

# Abundance and sighting patterns of bottlenose dolphins (*Tursiops truncatus*) at four northwest Atlantic coastal sites

CARA M. GUBBINS\*, MARTHAJANE CALDWELL<sup>†‡</sup>, SUSAN G. BARCO<sup>++</sup>, KEITH RITTMAS<sup>\*\*</sup>, NAN BOWLES<sup>\*\*</sup> AND VICTORIA THAYER<sup>¥</sup>

Contact e-mail: caragubbins@hotmail.com

## ABSTRACT

Researchers and managers studying Atlantic coastal bottlenose dolphins along the east coast of the United States have been working on the hypothesis that there are two units within the population. One unit migrates seasonally along the northwest Atlantic coast (moving north during summer and south during autumn and winter), while the other remains in local inshore waters year-round. As part of independent, on-going studies begun in the late 1980s and mid-1990s, the occurrence of dolphins was compared among four separate sites (Virginia, North Carolina, South Carolina and Florida) in 1997. The goals of the study were to test the current working hypothesis of one migrating stock of dolphins using data on abundance, distribution and sighting patterns and to calculate a minimum estimate of the population size of northwest Atlantic coastal bottlenose dolphins at the four sites. Dolphins were consistently present in Virginia from April to October and year-round in North Carolina, South Carolina and Florida. In total, 7,830 dolphins were counted and 2,839 identifications were made. Monthly dolphin counts and water temperatures were positively correlated at the Virginia, South Carolina and Florida sites. After adjusting for effort, monthly dolphin counts were significantly different among the four sites but new identification rates were not. The monthly resighting rates were significantly higher in Florida than at the other sites. Based on mark-recapture analysis, it was estimated that 2,392 coastal bottlenose dolphins were present at the four sites in 1997. This estimate is similar to published abundance estimates for dolphins along the entire US Atlantic coast (2,482). These results support the hypothesis of multiple population units with distinct movement patterns and suggest that published abundance estimates for coastal bottlenose dolphins are greatly underestimated.

KEYWORDS: ABUNDANCE ESTIMATE; ATLANTIC OCEAN; BOTTLENOSE DOLPHIN; DISTRIBUTION; MARK-RECAPTURE; MOVEMENTS; PHOTO-ID

## INTRODUCTION

Although bottlenose dolphins (*Tursiops truncatus*) are distributed along the Atlantic coast of the United States from the Florida Keys to New York, distribution and abundance change seasonally between northern Florida and New York (Kenney, 1990; Wang *et al.*, 1994). During the summer, dolphins are distributed throughout this range and abundance is greatest between North Carolina and New Jersey. In the autumn, the distribution of dolphins begins to shift south and by winter abundance is greatest between Cape Hatteras, North Carolina and northern Florida (Wang *et al.*, 1994). This shift in abundance suggests that at least some coastal animals migrate south to winter at the southern end of their range somewhere between Cape Hatteras and central Florida (Wang *et al.*, 1994). Against this background of seasonal movements, there is evidence that some individuals move little over the course of the year, particularly in the more southern parts of this range (Wang *et al.*, 1994; Gubbins, 2002a; b). These resident dolphins may comprise distinct population units that should be managed independently of migratory dolphins (CeTAP, 1982; Wang *et al.*, 1994; Hohn, 1997; Barco *et al.*, 1999a).

Attention was drawn to the question of population structure and movement patterns by analysis of stranding patterns associated with a mass mortality event. Between June 1987 and March 1988, more than 740 dead bottlenose dolphins washed ashore from New Jersey to Florida (Scott *et al.*, 1988; Wang *et al.*, 1994; Mead and Potter, 1995). Two agents were associated with the event: brevetoxin originating from a red tide (Geraci, 1989) and a morbillivirus (Lipscomb

*et al.*, 1994; Duignan *et al.*, 1996). Carcasses were recovered from North Carolina, Virginia and New York in June 1987, from Virginia, New York and New Jersey in July, and from North Carolina between August and November. In December, carcasses were found in South Carolina, Georgia and Florida but by January 1988, and through February, carcasses were recovered only in Florida. Carcasses were recovered in Florida, Georgia, South Carolina and North Carolina during March 1988.

Based on stranding data from the 1987-88 die-off and abundance data from aerial surveys, Scott *et al.* (1988) hypothesised that a single migratory stock of bottlenose dolphins ranged seasonally from Long Island, New York to central Florida. This hypothesis, known as the 'single stock' hypothesis, has been the working paradigm for researchers and managers along the east coast of the United States (Waring *et al.*, 2000, pp.141-149). However, due to the dearth of published data on the behavioural ecology of Atlantic bottlenose dolphins, this hypothesis excludes inshore dolphins and has not been formally tested.

Stranding data were also used to estimate a potential stock decline of 53% due to the die-off (Scott *et al.*, 1988). Consequently, this stock was officially classified as depleted under the US Marine Mammal Protection Act of 1972 (Wang *et al.*, 1994). As the agency responsible for implementation of the Marine Mammal Protection Act, the US National Marine Fisheries Service was required to develop a conservation plan for the coastal migratory stock. However, limited data on dolphin movement patterns and abundance has hampered development of a plan and, thus, management of the depleted migratory stock. Only five

\* Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV 89557-0015, USA.

† Department of Biology, University of Miami, Coral Gables, FL 33149, USA.

‡ Department of Marine Science, Savannah State University, PO Box 20467, Savannah, Georgia 31404, USA.

++ Virginia Marine Science Museum Stranding Program, 717 General Booth Boulevard, Virginia Beach, Virginia 23451, USA.

\*\* North Carolina Maritime Museum, 315 Front Street, Beaufort, NC 28516, USA.

¥ Duke University Marine Laboratory, 315 Duke Marine Lab Road, Beaufort, NC 28516, USA.

studies on the behavioural ecology of these bottlenose dolphins (Blaylock, 1988; Jacobs *et al.*, 1993; Barco *et al.*, 1999b; Gubbins, 2002a; b) have been published. Furthermore, none of these address large-scale movement patterns of dolphins. The paucity of published research is a hindrance to better understanding the consequences of the 1987-88 mortality event, the population biology of these animals and the development of a management plan for the depleted migratory stock.

In response to the 1987-88 die-off and the lack of data relevant to movement, status and risk questions, the Atlantic Coastal Dolphin Cooperative was formed in 1993. The goal of the cooperative was to share information, compare sightings among areas and provide data that would elucidate the population biology of coastal Atlantic bottlenose dolphins. As members of the Atlantic Coastal Dolphin Cooperative, the authors of this paper collaboratively analysed data collected during 1997 from the four independent sites. The first goal was to compare local abundance, distribution and sighting patterns between the four sites and to combine the data to examine large-scale movement patterns of population units in order to test the Scott *et al.* (1988) single stock hypothesis. The second goal was to calculate a minimum estimate of the population size of northwest Atlantic coastal bottlenose dolphins based on photo-identification rates at the four sites.

## MATERIALS AND METHODS

Coastal bottlenose dolphins were defined as those animals using inshore and alongshore waters (Wells *et al.*, 1999). Data collected during 1997 at four sites along the Atlantic coast of the United States were analysed (Fig. 1). These data were collected as part of independent research projects in: Virginia Beach, Virginia from 1989 to present; Beaufort, North Carolina from 1985 to present; Hilton Head, South Carolina from 1994-1998; and Jacksonville, Florida from 1994-1997. In 1997, data were collected from March-October in Virginia Beach, February-December in Hilton Head, and January-December in Beaufort and Jacksonville. The research goals at each study site were similar, resulting in similar data collection methods and compatible data.

At each site, small powerboats were used on standard transects to survey each study area; hours on survey in the field were recorded as a measure of effort. A survey team consisted of a vessel operator, a data recorder and one or two photographers. The vessel maintained a cruising speed of 30-40 km h<sup>-1</sup> until dolphins were encountered, at which time the boat slowed down and the time of initial observation was recorded. The boat then moved parallel to the group, and the location, number of dolphins and number of young of the year were recorded. A dolphin group was defined as a collection of individuals that were estimated to be within 100m of each other while being observed. Once location, number and group composition data were recorded, attempts were made to photograph the dorsal fin of each member of the group.

Unique nicks, marks and scars on dorsal fins were used to identify individual dolphins (Würsig and Jefferson, 1990). Using standard protocols, dorsal fin photos were compared to independent catalogues of fin photos of known dolphins at each site in order to confirm sightings of identifiable individuals (Urian and Wells, 1996). For each site, the total number of dolphins observed and identified per hour surveyed was calculated for each month. For each dolphin identified, it was determined whether the observation was

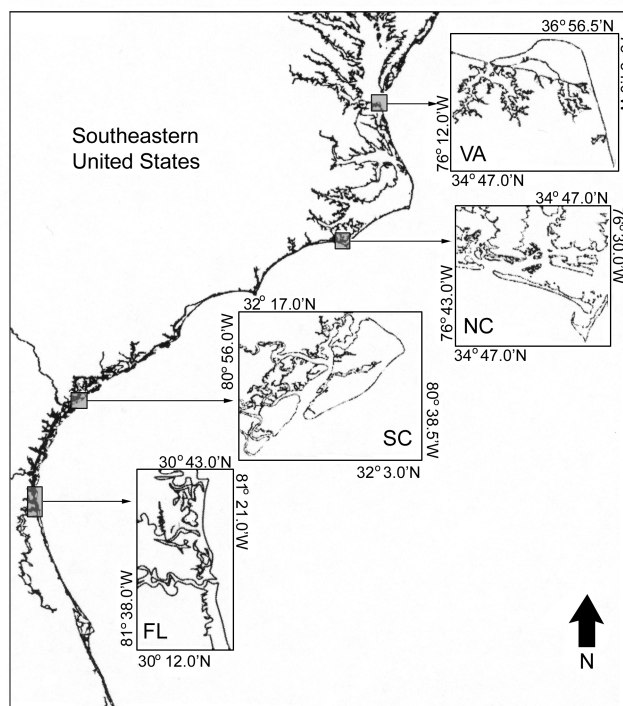


Fig. 1. Four study sites at Virginia Beach, Virginia; Beaufort, North Carolina; Hilton Head, South Carolina; and Jacksonville, Florida. The Virginia Beach site was exposed ocean coastline while the other three sites combined exposed ocean coast and inshore tidal rivers.

the initial sighting in 1997 (new) or a subsequent sighting (resight). The number of new and resighted dolphins per survey hour recorded each month was calculated for all four sites. Data were not normally distributed, therefore all data were transformed by adding 0.5 and then taking the square root (Zar, 1999).

Stranding patterns during the die-off suggested that one population unit of coastal dolphins was migrating seasonally along the northwest Atlantic coast (moving north during summer and south during autumn and winter). Based on this, a seasonal influx of dolphins was expected at the northern study sites and a concomitant decrease in abundance expected at the southern sites. Specifically, it was predicted that abundance and water temperature would be positively correlated in Virginia Beach and negatively correlated in Beaufort, Hilton Head and Jacksonville. To test this prediction, two types of analyses were performed. First, a simple linear regression was used to test for a correlation between mean monthly sea surface water temperature and the number of dolphins observed per survey hour per month within each site (Statistix; Analytical Software, 2000). Water temperatures were either measured directly during surveys (Jacksonville) or obtained from National Oceanic and Atmospheric Administration weather stations for the dates surveyed from the website [www.noaa.gov](http://www.noaa.gov) (Virginia Beach, Beaufort, Hilton Head). Second, a two-way analysis of variance was used to test for differences among the four sites in the number of dolphins observed per survey hour for the six months that dolphins were observed at all sites (May to October). Both analyses were then repeated using the number of new dolphins identified per hour per month and the number of resighted dolphins per hour per month.

With the CAPTURE program (Otis *et al.*, 1978), Chao *et al.*'s (1992)  $M_{th}$  model was used to estimate population size at each site. Wilson *et al.* (1999) suggest that the  $M_{th}$  model, which allows capture probability to vary by time and individuals, is the most appropriate model for bottlenose

dolphin populations given the behaviour of this species. Local abundance was calculated at each of the four sites using sighting records of all individuals identified from May to October. By restricting the analysis to this six-month time period, the possibility of violating the model's assumptions of geographic closure and mark retention (Wilson *et al.*, 1999) was reduced. To estimate the minimum number of dolphins using the northwest Atlantic coast between Jacksonville and Virginia Beach in 1997, the May to October mark-recapture data were combined. In this analysis, it was assumed that the dolphins using the northwest Atlantic comprised one closed population.

## RESULTS

During 917 survey hours in 1997, 7,830 dolphins were counted; 1,138 individual dolphins were identified a total of 2,839 times (Table 1). Each site had a unique abundance pattern (Fig. 2). In Virginia Beach (VA), dolphins were present from May through October, with the highest counts in July and September. In Beaufort (NC), dolphins were seen consistently year round, with the lowest abundance records in April and June. In Hilton Head (SC), dolphin abundance was lowest from February to April and two peaks were recorded in May and July. Jacksonville (FL) had oscillating abundance year round, with lows in January and December and a high peak in July.

As expected, dolphin abundance in Virginia Beach was positively correlated with water temperature ( $R^2=0.89$ ,  $p<0.001$ ). Dolphins were not observed in Virginia Beach when water temperature was less than 16°C (Fig. 2). Contrary to the prediction, a positive correlation between water temperature and dolphin abundance was found in Hilton Head and Jacksonville ( $R^2=0.48$ ,  $p=0.02$  and  $R^2=0.43$ ,  $p=0.03$ , respectively) and no significant correlation in Beaufort ( $R^2=0.18$ ,  $p=0.19$ ). In accordance with the prediction, there was a significant effect of site on dolphins observed per hour surveyed per month from May-October ( $f=4.46$ ,  $df=3$ ,  $p=0.01$ , Fig. 2). Significantly more dolphins were observed per hour per month in Virginia Beach than in Beaufort and Jacksonville (after Bonferroni correction  $p=0.025$  and  $p=0.016$ , respectively). However, there was no difference between Virginia Beach and Hilton Head or between Beaufort, Hilton Head and Jacksonville.

The number of new dolphins identified per survey hour per month was only correlated with water temperature in Virginia Beach ( $R^2=0.74$ ,  $p<0.007$ , Fig. 2). After square root transformation these data violated the assumption of homogeneity of variance, therefore a non-parametric Kruskal-Wallis one-way ANOVA was used rather than a parametric two-way ANOVA. From May-October, there

was no significant difference in the number of new dolphins identified per survey hour per month among the four sites ( $u=5.46$ ,  $p=0.14$ , Fig. 2).

The number of resighted dolphins per survey hour per month was positively correlated with water temperature in Virginia Beach and Jacksonville ( $R^2=0.71$ ,  $p=0.001$  and  $R^2=0.77$ ,  $p=0.0003$ , respectively, Fig. 2). A significant difference among the four sites was found in the number of dolphins resighted per hour surveyed each month from May through October ( $f=10.87$ ,  $df=3$ ,  $p<0.0001$ , Fig. 2). Significantly more dolphins were resighted per hour in Jacksonville than in any other site (after Bonferroni correction,  $p<0.003$ ).

The percentage of identified dolphins sighted only once was variable among the four sites (Virginia Beach = 72%, Beaufort = 59%, Hilton Head = 64% and Jacksonville = 44%). The frequency at which individual dolphins were resighted varied among the sites (Fig. 3). No identified dolphins were sighted more than nine times in Virginia Beach, Beaufort and Hilton Head, while 17% of dolphins identified in Jacksonville were sighted between 9-16 times. The mean number of sightings for individual dolphins identified in Jacksonville (mean = 6.6) was over 1.8 times greater than those for the other three sites (Virginia Beach: mean = 2.8; Beaufort: mean = 3.6; Hilton Head: mean = 3.0; Fig. 3).

The population estimates and confidence intervals obtained for each of the four sites using the  $M_{th}$  model and data from May-October are presented in Table 2. Combining data from all four sites resulted in a minimum population estimate for the northwest Atlantic coast of 2,392 dolphins, only 59 dolphins less than when the estimates from each site are summed (2,451).

## DISCUSSION

The 'single stock' hypothesis has not been formally tested and, until now, data were not available to do so. The hypothesis is not consistent with the results of this study using data on three aspects of the behavioural ecology of coastal dolphins: abundance, distribution and sighting patterns.

The single stock hypothesis predicts that abundance and distribution will change along the coast as the year progresses. Specifically, it predicts an increase in abundance at increasingly more northern sites until late summer. However, in this study, abundance increased at all four of the sites between May and October, peaking at the same time (in July) at Virginia Beach, Hilton Head and Jacksonville. Further, the predicted autumn southern shifts in abundance and distribution were not apparent – all three of these same sites showed a decrease in abundance in the autumn. Water

Table 1

Summary of data collection effort and results. The rates of identifying new dolphins were similar among the four study sites, but significantly more dolphins were counted per survey hour in Virginia Beach, Virginia (VA) ( $F=4.46$ ,  $df=3$ ,  $P=0.01$ ) and resighted in Jacksonville, Florida (FL) ( $F=10.9$ ,  $df=3$ ,  $P<0.0001$ , Bonferroni adjusted). NC = Beaufort, North Carolina; SC = Hilton Head, South Carolina.

Site	Effort (months surveyed)	Effort (survey hours)	Dolphins observed	Total dolphin identifications	Individual dolphins identified	Number of individuals resighted (% of total)	Dolphins observed per survey hour	New dolphins per survey hour	Dolphins resighted per survey hour
VA	8	105	2,147	513	337	176 (52)	10.0	1.3	0.8
NC	12	273	1,869	480	233	96 (41)	6.9	0.9	0.9
SC	11	206	1,729	399	234	84 (36)	7.2	1.0	0.7
FL	12	333	2,085	1,447	334	188 (56)	5.9	1.0	3.1
Total	43	917	7,830	2,839	1,138	544 (48)			

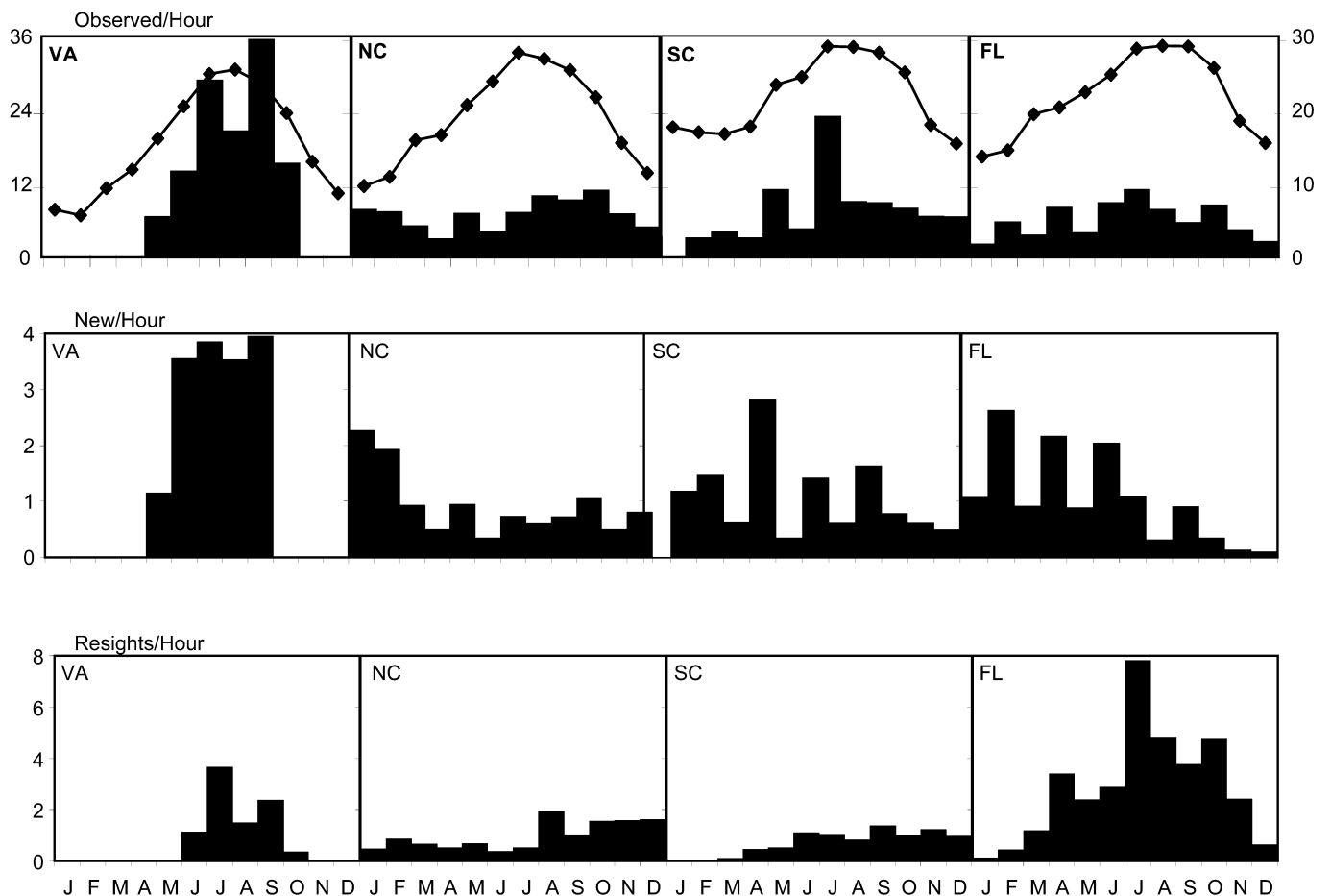


Fig. 2. Comparison of the total numbers of dolphins counted (observed), identified (new) and re-identified (resighted) per survey hour for each site. Sea surface water temperature from 0-30°C is shown on the right Y-axis in the observed/hour row and the number of dolphins counted per survey hour is on the left Y-axis of all rows. Dolphin abundance was positively correlated with water temperature at Virginia Beach (VA), Hilton Head (SC) and Jacksonville (FL), but there was no correlation in Beaufort (NC). Although there was no significant difference in the rate at which new dolphins were identified among sites, significantly more dolphins were counted per survey hour at Virginia Beach ( $f = 4.46$ ,  $df = 3$ ,  $p = 0.01$ ) and significantly more known dolphins were resighted per survey hour at Jacksonville ( $f = 10.9$ ,  $df = 3$ ,  $p < 0.0001$ , Bonferroni adjusted).

temperature was positively correlated with dolphin abundance in Virginia Beach, Hilton Head and Jacksonville: more dolphins were encountered at these sites when the water temperature exceeded 16°C.

Distribution was related between sites in the northern end of the study but not coast-wide or in the south. Abundance was lowest in Beaufort when it was highest in Virginia Beach. Detailed examination of sightings of individuals at both sites indicates that there is north-south movement of some dolphins between Virginia Beach and Beaufort: 120 dolphins have been photographed in both sites (Barco and Swingle, 1996; Barco *et al.*, 1997; Rittmaster and Thayer, 1998). In contrast, only two dolphins have been sighted in both Hilton Head and Jacksonville (Urian *et al.*, 1999) and there was no relationship between sighting or abundance patterns between these two sites in 1997. Similarly, none of the data suggest any relationship in changing abundance patterns between Hilton Head or Jacksonville and the two sites farther north.

Contrary to single stock predictions, sighting rates of new dolphins were not significantly different among the four sites between May and October. Sighting patterns of new and previously observed individuals suggest short-term use of Virginia Beach during the summer. In Beaufort, the highest identification rate of new dolphins occurred in January and February while resighting rates were highest from August to December, suggesting that dolphins were moving out of Beaufort mid-year and back into Beaufort during the end of

the year. These patterns coincide with the shifts in abundance between Virginia Beach and Beaufort noted above, further supporting seasonal movement between these two sites. Contrary to single stock predictions, few new dolphins were identified and relatively few known dolphins were resighted during autumn and winter months in Hilton Head and Jacksonville. While Hilton Head and Jacksonville populations included individual dolphins present year-round as well as seasonally, the seasonal patterns of resights were different from those predicted by the single stock hypothesis. Specifically, dolphins in Hilton Head were present for short periods of time during the summer and dolphins in Jacksonville were summer rather than winter residents. These residency and movement patterns are supported by multiple-year sighting data at each site (Rittmaster and Thayer, 1998; Barco *et al.*, 1999a; Gubbins, 2000; Caldwell, 2001).

Our results provide support for an alternative hypothesis that there are multiple population units of coastal dolphins with distinct movement patterns (Hohn, 1997). This is a likely scenario since the data (and additional unpublished data) show a relationship in dolphin movement patterns between Virginia Beach and Beaufort but no relationships among Beaufort, Hilton Head and Jacksonville or Virginia Beach, Hilton Head and Jacksonville. These patterns indicate that at least three independent population units: Virginia Beach/Beaufort, Hilton Head and Jacksonville. A second alternative hypothesis is that there is seasonal

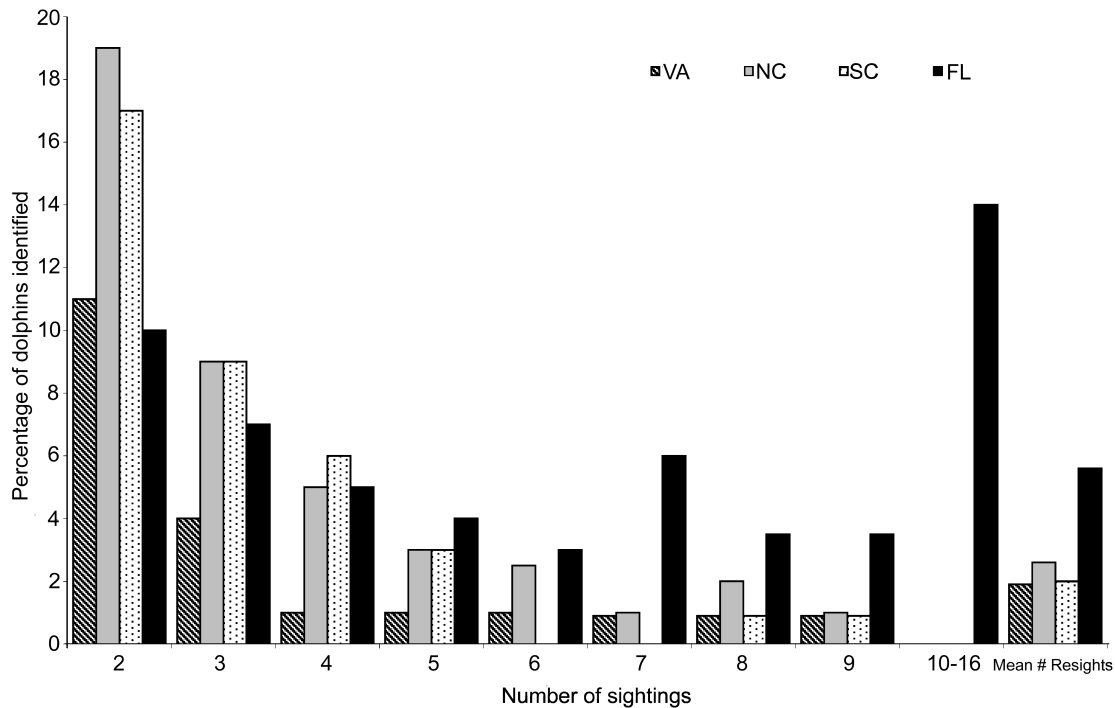


Fig. 3. Sighting frequencies of identified dolphins expressed as the percentage of identified dolphins sighted one or more times at each site. Sighting frequencies were similar in Virginia Beach (VA) and Hilton Head (SC), higher in Beaufort (NC) and highest in Jacksonville (FL).

Table 2

Abundance estimates for each site and for all four sites combined. The estimate for the four sites is as much as eight times larger than previous estimates for dolphins along the entire east coast. Estimates were calculated using the program CAPTURE.  $M_{th}$  estimate is the estimate of the population for each site. Estimated prob. of capture was automatically calculated. 'Number captured' represents the number of individual dolphins identified. 'Total captures' is the number of times all dolphins were identified, including first identifications and subsequent resightings. Study areas are Virginia Beach (VA), Beaufort (NC), Hilton Head (SC) and Jacksonville (FL).

Study area	$M_{th}$ estimate	Lower CI	Upper CI	SE	Estimated prob. of capture	Number captured	Total captures
VA	1,001	786	1,318	134.10	0.085	337	412
NC	513	405	680	69.09	0.154	205	299
SC	525	399	728	82.26	0.051	233	262
FL	412	374	468	23.69	0.392	333	719
Sum of estimations for all four sites	2,451						
Estimation of all four sites together	2,392	2,158	2,673	131.1909	0.2095	1,240	1,692
Difference	59						

longitudinal movement offshore in the winter and inshore during the summer months. The monthly abundance data coupled with no resights between southern and northern sites and only two between southern sites suggest that this might occur in Hilton Head and Jacksonville and may contribute to the high summer abundance in Virginia Beach.

One caveat inherent in this and all similar collaborative field studies is that there are gaps in areas surveyed. The four study areas were separated by hundreds of kilometres of coastline. When not observed in one study area, dolphins could simply have moved to adjacent coastal areas with no survey effort. Expansion of this format, by including more coastal sites closer together and incorporating offshore photo-identification surveys, would help test the alternative hypotheses presented here. Such additional data would help managers more accurately determine the existence and ranging patterns of distinct population units of coastal

dolphins and estimate the population size of all coastal dolphins, including those in inshore waterways. A cooperative photo-identification effort of 21 independent research sites (including those here) from Jacksonville, Florida to Cape May, New Jersey is currently underway (Urian *et al.*, 1999). Results from this collaboration should help elucidate stock structure of coastal dolphins throughout their known range. To date there has been no survey effort offshore to test the seasonal longitudinal movement hypothesis and this seems a fruitful area for future research since most coastal studies take place within a few kilometres of the shoreline.

Due in large part to data gaps, published stock assessments of *Tursiops* along the Atlantic coast of the United States group all animals into a single coastal stock (Waring *et al.*, 2000, pp.141-149). Informally, however, it is widely accepted among researchers and managers that this

population is comprised of multiple stocks most likely containing year-round and seasonal residents as well as transient dolphins. The data and analyses in this paper are the first to formally test this hypothesis and the results support this informal contention. Between northern Florida and Virginia, multiple population units of coastal dolphins were found with differing movement patterns.

The second goal of this study was to calculate a minimum estimate of the population size of northwest Atlantic coastal bottlenose dolphins. The estimate of 2,392 dolphins was as high as or higher than previous abundance estimates for dolphins along the entire US Atlantic coast. Kenney (1990) estimated that the population of coastal and offshore bottlenose dolphins off the northeastern USA was between 10,000 and 13,000 individuals in the early 1980s. Kenney (1990) further proposed that the inshore (coastal) stock comprised 3-4% of the total population, leading to an estimate of 300-400 coastal dolphins. The most recent estimate of abundance for the coastal population (2,482) was simply a count of the number of dolphins sighted during aerial surveys along the coast (Waring *et al.*, 2000, pp.141-149).

Previous estimates were based on aerial or ship-transect surveys conducted in oceanic waters and none have been based on photo-identification or included estuarine waters (CeTAP, 1982; Kenney, 1990; Waring *et al.*, 2000, pp.141-149). Line transect methods can be used to estimate dolphin density, and therefore abundance (Wilson *et al.*, 1997). However, cetaceans are wide-ranging and spend much of their time underwater, making this type of sampling difficult to implement (Wilson *et al.*, 1999). Several additional problems are associated with aerial and ship-transect surveys. Dolphin behaviour is often related to coastal topography and aerial and shipboard observers can miss submerged animals as they survey at a pre-determined, constant speed (Wilson *et al.*, 1997). Further, observers cannot differentiate offshore dolphins from coastal dolphins on sight in areas where both occur, such as the northwest Atlantic Ocean. These considerations, coupled with the highly variable group size of bottlenose dolphins (Wells *et al.*, 1980), can lead to estimates of abundance with poor precision (Wilson *et al.*, 1999). Mark-recapture methods use data on the number of animals marked and their proportion represented in subsequent samples to estimate population parameters including abundance (Seber, 1982). Mark-recapture techniques can provide unbiased estimates of population size that are more precise than those derived from line-transect sampling (Calambokidis *et al.*, 1990; Fairfield, 1990; Read *et al.*, 2001).

The combined population estimate of 2,392 dolphins, which represents an absolute minimum 'best' coastal estimate, is comparable to the recent estimate of 2,482 dolphins reported by Waring *et al.* (2000, pp.141-149). The estimate from this study is eight times greater than Kenney's (1990) coast-wide estimate based on aerial survey data from the Cetacean and Turtle Assessment Program (CeTAP, 1982). The differences between the four-site estimate and the two coast-wide estimates are even more important when one considers the fact that the study sites here encompass less than 300km of the > 2,000km of coastline available to Atlantic bottlenose dolphins. Further, during previous and subsequent years of research following the same data collection and photo-identification protocols, more individual dolphins have been identified at all four sites than the 1,138 identified in 1997 reported in this paper (Virginia Beach: 1,000; Beaufort: 1,300; Hilton Head: 503; Jacksonville: 905; total: 3,708; unpublished data). After

accounting for the two dolphins identified at both Hilton Head and Jacksonville and 120 dolphins identified at both Virginia Beach and Beaufort, this study identified a total of 3,694 individual dolphins in the four study areas. This number does not include the unmarked juveniles and calves in the populations. Assuming a 10% calving rate, this number jumps to over 4,000 individuals. Finally, Waring *et al.*'s (2000, pp.141-149) estimate did not include dolphins using bays, sounds and estuaries. The study sites in Beaufort, Hilton Head and Jacksonville included coastal and inshore waters and the mark-recapture estimate in this paper is likely more representative of the actual abundance of dolphins in the study sites than Waring *et al.*'s (2000, pp.141-149) estimate based on transect data collected during alongshore surveys. The results in this paper imply that a much larger number of individual dolphins are utilising the coastal waters of the northwest Atlantic than are currently considered.

[Authors' note: At meetings of the 'Tursiops Take Reduction Team in the mid-Atlantic and southeast US' in July and August 2001, new information was presented on stock structure and abundance estimates for coastal *Tursiops*. These data will be published in the US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments 2002.]

## ACKNOWLEDGEMENTS

We are grateful to the many volunteers who assisted us in the field and in analysing fin photos, particularly A. Groth (Virginia Beach) and C. Eckland (Hilton Head). In 1997, SGB was supported by a grant from National Marine Fisheries Service to the Virginia Marine Science Museum Stranding Program and to D.A. Pabst and B. McLellan of the University of North Carolina at Wilmington. Many volunteers and the staff of the Museum, particularly Stranding Program curator W.M. Swingle, supported the Virginia Beach research. The Beaufort team is grateful to the Friends of the Museum/North Carolina Maritime Museum and the National Marine Fisheries Service Beaufort Lab for providing much-needed equipment, supplies, logistical support, and dedicated students and volunteers. K. Merrels has spent countless hours in the darkroom and photo catalogues helping organise the Beaufort individual recognition data. John Russell contributed many hours of his time, boat driving expertise, and funds to this project. L. Barker, C. Jones and C. Spangler provided valuable help, inspiration and critical feedback. The Worthington Foundation, University of Nevada Reno Ecology, Evolution and Conservation Biology Program, University of Nevada Reno Biology Department and Mystic Aquarium provided field support for CMG. CMG was partially supported by fellowships and awards from the University of Nevada Reno Graduate School, Graduate Student Association, Biology Department, and Ecology, Evolution and Conservation Biology Program, and Mystic Aquarium. Many volunteers and the staff of Mystic Aquarium, particularly Director of Research and Veterinary Services, D. St Aubin, supported the Hilton Head research. MjC was supported by a grant from National Marine Fisheries Service to the University of Miami. MjC is grateful to the University of Miami for logistical support and Drs Gaines, Wells, Searcy, Hughes and Green for advice. Mayport Marine and a host of volunteers, especially J. Nangle and L. Reynolds, kept the Jacksonville project afloat. This research was conducted under National Marine Fisheries Service General Authorisations Number 9 (Virginia Beach), Number 2 (Hilton Head), Number 738 (Jacksonville) and National

Marine Fisheries Service research permit #779-1339 (Beaufort). Fin photographs of dolphins identified in Hilton Head (South Carolina) and in Jacksonville (Florida) and in Virginia Beach (Virginia) and Beaufort (North Carolina) were matched by K. Urian, curator of the Mid-Atlantic Bottlenose Dolphin Catalogue. E. Beever and J. Lewis kindly reviewed an earlier draft of this manuscript. Two anonymous reviewers provided helpful comments that improved this manuscript.

## REFERENCES

- Barco, S.G. and Swingle, W.M. 1996. Sighting patterns of coastal migratory bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia and North Carolina. Final Grant Report for VA DEQ Coastal Resources Management Grant No. NA47OZ0287-01. Virginia Marine Science Museum Scientific Report 1996-001. 31pp. [Available from: Virginia Marine Science Museum, Virginia Beach, VA 23451].
- Barco, S.G., Bowles, N.I., Rittmaster, K.A., Swingle, W.M. and Thayer, V.G. 1997. The Virginia/North Carolina coastal dolphin interstate. Paper presented to the Sixth Annual Atlantic Coastal Dolphin Conference, 2-4 April 1997, Wilmington, NC, USA. [Available from: Virginia Marine Science Stranding Program, 717 General Booth Boulevard, Virginia Beach, VA 23451, USA].
- Barco, S.G., Swingle, W.M., McLellan, W.A., Harris, R.N. and Pabst, D.A. 1999a. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Mar. Mammal Sci.* 15(2):394-408.
- Barco, S.G., Swingle, W.M., McLellan, W.A. and Pabst, D.A. 1999b. Using photoidentification to characterize seasonally occurring bottlenose dolphins in Virginia Beach, Virginia. Paper presented to the 13th Biennial Conference on the Biology of Marine Mammals, Maui, Hawaii, 28 November – 3 December 1999. [Available from: Virginia Marine Science Museum Stranding Program, 717 General Booth Boulevard, Virginia Beach, VA 23451, USA].
- Blaylock, R.A. 1988. Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), in Virginia. *Fish. Bull.* 86(4):797-805. LFS.
- Calambokidis, J., Cabbage, J.C., Steiger, G.H., Balcomb, K.C. and Bloedel, P. 1990. Population estimates of humpback whales in the Gulf of the Farallones, California. *Rep. int. Whal. Commn* (special issue) 12:325-33.
- Caldwell, M. 2001. Social and genetic structure of bottlenose dolphin (*Tursiops truncatus*) in Jacksonville, Florida. Ph.D. Thesis, University of Miami, Miami, Florida, USA. 143pp.
- CeTAP. 1982. A characterization of marine mammals and turtles in the mid- and north Atlantic areas of the US outer continental shelf. Cetacean and Turtle Assessment Program, University of Rhode Island. Final Report, Contract AA51-CT-48. US NTIS PB83-21555. Bureau of Land Management, Washington, DC. 538pp. [Available from <http://www.blm.gov>].
- Chao, A., Lee, S.M. and Jeng, S.L. 1992. Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* 48:201-16.
- Duignan, P.J., House, C., Odell, D.K., Wells, R.S., Hansen, L.J., Walsh, M.T., St Aubin, D.J., Rima, D.J. and Geraci, J.R. 1996. Morbillivirus in bottlenose dolphins: evidence for recurrent epizootics in the western North Atlantic and Gulf of Mexico. *Mar. Mammal Sci.* 12:499-515.
- Fairfield, C.P. 1990. Comparison of abundance estimation techniques for the western North Atlantic right whale (*Eubalaena glacialis*). *Rep. int. Whal. Commn* (special issue) 12:119-26.
- Geraci, J.R. 1989. Clinical investigation of the 1987-88 mass mortality of bottlenose dolphins along the US central and south Atlantic coast. Final report to National Marine Fisheries Service and US Navy Office of Naval Research, and Marine Mammal Commission, Guelph, Ontario, Canada. 63pp. [Available from <http://www.nmfs.gov>].
- Gubbins, C.M. 2000. Behavioral ecology and social structure of Atlantic coastal bottlenose dolphins (*Tursiops truncatus*) in South Carolina. Ph.D. Thesis, University of Nevada, Reno. 162pp.
- Gubbins, C.M. 2002a. Association patterns of resident bottlenose dolphins (*Tursiops truncatus*) in a South Carolina estuary. *Aquat. Mamm.* 28:24-31.
- Gubbins, C.M. 2002b. Use of home ranges by resident bottlenose dolphins (*Tursiops truncatus*) in a South Carolina estuary. *J. Mammal.* 83:178-89.
- Hohn, A.A. 1997. Design for a multiple-method approach to determine stock structure of bottlenose dolphins in the mid-Atlantic. NOAA Technical Memorandum. NMFS-SEFC-401. 22pp. [Available from <http://www.nmfs.noaa.gov/publications.htm>].
- Jacobs, M., Nowacek, D.P., Gerhart, D.J., Cannon, G., Nowicki, S. and Forward, R.B. 1993. Seasonal changes in vocalizations during behavior of the Atlantic bottlenose dolphin. *Estuaries* 16(2):241-6.
- Kenney, R.D. 1990. Bottlenose dolphins off the northeastern United States. pp. 369-86. In: S. Leatherwood and R.R. Reeves (eds.) *The Bottlenose Dolphin*. Academic Press, San Diego. 653pp.
- Lipscomb, T.P., Schulman, F.Y., Moffett, D. and Kennedy, S. 1994. Morbilliviral disease in Atlantic bottlenose dolphins (*Tursiops truncatus*) from the 1987-1988 epizootic. *J. Wildl. Dis.* 30(4):567-71.
- Mead, J.G. and Potter, C.W. 1995. Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: Morphological and ecological considerations. *Int. Bio. Res. Inst. Rep.* 5:31-43.
- Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* 62:1-135.
- Read, A.J., Foster, B., Urian, K., Waples, D., Wilson, B. and Pierce, A. 2001. Mark-recapture survey of bottlenose dolphins in the bays and sounds of NC. Final Report to the North Carolina Fishery Resource Grant Program, January 2001. 15pp. [Available from: [www.ncseagrant.org](http://www.ncseagrant.org)].
- Rittmaster, K. and Thayer, V. 1998. Temporal and spatial sighting patterns of bottlenose dolphins (*Tursiops truncatus*) stock(s) in Beaufort, North Carolina, USA. Paper presented to the World Marine Mammal Conference, 20-24 January 1998, Monaco. [Available from: [www.marinemammalogy.org](http://www.marinemammalogy.org) or North Carolina Maritime Museum, 315 Front Street, Beaufort, NC 28516, USA].
- Scott, G.P., Burn, D.M. and Hansen, L.J. 1988. The dolphin die-off; long term effects and recovery of the population. *Proc. Oceans* 88(3):819-23.
- Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd Edn. Charles Griffin and Company Ltd., London. i-xvii+654pp.
- Urian, K.W. and Wells, R.S. 1996. Bottlenose dolphin photo-identification workshop: March 21-22, 1996, Charleston, South Carolina. NOAA Technical Memorandum. NMFS-SEFSC-393. 72pp. [Available from <http://www.nmfs.noaa.gov/publications.htm>].
- Urian, K., Hohn, A.A. and Hansen, L.J. 1999. Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic. NOAA Tech. Mem. NMFS-SEFSC-425. 22pp. [Available from: <http://www.nmfs.gov>].
- Wang, K.R., Payne, P.M. and Thayer, B.G. 1994. Coastal stocks of Atlantic bottlenose dolphin: status review and management. NOAA Technical Memorandum. NMFS-OPR-4. 121pp. [Available from <http://www.nmfs.noaa.gov/publications.htm>].
- Waring, G.T., Quintal, J.M. and Swartz, S.L. 2000. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2000. NOAA Technical Memorandum NMFS-NE 162. 303pp. [Available from: <http://www.nmfs.gov>].
- Wells, R.S., Irvine, A.B. and Scott, M.D. 1980. The social ecology of inshore odontocetes. pp. 263-317. In: L.M. Herman (ed.) *Cetacean Behaviour: Mechanisms and Functions*. John Wiley & Sons, New York. xiii+463pp.
- Wells, R.S., Boness, D.J. and Rathburn, G.B. 1999. Behavior. pp. 324-421. In: J. Reynolds and S. Rommel (eds.) *Biology of Marine Mammals*. Smithsonian Institution Press, Washington and London. 578pp.
- Wilson, B., Thompson, P.M. and Hammond, P.S. 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *J. Appl. Ecol.* 34:1365-74.
- Wilson, B., Hammond, P.S. and Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl.* 9:288-300.
- Würsig, B. and Jefferson, T.A. 1990. Methods of photo-identification for small cetaceans. *Rep. int. Whal. Commn* (special issue) 12:43-52.
- Zar, J.H. 1999. *Biostatistical Analysis*. 4th Edn. Prentice Hall, New Jersey, USA. 663pp.

Date received: August 2001.

Date accepted: January 2003.