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Updated Abundance Estimate for Common Bottlenose Dolphins (*Tursiops truncatus*) inhabiting West Bay, Texas

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Abstract

1. West Bay is located along the south-west portion of Galveston Bay, Texas, and has been delimited as a bay, sound, and estuary (BSE) common bottlenose dolphin (*Tursiops truncatus*) stock area under the Marine Mammal Protection Act of 1972. The most recent abundance estimate available for the West Bay BSE stock is from 2001 and is considered outdated for management purposes.

2. This study provides an updated abundance estimate using photo-identification capture-mark-recapture (CMR) data collected from West Bay during the winter of 2014 and summer of 2015. The CMR data were analysed using both Pollock's robust design models and Poisson-log normal mark-resight models.

3. Differences between the model types are discussed, and the abundance estimates derived from the mark-resight models are recommended for management use (50.63 (Unconditional SE 2.23) in the winter and 44.36 (Unconditional SE 1.18) in the summer).

4. While the updated abundance estimate is higher than the previously reported estimates which vary between 28 and 38, they still indicate that West Bay supports a small population of bottlenose dolphins. As a result, the West Bay BSE stock should be closely monitored for impacts, particularly those related to human caused stressors.

Key Words: estuary, coastal, protected species, survey, distribution, mammals

1. Introduction

Common bottlenose dolphins (*Tursiops truncatus*) are found throughout temperate and tropical waters worldwide (Reynolds, Wells, & Eide, 2000). Marine mammals in U.S. waters are

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protected under the Marine Mammal Protection Act (MMPA) of 1972, and the units for management are "population stocks" (MMPA 16 U.S.C. §§ 1361-1421h; Rosel et al., 2011). A stock is defined as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement that interbreed when mature" (MMPA 16 U.S.C. §§ 1361-1421h). Often these population stocks represent communities of dolphins which Wells, Scott, and Irvine (1987) defined as dolphins that share "large portions of their ranges and interact with eachother to a much greater extent than with members of similar units in adjacent waters." Even though these communities are not necessarily genetically isolated and some genetic exchange may occur with neighbouring communities, they are recognized as a functioning element of the ecosystem of which they are a part and therefore should be managed as different stocks (MMPA 16 U.S.C. §§ 1361-1421h; NMFS, 2016).

Bottlenose dolphins in the Gulf of Mexico (GoM) are currently managed as 35 stocks including one large oceanic stock, three coastal stocks and 31 BSE stocks (Hayes, Josephson, Maze-Foley, & Rosel, 2017). The Western Coastal Stock extends from the Mississippi River Delta to the Texas-Mexico border from the shore to the 20m isobath (Waring, Josephson, Maze-Foley, & Rosel, 2016). In the same region, NOAA has defined 10 bay, sound, and estuary (BSE) stocks including the West Bay, Texas stock and neighbouring Galveston Bay stock (Waring et al., 2016). Throughout the Gulf of Mexico, long-term, year-round residency of bottlenose dolphins has been reported from nearly every BSE site where photo-identification (photo-ID) or tagging studies have been conducted including those in Texas (Balmer et al., 2008; Hayes et al., 2017; Hubard, Maze-Foley, Mullin, & Schroeder, 2004; A.B. Irvine & Wells, 1972; Maze & Würsig, 1999; Shane, 1980; Wells et al., 1987). The amount of movement between the BSE stocks and coastal stocks varies; however, in many cases residents primarily use BSE waters with limited movement into Gulf waters (Balmer et al., 2019; Fazioli, Hofmann, & Wells, 2006; Hayes et al., 2017; Wells et al., 2017). For example, in a study of Gulf waters off of Sarasota Bay, Florida, Fazioli et al. (2006) found 57 resident Sarasota Bay dolphins (23% of the dolphins identified) were sighted in Gulf waters and that the majority of those sightings appeared in nearshore waters near the passes.

Bottlenose dolphins inhabiting coastal and estuarine environments are exposed to a wide variety of threats and stressors including, but not limited to, pollution, interactions with commercial and recreational fisheries, toxic algal blooms, noise, and industrial activities including shipping. Phillips and Rosel (2014) developed a method for evaluating 19 threats with the potential to impact dolphins and assessed data availability for stocks as a way to prioritize research. They applied this method to seven Texas BSE stocks including West Bay and documented 6 of 19

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threat categories as “present and a characterized problem for this [West Bay] stock area” including oil and gas production, heavy metal pollution, chemical pollution, algal blooms, adverse weather, and previous mortality events of unknown etiology (Phillips & Rosel, 2014). The combination of the cumulative threat assessment score and the lack of up-to-date (within five years) assessment data led to the West Bay Stock being ranked as a high priority for further research (Phillips & Rosel, 2014).

West Bay, Texas, is a long, narrow bay in the south-west portion of the Galveston Bay Estuarine System and connects to several small bays including Chocolate Bay, Bastrop Bay, Christmas Bay, and Drum Bay (Figure 1). It has an approximate area of $180km^2$ and an average depth of 1.2m with a maximum depth of 7m (Phillips & Rosel, 2014). West Bay is connected to the GoM by San Luis Pass in the south and is connected to Galveston Bay to the north. In order to monitor and possibly mitigate the effects of stressors, managers need to understand the abundance and stock boundaries of populations. Photo-identification (photo-ID) is a common tool for capture-mark-recapture (CMR) studies of bottlenose dolphins for the purpose of estimating stock abundance using a variety of statistical methods (Rosel et al., 2011; Urian et al., 2015; Würsig & Würsig, 1977). Bottlenose dolphins often acquire distinct natural markings on their dorsal fins which can be photographed and used to identify individuals and track their sightings over time without requiring a physical capture to mark animals (Wells & Scott, 1999; Würsig & Jefferson, 1990; Würsig & Würsig, 1977). Maze and Würsig (1999) conducted three photo-ID surveys of dolphins in West Bay in 1990, 1995, and 1996 and showed evidence of two different communities which they defined as “Gulf animals” and “Bay animals” or “residents”. The Gulf animals were only sighted in coastal waters and had a low resighting rate; however, the Bay animals had a higher resighting rate (86.5%) and were sighted in the south-west areas of West Bay and San Luis Pass with some also sighted in Gulf waters (Maze & Würsig, 1999). Under the current stock structure described above, the dolphins identified as Gulf animals likely do not belong to the West Bay Stock and likely belong to the Western Coastal Stock. The same study also found evidence for long-term site fidelity as 14 dolphins sighted during the 1995/1996 surveys had also been sighted in the 1990 surveys (Maze & Würsig, 1999). Photo-ID surveys conducted in 2002 and 2003 also identified “resident” and “Gulf” dolphins with 75 of 110 identified individuals only sighted in coastal waters and most only sighted once (Henderson, 2004). The remaining 35 were considered resident to West Bay with residency defined as being sighted in three of four seasons and continued sightings in two of four seasons (Henderson, 2004; L.-J. Irwin & Würsig, 2004). Twenty-five of those 35 residents had been sighted in previous studies in West Bay, again confirming long-term site fidelity (Henderson, 2004). Photo-ID data collected between 1997 and 2001 identified between 28 and 34 individuals per year that met the

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residency criteria (L.-J. Irwin & Würsig, 2004). These data were analysed using CMR models and annual abundance estimates for all dolphins using West Bay ranged from 28 (95% CI 26 – 71) to 38 (95% CI 33 – 55) (L.-J. Irwin & Würsig, 2004).

The previous studies also identified some exchange between the West Bay surveys and the Galveston Bay study area (the current Galveston Bay BSE Stock area), though the movement between them appears to be limited. Maze and Würsig (1999) compared their 1995-1996 West Bay/San Luis Pass photo-ID catalogue with a photo-ID catalogue from 1995 Galveston Bay surveys and found three dolphins that were sighted in both survey areas. Two of the three were Gulf animals also seen in the Galveston area and one was a Bay animal sighted twice in Galveston Bay in the summer of 1995 and then seen in the West Bay catalogue 19 times beginning in December 1995, suggesting a temporary or permanent shift in its home range (Maze & Würsig, 1999). Maze-Foley and Würsig (2002) expanded this study to examine association patterns of dolphins in the West Bay study area and concluded that the West Bay community of dolphins is separate but not necessarily isolated from the Galveston Bay community and recommended that NMFS continue to manage West Bay and Galveston Bay as separate stocks.

Prior to the current study, the abundance estimates generated from the 2001 data were the most recently available (Hayes et al., 2017). The 1994 amendments to the Marine Mammal Protection Act of 1972 (MMPA) require the National Marine Fisheries Service and the U.S. Fish and Wildlife Service to conduct assessments of all marine mammal stocks in the U.S. Exclusive Economic Zone (EEZ) and guidelines state that abundance estimates more than eight years old should not be used for management purposes (Hayes et al., 2017; Wade & Angliss, 1997). For this reason, recent stock assessment reports have listed the minimum population size estimate (N_{min}) for common bottlenose dolphins utilizing West Bay as “unknown” which prevents the calculation of the potential biological removal level (PBR). The PBR is an important metric for management because if known human-caused mortality exceeds the PBR for a given stock, then the stock is classified as strategic which can trigger management actions to reduce mortality for that stock (Wade & Angliss, 1997). This could be particularly important in stocks such as West Bay where there are multiple stressors on a relatively small population.

This study analysed photo-ID CMR data collected within the currently defined West Bay stock boundaries during two seasons, December 2014 (winter) and June 2015 (summer), with the goal of providing updated abundance estimates. The data were analysed with the more commonly used Pollock’s closed capture robust design models and newer Poisson-log normal mark-resight

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models (McClintock & White, 2010; McClintock, White, Antolin, & Tripp, 2009; Pollock, 1982). The mark-resight models have been applied to estimate abundance of Irrawaddy dolphin in the Mekong River and Indo-Pacific bottlenose dolphins in Bangladesh, but we are not aware of them previously being used for bottlenose dolphin abundance estimates in the United States (Mansur, Strindberg, & Smith, 2012; Ryan, Dove, Trujillo, & Doherty, 2011). Differences between the models will be discussed in the methods section below.

While long-term, multi-year studies are always preferred, funding and resources do not always allow for long-term surveys. This paper provides updated abundance estimates derived from a relatively short-term dataset (<1 year) that will allow for the calculation of PBR which is critical to improve management of this stock. In addition, this paper applies a relatively new model, the Poisson-log normal mark-resight model, which may be of interest to other researchers using similar photo-ID methods to estimate abundances of small cetacean populations.

2. Methods

Field and photo-processing

Photo-ID CMR surveys were conducted following methods outlined in Rosel et al. (2011) and the Pollock's "Robust" survey design (Kendall & Nichols, 1995; Kendall, Nichols, & Hines, 1997; Kendall, Pollock, & Brownie, 1995; Pollock, 1982). Surveys were conducted in two primary sessions (December 2014 and June 2015) with three secondary surveys per season (Ronje, Whitehead, Piwetz, & Mullin, 2018). The survey area included West Bay proper, Chocolate Bay, Christmas Bay, and San Luis Pass (Figure 1). Christmas Bay was only surveyed in the summer survey as the water depth was too shallow for the research vessel during the winter survey (Ronje et al., 2018). The surveys also included two pre-determined transect lines in coastal waters, oriented parallel to the coastline at approximately 500m and 2km from shore and extending approximately 10km north and 10km south of San Luis Pass (Figure 1). Transect lines were transited by a small vessel with a three-member observer team. Surveys were planned for a Beaufort sea state of 3 or less; however, parts of some surveys were conducted in slightly worse conditions. Upon encountering a group of dolphins (a "sighting"), attempts were made to photograph the left and right sides of the dorsal fins of all dolphins in each group using digital cameras equipped with 100–400 mm telephoto lenses. Field data collection methods were similar to that outlined in Melancon et al. (2011), and collected data included the date, time, and

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GPS location of each group, group size and composition, behavioral observations, etc. Detailed field methods for this study are outlined in Ronje et al. (2018).

A FinBase database (Adams, Speakman, Zolman, & Schwacke, 2006) was used to store the field data, house the photo-catalogue, and facilitate the matching of photos collected during each sighting to the catalogue of individuals. It is critical for CMR analytical methods that both the quality of photographs and distinctiveness of animals be considered carefully in order to ensure marks are read without error each time (Rosel et al., 2011; K. Urian et al., 2015; K.W. Urian, Waples, Tyson, Hodge, & Read, 2013). Image quality and fin distinctiveness were scored independently within FinBase prior to fin matching (Melancon et al., 2011). Photo-quality was scored based on a sum of scores from five characteristics of the photo: focus/clarity, contrast, angle, partial, and distance. Only photos that scored with a photo quality score of average ("Q2") or excellent ("Q1") were used for analyses (Melancon et al., 2011; K.W. Urian, Hohn, & Hansen, 1999). Dorsal fins were assigned distinctiveness scores in four categories: non-distinct (clean fins, no marks, D4), marginally distinct (very subtle marks that may be difficult to distinguish each and every time, score D3), average distinctiveness (score D2) or high distinctiveness (marks evident even in poor quality photos, score D1; Melancon et al., 2011). For this study, fins with a score of D4 and D3 were considered "unmarked" and fins with scores of D2 and D1 were considered "marked." A single researcher scored the distinctiveness of all fins to ensure consistency. All matching of the fins to the catalogue was verified by a second independent researcher.

Previous studies have distinguished two different dolphin communities utilizing the coastal waters of this study area: animals with sightings inside West Bay, San Luis Pass, and the coastal waters, and those sighted only in the coastal waters with a much lower re-sighting rate (Henderson, 2004; L.-J. Irwin & Würsig, 2004; K.S. Maze & Würsig, 1999). The sighting histories of all marked individuals identified from the 10 sightings on the coastal track-lines were reviewed to see if a similar pattern emerged. Any sightings consisting primarily of dolphins with no sightings inside West Bay or San Luis Pass were presumed to be members of a neighbouring stock rather than the West Bay Stock and were excluded from the the "coastal parsed" dataset. The "coastal parsed" dataset, is the primary one used in this study, and is described in greater detail in the results section below. To be thorough the full data set including all 10 coastal sightings ("all sightings") and the dataset excluding all 10 coastal sightings ("inside only") were also examined.

Abundance estimation

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The CMR data were analysed with the software package MARK version 8.2 (http://www.phidot.org/software/mark/index.html, accessed 15 Nov. 2017) using two different groups of models: the Pollock's closed capture robust design models (Kendall et al., 1997; Kendall et al., 1995; Pollock, 1982) and the Poisson-log normal mark-resight models (McClintock & White, 2010; McClintock et al., 2009). Pollock's closed capture robust design models estimate the abundance of marked individuals in the population during each primary session along with probability of capture and probability of recapture for each secondary session. These models follow a set of assumptions including: all marks are unique and not lost or misread, survival is equal for all individuals between primary periods, each individual's capture probability and survival probability is independent of all others and the population is closed between primary sampling periods (Kendall et al., 1995). The duration of the primary sampling periods were short (14 days in winter and 17 days in summer) in an effort to meet the assumption of closure (e.g. limited births, deaths, immigration, emigration during that time) and also limit the number of fin changes that could occur (limiting lost marks). By selecting only the highest quality photos and highest levels of fin distinctiveness as marked, it is assumed any errors caused by either missing marks or mis-identifying fins are limited. We have no reason to believe the assumption for equal survival rates among individuals would be violated. It is possible that the assumption of independence of individual's capture probability was not met. Bottlenose dolphins are known to live in fission-fusion societies with members that form small groups that change composition frequently (Connor, Wells, Mann, & Read, 2000; Wells, 2003). There can be strong social associations between dolphins in a community where some dolphins are more likely to be found together than with other individuals, particularly male-pair bonds and mother-calf associations. The strength of these associations can vary considerably both between and within communities (Wells, 2003). In addition, calves stay with their mother for 3 – 6 years though some may begin moving independently before then (Wells, 2003). Violation of this assumption would presumably lead to individual capture heterogeneity which was tested for during the analysis. The direction of any potential bias on the abundance estimate is unknown though it is expected to be small given the high capture probability in this population.

The data were analysed using both the full-likelihood approach and the conditional likelihood approach (termed "Huggins p & c") of the Pollock's robust design models (Huggins, 1989, 1991; Otis, Burnham, White, & Anderson, 1978). In both approaches, p is the probability of first capture and c is the probability of recapture. With only two primary periods, it is not possible to estimate emigration or immigration. However, by running the no emigration model (γ" to 0), S is a valid survival estimate representing the probability of surviving and staying in the study area between primaries. Three models were analysed using both the full-likelihood and Huggins

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approaches. Using the Otis et al. (1978) notation, data were analysed using the M_t model where p and c are assumed to be time varying and equal, and the M_{tb} model where p and c were allowed to vary with time but were not equal to each other, thus allowing a behavioural difference between the probability of capture and the probability of recapture. The most basic model (M_0) was also analysed for comparison. Individual heterogeneity was not included in the closed capture models as more surveys were needed and models including heterogeneity could not converge. Model selection was based upon Akaike's Information Criterion (AIC_c) with the preferred model having the lowest AIC_c (Hurvich & Tsai, 1989; Sugiura, 1978) Models were averaged (weighted by AIC_c) to account for model selection uncertainty (Burnham & Anderson, 2016). The derived abundance estimate for the marked individuals was then divided by the proportion of marked fins (i.e., distinct animals) photographed to provide an estimate of total individuals (marked and unmarked) in the sampled population. The proportion marked was calculated by dividing the number of marked animals (D2 and D1) seen in each sighting by the total number of animals catalogued from that sighting and was calculated only from those sightings with complete photo coverage (photo completeness ≥ 1, calculated by the number of catalogued dolphins for a sighting divided by the field estimate of the number of dolphins present in that sighting (Balmer et al., 2013; Speakman, lane, Schwacke, Fair, & Zolman, 2010; Wilson, Hammond, & Thompson, 1999).

The zero-truncated Poisson-log normal model (ZPNE) was designed for use with mark-resight data (where encounters consist of sighting data not physical captures) and in cases where the number of marks in the population may be unknown and sampling within a survey is with replacement, which is the case for dolphin photo-ID studies (McClintock et al., 2009). The Poisson-log normal mark-resight models can also be used to estimate abundance when sampling is conducted following the robust design, as was done here. An important difference between the mark-resight model and the closed capture robust-design models is that the mark-resight approach uses a derived mean resighting rate of marked animals and incorporates counts of sightings of unmarked animals into the estimation framework thereby directly estimating the abundance of both marked and unmarked animals in the population for each primary session (McClintock et al., 2009). Assumptions for this model include: 1) geographic and demographic closure within each primary period; 2) no loss of marks within each primary period though it is permissible for new marks to appear in between primary periods; 3) no errors in distinguishing marked and unmarked animals; and 4) independently and identically distributed resighting probabilities for both marked and unmarked animals (McClintock & White, 2010; McClintock et al., 2009). The first three assumptions are very similar to those discussed above for the closed-capture robust design models. Every effort was made during our surveys to photograph each

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animal in the group regardless of fin distinctiveness which addresses assumption four. We have no reason to believe the capture probabilities would be any different for marked or unmarked fins.

In the analyses, the parameters for the mean resighting rate (α) and for the number of unmarked individuals in the population (U) were both allowed to vary with time. The parameter for individual heterogeneity in resighting rates (σ) was allowed to vary with time, remain constant, or was set to zero resulting in three models being analysed. The parameters for the probability of remaining outside the study area (probability of not immigrating - γ') and the probability of transitioning out of the study area (emigrating -γ") could not be estimated in this study with only two primary sessions. The apparent survival between primary sessions (θ) was estimated; however, it is important to note that this represents the estimate of true survival combined with the probability of staying in the study area since γ' and γ" could not be estimated and therefore, γ" was fixed to zero.

3. Results

There were 12 dolphin groups sighted in the winter and 24 in the summer with 45 and 80 marked animals sighted respectively (Table 1; 97 marked animals total in both seasons combined). Similar to previous studies, it appeared there were different communities of dolphins overlapping in the coastal region. Of the 97 marked animals, 49 were sighted either in West Bay only or in both West Bay and the coastal area. 84% of those 49 were seen more than once and 73% were seen in 3 – 11 sightings. Hereafter, we refer to these animals as the West Bay Community, which is consistent with what previous studies described as the "Bay" or "resident" dolphins (Henderson, 2004; Maze & Würsig, 1999). Forty-eight animals were only seen in coastal waters with a low re-sighting rate and are likely not a part of the West Bay Community. Forty-four of those (92%) were only seen on a single day (either one or two sightings, same day). The remaining four animals were seen on two different days (a maximum of three sightings on two days). These animals are consistent with what previous studies called "Gulf dolphins" and we will use the same terminology here. The "Gulf dolphins" are likely part of the Western Coastal Stock of common bottlenose dolphins though it is possible they are from a neighboring BSE stock such as Galveston Bay.

In an effort to exclude sightings from the dataset that were likely not representative of the West Bay Community, the 10 sightings from coastal transects outside of San Luis Pass (Table 2, Figure 2) were examined, and a clear pattern emerged. In four of these coastal sightings (3 winter, 1 summer), the majority of marked animals (>70%) had also been seen in West Bay

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and/or San Luis Pass while the remaining animals from those four sightings had either only been seen once or had unmarked fins. These sightings were considered West Bay Community sightings and were included in the "coastal-parsed dataset" (Figure 2). This was in contrast to the other six coastal sightings where all marked dolphins except for one had only been seen once or twice and never in West Bay or San Luis Pass. These six sightings were considered to be sightings of "Gulf dolphins" and they were excluded from the "coastal-parsed dataset" (Figure 2). The "coastal parsed" dataset was analysed as the primary dataset as it best represents the West Bay community. For comparison, we also analysed the "all sightings" dataset including all 10 coastal sightings and the "inside only" dataset excluding all 10 coastal sightings using the mark-resight model (Figure 2).

Results from the coastal-parsed dataset analysed using both of the Pollock's robust design closed capture model approaches (full-likelihood and Huggins) supported the M_t and M_{tb} models (Tables 3 & 4), while AIC_c values indicated no support for the M_0 models. The Delta AIC_c between the M_t and M_{tb} models using the full-likelihood model was 3.6, indicating slight support for the M_t model over the M_{tb} model; however, the Delta AIC_c was less than 2 using the Huggins model, indicating no support for one over the other (Tables 3 & 4). Therefore, the weighted average of the marked population size (N) was calculated using the model averaging function within MARK for each model type. Capture probabilities were low in the first secondary survey of the winter session (0.15) but were higher for the other five secondary surveys ranging from 0.63 – 0.93 (Tables 5 & 6). The model averaged N was then corrected by the proportion marked for each season (0.90 winter and 0.95 summer) calculated from the sightings with photo-completeness ≥ 1 (2 of 11 sightings in winter and 12 of 19 sightings in summer; Table 7). The resulting abundance estimates were 49.86 and 51.54 in the winter and 41.16 and 43.76 in the summer (Full-likelihood and Huggins respectively; Table 7). The variance for these abundance estimates applies only to the estimate of marked individuals and does not include uncertainty in the proportion of marked fins in the population (Table 7).

The results from the mark-resight ZPNE models were very similar with similar support among the tested models (ΔAIC of <2.5 across models, Tables 8 & 9). Therefore, the weighted average of the total derived population size (N) was calculated using the model averaging function within MARK, resulting in an estimated abundance of 50.63 (Unconditional SE 2.23) in the winter and 44.36 (Unconditional SE 1.18) in the summer (Table 7). For these mark-resight models, variance estimates include uncertainty in the number of unmarked individuals in the population. The abundance estimate derived from the "inside only" dataset was quite similar resulting in an estimated abundance of 52.40 (Unconditional SE 3.95) in the winter and 44.59 (Unconditional

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SE 1.24) in the summer (Table 10). The estimates derived from the “all sightings” dataset reflected a higher but similar estimate in the winter and a much higher estimate in the summer (Table 10; 55.40, unconditional SE 2.91 and 106.52, unconditional SE 5.96 respectively). Results for the ZPNE models analysing the “inside only” and “all sightings” datasets can be found in supplemental tables S1 – S4.

4. Discussion

Photo-ID CMR studies have proven to be effective in estimating abundances of BSE dolphin stocks. While long-term studies are beneficial for understanding a broader suite of population parameters (emigration, immigration, long-term survival, social structure, etc.); they can be time-consuming and expensive. The most recent Gulf of Mexico BSE Stock Assessment report shows that 28 stocks are in need of updated abundance estimates to calculate N_{min} and PBR (Hayes et al., 2017). In this study we were able to generate abundance estimates from a short-term study with data collected during only two primary periods of about two weeks each, contributing to improved management of this stock. In addition, the data were analysed using the less-commonly applied mark-resight model and compared with the results from the more commonly applied closed capture robust design models.

The abundance estimates from all model types applied to the “coastal-parsed” dataset were very similar ranging from 49.8 – 51.5 dolphins in the winter and 41.2 – 44.4 dolphins in the summer (Table 7). The mark-resight model is preferred in that it includes individual heterogeneity, and it directly incorporates data from unmarked animals accounting for the uncertainty in the proportion of animals with distinct fins, which we believe is an improvement over the closed capture robust design models. Given the small population size and the high resighting rate in this study, the model specification did not appear to have a meaningful impact on the West Bay abundance estimate. It would be interesting to apply the mark-resight model to a broader range of photo-ID datasets (e.g. larger populations, lower resight-rates) and compare performance to the robust design models under less ideal conditions with greater likelihood of significant capture heterogeneity.

Due to the relatively small size of this study area, it was possible to thoroughly examine the sighting histories of the marked animals seen on the coastal track-lines in an effort to exclude dolphins from neighbouring communities from the abundance estimate for the West Bay Community. As a result the estimates derived from the mark-resight model for three different datasets were compared. The results from the “coastal-parsed” dataset were very similar to the “inside-only” dataset, and the two had overlapping confidence intervals around the estimates.

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Interestingly, the two datasets had the same minimum number of known marked animals in the summer and only differed by four animals in the winter, and the standard error was lower for the "coastal-parsed" dataset. The "all-sightings" dataset included a similar minimum number of known animals in the winter compared to the coastal-parsed dataset (45 vs. 42 respectively) but a higher number of known individuals in the summer (80 vs. 39 respectively). This is reflected in the abundance estimates where the winter estimate was slightly higher but within the 95% confidence interval of the coastal-parsed dataset but the summer estimate of 106 dolphins was much higher, possibly reflecting a higher number of "Gulf dolphins" off of San Luis Pass in the summer. However, it is important to note that this difference could be related to two large sightings on the same day (6/8/2015) in the coastal waters, with 30 and 36 dolphins respectively (Table 2). More surveys would need to be conducted before drawing any strong conclusions on seasonality. It is interesting to note that the sigma parameter estimating individual capture heterogeneity (0.63) was high for the summer season in the "all sightings" dataset (Table S4) compared to the low sigma estimate in the other models, likely due to having different capture probabilities in the West Bay Community and the "Gulf dolphins". The comparison of these three datasets supports the decision to parse out the coastal sightings to obtain the data most accurately representing the range of the West Bay Community while including more data to increase our precision.

There is, however, some uncertainty in assigning sightings to the Gulf versus West Bay community as it does not account for the possibility of mixed sightings. There is evidence from previous studies that mixed sightings do occur. Maze-Foley and Würsig (2002) found that each sighting of Gulf animals included at least one Bay animal, and that all mixed sightings were in the coastal waters. Henderson and Würsig (2007) identified 8 of 44 sightings observed during their 2002 – 2003 surveys as mixed groups and stated that the mixed groups were primarily seen in Gulf waters (6 of 8 mixed groups). This is similar to findings from a study on the central west coast of Florida that found 14% (71 of 493) of sightings in the Gulf coastal waters were mixed groups of Gulf and inshore dolphins (Fazioli et al., 2006). In the present study, only one sighting in coastal waters included a single West Bay Community dolphin with 30 other marked dolphins that were presumed to be from another community since they were only ever seen in Gulf coastal waters (6/8/2015, sighting 2, Table 2). In addition, the four coastal sightings retained in analyses as West Bay Community sightings contained 0 – 30% of animals (0/11, 1/10, 3/10, and 1/8; Table 2) that were only sighted once. All dolphins in these four sightings were retained in the analyses as presumed West Bay community dolphins. However, it is possible that these were mixed sightings, and the five dolphins only observed once were from a neighbouring community. It is also possible that some coastal stock dolphins were present in estuarine waters

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and therefore incorrectly assigned as BSE animals and included in the analyses, although the studies by Henderson and Würsig (2007) and Maze-Foley and Würsig (2002) indicate this is likely rare, particularly inshore of San Luis Pass. Future research with a focus on understanding the habitat use, seasonality and movement of West Bay animals in coastal waters; movement of “Gulf dolphins” into West Bay and neighbouring Galveston Bay estuarine waters; and the degree of mixing between West Bay and neighbouring dolphin communities would be helpful. This could ideally be achieved with tagging studies but could also be accomplished with additional photo-ID surveys and comparisons among photo-ID catalogues.

Following the comparisons of the different model types and the three different datasets, we recommend the model results from the mark–resight model analysing the “coastal-parsed” dataset (50.63 winter, 44.36 summer, 47.5 mean) be used as the best abundance estimate for the management of the West Bay BSE Stock of common bottlenose dolphins (Table 7). The population of dolphins utilizing West Bay and San Luis Pass is relatively small and should be closely monitored for impacts from stressors, particularly human-caused stressors. The updated abundance estimate from this study will allow managers to calculate a PBR for the West Bay BSE stock. The PBR is used as a benchmark to compare to the numbers of known human-caused mortalities and can trigger management actions if the mortalities exceed the PBR level (Wade & Angliss, 1997). There have been documented cases of human-caused mortality in the West Bay Stock area in the past, including a stranded dolphin with a hook and line fishing gear interaction in 2014 (Hayes et al., 2017) and two stranded dolphins on the Gulf side of the barrier islands of West Bay with evidence of a boat collision (Phillips & Rosel, 2014). It is also important to note that strandings likely underestimate the extent of human-caused mortality because not all of the animals that die will wash ashore and if the carcass does wash ashore, it may not be reported (Authier et al., 2014; Wells et al., 2015). In addition, evidence of human-interaction on a carcass could be lost due to decomposition, scavenging, or other factors (Byrd et al., 2014). Continued monitoring for evidence of human-caused mortality and having a PBR level to compare with those mortality rates is critical for the management of the West Bay BSE stock.

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Tables

Table 1. Survey data per primary period (including all data – West Bay and coastal sightings) with total number of km of track-line surveyed, number of sightings, total number of dolphins sighted (sum of best group size estimate from field per season), number of calves sighted, number of neonates sighted, mean group size per season (mean of best group size field estimate per season).

	Winter 2014	Summer 2015
Km surveyed†	763	867
# of sightings†	12	24
Total # of dolphins sighted †	160	269
# of calves sighted†	15	46
# of neonates sighted†	0	2
Mean sighting group size	13.3	11.2

†Also presented in Ronje et al. 2018

Table 2. Characteristics of ten coastal sightings further evaluated. Sightings are listed in geographic order from the north-east to the south-west sightings (see locations in Fig. 2). WB = West Bay Community of dolphins

Date	Sight. #	No. animals per sighting	Characteristics	Outcome

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6/19/2015	1	3	All 3 seen 1 – 2 times and only coastal	Presumed not WB
6/19/2015	2	2	Both seen twice only on 6/19	Presumed not WB
12/6/2014	1	10	7 marked fins seen in Bay and/or Pass in addition to coastal sighting. 3 marked only seen once.	Presumed WB
12/6/2014	2	8	8 marked fins seen in Bay and/or Pass in addition to coastal sighting.	Presumed WB
12/6/2014	3	10	9 marked fins seen in Bay and/or Pass in addition to coastal sighting. 1 marked seen only once	Presumed WB
6/8/2015	1	30	24 marked fins seen 1 – 2 times and only coastal. Remaining 6 unmarked	Presumed not WB
6/19/2015	3	11	10 marked fins seen in Bay and/or Pass in addition to coastal sighting. 1 unmarked fin.	Presumed WB
6/11/2015	1	3	All 3 seen 1 – 3 times and only coastal	Presumed not WB
6/8/2015	2	36	30 marked fins seen 1 – 2 times and only coastal. 1 marked dolphin with multiple Bay and Pass sightings was present in this sighting. Remaining 5 were unmarked fins	Presumed not WB
12/10/2014	1	3	3 animals only seen once	Presumed not WB

Table 3. Model results from the Pollock's robust design full-likelihood p & c approach. M_t = detection probabilities assumed to be time varying; M_{tb} model where detection probabilities vary with time but also recapture probabilities are different from initial capture probabilities; $M_{0=}$ the null model with constant detection probabilities across all factors.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
M_t	-145.958	0	0.86125	1	8	8.9078
M_{tb}	-142.306	3.6514	0.13875	0.1611	11	5.7621
M_0	-110.100	35.8576	0	0	4	53.4341

Table 4. Model results from the Pollock's robust design Huggins p & c approach. M_t = detection probabilities assumed to be time varying; M_{tb} model where detection probabilities vary with time

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but also recapture probabilities are different from initial capture probabilities; $M_{0=}$ the null model with constant detection probabilities across all factors.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
M_{tb}	296.2786	0	0.62871	1	9	448.9073
M_t	297.332	1.0534	0.37129	0.5906	7	454.4056
M_0	332.5273	36.2487	0	0	3	498.1617

Table 5. Real function parameters from the Pollock's robust design Full-likelihood M_t model. Parameters: S=probability of surviving between primaries; Gamma'' = probability of transitioning from an observable state (on the study area) to unobservable (off the study area) in between primary periods; p=probability of capture in each secondary survey within each primary session, f_0=number of individuals with no sightings during each primary.

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:S	0.6691035	0.0730258	0.5144122	0.7942279
2:Gamma''	0.0000000(Fixed)	0.0000000	0.0000000	0.0000000
3:p Session 1	0.1559243	0.0548302	0.0754793	0.2947705
4:p Session 1	0.7127952	0.0782385	0.5398982	0.8399780
5:p Session 1	0.6905225	0.0789005	0.5197178	0.8214517
6:p Session 2	0.6923084	0.0739052	0.5326839	0.8162200
7:p Session 2	0.8461541	0.0577744	0.6973851	0.9292104
8:p Session 2	0.9230777	0.0426690	0.7870277	0.9749798
9:f_0 Session 1	2.8936006	2.4885424	0.6730632	12.440027
10:f_0 Session 2	0.1032339E-006	0.2546963E-003	0.4461190E-010	0.2388879E-003

Table 6. Real function parameters from the Pollock's robust design Huggins M_{tb} model. Parameters: S=probability of surviving between primaries; Gamma'' = probability of transitioning from an observable state (on the study area) to unobservable (off the study area) in between primary periods; p=probability of capture in each secondary survey within each primary session, c = probability of recapture in each secondary survey within each primary session.

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:S	0.7350427	0.1384527	0.4078118	0.9178689

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2:Gamma''	0.0000000(Fixed)	0.0000000	0.0950529	0.0950529
3:p Session 1	0.1496855	0.0543764	0.0708030	0.2891082
4:p Session 1	0.6538462	0.1338737	0.3720716	0.8575780
5:p Session 2	0.6279070	0.1251745	0.3712547	0.8282585
6:p Session 2	0.5000001	0.3061863	0.0831346	0.9168655
7:c Session 1	0.8571429	0.1322600	0.4193889	0.9803301
8:c Session 1	0.6666666	0.0820610	0.4923429	0.8048559
9:c Session 2	0.9259259	0.0504010	0.7475200	0.9814038
10:c Session 2	0.9142857	0.0473188	0.7656055	0.9720933

Table 7. Winter and summer population estimates (N), unconditional standard error (SE), coefficient of variation (CV), and 95% confidence intervals (95% CI) derived from the Pollock's closed capture (CC) robust design full-likelihood and Huggins approaches and the mark-resight zero-truncated Poisson log-normal mixed effects model (ZPNE) using the "coastal-parsed" dataset. "Min. known marked" represents the minimum number of identified marked fins in the catalog per season. The CIs for model averaged estimates were calculated as outlined in Cooch & White (2017) chapter 14.10.

	Winter	**Summer**
Min. known marked	42	39
Proportion marked	0.90	0.95
CC Full - likelihood		
Estimated Marked N	44.88	39.10
Unconditional SE[†]	2.65	0.88
CV[†]	0.06	0.02
95% CI[†]	42.6 – 55.4	39.0 – 45.0
Estimated Total N[‡]	**49.86**	**41.16**
CC Huggins		
Estimated Marked N	46.39	41.57
Unconditional SE[†]	4.15	5.8
CV[†]	0.09	0.14
95% CI[†]	42.9 - 63.0	39.2 - 74.8
Estimated Total N[‡]	**51.54**	**43.76**
ZPNE		
Estimated Total N	**50.63**	**44.36**
Unconditional SE	2.23	1.18

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CV	0.04	0.03
95% CI	47.2 - 56.2	42.5 - 47.2

‡ Estimated Total N is the estimated marked N corrected by the proportion marked for each season.
†The variance in the closed capture models apply only to the estimates of marked individuals and do not include uncertainty in the proportion of marked fins in the population and therefore are not directly comparable to the variance of the ZPNE models.

Table 8. Results for the Mark-Resight zero-truncated Poisson log-normal mixed effects models. Parameter definitions: α = intercept for the mean resighting rate during each primary interval; σ = individual heterogeneity in resighting rates during each primary interval; U = number of unmarked individuals in the population during each primary interval; γ'' = probability of transitioning from an observable state (on the study area) to unobservable (off the study area) in between primary periods; φ = apparent survival between primary periods. In the models below α, U, and φ were all allowed to vary with time, γ'' was fixed to 0 (no emigration model), and σ was fixed at 0, varied with time, or held constant over time (.)

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
α(t) **σ(0)** U(t) γ''(0) ϕ(t)	370.7809	0	0.71057	1	5	360.0016
α(t) **σ(t)** U(t) γ''(0) ϕ(t)	373.1064	2.3255	0.22214	0.3126	6	360.0012
α(t) **σ(.)** U(t) γ''(0) ϕ(t)	375.4950	4.7141	0.06729	0.0947	7	360.0016

Table 9. Real function parameters from the mark-resight model with σ(t). Alpha is the intercept for the mean resighting rate during each primary; sigma is the individual heterogeneity in resighting rates during each primary; U is the number of unmarked individuals in the population during each primary; phi is the apparent survival between primary periods in this case representing the combination of true survival and staying in the study area; Gamma'' is the probability of transitioning from an observable state (on the study area) to unobservable (off the study area) in between primary periods.

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:alpha	2.2025080	0.2534181	1.7591353	2.7576284
2:alpha	4.4041701	0.3714255	3.7342541	5.1942674
3:sigma	0.9654619E-004	0.2107618	0.4434260E-007	0.2102079
4:sigma	0.0340041	0.7955697	0.2476340E-003	4.6693110
5:U	3.4068232	1.2685080	1.6812591	6.9034238

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6:U	4.8796352	1.1104280	3.1413837	7.5797297
7:Phi	0.6748971	0.0736934	0.5180209	0.8003882
8:Gamma''	0.0000000 (fixed)	0.0000000	0.0000000	0.0000000

Table 10. Winter and summer population estimates (N), unconditional standard error (SE), coefficient of variation (CV), and 95% confidence intervals (95% CI) derived from the mark-resight zero-truncated Poisson log-normal mixed effects model (ZPNE) for “inside only”(excluding 10 sightings in coastal waters) and “all sightings” dataset (including all 10 coastal sightings). "Min. known marked" represents the minimum number of identified marked fins in the catalog for each dataset per season. The CIs for model averaged estimates were calculated as outlined in Cooch & White (2017) chapter 14.10.

	Winter	**Summer**
ZPNE - Inside only		
Min. known marked	38	39
Proportion marked	0.90	0.96
Estimated Total N	**52.4**	**44.59**
Unconditional SE	3.95	1.24
CV	0.08	0.03
95% CI	46.5 - 62.4	42.6 - 47.6
ZPNE - All sightings		
Min. known marked	45	80
Proportion marked	0.90	0.95
Estimated Total N	**55.99**	**106.08**
Unconditional SE	3.36	5.90
CV	0.06	0.06
95% CI	51.1 – 64.7	96.8 – 120.4

Figure Legends

Figure 1. Map of the West Bay, Texas, study site including track-lines and common bottlenose dolphin sightings from the December 2014 and June 2015 CMR surveys.

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Figure 2. The sighting histories of animals from ten sightings in coastal waters were evaluated (winter sightings in blue and summer sightings in red). Those represented by blue and red circles were presumed West Bay Community (WB) sightings and retained in the “coastal-parsed dataset” in addition to the sightings inside West Bay and San Luis Pass shown in green. Those represented by squares were presumed “Gulf dolphin” sightings (not WB) and excluded from the the “coastal-parsed” dataset. The “inside-only” dataset included only those sightings shown in green and the “all-sighitngs” dataset included all sightings shown on the map.

Supplemental Data

Parameter definitions for all tables below:

Parameter definitions: Alpha (α) = intercept for the mean resighting rate during each primary interval; Sigma (σ) = individual heterogeneity in resighting rates during each primary interval; U = number of unmarked individuals in the population during each primary interval; Gamma" (γ") = probability of transitioning from an observable state (on the study area) to unobservable (off the study area) in between primary periods; Phi (φ) = apparent survival between primary periods. In the models below α, U, and φ were all allowed to vary with time, γ" was fixed to 0 (no emigration model), and σ was fixed at 0, varied with time, or held constant over time (.)

Table S1. Results for the Mark-Resight zero-truncated Poisson log-normal mixed effects models using the inside only dataset.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
α(t) **σ(0)** U(t) γ"(0)ϕ(t)	319.0074	0	0.71306	1	5	308.1855
α(t) **σ(.)** U(t) γ"(0) ϕ(t)	321.3521	2.3447	0.22079	0.3096	6	308.1855
α(t) **σ(t)** U(t) γ"(0) ϕ(t)	323.7629	4.7555	0.06614	0.0928	7	308.1855

Table S2. Real function parameters from the mark-resight model using the inside only dataset with σ(.).

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:alpha	1.5936255	0.2372594	1.1922045	2.1302069
2:alpha	4.1380384	0.3345434	3.5325569	4.8472998
3:sigma	0.6898887E-004	0.1035106	0.3830718E-007	0.1242447
4:U	4.7085002	1.8087406	2.2755068	9.7428731

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5:U	4.9554553	1.1530602	3.1595348	7.7722002
6:Phi	0.7487861	0.0727057	0.5828728	0.8640941
7:Gamma''	0.0000000 (fixed)	0.0000000	0.0000000	0.0000000

Table S3. Results for the Mark-Resight zero-truncated Poisson log-normal mixed effects models using the all sightings dataset.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
α(t) **σ(t)** U(t) γ''(0)ϕ(t)	527.6406	0	0.76889	1	7	512.6994
α(t) **σ(.)** U(t) γ''(0) ϕ(t)	530.0502	2.4096	0.23048	0.2998	6	517.3502
α(t) **σ(0)** U(t) γ''(0) ϕ(t)	541.8591	14.2185	0.00063	0.0008	5	531.3632

Table S4. Real function parameters from the mark-resight model using the all sightings dataset with σ(t).

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:alpha	2.0810262	0.2399006	1.6613953	2.6066464
2:alpha	2.1883629	0.2829445	1.7002666	2.8165772
3:sigma	0.2092244E-004	0.0642882	0.8115209E-008	0.0539418
4:sigma	0.6323608	0.1273018	0.4278621	0.9346006
5:U	3.6056992	1.3428046	1.7791877	7.3073050
6:U	11.921063	3.4179558	6.8716608	20.680845
7:Phi	0.6683839	0.0789152	0.5007615	0.8019813
8:Gamma''	0.0000000 (fixed)	0.0000000	0.0000000	0.0000000

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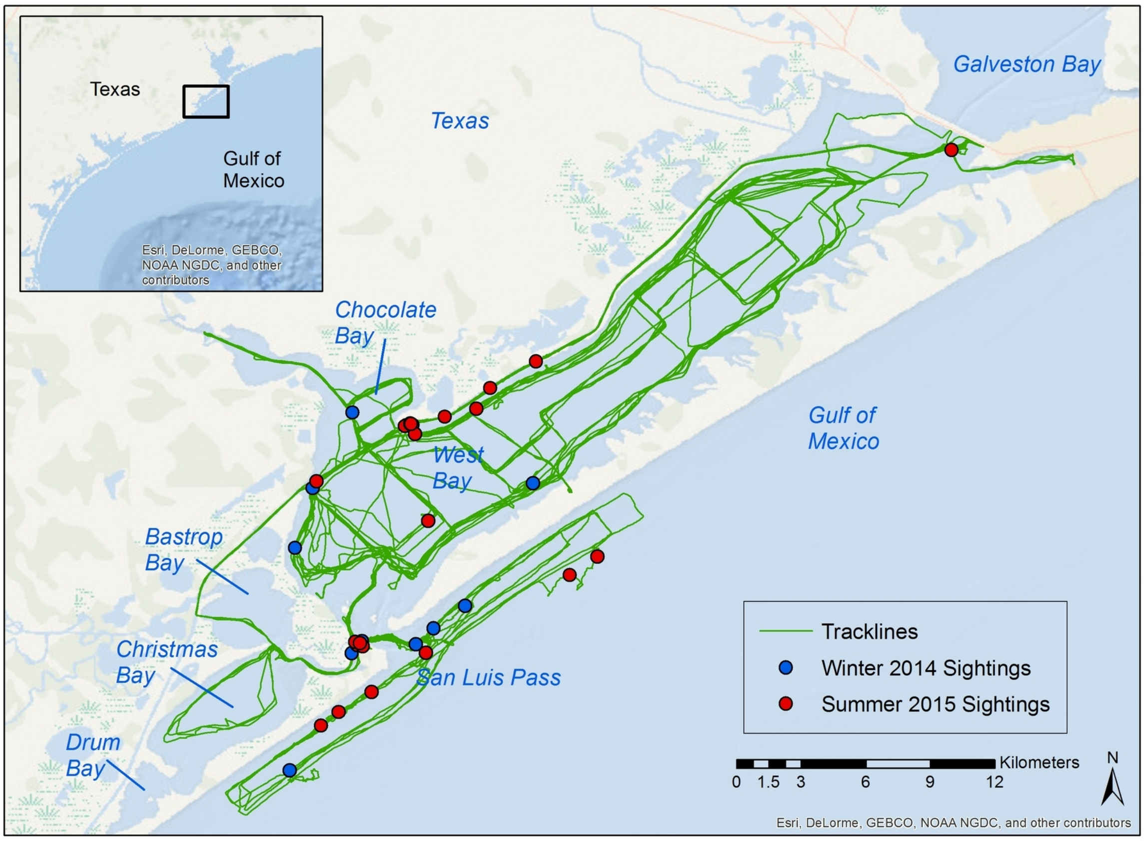

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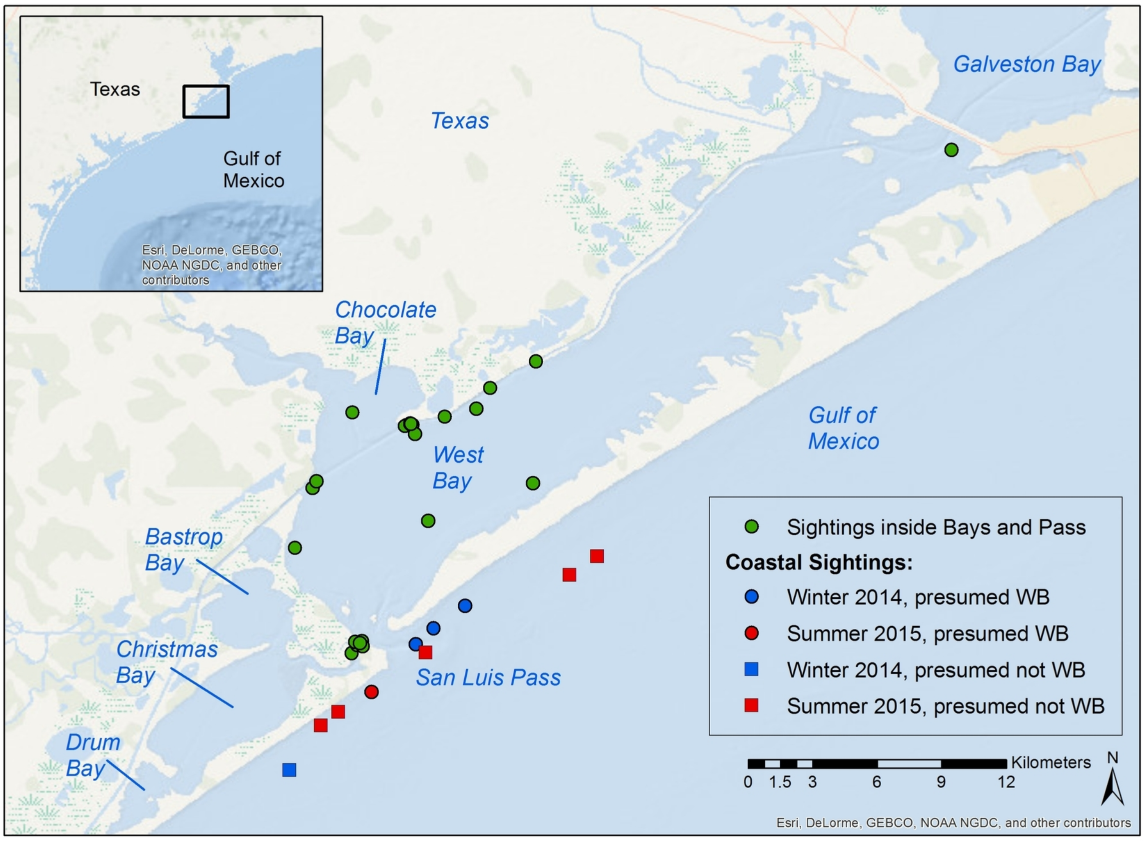

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