Contribution to the Theme Section 'Effects of the Deepwater Horizon oil spill on protected marine species'

Survival, density, and abundance of common bottlenose dolphins in Barataria Bay (USA) following the *Deepwater Horizon* oil spill

Trent L. McDonald[1],*, Fawn E. Hornsby[1], Todd R. Speakman[2], Eric S. Zolman[2], Keith D. Mullin[3], Carrie Sinclair[3], Patricia E. Rosel[4], Len Thomas[5], Lori H. Schwacke[2]

[1]Western EcoSystems Technology, Inc., Laramie, WY 82070, USA

[2]National Centers for Coastal Ocean Science, National Oceanic and Atmospheric Administration, Hollings Marine Laboratory, Charleston, SC 29412, USA

[3]National Marine Fisheries Service, Southeast Fisheries Science Center, Pascagoula, MS 39568, USA

[4]National Marine Fisheries Service, Southeast Fisheries Science Center, Lafayette, LA 70506, USA

[5]Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, St. Andrews KY16 9LZ, UK

ABSTRACT: To assess potential impacts of the *Deepwater Horizon* oil spill in April 2010, we conducted boat-based photo-identification surveys for common bottlenose dolphins *Tursiops truncatus* in Barataria Bay, Louisiana, USA (~230 km², located 167 km WNW of the spill center). Crews logged 838 h of survey effort along pre-defined routes on 10 occasions between late June 2010 and early May 2014. We applied a previously unpublished spatial version of the robust design capture-recapture model to estimate survival and density. This model used photo locations to estimate density in the absence of study area boundaries and to separate mortality from permanent emigration. To estimate abundance, we applied density estimates to saltwater (salinity > ~8 ppt) areas of the bay where telemetry data suggested that dolphins reside. Annual dolphin survival varied between 0.80 and 0.85 (95% CIs varied from 0.77 to 0.90) over 3 yr following the *Deepwater Horizon* spill. In 2 non-oiled bays (in Florida and South Carolina), historic survival averages approximately 0.95. From June to November 2010, abundance increased from 1300 (95% CI ± ~130) to 3100 (95% CI ± ~400), then declined and remained between ~1600 and ~2400 individuals until spring 2013. In fall 2013 and spring 2014, abundance increased again to approximately 3100 individuals. Dolphin abundance prior to the spill was unknown, but we hypothesize that some dolphins moved out of the sampled area, probably northward into marshes, prior to initiation of our surveys in late June 2010, and later immigrated back into the sampled area.

KEY WORDS: Robust design · Photo-identification · *Tursiops truncatus* · Capture-recapture · Spatial-capture model

INTRODUCTION

Photo-identification (photo-ID), the process of using photographs for individual recognition, has become a reliable, non-invasive technique for tracking small cetaceans temporally and spatially (Würsig & Jefferson 1990). The natural markings, principally nicks and notches along the trailing edge of common bottle-nose dolphin *Tursiops truncatus* dorsal fins, as well as body scars and pigmentation patterns, can persist throughout their lifetime (Lockyer & Morris 1990, Würsig & Jefferson 1990, Read et al. 2003). Capture-recapture analyses are commonly applied to photo-ID data to estimate abundance (Wilson et al. 1999, Read et al. 2003, Balmer et al. 2008) and survivorship (Speakman et al. 2010).

*Corresponding author: tmcdonald@west-inc.com

Currently, the National Marine Fisheries Service (NMFS) recognizes 31 Bay, Sound, and Estuary (BSE) stocks of common bottlenose dolphins in US waters of the northern Gulf of Mexico (GoM) (Waring et al. 2015). The 31 stocks are treated as discrete populations because photo-ID and tagging studies, where conducted, generally provide evidence of long-term residency in BSEs of the northern GoM, and genetic studies have supported this concept (reviewed by Waring et al. 2015). Barataria Bay, Louisiana (Fig. 1), along with its ancillary bays (e.g. Caminada Bay and Bay des Ilettes) is located in the north-central GoM just west of the Mississippi River Delta, and comprises a single NMFS BSE stock (Waring et al. 2015). Few studies have estimated abundance and survivorship of common bottlenose dolphins in GoM stocks, including Barataria Bay

(Waring et al. 2015). One study, conducted between June 1999 and May 2002 (Miller 2003), identified 133 dolphins in the lower reaches of Caminada and Barataria Bays. This study produced an abundance estimate of 180 (95% CI 159 to 213), but only sampled a portion of Barataria Bay and thereby underestimated the number of resident dolphins in the whole of Barataria Bay.

A catastrophic explosion on the *Deepwater Horizon* (DWH) oil drilling rig on 20 April 2010 resulted in a fire that ultimately destroyed the rig 80 km ESE of the Mississippi River Delta (Port Eads, LA). The flow of oil from the uncapped well resulted in the worst marine oil spill in US history and released millions of barrels of crude oil into the northern GoM (DWH NRDA Trustees 2016). An unknown portion of the released oil ultimately penetrated the inshore waters
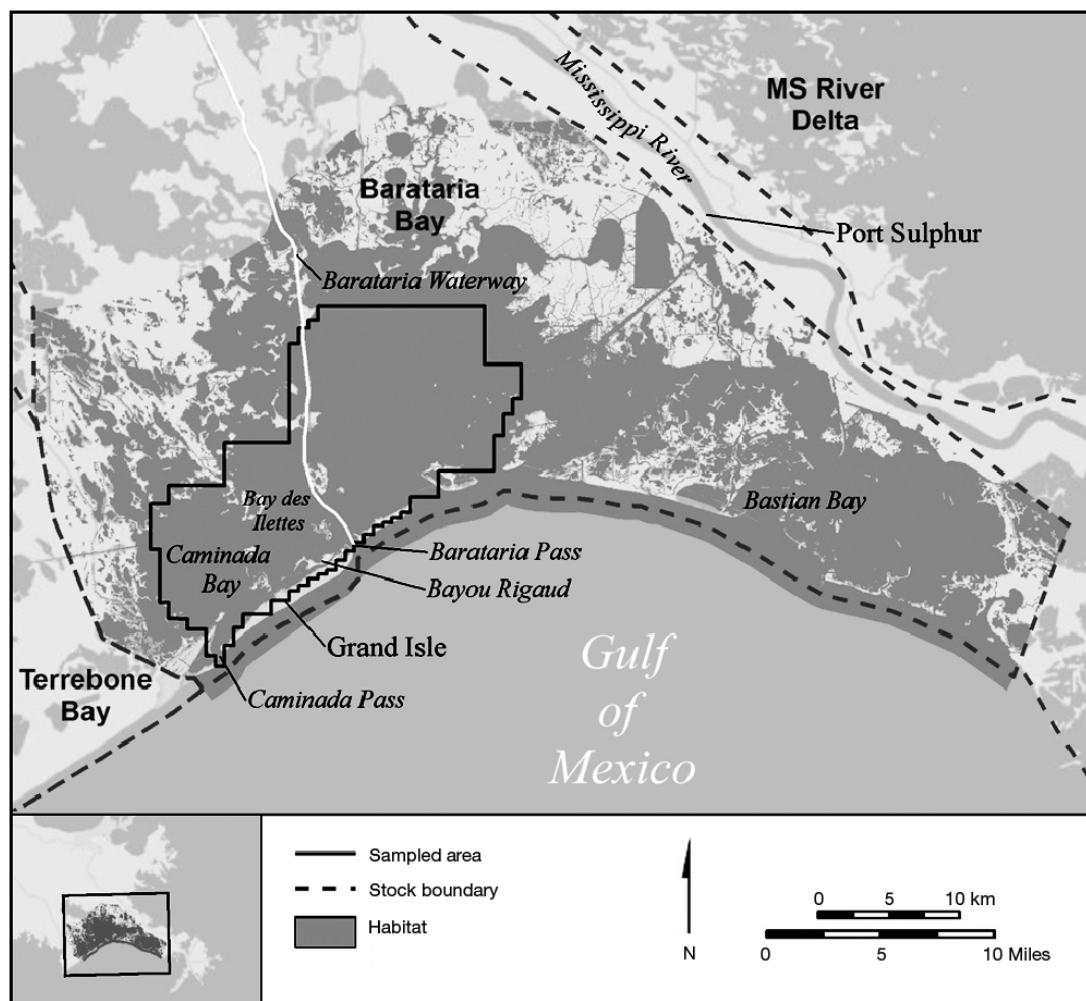

Fig. 1. Barataria Bay, Louisiana (USA), and study area. Habitat polygon defined by salinity models of Hornsby et al. (2017). Habitat mask (denoted **M** in text) covered habitat area and is shown in the lower-left inset

of Louisiana and Mississippi (DWH NRDA Trustees 2016), including Barataria Bay. In response, the National Oceanic and Atmospheric Administration (NOAA) led a Natural Resource Damage Assessment (NRDA) to estimate damages to a wide variety of marine resources, including the estuarine population of common bottlenose dolphins in Barataria Bay. NOAA researchers initiated boat-based photo-ID surveys in Barataria Bay in late June 2010. These surveys were designed to provide data on dolphin demographic parameters, specifically density, survival, and abundance. Following capping of the DWH well in August 2010, photo-ID surveys continued at sporadic intervals of 2 to 12 mo until April 2014, i.e. 4 yr after the spill began.

In this paper, we detail the photo-ID surveys in Barataria Bay, the photo processing necessary to identify individuals, and the subsequent statistical analysis of photo recaptures used to estimate survival and abundance. In doing so, we applied a previously unpublished variant of a spatially explicit capture-recapture model and made inference to changes in survival, density, and abundance during the 4 yr following the spill.

FIELD AND PHOTO ANALYSIS METHODS

Study area

The study area comprised estuarine waters of Barataria Bay near Grand Isle, Louisiana (29°14′ N, 90°00′ W), including Bayou Rigaud, Barataria Bay and Pass, Caminada Bay and Pass, Barataria Waterway, and Bay des Ilettes (Fig. 1). The study area is separated from the GoM by Grand Isle and the Grande Terre islands, but is connected by a series of passes to open GoM waters. The west, north, and northwest margins of the bay outside our study area include marsh, canals, channels, and bayous. The salinity of the bay's water varies from nearly fresh northwest of the study area to nearly seawater in the southeastern tidally influenced portions surrounding the barrier islands (US EPA 1999, Moretzsohn et al. 2010, and Hornsby et al. 2017, this Theme Section).

Photo-ID surveys

The field sampling methodology we employed has been standardized (reviewed by Rosel et al. 2011) and implemented by several studies in the southeast-

ern USA (e.g. Balmer et al. 2008, Speakman et al. 2010, Tyson et al. 2011). That methodology implements a robust capture-recapture design (Pollock 1982, Kendall et al. 1995, 1997) containing secondary sampling occasions nested within primary sampling occasions. The robust design assumes population closure among secondary occasions contained in the same primary, and openness between primaries.

Secondary occasions

We defined a secondary sampling occasion to be 1 complete transit of our photo-ID transect (Fig. 2), which required approximately 2 d to complete and followed standard photo-ID field protocols (Melancon et al. 2011, Rosel et al. 2011). We utilized two 5–6 m, center console, outboard vessels crewed by a minimum of 3 observers during all secondary surveys. On 1 day of a secondary survey, 1 vessel targeted Barataria Pass's southern half, while the other covered the pass's northern half (Fig. 1). This was done to coordinate and adequately photograph the large number of dolphins typically encountered there. Outside Barataria Pass, the 2 vessels operated independently and were nearly always out of line-of-sight.

We conducted most photo-ID surveys under optimal sighting conditions (Beaufort state < 3). Photo-ID vessels traversed the survey transect at 28–30 km h^{-1} until the crew sighted a dolphin or group of dolphins. We defined a dolphin group as all dolphins in relatively close proximity (<100 m), engaged in similar behavior, and generally heading in the same direction (Wells et al. 1980). After sighting a dolphin group, crews recorded the location of the boat after approaching within photographic range. A handheld GPS device (Garmin GPSmap 76Cx, stated accuracy 10 m) onboard the boat determined all locations. One member of the crew attempted to photograph all members of a group, regardless of fin marks, using Canon EOS digital cameras equipped with 100–400 mm variable length telephoto lenses.

We defined sightings as 'on-effort' when we encountered a group on an active search transect. Groups observed during transit to and from the dock or while between transects were considered 'off-effort.' After each survey, we downloaded GPS track logs and photos for both boats. We archived photos nightly after verifying frame numbers against the sighting sheets and renaming photos to include survey and sighting numbers.
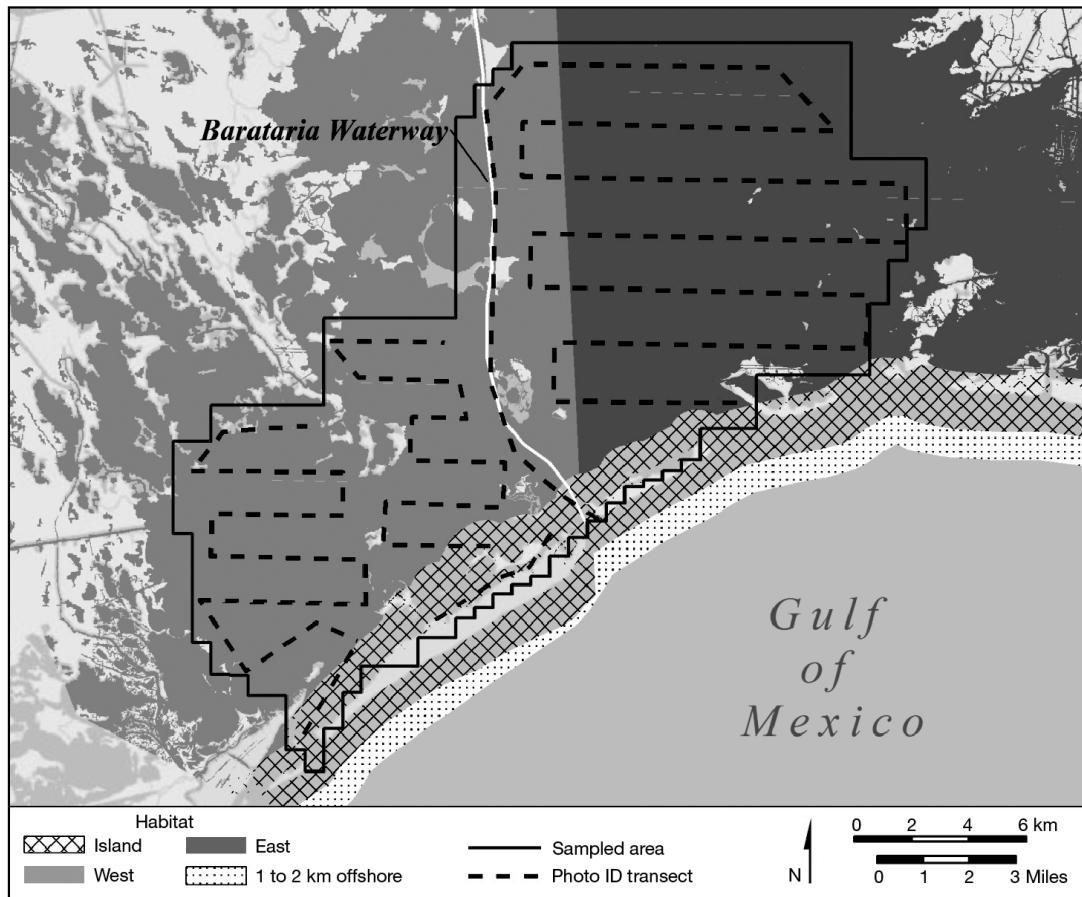
Fig. 2. Study area, showing common bottlenose dolphin *Tursiops truncatus* photo-ID transects and habitat strata. The rectangular habitat mask used in analysis covered all shaded areas here and in Fig. 1, with land and ocean >2 km offshore coded as 'non-habitat'

Primary occasions

We defined 3 consecutive secondary occasions, each separated by 1 d, to comprise a primary sampling occasion. The single day between secondary occasions was included to allow mixture of the dolphin population. The 3 secondary occasions that made up each primary required approximately 1 wk to complete. We conducted 10 primary photo-ID occasions from late June 2010 through early May 2014 (dates listed in Table 1).

Photo analysis

Initial processing of photographs involved 4 general steps (Mazzoil et al. 2004, Melancon et al. 2011). Step 1 identified duplicate photos of individuals taken during a single sighting event. Step 2 selected the highest quality left- and right-side dorsal photo for each individual during each sighting event.

Often, only 1 side of an individual's fin was photographed during a sighting. Step 3 cropped each photo to isolate the dorsal fin. Finally, when necessary, we rotated the photograph to make the dorsal fin's base parallel with the bottom of the frame. Occasionally, we adjusted brightness and contrast to improve image quality. We completed all processing in Photoshop 7.0 (Adobe Systems).

Correct identification of fins is critical to unbiased estimation of demographic parameters (Würsig & Jefferson 1990, Friday et al. 2000, Read et al. 2003). To help avoid false matches among photos, we graded the quality of images as Q-1 (excellent), Q-2 (average), or Q-3 (low) using a weighted scale based on 5 characteristics: focus, contrast, angle, fin visibility/obscurity, and proportion of the frame filled by the fin (Urian et al. 2014).

We identified and matched individuals by visually comparing Q-1 and Q-2 photographs to other Q-1 and Q-2 photos in a catalog of dorsal fin photos. Photographs of lesser quality were occasionally

Table 1. Estimated posterior mean common bottlenose dolphin *Tursiops truncatus* density (ind. km^{-2}) and abundance (no. dolphins) during primary capture sessions, and averaged over the study period in Barataria Bay, Louisiana (USA). CI: lower and upper credible interval. All values are plotted in Fig. 6. Abundances were calculated by expanding densities to the size of the stratum. Sizes of the strata were: 127.379, 355.278, and 684.728 km^2 for Island, West, and East, respectively. Stratum densities multiplied by stratum size do not sum to total Abundance due to rounding error

Session	Date	Island density Est (95% CI)	West density Est (95% CI)	East density Est (95% CI)	Abundance Est (95% CI)
1	26-Jun-10	8.2 (7.2, 9.2)	0.64 (0.61, 0.68)	0.038 (0.028, 0.061)	1303 (1164, 1424)
2	12-Nov-10	11.3 (9.9, 12.6)	0.95 (0.90, 1.00)	0.726 (0.532, 1.155)	2270 (1960, 2612)
3	9-Apr-11	11.8 (10.4, 13.2)	1.20 (1.14, 1.26)	0.270 (0.197, 0.429)	2115 (1877, 2290)
4	12-Jun-11	17.0 (14.9, 19.1)	1.18 (1.12, 1.24)	0.757 (0.555, 1.204)	3107 (2700, 3485)
5	14-Nov-11	10.0 (8.8, 11.2)	1.61 (1.53, 1.69)	0.625 (0.458, 0.994)	2278 (1998, 2576)
6	14-Feb-12	6.8 (5.9, 7.6)	1.14 (1.09, 1.20)	0.674 (0.494, 1.072)	1730 (1496, 2030)
7	15-Apr-12	10.8 (9.5, 12.1)	1.04 (1.00, 1.10)	0.971 (0.711, 1.544)	2412 (2064, 2847)
8	12-Apr-13	10.2 (8.9, 11.4)	0.69 (0.65, 0.72)	0.113 (0.083, 0.179)	1618 (1435, 1759)
9	13-Nov-13	13.6 (11.9, 15.2)	1.88 (1.79, 1.98)	0.991 (0.726, 1.577)	3078 (2673, 3537)
10	27-Apr-14	14.3 (12.5, 16.0)	2.11 (2.01, 2.22)	0.850 (0.622, 1.351)	3150 (2759, 3559)
Average density		11.4 (9.99, 12.8)	1.24 (1.19, 1.31)	0.601 (0.441, 0.957)	
SD(density)		0.884	0.0319	0.185	
Average abundance		1452 (1272, 1625)	442 (421, 465)	412 (302, 655)	2306 (2014, 2603)
SD(abundance)		112.6	11.3	126.6	195.9

matched to known individuals if the fin was highly distinct and constituted a clear match. We stored and managed our dorsal fin photo catalog in a customized Microsoft Access database (FinBase) (Adams et al. 2006). Two researchers verified all matches, and hence all identifications. Following identification, we assigned unique numerical codes to the individual in FinBase. FinBase records also contained location, age class, distinctiveness, and other information pertaining to the fin or photo. We assigned distinctiveness based on the extent of dorsal fin markings, regardless of photographic quality. We considered fins with none or few markings to be 'unmarked.' We considered very distinctive fins (coded D-1: obvious major marks) and average fins (coded D-2: 2 minor marks or 1 major mark) to be 'marked' (Urian et al. 2014). In each primary session, we estimated the proportion of marked dolphins in the population as the proportion of 'marked' fins among all high quality photographs (Q-1 and Q-2). Additional details of the photo analysis are available in Melancon et al. (2011).

DATA ANALYSIS METHODS

We applied the spatially explicit robust design (SERD) model of Ergon & Gardner (2014) to dolphin photo-ID data from Barataria Bay after extending it to include habitat boundaries (water). The SERD model of Ergon & Gardner (2014) incorporated a spatially explicit capture–recapture (SECR) model (Borchers & Efford 2008) into the closed (within-primary) portion of a standard robust design and estimated density, rather than abundance, for each primary occasion. SECR models estimate latent individual activity centers from the capture locations of every individual and use these locations to adjust capture probabilities based on distance to trapping locations. In turn, the distance-based capture probabilities estimate an effective study area, and density is essentially estimated as the number of activity centers divided by size of the effective study area. We extended the SERD model of Ergon & Gardner (2014) to include habitat boundaries (hereafter, 'habitat mask') that restricted dolphin movement and activity centers to water. The spatial capture heterogeneity induced by the SERD model allowed the open (between-primary) portion to infer both permanent and temporary emigration, thereby estimating 'true' rather than 'apparent' survival.

In the remainder of this section, we describe the SERD model and its estimation via Markov chain Monte Carlo (MCMC) sampling. Computer code to carry out estimation, written in the JAGS language (Plummer 2003), is provided in Supplement 2 at www.int-res.com/articles/suppl/n033p193_supp2.R. (with additional implementation details available in Supplement 1 at www.int-res.com/articles/suppl/n033 p193_supp1.pdf). We performed analyses in JAGS version 4.0.0.

Spatially explicit component for density

The SECR (i.e. closed) component of our SERD model mimicked that of previous SECR models (Borchers & Efford 2008, Royle et al. 2013, Schaub & Royle 2014). We divided the sampled area (Fig. 2) into a total of R square discrete pixels, each with size 1000×1000 m. These pixels were considered traps, and an individual became caught in a trap when its photo location plotted inside the pixel boundaries. Below, we use the term trap rather than pixel for generality, but in this study trap and pixel are synonymous. During a particular secondary sampling occasion, an individual could be caught in at most one trap, but one trap could capture multiple individuals during a secondary occasion. Individual capture histories for a primary session consisted of at most 3 trap identifiers, one for each secondary occasion. When an individual was not photographed, the trap identifier did not exist. For computational reasons that will become apparent later, the trap identifier for known un-captured individuals was set to 0.

Data and notation

The number of subscripts required to fully specify the model is excessive. In the following, we generally adopt the notation of Ergon & Gardner (2014), but use arrays for clarity and to make implementation straightforward. To reference an element of an array, we use brackets (i.e. [ ]) instead of subscripts. For example, when g is a parameter, we write $g[i,k,t]$ instead of g_{ikt}. When $\mathbf{G}$ is an array, we write $\mathbf{G}[i,j,k]$ to reference the ith row, j^{th} column, and k^{th} page. When we omit a dimension from the brackets, we reference the entire missing dimension, which is generally a vector. For example, $\mathbf{G}[i,,k]$ references all columns from the ith row and k^{th} page of $\mathbf{G}$. This latter notation is modeled after R language syntax (R Core Team 2015) for referencing multi-dimensional arrays. One-dimensional arrays are vectors. Two-dimensional arrays are matrices. Vectors, matrices, and arrays are in **bold** font, scalars are in *italic* font.

We start by defining np to be the number of primary occasions, and ***ns*** to be a vector of length np containing the number of secondary occasions in each primary. Here, ***ns*** = [3,3,…,3]. We define n to be the number of unique individuals captured during all primary and secondary occasions. We define ns_{max} to be the maximum number of secondary occasions that occurred during a single primary (i.e. ns_{max} = max(***ns***); here, ns_{max} = 3). Let ***dt*** be an $np-1$ vector of time intervals (fractions of a year) between each primary.

Trap locations are housed in matrix $\mathbf{X}$, which is size $R \times 2$. $\mathbf{X}[r,]$ is the (x,y) coordinate vector of the center of trap r. Capture histories in the form of trap indices are housed in a 3-dimensional array $\mathbf{H}$ which has size $n \times ns_{max} \times np$. $\mathbf{H}[i,j,k]$ is the row index of $\mathbf{X}$ for the trap that captured individual i during secondary occasion j of primary session k. In other words, the trap at location $\mathbf{X}[\mathbf{H}[i,j,k],]$ captured animal i during secondary j of primary k. Prior to first capture and when a previously captured animal was not captured, $\mathbf{H}[i,j,k]$ = 0; but values prior to first capture were inconsequential because the model conditions on first capture. For computational purposes $\mathbf{X}[0,]$ was understood to be the null, or nonexistent, location.

In regular SECR models (e.g. Borchers & Efford 2008, Ergon & Gardner 2014, Schaub & Royle 2014), individuals are viewed as having a single activity center during the study period. Activity centers are latent, or unobserved, in SECR models because locations are only known when an individual is seen. Here, we allow different activity centers on each primary occasion. For computational purposes, we define array $\mathbf{S}$ to be an $n \times 2 \times np$ array such that $\mathbf{S}[i,,k]$ is the (x,y) coordinate vector of individual i's activity center during primary session k.

We incorporated a habitat mask into the SERD model by defining $\mathbf{M}$ to be an $mx \times my$ matrix of 0's and 1's, where each cell was associated with a geographic pixel (1000×1000 m). Cells in $\mathbf{M}$ containing 1's indicated pixels where activity centers could be located, while 0's indicated pixels where activity centers could not be located. We set the size of $\mathbf{M}$ such that it covered a large area surrounding the sampled area (lower-left inset, Fig. 1). Values associated with pixels whose centers fell on land or were over 2 km offshore of the islands were set to 0. We set values in $\mathbf{M}$ to 1 when a pixel's center fell in water and within 2 km offshore of an island. For computational convenience, we set the origin of the mask so that habitat pixel centers coincided with trap pixel centers in the sampled area, but this was theoretically not necessary. To facilitate programming via simple indexing and to simplify specification of priors, we shifted the locations in $\mathbf{X}$, $\mathbf{M}$, and $\mathbf{Z}$ ($\mathbf{Z}$ defined in next paragraph) left and down so that the minimum horizontal and vertical coordinate was (0,0).

Based on dolphin movements in Barataria Bay documented by satellite-linked tags (Wells et al 2017, this Theme Section), and general knowledge of the number and location of dolphins in the bay, we

hypothesized that density varied among 3 habitat areas (i.e. strata). The 'Island' stratum encompassed waters less than 1 km from 1 of the barrier islands (Fig. 2). The 'West' stratum primarily encompassed non-island portions of Barataria Bay west of the Barataria Waterway (Fig. 2). The 'East' stratum encompassed non-island portions of the bay east of the waterway. Due to the shape and slight curvature of islands in the Island stratum, it was possible for a dolphin's activity center to fall outside the Island stratum (>1 km from islands) even though dolphins were only photographed inside the Island stratum. To allow this situation, we included a fourth stratum defined as waters between 1 and 2 km offshore of the barrier islands, but we do not report density estimates there because we inadequately sampled dolphins in this area. The stratum designation of all pixels in non-habitat ($\mathbf{M} = 0$ pixels) was unassigned because they were not used in calculations. The end result was an $mx \times my$ matrix $\mathbf{Z}$, similar to $\mathbf{M}$, of strata indicators 1, 2, ..., 5 with 1 = Island, 2 = West, 3 = East, 4 = 1–2 km offshore, and 5 = non-habitat.

Capture probability model

As in standard SECR models, we modeled the capture probability of an individual as a function of distance between its activity center and all traps. We used the exponential power series capture function (Pollock 1978) to model the decline in capture probability of activity centers far from the traps. During a particular primary occasion, we modeled the exposure of an individual with activity center at $\mathbf{S}[i,,k]$ to our photographic efforts in trap $\mathbf{X}[t,]$ as

$$g[i,k,t] = \lambda_m \exp\left(-\left(\frac{d[i,k,t]}{\sigma_m}\right)^{\kappa_m}\right) \quad (1)$$

where $d[i, k, t] = ((\mathbf{S}[i, 1, k] - \mathbf{X}[t, 1])^2 + (\mathbf{S}[i, 2, k] - \mathbf{X}[t, 2])^2)^{0.5}$ was distance (in units of pixels, here km) between the activity center and the trap. Parameters λ_m, σ_m, and κ_m ($m = 1, 2, 3, 4$) were strata-specific parameters that determined the height, extent, and shape of the capture function (Fig. 3).

The prior distributions for σ_m and κ_m were: $\sigma_m \sim$ Uniform(0.1, 15); $\kappa_m \sim$ Uniform(1, 3) for $m = 1, 2, 3, 4$. The prior for σ_m was considered uninformative because, at the upper limit of 15, substantial capture hazard existed at every trap for individuals in almost all parts of the sampled area. Note that the upper limit of 15 km was approximately the entire north–south extent of the study area (Fig. 2) and half of the east–west extent of the study area. Many authors do

not estimate κ_m and simply assume the half-normal capture function (i.e. $\kappa_m = 2$) (Borchers & Efford 2008, Schaub & Royle 2014), so we chose a mildly informative prior distribution for κ_m centered on 2.

The capture function intercept, λ_m, quantified the probability of detection at a single trap assuming that an activity center coincided with the trap location. The prior distribution for λ_m depends upon the number and configuration of traps, as well as the size of an individual's activity area. We did not have a prior estimate of λ_m and consequently specified a uniform prior as $\lambda_m \sim$ Uniform(0.002, 0.02). This prior for λ_m covers the approximate range of the number of traps in a dolphin's presumed activity area. Based on radio telemetry, we estimated a dolphin's activity area during a primary session to contain between 1 and 10 traps, and set the limits of λ_m's prior to approximately $1/R$ and $10/R$ (where R = number of traps).

The overall exposure of individual i to trapping during any secondary occasion in primary k was

$$G[i,k] = \sum_{t=1}^{R} g[i,k,t] \quad (2)$$

The overall probability of capturing a photograph of individual i's dorsal fin in any trap during any of the secondary occasions of primary occasion k was

$$p[i,j,k] = 1 - \exp(-G[i,k]) \quad (3)$$

Here, $G[i,k]$ does not contain an index for secondary occasion (i.e. j) and therefore does not vary by secondary occasion. Models which vary capture probability over secondary occasions are possible, but

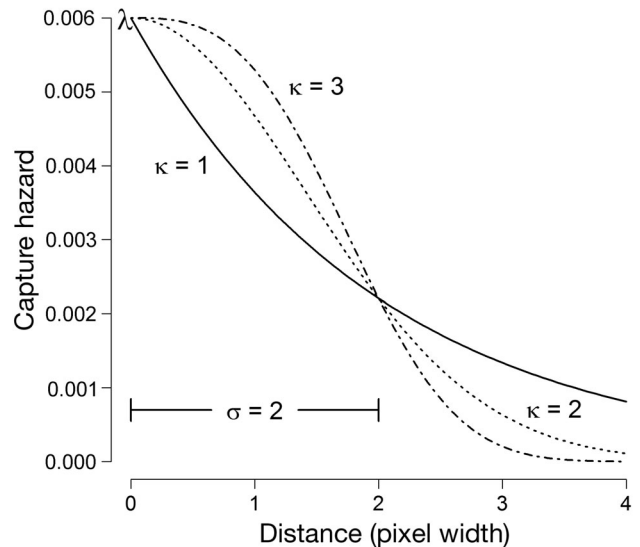
Fig. 3. Plots of capture exponential power series functions for an individual trap (Eq. 1) for 3 hypothetical values of shape parameter κ, height parameter $\lambda = 0.006$, and extent parameter $\sigma = 2$

were not needed here given the extremely short duration of primary sessions (~1 wk).

The probability of capturing a photograph of individual i in trap t during secondary occasion j of primary session k was modeled as

$$\Pr(\mathbf{H}[i, j, k] = t) = \frac{g[i, k, t]}{G[i, k]} p[i, j, k], \qquad (4)$$

and the probability of not photographing the individual was

$$\Pr(\mathbf{H}[i, j, k] = 0) = 1 - p[i, j, k] \qquad (5)$$

Derived density estimates

Given a sample of the capture parameters [λ_m, σ_m, κ_m] from their posterior distribution, we derived estimates of density after Borchers & Efford (2008). In this section, the number of indices is excessive if we maintain one for the primary occasion (i.e. k above). Consequently, we drop the index for primary occasions and conduct the following calculations for each primary.

Conceptually, we derived a density estimate in the mth stratum by hypothesizing activity centers in every pixel of valid habitat and computing probability of detection in every pixel. We then estimated density as the observed number of captures divided by the sum of all activity center capture probabilities in valid habitat.

Assume the number of valid habitat locations in $\mathbf{M}$ is q (i.e. q = number of 1's in $\mathbf{M} = \sum_{i=1}^{mx} \sum_{j=1}^{my} \mathbf{M}[i, j]$). Let $\mathbf{C}$ be a $q \times 2$ matrix containing the (x, y) coordinates for the centers of all valid habitat pixels in $\mathbf{M}$. Given an estimated parameter vector [λ_m^a, σ_m^a, κ_m^a] from the MCMC routine (a indicates the ath MCMC iteration), we evaluated the capture function (Eq. 1) as

$$g[i, a, m, t] = \lambda_m^a \exp\left(-\left(\frac{d[i, t]}{\sigma_m^a}\right)^{\kappa_m^a}\right) \qquad (6)$$

where $d[i, t] = ((\mathbf{C}[i, 1] - \mathbf{X}[t, 1])^2 + (\mathbf{C}[i, 2] - \mathbf{X}[t, 2])^2)^{0.5}$ is the distance from location $\mathbf{C}[i,]$ to trap t. We computed overall exposure of an activity center at $\mathbf{C}[i,]$ to capture as

$$G[i, a, m] = \sum_{t=1}^{R} g[i, a, m, t] \qquad (7)$$

and the probability of obtaining a photograph of an animal with activity center $\mathbf{C}[i,]$ during a single secondary occasion as

$$p[i, a, m] = 1 - \exp(-G[i, a, m]) \qquad (8)$$

Because we modeled constant capture probabilities across secondary occasions, the probability of photographing an individual during $\mathbf{ns}[k]$ secondary occasions was

$$P[i, a, m] = 1 - (1 - p[i, a, m])^{\mathbf{ns}[k]} \qquad (9)$$

Here, $P[i, a, m]$ was equivalent to '$p.(x)$' of Borchers & Efford (2008). For each iteration a we summed the $P[i, a, m]$ surface over all habitat locations i to arrive at a probability of detecting individuals in stratum m on iteration a, i.e.

$$A[a, m] = \sum_{i=1}^{q} P[i, a, m] \qquad (10)$$

Finally, we defined the number of individuals photographed in stratum m during the primary occasion to be $\mathbf{n}[m]$ and computed density as

$$D[a, m] = \left[\frac{\mathbf{n}[m]}{A[a, m]}\right]\frac{1}{b} \qquad (11)$$

where b is the proportion of distinctive fins seen during the primary session. We computed b as the fraction of all high quality photographs with enough distinctive marks to uniquely identify the individual. Inclusion of b inflated density estimates to account for the unmarked population fraction, which typically represented young individuals. Our model did not include variation in the estimated b because the proportion was relatively high (approximately 0.8) and based on hundreds of photos (consequently, $se(b) = \sqrt{b(1-b)/n}$ is small). The point estimate of density in stratum m was the posterior mean, obtained by computing average D over the MCMC iterations (i.e. over a) after a suitable burn-in period (see below). A 95% posterior credible interval (CI) for density was computed by calculating the 2.5$^{\text{th}}$ and 97.5$^{\text{th}}$ quantiles of $D[a, m]$ over all MCMC iterations.

Derived abundance estimates

We estimated abundance by expanding strata-specific density estimates to the area of estimated dolphin habitat in Barataria Bay. Estimated dolphin habitat was derived by Hornsby et al. (2017), who used daily salinity maps and daily dolphin satellite-tag-telemetry locations to estimate an average minimum salinity level tolerated by dolphins. Hornsby et al. (2017) estimated that 95% of dolphin locations occurred in waters more saline than 7.89 ppt. By averaging the daily location of the 7.89 ppt salinity contour over multiple years, Hornsby et al. (2017) estimated 1167.385 km^2 of dolphin habitat in Barataria Bay (grey areas in Fig. 1) apportioned among the strata as follows: Island habitat = 127.379 km^2;

West habitat = 355.278 km^2; and East habitat = 684.728 km^2.

Reinstating the subscript for primary session (i.e. k), we computed an estimate of abundance from every iteration of the MCMC routine as

$$N[k,a] = \sum_{m=1}^{3} K[m]D[k,a,m] \qquad (12)$$

where $K[m]$ is total area of stratum m (in km^2) and $D[k,a,m]$ is density estimated for the kth primary on the ath iteration of the MCMC sampler in stratum m. The final point estimate of abundance for the primary session was the mean $N[k,a]$ over MCMC iterations. We computed lower and upper CI limits as the 2.5th and 97.5th quantiles of the mean over MCMC iterations.

To arrive at a single estimate for the entire study period, we averaged N over the np primary occasions each MCMC iteration. Lower and upper CI limits were the 2.5th and 97.5th quantiles of this average.

Open component for survival

The SERD model allowed population changes and activity center movements between primary occasions. We estimated survival between primary occasions following Ergon & Gardner (2014) who conditioned on first capture and followed individuals afterwards, similar to Cormack-Jolly-Seber models (Jolly 1965, Seber 1965, Cormack 1972, Schaub & Royle 2014).

Movement model for activity centers

We assumed the activity center associated with an individual's first primary had a (bivariate) uniform prior over the habitat mask. We assumed

$$\mathbf{S}[i, ,f] \sim Uniform([0, \Delta x], [0, \Delta y]) \qquad (13)$$

where Δx is the horizontal extent of our habitat mask, Δy is the vertical extent of our habitat mask, and f is the first primary during which we encountered animal i. Here, $\Delta x = mx$ km and $\Delta y = my$ km because we used 1 km grid cell spacing. During MCMC sampling, we employed the habitat check of Meredith (2013) to assign probability 0 to $\mathbf{S}[i, ,f]$ if $M[sx, sy] = 0$, where $sx = floor(\mathbf{S}[i,1,f])$ and $sy = floor(\mathbf{S}[i, 2,f])$ and $floor(x)$ is the largest integer less than or equal to x. This prevented placement of activity centers in pixels with $M = 0$. Had we used a grid spacing other than 1 km, we would have divided $\mathbf{S}[i,1,f]$ and $\mathbf{S}[i,2,f]$ by their respective cell extents prior to applying $floor$.

Following first encounter, a simple movement model based on distance and angle allowed different activity center locations during each primary occasion (Schaub & Royle 2014). We computed a new activity center location for primary occasion $k > f$ as

$$S[i,1,k] = S[i,1,k-1] + d[i,k-1]\cos(\theta[i,k-1]) \quad (14)$$

$$S[i,2,k] = S[i,2,k-1] + d[i,k-1]\sin(\theta[i,k-1]) \quad (15)$$

where $\theta[i,k-1] \sim Uniform(-\pi, \pi)$, $d[i,k-1] \sim Exponential(\gamma_m^{-1})$ and γ_m ($m = 1, ..., 5$) was a stratum-specific hyper-parameter for movement distance. The prior for γ_m in stratum $m = 1, 2, 3,$ or 4 was uniform on the interval $[0, 20]$, while γ_5 was fixed at an arbitrary value (0.5) because activity centers were not allowed outside the habitat mask where stratum was 'non-habitat.' Again, a habitat check ensured that activity centers in non-habitat were assigned zero probability.

Conditional likelihood for survival

To aid interpretation and facilitate later summaries, we parameterized the open portion of the SERD model using equivalent annual survival, which we assumed had a $uniform(0,1)$ prior distribution. We adjusted for unequal time intervals between primaries by defining $\mathbf{w}[k]$ ($k = 1, 2, ... (np-1)$) to be the fraction of a year between primary occasion k and $k+1$ and raising the equivalent annual survival, $\boldsymbol{\Phi}[k]$ ($k = 1, 2, ... (np-1)$), to the $\mathbf{w}[k]$ power. For example, if 6 mo elapsed between primary occasions 1 and 2, while 15 mo elapsed between occasions 2 and 3, $\mathbf{w} = [0.5, 1.25]$ and the interval-specific survivals were $\boldsymbol{\Phi}[1]^{0.5}$ and $\boldsymbol{\Phi}[2]^{1.25}$.

More specifically, let $\mathbf{z}[i,k]$ be a $n \times np$ matrix of latent (unobserved) 0's and 1's where $\mathbf{z}[i,k] = 1$ if individual i was alive during primary k, and 0 otherwise. Note that $\mathbf{z}[i,f] = 1$ always, $\mathbf{z}[i,k+1] = 0$ if $\mathbf{z}[i,k] = 0$, and $\mathbf{z}[i,k]$ for $k < f$ were inconsequential because they did not enter the conditional likelihood. Given latent survival indicator $\mathbf{z}[i,k]$, the likelihood of animal i surviving to primary session $k+1$ was

$$Pr(z[i,k+1] = 1) = \mathbf{z}[i,k]\boldsymbol{\Phi}[k]^{\mathbf{w}[k]} \qquad (16)$$

(Ergon & Gardner 2014, Schaub & Royle 2014).

Schwacke et al. (2017, this Theme Section) used a structured model of population growth to characterize losses and recovery of the Barataria Bay population following the DWH spill. Their model, which estimated the transient dynamics in 1 yr time steps, required survival estimates over combined intervals

approximately 1 yr in length. We therefore summarized survival during 4 combined intervals (each starting and ending at a primary session, Table 2) by averaging the equivalent annual survival estimates over the between-primary periods in each. For example, the second combined interval following the spill started on 12 June 2011 and lasted until 15 April 2012, a period of 10 mo. This period contained 3 inter-primary intervals and hence 3 estimates of the equivalent annual survival (i.e. $\Phi[4]$, $\Phi[5]$, and $\Phi[6]$). We estimated probability of surviving the second combined interval as

$$\Phi^\star[2] = \left(\frac{\Phi[4] + \Phi[5] + \Phi[6]}{3}\right)^{10/12} \qquad (17)$$

We performed similar calculations for the other 3 combined intervals listed in Table 2, as well as averaged equivalent annual survivals over the same intervals.

MCMC estimation

We implemented 3 parallel MCMC chains in JAGS to estimate parameters. Each chain performed 500 burn-in steps and 200 sampling steps. Iterations took approximately 9 d to complete on a single-core 64-bit server, and ultimately yielded 600 observations of the parameter vector. The Gelman and Rubin procedure (Gelman & Rubin 1992) checked mixing of the λ_m, σ_m, κ_m, and Φ chains by computing potential scale reduction factors. Geweke z statistics checked convergence of the chains (Geweke 1991).

RESULTS

Crews photographed 1601 unique individual common bottlenose dolphins during 10 primary occasions in Barataria Bay. Intervals between primary occasions varied from 2 mo to 1 yr. The number of unique individuals per primary varied from 226 (Primary 1) to 591 (Primary 10) (Fig. 4). The cumulative number of new individuals (i.e. the discovery curve) leveled off between April 2012 and April 2013, but then continued to grow during late 2013 and 2014 at a rate only slightly lower than previously observed (Fig. 4).

Table 2. Estimated common bottlenose dolphin *Tursiops truncatus* survival probabilities ('Est.') and 95% credible intervals ('Low', 'High') in Barataria Bay. 'Interval' estimates are probability of surviving the specific interval, computed by Eq. 17. 'Annual' estimates are the equivalent annualized survival computed by averaging Inter-primary estimates (see Fig. 5). Dates are mo/yr

Inter-val	Start	End	Interval			Annual		
			Est.	Low	High	Est.	Low	High
1	Jun 10	Jun 11	0.846	0.787	0.901	0.862	0.808	0.916
2	Jun 11	Apr 12	0.827	0.790	0.862	0.792	0.738	0.839
3	Apr 12	Apr 13	0.804	0.766	0.847	0.803	0.764	0.846
4	Apr 13	Apr 14	0.973	0.937	0.996	0.973	0.934	0.996

Mixing of all parameters, especially survival parameters ($\Phi[k]$, $k = 1, \ldots, 9$), was good, except for capture parameters σ_1 and κ_1 associated with the Island stratum (with potential scale reduction factors of 4.9 and 5.7, respectively), and σ_3 and λ_3 associated with the East stratum (potential scale reduction factors 10.8 and 4.2, respectively). The Geweke statistics indicated convergence of all parameters except κ_1 associated with the Island stratum ($z = 2.08$), and σ_3 and λ_3 associated with the East stratum ($z = 9.01$ and 2.22, respectively). The estimated posterior mean σ_1 was 2.34 km (95% CI = 2.18 to 2.52 km), while mean κ_1 was 2.73 (95% CI = 2.17 to 2.99). The posterior mean of σ_3 equaled 11.3 km (95% CI = 5.3 to 15.0 km), while mean λ_3 was 0.00229 (95% CI = 0.00200 to 0.00353).

It is not surprising that detection parameters converged slowly. All 3 parameters (λ, σ, κ) are correlated, and the detection function (Eq. 1) was nearly horizontal (its theoretical upper limit) in the Island
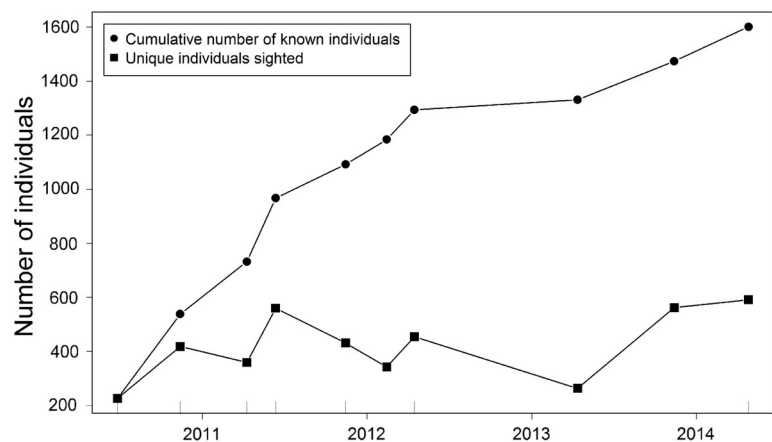

Fig. 4. Discovery curve (cumulative number of unique individuals) and the number of individual common bottlenose dolphins *Tursiops truncatus* caught per primary session. Tick marks on the *x*-axis are mid-point dates of the primary sessions (listed in Table 1)

and East strata. Nearly constant detection out to 2+ km in the Island stratum was not surprising given the size of the strata, the ubiquity of dolphins in these areas, and the relative ease of spotting dolphins in waters around the islands. A low and attenuated (long) detection function in the East stratum was not surprising given its low density and predominantly open water habitat.

Survival

Across the first 3 combined intervals (approximately 3 yr following the DWH spill), estimated annual survival of dolphins in Barataria Bay varied from 0.80 to 0.85, with upper credible limits at or below 0.90 (Table 2, Fig. 5). During the fourth and final 1 yr interval, we estimated survival to be 0.97 (95% CI = 0.94 to 0.99). The final interval includes survival between the last 2 occasions, which is generally considered unreliable in capture-recapture analyses due to partial or complete confounding with capture probability (Lebreton et al. 1992).

Density

Estimated density (ind. km^{-2}) of dolphins in the Island stratum was approximately 10 times higher than density in the 2 non-Island strata. Estimated density in the Island stratum increased from approximately 8.2 ind. km^{-2} in late June and early July 2010 to approximately 17.0 in June 2011 (Fig. 6). After June 2011, estimated density surrounding the islands varied from 6.7 to 10.8 ind. km^{-2} until November 2013. After November 2013, density increased to 13.60 and 14.25 ind. km^{-2} in late 2013 and spring, 2014, respectively.

Density in the 2 non-Island strata remained relatively constant until November 2013. In the West stratum, density varied from 0.64 to 1.6 ind. km^{-2} until the April 2013 session when density during the final 2 primaries increased to 1.87 and 2.11 ind. km^{-2}. In the East stratum, density varied between 0.03 and 0.97 ind. km^{-2} until April 2013. Afterwards, density in the East stratum increased to 0.99 in November 2013 and 0.85 ind. km^{-2} in April 2014.

Abundance

Temporal trends in abundance mirrored temporal trends in density. In the year following the DWH spill, the estimated number of dolphins within Barataria Bay increased from 1300 (95% CI ± ~130) to 3100 (95% CI ± ~400) (Table 1, Fig. 6). Between summer and late fall 2011, the number of dolphins in Barataria Bay declined to approximately 2300 (95% CI ± ~290) individuals, and remained between ~1600 and ~2400 individuals until spring 2013 (Table 1, Fig. 6). In fall 2013 and spring 2014, the estimated number of dolphins in Barataria Bay increased to higher levels of approximately 3100 individuals (Table 1, Fig. 6).
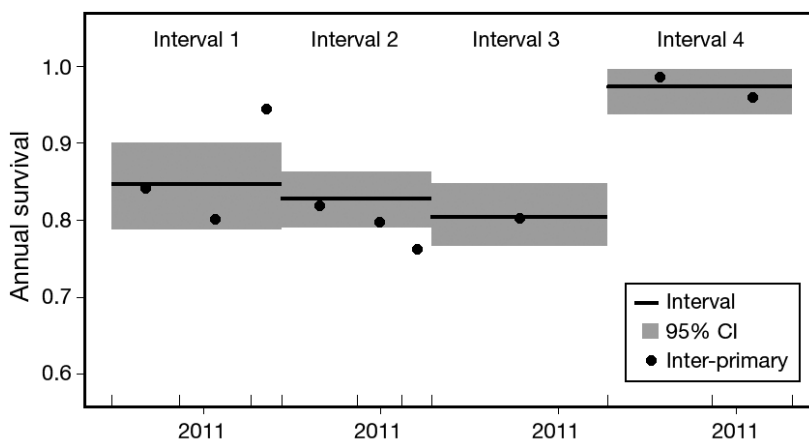

Fig. 5. Annual estimated survival rates of common bottlenose dolphins *Tursiops truncatus* in Barataria Bay. Estimates labeled 'Interval' (gray bars) are estimated probabilities of surviving the combined interval. 'Inter-primary' points estimate equivalent annual survival between primary sessions. Tick marks on the *x*-axes are mid-point dates of primary sampling sessions. The final 'Inter-primary' estimate is considered unreliable due to confounding factors (see 'Results'), and final 'Interval' estimate should be viewed with caution

DISCUSSION

Estimated survival rates for dolphins in Barataria Bay during the first 3 yr (2011–2013) after the April 2010 DWH oil spill were low (range 0.804–0.846, Table 2) relative to other BSE common bottlenose dolphin stocks along the southeast US coast that have been studied with similar mark-recapture techniques. An annual survival rate of 0.951 (95% CI = 0.88–1.00) was reported for the Charleston BSE common bottlenose dolphin stock surveyed between 2004 and 2006 (Speakman et al. 2010). Similarly, an annual survival rate of 0.962 was reported for common bottlenose dolphins in Sarasota Bay, Florida, surveyed over a 7 yr period
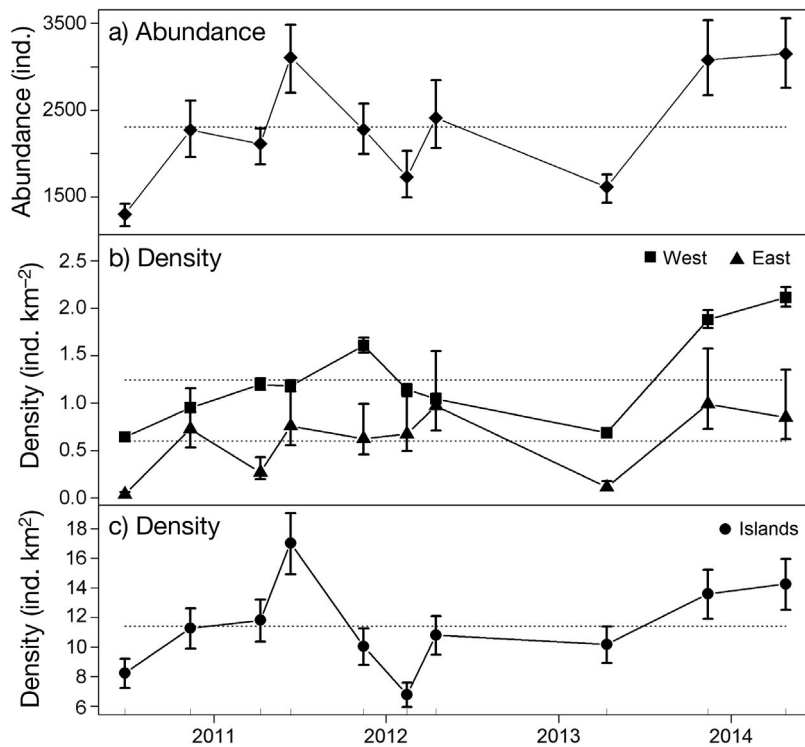
Fig. 6. Overall estimated (a) abundance and (b,c) density estimates of common bottlenose dolphins *Tursiops truncatus* by stratum in Barataria Bay from the spatially explicit, robust design capture-recapture model. Points are estimated posterior means and vertical bars are 95% credible intervals. Symbols are plotted at the mid-point dates of primary sampling sessions. Dashed horizontal lines are temporal averages of their respective time series. Note differences in *y*-axis scales

from 1980 to 1987 (Wells & Scott 1990). However, it was not surprising that we found lower survival rates in Barataria Bay dolphins given that an unusual mortality event (UME) in the northern GoM overlapped our study period (Litz et al. 2014, Venn-Watson et al. 2015). A UME as defined under the Marine Mammal Protection Act (116 USC 1421h) can be declared based on a number of criteria. In this case, the stranding rate was determined to be unusually high (over 2 SD above the historic mean rate). While the UME was declared for the broader northern GoM (Franklin County, FL, to the Louisiana–Texas border), dolphin strandings were particularly high in Barataria Bay. In fact, Louisiana recorded the highest stranding rates on record between the April 2010 DWH spill and December 2011 (Venn-Watson et al. 2015), and a large portion of these strandings were recovered in and around Barataria Bay. The number of dolphin strandings decreased in 2014 and the UME officially ended in July 2014. NOAA concluded that the DWH oil spill was the most likely explanation for the elevated stranding numbers that persisted for the 4 yr after the

spill (www.nmfs.noaa.gov/pr/health/mmume/cetacean_gulfofmexico.htm). Near the end of the UME period, our final survival estimate (April 2013 – April 2014) rebounded to 0.973 (95% CI: 0.937–0.996) and was similar to rates reported in previous studies of BSE dolphins (Wells & Scott 1990, Speakman et al. 2010). Despite our caution about confounding in the final survival estimate, the magnitude of the estimate makes it likely that survival increased during the fourth 1 yr study interval relative to previous intervals, and this increased survival in late 2013 is consistent with lower dolphin stranding numbers reported after April 2013 (relative to previous years).

The density of common bottlenose dolphins varied spatially across the photo-ID survey area, with nearly 10-fold higher density observed in the Island stratum as compared to the 2 non-Island strata (Fig. 6). It is known that interlinked physical and biological factors can cause increased density of top predators in specific areas (e.g. Wingfield et al. 2011). The multiple passes and estuarine entrances within the Island stratum (Fig. 1) likely provide attractive habitat for bottlenose dolphins. The entrances tend to concentrate fish moving between estuary and ocean waters (Shane 1990) and must be negotiated by spawning fish when they move from medium to higher salinity waters in the GoM (e.g. Lyczkowski-Shultz et al. 1990). Additionally, sloping bottom topography around islands can increase fish concentrations and facilitate dolphin foraging (Ingram & Rogan 2002). The higher density of dolphins observed in the Island stratum is also consistent with numerous prior studies in the GoM (Shane 1977, Barham et al. 1979, Leatherwood & Reeves 1983) and elsewhere (Ballance 1992, Ingram & Rogan 2002) that indicate a tendency of bottlenose dolphins to aggregate near the entrances to estuaries.

The densities estimated for the 3 strata, as well as the estimated overall abundance for the Barataria Bay stock, also varied temporally (Table 1, Fig. 5). Low densities for all 3 strata were observed in the first sampling occasion immediately following the DWH spill (June 2010). Densities increased over the following year, but then declined to varying degrees between June 2011 and April 2013. In the final 2

surveys (November 2013 and April 2014) densities across all 3 strata again increased and a concomitant uptick appeared in the discovery curve after a previous apparent leveling off (Fig. 4).

NRDA photo-ID surveys did not begin until approximately 2 mo after the DWH spill. Consequently, common bottlenose dolphin abundance in Barataria Bay prior to the DWH spill is unknown. By the time of the first photo-ID survey, oil response and cleanup activities were well underway. The heaviest and most persistent shoreline oiling occurred in portions of Barataria Bay (Michel et al. 2013), and thus this area immediately became a primary focus for oil spill response and the media. Hundreds of vessels responded to oil in the nearshore environment, and activities in the Barataria Bay area included placing and moving oil-retention booms, skimming, dredging activities offshore of the islands, transport of response workers, officials, and journalists, and releases of fresh water from the Mississippi River. Over 12.7 million feet of oil containment boom was deployed in the northern GoM, including in Barataria Bay, and both the boom deployment and subsequent deployment of boom removal teams significantly increased boat traffic (DWH NRDA Trustees 2016). The unprecedented level of boat activity and boom deployment damaged nearshore habitats and disturbed wildlife (DWH NRDA Trustees 2016). Much of these cleanup activities overlapped photo-ID survey routes, particularly the Island stratum. In addition, fishing and shrimping activities were temporarily banned in parts of the bay. While the spatial and temporal closures of fishing activity during 2010 were extremely complicated and not well documented, the general reduction in fishing would have reduced bycatch that is likely an attractive food source to some dolphins. We suggest that the combined effects of response, cleanup, preventative activities, and reduced fishing, as well as the oil itself, created an unfavorable environment for dolphins throughout much of Barataria Bay. Faced with this unfavorable environment, it is very plausible that dolphins responded by temporarily moving out of areas near barrier islands and passes where the most intense clean-up activities were occurring (Fig. 7a). Dolphins that may have moved to marshes in the extreme interior (north, west, or east) would not have been photographed.

While not comparable to the unprecedented level of disturbance in Barataria Bay, prior studies have also observed temporary shifts in distribution related to disturbance by industrial activities. A change in bottlenose dolphin density was observed in Sarasota Bay during bridge construction, with dolphin density increasing in the vicinity of the bridge once construction was complete (Buckstaff et al. 2013). A study of bottlenose dolphins in Aberdeen Harbor, Scotland, found that dredging operations temporarily displaced bottlenose dolphins from an important foraging area (Pirotta et al. 2013). Similarly, harbor porpoise density decreased in the vicinity of an offshore wind farm during construction that involved pile-driving activity (Dähne et al. 2013).

Estimated abundance increased during surveys after the well was capped, when spill-related anthropogenic activities slowed (November 2010 to June 2011) and eventually ceased. At that time, it is possible that the reduced activity level prompted displaced dolphins to return to portions of the bay subject to our photo-ID efforts (Fig. 7b).

The decline in densities across the 3 strata after June 2011 and continuing until April 2013 is consistent with a population experiencing increased mortality (Fig. 7c). Our low survival estimates for this period, concurrent high stranding rates, and general poor health of Barataria Bay dolphins documented during separate health assessments (Lane et al. 2015, Smith et al. 2017, this Theme Section) strongly support the notion that increased mortality occurred during this period.

The renewed increase in densities across strata during the final 2 surveys, concomitant with an uptick in the discovery curve, indicates an influx of previously unidentified dolphins, and we propose 2 plausible contributing sources for the new individuals. First, a portion of these dolphins could represent individuals that had been in the photo-ID study area but only recently acquired the necessary natural fin markings that allowed them to be recognized as unique individuals. Dolphins acquire dorsal fin nicks and notches over time, and therefore very young individuals are less likely to have distinctive and identifiable fin features. Analysis of fin markings on dolphins of known age from other BSE stocks suggest that the median age for dolphins to acquire distinctive markings is around 6 to 8 yr (Lane 2007, L. Schwacke unpublished data), but varies by sex, with males generally acquiring distinctive markings at an earlier age (Orbach et al. 2015). If the Barataria Bay dolphin population had been experiencing significant growth through an increased number of births during years just prior to the DWH spill, the fins of a large cohort of young dolphins could have become distinctive and contributed to the perceived influx of new individuals in November 2013 and April 2014. During 2007, Miller et al. (2010) hypothesized that a reported boom in dolphin calf numbers in nearby
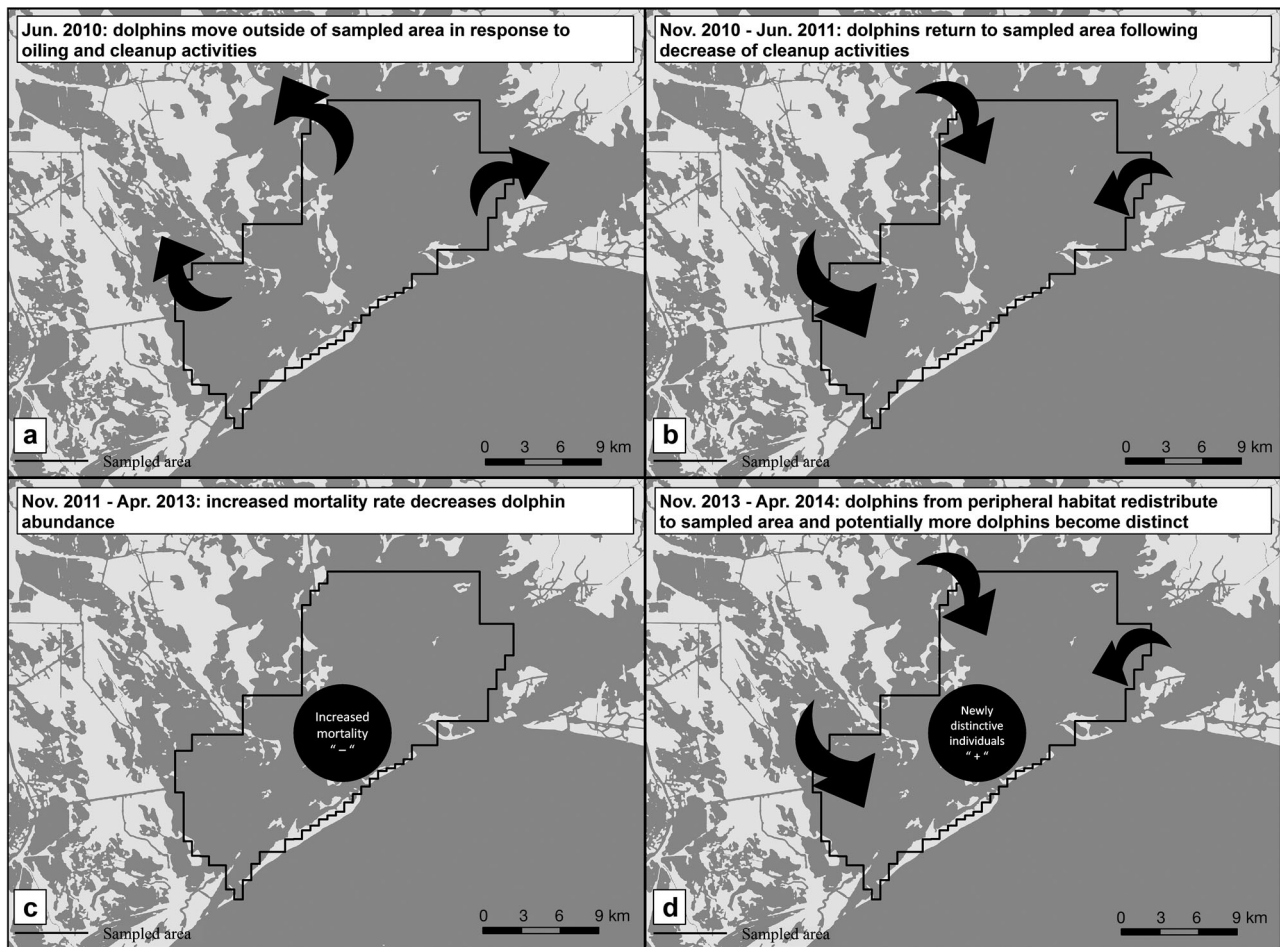
Fig. 7. Hypothesized movements of Barataria Bay common bottlenose dolphins *Tursiops truncatus* during the study period. Minus and plus signs in (c) and (d) imply decrease and increase, respectively, due to these sources

Mississippi Sound was a response to greater resource availability caused by decreased fishery activities after Hurricane Katrina 2 yr earlier. If a similar increase in dolphin reproduction occurred in Barataria Bay during the same time period, the larger-than-normal calf cohort would have been 6 to 7 yr old at the time of the final 2 photo-ID surveys.

However, despite the possibility that a large number of dolphins became distinctive in mid-2013, we believe that increased reproduction alone cannot explain the nearly 50% increase in density for the Island stratum, and the 3-fold and nearly 8-fold increase in density for the West and East strata, respectively, in a 1 yr period (April 2013 to April 2014). Even a significant increase in calving over a 2 to 3 yr period (e.g. beginning in 2007 concurrent with the calving boom reported for Mississippi Sound, and continuing until 2010 when the DWH oil spill occurred) would not be sufficient to produce such large proportional increases in densities. Such increases

translate into nearly doubling the estimated overall dolphin abundance, over a very short period.

Instead, we suggest that the apparent influx of new dolphins likely represents movement of distinctive individuals from peripheral habitat, within Barataria Bay but outside the photo-ID study area, into the photo-ID study area where they would be subject to our photographic efforts (Fig. 7d). The loss of dolphins through mortality over the prior 2 yr period would have created space and potentially freed other resources. The freeing of resources then could have prompted the movement of other dolphins into the photo-ID study area from more peripheral habitat, such as the more variable and generally lower salinity waters to the northwest. An analysis of telemetry data from Barataria Bay bottlenose dolphins integrated with a spatio-temporal model of salinity patterns, indicated that the tagged dolphins favored higher salinity waters (DWH MMIQT 2015, Hornsby et al. 2017). Furthermore, the increases in density

occurred across the 3 strata, but the largest absolute increase in density, from 10.2 to 14.3 ind. km^{-2}, occurred in the Island stratum. As previously discussed, the Island stratum likely represents prime foraging habitat, which would be a strong attractor for dolphins. If the increases in densities observed for the final 2 surveys were due to movement from peripheral areas into the photo-ID survey area, then this would not have been true recruitment (immigration), but rather a shift of bottlenose dolphin distribution within Barataria Bay. If this is the case, our final 2 abundance estimates (for November 2013 and April 2014), must be considered to be biased high because densities in peripheral habitat would be lower after re-distribution, and subsequent extrapolation of estimates on the study area would over-estimate the bay-wide population. In other words, the increases observed late in our study would only reflect a re-distribution of dolphins within the Barataria Bay stock boundaries rather than a true increase in the population of Barataria Bay.

A final possibility that must be considered for the increased abundance after mid-2013 is true recruitment (immigration) of dolphins from coastal waters or adjacent estuaries (e.g. Terrebonne and Timbalier Bays). For several reasons, we consider this alternative unlikely. First, estuarine populations of common bottlenose dolphins in the northern GoM show extremely high site fidelity (Wells 2003, Hubard et al. 2004, Bassos-Hull et al. 2013). Site fidelity is high because dolphin residency in an area is often accompanied by unique feeding habits that are specialized to their habitat (Hoese 1971, Lewis & Schroeder 2003, Weiss 2006, Mann et al. 2008). Recent studies suggest that feeding specialization largely determines a dolphin's habitat use and, rather than switch feeding strategies, dolphins seek habitats where they can successfully practice their specialized habits (Mann et al. 2008, Torres & Read 2009). Second, satellite-tag telemetry data from dolphins in Barataria Bay revealed no movement out of the bay over a 4 to 5 mo period (Wells et al. 2017). Third, there is ample evidence that coastal and estuarine dolphin populations are distinct and that permanent changes in residency are rare. Fazioli et al. (2006) found some interaction between coastal and estuarine dolphins on the west coast of Florida, but no long-term immigration to inshore areas. Sellas et al. (2005) used genetic data to show that coastal and estuarine populations off Florida are demographically independent. Given foraging specialties, we theorize that dolphins from coastal populations near Barataria Bay were unlikely to immigrate into an estuarine environment due to

significant differences in habitat and prey types. Therefore, immigration from the Western Coastal Stock is likely minimal.

In summary, we propose that low densities immediately following the spill were a result of dolphins moving away from the center of high disturbance (Fig. 7a), that they later returned once response activities had subsided and much of the heavy oiling was removed (Fig. 7b), that they experienced high mortality for approximately 3 yr following the spill (Fig. 7c), and that survival rebounded as dolphins from more peripheral habitat moved into the study area in late 2013. These hypotheses are ecologically reasonable, and alternative hypotheses (e.g. immigration from coastal stocks, or recruitment of young dolphins into the distinctively marked cohort) seem unlikely.

We can say with certainty that bottlenose dolphin movements and population responses to changes in Barataria Bay are complex. Proposed restoration activities, such as freshwater diversions to rebuild marsh, will likely alter salinity patterns across Barataria Bay and have significant impacts on Barataria Bay dolphins. This will only add to the difficult task of predicting the population's future trajectory. Intensive and continued study will be needed to determine the future viability of the stock.

LITERATURE CITED

Adams J, Speakman T, Zolman E, Schwacke LH (2006) Automating image matching, cataloging, and analysis for photo-identification research. Aquat Mamm 32:374–384

Ballance LT (1992) Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. Mar Mamm Sci 8:262–274

Balmer BC, Wells RS, Nowacek SM, Nowacek DP, Schwacke LH, McLellan WA, Scharf FS (2008) Seasonal abundance and distribution patterns of common bottlenose dolphins

(*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. J Cetacean Res Manag 10:157–167

Barham EG, Sweeney JC, Leatherwood S, Beggs RK, Barham CL (1979) Aerial census of the bottlenose dolphin, *Tursiops truncatus*, in a region of the Texas coast. Fish Bull 77:585–595

Bassos-Hull K, Perrtree RM, Shepard CC, Schilling S and others (2013) Long-term site fidelity and seasonal abundance estimates of common bottlenose dolphins (*Tursiops truncatus*) along the southwest coast of Florida and responses to natural perturbations. J Cetacean Res Manag 13:19–30

Borchers DL, Efford MG (2008) Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385

Buckstaff KC, Wells RS, Gannon JG, Nowacek DP (2013) Responses of bottlenose dolphins (*Tursiops truncatus*) to construction and demolition of coastal marine structures. Aquat Mamm 39:174–186

Cormack R (1972) The logic of capture-recapture experiments. Biometrics 28:337–343

Dähne M, Gilles A, Lucke K, Peschko V and others (2013) Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. Environ Res Lett 8:025002

DWH MMIQT (*Deepwater Horizon* Marine Mammal Injury Quantification Team) (2015) Models and analyses for the quantification of injury to Gulf of Mexico cetaceans from the *Deepwater Horizon* oil spill. https://pub-dwhdatadiver.orr.noaa.gov/dwh-ar-documents/876/DWH-AR0105866.pdf (accessed on 1 December 2016)

DWH NRDA (Deepwater Horizon Natural Resource Damage Assessment) Trustees (2016) *Deepwater Horizon* oil spill: final programmatic damage assessment and restoration plan and final programmatic environmental impact statement. Tech Rep. www.gulfspillrestoration.noaa.gov/restoration-planning/gulf-plan

Ergon T, Gardner B (2014) Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. Methods Ecol Evol 5:1327–1336

Fazioli KL, Hoffmann S, Wells R (2006) Use of Gulf of Mexico coastal waters by distinct assemblages of bottlenose dolphins (*Tursiops truncatus*). Aquat Mamm 32:212–222

Friday N, Smith TD, Stevick PT, Allen J (2000) Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whales (*Megaptera novaeangliae*). Mar Mamm Sci 16:355–374

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. Stat Sci 7:457–511

Geweke J (1991) Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. Vol 196. Research Department, Federal Reserve Bank of Minneapolis, Minneapolis, MN

Hoese HD (1971) Dolphin feeding out of water in a salt marsh. J Mammal 52:222–223

Hornsby FE, McDonald TL, Balmer BC, Speakman TR and others (2017) Using salinity to identify common bottlenose dolphin habitat in Barataria Bay, Louisiana, USA. Endang Species Res 33:181–192

Hubard CW, Maze-Foley K, Mullin KD, Schroeder WW (2004) Seasonal abundance and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in Mississippi Sound. Aquat Mamm 30:299–310

Ingram SN, Rogan E (2002) Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus.* Mar Ecol Prog Ser 244:247–255

Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration — stochastic model. Biometrika 52:225–247

Kendall WL, Pollock KH, Brownie C (1995) A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293–308

Kendall WL, Nichols JD, Hines JE (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578

Lane S (2007) Comparison of survival models using mark-recapture rates and age-at-death data for bottlenose dolphins, *Tursiops truncatus*, along the South Carolina coast. MSc thesis, College of Charleston, Charleston, SC

Lane SM, Smith CR, Mitchell J, Balmer BC and others (2015) Reproductive outcome and survival of common bottlenose dolphins sampled in Barataria Bay, Louisiana, USA, following the Deepwater Horizon oil spill. Proc R Soc B 282:20151944

Leatherwood S, Reeves RR (1983) Abundance of bottlenose dolphins in Corpus Christi Bay and coastal southern Texas. Contrib Mar Sci 26:179–199

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

Lewis JS, Schroeder WW (2003) Mud plume feeding, a unique foraging behavior of the bottlenose dolphin in the Florida Keys. Gulf Mex Sci 21:92–97

Litz JA, Baran MA, Bowen-Stevens SR, Carmichael RH and others (2014) Review of historical unusual mortality events (UMEs) in the Gulf of Mexico (1990-2009): providing context for the multi-year northern Gulf of Mexico cetacean UME declared in 2010. Dis Aquat Org 112:161–175

Lockyer CH, Morris RJ (1990) Some observations on wound healing and persistence of scars in *Tursiops truncatus.* Rep Int Whaling Comm 1990:113–118

Lyczkowski-Shultz J, Ruple DL, Richardson SL, Cowan JH Jr (1990) Distribution of fish larvae relative to time and tide in a Gulf of Mexico barrier island pass. Bull Mar Sci 46:563–577

Mann J, Sargeant BL, Watson-Capps JJ, Gibson QA, Heithaus MR, Connor RC, Patterson E (2008) Why do dolphins carry sponges? PLOS ONE 3:e3868

Mazzoil M, McCulloch SD, Defran RH, Murdoch E (2004) The use of digital photography and analysis for dorsal fin photo-identification of bottlenose dolphins. Aquat Mamm 30:209–219

Melancon RAS, Lane S, Speakman T, Hart LB and others (2011) Photo-identification field and laboratory protocols utilizing Finbase version 2. NOAA Tech Memo NMFS-SEFSC-627

Meredith M (2013) SECR in BUGS/JAGS with patchy habitat. www.mikemeredith.net/blog/1309_SECR_in_JAGS_patchy_habitat.htm

Michel J, Owens EH, Zengel S, Graham A and others (2013) Extent and degree of shoreline oiling: *Deepwater Horizon* oil spill, Gulf of Mexico, USA. PLOS ONE 8:e65087

Miller C (2003) Abundance trends and environmental habitat usage patterns of bottlenose dolphins (*Tursiops truncatus*) in lower Barataria and Caminada bays, Louisiana. PhD thesis, Louisiana State University, Baton Rouge, LA

Miller LJ, Mackey AD, Hoffland T, Solangi M, Kuczaj SA (2010) Potential effects of a major hurricane on Atlantic bottlenose dolphin (*Tursiops truncatus*) reproduction in the Mississippi Sound. Mar Mamm Sci 26:707–715

Moretzsohn F, Sanchez-Chavez JA, Tunnell JW Jr (2010) Gulfbase: Resource database for Gulf of Mexico research. Tech Rep. Harte Research Institute for Gulf of Mexico Studies at Texas A&M University, Corpus Christi, TX. www.gulfbase.org

Orbach DN, Packard JM, Piwetz S, Würsig B (2015) Sex-specific variation in conspecific-acquired marking prevalence among dusky dolphins (*Lagenorhynchus obscurus*). Can J Zool 93:383–390

Pirotta E, Laesser BE, Hardaker A, Riddoch N, Marcoux M, Lusseau D (2013) Dredging displaces bottlenose dolphins from an urbanised foraging patch. Mar Pollut Bull 74:396–402

Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proc 3rd Int Workshop on Distributed Statistical Computing (DSC 2003), Vienna, Austria, Vol 124, p 125

Pollock KH (1978) A family of density estimators for line-transect sampling. Biometrics 34:475–478

Pollock KH (1982) A capture-recapture design robust to unequal probability of capture. J Wildl Manag 46:752–757

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Read AJ, Urian KW, Wilson B, Waples DM (2003) Abundance of bottlenose dolphins in the bays, sounds, and estuaries of North Carolina. Mar Mamm Sci 19:59–73

Rosel PE, Mullin KD, Garrison L, Schwacke LH and others (2011) Photo-identification capture-mark-recapture techniques for estimating abundance of bay, sound and estuary populations of bottlenose dolphins along the U.S. East coast and Gulf of Mexico: a workshop report. NOAA Tech Memo NMFS-SEFSC-621

Royle JA, Chandler RB, Sollmann R, Gardner B (2013) Spatial capture-recapture. Academic Press, Waltham, MA

Schaub M, Royle JA (2014) Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. Methods Ecol Evol 5:1316–1326

Schwacke LH, Thomas L, Wells RS, McFee WE and others (2017) Quantifying injury to common bottlenose dolphins from the *Deepwater Horizon* oil spill using an age-, sex- and class-structured population model. Endang Species Res 33:265–279

Seber GAF (1965) A note on the multiple-recapture census. Biometrika 52:249–259

Sellas AB, Wells RS, Rosel P (2005) Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. Conserv Genet 6:715–728

Shane SH (1977) The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. PhD thesis, Texas A&M University, College Station, TX

Shane SH (1990) Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic Press, San Diego, CA, p 541–558

Smith CR, Rowles TK, Hart LB, Townsend FI and others (2017) Slow recovery of Barataria Bay dolphin health following the *Deepwater Horizon* oil spill (2013–2014), with evidence of persistent lung disease and impaired stress response. Endang Species Res 33:127–142

Speakman TR, Lane SM, Schwacke LH, Fair PA, Zolman ES (2010) Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. J Cetacean Res Manag 11:153–162

Torres LG, Read AJ (2009) Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. Mar Mamm Sci 25:797–815

Tyson RB, Nowacek SM, Nowacek DP (2011) Community structure and abundance of bottlenose dolphins *Tursiops truncatus* in coastal waters of the northeast Gulf of Mexico. Mar Ecol Prog Ser 438:253–265

Urian KW, Waples DM, Tyson RB, Hodge LE W, Read AJ (2014) Abundance of bottlenose dolphins (*Tursiops truncatus*) in estuarine and near-shore waters of North Carolina, USA. J North Carol Acad Sci 129:165–171

US EPA (United States Environmental Protection Agency) (1999) Ecological condition of estuaries in the Gulf of Mexico. Tech Rep 620-R-98-004. US EPA, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Gulf Ecology Division, Gulf Breeze, FL

Venn-Watson S, Garrison L, Litz J, Fougeres E and others (2015) Demographic clusters identified within the northern Gulf of Mexico common bottlenose dolphin (*Tursiops truncatus*) Unusual Mortality Event: January 2010–June 2013. PLOS ONE 10:e0117248

Waring GT, Josephson E, Maze-Foley K (2015) U.S. Atlantic and Gulf of Mexico marine mammal stock assessments: 2014. NOAA Tech Memo NMFS-NE-221

Weiss J (2006) Foraging habitats and associated preferential foraging specializations of bottlenose dolphin (*Tursiops truncatus*) mother-calf pairs. Aquat Mamm 32:10–19

Wells RS (2003) Dolphin social complexity: lessons from long-term study and life history. In: de Waal FBM, Tyack PL (eds) Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA, p 32–56

Wells RS, Scott MD (1990) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Rep Int Whaling Comm Spec Issue 12:407–415

Wells RS, Irvine AB, Scott MD (1980) The social ecology of inshore odontocetes. In: Herman LM (ed) Cetacean behavior: mechanisms and functions. Wiley, New York, NY, p 263–317

Wells RS, Schwacke LH, Rowles TK, Balmer BC and others (2017) Ranging patterns of common bottlenose dolphins *Tursiops truncatus* in Barataria Bay, Louisiana, following the *Deepwater Horizon* oil spill. Endang Species Res 33: 159–180

Wilson B, Hammond PS, Thompson PM (1999) Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecol Appl 9:288–300

Wingfield DK, Peckham SH, Foley DG, Palacios DM and others (2011) The making of a productivity hotspot in the coastal ocean. PLOS ONE 6:e27874

Würsig B, Jefferson TA (1990) Methods of photo-identification for small cetaceans. Rep Int Whaling Comm 1990: 43–50