

Historical Abundance and Spatial Distribution of the Atlantic Bottlenose Dolphin (*Tursiops truncatus*) Along the Southeast Coast of the United States

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Abstract

The Atlantic coastal bottlenose dolphin (*Tursiops truncatus*) has a complex distribution along the southeast coast of the United States. The current population estimates for the 15 stocks of these dolphins are based primarily on a series of surveys, with the incorporation of stranding data and trends observed during a series of mass strandings caused by a morbillivirus epizootic in 1987-1988. Currently, there are no density or abundance estimates for areas south of Cape Hatteras, North Carolina, before these stranding events. From April 1982 to August 1984, aerial sightings of dolphins were recorded seasonally along the continental shelf from Cape Hatteras to Key West, Florida. These data were collected in conjunction with the Southeast Turtle Surveys (SETS) conducted by the National Marine Fisheries Service. We analyzed these datasets to determine population density and abundance across locations, seasons, and years prior to the 1987-1988 event. The average abundance estimate from 1982 to 1984 was 10,931 dolphins (CV = 0.06). Abundance estimates for 1982 (11,720, CV = 0.14), 1983 (11,393, CV = 0.09), and 1984 (14,408, CV = 0.12) were not significantly different ($p \leq 0.05$). Nor were the summer (10,324, CV = 0.14), spring (13,312, CV = 0.09), and fall (15,900, CV = 0.19) estimates. Results demonstrate that dolphins in the early 1980s followed similar migratory patterns as currently observed, including a shift of dolphins north in the summer and south in the winter. The estimated abundance in the winter of 1983 was less than estimates from replicate studies in the winter of 1992 and 1995, while estimated abundance of dolphins in the summers of the early 1980s was approximately half that estimated in a summer 2002 survey. These data present a baseline of density and abundance estimates before the mass stranding events of 1987-1988, and preliminary comparisons indicate that the mortality

rate may have been low for the overall population of dolphins between Cape Hatteras and Key West.

Key Words: Atlantic bottlenose dolphin, *Tursiops truncatus*, distribution, abundance, line transects, distance sampling, estimate, SETS

Introduction

The Atlantic bottlenose dolphin (*Tursiops truncatus*) has a complex distribution along the Atlantic coast of the United States, and it is comprised of estuarine, coastal, and offshore stocks. Two of these stocks are morphologically and genetically distinct ecotypes that occur in waters over the continental shelf, and are described as the *offshore* and *coastal* ecotypes (Duffield et al., 1983). The coastal ecotype is typically found between 7.5 and 34 km from shore, and the offshore ecotype is found in water ≥ 34 km offshore and ≥ 34 m deep (Torres et al., 2003).

The coastal bottlenose dolphin ecotype includes migratory, resident, and transient stocks found within estuarine habitats and nearshore continental shelf waters from northern New Jersey to central Florida (Waring et al., 2011). Two migratory stocks are hypothesized to move seasonally over large spatial scales. The Northern Migratory stock occurs in waters off of North Carolina during the winter months and ranges as far north as New Jersey during the summer (Rosel et al., 2009). The movement of the Southern Migratory stock is less well understood, but it likely ranges as far south as northern Florida during winter months and occurs off the coast of North Carolina and perhaps Virginia during the summer (Waring et al., 2011). In addition, there appear to be resident animals within nearshore coastal waters off of South Carolina, Georgia, and northern Florida that do not undertake large-scale seasonal migrations (Waring et al., 2011) (Figure 1). Finally, there are resident bottlenose dolphin populations that occupy the waters of

estuarine systems, including those near Charleston, South Carolina (Speakman et al., 2006); Indian River Lagoon, Florida (Mazzoil et al., 2005, 2008); and Biscayne Bay, Florida (Litz, 2007). Animals from these stocks may occur intermittently in near-shore coastal waters (Waring et al., 2011).

The complexity of the stock structure of bottlenose dolphins on the Atlantic coast has hampered assessments of population status and the evaluation of the impacts of both natural and anthropogenic sources of mortality. A series of mass strandings caused by a morbillivirus epizootic (Lipscomb et al., 1994) occurred in 1987-1988 between Florida and New Jersey. Initially, the spatial and temporal patterns of strandings were interpreted to represent a single coastal migratory stock ranging seasonally between Florida and New Jersey, and the impact on

this putative stock was estimated to have resulted in mortality rates up to 50% (Scott et al., 1988). However, later evaluation by McLellan et al. (2002) was not consistent with the single stock hypothesis, and genetic analyses indicated multiple distinct populations throughout the range of the epizootic event (Rosel et al., 2009). Reanalysis of the stranding patterns suggested that the mortality rate for some stocks was likely close to 10% (Eguchi, 2002). Following the mass strandings of 1987-1988, the coastal migratory stock of bottlenose dolphins was declared *depleted* under the Marine Mammal Protection Act, and the entire coastal ecotype retains that status despite the revisions to the stock structure.

The abundance and spatial distribution of bottlenose dolphins in coastal waters of the southeast U.S. has been assessed using aerial surveys conducted

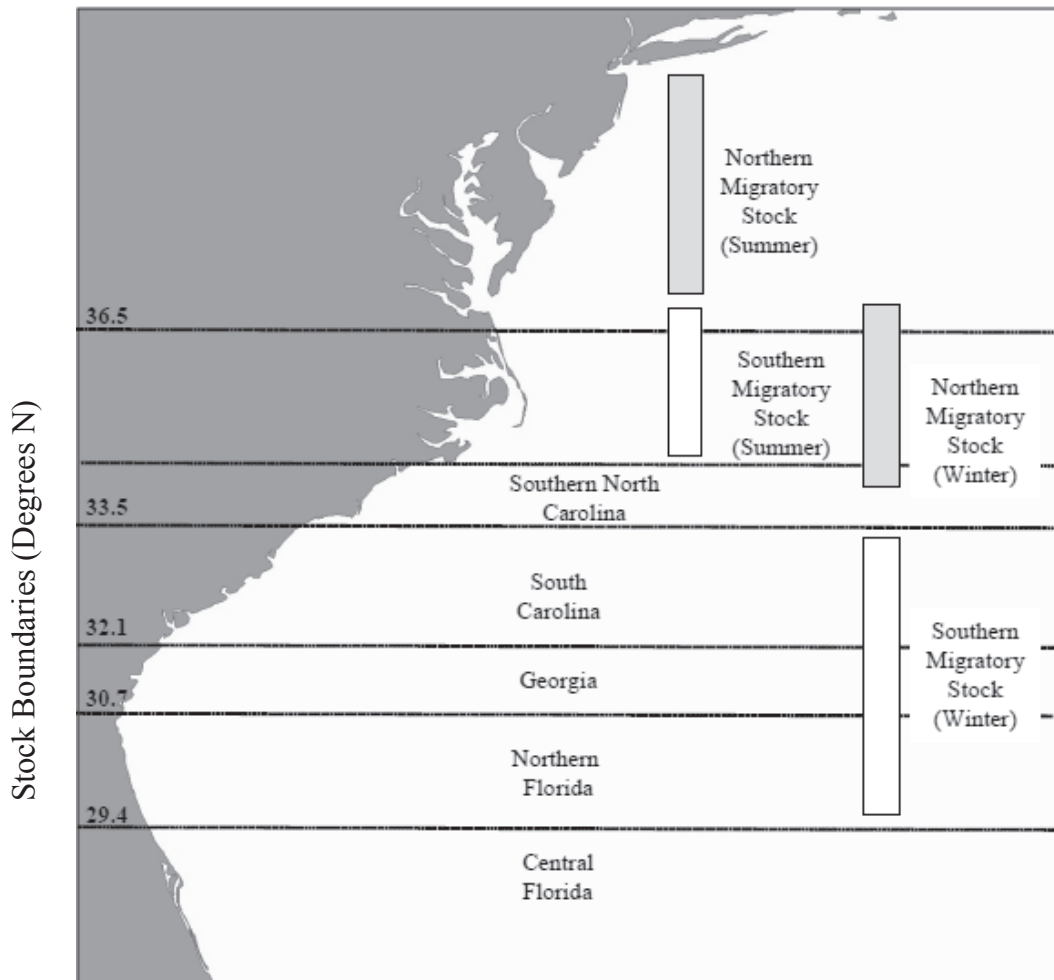


Figure 1. Current boundaries for prospective stocks of Western North Atlantic Coastal morphotypes of bottlenose dolphins; although several estuarine stocks of dolphins are found south of central Florida, there are no separate coastal stocks. Taken from the October 2008 Stock Assessment Report (Waring et al., 2009).

between 1992 and 2005 (Waring et al., 2011). These included a survey in the winter of 1992 (Blaylock & Hoggard, 1994), in the winter of 1995 (Blaylock et al., 1995), and in the summer of 2002 (Garrison et al., 2003). These surveys provide excellent estimates of a single seasonal time point, but they have not been of sufficient frequency to assess potential trends in population size. Also, in the absence of data prior to the epizootic event, it is difficult to evaluate the status of the stocks relative to the decades preceding the event. Another set of aerial surveys were conducted over the continental shelf from Cape Hatteras, North Carolina, to the Gulf of Maine between 1978 and 1982, and these surveys have been analyzed to provide information on seasonal abundance and spatial distribution of bottlenose dolphins from the Northern Migratory stock and the offshore ecotype (Kenney, 1990). These do not include the waters primarily affected by the epizootic event, and no such analysis of historical data has been conducted for waters south of Cape Hatteras.

From 1982 to 1984, aerial surveys to assess sea turtle distribution were conducted seasonally during the Southeast Turtle Survey (SETS). The survey area ran along the U.S. coast from Cape Hatteras to Key West, Florida, and distribution data were collected for sea turtles and dolphins as well as any other discernible sightings (Thompson & Shoop, 1983). Using the data collected during SETS, we calculated estimates of the abundance and density of bottlenose dolphins both collectively and seasonally for the years 1982 to 1984. These results provide a baseline for comparison with estimates from after the morbillivirus epizootic and contribute to the understanding of the bottlenose dolphin population status along the southeast coast of the U.S.

Materials and Methods

Data Collection

From April 1982 to August 1984, aerial surveys were conducted seasonally along the continental shelf from Cape Hatteras, North Carolina, to Key West, Florida. These data were collected in conjunction with SETS conducted by the National Marine Fisheries Service (NMFS) along randomly selected line transects within sampling blocks (Thompson & Shoop, 1983; Aero-Marine Surveys, 1984). Each survey included coverage of the study area from the shoreline to the western edge of the Gulf Stream. The study area covered 107,242 km² and was divided into ten sampling blocks approximately 10,000 km² each (Figure 2) designed to allow each block to be flown in a single day. Surveys were flown seasonally, and each season was comprised of two months: winter (January-February), spring (April-May), summer (July-August), and fall (October-November). Transects of lengths

between 16 and 153 km were selected to sample a total of more than 8% of the area within each block (Thompson & Shoop, 1983). There were a total of eight surveys flown from 1982 to 1984.

Sightings were collected from a twin-engine, Beechcraft AT-11 aircraft flown at an altitude of 152.4 m. A Plexiglas nose bubble allowed for an unobstructed view of the trackline directly below the plane. Before data collection, five intervals were marked on the bubble window using a reference air-strip at increments of $\frac{1}{6}$ nmi or 115.75 m. The perpendicular distance to the trackline from the aircraft for each sighting was recorded within one of these five intervals that encompassed 0 to 578.75 m; therefore, no exact distances from the aircraft were taken (Thompson & Shoop, 1983).

Study observer positions ($n = 4$) included a right and left observer, resting position, and data entry in addition to the pilot. Location, number, and distance from the aircraft of each bottlenose dolphin sighted were recorded as clusters, or estimated number of animals, within one sighting. Since bottlenose dolphins are typically detected in clusters, the distance measurement was taken to the center of the cluster, and the number of individuals in the cluster were counted (Thompson & Shoop, 1983).

The intervals were converted to distances using a random conversion within the interval to avoid problems of curve fitting. Sightings may include any combination of offshore, coastal, or estuarine dolphin stocks. However, the surveys did not extend far into the range of offshore dolphins nor would the survey area allow for adequate coverage of the estuarine stocks. Therefore, the SETS coverage area most likely contains primarily coastal resident and migratory stocks.

Data Analysis

These datasets were analyzed using the computer program *Distance*, Version 5.0, to determine population density and abundance across locations, seasons, and years (Thomas et al., 2010). Each of the eight datasets—spring 1982, 1983, 1984, summer 1982, 1984, fall 1982, 1983, and winter 1983—was analyzed to estimate density and abundance of bottlenose dolphins both across the total area and within each of the ten survey blocks. The individual datasets from each survey were combined to provide seasonal, annual, and overall abundance estimates. The models included the assessment of the covariate effects on sighting (Buckland et al., 2004). Covariates included sea surface temperature (SST) recorded by the Barnes PRT-5S radiometer, time and position of sighting measured by the Loran-C navigation computer, glare, sea state, turbidity, cloud condition (cloudcon), cloud cover, visibility, and any notes about the individual sightings (Thompson & Shoop, 1983).

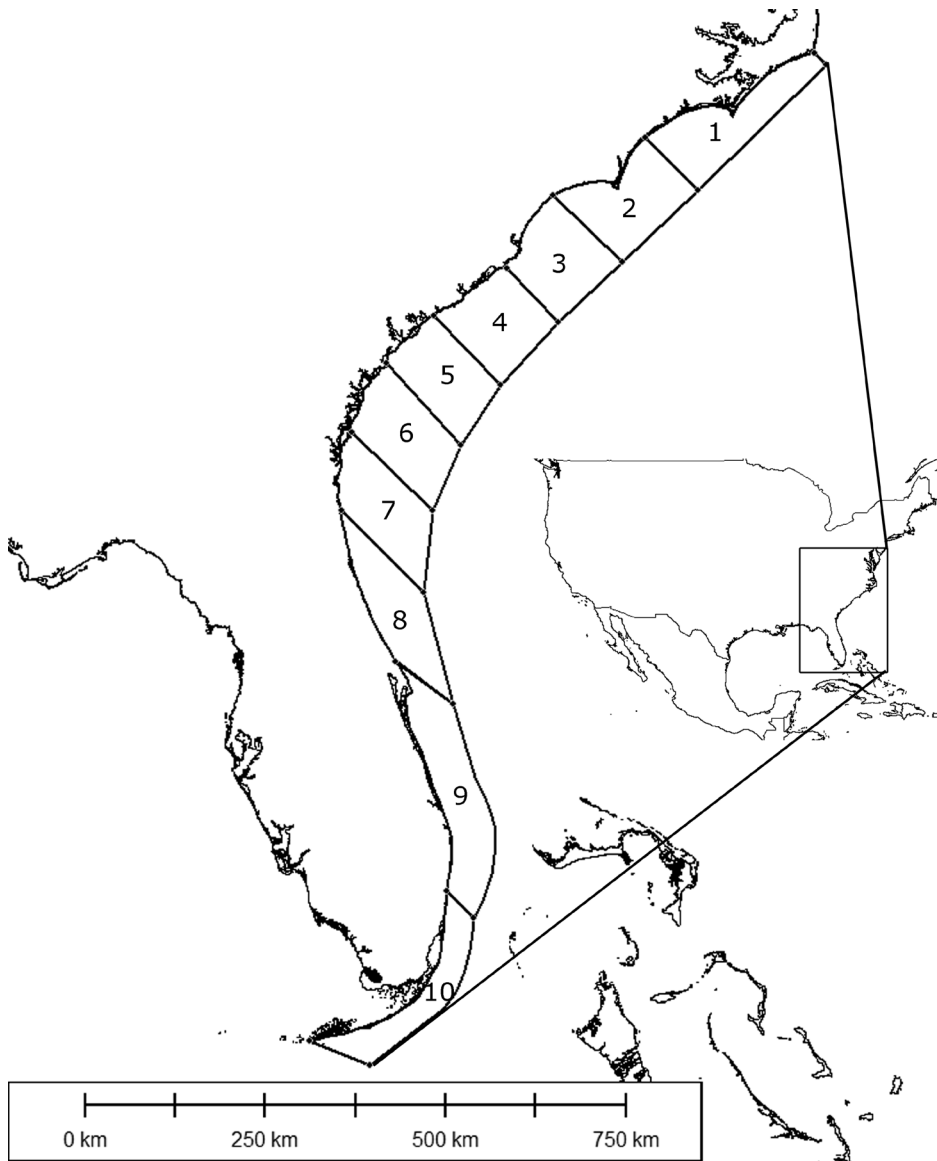


Figure 2. Division of 10,000 km² block areas along the southeast coast of the United States

Each of the eight datasets examined covered Blocks 1 through 10 with at least an 8% effort unless there was interference due to weather or military activity. Three surveys were affected by interference: winter, summer, and fall 1983. During the winter 1983 survey, Block 1 was not surveyed, and Block 2 only had 4.46% coverage due to weather interference. In summer 1983, all blocks had 4% coverage except for Blocks 8 and 9, which had over 8%. During the fall 1983 survey, Blocks 4, 5, 6, and 7 were combined with only 4% coverage of all blocks. Blocks 1 and 2 were missed due to weather,

and Block 3 was cut from the survey (Aero-Marine Surveys, 1984). All estimates incorporate these variations in effort. To determine the actual area contained within each of the ten blocks surveyed, the GPS points (Thompson & Shoop, 1983) of the outer limits of these blocks were plotted using *Globalmapper*, Version 7.0 (2005). The points were then connected and the area contained within the outlined block determined. These areas were used in the density calculations.

All datasets were mapped using *Globalmapper* to examine the position of transects and sightings

within blocks to ensure that all data were recorded correctly. Any transect which crossed blocks or extended more than $\frac{1}{3}$ of its length outside of the block was removed from the analysis. Any sighting associated with these transects was also removed, and any sighting that did not correspond to a transect or block was removed.

The best model for each dataset was chosen based on several factors, most importantly Akaike's Information Criterion (AIC) and secondly the Coefficient of Variance (CV). The best fit model is that which has the lowest AIC and CV (Buckland et al., 2001).

The resultant estimates of density from seasons and years were compared using a Z-statistic. This was calculated using the equation given by Buckland et al. (2001). The difference in density variance between two densities is equal to the addition of the individual variances:

$$\hat{\text{var}}(\hat{D}_1 - \hat{D}_2) = \hat{\text{var}}(\hat{D}_1) + \hat{\text{var}}(\hat{D}_2)$$

This difference in density variance can then be used to calculate the z-score:

$$Z = \frac{(\hat{D}_1 - \hat{D}_2) - (D_1 - D_2)}{\sqrt{\hat{\text{var}}(\hat{D}_1 - \hat{D}_2)}}$$

To test the null hypothesis that the density of one area was equal to the density of another, the

densities were set equal to each other ($D_1 = D_2$) and therefore ($D_1 - D_2 = 0$). The resultant z-score was located in the z-table, which gives the probability of the values being larger, or a one-tailed test. This probability was then multiplied by 2 to determine the two-tailed result (Buckland et al., 2001).

To further test the null hypothesis that densities during separate surveys are equal, the z-based 95% CI were calculated. These are given by the difference in density plus or minus the z-score multiplied by the variance of the difference:

$$(\hat{D}_1 - \hat{D}_2) \pm z(\alpha) \sqrt{\hat{\text{var}}(\hat{D}_1 - \hat{D}_2)}$$

If the resultant range contains zero—in other words, goes from a negative to a positive value—then this indicates that the difference in abundance or density estimates is not significant (Buckland et al., 2001).

Results

All datasets supported robust results with the AIC varying by less than 2 in almost all model comparisons and less than 3 in all comparisons (Burnham & Anderson, 2002). The chosen sighting functions each had a CV less than 0.23 with a low of 0.018 when all datasets were merged (Table 1). The sighting functions had relatively good fits with all of the chi-square goodness of fit *p*-values well above 0.05 (Table 2). All of these factors are indicative of robust datasets that result in the

Table 1. Model selection for all datasets

Dates	Key function	Series adjustment	Truncation	Interval (m)	Covariate
Spring 1982	Hazard-Rate	Simple polynomial	250 m	50	None
Summer 1982	Hazard-Rate	Simple polynomial	5%	50	None
Fall 1982	Half-Normal	Cosine	300 m	75	None
Winter 1983	Half-Normal	Cosine	N/A	115.75	None
Spring 1983	Hazard-Rate	Simple polynomial	7%	33	None
Summer 1983	Half-Normal	Cosine	250 m	50	None
Fall 1983	Half-Normal	Cosine	N/A	86	None
Spring 1984	Hazard-Rate	Simple polynomial	250 m	50	None
Summer 1984	Half-Normal	Cosine	300 m	75	Sea state Cloudcon SST
1982	Hazard-Rate	Simple polynomial	5%	75	None
1983	Hazard-Rate	Simple polynomial	350 m	115.75	None
1984	Half-Normal	Cosine	250 m	50	Sea state
Spring	Hazard-Rate	Simple polynomial	350 m	115.75	SST
Summer	Half-Normal	Cosine	250 m	50	None
Fall	Half-Normal	Cosine	275 m	18	Cloudcon
Winter	Half-Normal	Cosine	N/A	115.75	None
Total	Hazard-Rate	Simple polynomial	300 m	75	Cloudcon

Table 2. Sighting function evaluation criteria: ESW = Effective Swath Width, CV = Coefficient of Variance, GOF = Goodness of Fit, SE = Standard Error; all calculated by the *Distance*, Version 5.0.

Dates	ESW	CV	GOF chi-square <i>p</i> -value	SE
Spring 1982	178	0.08	0.33475	14.722
Summer 1982	207	0.07	0.78249	14.871
Fall 1982	127	0.09	0.64269	11.409
Winter 1983	171	0.08	0.71770	14.144
Spring 1983	238	0.03	0.41765	7.258
Summer 1983	179	0.11	0.87188	20.385
Fall 1983	258	0.23	0.63735	59.711
Spring 1984	211	0.06	0.93570	14.214
Summer 1984	142	0.10	N/A	14.829
1982	185	0.05	0.73214	9.567
1983	214	0.04	N/A	9.516
1984	183	0.03	0.84636	6.454
Spring	213	0.03	N/A	5.973
Summer	174	0.06	0.80738	11.482
Fall	157	0.07	0.66283	11.440
Total	215	0.02	N/A	3.857

Table 3. Density and abundance estimates for all datasets, including the mean group size

Dates	Mean density (dolphins/km ²)	SE density	Mean abundance	SE abundance	CV	Mean group size	SE group size
Spring 1982	0.07690	0.00186	8,247	199.65	0.23	4.25	0.52230
Summer 1982	0.11011	0.00327	11,808	351.03	0.25	8.15	1.62510
Fall 1982	0.17131	0.00438	11,941	305	0.22	7.76	1.07700
Winter 1983	0.12318	0.00237	11,884	228.17	0.20	4.82	1.09070
Spring 1983	0.14401	0.00111	15,444	199.16	0.11	4.83	0.57120
Summer 1983	0.05950	0.00146	6,381	156.61	0.20	3.10	0.37323
Fall 1983	0.08528	0.01641	6,430	489.04	0.39	6.44	1.57200
Spring 1984	0.13473	0.00158	14,449	169.56	0.13	4.30	0.37030
Summer 1984	0.15309	0.01914	14,928	567.08	0.30	5.64	0.93259
1982	0.10928	0.00100	11,720	107.2	0.14	6.51	0.63647
1983	0.10623	0.00048	11,393	51.5	0.09	4.59	0.40059
1984	0.13435	0.00113	14,408	120.87	0.12	4.56	0.35757
Spring	0.12413	0.00048	13,312	51.62	0.08	4.57	0.31573
Summer	0.09627	0.00097	10,324	103.69	0.14	5.54	0.65695
Fall	0.14827	0.00283	15,900	303.53	0.19	7.43	0.89135
Total	0.10193	0.00022	10,931	23.81	0.06	5.16	0.27870

most accurate estimates from the chosen models (Buckland et al., 2001).

The total abundance estimates for the study area were generally higher in the winter and spring and lower in the summer and fall (Table 3). For any given time period, Block 8 (coastal northern Florida) typically had the highest density and abundance estimates, while Blocks 3 and 4 (coastal South Carolina) and Block 10 (southern Florida and the Keys) had the lowest density and abundance estimates (Tables 4 & 5). For several of the datasets, covariate inclusion was indicated by both AIC and CV. These included sea state, SST,

and cloud condition. All three were indicated in summer 1984, sea state in the pooled 1984, SST in both spring and total pooled data, and cloud concentration in fall (Table 1). There were no significant differences ($p \geq 0.05$) in estimated density between seasons or years (Table 6).

Seasonal Comparisons

In spring, the total estimated dolphin abundance for 1982 to 1984 was 13,312 individuals and the estimated density was 0.124 dolphins/km² (CV = 0.08) (Table 3). The highest abundance in the spring was in Block 8 along the northern Florida

Table 4. Dolphin abundance and density seasonally as pooled by years along the southeast coast of the United States from 1982 to 1984

Block (north to south)	Spring		Summer		Fall		Winter	
	mean abundance (CV)	mean density (dolphins/km ²) (CV)	mean abundance (CV)	mean density (dolphins/km ²) (CV)	mean abundance (CV)	mean density (dolphins/km ²) (CV)	mean abundance (CV)	mean density (dolphins/km ²) (CV)
1	534 (0.24)	0.05 (0.24)	703 (0.26)	0.07 (0.26)	3,312 (0.32)	0.31 (0.32)	NA	NA
2	943 (0.21)	0.09 (0.21)	443 (0.52)	0.04 (0.52)	2,915 (0.39)	0.27 (0.39)	0	0
3	1,300 (0.20)	0.13 (0.20)	786 (0.41)	0.08 (0.41)	2,158 (0.29)	0.21 (0.29)	483 (0.46)	0.05 (0.47)
4	1,186 (0.22)	0.12 (0.22)	984 (0.28)	0.10 (0.28)	1,356 (0.43)	0.13 (0.43)	1,765 (0.31)	0.17 (0.32)
5	1,799 (0.20)	0.18 (0.20)	418 (0.39)	0.04 (0.39)	1,751 (0.43)	0.17 (0.43)	450 (0.40)	0.05 (0.40)
6	1,868 (0.18)	0.17 (0.18)	1,173 (0.41)	0.10 (0.41)	717 (0.47)	0.06 (0.47)	288 (0.93)	0.03 (0.93)
7	1,799 (0.16)	0.16 (0.16)	899 (0.30)	0.08 (0.30)	1,053 (0.34)	0.09 (0.34)	1,474 (0.39)	0.13 (0.39)
8	2,488 (0.19)	0.23 (0.19)	2,984 (0.20)	0.27 (0.20)	938 (0.51)	0.09 (0.51)	3,729 (0.27)	0.34 (0.27)
9	1,040 (0.20)	0.09 (0.20)	1,273 (0.27)	0.11 (0.27)	786 (0.42)	0.07 (0.42)	3,340 (0.34)	0.28 (0.34)
10	356 (0.29)	0.04 (0.29)	661 (0.36)	0.07 (0.36)	915 (0.51)	0.09 (0.51)	353 (0.55)	0.04 (0.55)
Total	13,312 (0.08)	0.12 (0.08)	10,324 (0.14)	0.10 (0.14)	15,900 (0.19)	0.15 (0.19)	11,884 (0.20)	0.12 (0.20)

Table 5. Dolphin abundance and density for the years 1982, 1983, 1984, and the combined (1982 to 1984) datasets, along the southeast coast of the United States

Block (north to south)	1982		1983		1984		Combined	
	Mean abundance (CV)	Mean density (dolphins/km ²) (CV)	Mean abundance (CV)	Mean density (dolphins/km ²) (CV)	Mean abundance (CV)	Mean density (dolphins/km ²) (CV)	Mean abundance (CV)	Mean density (dolphins/km ²) (CV)
1	1,364 (0.23)	0.13 (0.23)	329 (0.28)	0.03 (0.28)	1,023 (0.32)	0.10 (0.32)	733 (0.16)	0.07 (0.16)
2	1,030 (0.32)	0.10 (0.32)	641 (0.35)	0.06 (0.35)	1,199 (0.27)	0.11 (0.27)	793 (0.18)	0.07 (0.18)
3	1,078 (0.24)	0.10 (0.24)	1,107 (0.25)	0.11 (0.25)	1,129 (0.33)	0.11 (0.33)	978 (0.16)	0.09 (0.16)
4	830 (0.27)	0.08 (0.27)	1,220 (0.17)	0.12 (0.17)	1,702 (0.38)	0.17 (0.38)	1,066 (0.15)	0.10 (0.15)
5	923 (0.29)	0.09 (0.29)	1,159 (0.24)	0.12 (0.24)	1,852 (0.38)	0.18 (0.38)	1,113 (0.18)	0.11 (0.18)
6	451 (0.35)	0.04 (0.35)	1,832 (0.19)	0.16 (0.19)	1,846 (0.29)	0.16 (0.29)	1,239 (0.16)	0.11 (0.16)
7	1,409 (0.33)	0.13 (0.33)	1,077 (0.18)	0.10 (0.18)	1,859 (0.25)	0.17 (0.25)	1,227 (0.14)	0.11 (0.14)
8	2,979 (0.29)	0.27 (0.29)	2,431 (0.14)	0.22 (0.14)	2,040 (0.24)	0.19 (0.24)	2,255 (0.12)	0.21 (0.12)
9	1,056 (0.27)	0.09 (0.27)	1,136 (0.22)	0.09 (0.22)	1,569 (0.27)	0.13 (0.27)	1,103 (0.15)	0.09 (0.15)
10	599 (0.35)	0.06 (0.35)	462 (0.25)	0.05 (0.25)	191 (0.67)	0.02 (0.67)	425 (0.20)	0.04 (0.20)
Total	11,720 (0.14)	0.11 (0.14)	11,393 (0.09)	0.11 (0.09)	14,408 (0.13)	0.13 (0.13)	10,931 (0.06)	0.10 (0.06)

Table 6. Z-based confidence interval and *p*-value for seasonal density comparisons

Seasonal/yearly comparison	95% Z-based CI		<i>p</i> -value
	Lower (difference)	Upper	
Spring to Summer	-0.0033 (0.0312)	0.0318	0.08
Spring to Winter	-0.0475 (0.0043)	0.0057	0.87
Fall to Spring	-0.0391 (0.0208)	0.0226	0.50
Fall to Summer	-0.0103 (0.0520)	0.0540	0.10
Fall to Winter	-0.0482 (0.0251)	0.0278	0.50
Winter to Summer	-0.0277 (0.0269)	0.0284	0.33
1982 to 1983	-0.0331 (0.0031)	0.0392	0.87
1982 to 1984	-0.0108 (0.0251)	0.0670	0.31
1983 to 1984	-0.0202 (0.0281)	0.0703	0.16

coastline. Looking at trends north to south, the abundance increased gradually up to Block 8 followed by a drastic decline in central Florida and the Keys. The Florida Keys had the lowest abundance: 356 dolphins (CV = 0.19).

The total estimated abundance and density for summer 1982-1984 were 10,324 individuals and 0.096 dolphins/km² (CV = 0.14) (Table 3). The dolphin density was consistent across the blocks except for Block 8 in northern Florida, which had a density more than twice that of any other block at 0.273 dolphins/km² (0.20). Blocks 2 and 5 had the smallest density at 0.041 (CV = 0.52) and 0.042 (CV = 0.39) dolphins/km², respectively (Table 4).

The total mean estimated abundance and density for fall of 1982-1983 was 15,900 individuals and 0.148 (CV = 0.19) dolphins/km² (Table 3). Generally, the densities increased with an increase in latitude. Block 1 had the highest density at 0.308 (CV = 0.32) dolphins/km². Blocks 6 and 9 had the lowest densities at 0.063 (CV = 0.47) and 0.065 (CV = 0.42) dolphins/km², respectively (Table 4).

The only winter survey was conducted in January-February of 1983, so this dataset represents the full seasonal data for winter. Block 1 was not surveyed due to inclement weather, and there were no sightings in Block 2. Blocks 8 and 9 along the Florida coastline had the highest estimated density of 0.34 (CV = 0.27) and 0.28 (CV = 0.34) dolphins/km², respectively. Block 6 along the Georgia coastline had the lowest density: 0.026 (CV = 0.93) dolphins/km². The total estimated density and abundance for winter 1983 was 0.123 individuals/km² and 11,884 (CV = 0.20) individuals with a CV of 0.20 (Table 4).

Yearly Comparisons

The combined 1982 data, which included spring, summer, and fall of 1982, had a total abundance estimate of 11,720 dolphins and a density estimate of 0.109 (CV = 0.14) dolphins/km². In 1982, the highest density area was along the central Florida

coastline (0.27 dolphins/km²; CV = 0.29). The lowest density was along the Georgia coastline (0.04 dolphins/km²; CV = 0.35) (Table 5).

Overall density estimates for 1983 (0.106 dolphins/km²; CV = 0.09), which included winter, spring, summer, and fall of 1983, were very close to the 1982 estimates. As in 1982, the area with the highest density was along the northern Florida coastline in Block 8 (0.223 dolphins/km²; CV = 0.14), while in contrast, the Georgia coastline in Block 6 was the second highest (0.16 dolphins/km²; CV = 0.19) (Table 5). Blocks 1 and 10 at the extreme north and south of the survey area had the lowest densities and abundances.

The total abundance and density for 1984 was calculated from the spring and summer 1984 surveys at 14,408 and 0.134 dolphins/km² (CV = 0.13) (Table 3). These estimates were slightly higher than the previous 2 y. The highest density was in Block 8 (0.185 dolphins/km²; CV = 0.24). Block 10 in the Florida Keys was the lowest density area (0.0197 dolphins/km²) (Table 5).

Overall Comparisons

All datasets combined had a mean abundance estimate of 10,931 and density of 0.102 (CV = 0.06) dolphins/km². The area with the largest overall density was Block 8 with 0.21 (CV = 0.12) dolphins/km², while the smallest overall density was 0.04 (CV = 0.20) dolphins/km² in Block 10 (Table 5). The density increased gradually from north to south from southern North Carolina to northern Florida and then dropped in central Florida and the Keys (Table 5).

Discussion

Generally, over season and year, Block 8 off of the northern Florida coastline had the highest dolphin density estimates, while Block 10 in southern Florida and the Keys had the lowest. This differed from the fall estimates when Block 1 in North Carolina was the highest, and Blocks 6 and

9 in South Carolina and central Florida were the lowest (Table 4). This likely is an indication of movement during the fall months—perhaps that of the Southern Migratory stock (Waring et al., 2011).

Although not statistically significant, there was a trend of higher dolphin abundance estimates within the study area in the spring ($p = 0.08$) and winter ($p = 0.10$) compared to the summer (Table 6). This may be from a group of dolphins leaving the study area during the summer, again consistent with the hypothesized large-scale movements of the Southern Migratory stock as far south as northern Florida during winter months and off the coast of North Carolina and perhaps Virginia during the summer (Waring et al., 2011). In comparing the combined seasonal data, there was an increase in total dolphin abundance from summer to fall and then a decrease to approximately the same number in winter and spring. During the fall, the estimated abundance in the northern blocks was five to seven times higher than during the other seasons (Table 4). This may be a result of the presence of the Southern Migratory stock or an influx of dolphins from another area.

These findings support the current stock boundaries hypothesized for coastal bottlenose dolphins (Figure 1). The dolphins appear to shift from Georgia and northern Florida in the spring and summer to northern South Carolina and North Carolina in the fall before returning to Georgia in the winter. These results corroborate other findings (National Marine Fisheries Service [NMFS], 2001; McLellan et al., 2002; Garrison et al., 2003) and may be a result of sea temperature changes and prey distribution associated with the fall season that would correlate with previous studies in which dolphin density increased south of Cape Hatteras in the fall (Torres et al., 2005).

From 1982 to 1984, there was not a significant change in dolphin density. For all 3 y, northern Florida had the highest densities. In 1983, there was a two- to threefold decrease in the number of dolphins in the two most northern blocks. This is likely the result of the inclusion of the winter data in that dataset. This indicates the importance of estimating from data that is divided by season since most dolphin stocks are known to migrate seasonally (Torres et al., 2005). From 1982 to 1984, there was a general increase of dolphin abundance from North Carolina moving south toward northern Florida, followed by a decrease continuing south toward central Florida and the Keys (Table 5). This again indicates the importance of the area off of the coast of northern Florida.

Advances in our knowledge of the dolphin distribution along the southeast coast of the U.S. have allowed current stocks to be divided using more

natural boundaries as opposed to the generically created, equal sized, ten blocks that were used for the SETS data. These variations in boundaries make it difficult to compare the most current estimates to the SETS estimates. However, two surveys were run in the winters of 1992 (Blaylock & Hoggard 1994) and 1995 (Blaylock et al., 1995) using the same blocks and methods as those employed during SETS. During the winter of 1992, the estimated dolphin abundance of the same area and covering the same 10 blocks was 12,435 (CV = 0.18) dolphins (Blaylock & Hoggard, 1994); and in the winter of 1995, the abundance estimate was 20,005 (CV = 0.21) (Blaylock et al., 1995). The population in the winter of 1983 was estimated at 11,884 (CV = 0.20) dolphins, which is less than both of the estimates in the winter of 1992 and 1995.

Additionally, in 2002, Garrison et al. (2003) conducted a survey of bottlenose dolphins from the southern Delaware Bay to Cape Canaveral, Florida. This analysis estimated that for the management units from southern North Carolina to central Florida there were 21,527 (CV = 0.24) dolphins. The summer estimates show that there appeared to be almost double the dolphin abundance in the summer of 2002 compared to the combined summers of 1982-1984 (10,324; CV = 0.14) or the individual summers of 1982 (11,808; CV = 0.25), 1983 (6,381; CV = 0.20), and 1984 (14,928; CV = 0.30).

There were several factors that varied between the 2002 study and those previous. The largest change was the adjustment for $g(0)$. This creates a negative bias through insufficient sightings of animals along a trackline and can be corrected for through the use of observers on a double platform. The 2002 survey employed this strategy which consists of two observation groups that make observations independent of one another to determine the proportion of animals missed (Buckland et al., 2001). In addition, a generalized additive model was used to determine any spatial relationship between abundance and characteristics such as sea surface temperature or depth. These analyses found that depth, distance from shore, and temperature were the main covariates to explain dolphin distribution (Garrison et al., 2003). Therefore, some of the increase in population between the SETS and 2002 data may be due to insufficient sightings during SETS.

A more in-depth analysis comparing these data on an equivalent level is needed—for example, taking into account differences in study area coverage and advances in data collection between 1982 and 2002. However, a preliminary comparison indicates that there may have been a low mortality rate caused by the 1987-1988 morbillivirus epizootic. This supports the findings of Eguchi

(2002), who found that a much smaller proportion (~10%) of the population was affected than the 50% originally calculated by Scott et al. in 1988.

Conclusions

Our data corroborate seasonal movement of coastal bottlenose dolphin stocks along the southeastern coast of the U.S. High densities of dolphins off the coast of northern Florida and low densities in the Florida Keys during the early 1980s offer baseline data for future use in population trends and abundance estimation.

The nearly equal estimates of dolphins between 5 to 7 y before the epizootic and 3 y following it indicate that, overall, Eguchi (2002) had a more accurate estimate of the affected population than Scott et al. (1988). Even with the crude comparisons of abundance estimates between the SETS data and data collected in 1992, 1995, and 2002, it appears that there were no long-term effects on the abundance of Atlantic bottlenose dolphins from Cape Hatteras, North Carolina, to the Florida Keys as a result of the morbillivirus epizootic of 1987-1988 from the population abundance of the early 1980s. A more detailed analysis, with SETS data broken into the current stock units, would give a better idea of how individual populations were affected. These data do not include what may have been the effects of the epizootic north of Cape Hatteras, so this should be a consideration in future studies. Additionally, future research should take into account the apparent increase in dolphin estimates over the past 20 y.

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