Distribution, abundance and sighting patterns of multiple stocks of bottlenose dolphins (*Tursiops truncatus*) in coastal Virginia waters

**Amy Engelhaupt**, **Thomas A. Jefferson**, **Jessica M. Aschettino** and **Joel T. Bell**

Contact e-mail: amyengelhaupt@gmail.com

**ABSTRACT**

Three stocks of bottlenose dolphins (*Tursiops truncatus*) are currently known to co-occur in the coastal waters off Virginia. A combination of visual line-transect survey and photo-identification (photo-ID) methods was used to gather information on the occurrence, distribution and density of bottlenose dolphins in the coastal areas of Norfolk and Virginia Beach. Sixty-one line-transect surveys were completed in two zones (inshore and offshore) between August 2012 and August 2015, with on-effort coverage of 6,550 kilometres (km) of trackline over 349.6 hours. Conventional line-transect analysis of bottlenose dolphin sightings showed both spatial and temporal variation in density (D) and abundance (N), with highest density in the inshore zone during warm-water months (June–November). Inshore densities were calculated as 3.51 individuals per square kilometre (km$^2$) (N = 1,090) in the warm-water season and 0.73 individuals/km$^2$ (N = 225) in cool-water months (December–May). Densities in the offshore zone were 1.24 individuals/km$^2$ (N = 741) in the warm-water season and 0.61 individuals/km$^2$ (N = 366) in the cool-water season. Warm-water density peaks support previous research; however, this study documents a cold-season presence of dolphins in both zones not previously reported. Twenty-seven photo-ID surveys were completed and a photo-ID catalogue was created using photos taken during both dedicated photo-ID and line-transect surveys, containing 1,335 unique individuals. Re-sighting numbers were low, with less than 17% of individuals documented on more than one occasion, and only 4% sighted on three or more occasions, with a maximum of 4 re-sightings. Days between re-sightings ranged from 5 to 970, though distance between re-sightings spanning greater time was minimal (less than 25km). Sighting locations of photo-IDed dolphins were broken into three regions to investigate seasonal and spatial patterns of individual distribution; dolphins sighted only in the Cape Henry (CH) or Inner Bay (IB) region were observed mostly during summer and fall seasons (93% CH, 100% IB) with none occurring during winter. For the Outer Coastline (OC) region, the majority of sightings (88%) occurred during fall and winter. Additionally, there were two individuals sighted during winter months also sighted during summer more than 130km to the north inside Chesapeake Bay (matched to a different catalogue). These sightings support the possibility that the current stock structure does not account for all dolphins in the region. Stock structure as currently understood is complicated, with overlapping spatial distribution of three stocks that separate seasonally. Our study provides information that may be useful for management, but also additional findings that could impact future stock designations.

**KEYWORDS:** BOTTLENOSE DOLPHIN; ATLANTIC OCEAN; MID-ATLANTIC, VIRGINIA; CHESAPEAKE BAY; CONSERVATION; ABUNDANCE ESTIMATE; SURVEY – VESSEL; DISTRIBUTION; MOVEMENTS; SITE FIDELITY; PHOTO-ID
INTRODUCTION

Bottlenose dolphins are common in Chesapeake Bay and in waters off the Virginia coastline. This region appears to be an area of overlapping stock ranges (Fig. 1), where the majority of individuals utilising the area are part of either the Western North Atlantic Southern Migratory Coastal Stock (SMCS), which ranges in summer from Cape Lookout, North Carolina, to central Virginia; or the Western North Atlantic Northern Migratory Coastal Stock (NMCS), which ranges from northern Virginia to Long Island, New York, in the summer, but migrates through the Chesapeake Bay mouth area to spend cold winter months in North Carolina waters (Hayes et al., 2018). Individuals from an additional stock, the Northern North Carolina Estuarine System Stock (NNCES), are also reported to move as far north as Chesapeake Bay in summer months (Hayes et al., 2018). These stocks are managed by the National Marine Fisheries Service (NMFS) and both the Northern and Southern Migratory Coastal Stocks are designated as depleted (Hayes et al., 2018). All three are considered strategic, which is defined by the US Marine Mammal Protection Act of 1972 (16 USC, § 1361) as a marine mammal stock for which the level of direct human-caused mortality exceeds the potential biological removal level; which, based on the best available scientific information, is declining and is likely to be listed as a threatened species under the Endangered Species Act of 1973 (16 USC §1531) within the foreseeable future; or which is listed as a threatened species or endangered species under the Endangered Species Act of 1973, or is designated as depleted. Total abundance of the SMCS is estimated at 3,751 dolphins (coefficient of variation [CV] = 0.06), the NMCS is estimated at 6,639 dolphins (CV = 0.41) and the NNCES Stock is estimated at 823 dolphins (CV = 0.06, Hayes et al., 2018).

Significant seasonal fluctuations in bottlenose dolphin distribution and numbers exist in this area, with peak abundance occurring in late summer/early fall when water temperatures are highest (Winn, 1982; Blaylock, 1984; Barco et al., 1999). Although previous work investigated metrics to estimate bottlenose dolphin abundance in this region (e.g., Blaylock, 1988; Barco et al., 1999; Baker, 2000), actual local abundance estimated in parts of this area is not thoroughly understood. For example, Blaylock (1988) estimated that there were on average 340 bottlenose dolphins in the Chesapeake Bay mouth and southern Virginia coast, but this is derived from a combination of Chesapeake Bay mouth transects and a coastline strip transect. Surveys conducted by Barco et al. (1999) showed variation in abundance by month, but coverage did not extend as far south as the North Carolina border, or more than 10km into the Chesapeake Bay. Distribution has also been documented much further in the bay, as far as 180km inside the bay mouth (Blaylock, 1988; Baker, 2000). Survey coverage was also limited to the months of April–November for the Blaylock et al. (1988) and Barco et al. (1999) abundance estimates. Multiple abundance surveys, including the University of Rhode Island’s (Cetacean and Turtle Assessment Program (CETAP) in 1978–1982, NMFS’ Mid-Atlantic Tursiops Surveys (MATS) in 2002 and 2004, and NMFS’ Atlantic Marine Assessment Program for Protected Species (AMAPPS) in 2010, 2011 and 2016) surveyed the coastal area for bottlenose dolphins, but abundance estimates did not include Chesapeake Bay nor any other estuary (Winn, 1982; Garrison et al., 2017).

The waters off the Virginia coast are heavily used by the US Navy and are home to the sixth busiest container port in the US. The area is utilised by recreational and charter fishing vessels and the marine environment is particularly vulnerable to pollution given the large size of the Chesapeake Bay watershed. Climate change, commercial fishing and oil and gas exploration are additional threats to marine species occurring in the area. The region’s bottlenose dolphin populations have also been affected by two mass die-off events, first in 1987–1988 where 742 dolphins stranded (Lipscomb et al., 1994; Scott et al., 1988; Geraci, 1989) and again in 2013–2015 with more than 1,600 strandings (Morris et al., 2015). Scott et al. (1988) estimated that the mortality rate during the 1987–1988 event was ten times that of the prior historical rates. According to NMFS, the stranding rate during the 2013–2015 period was approximately five times the average from the five years prior.

Visual surveys were conducted during 2012–2015 as part of the US Navy’s Marine Species Monitoring Program supported by HDR Inc. The primary goal for the work was to provide a more complete assessment of the seasonal occurrence of bottlenose dolphins in the area and investigate site fidelity within the region. Two survey

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5 https://usace.contentdm.oclc.org/digital/collection/p16021coll2/id/1415/rec/1
6 https://www.chesapeakebay.net/discover/watershed
Fig. 1. Map of east coast of U.S, adapted from Hayes et al. (2018) and NOAA Fisheries, showing estimated latitudinal limits and best abundance estimates (N) of three bottlenose dolphin stocks that occur in the study area. The red color shows the approximate warm-season boundaries for each stock and the blue shows the approximate cold-season boundaries.
techniques were employed: systematic line-transect surveys and photo-identification (photo-ID), both to be completed monthly, whenever possible, for year-round coverage. Line-transect survey data were analysed to determine distribution and density/abundance of marine mammals in the study area, using NMFS’ standard Distance sampling protocols (Jackson, 2001). The study area and zones were determined through coordination with the US Navy to best represent areas most utilised for exercises and construction. The objective of the photo-ID surveys was to determine site fidelity and distributional patterns of marine mammals using the study area.

MATERIALS AND METHODS

Study Area
Norfolk and Virginia Beach border the southern end of Chesapeake Bay and the coastline of Virginia Beach extends along the Atlantic Ocean (Fig. 2). Within the study area construction is widespread; military, commercial and recreational vessels transit in large numbers; and military training exercises occur on a regular basis.

Prior to initial surveys in 2012, two primary survey zones were established, as shown in Fig. 2a. Following supplementary information and input and taking into account results from the first 19 months of this study, the offshore zone was adjusted in March 2014 to optimise coverage. The amended zones are shown in Fig. 2b:

(1) Inshore – a 310.4 square kilometre (km²) area covering a strip extending from shore out to 3.7km (2.0NM). The inshore zone includes the coastal Chesapeake Bay waters near Naval Station Norfolk, extends past Cape Henry and extends down the Atlantic coast towards the Virginia/North Carolina border.

(2) Offshore – a 596.6km² area covering Atlantic waters from 3.7km (2.0NM) to 25.7km (13.9NM) from shore. The offshore zone was designed to include nearly the entire Virginia Capes Operation Area Mine Neutralisation Exercise (MINEX) W-50a and W-50b Navy training areas.

Vessel Line-transect Surveys
Line-transect surveys were scheduled for two full days (approximately 8–10 hours [hr]) each month (one for each survey zone) beginning in August 2012. Zig-zag transect lines were created to cover the 3.7km inshore strip and two alternating sets of five parallel transect lines were created to cover the MINEX W-50 range boxes in the offshore zone (Fig. 2b). Offshore transect lines were 22km in length and spaced at a distance of 5.4km apart. The modifications made in early 2014 allowed better alignment with Navy training activity and addressed potential biases of the original design. The offshore transect lines were shifted north and extended inshore to meet the inshore zone boundary. The inshore boundary did not change; however, the initial zig-zag pattern (Fig. 2a) of the inshore transects introduced a potential positive bias along the inside corners when compared to the outside of the corners and the tighter grouping of lines on the Chesapeake Bay side of the area lead to uneven coverage (see Thomas et al., 2007). Adjustments were made with assistance from experts at the Centre for Research into Ecological and Environmental Modelling, using tools in the program DISTANCE 6.2 (Thomas et al. 2010) to reduce potential bias, while using as much of the earlier-collected data as possible in later analyses (Fig. 2b). Data collected prior to the adjustment that were still within the new boundaries were included in the analysis for both zones.

Departures were timed to maximise survey duration in daylight hours (approximately 1hr after dawn through 1hr before dusk) and optimal weather conditions (i.e., Beaufort Sea State [BSS] 0–3, no heavy rain and visibility of greater than 1.8km). Beginning and end times for the survey days were dependent on weather conditions and daylight available.

Line-transect surveys were conducted using the Research Vessel (R/V) Ocean Explorer, or charter fishing vessels (M/V) Flat Line and M/V Matador, which range in length from 12.8 to 13.7 metres (m) and all possessing elevated viewing platforms. The height of the observers’ eyes above the water’s surface was approximately 4m. The vessel transited the survey lines at a constant speed of 15 to 19km/hr (8–10 knots). Three observers comprised the on-effort survey team. Two of the observers searched for marine mammals continuously through
Fig. 2. Study area delineated into inshore and offshore zones with transect lines used for year 1 of study (a) and revised transect lines for inshore and offshore zones for years 2 and 3 of study (b).
Baker Marine 7 × 50 binoculars, with the port observer focused on the 100° arc from 10° to 270° (all angles are given in relation to the bow, which is defined as 0°) and the starboard observer from 350° to 90°. The third on-effort observer searched primarily with the naked eye, to avoid missing groups near the trackline. This observer also served as the data recorder. The resulting search area covered by the three-person team included the bearings ahead of the vessel, between 90° and 270°, with a 10° overlap centred on the trackline. To minimise fatigue, observers rotated positions approximately every 30 minutes (min).

Effort data collected during on-effort survey periods included time and position for the start and end of search effort, BSS, visibility, presence and percentage of glare and percent cloud cover. Survey software automatically recorded vessel speed and tracked position at 30-second intervals. When marine mammals were sighted, the monitoring team collected associated sighting data and, if necessary, the vessel diverted from its current course to approach the sighting to confirm group size estimates and species identification. A decision was made whether or not to obtain photographs based on time constraints and priority of completing trackline effort for the day. In these instances where the vessel left the track, the data recorder indicated in the software that the team went off-effort. The monitoring team also prioritised completing the tracklines within the available survey time each day over collecting additional ancillary data. Sighting information collected included data on initial sighting angle and distance, initial sighting position, environmental conditions, group size and composition and behavioural state (travel, mill, social, play, or unknown), including any response to the survey vessel.

Actual animal locations were calculated by VisVessel (version 1.1.0.0, Read et al., 2014), Mysticetus8 (version 1.9.0.158) or WILD9 (Whale Identification, Logging and Display System version 1.9.02) software, using the input values for bearing to the individual or group and a measure of distance. Sighting distances were calculated using reticles in the binoculars or by visual estimation, if no horizon was visible. Training in distance estimation using Bushnell Fusion 1600 laser rangefinder binoculars was completed prior to project startup, and for new observers before surveys. Location data and vessel speed were obtained from a Globalsat BU-353 or Garmin 78s global positioning system. Photographs were taken opportunistically during sightings (time permitting) using a Canon 7D digital camera with a 100 to 400-millimeter (mm) zoom lens or a fixed 300mm lens. Photographs of bottlenose dolphins were added to the photo-ID catalogue described below.

Data Analysis

Conventional line-transect methods (also known as Conventional Distance Sampling or CDS) were used to analyse the vessel survey data (Buckland et al., 2001). Estimates of density and abundance (and their associated CV) were calculated using the following formulae:

\[
\hat{D} = \frac{n \hat{f}(0) \hat{E}(s)}{2L \hat{g}(0)}
\]

\[
\hat{N} = \frac{n \hat{f}(0) \hat{E}(s) A}{2L \hat{g}(0)}
\]

\[
CV = \sqrt{\frac{\text{var}(n)}{n^2} + \frac{\text{var} [ \hat{f}(0) ]}{[ \hat{f}(0) ]^2} + \frac{\text{var} [ \hat{E}(s) ]}{[ \hat{E}(s) ]^2} + \frac{\text{var} [ \hat{g}(0) ]}{[ \hat{g}(0) ]^2}}
\]

Where,

\(D\) = density (of individuals),

\(n\) = number of on-effort sightings,

\(f(0)\) = probability density function evaluated at zero distance,

\(E(s)\) = expected average group size (using size-bias correction in DISTANCE),

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8 https://www.mysticetus.com/
L = length of transect lines surveyed on effort,
g(0) = trackline detection probability,
N = abundance,
A = size of the study area,
CV = coefficient of variation and
var = variance.

The probability density function and encounter rates were calculated for bottlenose dolphins using the software DISTANCE 6.2, making use of all on-effort data collected in BSS conditions of 0–3, which was considered acceptable sighting conditions. Estimates were not stratified by BSS or other environmental parameters due to limited sample sizes. Estimates of density and abundance (in terms of sighting rate and group size) and main survey zone, producing four separate estimates. The seasons were defined as warm-water (June–November) and cool-water (December–May), which aligns with the seasonal designations discussed in the NMFS Stock Assessment Reports (Hayes et al., 2018). Sighting rates and average group size were calculated separately for each of the four strata. Due to sample size considerations and the consistency of data collection across all years of the study, data were pooled from all strata to produce a single estimate of the probability density function, f(0).

To avoid potential overestimation of group size, the size-bias-adjusted estimate of average group size was calculated in DISTANCE. Group size for each estimate was calculated using a stratified approach (i.e., only groups from within a particular stratum were used to calculate average group size for that stratum).

Several approaches to truncation of the perpendicular sighting distance (PSD) data were tested and truncation at 0.35km produced the PSD histogram with the best fit satisfying the ‘shape criterion’ and lowest variance (see Buckland et al., 2001). The data were modelled using hazard rate (with cosine and simple polynomial adjustments) and half normal (with cosine and hermite polynomial adjustments) models; the model with the lowest value for Akaike's Information Criterion was selected and used for the final estimates.

Data were not available to estimate trackline detection probability [g(0)] for this study, thus g(0) was assumed to equal 1.0. While this may not be strictly true, the study area is relatively shallow (< 20m) and bottlenose dolphins do not normally conduct long, deep dives in such habitats. Therefore, if there is any availability bias resulting from the assumption of g(0) = 1.0, it should be minimal. Perception bias could, however, result in a negative bias in the resulting estimates, though we had no data available to evaluate this in the current study.

Photo-identification Surveys
During the first year, photo-ID surveys were conducted only during summer months, but funding allowed for monthly surveys throughout all seasons in subsequent years when weather conditions permitted. Departures by the survey team were timed for optimal light conditions for photography and optimal weather conditions (e.g., BSS 0–3, no heavy rain and visibility of greater than 1.8km).

Initially we attempted systematic coverage of the ‘Inner Bay’ zone areas using the small M/V Double OO’s, a 9.4m centre-console vessel to collect data suited for mark-recapture population estimates. However, it was determined that the significant seasonal fluctuation of dolphins in/out of the study area violates the assumption of geographic closure for conventional capture-recapture models (Wilson et al., 1999) and would not allow such analysis. As a result, it was decided that a more efficient use of time would be to extend the survey area towards Cape Henry and to the south along the coast and spend more time with dolphin groups rather than focusing on systematic coverage of particular areas for photo-ID surveys. The vessel transited the nearshore waters at a speed of 13 to 15km/hr (7–8 knots) while observers searched for marine mammals using Canon IS (image stabilised) 10 × 30 binoculars and with the naked eye.

Upon sighting a group of dolphins, data were recorded on printed data sheets, including group size estimates, species identification, initial behavioural category, sighting location, bottom depth, sea surface temperature and frame numbers of photographs taken. Location data were obtained from a handheld Garmin global positioning system receiver. Photographs were taken when possible using a Canon 7D digital camera with a 100–400mm
zoom lens. Observers adjusted the amount of time spent with each group as necessary to obtain photographs of as many individuals within the group as possible while allowing additional survey time to optimise coverage and encounter additional groups.

All photos taken were for identification purposes and the photographer focused on perpendicular views of the dolphins’ dorsal fins. Unique patterns of nicks and notches on the trailing edge of the dorsal fins were used to identify individuals, a technique utilised by numerous researchers and first described by Würsig and Würsig (1977). Photos went through a process of digital sorting and cataloguing, starting with the initial removal of poor quality photos (i.e., out of focus, poor angle, obscured fins, or too distant). Photos rated fair, good, or excellent quality then went through the next steps in the process. The program ACDSee Pro\(^{10}\) (Versions 3–8) was used to crop, zoom and sort the dorsal fin photos within each group sighting by matching up all duplicate photos of the same individual and choosing the best image to proceed to cataloguing. Each image used was assigned a distinctiveness rating number 1–4 (1 = very distinctive, 2 = moderately distinctive, 3 = marginally distinctive and 4 = not distinctive), using criteria similar to that described in Urian et al. 1999. Category 4 photos were eliminated from catalogue comparisons. The Norfolk-Virginia Beach (NVB) catalogue was then created (also using ACDSee) by designating an ID number for each individual in a sighting group. For each subsequent group sighting, each image was first compared to each previously catalogued individual to see if it matched any of those fins before designating as a new individual and assigning an ID number. Any potential matches found were verified by a second experienced reviewer before confirming as a re-sighting. A spreadsheet was used to track additional details, such as latitude and longitude of the sighting; date and time of the sighting; the date the ID was added to the catalogue; whether left, right or photos from both sides were obtained; presence of *Xenobalanus globicipitis*, an assigned distinctiveness rating; and whether the ID was the original or if it was a within-year or between-year re-sighting.

Supplementary images collected during the line-transect surveys outlined above, within the same study area, were included in the photo-ID catalogue. Matches of catalogued animals to a catalogue of 56 individuals photographed during cruises to refurbish acoustic recording devices approximately 75–100km north of the study area in the Chesapeake Bay, near Patuxent River (PAX) (Richlen *et al.*, 2018) were also included in the comparison.

**RESULTS**

**Line-Transect Surveys**

Thirty-three inshore line-transect surveys and 28 offshore line-transect surveys were completed between August 2012 and August 2015 covering a total of 6,550km and 348.8hrs on-effort. The total on-effort distance and time spent in the inshore zone was 3,634km and 192.8hrs, respectively, while 2,916km and 156.8hrs of on-effort time was spent in the offshore zone.

A total of 517 sightings of bottlenose dolphins was recorded during transect surveys from August 2012 through August 2015 (Fig. 3). Seventy-seven dolphin groups were sighted in the offshore zone, while 440 were sighted in the inshore zone (Table 1).

Sighting numbers varied by season, with overall sightings totals as few as 28 sightings during cool-water months and as many as 49 in the warm-water season in the offshore zone; and as few as 81 in the cool-water season and a maximum of 359 during warm-water months in the inshore zone (Fig. 3, Table 1).

**Density and Abundance Estimates**

Estimates of density and abundance were calculated for bottlenose dolphins using 413 sightings and 3,535.3km of line-transect survey effort in the inshore zone, and 63 sightings and 2,478.3km of effort in the offshore zone, after excluding effort and sightings that fell outside of the final boundaries as shown in Fig. 2a. The detection function was modelled using the hazard rate key function, with a cosine adjustment. The calculated value of f(0) was 6.4689 (CV = 11.2%) and the effective strip width (1/f(0)) was 155m. The histogram of perpendicular sighting distances and fitted model are shown in Fig. 4. A positive reaction to the vessel was noted for one offshore

\(^{10}\)https://www.acdsee.com
sighting and for 13 inshore sightings, which is 1.3 and 2.9% of all sightings, respectively. Line-transect parameters and resulting estimates are provided in Table 2.

**Photo-Identification Surveys**

Twenty-seven photo-ID surveys were completed between August 2012 and August 2015 with a total of 193 groups of bottlenose dolphins sighted (Table 3). A catalogue was created using photos collected from both photo-ID and transect surveys. Fig. 5 shows the locations of all sightings used in the catalogue. To date, the NVB catalogue contains 1,335 identifiable individuals. The catalogue was also compared to HDR’s Patuxent River (PAX) bottlenose dolphin catalogue consisting of 56 individual dolphins photographed on three separate days in 2015 and 2016.
Fig. 4. Perpendicular distance histogram and fitted detection function for bottlenose dolphins.

Table 2

<table>
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<tr>
<th>Zone</th>
<th>Season</th>
<th>No. sightings*</th>
<th>Effort (km)</th>
<th>Avg. Grp. Size</th>
<th>Stg. Rate³</th>
<th>Density⁴</th>
<th>Abundance</th>
<th>CV</th>
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<td>Inshore</td>
<td>Cool-water</td>
<td>63</td>
<td>1,791</td>
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<td>1,427</td>
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<td>741</td>
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*After truncation. § Measured as individuals per linear km. # Measured as individuals per km².

Table 3

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<th>Total survey minutes</th>
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Re-sighting rates across surveys were low. Of the 1,335 individuals catalogued, excluding same day re-sightings, 228 (17.1%) individuals were seen on more than one occasion and 56 of those (4.2% of catalogued individuals) were seen on three or more occasions with a maximum of 5 sightings for one individual (Table 4). Days between sightings ranged from 5 to 970 days (mean = 282) within the study area and as many as 1,336 days for individuals matched to the PAX catalogue. There were 87 individuals with less than 150 days between sightings, which were considered within-season re-sightings and 141 were greater than 150 days, categorised as between-season re-sightings.

Distance between sighting locations for a re-sighted individual did not always increase as time between sightings increased. Table 4 shows the number of days between first and last sighting of an individual, as well as the distance between the first and last sighting for all individuals sighted greater than 500 days apart – 18 of the 20 individuals (90.0%) had a distance of less than 25km between all sightings.

Sighting locations for the 228 re-sighted individuals were broken into regions: Inner Bay (IB), Cape Henry (CH) and Outer Coastline (OC) (Fig. 5). While there was overlap between regions (38.2% seen in more than one region), 105 individuals (46.1%) were sighted only in the CH region; 25 (11.0%) were only sighted in the OC region and 11 (4.8%) were only sighted in the IB. The greatest overlap was between the IB/CH regions; 56 individuals (24.6%) were sighted in both of these areas. Twenty-seven (11.8%) were sighted in both CH and the OC and just 4 (1.8%) in both CH and the IB.

For those individuals sighted only in CH, 93.3% (98 of 105) were sighted during summer and fall seasons only. The remaining sightings were in spring (May) and none were during winter months. Of the 25 individuals sighted
only in OC, 88% (22 of 25) occurred during fall and winter months. The remaining were in spring (March or April) and none were in summer. Summer sightings were recorded within the boundaries of the OC region, but the individuals sighted within that region during the summer were also sighted elsewhere within the study area. The 11 individuals sighted only within the IB region were all observed during summer and fall months.

Table 4

<table>
<thead>
<tr>
<th>Catalog ID no.</th>
<th>Number of days sighted</th>
<th>Days between first and last re-sighting</th>
<th>Distance between first and last sightings (km)</th>
<th>Regions sighted</th>
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</thead>
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<tr>
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<td>8.5</td>
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<tr>
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<td>694</td>
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</table>

Two matches were made between the NVB and PAX catalogue. Both of those individuals were sighted during winter months in the OC region of the study area and in the PAX area during summer months. Fig. 6 shows the sighting location of the PAX individuals in relation to the other sightings included in the NVB catalogue.

Epizoic barnacles (*Xenobalanus globicipitis*) were present on dorsal fins of catalogued dolphins during all months from April to December; none were recorded from January to March. Of the 228 individuals photographed on more than one day, 51.3% (117) had barnacles recorded. For individuals sighted within only one of the three sighting location regions, 70 of the 105 CH only (66.7%), one of the 25 OC only (4.0%), and three of the 11 IB only (27.3%) individuals had a barnacle present during one or more sighting.

**DISCUSSION**

The results from this project confirm earlier findings that bottlenose dolphins are common in the study area, with highest densities in the inshore coastal waters in summer and fall months. Peak estimated abundance in coastal waters of the study area was 1,090 individuals present during the warm-water season (density = 3.51 individuals per km$^2$, CV = 16%). Bottlenose dolphins do not, however, completely leave this area during cool-water months, with approximately 225 individuals still present in winter and spring months. Previous studies reported that this region had no presence of bottlenose dolphins in winter months (Winn, 1982; Barco et al., 1999; Blaylock, 1988). Hayes et al. (2018) also designated the VA/NC border as the northern boundary for winter occurrence for the NMCS. The 20 sightings recorded during inshore coastal surveys in winter months clearly challenge the previously accepted seasonal residency concept, but considering the majority of these sightings were located to the southern end of the inshore zone, a possible explanation could be the boundary designated by the current stock assessment simply needs to be extended to the north. There are, however, sightings in the months of January and February that are near Cape Henry or further inside Chesapeake Bay (Fig. 3). Winter survey effort has definitively shown that dolphins are present during winter months, which has not been previously considered.
Fig. 6. Bottlenose dolphin group sighting locations from PAX and NVB catalogs.
Densities in the waters of the offshore zone were generally lower than in the coastal strip (D = 1.24 individuals/km² in summer/fall and 0.61 individuals/km² in winter/spring) (Table 2). This area falls close to the existing winter boundary for the NMCS and well within the northern limit of the summer boundary of the SMCS. It is likely the density estimate for the offshore zone encompasses parts of both migratory coastal stocks, while the inshore zone is a much more complicated area of overlapping ranges.

The transect line modifications made in early 2014 improved the overall design, and allowed for better correspondence with Navy activities. The inclusion of relevant data from before the redesign is not expected to have resulted in any significant bias, as the modifications were relatively minor, and we ensured that only data that fell within the new boundaries were used in the final analysis. In addition, although there might be a slight bias as a result of attraction of some dolphins to the survey vessel, dolphin groups only showed a positive response to the survey vessel in a very small proportion of cases (< 3% for each survey area). We do not think this would have had a significant impact on our results. A more important issue of potential bias involves the fact that perception bias can be significant for bottlenose dolphins, especially in moderate to high Beaufort states (Barlow, 2015). Therefore, since we were not able to account for this in our study, our estimates may show a significant downward bias, as a result.

Most of our final estimates are more precise than previously available estimates (and most of our inshore estimates are reasonably precise, with CVs in the 16–28% range). This is likely due to both the improved survey design and also to the increased sample sizes that went into producing year-round estimates. We feel that these estimates could be useful as baselines for future managements actions, but with due consideration to the potential biases that we have identified (e.g., potential missed trackline sightings, and responsive movement).

Photo-ID results indicate a very open population, with short-term visits to the area with localised sightings for most individuals. Range boundaries are not distinct, however and there is no clear way to draw lines given the level of overlap. With 17.1% of identified individuals being re-sighted, that leaves 82.9% of catalogued individuals sighted only once, which is greater than that described by Barco (1999) of 75%. These two studies include the same region, though coverage in the current photo-ID study extended further inside Chesapeake Bay, as well as farther south along the Virginia coast.

Re-sightings in the Cape Henry region are clear evidence of seasonal fidelity, shown by multiple between-season re-sightings in close proximity (within 20km) to their original sighting locations, occurring within the same year or during the same warm season in subsequent years. Previous studies have also suggested seasonal fidelity (Blaylock, 1984; Barco, 1995). The re-sightings within the Cape Henry region are also evidence of the overlapping range from individuals of different stocks. Recent stock assessments place the region as part of the warm-month distribution of the SMCS (Hayes et al., 2018), however, the region is also positioned between the reported warm- and cold-month distribution of the NMCS, so individuals from both stocks are expected to occur. The results of a satellite tracking effort summarised by (Hayes et al., 2018) further complicate the picture by showing members of the NNCES also using Virginia waters. Too few re-sightings exist to allow for home range estimates, which is also problematic because of the lack of clear boundaries. Comparison of catalogues to other regions as a next step will be key to confirming these seasonal residents as part of the appropriate NMFS-managed stock and may help to stratify the occurrence by season and the level of overlap of these stocks. Such comparisons have the potential to identify individuals not observed in any of the other regions, which is also of importance.

Individuals sighted during winter months in the Outer Coastline region are of particular interest. According to the described distribution of bottlenose dolphin stocks, one would expect all individuals sighted within the study area during cold months to be a part of the NMCS. However, the two individuals re-sighted to the north inside Chesapeake Bay suggest some individuals are not falling into the previously described ranges or stock boundaries. The absence of *Xenobalanus* on the majority of these individuals further supports the discrepancy, assuming the absence of the barnacles would suggest those individuals belong to the estuarine stock NNCES rather than the NMCS stock, as suggested by Urian et al. 2019, however the timing doesn’t match the cold-month distribution of that stock as currently understood. If additional matches are found of animals sighted in the OC region during cold months and farther north inside Chesapeake Bay, it could warrant expanding the northern extent of the range of the NMCS to include Chesapeake Bay. Alternatively, it could suggest the presence of a Chesapeake Bay estuarine stock that does not migrate to the regions of the other three defined
stocks. The large size, open mouth, and seasonal variability of Chesapeake Bay may make discerning a resident estuarine population somewhat more complicated compared to closed estuarine systems, such as in North Carolina, South Carolina and Florida (Wang et al., 1994; Gubbins, 2002; Zolman, 2002; Mazzoil et al., 2008; Urian et al., 2013).

Further comparisons will also benefit the determination of stock assignment for the dolphins sighted within the Inner Bay region. It is unknown whether summer, fall and spring sightings inside the bay to the far west such as these, are members of the SMCS, the NNCES stock, or even similar to those discussed above, sighted in PAX during warm months (inside Chesapeake Bay, Fig. 6) and in the OC zone during winter. Even the current study leaves much of the Chesapeake Bay area of dolphin distribution undocumented. Sighting data show dolphins utilise much more of Chesapeake Bay, including areas surrounding the northern end of the bay mouth (near Cape Charles, Wang et al., 1994) and farther north inside the bay (Baker, 2000; Rodriguez et al., 2021), and the stock to which these dolphins belong is unclear.

The progression of stock structure designations and ability to assess impacts is an important consideration. For example, abundance estimates conducted to assess the impact of the 1987–1988 morbillivirus outbreak showed no difference locally (Keinath and Musick, 1988), but back when the coastal stock was considered to be one large stock that migrated north and south, Scott et al. (1988) estimated a decline in abundance of up to 53%. Similarly, Garrison et al. (2017) found a potential decrease in abundance before and after the 2013–2015 die-off, but stratification of the local estimates performed on this dataset that was presented in Engelhaupt et al. (2016) showed no decrease in abundance following the event. This was not included in the present publication, however, as results did not have enough power and should be taken with caution.

Further changes may be forthcoming as more detailed studies reveal departures from the existing boundaries and possible ‘new’ stocks that have yet to be documented. Toth et al. (2012) thought further partitioning of the NMCS was warranted. Interestingly though, the suggested differentiation was within the coastal stock, not a separate estuarine stock; the authors suggest in another publication that dolphins from the NMCS do not commonly occur in nearby estuaries even on a seasonal basis (Toth et al., 2011).

Overall, the results from this study provide more detailed and up-to-date information by estimating bottlenose dolphin abundance throughout the year and providing information for recent years. These results support findings from previous research, but also show substantial presence of bottlenose dolphins throughout the year in nearshore areas of southern Virginia, with a level of occurrence that fluctuates seasonally. Density estimates confirm an expected seasonal peak in summer and fall, corresponding with warm water temperatures, but the study takes the next step to include estimates for all seasons. These estimates, however, cannot be clearly separated and assigned to management stocks as they are currently defined. Further refining stock designations is important for management purposes since smaller populations, such as estuarine stocks, may have a greater vulnerability to significant impacts from the multitude of threats.

It is a complicated labyrinth of varied factors that lead to the distribution of bottlenose dolphins in this area, and lines between the stocks are not discrete or easily identified. This compounds the difficulty in defining stock boundaries and further complicates our ability to assess potential impacts that come from multiple anthropogenic sources, climate change, compromised water quality, stress from military activities, vessel traffic, fisheries competition and direct fisheries interactions. Levels of impacts vary geographically and therefore differential occurrence patterns need to be considered when managing the species. One particular stock may be more vulnerable to a specific threat than others. Still, progress has been made and our understanding has greatly improved. We now understand that the situation is more complex than the previously described single coastal migratory stock, but some dolphins may still not be accounted for in management decisions. Future work should address this.

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