

IMPROVING MANAGEMENT OF OVERLAPPING BOTTLENOSE DOLPHIN ECOTYPES THROUGH SPATIAL ANALYSIS AND GENETICS

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ABSTRACT

In the Northwest Atlantic the distribution of coastal bottlenose dolphins (*Tursiops truncatus*) overlaps with that of the offshore ecotype. We hypothesized that the distribution of the two ecotypes could be delineated by depth and/or distance from shore, facilitating their identification during surveys. We obtained 304 skin biopsy samples and identified each as either coastal or offshore using analysis of mitochondrial DNA. We then interpreted the spatial distribution of coastal and offshore forms using spatial analysis. Using a Classification and Regression Tree (CART) analysis, we found a statistically significant break in ecotype distribution at 34 km from shore. In waters beyond 34 km from shore and deeper than 34 m, all bottlenose dolphins were of the offshore ecotype. Within 7.5 km of shore, all 65 samples were of the coastal ecotype. Between these two areas only nine samples were collected, so the genetic composition of bottlenose dolphins in this area remains poorly known. To enhance our understanding of the spatial distribution of the two ecotypes, future research should obtain more biopsy samples in this zone. Nevertheless, our results indicate that a conservative abundance estimate for the coastal ecotype could be generated from surveys of bottlenose dolphins within 7.5 km of shore.

Key words: bottlenose dolphin, *Tursiops truncatus*, spatial analysis, molecular

analysis, management, stock structure, abundance estimates, overlapping populations.

The Marine Mammal Protection Act (MMPA) defines a stock as “a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature” (MMPA [16 U.S.C. 1362]). This definition implies that, whenever possible, delineation of marine mammal stocks should reflect natural biological populations. Management of marine mammals under the MMPA is conducted on a stock-by-stock basis. Sustainable anthropogenic mortality levels, called Potential Biological Removals (PBR), are calculated for each stock using several parameters, including population abundance estimates (Wade 1998). As noted by Taylor (1997), the success of this management scheme requires knowledge of population structure. Thus, the process of accurately identifying discrete stocks of marine mammals and generating representative abundance estimates are two critical, yet challenging, tasks in marine mammal management (Wade and Angliss 1997).

Management of bottlenose dolphins (*Tursiops truncatus*) in the NW Atlantic is hindered by the unresolved state of the systematics of the genus *Tursiops*. In the western North Atlantic, two ecotypes of bottlenose dolphins have been identified using a variety of techniques, including morphology (Mead and Potter 1995), parasite loads (Mead and Potter 1995), stomach contents (Mead and Potter 1995), and hemoglobin analysis (Hersh and Duffield 1990). Moreover, analysis of mitochondrial DNA and nuclear genetic markers have revealed that the two ecotypes are genetically divergent with fixed differences, allowing genetic assignment without error (Hoelzel *et al.* 1998). These two ecotypes of bottlenose dolphins are designated as separate management units under the MMPA (Waring *et al.* 2001), and may be reproductively isolated species (Curry and Smith 1997) with overlapping geographic distributions.

It is believed that the coastal ecotype is distributed primarily in neritic waters and the offshore ecotype is found in deeper waters farther from shore (Kenney 1990, Wells *et al.* 1999). However, these are vague distribution descriptions, which do not improve stock definition. To date, there have been no attempts to determine boundaries between the two ecotypes, although Kenney (1990) speculated that the 25-m isobath might define the upper limit of the depth range of coastal bottlenose dolphins in waters north of Cape Hatteras, NC. Aerial surveys conducted in the 1980s documented that the density of *T. truncatus* varied with distance from shore, creating a significant gap in sightings of bottlenose dolphins between coastal and offshore waters north of Cape Hatteras, NC (Kenney 1990).

Abundance estimates for both ecotypes suffer from a high level of uncertainty because it is impossible to differentiate between coastal and offshore bottlenose dolphins during abundance surveys (Waring *et al.* 2001). The coastal form is listed as depleted under the MMPA as a result of an epizootic in 1987–1988, which is estimated to have killed 53% of the population (Scott *et al.* 1988) and continues to experience anthropogenic mortality as a result of bycatch in commercial fisheries, particularly by coastal gill nets. Therefore, management action to reduce bycatch rates for this ecotype is a high priority, and a Take Reduction Team has been formed to mitigate these high rates of incidental mortality. The current published abundance estimate for the coastal ecotype is based on sightings of bottlenose dolphins within 1 km of shore (Waring *et al.* 2001) because managers are confident

no offshore bottlenose dolphins inhabit these neritic waters. However, it has been recognized by both managers and the Take Reduction Team that abundance of the coastal ecotype is underestimated using this 1-km limit because the distribution of this ecotype extends beyond 1 km from shore. In fact, in our sampling, many coastal dolphins were sampled beyond 1 km from shore. Therefore, the true risk imposed on the coastal ecotype by incidental mortality in fisheries cannot be properly assessed at the present time because of the uncertainty in abundance estimates and population structure.

If it was possible to identify physical boundaries that separate the two ecotypes and determine that these boundaries did not change seasonally or over time, we could determine the ecotype of bottlenose dolphins observed during surveys based on geographic location. Additionally, managers could estimate abundance for the two ecotypes through poststratification of observations from past surveys. We hypothesized that bathymetry and/or distance from shore could be used to partition the distributions of the two ecotypes of bottlenose dolphins in the Northwest Atlantic. We chose to analyze depth and distance from shore because they are static features of the environment. Nevertheless, we recognize that other parameters, such as currents, fronts, temperature at depth, and salinity, are also likely to influence the distribution of these two ecotypes. Although the effect of these parameters on the distribution of the animals is significant, they are less tractable to stock definition because they are fluid and not readily delineated on a map, and these data are not always collected or obtainable for each dolphin sighting.

In the present study we combined two powerful tools for analyzing biogeography of population units: molecular genetic analysis and Geographic Information Systems (GIS). We used genetics to identify coastal or offshore ecotypes and used GIS to display and analyze spatial distribution relative to environmental parameters. When management goals are explicit, conservation genetics has successfully provided resource managers unambiguous criteria for designating management units (Taylor and Dizon 1999). This unique approach to determine the spatial distribution and level of overlap of genetically distinct ecotypes allowed us to assess the influence of environmental parameters on two poorly understood management units.

METHODS

The study area for this analysis was the Northwest Atlantic from New York to the central Florida coast, up to 515 km from shore (Fig. 1). A total of 304 skin biopsy samples of bottlenose dolphins were collected from various sources (Table 1). Two hundred and thirty-five samples were obtained from five National Oceanographic and Atmospheric Administration (NOAA) large-vessel research cruises conducted in pelagic waters of the Northwest Atlantic in 1997, 1998, and 1999. This sampling was conducted during July, August, and September. Samples were collected from bow-riding dolphins in front of the research vessel and from dolphins surfacing near a small boat deployed from the main vessel. One sample was obtained by a federal observer from a bottlenose dolphin incidentally caught in a coastal gill net off New Jersey. The remaining 68 samples were obtained from shore-based sampling efforts from small boats conducted throughout the year out of Virginia, Charleston, SC, and Jacksonville, FL (Table 1). Biopsy samples were obtained using custom-made biopsy darts designed to extract a small plug of skin tissue from the animal. The biopsies were collected with a pull crossbow, a pole

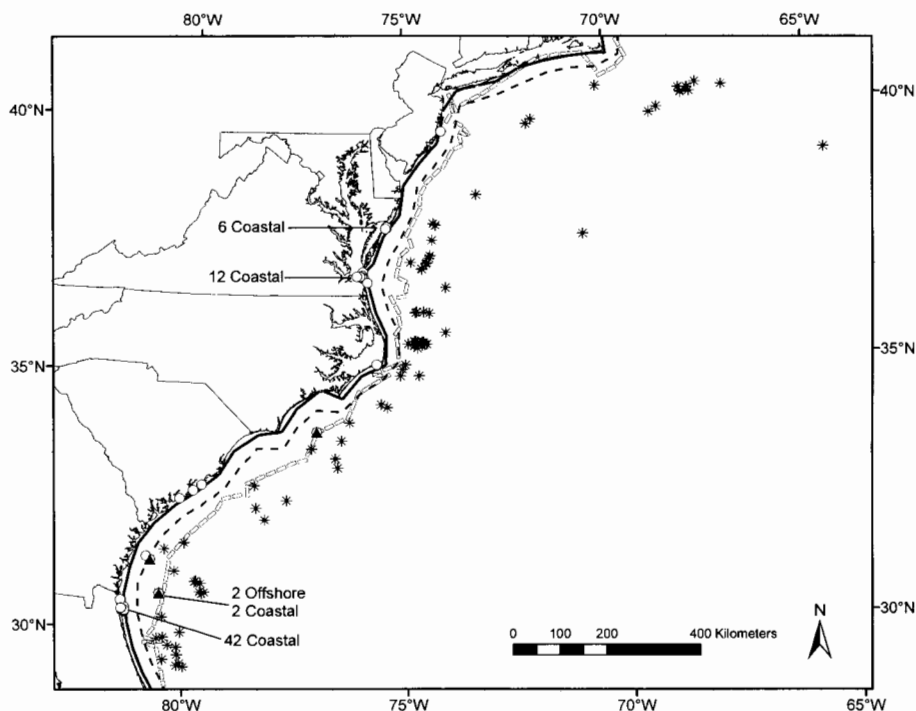


Figure 1. Distribution of sampling locations of coastal and offshore bottlenose dolphin ecotypes in the NW Atlantic, the habitat partitions generated by the CART analysis, and the 7.5-km isohaline. Coastal sampling locations (open circles), offshore sample locations (asterisks), three locations where both coastal and offshore ecotypes were sampled in the same sighting (triangles), 7.5 km from shore isohaline (solid line), 34 km from shore isohaline (dashed line), 34-m isobath (blocked line). The area between the solid line (7.5 km from shore) and the most eastward edge of both the 39-km isohaline and the 34-m isobath encompasses the "Gray Zone." Note the lack of sampling locations in this area as well as the ecotype overlap.

spear, or a modified .22 caliber rifle. The skin portion of the biopsies used for genetic analysis was stored in vials filled with a solution of saturated sodium chloride in 20% dimethylsulphoxide (DMSO). Each sample is assumed to represent an individual bottlenose dolphin.

Some bias in the sampling distribution occurred because the large NOAA research vessels could not survey in shallow water and the small boats could not travel far from shore. The biopsy samples were collected randomly within each area (shallow or deep water; close to shore or far from shore), but the samples were collected non-systematically across the entire study area. Additionally, the shore-based efforts were not systematic or even across our entire study area, creating gaps in sampling locations along the coast (Fig. 1). Despite this clumped shore-based sampling effort, we assume that the 68 samples collected are representative of coastal *T. truncatus* distribution along the US east coast.

To identify each biopsy as a coastal or offshore ecotype, a 400 base-pair portion of the control region of the mitochondrial DNA (mtDNA) genome was amplified and sequenced for each of the 304 samples (P. Rosel, unpublished data) following

Table 1. Description of where and when the 304 biopsy samples and 153 sampling locations of bottlenose dolphins (*Tursiops truncatus*) used in this analysis were acquired.

Sampling effort	Collection dates	Number of biopsies	Number of sampling locations
R/V <i>Albatross</i> AL9708	July 1997	7	5
R/V <i>Able J</i> AJ9701	August 1997	5	1
R/V <i>Gunter</i> RS98-01	July–August 1998	14	12
R/V <i>Delaware II</i> DE98-07	July 1998	115	30
R/V <i>Oregon II</i> OII99-05	August–September 1999	94	42
Charleston, SC	June, December 1998; May 1999	3	3
Jacksonville, FL	March, April, May, October 1998	42	42
VA	October 1998; October 1999	23	17
NJ bycatch	June 1999	1	1
Total		304	153

protocols described in Rosel and Block (1996) and Rosel *et al.* (1999). This portion of mtDNA was analyzed because the control region has a high mutation rate, providing a higher level of resolution when examining closely related taxa (Brown 1983), such as the coastal and offshore bottlenose dolphin ecotypes. Mitochondrial DNA's unique characteristics of maternal inheritance and haploid state increase our ability to elucidate differences among population units. Avise (1995) and Taylor *et al.* (2000a) agree that mtDNA is currently the best genetic marker for directing conservation decisions about population structure. The control region fragment analyzed here exhibits fixed differences in the mtDNA sequence between the two ecotypes (Hoelzel *et al.* 1998) allowing each biopsy to be identified as either the coastal or offshore ecotype.

Due to the large geographic area covered by this project, bathymetric and coastline data were attained from several sources. 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 U.S. 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 500 m and projected in Albers, assuming a spheroid Clarke 1866. This projection and cell size was used for all subsequent coverages and grids. 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.

All 304 biopsy samples were analyzed genetically, but not all the samples were used in the spatial analysis. Instead, 153 different sampling locations were used to sample both the bathymetry and distance from shore grids. This approach was used because, in many cases, biopsies from multiple individual dolphins were collected at the same sighting and, therefore, the same geographic location. Locations were not weighted by the number of samples collected at the site because the number of

biopsies collected did not necessarily reflect the size of the group for that sighting. For example, the research team may have sampled all 12 dolphins present in one sighting but only 12 of 200 dolphins in another sighting. Therefore, the data were analyzed as presence/absence of each ecotype at each sampling location. This manner of interpreting the data allows each location to have equal influence when testing for statistical significance of bathymetry and distance from shore. The entire data set of biopsy samples includes 150 different sampling locations. However, at three of these 150 locations, molecular analysis revealed that both coastal and offshore dolphins were present (see below). Therefore, these three locations were used twice in the data set with the same values of environmental parameters for both ecotypes. Hence, the 304 individual biopsies were reduced to 153 sampling locations to sample the bathymetry and distance from shore grids.

It is possible to describe habitat use for population units from point observations using a Classification and Regression Tree (CART) analysis (Venables and Ripley 1997). CART analysis is used to define the relationship of each population unit to predictor variables. CART recursively partitions data using an algorithm that splits observations into groups based on a single best predictor variable, in this case depth or distance from shore, until all points are classified. This method of partitioning gives the maximum deviance in the response variable and the resulting subgroups are partitioned until the final groups are relatively homogeneous. A CART analysis is non-parametric and does not assume linearity, homogeneous variables, or independence of data (Venables and Ripley 1997). The output is a tree with branches leading to terminal nodes representing final classifications. CART was originally created by Breiman *et al.* (1984) for use in the medical field. However, since 1987 CART methods have been applied to ecological studies (Verbyla 1987), coincident with the rise of GIS applications for landscape and geographic distribution analysis (Iverson and Prasad 1998). CART has been used in previous ecological studies to decipher the relationships between environmental factors and species distribution (Michaelsen *et al.* 1994, Iverson and Prasad 1998).

We used a CART analysis to examine the relationships between bathymetry, distance from shore, and the spatial distribution of the coastal and offshore ecotypes of bottlenose dolphins. The CART analysis was run in S-Plus version 5.1 (Venables and Ripley 1997) using the following model: clade as a function of depth and distance from shore.

A scatterplot was created to examine the distribution of each sampling location relative to depth and against distance from shore. Additionally, a non-parametric, two-tailed Mann-Whitney test was used to assess significance between means of each ecotype for depth and distance from shore.

RESULTS

Samples of the offshore ecotype were obtained from Long Island, NY, to the coast of central Florida and samples of the coastal ecotype were obtained from Jacksonville, FL, to the central New Jersey coast (Fig. 1). At three sampling locations, coastal and offshore animals were sampled at the same location during the same sighting, indicating mixed groups. Of 235 biopsy samples collected during pelagic sampling, only nine (six locations) were from coastal animals. No offshore samples were collected from shore-based sampling efforts. A total of 69 coastal biopsy locations and 84 offshore biopsy locations were used in the analysis. There were significant differences (two-tailed Mann-Whitney test, $P < 0.0001$) between

Table 2. Comparison of depth and distance from shore for coastal and offshore sampling locations. (*P*-values calculated using a non-parametric two-tailed Mann-Whitney test.)

	Minimum	Maximum	Mean (SE)	<i>P</i>
Depth (m)				
Coastal	1	33	14.9 (7.45)	<0.0001
Offshore	19	4,925	772.3 (952.95)	
Distance (km)				
Coastal	0.25	81	6.2 (13.74)	<0.0001
Offshore	17	515	114.4 (69.74)	

the mean depth and the mean distance from shore of coastal and offshore sampling locations (Table 2).

In classifying the data, the CART returned the same input function: clade as a function of depth and distance from shore, indicating that both variables were influential. The CART correctly classified 98% of the samples as coastal or offshore (misclassification error rate: $0.02 = 3/153$). The residual mean deviance was 0.08, indicating that approximately 92% of the variability in the data was explained correctly by the variables.

The CART analysis created two terminal nodes of unmixed groups and one terminal node of mixed ecotypes (Table 3) based on maximum deviance within the data set. Terminal node 1, an unmixed group, included 66 coastal sampling locations within 34 km of shore. Terminal node 3, also an unmixed group, included 78 offshore sampling locations in waters farther than 34 km from shore and deeper than 34 m. Terminal node 2, the only mixed node, resulted in the highest level of uncertainty with a misclassification rate of 0.33. Of the nine sampling locations in Terminal node 2, greater than 34 km from shore and less than 34 m deep, three coastal sampling locations were misclassified as offshore. This node contained all three locations where both coastal and offshore ecotypes were sampled at the same sighting, meaning that this area really contains only six different sampling locations. Node 2 also includes the offshore animal found closest to shore (39.4 km) and in the shallowest water (19 m). The coastal animal farthest from shore (82 km) and the coastal animal found in the deepest water (33 m) were also grouped into node 2.

The statistical breaks determined by the CART do not depict an important feature of the data: within 7.5 km of shore all 65 samples were of the coastal ecotype (Fig. 2). This represents 94% of all coastal samples used in the analysis. Despite the fact that no offshore animals were sampled within 39 km from shore, the CART analysis found a statistically significant break at 34 km from shore, not at the 7.5- or 39-km isoline. This result is likely due to the dearth of samples collected between 7.5 and 39 km from shore. Only one bottlenose dolphin was sampled in this area (a coastal dolphin), at 28.4 km from shore. Because a CART attempts to define homogeneous groups, our CART analysis grouped this data point with the other coastal samples within 7.5 km of shore and averaged the distance between 28.4 and 39 km to derive the break at 34 km. However, we are reluctant to conclude that all bottlenose dolphins sighted within 39 km of shore are of the coastal ecotype because the sample size between 7.5 and 39 km from shore is so small.

Table 3. Distribution of 153 sampling locations within the three terminal nodes created by the CART analysis; 65 of the 66 coastal samples in Terminal node 1 are within 7.5 km of shore. All sampling locations in Terminal node 3 are of the offshore ecotype. Notice the relative lack of biopsy sampling locations in Terminal node 2 which comprises most of the "Gray Zone."

	Terminal node 1	Terminal node 2	Terminal node 3
	Within 34 km of shore	Farther than 34 km of shore and less than 34 m deep	Farther than 34 km from shore and deeper than 34 m
Number of coastal dolphin locations	66	3	0
Number of offshore dolphin locations	0	6	78
Total	66	9	78

Moreover, the probability of an offshore bottlenose dolphin occurring in waters less than 7.5 km from shore is less than $1/n$, where n is the number of collected samples within 7.5 km of shore. There were a total of 65 sampling sites within 7.5 km of shore, making the probability of an offshore animal occurring in this area less than 0.015. Due to these findings, we identify the 7.5 km from shore line as the boundary of pure coastal ecotype habitat, not 34 km as the CART analysis found. In addition, the probability of a coastal bottlenose dolphin occurring in waters deeper than 34 m and beyond 34 km from shore (Terminal node 3) is less than 0.013 (1/78).

Terminal node 2 was the only node with misclassifications and comprises part of what we term the "Gray Zone": waters of the Northwest Atlantic between 7.5 km from shore and the combined eastward edge of the 34-m isobath and the isoline 34 km from shore (Fig. 1, 2). Table 3 shows the distribution of bottlenose dolphin sampling locations in the Northwest Atlantic in the three terminal nodes created by the CART. Note the relative paucity of samples in terminal node 2, comprising most of the "Gray Zone." Less than 6.5% (10/153) of the total biopsy locations are from the "Gray Zone."

The scatterplot of sampling locations (Fig. 2) supports our results by illustrating the area of only coastal ecotypes (within 7.5 km of shore) and the area of only offshore ecotypes (beyond 34 km from shore and waters deeper than 34 m). The "Gray Zone" in Figure 2 displays the dearth of sampling and degree of ecotype overlap in this area. Figure 2 further supports the results by reinforcing the conclusion that depth can be used to partially separate the two ecotypes. No coastal bottlenose dolphins in this dataset were sampled in waters deeper than 34 m. Furthermore, no offshore dolphins in this dataset were sampled in waters shallower than 19 m. Additionally, the distribution histogram (Fig. 3) indicates that the two populations show inverse trends in abundance relative to distance from shore.

DISCUSSION

Our spatial and molecular analyses allowed us to distinguish areas in which only the coastal or only the offshore ecotype of bottlenose dolphins were present off the eastern coast of the United States. Within 7.5 km of shore, all bottlenose dolphins sampled were genetically identified as coastal dolphins. Furthermore, all 78 samples collected beyond 34 km from shore and in waters deeper than 34 m (Terminal node

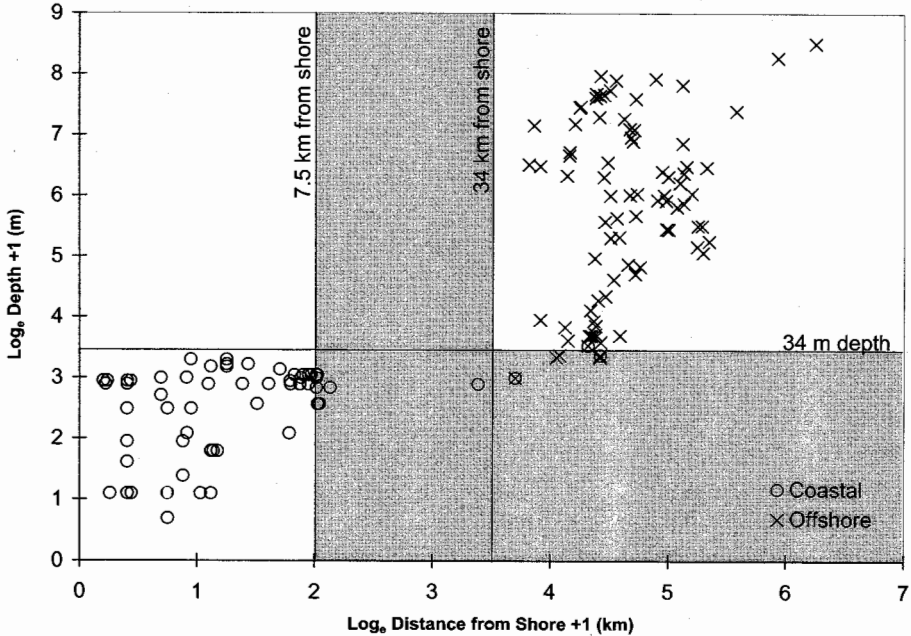


Figure 2. Distribution of all coastal and offshore bottlenose dolphin biopsy sampling locations relative to log of distance from shore and log of depth. The shaded area represents the "Gray Zone" (from 7.5 km to 34 km from shore and less than 34 m depth). Note that within 7.5 km from shore all samples are coastal and beyond 34 km from shore and above 34 m (Terminal node 3) in depth all samples are offshore.

3) were from the offshore ecotype. Thus, any bottlenose dolphin observed within 7.5 km from shore has a 99.98 probability of being a coastal animal, and any bottlenose dolphin beyond 34 km from shore and in waters deeper than 34 m has a 99.99 probability of being of the offshore ecotype.

Future surveys aimed at estimating the abundance of the coastal ecotype could minimize the probability that offshore dolphins are mistakenly included by restricting track lines to within 7.5 km of shore. However, use of the 7.5-km boundary between ecotypes will still lead to an underestimate of true population size because we know that some coastal animals are present in waters beyond 7.5 km from shore, and can occur as far as 81 km from shore. On the other hand, an abundance estimate made within 7.5 km from shore could include some estuarine bottlenose dolphins (not considered members of the coastal stock[s]) that make short forays into coastal waters (Read *et al.* 2003). Under the MMPA, sustainable mortality levels for each stock are calculated by a formula that requires a minimum abundance estimate, not an absolute abundance estimate (see Waring *et al.* 2001). Therefore, the use of an abundance estimate for the coastal bottlenose dolphin ecotype based on the 7.5-km line rather than the 1-km line currently used would yield a more reliable, yet still conservative, minimum abundance estimate that could be used to calculate sustainable removal levels in a precautionary manner.

The region between 7.5 km from shore and the combined eastward edge of the 34-m isobath and 34-km isoline comprises an area of ecotype overlap (Fig. 1 and 2). Therefore, this area is termed the "Gray Zone" because it is both an area of

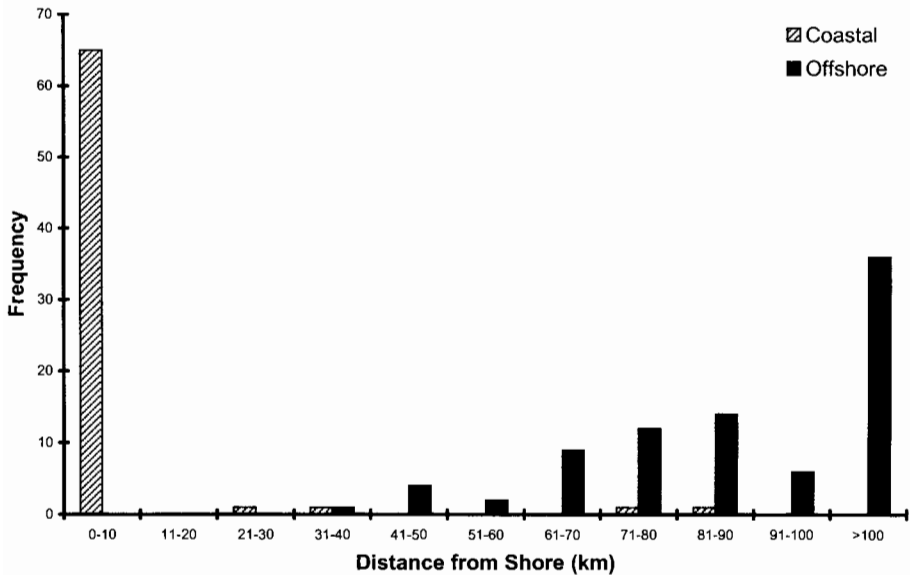


Figure 3. Distribution of coastal and offshore bottlenose dolphin ecotype sampling locations according to distance from shore. All bins are equal 10-km bins except the last bin which are all sampling locations farther than 100 km from shore.

population overlap between the coastal and offshore ecotypes, as well as the area with the fewest biopsy samples. Together, these attributes make it impossible to draw any conclusions about the distribution patterns of either ecotype in the area at this time.

It may be possible that after further sampling, the "Gray Zone" can be reduced in size, providing more accurate boundaries of pure ecotype habitat. However, because three mixed groups, containing individuals of both ecotypes, were documented in the "Gray Zone," we can conclude that no rigid boundary between the ecotypes exists. Additionally, this region of low sampling may represent a true hiatus in bottlenose dolphin density, as suggested by Kenney (1990), who analyzed aerial survey data. Dedicated surveys within the "Gray Zone," with increased biopsy effort, would help define the spatial boundaries of this area of overlap, quantify the level of habitat use by both ecotypes, and aid in estimating the proportions of both ecotypes present within the region. This might require considerable survey and biopsy effort if dolphin densities are in fact low in this area. In addition, further sampling in the ranges of both the coastal and offshore ecotypes will improve our understanding of the ranges and overlap of these two forms.

Once accurate proportions are available in the area of mixing, estimates of the abundance of all bottlenose dolphins in this area could be prorated based on these proportions to obtain separate abundance estimates for the coastal and offshore ecotypes in the region. This estimate for the coastal ecotype in the area of overlap can then be combined with the abundance estimate calculated within 7.5 km of shore to provide a more accurate total abundance estimate for the coastal ecotype. Additionally, abundance estimates could be calculated by poststratifying past aerial

and boat-based surveys based on the 7.5-km isoline and, if available, include the proportions of coastal animals in the "Gray Zone."

The results of our CART analysis should be considered provisional because there is a significant lack of data in the "Gray Zone." However, if this area of distribution overlap between the two ecotypes is indeed an area of low density, our inability to classify animals in this region may not result in a substantial underestimate of abundance for the coastal ecotype solely using the 7.5-km limit.

Most samples were collected between July and September and, therefore, our analysis may only reflect the distribution patterns of the two bottlenose dolphin ecotypes during the summer months (Table 1). Although the seasonal distribution patterns of the offshore ecotype are unknown, the coastal ecotype is known to exhibit seasonal changes in distribution (Waring *et al.* 2001), and other pelagic delphinids, such as the common dolphin (*Delphinus delphis*), exhibit seasonal movements (Waring *et al.* 2001). Therefore, it is possible that the offshore bottlenose dolphin ecotype, like the coastal ecotype, varies its habitat use seasonally. Because environmental stochasticity can dramatically alter the distribution of highly mobile marine animals, such as cetaceans, efforts to estimate abundance in fixed geographic regions can be complicated (Forney 2000). Therefore, to provide a better understanding of whether there are seasonal shifts in the distribution of the ecotypes, biopsies should be collected in both the summer and winter seasons, and, if there are seasonal changes in distribution, this analysis should be replicated using samples collected during the winter season. As Taylor *et al.* (2000b) recommend, uncertainty should be incorporated into management schemes, not ignored. At this time, without knowledge on the seasonal distribution patterns of the offshore bottlenose dolphin ecotype, the habitat partitions proposed by our results should be applied only to summer abundance surveys so that similar trends in distribution are most likely to occur.

This study showed that population management can be improved by combining the techniques of spatial analysis and genetics to discern population structure and distribution of overlapping, cryptic and poorly understood populations. The objective of our study was to provide managers with empirical evidence of a habitat partition between two overlapping bottlenose dolphin ecotypes in the Northwest Atlantic, to facilitate estimation of abundance for both ecotypes. While a larger suite of samples, particularly within the "Gray Zone," would provide the basis for a stronger analysis, and may change the best estimate of a distance from shore with which to estimate abundances, our results indicate that a realistic minimum abundance estimate for the coastal ecotype can be generated from surveys conducted within 7.5 km from shore, allowing a pragmatic evaluation of anthropogenic threats.

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