2011	21	55	8 (1–20)

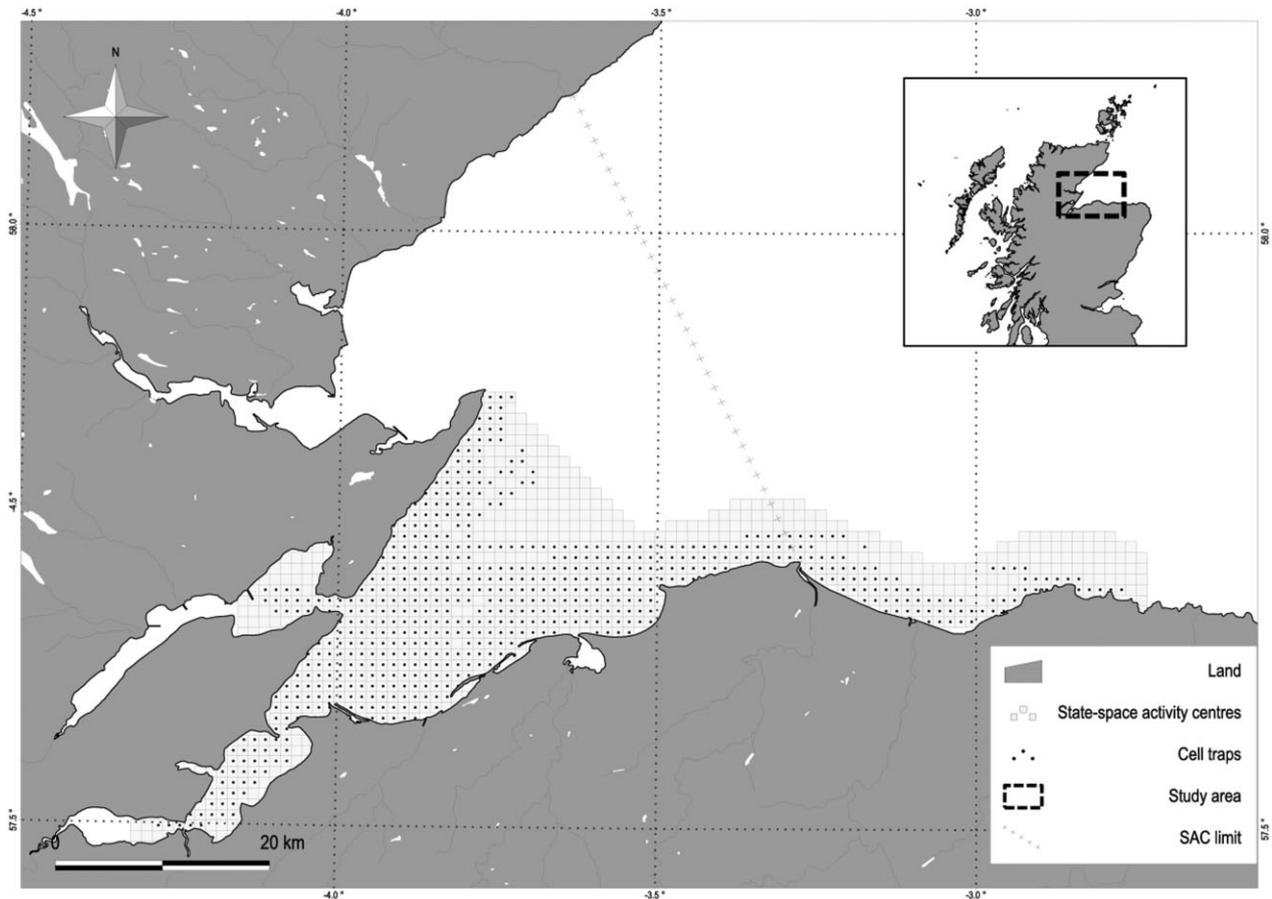


Figure 1 Map of the study area showing the 1 km by 1 km state-space of activity centres and the 630 cell traps.

Modelling animal distribution with spatially explicit capture–recapture models

We used a Bayesian spatially explicit capture–recapture approach (Royle *et al.*, 2009b) to model the probability of observing individual dolphins across the study area based on the photo-identification data. Although these methods have been originally developed for the analysis of camera-trap data, the data collected through photo-identification surveys can be adapted to the framework by gridding the sampled area and treating each grid cell as a sampling unit (Thompson, Royle & Garner, 2012).

A grid of 959 1 km by 1 km cells was used as the state-space of potential individual activity centres (Fig. 1). The grid enclosed the known suitable habitat for bottlenose dolphins in the Moray Firth (i.e. the inner firth and the coastal areas of the outer firth) (Hastie *et al.*, 2004; Bailey & Thompson, 2009) and the area consistently covered by boat surveys across the years. We preliminarily tested a series of grids with different extents to ensure that this was not affecting the stability of the parameter estimates.

Different years were modelled separately to reduce the effects of mortality, immigration and emigration, as the models assume that the population is closed within

the sampling period. Surveys in a given year were treated as different sampling occasions. Of the 959 cells of the grid, 630 were visited at least once during the boat surveys and represented the potential traps (Fig. 1). If, during a given survey, the boat visited one of the 630 cell traps, that trap was considered active during that survey. Information on where the animals were captured on each sampling occasion (i.e. in which cell trap they were photo-identified) was used to build the spatially explicit capture history. We assumed that the captures were the result of a Bernoulli process, that is $y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k})$ (equation 1), where $y_{i,j,k}$ indicates whether individual i was photo-identified in cell trap j on sampling occasion k and is either 0 or 1. $p_{i,j,k}$ is the probability of observing individual i in cell trap j during survey k and depends on the distance of trap j from the individual's activity centre cell.

Analyses were carried out using the package SPACECAP (Gopalaswamy *et al.*, 2012) available for R v. 2.14.1 (R Development Core Team, 2013). The open-access code was customized to address some specific features of the data (Supporting Information Appendix S1).

(1) Because the study area is an estuarine embayment with promontories and bays, we did not use Euclidean distance to calculate distances. Instead, a matrix of at-sea distances

(in km) between the centroids of the grid cells was calculated. This modification also required us to recalculate the neighbourhood for every cell, that is the cells within a distance of 5 km. This information is used by SPACECAP to select suitable candidate activity centres at each Monte Carlo Markov chain (MCMC) iteration.

(2) During each survey, the research vessel spent a variable amount of time in each cell trap, depending on travel speed. The amount of time spent in each trap looking for the animals affects encounter rate. Therefore, we altered the SPACECAP code to account for the influence of survey effort on capture probabilities during each sampling occasion. Effort in minutes was included in the model as in Thompson *et al.* (2012) and Russell *et al.* (2012). Under this approach, effort is treated as a covariate having a multiplicative effect on the basal encounter rate. An additional parameter is used to describe the shape of this relationship, which we called a_2 for consistency with the cited paper. The probability of observing individual i in cell trap j on sampling occasion k ($p_{i,j,k}$) was therefore modelled as $\text{cloglog}(p_{i,j,k}) = \log(\lambda_0) - (1/\sigma^2) \times d_{i,j}^2 + a_2 \times \log(\text{effort}_{j,k})$ (equation 2), where λ_0 is the basal encounter rate, σ is the standard deviation of the half-normal detection function, $d_{i,j}$ is the distance between the activity centre of individual i from trap j and $\text{effort}_{j,k}$ represents the number of minutes spent in trap j during occasion k .

SPACECAP uses the method of data augmentation to estimate population size N (Royle *et al.*, 2009b). N has a discrete uniform prior $U(0, M)$, where M is the number of pseudo-individuals. M includes the n observed individuals and the A augmented individuals, which is the maximum number of marked individuals with all-zero capture histories, that is not captured on any occasion (Royle *et al.*, 2009b). For all models, we used an initial A of 150, which was chosen to be large enough to avoid posterior truncation (Royle *et al.*, 2009b). The MCMC were run for 150 000 iterations, with an initial burn-in of 10 000 iterations and a thinning rate of 10. Convergence was assessed using trace plots, autocorrelation plots and Geweke's diagnostic provided by SPACECAP (Royle, Kéry & Guélat, 2011). When the absolute value of this diagnostic for any parameter of the model was greater than 1.6, we progressively increased the burn-in, until Geweke's diagnostic was below 1.6 for all parameters. The Bayesian P -value, which measures the discrepancy between observed data and expected values, was used as a measure of the goodness-of-fit of the model to the data (Gelman, Meng & Stern, 1996; Royle *et al.*, 2011). This statistic varies between 0 and 1, and a value close to either extreme indicates a poor fit. Finally, we modified the code to retain the estimated individuals' activity centres at each iteration.

Exposure rates

We used the parameter estimates at each retained iteration (i.e. excluding the burn-in period) in equation 2 to calculate the probability of observing each individual in every cell of the state-space, given a unit of effort (1 minute). The cell

median of these probabilities across iterations gave us an estimate of the individuals' home ranges. The boat model predicted the number of minutes boats were present in cell j in day d ($m_{j,d}$). Therefore, the expected number of minutes that dolphin i spent in the presence of boats in cell j , day d and year y could be calculated as: $t_{i,j,d,y} = m_{j,d} \times p_{i,j,y}$ (equation 3), where $p_{i,j,y}$ was the estimated probability of observing dolphin i in cell j on year y , given 1 minute of effort. This assumed that both boats and dolphins showed similar daily patterns of use at each site, for example boats did not occur in a given cell at specific hours of the day when dolphins were consistently not using that cell. Because our data only covered the summer season, we only considered boat exposure between the 1st of May and the 1st of October.

We derived the median individual exposure in each sampled summer. We then assessed the distribution of the exposure in space, that is how exposure varied between different grid cells. The overall variability in exposure between individuals within each summer was evaluated using histograms. Finally, for a subset of individuals that were encountered in at least five summers out of the six analysed, we investigated whether they tended to be consistently over- or underexposed, and how these individual differences contributed to explain the variation in exposure in comparison with differences among years. To do so, we ran a mixed-effects model with year as a categorical fixed effect and individual ID as a random effect and carried out model selection using the Akaike Information Criterion (AIC). The analysis was carried out using the library lme4 (Bates, Maechler & Bolker, 2012) in R.

Results

An average of 28 trips was carried out each year. On average, 50 marked individuals were encountered per year, each sighted on seven different occasions (Table 1). Trace plots and Geweke's diagnostics suggested that the spatially explicit capture–recapture models converged after a variable number of burn-in iterations (Table 2). Autocorrelation plots were used to decide whether additional thinning of the chains was required. The 2006 and 2010 were the years with the least satisfactory goodness-of-fit, as suggested by the Bayesian P -value. We found variability across years both in σ (which can be interpreted as a measure of the amount of movement of each individual around its activity centre) and the basal encounter rate λ_0 (Table 3). The estimates of a_2 were close to 1, suggesting that effort increased the

Table 2 Goodness-of-fit and number of iterations to convergence for the yearly models

Year	Bayesian P -value	No. of burn-in iterations
2006	0.84	35 000
2007	0.55	25 000
2008	0.59	25 000
2009	0.73	10 000
2010	0.77	25 000
2011	0.68	30 000

Table 3 Parameter estimates and uncertainty for the yearly models. λ_0 is the basal encounter rate, σ is the standard deviation of the half-normal detection function, N is the number of marked individuals in the population and a_2 is the parameter describing the effect of effort. The 95% HPD is the Bayesian highest posterior density (HPD) interval, that is the shortest interval enclosing 95% of the posterior distribution

Year	Parameter	Median	95% HPD
2006	σ	2.31	1.79–2.98
	λ_0	0.0018	0.0012–0.0024
	N	66	54–80
	a_2	1.09	0.94–1.23
2007	σ	2.23	1.89–2.65
	λ_0	0.0102	0.0078–0.0130
	N	78	63–95
	a_2	0.51	0.37–0.65
2008	σ	4.67	3.78–5.80
	λ_0	0.0051	0.0038–0.0069
	N	37	34–42
	a_2	0.84	0.69–0.99
2009	σ	8.24	7.18–9.35
	λ_0	0.0021	0.0017–0.0025
	N	52	52–53
	a_2	1.01	0.90–1.12
2010	σ	4.24	3.77–4.78
	λ_0	0.0039	0.0031–0.0048
	N	63	60–66
	a_2	0.93	0.83–1.04
2011	σ	4.75	4.05–5.60
	λ_0	0.0037	0.0029–0.0045
	N	58	55–62
	a_2	0.95	0.86–1.07

encounter rate in an approximately linear way, although in 2007 and 2008, this relationship was plateauing for greater effort (i.e. $a_2 < 1$) (Supporting Information Fig. S2).

The analysis of the individuals' distributions in a given summer showed that there was variability in the way different animals used the area (e.g. Fig. 2). Moreover, individuals also had a variable distribution across different summers (e.g. Fig. 3). The variability in the basal encounter rate between summers (Table 3) resulted in a widely variable exposure to boat traffic (Fig. 4). Nevertheless, the relative spatial distribution of such exposure was stable across summers (Fig. 5), concentrating in the inner Moray Firth and around harbours.

Plotting the within-summer variability in exposure highlighted marked inter-individual differences in exposure rate (Fig. 6). There were also differences in the distribution of such exposure between different years. In the summers 2008–2011, most individuals were exposed to higher levels of boat interactions, with a few relatively underexposed individuals (Fig. 6). In 2007, individual exposure was more evenly spread across the exposure range, whereas in 2006, most individuals showed an intermediate exposure rate. The inter-quartile range of individual exposures was particularly wide in 2007 but did not show any relevant trend in the other years (Fig. 4).

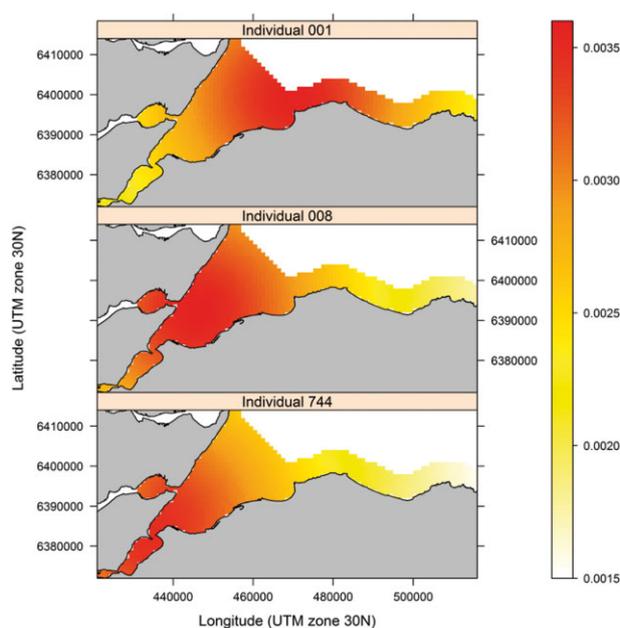


Figure 2 Estimated probability of encountering specific individuals across the study area in 2010.

Mixed-effect analysis on the 34 individuals encountered in at least 5 years showed that the model with year as a fixed effect and individual ID as a random effect was better (AIC = 3122) than both the model only including year (AIC = 3223) and the model only including individual ID (AIC = 3895). Year explained 96% of the variance and individual ID 1.5%, suggesting that while the differences between years drove the variability in exposure (e.g. Supporting Information Fig. S3), there was some individual consistency over time. The dot plot for the random effects shows that some individuals were consistently over- or underexposed (Fig. 7). Exposure in 2006 was considerably lower than in subsequent years. When we removed 2006 and re-ran the models using data from 2007–2011, year explained 92% of the variability and individual ID 2.7%.

Discussion

Modelling individual exposure to human activities

Our study outlines a framework to model exposure rates of individual animals to an anthropogenic stressor and to characterize how this exposure varies in space and time. A similar approach is used in ecological risk assessments for chemical contamination to understand the degree of overlap between the contaminant and the population under threat (Hope, 2000; Linkov *et al.*, 2002; Wickwire *et al.*, 2011). Exposure of marine mammals to ship-strike risk has also been previously quantified using spatially explicit models (Vanderlaan *et al.*, 2008; Williams & O'Hara, 2010; Bauduin *et al.*, 2013; Redfern *et al.*, 2013; Vaes & Druon,

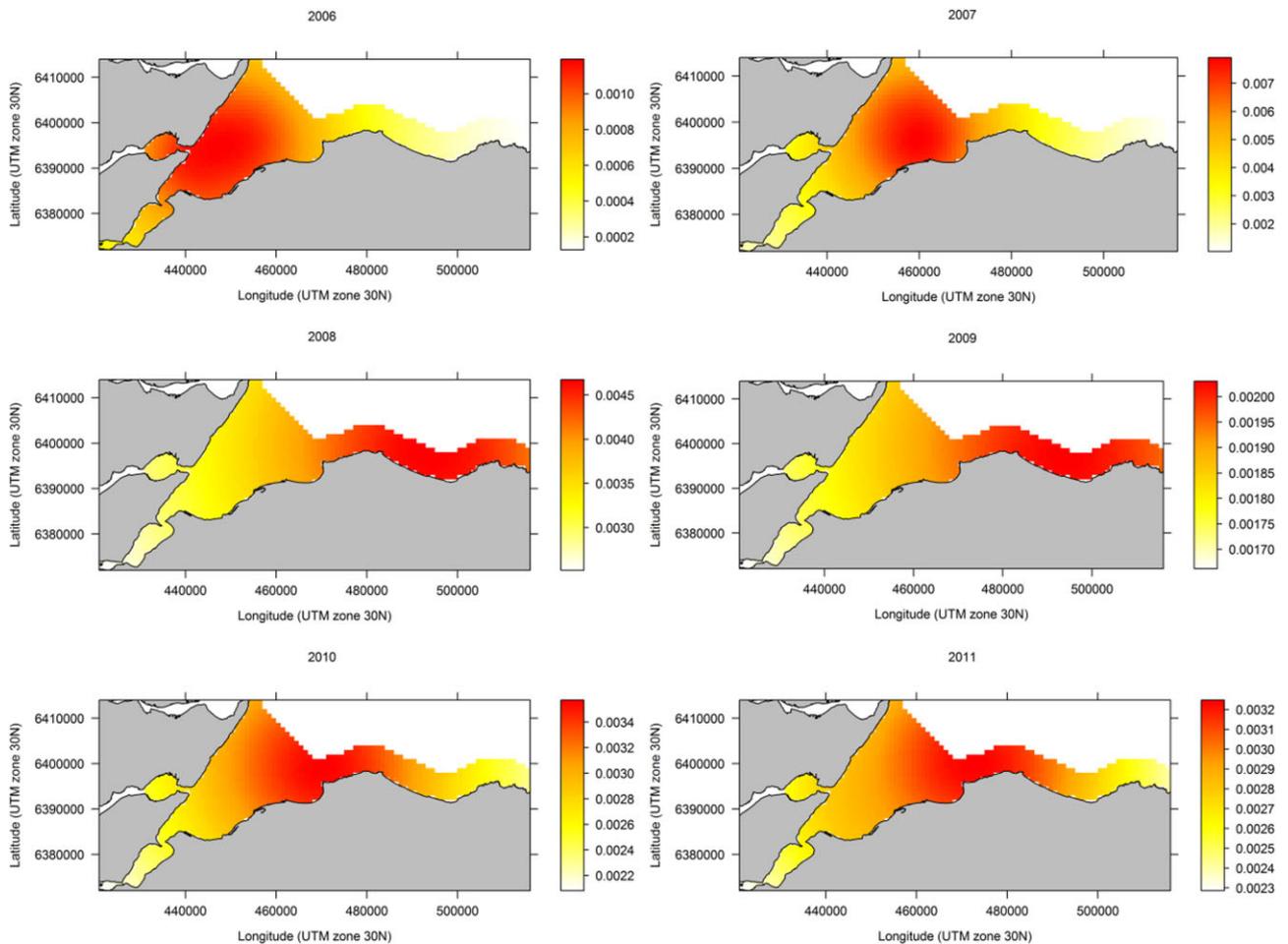


Figure 3 Estimated probability of encountering individual 001 in each analysed summer.

2013), but these studies did not consider the variability in habitat use between specific individuals.

Here, we used spatially explicit capture–recapture techniques to model individual home ranges and estimate the probability of observing each individual across the area of interest (Borchers & Efford, 2008; Royle *et al.*, 2009b). We then combined the results with a separate model for boat traffic to account for the heterogeneous distribution of this human activity (Halpern *et al.*, 2008; Lusseau *et al.*, 2011). This analytical approach could be extended to other situations where individuals can be recognized over subsequent capture occasions and where spatial information is available on the capture locations and on the distribution of the anthropogenic stressors.

Variability in exposure rates

The variability in exposure was mainly attributable to yearly variations in the basal encounter rate, that is the probability of encountering any specific dolphin in the area. Such large yearly variability could be associated with fluctuations of the environment that the animals inhabit. For instance,

the availability of food resources in different parts of the animals' range would imply that the relative usage of the various subareas changes over time (Lusseau *et al.*, 2004; Wilson *et al.*, 2004). Animals might roam more in some years, for example when more limited resources are available in the Moray Firth. This factor is known to affect other characteristics of the population's behavioural ecology (Lusseau *et al.*, 2004) and would result in spending less time in the study area and being captured with a lower probability. Alternatively, yearly variations could reflect changes in the social and spatial arrangements of the population. There are some individuals that are known to concentrate their activity in other areas along the east coast of Scotland (Wilson *et al.*, 2004; Lusseau *et al.*, 2006; Cheney *et al.*, 2013), but in some summers they could be visiting the Moray Firth more often. If in these instances they are encountered and photo-identified, this would reduce the estimate of the basal encounter rate λ_0 and increase the estimate of σ . The models could be further developed to address the existence of different social groups in the population by allowing for heterogeneity in λ_0 and σ . Although the modelling approach we used assumed that capture

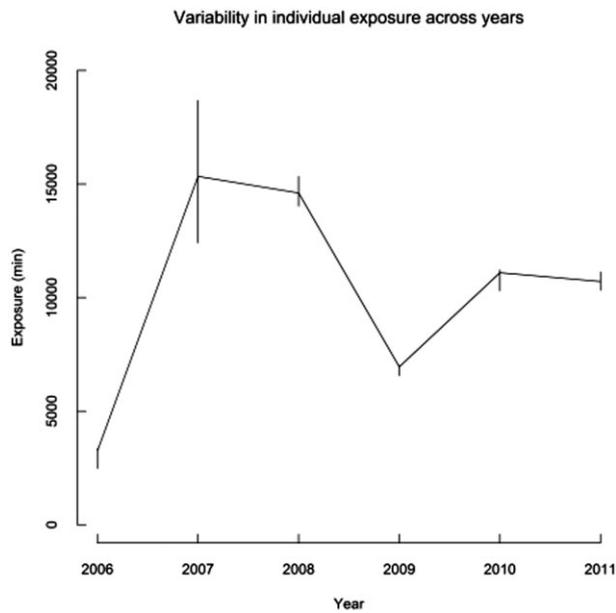


Figure 4 Variability in the median estimated individual exposure to boat traffic across years. The vertical lines represent the inter-quartile range.

probability was constant across individuals, allowing for heterogeneity either between groups or single dolphins would improve its biological realism. Moreover, a spatially explicit version of the Jolly-Seber model (Pollock *et al.*, 1990) could be implemented to avoid running separate yearly models. However, these adjustments would require a larger dataset with many recaptures for each individual to estimate the greater number of parameters.

Despite the large variability in absolute values of exposure, the relative pressure of boat traffic in different regions of the Firth remained more stable. Although this was partly driven by the use of a single map for boat traffic distribution in the area for the whole study period, the dolphins' distribution also influenced the distribution of the exposure risk. From our results, it is thus possible to identify specific cells or areas where the probability and magnitude of the interactions between dolphins and boats are greater. As we estimated the exposure to a source of disturbance that has been operating in the area for decades, dolphins' distribution could have already been responding to this stressor. The space use that we observe might have evolved through time to minimize the interactions with regular (and hence predictable) boat traffic (Rako *et al.*, 2013). Similarly, dolphins may have responded to these stressors by avoiding periods of the day or tidal cycle with peak boat traffic. Furthermore, our work focused on the summer months, when dolphins

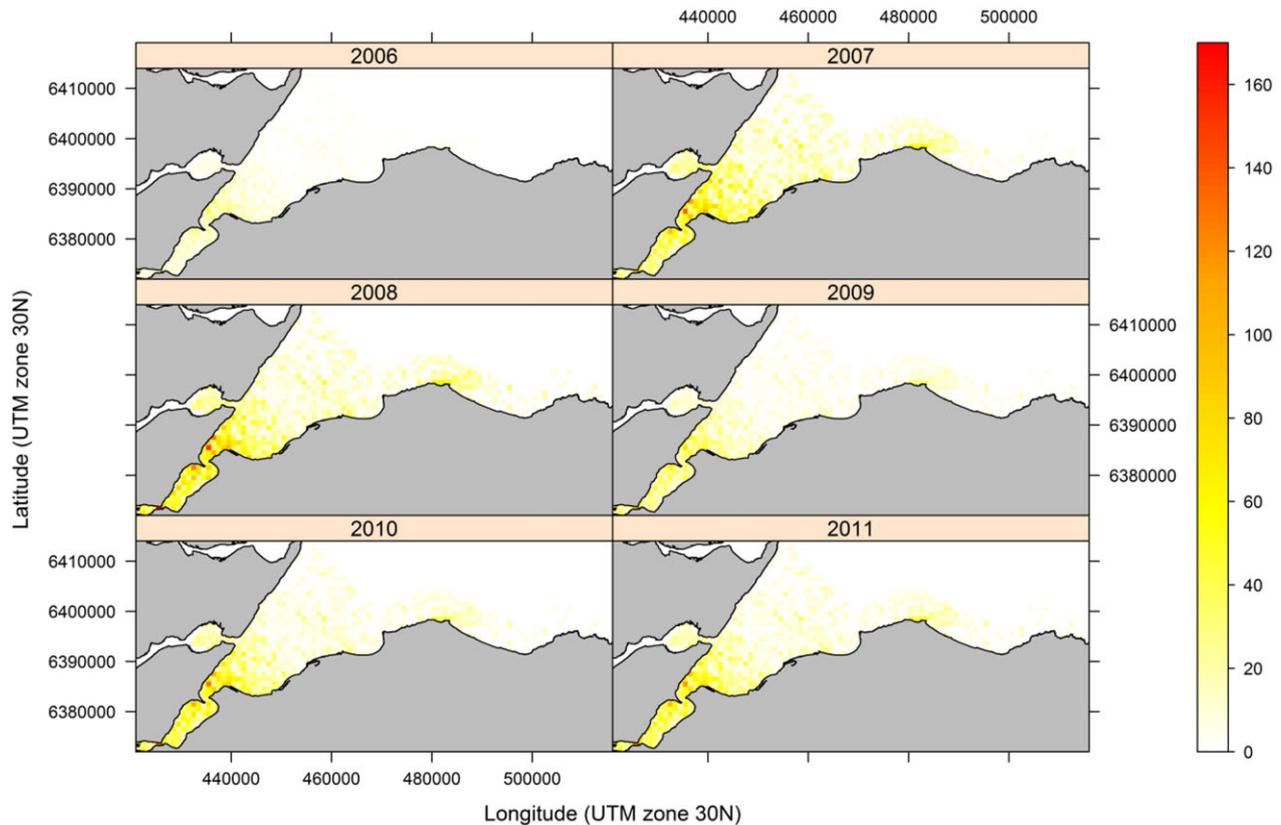


Figure 5 Distribution of dolphin exposure to boat traffic across the study area. Exposure is the median estimated number of minutes spent by one dolphin in the presence of boats in each grid cell.

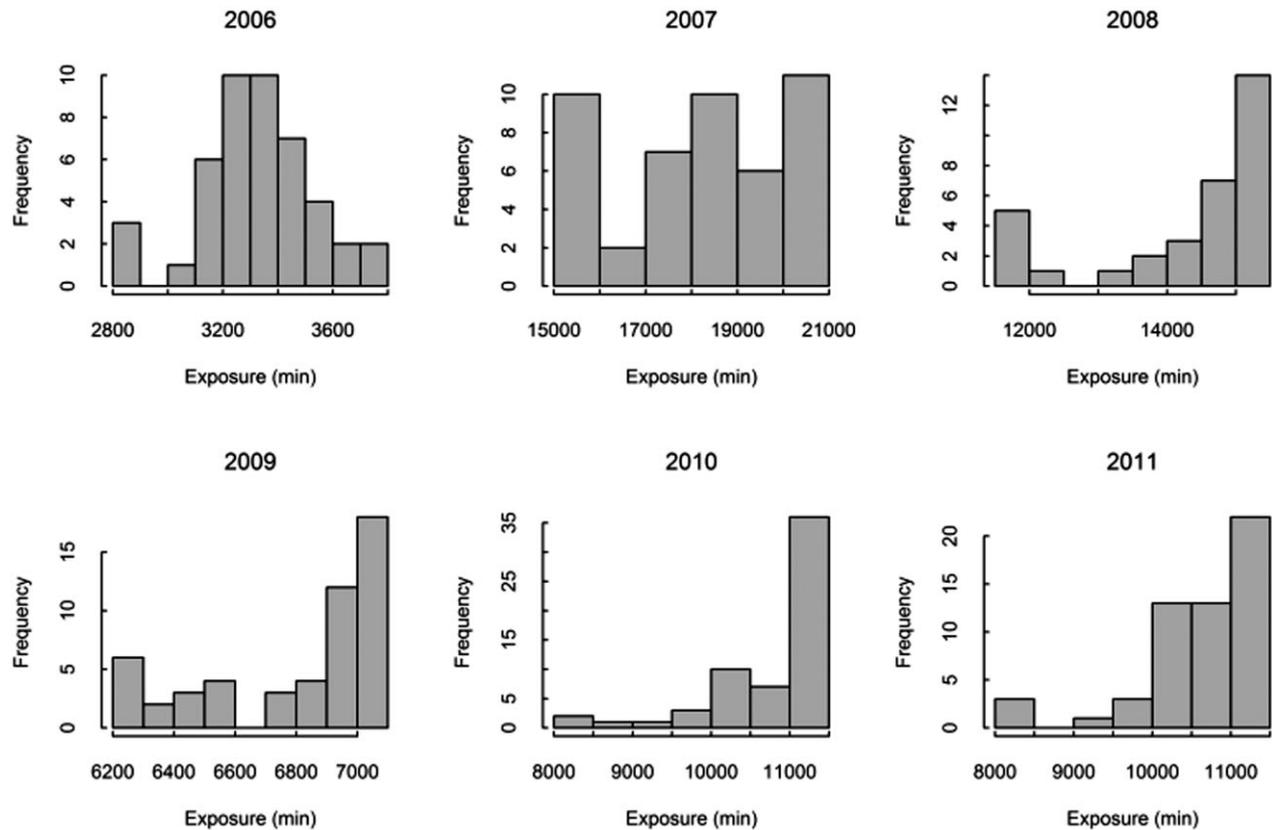


Figure 6 Variability of median individual exposure in each sampled year.

abundance in the area is highest (Wilson, Thompson & Hammond, 1997), but it would be valuable to extend this approach to other periods of the year, or other parts of the population's range where it is not currently possible to assess exposure to boat traffic.

Within years, individual animals showed marked differences in space usage, both in terms of the location of their activity centre within the Moray Firth, and of the realized space usage around such centre. Although the model assumed that capture probability was constant across individuals, this variation in space usage could arise from the procedure we followed to estimate an individual's home range. By calculating the probability of observing a specific dolphin across the grid cells at each iteration, we incorporated the uncertainty associated with the position of the activity centre. Therefore, an individual whose activity centre was less defined had a more diffuse home range than another for which the activity centre was consistently estimated in a specific grid cell (e.g. Supporting Information Fig. S4). The uncertainty on the position of the activity centre could depend on both the number of times an individual was encountered within a year and the individuals' natural differences in the use of their home range. A different use of space then resulted in a variable exposure to boat traffic. This should not be ignored when planning management, especially for long-lived marine top predators showing complex interactions with their environment and

social structures (Natoli *et al.*, 2005; Mattisson *et al.*, 2013). The differential habitat use appeared to be partially consistent across time, suggesting that some individuals might be chronically exposed to more traffic than others, although this variability was small compared with the year-to-year changes. Consistently overexposed individuals belonged to the social unit that was found to use the inner Moray Firth during earlier studies, whereas underexposed individuals ranged over a wider area including the outer part of the firth (Fig. 7) (Lusseau *et al.*, 2006). In future, the survival and reproductive performance of individual dolphins could be compared with their relative exposure to traffic, thereby informing efforts to predict the consequences of this human activity at a population level (New *et al.*, 2013).

Conservation implications

Boat traffic (both commercial and recreational) is increasing worldwide (Hildebrand, 2009). This raises concern for the potential effects on marine mammal populations, deriving from both the noise introduced in the environment (e.g. Aguilar Soto *et al.*, 2006) and the physical interactions between animals and vessels (e.g. Lusseau, 2003). Any long-term consequence of this disturbance on the exposed populations will be mediated by the repeated disruption of the activity patterns of individual animals (New *et al.*, 2013). European conservation legislation now requires regulators

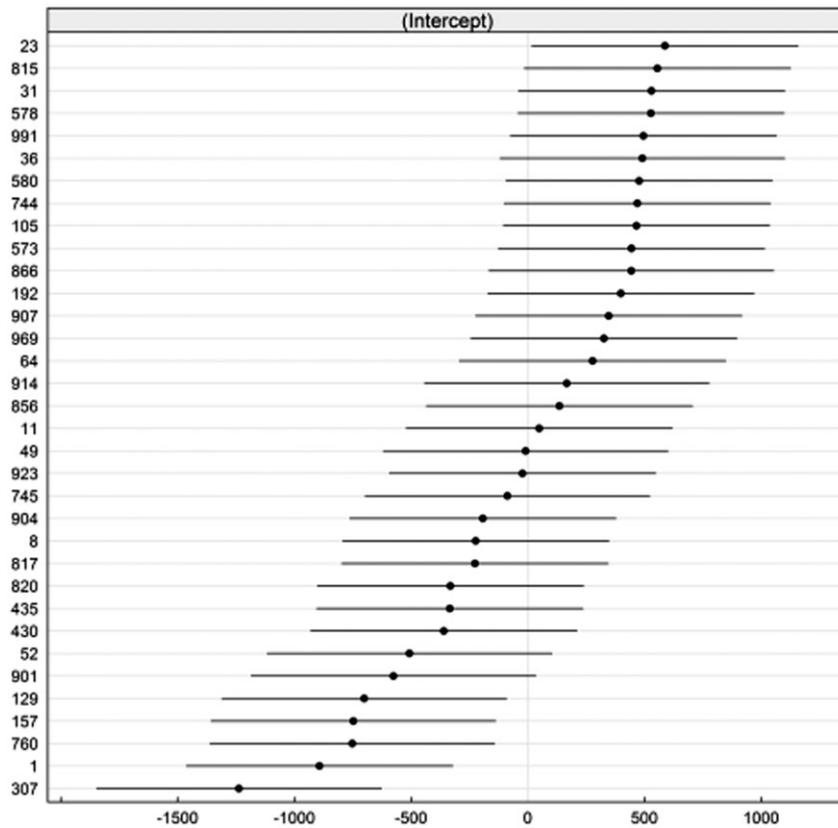


Figure 7 Dot plot for the random effects in the model for the exposure of the 34 individuals that were encountered in at least 5 years.

to estimate the cumulative exposure of individuals to such stressors in order to infer the population consequences of these disturbances (Cooper & Sheate, 2002). Our results highlight the importance of analytical approaches that incorporate individual heterogeneity in behaviour and habitat use in this process. For example, if a vulnerable class in the population tended to have higher exposure rates (e.g. juveniles, or mothers with calves), ignoring differences between individuals would lead to underestimating any potential consequences. We also show that animals that primarily use the inner portion of the Moray Firth were consistently more exposed to traffic, indicating that spatial differences could affect the individuals' requirements for conservation.

Characterizing individual differences in exposure and, consequently, performance provides a basis to assess the contribution of individuals to the population's demographic rates (Coulson *et al.*, 2006) and how this varies as the intensity and distribution of a stressor evolves in time. Moreover, by providing a framework to quantify individual heterogeneity in exposure to risk, our approach could be applied to other ecological questions. For example, it could be used to evaluate the behaviourally mediated effects of spatially heterogeneous predation risk (Laundré, Hernández & Altendorf, 2001; Wirsing *et al.*, 2008) and the cascade of responses that such risk could cause at a community level (Schmitz, Beckerman & O'Brien, 1997).

We found marked yearly variation in the basal probability of encounter, suggesting that the quality of the study area

and its resulting importance for the animals could be changing over time. As a result, animals' tolerance of boat disturbance is also expected to vary (Beale & Monaghan, 2004), and in some years, the risk from boat traffic in the Moray Firth could be lower. Such fluctuations complicate the management of any anthropogenic impact on the animals. For example, the existing SAC, which protects a part of the animals' overall range, does not account for the detected variability in occurrence and exposure. Patterns of exposure in other parts of the range need to be quantified for a complete understanding of the effects on the individuals, and a more flexible management scheme could then be developed. However, we identified where boats and dolphins are most likely to overlap within the existing marine protected area, which can focus management efforts on localized regions with higher risk (Cañadas *et al.*, 2005). Despite the absolute yearly differences, the stability of the relative spatial risk across years further reinforces a long-term management strategy.

Conclusion

Given the increasing range of human activities targeting the marine environment (Halpern *et al.*, 2008), robust quantitative tools are necessary to evaluate any effect on animal populations. Spatially explicit agent-based models for the interactions between such activities and animals require information on where and when these interactions are more likely

to occur (Anwar *et al.*, 2007; McLane *et al.*, 2011; New *et al.*, 2013). Our study provides a useful framework to inform these models while accounting for individual heterogeneity.

Acknowledgements

This work received funding from the MASTS pooling initiative (the Marine Alliance for Science and Technology for Scotland) and their support is gratefully acknowledged. MASTS is funded by the Scottish Funding Council (grant reference HR09011) and contributing institutions. We would like to thank Marine Scotland and Scottish Natural Heritage for partly funding this work. We would particularly like to thank Ben Leyshon for all his support. Photo-identification data were collected during a series of grants and contracts from the BES, ASAB, Greenpeace Environmental Trust, Scottish Natural Heritage, Scottish Government, Whale and Dolphin Conservation, Talisman Energy (UK) Ltd., Department of Energy and Climate Change, Chevron and the Natural Environment Research Council. All survey work was carried out under Scottish Natural Heritage Animal Scientific Licences. We also would like to thank Andrew Royle, David Borchers, Darren Kidney and Steve Palmer for their useful advice at the early stages of this work, and Fredrik Christiansen for invaluable discussions on spatially explicit capture–recapture techniques. Finally, we thank Tim Barton and all the people who have helped during data collection.

References

- Aguilar Soto, N., Johnson, M., Madsen, P.T., Tyack, P.L., Bocconcelli, A. & Fabrizio Borsani, J. (2006). Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*)? *Mar. Mamm. Sci.* **22**, 690–699.
- Anwar, S.M., Jeanneret, C.A., Parrott, L. & Marceau, D.J. (2007). Conceptualization and implementation of a multi-agent model to simulate whale-watching tours in the St. Lawrence Estuary in Quebec, Canada. *Environ. Model. Softw.* **22**, 1775–1787.
- Bailey, H. & Thompson, P. (2009). Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. *Mar. Ecol. Prog. Ser.* **378**, 279–287.
- Bates, D., Maechler, M. & Bolker, B. (2012). lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999999-0. Available at: <http://cran.r-project.org/package=lme4>
- Bauduin, S., Martin, J., Edwards, H.H., Gimenez, O., Koslovsky, S.M. & Fagan, D.E. (2013). An index of risk of co-occurrence between marine mammals and watercraft: example of the Florida manatee. *Biol. Conserv.* **159**, 127–136.
- Beale, C.M. & Monaghan, P. (2004). Behavioural responses to human disturbance: a matter of choice? *Anim. Behav.* **68**, 1065–1069.
- van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M. & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J. Anim. Ecol.* **80**, 771–785.
- Bixler, A. & Gittleman, J.L. (2000). Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). *J. Zool. (Lond.)* **251**, 525–533.
- Borchers, D.L. & Efford, M.G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* **64**, 377–385.
- Campioni, L., Delgado, M.D.M., Lourenço, R., Bastianelli, G., Fernández, N. & Penteriani, V. (2013). Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. *Oecologia* **172**, 371–385.
- Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E. & Hammond, P.S. (2005). Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquat. Conserv.* **15**, 495–521.
- Cheney, B., Corkrey, S., Quick, N., Janik, V.M., Islas-Villanueva, V., Hammond, P.S. & Thompson, P.M. (2012). *Site condition monitoring of bottlenose dolphins within the Moray Firth Special Area of Conservation: 2008–2010*. Scottish Natural Heritage Commissioned Report No. 512.
- Cheney, B., Thompson, P.M., Ingram, S.N., Hammond, P.S., Stevick, P.T., Durban, J.W., Culloch, R.M., Elwen, S.H., Mandleberg, L., Janik, V.M., Quick, N.J., Islas-Villanueva, V., Robinson, K.P., Costa, M., Einfeld, S.M., Walters, A., Phillips, C., Weir, C.R., Evans, P.G.H., Anderwald, P., Reid, R.J., Reid, J.B. & Wilson, B. (2013). Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters. *Mamm. Rev.* **43**, 71–88.
- Cooper, L. & Sheate, W. (2002). Cumulative effects assessment: a review of UK environmental impact statements. *Environ. Impact Assess. Rev.* **22**, 415–439.
- Coulson, T., Benton, T.G., Lundberg, P., Dall, S.R.X., Kendall, B.E. & Gaillard, J.-M. (2006). Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc. Roy. Soc. Lond. B Bio.* **273**, 547–555.
- Crocker, D.R. (2005). Estimating the exposure of birds and mammals to pesticides in long-term risk assessments. *Ecotoxicology* **14**, 833–851.
- Efford, M. (2004). Density estimation in live-trapping studies. *Oikos* **106**, 598–610.
- Gelman, A., Meng, X. & Stern, H. (1996). Posterior predictive assessment of model fitness via realized discrepancies. *Stat. Sin.* **6**, 733–807.
- Gopalaswamy, A.M., Royle, A.J., Hines, J.E., Singh, P., Jathanna, D., Kumar, N.S. & Karanth, K.U. (2012). SPACECAP: a program to estimate animal abundance and density using Bayesian spatially-explicit capture–

- recapture models. R package version 1.0.6. Available at: <http://cran.r-project.org/package=SPACECAP>
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. (2008). A global map of human impact on marine ecosystems. *Science* **319**, 948–952.
- Hastie, G.D., Wilson, B., Wilson, L.J., Parsons, K.M. & Thompson, P.M. (2004). Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Mar. Biol.* **144**, 397–403.
- Hildebrand, J.A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* **395**, 5–20.
- Hope, B. (2000). Generating probabilistic spatially-explicit individual and population exposure estimates for ecological risk assessments. *Risk Anal.* **20**, 573–589.
- Laundré, K.B., Hernández, J.W. & Altendorf, L. (2001). Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, U.S.A. *Can. J. Zool.* **79**, 1401–1409.
- Linkov, I., Burmistrov, D., Cura, J. & Bridges, T.S. (2002). Risk based management of contaminated sediments: consideration of spatial and temporal patterns in exposure modeling. *Environ. Sci. Technol.* **36**, 238–246.
- Lusseau, D. (2003). Effects of tour boats on the behavior of bottlenose dolphins: using Markov chains to model anthropogenic impacts. *Conserv. Biol.* **17**, 1785–1793.
- Lusseau, D., Williams, R., Wilson, B., Grellier, K., Barton, T.R., Hammond, P.S. & Thompson, P.M. (2004). Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecol. Lett.* **7**, 1068–1076.
- Lusseau, D., Wilson, B., Hammond, P.S., Grellier, K., Durban, J.W., Parsons, K.M., Barton, T.R. & Thompson, P.M. (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *J. Anim. Ecol.* **75**, 14–24.
- Lusseau, D., New, L., Donovan, C., Cheney, B., Thompson, P.M., Hastie, G. & Harwood, J. (2011). *The development of a framework to understand and predict the population consequences of disturbances for the Moray Firth bottlenose dolphin population*. Scottish Natural Heritage Commissioned Report No. 468.
- Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R. & Pedersen, H.C. (2013). Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia* **173**, 813–825.
- McLane, A.J., Semeniuk, C., McDermid, G.J. & Marceau, D.J. (2011). The role of agent-based models in wildlife ecology and management. *Ecol. Modell.* **222**, 1544–1556.
- Naidoo, R., Preez, P.D., Stuart-Hill, G., Weaver, L.C., Jago, M. & Wegmann, M. (2012). Factors affecting intraspecific variation in home range size of a large African herbivore. *Landsc. Ecol.* **27**, 1523–1534.
- Naidoo, R., Preez, P.D., Stuart-Hill, G., Weaver, L.C., Natoli, A., Birkun, A., Aguilar, A., Lopez, A. & Hoelzel, A.R. (2005). Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proc. Roy. Soc. Lond. B Bio.* **272**, 1217–1226.
- New, L.F., Harwood, J., Thomas, L., Donovan, C., Clark, J.S., Hastie, G., Thompson, P.M., Cheney, B., Scott-Hayward, L. & Lusseau, D. (2013). Modeling the biological significance of behavioral change in coastal bottlenose dolphins in response to disturbance. *Funct. Ecol.* **27**, 314–322.
- Pelc, R. & Fujita, R. (2002). Renewable energy from the ocean. *Mar. Policy* **26**, 471–479.
- Pollock, K., Nichols, J.D., Brownie, C. & Hines, J.E. (1990). Statistical inference for capture-recapture experiments. *Wildl. Monogr.* **107**, 3–97.
- R Development Core Team (2013). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0. URL: <http://www.R-project.org/>
- Rako, N., Fortuna, C.M., Holcer, D., Mackelworth, P., Nimak-Wood, M., Pleslić, G., Sebastianutto, L., Vilibić, I., Wiemann, A. & Picciulin, M. (2013). Leisure boating noise as a trigger for the displacement of the bottlenose dolphins of the Cres-Lošinj archipelago (northern Adriatic Sea, Croatia). *Mar. Pollut. Bull.* **68**, 77–84.
- Read, A.J., Drinker, P. & Northridge, S. (2006). Bycatch of marine mammals in U.S. and global fisheries. *Conserv. Biol.* **20**, 163–169.
- Redfern, J.V., McKenna, M.F., Moore, T.J., Calambokidis, J., Deangelis, M.L., Becker, E.A., Barlow, J., Forney, K.A., Fiedler, P.C. & Chivers, S.J. (2013). Assessing the risk of ships striking large whales in marine spatial planning. *Conserv. Biol.* **27**, 292–302.
- Royle, J., Nichols, J., Karanth, K.U. & Gopalaswamy, A.M. (2009a). A hierarchical model for estimating density in camera-trap studies. *J. Appl. Ecol.* **46**, 118–127.
- Royle, J.A., Karanth, K.U., Gopalaswamy, A.M. & Kumar, N.S. (2009b). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology* **90**, 3233–3244.
- Royle, J.A., Kéry, M. & Guélat, J. (2011). Spatial capture-recapture models for search-encounter data. *Methods Ecol. Evol.* **2**, 602–611.
- Russell, R.E., Royle, J.A., Desimone, R., Schwartz, M.K., Edwards, V.L., Pilgrim, K.P. & McKelvey, K.S. (2012). Estimating abundance of mountain lions from unstructured spatial sampling. *J. Wildl. Mgmt.* **76**, 1551–1561.

- Schmitz, O., Beckerman, A. & O'Brien, K. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* **78**, 1388–1399.
- Schoener, T. & Schoener, A. (1982). Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology* **63**, 809–823.
- Schofield, G., Hobson, V.J., Lilley, M.K.S., Katselidis, K.A., Bishop, C.M., Brown, P. & Hays, G.C. (2010). Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. *Biol. Conserv.* **143**, 722–730.
- Schradin, C., Schmohl, G., Rödel, H.G., Schoepf, I., Treffler, S.M., Brenner, J., Bleeker, M., Schubert, M., König, B. & Pillay, N. (2010). Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. *Anim. Behav.* **79**, 195–203.
- Schreier, M., Mannstein, H., Eyring, V. & Bovensmann, H. (2007). Global ship track distribution and radiative forcing from 1 year of AATSR data. *Geophys. Res. Lett.* **34**, 1–6.
- Thompson, C.M., Royle, J.A. & Garner, J.D. (2012). A framework for inference about carnivore density from unstructured spatial sampling of scat using detector dogs. *J. Wildl. Mgmt.* **76**, 863–871.
- Thompson, P.M., Lusseau, D., Barton, T., Simmons, D., Rusin, J. & Bailey, H. (2010). Assessing the responses of coastal cetaceans to the construction of offshore wind turbines. *Mar. Pollut. Bull.* **60**, 1200–1208.
- Vaes, T. & Druon, J.-N. (2013). *Mapping of potential risk of ship strike with fin whales in the Western Mediterranean Sea: a scientific and technical review using the potential habitat of fin whales and the effective vessel density*. European Commission Joint Research Centre, Scientific and Technical Research Report No. JRC79841.
- Vanderlaan, A., Taggart, C., Serdynska, A., Kenney, R. & Brown, M. (2008). Reducing the risk of lethal encounters: vessels and right whales in the Bay of Fundy and on the Scotian Shelf. *Endanger. Species Res.* **4**, 283–297.
- Vindenes, Y., Engen, S. & Saether, B.-E. (2008). Individual heterogeneity in vital parameters and demographic stochasticity. *Am. Nat.* **171**, 455–467.
- Wang, M. & Grimm, V. (2007). Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*. *Ecol. Modell.* **205**, 397–409.
- Wickwire, T., Johnson, M.S., Hope, B.K. & Greenberg, M.S. (2011). Spatially explicit ecological exposure models: a rationale for and path toward their increased acceptance and use. *Integr. Environ. Assess. Manag.* **7**, 158–168.
- Williams, R. & O'Hara, P. (2010). Modelling ship strike risk to fin, humpback and killer whales in British Columbia, Canada. *J. Cetacean. Res. Manag.* **11**, 1–10.
- Wilson, B., Thompson, P. & Hammond, P. (1997). Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *J. Appl. Ecol.* **34**, 1365–1374.
- Wilson, B., Reid, R.J., Grellier, K., Thompson, P.M. & Hammond, P.S. (2004). Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. *Anim. Conserv.* **7**, 331–338.
- Wirsing, A.J., Heithaus, M.R., Frid, A. & Dill, L.M. (2008). Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. *Mar. Mamm. Sci.* **24**, 1–15.

Supplementary information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Distribution of survey effort in each summer of data collection.

Figure S2. Estimated relationship between encounter rate and effort.

Figure S3. Estimated probability of encountering individual 001 in each analysed summer (same scale used for plotting).

Figure S4. Estimated probability of encountering individual 907 and individual 001 in summer 2006.

Appendix S1. Customized SPACECAP code for R.