

Gulf and Caribbean Research

Volume 31 | Issue 1

2020

Abundance and Occurrence of Common Bottlenose Dolphins (*Tursiops truncatus*) in Three Estuaries of the Northwestern Gulf of Mexico

Errol Ronje

University of Florida, School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program, errol.ronje@gmail.com

Heidi Whitehead

Texas Marine Mammal Stranding Network, hwhitehead@tmmsn.org

Kevin Barry

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, kevin.barry@noaa.gov

Sarah Piwetz

Texas Marine Mammal Stranding Network, spiwetz@tmmsn.org

See next page for additional authors

Follow this and additional works at: <https://aquila.usm.edu/gcr>



Part of the [Marine Biology Commons](#), and the [Zoology Commons](#)

To access the supplemental data associated with this article, [CLICK HERE](#).

Recommended Citation

Ronje, E., H. Whitehead, K. Barry, S. Piwetz, J. Struve, V. Lecours, L. Garrison, R. S. Wells and K. D. Mullin. 2020. Abundance and Occurrence of Common Bottlenose Dolphins (*Tursiops truncatus*) in Three Estuaries of the Northwestern Gulf of Mexico. *Gulf and Caribbean Research* 31 (1): 18-34.

Retrieved from <https://aquila.usm.edu/gcr/vol31/iss1/9>

DOI: <https://doi.org/10.18785/gcr.3101.09>

This Article is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in *Gulf and Caribbean Research* by an authorized editor of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.

Abundance and Occurrence of Common Bottlenose Dolphins (*Tursiops truncatus*) in Three Estuaries of the Northwestern Gulf of Mexico

Authors

[Errol Ronje](#), *University of Florida, School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program*; [Heidi Whitehead](#), *Texas Marine Mammal Stranding Network*; [Kevin Barry](#), *National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories*; [Sarah Piwetz](#), *Texas Marine Mammal Stranding Network*; [Juliane Struve](#), *University of Florida, School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program*; [Vincent Lecours](#), *University of Florida, School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program*; [Lance Garrison](#), *National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center*; [Randall S. Wells](#), *Chicago Zoological Society's Sarasota Dolphin Research Program, c/o: Mote Marine Laboratory*; and [Keith D. Mullin](#), *National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories*

GULF AND CARIBBEAN

R E S E A R C H

Volume 31
2020
ISSN: 2572-1410



Published by

**THE UNIVERSITY OF
SOUTHERN MISSISSIPPI**

GULF COAST RESEARCH LABORATORY

Ocean Springs, Mississippi

ABUNDANCE AND OCCURRENCE OF COMMON BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN THREE ESTUARIES OF THE NORTHWESTERN GULF OF MEXICO

Errol I. Ronje^{1,2}, Heidi R. Whitehead³, Kevin Barry⁴, Sarah Piwetz³, Juliane Struve¹, Vincent Lecours¹, Lance P. Garrison⁵, Randall S. Wells⁶, Keith D. Mullin⁴

¹ University of Florida, School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program, 136 Newins–Ziegler Hall, Gainesville, FL, 32611, USA; ² Riverside Technology, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, 3209 Frederic St., Pascagoula, Mississippi, 39567, USA; ³ Texas Marine Mammal Stranding Network, 4700 Avenue U, Galveston, Texas, 77551, USA; ⁴ National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, 3209 Frederic St., Pascagoula, Mississippi, 39567, USA; ⁵ National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, Florida, 33149, USA; ⁶ Chicago Zoological Society's Sarasota Dolphin Research Program, c/o: Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida, 34236, USA; Corresponding author, email: errol.ronje@gmail.com

ABSTRACT: Current abundance estimates for populations of common bottlenose dolphins (*Tursiops truncatus*, Montagu, 1821) in bays, sounds, and estuaries are lacking throughout most of the northwestern Gulf of Mexico (GOM), including areas of Texas and western Louisiana. To address this issue, we conducted 92 small-boat photographic identification surveys covering ~2000 km² and comprising ~11,000 km of track-line in winter and summer seasons in West Bay, TX (2014–2015, n = 25), the Galveston Bay, TX system (2016, n = 50), Sabine Lake, TX (2017, n = 17), and adjacent coastal waters. Individual dolphin encounter histories were constrained by spatiotemporal parameters to approximately represent 1) a “Bay” estimate of individuals limited to the interior of each embayment, and 2) a “Selective” estimate of the number of individuals in each survey area (including nearshore coastal waters), filtered for potential transient dolphins. Using the Selective dataset, estimated bottlenose dolphins (95% CI) were (winter and summer, respectively) 38 (29–47) and 37 (33–40) for West Bay, 842 (694–990) and 1,132 (846–1,417) for Galveston Bay, and 122 (73–170) and 162 (114–210) for Sabine Lake. A range of 4–15% of marked individuals in each study area were identified as inter-bay matches. These results provide new insights on the potential spatial range of each population, update previous abundance estimates for West Bay and Galveston Bay, and contribute novel population information for Sabine Lake and adjacent coastal waters of the northwestern GOM.

KEY WORDS: marine mammal, mark-recapture, population, abundance, photo-ID

INTRODUCTION

Common bottlenose dolphins (*Tursiops truncatus*, Montagu, 1821) are globally distributed between the 60th parallels in temperate to tropical oceanic and coastal waters, and estuarine populations have been documented throughout their range (Jefferson et al. 2008, Wells and Scott 2018). In the Gulf of Mexico (GOM), common bottlenose dolphins (hereafter referred to as “bottlenose dolphins”) are widely distributed in bays, sounds, estuaries, and coastal waters, including the waters of Texas (Gunter 1942, Shane 1977, Gruber 1981, Henningsen and Würsig 1991, Maze and Würsig 1999). In the U.S., the Marine Mammal Protection Act (MMPA) of 1972 includes bottlenose dolphins, and mandates that current information on abundance and geographic distribution be collected for each stock unit to assess risks to the populations and devise conservation measures (Wade and Angliss 1997). Bottlenose dolphin stock units are defined for 31 northern GOM embayments based on the nature of their geographic separation and the assumption that each embayment likely includes at least some individuals with long-term site-fidelity and social bonds that would be difficult to replace should the stock be significantly depleted or exterminated (Wells et al. 1987, Mullin et

al. 2007). Periodic assessments of abundance and distribution are required for management purposes and for long-term monitoring programs to detect population trends, unusual mortality events, and updating the geographic range of stock areas. These assessments also provide baseline data for population-level impacts associated with habitat modifications, sea-level rise, catastrophic events (e.g., major hurricanes, harmful algal blooms), and other natural and anthropogenic pressures. However, long-term population trends for the northwestern GOM bottlenose dolphin stocks cannot be assessed due to large temporal or spatial data gaps (Phillips and Rosel 2014). Out of 7 northwestern GOM estuarine bottlenose dolphin stocks delineated by the National Marine Fisheries Service (NMFS), 3 are in the upper Texas coast: West Bay, Galveston Bay, and Sabine Lake. Up-to-date abundance estimates are part of a suite of population information required by the NMFS to assess the viability of each bottlenose dolphin stock (Hayes et al. 2017).

The upper Texas coast is home to > 7 million people and contains highly concentrated industries related to petroleum and chemical production. Shrimp, finfish, and shellfish are among the natural resources harvested from

upper Texas coastal waters, and in total some 36 million pounds of commercial fisheries landings were recorded at just 2 of the largest ports in the region during 2017 (Galveston and Port Arthur, NOAA 2019). The Gulf Intracoastal Waterway (GIWW), a dredged canal spanning much of the GOM coast, connects coastal bodies of water. Anthropogenic threats (e.g., ship strikes, oil spills, cumulative industrial pollution, and fisheries interactions) exist for bottlenose dolphins inhabiting the upper Texas coast, as reviewed in Phillips and Rosel (2014). Therefore, this region was scored as a high research priority for bottlenose dolphins due to the anthropogenic threats (Phillips and Rosel 2014).

Photographic identification (photo-ID) capture–mark–recapture (CMR, or “mark–recapture”) methods are based on the unique, naturally occurring marks on the dorsal fins of free–ranging cetaceans used to identify individuals (Würsig and Würsig 1977) across a time series of sampling occasions. Photo-ID mark–recapture methodology has been used for a wide range of cetacean population studies and can serve as a foundation for insights into population size, behavior, migration, survival, fecundity, and the delineation of stock boundaries (Wells 2018). The purpose of this study was to assess the stock range, estimate abundance, and investigate connectivity among 3 stocks of bottlenose dolphins in estuarine and coastal waters along the northwestern GOM coast from 2014 – 2018.

MATERIALS AND METHODS

Survey Area

The geographic range of this study includes about 1,800 km² of the estuarine and coastal waters of the northeast Texas Gulf Coast, from the western Louisiana border to just southwest of Galveston Island, TX (Figure 1). Surveys were conducted in 3 research areas—West Bay, Galveston Bay, and Sabine Lake—as well as coastal waters near the inlet to each embayment.

West Bay. West Bay (~150 km², mean depth 1.5 m) is oriented southwest to northeast along Galveston Island, and is about 30 km in length and 3.5 – 6 km wide. West Bay is located to the southwest of Galveston Bay and is adjacent to a “Back Bay” of the Galveston Bay system, with a loose boundary of shoals or islands delineating the 2 bodies of water. San Luis Pass is at the southeastern point of West Bay and is the primary point of seawater exchange with the GOM.

Galveston Bay. Galveston Bay (~1400 km², mean depth 2.5 m) is the largest bay on the upper Texas coast (USEPA

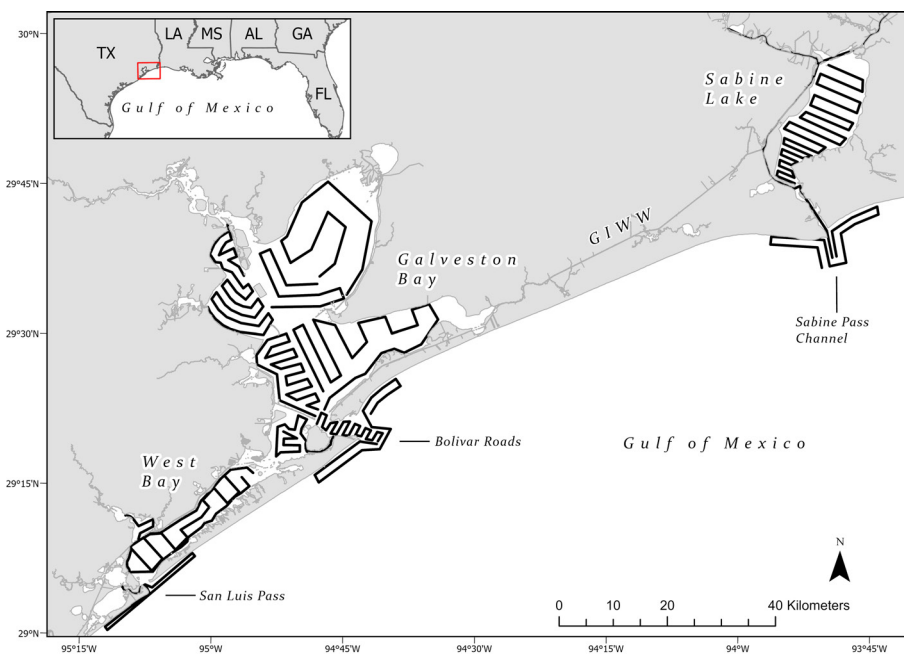


FIGURE 1. Map of West Bay, Galveston Bay, and Sabine Lake, TX survey areas in the northwestern Gulf of Mexico. Black lines represent pre-determined photo-ID survey routes.

1999). The primary sources of freshwater input to Galveston Bay are the San Jacinto and Trinity Rivers. Bolivar Roads serves as a vessel anchorage and key pass from the GOM into Galveston Bay and intersects the Houston Ship Channel, Galveston Ship Channel, and the GIWW. The entrance to Bolivar Roads from the GOM is positioned about 50 km and 90 km from the GOM passes into West Bay and Sabine Lake, respectively.

Sabine Lake. Sabine Lake (~240 km², mean depth 2 m) is a brackish estuarine embayment bisected by the Texas – Louisiana border (USEPA 1999). Sabine Lake receives the highest freshwater inflow per unit volume of any GOM embayment, primarily from the Sabine and Neches rivers flowing into its northern end (Ward 1980). The lake is adjacent to deep-draft engineered channels on its southern and western boundaries, including the Port Arthur Ship Canal, Sabine–Neches Waterway, GIWW, and the Sabine Pass Channel, which is the only GOM access point into Sabine Lake.

Survey Procedure

Photo-ID mark–recapture surveys were conducted from 7 m center console boats equipped with one or 2 four-stroke outboard engines. Each survey team consisted of 3 individuals. All members visually scanned for bottlenose dolphin groups 180° ahead of the research vessel, and individual operational duties included driving, photographing bottlenose dolphins, and recording data. Surveys were conducted in a Beaufort sea state ≤ 3 on predetermined survey routes (Figure 1) at a speed of 28 – 32 km/h. We completed a survey effort log (e.g., start and end time, weather conditions, effort status) for each survey and the vessel track lines were recorded on a handheld global positioning sys-

tem (GPS) receiver unit. The survey team recorded data only in “on-effort” status when following the prescribed visual survey methodology. If those conditions were not met (e.g., transiting at higher speeds to or from the dock) the team was working in “off-effort” status.

When a bottlenose dolphin or group of individuals was sighted on-effort, it was approached for data collection consistent with photo-ID methods described by Melancon et al. (2011); data included date, start and end time, start and end GPS locations, environmental conditions, group size and composition (e.g., observations of mom/calf associations), behavioral observations, and general notes. A group was defined as all individuals in proximity (< 100 m) to one another, generally moving in the same direction and engaging in similar behavior (Rosel et al. 2011). We photographed dorsal fins with digital single lens reflex (DSLR) cameras equipped with 100–400 mm telephoto zoom lenses. We attempted to photograph every individual in each group regardless of dorsal fin distinctiveness, with passes on both left and right sides. Occasionally, the team stopped to photograph and collect data from groups observed while off-effort using similar protocols.

Survey Design

We conducted small-boat photo-ID surveys from October 2014–April 2018. Systematic photo-ID mark-recapture surveys were completed to estimate bottlenose dolphin abundance. We only used data from the structured mark-recapture surveys to estimate abundance, but other data collected during opportunistic photo-ID surveys from 2014–2018 were used to investigate potential population connectivity. Our mark-recapture surveys followed a temporal structure with “primary” seasonal sessions (i.e., winter and summer) and multiple “secondary” survey occasions within each season (Pollock 1982). Within each primary session, we assumed the population was “closed.” When closure assumptions are valid, it can be inferred that the data collected in each survey area are representative of the population during the study period (Williams et al. 2002). Our 2 primary sessions were conducted in presumed non-transitional meteorological seasons, e.g., December–February in winter and June–August in summer (Trenberth 1983). A primary session (12–20 days) consisted of 3–4 secondary occasions, where each consisted of complete coverage of the survey area completed in as few days as possible (consecutive days ranged from 2–4 in each survey area), weather permitting, to help improve the likelihood that the closure assumption was met. One “mixing day” was allotted between secondary occasions to allow time for marked and unmarked dolphins to mix spatially (Rosel et al. 2011). Due to inclement weather or differences in the time to completion, survey coverage was temporally distributed for all areas (i.e., transects were not surveyed at the same time of day during each secondary occasion). Some bottlenose dolphin stock ranges have not

been well defined by the NMFS, so care was taken to ensure the geographic scope of the surveys provided complete spatial coverage of the potential stock range (Rosel et al. 2011), including waters of the entire bay system that were practical to survey.

The survey transect–line design (Figure 1) was spatially stratified based on several factors: maximizing coverage of the study area, minimizing heterogeneity in capture probability, bottlenose dolphin group density noted during exploratory surveys, anecdotal reports of sightings, and the presumed salinity gradient (i.e., salinity decreases as distance from the GOM increases). The survey design for each embayment also included 2 parallel coastal transects. The first transect followed along the beach contour 300–500 m from the beach and the second transect was placed ~2 km from shore; each transect extended ~5 km or more in each direction away from the inlet. These coastal transects were included in the study design because telemetry tag and photo-ID data from other embayments within the GOM have demonstrated that resident estuarine animals may regularly use nearshore coastal waters (Balmer et al. 2008, Wells et al. 2017). Those data support the inclusion of nearshore coastal waters within the boundaries of some stocks (Maze and Würsig 1999, Mullin et al. 2017, Litz et al. 2019, Maze–Foley et al. 2019).

West Bay. Other ecological studies of the Galveston Bay system include West Bay as a sub-embayment of Galveston Bay. However, the NMFS has delineated the West Bay bottlenose dolphin stock as a management unit separate from the rest of the Galveston Bay system (Hayes et al. 2017) and previous research in West Bay indicates its population is comprised of a core resident group of animals with long-term site fidelity (Maze and Würsig 1999, Irwin and Würsig 2004). Our West Bay surveys were conducted with one research vessel in December 2014 and June 2015. Previous studies identified the southwestern end of West Bay as the area most likely inhabited by bottlenose dolphins (Maze and Würsig 1999, Irwin and Würsig 2004, Henderson and Würsig 2007); however, we included the entirety of West Bay for a geographically comprehensive assessment. Survey transects across the middle of the bay were separated by about 3 km, with a single line or loop in the adjacent bay areas and connecting water ways. On the initial December 2014 survey, Christmas Bay and Bastrop Bay were found to be too shallow for the research vessel. However, the water depth was acceptable in Christmas Bay during June 2015, so it was added for the summer sampling session.

Galveston Bay. Galveston Bay surveys were conducted with 2 research vessels in January and July of 2016. Research indicates deep water channels are important components of bottlenose dolphin habitat in Galveston Bay (Moreno and Mathews 2018, Piwetz 2019). Therefore, the highest concentration of animals was anticipated in the southern and western areas of the bay, where deep shipping channels are

dredged. Bolivar Roads is often congested with industrial vessels, cruise ships, commercial fisheries activity, and recreational boaters that create visual obstacles to bottlenose dolphin group detection. Therefore, survey transect lines were drawn to a finer scale in Bolivar Roads to compensate for potential visual obstructions and maximize the capture probability for groups. Survey transect line spacing ranged from 1–1.25 km in the southern area of the bay. In the central section of the bay, transect line spacing ranged from 1.5 km in Galveston Bay out to 5 km in East Bay. In Upper Galveston Bay, transect lines were spaced 1.5 km apart. Few bottlenose dolphin encounters were expected in Trinity Bay due to the low salinity levels (~1–2) found during all surveys. Thus, the perimeter and inner transect lines of Trinity Bay were surveyed only once per season on the first sampling occasion; thereafter only the western–most lines of Trinity Bay were surveyed.

Sabine Lake. Sabine Lake surveys were conducted with one research vessel in February and June of 2017. The Texas Marine Mammal Stranding Network has performed multiple out-of-habitat interventions or stranding responses for bottlenose dolphins in fresh water in the outer reaches of Sabine Lake (Whitehead and Ronje 2017¹), and reports archived from the general public indicate groups of individuals use the engineered navigation channels and rivers. Therefore, survey routes included the Sabine Pass Channel, Port Arthur Ship Canal, Sabine–Neches Waterway, and Neches and Sabine Rivers. We graduated survey line spacing in the open water of Sabine Lake from ~1–2 km to concentrate survey effort with the presumption of encountering more bottlenose dolphin groups closer to the Sabine Pass Channel, where surface salinity was presumably greater. We surveyed upper lake lines in alternate sessions, so that each upper lake line was surveyed by the end of each primary session.

Photo Analysis

Dorsal fin marks were assumed unique and not mismatched or misread during photo analysis. Bottlenose dolphins accumulate nicks and notches over time and the long-lasting nature of the marks is well established (Würsig and Würsig 1977). Primary sessions were completed in about 2 weeks, and while new marks could have been acquired between primary sessions, or during the 3 year period over which these surveys were conducted, it was unlikely changes in marks would alter the fin beyond recognition (Urian et al. 2014). Photos were processed for primary matching and verification similar to the protocols outlined in Melancon et al. (2011) and combined with their associated data to cre-

ate a catalog of bottlenose dolphin dorsal fins for northern Texas and western Louisiana embayments (NorTex catalog). Photo analysis was done with the aid of FinBase, a software package designed for bottlenose dolphin photo-ID that consolidates data tracking, image analysis, and a multiple-attribute catalog sorting algorithm to expedite photo analysis and generate encounter histories for use in mark-recapture studies (Adams et al. 2006). Primary matching and verification were conducted by at least 2 experienced technicians. We assigned photo quality scores and dorsal fin distinctiveness grades to each photo to determine their suitability for analysis. Photo quality is cumulatively scored for each image in FinBase using 5 categories of quality: focus, contrast, angle, partial (e.g., a dorsal fin partially submerged), and distance, and ranged from a photo quality (PQ) score of PQ 1–3, with PQ 1 and 2 considered acceptable for analyses. Distinctiveness levels assigned to each dorsal fin were classified similar to Urian et al. (2014): D4 (not distinct, includes calves)–no useful mark information (≤ 1 small nick or tiny notch); D3 (low or marginally distinct)–few and/or small marks (e.g., 2 small nicks); D2 (average)–1 or more permanent marks or notches; D1 (highly distinct)–major, prominent feature(s) unlikely to be mistaken even in poor quality photos. We used only those individuals classified as D1 or D2 and PQ1 or PQ2 for mark-recapture abundance estimation and inter-bay matching. When possible, “not distinct” calf dorsal fins were matched to avoid duplication, typically using recorded mom/calf associations (if confirmed through re-sights), or other temporary marks (e.g., skin disorders). After photo analysis, we constructed discovery curves for each survey area to visualize the newly marked individuals encountered, the recaptured individuals, and the cumulative total of individuals (D1 + D2, PQ1 + PQ2) for each survey area in mark-recapture sessions.

Photo-ID studies of bottlenose dolphins in many areas indicate some individuals exhibit long-term site fidelity to specific embayments (Wells 2014), and individual movements may range from within an estuary to adjacent passes and coastal waters (Irvine et al. 1981, Fazioli et al. 2006, Laska et al. 2011). Individuals from other populations may travel along the coast and use the habitat within the stock boundaries of a different population (Wells et al. 1987, Maze and Würsig 1999, Speakman et al. 2010, Urian et al. 2018). Including transient individuals in the abundance estimate may over-estimate the size of a given stock, with potential implications for management decisions. Therefore, for each of the 3 embayments in this study, we used a novel approach to classify the number of bottlenose dolphins present during this study and exclude some transient animals by parsing encounter histories of individuals by spatiotemporal parameters before estimating the abundances of each survey area. Encounter histories were subset as Bay or Selective for each survey area (Table 1). A Bay classification includes only en-

¹Whitehead, H.R. and E.I. Ronje. 2017. Case reports of out-of-habitat marine mammals: Common bottlenose dolphins (*Tursiops truncatus*) and North Atlantic right whales (*Eubalaena glacialis*) in the western Gulf of Mexico. Poster presented at the 22nd Biennial Conference on the Biology of Marine Mammals. 23-27 October 2017, Halifax, Nova Scotia, Canada. <https://marinemammalscience.org/conference/past-and-future-conferences/>

TABLE 1. Summary of the data parsing criteria for the Bay and Selective datasets.

Criteria	Bay	Selective
Sighting of a bottlenose dolphin in bay or Gulf channel to bay	Included	Included
Sighting in bay of a bottlenose dolphin also seen in another bay (inter-bay match)	Included	Excluded
Sighting in coastal waters of a bottlenose dolphin also seen in bay or channel to bay	Included	Included
Sighting in coastal waters of a bottlenose dolphin only ever seen in coastal waters in just 1 season	Excluded	Excluded
Sighting in coastal waters of a bottlenose dolphin only ever seen in coastal waters in 2 seasons	Excluded	Included

counters within the boundary of the embayment and channel connecting to the GOM in ≥ 1 season. A Selective classification includes encounters within the boundary of the embayment and channel connecting to the GOM in ≥ 1 season and encounters in coastal waters within 2 km from shore that were observed in both seasons. Additionally, the Selective dataset excludes individuals that used > 1 stock management area (inter-bay matches). Data were filtered using a custom python script in ArcGIS Desktop 10.4 (ESRI 2019). The delineation of the coastal waters began at the mouth of the engineered channel (or natural pass in the case of West Bay) where the coastal waters enter the estuary.

Abundance Estimation

After parsing the data for the above criteria, photo-ID encounter histories for each individual in a primary session (winter or summer) were analyzed in program MARK 9.0 (White and Burnham 1999) using the closed capture “Huggins’ p and c ” conditional likelihood approach (Huggins 1991). Estimating abundance may also be described as an estimation of the parameters of capture (p) and recapture (c) probabilities in a population, from which an estimate of abundance (\hat{N}) is derived. The Huggins’ p and c approach is conditional only on the number of animals encountered, requiring only 2 parameters to estimate, and is suitable for sparse data. The “full-likelihood” approach (an approach that accounts for animals in the population that were not encountered by including their probabilities of capture in the likelihood (Darroch 1958)) was also explored but models did not consistently converge for the smaller data sets. Using the Otis et al. (1978) notation, the closed capture models considered under each approach to estimate abundance were:

(Equation 1) M_0 : $p(.) = c(.)$; time constant capture probability

(Equation 2) M_1 : $p(.)$, $c(.)$; capture probability is constant in time; however, behavioral response influences capture probability and therefore initial capture probability (p) may differ from subsequent recapture probability (c)

(Equation 3) M_2 : $p(t) = c(t)$; time variable capture probability allowing differences in recapture probability between secondary sampling occasions.

Overdispersion (when sampling variance is greater than expected) is a common problem with capture–recapture studies on species that aggregate in groups or form long-lasting social bonds. Such behavior may result in dependent or heterogeneous individual capture probabilities, potentially resulting in an underestimated sampling variance (Anderson et al. 1994). Individual heterogeneity, M_h (Chao et al. 1992), in capture probability was not modeled in this study due to the low number of sampling occasions (3–4 sampling occasions per primary session in this study) compared to the minimum of 5 or 6 recommended (Conn et al. 2006, Lukacs 2018). Model results were evaluated by estimating a variation inflation factor (Fletcher’s \hat{c}) to quantify the amount of overdispersion and gauge goodness–of–fit (Fletcher 2012, Cooch and White 2018). A Fletcher’s $\hat{c} < 4$ has been suggested as an acceptable measure–of–goodness of fit (Anderson et al. 1994); however, if overdispersion was indicated (Fletcher’s $\hat{c} > 1$), \hat{c} was manually adjusted within program MARK to match Fletcher’s \hat{c} for the most parameterized model of each dataset (time dependent model, M_t) to determine if overdispersion affected model rank. Model selection was guided by an examination of Akaike’s Information Criterion (Akaike 1973), corrected for small sample sizes (AIC_c) and a quasi-likelihood adjusted AIC_c ($QAIC_c$) within program MARK. The most parsimonious model was selected as the model with the lowest $QAIC_c$ score. If the difference ($\Delta QAIC_c$) in one or more models was $\leq 4 QAIC_c$ points of the minimum score (Burnham et al. 2011, Symonds and Moussalli 2011), those model outputs were combined using the weighted model–averaging function within program MARK.

Closed capture models only estimate the number of marked individuals, so we made a correction to account for the number of unmarked individuals in each sample. We calculated a corrected estimate of abundance (\hat{N}_c) to account for both marked and unmarked individuals by dividing \hat{N} by the proportion of marked fins, also known as theta (θ). Since the proportion of distinctive fins can change between and within survey areas (Balmer et al. 2019), seasonal θ values were calculated for each of the 3 survey areas. As with previous studies, θ was derived by calculating the proportion of distinctive fins (D1 + D2) out of all fins (D1+D2+D3+D4) that met photo quality criteria (i.e., PQ1 and PQ2) and were collected during on–effort group encounters (Read et al. 2003)

for each of the Bay and Selective datasets. Subsequently using θ , we calculated a corrected estimate for total abundance for each winter/summer primary session: $\hat{N}_c = \hat{N}/\theta$. We generated the variance and confidence intervals of the corrected estimates using the delta method (Wilson et al. 1999).

An encounter index derived from only the mark–recapture data was created for each dataset (Bay and Selective) by survey area and season. The encounter indices provide an indication of the number of marked (D1 + D2, PQ1 + PQ2) dorsal fins re–sighted in each primary session, where the maximum number of re–sights is limited to the number of secondary sampling occasions within each primary session. The indices are not necessarily good indicators of long–term site fidelity of an individual to each stock area, as they are based on data collected within a short period of time (2–3 weeks), but are helpful to visualize recapture rates within each primary session.

RESULTS

In total, 92 small–boat photographic identification surveys covering ~2,000 km² comprising ~11,000 km of track–line were conducted over ~607 h during summer and winter seasons in West Bay (n = 25, 2014–2015), the Galveston Bay system (n = 50, 2016), Sabine Lake (n = 17, 2017); these surveys included GOM coastal waters adjacent to each embayment (Table 2). During each seasonal primary session, 3 secondary sampling occasions were conducted in West Bay and Sabine Lake. Resources allowed for an additional secondary sampling session during the winter in Galveston Bay, where we conducted 4 secondary sampling sessions in winter and 3 in summer. Overall, we collected photos from 404 bottlenose dolphin groups in West Bay (n = 52), Galveston

Bay (n = 260), and Sabine Lake (n = 92). Generally, we documented bottlenose dolphin groups more often in or near the deep–water channels and passes that connect to the GOM, particularly during the winter (Figure 2).

Photo Analysis

We collected and sorted ~36,000 photos of bottlenose dolphin dorsal fins for the identification of individuals. In total, 1,271 individuals were identified during mark–recapture surveys (n = 99 West Bay, n = 843 Galveston Bay, n = 329 Sabine Lake; Table 2). The mean (± SE) number of marked animals in each group were 10.2 ± 0.42, 8.9 ± 1.0, and 7.8 ± 0.16 for West Bay, Galveston Bay, and Sabine Lake, respectively (Table 2). By survey area and season, the number of distinctive (D1 + D2, PQ1 + PQ2) individuals encountered (and proportion distinct) were 40 (82%) and 72 (86%) in West Bay, 336 (76%) and 539 (73%) in Galveston Bay, and 130 (61%) and 185 (84%) in Sabine Lake for winter and summer, respectively. However, the number of individuals in each dataset used for abundance estimation decreased when we applied the Bay and Selective criteria (see “n”, Table 3). The discovery curves indicate more new individuals were encountered for all 3 survey areas during the summer surveys (Figure 3). Discovery curves increased for all survey areas during the winter primary session. During the second primary session, in summer, the West Bay discovery curve approached a plateau, while the rate of new individuals in Galveston Bay and Sabine Lake increased throughout both seasonal primary sessions.

In total, 40 inter–bay matches were found in the Galveston Bay survey area; 15 individuals in West Bay and 25 individuals in Sabine Lake (Figure 4). Inter–bay matches repre-

TABLE 2. Summary of 2014–2018 common bottlenose dolphin photo-ID survey effort along the upper Texas coast. We conducted photo-ID capture-mark-recapture (CMR) surveys during winter and summer seasons (primary sessions) and specific sampling sessions (secondary occasions). Photo-ID surveys for other research questions (mixed) were conducted opportunistically. Mean catalogued group size represents the group size for all bottlenose dolphins catalogued in FinBase for each group, and total catalogued dolphins are the total distinctive (D1 + D2) and marginally distinctive (D3) identified in each survey area. We found 40 inter-bay matches, all having Galveston Bay in common.

Survey Area and Season	CMR Primary Session Dates (length in days) and non-CMR surveys	CMR Secondary Occasions (length of each in days)	Surveys	Survey Hours	Survey Effort (km)	Bottlenose Dolphin Groups	Mean Catalogued Group Size (±SE)	Total Catalogued Bottlenose Dolphins (D1+D2+D3)	Inter-bay Matches
West Bay									
Winter	1–12 Dec 2014 (12)	3 (3,4,3)	10	46	763	12	9.6 ± 2.1		
Summer	7–20 June 2015 (14)	3 (3,2,3)	8	50	867	24	11.2 ± 2.4		
Mixed	Other 2014–2018		7	34	497	16	9.8 ± 2.2		
	Cumulative	6	25	130	2,127	52	10.2 ± 0.42	99	15
Galveston Bay									
Winter	10–29 Jan 2016 (20)	4 (4,4,3,2)	25	169	3,348	117	6.4 ± 0.52		
Summer	7–22 July 2016 (16)	3 (4,3,3)	17	148	2,561	100	10.7 ± 0.78		
Mixed	Other 2014–2018		8	31	537	58	9.5 ± 2.7		
	Cumulative	7	50	348	6,446	260	8.9 ± 1.0	843	40
Sabine Lake									
Winter	4–18 Feb 2017 (15)	3 (3,4,3)	7	53	1,087	30	7.7 ± 2.0		
Summer	13–25 June 2017 (13)	3 (3,2,2)	7	62	1,139	48	8.2 ± 1.2		
Mixed	Other 2014–2018		3	14	297	14	7.5 ± 3.1		
	Cumulative	6	17	129	2,523	92	7.8 ± 0.16	329	25
Total		19	92	607	11,096	404	8.6 ± 0.43	1,271	40

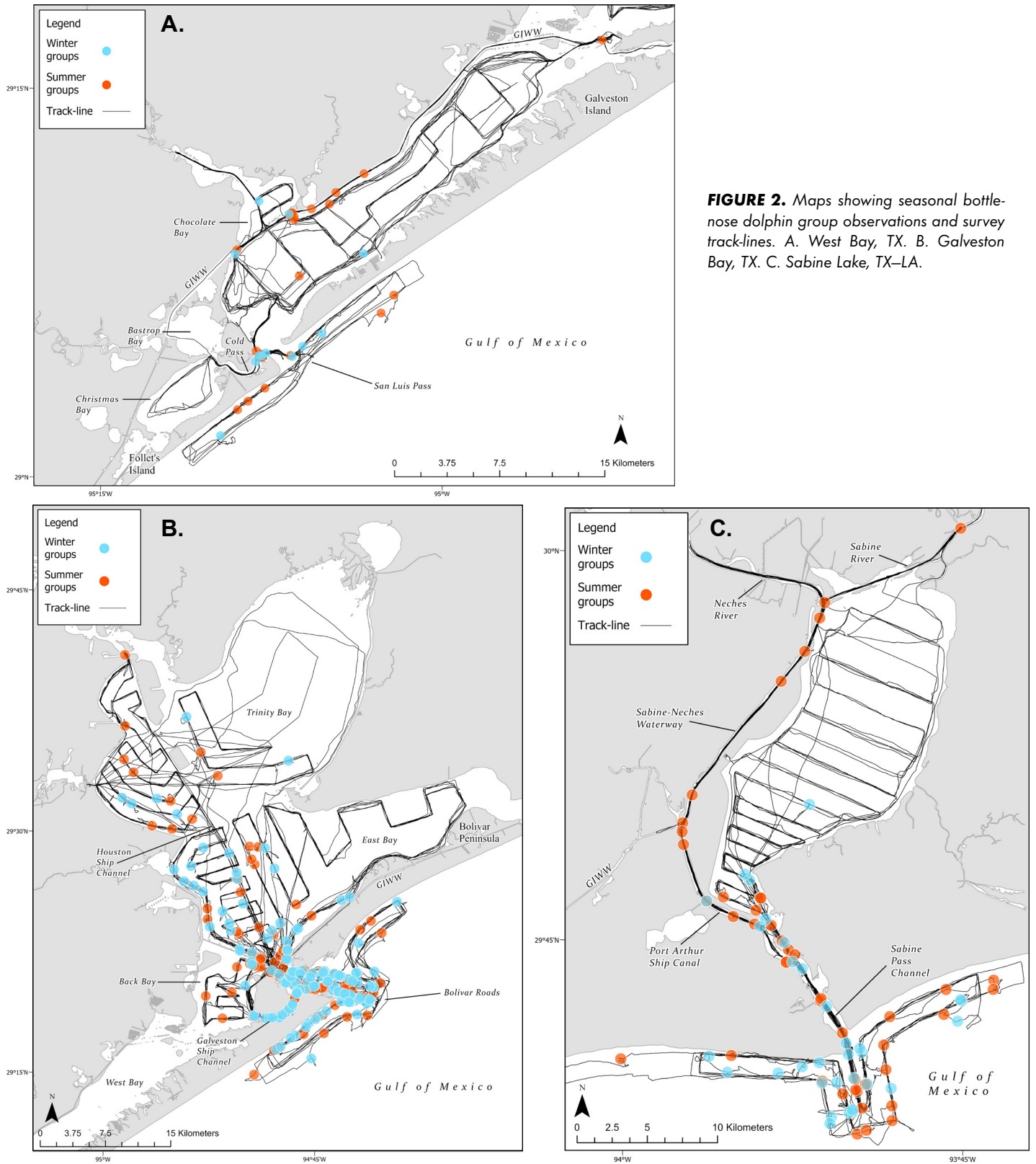


FIGURE 2. Maps showing seasonal bottlenose dolphin group observations and survey track-lines. A. West Bay, TX. B. Galveston Bay, TX. C. Sabine Lake, TX-LA.

sented 15.2% of individuals in West Bay, 4.7% in Galveston Bay, and 7.6% in Sabine Lake. We noted no inter-bay matches between the West Bay and Sabine Lake survey areas, yet individuals from both populations were found inside the Galveston Bay stock area (Figure 4). For example,

individual #2 (Table S1) was observed in West Bay in the winter–summer survey seasons during 2014–2015, observed in Galveston Bay during the summer of 2016, and then resighted in West Bay during the spring of 2017 and 2018. Similar movement patterns were observed for the other in-

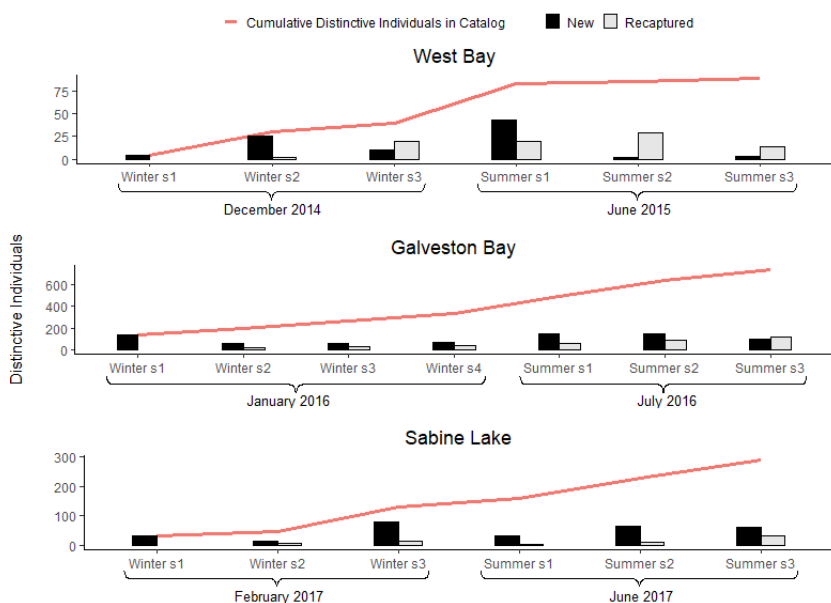


FIGURE 3. Plot of discovery curves for West Bay, TX, Galveston Bay, TX, and Sabine Lake, TX–LA. The cumulative line represents the total number of distinctive individual bottlenose dolphins used for abundance estimation in the photo-ID catalog for each survey area. Secondary sampling occasions designated with “s1” at the beginning of each seasonal primary. Note different y-axis scale for each bay.

ter–bay matching individuals. The 40 inter–bay matching individuals were recorded in coastal waters (28%), in the pass or channel entrance to each bay (33%), and inside the interior of an embayment (39%). From the entrance of the channel into Galveston Bay, these inter–bay movements represent an approximate distance of 50 km and 90 km, from the West Bay and Sabine Lake passes, respectively.

Abundance Estimation

Model selection varied by survey area and dataset. Some overdispersion was indicated by Fletcher’s \hat{c} for the most general model (M_t , Table 3). The Fletcher’s \hat{c} results using the Selective dataset for West Bay, Galveston Bay, and Sabine

Lake were 1.2, 1.6, and 2.1 for winter, and 1.8, 0.9, and 1.8 for summer, respectively. Results were similar for the Bay datasets. Since \hat{c} was ≤ 2.1 for all of our models (Table 3), we considered each model to have an acceptable measure of goodness–of–fit. The QAIC_c results (Table S2) were consistent with the AIC_c results and indicated the M_t model was consistently supported by West Bay data, while a combination of the M_t model and model–averaging was used for Galveston Bay and Sabine Lake, depending on the season (Table 3). The QAIC_c results consistently supported the M_t model for winter Galveston Bay data subsets and model–averaging of all 3 models (M_o , M_b , M_t) for the summer data subsets. Sabine Lake QAIC_c results indicated support for the M_t model for all data subsets except for the winter Bay dataset that was model–averaged between all 3 models (M_o , M_b , M_t). The M_b model failed with certain datasets (West Bay winter data, Sabine Lake Selective winter and all Sabine Lake summer data). For all survey areas, the estimates based on the Selective dataset were

derived from a filtered dataset that removes potential migratory and transient animals yet includes animals with at least dual–season site fidelity to the nearshore coastal waters of the stock area. Hereafter, results will describe the “best” abundance and parameter estimates based on the Selective dataset model selection, but we note that the Bay estimate may also be useful for management decisions.

The best abundance estimates corrected for unmarked individuals in West Bay were 37.9 (95% CI = 28.7–47.1) and 36.5 (95% CI = 32.7–40.3) for the winter and summer primary sampling sessions, respectively (Table 3, Figure 5).

West Bay capture probabilities for each sampling occasion ranged from 0.16–0.67 in winter and 0.13–0.89 in summer (Table S3), and the mean (\pm SE) capture probability was 0.50 ± 0.08 and 0.58 ± 0.16 in winter and summer, respectively (Table 3).

The best abundance estimates corrected for unmarked individuals in Galveston Bay were 841.9 (95% CI = 693.5–990.4) and 1,131.5 (95% CI = 846.3–1,416.7) for the winter and summer primary sampling sessions, respectively (Table 3, Figure 5). Capture probabilities for each Galveston Bay sampling occasion ranged from 0.11–0.19 in winter and 0.22–0.23 in summer (Table S3) and the mean (\pm SE) capture probability was 0.14 ± 0.01 and 0.22 ± 0.002 in winter and summer, respectively (Table 3).

The best abundance estimates corrected for unmarked individuals in Sabine Lake were 121.6

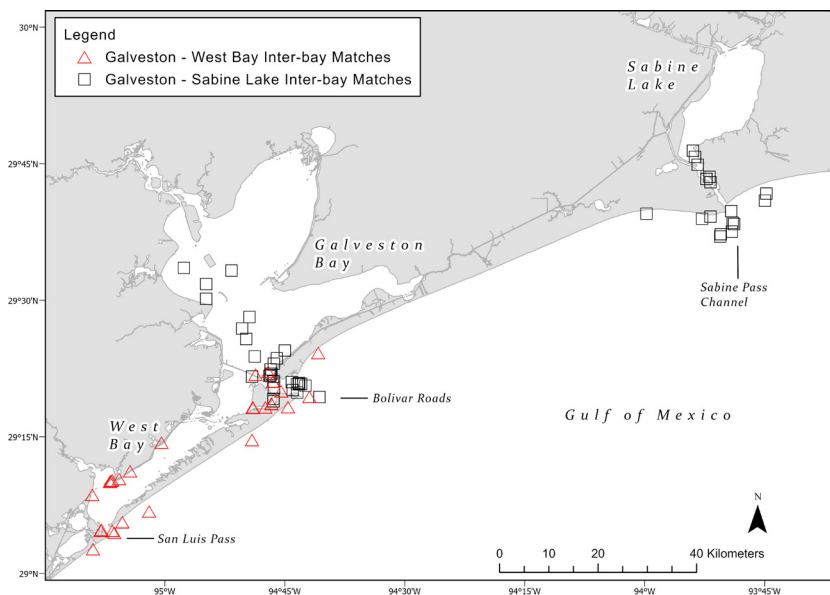


FIGURE 4. Map of sighting locations for bottlenose dolphin inter-bay matches along the upper Texas coast from 2014 – 2018.

TABLE 3. Bay and Selective bottlenose dolphin abundance estimates for West Bay, TX, Galveston Bay, TX, and Sabine Lake, TX–LA. Datasets are parsed encounter histories. The Bay dataset included all distinctive individuals observed in the bay or Gulf pass to the bay in ≥ 1 season. The Selective dataset included all individuals in the Bay dataset, and additionally included individuals observed in coastal waters during both summer and winter seasons but excluded dolphins found to use more than one survey area (inter-bay matches). W = winter, S = summer, Models: M_0 = constant capture probability, M_b = capture probability influenced by behavioral response to initial capture, M_t = time variable capture probability. Multiple models (e.g., M_0 , M_b , M_t) indicate the estimate was derived using model averaging; n = number of distinctive (D1 + D2) individuals in NorTex catalog for each dataset), \hat{c} = Fletcher's c-hat, a measure of overdispersion, \hat{p} = estimated mean capture probability, \hat{N} = estimated abundance, \hat{N}_c = abundance estimate corrected for unmarked fins. The % marked was calculated using only animals observed in the bay and channel for the Bay dataset, and using all animals observed in the survey area (bay, channel, and coastal waters) for the Selective dataset.

Dataset	Model		n		\hat{c}		\hat{p} ± SE		\hat{N} ± SE		% Marked		\hat{N}_c (95% CI)	
	W	S	W	S	W	S	W	S	W	S	W	S	W	S
West Bay														
Bay	(M_t)	(M_t)	33	33	1.5	1.6	0.50 ± 0.10	0.60 ± 0.16	38.1 ± 3.5	33.6 ± 0.9	0.83	0.82	45.9 (35.4–56.4)	41.0 (36.0–46.0)
Selective	(M_t)	(M_t)	27	31	1.2	1.8	0.50 ± 0.08	0.58 ± 0.16	31.1 ± 3.1	31.4 ± 0.7	0.82	0.86	37.9 (28.7–47.1)	36.5 (32.7–40.3)
Galveston Bay														
Bay	(M_t)	(M_0, M_b, M_t)	301	464	1.6	0.30	0.13 ± 0.01	0.21 ± 0.002	646.8 ± 58.6	918.31 ± 134.1	0.76	0.73	851.1 (691.5–1,010.7)	1,258.0 (892.2–1,623.8)
Selective	(M_t)	(M_0, M_b, M_t)	311	440	1.6	0.90	0.14 ± 0.01	0.22 ± 0.002	639.9 ± 54.1	826.0 ± 104.0	0.76	0.73	841.9 (693.5–990.4)	1,131.5 (846.3–1,416.7)
Sabine Lake														
Bay	(M_0, M_b, M_t)	(M_t)	20	58	1.5	1.4	0.25 ± 0.02	0.28 ± 0.04	34.8 ± 16.7	94.7 ± 14.9	0.58	0.62	60.0 (2.9–117.1)	152.7 (102.6–202.8)
Selective	(M_t)	(M_t)	44	79	2.1	1.8	0.26 ± 0.05	0.26 ± 0.04	74.2 ± 14.2	136.3 ± 20.1	0.61	0.84	121.6 (73.0–170.3)	162.2 (114.3–210.2)

(95% CI=73.0–170.3) and 162.2 (95% CI=114.3–210.2) for the winter and summer primary sampling sessions, respectively (Table 3, Figure 5). Capture probabilities for each Sabine Lake sampling occasion ranged from 0.15–0.39 in winter and 0.15–0.37 in summer (Table S3), and the mean (\pm SE) capture probability was 0.26 ± 0.05 and 0.26 ± 0.04 in winter and summer, respectively (Table 3).

The encounter indices indicate the proportion of individuals re-sighted in the Bay and Selective datasets were similar (Table 4, Figure 6). For West Bay, ~50% of individuals were seen only once in winter, while ~75% of individuals were observed twice in summer. We observed few individuals in West Bay 3 times in either season (~6%). Those rates were markedly different from the encounter frequencies observed in Galveston Bay and Sabine Lake, where over 70% of individuals were seen only once in both seasons, and ~20–30% observed twice in either season, with very few animals encountered ≥ 3 times in either season (1–2%).

DISCUSSION

These results provide updated bottlenose dolphin population estimates for 3 northwestern GOM embayments and NMFS marine mammal stock management areas. Using the Huggins' p and c approach, we found the M_t model, or a combination of averaged models, best applied across these sparse data. The M_b model failed for several of the datasets, particularly for winter West Bay and summer Sabine Lake data, likely due to a combination of low capture probability, few sampling occasions (< 5), and heterogeneity in individual capture probabilities (White and Cooch 2017). For both the Bay

and Selective datasets, mean West Bay capture probability was high (0.5–0.6) relative to the mean capture probabilities for Galveston Bay (0.13–0.22) and Sabine Lake (0.25–0.28). Otis et al. (1978) suggested minimum thresholds of capture probability for each of the models used here ($M_0 > 0.1$, $M_b > 0.2$, $M_t > 0.1$) to avoid bias in an abundance estimator with > 5 sampling occasions. The M_t model was selected as the most parsimonious model for all of the West Bay abundance

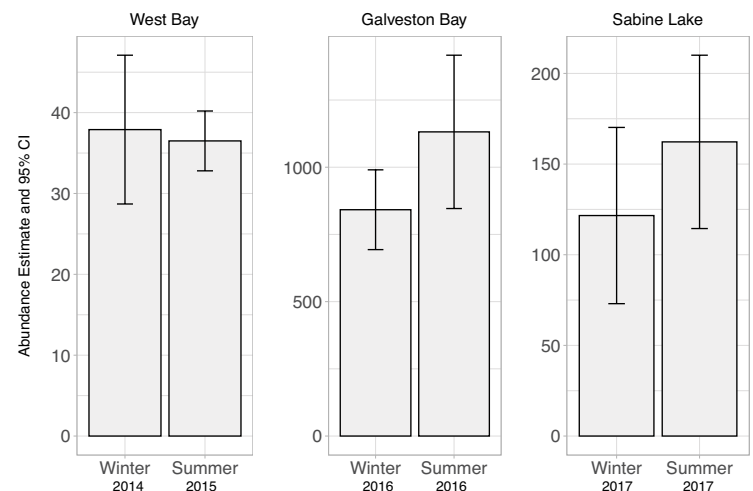


FIGURE 5. Best-estimated abundance (95% CI) corrected for unmarked dorsal fins of bottlenose dolphins for each survey area along the upper Texas coast. Data based on seasonal primary session using the Selective dataset. The Selective dataset included all individuals in the bay and Gulf pass to the bay in ≥ 1 season, and included individuals observed in coastal waters during both summer and winter seasons but excluded dolphins that used more than one survey area (inter-bay matches). Note different y-axis scale for each bay.

TABLE 4. Encounter frequency index for distinctive (D1 + D2) individual bottlenose dolphins in each survey area along the upper Texas coast and datasets (parsed encounter histories) used for abundance estimation. The Bay dataset included all distinctive individuals observed in the bay or Gulf pass to the bay in ≥ 1 season. The Selective dataset included all individuals in the Bay dataset, and additionally included individuals observed in coastal waters during both summer and winter seasons but excluded dolphins that used more than one survey area (inter-bay matches). Percentages were rounded to the nearest whole number.

Dataset	Encounter Frequency			
	1	2	3	4
West Bay				
Winter Bay	18 (55%)	13 (39%)	2 (6%)	
Summer Bay	7 (21%)	24 (73%)	2 (6%)	
Winter Selective	14 (52%)	11 (41%)	2 (7%)	
Summer Selective	5 (16%)	24 (77%)	2 (6%)	
Galveston Bay				
Winter Bay	241 (80%)	50 (17%)	8 (3%)	2 (1%)
Summer Bay	356 (77%)	97 (21%)	11 (2%)	
Winter Selective	244 (78%)	56 (18%)	9 (3%)	2 (1%)
Summer Selective	333 (76%)	96 (22%)	11 (3%)	
Sabine Lake				
Winter Bay	14 (70%)	6 (30%)		
Summer Bay	41 (71%)	17 (29%)		
Winter Selective	33 (75%)	10 (23%)	1 (2%)	
Summer Selective	58 (73%)	21 (27%)		

estimates, for the Galveston Bay winter estimates, and all but the winter estimate for the Sabine Lake Bay dataset, and in each instance the estimated capture probability was greater than the threshold of 0.1 suggested by Otis et al. (1978). The remaining abundance estimates (summer Galveston Bay and winter Sabine Lake) were model-averaged (i.e., M_o , M_b , M_i) with mean capture probabilities ≥ 0.21 . However, this study estimated abundance using closed capture models for each season separately and had at most 4 sampling occasions in a single primary session. Ideally, we would include more sampling periods for future studies of these areas to provide enough data to allow better diagnostics and modeling of additional parameters (e.g., individual heterogeneity, temporary migration, and survival). The large spatial range of our survey areas made additional sampling occasions impractical. However, the distribution of bottlenose dolphin groups presented here may guide future photo-ID mark-recapture studies to direct resources to areas where encounters are more likely, allowing for additional primary sessions and ≥ 5 survey iterations within each primary session, as recommended by Conn et al. (2011) and Lukacs (2018). The Selective dataset was parsed to reduce the probability of including animals sighted in nearshore coastal waters with low site fidelity in our estimates. It is possible transient individuals were observed in coastal waters in both primary sampling sessions, and therefore included in the Selective abundance estimate. If so, those individuals were using the nearshore coastal waters in a minimum of 2 non-contiguous seasons

in a single survey area, which is similar to the definition for residency (“at least 50% of time”) as suggested in Rosel et al. (2011). The Selective method of parsing the datasets resulted in fewer individuals input for both seasons in West Bay and summer in Galveston Bay, and a net addition of only 10 individuals during the winter Galveston Bay primary session, resulting in a lower estimate (relative to the Bay dataset) for the Galveston Bay population in each season. However, the Selective parsing method added a considerable number of individuals (an increase of ~120% and 36% in winter and summer, respectively) to the Sabine Lake mark-recapture dataset, relative to the Bay parsing method.

Previous researchers have estimated abundances for each of the survey areas in this study (Table 5). Maze and Würsig (1999) identified 71 individuals during their 1995–1996 study in West Bay and concluded that 37 animals using both bay and GOM coastal waters were residents of that embayment. Using data collected from 1997–2001, Irwin and Würsig (2004) estimated the West Bay population was 28–34 resident bottlenose dolphins. The research conducted by Maze and Würsig (1999) and Irwin and Würsig (2004) was supported by long-term studies of West Bay dating to 1990 (Henningsen and Würsig 1991), and Irwin and Würsig (2004) posited the carrying capacity of the West Bay habitat may be about 30 individuals. Litz et al. (2019) estimated abundance for West Bay using an earlier variation of the West Bay study data we used here. Because this study was combining data from 3 study areas into a single catalog for comparison, the fin distinctiveness of the entire catalog was re-scored for consistency across study areas resulting in some slight changes to the categorization of marked and unmarked animals between the 2 studies. Our study also used only on-effort sighting data for abundance estimation (a difference of 1 winter and 6 summer group encounters) resulting in different proportions of marked animals between the Litz et al. (2019) winter and summer study (θ of 0.90 and 0.95, respectively) and this study (θ of 0.82 and 0.86, respectively). Litz et al. (2019) included certain individuals in coastal sightings in the abundance estimate. The method Litz et al. (2019) used to parse the potential West Bay stock from presumed transient individuals along the coast involved a thorough review of individual sighting histories that supported the presumption of site-fidelity to West Bay, but without the inter-bay match information available to this study. The best West Bay estimate from Litz et al. (2019) was 50.6 (95% CI 47.2–56.2) and 44.4 (42.5–47.2) in winter and summer, respectively. The differences between those estimates and our West Bay abundance estimates are primarily due to our exclusion of 15 probable transient individuals observed using the combination of West Bay and Galveston Bay data. The best abundance estimate of the West Bay population presented here, 37.9 (95% CI 28.7–47.1) and 36.5

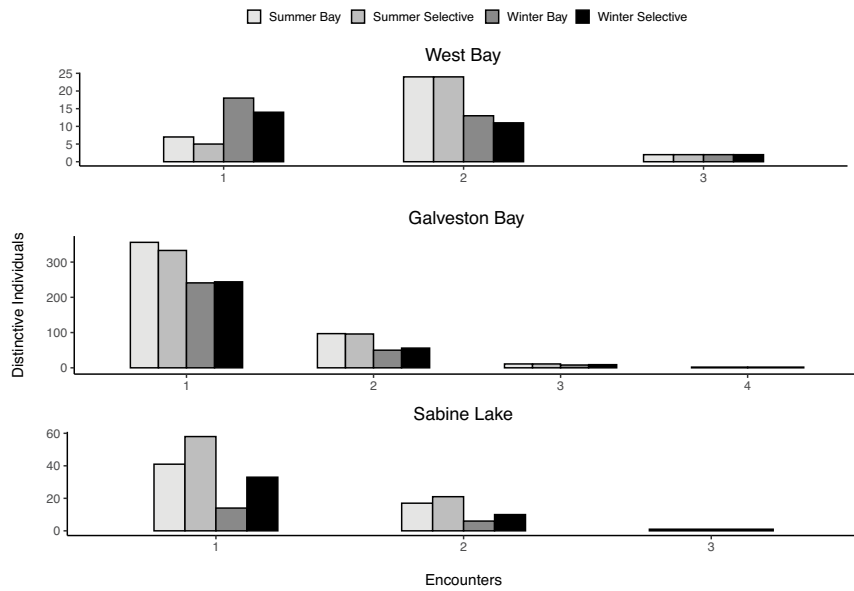


FIGURE 6. Encounter indices for distinctive individual bottlenose dolphins included in mark-recapture abundance estimation in 3 embayments along the upper Texas coast during 2014–2017. Data displayed by season and dataset (parsed encounter histories). The Bay dataset included all distinctive individuals observed in the bay or Gulf pass to the bay in ≥ 1 season. The Selective dataset included all individuals in the Bay dataset, and additionally included individuals observed in coastal waters during both summer and winter seasons but excluded dolphins that used more than one survey area (inter-bay matches). Note different y-axis scale for each bay.

(32.7–40.3) in winter and summer, respectively, is similar to the range of previous West Bay abundance estimates (Irwin and Würsig 2004), suggesting the West Bay population remains relatively stable and close to the suggested carrying capacity of 30. This is strong support for the use of the Selective data parsing method used for West Bay, as our resident abundance estimate derived from only 2 primary sessions (winter and summer) is consistent with long-term studies of the same population (Maze and Würsig 1999, Irwin and Würsig 2004).

The NMFS conducted line transect aerial surveys from 1984–1985 and 1992–1993 during all seasons over Sabine Lake and the Galveston Bay system, with distance sampling methodology resulting in estimates of 0–2 bottlenose dolphins for Sabine Lake and 152 bottlenose dolphins for Galveston Bay (Scott et al. 1989, Blaylock and Hoggard 1994). Henningsen and Würsig (1991) conducted visual small-boat surveys in the general Galveston Bay area including coastal waters and identified 1,002 individuals, although only 135 were re-sighted primarily in the bay during their 7 month study. Bräger (1993) conducted 97 surveys from June

to November 1991 around the northeastern end of Galveston Island, including the Galveston Ship Channel, Back Bay, Bolivar Roads, and adjacent coastal waters, and estimated that ~200 dolphins used Galveston Bay year-round. The count of 1,002 distinct individuals in Galveston Bay (Henningsen and Würsig 1991) is similar to the range of best estimates calculated in this study of 841.9 (95% CI 693.5–990.4) and 1,131.5 (95% CI 846.3–1416.7), winter and summer, respectively, and clearly much higher than the estimate of Galveston Bay resident bottlenose dolphins from previous estimates. Our study has several important differences relative to earlier Galveston Bay studies that may be responsible for the discrepancies between abundance estimates.

First, unlike previous studies, we adjusted abundance estimates in all survey areas to account for unmarked individuals, thus further contributing to our higher estimates of abundance. The θ used in the correction for unmarked fins is based on current standard photo-ID protocol (Urian et al. 2014). It is possible that some of our abundance estimates are inflated due to the presence of transient individuals. The discovery curve for West Bay tends to level off through the

TABLE 5. Abundance estimates from this study for bottlenose dolphins along the upper Texas coast compared to previous studies. Sampling methods include capture-mark-recapture (CMR), distance sampling (Distance), and a count of unique catalogued individuals with observed site fidelity to the stock area (Catalog).

Study	Survey Year	Platform	Method	West Bay	Galveston Bay	Sabine Lake
Scott et al. 1989	1984-1985	Aerial	Distance	0	45	2
Henningsen and Würsig 1991	1990	Small Boat/Helicopter	Catalog	NA	135*	NA
Bräger 1992, 1993	1991	Small Boat	CMR, Catalog	NA	200*	NA
Blaylock and Hoggard 1994	1992-1993	Aerial	Distance	29	152	0
Maze and Würsig 1999	1995-1996	Small Boat	Catalog	37	NA	NA
Irwin and Würsig 2004	1997-2001	Small Boat	CMR, Distance, Catalog	28–34	NA	NA
Litz et al. 2019	2014-2015	Small Boat	CMR	44–51	NA	NA
Present study	2014-2018	Small Boat	CMR	37–38	842–1,132	122–162

*Over 1,000 unique individuals were identified

secondary primary session, but those for Galveston Bay and Sabine Lake increase throughout our sampling sessions, suggesting incomplete marking of those populations, possibly due to mixing with members of some other population. Although the Selective dataset limited the inclusion of coastal sightings to only those individuals present in both seasons, individuals observed within the bay and pass boundaries were counted towards the abundance estimate even if only present during one season for both the Bay and Selective datasets. Previous researchers studying bottlenose dolphins in Galveston Bay suggested a high number of transient dolphins frequent the Houston Ship Channel and nearshore GOM coastal waters (Henningsen and Würsig 1991, Bräger 1993, Beier 2001), and over 70% of individuals in the Galveston Bay survey area included in our mark–recapture estimates were seen only once. These results may signal Galveston Bay is host to a highly mixed or predominantly open population; however, differences in survey design, photo collection and analysis methods, and spatial scope make a comparison of study results challenging. Even long–term monitoring research programs encounter difficulties in distinguishing resident bottlenose dolphin populations from those of another stock (Urian et al. 2018). Previous Galveston Bay abundance estimates were based on a count of distinctive individuals with multi–seasonal site fidelity (Henningsen and Würsig 1991, Fertl 1994). The abundance estimate provided by Bräger (1993) was derived from a catalog subset of distinctive individuals resighted multiple times over the course of 2 years, and those individuals were used to calculate abundance using a weighted–mean Lincoln–Petersen estimator (Bräger 1992). However, those data were collected in a smaller study area (~100 km²) on the northeastern end of Galveston Island that also included coastal waters, in contrast to the broader spatial coverage of our study (~1400 km²) that extended to the perimeters of upper Galveston Bay, where growing evidence indicates use by at least a summer seasonal population (Fazioli et al. 2017²). An additional consideration is that the Galveston Bay abundance estimate of ~200 provided by Bräger (1993) is very similar to the 240 individuals identified by Fertl (1994) during a 3 year study of bottlenose dolphin behavior in the Galveston Ship Channel—a narrow seaport habitat that was encapsulated within the study area of Bräger (1992). The results of both studies are consistent, but they may represent only a partial segment of the total Galveston Bay population.

Similar to the Galveston Bay survey area, most bottlenose dolphin groups sighted in Sabine Lake during this study

were in the Gulf pass and nearshore coastal waters, and the spatial inconsistencies in study design are likely responsible for the large difference in our abundance estimates compared to the NMFS aerial surveys (Scott et al. 1989, Blaylock and Hoggard 1994). The NMFS aerial survey crews were primarily assessing Sabine Lake proper, and not the Sabine Pass Channel and adjacent coastal waters and used different statistical methods. The encounter index for Sabine Lake in our study was very similar to that of Galveston Bay (over 70% of individuals encountered only once in each primary session), however, unlike the Selective dataset for Galveston Bay and West Bay, the Selective dataset for Sabine Lake included a greater number of individuals used for abundance estimation relative to the Bay dataset. This resulted in a 50% increase in winter abundance estimates between the Bay dataset (60.0, 95% CI 2.9–117.1), and the Selective dataset (121.6, 95% CI 73.0–170.3), although summer abundance estimates were very similar between the two datasets (~6% difference). The low number of distinctive individuals encountered inside the boundaries of the Sabine Lake stock area (i.e., the Sabine Pass Channel, Sabine Lake proper, and adjacent shipping channels) may pose a problem for the reliability of our Sabine Lake winter abundance estimate using the Bay parsing method. Otis et al. (1978) cautioned against modeling attempts where $n < 25$ or mean capture probabilities < 0.1 , with few sampling occasions (≤ 10). Although the mean (\pm SE) capture probability for the Sabine Lake winter Bay dataset was 0.25 ± 0.02 , the sample size was only 20, with 3 secondary sampling occasions within the winter primary session. Thus, our capacity for inference may be limited using that dataset. However, the difference in the number of distinctive individuals catalogued between the Bay and Selective datasets is based on a direct count resulting from photo analysis and provides at least enough information to infer more marked individuals present in the survey area were using coastal waters in both seasons. This may indicate there are bottlenose dolphins (potentially the majority in winter) with site–fidelity to the Sabine Lake survey area that prefer to use the Gulf waters near the end of and adjacent to the Sabine Pass Channel. This is not surprising given that Sabine Lake salinity is typically lowest in winter due to increased freshwater riverine flow bypassing upstream hydroelectric reservoirs draining into Sabine Lake (Orlando et al. 1993). The abundant natural freshwater inflow into Sabine Lake, the anthropogenic manipulation of river flow, and the extensively dredged channels that removed previous impediments to Gulf tidal influx have resulted in a highly engineered environment of stratified salinities (Ward 1980) that may have resulted in a novel exception to typical estuarine bottlenose dolphin habitat use.

The winter spatial distribution of the bottlenose dolphins we observed is consistent with the winter spatial distribution of individuals noted by other researchers who suggest

²Fazioli, K.L., V. Mintzer, and G. Guillen. 2017. Site fidelity of bottlenose dolphins (*Tursiops truncatus*) in a highly-industrialized estuary. Poster presented at the 22nd Biennial Conference on the Biology of Marine Mammals. 23-27 October 2017, Halifax, Nova Scotia, Canada. <https://marinemammalscience.org/conference/past-and-future-conferences/>

they tend to favor the deep waters of the pass or channels to embayments during winter (Irvine et al. 1981, Wells et al. 1987). Other research conducted in central and southern areas of the Texas coast (e.g., Matagorda Bay and Corpus Christi Bay areas) indicate an increase in winter populations using the Gulf passes and deep shipping channels (Shane 1980, Gruber 1981). Maze and Würsig (1999) found no seasonal occurrence pattern for West Bay, but like Irwin and Würsig (2004) and Henderson and Würsig (2007), noted a tendency for higher resident density in the Gulf during cold months and in the bay during warm months. Researchers focused on the northeast end of Galveston Island suggested an increase in abundance between late spring and early fall (reviewed in Fertl (1994) and Maze and Würsig (1999)), which temporally overlaps with our summer Galveston Bay and Sabine Lake surveys. The seasonal trends we observed are consistent with the seasonal observations of past researchers. We documented increased bottlenose dolphin density in the deep shipping channels and Gulf passes during winter, no strong seasonal variation in West Bay abundance, and higher abundance estimates during summer for Galveston Bay and Sabine Lake.

The general spatial distribution of the inter-bay matches identified here also corresponds, in part, to natural and engineered deep-draft channels present in each survey area (e.g., San Luis Pass and the GIWW in West Bay, the Houston Ship Channel, and the Sabine Pass Channel). The presence of a federally protected species in high-traffic areas may have implications for future coastal engineering projects, particularly in winter, when group density was greater in the coastal inlets and major shipping channels of this study. For example, in recent years, Bolivar Roads (the channel between Galveston Bay and the GOM) has been a focal point in a broader plan by the state and federal government to protect the economic interests of the community and industry making use of Texas shorelines. The tentatively selected plan (TSP) includes a sea gate that will potentially alter or close Bolivar Roads as a storm-surge protection device for oil refineries and communities near Galveston Bay (USACE 2018). The impacts of large scale human modifications to Bolivar Roads (e.g., the TSP) or other bay access points for bottlenose dolphins should be considered (Ronje et al. 2018). The matches identified in different survey areas in this study all had the Galveston Bay survey area in common, and notably, there was no crossover in matches between West Bay and Sabine Lake. Tyson et al. (2011) and Urian et al. (2013) posited community boundaries for adjacent bottlenose dolphin populations by identifying a geographical boundary line on which the fewest number of overlapping dorsal fin matches were found. It is possible Bolivar Roads is the location of a similar type of community boundary, yet also serves as a potential mixing area or functions as a “hub” for the populations of West Bay, Galveston Bay, Sabine Lake, and

potentially an open population occurring primarily in near-shore coastal waters (Beier 2001).

Long-distance or inter-bay movements of individuals or groups to multiple embayments have been noted in the north-central GOM (Balmer et al. 2016, Ronje et al. 2017) and Texas Gulf coast (Gruber 1981, Würsig and Lynn 1996, Maze and Würsig 1999). It is possible these bottlenose dolphins are part of 3 distinct GOM coastal stocks, (i.e., northern, western, and eastern coastal stocks) delineated by the NMFS (Waring et al. 2016). The Western Coastal Stock range extends from the Mississippi River Delta to the Texas-Mexico border from the coastal shoreline out to the 20 m isobath in the GOM. Few studies have identified bottlenose dolphins belonging specifically to the Western Coastal Stock; however, the animals found to match in > 1 survey area in this study (and possibly some animals included in the Bay and Selective datasets) are potential members of the Western Coastal Stock, or some other population. They may also be individuals exhibiting a temporary or permanent shift in their home range. Maze and Würsig (1999) reported a bottlenose dolphin sighted in areal Galveston Bay surveys during summer also appeared in West Bay the following winter, and was thought to have remained in West Bay for at least 9 months. The biological importance of transient individuals or short-term residents from other stocks mixing with the populations studied here is the potential for the transmission of communicable disease between populations (Rosel et al. 2009). While genetic exchange may also occur, studies in the eastern GOM concluded little interbreeding occurs between those coastal and estuarine populations (Sellas et al. 2005). Additional research could provide insights into determining if the population studied here fit the description of a metapopulation (Kritzer and Sale 2004). Photo-ID mark-recapture techniques can provide insight into metapopulations of bottlenose dolphins occupying discrete geographic areas. For example, Chabanne et al. (2017) applied multistate capture-recapture robust design to characterize the metapopulation structure of Indo-Pacific bottlenose dolphin (*T. aduncus*) subpopulations in Western Australia occupying habitats in 3 distinct geographic sites. Similar studies in the northwestern GOM could further elucidate the movement patterns of bottlenose dolphins in our study region and determine the significance of inter-population demographic influence among the 3 embayments studied here and potentially within the Western Coastal Stock. The limited data from this study demonstrate that the ranging patterns of some individuals include Galveston Bay, the adjacent estuaries, and nearshore coastal waters. The magnitude of the population connectivity observed here, and its role in the dynamics of each of these populations, requires additional study likely including multi-year photo-ID studies, telemetry studies, and assessment of the genetic independence of the defined stocks. Given the high degree of

commercial activity, history of industrial pollution in the region, and anthropogenic modification to the environment, research should be directed to collect more information on the degree to which bottlenose dolphin populations or sub-

populations are mixing in Galveston Bay. These data are vital to improve impact assessments of future coastal engineering projects or other anthropogenic activities occurring in bottlenose dolphin habitat in the northwestern GOM.

ACKNOWLEDGMENTS

Special thanks to J. Adams for FinBase technical support. We thank S. Hall, C. Teague, C. Toms, P. Secker, the many other individuals that generously contributed their time and skills to the collection of data in the field, and B. Würsig and R. Davis for field logistics support. We thank S. Bräger, K. Maze-Foley, J. Litz, P. Rosel, and 4 anonymous reviewers for their constructive remarks. The National Marine Fisheries Service, the Texas Marine Mammal Stranding Network, SeaWorld San Antonio, the SeaWorld Busch Gardens Conservation Fund, and the Marine Mammal Behavioral Ecology Group at Texas A&M University at Galveston contributed funding, staff, or in-kind resources. We conducted this work under MMPA Permit No. 14450 issued to the Southeast Fisheries Science Center by the National Marine Fisheries Office of Protected Resources, Louisiana Wildlife and Fisheries Scientific Collecting Permit SCP#46 and approved by the National Marine Fisheries Service Atlantic Institutional Animal Care and Use Committee.

LITERATURE CITED

- Adams, J.D., T. Speakman, E. Zolman, and L.H. Schwacke. 2006. Automating image matching, cataloging, and analysis for photo-identification research. *Aquatic Mammals* 32:374–384. <http://doi.org/10.1578/AM.32.3.2006.374>
- Akaike, H. 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika* 60:255–265. <https://doi.org/10.1093/biomet/60.2.255>
- Anderson, D., K. Burnham, and G. White. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780–1793. <https://doi.org/10.2307/1939637>
- Balmer, B., R. Wells, S. Nowacek, D. Nowacek, L. Schwacke, W. McLellan, and F. Scharf. 2008. Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. *Journal of Cetacean Research and Management* 10:157–167.
- Balmer, B., C. Sinclair, T. Speakman, B. Quigley, K. Barry, C. Cush, M. Hendon, K. Mullin, E. Ronje, P. Rosel, L. Schwacke, R. Wells, and E. Zolman. 2016. Extended movements of common bottlenose dolphins (*Tursiops truncatus*) along the northern Gulf of Mexico's central coast. *Gulf of Mexico Science* 1:93–97. <https://doi.org/10.18785/goms.3301.08>
- Balmer, B., S. Watwood, B. Quigley, T. Speakman, K. Barry, K. Mullin, P. Rosel, C. Sinclair, E. Zolman, and L. Schwacke. 2019. Common bottlenose dolphin (*Tursiops truncatus*) abundance and distribution patterns in St. Andrew Bay, Florida, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29:486–498. <https://doi.org/10.1002/aqc.3001>
- Beier, A.G. 2001. Occurrence, Distribution, and Movement Patterns of Outer Coastline Bottlenose Dolphins Off Galveston Island, Texas. MSc. thesis. Texas A&M University, Galveston, TX, USA, 108 p.
- Blaylock, R.A. and W. Hoggard. 1994. Preliminary estimates of bottlenose dolphin abundance in southern US Atlantic and Gulf of Mexico continental shelf waters. NOAA Technical Memorandum NMFS-SEFSC-356. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL, USA. 10 p.
- Bräger, S. 1992. Site fidelity and association patterns of the bottlenose dolphin, *Tursiops truncatus*. MSc. thesis. Christian-Albrechts-Universität, Kiel, Germany, 97 p.
- Bräger, S. 1993. Diurnal and seasonal behavior patterns of bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science* 9:434–438. <https://doi.org/10.1111/j.1748-7692.1993.tb00477.x>
- Burnham, K.P., D.R. Anderson, and K.P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23–35. <https://doi.org/10.1007/s00265-010-1029-6>
- Chabanne, D.B., K.H. Pollock, H. Finn, and L. Bejder. 2017. Applying the multistate capture-recapture robust design to characterize metapopulation structure. *Methods in Ecology and Evolution* 8:1547–1557. <https://doi.org/10.1111/2041-210X.12792>
- Chao, A., S. Lee, and S. Jeng. 1992. Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* 48:201–216. <https://doi.org/10.2307/2532750>
- Conn, P.B., A.D. Arthur, L.L. Bailey, and G.R. Singleton. 2006. Estimating the abundance of mouse populations of known size: Promises and pitfalls of new methods. *Ecological Applications* 16:829–837. [https://doi.org/10.1890/1051-0761\(2006\)016\[0829:ETAOMP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0829:ETAOMP]2.0.CO;2)
- Conn, P.B., A.M. Gorgone, A.R. Jugovich, B.L. Byrd, and L.J. Hansen. 2011. Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. *Journal of Wildlife Management* 75:569–579. <https://doi.org/10.1002/jwmg.94>
- Cooch, E.G. and G.C. White. 2018. Program MARK a gentle introduction. 18th edition. p. 5–1 to 5–40. <http://www.phidot.org/software/mark/docs/book/>

- Darroch, J.N. 1958. The multiple–recapture census: I. Estimation of a closed population. *Biometrika* 45:343–359. <https://doi.org/10.2307/2333183>
- ESRI. 2019. Environmental Research Systems Institute. ArcGIS Pro 2.4.1. Redlands, CA, USA.
- Fazioli, K.L., S. Hofmann, and R.S. Wells. 2006. Use of Gulf of Mexico coastal waters by distinct assemblages of bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 32:212–222. <https://doi.org/10.1578/am.32.2.2006.212>
- Fertl, D. 1994. Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston ship channel, Texas. *Texas Journal of Science* 46:299–318.
- Fletcher, D. 2012. Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika* 99:230–237. <https://doi.org/10.1093/biomet/asr083>
- Gruber, J.A. 1981. Ecology of the Atlantic bottlenosed dolphin (*Tursiops truncatus*) in the Pass Cavallo area of Matagorda Bay, Texas. MSc. thesis. Texas A&M University, College Station, TX, USA, 182 p.
- Gunter, G. 1942. Contributions to the natural history of the bottle–nose dolphin *Tursiops truncatus* (Montague) on the Texas coast. *Journal of Mammalogy* 23:267–276. <https://doi.org/10.2307/1374993>
- Hayes, S.A., E. Josephson, K. Maze–Foley, P.E. Rosel, B.L. Byrd, T.V. Cole, L. Engleby, L.P. Garrison, J.M. Hatch, and A. Henry. 2017. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2016. NOAA Technical Memorandum NMFS–NE–241. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA, USA. 282 p.
- Henderson, E.E. and B. Würsig. 2007. Behavior patterns of bottlenose dolphins in San Luis Pass, Texas. *Gulf of Mexico Science* 2:153–161. <https://doi.org/10.18785/goms.2502.06>
- Henningsen, T. and B. Würsig. 1991. Bottle–nosed dolphins in Galveston Bay, Texas: Numbers and activities. Proceedings of the Fifth Annual Conference of the European Cetacean Society, Sandefjord, Norway, 21 – 23 February 1991, p. 36–38.
- Huggins, R. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732. <https://doi.org/10.2307/2532158>
- Irvine, A.B., M.D. Scott, R.S. Wells, and J.H. Kaufmann. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin* 79:671–688.
- Irwin, L.J. and B. Würsig. 2004. A small resident community of bottlenose dolphins, *Tursiops truncatus*, in Texas: Monitoring recommendations. *Gulf of Mexico Science* 2:13–21. <https://doi.org/10.18785/goms.2201.02>
- Jefferson, T.A., M.A. Webber, and R.L. Pitman. 2008. *Marine Mammals of the World: A Comprehensive Guide to their Identification*. Elsevier, Canada. 592 p.
- Kritzer, J.P. and P.F. Sale. 2004. Metapopulation ecology in the sea: From Levins’ model to marine ecology and fisheries science. *Fish and Fisheries* 5:131–140. <https://doi.org/10.1111/j.1467–2979.2004.00131.x>
- Laska, D., T. Speakman, and P.A. Fair. 2011. Community overlap of bottlenose dolphins (*Tursiops truncatus*) found in coastal waters near Charleston, South Carolina. *The Journal of Marine Animals and Their Ecology* 4:10–18.
- Litz, J.A., E.I. Ronje, H. Whitehead, and L.P. Garrison. 2019. Updated abundance estimate for common bottlenose dolphins (*Tursiops truncatus*) inhabiting West Bay, Texas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29(11):1–12. <https://doi.org/10.1002/aqc.3195>
- Lukacs, P. 2018. Closed population capture–recapture models. In: E. G. Cooch and G. C. White, eds. Program MARK—a gentle introduction, 18th edition. *Advanced Methods*. Vol. 2, p. 14–1 to 14–53. <http://www.phidot.org/software/mark/docs/book/>
- Maze–Foley, K., B.L. Byrd, S.C. Horstman, and J.R. Powell. 2019. Analysis of stranding data to support estimates of mortality and serious injury in common bottlenose dolphin (*Tursiops truncatus truncatus*) stock assessments for the Atlantic Ocean and Gulf of Mexico. NOAA Technical Memorandum NMFS–SEFSC–742. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL, USA. 51 p. <https://doi.org/10.25923/jtlx–jv75>
- Maze, K.S. and B. Würsig. 1999. Bottlenosed dolphins of San Luis Pass, Texas: Occurrence patterns, site–fidelity, and habitat use. *Aquatic Mammals* 25:91–104.
- Melancon, R., S. Lane, T. Speakman, L. Hart, C. Sinclair, J. Adams, P. Rosel, and L. Schwacke. 2011. Photo–identification field and laboratory protocols utilizing FinBase version 2. NOAA Technical Memorandum NMFS–SEFSC–627, US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Lafayette, LA, USA. 52 p.
- Moreno, P. and M. Mathews. 2018. Identifying foraging hotspots of bottlenose dolphins in a highly dynamic system: A method to enhance conservation in estuaries. *Aquatic Mammals* 44:694–710. <https://doi.org/10.1578/AM.44.6.2018.694>
- Mullin, K.D., P.E. Rosel, A.A. Hohn, and L.P. Garrison. 2007. Bottlenose dolphin stock structure research plan for the central northern Gulf of Mexico. NOAA Technical Memorandum NMFS–SEFSC–563. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Pascagoula, MS, USA. 27 p.
- Mullin, K.D., T. McDonald, R.S. Wells, B.C. Balmer, T. Speakman, C. Sinclair, E.S. Zolman, F. Hornsby, S.M. McBride, K.A. Wilkinson, and L.H. Schwacke. 2017. Density, abundance, survival, and ranging patterns of common bottlenose dolphins (*Tursiops truncatus*) in Mississippi Sound following the Deepwater Horizon oil spill. *PLoS One* 12:e0186265. <https://doi.org/10.1371/journal.pone.0186265>
- NOAA. 2019. National Oceanic and Atmospheric Administration, National Marine Fisheries Service. Total commercial fishery landings at an individual U. S. port for all years af-

- ter 1980, <https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/other-specialized-programs/total-commercial-fishery-landings-at-an-individual-us-port-for-all-years-after-1980/index>, viewed on 5/29/2019.
- Orlando, S.P.J., L.P. Rozas, G.H. Ward, and C.J. Klein. 1993. Salinity characteristics of Gulf of Mexico estuaries. NOAA's National Estuarine Inventory Series. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of Ocean Resources Conservation and Assessment, Silver Spring, MD, USA. 209 p.
- Otis, D.L., K.P. Burnham, G.C. White, and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:3–135. <https://www.jstor.org/stable/3830650>
- Phillips, N.M. and P.E. Rosel. 2014. A method for prioritizing research on common bottlenose dolphin stocks through evaluating threats and data availability: Development and application to bay, sound and estuary stocks in Texas. NOAA Technical Memorandum NMFS–SEFSC–665. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center. Lafayette, LA, USA. 154 p. <https://doi.org/10.7289/V5F769H8>
- Piwetz, S. 2019. Common bottlenose dolphin (*Tursiops truncatus*) behavior in an active narrow seaport. *PloS One* 14:e0211971. <https://doi.org/10.1371/journal.pone.0211971>
- Pollock, K.H. 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757. <https://doi.org/10.2307/3808568>
- Read, A.J., K.W. Urrian, B. Wilson, and D.M. Waples. 2003. Abundance of bottlenose dolphins in the bays, sounds, and estuaries of North Carolina. *Marine Mammal Science* 19:59–73. <https://doi.org/10.1111/j.1748-7692.2003.tb01092.x>
- Ronje, E.I., K.P. Barry, C. Sinclair, M.A. Grace, N. Barros, J. Allen, B. Balmer, A. Panike, C. Toms, K.D. Mullin, and R.S. Wells. 2017. A common bottlenose dolphin (*Tursiops truncatus*) prey handling technique for marine catfish (Ariidae) in the northern Gulf of Mexico. *PLoS One* 12:e0181179. <https://doi.org/10.1371/journal.pone.0181179>
- Ronje, E.I., H.R. Whitehead, and K.D. Mullin. 2018. The 1990 common bottlenose dolphin (*Tursiops truncatus*) mass die–off in East Matagorda Bay, Texas – New insight into a cold case. *Southeastern Naturalist* 17:411–422. <https://doi.org/10.1656/058.017.0306>
- Rosel, P., K. Mullin, L. Garrison, L. Schwacke, J. Adams, B. Balmer, P. Conn, M. Conroy, T. Eguchi, A. Gorgone, A. Hohn, M. Mazzoil, C. Schwartz, C. Sinclair, T. Speakman, K. Urrian, N. Vollmer, P. Wade, R. Wells, and E. Zolman. 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. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Lafayette, LA, USA. 38 p.
- Rosel, P.E., L. Hansen, and A.A. Hohn. 2009. Restricted dispersal in a continuously distributed marine species: Common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. *Molecular Ecology* 18:5030–5045. <https://doi.org/10.1111/j.1365-294X.2009.04413.x>
- Scott, G.P., D.M. Burn, L.J. Hansen, and R.E. Owen. 1989. Estimates of bottlenose dolphin abundance in the Gulf of Mexico from regional aerial surveys. Contribution Number CRD 88/89–07. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, Coastal Resources Division. Miami, FL, USA. 71 p.
- Sellas, A.B., R.S. Wells, and P.E. Rosel. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conservation Genetics* 6:715–728. <https://doi.org/10.1007/s10592-005-9031-7>
- Shane, S.H. 1977. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. MSc. thesis. Texas A&M University, College Station, TX, USA, 257 p.
- Shane, S.H. 1980. Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas. *Fishery Bulletin* 78:593–601.
- Speakman, T.R., S.M. Lane, L.H. Schwacke, P.A. Fair, and E.S. Zolman. 2010. Mark–recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. *Journal of Cetacean Research and Management* 11:153–162.
- Symonds, M.R. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65:13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Trenberth, K.E. 1983. What are the seasons? *Bulletin of the American Meteorological Society* 64:1276–1282. [https://doi.org/10.1175/1520-0477\(1983\)064<1276:WATS>2.0.CO;2](https://doi.org/10.1175/1520-0477(1983)064<1276:WATS>2.0.CO;2)
- Tyson, R.B., S.M. Nowacek, and D.P. Nowacek. 2011. Community structure and abundance of bottlenose dolphins (*Tursiops truncatus*) in coastal waters of the northeast Gulf of Mexico. *Marine Ecology Progress Series* 438:253–265. <https://doi.org/10.3354/meps09292>
- Urrian, K.W., D.M. Waples, R.B. Tyson, L.E. Hodge, and A.J. Read. 2013. Abundance of bottlenose dolphins (*Tursiops truncatus*) in estuarine and near–shore waters of North Carolina, USA. *Journal of the North Carolina Academy of Science* 129:165–171. <https://doi.org/10.7572/2167-5880-129.4.165>
- Urrian, K.W., A. Gorgone, A. Read, B. Balmer, R.S. Wells, P. Berggren, J. Durban, T. Eguchi, W. Rayment, and P.S. Hammond. 2014. Recommendations for photo–identification methods used in capture–recapture models with cetaceans. *Marine Mammal Science* 31:298–321. <https://doi.org/10.1111/mms.12141>
- Urrian, K.W., R. Kaufmann, D.M. Waples, and A.J. Read. 2018. The prevalence of ectoparasitic barnacles discriminates stocks of Atlantic common bottlenose dolphins (*Tursiops truncatus*) at risk of entanglement in coastal gill net fisheries. *Ma-*

- rine Mammal Science 35:290–299. <https://doi.org/10.1111/mms.12522>
- USACE. 2018. Coastal Texas protection and restoration feasibility study. Draft integrated feasibility report and environmental impact statement. DIFR–EIS. U.S. Army Corps of Engineers, Galveston District Southwestern Division, Galveston, TX, USA. 442 p.
- USEPA. 1999. Ecological condition of estuaries in the Gulf of Mexico. EPA 620–R–98–004. U.S. Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Gulf Ecology Division, Gulf Breeze, FL, USA. 80 p.
- Wade, P.R. and R.P. Angliss. 1997. Guidelines for assessing marine mammal stocks: Report of the GAMMS Workshop April 3–5, 1996, Seattle, Washington. NOAA Technical Memorandum NMFS–OPR–12. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. Silver Springs, MD, USA. 97 p.
- Ward, G.H. 1980. Hydrography and circulation processes of Gulf estuaries. In: P. Hamilton and K. B. Macdonald, eds. Estuarine and Wetland Processes, Marine Science Book Series. Vol. 11. Springer Science+Business Media, New York, NY, USA, p. 183–215. <http://doi.org/10.1007/978-1-4757-5177-2>
- Waring, G.T., E. Josephson, K. Maze–Foley, and P.E. Rosel. 2016. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2015. NOAA Technical Memorandum NMFS–NE–238. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Woods Hole, MA, USA. 501 p.
- Wells, R.S. 2014. Social structure and life history of bottlenose dolphins near Sarasota Bay, Florida: Insights from four decades and five generations. In: J. Yamagiwa and L. Karczmarski, eds. Primates and Cetaceans, Primatology Monographs. Springer, Tokyo, Japan, p. 149–172. https://doi.org/10.1007/978-4-431-54523-1_8
- Wells, R.S. 2018. Identification Methods. In: B. Würsig, J. G. M. Thewissen and K. M. Kovacs, eds. Encyclopedia of Marine Mammals. 3rd ed. Academic Press/Elsevier, San Diego, CA, USA, p. 503–507. <http://dx.doi.org/10.1016/B978-0-12-804327-1.00009-1>
- Wells, R.S. and M.D. Scott. 2018. Bottlenose dolphin, *Tursiops truncatus*, common bottlenose dolphin. In: B. Würsig, J. G. M. Thewissen and K. M. Kovacs, eds. Encyclopedia of Marine Mammals. 3rd ed. Academic Press/Elsevier, San Diego, CA, USA, p. 118–125. <https://doi.org/10.1016/B978-0-12-804327-1.00072-8>
- Wells, R.S., M.D. Scott, and A.B. Irvine. 1987. The social structure of free–ranging bottlenose dolphins. In: H. H. Genoways, eds. Current Mammalogy. Springer. Boston, MA, USA, p. 247–305. https://doi.org/10.1007/978-1-4757-9909-5_7
- Wells, R.S., L.H. Schwacke, T.K. Rowles, B.C. Balmer, E. Zolman, T. Speakman, F.I. Townsend, M.C. Tumlin, A. Barleycorn, and K.A. Wilkinson. 2017. Ranging patterns of common bottlenose dolphins *Tursiops truncatus* in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. Endangered Species Research 33:159–180. <https://doi.org/10.3354/esr00732>
- White, G.C. and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:S120–S139. <https://doi.org/10.1080/00063659909477239>
- White, G.C. and E.G. Cooch. 2017. Population abundance estimation with heterogeneous encounter probabilities using numerical integration. Journal of Wildlife Management 81:322–336. <https://doi.org/10.1002/jwmg.21199>
- Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, CA, USA, 817 p.
- Wilson, B., P.S. Hammond, and P.M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecological Applications 9:288–300. <https://doi.org/10.2307/2641186>
- Würsig, B. and M. Würsig. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198:755–756. <http://doi.org/10.1126/science.198.4318.755>
- Würsig, B. and S.K. Lynn. 1996. Movements, site fidelity, and respiration patterns of bottlenose dolphins on the central Texas coast. NOAA Technical Memorandum NMFS–SEFSC–383. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL, USA. 111 p.