Photographic mark–recapture analysis of local dynamics within an open population of dolphins

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Abstract. Identifying demographic changes is important for understanding population dynamics. However, this requires long-term studies of definable populations of distinct individuals, which can be particularly challenging when studying mobile cetaceans in the marine environment. We collected photo-identification data from 19 years (1992–2010) to assess the dynamics of a population of bottlenose dolphins (*Tursiops truncatus*) restricted to the shallow (<7 m) waters of Little Bahama Bank, northern Bahamas. This population was known to range beyond our study area, so we adopted a Bayesian mixture modeling approach to mark–recapture to identify clusters of individuals that used the area to different extents, and we specifically estimated trends in survival, recruitment, and abundance of a "resident" population with high probabilities of identification. There was a high probability ($p = 0.97$) of a long-term decrease in the size of this resident population from a maximum of 47 dolphins (95% highest posterior density intervals, HPDI = 29–61) in 1996 to a minimum of just 24 dolphins (95% HPDI = 14–37) in 2009, a decline of 49% (95% HPDI = −5% to −75%). This was driven by low per capita recruitment (average ~0.02) that could not compensate for relatively low apparent survival rates (average ~0.94). Notably, there was a significant increase in apparent mortality (~5 apparent mortalities vs. ~2 on average) in 1999 when two intense hurricanes passed over the study area, with a high probability ($p = 0.83$) of a drop below the average survival probability (~0.91 in 1999; ~0.94, on average). As such, our mark–recapture approach enabled us to make useful inference about local dynamics within an open population of bottlenose dolphins; this should be applicable to other studies challenged by sampling highly mobile individuals with heterogeneous space use.

Key words: Bayesian statistics; bottlenose dolphin; capture–recapture; clusters; Jolly-Seber; Little Bahama Bank, northern Bahamas; mixture models; population dynamics; transients; Tursiops truncatus.

INTRODUCTION

Identifying demographic changes is key to understanding population dynamics (e.g., Chapron et al. 2009). However, this requires long-term studies of definable populations of distinct individuals, which can be particularly challenging when studying mobile cetaceans in the marine environment. In exceptional circumstances, cetaceans can be monitored through complete annual censuses of individuals (e.g., Ford et al. 2009), but in most cases demographic analyses rely on following the fates of individually marked animals using mark–recapture sampling (Lebreton et al. 1992). Specifically, photo-identification of natural markings has allowed individual cetaceans to be monitored in photographic "capture" and "recapture" samples (Ham-

mond 1990*a*, Hammond et al. 1990), and in a limited number of cases this approach has been used to make inference about demographic changes and population dynamics (Whitehead et al. 1997, Cameron et al. 1999, Caswell et al. 1999, Fujiwara and Caswell 2001, Mizroch et al. 2004, Leaper et al. 2006, Corkrey et al. 2008).

However, despite a growing number of long-term photo-identification studies of dolphins, inference about demographic changes has been constrained by the large-scale movements of individuals relative to the small coastal study sites that are logistically feasible (Durban et al. 2005). This mobility results in uncertainty over population definition, heterogeneity in ranging patterns (e.g., Lusseau et al. 2006), temporary emigration beyond the study area (Whitehead 1990), and the presence of "transient" individuals among local or "resident" populations (Pradel et al. 1997, Conn et al. 2011): all violate assumptions of traditional mark–recapture approaches and constrain inferences about demographic parameters.
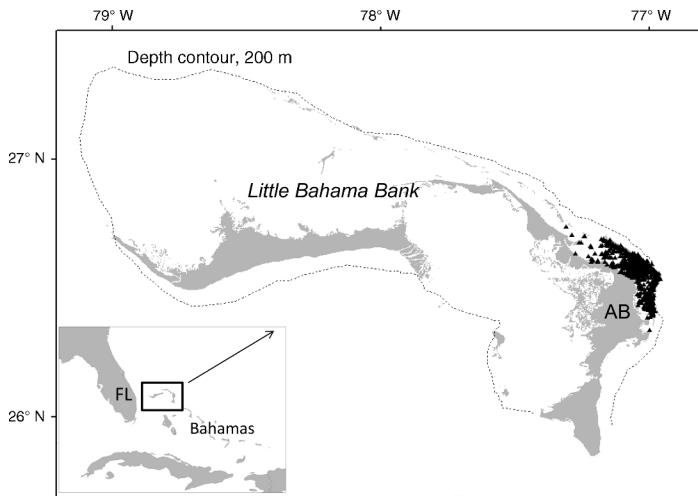
Fig. 1. Map of the study area east of Abaco Island (AB) on Little Bahama Bank, off the coast of Florida (FL), USA. Solid triangles show locations of 881 encounters with bottlenose dolphins (*Tursiops truncatus*) between 1992 and 2010, from which photo-identification data were collected.

Although modern mark–recapture approaches provide tools to separate the effects of movement from survival estimates (e.g., Whitehead 1990, Pradel et al. 1997, Cameron et al. 1999, Silva et al. 2009), these approaches require sampling designs that are often impractical for wide-ranging dolphins, or have unrealistic assumptions about movements. Specifically, it is generally impossible to obtain an adequate sample from "secondary" periods within each year that are sufficiently short to guarantee an absence of movement beyond the study area (e.g., Durban et al. 2000), and therefore provide unbiased estimation of detection probability using the "robust design" (Pollock et al. 1990). Furthermore, assumptions of constant or random temporary emigration between "primary" annual periods (Whitehead 1990, Kendall and Nichols 2002) are unlikely to be met in populations with heterogeneous ranging patterns (e.g., Lusseau et al. 2006). Similarly, within-year movements between study areas (e.g., Durban et al. 2005) violate assumptions of a multistate mark–recapture approach (Cameron et al. 1999). Furthermore, sparse data samples and low detection probabilities can lead to uncertainty in distinguishing "resident" and "transient" individuals based on recapture histories alone (Pradel et al. 1997).

To overcome these issues, we applied a new parameterization of the established Jolly-Seber model (Royle and Dorazio 2008, Gardner et al. 2010) to photographic identification records to make inference about the population dynamics of bottlenose dolphins (*Tursiops truncatus*) occurring in a coastal study area in the northern Bahamas. Long-term re-identifications over a 19-year period allowed us to monitor the "super-population" using the area, even though the entire population was not always present, through imputation of out-of-sample identification data. In contrast to existing estimators for open populations (Schwarz and Arnason 1996), this new parameterization adopted an individual-specific factorization that was amenable to modeling individual effects, which allowed us to identify

distinct population clusters (e.g., Durban et al. 2010) that used the study area to different extents (Whitehead and Wimmer 2005). Specifically, we used hierarchical Bayesian mixture modeling to identify a "resident" cluster, or population, of individuals with relatively high probabilities of identification, allowing us to reduce the influence of "transient" individuals (e.g., Pradel et al. 1997) and providing increased power for estimating trends in survival, recruitment, and abundance. We discuss between-year changes in demographic parameters and abundance in relation to key environmental covariates, notably the incidence and intensity of hurricanes, highlighting the utility of this approach.

METHODS

Population definition and field sampling

Annual surveys were conducted in each of 19 years between 1992 and 2010 in a 160-km² study site on the east side of Abaco Island (~26°33′ N, ~077°04′ W), part of Little Bahama Bank in the northern Bahamas (Fig. 1). Dolphins in this area are part of a larger population of ~1100 individuals (Durban 2002) that are restricted to the shallow waters (generally <7 m) of Little Bahama Bank by the deep surrounding waters of the Northwest Atlantic Ocean (Parsons et al. 2006). Although only a fraction of this overall population uses the east Abaco study area (Fearnbach et al. 2011), there is a high resighting rate of individuals within the study area (Claridge 1994, Durban et al. 2000, Parsons et al. 2003, Parsons et al. 2006, Fearnbach et al. 2011), implying site fidelity of at least some of the individuals over the two decades of study.

Small (~5 m), rigid-hulled inflatable boats were used to survey in a primarily opportunistic fashion: either in response to reported dolphin sightings and shore-based observations or by visiting areas where dolphins had been previously seen. As a result, survey effort was not uniformly distributed throughout the study area, but rather was focused on areas of high dolphin occurrence

to maximize the population coverage through photographic samples. Additionally, randomized line-transect surveys were conducted during seven years (1997–2000, 2007–2009) to ensure that the full extent of the study area was surveyed. When dolphins were encountered, dorsal fin photographs were taken of as many individuals as possible. Between 1992 and 2003, Ilford HP5 black and white film was shot using Nikon 35-mm cameras. The film was later push-processed to enhance contrast and reveal markings on the photographed dorsal fins. Between 2004 and 2010, Nikon digital SLR cameras were used to shoot high-resolution images of at least 6 megapixels (MP).

The timing and number of surveys each year varied due to weather, logistic support, and personnel availability. We therefore defined an annual census period between January and October, overlapping with the majority of dolphin encounters. In addition to mark–recapture analyses of data from each year, we also compared sighting frequencies for the month of October in six "index" years between 1998 and 2010. These index months were chosen because of high and comparable survey effort.

Photographic mark–recapture

Each identification image was examined on either a light table (black and white negatives) or on a high-resolution computer monitor (digital images). Photographs were assigned a quality grade (Q value ranging from 1 to 3) based on the image size, focus, lighting, angle of the fin, and exposure of the photograph (Durban et al. 2000). Only high-quality ($Q \geq 2$) photos were used for individual recognition. Individual dolphins were identified based on either the pattern of naturally acquired nicks in the dorsal fin or distinctive fin profiles. These features have been demonstrated to provide reliable individual identification of bottlenose dolphins over time periods of at least several years (Scott et al. 1990, Wilson et al. 1999). Individual identity was assigned by comparing photographs with a photo-identification catalog comprising distinct individuals identified during the duration of the study. If matched, the photograph was linked to the existing identification number. If no match was found, it was given a new number and added to the catalog. The best photograph of each dolphin from each group encountered was selected and added to the database.

We treated these photographic identifications and re-identifications of individuals as "captures" and "recaptures" to which analytical mark–recapture techniques could be applied. Specifically, we pooled all identifications into binary identification histories for each dolphin in each annual period, and constructed a matrix of identification histories with elements h_{ij} taking the values 1 or 0 to indicate whether or not each observed individual $i = 1, \ldots, n$ was identified during each of the $t = 1, \ldots, T = 19$ annual sampling periods. To make inference about population dynamics, we adopted a new

parameterization of the Jolly-Seber mark–recapture model that allowed for estimation of both survival and recruitment (Royle and Dorazio 2008, Gardner et al. 2010). Because the size of the "superpopulation" available to be identified was not fixed, but unknown, we augmented the list of individuals observed with a large number ($M = 50$) of all zero-identifications histories to represent the pool of unidentified individuals available for recruitment.

For each identification history h_i, there was a corresponding population history given by $\mathbf{x}_i$, a vector of binary state variables describing whether or not individual i was alive or not. Estimation of these population states was accomplished through a model for the demographic processes of survival and recruitment (Royle and Dorazio 2008):

$$x_{i,t+1} \sim \text{Bern}\left\{ \varphi_{it}x_{it} + \gamma_{it+1}\left[\prod_{k=1}^{t}(1 - x_{ik})\right] \right\}$$

with the initial state given by $x_{i1} \sim \text{Bern}(\gamma_{i1})$. Thus, if an individual was alive at time t (i.e., $x_{it} = 1$), then its status at time $t + 1$ was modeled as the outcome of a Bernoulli random variable with parameter φ_{it}, the probability of surviving from time interval t to $t + 1$. If an individual was not alive during the previous time intervals $1, \ldots, t$ (i.e., $x_{it} = 0$), then the outcome was a Bernoulli trial with parameter γ_{it+1}, the probability of entry into the population between intervals t and $t + 1$.

Known deaths were incorporated by inputting values of 0 for x following the recovery of a carcass of a known individual: this occurred once during the study. Similarly, values of 1 were inputted for x in years when any dolphin was not identified ($h = 0$) between years of repeated identifications ($h = 1$), and similar imputation was based on identifications in the out-of-sample months (November and December) subsequent to annual sampling intervals when a dolphin was not seen, but was previously known to be alive. Where the status was unknown following the interval of last identification or before first identification, and for all unobserved augmented individuals, we treated x_{ij} as a missing value about which inference may be made. Annual estimates of population abundance, N_t, were therefore simply derived as a function of the latent state variable x_{it}, indicating how many individuals were alive in each year:

$$N_t = \sum_{i=1}^{n+M} x_{it}.$$

Similarly, contributions to changes in the abundance were assessed by monitoring changes in the latent state variable x_{it} to derive the number of deaths D_{t+1} and recruits R_{t+1} occurring between each consecutive pair of years $t: t + 1$:

$$R_{t+1} = \sum_{i=1}^{n+M} (1 - x_{it})x_{it+1}$$

$$D_{t+1} = \sum_{i=1}^{n+M} x_{it}(1 - x_{it+1}).$$

Per capita recruitment, b_t, was then derived as a simple ratio of the number of recruits to abundance in each year R_t/N_t.

The parameters and missing data of the population process were estimated from the observed data through an observation model for the identification histories h_{it}. Conditional on the partly observed population process x, the binary observations were modeled as independent random variables:

$$h_{it} \sim \text{Bern}(p_{it}x_{it}).$$

The model for the observed identification histories h therefore reflected the fact that an animal can only be identified if it is alive. If $x_{it} = 0$ (individual i has either died, or has not yet recruited) then $h_{it} = 0$ with probability 1; otherwise h_{it} was a Bernoulli trial with parameter p_{it} describing the identification probability. Not all individuals that were known or estimated to be alive necessarily used the study area in each year, so this identification probability inherently encompassed the combined process of temporary emigration away from the area and detection probability when in the area (e.g., Whitehead 1990). This alleviated the requirement to impose unrealistic assumptions about random or constant temporary emigration (Whitehead 1990, Kendall and Nichols 2002), and allowed for temporary emigration beyond the study area to vary across time and across individuals in response to both individual movement and effort-dependent changes in the effective size of the study area. As a consequence, the population size N_t referred to the size of the sample population that used the study area, despite the realization that all of these individuals are not necessarily present in the study area in each year.

Temporal and individual variation in identification probabilities were specified by modeling p as a function of a mean (μ) and time-varying individual random effects terms (ε):

$$\text{logit}(p_{it}) = \text{logit}(\mu^p) + \varepsilon^p_{z[i]=c,t}$$

$$\varepsilon^p_{ct} \sim \mathcal{N}(0, \sigma^p)$$

where $\text{logit}(a) = \log(a/(1-a))$. Instead of a separate effect for each individual in each year, we adopted a mixture formulation in which each annual random effect was drawn from a specific cluster, c, with assignment of individuals to clusters through estimation of the indicator variable $z_i = c$. For a ceiling of $C = 10$ potential clusters, we used a Dirichlet process to draw a set of C values of ε^p_{ct} for each year t from a baseline distribution with mean 0 and standard deviation σ^p, and estimated which value $z_i = c = 1, \ldots, C$ was appropriate for each individual (following Durban et al. [2010]). The model therefore identified clusters of dolphins with

similar vectors of capture probabilities across years. We used a similar stratification of survival (φ) and recruitment (γ) probabilities, with annual random effects terms drawn from a distribution stratified by the cluster indicators that were estimated from the capture probabilities:

$$\text{logit}(\varphi_{it}, \gamma_{it}) = \text{logit}(\mu^{\varphi,\gamma}) + \varepsilon^{\varphi\gamma}_{c,t}$$

$$\varepsilon^{\varphi,\lambda}_{ct} \sim \mathcal{N}(0, \sigma^{\varphi,\lambda}).$$

Therefore the model did not estimate clusters of dolphins with similar survival or recruitment histories, but rather estimated survival and recruitment for the clusters with similar capture probabilities.

Bayesian inference

The Bayesian approach is well suited to conveying uncertainty due to small sample sizes, because inference is based on full probability distributions (Gelman et al. 1995, Wade 2000). This approach required prior distributions to be specified for all model parameters, and we adopted similar priors for the mean and standard deviation of each parameter set: Uniform (0,1) prior distributions were placed on each of the mean probabilities $\mu^{\varphi,\gamma,p}$ and a Uniform (0,10) was adopted for the standard deviations $\sigma^{\varphi,\gamma,p}$ to allow annual differences from the means to emerge. This hierarchical prior allowed years in the set with relatively informative data to contribute largely toward the mean, and estimates from sparse data years were drawn toward the overall mean. This had the effect of smoothing estimates across each set so that notable variability from the mean was detected, but there was "borrowing strength" across each set to allow for more precise estimates in sparse data years. Note that we set $p_1 = p_2$ and $p_T = p_{T-1}$ to ensure parameter identifiability (Link and Barker 2005), and therefore we only present estimates for $t = 2, \ldots, T - 1$.

Once these priors had been assigned, the model described a series of probability distributions for the unknown parameters and missing data components conditional on the observed data. Missing data were thus treated the same as the other unknown parameters, and updated based on the observed data. We used WinBUGS software (Lunn et al. 2000) to implement Markov Chain Monte Carlo (MCMC) sampling to make repeated draws from the conditional distributions and estimate the posterior distribution for each parameter. We based inference on 30 000 MCMC iterations after discarding a "burn-in" of 10 000 iterations prior to convergence of three different chains (Brooks and Gelman 1998). With repeated iterations, the modal cluster allocation z_i attaching to individual i was taken over the candidate values assigned at each iteration of the chain, and variability in the sampled values represented uncertainty about cluster membership. Simultaneous MCMC sampling from the multiple

parameters in the model enabled this uncertainty to be propagated into uncertainty about the cluster-specific parameters. Similarly, by simultaneously monitoring estimates of parameter values across MCMC iterations, we were able to make probabilistic statements about hypotheses, for example, the probability that a specific annual survival probability was less than the average that was estimated from the proportion of iterations for which $\varepsilon_{c,t}^{\varphi} < 0$.

We employed the same MCMC simulation approach to generate predictive observations to compare the fit of the competing models using a posterior predictive criterion (Gelfand and Ghosh 1998). In order to assess the utility of allowing for clustered heterogeneity, we tested the fit of this Jolly-Seber model with clustered time-varying individual effects (JS_{tc}) to a model with just time-varying random effects (JS_t):

$$\text{logit}(p_{it}, \varphi_{it}, \gamma_{it}) = \text{logit}(\mu^{p,\varphi,\gamma}) + \varepsilon_t^{p,\varphi,\gamma}$$

$$\varepsilon_t^{p,\varphi,\gamma} \sim \mathcal{N}(0, \sigma^{p,\varphi,\gamma}).$$

For each model, we predicted a new set of data (X^{new}) of the same dimensions as the observed data (i in $1, \ldots, n$ and t in $1, \ldots, T$) by generating samples directly from the posterior distributions of the fitted model parameters. We then calculated a loss function that measured the discrepancy between the observed data, X, and the predicted data, X^{new}. As a loss function, we used the sum of the predicted errors (PE):

$$\text{PE} = \sum_{i=1}^{n} \sum_{t=1}^{T} [x_{it}^{new} - x_{it}]^2.$$

As with other model selection methods, the predictive criterion achieves a compromise between the goodness of fit and a penalty for the number of free parameters in the model (Gelfand and Ghosh 1998). The model with the smallest criterion value was estimated to be the model that would best predict a replicate data set of the same structure as that currently observed.

However, the predictive model selection criterion did not reveal whether the selected model was a plausible fit for the observed data. We therefore also adopted a posterior predictive approach for goodness-of-fit checking (Gelman et al. 1996) by drawing predicted data from the posterior distributions of model parameters for each selected cluster, c, and calculating a discrepancy measure, D_c, for both the predicted H^{new} and observed data H (e.g., Durban et al. 2010):

$$D(H)_c = \sum_{i=1}^{n} \sum_{t=1}^{T} \left| h_{z[i]=c,t} - p_{z[i]=c,t} \right|$$

$$D(H^{new})_c = \sum_{i=1}^{n} \sum_{t=1}^{T} \left| h_{z[i]=c,t}^{new} - p_{z[i]=c,t} \right|.$$

Because the discrepancy measures themselves both had posterior distributions, they were compared by

TABLE 1. Number of encounters with bottlenose dolphins (*Tursiops truncatus*) and number of distinct individuals identified from high-quality photographs in the annual January–October sampling intervals.

Year	No. encounters	No. individuals
1992	31 (25)	35 (14)
1993	32 (24)	46 (12)
1994	31 (13)	45 (6)
1995	72 (15)	67 (7)
1996	135 (11)	81 (8)
1997	31 (0)	32 (0)
1998	194 (9)	86 (14)
1999	78 (0)	90 (0)
2000	35 (2)	35 (0)
2001	3 (0)	5 (0)
2002	3 (0)	13 (0)
2003	11 (0)	49 (0)
2004	2 (0)	4 (0)
2005	9 (0)	36 (0)
2006	4 (0)	13 (0)
2007	20 (0)	33 (0)
2008	25 (3)	50 (0)
2009	21 (0)	32 (0)
2010	42 (0)	68 (0)

Note: Values in parentheses are the November–December out-of-sample encounters and additional individuals.

estimating the exceeding tail area probability, termed the posterior predictive p value, as the percentage of MCMC draws for which $D(H^{new})_c$ exceeded $D(H)_c$. Values close to 0.5 indicated that the realized discrepancy of the data was very similar to what one might expect from replications under the model; values close to 0 or 1 implied a poor fit (Gelman et al. 1996).

RESULTS

Mark–recapture sample

Photographs were taken during 881 encounters with dolphins (Fig. 1), resulting in 3558 individual identifications. Most (779 encounters, 3121 identifications) occurred within the January–October sampling interval, comprising 284 individual dolphins. After constraints for photographic quality and individual distinctiveness were applied, the mark–recapture sample was restricted to 237 individuals, representing 820 nonzero entries in the identification matrix (h). There were 52 additional identifications of these same individuals that were used as out-of-sample resightings, and 513 additional annual records that were imputed as "alive" ($x_{it} = 1$) for years when dolphins were not identified between years of repeated identifications. The number of these individuals identified in each annual sample varied across years (median = 36 individuals, range = 4–90), reflecting variability in the number of encounters (Table 1). Individuals were identified in an average of two different years (median = 2 years, range = 1–15), but there was evidence of some bimodality to the frequency of identification, and 18 dolphins were seen in 10 or more years (Fig. 2). The cumulative number of distinct individuals increased throughout the study period (Fig.
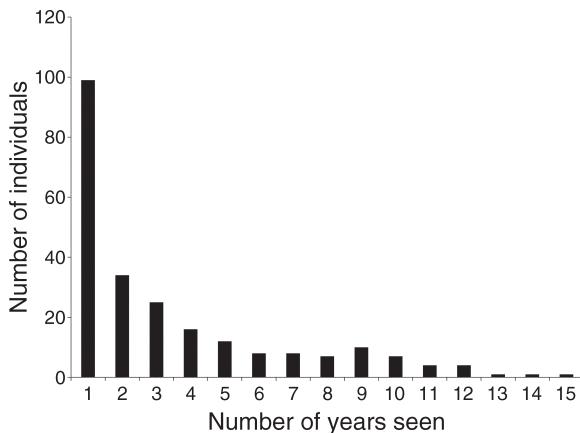
Fig. 2. Number of years in which distinctly marked individual dolphins were documented from high-quality photographs.

3), suggesting an open population with regular recruitment of new animals to the study area.

Model fitting

There were notable differences in the estimates produced using the Jolly-Seber model with clustered time-varying individual effects (JS_{tc}) compared to the standard model with only time-varying parameters (JS_t) (Table 2). The incorporation of heterogeneous individual effects into the model had the effect of lowering the estimated average probability of identification, therefore raising the average size of the estimated superpopulation using the area. Estimates of the average survival and recruitment probabilities were comparable under both models, but both were higher for the JS_{tc}. Model selection supported the incorporation of clustered individual effects, with predicted values from the JS_{tc} model (with 648 predicted errors over the 4503 binary observations) displaying closer agreement to the observed identification histories than the JS_t model (with 669 predicted errors over the 4503 binary observations; Table 2). Further inference was therefore based solely on the JS_{tc} model, which had the smallest predictive error (Gelfand and Ghosh 1998).

Up to nine different clusters were sampled during the MCMC iterations from the JS_{tc} model, reflecting uncertainty about the number of clusters and cluster allocation of individuals. However, dolphins were only assigned with maximum probability to two distinct clusters of approximate sizes of 68 and 153 individuals (Table 3). Most of these individuals could be assigned to a specific cluster with high probability, with 50 and 111 dolphins having the majority of their allocation density ($p_{z_i=c} > 0.50$) associating them with clusters 1 and 2, respectively. Notably, individuals in cluster 2 had a relatively low average identification probability, whereas individuals in cluster 1 had an average identification probability more than three times as high (Table 3), indicating greater site fidelity to the study area. Indeed, dolphins assigned with

high probability ($p_{z_i=c} > 0.50$) to this "resident" cluster were identified in more years (median = 2 years, range = 2–15), compared to the "transient" cluster (median = 1 year, range = 1–5). The identification probability of dolphins within the "resident" cluster varied between years, with posterior medians ranging from 0.07 to 0.90, reflecting the degree of survey effort (Fig. 4, Table 1); this was close to 1.0 in years with high photo-identification coverage. This relatively high probability of identification provided more power for monitoring demographic changes, because estimates of survival and recruitment parameters were more precise compared to the "transient" cluster (Table 3). There was good agreement between the posterior predictive distribution of $D(H^{new})_c$ and the posterior distribution of $D(H)_c$ for the resident cluster 1. The posterior predictive p value equaled 0.46, indicating that the discrepancy of the data was similar (close to 0.5) to what one might expect from replications under the model (Gelman et al. 1996), and supporting that the model was a plausible fit to the data. The posterior predictive p value for the transient cluster 2 was only 0.23, implying the limited utility of the model for making inference about the infrequently seen transient individuals. We therefore focused assessment of demographic trends on this "resident" cluster, which could be thought of as a local population.

There was a high probability ($p = 0.97$) of a long-term decrease in the size of this resident population from a high of 47 dolphins (95% highest posterior density intervals, HPDI = 29–61) in 1996, to a low of just 24 dolphins (95% HPDI = 14–37) at the end of the time series in 2009 (Fig. 5), a decline of 49% (95% HPDI = −5% to −75%). This decline was based on low per capita recruitment that could not compensate for high apparent mortalities. Estimates of per capita recruitment rate were low, on average [mean($b_{z=1,t}$) posterior median = 0.02; 95% HPDI = 0–0.09], corresponding to an average of 1 recruit per year (95% HPDI = 0–5), with relatively
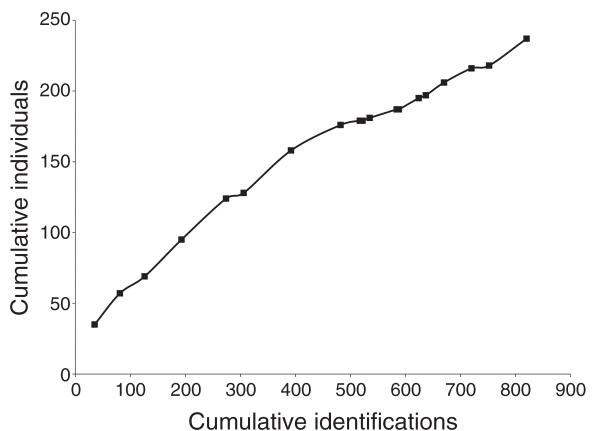

Fig. 3. Discovery curve of the total number of distinctly marked individual dolphins identified from the growing number of cumulative identifications made in each year between 1992 and 2010.

TABLE 2. Comparison of the of two mark–recapture models fit to the photo-identification data: a Jolly-Seber formulation with time-varying parameters (JS_t) and a model with heterogeneity incorporated through clustered time-varying individual effects (JS_{tc}).

Model	PE	Probability of identification, μ_p	Survival, μ_φ	Recruitment, mean(b_t)	Superpop., $\hat{N}$	Clusters, C
JS_t	699	0.42 (0.28−0.59)	0.92 (0.87−0.96)	0.07 (0.02−0.17)	95 (79−113)	
JS_{tc}	648	0.29 (0.14−0.48)	0.95 (0.92−0.97)	0.04 (0−0.10)	142 (96−187)	2

Notes: Best fit was determined by the sum of the predicted errors (PE) from each model across the 4503 binary observations. Posterior median values, with 95% highest probability density intervals (HPDI) in parentheses, are shown for the average annual probability of identification, survival, and per capita recruitment, and size of the superpopulation using the study area. For the JS_{tc} model, the number of clusters to which individuals could be assigned with the majority of their probability density ($p_{z_i=c} > 0.50$) is shown, from a ceiling of 10 possible clusters. Terms are: t, annual sampling interval; c, a specific cluster, equivalent to a component of the mixture model; z, cluster indicator variable; i, individual dolphin; estimation of $z_i = c$ indicates the assignment of an individual to a particular cluster.

low estimates of survival rate [mean($\varphi_{z=1,t}$) posterior median = 0.94, 95% HPDI = 0.82–0.99) equating to a comparatively high average of 2 deaths per year (95% HPDI = 0–7). Therefore, the apparent mortalities were estimated to be twice as high as the recruitments, on average, and mortalities exceeded recruitment in all years following the peak abundance in 1996 (Fig. 6).

Notably, there was an anomalous drop in survival in 1999, with a survival rate estimate of 0.91 (95% HPDI = 0.78–0.97), representing 5 deaths (95% HPDI = 1–10). This was the largest annual departure from the average survival rate, with a probability of 0.83 that this annual estimate deviated from the average. This peak in apparent mortality corresponded to the largest between-year decline in abundance, with an estimated 11% drop (95% HPDI = −88% to +58%) in the size of the "resident" population in 1999 (posterior median = 40, 95% HPDI = 25–55) compared to the previous year (posterior median = 45, 95% HPDI = 24–54). Despite uncertainty in these adjacent estimates, MCMC draws from the full posterior distributions and estimated a probability of 0.66 of a decline.

Although demographic estimates were less precise, these abundance trends were mirrored in the larger "superpopulation" that used the area, which declined from an estimated high of 187 dolphins in 1996 (95% HPDI = 154–221) to a low of 96 (95% HPDI = 72–117) in 2009, an overall reduction of 49% (95% HPDI = −32% to −62%). Again the largest drop (posterior median = −12 %; 95% HPDI = −44% to +31%) was estimated to occur in 1999 when the size of the "superpopulation" was estimated to decline from a posterior median of 175

to 154 (Fig. 5), with a probability of 0.73 of a decline occurring between adjacent estimates.

Sighting frequencies during our October index months over six years showed a similar decrease in the frequency of dolphin sightings from 1999 onward, despite comparable survey effort and extent (Fig. 7). The total days of survey effort (median = 20 days, range = 14–25), and total kilometers surveyed (median = 1660 km, range = 1023–2029 km) were relatively high for the month of October for all six years. However, there was a marked decline in the number of dolphin sightings, and thus sighting frequency after 1999 (1999–2010: median encounters = 24, range = 19–35 and median encounters per km = 0.02 groups per km of survey effort, range = 0.01–0.02) compared to 61 encounters and 0.04 groups per km of survey effort in 1998, with dolphins being sighted half as frequently in recent years (Table 4, Fig. 7).

DISCUSSION

The bottlenose dolphins that we surveyed displayed heterogeneous sighting frequencies in our study area, due to their mobility relative to the limited extent of the area that we could consistently survey using small boats. This presented problems for population definition and monitoring using conventional mark–recapture models. We overcame this by using a Bayesian mixture model to identify a defined cluster, or local population, from a larger superpopulation of dolphins that were more "transient" in their use of our study area (e.g., Conn et al. 2011). Although members of the local population probably did not spend their entire time within our study area, these comparatively "resident" dolphins had

TABLE 3. Estimates of parameters from the Jolly-Seber model with clustered time-varying individual effects (JS_{tc}) for two clusters to which individuals could be assigned with the majority of their probability density ($p_{z_i=c} > 0.50$).

Cluster	Probability of identification, mean ($p_{z=c,t}$)	Survival, mean ($\varphi_{z=c,t}$)	Recruitment, mean($b_{z=c,t}$)	Cluster size
$c = 1$, "residents"	0.56 (0.39−0.73)	0.94 (0.82−0.99)	0.02 (0−0.09)	68
$c = 2$, "transients"	0.17 (0.01−0.79)	0.94 (0.77−0.99)	0.02 (0−0.13)	153

Notes: Posterior median values (with 95% highest probability density intervals in parentheses) are shown for the average annual probability of identification, survival, and per capita recruitment for each cluster. The size of the cluster reflects the number of dolphins that were assigned with maximum probability.
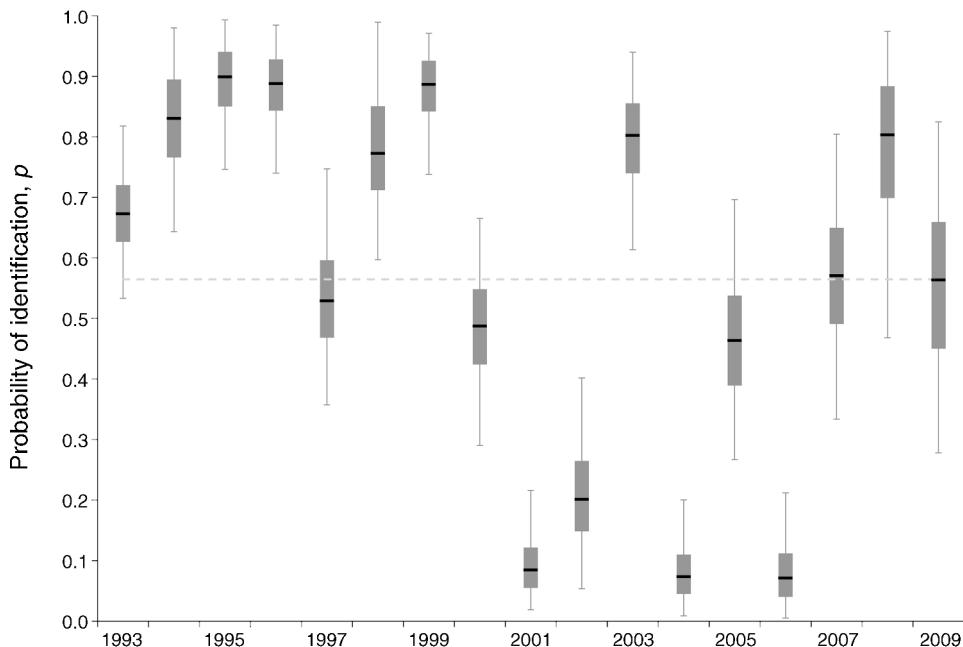
FIG. 4. Annual estimates of identification probability for the "resident" cluster of dolphins, 1993–2009. Estimates are presented as posterior medians (horizontal solid lines within bars), with 75% (gray bars) and 95% (vertical lines) highest posterior density intervals. The average annual probability of identification [mean($p_{z=1,t}$) = 0.56] is represented by the horizontal dashed line.

relatively high identification probabilities, which were essentially 1.0 (always identified) in years with high survey coverage. This not only indicated a high chance of encountering these study dolphins during the course of an annual survey period, but also provided increased power for monitoring their fates.

Less than half of the dolphins that we documented could be classified as "resident," and the size of this population declined to approximately half its earlier size over the course of the study. Although there are many factors that could have led to this decline, estimates of demographic parameters suggest that intense tropical
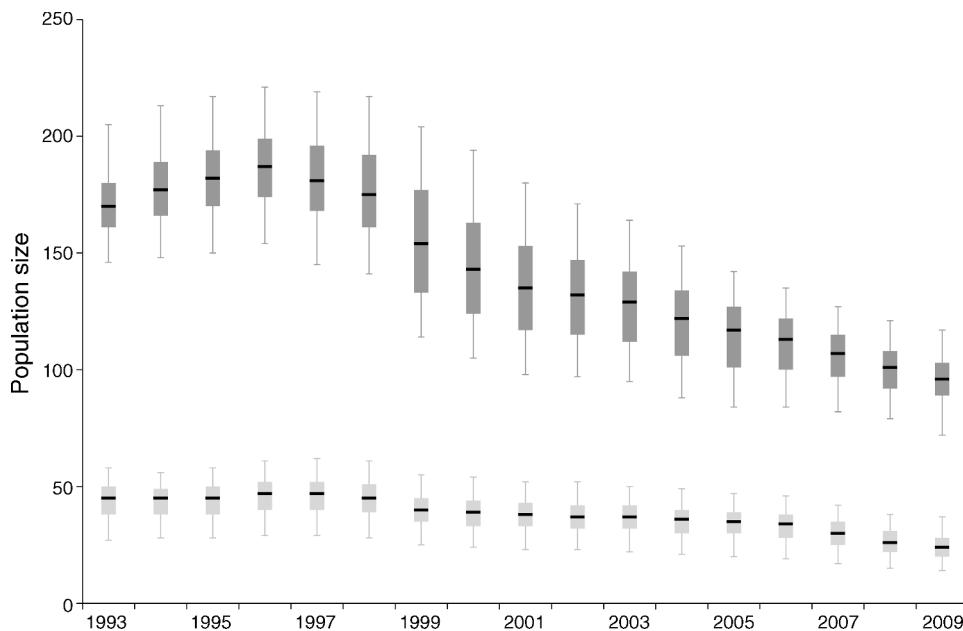

FIG. 5. Annual estimate of abundance of the "superpopulation" using the study area during the study period (1992–2009) (dark gray fill, top) and the "resident" population (light gray fill, bottom). Estimates are presented as posterior medians (horizontal line), with 75% (gray bars) and 95% (vertical lines) highest posterior density intervals.
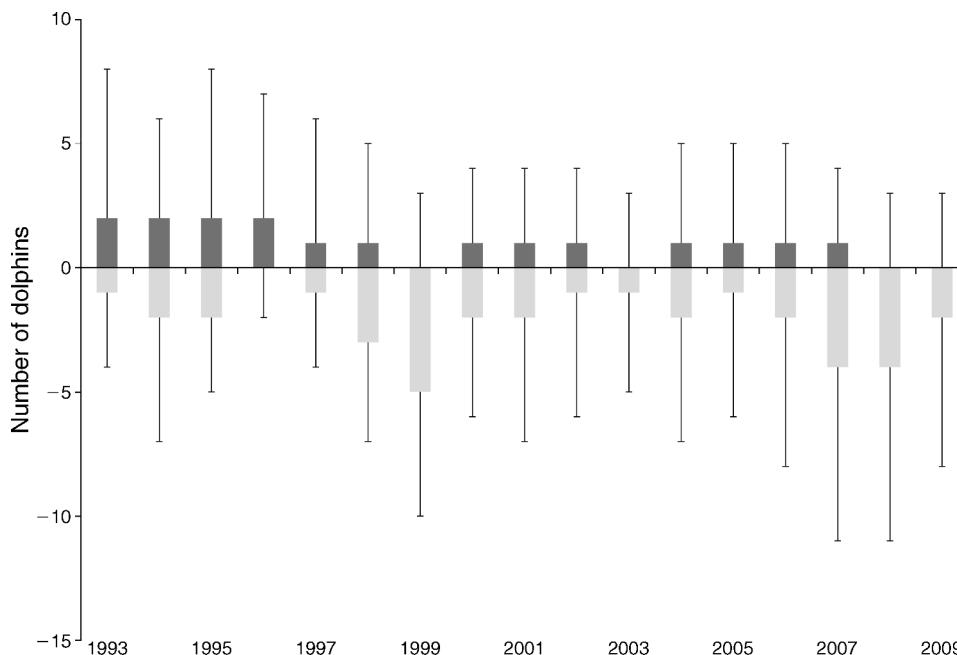
FIG. 6. Annual estimates of apparent mortalities (below the x-axis, light gray bars) and recruitments (above the x-axis, dark gray bar) for the "resident population" of dolphins using the study area. Estimates are presented as posterior medians (bars), and upper 95% highest posterior density intervals are shown with vertical lines.

cyclones may have an abrupt impact on mortality trends. Specifically, the greatest between-year decline in estimated abundance occurred in 1999, with a significant spike in apparent mortalities. This was the year when two intense hurricanes struck our study area just three weeks apart in August and September. One of these storms, Hurricane Floyd, was the largest and strongest during the study period (and the strongest for more than 30 years), bringing sustained winds of 233 km/h when it passed directly over the study area; data *available online*).[7] This abrupt decline in abundance was mirrored in both the local population (~11% decline) and the larger superpopulation using the area (~12%). Furthermore, the population-level impact was supported by a decrease in the sighting frequency of dolphins in years following these storms.

This abrupt decline in abundance could be the result of movement (permanent emigration) away from the study area, perhaps due to habitat disturbance (e.g., Preen and Marsh 1995, Spiller et al. 1998, Gales et al. 2004, Gardner et al. 2005), but we suggest that real mortalities contributed significantly to the observed demographic changes. Mortality could occur through direct physical challenges posed by abrupt changes in environmental conditions, specifically wave heights and storm surge that probably make the shallow-water sandbank system uninhabitable. However, it is likely that there are also indirect effects of abrupt environ-

mental changes, specifically if dolphins are forced from their shallow-water habitat during intense storms to seek refuge, probably in deep, oceanic waters where they are exposed to increased predation risk from oceanic sharks. We have documented an increase in the incidence of fresh shark-bite wounds on surviving dolphins following hurricanes (Fearnbach et al. 2011), providing support for an associated increase in predation risk. Although the plausible relationship between tropical cyclones and dolphin population dynamics is based on our observations of covariance in just a single year of anomalous hurricane activity, this is consistent with recent data suggesting that hurricanes may have impacts on the reproduction and social structure of coastal cetaceans (Miller et al. 2010, Elliser and Herzing 2011, Fearnbach et al. 2011) and abrupt mortality of even pelagic species (Mignucci-Giannoni et al. 1999).

In addition to the abrupt impact in 1999, our analyses suggest long-term declines in abundance from 1996 until the end of the time series in 2009, with relatively high mortality exceeding estimates of per capita recruitment. This is supported by continued low sighting frequencies in index survey months over the past decade. This long-term decline could represent mortality or permanent emigration resulting from the prolonged and combined effects from earlier storms (e.g., Preen and Marsh 1995); it is notable that mortality exceeded recruitment in all years following 1996, when the area experienced the first intense hurricane (winds >150 km/h) since 1965. Similarly, this apparently gradual decline could be a
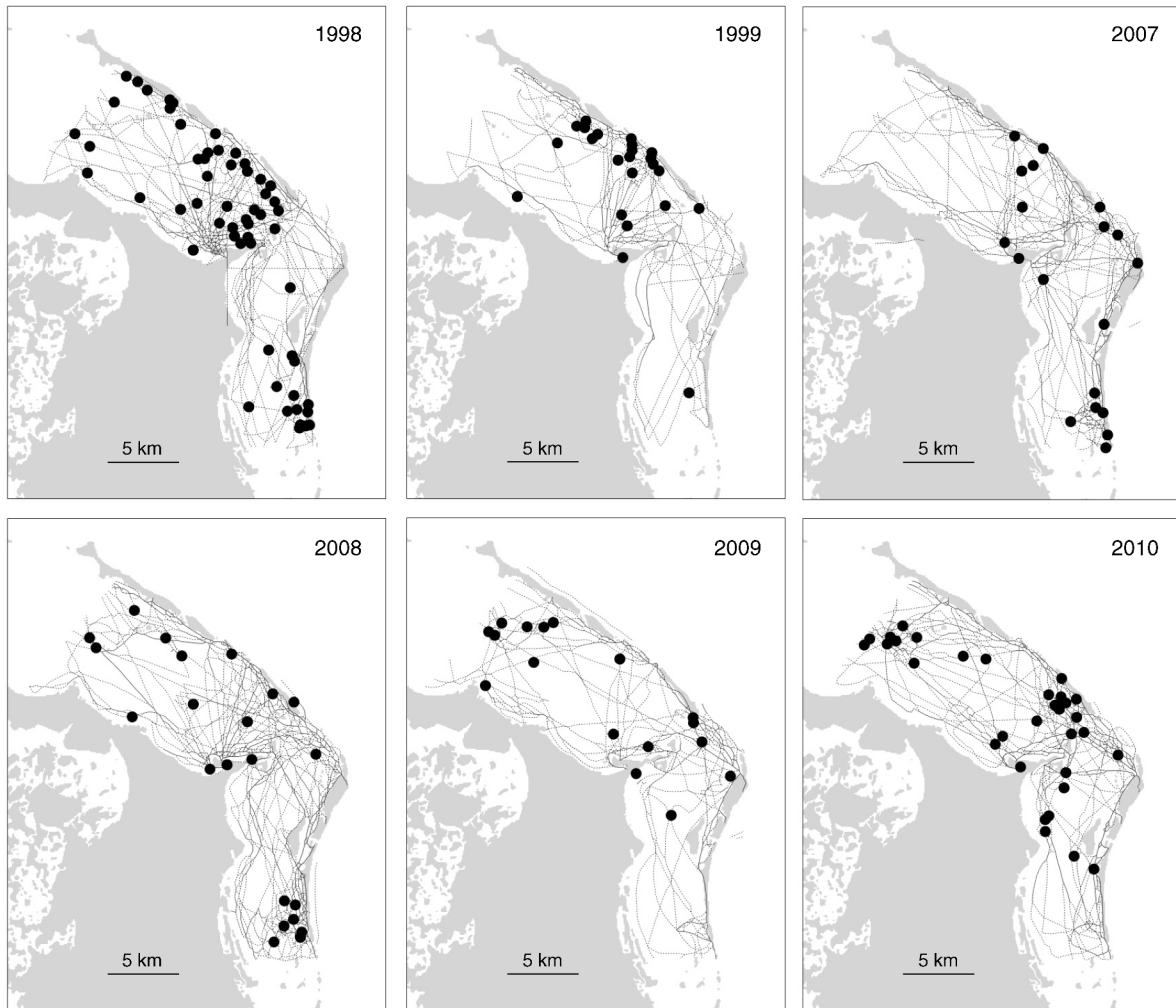
[7] http://www.nhc.noaa.gov/1999floyd.html

FIG. 7. Map of the east Abaco study area showing all the tracks of the survey vessel during visual surveys (stippled lines) and bottlenose dolphin encounters (solid black circles) for the month of October for six years (1998, 1999 and 2007–2010).

response to unobserved effects following later hurricanes; two further intense hurricanes passed through the study area in 2004, but an extremely low level of photo-identification effort in this year resulted in low capture probability, and further nonlinearities may have gone unobserved due to relatively high uncertainty in demographic estimates. The dolphins probably also have responded to variability in other natural and anthropogenic factors, perhaps compounding the effects of these storms. For example, both coastal development and recreational boat traffic escalated in the study area in recent years, most likely creating a habitat that is increasingly undesirable for dolphins (e.g., Caron and Sergeant 1988, Lusseau 2005, Bedjer et al. 2006), and perhaps leading to permanent emigration to other areas on Little Bahama Bank that remain largely undisturbed. It is also possible that predation risk by sharks may have increased in recent years due to a recovery of the sea turtle population following a ban on harvesting (Baha-

mas Marine Mammal Research Organisation, *unpublished data*). Dolphins have been shown to alter their use of certain habitats in response to fluctuations in predation risk resulting from shifts in the availability

TABLE 4. Survey effort for the month of October in six years (1998–1999, 2007–2010) with comparable survey effort (>1000 km) and spatial extent.

Year	Effort (days)	Effort (km)	No. encounters	Sighting frequency (encounters/km)
1998	23	1458	61	0.04
1999	14	1023	25	0.02
2007	25	2029	21	0.01
2008	20	1724	24	0.01
2009	16	1616	19	0.01
2010	20	1704	35	0.02

Note: Effort is shown as number of days with sightings surveys, total distance (km) surveyed, number of dolphin encounters, and sighting frequency (ratio of number of encounters to total kilometers surveyed).

of key prey species for sharks (Heithaus et al. 2002, Heithaus and Dill 2002).

Despite uncertainty about the influence of environmental covariates, the ability to define a local population and estimate changes to its demographics has allowed us to frame discussions about the possible causes of population dynamics, which is rarely possible for cetaceans due to problems of population definition. In the presence of movement beyond a study area, inference from mark–recapture generally refers to the level of the superpopulation, which may be largely undefined unless unrealistic assumptions are made to separate temporary emigration from capture probability of locally available individuals (Pollock et al. 1990, Whitehead 1990, Kendall and Nichols 2002). However, when the heterogeneity of ranging patterns induces a bimodal structure to capture probabilities, it is possible to distinguish "resident" and "transient" individuals based on capture histories alone (Pradel et al. 1997, Whitehead and Wimmer 2005, Conn et al. 2011). Our model generalizes this concept to two or more structural clusters, if they exist, and estimates individual effects to infer each individual's cluster assignment (e.g., Durban et al. 2010). The Bayesian approach allows uncertainty to be effectively incorporated into inference about cluster membership, addressing problems caused by low capture probabilities. Although we estimated latent individual effects in our case, this formulation provides a promising direction for the future development of models that incorporate individual covariates for clustered capture probabilities, in order to learn about the mechanisms underlying heterogeneous space use.

This structure of differential site fidelity by social clusters or "communities" is common in populations of bottlenose dolphins (Lusseau et al. 2006, Parsons et al. 2006, Urian et al. 2009, Conn et al. 2011), and we propose that this clustered mark–recapture approach will be useful for defining units to monitor in other similar open populations. However, we also suggest that its utility also extends more generally to mark–recapture studies in which high mobility and differential ranging patters of the target animals induce heterogeneous capture probabilities of individuals within local study areas (e.g., Hammond 1990b). The approach might be particularly suitable for opportunistic and nonstandard mark–recapture samples (e.g., Karanth et al. 2006, Petit and Valière 2006), where it can be harder to design and control for appropriate spatial coverage.

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