

Seasonal Density Estimates of *Tursiops truncatus* (Bottlenose Dolphin) in the Mississippi Sound from 2011 to 2013

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Abstract - We conducted vessel-based line-transect sampling from December 2011 to November 2013 to quantify *Tursiops truncatus* (Bottlenose Dolphin) density over 8 consecutive seasons in the Mississippi Sound. Density estimates showed temporal variation ranging from 0.27 Dolphins/km² (CV% = 31.3) in spring 2013 to 1.12 Dolphins/km² (CV% = 21.6) in spring 2012. Density in winter and summer was stable compared to fall and spring, which fluctuated across years. We also noted spatial variation—density was commonly highest in the central and eastern portions of the Mississippi Sound. Spatial and temporal variation in temperature and salinity were potentially driving shifts in Bottlenose Dolphin density. Additional regularly collected density estimates using standardized protocols are needed in order to draw more definitive conclusions regarding the status and trend of this population.

Introduction

Bays, sounds, and estuaries (BSEs) within the northern Gulf of Mexico (nGOM) have shown a variety of *Tursiops truncatus* (Montagu) (Bottlenose Dolphin, hereafter Dolphin) abundance and distribution patterns including no change between seasons (McClellan et al. 2000), peaks in spring (Shane 2004), summer (Hubard et al. 2004), and winter (Bassos-Hull and Wells 2007, Shane 1980), or bimodal peaks in spring and fall (Balmer et al. 2008). Recent National Oceanic and Atmospheric Administration (NOAA) reports estimate that the Bay Boudreau, Mississippi Sound (BB-MSS) BSE Dolphin stock is among the most densely populated within the nGOM (Waring et al. 2014). The geographic extent of the stock area spans 3711 km² (Scott et al. 1989) from the western edge of Mobile Bay, AL to Lake Borgne, LA in the west. The southern border includes the mouth of Bay Boudreau in the west and a chain of barrier islands (Cat, Ship, Horn, Petit Bois, and Dauphin islands) in central and eastern portions of the stock area (NOAA 2015). Previous research has shown that Dolphins in this area exhibit seasonal variation in abundance (Hubard et al. 2004, Lohefener et al. 1990, Miller et al. 2013), but differences in survey methods, study areas, and timing of surveys make interpretation of long-term trends difficult. More study is needed to increase understanding of the biology and spatial and temporal distribution of Dolphins in the MSS to better understand stock structure in this region.

Previous research designed to quantify Dolphin abundance has included variable methodologies and density estimates for the MSS. Density estimates derived

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from aerial surveys for the fall of 1985 and 1992 were 0.07 Dolphins/km² and 0.2 Dolphins/km², respectively, for the MSS and Lake Borgne (Blaylock and Hoggard 1994). Mullin et al. (1990) conducted aerial surveys in 1987 and estimated 0.37 Dolphins/km² in May and 0.16 Dolphins/km² in September within inshore waters from the mouth of the Mississippi River to the Alabama–Florida border. Boat-based surveys have resulted in higher estimates for the region; surveys conducted from 1995 to 1996 in an area directly north of Horn and Petit Bois islands resulted in density estimates that ranged from 0.6 Dolphins/km² in winter to 1.3 Dolphins/km² in the summer (Hubard et al. 2004). Boat-based density estimates within the MSS ranged from 0.67 Dolphins/km² in winter (from November 2007 to February 2008) to 1.07 Dolphins/km² in summer (May–August 2007) for an area that extends from the Mississippi–Louisiana border to the eastern end of Horn Island, including an area up to 15 km south of the barrier islands. Density was highest inshore in summer months (1.69 Dolphins/km²), but was reduced in these areas during winter (0.89 Dolphins/km²), suggesting higher use of deeper, offshore areas in winter (Miller et al. 2013). Pitchford et al. (2015) predicted occurrence of Dolphins with spatial distribution models (SDMs) for the MSS that showed seasonal shifts. In winter (December–February), occurrence was highest south of East Ship and Horn Islands. In spring (March–May), predicted occurrence was highest north of Horn and Petit Bois islands and in an area south of Bay St. Louis, MS. During summer, predicted occurrence was high throughout the MSS extending into Lake Borgne, LA. In fall (September–November), a westward shift was noted, including high levels of predicted occurrence in Lake Borgne, LA. The results of the Pitchford et al. (2015) study did not include abundance estimates, but did suggest that shifting environmental conditions and prey distributions drive seasonal shifts in Dolphin occurrence. Aerial surveys were conducted from 2011–2012 in the MSS from Alabama in the east to the mouth of Lake Borgne in the west (Lake Borgne was not surveyed) and extending south into the Bay Boudreau region, but did not include areas south of the barrier islands. Density estimates extrapolated to the BB-MSS geographic region were 0.65 Dolphins/km² in spring (March–April 2011), 0.46 Dolphins/km² in summer (July–August 2011), 0.31 Dolphins/km² in fall (October–November 2011), and 0.24 Dolphins/km² in winter (January–February 2012) (NOAA 2015). These estimates are lower than those reported by Miller et al. (2013), but the differences in sampling method (i.e., aerial vs. boat) and survey area likely contributed to these disparities. Large coefficients of variation associated with both sets of estimates further confound comparisons between the Miller et al. (2013) and Pitchford et al. (2015) studies.

Regular abundance estimates can be used for several purposes including trend analysis and calculations of potential biological removal (PBR), which require abundance estimates that are ≤ 8 years old (Waring et al. 2014). This consideration is important for the MSS because several anthropogenic and natural disturbances have occurred in the nGOM in recent years, including the Deepwater Horizon (DWH) oil spill (Schwacke et al. 2013), freshwater floods (Carmichael et al. 2012), and several hurricanes (Miller et al. 2010, Smith et al. 2013) that have been implicated as sources of stress to Dolphins in this region. Coinciding with these disturbances

is the longest-running unusual mortality event (UME) on record within the nGOM that began in 2010 and continues to date (Litz et al. 2014, Venn-Watson et al. 2015a). Currently, the UME has included 1259 Bottlenose Dolphin strandings over a ~2712-km² region extending from the western border of Louisiana to the Florida Panhandle (data available at <http://www.nmfs.noaa.gov/pr/health/mmume/>). Although the actual cause is unclear, several factors have been cited as contributors to this UME including the combination of prolonged cold weather and unusually large freshwater floods (Carmichael et al. 2012) and petroleum exposure associated with the DWH oil spill (Litz et al. 2014, Schwacke et al. 2013). The DWH oil spill released 4.9 million barrels of oil into the nGOM, and response efforts resulted in the application of 1 million gallons of Corexit[®] dispersant into the nGOM (National Commission 2010) that have since been implicated as a source of stress for many marine species (White et al. 2012, Whitehead et al. 2011) including Dolphins (Lane et al. 2015, Schwacke et al. 2013, Venn-Watson et al. 2015b). Large numbers of stranded Dolphins were recovered in Mississippi following the oil spill, including an usually large number of perinate Dolphins (Venn-Watson et al. 2015a). Considering the importance of the MSS for Dolphins and the existence of numerous threats, regular population assessments are needed to gauge trends in Dolphin density in this region (Balmer et al. 2013, Speakman et al. 2010). Such assessments provide important information for the management of this protected species and can be used to indicate the health of the regional ecosystem (Balmer et al. 2015, Kucklick et al. 2011, Wells et al. 2004).

The purpose of this paper is to present density estimates derived from boat-based, line-transect distance-sampling conducted within the MSS from 2011 to 2013. The results include seasonal estimates for multiple strata arranged from west to east to provide a high level of spatial resolution. Although our results do not present any direct evidence of the effects of recent disturbances in the MSS, they provide much-needed density estimates for a protected species within a region that has experienced a variety of natural and anthropogenic disturbances. In addition, we collected data across all seasons for 2 y and from areas that have not been included in some previous abundance estimates (e.g., areas south of the barrier islands, Lake Borgne). Our results contribute to greater understanding of spatial and temporal shifts in the distribution of estuarine Dolphins in this region.

Materials and Methods

Study area

The MSS is a ~2000-km² microtidal embayment that is heavily influenced by wind forcing (Kjerfve 1986) and is separated from the Gulf of Mexico by a series of barrier islands (Cat, Ship, Horn, Petit Bois, and Dauphin islands) (Eleuterius 1978; Fig. 1). Average annual water-temperature range = 9–32 °C, salinity range = 0–33 ppt, and water-depth range = 1–7 m (Christmas and Eleuterius 1973). Structured habitats within the region are limited to seagrass beds along the barrier-island shorelines and marsh-edge habitats, which have been altered from their historic extent (Rakocinski et al. 2003).

Data collection

From December 2011 through November 2013, we recorded Dolphin sightings using line-transect, distance-sampling methods as outlined in Buckland et al. (2001). We employed a stratified sampling design to achieve fine-scale spatial resolution. We divided the study area into 7 strata, $\sim 20 \text{ km} \times 20 \text{ km}$ in size arranged and numbered from west to east. Each stratum contained four $\sim 20\text{-km}$ quasi-parallel transects that we surveyed twice within each season including winter (December–February), spring (March–May), summer (June–August), and fall (September–November) (Fig. 1). The transects were separated by a minimum perpendicular distance of 2.2 km. We considered the orientation of the transects (i.e., parallel to the shoreline) appropriate due to the highly uniform depth and substrate within the MSS. We surveyed alternating transects (i.e., A and C or B and D) from either stratum 1–4 or 5–7 each survey day to maintain high probability of independence among sightings. Typically, we conducted surveys during the period 0700–1500 h, only when winds were $\leq 16 \text{ km per hour}$, and wave heights were $\leq 0.6 \text{ m}$. We surveyed all transects before initiation of a second seasonal survey. It took an average of 4.25 d (SE = 0.14) to cover all transects once and 8.5 d (SE = 0.27) to cover all transects twice. The survey platform was a 9.5-m Stamas Tarpon

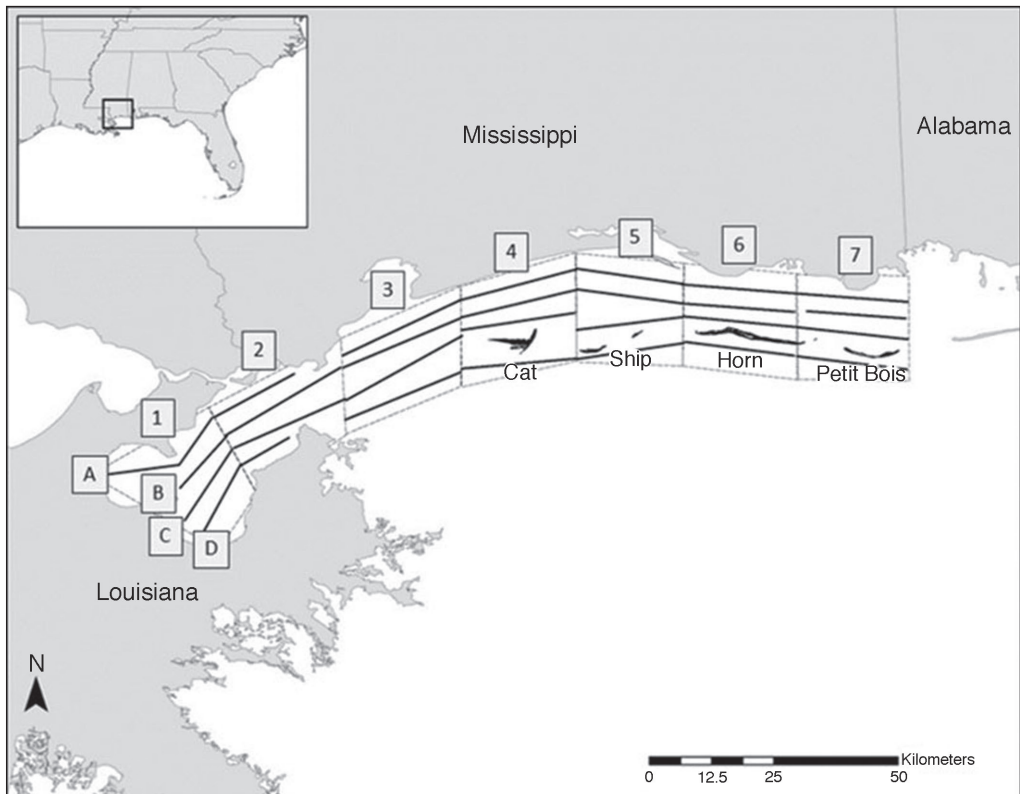


Figure 1. Study area used to develop seasonal spatial distribution models for Bottlenose Dolphins (*Tursiops truncatus*) within the Mississippi Sound. Survey strata are numbered 1–7 and transects are labeled A–D.

(Stamas Yacht, Inc., Tarpon Springs, FL) powered by twin 250-hp, 4-stroke engines carrying a boat captain and 4 observers at 25 km per hour. At the beginning of each transect within each stratum, we recorded Beaufort sea state (BSS), glare, sightability, and sea-surface environmental conditions (i.e., dissolved oxygen, salinity, pH, temperature, and depth). Sightability was a composite measure of BSS and glare and contained 4 levels (i.e., poor, moderate, good, and excellent) to quantify the ability of observers to detect Dolphins. During the survey, 2 observers scanned the area between the transect and 90° to port, and 2 observers scanned the area between the transect and 90° to starboard (Melancon et al. 2011, Miller et al. 2013). We classified a Dolphin sighting as an observation of at least 1 Dolphin by more than 1 observer. When only 1 observer sighted a Dolphin, the boat stopped briefly on the transect to allow all observers to search for the animal before continuing on the survey. When Dolphins were observed, the boat traveled directly to the original sighting location to estimate the total number of Dolphins in the group (i.e., cluster size) using the 10-m chain rule (Smolker et al. 1992) and to determine geographic coordinates using a Garmin GPSmap76 global positioning system (GPS) with differential accuracy of 3–5 m. Travel to the original sighting location provided the best estimate of actual distance, which reduced the likelihood of bias and improved the accuracy of our density estimates (Buckland et al. 2001). After recording coordinates of the sighting and estimating group size, the boat traveled back to the transect at the location where it departed and the survey resumed. We imported sighting-location coordinates for each season into ESRI® ArcMap™ 10.2 (Redlands, CA) and used the measuring tool to determine the distance from each sighting to the transect line.

Data analysis

We used Program Distance 6.0 (Thomas et al. 2010) to estimate density (D), population size (N), and cluster size among seasons of the year (i.e., winter, spring, summer, and fall) from 2011 to 2013. We employed both the conventional-distance sampling (CDS) and the multiple covariates distance sampling (MCDS) engines to generate a model set for each season (Thomas et al. 2010). Initial analyses revealed that several sightings associated with unusually large distances from the survey platform were skewing detection functions; thus, we discarded from density-estimation analyses the sightings associated with the largest 5% of perpendicular distances from the survey vessel (Buckland et al. 2001). Detection functions for selected models did not indicate violation of the assumption that all Dolphins on the transect line were seen during surveys, so we did not need to truncate the smallest observed distance values. We used a global detection function to estimate stratum-specific densities, global densities, and post-stratified sightings by survey stratum to account for variation in the spatial distribution of Dolphins among seasons. We did not employ stratum-specific detection functions because small sample sizes among survey strata prevented reliable assessment of differences in detectability among strata. We estimated cluster size for each season and stratum by regressing log cluster size against detection-probability estimates. We estimated total

abundance (\hat{N}) with the equation

$$\hat{N} = \sum_{i=1}^n (s_i / \hat{P}_i),$$

where \hat{P}_i represents the inclusion probability and s_i represents cluster size (Thomas et al. 2010).

We developed a set of candidate models for each season over the study period (2011/12–2013) using a variety of combinations of covariates that could influence detectability of Dolphins. Each set contained models with no covariates and models with sightability, glare, BSS, glare and BSS, and cluster size as covariates with all possible combinations of uniform (no covariates), half-normal, and hazard-rate detection-functions and cosine, simple polynomial, and hermite polynomial-series expansions. We employed Kolmogorov-Smirnov and chi-square goodness-of-fit tests to assess model fit. We calculated Akaike's information criterion (AIC) (Akaike 1973) and Akaike weights (Burnham and Anderson 2002) for each model and used them to select a final model for each season. We determined global density and cluster size-estimates across the entire study area from the mean of strata estimates weighted by stratum area. Where possible, we also made stratum-specific estimates to examine the spatial variation in density across the MSS. Following density estimation, we used least-squares regression, including calculation of R^2 values, in Microsoft Excel[®] to conduct trend analyses. Finally, we ran a multiple linear regression to examine the relation between Dolphin density (Dolphins/km²) within each stratum for each season ($n = 56$), and dissolved oxygen, salinity, temperature, and depth using the R 2.12.1 (R Core Team, 2015). We set a priori significance at $\alpha = 0.05$.

Results

We spent a total of 456 hours surveying during 66 days over the course of this study. During this time, we documented 539 Dolphin sightings—165, 128, 106, and 140 during winter, spring, summer, and fall, respectively (Fig. 2). Seasonal encounter rates across the study period ranged from 0.07 sightings/km (CV% = 47) in spring 2013 to 0.15 sightings/km (CV% = 38) in spring 2012. Average cluster size ranged from 3.0 Dolphins per group in winter 2012/13 to 5.7 Dolphins per group in summer of 2013 (Fig. 3). Average depth recorded during surveys ranged from 3.7 m (SE = 0.2) during winter of 2011/12 to 4.6 m (SE = 0.4) in summer of 2012 (Table 1). Average water temperature ranged from 14.2 °C (SE = 0.3) in winter 2011/12 to 29.5 °C (SE = 0.2) during summer 2012. Average salinity ranged from 11.3 ppt (SE = 0.9) in spring 2013 to 26.2 ppt (SE = 4.3) in winter 2011/12. Average dissolved oxygen ranged from 4.6 mg/L (SE = 0.1) during summer 2012 to 8.1 mg/L (SE = 0.3) during fall 2013. We noted spatial variation when examining environmental conditions by stratum. Specifically, we observed a west–east salinity gradient that ranged from 2.4 (spring 2013) to 9.4 ppt (winter 2011/12) in stratum 1 and from 17.7 (spring 2013) to 28.3 (fall 2013) ppt in stratum 7. Spring salinity levels also varied notably across years from 4.7 (stratum 1) to

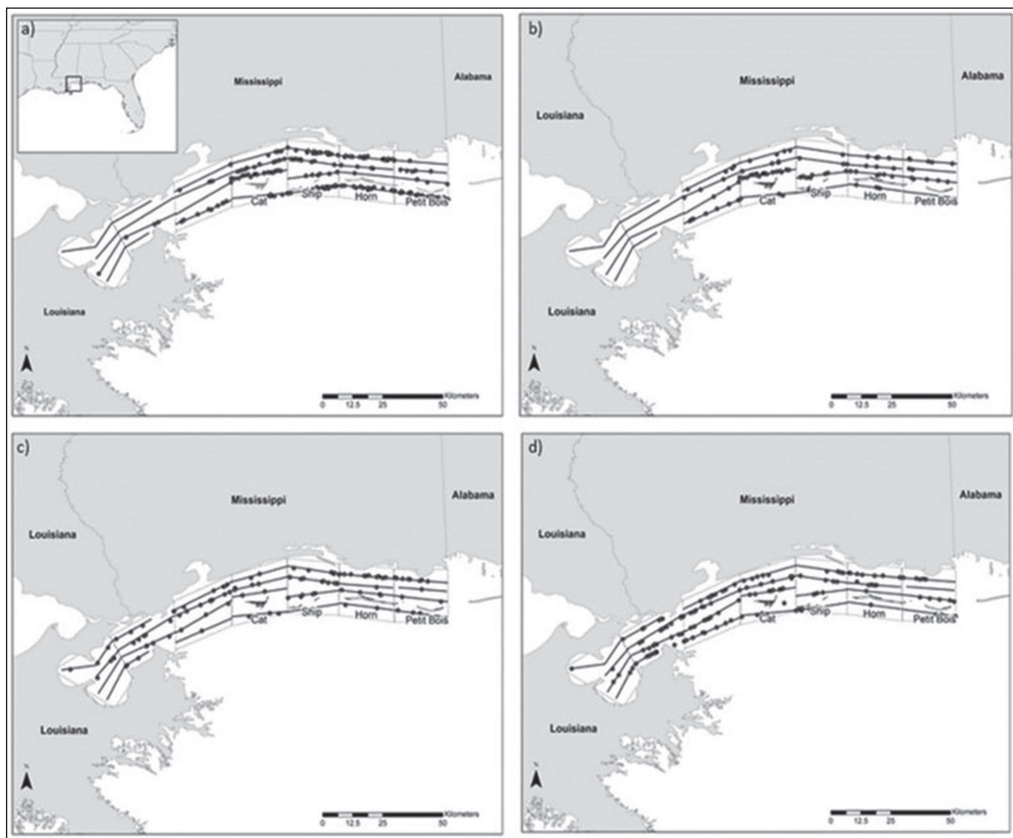


Figure 2. Bottlenose Dolphin (*Tursiops truncatus*) sightings in winter (a), spring (b), summer (c), and fall (d) in the Mississippi Sound from 2011 to 2013.

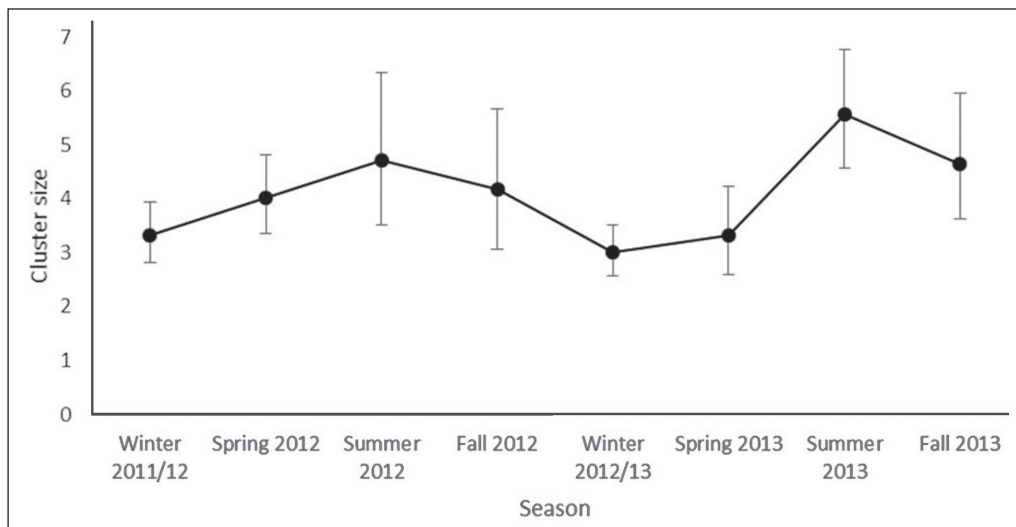


Figure 3. Bottlenose Dolphin (*Tursiops truncatus*) cluster size in the Mississippi Sound among seasons of the year from 2011/12 to 2013. The error bars on each estimate are 95% confidence intervals around the mean.

23.5 ppt (stratum 7) in spring 2012 and from 2.4 ppt (stratum 1) to 17.7 ppt (stratum 7) in spring 2013. (for full data on environmental conditions by stratum, see Supplemental Table 1, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2264-Pitchford-s1>, and, for BioOne subscribers, at <http://dx.doi.org/10.1656/S2264.s1>).

AIC values indicated that the best models for all seasons had no covariates, with the exception of the spring 2012 model, which included sightability as a covariate (for summary information on all analyzed models, see Supplemental Table 2, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2264-Pitchford-s1>, and, for BioOne subscribers, at <http://dx.doi.org/10.1656/S2264.s1>). There was considerable model-competition for each season as indicated by AIC values; thus, we calculated AIC weights. Of models generated for fall 2012, a model that included sightability as a covariate (AIC weights = 0.22) was very competitive with the model with no covariates (AIC weights = 0.24). Kolmogorov-Smirnov goodness-of-fit test statistics and *P*-values for the highest-ranking seasonal models are provided in Table 2.

Dolphin density estimates ranged from 0.27 Dolphins/km² (CV% = 31.3) in spring 2013 to 1.12 Dolphins/km² (CV% = 21.6) in spring 2012 (Table 2, Fig. 4).

Table 1. Average depth, temperature, salinity, dissolved oxygen, and associated standard error of the mean (SE) among seasons of the year in the Mississippi Sound from winter 2011/12 to fall 2013.

Season	Depth (m)	Temp (°C)	Salinity (ppt)	Dissolved oxygen (mg/L)
Winter 2011/12	3.7 (0.2)	14.2 (0.3)	26.2 (4.3)	7.0 (0.2)
Spring 2012	4.2 (0.3)	23.5 (0.4)	14.3 (0.8)	5.4 (0.1)
Summer 2012	4.6 (0.4)	29.5 (0.2)	19.7 (1.1)	4.6 (0.1)
Fall 2012	4.1 (0.2)	23.6 (0.5)	17.6 (1.0)	4.9 (0.1)
Winter 2012/13	4.1 (0.3)	14.8 (0.3)	16.1 (1.1)	6.3 (0.1)
Spring 2013	4.4 (0.3)	21.1 (0.5)	11.3 (0.9)	5.8 (0.1)
Summer 2013	4.4 (0.3)	28.9 (0.1)	16.3 (0.9)	6.3 (0.2)
Fall 2013	4.2 (0.3)	20.8 (0.8)	19.9 (1.0)	8.1 (0.3)

Table 2. Estimates of Bottlenose Dolphin (*Tursiops truncatus*) density (D; Dolphins/km²) and population size (N) among seasons of the year in the Mississippi Sound from winter 2011/12 to fall 2013. CI = confidence interval, CL = confidence limit, CV = coefficient of variation, K-S GoF = Kolmogorov-Smirnov goodness-of-fit statistic (and associated *P* value).

Season	D	Lower CI	Upper CI	N	Lower CL	Upper CL	CV%	Cluster size	K-S GoF
Winter 2011/12	0.66	0.40	1.10	1793	1076	2988	25.1	3.3	0.09 (0.6)
Spring 2012	1.12	0.71	1.71	3236	1927	4627	21.6	4.0	0.08 (0.5)
Summer 2012	0.86	0.51	1.43	2322	1394	3868	25.9	4.7	0.07 (1.0)
Fall 2012	0.46	0.29	0.73	1248	790	1973	23.3	4.2	0.08 (0.7)
Winter 2012/13	0.75	0.42	1.32	2023	1144	3578	28.3	3.0	0.05 (0.9)
Spring 2013	0.27	0.15	0.50	738	397	1369	31.3	3.3	0.08 (0.9)
Summer 2013	0.71	0.45	1.11	1923	1231	3003	22.8	5.7	0.08 (0.9)
Fall 2013	0.83	0.50	1.36	2239	1362	3680	24.9	4.6	0.04 (1.0)

Population estimates for the study area ranged from 738 (95% CI = 397–1369) in spring 2013 to 3236 (95% CI = 1927–4627) in spring 2012. Densities in winter and summer seasons were fairly constant relative to those in spring and fall seasons, which fluctuated during the 2-y study period. Overall, we detected a slight decreasing trend in Dolphin density ($R^2 = 0.08$; $m = 0.03$). We also detected a slight increasing trend in cluster size ($R^2 = 0.15$). Model coefficients of variation for each season within each year ranged from 21.6% in spring 2012 to 31.3% in winter 2013 (Table 2). Full data on variance attributed to detection probability, encounter rate, and cluster size are provided in Supplemental Table 3 (available online at <http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2264-Pitchford-s1>, and, for BioOne subscribers, at <http://dx.doi.org/10.1656/S2264.s1>).

Dolphin density varied among strata and strata within season ranging from 0 Dolphins/km² in strata 1 and 2 in spring 2012 and in stratum 2 in spring 2013 to 2.1 Dolphins/km² (CV% = 56.1) in stratum 4 in spring 2012 (Fig. 5; see Supplemental Table 2, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2264-Pitchford-s1>, and, for BioOne subscribers, at <http://dx.doi.org/10.1656/S2264.s1>). Differences in density estimates among strata 3–7 compared to strata 1–2 in the westernmost portion of the Mississippi Sound were also notable. While Dolphin density in stratum 1 was similar to levels in the other strata during the summer and fall seasons of 2012 and 2013, it remained relatively low in the winter and spring seasons during both survey years. Variation in encounter rates ranged from 0 sightings/km in strata 1 and 2 in spring 2012 and in stratum 2 in spring 2013, to 0.33 sightings/km in strata 5 in winter 2012/13. Encounter rate was the main source of variance for all models across all seasons as encounter rate variance ranged from 28.7% in stratum 6 in spring 2012 to 98.3% in stratum 1 in winter 2011/12 (see Supplemental Table 2, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2264-Pitchford-s1>, and, for BioOne subscribers, at <http://dx.doi.org/10.1656/S2264.s1>).

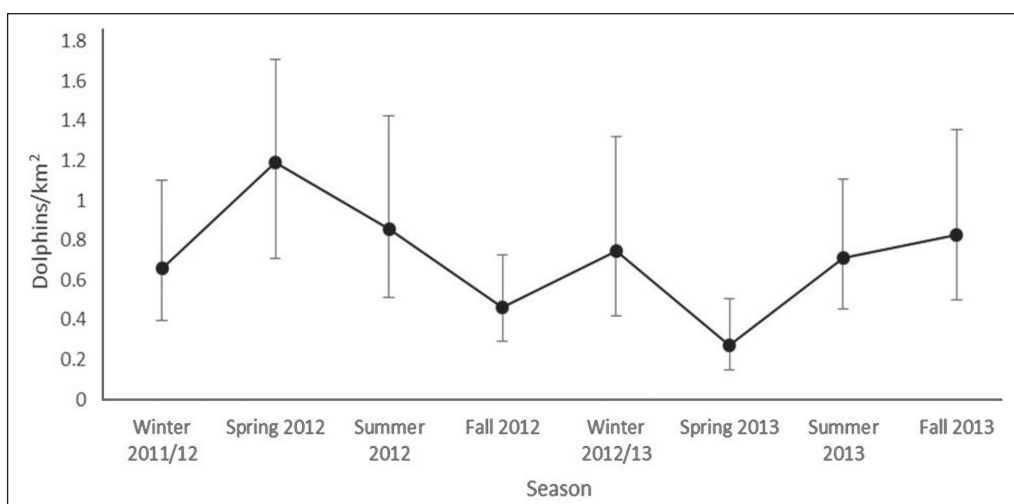


Figure 4. Bottlenose Dolphin (*Tursiops truncatus*) density (Dolphins/km²) in the Mississippi Sound among seasons of the year from 2011/12 to 2013. The error bars on each estimate are 95% confidence intervals around the mean.

org/10.1656/S2264.s1). Results of a multiple linear regression showed that only salinity was a significant predictor of Dolphin density ($P = 0.003$; $R^2 = 0.23$).

Discussion

Spatiotemporal variation in density

Overall, these results suggest that there is spatial variation in Dolphin density in the MSS over seasonal and annual timescales. Differences in density among survey strata across both season and year suggests that the region is dynamic with regard to environmental variants (e.g., temperature, salinity) that influence Dolphin occurrence and distribution (Pitchford et al. 2015). The largest difference among seasons included a 4-fold decrease in density from the spring of 2012 to the spring of 2013 and an almost 2-fold increase from the fall 2012 to the fall of 2013. Conversely, summer and winter densities were similar throughout the study period. Differences in density estimates among the 2 spring seasons potentially reflect differences in environmental conditions. The spring of 2012, which contained the greatest estimated density over the 2 years sampled (1.12 Dolphins/km²), coincided with lower-flow rates on the Pascagoula and Pearl rivers (484 m³/s and 305 m³/s average minimum daily flow rates, respectively, for 1 February 2012–11 May 2012) (US Geological Survey 2015) and was characterized by higher average sea-surface temperature (SST) (23.5 °C; SE = 0.4) and higher average salinity (14.3 ppt; SE = 0.1). Spring 2013 coincided with higher-flow rates on the Pascagoula and Pearl Rivers (721 m³/s and 557 m³/s average minimum daily flow rate, respectively, for 1 February

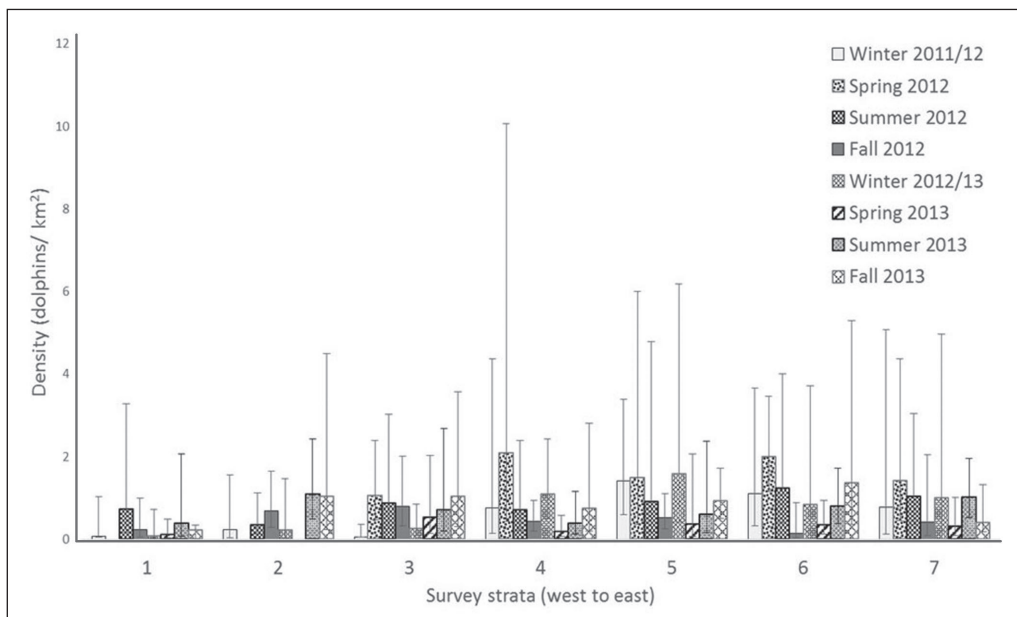


Figure 5. Dolphin density (Dolphins/km²) among survey strata for each survey season from 2011/12 to 2013. Survey strata are numbered 1–7 from the western portion of the Mississippi Sound in Lake Borgne, LA to the Mississippi–Alabama state border in the east. The error bars on each estimate are 95% confidence intervals around the mean.

2013–11 May 2013) (US Geological Survey 2015), lower average SST (21.1 °C; SE = 0.5), and lower average salinity (11.3 ppt; SE = 0.9) within the MSS, and the lowest estimated density during the study period (0.27 Dolphins/km²). Salinity was also higher in all strata during the spring of 2012 relative to spring 2013, excepting stratum 4. Similarly, low estimates in fall 2012 (0.46 Dolphins/km²) coincided with the occurrence of Hurricane Isaac, which produced over 10 inches of rain in South Mississippi from 25 August to 3 September 2012 (Berg 2013). During the late summer and fall of 2013, the MSS was unaffected by tropical systems and our estimated density estimate for that period was 0.83 Dolphins/km². Changes in average temperature, salinity, and flow rates among both spring and fall seasons of the study period reflect overall differences in climate that may have played a role in the abundance of Dolphins within the MSS. Further, the significance of salinity as a predictor of density also suggests that increased precipitation and river flow into the MSS is linked with periods of reduced Dolphin population density.

Density was commonly highest within the central and eastern MSS (i.e., strata 4–7) regardless of season, and density in the extreme western MSS (i.e., strata 1–2) was consistently low in the winter and spring relative to the other strata. However, during the summer and fall, density in strata 1–2 was typically higher than it was during winter and spring, suggesting that use of this area was somewhat restricted to the warm season. During the winter and spring, low temperature and salinity are common in this area, as is low predicted occurrence of Dolphins (Pitchford et al. 2015). Specifically, salinity is consistently lower in the western MSS, especially in the winter and spring. Possible reasons for low densities in the cooler months include discomfort associated with inhabiting cold water (Loheofener et al. 1990), suppressed immune response (Carmichael et al. 2012), development of skin lesions (Hart et al. 2012), and seasonal changes in the distribution of prey (Hastie et al. 2004, Hubard et al. 2004, Loheofener et al. 1990, Miller et al. 2013, Pitchford et al. 2015). While the potential direct effects of temperature and salinity on Dolphins has been noted in other studies (Carmichael et al. 2012, Hart et al. 2012), there is less information available regarding the indirect effects of changing environmental conditions on Dolphin distribution. An exception includes hydrographic fronts, which readily form in estuarine systems near the mouths of rivers and have the propensity to concentrate fish (Franks 1992) and increase foraging efficiency for Dolphins (Mendes et al. 2002). Although there are a variety of prey species that inhabit the MSS (Barros and Odell 1990, Barros and Wells 1998, Hoese and Moore 1998) and have seasonal-movement regimes that could influence the distribution of Dolphins (Hubard et al. 2004, Loheofener et al. 1990, Miller et al. 2013, Pitchford et al. 2015), it is difficult to relate Dolphin density to occurrence of these species without more-specific information regarding both Dolphin diet and seasonal shifts in the distribution of prey species within the MSS. Researchers noted a seasonal shift in diet in their study of stomach contents of stranded oceanic Dolphins in North Carolina—the majority of prey items across all seasons were from the family Scianidae, the relative proportions of Sciaenids (e.g., *Micropogonias undulatus* vs. *Cynoscion regalis*) differed significantly across seasons (Gannon and Waples

2004). The lack of substantial information on Dolphin prey- and forage-species distribution in the nGOM, should be addressed in the future to better understand Dolphin distribution, activity, and movement in this region. Work similar to Gannon and Waples (2004) or McCabe et al. (2010), which examined prey selection of Dolphins by incorporating prey-availability sampling, should help to illuminate the relation between shifting environmental conditions and seasonal spatial distributions of Dolphins in the MSS.

Variation in cluster size of sighted groups was evident during the course of our study; the number of Dolphins within each group was lowest in winter (3.3 and 3.0 Dolphins/group in winter 2011/12 and winter 2012/13, respectively) and highest in summer (4.7 and 5.7 Dolphins per group in summer 2012 and 2013, respectively). These numbers are consistent with group sizes reported by Mullin et al. (1990), but are lower than the average cluster size reported by Miller et al. (2013), which ranged from 7.7 Dolphins per cluster during winter to 11.7 Dolphins per cluster during summer. A possible explanation for lower estimated cluster sizes in this study is the location of our sampling area. Miller et al. (2013) surveyed up to 15 km south of the barrier islands, potentially observing larger groups from the Northern Coastal Stock (NCS).

Sources of error

Boat-based surveys may positively bias density estimates because Dolphins may actively seek boats in order to bowride, although this phenomenon is more common with large, slow moving vessels that produce a bow wave (Würsig et al. 1998). Conversely, aerial surveys often result in negatively biased density estimates, particularly in turbid waters or for small BSE stocks in which aerial-survey speed and geography of the region may reduce sightings (Hubard et al. 2004, Marsh and Sinclair 1989). The first published density estimates for the MSS were derived from aerial surveys (0.07–0.2 Dolphins/km²; Blaylock and Hoggard 1994) and seem low when compared with boat-based estimates (0.16–0.37 Dolphins/km², Mullin et al. 1990). Other factors that could negatively bias estimates include responsive movement away from the survey vessel, sighting conditions, and observer variation and fatigue (Buckland et al. 2001). We did not control for responsive movement in this study, but histograms of detection probability produced by the Program Distance 6.0 (Thomas et al. 2010) did not suggest that Dolphins were either attracted to or repelled from the survey vessel. To control for effects of survey conditions, we measured variables such as BSS, glare, and sightability—which accounts for BSS, glare and other factors (e.g., weather) that could affect detection—during each survey and included them in the analysis as a covariate. However, only during spring 2012 was a model that included sightability selected as the best model. We did not control for observer variation and fatigue, but designed the study to avoid long surveys, and we used inter-transect travel time as an observer rest-period to minimize fatigue. Also, to avoid potential bias arising from interobserver variability, we counted only sightings observed by 2 or more observers.

Trend detection

We detected a decreasing trend in density from 2011 to 2013 ($R^2 = 0.08$; $m = 0.03$), but this result may not reflect actual population trends. Although our study included the high frequency of sampling needed for trend detection, seasonal estimates had low precision (i.e., large confidence intervals). When compared with previous estimates, winter densities from 2011 to 2013 were higher and summer densities were lower than those published by Loheofener et al. (1990) and Hubard et al. (2004); however, these estimates may not be directly comparable because they were made within the MSS embayment only. Estimates from Miller et al. (2013), when including only their values for coastal and island waters, correspond closely to those for strata 3–6 in this study. Miller et al. (2013) reported a density in the same area of 0.88 Dolphins/km² in winter 2007/08, very similar to estimates presented here for the 2011/12 and 2012/13 winters (0.86 and 0.95 Dolphins/km², respectively). This finding suggests that the number of Dolphins using this region during winter has not decreased during the intervening years. Conversely, 2007 summer estimates of 1.54 Dolphins/km² (Miller et al. 2013) were higher than 2012 and 2013 summer estimates in our study (0.94 and 0.63 Dolphins/km², respectively), suggesting that the summer population in strata 3–6 may have decreased. Again, the magnitude of variation in estimates and seasonal and annual variation in physical conditions in the MSS suggests that to accurately quantify population trends, longer study periods to record both Dolphin density and physical oceanographic data are needed. The survey area employed in the current study encompasses the majority of the geographic region delineated as the BB-MSS stock; however, coverage of this area required a minimum of 4 days, which may have inflated the variance around seasonal estimates. Future studies could employ the use of multiple boats to reduce the amount of time required to complete all transects, thus reducing the variance around estimates. Another strategy to increase the precision of estimates and facilitate trend detection would be to select a smaller trend-site for repeated (e.g., annual, biannual) surveys in a location and during a time of year when density has historically been stable and, thus, distributional shifts would be less likely to confound trend detection (Taylor et al. 2007). In this study, density in strata 4–7 was relatively constant during summer, suggesting that this area would be a reasonable location for trend detection during the summer (June–August). However, it is unknown how well this area represents the BB-MSS stock, which encompasses a large geographic area and has the potential to house multiple independent populations.

Aerial stock-assessment surveys conducted in the MSS in 2011 were completed just as this study was beginning (both studies were underway during winter 2012). The resulting best estimate of 900 Dolphins (CV = 0.63) based on winter aerial surveys (NOAA 2015) was lower than the estimate for the same time period presented in this study ($N = 1793$; CV = 0.25). This result is not surprising because the stock assessment was based on aerial surveys, which are often biased low (Hubard et al. 2004, Marsh and Sinclair 1989) and did not include areas south of the barrier islands. The results of our study and others (Miller et al. 2013, Pitchford

et al. 2015) have shown that occurrence of Dolphins south of the barrier islands is high during the winter when occurrence is lower in near-shore areas, suggesting that the southern boundary for this stock has little biological significance. The proximity of the NCS to the BB-MSS stock and the potential for movement of NCS Dolphins into shallow waters of the MSS (NOAA 2015), further confounds stock delineation. These factors must be considered when designing future studies, and we recommend establishment of trend sites to improve delineations. While inclusion of areas south of the barrier islands in winter increases the potential for inclusion of Dolphins from the NCS, winter surveys excluding this area are likely underestimating abundance of the BB-MSS stock. Future surveys should include these areas, specifically in winter, to more accurately quantify regional population size. Implementation of a broad-scale photo-identification project that includes Pollock's (1982) robust design could help to determine where biologically significant boundaries lie through estimation of home ranges (Defran et al. 1999; Gubbins 2002) and the use of mark–recapture analyses that include estimates of emigration, immigration, survival rate, and population size (Rosel et al. 2011).

Conclusions

Although Dolphins are a protected species (Marine Mammal Protection Act of 1972) and are often cited as sentinels of marine ecosystems (Kucklick et al. 2011, Wells et al. 2004), there has been little effort to quantify long-term trends in density and to use this information to improve management of the species. Also, there has been no investigation of a carrying capacity of Dolphins in the MSS and no effort to examine changes in demographic rates in response to changes in density. This lack of information is a barrier to understanding how population changes resulting from large-scale mortality, including changes to population demographics, affect recovery of the species. Our results showed that the density of Dolphins varied over spatial and temporal scales, suggesting that seasonal abundance and distribution of Dolphins in the MSS is complex and is likely related, either directly or indirectly, to changes in environmental conditions (e.g., salinity). Due to the infrequency of Dolphin density estimations within this region, differences in study areas and methodologies, and a lack of precision in estimates, only large changes in the population are likely detectable. This inability to accurately detect change is unfortunate given the occurrence of several large disturbances including the DWH oil spill and the ongoing UME. Undoubtedly, more work needs to be done to more accurately quantify abundance and distribution of Dolphins within the MSS and to better delineate stock boundaries to improve our understanding of this population.

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