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Original research article

Long-term trends in the use of a protected area by small cetaceans in relation to changes in population status

Barbara Cheney[a,*], Ross Corkrey[a,1], John W. Durban[a,2], Kate Grellier[a,b,3], Philip S. Hammond[b], Valentina Islas-Villanueva[b,4], Vincent M. Janik[b], Susan M. Lusseau[a,5], Kim M. Parsons[a,6], Nicola J. Quick[b,7], Ben Wilson[a,8], Paul M. Thompson[a]

[a] University of Aberdeen, Institute of Biological and Environmental Science, Lighthouse Field Station, Cromarty, IV11 8YL, UK

[b] Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, Fife KY16 8LB, UK

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A B S T R A C T

The requirement to monitor listed species in European designated sites is challenging for long-lived mobile species that only temporarily occupy protected areas. We use a 21 year time series of bottlenose dolphin photo-identification data to assess trends in abundance and conservation status within a Special Area of Conservation (SAC) in Scotland. Mark–recapture methods were used to estimate annual abundance within the SAC from 1990 to 2010. A Bayesian mark–recapture model with a state-space approach was used to estimate overall population trends using data collected across the populations' range. Despite inter-annual variability in the number of dolphins within the SAC, there was a >99% probability that the wider population was stable or increasing. Results indicate that use of the SAC by the wider population has declined. This is the first evidence of long-term trends in the use of an EU protected area by small cetaceans in relation to changes in overall population status. Our results highlight the importance of adapting the survey protocols used in long-term photo-identification studies to maintain high capture probabilities and minimise sampling heterogeneity. Crucially, these data demonstrate the value of collecting

* Corresponding author. Tel.: +44 0 1381600548.
E-mail addresses: b.cheney@abdn.ac.uk (B. Cheney), scorkrey@utas.edu.au (R. Corkrey), john.durban@noaa.gov (J.W. Durban), kateg@naturalpower.com (K. Grellier), psh2@st-andrews.ac.uk (P.S. Hammond), v.islas.villanueva@gmail.com (V. Islas-Villanueva), vj@st-andrews.ac.uk (V.M. Janik), susan.lusseau@scotland.gsi.gov.uk (S.M. Lusseau), kim.parsons@noaa.gov (K.M. Parsons), nicola.quick@duke.edu (N.J. Quick), ben.wilson@sams.ac.uk (B. Wilson), lighthouse@abdn.ac.uk (P.M. Thompson).

1 Present address: Tasmanian Institute of Agriculture, University of Tasmania, Private Bag 54, Hobart, Tasmania, 7001, Australia.

2 Present address: Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Dr., La Jolla, CA 92037, USA.

3 Present address: Natural Power, The Green House, Forrest Estate, Dalry, Castle Douglas DG7 3XS, UK.

4 Present address: Instituto de Ciencias del Mar y Limnología, UNAM, 04510, Mexico.

5 Present address: Marine Scotland Science, Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK.

6 Present address: National Marine Mammal Laboratory, NOAA, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA.

7 Present address: Nicholas School of the Environment, Duke Marine Lab, 135 Duke Marine Lab Road, Beaufort, NC, USA.

8 Present address: Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll PA37 1QA, UK.

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data from the wider population to assess the success of protected areas designated for mobile predators.

1. Introduction

Estimation of abundance and trends underpins population ecology and is essential information for management and conservation efforts (Krebs, 2001). In some countries, regular assessments of abundance are also a legislative requirement to support conservation of protected species (e.g. Wade and Angliss, 1996) or areas (Cowx et al., 2009). In Europe, the Habitats Directive (92/43/EEC) requires the designation of Special Areas of Conservation (SACs) as a measure to help protect species listed in Annex II. The Directive requires Member States to report on the conservation status of these species on a six year cycle, including information on their abundance within the protected area (European Union, 1992). However, it is challenging to design cost-effective survey programmes that can assess population status, particularly for mobile species that commonly range across the boundaries of protected areas (Hammond et al., 2013).

This problem is particularly acute for cetaceans as they are often widely distributed, highly mobile and spend a high proportion of time underwater, making it difficult to obtain accurate and precise abundance estimates. A long time series of data is typically needed to provide sufficient statistical power to detect trends from estimates of abundance (Taylor et al., 2007; Thompson et al., 2000; Wilson et al., 1999). For example, Taylor et al. (2007) highlight that most marine mammal stocks in the USA have inadequate data to detect a 50% decline in abundance over 15 years. While some studies have used sightings surveys to identify long-term trends in large whale populations (Branch and Butterworth, 2001; Buckland and Breiwick, 2002; Moore and Barlow, 2011), published data on abundance trends in coastal small cetaceans are rare (see Fearnbach et al., 2012, for a recent exception). Nevertheless, information on abundance is available from many small cetacean populations through photo-identification based mark–recapture methods (Berrow et al., 2012; Currey et al., 2011; Durban et al., 2000; Gormley et al., 2012; Nicholson et al., 2012; Pesante et al., 2008). These long-term studies can provide time series of abundance estimates for evaluating trends and informing the management of protected areas established for these populations. However, there are two issues that need to be considered when developing survey programmes for small cetaceans in these areas.

First, whilst standardised survey protocols are preferred in long-term ecological studies (Currey et al., 2007; Magurran et al., 2010), these can overlook the dynamic way in which populations use their range, introducing bias and increasing uncertainty in abundance estimates (Forney, 2000). In mark–recapture studies, both short term (e.g. Nicholson et al., 2012; Parra et al., 2006) and long-term (e.g. Wilson et al., 2004) temporal changes in distribution or ranging patterns may introduce heterogeneity in capture probabilities along otherwise standardised survey routes, resulting in biased abundance estimates. Where these changes occur during a longer-term study, survey protocols may need to be adapted to reduce sampling heterogeneity. Similarly, developments in technology, statistical techniques, changing research priorities, logistics or financial constraints may all lead to modifications to survey protocols over time (Lindenmayer and Likens, 2009; Ringold et al., 1996). The consequences of such flexible approaches must be explored before drawing inference from a long-term time series. Of particular concern to photo-identification mark–recapture studies, where some individuals do not have markings that can be reliably identified between annual survey seasons, are potential changes in the proportion of distinctive or well-marked animals. An accurate estimate of this proportion is required to account for non-distinct animals when estimating total abundance (e.g. Durban et al., 2010; Gormley et al., 2005; Lukoschek and Chilvers, 2008; Read et al., 2003; Wilson et al., 1999). Longer-term temporal changes in this proportion may have an underlying biological basis, for example if age or sex differences in the occurrence of distinctive marks exist, a trend may reflect changes in population age or sex structure. However, it may also be affected by survey protocols. For example, photo quality and mark distinctiveness can be correlated due to photographer bias if more time is spent obtaining quality pictures of well-marked animals (Read et al., 2003).

Secondly, survey effort is typically focused on monitoring abundance trends within only part of the overall range of the population. This means that monitoring programmes generally only provide information on variation in the abundance of individuals using a specific area rather than changes in the population itself (Forney, 2000). In some cases, monitoring may only be conducted within a protected area (Berrow et al., 2012; Gnone et al., 2011; Gormley et al., 2005). Yet European Directives aim to designate networks of core sites that support the conservation status of the wider population (European Union, 1992). Robust design methods could be used to assess the extent of seasonal emigration in and out of such sites (e.g. Nicholson et al., 2012; Smith et al., 2013). However, the collection of at least some information from the wider population may be needed to assess the relative value of the protected area itself (Hooker and Gerber, 2004), and this typically requires a modelling framework that can be used with much sparser data from less frequent surveys (e.g. Corkrey et al., 2008).

Here, we explore these issues using a continuous 21 year time series of data from photo-identification surveys of bottlenose dolphins (*Tursiops truncatus*) off north-east Scotland. Our aim was firstly to use core annual survey data to assess trends in abundance within an SAC over the last two decades, thereby allowing the UK government to contribute to their reporting requirements under the EU Habitats Directive. We then go on to use Corkrey et al. (2008) state-space mark–recapture

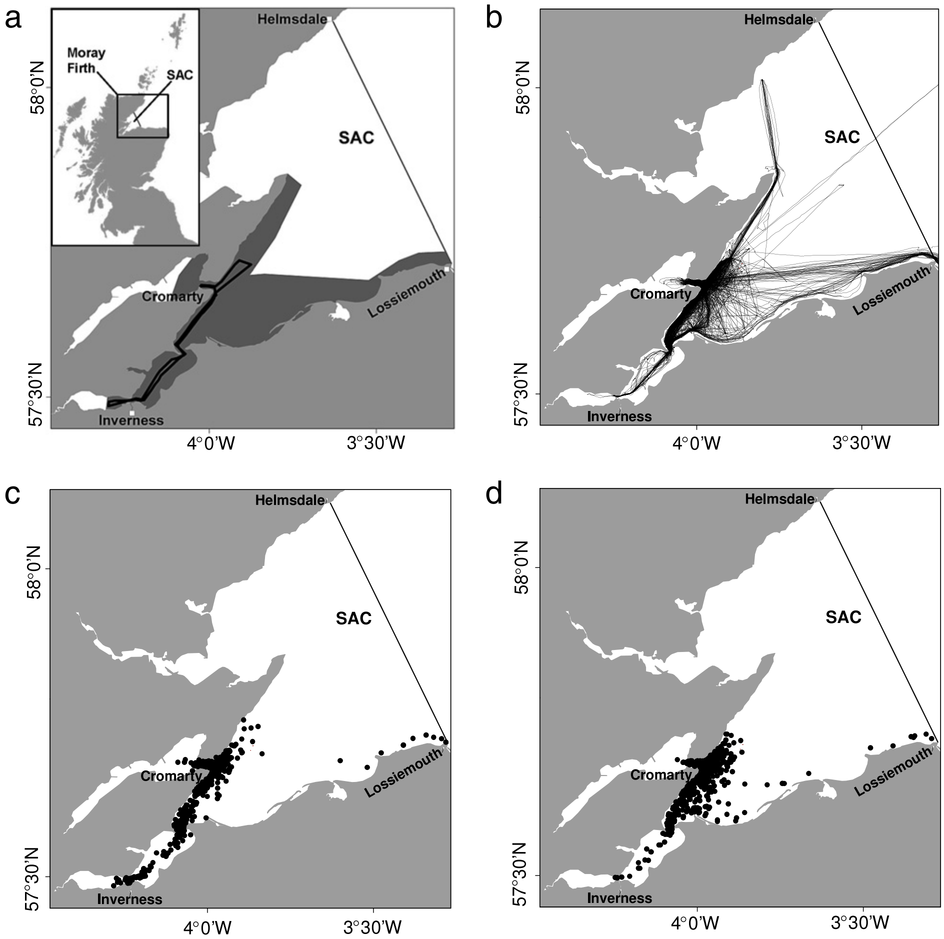

Fig. 1. The Moray Firth Special Area of Conservation (SAC) with photo-identification surveys (a) the fixed survey route for the majority of surveys (>80%) from 1990 to 2000 (black line), with occasional surveys in other areas (grey shading), (b) GPS tracks of flexible surveys from 2001 onward, and the location of all bottlenose dolphin encounters in (c) 1990–2000, and (d) 2001–2010. Inset shows the location of the Moray Firth and the boundary of the SAC.

model which incorporates other data sources to estimate overall trends across the entire population range, and combine these data to investigate temporal changes in the use of this protected area.

2. Methods

2.1. Study population and photo-identification survey methods

The study monitored the bottlenose dolphin population that occurs along the east coast of Scotland (Cheney et al., 2013; Wilson et al., 2004). In response to the 1992 EU Habitats Directive, part of this population's range was designated as the Moray Firth Special Area of Conservation in 2005 (Fig. 1(a)).

Between 1990 and 2010, multiple boat-based photo-identification surveys were carried out each summer (May to September) within the area that was subsequently designated as the Moray Firth SAC (Tables 1 and A1 in Supporting information (see Appendix A). From 1990 to 2000, most surveys followed a fixed route through the core areas that were used regularly by dolphins at that time (Fig. 1(a)) (Wilson et al., 1997). From 2001 onwards, in response to changes in the distribution of dolphins within this area (Wilson et al., 2004), more flexible survey routes were chosen to maximise sighting probability both within the original core study area and other parts of the SAC (Fig. 1(b)). All surveys were made from small (5–6 m) boats with outboard engines (Thompson et al., 2011; Wilson et al., 1997). The time and position of all encounters were noted, and the boat was carefully manoeuvred at slow speed around dolphins to obtain high quality pictures of the left and right sides of the dorsal fins of as many individuals as possible. Photographs were taken with an SLR camera, with transparency film until 2001 and digital imagery thereafter.

In most years, some data were also collected during less regular summer (May to September) surveys in other parts of the population's range (see Fig. A1) (Cheney et al., 2013). These data were collected using standardised photo-identification

Table 1
Summary of the survey protocols and variables used in the generalised linear mixed models from the two decades of photo-identification surveys in the Moray Firth Special Area of Conservation. The annual mean (± standard error) are shown (full details in Table A2).

Survey protocols & variables	1990–2000	2001–2010
Survey Route	Fixed	Flexible
Camera	Film	Digital
Number of SAC surveys	19 (±2)	29 (±2)
Survey duration (hours)	6.1 (±0.3)	4.2 (±0.5)
Number of encounters	58 (±6)	80 (±5)
Encounter duration (minutes)	31 (±2)	30 (±2)
Survey time spent with dolphins	28% (±2%)	35% (±3%)
Number of well-marked dolphins	35 (±2)	47 (±2)
Number of new calves identified	7 (±2)	7 (±1)
Number of capture occasions	13 (±2)	24 (±1)
Number of captures	74 (±9)	230 (±24)

procedures (Cheney et al., 2013; Islas-Villanueva, 2010; Quick and Janik, 2008; Quick et al., 2008; Wilson et al., 2004) but the design and number of surveys varied among years and survey areas (see Table A1).

All photo-identification pictures were graded for photographic quality (Wilson et al., 1999) and analyses restricted to the highest quality photographs (Cheney et al., 2013). Each image was matched against a catalogue of known individuals from the east coast of Scotland and all matches were confirmed by at least two experienced researchers.

2.2. Trends in abundance within the Special Area of Conservation

Annual abundance was estimated using a modification of the approach developed by Wilson et al. (1999). Previously, estimates were derived separately for the left and right sides, but this led to high sampling variation in some years. Here, we based estimates on well-marked individuals with nicked dorsal fins that could be identified from both sides, and produced a single capture history combining the left and right sides for each year. Goodness of fit tests in program CAPTURE (Rexstad and Burnham, 1991) suggested that the Chao et al. (1992) M_{th} model was the most appropriate model for the majority of years with the M_t model for the remaining years. We implemented both models in CAPTURE. In all but four years the M_{th} model estimates were larger, indicating that there was heterogeneity of capture probabilities in our data (Chao et al., 1992). Therefore the M_{th} model was used to estimate the number of well-marked individuals during each summer field season and capture probabilities for each survey. This closed model was appropriate as abundance estimates were made independently for each year.

High quality pictures were used to assess the proportion of well-marked animals on each survey (θ), calculated separately for the left and right sides (because dolphins with no nicks may not be identified from both sides). Trend in θ over time was explored using a generalised linear model (GLM) with binomial error distribution and logit link. Variability in θ in relation to different biological and sampling variables was then considered using generalised linear mixed models (GLMMs) with binomial error distribution and logit link. This GLMM approach accounted for repeated measures and non-independence between the left and the right side estimation of θ, using survey as a random effect. Biological variables included mark-recapture estimates of the number of well-marked animals and the number of new calves identified each year. Sampling variables included the total number of surveys, number of encounters, cumulative number of well-marked individuals identified (captures) and the number of surveys where at least one well-marked dolphin was identified in a high quality picture (capture occasions). Changes to our survey protocols were also considered, including the change from a fixed survey route to flexible surveys and from film to digital cameras (see Table A2 for details). As some of these explanatory variables were collinear, each was separately considered in its own GLMM fitted with maximum likelihood in the lme4 package (Bates et al., 2014). Model selection was carried out using Akaike Information Criterion (AIC) (Burnham and Anderson, 2002) and all analyses were carried out in R version 3.0.2 (R Core Team, 2013).

The proportion of well-marked animals (θ) was estimated using the GLMM with the lowest AIC (see results). This was used to inflate the annual mark–recapture estimates of well-marked animals ($\hat{N}_t$) for each year t 1990–2010 to estimate total annual abundance ($N_{t\,total} = \hat{N}_t/\theta$) (see results). Assuming $N_{t\,total}$ is log normally distributed, the upper and lower 95% confidence intervals were estimated, by dividing and multiplying $N_{t\,total}$, respectively, by:

$$e^{1.96\sqrt{\ln(1+CV^2_{N_{t\,total}})}}$$

where:

$$CV^2_{N_{t\,total}} = \frac{var\left(\hat{N}_t\right)}{\hat{N}_t^2} + \frac{var\,(\theta)}{\theta^2}.$$

A linear regression was used to determine whether there was a trend in abundance within the SAC between 1990 and 2010.

2.3. Trends in population size

Data from outside the SAC were sparser (see Table A1), especially in the early part of the time-series, and capture probabilities were often low. Therefore, a Bayesian mark–recapture model with a state-space approach (Corkrey et al., 2008) was used to estimate abundance and trends for the total population. Capture histories were created to record whether or not well-marked individuals were sighted anywhere in the population's known range (see Cheney et al., 2013) during each summer (May–September) field season. This model incorporates a series of sub-models including an underlying population model (to provide probability distributions for modelling the well-marked population), an observation model (to provide probability distributions of capture probabilities to estimate the size of the well-marked population), a model to inflate for non-distinct individuals and a Cormack–Jolly–Seber recapture model (which incorporates heterogeneity of capture probabilities across individuals). This model explicitly accounts for heterogeneity and uncertainty, can use sparse sightings data and provides a probability of whether the population is on the decline or increasing (for full model details see Corkrey et al., 2008). Markov chain Monte Carlo (MCMC) simulation was used to obtain estimates of the posterior distribution of abundance estimates, and derive posterior means and variances. The model was fitted in Fortran compiler G95, version 0.93, for 1,000,000 iterations with a 50% burn in. This produced annual estimates from 1990 to 2010 of the total number of bottlenose dolphins using the east coast of Scotland with 95% highest posterior density intervals (HPDI).

A Bayesian linear regression model ($W_t' = W_I + W_S \times (t - 1)$) was used to determine whether or not there was a trend in total population abundance between 1990 and 2010 where W_t' is the predicted total population, W_I and W_S are intercept and slope parameters to be estimated and t is time (with $t = 1$ corresponding to 1990). The intercept and slope parameters were assigned vague normal priors with high variance (=1000), $W_I \sim N(0, 1000)$, $W_S \sim N(0, 1000)$ and $W_t \sim N(W_t', 1000)$ in which W_t is the estimated posterior total population.

2.4. Use of the Special Area of Conservation

To investigate trends in the proportion of the total population using the SAC from 1990 to 2010 we used a parametric bootstrap procedure to account for the uncertainty around our abundance estimates. For each year, estimates of abundance for the SAC and total population were drawn from lognormal distributions of the mean and variance of our SAC and total population abundance estimates. The annual proportion of the total population using the SAC was then calculated. A GLM with quasi-binomial error distribution to account for overdispersion in the data and logit link was fitted to these annual proportions to estimate the slope. This bootstrapping procedure was repeated 1000 times.

3. Results

3.1. Trends in abundance within the Special Area of Conservation

The change in survey protocols resulted in some differences in key variables between the first (1990–2000) and second decade (2001–2010) including a greater number of more frequent but shorter surveys during the second decade (Table 1).

A minimum of 21 and maximum of 60 well-marked individuals were identified in each year from high quality photographs. Mark–recapture estimates of the number of well-marked individuals ranged from 24 to 75, but there was no significant trend in the estimates of well-marked individuals using the SAC ($t_{19} = -0.738$, $p = 0.469$) (see Table A4). The coefficient of variation (CV) of estimates ranged from 0.03 to 0.28 (mean = 0.13) (see Table A4), decreasing as the number of surveys increased (linear regression, slope = −0.007, SE = 0.001, $t_{19} = -5.349$, $p < 0.0001$). Median capture probabilities for each year varied from 0.04 to 0.23, and were higher from 2001 onwards during the flexible rather than fixed survey protocol (1990–2000 median = 0.09, IQR = 0.06–0.10; 2001–2010 median = 0.17, IQR = 0.11–0.20).

Annual estimates of the proportion of well-marked animals (θ) varied among years (Fig. 2), with no significant difference between sides (Pearson's Chi-squared test, $\chi^2 = 0.069$, d.f. = 1, $p = 0.793$). There was an increasing trend in θ between 1990 and 2010 (right side: $z = 5.102$, $p < 0.001$; left: $z = 3.625$, $p = 0.0003$, Table A3), but no trend was detected within either the first or the second decade of research ($p > 0.05$, Fig. 2). None of the biological variables in the GLMMs explained significant variability in θ; instead, much of the variation was accounted for by covariates relating to survey protocols (Table 2). The best model included the change in survey protocol in 2001, from the fixed survey route to flexible surveys (Table 2). This model provided two estimates of θ, one for 1990–2000 for the fixed survey route ($\theta_1 = 0.4720$, SE = 0.0345) and one for 2001–2010 for the flexible survey route ($\theta_2 = 0.5609$, SE = 0.0425), resulting in a step increase in θ coinciding with the change in survey protocol (Fig. 2). There are two plausible causes for this change. One is that the population age structure has changed in such a way that θ has increased. However, there is no evidence for this (e.g. Table 2). The other, more likely, explanation is that estimates of θ have changed as a result of changes in sampling. A priori, one might expect any sampling differences that affected the estimation of θ to also affect the estimate of well-marked animals. However, there was no increase in the mean estimate of the number of well-marked dolphins (1990–2000: 52 (SE = 5), 2001–2010: 53 (SE = 2)). Given the possibility that the change in the estimate of θ is a result of sampling bias, the higher capture probabilities and reduced capture heterogeneity in the second decade, and the absence of biological explanations for a step change in θ, we argue that the estimate of θ from the second decade probably reflects the proportion of well-marked animals

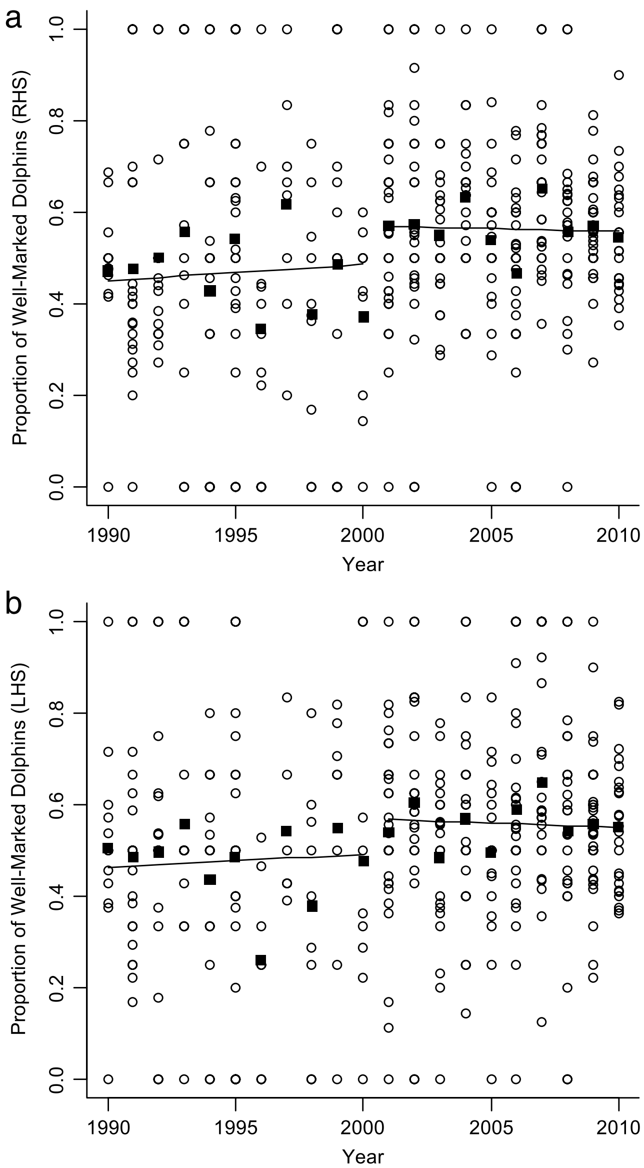

Fig. 2. The proportion of well-marked individuals (θ) for each survey, (a) right side and (b) left side from 1990 to 2010 (clear circles) and annual average estimates of θ (black squares) with binomial GLM fitted lines (black lines) for 1990–2000 (right side: $z = 0.784$, $p = 0.433$; left side: $z = 0.533$, $p = 0.594$) and 2001–2010 (right side: $z = -0.379$, $p = 0.705$; left side: $z = -0.663$, $p = 0.507$) (full GLM results in Table A3).

in this population throughout the time series. Accordingly θ_2 was applied to all annual mark–recapture estimates to estimate abundance within the SAC. However, given that we cannot rule out the possibility of a step-change in θ, we also explore the consequences of applying θ_1 to annual abundance estimates from 1990–2000 and θ_2 to estimates from 2001–2010 (see Table A4). We return to this point in the discussion.

Using θ_2 throughout the time series, estimates of the number of dolphins using the SAC ranged from 43 (95% confidence interval (CI): 32–57) in 1998 to 134 (95% CI: 92–193) in 1990 (Fig. 3 and Table A4), and there was no significant linear trend in annual estimates ($t_{19} = -0.729, p = 0.475$). However, applying the two different estimates of θ to data from the first and second decades of surveys (see Table A4) resulted in significant linear decline in annual estimates (slope $= -1.968$, SE $= 1.128$, $t_{19} = -2.348$, $p = 0.03$).

3.2. Trends in population size

Between 1990 and 2010 a minimum of 26 and maximum of 92 well-marked individuals were identified each year off the east coast of Scotland. Annual estimates of total population size using the Bayesian mark–recapture model ranged from

Table 2
The results of generalised linear mixed models to explore how the proportion of well-marked animals (θ) varied in relation to biological and sampling variables and changes to survey protocols. The model with the lowest AIC is in bold.

Fixed effects	Coefficient	Std. error	Z	P	Random effects	Variance	Std. dev.	AIC
Intercept	−0.1557	0.1142	−1.363	0.1730				
Total surveys	0.0111	0.0041	2.722	0.0065	Survey	0.1152	0.3395	2674.6
Intercept	0.0646	0.1226	0.526	0.599				
Encounters	0.0010	0.0015	0.673	0.501	Survey	0.1224	0.3499	2681.4
Intercept	−0.0840	0.0600	−1.399	0.162				
Captures	0.0015	0.0004	4.361	<0.0001	Survey	0.1096	0.331	2663.3
Intercept	−0.2915	0.0968	−3.012	0.0026				
Capture occasions	0.0207	0.0044	4.725	<0.0001	Survey	0.1045	0.3232	2660.3
Intercept	−0.0451	0.0483	−0.934	0.35				
Camera	0.2956	0.0603	4.903	<0.0001	Survey	0.1024	0.32	2658.8
Intercept	**−0.1146**	**0.0533**	**−2.149**	**0.0316**				
Survey route	**0.3620**	**0.0630**	**5.750**	**<0.0001**	**Survey**	**0.0924**	**0.3039**	**2650.8**
Intercept	0.0783	0.1068	0.734	0.463				
Mark–recapture estimate	0.0013	0.0020	0.647	0.518	Survey	0.1211	0.348	2681.5
Intercept	0.1676	0.0688	2.437	0.0148				
New calves	−0.0032	0.0085	−0.370	0.7110	Survey	0.1216	0.3487	2681.7

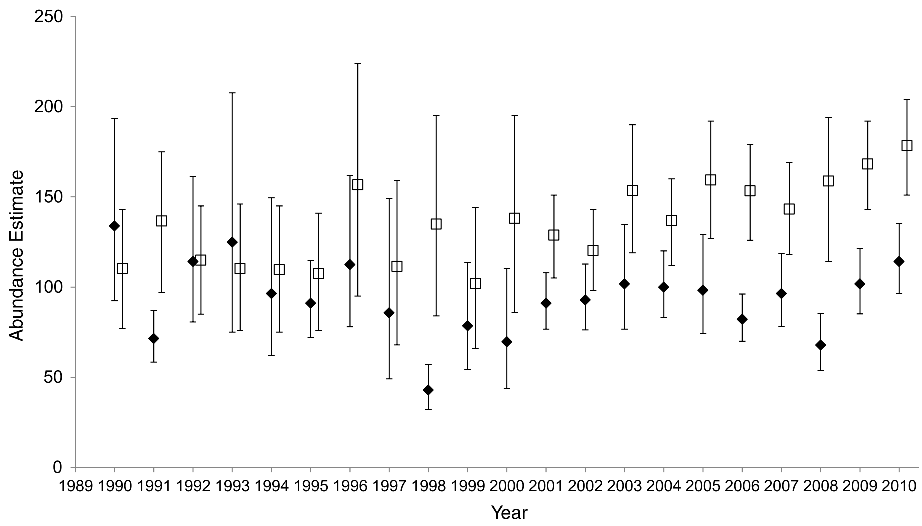

Fig. 3. Annual estimates of the number of bottlenose dolphins using the Moray Firth Special Area of Conservation from 1990 to 2010 (black diamonds) with 95% confidence intervals and of the total east coast of Scotland bottlenose dolphin population with posterior means (clear squares) and 95% highest posterior density intervals.

102 (95% HPDI: 66–144) in 1999 to 178 (95% HPDI: 151–204) in 2010 (Fig. 3 and Table A5). The Bayesian linear regression suggests there is a >99% probability that this population is either stable or increasing.

3.3. *Use of the Special Area of Conservation*

The proportion of the total population using the SAC was investigated using annual estimates of abundance in the SAC based upon θ_2, and the estimates of population abundance. The parametric bootstrap took uncertainty around these estimates into account and provided evidence that the proportion of the population using the SAC has declined, with all the bootstrap replicate GLMs showing negative slope coefficients (mean $= -0.0621$, SE $= 0.0007$). 93% of bootstrap replicates showed that >50% of the population use the SAC.

4. Discussion

Protected areas are commonly promoted for *in situ* conservation, yet there is little published information on long-term abundance and trends of top predator populations to evaluate their effectiveness (Gaston et al., 2006; Hooker and Gerber, 2004) (see Gormley et al., 2012, for a recent exception). We investigated some of the issues that could impact estimates of abundance, and present evidence of long-term trends in the use of a protected area for small cetaceans in relation to overall changes in population status. Results show that, despite inter-annual variability, the Moray Firth SAC has been used consistently for at least the last two decades by the majority of a stable or increasing population of bottlenose dolphins.

4.1. Influence of changes in survey protocols on sampling variability

Survey protocols used to monitor dolphin abundance within the Moray Firth SAC were adapted primarily in response to changes in dolphin distribution (Wilson et al., 2004) and partly due to the development of digital photography. We investigated how these changes to survey protocols might influence trend estimates (see also Moore and Barlow, 2011) and found evidence that they did affect estimates of the proportion of well-marked individuals, θ. The change in this populations' distribution (Wilson et al., 2004) decreased sighting frequencies along parts of our original fixed survey route but, by targeting areas that were more regularly used by dolphins, we successfully increased overall capture probabilities. Furthermore, shorter flexible surveys were less constrained by weather, resulting in an increase in the number of surveys and captures during the second decade of research (Table 1). This more intensive sampling of the dolphins using the SAC and switch to digital photography produced larger numbers of photographs, which is known to reduce capture heterogeneity (Hammond, 1986). This potentially also resulted in a larger, more representative sample of animals being photographed. Sampling variability was further reduced by only using nicked animals that could be identified from both sides, allowing annual abundance to be estimated from a single capture history (see also Corkrey et al., 2008). This resulted in CVs that were generally lower than previous estimates that averaged the left and right side estimates (Wilson et al., 1999).

4.2. Trends in population size and use of the Special Area of Conservation

There was no significant trend in mark–recapture estimates of the number of well-marked dolphins using the SAC over this study period. However, investigations of variation in the observed proportion of well-marked individuals highlight that estimates of θ are critical to any assessment of trends in the total number of animals using this protected area. Given that bottlenose dolphins are long-lived species with low recruitment, the extreme fluctuations in annual estimates of θ, particularly in the first decade (Fig. 2 and Table A4), are biologically implausible. Nevertheless, whilst high inter-annual variability in estimates of θ must be driven largely by sampling variation, longer term change in θ could result from gradual changes in population age or sex structure. Our best model of variation in θ produced different estimates for the first ($\theta_1 = 0.4720$) and second ($\theta_2 = 0.5609$) decade of the study. We identified no biological reason for such a change. Instead the higher estimate of θ in the second decade was co-incident with changes in survey protocols that also resulted in higher capture probabilities and reduced capture heterogeneity. We might expect any sampling bias that affected θ to also affect the estimate of well-marked animals. However, despite observing a step change in θ we found no systematic change in the estimate of well-marked animals. Therefore, we suggest that θ_2 more accurately reflects the actual proportion of well-marked animals in this population throughout this time-series.

At the same time, we note that inferences about whether or not there was a decreasing trend in the total number of individuals using the SAC are dependent upon the choice of using a single value of θ or the two values from the model. Applying θ_2 to the complete time-series resulted in no significant trend in the number of dolphins using the Moray Firth SAC between 1990 and 2010. However, if modelled estimates of θ were used for their respective time periods (θ_1 for 1990–2000 and θ_2 for 2001–2012) there was a declining trend in the number of dolphins using the SAC over this period. It is well recognised that trends can be difficult to detect when sampling variability is high (Moore and Barlow, 2011). Effort therefore typically focuses on reducing CVs, which in our case were relatively precise and comparable with other studies of cetaceans (Berrow et al., 2012; Gormley et al., 2005; Read et al., 2003; Silva et al., 2009). Other studies have previously highlighted how factors such as photographer behaviour can affect estimation of θ (Read et al., 2003). Whilst the influence of such factors can be incorporated in model based estimates of θ, our results highlight the value of conducting parallel studies that can directly investigate whether there are trends in population age, size or sex structure (Fearnbach et al., 2011; Fortune et al., 2012).

A wider issue is that protected areas for mobile species such as this rarely encompass the entire population range. Indeed, the European Habitats Directive aims to provide a network of SACs that supports the favourable conservation status of the population. Whilst it has been recommended that broader-scale surveys are required to interpret abundance trends within SACs (Cañadas and Hammond, 2006), monitoring typically occurs only within site boundaries (Berrow et al., 2012; Pierpoint et al., 2009). Our study is the first to assess trends within an SAC in relation to trends in overall population size. By updating the previous assessment by Corkrey et al. (2008) using data collected over the last decade (Cheney et al., 2013; Islas-Villanueva, 2010; Quick and Janik, 2008), these analyses suggest that there is a $>99\%$ probability that the overall population is either stable or increasing (Fig. 3). Integration of this result with data from the more regular surveys within the SAC indicates that $>50\%$ of the population use the protected area at some point in any one year. This supports findings from intensive surveys in 2006 and 2007 that showed that $>80\%$ of well-marked animals in the population had been observed in the SAC at some point in the previous two decades (Cheney et al., 2013).

Irrespective of whether the number of individuals using the SAC has remained stable or decreased, there is an indication that use of the SAC has declined over the past two decades (Fig. 3); a trend that would be more pronounced if the two values of θ were used. On the one hand, this could be interpreted as a reduction in the importance of the SAC relative to surrounding areas. Alternatively, relatively stable numbers within the SAC may indicate that the area is at carrying capacity, and a decline in relative use might be expected if protective measures are facilitating the recovery and expansion of the wider population. The cause(s) of changes in habitat use or local abundance tend to be difficult to ascertain (Hartel et al., 2014; Tezanos-Pinto et al., 2013). Evaluation of these alternatives requires further research on how variation in environmental conditions (e.g. habitat and prey availability), anthropogenic disturbance (e.g. noise) and demographic parameters both in the SAC and in other parts of the population's range, influence use of this protected area. This, in turn, serves to highlight our limited ability to predict the dynamics of coastal delphinid habitat use at larger temporal scales. There is little evidence of the presence of bottlenose dolphins in the Moray Firth before the mid-20th century (Cheney et al., 2013), and populations that we consider 'resident' may change their ranging patterns at inter-generational scales.

Even when long-time series are available, the limited power to demonstrate changes in the relative use of SACs must be recognised by conservation managers and legislators. Crucially, this dataset only provides an estimate of the number of individuals using the SAC during the summer sampling period. These investigations of the importance of protected areas should therefore be complemented by other approaches (e.g. passive acoustic monitoring) that can explore variation in the amount of time that animals spend in key areas within their range (Bailey et al., 2010; Pierpoint et al., 2009).

5. Conclusion

The population of bottlenose dolphins inhabiting the east coast of Scotland has remained stable over the past two decades. Estimates of abundance within the Moray Firth SAC varied over that period, coinciding with changes in the way the population uses its range and expanded it. This study was underpinned by a long-term research project and it is impractical to expect this level of survey effort in and around all protected areas. However, where photo-identification is used to support monitoring of abundance trends, our results highlight the importance of adapting survey protocols to maintain high capture probabilities and minimise sampling heterogeneity and the need for accurate estimation of θ to correctly assess trends. A long time series is required to assess trends in the abundance of these long-lived mobile marine predators, and shorter-term variations in abundance within specific areas should be interpreted cautiously. Most critically, assessment of the effectiveness of protected areas for mobile predators requires at least some information on the wider population. Use of these data within a state-space modelling framework highlights how even sparse data from the wider population can help managers interpret abundance trends within a protected area.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.08.010.

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