Habitat and abundance of cetaceans in Atlantic Ocean continental slope waters off the eastern USA

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ABSTRACT

This study quantifies the abundance and spatial distribution of the cetacean community occupying continental shelf edge and inner continental slope waters along the US southeast Atlantic coast. A shipboard visual line-transect survey was conducted between June and August of 2004 that included effort in waters >50m deep encompassing the shelf break and inner continental slope off the US east coast between 28°N and 38°N latitude. The abundance of nine cetacean taxa was estimated using line-transect distance analysis and an independent observer approach to correct for visibility bias. Canonical correspondence analysis was used to examine the spatial distribution of the cetaceans encountered during the survey as a function of surface temperature, surface salinity, surface fluorescence, bottom depth, and bottom slope. The abundance estimates for most species were much higher than those from a study of the area conducted in 1998. This is primarily due to increased coverage of the shelf-break region and correction for visibility bias. The multivariate analysis indicated four distinct groups of cetaceans that partitioned habitat as a function of salinity, depth, and a latitudinal gradient. These groups were associated with specific water masses and hydrographic features including mid-Atlantic shelf waters (Group I), the shelf break (Group II), mid-Atlantic slope waters (Group III), and south Atlantic slope water (Group IV). Areas where water masses converge such as the continental shelf break along the mid-Atlantic and near Cape Hatteras, North Carolina are therefore areas of both high diversity and density of cetaceans.

KEY WORDS: CETACEAN HABITAT; LINE-TRANSECT SURVEY; MULTIVARIATE ANALYSIS

INTRODUCTION

Cetaceans are highly mobile predators that occupy a diverse range of habitats throughout the world's oceans. Habitat selection and spatial distribution are thought to be largely determined by prey density, particularly for the odontocetes (e.g. Baumgartner *et al.*, 2001; Kenny *et al.*, 1995). Cephalopods and pelagic fish are the primary prey of odontocetes occurring in deep continental shelf and slope waters (e.g. Cañadas *et al.*, 2002; Gannon *et al.*, 1997; Mintzer *et al.*, 2008). The density of such prey varies both seasonally and spatially. Oceanographic features such as water mass boundaries, mesoscale eddies, upwelling or downwelling regions and convergence zones have the potential to locally increase prey densities in response to increases in secondary production. These features may also increase the availability of prey to shallow-diving cetaceans by increasing the abundance of prey near the surface (Baumgartner *et al.*, 2001).

Given the strong correlation between bathymetry and underlying circulation patterns in shelf and slope systems, many studies have demonstrated differentiation of cetacean habitats within bathymetric zones (e.g. Azellino *et al.*, 2008; Cañadas *et al.*, 2002). In the northern Gulf of Mexico, for example, several species of delphinids showed preferences for distinct bathymetric zones separating species that occurred near the shelf break with steeper bathymetry from those with a more broad distribution over deeper waters. However, finer scale partitioning of habitat within these groups was driven by hydrographic features such as thermocline depth (Baumgartner *et al.*, 2001). Similarly, beaked whales (family Ziphiidae) and sperm whales (*Physeter macrocephalus*) along the northeast coast of the US occupied waters near the shelf-break and inner continental slope but partitioned habitat at smaller scales based upon water temperature (Waring *et al.*, 2001). A broader study of the northeast US pelagic cetacean community likewise demonstrated groupings of species by bathymetry and latitudinal range corresponding to water temperature (Hamazaki, 2002). The spatial distribution of these species groups shifted between years as a result of variations in water temperature. These studies demonstrate that cetaceans, like their pelagic prey, respond to environmental variation by moving to track preferred habitats (Redfern *et al.*, 2006).

The outer continental shelf and inner slope of the Atlantic Ocean along the US east coast between 28°N and 38°N (Fig. 1) encompasses a diverse suite of cetacean habitats. Over the southern portion of the survey area (south of Cape Hatteras, North Carolina), the shelf break (roughly the 200m isobath) is dominated by warm, high salinity waters of the Gulf Stream. On the western side of the Gulf Stream, South Atlantic Shelf waters are present, while the eastern side is dominated by the low productivity waters of the Sargasso Sea (Schmitz *et al.*, 1987). The Blake Plateau, with bottom depths of approximately 1,000m, extends approximately 300km east of the continental shelf break. North of Cape Hatteras, the Gulf Stream diverges from the continental shelf break. Between the shelf break and the Gulf Stream are slope waters with surface temperatures of 20–24°C and salinity ranging between 34–35psu. The waters over the shelf (Mid-Atlantic Shelf Water) in this region are both cooler and of lower salinity than the adjacent slope water. The shelf water

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bulges out over the shelf break in a wedge extending from the 100m isobath to the surface 30–50km seaward. Associated with this bulge is a pool of cold, low salinity (~33psu) water occurring at depths of 50–80m (Schmitz *et al.*, 1987). At the surface, the boundary between the shelf and slope waters is evinced as the shelf-break front with a strong cross-shelf salinity gradient (Gawarkiewicz *et al.*, 1996). Near Cape Hatteras, the hydrography is complex due to the interaction between the Gulf Stream and both the Mid-Atlantic and South Atlantic Shelf water masses.

Against the backdrop of this complex oceanographic structure, the cetacean community includes both sub-tropical and temperate species responding to a range of bathymetric and oceanographic regimes. In this study, we assess the abundance and spatial distribution of this diverse cetacean community and use constrained ordination analysis to examine the relationships between species groups and large-scale oceanographic and bathymetric features.

METHODS

Survey methods

A visual line-transect survey was conducted aboard the NOAA Ship *Gordon Gunter* from 22 June to 19 August 2004. The survey was conducted in water depths greater than 50m and covered waters including the outer continental shelf, the shelf break and the inner continental slope to the US Exclusive Economic Zone. Survey effort was conducted in three strata: South Atlantic slope (Area = 146,933km^2); the Mid-Atlantic shelf break (Area = 74,114km^2); and the Mid-Atlantic slope (Area = 194,326km^2, Fig. 1). Tracklines were arranged in a 'double saw-tooth' pattern perpendicular to the bathymetry with a randomised starting point to provide uniform coverage probabilities within each stratum. However, not all planned tracklines were covered due to weather conditions. Survey speed was typically 18km hr^{-1} (~10 knots). Survey effort was suspended during heavy seas (swell height >2m), rain, or other poor visibility conditions (sea state >5 on the Beaufort scale).

The survey was conducted using a two-team independent observer approach to estimate abundance and account for visibility bias (Laake and Borchers, 2004). The first observer team was stationed on the ship's flying bridge (average eye height above water = 13.7m), and the second team was stationed at a lower platform on the bridge wings (average eye height above water = 11.0m). The two teams were isolated from one another to avoid cueing each other to the presence of marine mammals. The flying bridge team included two observers searching with 25 × 150 'bigeye' binoculars and a centre observer searching with handheld binoculars and the naked eye. The bridge wing team consisted of two observers searching with bigeye binoculars. The bigeye observers searched the arc from the ship's bow (the trackline) to the vessel beam on each side, while the third observer on the flying bridge primarily concentrated on the trackline and near the ship.

A data recorder maintained independent communication with both teams and recorded data on sightings by each team. This coordinating observer was also responsible for identifying sightings that were seen by both teams. Upon a marine mammal sighting made by one of the teams, the position of the group was plotted, and the sighting team went off effort to continue to track the group. The second team was not informed of the sighting and remained on effort. If the mammal group went past the vessel's beam (relative bearing 90°) without being seen by the second team, then it was considered missed. Once the group was 'missed' or seen by the second team, then both teams went off effort, and the vessel was turned to approach the group for species identification and group size estimation. If the two teams saw two separate sightings of marine mammals at the same time, then the vessel typically turned to identify the closest group first and then attempted to relocate the farther group.

For each cetacean group sighted, time, position, bearing to the sighting, radial distance to the sighting, species, group size, behaviour, bottom depth, sea surface temperature, and associated animals (e.g. seabirds and fish) were recorded. The radial distance to sightings made from the bigeye binoculars was measured with reticles, while distances were visually estimated for groups sighted by naked eye or handheld binoculars. Survey effort data were recorded every two minutes and included the ship's position and heading, effort status, observer positions, and environmental conditions which could affect the observers' ability to sight animals (e.g. Beaufort sea state, trackline glare, cloud cover, etc.). Typically, if a sighting was within 3 n.miles on either side of the ship, the ship was diverted from the trackline to approach the group to identify species and estimate group size. Cetaceans were identified to the lowest taxonomic level possible. Unidentified animals were typically those that were not re-sighted after the initial cue.

There are three abundant taxonomic groups used in this study that combine species or genetically distinct populations that cannot be differentiated at sea and may have different habitat associations. The first is the pilot whales (*Globicephala* sp.) which may include both the short-finned (*G. macrorhynchus*) and long-finned (*G. melas*) species. The spatial range of the two species overlaps in the region between 35°N and 41°N, with the short-finned species having a generally more southern tropical and sub-tropical distribution (Leatherwood *et al.*, 1983). Given the spatial range of our survey, it is likely that our results are more indicative of the distribution of the short-finned pilot whale. The second group is the Atlantic spotted dolphin (*Stenella frontalis*) which occurs in a more near-shore coastal form and a more offshore form (Adams and Rosel, 2006). These two groups are genetically distinct from one another, and there is evidence for differentiation of habitat near Cape Hatteras. It is unclear if both groups are included in the current analysis. Finally, there are two distinct forms of bottlenose dolphins (*Tursiops truncatus*), a larger more robust type with a more offshore distribution and a smaller type with a more coastal distribution (Hersh and Duffield, 1990; Torres *et al.*, 2003). It is most likely that the current survey includes predominantly the offshore morphotype.

Abundance estimation

Abundance estimates for observed cetacean species were derived using the independent observer approach assuming point independence (Laake and Borchers, 2004) as implemented in the Distance computer program (version 5.0 release 2; Thomas *et al.*, 2006). Briefly, this approach is an extension of standard line-transect distance analysis that includes direct estimation of sighting probability on the trackline. The probability of sighting a particular group is the product of two probability components. The first probability corresponds to the 'standard' sighting function such that the probability of detection declines with increasing distance from the trackline following a known functional form (typically the half-normal or hazard function). The second component is the likelihood of detection on the trackline which is modelled using a logistic regression approach and the 'capture histories' of each sighting (i.e. seen by one or both teams). The logistic model can include factors that may affect the probability of detection such as viewing or weather conditions. Details on the derivation, assumptions, and implementation of the estimation approach are provided in Laake and Borchers (2004).

Sighting probability analyses were conducted separately for three groups of cetaceans, dolphins, pilot whales, and large whales, to account for differences in body size and surface behaviour and associated differences in sighting probability (Table 1; Barlow, 1995; Mullin and Fulling, 2003). While 'cryptic' species including beaked whales (family Ziphiidae) and pygmy/dwarf sperm whales (*Kogia* spp.) were observed, there were insufficient sightings of these species for reliable abundance estimation. For each species group, sighting probability was estimated globally across strata. The perpendicular sighting distances were right-truncated to remove roughly 10% of the sightings with the farthest distances (Buckland *et al.*, 2001) which corresponded to 5,000m for the dolphins and large whale groups and 4,000m for the pilot whales. The form of the sighting function (hazard vs. half-normal) and the inclusion of covariates (including group size, sea state, glare, swell height, wind speed) in the mark-recapture model were evaluated through model selection based upon the Akaike Information Criterion (AIC; Laake and Borchers, 2004). There was no evidence of reactive movements to the survey vessel, and environmental covariates had little effect on either the sighting distance or mark-recapture components of the model with the exception of group size which was important in the mark-recapture portion of the model for pilot whales and large whales. Stratified abundance estimates for each individual taxon were calculated using stratum and species level encounter rates (groups per km of trackline) and mean group size.

Habitat associations

Surface layer (measurements taken at <5m depth) salinity, temperature and fluorescence (recorded in micrograms per litre and used as a proxy for chlorophyll concentration) were recorded continuously throughout the survey using sensors deployed aboard the vessel. These hydrographic data were used to assess habitat associations and groupings amongst the species encountered during the survey. Bottom depth along the trackline was derived from the ETOPO2 global bathymetry dataset[1]. The bathymetric slope was derived from the bathymetry grid using tools in ArcGIS Spatial Analyst (ESRI, Inc.).

Habitat variables (temperature, salinity, fluorescence, bottom depth, and bathymetric slope) were summarised into 10 × 10km grid cells. For each cell, the mean of the environmental variables, total survey effort and number of marine mammal groups and individuals (by species) were calculated. The spatial cells were treated as the sampling unit in a multivariate analysis of marine mammal habitat associations.

Canonical correspondence analysis (CCA; Ter Braak, 1986) was used to examine the habitat associations of the marine mammal species encountered during the survey. CCA is a constrained ordination approach that quantifies the amount of variation in a multivariate response (i.e. species abundance) that can be explained by a selected suite of environmental/habitat characteristics (Ter Braak, 1986). The response matrix was the species composition within each cell expressed as the total number of animals of each species sighted in the cell. Several metrics of species occurrence were explored including dividing the number of animals observed by the amount of trackline in the cell as a proxy for animal density. In addition, log- and square-root transformations were applied to reduce the influence of rare species. The results of the analysis were insensitive to these transformations, and therefore simple counts were used. The explanatory matrix included the suite of environmental variables described above for each cell in addition to the X ('Easting') and Y ('Northing') location of the cell based on the Universal Transverse Mercator (WGS 1984, Zone 18N) projection of the grid. These spatial variables were included as main effects in the models after exploratory analyses indicated no significant spatial confounding of habitat relationships (Borcard *et al.*, 1992). All CCA analyses were conducted using the package 'vegan' implemented in the R statistics package (Oksanen *et al.*, 2008).

A stepwise selection approach was used to select explanatory variables to constrain the ordination. Each variable was first submitted as a single term, and its significance was tested using permutation tests (1,000 permutations) of the F-statistic. Those variables that were statistically significant ($p<0.05$) were then included in progressive two and three term models until all significant variables were included. Single terms were then sequentially dropped from this full model to verify their explanatory significance. The multiple term significance tests in CCA may be sensitive to the order of entry into the model (Oksanen *et al.*, 2008); therefore, the stepwise approach included the entry and removal of terms in differing orders to avoid this artifact. The model including all significant effects was used to examine correlations between species distribution and habitat variables, associations between species, and spatial patterning in marine mammal habitats.

RESULTS

Survey results

A total of 5,139km of effort was completed during the survey including 1,601km in the South Atlantic slope stratum, 1,798km in the Mid-Atlantic shelf break stratum, and 1,739km in the Mid-Atlantic slope stratum (Fig. 1). Several survey days were lost due to poor weather conditions including Hurricanes Alex and Charley. The vast majority (>90%) of the survey effort was conducted in Beaufort sea states of three or less. There were a total of 364 marine mammal groups sighted by one or more survey teams including 17 taxa (Table 1). The most common species sighted were bottlenose dolphins, sperm whales and pilot

[1] *http://www.ngdc.noaa.gov/mgg/global/global.html*.

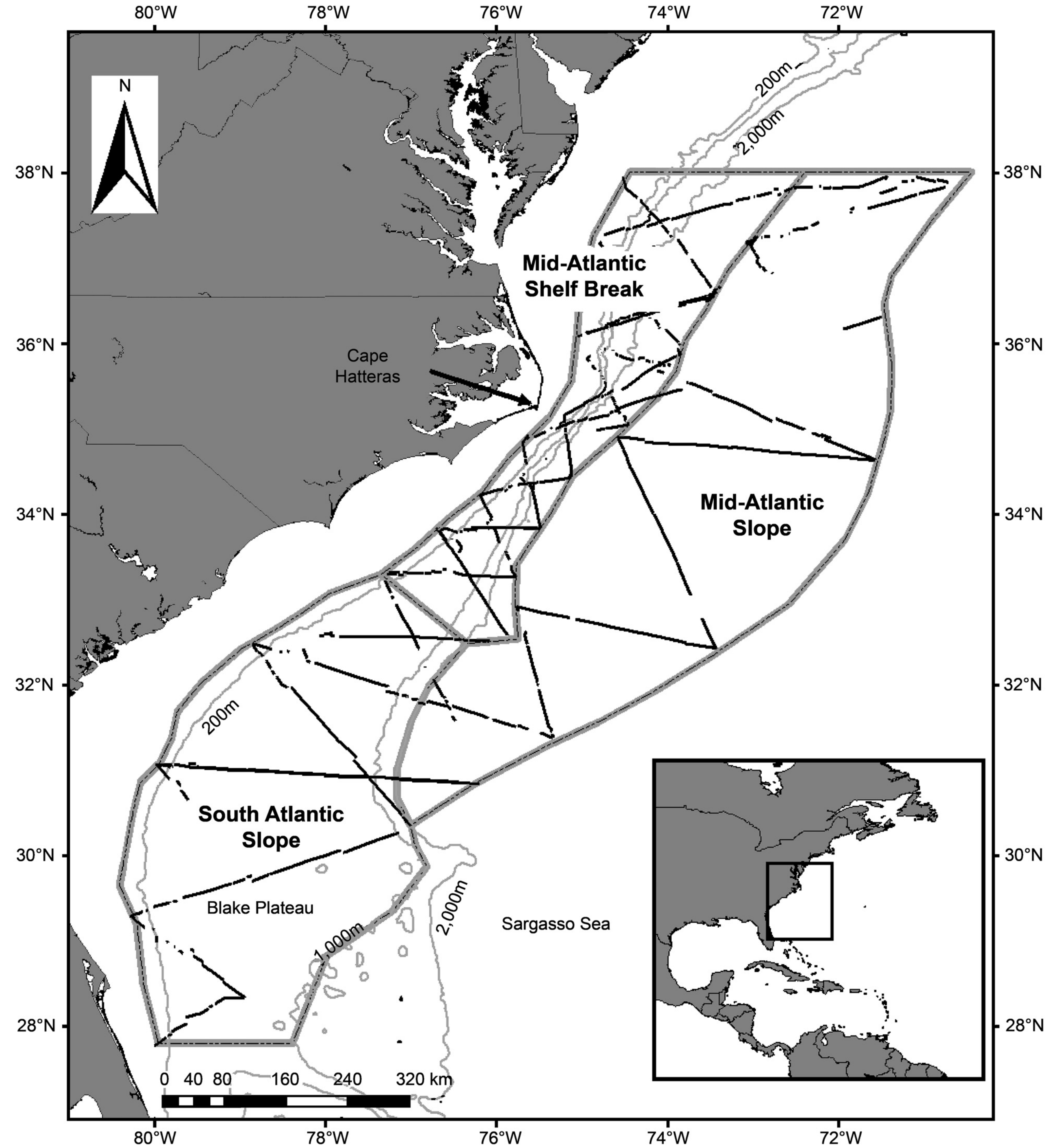

Fig. 1. Survey effort (black lines) and strata (within thick grey lines) during the summer 2004 Atlantic Cetacean Survey. Contours derived from the ETOPO-2 bathymetry grid are shown.

whales. Both the number of sightings and the number of species observed in the Mid-Atlantic shelf break stratum were much higher than in either of the other two strata. Mean group sizes for most taxa were consistent across strata (Table 1).

Abundance estimates

For each group, the best-fitting models were selected based upon the model with the lowest value of AIC. There was little evidence that covariates, other than group size for large whales and pilot whales, improved the overall model fit. In most cases, the addition of covariates to the models resulted in small increases in AIC (generally less than 2), indicating that the parsimonious model excluding covariates was at least as appropriate as the more complex models. Models including all covariates resulted in ΔAIC values greater than 7, indicating that there was little support for including this additional complexity. The choice of the form of the sighting function (hazard vs. half-normal) had strong support for each group with ΔAIC values of 4 or greater in each case. The selected models were effective at fitting the sighting probabilities of the different capture histories (seen by team 1 only, seen by team 2 only, or duplicates) as demonstrated by Chi-sq goodness of fit tests for all cases.

For the dolphin sub-group, the best fitting sighting function was a hazard model including no additional covariates in the mark-recapture component of the model (Fig. 2a). The average estimated sighting probability within the surveyed strip was 0.27 (CV = 0.157). The sighting

Table 1

Number of groups sighted (N) and mean group size by stratum for each marine mammal taxon encountered during the summer 2004 Atlantic cetacean survey. The coefficient of variation (CV) of the mean is indicated in parentheses.

	South Atlantic Slope		Mid-Atlantic Shelf Break		Mid-Atlantic Slope	
Species	N	Mean group size (CV)	N	Mean group size (CV)	N	Mean group size (CV)
Subgroup – dolphins						
Atlantic spotted dolphin (*Stenella frontalis*)	1	73.0 (–)	21	83.0 (0.19)	9	73.6 (0.44)
Bottlenose dolphin (*Tursiops truncatus*)	28	25.6 (0.19)	43	33.1 (0.17)	4	34.3 (0.14)
Bottlenose/Atlantic spotted dolphin	4	10.0 (0.44)	0	–	0	–
Short-beaked common dolphin (*Delphinus delphis*)	0	–	10	267.2 (0.36)	0	–
Pantropical spotted dolphin (*Stenella attenuata*)	2	52.5 (0.71)	0	–	1	70.0 (–)
Risso's dolphin (*Grampus griseus*)	6	23.3 (0.52)	8	24.3 (0.39)	1	15.0 (–)
Stenella sp.	0	–	0	–	2	6.5 (0.23)
Striped dolphin (*Stenella coeruleoalba*)	0	–	4	80.0 (0.21)	6	136.5 (0.21)
Unidentified dolphins	11	3.2 (0.27)	21	20.6 (0.35)	7	6.0 (0.54)
Unidentified odontocetes	3	2.0 (0.29)	2	1.0 (0.0)	3	2.0 (0.50)
Subgroup – pilot whales						
Pilot whales (*Globicephala sp.*)	11	24.2 (0.22)	37	19.8 (0.12)	5	12.6 (0.17)
Subgroup – large whales						
Fin whale (*Balaenoptera physalus*)	0	–	1	2.0 (–)	0	–
Unidentified baleen whales	0	–	1	12.0 (–)	1	1.0 (–)
Sperm whale (*Physeter macrocephalus*)	2	2.0 (0.50)	69	2.3 (0.08)	14	1.9 (0.15)
Unidentified large whales		–	3	1.0 (0.0)	4	1.0 (0.0)
Subgroup – cryptic species						
Beaked whales (*Ziphiidae*)	5	1.4 (0.17)	8	1.4 (0.27)	4	2.0 (0.20)
Pygmy/dwarf sperm whale (*Kogia* sp.)	0	–	1	1.0 (–)	1	1.0 (–)

function had a good overall fit to the observed sighting distances (Chi-sq Goodness of Fit [GOF], $p = 0.228$). The estimated sighting probability on the trackline for each team independently was 0.596 (CV = 0.068) and for the two teams jointly was 0.837 (CV = 0.039).

A hazard rate model including cluster size and sighting distance was the best fitting mark-recapture model for pilot whales and had a good fit to the observed data (Chi-sq GOF, $p = 0.281$; Fig. 2b). The average estimated sighting probability for pilot whales in the survey strip was 0.35 (CV = 0.31). The estimated sighting probability on the trackline for each team independently was 0.47 (CV = 0.18) and was 0.69 (CV = 0.13) for the two teams jointly.

For the large whales, the best mark-recapture model was a half-normal function including cluster size as a covariate (Fig. 2c). The sighting function model was a good fit to the observed data (Chi-sq GOF, $p = 0.640$), and the resulting estimated sighting probability in the survey strip was 0.483 (CV = 0.08). The sighting probability on the trackline for each team independently was 0.52 (CV = 0.13) and was 0.76 (CV = 0.08) for the two teams jointly.

The abundance and density estimates for each stratum, and overall, are shown in Table 2 for species where estimation was possible. The 'baleen whale' group in Table 2 includes both identified fin whales and unidentified baleen whales. The precision of the abundance estimates varied widely as a result of variable encounter rates and group sizes. The most precise estimates approach CV values of 0.30 for bottlenose dolphins and Risso's dolphins, while the least precise approach CVs of 1.0 for Atlantic spotted dolphins and the baleen whales (Table 2).

Among the abundant dolphin species, there are clear differences in density across strata. For example, Atlantic spotted dolphins occurred in high densities in the Mid-Atlantic shelf break and Mid-Atlantic slope strata while bottlenose dolphins were more abundant in the Mid-Atlantic shelf break and the South Atlantic slope strata (Table 2). In

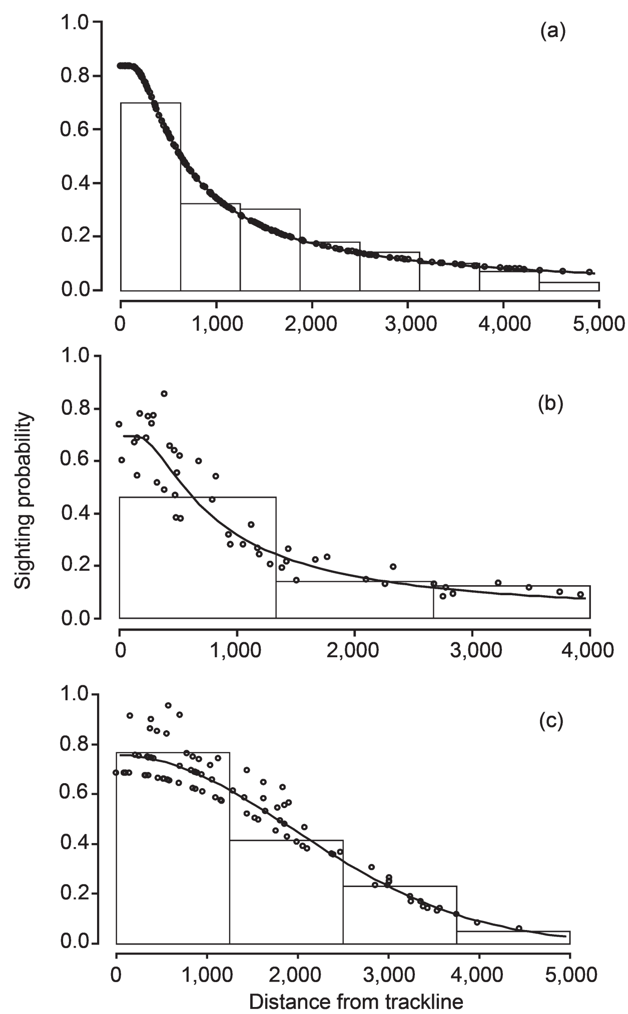

Fig. 2. Sighting detection functions pooled across observer teams for (a) dolphins, (b) pilot whales, and (c) large whales. The line indicates the fitted sighting function, and points are estimated sighting probabilities for individual groups. Bars are grouped distance intervals used for chi-square goodness of fit tests, though sighting function fits are based on ungrouped data. Plots were generated using Distance 5.0 (release 2, Thomas *et al.*, 2006).

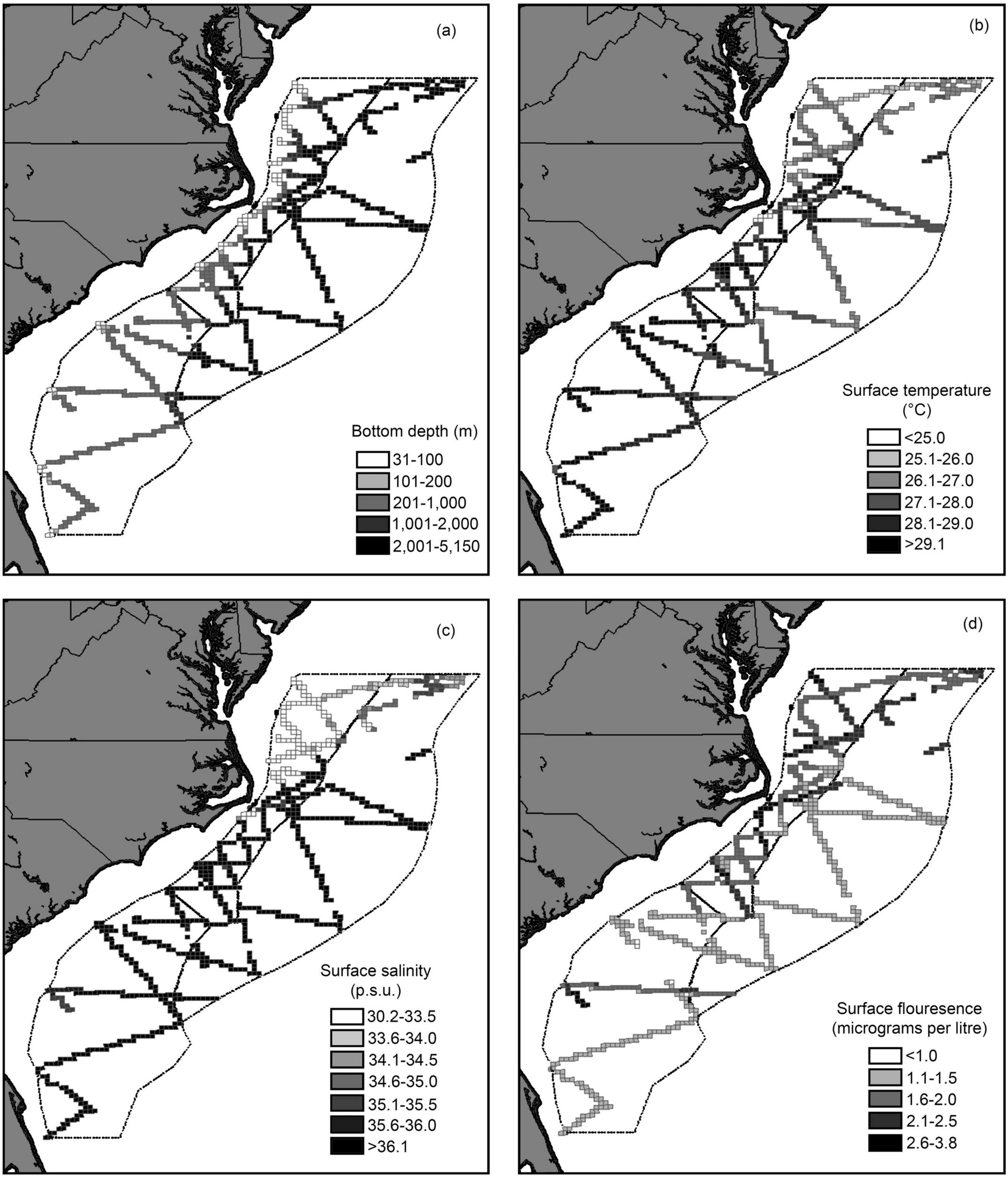

Fig. 3. Mean of environmental variables in sampled 10 × 10km spatial cells: (a) bottom depth, (b) surface temperature, (c) surface salinity, and (d) surface fluorescence.

contrast, striped dolphins occurred almost exclusively in the Mid-Atlantic slope stratum while short-beaked common dolphins were confined to the Mid-Atlantic shelf break stratum (Table 2).

Habitat associations

The sampled area included broad regions with distinct environmental conditions. In the northern portion of the survey range in waters generally < 2,000m depth corresponding to the outer continental shelf and shelf break, the water temperature was cool (< 26°C) and salinity was low (< 33.5psu, Fig. 3). Further offshore in the northern part of the region, water temperature was also cool, but salinity was greater than 35psu. The Gulf Stream (high water temperature, high salinity) was apparent near Cape Hatteras, North Carolina (~35.2°N Latitude) in close proximity to

Table 2

The estimated density (number/km²) and abundance for each species by stratum from the summer 2004 Atlantic cetacean survey. The coefficient of variation (CV) for density estimates is indicated in parentheses.

	South Atlantic Slope		Mid-Atlantic Shelf Break		Mid-Atlantic Slope		Total	
Species	Density (CV)	Abundance	Density (CV)	Abundance	Density (CV)	Abundance	Density (CV)	Abundance
Atlantic spotted dolphin	0.020 (0.74)	2,891	0.418 (0.52)	30,997	0.164 (1.81)	31,923	0.158 (0.92)	65,812
Bottlenose dolphin	0.183 (0.37)	26,892	0.312 (0.46)	23,172	0.034 (0.69)	6,606	0.136 (0.30)	56,671
Short-beaked common dolphin	0 (–)	0	0.512 (0.85)	37,951	0 (–)	0	0.512 (0.85)	37,951
Pantropical spotted dolphin	0.028 (1.00)	4,158	0 (–)	0	0.017 (0.76)	3,375	0.018 (0.66)	7,534
Risso's dolphin	0.038 (0.53)	5,545	0.026 (0.56)	1,938	0.004 (0.96)	723	0.020 (0.41)	8,207
Striped dolphin	0 (–)	0	0.077 (0.48)	5,690	0.203 (0.694)	39,494	0.109 (0.61)	45,185
Pilot whales	0.029 (0.87)	4,262	0.176 (0.66)	13,055	0.019 (0.62)	3,737	0.0507 (0.52)	21,056
Baleen whales	0 (–)	0	0.002 (1.06)	125	0.0002 (1.35)	34	0.0004 (0.88)	159
Sperm whale	0.001 (0.53)	97	0.021 (0.42)	1,615	0.004 (0.98)	743	0.006 (0.42)	2,455

Mid-Atlantic Shelf and Slope waters. While South of Cape Hatteras, over the Blake Plateau, both water temperature (>28°C) and salinity (>35.5psu) were high (Fig. 3).

In the CCA analysis, salinity ($F = 0.332$, $p = 0.022$), depth ($F = 0.956$, $p = 0.002$), and the Y-coordinate ($F = 0.716$, $p = 0.002$) were retained as significant explanatory factors. The ordination including these variables explained 16.7% of the total inertia in the data. The first two canonical axes accounted for 89.4% of this explained variance. The CCA biplot arrows (Fig. 4) indicate the correlation between the canonical axes (CA) and the explanatory variables. The first axis (CA I) scores were negatively correlated with depth and salinity. The second axis (CA II) was primarily correlated with the Y-coordinate with northern sites having more negative scores and southern sites having more positive scores (Fig. 4). The large scale gradient indicated by the Y-coordinate is partially correlated with the latitudinal temperature gradient; however, accounting directly for this large scale spatial effect by including the Y-coordinate as a conditional variable did not improve the explanatory power of the CCA nor did it result in temperature being included in the selected model.

The CCA indicated four clearly differentiated groups of species based upon the species-environment relationships (Fig. 4). First, the baleen whales (including both unidentified baleen whales and fin whales) and short-beaked common dolphins were grouped and occurred in habitats of shallow water depth and low salinity (Table 3). These two taxa occurred in waters north of Cape Hatteras at depths <1,000m (Fig. 5a). The second group included bottlenose dolphins, Risso's dolphins and pilot whales. These species were distributed more broadly throughout the latitudinal range of the survey in waters between the 1,000–2,000m isobaths. In the northern portion of the survey range, this corresponded to waters near the shelf break, while south of Cape Hatteras, this corresponded to the shallow portion of the Blake Plateau (Fig. 5b). These species had mean temperature values of

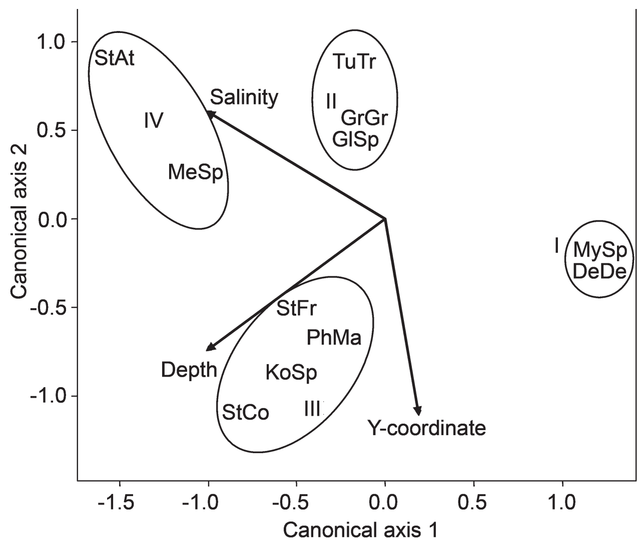

Fig. 4. Canonical correspondence analysis biplot. Arrows indicate the relative importance (length) and correlation (angle with axis) between each variable retained in the model and the canonical axes. Species scores on the canonical axes are indicated by abbreviations (see Table 3). Species groupings are indicated.

Table 3

Mean (weighted by abundance) environmental variable values for each species. The CCA group assignment for each species is shown in Figure 4. The standard deviation of the mean is indicated in parentheses.
'Northing' refers to Latitude projected into the Universal Transverse Mercator (Zone 18N) coordinate system.

CCA Group	Species (abbreviation)	Depth (m)	Temperature (°C)	Salinity (ppt)	Northing (km)
I	Common dolphin (DeDe)	305.6 (148.5)	26.6 (0.12)	31.4 (0.25)	4,020 (23)
	Baleen whales (MySp)	272.7 (546.5)	26.4 (0.33)	31.8 (0.94)	4,062 (122)
II	Pilot whales (GlSp)	1,341.8 (164.8)	28.3 (0.24)	34.9 (0.33)	3,829 (35)
	Risso's dolphin (GrGr)	1,161.4 (293.4)	28.5 (0.51)	35.0 (0.55)	3,839 (76)
	Bottlenose dolphin (TuTr)	1,002.1 (112.8)	28.2 (0.19)	35.5 (0.19)	3,765 (36)
III	Dwarf/pygmy sperm whale (KoSp)	2,605.6 (432.8)	26.7 (0.31)	33.9 (0.84)	4,060 (45)
	Sperm whale (PhMa)	2,186.9 (92.9)	27.0 (0.14)	33.6 (0.22)	4,031 (21)
	Striped dolphin (StCo)	3,050.3 (135.6)	26.5 (0.29)	34.5 (0.31)	4,150 (18)
	Atl. spotted dolphin (StFr)	2,377.4 (188.5)	27.5 (0.34)	34.4 (0.33)	3,998 (24)
IV	Beaked whales (MeSp)	2,280.7 (208.9)	27.8 (0.34)	35.8 (0.25)	3,790 (77)
	Pantropical spotted dolphin (StAt)	2,369.4 (1,230.9)	28.7 (0.82)	36.4 (0.06)	3,473 (229)

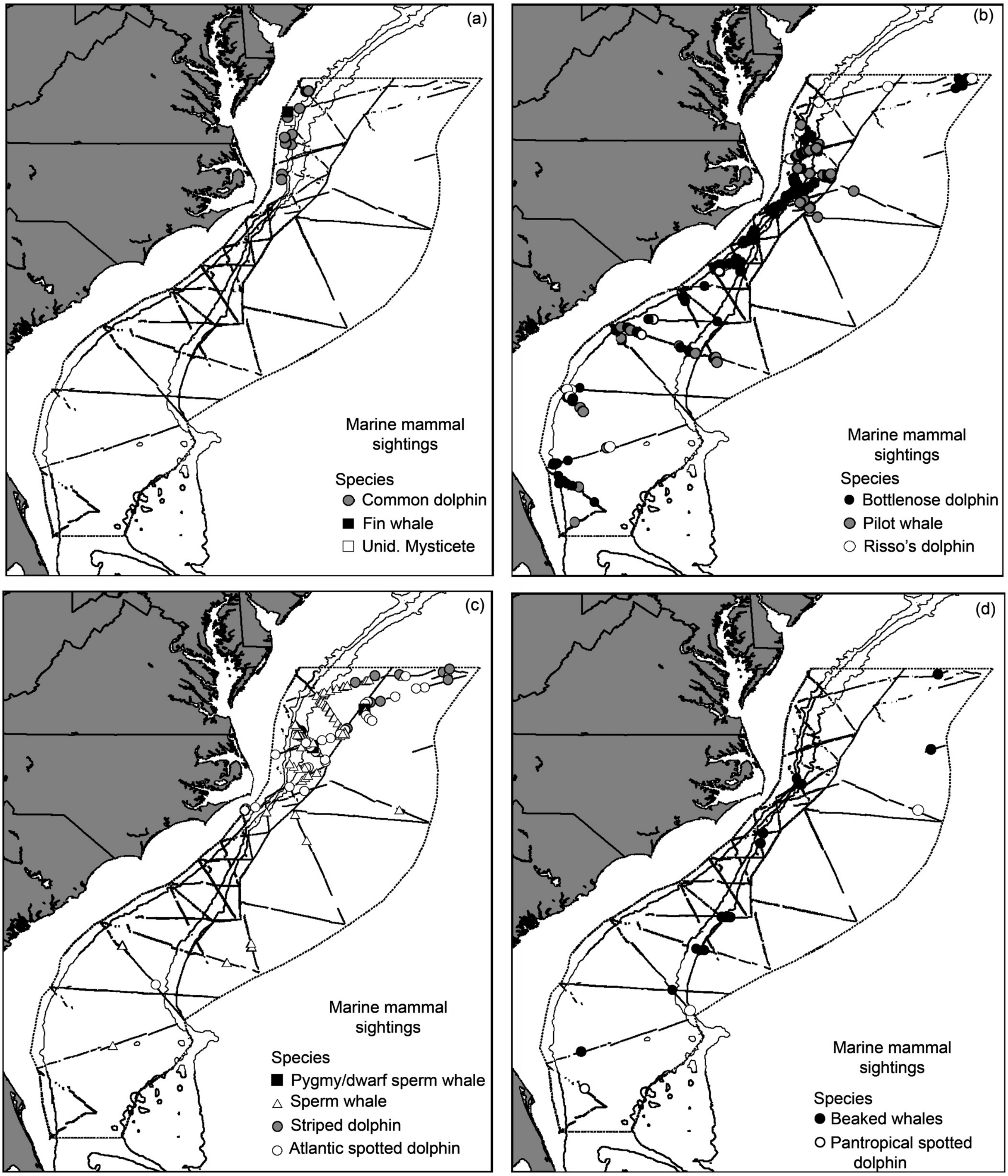

Fig. 5. Sightings of each species in groups identified by CCA including (a) Group I, (b) Group II, (c) Group III, and (d) Group IV.

28–28.5°C, mean salinity of 34.9–35.5psu, and mean depths of 1,000–1,300m (Table 3). The third group included sperm whales, Atlantic spotted dolphins, striped dolphins and *Kogia* sp. (Fig. 4). These species occupied the northern offshore waters deeper than 2,000m (Fig. 5c), and their habitats were characterised by lower water temperatures and intermediate salinities (Table 3). Finally, the beaked whales and pantropical spotted dolphins formed a group of more southern offshore species occurring in waters deeper than the 2,000m isobath (Fig. 5d) with high water temperatures (>28°C) and high salinities (>35.5psu, Table 3).

DISCUSSION

This study demonstrates that there are distinct communities of cetaceans inhabiting oceanic waters along the southeast US Atlantic coast, and that these communities correspond to distinct oceanographic regimes. Our study also provides improved and updated abundance estimates for the cetacean species encountered, which is a critical part of the management of these protected species.

This region was also surveyed during the summer of 1998 (Mullin and Fulling, 2003). The previous survey also conducted line transect sampling; however, there was no correction for visibility bias in the associated abundance estimates. In addition, the previous survey used a uniform sampling design that also included areas over the continental shelf. As a result, there was relatively little effort expended over the shelf break in the 1998 survey (Mullin and Fulling, 2003). Given these differences in survey design and analysis, it is not surprising that there are significant differences in estimated abundance. The 1998 survey used the same observer configuration as the flying bridge team in the 2004 survey. Based upon estimated sighting probabilities for individual teams (ranging from 0.470 to 0.596), it is expected that the estimates from the 2004 survey would be approximately 2× higher than those from 1998. Accordingly, the abundance estimates from the 2004 survey are much higher than those from 1998 for Atlantic spotted dolphins (2004: 65,812 vs. 1998: 14,438), bottlenose dolphins (2004: 56,671 vs. 1998: 24,671), pilot whales (2004: 21,056 vs. 1998: 5,109), striped dolphins (2004: 45,185 vs. 1998: 10,225), and sperm whales (2004: 2,455 vs. 1998: 1,181; Mullin and Fulling, 2003). The increased level of survey effort along the shelf break during 2004 is also an important component of these differences as the majority of pilot whales, Atlantic spotted dolphins, and Atlantic bottlenose dolphins were seen in this stratum, which was undersampled in the 1998 survey (Table 1).

The majority of species observed in 2004 were also observed in 1998. However, the 2004 survey did not include sightings of minke whales (*Balaenoptera acutorostrata*), Clymene dolphins (*Stenella clymene*) or rough-toothed dolphins (*Steno bredanensis*). These species were rare in the 1998 survey with a total of four sightings. Interestingly, the 1998 survey did not observe short-beaked common dolphins, which was one of the more abundant species in the 2004 survey and included encounters of large groups. During summer months, common dolphins occur primarily to the north of the surveyed area along the shelf break near Georges Bank (Selzer and Payne, 1988), and it is therefore expected that the abundance of this species may vary strongly between years as a function of environmental variation.

Risso's dolphin abundance was similar between the two surveys with an estimated abundance of 8,207 (CV = 0.41) during the 2004 survey and 9,533 (CV = 0.50) during 1998 (Mullin and Fulling, 2003). The spatial distribution of Risso's dolphins was similar between the two surveys with sightings occurring throughout the survey range but primarily in the South Atlantic slope and Mid-Atlantic shelf break strata (Fig. 5). As with common dolphins, Risso's dolphins occur primarily along Georges Bank during summer months (Waring *et al.*, 2007), and hence the abundance in the Mid-Atlantic strata may vary. However, it does appear that there is a relatively constant, but lower density, occurrence of Risso's dolphins in the south Atlantic slope stratum.

A study of marine mammal habitats just to the north of the current survey area identified four species groups as a function of water temperature, bottom depth, bottom slope and surface front probability (Hamazaki, 2002). This study included most of the species evaluated in the current analysis. Interestingly, Hamazaki's (2002) grouping of 'Mid-Atlantic Shelf Species' included bottlenose dolphins, Risso's dolphins, pilot whales, and common dolphins. The first three species correspond to our Group II and include species that are associated with shelf break waters and a broad latitudinal distribution. Common dolphins, however, have a markedly different distribution compared to these species as they are associated with shallow, low salinity waters on the eastern side of the shelf break front along with the fin whales (included Hamazaki's Northern Atlantic shelf species group). This difference in groupings is primarily a function of the more southerly spatial range of our study that better covers the range of the Group II species. In addition, our study included salinity as an explanatory factor. The boundary between the Mid-Atlantic shelf water and the Mid-Atlantic slope water is better defined by a salinity gradient in surface waters as opposed to a temperature gradient (Gawarkiewicz *et al.*, 1996). Our Group I species were associated with this cool, lower salinity shelf water, and this reflects the fact that our survey covered the southward extension of their more northerly habitats during summer months. Spatially, this results in dramatic changes in cetacean habitats over relatively small spatial scales. On the shoreward side of the shelf-break front we observed concentrations of these more northerly species. However, on the seaward side of the front, over distances <30km, both the underlying hydrography and the cetacean community are markedly different.

The convergence of water masses, and associated increases in both the density and diversity of the cetacean communities is most apparent near Cape Hatteras. In this region, there is a convergence of Mid-Atlantic shelf water, South Atlantic shelf water, the Gulf Stream, and Mid-Atlantic slope waters (Gawarkiewicz *et al.*, 1996). As a result, there is an associated convergence of all four of our identified species groups within a small and extremely dynamic region. Within the area between Cape Hatteras and the mouth of the Chesapeake Bay (~37ºN latitude) near the shelf-break we observed 9 of our 11 identified species (only fin whales and *Kogia* sp. were not observed) in 138 groups of marine mammals totalling 5,648 individuals. In addition, this area included numerous large groups of dolphins including 9 groups of more than 100 Atlantic spotted dolphins and 5 groups of common dolphins ranging between 350 and more than 1,000 individuals. This dynamic hydrographic region and the associated high productivity clearly supports a very dense and rich cetacean fauna.

The habitat associations of species in this study are consistent with findings in other areas of the world's oceans. For example, Risso's dolphins were found to be associated with areas of high bathymetric slope in the northern Gulf of Mexico (Baumgartner, 1997; Baumgartner *et al.*, 2001) and in two areas of the Mediterranean Sea (Azellino *et al.*, 2008; Cañadas *et al.*, 2002). These authors note that Risso's dolphin and other species associated with strong bathymetric slope primarily feed upon squids. Similarly, pilot whales (both long-finned and short-finned) are typically grouped with Risso's dolphins and other shelf-break associated species, as they are in our study, again presumably associated with a preference for squid prey.

The inclusion of bottlenose dolphins in this group is interesting as it suggests that perhaps they are also primarily squid predators in this habitat. The bottlenose dolphins encountered during this survey are certainly of the more pelagic 'offshore' morphotype as opposed to the 'coastal' morphotype that occurs in near shore continental shelf and estuarine waters (Torres *et al.*, 2003). These offshore animals appear to be more adapted to longer, deeper duration dives than coastal animals based upon hemoglobin profiles (Hersh and Duffield, 1990). This is consistent with the characterisation of the deep diving shelf-break associated species that consume primarily squids in pelagic habitats. Most diet studies characterise bottlenose dolphins as primarily piscivorous (e.g. Barros and Odell, 1990; Kenny *et al.*, 1995), but many of these previous studies are from animals inhabiting coastal habitats. The remaining abundant delphinids including common dolphins, Atlantic spotted dolphins and striped dolphins, are thought to be opportunistic piscivores with a diverse diet including small mesopelagic and pelagic fishes (Kenny *et al.*, 1995; Pauly *et al.*, 1998; Young and Cockcroft, 1994).

Interestingly, in some studies (e.g. Baumgartner *et al.*, 2001; Cañadas *et al.*, 2002; Davis *et al.*, 1998) sperm whales are also grouped with the shelf-break species, presumably associated with the similar dependence on squid prey. However, in our study, and similarly in Hamazaki (2002), sperm whale habitats were not as strongly associated with the shelf break areas and were spread more broadly across the inner continental slope. This suggests segregation of habitat, and perhaps prey resources, among the teuthophagic species in this region. Alternatively, sperm whales may be exploiting less persistent areas of high productivity associated with Gulf Stream eddies and rings. Similar associations of sperm whales with mesoscale physical features have been observed with Loop current eddies in the northern Gulf of Mexico (Biggs *et al.*, 2005).

The 'cryptic species', beaked whales and *Kogia* sp., present a challenge for assessment using visual surveys (Barlow, 1999). Both taxa have long dive intervals and relatively short surface intervals and thus have limited availability for observation. Likewise, both groups are difficult to see at the surface and generally dive before they can be approached by the vessel. Hence, sighting conditions and other factors strongly influence the number and types of these species encountered. It is likely that our characterisations of their spatial distribution and habitat preferences are incomplete. For example, during the summer 1998 survey, there was a greater number of *Kogia* sp. sightings in the southern offshore portion of the survey area (Mullin and Fulling, 2003), and *Kogia* are regularly seen stranded along the southeastern US coastline (Waring *et al.*, 2007).

The majority of beaked whales encountered in this survey were in the southern portion of the survey range. We had very few beaked whale sightings north of Cape Hatteras, and those occurred only in deeper water. Beaked whales are well documented to occur north of our survey area along the southern flank of Georges Bank and along the shelf break off the coast of southern New England (Kenny and Winn, 1987; Waring *et al.*, 2001). However, in Waring *et al.* (2001) there was a lack of sightings along the mid-Atlantic shelf break south of approximately 38ºN latitude, which is the northern extent of our survey. These data do suggest that there is a discontinuity in the spatial distribution of beaked whales in the mid-Atlantic region which may correspond to a faunal break in the distribution of this diverse species group which potentially includes four species of the genus *Mesoplodon* along with *Ziphius cavirostris* (Cuvier's beaked whale; Waring *et al.*, 2007).

This study demonstrates that groups of cetaceans are closely associated with distinct hydrographic regimes over broad spatial scales. The separation between continental shelf and slope water masses represent transitions in the underlying physical characteristics of the water column, changes in the composition and density of the prey field, and hence changes in the composition of the cetacean community. The convergence of water masses along the shelf-break in the mid-Atlantic and at Cape Hatteras results in localised increases in the diversity of the cetacean community. The increased surface water primary and secondary production at these boundaries results in very high densities of cetaceans. Evaluating finer scale physical variability and the associated variation in the species composition and density of cetacean species will further improve the understanding of the habitat associations, partitioning of prey resources, and spatial distribution of cetacean communities.

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