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SPATIOTEMPORAL PREDICTION MODELS OF CETACEAN HABITATS IN THE MID-WESTERN NORTH ATLANTIC OCEAN (FROM CAPE HATTERAS, NORTH CAROLINA, U.S.A. TO NOVA SCOTIA, CANADA)

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ABSTRACT

Habitat prediction models were developed for 13 cetacean species of the mid-western North Atlantic Ocean: beaked whale, fin whale, humpback whale, minke whale, pilot whale, sperm whale, bottlenose dolphin, common dolphin, Risso's dolphin, spotted dolphin, whitesided dolphin, and harbor porpoise. Using the multiple logistic regression, sightings of cetaceans during the 1990–1996 summer (June–September) surveys were modeled with oceanographic (sea surface temperature, monthly probability of front occurrence) and topographic (depth, slope) variables for the same period. Predicted habitat maps for June and August were created for each species using a Geographical Information System. The predicted habitat locations matched with current and historic cetacean sighting locations. The model also predicted habitat shifts for some species associated with oceanographic changes. The correct classification rate of the prediction models with 1997–1998 summer survey data ranged from 44% to 70%, of which most of the misclassifications were caused by false positives (*i.e.*, absence of sightings at locations where the models predicted).

Key words: cetaceans, habitat prediction model, Geographical Information System, western North Atlantic Ocean.

Identification of habitats plays a significant role in the management and conservation of terrestrial species (*e.g.*, Gap Analysis Program [GAP], Jennings 2000). Products of these efforts are incorporated into the Geographical Information System (GIS) to produce layers of spatial information on location and extent

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of habitat of the species. However, in marine systems the same effort is still at an emergent stage (*e.g.*, Living Marine Resources Information Systems [LMRIS], US Navy 1999). Past efforts to identify cetacean habitats include: plotting cetacean sighting locations from surveys (*e.g.*, Silber *et al.* 1994, Jefferson and Schiro 1997, Ballance and Pitman 1998, Kingsley and Reeves 1998, Waring *et al.* 1999), encircling entire areas of cetacean sighting locations (Au and Perryman 1985), and selecting areas of high cetacean sighting frequency, density, or biomass (*e.g.*, Kenney and Winn 1986, Hooker *et al.* 1999). While these methods can identify cetacean habitats where surveys are conducted, they cannot identify habitats in unsurveyed areas or predict spatiotemporal habitat shifts associated with oceanic changes.

To address these deficiencies several authors have constructed cetacean habitat prediction models (*e.g.,* Reilly 1990, Fiedler and Reilly 1994, Reilly and Fiedler 1994, Moses and Finn 1997, Hedley *et al.* 1999, Forney 2000, Gregr and Trites 2001, Waring *et al.* 2001). These models are based on statistical regression in which presence or abundance of cetaceans is regressed with a set of predictor variables, such as oceanographic, topographic, and biological variables. The models are also incorporated into a GIS to show location and extent of (potential) cetacean habitats. Applications of these models have been discussed; however, many prediction models are limited to only a few species (Reilly 1990, Fiedler and Reilly 1994, Reilly and Fiedler 1994, Moses and Finn 1997, Forney 2000, Waring *et al.* 2001), and a few have examined the validity of the models (*e.g.,* Hedley *et al.* 1999, Gregr and Trites 2001).

Using cetacean data in the mid-western North Atlantic Ocean as a case study, I developed cetacean habitat prediction models. Specifically, this study classified common cetaceans in this area by their habitats, developed habitat prediction models for each species, and tested the predictive power of these models using survey data.

Methods

Data Sources

Cetacean survey sighting data—Cetacean sighting data were collected by staff of the Protected Species Branch of the National Marine Fisheries Service (NMFS) at the Northeast Fisheries Science Center (NEFSC), Woods Hole, MA. From 1990 to 1998, 12 line-transect shipboard surveys were conducted in the early June to early September season. Except for the 1997 survey along the sea mounts region, most of the surveys were concentrated along the continental shelf edge and in the Gulf of Maine/Bay of Fundy area (Fig. 1). Primary objective of the surveys along the continental shelf edge was to estimate abundance of all cetaceans in this region, while those in the Gulf of Maine/Bay of Fundy area were primarily to estimate abundance of harbor porpoise (*Phocoena phocoena*). In all the surveys, the survey track-lines were constructed to provide maximum and unbiased coverage of the surveyed area.[2] Generally, the lower mid-Atlantic (35°N–40°N) was surveyed in June and July, the upper mid-Atlantic (40°N–43°N) and the Gulf of Maine/Bay of Fundy were surveyed in August and early September.

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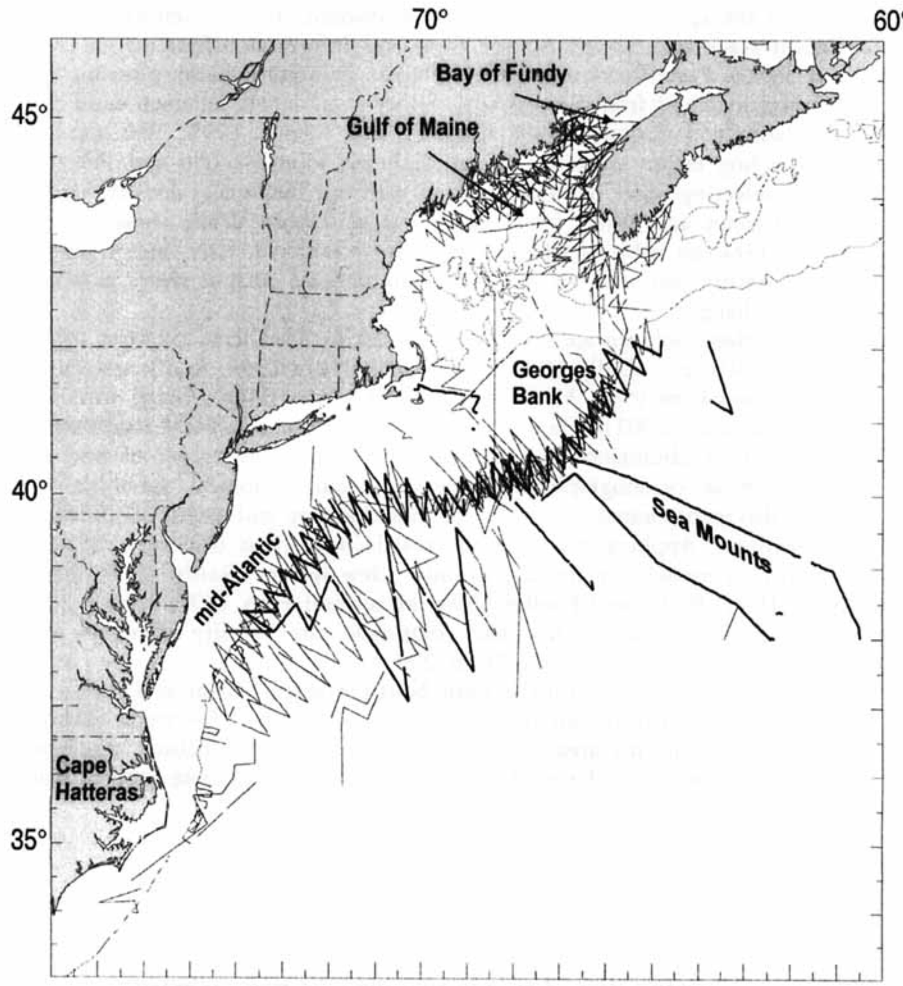


Figure 1. Sighting survey track lines during 1990–1998. Bold lines show track lines of 1997 (along sea-mount region) and 1998 (along continental shelf edge region) surveys. The 200 m bathymetry line represents continental shelf edge.

The sighting surveys were conducted along predetermined track lines at an average speed of 18.5 km/h (10 kn) from 0600 to 1800 (no observations from 1200 to 1300) when Beaufort sea state conditions were below five. Presence of cetaceans was observed with the naked eye, and 25 × 150, or 20 × 60 binoculars, from the flying bridge and crow's nest, 8 and 14 m above water line, respectively. When cetaceans were sighted, the following data were recorded: (1) species; (2) maximum, minimum, and best estimate of group size; (3) estimated distance, radial angle, and swimming direction of the animals relative to the ship; and (4) date, time, latitude, and longitude of the ship at the time of sighting.

Oceanographic and topographic data—To construct cetacean habitat prediction models, data for predictor variables must be available for the entire mid-western North Atlantic region during the sighting survey periods. Variables that met the criteria were sea surface temperature (SST), monthly front probability, and ocean depth and slope.

Sea surface temperature (SST)—Weekly averaged SST data were obtained from the Physical Oceanography Distributed Active Archive Center (PODAAC), a component of the Earth Observing System Data and Information System (EOSDIS) for NASA's Earth Observing System (EOS) project. The Multi-Channel Sea Surface Temperature (MCSST) data were derived from the 5-channel Advanced Very High Resolution Radiometers (AVHRR) on board the NOAA-7, -9, -11, and -14 polar orbiting satellites. The data were provided on an equal-angle grid of 2,048 pixels longitude by 1,024 pixels latitude that is nominally referred to as 18 × 18 km resolution.

Monthly front probability—Monthly front probability data were obtained from the Department of Oceanography, University of Rhode Island (see Acknowledgments). These were derived from SST data obtained from the National Geophysical Data Center (NGDC) of NOAA. Each year's collection of SST data was declouded by an automated cloud detection algorithm (Ullman and Cornillon 1999), and then processed by a multi-image edge detection algorithm (Cayula and Cornillon 1995) to detect the presence of a front at each pixel (4.8 × 4.8 km). The monthly probability of front occurrence at each pixel was calculated as a percent of the number of images with fronts divided by the total number of available images per month. Because the de-clouding and edge detection processes require a full year of SST data (Cayula and Cornillon 1995, Ullman and Cornillon 1999), monthly front probability data were available only for 1990–1996 at the time of the study.

Ocean topography: depth and slope—Ocean-bottom depth data were obtained from the NGDC, generated from a digital database of land and sea-floor elevations on a 5 × 5 min (*ca.* 9 × 9 km) grid. Slope of the ocean floor (0°–90°) was calculated using the SLOPE command of the Arc/Info® Grid module.

Data integration—All the data were integrated using Arc/Info®. The entire mid-western North Atlantic Ocean was divided into 10-minute square (*ca.* 18.5 × 18.5 km) grids that are conventionally used as a standard fishery management unit by the NMFS NEFSC.[3] Each survey track line was segmented and identified by each grid square it crossed through (*i.e.,* "effort grids"). Topographic and oceanographic data of the closest survey date (<7 d) were collected, using the LATTICESPOT command for the center of the each effort grid square. Each grid was also associated with cetacean sighting data using the IDENTITY command.

Data Analyses

Classification of cetaceans by habitat type—Before a prediction model was constructed for each species, each species was classified by habitat type using standardized cluster analysis, with the average linkage method applied to mean value of the SST, monthly front probability, depth, and slope where each species had

[3] Personal communication with Daniel Sheehan, NMFS Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

been sighted. Within each classified species group, analysis of valiance (ANOVA) with the least square distance mean separation method was used to characterize habitat of each species and to identify variables that separate habitats of various species within each habitat type.

Construction of the cetacean habitat prediction model—A multiple logistic regression was used to construct the cetacean habitat prediction model. Logistic regression predicts probability of presence of each species in each grid square, instead of its abundance/density. For the prediction of cetacean abundance/density, numbers of each species sighted in each grid square need to be corrected by efforts, survey design (*e.g.*, choice of survey track lines, target or non-target species survey, height of survey platform, choice of binoculars), and survey condition (*e.g.*, Beaufort sea states) (Hedley *et al.* 1999). These corrections are not necessary for logistic regression models that use presence/absence data. Each effort grid square was classified as either 1 (cetacean sighting) or 0 (absence of sighting). Probability of the presence of the species was calculated as:

$$p = e^y/(1 + e^y) \quad y = a_0 + a_1x_1 + a_2x_2 + \ldots a_ix_i$$

where a_i was the regression coefficient, and x_i was the predictor variable (SST, monthly front probability, depth, slope, and quadratic forms and interaction terms of these variables).

For selection of predictor variables, the forward and backward stepwise selection method was applied. Habitat prediction models were constructed using only the 1990–1996 survey data, so that the 1997–1998 survey data could be used to evaluate the accuracy of the models' predictions.

Evaluation of prediction models—Predictive power of the models was evaluated by cross-validating the model prediction of presence-absence of each species in each effort grid square with those of the 1997–1998 surveys. For each effort grid square, the prediction models calculated probability of presence of each species that was classified as either present or absent based on a threshold value, the observed sighting probability of the 1990−1996 surveys for each species, and the number of sighting grids divided by the total number of effort grids. Correct classification rate of the model prediction was calculated with actual sighting data.

Since monthly front probability data were not available for 1997–1998, the predictive power of the models could not be evaluated when the monthly front probability was included. For such cases, alternative prediction models without monthly front probability were constructed and their predictive power was evaluated. Because the alternative models were less fit than the original models, evaluation of the alternative models provides minimum predictive power compared with the original models.

Further, because 1997–1998 surveys were conducted along the mid-Atlantic shelf and sea mounts regions, sighting data were not available for several species that are sighted mostly in the Gulf of Maine/Bay of Fundy area (harbor porpoises, whitesided dolphins, humpback whales, minke whales). Consequently, predictive power of the models for those species was not evaluated.

Identification of cetacean habitats and prediction of spatiotemporal habitat shifts—The models were incorporated into GIS maps projecting probability distribution of cetacean presence; from this, cetacean habitats were identified. The predicted habitat maps were based on oceanographic conditions of 1 August 1995 because

SST of that date showed the clearest and the most typical oceanographic conditions of any August.[4] As a reference, August sighting locations of each species (<1986, 1990–1996, and 1997–1998) were plotted on the prediction maps. The majority of the historic (<1986) sighting records were from surveys of the Cetacean and Turtle Assessment Program (CETAP) (CETAP 1982). CETAP conducted surveys monthly in the entire mid-western North Atlantic region during 1978 and 1982. Although consistency or inconsistency of the predicted habitat areas with sighting locations does not necessarily indicate a predictive power of the models, these sighting locations could serve as references for power of the models to predict in unsurveyed areas.

In the mid-western North Atlantic, oceanographic conditions often change during summer. From June to August sea-surface temperature increases 5°–10°C along with the northward shift of the Gulf Stream. This may cause a northward shift of habitat locations for some species. To examine whether the models could predict these potential spatiotemporal shifts of cetacean habitats, prediction maps for June were constructed using the oceanographic conditions of 17 June 1991 because SST of that date showed the clearest and the most typical oceanographic conditions any June.[4] Because no comprehensive multimonths survey has been conducted since 1982 (CETAP 1982), quantitative assessment of this habit was not possible. Instead, locations of predicted habitats in these maps were visually compared with those of August. When predicted habitat areas were significantly different in a visually noticeable manner, it was assumed that the species shifted its habitat.

Examination of spatial-scale effects on prediction models—Because the choice of the 10-minute square grid was arbitrary, sensitivity analyses were conducted on the effects of scaling, using six scales: 4-km squares (4 × 4 km), 8-, 16-, 32-, 48-, and 96-km squares (96 × 96 km). The 4-km square approximates the maximum distance between the ship and observed cetaceans, and the 96-km square approximates the maximum daily survey effort. For each species and scale, a prediction model was constructed and its predictive power was evaluated in the same way described above. In this analysis, instead of weekly averaged SST data, full resolution (1.2 × 1.2 km) five-day warmest SST composite data were used as the predictor variable (see Waring *et al.* 2001).

RESULTS

Over the nine-year survey period, the following 13 species each had more than 30 sighting grid cells: bottlenose dolphin (*Tursiops truncatus*, coastal and offshore types),[5] common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*), spotted dolphin (Atlantic: *Stenella frontalis*, and pantropical: *S. attenuata*),[5] striped dolphin (*S. coeruleoalba*), whitesided dolphin (*Lagenorhynchus acutus*), harbor porpoise (*Phocoena phocoena*), beaked whale (*Mesoplodon spp.*, and *Ziphius cavirostris*),[5] fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), minke whale (*B. acutorostrata*), pilot whale (longfinned: *Globicephala melas*, and shortfinned: *G. macrorhynchus*),[5] and sperm whale (*Physeter macrocephalus*).

[4] Personal communication with Grayson Wood, NMFS Northeast Fisheries Science Center, Narragansett Laboratory, 28 Tarzwell Drive, Narragansett, RI 02882.

[5] These species were not distinguished in the sighting surveys.

Table 1. Mean (± SD) of environmental variables associated with the cetacean sightings.

Species	Temperature (°C)	Front probability (%)	Depth (m)	Slope (°)
1. Mid-Atlantic species				
1a. Mid-Atlantic offshore species				
Beaked whale	21.1 ± 5.4[a]	5.6 ± 5.5[a]	−1,734 ± 1,014[a]	2.6 ± 1.9[a]
Sperm whale	22.5 ± 4.8[a]	6.5 ± 4.9[a]	−2,011 ± 1,023[a]	1.9 ± 1.5[b]
Striped dolphin	21.9 ± 4.8[a]	6.2 ± 6.7[a]	−1,899 ± 963[a]	2.0 ± 1.6[b]
Spotted dolphin	25.0 ± 3.0[b]	5.6 ± 3.1[a]	−2,068 ± 1,061[a]	1.3 ± 1.2[c]
1b. Mid-Atlantic shelf species				
Bottlenose dolphin	21.7 ± 4.0[a]	6.3 ± 4.9[a]	−972 ± 925[a]	1.9 ± 1.6[a]
Risso's dolphin	22.5 ± 3.2[a]	6.4 ± 4.7[a]	−1,257 ± 1,066[b]	1.9 ± 1.5[a]
Common dolphin	18.0 ± 5.7[c]	7.4 ± 6.0[a]	−931 ± 795[a]	2.4 ± 1.9[b]
Pilot whale	19.6 ± 5.7[b]	7.3 ± 7.4[a]	−1,197 ± 917[b]	2.4 ± 1.9[b]
2. Northern Atlantic species				
2a. Northern Atlantic nearshore species				
Harbor porpoise	14.0 ± 2.2[a]	10.0 ± 8.0[a]	−85 ± 46[a]	0.2 ± 0.1[a]
Minke whale	14.7 ± 3.6[b]	6.3 ± 5.2[a]	−215 ± 474[a]	0.4 ± 0.7[a]
Whitesided dolphin	13.2 ± 3.1[a]	6.5 ± 5.7[a]	−439 ± 695[b]	0.9 ± 1.6[b]
2b. Northern Atlantic shelf species				
Fin whale	18.2 ± 3.8[a]	6.3 ± 4.9[a]	−337 ± 449[a]	1.1 ± 1.3[a]
Humpback whale	17.2 ± 3.4[a]	6.3 ± 3.2[a]	−261 ± 465[a]	0.7 ± 1.1[a]

Letters indicate mean groups ($P < 0.05$) by Duncan's multiple comparison tests.

Classification of cetaceans by habitat use—The 13 cetacean species were classified into two major habitat groups: (1) pelagic Atlantic species, and (2) northern Atlantic species (Normalized Root Mean Square Distance: NRMSD = 1.0) and four subgroups (NRMSD = 0.7): (1a) mid-Atlantic offshore species (beaked whale, sperm whale, striped dolphin, and spotted dolphin), (1b) mid-Atlantic shelf species (bottlenose dolphin, Risso's dolphin, common dolphin, and pilot whale), (2a) northern Atlantic nearshore species (harbor porpoise, minke whale, whitesided dolphin), and (2b) northern Atlantic shelf species (fin whale, humpback whale) (Table 1, Fig. 2).

Mid-Atlantic offshore species were sighted in waters of SST 21°–26°C over depths greater than 1,500 m, offshore of the shelf/slope and sea mounts regions (Table 1, Fig. 3). Habitats of the four species were separated by temperature and slope (Table 1). Spotted dolphins were sighted in the warmest waters over the mildest slopes, whereas beaked whales occurred in the water over the steepest slopes. Sperm whales and striped dolphins were sighted in waters between these two.

Mid-Atlantic shelf species were sighted in waters of SST 18°–23°C over depths of less than 1,500 m in the entire continental shelf, offshore, and sea mounts regions (Table 1, Fig. 4). Habitats of the four species were separated by temperature and depth (Table 1): bottlenose dolphins in warm and shallow water, Risso's dolphins in warm and deep water, common dolphins in cool and shallow water, and pilot whales in cool and deep water.

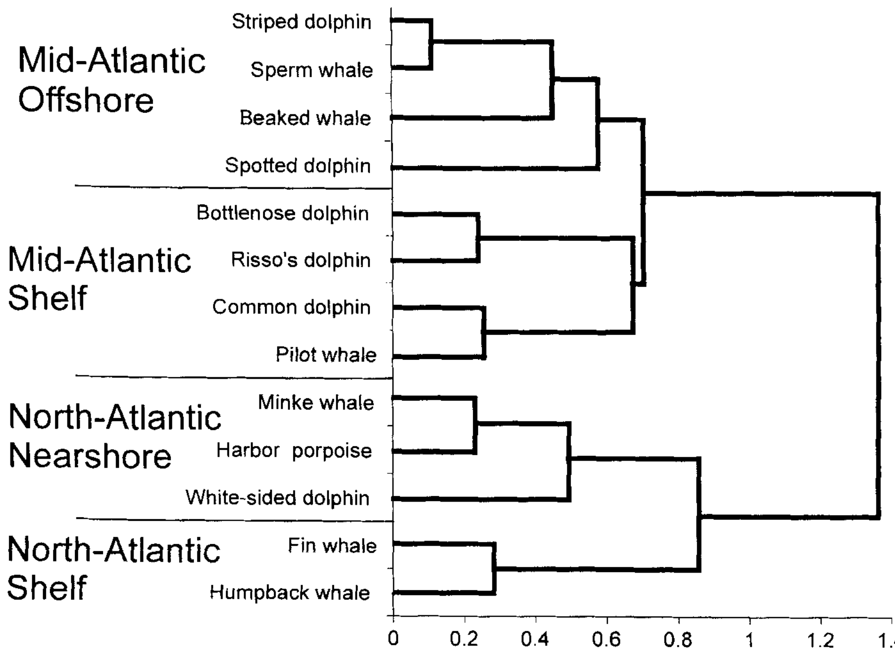


Figure 2. Cluster analysis of cetacean fauna in western North Atlantic Ocean.

Northern Atlantic nearshore species were sighted in waters of SST 10°–15°C over depths less than 500 m in the entire northern nearshore and Georges Bank regions (Table 1, Fig. 5). Harbor porpoises were sighted in the shallowest water, whereas whitesided dolphins tended to be sighted in waters of 400–500 m depth (Table 1).

Northern Atlantic shelf species were sighted in waters of SST 17°–18°C over depths less than 400 m in the northern coastal side of the mid-Atlantic shelf regions (Table 1, Fig. 6). Although predicted habitat of fin whales was geographically larger than that of humpback whales, no difference was found between the oceanographic and topographic variables preferred by the two species (Table 1, Fig. 6).

Cetacean Habitat Prediction Model

Sighting probability of each species was low, ranging from 2% to 11%. Despite this low sighting probability, logistic regression models were significant for all species (Chi-square test: $P < 0.05$) and were a good fit to the data (1990–1996) (lack of fit test: $P > 0.05$) (Table 2). The correct classification rate of the model with 1997–1998 survey data ranged from 44% to 70%. This trend was the same across the six scales. From 4- to 96-km squares, sighting probability increased about 10 times while the number of effort grids decreased to about one-twentieth as many (Table 3); however, the correct classification rate for each species remained relatively the same across the scales (Table 4). Predictor variables included in the models for each species differed across the scales. Regardless

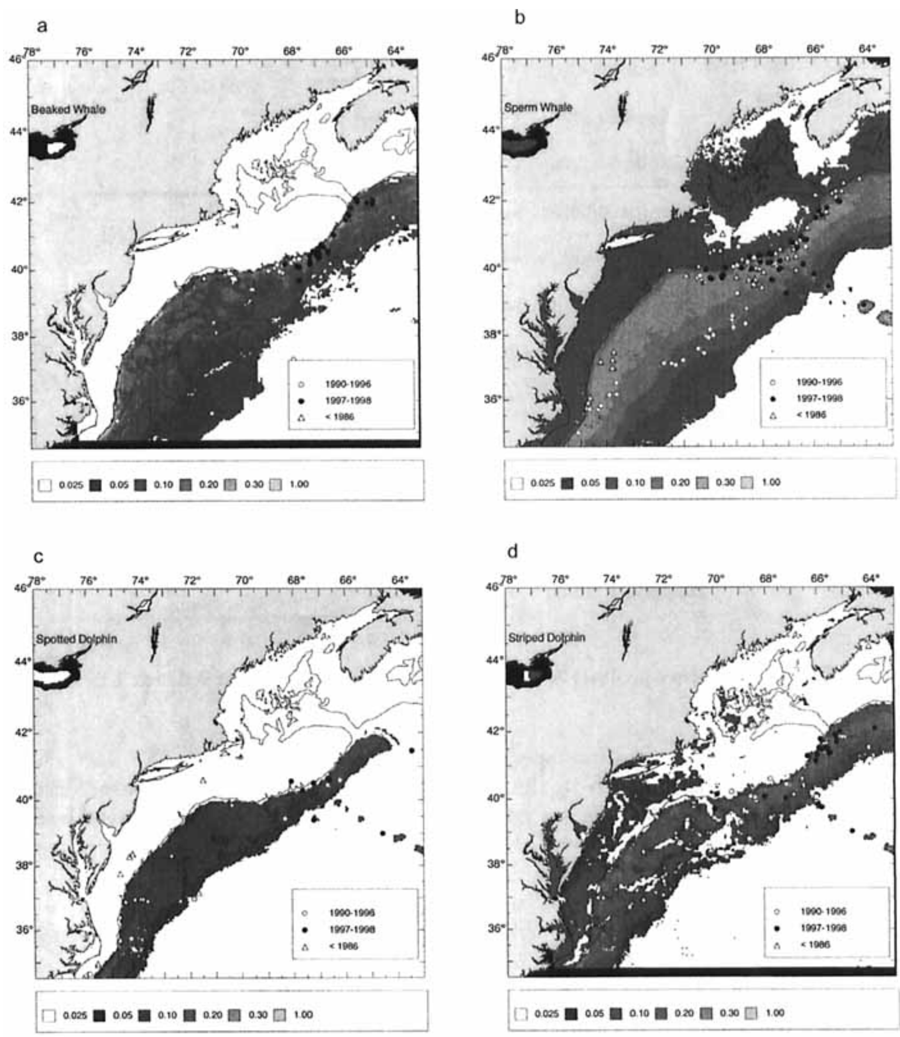


Figure 3. Predicted habitat areas and sighting locations (August) of mid-Atlantic offshore species: (a) beaked whales, (b) sperm whales, (c) spotted dolphins, and (d) striped dolphins. Predicted habitat distribution is based on oceanic conditions of 1 August 1995. Number indicates probability of occurrence of animals.

of the scale, most of the incorrect classifications were caused by false positives (*i.e.*, absence of sightings in grids where predicted present). Of the predicted-present grid squares, the percentage of actual sighting was less than 25%. These false positives were also apparent when areas of survey track line and locations of cetacean sightings were compared with predicted habitat areas (*e.g.*, areas of sighting probability > 0.05). Although the models predicted many of the surveyed areas as cetacean habitat, cetaceans were not sighted at every segment of each track line (Fig. 1, 3, 4, 5, 6).

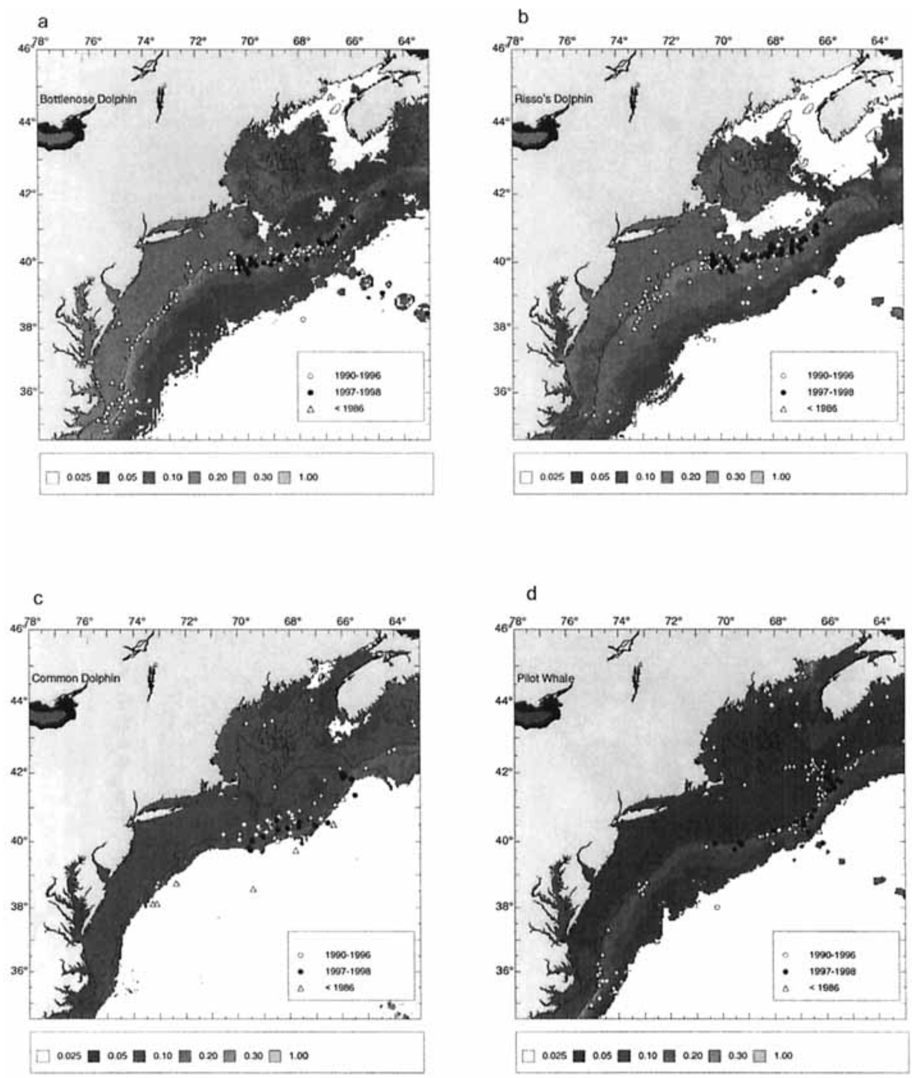


Figure 4. Predicted habitat areas and sighting locations (August) of mid-Atlantic shelf species: (a) bottlenose dolphins, (b) Risso's dolphins, (c) common dolphins, and (d) pilot whales.

For identification of potential habitats in unsurveyed areas, the models correctly predicted sea mounts areas as cetacean habitats; this was confirmed in the 1997 sighting survey. The model also predicted potential offshore habitat of common dolphin in June (Fig. 7). However, some inconsistencies were found between prediction models and sightings. Georges Bank was predicted as a habitat of northern species; however, no sightings were recorded in this area (Fig. 5). The models did not predict sightings of spotted dolphin and bottlenose dolphin

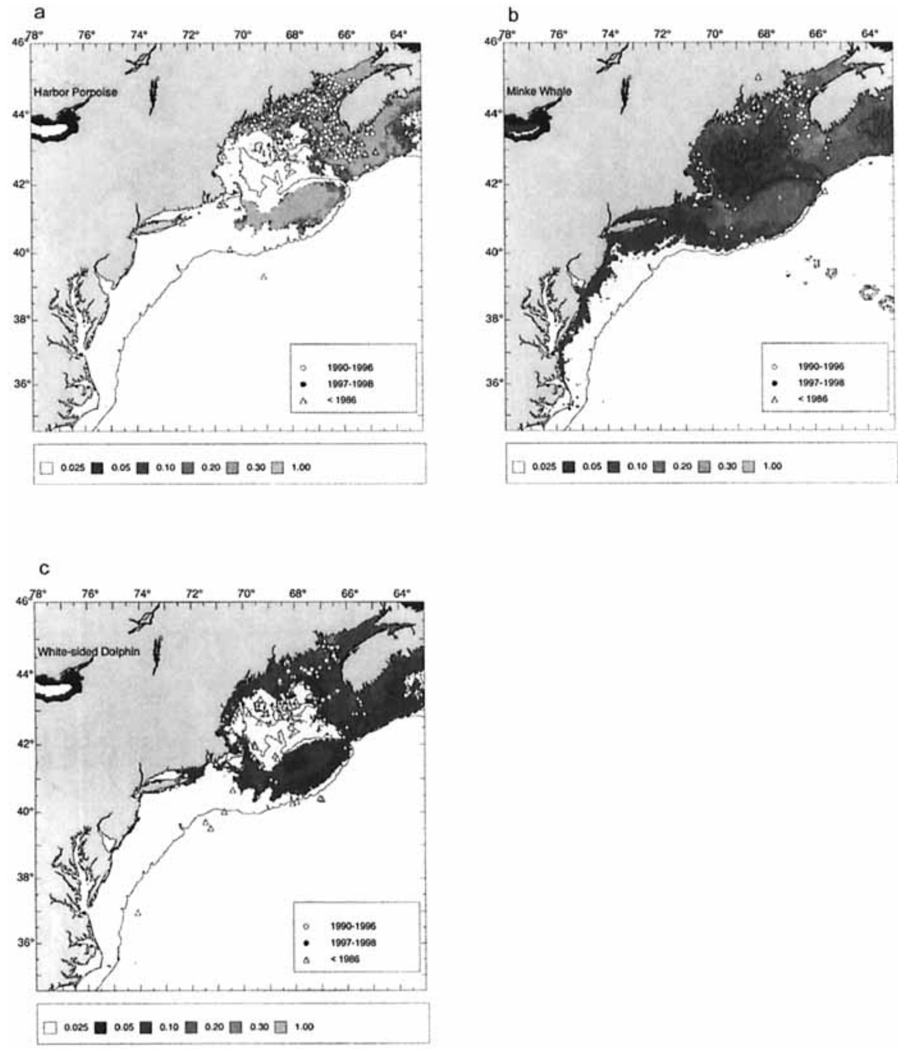


Figure 5. Predicted habitat areas and sighting locations (August) of northern Atlantic nearshore species: (a) harbor porpoises, (b) minke whales, and (c) whitesided dolphins.

along the coastal region (Fig. 3c, 4a) and whitesided dolphin in the mid-Atlantic shelf region (Fig. 5c) where they have been seen.

Effects of Oceanography on Cetacean Habitats

Comparison of maps of predicted habitats for June and August showed seasonal habitat shifts for common dolphins, spotted dolphins, whitesided dolphins, humpback whales, and harbor porpoises. These were consistent with the shifts of sighting locations recorded by CETAP monthly region-wide surveys (<1986 in Fig. 3, 4, 5, 6, 7). Compared with predicted habitats for June, August habitats

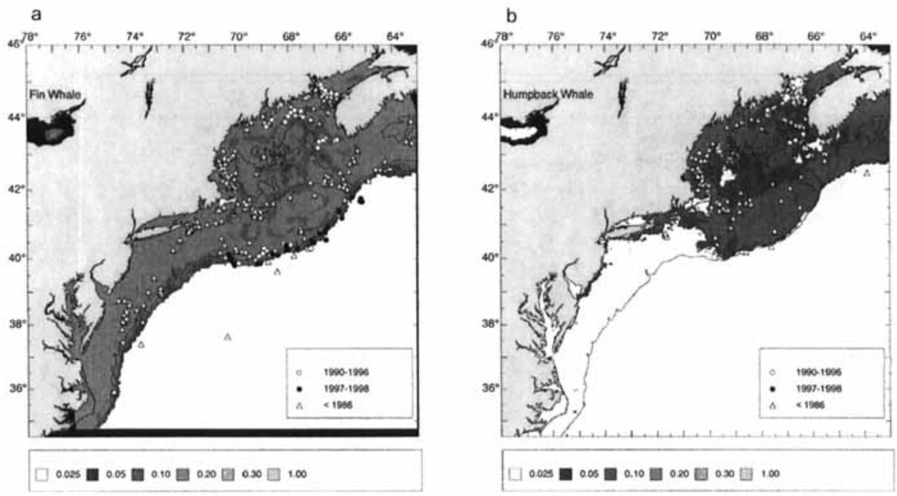


Figure 6. Predicted habitat areas and sighting locations (August) of northern Atlantic shelf species: (a) fin whales and (b) humpback whales.

shifted or expanded north. Habitat of common dolphins shifted from the southern offshore range of the continental shelf to surround Nova Scotia (*cf.* Fig. 7a, 4c). Habitat of whitesided dolphins contracted from almost to Cape Hatteras in June, to only as far south as Massachusetts in August (*cf.* Fig. 7b, 5c). Humpback whale distribution, which also extended south to Cape Hatteras in June, but at that time only as far north as Labrador, shifted most of its habitat north, to the eastern end of Long Island north to all around Nova Scotia (*cf.* Fig. 7d, 6b). Harbor porpoises shifted most of their June predicted habitat range of southern New York to northern Labrador, to south off Labrador and all around Nova Scotia in August (*cf.* Fig. 7c, 5a). Spotted dolphin predicted habitat, confined to the southern half of the mid-western Atlantic in June, expanded north to occupy the entire mid-western Atlantic in August (*cf.* Fig. 7e, 3d).

Discussion

Results of this study clearly demonstrate that cetaceans can be classified by habitats, and that the habitat prediction modeling has potential for not only identifying habitats, but also to predict shifts of habitats associated with oceanographic changes. Nevertheless, this approach also has some constraints.

Potential Application of Prediction Models

The major advantage of a prediction model is its capability to identify potential habitats in unsurveyed areas and track habitat shifts along with oceanographic changes (Reilly 1990, Fiedler and Reilly 1994, Reilly and Fiedler 1994, Moses and Finn 1997). The predicted potential habitats were sea mounts areas for pelagic Atlantic species and June offshore areas for common dolphins (Fig. 3, 4, 7a). Sea mounts have been suspected as potential cetacean habitats; this

Table 2. Results of regression analysis for each species based on 1990–1996 sighting data. All regression and selected predictor variables were significant ($P < 0.05$).

	Predictor variables[a]	SP[b]	LF[c]	CR[d]
1. Mid-Atlantic species				
1a. Mid-Atlantic offshore species				
Beaked whale	$-D$, $-D^2$, S, $-F$, $D \times S$	0.054	0.372	0.53[e]
Sperm whale	T, $-D$, $-D^2$	0.110	0.143	0.54
Striped dolphin	T, $-D$, $-D^2$, F, $-T \times F$, $T \times D$	0.056	0.711	0.58[e]
Spotted dolphin	T, $-D$, $-D^2$	0.022	0.459	0.54
1b. Mid-Atlantic shelf species				
Bottlenose dolphin	T, $-T^2$, D, S, $-S^2$	0.081	0.096	0.64
Risso's dolphin	T, $-T^2$, $-D^2$, $-T \times D$	0.076	0.289	0.44
Common dolphin	T, $-T^2$, $-D$, S, $T \times D$	0.072	0.232	0.68
Pilot whale	$-T$, T^2, $-D$, $-D^2$, S	0.066	0.399	0.66
2. Northern Atlantic species				
2a. Northern Atlantic nearshore species				
Harbor porpoise	T, $-T^2$, D, $-S$, $T \times D$	0.072	0.443	N/A
Minke whale	$-T$, D, $-S$, $-D \times S$	0.039	0.569	N/A
Whitesided dolphin	$-T$, $-D$, $T \times D$	0.021	0.271	N/A
2b. Northern Atlantic shelf species				
Fin whale	$-F$, D	0.066	0.181	0.70[e]
Humpback whale	T, $-T^2$, D, $-T \times D$	0.020	0.276	N/A

[a] T: temperature, D: depth, S: slope, F: monthly front probability (All parameters were significant; Chi-square test $P < 0.05$).
[b] SP: Observed mean sighting probability (number of sighting cells/total number of effort cells).
[c] LF: Lack of fit test; Comparison of predicted *vs.* observed ($P < 0.05$: poor fit; $P > 0.05$: good fit).
[d] CR: Rate of correct classification between the regression model prediction and 1997–1998 sighting survey data.
[e] Based on alternative prediction model.
N/A: Not available because sighting record was less than 3.

prompted an exploratory survey in these areas in 1997. Common dolphin was believed to reside in outer continental shelf waters from winter to spring (CETAP 1982). Predicted habitat shifts of some species (common dolphins, spotted dolphins, whitesided dolphins, humpback whales, and harbor porpoises) was also consistent with ecology of these species in this region (see Waring *et al.* 1999 for review). Although other species are known to migrate seasonally (*e.g.*, minke whales, pilot whales, sperm whales) (CETAP 1982, Waring *et al.* 1999), their migration was not predicted because they remain in the same area through the summer months.

Prediction models can show gradients of abundance or probability of cetacean presence (Fig. 3, 4, 5, 6, 7), which can be used to improve cetacean abundance estimations (Reilly 1990, Fiedler and Reilly 1994, Reilly and Fiedler 1994, Forney 2000). For instance, the survey areas can be stratified based on prediction models (Reilly and Fiedler 1994), or the models can be used to factor out the effects of oceanographic changes or seasonal habitat shifts on abundance estimates

Table 3. Comparisons of sample size and mean sighting probability for each species at 7 scales.

	4k	8k	16k	32k	48k	64k	96k
Total effort grid cells	12,543	6,146	2,974	1,487	1,043	812	625
1a. Mid-Atlantic offshore species							
Beaked whale	0.013	0.023	0.042	0.072	0.092	0.110	0.131
Sperm whale	0.028	0.048	0.077	0.126	0.157	0.184	0.229
Striped dolphin	0.016	0.029	0.049	0.080	0.098	0.123	0.142
Spotted dolphin	0.005	0.010	0.017	0.033	0.045	0.058	0.069
1b. Mid-Atlantic shelf species							
Bottlenose dolphin	0.020	0.034	0.062	0.103	0.127	0.150	0.186
Risso's dolphin	0.023	0.038	0.064	0.099	0.120	0.138	0.160
Common dolphin	0.016	0.028	0.050	0.085	0.106	0.129	0.158
Pilot whale	0.017	0.030	0.049	0.079	0.095	0.123	0.146
2a. Northern Atlantic nearshore species							
Harbor porpoise	0.111	0.144	0.180	0.213	0.220	0.238	0.221
Minke whale	0.008	0.014	0.015	0.039	0.051	0.059	0.066
Whitesided dolphin	0.004	0.008	0.015	0.022	0.034	0.034	0.048
2b. Northern Atlantic shelf species							
Fin whale	0.015	0.026	0.046	0.078	0.094	0.121	0.138
Humpback whale	0.005	0.009	0.013	0.023	0.030	0.039	0.045

(Reilly 1990, Fiedler and Reilly 1994, Forney 2000). These adjustments would provide more accurate abundance estimates, and thus population trends could be properly assessed (Forney 2000).

Predicted areas of high cetacean abundance/presence could be designated as cetacean conservation and management priority areas (*e.g.*, Hooker *et al.* 1999). In many cases, location and extent of a conservation/management zone (*e.g.*, marine protection area) is permanently fixed once it is designated. However, since many cetaceans are highly mobile and migratory, they are likely to reside in those zones only temporarily. Further, areas of high cetacean abundance/presence could shift outside the designated zone because of oceanographic changes. To accommodate non-stationary cetacean habitats, it could be more effective to shift location and extent of these zones as necessary, based on habitat prediction models. This method is under development for the protection of North Atlantic right whales (*Eubalaena glacialis*) in the western North Atlantic near the US coast.[6]

Finally, prediction models can shed insights on the ecology of cetaceans. For instance, prediction models were used to study habitat segregation of ecologically similar species, or a species of different habitat ecotypes (Reilly 1990, Waring *et al.* 2001). In this study the models seemed to show habitat separation of species of different ecotypes (*i.e.*, pantropical *vs.* Atlantic spotted dolphin; coastal vs. offshore bottlenose dolphin), as discrepancies were seen between sightings of these species in coastal areas and predicted habitat areas (Fig. 3c, 4a). Atlantic spotted dolphin primarily occurs in tropical coastal areas, whereas pantropical spotted

[6] Personal communication with Phil Clapham, NMFS Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

Table 4. Comparison of correct classification rates for each species at seven scales.

	4k	8k	16k	32k	48k	64k	96k
1a. Mid-Atlantic offshore species							
Beaked whale	0.50	0.50	0.46	0.47	0.55	0.62	0.36
Sperm whale	0.47	0.49	0.48	0.56	0.60	0.48	0.46
Striped dolphin	0.52	0.52	0.54	0.53	0.60	0.62	0.44
Spotted dolphin	0.45	0.46	0.49	0.38	0.54	0.46	0.48
1b. Mid-Atlantic shelf species							
Bottlenose dolphin	0.56	0.58	0.60	0.67	0.58	0.66	0.70
Risso's dolphin	0.44	0.53	0.31	0.46	0.39	0.56	0.56
Common dolphin	0.56	0.61	0.65	0.67	0.67	0.67	0.60
Pilot whale	0.68	0.61	0.64	0.70	0.57	0.56	0.50
2a. Northern Atlantic nearshore species							
Harbor porpoise	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Minke whale	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Whitesided dolphin	N/A	N/A	N/A	N/A	N/A	N/A	N/A
2b. Northern Atlantic shelf species							
Fin whale	0.63	0.63	0.63	0.67	0.70	0.72	0.63
Humpback whale	N/A	N/A	N/A	N/A	N/A	N/A	N/A

dolphin primarily occurs in tropical and subtropical oceans (Perrin *et al.* 1987). Coastal bottlenose dolphins occur primarily in shallow and warm water, whereas offshore bottlenose dolphins occur primarily in deep and cold water (Mead and Potter 1995). Thus, it is most probable that the spotted dolphins and bottlenose dolphins sighted in offshore regions were pantropical spotted dolphins and offshore bottlenose dolphins, whereas those in coastal areas were Atlantic spotted dolphins and coastal bottlenose dolphins (Waring *et al.* 1999). Failure of the models to predict these coastal types is consistent with the fact that these types have separate habitats.

Prediction models could also show areas of distinctive ecological characteristics. Habitat classification of the cetaceans in this study was similar to that found in the Gulf of Mexico (GOM) (Davis *et al.* 1998) and in the eastern tropical Pacific (ETP) (Polacheck 1987). In these regions, Risso's dolphin, pilot whale, and common dolphin were classified as the continental shelf or inshore group, and beaked whale, striped dolphin, spotted dolphin, and sperm whale were classified as the offshore group (Polacheck 1987, Davis *et al.* 1998). However, topographic and oceanographic conditions (*e.g.*, SST, depth, slope) of their habitats were different among the three regions. This suggests the existence of distinctive ecological habitats that are similar across the three regions and that cannot be characterized by physical measurements alone.

Constraints on Prediction models

While potential applications of prediction models are expanding, constraints of the prediction models should also be recognized. Because a prediction model is based on a statistical relationship between cetacean sightings and a predictor variables, accuracy and precision of models depend on quality of predictor variables and sighting data, and the strength of the statistical relationship between the two.

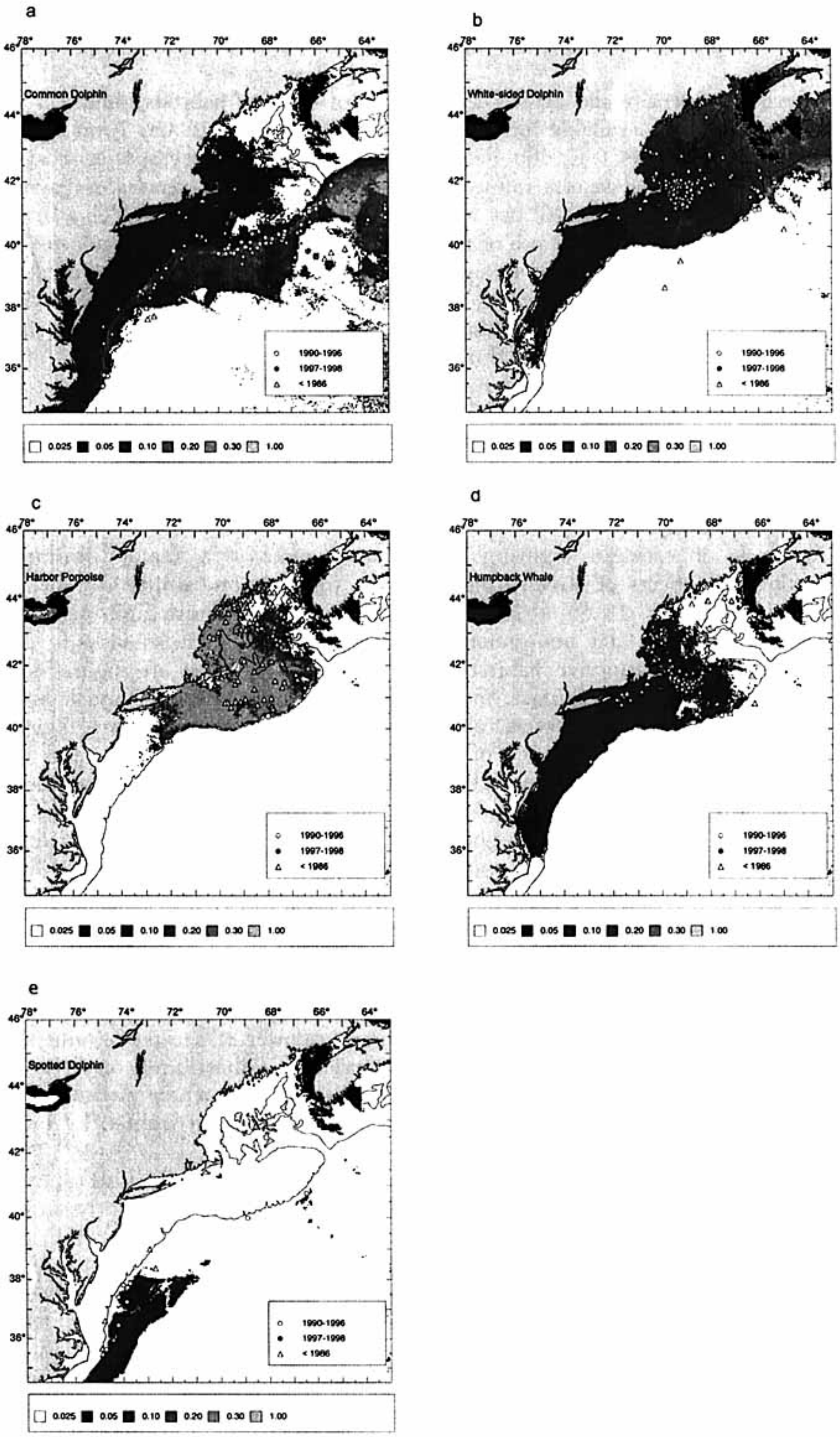
In order to identify and predict the location of cetacean habitats, predictor variable data must be available for those unsurveyed areas. This may limit the use of biological variables (*e.g.*, abundance and distribution of prey species) that are considered the prime factors influencing the distribution of cetaceans (Payne *et al.* 1986, Kenney *et al.* 1996) but are difficult to obtain oceanwide. This limitation may be lessened by the use of remote-sensing technology. For instance, general abundance of prey might be estimated using ocean color satellite data, the Coastal Zone Color Scanner (CZCS) (available for 1978–1986) and the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) (available for 1997–present). Neither of these data sets were available during the years (1990–1998), the period of interest in this study. The lack of historical predictor data also limits the use of historical sighting and whaling data as response variables. Some studies associate historical sighting/whaling data with present predictor data, implicitly assuming that historical oceanographic conditions were the same as present ones (*e.g.*, Moses and Finn 1997, Gregr and Trites 2001); however, validity of this assumption remains unknown.

Accuracy of cetacean sighting survey data remains a major limitation. Although the effects of survey conditions on sighting probability can be corrected (Hedley *et al.* 1999), a sighting survey cannot distinguish sightings of cetaceans in preferred and non-preferred habitats. The ocean lacks visually clear and ecologically distinctive habitat indicators, and cetaceans are sighted only when they appear at the surface, mostly while they are swimming and logging. Consequently, sighting observers cannot distinguish the following three pairs of survey occasions: (1a) sightings of cetaceans at a preferred habitat, and (1b) sightings of cetaceans at a non-preferred habitat; (2a) non-sightings (absence) of cetaceans at a preferred habitat, and (2b) non-sightings (absence) of cetaceans at a non-preferred habitat; (3a) non-sightings (unobserved) of cetaceans at a preferred habitat, and (3b) non-sightings (unobserved) of cetaceans at a non-preferred habitat. In this study, it is assumed that all sightings occurred at preferred habitat (1a) and that all the non-sighting areas were non-preferred habitat (2b); however, this assumption remains questionable. This limitation could also be overcome by simultaneous use of hydroacoustics with sighting surveys.[2]

These limitations lead to weak statistical relationships between predictor and response variables, which result in low predictive power of the model and misidentification of potential habitats. For instance, it is most probable that the models misidentified the Georges Bank area as habitat of northern Atlantic nearshore species (Fig. 5) because few nearshore species have been sighted by intensive air surveys in August (unpublished).[7]

Verification of model predictions also remains very difficult. Because cetaceans are highly mobile and their sighting probability is very low, they can be missed at the predicted habitat areas due to chance or to suboptimal survey conditions. Low sighting probability is also troublesome when model predictions are compared with survey data. Low sighting probability gives the null model (*i.e.*, no cetaceans in all the effort grids), higher correct classification rate (*i.e.*, 100%

[7] Unpublished data from Gordon Waring, NMFS Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.


a
Common Dolphin
b
White-sided Dolphin
c
Harbor Porpoise
d
Humpback Whale
e
Spotted Dolphin
78° 76° 74° 72° 70° 68° 66° 64°
46° 44° 42° 40° 38° 36°
1990-1996
1997-1998
< 1986
0.025 0.05 0.10 0.20 0.30 1.00

sighting probability) than those of prediction models. In this study, since sighting probability is less than 12%, the null model yields a higher correct classification rate (>88%) than that of the prediction model (44%–70%) (Table 2).

Statistical relationships between cetacean sightings and predictor variables are influenced by the choice of spatial and temporal scales. Generally, a large scale (*i.e.*, large unit survey effort in distance and time) would increase sighting probability (Table 3) but reduce precision of oceanographic and topographic conditions where cetaceans are sighted, whereas a small scale has the opposite effect. Higher sighting probability may increase predictive power of the model; however simultaneously, imprecise data could decrease accuracy of the model. Interestingly, choice of scale had little effect on predictive power of the model in this study. This suggests that 96-km squares and possibly larger grid scales are sufficient for prediction of oceanwide cetacean habitat (Table 4).

Choice of scale also depends on ecology of species, on scope of a study, on protocol and extent of a study, and on availability of data. As in this study, oceanwide habitat prediction of highly mobile species may not require detailed information on habitat characteristics. In contrast, data from ocean wide surveys may not be useful for prediction of residential cetaceans within local habitats. In addition to choice of spatial scale, choice of temporal scale should be considered. While detailed instantaneous data (*e.g.*, SST) may be available, cetaceans may not respond to instantaneous changes of ocean conditions. There may also be a time lag between change of oceanographic conditions and cetacean responses. For instance, it takes some time from oceanographic change, to algal bloom, to attraction of prey species, and then to attraction of cetaceans (Jaquet 1994). In such cases, there may be no relationship between cetacean sightings and instantaneous oceanographic conditions. Choice of spatiotemporal scales would also influence the variety and significance of predictor variables associated with cetacean sightings; this has often been ignored. Many studies lack a description of rationales for why particular scales were selected and none have done sensitivity analyses (*e.g.*, Reilly 1990, Fiedler and Reilly 1994, Reilly and Fiedler 1994, Moses and Finn 1997, Forney 2000, Waring *et al.* 2001). This poor definition of spatiotemporal scales is the primary cause for confusion and disagreements among studies about factors that associate with cetacean distribution (Jaquet 1996). It should also be remembered that significance of predictor variables in statistical regression models does not necessarily imply that the variables have ecological significance on habitat choices of the cetaceans.

Finally, inferences of prediction models are limited to the range of data. In this study inferences of this study's prediction models are limited to the mid-western North Atlantic during the summer season. To extend inference of the models beyond this range, additional survey data are needed. In this region, a multiseasonal comprehensive cetacean survey has not been conducted since 1982 (CETAP 1982). Considering the advancement of remote-sensing technology and

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Figure 7. Predicted habitat areas and sighting locations (June) of species: (a) common dolphins, (b) whitesided dolphins, (c) harbor porpoises, (d) humpback whales, and (e) spotted dolphins. Predicted habitat distribution is based on oceanic conditions of 17 June 1991. Black areas surrounding Nova Scotia indicate absence of data.

cetacean survey methodologies since then, another region-wide multiseasonal comprehensive survey could provide useful additional information.

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