Seasonal distribution and relative abundance of bottlenose dolphins, *Tursiops truncatus*, along the US mid-Atlantic Coast

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ABSTRACT

In the US mid-Atlantic, multi-disciplinary studies are underway to elucidate the complex stock structure of coastal bottlenose dolphins (*Tursiops truncatus*), as well as the degree of overlap between coastal and offshore ecotypes. In this study we use geo-referenced data, collected during aerial surveys in 2000-2002, to describe the distribution and relative abundance of bottlenose dolphins along the US mid-Atlantic coast. Two aerial survey designs were used: (1) onshore/offshore surveys out to 35 n.miles during winter from Georgia to Virginia; and (2) coastal surveys throughout the year along North Carolina (NC). The winter onshore/offshore surveys demonstrated that significantly more bottlenose dolphins occur in Raleigh Bay (between Cape Hatteras and Cape Lookout, NC), than in all other regions. Additionally, in winter most bottlenose dolphins occur in the coastal waters of NC; nearly half of all sightings occurred between the shoreline and 3km from shore. The year-round, coastal surveys demonstrated that this winter distribution pattern is the result of a distinct seasonal increase in the number of dolphins within the coastal waters of NC. Circular statistical analyses demonstrated a strong influence of season on dolphin abundance. Relatively few bottlenose dolphins were observed in late spring, summer, and early autumn, with increased numbers observed during winter. In all seasons but summer, dolphin numbers were highest in Raleigh Bay. Thus, the results of both surveys indicate the importance of the habitat surrounding Cape Hatteras to bottlenose dolphins. Dolphins may preferentially use these waters in response to changes in prey distribution and/or abiotic factors such as water temperature. These results reveal an overall seasonal movement pattern along the US Atlantic coast, which appears to be correlated, at least in part, to water temperature gradients and prey availability. Although the stock identity of dolphins sighted during these aerial surveys could not be ascertained, focused photo-identification efforts, together with enhanced genetic sampling, would provide insights into the movement patterns, and, thus, stock identity, of dolphins in this region.

KEYWORDS: BOTTLENOSE DOLPHIN; MANAGEMENT PROCEDURE; CONSERVATION; SURVEY–AERIAL; DISTRIBUTION; MOVEMENTS; ATLANTIC OCEAN; SITE FIDELITY; FOOD/PREY

INTRODUCTION

Coastal bottlenose dolphins (*Tursiops truncatus*) were the target of a directed drive fishery along the US mid-Atlantic coast from the late 1700s through the 1920s (Mead, 1975; Mitchell, 1975; Leatherwood and Reeves, 1982; Reeves and Read, 2003). These dolphins experienced a large-scale epizootic in 1987-88 (Geraci, 1989; Duignan *et al.*, 1996; McLellan *et al.*, 2002) and currently experience rates of fisheries bycatch that exceed their allowable removal levels (Waring *et al.*, 2002). Because of these impacts, coastal bottlenose dolphins in the mid-Atlantic are the focus of an ongoing, multi-disciplinary study to understand their stock structure and enhance their recovery (reviewed in Hohn, 1997). The present study provides insight into the temporal and spatial distribution and relative abundance of bottlenose dolphins along the US mid-Atlantic coast. These data were collected using two aerial survey designs: (1) an onshore/offshore survey out to 35 n.miles during winter from Georgia (GA) to Virginia (VA); and (2) a coastal survey throughout the year along North Carolina (NC).

The first goal of our study was to describe the winter distribution and relative abundance of bottlenose dolphins in US mid-Atlantic and southeastern US waters. In the northwest Atlantic there are two genetically separable and partially sympatric, but visually indistinguishable, populations of bottlenose dolphins. These are the coastal and offshore ecotypes (Hersh and Duffield, 1990; Mead and Potter, 1995; Hoelzel *et al.*, 1998; Torres *et al.*, 2003). Kenney (1990), using seasonal aerial survey data collected from Cape Hatteras, North Carolina (NC), north to the Gulf of Maine, determined that bottlenose dolphins were rarely observed north of Cape Hatteras in winter. Barco *et al.* (1999) demonstrated that dolphins were abundant in summer and absent in winter in the nearshore waters of Virginia Beach, VA. Kenney (1990) postulated that both the coastal and offshore ecotypes 'are seasonally migratory, with much lower abundance and a more southerly sighting distribution in the winter'. Using a 25-year database, McLellan *et al.* (2002) demonstrated that there were seasonal differences in the distribution of bottlenose dolphin strandings along the entire US Atlantic Coast. To date, though, there have been few survey efforts conducted south of Cape Hatteras, NC.

Torres *et al.* (2003), using both sightings and genetic samples collected during summer ship-board surveys, demonstrated that distance from shore and water depth could be used to stratify bottlenose dolphins into coastal and offshore ecotypes in the mid-Atlantic: all dolphins sampled within 7.5km of shore were of the coastal type and all those sampled beyond 34km and in waters deeper than 34m were of the offshore type. Torres *et al.* (2003) also described a 'gray zone' between 7.5 and 34km from shore and in waters less than 34m deep, where there was a dearth of samples of both ecotypes and an overlap between ecotypes. In the present study we use data gathered from recent winter aerial surveys (2000 and 2001) from VA to GA and spatial analytical techniques similar to those of Torres *et al.* (2003), to describe dolphin relative abundance and distribution in relation to distance from shore and depth.

The second goal of this study is to describe seasonal patterns of dolphin relative abundance and distribution in the coastal waters of NC. Dolphins inhabit both estuarine (Jones and Sayigh, 2002; Read *et al.*, 2003b) and coastal waters in NC (Waring *et al.*, 2002). Results of photo-identification studies (Urian *et al.*, 1999) and regional

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surveys (Friedlaender *et al.*, 2001) strongly suggest that seasonal differences in dolphin distribution exist within NC coastal waters. To date, however, no year-round, coast-wide survey data are available to evaluate such differences.

The above mentioned studies offer evidence of: (1) seasonal shifts in abundance and distribution of bottlenose dolphins along the US mid-Atlantic coast; and (2) spatial separation of coastal and offshore ecotypes. By analysing data from two aerial survey methods, our present study builds upon these results and offers a more comprehensive understanding of the spatial and temporal distribution of bottlenose dolphins along the US mid-Atlantic coast.

METHODS

Surveys were conducted in either single or twin-engine, over-wing planes. A Cessna 182 was used for coastal surveys and military versions of the Cessna 337 (O2) for onshore/offshore surveys. These aircraft designs provided high wing visibility, easy manoeuvrability, and retractable landing gear. The offshore flights were flown with additional safety equipment including an emergency position indicating radio beacon (EPIRB), an emergency locating transmitter (ELT), handheld VHF marine radios, a life raft and life vests.

Data collection

Both planes carried at least two global positioning system (GPS) units during each survey. One aviation GPS was used by the pilot to navigate tracklines, while sighting positions were collected and stored on a *Garmin* 12XL GPS with an external antenna. All sighting data were also recorded on data sheets in real time. Sighting locations were downloaded to a computer following surveys with associated sighting data, effort data and photography information. Standard event codes were used to differentiate between sighting events and effort events. The recorder collected data on cloud cover, visibility, Beaufort Sea State (BSS) and glare for each side of the plane on each trackline throughout the survey.

When an animal or group of animals was sighted, time and location on the trackline, species and the maximum, minimum and best estimate of the number of animals sighted were recorded. Observers used 7 $\times$ 50 *Fujinon* binoculars to confirm sightings. If large whales or large groups of dolphins were encountered, the track was broken and the plane circled over the sighting, collecting specific sighting locations and identification photographs. Group size was discussed among the observers and resolved to determine the best estimate. After identifying the species, the plane returned to the trackline at the position where it had left and continued the survey. Methodologies specific to each survey type are described below.

Onshore/offshore surveys

The crew for onshore/offshore surveys consisted of a pilot and a data recorder in the front seats and a left and right observer in the rear seats. The rear seat observers were responsible for reporting all animal sightings and shipping traffic. The individual in the co-pilot's seat acted as the data recorder.

The offshore survey area extended from 32°N at Savannah, GA to 37°N at the mouth of the Chesapeake Bay, VA. The tracklines started at the surf line and extended 35 n.miles (64.82km) offshore. In 2001, 76 tracklines were run in the survey area (Fig. 1). Tracklines were spaced parallel to each other at a distance of 4 n.miles apart and ran east to west. Tracklines at Cape Fear, Cape Lookout and Cape Hatteras were extended beyond 35 n.miles (64.82km) to provide additional offshore coverage. To increase coverage in 2002, while limiting tracklines to a length of 35 n.miles, the tracklines were flown at a 45% angle to latitude, in a northwest/southeast direction (Fig. 1). In 2002, the tracklines remained 4 n.miles apart, but 109 lines were flown from GA to VA.

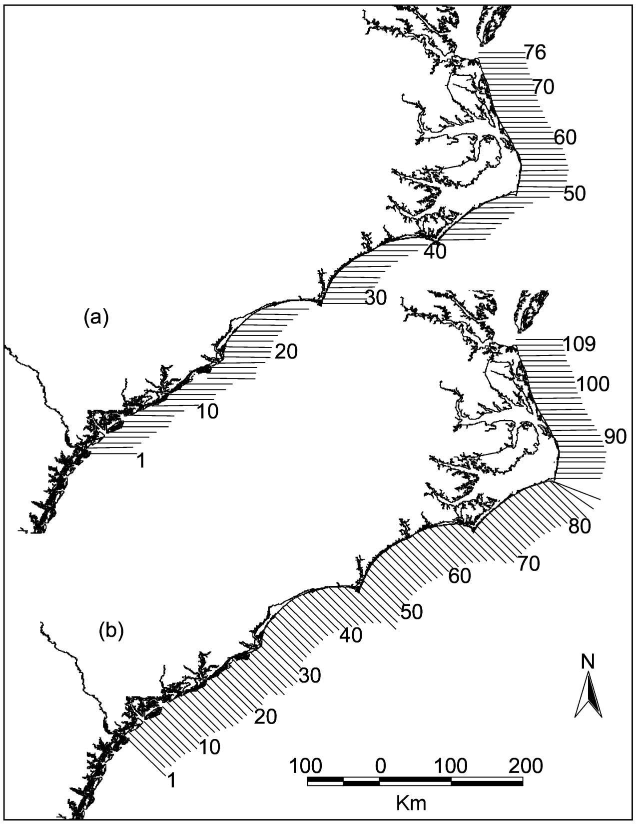

Fig. 1. Onshore/offshore survey tracklines in (a) 2001 and (b) 2002. Numbers denote individual trackline numbers.

The plane flew at 100kts, at a height of 300m. Observers were on-effort only in weather conditions of a BSS of 5 or less to standardise survey effort to optimal weather conditions. Given weather constraints across the geographically large survey area, tracklines were not systematically flown from north to south. Rather, survey effort was focused in areas with favourable weather conditions. Additional constraints were imposed by the necessity to adhere to closures imposed on military controlled airspaces in the nearshore waters of NC and VA and in coordination with the Air Defense Identification Zone (ADIZ). All tracklines were flown at least twice during the survey period, though some were flown as many as four times. However, only the first two surveys of each trackline in each year were used in this analysis, permitting similar effort to be analysed in both years. The offshore surveys were conducted from 6 February to 2 March 2001 and 22 January to 16 March 2002.

Coastal surveys

The coastal surveys were conducted along the NC coast from the South Carolina (SC) border, north to the VA border (See Table 1 for flight dates). The plane flew at 230m and at 100kts at a distance of approximately 500m offshore, parallel to the coastline. The crew for coastal surveys consisted of the pilot and a front seat recorder/observer and one left side rear observer. The plane flew northerly along the coast so that the rear observer monitored from the trackline to the shore while the front seat recorder/observer monitored from the trackline offshore. These surveys were occasionally broken to transit around regions of military activities that required restricted airspace. Due to unplanned military activity and occasional weather limitations, some surveys were terminated before they were completed. Only complete surveys, defined as one full survey of the entire NC coast in one day, were used in this analysis.

Table 1

Dates of coastal surveys, 2000 and 2001, with corresponding information on bottlenose dolphin sightings. The northernmost latitude indicates the latitude of the most northerly dolphin sighting; all surveys terminated at the NC/VA border (approximately latitude 36.6°N).

Date	Number of sightings	Total animals	Northernmost latitude (°N)
23 Feb. 00	46	296	35.9892
1 Mar. 00	92	633	35.6440
1 Apr. 00	63	441	36.0916
6 May 00	70	318	36.5114
9 May 00	12	72	36.5102
26 May 00	61	191	36.6200
1 Jun. 00	42	393	36.3156
17 Jun. 00	8	18	36.2677
22 Jun. 00	3	27	36.5305
30 Jun. 00	25	130	36.5055
3 Jul. 00	7	48	36.5474
15 Aug. 00	24	227	36.4791
19 Aug. 00	3	7	34.4677
20 Sep. 00	23	155	36.5498
4 Oct. 00	34	367	36.4502
13 Oct. 00	102	1,746	36.2160
20 Oct. 00	81	1,118	36.5490
13 Nov. 00	96	861	36.3727
27 Nov. 00	38	191	35.8521
29 Nov. 00	82	27	35.9357
17 Jan. 01	79	664	36.0695
2 Feb. 01	87	1,031	36.2344
23 Mar. 01	84	517	36.2742
20 Apr. 01	103	944	36.5054
14 May 01	52	420	36.5468
30 May 01	22	138	36.3632
12 Jun. 01	26	260	36.5349
19 Jun. 01	40	443	36.542001
26 Jun. 01	56	522	36.5057
16 Jul. 01	41	555	36.5543

Data analysis

Data from the onshore/offshore and coastal surveys were edited and sorted in Microsoft *Excel*. Graphs and figures were generated using Excel and the statistical package *SPSS* for Windows (SPSS Inc.; Version 11.5.0).

ArcGIS (ESRI; Version 8.2) was used to map tracklines and sighting locations from the onshore/offshore surveys. Despite the difference in survey methods used in 2001 and 2002, the same geographic area was covered in both years. Therefore, the mid-Atlantic coast was divided into six regions based on geographically prominent capes, bays or inlets: (1) Oregon Inlet, NC to the NC-VA border; (2) Cape Hatteras, NC to Oregon Inlet, NC; (3) Raleigh Bay; (4) Onslow Bay; (5) Long Bay; (6) south of Long Bay to the GA border (Fig. 2).

Values of depth and distance from shore for each sighting were sampled using *Arc/Info* (ESRI 1999; Version 8.0.1). The bathymetry coverage was created in *Arc/Info* (ESRI 1999; Version 8.0.1) from a combination of grids from the National Geophysical Data Center's Coastal Relief Model and the US Geological Survey's Gulf of Maine Bathymetry, points from the Geophysical Data System for Hydrographic Survey Data, and lines from the General Bathymetric Chart of the Oceans. The bathymetry grid was resampled to an integer grid with a cell size of $500m^2$ and projected in *Albers*, assuming a spheroid Clarke 1866 projection. The eastern US coastline was created with data obtained from NOAA's Medium Resolution Digital Vector Shoreline. A 'distance from shore' grid was generated from this coastline coverage using the Euclidean distance to the closest point of land for each location.

Arc/Info was also used to determine the amount of survey effort relative to depth and distance from shore during the onshore/offshore surveys. Each trackline from 2001 and 2002 was buffered 2km on each side, the approximate visual sighting distance during the aerial surveys. These buffered tracks were then converted to grids and used to sample the total area of depth and distance from shore surveyed. These values were converted to square km of effort and used to make histograms of dolphins sighted per unit effort relative to depth and distance from shore.

Bottlenose dolphin group size tends to increase with increased water depth and openness of habitat (reviewed in Shane *et al.*, 1986). Therefore, group size was related to distance from shore using a Kruskal-Wallis non-parametric test.

For analysis of the coastal surveys, seasons were defined as winter (December-February), spring (March-May), summer (June-August), and autumn (September-November). Circular statistics were employed to analyse seasonal trends in relative abundance of bottlenose dolphins along the NC coast (*Oriana* software; Version 2.0; Kovach Computing Services). Unlike conventional linear statistical analysis, circular statistics assume there is no true zero, but rather 360 equal intervals called degrees. This statistical approach is appropriate for detecting seasonal trends in data collected across multiple years (e.g. Thayer *et al.*, 2003; Barlow, 1984). The date of each coastal survey was converted to a Julian day for all 32 complete surveys. Additionally, 31 was added to each Julian date to position the first day of winter at 0° and, thus, make each quadrant of the circular diagram representative of an individual season (see Fig. 3). This dating method made Julian day 1 = December 1 and Julian day 365 = November 30. The Julian date of each survey was then converted to a degree (based on a 360° circle) using the formula: a = (360°) (Julian date) / 365 (366 for surveys in 2000 because it was a leap year) (Zar, 1984). An angular-linear correlation analysis was used to relate season and relative bottlenose dolphin abundance along the NC coast derived from the coastal surveys. The angular variable (date) was correlated with the linear variable (abundance). This correlation coefficient ranges from 0 to 1 and the significance of the correlation is calculated following the methods of Mardia and Jupp (2000).

RESULTS

Onshore/offshore aerial surveys (January-March 2001 and 2002)

Although their distribution was not uniform, a total of 494 sightings of bottlenose dolphins were made throughout the study area during the two winter seasons of onshore/offshore aerial surveys (Fig. 2). When corrected for effort (number of dolphins sighted per km of trackline flown within each region), there were significantly more

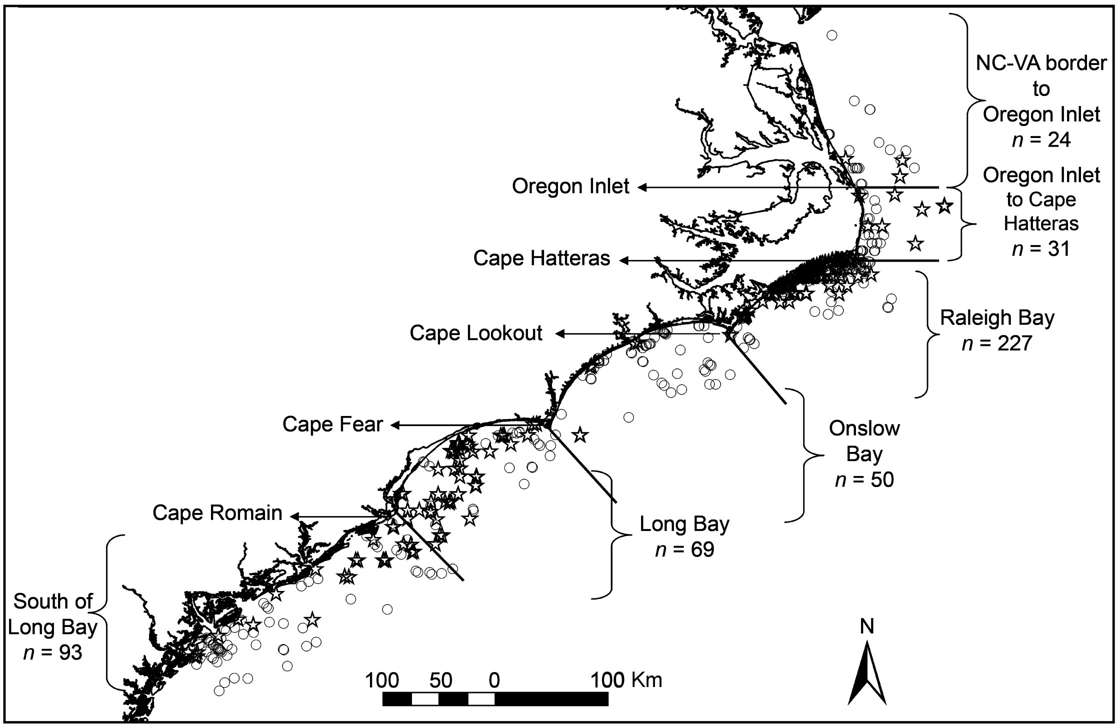

Fig. 2. The US mid-Atlantic coast was divided into six geographic regions based on prominent capes, bays and inlets, for analysis of bottlenose dolphin sightings from onshore/offshore aerial surveys in 2001 and 2002. The open stars indicate 2001 bottlenose dolphin sightings and the open circles indicate 2002 bottlenose dolphin sightings. *n* = total number of sightings within each region from the 2001 and 2002 surveys.

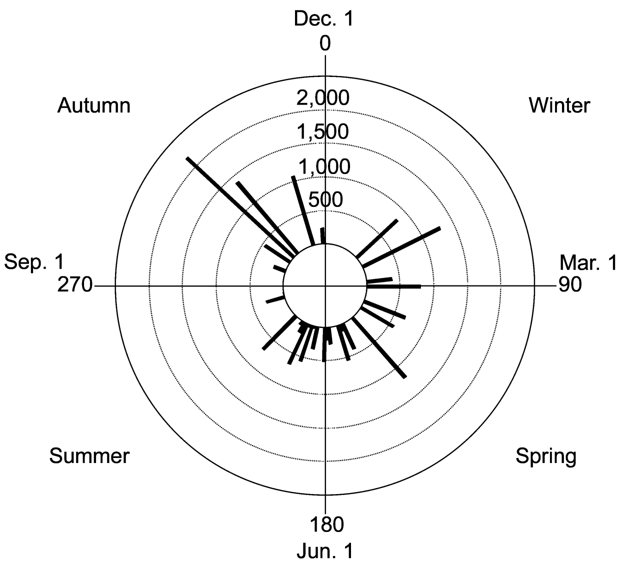

Fig. 3. A two-variable vector plot of all coastal surveys transformed into angles based on Julian date. Each bar corresponds to a single survey. The direction of the bar indicates the date (degree) of the survey, while the length of the bar denotes the total number of bottlenose dolphins counted on that survey. Each ring of the plot indicates the number of dolphins observed.

bottlenose dolphins counted in Raleigh Bay, between Cape Hatteras, NC and Cape Lookout, NC than all other regions (Exact Wilcoxon signed-rank test, V=21, *n*=6, *p*-value=0.0312) (Fig. 4). Nearly 30% of all bottlenose dolphin sightings occurred just south of Cape Hatteras, between 35.00°N and 35.20°N (Fig. 5b). Smaller peaks in sighting frequency occurred south of Cape Fear, south of Cape Romain, and north of Savannah, GA (Fig. 5b). The largest groups, containing more than 40 dolphins, were limited to the areas just south of Cape Hatteras, NC, in Raleigh Bay (14 sightings), and south of Cape Lookout, NC, in Onslow Bay (4 sightings). The four large group sightings in Onslow Bay were all offshore (>34.5km from shore). However, of the 14 sightings in Raleigh Bay, all but two large group sightings were within 2.5km of shore, including a single sighting of 150 individual dolphins 1km from shore. The remaining two large group sightings in Raleigh Bay were at 6 and 13km from shore.

Nearly half (45.7%) of all bottlenose dolphins sighted were within 3km of shore. Furthermore, 30.6% of dolphins were within 2km of shore and 9.3% were within 1km of shore (Fig. 6a). The greatest number of bottlenose dolphins sighted (871 individuals) was between 1 and 2km from shore. Bottlenose dolphins were observed frequently nearshore, but numbers of dolphins observed rapidly decreased beyond 3km of shore, with a slight increase between 34 and 46km. Beyond 46km from shore, very few bottlenose dolphins were sighted aside from a spike at 53km from shore.

There was no relationship between dolphin group size and distance from shore. A Kruskal-Wallis non-parametric test demonstrated that group sizes of sightings between 0-32, 33-46, and 33-64km from shore were similar. Moreover, of the 19 sightings beyond 50km from shore, no pattern of group size was evident.

The relative abundance of bottlenose dolphins in relation to water depth showed a similar trend as distance from shore. Sightings of bottlenose dolphins were most frequent in shallow waters and gradually declined with increasing depth (Fig. 6b). Beyond 10m depth, bottlenose dolphin observations were rare, except for two spikes in occurrence at 37m and between 401-500m. Twenty four percent of bottlenose dolphins were sighted in water less than 4m and nearly half (48.6%) were sighted in water less than 12m. All

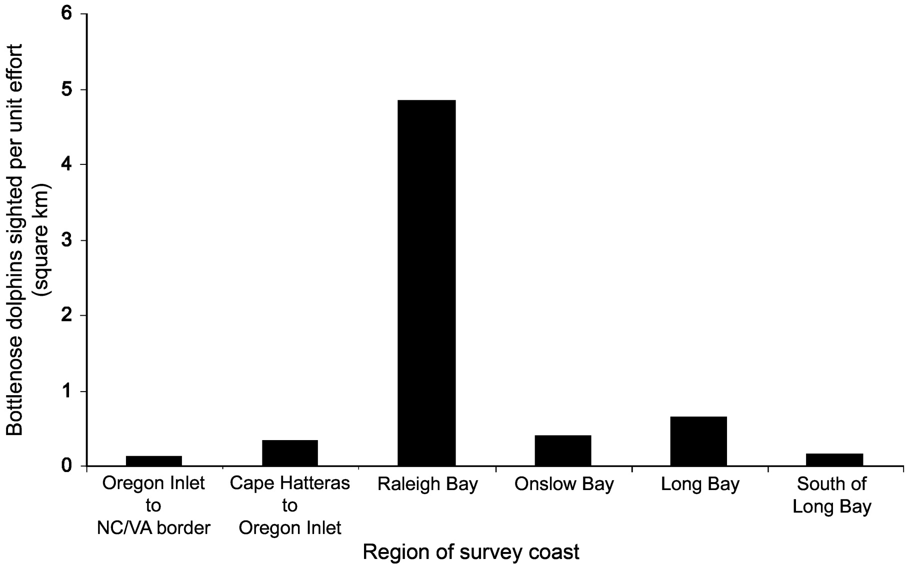

Fig. 4. Frequency of individual bottlenose dolphin observations during 2001 and 2002 onshore/offshore surveys, corrected for survey effort within each region.

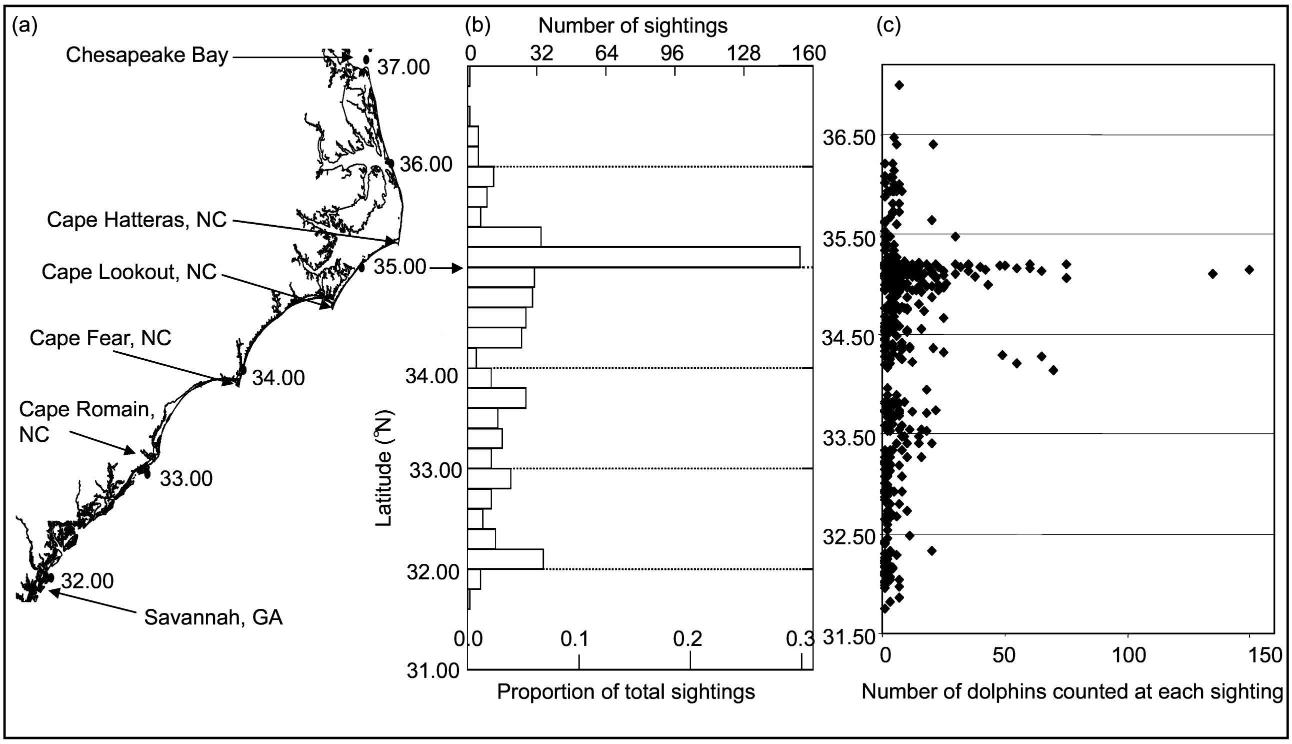

Fig. 5. Bottlenose dolphin sighting distribution from 2001 and 2002 onshore/offshore surveys relative to the coastline. (a) The onshore/offshore survey area for 2001 and 2002 (not to scale). (b) The proportional frequency of sightings by latitude. (c) The spatial frequency of sightings by group size relative to latitude.

17 sightings in water over 45m deep were between 34.81° N and 35.64° N, in offshore waters just north and south of Cape Hatteras, NC.

North Carolina coastal surveys (February 2000 – July 2001)

The onshore/offshore surveys demonstrate that, within the study area, in winter, most mid-Atlantic bottlenose dolphins occur in the coastal waters of NC (Figs 2, 4, 5 and 6). The NC coastal surveys permitted a quantitative description of seasonal patterns of bottlenose dolphin distribution within these nearshore waters.

A total of 5,431 bottlenose dolphins were observed on complete surveys during the two years of NC coastal aerial surveys. The relative abundance of bottlenose dolphins within NC coastal waters varied throughout the year. The circular statistical analysis demonstrated a correlation between dolphin abundance and season (Fig. 3). There was a significant correlation between the Julian date of each survey and total dolphins sighted (angular – linear correlation: r=0.436, p=0.006). Relatively few bottlenose dolphins were observed in late spring, summer, and early autumn (May-August). The greatest numbers of bottlenose dolphins were observed in late-autumn (October/

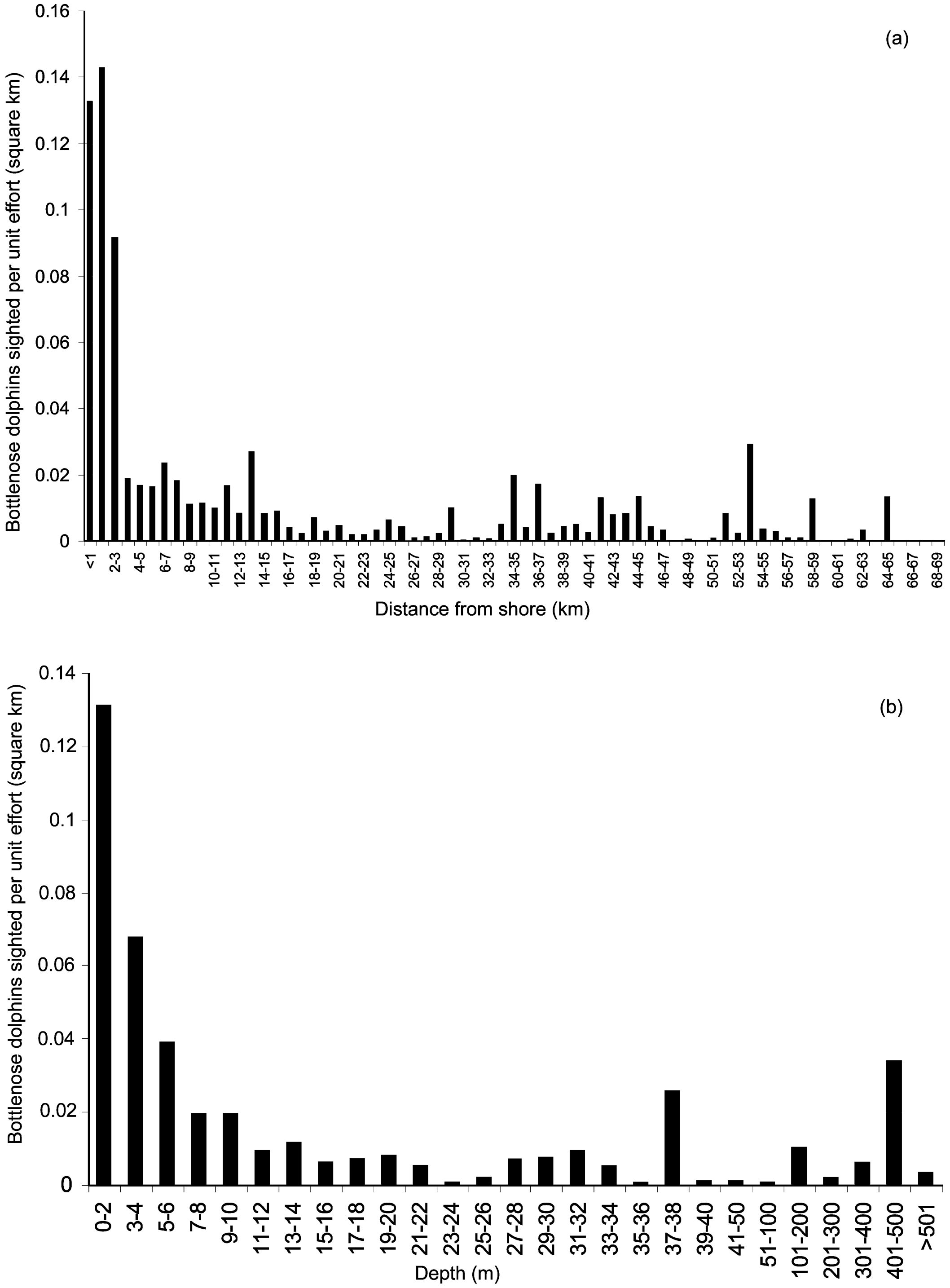

Fig. 6. Frequency of individual bottlenose dolphin observations per unit effort from 2001 and 2002 onshore/offshore surveys relative to distance from shore (a) and depth (b). The amount of survey effort conducted within each depth and distance from shore bin was calculated (see text for methods) in order to make relative sighting frequencies based on effort within each value range.

November). Intermediate numbers of bottlenose dolphins were sighted during the winter and early spring months of January-March.

This temporal fluctuation in relative abundance along the NC coast is also evident in Fig. 7, which spatially describes the seasonal distribution of bottlenose dolphin sightings. In winter, few bottlenose dolphins were sighted north of Cape Hatteras. During this period, bottlenose dolphin numbers were highest in the area just south of Cape Hatteras. In spring, more bottlenose dolphins were sighted north of Cape Hatteras than during winter. In summer, fewer dolphins were sighted than every other season and their distribution along the NC coast was more diffuse. During autumn, bottlenose dolphin sightings again clustered south of Cape Hatteras, with smaller peaks in abundance also observed at Cape Lookout and Cape Fear. In all seasons but summer, dolphin abundance was highest just south of Cape Hatteras.

Additionally, if season is ignored and sightings throughout the year are summed, individual bottlenose dolphin observations were most frequent at Cape Hatteras (Fig. 7, *n* values). A secondary peak in summed relative abundance occurred at Cape Lookout (742 dolphins sighted), and a third, slightly smaller peak at Cape Fear (398 dolphins sighted).

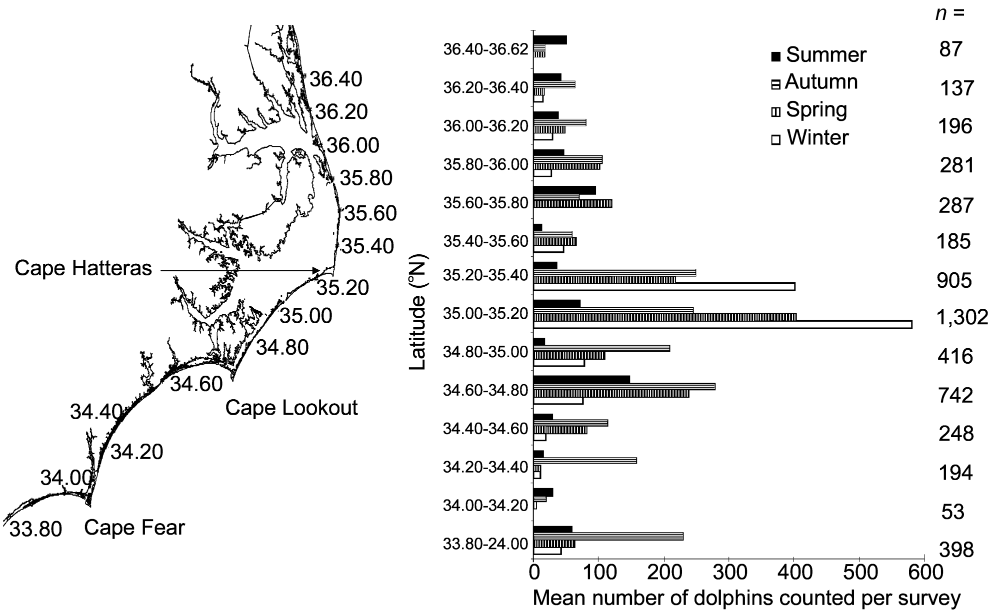

Fig. 7. Histogram of the seasonal distribution of bottlenose dolphins from 2000 and 2001 NC coastal surveys. Latitudinal bins were divided into equal 0.20° intervals. Note distinct peaks in abundance south of Cape Hatteras in all seasons but summer. *n* = number of dolphins observed within each latitudinal bin regardless of season. The NC coast is not drawn to scale.

The northernmost latitude of sightings in January, February and March of both years was further south than in all other months (Table 1). The mean latitude of bottlenose dolphin sightings November-March (late autumn through to early spring) was significantly less than the mean latitude between April-August (mid-spring through to summer) (one-tailed *t*-test: p=0.015).

DISCUSSION

This study used geo-referenced data from two complementary aerial surveys to describe the spatial and temporal distribution of bottlenose dolphins along the US mid-Atlantic coast. The onshore/offshore surveys demonstrate that in winter, dolphin abundance is greatest nearshore (<3km) in NC coastal waters, although dolphin abundance is relatively high out to 14km from shore. The coastal surveys demonstrated that dolphin relative abundance and distribution change seasonally in the nearshore waters of NC. Both surveys illustrate that bottlenose dolphin abundance is highest near Cape Hatteras, NC in all seasons except summer, suggesting that this area is an important habitat for bottlenose dolphins in the US mid-Atlantic.

Coupling our results with those of previous studies on bottlenose dolphin distribution north of Cape Hatteras, NC (Kenney, 1990; Barco *et al.*, 1999) reveals an overall seasonal movement pattern along the US Atlantic coast, which is likely correlated, at least in part, to water temperature gradients and prey availability. During the summer months, when water temperatures are relatively warm along the entire US east coast, Kenney (1990) found that bottlenose dolphins are distributed as far north as New Jersey (NJ). As water temperatures decline during the autumn, bottlenose dolphins appear to move south, reducing the frequency of sightings north of Cape Hatteras (Kenney, 1990) and increasing them south of Cape Hatteras (see Figs 3 and 7). When water temperatures decline further in winter, coastal bottlenose dolphins are extremely sparse north of Cape Hatteras, NC and abundant just south of Cape Hatteras. Finally, during the spring, as water temperatures rise, bottlenose dolphins are sighted more frequently north of Cape Hatteras. Thus, Cape Hatteras appears to be an important spatial boundary in the seasonal distribution of bottlenose dolphins along the US mid-Atlantic coast.

Although the stock identity of bottlenose dolphins sighted during these aerial surveys could not be ascertained, collaborative studies are being conducted to elucidate the movement patterns and stock identity of individual dolphins along the mid-Atlantic coast (Urian *et al.*, 1999). For example, in a photo-identification study conducted near Cape Hatteras during February/March 2003, Read *et al.* (2003a) matched individual dolphins from Cape Hatteras to dolphins photographed in the summer in NJ and VA. The results of this photo-identification study demonstrate that dolphins present in NJ during the summer move south to Cape Hatteras in winter. A combination of photo-identification techniques and temporal-spatial distribution analyses may provide further insight into the movement patterns of individual dolphins and, thus, their stocks along the US mid-Atlantic coast.

The onshore/offshore surveys demonstrated that, during winter, most dolphin sightings were within 3km of shore. Relative abundance remained high, though, out to 14km from shore. Because no genetic samples were obtained, we could not identify the dolphins as coastal or offshore ecotypes. However, we can speculate on the distribution patterns of the two ecotypes based on the results of Torres *et al.* (2003). Through spatial analysis of genetic samples of dolphins acquired during summer months, Torres *et al.* (2003) suggested spatial boundaries for each ecotype. All dolphins sampled within 7.5km of shore were of the coastal ecotype, while all those sampled beyond 34km of shore and in water deeper than 34m depth were of the offshore ecotype. Both ecotypes were found between 7.5km and this 34km/34m isoline, an area defined by Torres *et al.* (2003) as the 'gray zone'. These results suggest that dolphins within 3km of shore, which represent nearly half of all dolphins sighted during the winter onshore/offshore surveys, are of the coastal ecotype. Likewise, those dolphins sighted beyond 34km from shore are probably offshore ecotype bottlenose dolphins. Unlike the study of Torres *et al.* (2003), however, which documented a dearth of dolphins sampled within the 'gray zone' in summer, our study demonstrated that dolphin sightings remained relatively high out to 14km in winter. Whether this offshore extension represents a seasonal increase of either ecotype's abundance, or an extension of either ecotype's range, is currently unknown. For these reasons, we recommend focused genetic sampling of dolphins in this area during the winter months in the US mid-Atlantic region to provide insight into the identity of dolphins inhabiting the 'gray zone'.

The winter distribution pattern described above coincides with a distinct seasonal increase in the relative abundance of dolphins within the coastal waters of NC, especially around Cape Hatteras (see Figs 3 and 7). It is likely that at least part of this increase is due to coastal dolphins moving into the area from the north (see Read *et al.*, 2003a). With more dolphins using the waters off Cape Hatteras, competition for prey resources and habitat is likely to increase, as well as conflicts with seasonally increased fishing activity in this area (Street, 1996; Thayer and Montgomery, 1996; Watterson, 1999).

The results presented here, from both aerial surveys methods, clearly depict the importance of the habitat surrounding Cape Hatteras to bottlenose dolphins. The onshore/offshore winter surveys demonstrated a distinct peak in abundance, accounting for nearly 30% of all dolphins sighted, in Raleigh Bay, just south of Cape Hatteras (Fig. 5b). The coastal surveys also demonstrated that dolphin abundance was highest in Raleigh Bay in all seasons but summer (Fig. 7). The high relative abundance of dolphins in the Cape Hatteras marine ecosystem suggests that dolphins may be moving into these waters in response to changes in prey distribution and/or abiotic factors such as water temperature (e.g. Gaskin, 1982; Barco *et al.*, 1999; Zolman, 2002). The seasonal coastal surveys and onshore/offshore surveys also show the importance of the Cape Lookout, Cape Fear and Cape Romain habitats for bottlenose dolphins during the autumn and winter months.

The precise oceanographic conditions and processes that make Cape Hatteras and the other less prominent capes a preferred habitat for bottlenose dolphins and their prey are difficult to identify. The waters off the capes of the US mid-Atlantic are dynamic, with vertical and horizontal currents constantly mixing and shifting to produce seasonally and spatially determined productive habitats for the prey species of the dolphins (Worthington, 1976; Auer, 1987; Frankignoul *et al.*, 2001; Grothues *et al.*, 2002). Although the causal relationship between ocean processes and the influx of prey species is difficult to determine, Friedlaender *et al.* (2001) demonstrated a correlation between bottlenose dolphin abundance and that of an important prey fish species, spot (*Leiostomus xanthurus*), in the coastal waters near Cape Fear, NC. Both dolphin and spot abundance peaked in autumn, suggesting that the seasonal increase in dolphin abundance in this area was in response to increased prey availability. Moreover, Barco *et al.* (1999) found that dolphin abundance in waters off Virginia Beach, VA was highly correlated with sea surface temperature. Future research should investigate these relationships between dolphin occurrence, cape prominence, sea surface temperature, current patterns, productivity, and prey availability.

Many factors contribute to the complexity of managing the mid-Atlantic bottlenose dolphin stocks and defining their spatial boundaries. These include the existence of both resident and transient stocks of coastal dolphins, overlapping ranges of coastal and offshore ecotypes, and complicated seasonal movement patterns (Hohn, 1997; Barco *et al.*, 1999; McLellan *et al.*, 2002; Read *et al.*, 2003a; b; Reeves and Read, 2003; Torres *et al.*, 2003). The temporally and spatially dynamic nature of the oceanographic processes in the US mid-Atlantic further challenges researchers and managers. However, by linking the driving processes of biological and physical oceanography together with the distributional ecology of dolphins (e.g. prey availability and thermal limits) a coherent picture of bottlenose dolphin biogeography will likely emerge. This study provides results from the first comprehensive seasonal survey of bottlenose dolphin distribution south of Cape Hatteras, NC and, when combined with the results from previous research (Kenney, 1990; Barco *et al.*, 1999; Read *et al.*, 2003a), depicts a clear seasonal north/south migration pattern of coastal bottlenose dolphins along the entire US mid-Atlantic coast. This research also demonstrates that the waters off Cape Hatteras, NC are an important habitat for the bottlenose dolphin, particularly during the winter season when bottlenose dolphins appear to congregate in this area.

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