

Long-term trends in a northern Gulf of Mexico common bottlenose dolphin (*Tursiops truncatus*) population in the wake of the Deepwater Horizon oil spill

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ABSTRACT

Bottlenose dolphins along the northern Gulf of Mexico continue to be impacted by numerous stressors including harmful algal blooms, infectious disease epizootics, and oil exposure following the *Deepwater Horizon* (DWH) oil spill. Studies to assess the potential impacts of the DWH oil spill on dolphins in the northern Gulf of Mexico were initiated as part of a Natural Resource Damage Assessment and included photographic-identification (photo ID) surveys to determine abundance, density, and site fidelity in St. Joseph Bay, Florida (SJB). Although significant oiling did not occur in SJB, long-term data have been collected in this region to provide insight into population-level trends in abundance/density over time. Thus, SJB dolphins could serve as a reference for comparison to other dolphin populations exposed to DWH oiling. During 2005–2007, the results of photo ID and telemetry surveys determined seasonal fluctuations in abundance and identified two different dolphin populations in SJB: residents sighted across multiple seasons and years (St. Joseph Bay Stock), and visitors that were present during the spring and fall and associated with a 2–3fold increase in abundance (Northern Coastal Stock). The goals for the current study were to compare dolphin abundance, density, and site fidelity, prior to (2005–2007), during (2010), and post-DWH (2011 and 2013) using photo-ID surveys and a spatially explicit robust-design capture-recapture (SERDCR) model. The data collected during and post-DWH paralleled previous research in that a low number of individuals with high site fidelity were sighted across seasons and years (St. Joseph Bay Stock), and abundance/density increased in the fall as a result of an influx of dolphins that were likely members of the Northern Coastal Stock. However, June and August 2010 abundance (347; 193–498, 95% CI and 394; 288–534, 95% CI, respectively), density (dolphins/km²) (2.60; 1.36–3.70, 95% CI and 2.55; 1.89–3.29, 95% CI, respectively), and site fidelity patterns were more similar to previous years' spring and fall data, with high abundance estimates, increased dolphin density in coastal waters, and elevated numbers of individuals with low site fidelity in the SJB region. Factors that could have contributed to this increase in abundance include immigration of dolphins from adjacent estuaries, population growth within the St. Joseph Bay Stock, impacts from DWH oiling, and environmental and/or prey-based cues that influence movements of the Northern Coastal Stock. The results of this study demonstrate the importance of long-term monitoring to assess impacts of current and future stressors on the dolphins in the northern Gulf of Mexico.

KEYWORDS: ABUNDANCE ESTIMATE; MARK-RECAPTURE; SURVEY – VESSEL; SITE FIDELITY; PHOTO-ID

INTRODUCTION

The *Deepwater Horizon* (DWH) oil spill, which started on 20 April 2010, was the largest oil spill in the history of the US, released over 700 million litres of crude oil into the northern Gulf of Mexico, and contaminated over 1,600km of shoreline from Louisiana to northwestern Florida (e.g. Barron, 2012; Michel, 2013; Nixon, 2016) (Fig. 1A). The oil spill was an additional stressor to common bottlenose dolphins (*Tursiops truncatus*) in a region that had already been impacted by a series of Unusual Mortality Events (UMEs) since 1999 (Litz *et al.*, 2014; NOAA, 2004). As authorised under the Oil Pollution Act (101 H.R. 1465, P.L. 101–380), a Natural Resource Damage Assessment (NRDA) to assess the impacts of the DWH oil spill was conducted by the National Oceanic and Atmospheric Administration (NOAA), other federal agencies, and Gulf states' trustees. As part of the NRDA, studies were initiated to determine abundance, density, and site fidelity of dolphins in the bays, sounds, and estuaries (BSEs) at several sites in the northern Gulf of Mexico.

One of these study sites was St. Joseph Bay (SJB), located along the northwestern Florida coastline (Florida Panhandle) (Fig. 1). Since 1999, SJB has been impacted by numerous UMEs (Litz *et al.*, 2014), and was the geographic focus of a 2004 UME in which more than 100 dolphins stranded during March and April (NOAA, 2004; Twiner *et al.*, 2012). Following the 2004 UME, there have been multiple projects focusing on the health and population structure of SJB dolphins. Balmer *et al.* (2008; 2010) utilised photographic-identification (photo-ID) and telemetry surveys to determine seasonal fluctuations in abundance, and identified two different groups of dolphins within SJB: residents sighted across multiple seasons and years (likely members of the St. Joseph Bay Stock), and seasonal visitors (likely members of the Northern Coastal Stock) that were present during the spring and fall, associated with a 2–3 fold increase in abundance, and ranged over 100km to the west of SJB. Remote biopsy sampling and capture-release health assessment studies have established health parameters

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(Schwacke *et al.*, 2010) and baseline concentrations of persistent organic pollutants (POPs) for SJB dolphins (Balmer *et al.*, 2015; Kucklick *et al.*, 2011; Wilson *et al.*, 2013). Ultimately, significant oiling from the DWH oil spill was not observed in SJB (Michel *et al.*, 2013; Nixon *et al.*, 2016). However, dolphins in this region are one of the best-studied groups along the coast of the northern Gulf of Mexico and could be used as a reference for comparison to dolphins in other regions that were directly impacted by the DWH oil spill.

Balmer *et al.* (2008) conducted seasonal, small vessel-based, photo-ID surveys, and a robust-design capture-recapture model (Pollock, 1982) to estimate abundance and determine site fidelity in SJB from 2005–2007. The goals for this current study were to expand on the pre-DWH oil spill results (2005–2007) and conduct additional surveys during (2010) and post-spill (2011 and 2013) to estimate dolphin abundance, density, and site fidelity across all survey periods (2005–2013), using a spatially explicit robust-design capture-recapture (SERDCR) model. The SERDCR model was selected over other robust-design capture-recapture models because it incorporates capture heterogeneity, based upon activity centres from capture locations of all individuals, and estimates density across different habitats within a study area.

MATERIALS AND METHODS

Data collection

The SJB study site, defined by Balmer *et al.* (2008), included the coastal waters of the northern Gulf of Mexico (shoreline to 1.5km offshore) from Cape San Blas northwest to and including Crooked Island Sound, and St. Joseph Bay proper (Fig. 1B). Small vessel-based, photo-ID surveys began in February 2005 and occurred across several seasons during 2005–2007 (Balmer *et al.*, 2008). The survey design during (June and August 2010) and post (February 2011 and October 2013) the DWH oil spill followed the same transects and methodology as Balmer *et al.* (2008) with one, 5–6m, outboard vessel crewed by a minimum of three observers surveying at a speed of approximately 30km/hr. Full digital photographic coverage of each dolphin's dorsal fin was attempted with digital single-lens-reflex (DSLR) cameras equipped with a 100–400mm telephoto lens. Geographic location (GPS coordinates) and a suite of environmental and behavioural data (reviewed in Melancon *et al.*, 2011) were recorded during each sighting. Capture-recapture surveys were temporally divided into primary periods (i.e. each sampling season) and three secondary sessions were completed within each primary period (pre-DWH: N = 7 primary periods; during-DWH: N = 2 primary periods; post-DWH: N = 2 primary periods; total: N = 11 primary periods). Each secondary session required two survey days for completion and more than 75% of all transects in the study site were completed in optimal sighting conditions (Beaufort Sea State ≤ 3). Once a secondary session was completed, the study site was not surveyed for a minimum of one to two days to allow for sufficient population mixing and to meet the assumptions of capture-recapture population modelling (e.g. Balmer *et al.*, 2008; Speakman *et al.*, 2010; Balmer *et al.*, 2013).

Data analysis

Dorsal fin images were graded on both photographic quality and distinctiveness of the dorsal fin, following the methods of Urian *et al.* (1999; 2015). Photographic quality of the best left and/or right side image was graded based upon focus, contrast, angle, dorsal fin visibility, and proportion of dorsal fin within the frame of the image. Only images with excellent (Q-1) and average (Q-2) quality were included in subsequent analyses. Dorsal fin distinctiveness ratings were determined separate of photographic quality. Marked individuals were identified as those with very distinctive (D-1; obvious major marks) and moderately distinctive fins (D-2; 2 minor or 1 major mark). Unmarked individuals were identified as those that could be distinguished from others within a sighting but which lacked long-term markings that would allow reliable repeated identifications across sightings (D-3). Images were matched and verified by two experienced researchers to the SJB photo-ID catalogue using FinBase (Adams *et al.*, 2006), a customised Microsoft Access (Microsoft Corporation, Redmond, WA, USA) database. Photo-ID sighting histories for each D-1 and D-2 individual encountered during all primary periods (N = 11) during 2005–2013 were used to estimate dolphin abundance, density, and site fidelity.

Abundance, density and site fidelity

Discovery curves, which are cumulative counts of distinctive individuals over time, are used to provide insight into population closure and to illustrate photo-ID catalogue size (Wilson *et al.*, 1999). The total numbers of previously sighted and new distinctive individuals were calculated across the 11 primary periods (2005–2013). Site fidelity was investigated by grouping individuals into one of three sighting frequency bins based on the total number of primary periods each individual was observed in, out of 11 possible primary periods (Balmer *et al.*, 2008; Balmer *et al.*, 2013). Dolphins sighted in 1–2 primary periods were classified as having low site fidelity (LSF) and those sighted in 3–5 primary periods were classified as moderate site fidelity (MSF). High site fidelity (HSF) dolphins were sighted in 6 or more primary periods. The criteria for the HSF bin were based on the Rosel *et al.* (2011) definition of a resident dolphin as an individual that spends more than 50% of its time within a given BSE. The number of primary periods totaling less than 50% (<6) was divided into the LSF and MSF classifications.

Robust-design capture-recapture models have been used extensively with dolphin photo-ID data to estimate abundance (e.g. Speakman *et al.*, 2010; Tyson *et al.*, 2011; Sprogis *et al.*, 2016). However, depending on animals' movements and survey area boundaries, these models may violate the assumption of capture homogeneity. Spatially-explicit capture-recapture (SECR) models estimate activity centres for identified individuals from capture locations and modify capture probabilities based upon the distance between these activity centres (Borchers and Efford, 2008). In addition, SECR models incorporate habitat masks (strata) that can be used to group animals based upon their activity centres. Recently, McDonald *et al.* (2017) developed a spatially explicit robust design capture-recapture (SERDCR)

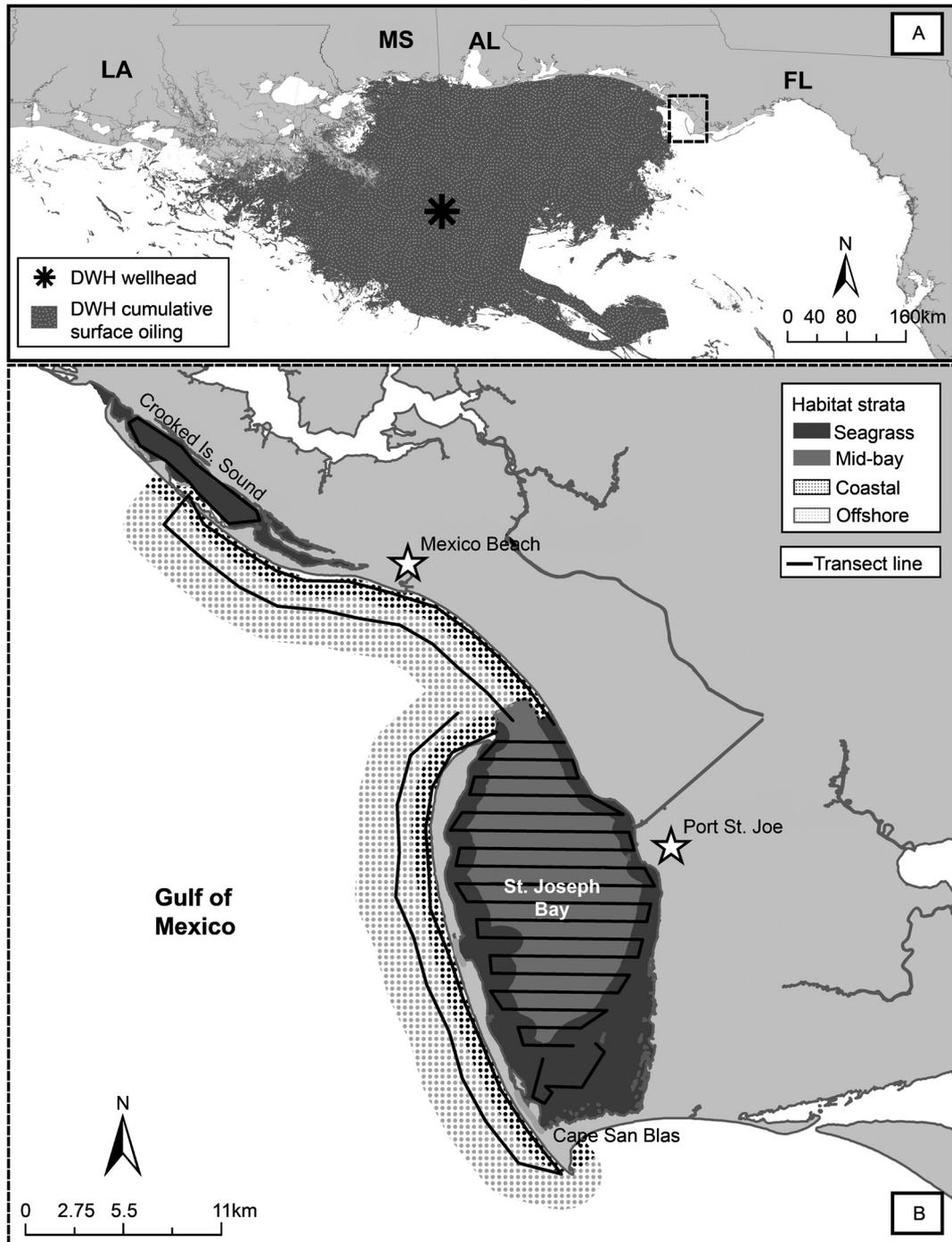


Fig. 1. (A) Extent of *Deepwater Horizon* (DWH) surface oiling, and (B) St. Joseph Bay, Florida (SJB) study site, habitat strata, and photo ID transect lines.

model that incorporated capture heterogeneity, based upon spatial locations of all sampled individuals, to estimate dolphin density in Barataria Bay, Louisiana. Abundance estimates for the Barataria Bay Stock were calculated using Bayesian Markov Chain Monte Carlo (MCMC) sampling methods with total area of the study site and density estimates as input variables. The SERDCR model was applied to SJB photo-ID data to estimate density and abundance across all primary periods (2005–2013). Based upon dolphin movement patterns and habitat use identified from photo-ID and telemetry data (Balmer *et al.*, 2008), SJB was divided into four strata: Seagrass, Mid-bay, Coastal and Offshore (Fig. 1B). The Seagrass stratum was defined by

using the Florida Fish and Wildlife Research Institute (FWRI) Seagrasses in Florida dataset⁸. The Mid-bay stratum included all waters inside St. Joseph Bay proper that were not part of the Seagrass stratum. The Coastal stratum extended from the shoreline to 1km offshore while the Offshore stratum included all waters from 1km to 3km offshore for the study site. Density estimates were calculated for the Seagrass, Mid-bay and Coastal strata as well as cumulatively. For the Offshore stratum, density was not calculated because of logistical challenges in surveying this area adequately across primary periods. Area for each stratum and total area for the SJB study site were calculated

⁸ See: <http://geodata.myfwc.com/datasets>.

using ArcMap 10.4.1 (ESRI, Redlands, CA, USA). Cumulative abundance and 95% confidence interval (CI) limits for the SJB study site, during each primary period, were determined using Bayesian MCMC methods as described in McDonald *et al.* (2017). Sighting histories used in the SERDCR model were only for marked individuals (D-1 and D-2). To estimate total density and abundance, the proportion of distinctive fins was calculated by determining the total number of marked and unmarked individuals during each sighting (Balmer *et al.*, 2013; Wilson *et al.*, 1999). Only sightings in which all individual dolphins were photographed (full photo coverage) were considered for estimating the distinctiveness rate. Degree of photo coverage was determined for each sighting by comparing the number of marked and unmarked individuals identified from photo-ID analysis and the best field estimate of total dolphins sighted. If these two numbers were equal, or the number from the photo-ID analysis was greater than the estimate of total dolphins sighted in the field, then the sighting was used for calculating the proportion of distinctive individuals. For each primary period, the distinctiveness proportion was calculated (the sum of distinctive individuals divided by total number of individuals within each primary period) and applied to estimate total dolphin density and abundance.

RESULTS

Discovery curve and site fidelity

From February 2005 through October 2013, 79 photo-ID surveys were completed across 11 primary periods, covering 10,738 km, obtaining 42,572 photos, recording 752 sightings, and a catalogue size of 686 individuals (D-1 and D-2). Mean dolphin group size was 8 (range 1–34), and was lowest in winter (mean = 5.0, SE = 0.5) and comparable across spring (mean = 9.9, SE = 0.9), summer (mean = 9.1, SE = 1.2), and

fall (mean = 12.0, SE = 2.0). The discovery curve slowed between July 2005 to February 2006, and September/October 2006 to June/July 2007 (Fig. 2). Mean distinctiveness rate was 0.73 (range 0.59–0.88) (Table 1). The highest number of previously identified individuals was in August 2010 (N = 104) and highest number of new individuals, excluding the first primary period (February/March 2005), was in May 2005 (N = 69). High numbers of LSF individuals were observed in May 2005, September/October 2006, June and August 2010, and October 2013, while low numbers of HSF individuals were sighted across all primary periods (range 23–42 individuals) (Fig. 3). The number of MSF individuals fluctuated throughout the primary periods (range 12–43 individuals).

Density and abundance

SJB dolphin densities fluctuated by year, season and strata (Table 1, Fig. 4). Mean dolphin density was highest in the Coastal stratum (1.34 dolphins/km²) and had the largest fluctuations across primary periods (range 0.04–2.69 dolphins/km²). Mean dolphin densities were lower in the Mid-bay (0.53 dolphins/km²) and Seagrass (0.30 dolphins/km²) strata with smaller fluctuations across primary periods (ranges 0.11–1.11 and 0.11–0.79 dolphins/km², respectively). Cumulative dolphin densities and abundance were highest in May 2005, September/October 2006, June 2010, August 2010, and October 2013, and lowest in February (2005, 2006, and 2011) and July 2005.

DISCUSSION

The long-term photo-ID data collected in SJB provide an opportunity to build upon initial hypotheses for stock structure in this region; compare abundance, density and site fidelity prior to, during, and post-DWH oil spill; and assess

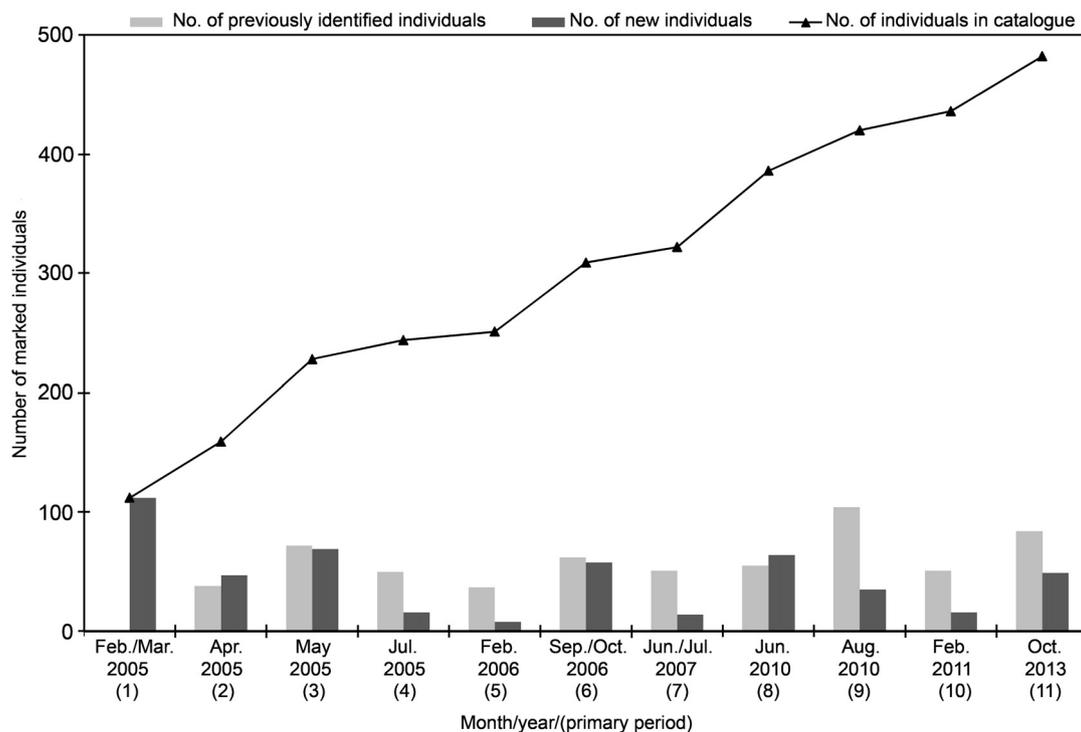


Fig. 2. Number of previously identified and new, marked individuals sighted during all photo-ID primary periods (2005–2013) and discovery curve for the St. Joseph Bay (SJB) study site.

Table 1
St. Joseph Bay dolphin densities by year, season and strata.

Month and year	Primary period	Distinctiveness rate	Density and 95% CI (dolphins/km ²)				Cumulative abundance and 95% CI
			Seagrass (278km ²)	Mid-bay (93km ²)	Coastal (109km ²)	Cumulative (480km ²)	SERDCR model
Feb./Mar. 2005	1	0.88	0.25 (0.18–0.37)	0.53 (0.51–0.57)	0.84 (0.32–1.26)	1.64 (1.02–2.19)	212 (134–292)
Apr. 2005	2	0.79	0.27 (0.20–0.39)	0.48 (0.45–0.51)	1.46 (0.57–2.17)	2.21 (1.21–3.07)	279 (159–392)
May 2005	3	0.85	0.22 (0.16–0.32)	0.17 (0.16–0.18)	2.69 (1.04–3.99)	3.09 (1.37–4.50)	371 (174–542)
Jul. 2005	4	0.85	0.39 (0.28–0.56)	0.62 (0.59–0.66)	0.04 (0.02–0.06)	1.04 (0.89–1.28)	169 (135–223)
Feb. 2006	5	0.68	0.11 (0.08–0.16)	0.30 (0.28–0.31)	0.84 (0.32–1.25)	1.25 (0.69–1.73)	150 (84–209)
Sep./Oct. 2006	6	0.84	0.36 (0.27–0.53)	0.11 (0.11–0.12)	2.42 (0.94–3.58)	2.89 (1.31–4.23)	375 (186–548)
Jun./Jul. 2007	7	0.67	0.16 (0.12–0.23)	0.60 (0.57–0.64)	0.66 (0.25–0.97)	1.41 (0.94–1.84)	171 (112–229)
Jun. 2010	8	0.59	0.41 (0.30–0.60)	0.36 (0.34–0.39)	1.83 (0.70–2.72)	2.60 (1.36–3.70)	347 (193–498)
Aug. 2010	9	0.63	0.79 (0.58–1.15)	1.11 (1.06–1.18)	0.65 (0.25–0.96)	2.55 (1.89–3.29)	394 (288–534)
Feb. 2011	10	0.64	0.12 (0.08–0.17)	0.50 (0.48–0.53)	0.58 (0.22–0.86)	1.20 (0.79–1.56)	142 (92–190)
Oct. 2013	11	0.65	0.18 (0.13–0.26)	1.06 (1.00–1.12)	2.66 (1.03–3.95)	3.90 (2.17–5.33)	438 (242–607)

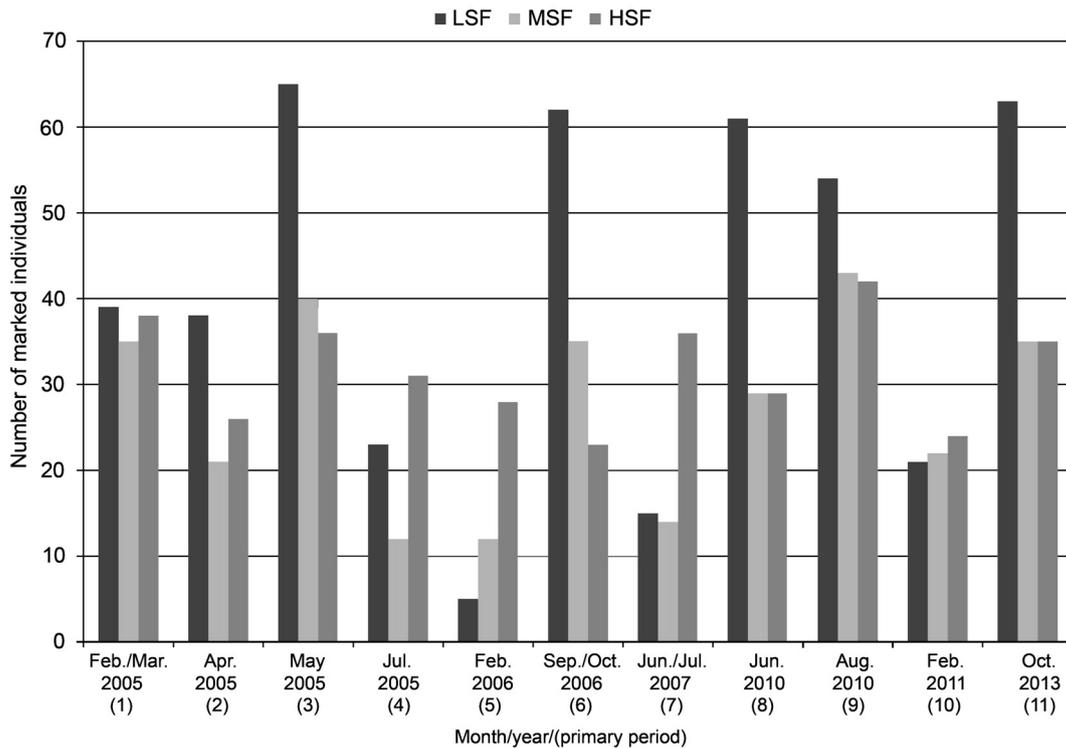


Fig. 3. Number of marked individuals sighted by site-fidelity classification and primary period year the St. Joseph Bay (SJB) study site. Low site fidelity (LSF): 1–2 primary periods, Moderate site fidelity (MSF): 3–5 primary periods, High site fidelity (HSF): 6–11 primary periods.

capture-recapture population modelling techniques that have evolved over the past 10 years. Balmer *et al.* (2008) identified two stocks within the boundaries of the SJB study site: the Northern Coastal Stock, characterised by a 2–3 fold increase in dolphin abundance during the spring and fall which was associated with LSF individuals sighted primarily in coastal waters; and the St. Joseph Bay Stock, characterised by a low number of HSF individuals sighted across seasons

and years. Thus, the most appropriate seasons to estimate St. Joseph Bay Stock abundance were winter and summer when the Northern Coastal Stock was not present in this region. The results from the analyses conducted on the recent data (2010, 2011 and 2013) support some of the findings from previous research (2005–2007), in that a low number of HSF individuals were sighted across seasons and years (indicative of the St. Joseph Bay Stock), winter was the optimal season

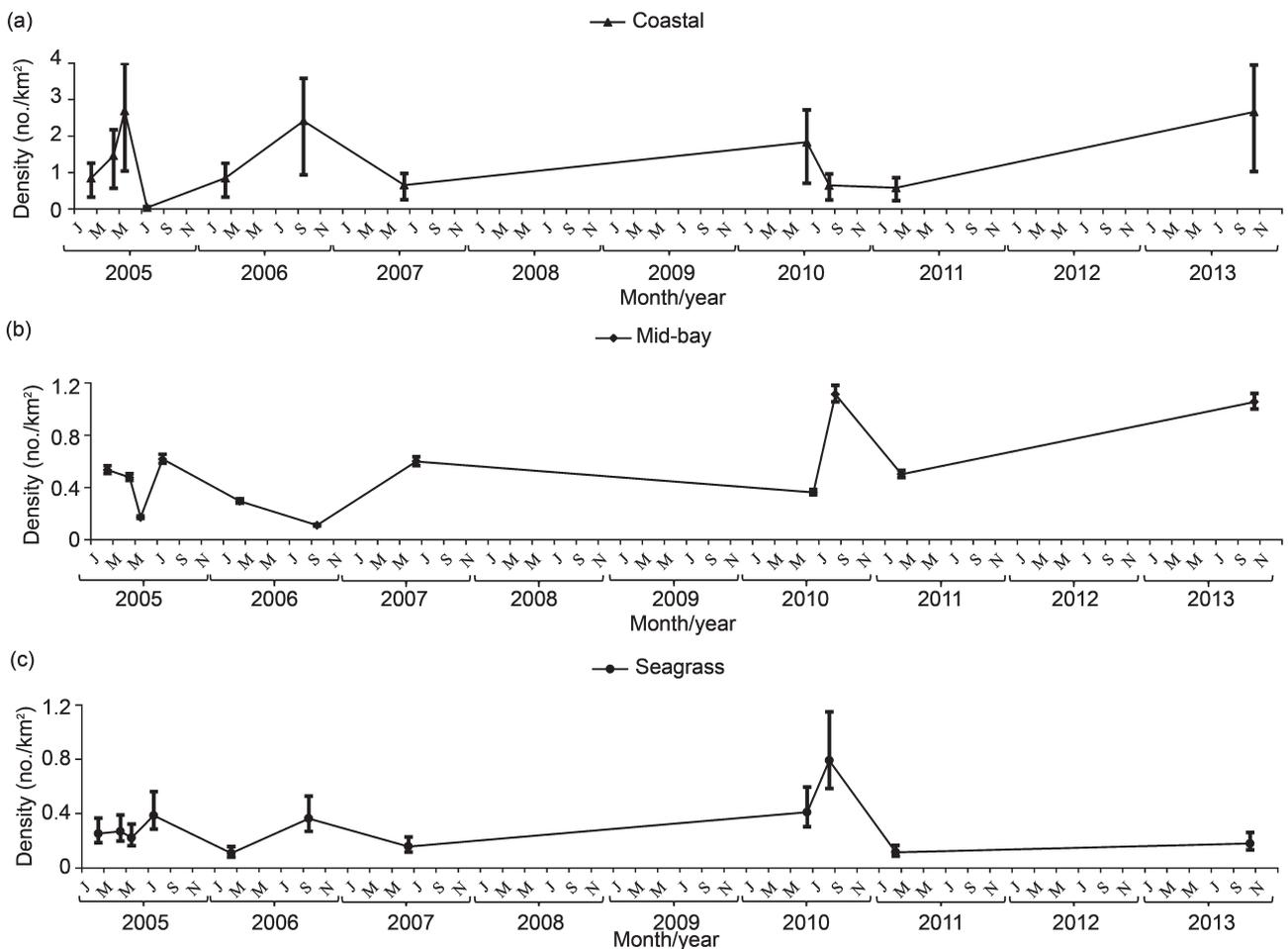


Fig. 4. Spatially explicit robust-design capture-recapture (SERDCR) dolphin density estimates and 95% CIs (dolphins no./km²) for all primary periods (2005–2013), grouped by habitat strata: (A) Coastal, (B) Mid-bay, and (C) Seagrass.

to estimate St. Joseph Bay Stock abundance, and abundance/density increased in the fall as a result of an influx of LSF individuals that were likely members of the Northern Coastal Stock. However, summer 2010 abundance, density, and site fidelity patterns were more similar to previous years' spring and fall data, with high abundance estimates, increased dolphin density in the Coastal strata, and elevated numbers of LSF individuals.

There are several hypotheses for this influx observed during summer 2010. Between summer 2007 and 2010, there was a three-year data gap in which St. Joseph Bay Stock abundance could have increased by immigration of new individuals from outside the population, or an increase in population growth within the St. Joseph Bay Stock via unmarked individuals (i.e. subadults and calves) becoming marked. If the 2004 UME impacted the St. Joseph Bay Stock, the high mortality of residents in this region may have created a situation where reduced competition for resources led dolphins from other BSEs to move into SJB. Numerous terrestrial and avian studies have identified range shifts and repopulation of a region by immigration following large-scale mortalities (e.g. Robinson *et al.*, 2008; Schaub *et al.*, 2010). For example, in a seven-year study of common barn owls (*Tyto alba*), Marti and Wagner (1985) determined that the largest breeding population of owls was observed two years after a large scale mortality of 77 owls. This influx was attributed to immigration of new owls into the region from adjacent study sites. However, BSE dolphins in the northern

Gulf of Mexico have high site fidelity to specific habitats (Bassos-Hull *et al.*, 2013; Hubard *et al.*, 2004; Wells, 2003) and specialised foraging behaviours (Lewis and Schroeder, 2003; Weiss, 2006), suggesting that permanent immigration may not be a primary factor for the influx of summer 2010 dolphins. Dolphin abundance has been estimated to increase due to population growth by a maximum of 4–5% per year (Barlow *et al.*, 1995; Wilson *et al.*, 1999). Assuming a maximum 5% increase each year since 2007, it is unlikely that population growth alone could account for the approximate two-fold increase in abundance between summer 2007 and summer 2010. The continuation of long-term photo-ID studies and development of collaborations among northern Gulf of Mexico study sites are necessary to assess movements of individuals between BSEs and better understand population-level effects in a region impacted by numerous UMEs. One example of successful collaborations among photo-ID study sites is the development of the Gulf of Mexico Dolphin Identification System (GoMDIS); an online tool to compare individual project-submitted photo-ID catalogues throughout the northern Gulf of Mexico (Cush and Wells, 2015).

Following the DWH oil spill, the presence of oil in coastal and offshore waters west of SJB may have prompted temporary movement of dolphins from oiled regions to those with less oiling during summer 2010. Although a different type of disturbance, dolphins in Sarasota Bay, Florida had been observed to have expanded ranging patterns as a result

of several severe biotoxin (*Karenia brevis*) events (McHugh *et al.*, 2011). This scenario was not observed following the *Exxon Valdez* oil spill in which resident and transient killer whale (*Orcinus orca*) pods in Prince William Sound, Alaska did not shift ranging patterns in response to heavy oiling (Dahlheim and Matkin, 1994; Matkin *et al.*, 2008). However, the *Exxon Valdez* and DWH oil spills were very different events in magnitude, oil type, spill location, environmental impact, and remediation techniques (Atlas and Hazen, 2011). The NRDA estimated that 38% (26–58%, 95% CI) of the Northern Coastal Stock were killed as a result of the DWH oil spill (Deepwater Horizon National Resource Damage Assessment Trustees, 2016). However, ranging patterns of this stock are not well-understood; thus, it is unclear if Northern Coastal Stock dolphins sighted in SJB were the same individuals impacted by the DWH oil spill. Recently, two dolphins sighted in SJB (2005–2010) were also identified in Mississippi Sound (2015), 300km to the west of SJB that received heavy DWH oiling (Balmer *et al.*, 2016; Michel *et al.*, 2013; Nixon *et al.*, 2016). Although a limited sample size, these results combined with the influx of LSF individuals in the Coastal strata during summer 2010 suggest that some members of the Northern Coastal Stock have extended movements along the northern Gulf of Mexico and could be exposed to stressors outside of the SJB study site, such as the DWH oil spill. Identification of individual dolphins to their respective stock is an essential component for assessing the impacts of a given anthropogenic stressor. Rosel *et al.* (2017) applied genetic assignment methods to differentiate stranded dolphins from southeastern Louisiana as either members of the local BSE or adjacent coastal stock. This analysis required a large sample size ($N = 156$) of dolphins remotely biopsied from the two stocks of origin. Future research, collecting samples from BSE stocks and the adjacent Northern Coastal Stock in the Florida Panhandle, would provide the necessary data for similar comparisons to assess the impacts of mortality events in this region.

An alternative hypothesis to the Northern Coastal Stock shifting its range in response to the DWH oil spill is that our current understanding of seasonal movements of this stock needs further refinement. Balmer *et al.* (2008) identified spring and fall as the seasons in which the Northern Coastal Stock were within the SJB study site. However, seasonality and dolphin movements in the northern Gulf of Mexico are likely different than those in the western North Atlantic (WNA) in which coastal dolphin movements are better understood. There are two stocks of dolphins in the WNA (Northern and Southern Migratory Coastal Stocks) that migrate seasonally from New York to North Carolina and North Carolina to Florida, respectively (Waring *et al.*, 2016). Although the exact cues for these migrations are not known, it has been hypothesised that water temperature and/or prey movements may be factors (Barco *et al.*, 1999; Gannon and Waples, 2004). The WNA Northern and Southern Migratory Coastal Stocks' north-south (latitudinal) movements differ from the Northern Coastal Stock's hypothesised east-west (longitudinal) movements. Thus, there are likely different environmental and/or prey-based cues between WNA and northern Gulf of Mexico dolphins. For example, the Northern Migratory Stock's water temperature range is approximately 23°C during summer in New Jersey and as

these animals migrate south in winter, water temperature is approximately 8°C in North Carolina waters (NOAA-NCEI, 2017). In contrast, water temperature across the northern Gulf of Mexico coastline is comparable during a given season but fluctuates across seasons (winter: 12°C \pm 2°C SD, summer 30°C \pm 1°C SD; $N = 4$ data collection sites), (NOAA-NCEI, 2017). The environmental and/or prey-based cues that influence Northern Coastal Stock movements may not fit into the four season structure of spring and fall movements of WNA Migratory Coastal Stocks. Based upon the long-term data in SJB, abundance estimates from winter are an appropriate representation of local abundance for the St. Joseph Bay Stock with low numbers of total individuals that have HSF. There is currently no clear pattern as to when the Northern Coastal Stock enters the SJB study site but this can occur during spring, summer or fall. Future research investigating factors that may influence dolphin and prey movements may provide essential data to better understand population structure of the Northern Coastal Stock.

Since Balmer *et al.* (2008), there have been numerous refinements in robust-design capture-recapture methodologies to develop models that more appropriately fit with marine mammal population structure and survey design (e.g. Conn *et al.*, 2011; Rehman *et al.*, 2016; Sprogis *et al.*, 2016). The SERDCR model used in this study grouped individual dolphins by habitat strata based upon their sighting locations (activity centres) and allowed for an assessment of dolphin density across habitat types. In addition to overlapping BSE and coastal stocks in the northern Gulf of Mexico (Waring *et al.*, 2016), sub-populations within stocks have been identified, for dolphins in the more interior estuarine waters and those in the larger sounds and surrounding barrier islands (Urian *et al.*, 2009; Wells *et al.*, 2017). The SERDCR model is a useful tool to determine density and abundance of different stocks and sub-populations within a study site and account for capture heterogeneity in these estimates. The abundance estimates derived from the Markovian robust-design model used by Balmer *et al.* (2008) and the SERDCR model were comparable. For the most part, total abundance estimates were slightly higher using the SERDCR model than the Markovian robust-design but 95% CIs for both models overlapped across all primary periods. The SERDCR model estimated dolphin density 2–3 times higher in the Coastal stratum than the Mid-bay and Seagrass strata during primary periods when the Northern Coastal Stock was likely in the study site which parallels the results of Balmer *et al.* (2008). For primary periods in which the Northern Coastal Stock was not present, SERDCR dolphin densities were generally similar across all strata. These results suggest that the St. Joseph Bay Stock uses all three of these habitat types throughout the year and corroborate with previous photo-ID/telemetry (Balmer *et al.*, 2008; Balmer *et al.*, 2010) and stable isotope (Wilson *et al.*, 2013) studies in the SJB region. As DWH restoration efforts begin in the northern Gulf of Mexico, it is essential for collaborations between all northern Gulf of Mexico study sites to develop survey methodologies and population models that best fit the complex stock structure for dolphins in this region. The results of these studies will provide the framework for long-term assessment of DWH restoration projects.

CONCLUSIONS

Prior to the 2004 UME, little was known about dolphin health and population structure in the Florida Panhandle. Although the cause of this UME was identified to be brevetoxin (NOAA, 2004; Twiner *et al.*, 2012), without baseline data prior to this UME, it still remains unclear which stock(s) were impacted and how the impacts were distributed if multiple stocks were involved. Over the past 10+ years, long-term data have been collected for dolphins in SJB (e.g. Balmer *et al.*, 2008; Schwacke *et al.*, 2010; Twiner *et al.*, 2012) as well as the development of projects in other study sites along the Florida Panhandle (e.g. Bouveroux *et al.*, 2014; Tyson *et al.*, 2011) and extended northern Gulf of Mexico waters (e.g. McDonald *et al.*, 2017; Miller *et al.*, 2013). Dolphins in the northern Gulf of Mexico continue to be exposed to numerous cumulative stressors including biotoxins (Fire *et al.*, 2011; Schwacke *et al.*, 2010; Twiner *et al.*, 2012), disease (Litz *et al.*, 2014), human interactions (Samuels and Bejder, 2004), the DWH oil spill (Schwacke *et al.*, 2014; Smith *et al.*, 2017), and other persistent organic pollutants (Balmer *et al.*, 2015; Kucklick *et al.*, 2011). Long-term monitoring is essential for assessing the impacts of current and future anthropogenic stressors on marine mammal populations (Wells *et al.*, 2004).

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REFERENCES

- Adams, J., Speakman, T., Zolman, E. and Schwacke, L.H. 2006. Automating image matching, cataloging, and analysis for photo identification research. *Aquat. Mamm.* 32: 374–84.
- Atlas, R.M. and Hazen, T.C. 2011. Oil biodegradation and bioremediation: a tale of the two worst oil spills in US history. *Environ. Sci. Technol.* 45: 6,709–15.
- Balmer, B.C., Wells, R.S., Nowacek, S.M., Nowacek, D.P., Schwacke, L.H., McLellan, W.A., Scharf, F.S., Rowles, T.K., Hansen, L.J., Spradlin, T.R. and Pabst, D.A. 2008. Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. *J. Cetacean Res. Manage.* 10: 157–67.
- Balmer, B.C., Schwacke, L.H. and Wells, R.S. 2010. Linking dive behavior to satellite-linked tag condition for a bottlenose dolphin (*Tursiops truncatus*) along Florida's northern Gulf of Mexico coast. *Aquat. Mamm.* 36: 1–8.
- Balmer, B.C., Schwacke, L.H., Wells, R.S., Adams, J.D., George, C.G., Lane, S.M., McLellan, W.A., Rosel, P.E., Sparks, K., Speakman, T., Zolman, E.S. and Pabst, D.A. 2013. Comparison of abundance and habitat usage for common bottlenose dolphins between sites exposed to differential anthropogenic stressors within the estuaries of southern Georgia, USA. *Mar. Mamm. Sci.* 29: E114–35.
- Balmer, B.C., Ylitalo, G.M., McGeorge, L.E., Baugh, K.L., Boyd, D., Mullin, K.D., Rosel, P.E., Sinclair, C., Wells, R.S. and Zolman, E.S. 2015. Persistent organic pollutants (POPs) in blubber of common bottlenose dolphins (*Tursiops truncatus*) along the northern Gulf of Mexico coast, USA. *Sci. Total Environ.* 527: 306–12.
- Balmer, B., Sinclair, C., Speakman, T., Quigley, B., Barry, K., Cush, C., Hendon, M., Mullin, K., Ronje, E., Rosel, P., Schwacke, L., Wells, R. and Zolman, E. 2016. Extended movements of common bottlenose dolphins (*Tursiops truncatus*) along the northern Gulf of Mexico's central coast. *Gulf Mex. Sci.* 33: 93–7.
- Barco, S.G., Swingle, W.M., McLellan, W.A., Harris, R.N. and Pabst, D.A. 1999. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Mar. Mamm. Sci.* 15: 394–408.
- Barlow, J., Swartz, S.L., Eagle, T.C. and Wade, P.R. 1995. U.S. marine mammal stock assessments: Guidelines for preparation, background, and a summary of the 1995 assessments. NOAA Technical Memorandum NMFS-OPR-6. 73pp. [Available at: <https://repository.library.noaa.gov/>].
- Barron, M.G. 2012. Ecological impacts of the Deepwater Horizon oil spill: implications for immunotoxicity. *Toxicol. Pathol.* 40: 315–20.
- Bassos-Hull, K., Perrtree, R., Shepard, C., Schilling, S., Barleycorn, A., Allen, J., Balmer, B., Pine, W. and Wells, R. 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. Manage.* 13: 19–30.
- Borchers, D.L. and Efford, M. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64: 377–85.
- Bouveroux, T., Tyson, R. and Nowacek, D. 2014. Abundance and site fidelity of bottlenose dolphins in coastal waters near Panama City, Florida. *J. Cetacean Res. Manage.* 14: 37–42.
- Conn, P.B., Gorgone, A.M., Jugovich, A.R., Byrd, B.L. and Hansen, L.J. 2011. Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. *J. Wild. Manage.* 75: 569–79.
- Cush, C.C. and Wells, R.S. 2015. Gulf of Mexico Dolphin Identification System (GoMDIS) – A Collaborative Tool for Bottlenose Dolphin Conservation and Monitoring. Gulf of Mexico Marine Mammal Research and Monitoring Meeting, New Orleans, LA, 7–8 April 2015. [Available from C. Cush cenglund@mote.org]
- Dahlheim, M.E. and Matkin, C.O. 1994. Assessment of injuries to Prince William Sound killer whales. pp.163–172. In: Loughlin, T.R. (ed.) *Marine Mammals and the 'Exxon Valdez'*. Academic Press, San Diego, California. 395pp.
- Fire, S. E., Wang, Z., Byrd, M., Whitehead, H.R., Paternoster, J. and Morton, S.L. 2011. Co-occurrence of multiple classes of harmful algal toxins in bottlenose dolphins (*Tursiops truncatus*) stranding during an unusual mortality event in Texas, USA. *Harmful Algae* 10: 330–6.
- Gannon, D.P. and Waples, D.M. 2004. Diets of coastal bottlenose dolphins from the US mid-Atlantic coast differ by habitat. *Mar. Mamm. Sci.* 20: 527–45.
- Hubard, C.W., Maze-Foley, K., Mullin, K.D. and Schroeder, W.W. 2004. Seasonal abundance and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in Mississippi Sound. *Aquat. Mamm.* 30: 299–310.
- Kucklick, J., Schwacke, L., Wells, R., Hohn, A., Guichard, A., Yordy, J., Hansen, L., Zolman, E., Wilson, R., Litz, J., Nowacek, D., Rowles, T., Pugh, R., Balmer, B., Sinclair, C. and Rosel, P. 2011. Bottlenose dolphins as indicators of persistent organic pollutants in waters along the US East and Gulf of Mexico coasts. *Environ. Sci. Technol.* 45: 4,270–77.
- Lewis, J. and Schroeder, W. 2003. Mud plume feeding, a unique foraging behavior of the bottlenose dolphin in the Florida Keys. *Gulf Mex. Sci.* 21: 92–7.
- Litz, J.A., Baran, M.A., Bowen-Stevens, S.R., Carmichael, R.H., Colegrove, K.M., Garrison, L.P., Fire, S.E., Fougères, E.M., Hardy, R. and Holmes, S. 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: 161–75.
- Marti, C.D. and Wagner, P.W. 1985. Winter mortality in common barn-owls and its effect on population density and reproduction. *Condor* 87: 111–15.
- Matkin, C.O., Saulitis, E.L., Ellis, G.M., Olesiuk, P. and Rice, S.D. 2008. Ongoing population-level impacts on killer whales *Orcinus orca* following the 'Exxon Valdez' oil spill in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* 356: 269–81.

- McDonald, T.L., Hornsby, F.E., Speakman, T.R., Zolman, E.S., Mullin, K.D., Sinclair, C., Rosel, P.E., Thomas, L. and Schwacke, L.H. 2017. Survival, density, and abundance of common bottlenose dolphins in Barataria Bay following the Deepwater Horizon oil spill. *Endanger. Species Res.* 33: 69–82.
- McHugh, K.A., Allen, J.B., Barleycorn, A.A. and Wells, R.S. 2011. Severe *Karenia brevis* red tides influence juvenile bottlenose dolphin (*Tursiops truncatus*) behavior in Sarasota Bay, Florida. *Mar. Mamm. Sci.* 27: 622–43.
- Melancon, R.A.S., Lane, S., Speakman, T., Hart, L.B., Sinclair, C., Adams, J., Rosel, P. and Schwacke, L. 2011. Photo IDentification field and laboratory protocols utilizing FinBase version 2. NOAA Technical Memorandum NMFS-SEFSC-627. 46pp. [Available at: <https://repository.library.noaa.gov>].
- Michel, J., Owens, E.H., Zengel, S., Graham, A., Nixon, Z., Allard, T., Holton, W., Reimer, P.D., Lamarche, A., White, M., Rutherford, N., Childs, C., Mauseth, G., Challenger, G. and Taylor, E. 2013. Extent and degree of shoreline oiling: Deepwater Horizon oil spill, Gulf of Mexico, USA. *PLoS One* 8:e65087.
- Miller, L.J., Mackey, A.D., Solangi, M. and Kuczaj II, S.A. 2013. Population abundance and habitat utilization of bottlenose dolphins in the Mississippi Sound. *Aquat. Conserv.* 23: 145–51.
- Nixon, Z., Zengel, S., Baker, M., Steinhoff, M., Fricano, G., Rouhani, S. and Michel, J. 2016. Shoreline oiling from the Deepwater Horizon oil spill. *Mar. Pollut. Bull.* 107: 170–8.
- NOAA. 2004. Interim report on the bottlenose dolphin (*Tursiops truncatus*) Unusual Mortality Event along the Panhandle of Florida March–April 2004 (unpublished). 36pp. [Available at: <http://www.nmfs.noaa.gov/pr/health/mmume/event2004.htm>].
- NOAA-NCEI. 2017. Coastal water temperature guide: water temperature table of the eastern Gulf of Mexico. [Available at: <https://www.nodc.noaa.gov/dsdt/cwtg/>].
- Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage.* 46: 757–760.
- Rehman, Z., Toms, C.N. and Finch, C. 2016. Estimating abundance: a non-parametric mark recapture approach for open and closed systems. *Environ. Ecol. Stat.* 23: 623–38.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S. and Cooley, S.W. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecol. Appl.* 18: 1,028–37.
- Rosel, P.E., Mullin, K.D., Garrison, L., Schwacke, L.S., Adams, J., Balmer, B., Conn, P., Conroy, M.J., Eguchi, T., Gorgone, A., Hohn, A., Mazzoil, M., Schwarz, C., Sinclair, C., Speakman, T., Urian, K., Vollmer, N., Wade, P., Wells, R. and Zolman, E. 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 Technical Memorandum NMFS-SEFSC-621. 30pp. [Available at: <https://repository.library.noaa.gov>].
- Rosel, P.E., Wilcox, L.A., Sinclair, C., Speakman, T.R., Tumlin, M.C., Litz, J.A. and Zolman E.S. 2017. Genetic assignment to stock of stranded common bottlenose dolphins in southeastern Louisiana after the Deepwater Horizon oil spill. *Endanger. Species Res.* 33: 221–34.
- Samuels, A. and Bejder, L. 2004. Chronic interaction between humans and free-ranging bottlenose dolphins near Panama City Beach, Florida. *J. Cetacean Res. Manage.* 6: 69–77.
- Schaub, M., Aebischer, A., Gimenez, O., Berger, S. and Arlettaz, R. 2010. Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biol. Conserv.* 143: 1,911–18.
- Schwacke, L.H., Twiner, M.J., DeGuise, S., Balmer, B.C., Wells, R.S., Townsend, F.I., Rotstein, D.C., Varela, R.A., Hansen, L.J., Zolman, E.S., Spradlin, T.R., Levin, M., Leibrecht, H., Wang, Z. and Rowles, T.K. 2010. Eosinophilia and biotoxin exposure in bottlenose dolphins (*Tursiops truncatus*) from a population impacted by repeated mortality events. *Environ. Res.* 110:548–55.
- Schwacke, L.H., Smith, C.R., Townsend, F.I., Wells, R.S., Hart, L.B., Balmer, B.C., Collier, T.K., DeGuise, S. Fry, M.M. and Guillette, L.J., Jr 2014. Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. *Environ. Sci. and Technol.* 48: 93–103.
- Smith, C.R., Hart, L.B., Townsend, F.I., Zolman, E.S., Wells, R.S., Quigley, B., Ivančić, M., McKercher, W., Tumlin, M., Mullin, K., Adams, J.D., Wu, D., McFee, W., Collier, T.K., Rowles, T.K. and Schwacke, L.H. 2017. The slow recovery of Barataria Bay dolphin health in the years following the Deepwater Horizon oil spill (2013–2014), with evidence of persistent lung disease and impaired stress response. *Endanger. Species Res.* 33: 127–42.
- Speakman, T.R., Lane, S.M., Schwacke, L.H., Fair, P.A. and Zolman, E.S. 2010. Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. *J. Cetacean Res. Manage.* 11: 153–62.
- Sprogis, K.R., Pollock, K.H., Raudino, H.C., Allen, S.J., Kopps, A.M., Manlik, O., Tyne, J.A. and Bejder, L. 2016. Sex-specific patterns in abundance, temporary emigration and survival of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in coastal and estuarine waters. *Front. Mar. Sci.* 3: 12.
- Trustees. 2016. Deepwater Horizon oil spill: Final programmatic damage assessment and restoration plan and final programmatic environmental impact statement. Technical report. [Available at: <http://www.gulfspillrestoration.noaa.gov/restoration-planning/gulf-plan/>].
- Twiner, M.J., Flewelling, L.J., Fire, S.E., Bowen-Stevens, S.R., Gaydos, J.K., Johnson, C.K., Landsberg, J.H., Leighfield, T.A., Mase-Guthrie, B., Schwacke, L., VanDolah, F.M., Wang, Z. and Rowles, T.K. 2012. Comparative analysis of three brevetoxin-associated bottlenose dolphin (*Tursiops truncatus*) mortality events in the Florida panhandle region (USA). *PLoS One* 7: 1–19.
- Tyson, R.B., Nowacek, S.M. and Nowacek, D.P. 2011. Community structure and abundance of bottlenose dolphins *Tursiops truncatus* in coastal waters of the northeast Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 438: 253–65.
- Urian, K.W., Hohn, A.A. and Hansen, L.J. 1999. Status of the photo identification catalog of coastal bottlenose dolphins of the western North Atlantic: report of a workshop of catalog contributors. NOAA Technical Memorandum NMFS-SEFSC-425. 29pp. [Available at: https://grunt.sefsc.noaa.gov/P_OryLDS/download/TM588_TM-425.pdf?id=LDS].
- Urian, K.W., Hofmann, S., Wells, R.S. and Read, A.J. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. *Mar. Mamm. Sci.* 25: 619–38.
- Urian, K., Read, A., Gorgone, A., Balmer, B., Wells, R., Hammond, P., Berggren, P., Durban, J., Eguchi, T. and Rayment, W. 2015. Recommendations for photo identification methods used in capture-recapture models with cetaceans. *Mar. Mamm. Sci.* 31: 298–321.
- Waring, G.T., Josephson, E., Maze-Foley, K. and Rosel, P.E. 2016. US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments-2015. Report No. NMFS-NE-238. 501pp. [Available at: <http://www.nmfs.noaa.gov/pr/sars/>].
- Weiss, J. 2006. Foraging habitats and associated preferential foraging specializations of bottlenose dolphin (*Tursiops truncatus*) mother-calf pairs. *Aquat. Mamm.* 32: 10–19.
- Wells, R.S. 2003. Dolphin social complexity: lessons from long-term study and life history. pp.32–56. In: F.B.M. de Waal and P.L. Tyack (eds.). *Animal Social Complexity: Intelligence, Culture and Individualized Societies*. Harvard University Press, Cambridge, Massachusetts. 640pp.
- Wells, R.S., Rhinehart, H.L., Hansen, L.J., Sweeney, J.C., Townsend, F.I., Stone, R., Casper, D.R., Scott, M.D., Hohn, A.A. and Rowles, T.R. 2004. Bottlenose dolphins as marine ecosystem sentinels: Developing a health monitoring system. *EcoHealth* 1: 246–54.
- Wells, R.S., Schwacke, L.H., Rowles, T.K., Balmer, B.C., Zolman, E., Speakman, T., Townsend, F.I., Tumlin, M.C., Barleycorn, A. and Wilkinson, K.A. 2017. Ranging patterns of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. *Endanger. Species Res.* 33: 159–80.
- Wilson, B., Hammond, P.S. and Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl.* 9: 288–300.
- Wilson, R.M., Nelson, J.A., Balmer, B.C., Nowacek, D.P. and Chanton, J.P. 2013. Stable isotope variation in the northern Gulf of Mexico constrains bottlenose dolphin (*Tursiops truncatus*) foraging ranges. *Mar. Biol.* 160: 2,967–80.