# Historic Population Estimates for Bottlenose Dolphins (*Tursiops truncatus*) in Aragua, Venezuela, Indicate Monitoring Need

Sergio Cobarrubia-Russo,[1,2] Shannon Barber-Meyer,[3,4] Guillermo R. Barreto,[2] and Alimar Molero-Lizarraga[5]

[1]*Laboratorio de Ecosistemas y Cambio Global, Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 20632, Caracas 1020-A, Venezuela*
[2]*Departamento de Biología de Organismos, Laboratorio de Manejo y Conservacíon de Fauna Silvestre, Universidad Simón Bolívar, Apartado 89000, Caracas 1080-A, Venezuela*
[3]*U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711–37th Street, SE, Jamestown, ND 58401, USA*
[4]*U.S. Geological Survey, 1393 Highway 169, Ely, MN 55731, USA*
*E-mail: sbarber-meyer@usgs.gov*
[5]*Unidad de Diversidad Biológica, Instituto Venezolano de Investigaciones Cientificas, Caracas 1020-A, Venezuela*

## Abstract

This study reports historic capture-mark-recapture survival and abundance estimates of common bottlenose dolphins (*Tursiops truncatus*) based on photo-identification surveys of coastal Venezuela (along the Aragua coast between Turiamo Bay and Puerto Colombia). We used the most recent data available: dolphins identified by unique dorsal fin marks during wet and dry season surveys conducted from 2004 to 2008. Dolphin encounter histories were analyzed in the Closed Capture Robust Design framework, with the top model including random movement, constant survival, and capture-recapture probabilities that varied by secondary periods. Survival of marked adults was estimated at 0.99 (95% CI = 0.97 to 1.00). Population estimates for all adults (marked and unmarked) averaged 31 animals (SD = 13.8), and for all dolphins (all adults and calves), 41 animals (SD = 17.2). Coastal bottlenose dolphins face numerous threats, including ship strikes, oil spills, conflict with recreational and industrial fisheries, other negative human interactions, biotoxins, chemicals, noise, freshwater discharge, and coastal development. Further, small populations are, in general, at increased risk due to reduced resiliency and recovery potential when exposed to such threats and to expected environmental and demographic stochasticity. These historic estimates of abundance and survival are critical for establishing a reference state and indicate a need for ongoing monitoring of the small dolphin population while the Aragua coast is still, as of yet, relatively little impacted by humans. Should coastal development increase (as is the global trend) and/or environmental catastrophes (e.g., harmful algal blooms, hurricanes, and oil spills) occur, these historic estimates will be essential for assessing impacts and guiding management and conservation interventions. Our results show year-round dolphin presence and highlight the Venezuelan coastal–oceanic landscape as an area of both future research and conservation importance.

**Key Words:** abundance, capture-mark recapture, cetacean, closed capture, robust design, survival, temporary emigration, bottlenose dolphin, *Tursiops truncatus*

## Introduction

Bottlenose dolphins (*Tursiops* sp.) are widespread, with populations found from equatorial to temperate seas and coastal to pelagic habitats all over the planet (coastal and oceanic ecotypes) (Leatherwood & Reeves, 1983; Shane et al., 1986; Wells & Scott, 1999; Reynolds et al., 2000). Populations of common bottlenose dolphins (*T. truncatus*; National Marine Fisheries Service [NMFS], 2016) vary in number depending, in part, on habitat, with those in neritic and pelagic zones ranging from 200 to 1,000 individuals, while those in coastal areas usually comprise less than 200 individuals (Bearzi et al., 1997; Defran & Weller, 1999; Wilson et al., 1999; Read et al., 2003; Fruet et al., 2011; Litz et al., 2019).

The western coast of Aragua, Venezuela (Figure 1), is a year-round host for two species of dolphins: (1) the common bottlenose dolphin and (2) the Atlantic spotted dolphin (*Stenella frontalis*). From 2004 to 2008, 100 small-boat transect surveys were conducted resulting in a daily encounter ratio between 0.79 and 1.11 dolphins/survey (Cobarrubia-Russo et al., 2019). During that period,
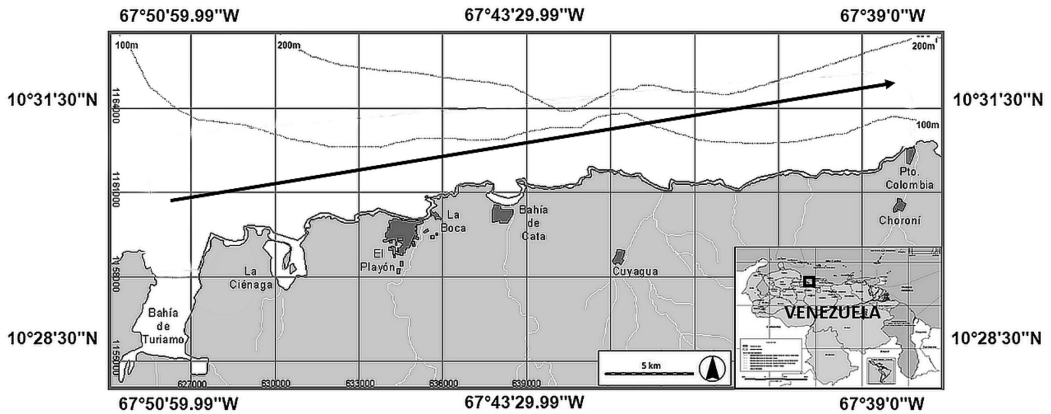
**Figure 1.** Map of the coastal Venezuela study area and transect surveyed (black arrow) during the 2004-2008 study period. Also depicted are the inset (location of study area in Venezuela), scale bar (5 km), and north arrow (open circle with line pointing north).

the accumulated number of unique bottlenose dolphins sighted never exceeded 100 (Cobarrubia-Russo et al., 2019). Observed groups of bottlenose dolphins that collectively comprised the superpopulation of the area included a local group of mother-calf pairs, other near-coast mother-calf groups, and all-male groups during the November to February reproductive season (Cobarrubia-Russo et al., 2019).

Although exploitation of cetaceans in Venezuela has occurred in the past (Romero et al., 1997), the government currently attempts to protect common bottlenose dolphins and the more than 20 other cetacean species recorded there (Romero et al., 2001; Bolaños & Villarroel-Marín, 2003) through the Law on the Protection of Wildlife and its Regulations (GORV Number 29.289, 8/11/1970), the Law on the Management of Biodiversity (GORBV Number 39.070, 12/1/2008), and Article 127 of the Constitution of the Bolivarian Republic of Venezuela (1999). Venezuela is also a signatory nation to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). However, major threats facing cetaceans persist, including incidental fishing, poaching as shark bait, and pollution (Rodríguez & Rojas-Suárez, 2008). In particular, small coastal populations of common bottlenose dolphins face myriad threats from human activities (Methion & Díaz López, 2018; Silva et al., 2020). Further, populations of less than 100 animals are more prone to extinction due to demographic and environmental stochasticity (Gilpin & Soulé, 1986; Traill et al., 2007). It is critical to document the population size of Venezuela's small coastal bottlenose dolphin population while the Aragua coast is still relatively less impacted by humans, before major impacts such as increased coastal development, sea-level rise, and other environmental disasters (e.g., oil spills, hurricanes, and harmful algal blooms)

potentially occur (Balmer et al., 2015; B. Balmer et al., 2018; J. Balmer et al., 2018; Labach et al., 2019; Durden et al., 2020; Ronje et al., 2020).

The primary goal of this study was to use historic data (the most recent data available) to generate the first abundance and survival estimates for Venezuela's coastal bottlenose dolphin population using photo-identification of marked (natural "marks" on their dorsal fins) adults. Capture-mark-recapture of dolphins based on photo-identification is a well-established method to determine abundance and survival (Rosel et al., 2011; Balmer et al., 2019; Labach et al., 2019; Durden et al., 2020; Silva et al., 2020). Capture-mark-recapture methods are preferred as abundance estimators over line-transect methods that estimate density because highly variable group sizes produce imprecise line-transect estimates, and, unless the range is defined, it is not possible to convert density to abundance (Wilson et al., 1999). Increasingly, Pollock's (1982) capture-mark-recapture robust design has been used to obtain accurate estimates of abundance and other demographic variables by expanding on traditional "open" population (primary periods) models to include secondary periods of "closure" within primary periods (Kendall et al., 1997). In this study, we used such Closed Capture Robust Design (CCRD) models to determine the abundance and survival of the marked adults, and to extend the abundance estimates to all adults and all dolphins (adults and calves) in the superpopulation (Kendall, 1999). This study provides benchmark historic status information (abundance and survival) on a coastal population of common bottlenose dolphins along the west-central coast of Venezuela, which will be useful for future demographic parameter comparisons within this population and with other populations. These

historic estimates indicate the need for ongoing monitoring of this small coastal (and, therefore, more vulnerable) common bottlenose dolphin population (Gilpin & Soulé, 1986; Traill et al., 2007; Methion & Díaz López, 2018; Silva et al., 2020).

## Methods

*Study Area*
The coast of Aragua State in Venezuela, South Caribbean, extends for ~60 km, with the western portion (~30 km) located between Turiamo Bay (10º 28' N, 67º 50' W, western terminus) and Puerto Colombia (10º 30' N, 67º 36' W, eastern terminus). The study area extended approximately 3 km from the coastline of the western portion out to the open sea, representing an area of ~92 km$^2$ (Figure 1). The coast was comprised of sandy beaches and rocky cliffs (Gowans et al., 2007). Sea surface temperatures range from 25 to 27°C, whereas salinity generally varies from 34 to 36 ppm (Novoa et al., 1998). The tidal regime is ±24 cm (in a mixed tidal pattern), and the primary weather seasons are dry (November to April) and wet (May to October) (Novoa et al., 1998).

*Data Collection and Photo-Identification*
Where possible, we generally followed the recommendations from Rosel et al. (2011) regarding photo-identification capture-mark-recapture techniques for estimating abundance of bottlenose dolphins. During the 2004-2008 study period, 100 field surveys were conducted via small motorboat (Cobarrubia-Russo et al., 2019). Data from these surveys were the most recent data available for our analysis (Cobarrubia-Russo et al., 2019). These observational surveys were conducted under the Scientific Hunting Permit from the Ministry of the Environment granted by the National Office of Biological Diversity, Venezuela. Each survey started on the western end of the survey transect (Figure 1), lasted 3 to 4 h, and covered ~30 km straight line, with a sea state from one to three (Douglas Scale). Each survey was completed within one day. Observers were able to detect marine mammals out to ~1.5 km (visual domain distance) while surveying common bottlenose dolphins from the superpopulation available in the wider area (Kendall, 1999). A 9-m-long × 2-m-wide "peñero" (Venezuelan fishing motorboat) vessel with a 45-hp outboard engine was used to conduct the surveys at a speed of ~7 kts with three observers—one at the bow, one on port, and one on starboard—all observing from a height of 2 m above sea level.

When a group of dolphins was sighted, the vessel cautiously approached at a slow speed (~0.5 kts) and in a parallel direction to the group's travel so their behavior was not altered by our presence. Once in proximity to the group, we recorded the observation time, group size, and location (using a hand-held Global Positioning System). The bow observer photographed individuals using a Digital Rebel XT Reflex SRL Canon camera with a Tamron 18 to 250 mm zoom lens set to Large/Fine resolution. Individual adult common bottlenose dolphins were later identified by natural, permanent marks (e.g., scars, notches, and deformations) (see below) (Würsig & Würsig, 1977; Wilson et al., 1999; Rosel et al., 2011). Calves were considered part of the unmarked population.

*Data Processing*
For photo-identification and the subsequent capture-mark-recapture analysis, we only used high-quality photographs with clear identification of individuals (good focus, sufficient closeness to detail the notches, and fin perpendicular to the plane of the photo) that was based on one or more distinctive marks (Rosel et al., 2011; Cobarrubia-Russo et al., 2019). Individuals without marks (all calves and some adults) or poorly marked were excluded (Rosel et al., 2011; Cobarrubia-Russo et al., 2019). Multiple sightings of an individual during a single field survey were combined and considered a single sighting. All identifications by photograph were visually determined and also checked with *Finscan*, Version 1.6.1, by three independent observers to minimize errors (Hillman et al., 1999, 2003; Cobarrubia-Russo et al., 2019). Each identified adult was assigned a unique alphanumeric ID (i.e., A, B, C, . . .) indicating the group it was with when first sighted and the chronological order of new dolphins sighted within that group (i.e., 1, 2, 3, . . .). The complete catalogue of photographs compiled from all surveys was used to construct individual encounter histories (date of survey and detection/non-detection by individual).

*Mark-Recapture Analysis*
We analyzed dolphin encounter histories using the 'Huggins p and c' Pollock's CCRD models (Pollock, 1982; Kendall et al., 1997) in *Program MARK*, Version 9.0 (www.phidot.org/software/mark/downloads). These models included primary periods between which the population was considered "open" and secondary periods within primary periods during which the population was considered "closed" (Kendall et al., 1997).

We used wet and dry seasons to form primary periods (rather than the four seasons of a year) (Cagnazzi et al., 2011) to analyze the superpopulation (Kendall, 1999) of Venezuela's coastal bottlenose dolphin population. Because survey effort varied over years (Cobarrubia-Russo et al., 2019), in some years, we analyzed data for more than one

primary period within a single wet or dry season. From the 100 surveys conducted during 2004 to 2008, we selected 39 surveys based on temporal clustering that comprised secondary periods across 13 primary periods (see details below). We did not include dolphins sighted in only one secondary period in the mark-recapture analysis. Although we did not use encounter history data from all 100 surveys, those surveys were still valuable for monitoring changes in fin "marks" over time (Cobarrubia-Russo et al., 2019).

Assumptions for the CCRD models we evaluated included (1) marks are unique, not lost, and correctly identified; (2) all individuals have the same probability of capture; (3) captures of individuals are independent between individuals; (4) marked animals have the same recapture probability as unmarked animals (i.e., no trap response); (5) individuals have the same probability of survival; (6) secondary sampling is instantaneous; and (7) geographic and demographic closure within (but not between) primary periods (Wilson et al., 1999; Methion & Díaz López, 2018). Our photo-identification methods (described above)

ensured assumption 1 was met. Whether marked or unmarked, all individuals in all encounters were counted and photographed on both sides of their dorsal fin whenever possible (Cobarrubia-Russo et al., 2019) to maximize equal probability of capture within a sampling session (assumption 2). Dolphins exhibit non-random associations (Wells et al., 1987; Rossbach & Herzing, 1999; Louis et al., 2015) and, thus, captures are unlikely to be independent among individuals (assumption 3). However, this violation is not likely to cause bias in the estimates, although the standard errors of those estimates may be biased low (Williams et al., 2002). Because the capture method (photography) is non-invasive, no trap response is expected (assumption 4). To ensure equal probability of survival (assumption 5), only adult animals were used in the capture-mark-recapture analysis. Furthermore, we excluded animals that were not observed in more than one secondary period as transients (Methion & Díaz López, 2018) to avoid bias (Hines et al., 2003). We completed secondary surveys within 1 d and primary periods averaged 25 d (range 2 to 52 d) to

**Table 1.** Results of 16 Closed Capture Robust Design (CCRD) movement models fitted to common bottlenose dolphin (*Tursiops truncatus*) encounter histories (*n* = 37 dolphins; *n* = 35 unique encounter histories) generated from 39 surveys along the coast of Venezuela during the 2004-2008 study period across 13 primary periods in *Program MARK* to estimate the population of marked adults, survival (S), emigration probabilities, and capture (P) and recapture (C) probabilities (Kendall et al., 1997). Survival and capture-recapture parameters were assessed as temporally constant (.) or allowed to vary with time (t). AICc = Akaike's Information Criterion corrected for small sample sizes.

| Model | AICc | Δ AICc | AICc weights | Model likelihood | Parameters | Deviance |
|---|---|---|---|---|---|---|
| Random, S(.), P = C(t) | 1,032.32 | 0 | 0.9976 | 1 | 52 | 1,347.86 |
| Markov, S(.), P = C(t) | 1,044.54 | 12.22 | 0.00222 | 0.0022 | 63 | 1,325.03 |
| No movement, S(.), P = C(t) | 1,050.99 | 18.66 | 0.00009 | 0.0001 | 40 | 1,401.09 |
| No emigration, S(.), P = C(t) | 1,050.99 | 18.66 | 0.00009 | 0.0001 | 40 | 1,401.09 |
| Random, S(t), P = C(t) | 1,056.99 | 24.67 | 0 | 0 | 62 | 1,340.81 |
| Markov, S(t), P = C(t) | 1,069.15 | 36.82 | 0 | 0 | 72 | 1,318.19 |
| No movement, S(t), P = C(t) | 1,071.80 | 39.47 | 0 | 0 | 51 | 1,390.36 |
| No emigration, S(t), P = C(t) | 1,071.80 | 39.47 | 0 | 0 | 51 | 1,390.36 |
| Random, S(.), P = C(t, .) | 1,106.61 | 74.29 | 0 | 0 | 26 | 1,492.89 |
| Markov, S(.), P = C(t, .) | 1,114.16 | 81.83 | 0 | 0 | 37 | 1,472.36 |
| No movement, S(.), P = C(t, .) | 1,123.51 | 91.19 | 0 | 0 | 14 | 1,537.75 |
| No emigration, S(.), P = C(t, .) | 1,123.51 | 91.19 | 0 | 0 | 14 | 1,537.75 |
| Random, S(t), P = C(t, .) | 1,124.79 | 92.46 | 0 | 0 | 36 | 1,485.65 |
| Markov, S(t), P = C(t, .) | 1,129.31 | 96.99 | 0 | 0 | 45 | 1,465.44 |
| No movement, S(t), P = C(t, .) | 1,140.31 | 107.99 | 0 | 0 | 25 | 1,529.02 |
| No emigration, S(t), P = C(t, .) | 1,140.31 | 107.99 | 0 | 0 | 25 | 1,529.02 |

comply with closure assumptions (assumptions 6 and 7). In photo-identification studies of long-lived, adult, non-transient bottlenose dolphins, closure is reasonably met during relatively short primary periods such as ours (Daura-Jorge et al., 2013; Balmer et al., 2019).

We tested four CCRD movement models including Markovian movement (time-dependent and different immigration and emigration probabilities across primary periods), random movement (equal immigration and emigration probabilities), no temporary emigration, and no movement. These models were evaluated with either constant or time-varying survival and with recapture probabilities that were either time-varying by secondary periods or constant within primary periods for a total of 16 models (Table 1). In models with time-varying survival, constraints were applied to final emigration parameters, allowing all parameters to be estimated (Methion & Díaz López, 2018). The model with the lowest value of Akaike's Information Criterion corrected for small sample sizes (AICc) was selected as the top model (Burnham & Anderson, 2004). Models within two AICc of the top model were assessed as potentially competing models (Burnham & Anderson, 2004). We did not explore Pledger's (2000) mixture models for heterogeneity in capture probabilities because they can only be modeled with no emigration (full-likelihood estimators have not yet been developed for temporary emigration models; Kendall et al., 1997). In similar coastal dolphin studies, those models have suffered from overparameterization (Daura-Jorge et al., 2013) and were not selected as competitive models among a larger suite of models, including those we tested (e.g., Methion & Díaz López, 2018). Furthermore, Pollock's (1982) CCRD allows for heterogeneity of capture probabilities because the secondary sampling periods are temporally relatively close together (Williams et al., 2002).

We followed methods from Wilson et al. (1999) to extend the population estimate of marked adults to (1) the population of all adults (marked and unmarked) and (2) the population of all dolphins (marked and unmarked adults plus calves) (Cagnazzi et al., 2011). We generated log-normal confidence intervals (CIs) for the adjusted population estimates (Burnham et al., 1987; Daura-Jorge et al., 2013). We assessed potential population trends using regression analysis in *Statistix*, Version 10.0.

## Results

### Photo-Identified and Resighted Individuals

Eighty-four sightings (one sighting could consist of more than one dolphin) of common bottlenose dolphins were recorded during 56 of the 100 surveys from 2004 to 2008, consisting of five sightings in 2004, 11 in 2005, 15 in 2006, 33 in 2007, and 20 in 2008. In total, we collected 3,360 photographs of which 660 were suitable for photo-identification analysis and used to create a catalogue of 86 fully identified adult individuals. Of these, 42 (48.83%) individuals were sighted more than once.

### Group Size and Abundance Estimation

Group sizes of bottlenose dolphins we encountered averaged 13 and ranged from 1 to 28. The number of calves per group averaged 3 and ranged from 0 to 9. The proportion of marked adults to total adults within a primary period averaged 0.63 (ranged 0.41 to 0.95). The proportion of marked adults to total group size within a secondary survey averaged 0.47 (ranged 0.30 to 0.76).

The top model included random movement, constant survival, and capture-recapture probabilities that varied by secondary periods (Table 1). There were no other competing models (Table 1). Survival of marked adults was estimated at 0.99 (95% CI = 0.97 to 1.00). The population estimates for marked adults for the 13 primary periods averaged 19 animals (SD = 7.8) and ranged from a low of seven animals in the wet season during 2004 to a high of 34 during the wet season in 2008 (Table 2).

Extended population estimates for all adults (marked and unmarked) averaged 31 animals (SD = 13.8; mean coefficient of variation [CV] = 0.26), and estimates for all dolphins (marked and unmarked adults plus calves) averaged 41 (SD = 17.2; mean CV = 0.28) (Table 2; Figure 2). Extended estimates for wet seasons only averaged 33 adults (SD = 17.6) and 45 adults and calves (SD = 21.6) (Table 2). Extended estimates for dry seasons only averaged 28 adults (SD = 8.5) and 37 adults and calves (SD = 10.4) (Table 2). The estimated adults-only and total population trends appeared generally stable except for an apparent peak in the first wet season estimate in 2008 (Figure 2).

## Discussion

The use of photo-identification in capture-recapture models has now become a standard and efficient method for the estimation of dolphin stocks (NMFS, 2016; Litz et al., 2019). Our study reports historic capture-mark-recapture population estimates of the common bottlenose dolphin along the Aragua coast, Venezuela. Although our data were collected during the 2004-2008 study period, they, nevertheless, form the basis of the first estimates of abundance and survival for the common bottlenose dolphin population along the Aragua coast. While more recent demographic data are ideal, it is not always as feasible (financially and/or logistically) to carry out more frequent surveys. Still, only approximately two to three dolphin generations have transpired since our

**Table 2.** Abundance estimates for the marked population (Nhat_Marked) of adult common bottlenose dolphins from the top model (Burnham & Anderson, 2004) generated by *Program MARK* and extended to all adults (marked and unmarked: Nhat_All_Adults) and to the total population (all adults plus calves: Nhat_Total) surveyed along the coast of Venezuela from 2004 to 2008. Confidence intervals (95% Lower CI [LCI] and Upper CI [UCI]) and coefficient of variation (CV) are also reported.

| Year | Season | Nhat_Marked | LCI | UCI | Nhat_All_Adults | CV | LCI | UCI | Nhat_Total | CV | LCI | UCI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2004 | Wet | 6.67 | 6.06 | 13.16 | 16.30 | 0.31 | 8.92 | 29.76 | 22.22 | 0.33 | 11.76 | 41.98 |
| 2005 | Wet | 12.20 | 8.94 | 26.81 | 20.74 | 0.37 | 10.32 | 41.71 | 34.16 | 0.40 | 16.11 | 72.46 |
| 2005 | Dry | 18.77 | 13.23 | 38.09 | 35.98 | 0.35 | 18.33 | 70.61 | 51.62 | 0.37 | 25.46 | 104.65 |
| 2006 | Wet | 15.21 | 7.29 | 71.94 | 26.08 | 0.84 | 6.26 | 108.56 | 41.29 | 0.85 | 9.68 | 176.06 |
| 2006 | Dry | 29.26 | 22.54 | 48.71 | 30.66 | 0.21 | 20.39 | 46.09 | 40.41 | 0.23 | 25.65 | 63.65 |
| 2006 | Dry | 10.31 | 10.02 | 13.86 | 18.75 | 0.16 | 13.84 | 25.40 | 28.12 | 0.18 | 19.79 | 39.95 |
| 2007 | Dry | 19.88 | 18.36 | 27.89 | 39.17 | 0.15 | 28.99 | 52.93 | 42.68 | 0.16 | 31.34 | 58.11 |
| 2007 | Dry | 17.48 | 16.27 | 24.06 | 18.94 | 0.10 | 15.56 | 23.05 | 23.31 | 0.12 | 18.36 | 29.58 |
| 2007 | Wet | 23.93 | 22.42 | 30.77 | 45.86 | 0.12 | 36.03 | 58.38 | 54.84 | 0.13 | 42.50 | 70.75 |
| 2007 | Wet | 12.22 | 12.01 | 15.46 | 23.86 | 0.16 | 17.51 | 32.52 | 34.34 | 0.18 | 24.16 | 48.80 |
| 2008 | Wet | 34.03 | 24.18 | 59.57 | 66.36 | 0.29 | 38.09 | 115.60 | 88.48 | 0.30 | 49.78 | 157.26 |
| 2008 | Wet | 20.00 | 17.43 | 37.90 | 28.95 | 0.21 | 19.13 | 43.79 | 38.95 | 0.22 | 25.23 | 60.12 |
| 2008 | Dry | 25.20 | 23.40 | 35.20 | 27.14 | 0.10 | 22.20 | 33.18 | 32.96 | 0.12 | 25.99 | 41.78 |
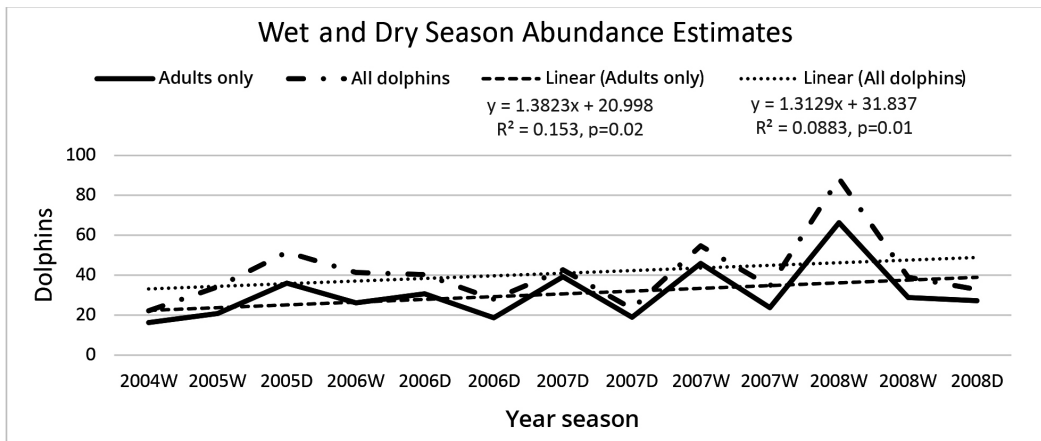


**Figure 2.** Coastal bottlenose dolphin (*Tursiops truncatus*) abundance estimates and trend lines for adults only (marked and unmarked) and for all dolphins (all adults plus calves) along the coast of Venezuela during the 2004-2008 study period in wet (W) and dry (D) seasons

data were collected (Reynolds et al., 2000). Further, because our results represent the first demographic estimates for this population, they are important in the documentation of historic benchmark estimates and for establishing the need for ongoing monitoring for future comparisons (Labach et al., 2019). Moreover, such estimates are vital to establish before major environmental impacts occur (Ronje et al., 2020).

Our top model included random movement between availability states indicating that the probability of an animal being available for capture during a current survey was independent of an animal's previous state and was the same for those animals previously in and out of the study area during the previous survey (i.e., the probability of temporarily emigrating is the same as the probability of an animal staying away if it was absent the previous session) (Kendall, 1999). The superpopulation estimates we report (based on the CCRD) are robust to these types of closure violations that include random movement in and out of a study area

(Kendall, 1999). Our estimates indicate the 2004-2008 coastal bottlenose dolphin total population was quite small, averaging less than 50 individuals. Our top model also included constant and high survival of adult common bottlenose dolphins, similar to what other studies have found (e.g., Methion & Díaz López, 2018). Relatively constant, high adult survival is typically a feature of long-lived mammals as even small perturbations can exact a large influence on population dynamics (Eisenberg, 1981; Harvey et al., 1989; Gaillard et al., 1998; Eberhardt, 2002).

Venezuela's Aragua coast forms the northern border of the Henry Pittier National Park, and its western end is occupied by only six small artisanal fishing villages and a Navy base in the Bay of Turiamo (which has relatively low maritime traffic). Therefore, among human-induced stressors, such as coastal development, vessel traffic, biotoxins and other pollutants, noise, and diseases, the main environmental stressor during our study was likely artisanal boats. However, the average number of boats observed during one of our typical 3 to 4 h field surveys (traversing ~30 km) was only approximately 25, a relatively small number of boats for a coastal region. Therefore, we suspect that this stressor was minimal compared to other locations with much greater fishery, recreational, and other boat traffic.

Considering the relatively low overall human impact to this population, our results revealed a lower population abundance than might be expected (estimated average of 41 total dolphins), all else being equal (e.g., Methion & Díaz López, 2018; Silva et al., 2020). For example, along an Uruguayan coast that is relatively more human-impacted than the Aragua coast of Venezuela, the Department of Rocha (Uruguay), nevertheless, reported more individuals than our study population (estimates of 63 [95% CI = 54 to 74] and 61 [95% CI = 53 to 73] dolphins were obtained from closed and open population models, respectively; Laporta et al., 2016). Similarly, in San Antonio Bay (Argentina), a population of 83 individuals (95% CI = 45.8 to 151.8) was estimated (Vermeulen & Cammareri, 2009; Vermeulen & Bräger, 2015; Vermeulen et al., 2015, 2016). More recently, two studies conducted in the United States highlight differences in abundance. One study in West Bay, Texas, considered to be a highly impacted area, estimated an abundance of 47.5 dolphins (95% CI = 44.36 to 50.63) (Litz et al., 2019); whereas Balmer et al. (2019) reported common bottlenose dolphin seasonal abundances in the bay, sound, and estuary population of St Andrew Bay, Florida, from a low of 199 individuals (95% CI = 173 to 246) during April 2016 to a high of 315 (95% CI = 274 to 378) in October 2016. Even the Turneffe Atoll (Belize),

which has no major human impact but is considered to have scarce food resources, reported more dolphins with abundances of 82 (95% CI = 73 to 103) between 1992 and 1993 and 86 (95% CI = 76 to 109) between 1994 and 1996 (Campbell et al., 2002). However, as Laporta et al. (2016) maintained, abundance disparities could be related to factors such as threats, population dynamics, ecological requirements, and the carrying capacity of the coast in addition to genetics, habitat differences, and interspecies relationships—that is, they are complex systems with multiple factors at play that reach beyond human impacts alone. Although smaller than others, our historic abundance estimate, nevertheless, similarly reflects that coastal common bottlenose dolphin populations tend, in general, to be small (Bearzi et al., 1997; Defran & Weller, 1999; Wilson et al., 1999; Read et al., 2003; Fruet et al., 2011).

We suggest that there were at least two factors that could have influenced our low abundance result: (1) insufficient prey base and (2) limited preferred habitat. Oceanic upwelling along the coast of Venezuela is generally considered weak and restricted to areas adjacent to the coast due to the absence of a continental shelf (Cervigón & Rodríguez, 1997). Furthermore, there are just five small rivers that serve to transport nutrients from the coastal mountain rainforests in Henry Pittier National Park down to the ocean (Cobarrubia-Russo, 2010; Bolaños-Jiménez et al., 2013). Although the coast of Aragua is an annual source of important prey for bottlenose dolphins, including more than 20 species of fishes and one cephalopod (Cervigón, 1986; Cervigón & Rodríguez, 1997), it may have been that the relatively weak coastal upwelling in combination with minimal river plume deposition resulted in an overall reduced nutrient supply insufficient to allow for a larger prey base that could support more dolphins. The presence of a potential competitor (i.e., the Atlantic spotted dolphin) may also have had an effect on prey availability. However, at least some spatial niche separation was apparent as Atlantic spotted dolphins mainly fed near the 200 m isobaths (Cobarrubia-Russo et al., 2020), whereas common bottlenose dolphins fed closer to shore, preferring shallower waters (usually in isobaths between 30 and 100 m) or at the beginning of underwater valleys or crevices (Shane, 1990).

Given common bottlenose dolphin habitat preferences, another factor that may have influenced their low abundance in our study was the pronounced steepness of the continental shelf slope that resulted in the 100 m isobath being a relatively short distance from the coast. Therefore, the available preferred habitat of common bottlenose dolphins in our study was generally reduced to an

area of coastal and neritic habitats along a relatively narrow west-east corridor (Figure 1). We hypothesize that this transit area had a relatively low carrying capacity in view of its size and probable nutrient supply (Cobarrubia-Russo, 2010; Cobarrubia-Russo et al., 2020).

We do not suspect overfishing was a cause for the relatively small common bottlenose dolphin population. Trawling has been banned in Venezuela since 2007 for conservation reasons, and the fishing activity in the study area was exclusively artisanal. Thus, during our study, there was no known overfishing along Aragua's coast that might have caused a reduction in dolphin presence, which is in contrast to the situation in the Ionian and Adriatic Seas that experienced a decrease in the encounter rates of *Delphinus* sp. and common bottlenose dolphins related to overfishing (Bearzi et al., 2004, 2005, 2006). Furthermore, in our experience, the fisherman–dolphin relationship in Aragua is quite positive.

Evaluation of trends in our population estimates were hampered by the relative imprecision of the estimates. Other coastal transect surveys for common bottlenose dolphins have had similar issues with relatively wide CIs around CCRD estimates (Balmer et al., 2019). Overall, we conclude the population appeared generally stable during the 2004-2008 study period, with a possible uptick during the wet season of 2008. The 2008 wet season peak (observed in the first estimate of that wet season) could have been an artifact of increased survey effort or it could have been due to one group of dolphins (group C) that joined the study area near the end of 2007. That group included mothers and calves, and the daily encounter rate increased after 2007 by 10 to 15% relative to other years (Cobarrubia-Russo et al., 2019). It is possible that the addition of these breeding females attracted more reproductive males that then arrived in the wet season of 2008 (November to February), resulting in the peak in our trend (Cobarrubia-Russo et al., 2019). Following the ostensible peak that we observed in the first wet season estimate of 2008, the second 2008 wet season estimate returned to levels similar to previous years (Figure 2). We suggest this coastal dolphin population consists of a community of neighbors (several groups) that visits the transect area (Shane et al., 1986; Félix, 1997; Rossbach & Herzing, 1999; Wells & Scott, 2002), comprising the wider superpopulation (Bradford et al., 2018) in the relatively open habitat (Defran & Weller, 1999). To increase the precision of estimates of the superpopulation (Kendall, 1999), future work could benefit from conducting surveys that include our primary survey transect but also survey the wider area.

Coastal bottlenose dolphins face numerous threats such as ship strikes, conflict with recreational and industrial fisheries, other negative human interactions, biotoxins, chemicals, noise, freshwater discharge, oil spills, and coastal development (Balmer et al., 2015; B. Balmer et al., 2018; J. Balmer et al., 2018; Litz et al., 2019; Ronje et al., 2020; Silva et al., 2020). Furthermore, because many coastal bottlenose populations are small (Daura-Jorge et al., 2013), they are at greater risk due to reduced resiliency and recovery potential when exposed to the threats noted above, and to expected environmental and demographic stochasticity (Gilpin & Soulé, 1986). Alarmingly, one study concluded populations of less than 50 animals (such as our study population) were likely to become extinct within the next 50 years (Berger, 1990). Our baseline historic population estimates of Aragua's common bottlenose dolphins reveal the need for ongoing monitoring of and conservation efforts for this small coastal population. Spatially expanded annual surveys of at least three secondary surveys in each wet and dry season are likely to improve the ability to manage and conserve this population and to better assess the influence of emerging threats on Venezuela's relatively small coastal bottlenose dolphin population. Our results and the year-round presence of dolphins highlight the Venezuelan coastal–oceanic landscape as an area important in terms of both conservation and future research (e.g., life histories, social organization, sympatry, global change, etc.).

## Literature Cited

Balmer, B., Watwood, S., Quigley, B., Speakman, T., Barry, K., Mullin, K., Rosel, P., Sinclair, C., Zolman, E., & Schwacke, L. (2019). Common bottlenose dolphin (*Tursiops truncatus*) abundance and distribution patterns in St Andrew Bay, Florida, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(3), 486-498. https://doi.org/10.1002/aqc.3001

Balmer, B. C., Ylitalo, G. M., McGeorge, L. E., Baugh, K. A., Boyd, D., Mullin, K. D., Rosel, P. E., Sinclair, C., Wells, R. S., Zolman, E. S., & Schwacke, L. H. (2015). Persistent organic pollutants (POPs) in blubber of common bottlenose dolphins (*Tursiops truncatus*) along the northern Gulf of Mexico coast, USA. *Science of the Total Environment*, *527*, 306-312. https://doi.org/10.1016/j.scitotenv.2015.05.016

Balmer, B., McDonald, T., Hornsby, F., Adams, J., Allen, J., Barleycorn, A., Clarke, P., Cush, C., Honaker, A., McHugh, K., Speakman, T., Wells, R., & Schwacke, L. (2018). Long-term trends in a northern Gulf of Mexico common bottlenose dolphin (*Tursiops truncatus*) population in the wake of the Deepwater Horizon oil spill. *Journal of Cetacean Research and Management*, *18*, 1-9.

Balmer, J. E., Ylitalo, G. M., Rowles, T. K., Mullin, K. D., Wells, R. S., Townsend, F. I., Pearce, R. W., Bolton, J. L., Zolman, E. S., Balmer, B. C., & Schwacke, L. H. (2018). Persistent organic pollutants (POPs) in blood and blubber of common bottlenose dolphins (*Tursiops truncatus*) at three northern Gulf of Mexico sites following the Deepwater Horizon oil spill. *Science of the Total Environment*, *621*, 130-137. https://doi.org/10.1016/j.scitotenv.2017.11.209

Bearzi, G., Holcer, D., & Notarbartolo di Sciara, G. (2004). The role of historical dolphin takes and habitat degradation in shaping the present status of northern Adriatic cetaceans. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *14*(4), 363-379. https://doi.org/10.1002/aqc.626

Bearzi, G., Notarbartolo di Sciara, G., & Politi, E. (1997). Social ecology of bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *Marine Mammal Science*, *13*(4), 650-668. https://doi.org/10.1111/j.1748-7692.1997.tb00089.x

Bearzi, G., Politi, E., Agazzi, S., & Azzellino, A. (2006). Prey depletion caused by overfishing and the decline of marine megafauna in eastern Ionian Sea coastal waters (central Mediterranean). *Biological Conservation*, *127*(4), 373-382. https://doi.org/10.1016/j.biocon.2005.08.017

Bearzi, G., Politi, E., Agazzi, S., Bruno, S., Costa, M., & Bonizzoni, S. (2005). Occurrence and present status of coastal dolphins (*Delphinus delphis* and *Tursiops truncatus*) in the eastern Ionian Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *15*(3), 243-257. https://doi.org/10.1002/aqc.667

Berger, J. (1990). Persistence of different-sized populations: An empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology*, *4*(1), 91-98. https://doi.org/10.1111/j.1523-1739.1990.tb00271.x

Bolaños, J., & Villarroel-Marín, A. (2003). Three new records of cetacean species for Venezuelan waters. *Caribbean Journal of Science*, *39*, 230-232.

Bolaños-Jiménez, J., Castro-Pérez, G., Herrera-Trujillo, O., Oviedo, L., Palacios, D., Sánchez-Criollo, L., Puerto, M. F., Sifontes, L., Silva-Hernández, M. G., & Villarroel-Marín, A. (2013). Presence of long-beaked common dolphins (*Delphinus* spp.) off central-western Venezuela. *Anartia*, *25*, 32-46.

Bradford, A. L., Baird, R. W., Mahaffy, S. D., Gorgone, A. M., McSweeney, D. J., Cullins, T., Webster, D. L., & Zerbini, A. N. (2018). Abundance estimates for management of endangered false killer whales in the main Hawaiian Islands. *Endangered Species Research*, *36*, 297-313. https://doi.org/10.3354/esr00903

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*(2), 261-304. https://doi.org/10.1177/0049124104268644

Burnham, K. P., Anderson, D. R., White, G. C., & Brownie, C. P. (1987). Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph*, *5*, 273-282.

Cagnazzi, D. D. B., Harrison, P. L., Ross, G. J., & Lynch, P. (2011). Abundance and site fidelity of Indo-Pacific humpback dolphins in the Great Sandy Strait, Queensland, Australia. *Marine Mammal Science*, *27*(2), 255-281. https://doi.org/10.1111/j.1748-7692.2009.00296.x

Campbell, G. S., Bilgre, B. A., & Defran, R. H. (2002). Bottlenose dolphins (*Tursiops truncatus*) in Turneffe Atoll, Belize: Occurrence, site fidelity, group size, and abundance. *Aquatic Mammals*, *28*(2), 170-180.

Cervigón, F. (1986). Peces marinos, en fauna de Venezuela: Vertebrados [Marine fishes in fauna of Venezuela: Vertebrates]. In C. Gremone (Ed.), *Biosfera* (pp. 167-226). Editorial Ex Libris.

Cervigón, F., & Rodríguez, B. (1997). Lista actualizada de los peces marinos de Venezuela, en vertebrados actuales y fósiles de Venezuela [Updated list of marine fishes of Venezuela in current vertebrates and fossils of Venezuela]. In E. La Marca (Ed.), *Serie catálogo zoológico de Venezuela* [Venezuela zoological catalog series] (Vol. 1, pp. 17-52). Museo de Ciencia y Tecnología de Mérida.

Cobarrubia-Russo, S. (2010). *Ecology and behavior of the bottlenose dolphin* Tursiops truncatus *at the coast of Aragua State* (Master's thesis). Simon Bolivar University, Caracas, Venezuela.

Cobarrubia-Russo, S. E., Barreto-Esnal, G. R., Molero-Lizarraga, A. E., & Mariani-Di Lena, M. A. (2020). Individual home ranges of *Tursiops truncatus* and their overlap with ranges of *Stenella frontalis* and fishermen in Aragua, Venezuela, South Caribbean. *Journal of the Marine Biological Association of the United Kingdom*, 1-10. https://doi.org/10.1017/S0025315420000557

Cobarrubia-Russo, S., Barreto, G., Quintero-Torres, E., Molero-Lizarraga, A., & Wang, X. (2019). Occurrence, abundance, range, and residence patterns of *Tursiops*

*truncatus* on the coast of Aragua, Venezuela. *Mammal Research*, *64*(2), 289-297. https://doi.org/10.1007/s13364-018-0401-1

Daura-Jorge, F. G., Ingram, S. N., & Simões-Lopes, P. C. (2013). Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. *Marine Mammal Science*, *29*(2), 293-311. https://doi.org/10.1111/j.1748-7692.2012.00571.x

Defran, R. H., & Weller, D. W. (1999). Occurrence, distribution, site fidelity and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Marine Mammal Science*, *15*(2), 366-380. https://doi.org/10.1111/j.1748-7692.1999.tb00807.x

Durden, W. N., Stolen, E. D., Moreland, L., Howells, E., Jablonski, T., Sleeman, A., Denny, M., Biedenbach, G., & Mazzoil, M. (2020). Robust design capture-recapture analysis of abundance and demographic parameters of Indian River Lagoon common bottlenose dolphins (*Tursiops truncatus truncatus*). *bioRxiv*. https://doi.org/10.1101/2020.01.30.926683

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology*, *83*(10), 2841-2854. https://doi.org/10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2

Eisenberg, J. F. (1981). *The mammalian radiations: An analysis of trends in evolution, adaptation, and behavior*. The University of Chicago Press.

Félix, F. (1997). Organization and social structure of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf de Guayaquil, Ecuador. *Aquatic Mammals*, *23*(1), 1-16.

Fruet, P., Secchi, E., Di Tullio, J., & Kinas, P. (2011). Abundance of bottlenose dolphins, *Tursiops truncatus* (Cetacea: Delphinidae), inhabiting the Patos Lagoon estuary, southern Brazil: Implications for conservation. *Zoologia*, *28*(1), 23-30. https://doi.org/10.1590/S1984-46702011000100004

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, *13*(2), 58-63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gilpin, M. E., & Soulé, M. E. (1986). Minimum viable populations: Processes of extinction. In M. E. Soulé (Ed.), *Conservation biology: The science of scarcity and diversity* (pp. 19-34). Sinauer Associates.

Gowans, S., Würsig, B., & Karczmarski, L. (2007). The social structure and strategies of delphinids: Predictions based on an ecological framework. *Advances in Marine Biology*, *53*, 195-294. https://doi.org/10.1016/S0065-2881(07)53003-8

Harvey, P. H., Read, A. F., & Promislow, D. E. L. (1989). Life history variation in placental mammals: Unifying the data with theory. *Oxford Surveys in Evolutionary Biology*, *6*, 13-31.

Hillman, G. R., Würsig, B., Gailey, G. A., Kehtarnavaz, N., Drobyshevsky, A., Araabi, B. N., Tagare, H. D., & Weller, D. W. (2003). Computer-assisted photo-identification of individual marine vertebrates: A multi-species system. *Aquatic Mammals*, *29*(1), 117-123.

Hillman, G. R., Würsig, B., Kehtarnavaz, N., Weller, D. W., Kreho, A., Drobyshevskyy, A., Elder, K., Araabi, B. N., McKinney, T., Gailey, G., & Tagare, H. (1999, December). Individual identification of dolphins in field photographs: A computer-based system. *Proceedings of the 13th Biennial Conference on the Biology of Marine Mammals*, Maui, HI.

Hines, J. E., Kendall, W. L., & Nichols, J. D. (2003). On the use of the robust design with transient capture-recapture models. *The Auk*, *120*(4), 1151-1158. https://doi.org/10.2307/4090285

Kendall, W. L. (1999). Robustness of closed capture–recapture methods to violations of the closure assumption. *Ecology*, *80*(8), 2517-2525. https://doi.org/10.1890/0012-9658(1999)080[2517:ROCCRM]2.0.CO;2

Kendall, W. L., Nichols, J. D., & Hines, J. E. (1997). Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology*, *78*, 563-578. https://doi.org/10.1890/0012-9658(1997)078[0563:ETEUCR]2.0.CO;2

Labach, H., Azzinari, C., Barbier, M., Cesarini, C., Daniel, B., David, L., Dhermain, F., Di-Meglio, N., Guichard, B., Jourdan, J., Robert, N., Roul, M., Tomasi, N., & Gimenez, O. (2019). Distribution and abundance of bottlenose dolphin (*Tursiops truncatus*) over the French Mediterranean continental shelf. *bioRxiv*. https://doi.org/10.1101/723569

Laporta, P., Fruet, P. F., & Secchi, E. R. (2016). First estimate of common bottlenose dolphin (*Tursiops truncatus*) (Cetacea, Delphinidae) abundance off Uruguayan Atlantic coast. *Latin American Journal of Aquatic Mammals*, *11*(1-2), 144-154. https://doi.org/10.5597/00223

Leatherwood, S., & Reeves, R. R. (1983). *The Sierra Club handbook of whales and dolphins*. Sierra Club Books.

Litz, J. A., Ronje, E. I., Whitehead, H. R., & Garrison, L. P. (2019). Updated abundance estimates for common bottlenose dolphins (*Tursiops truncatus*) inhabiting West Bay, Texas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(11), 1959-1970. https://doi.org/10.1002/aqc.3195

Louis, M., Gally, F., Barbraud, C., Béesau, J., Tixier, P., Simon-Bouhet, B., Le Rest, K., & Guinet, C. (2015). Social structure and abundance of coastal bottlenose dolphins, *Tursiops truncatus*, in the Normano-Breton Gulf, English Channel. *Journal of Mammalogy*, *96*(3), 481-493. https://doi.org/10.1093/jmammal/gyv053

Methion, S., & Díaz López, B. (2018). Abundance and demographic parameters of bottlenose dolphins in a highly affected coastal ecosystem. *Marine and Freshwater Research*, *69*(9), 1355-1364. https://doi.org/10.1071/MF17346

National Marine Fisheries Service (NMFS). (2016). *Guidelines for preparing stock assessment reports pursuant to the 1994 amendments to the MMPA* (NMFS Instruction 02-204-01). https://www.fisheries.noaa.gov/webdam/download/64669267

Novoa, D., Mendoza, J., Marcano, L., & Cárdenas, J. (1998). *Atlas pesquero marítimo de Venezuela* [Maritime fishing atlas of Venezuela]. MAC-SARPACONGEPESCA, VENCEP.

Pledger, S. (2000). Unified maximum likelihood estimates for closed capture-recapture models with heterogeneity. *Biometrics*, *56*, 434-442. https://doi.org/10.1111/j.0006-341X.2000.00434.x

Pollock, K. H. (1982). A capture–recapture design robust to unequal probability of capture. *The Journal of Wildlife Management*, *46*, 752-757. https://doi.org/10.2307/3808568

Read, A. J., Urian, K. W., Wilson, B., & Waples, D. M. (2003). Abundance of bottlenose dolphins in the bays, sounds and estuaries of North Carolina, USA. *Marine Mammal Science*, *19*(1), 59-73. https://doi.org/10.1111/j.1748-7692.2003.tb01092.x

Reynolds III, J. E., Wells, R. S., & Eide, S. D. (2000). *Biology and conservation of the bottlenose dolphin*. University Press of Florida.

Rodríguez, J. P., & Rojas-Suárez, F. (Eds.). (2008). *Libro rojo de la fauna Venezolana* (Tercera edición) [Red book of Venezuelan fauna (3rd ed.)]. Provita and Shell Venezuela.

Romero, A., Jr., Agudo, A. I., & Green, S. M. (1997). Exploitation of cetaceans in Venezuela. *Reports of the International Whaling Commission*, *47*, 735-746.

Romero, A., Jr., Agudo, A. I., Green, S. M., & Notarbartolo di Sciara, G. (2001). *Cetaceans of Venezuela: Their distribution and conservation status* (NOAA/National Marine Fisheries Service Technical Report NMFS 151). National Oceanic and Atmospheric Administration, U.S. Department of Commerce. 60 pp.

Ronje, E., Whitehead, H., Barry, K., Piwetz, S., Struve, J., Lecours, V., Garrison, L., Wells, R. S., & Mullin, K. D. (2020). Abundance and occurrence of common bottlenose dolphins (*Tursiops truncatus*) in three estuaries of the northwestern Gulf of Mexico. *Gulf and Caribbean Research*, *31*, 18-34. https://doi.org/10.18785/gcr.3101.09

Rosel, P. E., Mullin, K. D., Garrison, L., Schwacke, L., Adams, J., Balmer, B., Conn, P., Conroy, M. J., Eguchi, T., Gorgone, A., Hohn, A., Mazzoil, M., Schwartz, C., Sinclair, C., Speakman, T., Urian, K., Vollmer, N., Wade, P., Wells, R., & Zolman, E. (2011). *Photo-identification capture-mark-recapture techniques for estimating abundance of bay, sound and estuary populations of bottlenose dolphins along the U.S. East Coast and Gulf of Mexico: A workshop report* (NOAA Technical Memorandum NMFS-SEFSC-621). National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

Rossbach, K. A., & Herzing, D. L. (1999). Inshore and offshore bottlenose dolphin (*Tursiops truncatus*) communities distinguished by association patterns near Grand Bahama Island, Bahamas. *Canadian Journal of Zoology*, *77*(4), 581-592. https://doi.org/10.1139/z99-018

Shane, S. H. (1990). Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 245-266). Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50016-0

Shane, S. H., Wells, R. S., & Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science*, *2*(1), 34-63. https://doi.org/10.1111/j.1748-7692.1986.tb00026.x

Silva, D., Young, R. F., Lavin, A., O'Shea, C., & Murray, E. (2020). Abundance and seasonal distribution of the southern North Carolina Estuarine System stock of common bottlenose dolphins (*Tursiops truncatus*). *Journal of Cetacean Research and Management*, *21*, 33-43. https://doi.org/10.47536/jcrm.v21i1.175

Traill, L. W., Bradshaw, C. J., & Brook, B. W. (2007). Minimum viable population size: A meta-analysis of 30 years of published estimates. *Biological Conservation*, *139*(1-2), 159-166. https://doi.org/10.1016/j.biocon.2007.06.011

Vermeulen, E., & Bräger, S. (2015). Demographics of the disappearing bottlenose dolphin in Argentina: A common species on its way out? *PLOS ONE*, *10*(3), e0119182. https://doi.org/10.1371/journal.pone.0119182

Vermeulen, E., & Cammareri, A. (2009). Residency, abundance and social composition of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. *Aquatic Mammals*, *35*(3), 378-385. https://doi.org/10.1578/AM.35.3.2009.378

Vermeulen, E., Holsbeek, L., & Das, K. (2015). Diurnal and seasonal variation in the behaviour of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. *Aquatic Mammals*, *41*(3), 272-283. https://doi.org/10.1578/AM.41.3.2015.272

Vermeulen, E., Balbiano, A., Beleguer, F., Colombil, D., Failla, M., Intrieri, E., & Bräger, S. (2016). Site-fidelity and movement patterns of bottlenose dolphins in central Argentina: Essential information for effective conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*, 282-292. https://doi.org/10.1002/aqc.2618

Wells, R. S., & Scott, M. D. (1999). Bottlenose dolphin *Tursiops truncatus* (Montagu 1821). In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals*: *Vol. 6. Second book of dolphins and porpoises* (pp. 137-182). Academic Press.

Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy* (Vol. 1, pp. 247-305). Springer. https://doi.org/10.1007/978-1-4757-9909-5_7

Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and management of animal populations: Modeling, estimation, and decision making*. Academic Press.

Wilson, B., Hammond, P. S., & Thompson, P. M. (1999). Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications*, *9*(1), 288-300. https://doi.org/10.1890/1051-0761(1999)009[0288:ESAATI]2.0.CO;2

Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science*, *198*, 755-756. https://doi.org/10.1126/science.198.4318.755