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CETACEAN TROPHIC INTERACTIONS OFF THE NORTHEAST USA INFERRED FROM SPATIAL AND TEMPORAL CO-DISTRIBUTION PATTERNS

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Abstract

Data collected in several research programs over a nine year period (1978-1987) off the northeast U.S. coast were used to delineate potential trophic interactions of cetaceans by examining spatial/temporal co-distribution patterns between cetaceans and prey species. Analyses were conducted for five cetaceans and eight prey species.

A dichotomy exists between contemporaneously collected cetacean and marine fish and squid data. While bottom trawl survey coverage extends only to the shelf edge (360m), survey coverage for cetaceans extends out to 2,000m.

Visual inspection of spatial and temporal patterns in the data sets indicate a greater range overlap between pilot whales, common dolphins, bottlenose dolphins and prey in spring; in autumn the overlap is more prominent for fin whales. We suggest that these patterns reflect the strong inshore and offshore migration of fish and squid in response to seasonal water temperatures.

Fourteen percent (11/80) of the linear regressions between prey abundance and cetacean sighting rates were significant (P<0.05), although coefficients of determination (r²) were all below 0.38. Significant relationships were obtained between fin whales and sandlance in autumn, and between pilot whales and Illex squid in spring. These analyses suggest that broadscale trophic interrelationships exist within the northeast region, and need to be considered when assembling trophic models, and formulating management advice.

Key words: cetaceans, ecology, northeast U.S. shelf.

INTRODUCTION

Assessment and management of living marine resources increasingly focus on ecosystem approaches rather than single species approaches (FAO, 1978; Beverton, 1985; Sherman and Alexander, 1986; Overholtz et al., 1991; Smith et al., 1993). A holistic approach to management of marine mammal populations requires information on population dynamics, direct and indirect ecological impacts of commercial fishing, habitat requirements, and spatial and temporal trophic interactions (Beverton, 1985; Hoydal, 1990). Within the U.S. Exclusive Economic Zone (EEZ), both the Marine Mammal Protection Act (1972) and the Magnuson Fisheries Conservation and Management Act (1976) advocate ecosystem management.

Ecological impacts of commercial fishing on the prey of marine mammals have received widespread attention (Mercer, 1975; Jones, 1981; Harwood and Croxall, 1988; Hoover, 1988; Read and Gaskin, 1988; Payne et al., 1990; Anonymous, 1992; Haug et al., 1992). These studies have attempted to link spatial and temporal fluctuations in prey abundance to changes in marine mammal abundance, habitat shifts, and biological parameters. For many marine mammal stocks, current carrying capacity may be below historical levels (NMFS, 1992) due to reductions in prey caused by fishing. Conversely, it has been hypothesized that marine mammal predation on commercially overexploited fishery resources has contributed to stock collapses and recruitment failure (Sissenwine et al., 1984; Gulland, 1987; Nordoy and Blix, 1992). Marine mammals are frequently viewed as competitors for commercially valuable species, and their consumption of fish has been estimated to be equivalent to commercial harvests (Furness 1982; Sissenwine et al., 1984; Hain et al., 1985; Kenney et al. 1985; Gulland, 1987; Sherman, 1990; Sigurjonsson and Vikingsson,

For most species of marine mammals in the northwest Atlantic, recent data on food habits and prey preferences are not available. Most of the existing data are from whaling studies, opportunistic at-sea observations, fecal analyses, and stomach contents of incidentally caught and stranded animals (Sutcliffe and Brodie, 1977; Overholtz and Nicolas, 1979; Mayo, 1982; Whitehead and Carlson, 1986; Payne and Selzer, 1989; Mayo and Marx, 1990; Waring et al., 1990; Early and McKenzie, 1991). Despite biases, such as limited spatial and temporal coverage, reliance on remains of prey hard parts, and health of the animals (particularly stranded individuals) these data provide some insights into food habits, and have been used to estimate the predatory impact of marine mammals off the northeastern U.S. coast (Scott et al., 1983; Kenney et al., 1985; Overholtz et al., 1991).

The objective of this study was to deduce trophic interactions between five cetaceans and eight potential prey species off the northeast U.S. coast (Figure 1) using information derived from contemporaneous multiplatform research surveys, and examination of co-distribution data.

DATA SOURCES

Marine mammal data were obtained from the Cetacean and Sea Turtle Assessment Program (CETAP) and the Cetacean and Sea Bird Assessment Program (CSAP). Copies of CETAP and CSAP data bases are archived at the Northeast Fisheries Science Center (NEFSC), Woods Hole, MA.

The CETAP study, conducted by the University of Rhode Island from November 1978 to January 1982 (CETAP, 1982), covered shelf and shelf-edge waters (0-2000 m) between Cape Hatteras and Nova Scotia (Figure 1). The study was designed to characterize and assess the cetacean and sea turtle community off the U.S. northeastern coast. Although data were principally collected using aerial line-transect surveys, animal sightings obtained from historical records and from observers placed aboard platforms-of-opportunity have been included in the data base (CETAP, 1982; Scott et al., 1983).

The CSAP program, conducted by Manomet Bird Observatory from 1980 to 1987, involved the placement of dedicated marine mammal and sea bird observers aboard NEFSC, and other fishery research vessels (Powers et al., 1980; Smith et al., 1990; Payne et al., 1984). The NEFSC surveys were conducted in continental shelf waters (10-360 m) between Cape Hatteras and Nova Scotia with marine mammal searching effort dictated by survey type (Smith et al., 1990; Payne et al., 1984). The CSAP program was designed to provide long-term monitoring of cetaceans, sea birds and sea turtle abundance and distribution in waters off the northeastern U.S. (Powers et al., 1980; Payne et al., 1984)

Fish and squid data were derived from the 1979-1987 NEFSC bottom trawl surveys. These years correspond to the CETAP and CSAP survey periods. Since 1968, NEFSC spring and autumn surveys have been conducted annually in the aforementioned region in waters between 27-360 m (Azarovitz, 1981; Anonymous, 1992). A stratified random sampling scheme is used, with the number of survey stations proportional to survey stratum area. At each station a 30 minute tow is made. Stratum boundaries (Figure 2) are primarily based on depth and secondarily bottom type (Grosslein, 1969). Detailed descriptions of survey design, gear, and data processing are provided in Grosslein (1969) and Azarovitz (1981).

METHODS

Cetaceans considered in this study are pilot whales (Globicephala spp.), common dolphins (Delphinus delphis), white-sided dolphins (Lagenorhynchus acutus), bottlenose dolphins (Tursiops truncatus), and fin whales (Balaenoptera physalus). Species selection criteria were based on a priori knowledge on the general ecology of these species, and familiarity with data bases. These species constitute a representative cross section of the cetacean community off the northeast U.S. coast based on size, feeding behavior, diet, and habitat use. They are among the most frequently observed in systematic sighting surveys conducted between Cape Hatteras and Nova Scotia.

Eight potential prey species were considered: Atlantic herring, (Clupea harengus), sandlance (Ammodytes spp.), silver hake (Merluccius bilinearis), red hake (Urophycis chuss), butterfish (Peprilus triacanthus), Atlantic mackerel (Scomber scombrus), long-finned squid (Loligo pealei), and short-finned squid (Illex illecebrosus). These species comprise an important component of the fish and squid biomass, and are actual or potential prey items for the five cetacean species mentioned above (Waring et al., 1990; Overholtz and Waring, 1991).

Data bases were entered into ARC-INFO (a Geographic Information System (GIS)), for mapping, and for calculating distances from the 200m and 1000m isobaths to the center of 10 minute grids of latitude and longitude.

Using 10 minute squares of latitude and longitude, seasonal plots (March to May = spring, September to November = autumn), depicting relative densities of cetaceans and potential prey codistribution were constructed, with the 1979-1981 CETAP (R. Kenney, personal communication) and NEFSC bottom trawl survey data.

Relationship between prey abundance and environmental data obtained from NEFSC autumn (1982-1987) and spring (1983-1987) bottom trawl surveys were explored using General Linear Models (GLM) (SAS, 1985). This modeling investigated whether fish and squid abundance were interrelated with environmental variables over a broad geographic area.

Initially a factorial model (2-way classification) was used to examined relationships between prey abundance (survey catch in ln numbers per tow; dependent variable) and several environmental and geographic parameters (independent variables). Surface temperature, bottom temperature, distance to 200m and 2,000m isobaths were continuous variables; whereas, depth and latitude were class variables. Temperature was treated as a continuous variable. Depth classes used (i.e., 27-55 m, 56-110 m, 111-185 m, and greater than 185 m) corresponded to bottom trawl survey

depth zones (Figure 2). The nine latitude classes were $(36.00^{\circ} - 37.00^{\circ}, 37.00^{\circ} - 38.00^{\circ}, ..., 44.00^{\circ}, - 45.00^{\circ})$.

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The initial model form was:

 $Ln(Y) = b_o + b_1 * BT + b_2 * ST + b_3 * DI_1 + b_4 * DI_2 + b_5 * BD + b_6 * LA + B_7 T * LA + B_8 ST * LA + B_9 BD * LA + e$

3.1

where BT is bottom temperature, ST is surface temperature, DI₁ and DI₂ were the distances from the 2,000 m and 200 m isobaths, respectively, to the center of a 10 minute square, BD is bottom depth, LA is the latitude, and BT*LA, ST*LA, and BD*LA are interaction terms. The choice of interaction terms was based on information regarding depth and seasonal temperature changes over the latitude range considered in this study. Data were analyzed by season, and tows missing bottom or surface temperature were excluded from the analysis.

After inspection of model output, variables nonsignificant in all runs were removed and a more parsimonious model chosen. This model had the form:

 $Ln(Y) = b_o + b_1 * BT + b_2 * ST + b_3 * BD + b_4 * LA + b_5 * BT * LA + e$

3.2

Annual and seasonal abundance indices (stratified mean number per tow) of prey species were determined for six bottom trawl survey strata sets (Figure 2) using SURVAN (Groundfish Survey Analysis Program). These were defined as shelf edge south (strata = 03-04, 07-08, 11-12, 63-64, 67-68, 71-72), mid-Atlantic and southern New England shelf (strata = 01-02, 05-06, 09-10, 61-62, 65-66, 69-70, 73-74), Georges Bank edge (strata = 14-15, 17-18), Georges Bank (strata = 13, 16, 19-20, 21-22), southwestern Gulf of Maine (strata = 23, 25, 26), and central Gulf of Maine (strata = 28-30, 36, 39-40). Strata sets were defined based on bathymetry, a priori knowledge of fish and squid distributions, and geographic features (e.g., shelf edge south and Georges Bank edge encompasses the same depths, but adjoin geographically different regions).

Using CSAP data, a measure of cetacean seasonal abundance within each of the six strata sets was obtained by calculating the numbers of animals per kilometer searched (S. Northridge, personal communication). Following Payne et al. (1986), only data collected in optimal sea conditions (i.e., Beaufort 3 or less, wind <16 nm/h) were used. The Chi-square statistic was used to test the null hypothesis that line transect effort (i.e.,

kilometers searched) was proportional to survey strata set areas. Similar analyses were not conducted using the CETAP data due to major differences in survey design between that program and NEFSC research vessel surveys.

The relationship between the seasonal and spatial abundance of each cetacean and prey species was examined using regression analysis (Zar, 1974).

The model form was:

 $Cet = B_0 + B_1 * PRA + \epsilon_i$

3.3

where Cet is cetacean density (sighting per kilometer) and PRA is prey abundance (stratified mean number per tow) by season. The coefficient of determination (r²) was used as a measure of association between predator and potential prey species.

Results

Visual inspection of spatial and temporal patterns in contemporaneously collected NEFSC and CETAP data (Appendix A) indicate that several species of fish and squid (e.g., sandlance, (A.3, A.5), herring (A.4, A.6) and butterfish (A.9) can be excluded as likely prey for some cetaceans over the entire or parts of the study area. The co-distribution data indicate a greater range overlap between pilot whales, common dolphins, bottlenose dolphins and potential prey species in spring; whereas, in autumn the overlap is more prominent for fin whales. These patterns may reflect the strong inshore and offshore migration of fish and squid in response to seasonal water temperatures. Specific comparisons between predators and potential prey based solely on visual inspection of Appendix A, follow.

Pilot Whales

In spring, the spatial overlap between pilot whales and squid (Loligo and Illex), and to a lesser extent butterfish and mackerel, is almost entirely along the shelf edge (Appendices A.1 & A.2). Silver hake and red hake are also found in this habitat, as well as in shelf waters from Long Island to Georges Bank (Appendix A.2). Pilot whales co-occur with sandlance and herring on Georges Bank (Appendices A.1 & A.2) in spring. During autumn, pilot whales are associated with Loligo, Illex and butterfish, and less so with the hakes along the entire shelf edge (Appendices A.3 & A.4). Co-occurrence with the hakes and Illex occurs along the western edge of Georges Bank.

Common dolphins

Common dolphins co-occur with both squids and butterfish (and to a lesser extent mackerel) along the shelf edge in spring (Appendices A.5 & A.6). While silver hake and red hake distributions also overlap common dolphins, the hakes are more abundant in shelf than shelf edge waters (Appendix A.6). In autumn, common dolphins are co-distributed with squid, hake, and butterfish on Georges Bank (Appendices A.7 & A.8).

White-sided dolphins

White-sided dolphins are largely distributed in Gulf of Maine and adjacent waters in both seasons, concentrating along the 100m isobath. Their distribution in this region overlaps silver hake, red hake, and sandlance in both seasons, herring in spring, and Loligo and Illex in autumn (Appendices A.9 - A.12). In the southern New England and mid-Atlantic regions, the distribution of white-sided dolphins overlaps herring, sandlance and the hakes in inshore waters. On Georges Bank in autumn, white-sided dolphins co-occur with the hakes and squids, butterfish, and to a lesser extent sandlance (Appendices A.11 & A.12).

Bottlenose dolphins

In spring, bottlenose dolphins overlap the same prey species along the shelf edge as common dolphins (i.e., squids, butterfish, mackerel and to a lesser degree with the hakes (Appendices A.13 & A.14). South of Chesapeake Bay, bottlenose dolphins overlap the squids and butterfish, and again to a lesser degree with the two hake species. Overlap with mackerel, however, does not occur south of 38° 00', where mackerel are on the shelf proper (Appendix A.14). In autumn, bottlenose dolphins are more associated with Illex, hakes and butterfish along the shelf edge, particularly south of 38° 00' (Appendices A.15 & A.16).

Fin_whales

In spring, fin whale distribution overlaps (1) sandlance, silver hake and red hake throughout the shelf region; (2) sandlance in the mid-Atlantic and Georges Bank regions and northward onto Jeffreys' Ledge; (3) mackerel in the mid-Atlantic area; and (4) herring along a corridor extending from the southwest part of Georges Bank into the southwest corner of the Gulf of Maine (Appendices A.17 & A.18). In autumn, fin whales and the two hakes co-occur in many regions; whereas, co-occurrence with sandlance, the squids, and mackerel is predominantly along the corridor extending from the Great South Channel to Jeffrey's Ledge (Appendices A.19 & A.20). The autumn distribution of fin whales overlaps historical herring spawning

grounds (Anthony, 1972) on Georges Bank and in the Gulf of Maine.

Fish and Squid Versus Environmental Variables

Results of multiple regressions of spring and autumn species catch per tow values versus "environmental" variables are presented in Table 1. Most regressions were significant (P < .05), except for Illex, sandlance, and mackerel in spring, and sandlance and mackerel in autumn. However, the amount of variation explained by the significant regressions was quite low; the best fit accounted for only 43% of the variance (Table 1): Generally, for most species, depth was a significant explanatory variable in both seasons. Surface temperature was a significant factor only in autumn. In addition, interaction variables (bottom temperature * latitude) were only significant for herring (spring) and red hake (autumn).

Species Abundance Indices

The stratified mean number per tow for the eight prey species, and number of cetaceans per kilometer searched by strata sets are summarized in Appendix B. Generally, herring and sandlance were not captured in the shelf edge (strata sets 1 and 2). Herring were most abundant in sets 4-6 (Georges Bank and Gulf of Maine); whereas, sandlance were abundant in sets 3-5 (set 3 = mid-Atlantic and southern New England shelf). Overall, butterfish, Loligo, and Illex indices were highest in sets 1-3 in all seasons. These three species were also caught during autumn in sets 4-6.

Mackerel were taken in low numbers in all strata sets, although in some areas they were seasonally absent for several consecutive years. Red and silver hake were ubiquitous in all seasons and strata sets. Abundance indices for both hakes, however were highest in set six.

Cetacean abundance indices (number per kilometer searched) (Appendix B) indicate that most species were sighted throughout the survey region. Multi-year gaps, however, are evident, particularly in spring, in at least one strata set for each species. Numbers of zero data cells were highest for bottlenose and white-sided dolphins.

Searching effort per stratum set was significantly different (P<0.05) than proportional allocation in all years, but no clear trends were evident. For example, searching effort ranged from 550 to 1996 km, and 15 to 218 km, respectively, in strata sets 3 (largest) and 4 (smallest). Sampling variability can be attributed to several factors including survey protocol, weather, and space availability for marine mammal observers (Payne et al., 1984; Smith et al., 1990).

Correlation Between Prey and Cetaceans

Only fourteen percent (11/80) of the linear regressions between prey abundance and cetacean sighting rates were significant (P<0.05), and coefficients of determination (r^2) for these regressions were all below 0.38 (Table 2). The number of significant relationships ranged from five for bottlenose dolphins to zero for common dolphins (although, visual inspection of Appendix A plots suggests common dolphins are associated with several species). For bottlenose dolphins significant relationships were detected with the abundance of Loligo, Illex, and butterfish in spring, and Illex and silver hake in autumn. Sighting rates of white-sided dolphins were positively correlated with sandlance in spring and negatively associated with butterfish, Loligo and silver hake in autumn. Significant relationships were also obtained between fin whales and sandlance in autumn, and between pilot whales and Illex in spring. Negative intercepts were obtained in nine regressions (Table 2) suggesting that a linear model may not be appropriate (i.e., relationships may be non-linear near zero).

DISCUSSION

Potentials for broad-scale ecological interactions between cetaceans and potential prey off the northeast U.S. coast are suggested by spatial and temporal patterns in both their distribution and abundance. However, strong correlations were not observed between the density of most cetaceans and the seasonal and temporal abundance of prey species. Cetaceans considered in this study are opportunistic predators (Mitchell, 1975; Gaskin, 1985), and their prey selection will likely change during migration and occupation of northeast shelf and shelf-edge waters. Reliable evaluation of the importance of the eight potential prey species in deep water (> 300 m) cetacean habitats is precluded by the lack of NEFSC survey sampling in depths beyond 320 m.

Depth was the most important explanatory variable in GLM models which examined relationships between fish and squid catch per tow and several "environmental" variables. Generally bottom and surface temperature were not significant factors. This is contrary to other studies (Colton, 1972; Grosslein and Azarovitz, 1982; Sherman et al., 1988) which indicate seasonal patterns in fish and squid distribution in the northeast region are broadly related to environmental conditions, particularly water temperature. Studies focused on smaller geographic areas (i.e.; Georges Bank) have shown stronger correlations between temperature and NEFSC research vessel catches (Murawski and Finn, 1988; Murawski and Mountain, 1990). The likelihood of greater variability in parameter values over a broad geographic region (e.g., thermal edge effects may be important) may possibly

explain why temperature was not an important explanatory variable in this study.

Within the broad areal habitats considered in this study, significant relationships between prey abundance and cetacean sighting rates were found for only a few species. Significant correlations between fin whales and herring in spring, and sandlance in autumn are concordant with fine scale surface feeding observations made aboard research and whale watching vessels (Overholtz and Nicolas, 1979). Herring and sandlance are known to be important prey for fin whales in the northeast region during spring, summer and autumn (Mayo, 1982; Kenney et al., 1985; Hain et al., 1992). A relationship between pilot whales and Illex squid is also consistent with previous prey preference studies (Sergeant 1962; Mercer, 1975), but only in spring when both species are concentrated along the shelf edge. Significant regressions were also found between bottlenose dolphins and four prey species (butterfish, Loligo, Illex, and silver hake).

Most of the correlations between prey abundance and cetacean sighting rates were not significant (69/80; 84%). Strata set specification, data variability, small sample sizes (particularly cetacean sighting rates) and differential seasonal habitat use by prey and predators likely contributed to the low number of significant relationships.

The objective of this study was to deduce trophic interactions between five cetaceans and eight potential prey species. Visual inspection of (1979-81) spatial and temporal codistribution patterns suggest a broad overlap range exists, but this was generally not supported by species-specific regression analyses. The former were summaries of multiyear data sets, and hence may magnify the perceived level of association. Cetaceans are opportunistic predators and appear to be less constrained by oceanographic parameters than their prey (Mitchell, 1975; Gaskin, 1985; Katona and Whitehead, 1988). This may help explain the low number of significant correlations.

Determining cetacean food-web relationships may require fine scale sampling, since prey density, rather than prey abundance may be the critical factor (Piatt et al., 1989). For example, during spring, pilot whales are known to aggregate at the heads of submarine canyons in the mid-Atlantic Bight to feed on dense schools of mackerel (Kenney and Winn, 1986; Overholtz and Waring, 1991; Waring 1995). However, such events are not reflected in survey data. One approach to delineating 'broadscale relationships via fine scale sampling' would be to simultaneously collect fishery and cetacean data in areas of high use cetacean habitats. This may require hydroacoustic and pelagic trawl surveys, as cetaceans are capable of foraging throughout the water column and are known to feed on vertically migrating prey. Data analyses will require statistical models that incorporate

multispecies and environmental interactions.

Analyses of stomach contents from cetaceans incidentally caught in shelf edge fisheries suggest myctophids may be an important dietary item. The importance of slope water prey (myctophids) in meeting energetic requirements was not considered in this study due to survey depth limitations, but must be evaluated. Myctophids are mesopelagic fishes that migrate vertically, coming to the surface at night, descending to deeper water by day (Backus et al., 1977; Olson and Backus, 1985). Myctophids are an important component in oceanic food webs (Backus et al., 1977), and dense aggregations of these fishes make them suitable potential prey for smaller cetaceans (Fitch and Brownell, 1968). The slope water region is a likely winter habitat for most cetaceans that occur between spring and autumn in northeast shelf and shelf edge waters.

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Table 1. Regression parameters for regression between fish and squid catch per tow, and environmental and bathymetric variables. Values' listed under BT, ED, LA, ST, and BT*LA are probability levels (P > F).

Species	R²	P**	вт	ED	LA	ST	BT*LA
				Spring			
Loligo	0.43	0.0001	0.44	0.01	0.03	0.95	0.23
Illex	0.32	0.4991	0.61	0.98	0.46	0.18	0.27
Butterfish	0.36	0.0004	0.71	0.02	0.19	0.33	0.14
Herring	0.26	0.0041	0.88	0.07	0.00	0.98	0.02
Silver hake	0.17	0.0001	0.21	0.00	0.06	80.0	0.14
Red hake	0.15	0.0020	0.03	0.00	0.46	0.11	0.58
Sandlance	0.18	0.3878	0.47	0.16	0.89	0.56	0.89
Mackerel	0.11	0.8944	0.41	0.56	0.92	0.14	0.86
				Autumr	ı		
Loligo	0.25	0.0001	0.00	0.00	0.52	0.14	0.34
Illex	0.21	0.0001	0.89	0.00	0.04	0.08	0.10
Butterfish	0.23	0.0001	0.11	0.00	0.10	0.00	0.06
Herring	0.28	0.0045	0.20	0.16	0.49	0.01	0.29
Silver hake	0.11	0.0001	0.81	0.33	0.04	0.00	0.07
Red hake	0.16	0.0001	0.40	0.02	0.01	0.37	0.01
Sandlance	0.25	0.3422	0.58	0.01	0.94	0.15	0.94
Mackerel	0.45	0.3102	0.12	0.03	0.72	0.12	0.78

^{*}BT = bottom temperature, ED = depth, LA = latitude, ST = surface temperature, BT*LA = interaction term

[&]quot; Significance of overall model

Table 2. Parameters for linear regression between prey abundance indices (Ln +1) stratified mean number per tow and cetacean sighting per kilometer, 1982-1987.

Prey	Season	Intercept(a)	Slope (b)	<u>R²</u>	Prob	<u>F</u>	<u>n</u>
		Bot	tlenose dol	phin			
Loligo	spr aut		0.028 0.011	0.380	0.001° 0.342	17.04 0.92	30 36
Illex	spr aut		0.124 0.060	0.200 0.150	0.014° 0.020°	6.83 5.94	30 36
Butterfis	h spr aut		0.047 0.025*	0.380	0.001° 0.094	17.06 2.96	30 36
Herring	spr	0.049	-0.057*	0.080	0.133	2.39	30
	aut	0.041	-0.032*	0.022	0.393	0.75	36
Mackerel	spr	0.022*	0.021*	0.010	0.526	0.41	30
	aut	0.045	-0.132*	0.027	0.337	0.95	36
Sandlance	spr	0.045	-0.048*	0.070	0.150	2.19	30
	aut	0.046	-0.066*	0.030	0.295	1.13	36
Silver ha	ke spr	-0.003*	0.016°	0.030	0.366	0.85	30
	aut	0.121	-0.040	0.130	0.028*	5.25	36
Red hake	spr	0.0 47 *	-0.019*	0.020	0.516	0.43	30
	aut	0.088	-0.053*	0.090	0.077	3.31	36
		<u>C</u>	ommon dolph	<u>in</u>			
Loligo	spr	0.015°	0.011°	0.114	0.069	3.59	30
	aut	0.658°	-0.083°	0.011	0.542	0.38	36
Illex	spr	0.024*	0.037°	0.032	0.342	0.93	30
	aut	0.125*	0.335°	0.033	0.292	1.14	36
Butterfis	h spr aut	0.019* 0.638*	0.014* -0.107*	0.068	0.163 0.554	2.05 0.36	30 36
Herring	spr	0.038	-0.022*	0.022	0.435	0.63	30
	aut	0.567	-0.378*	0.022	0.391	0.76	36
Mackerel	spr	0.021°	0.031°	0.057	0.203	1.70	30
	aut	0.566	-1.010°	0.011	0.538	0.39	36
Sandlance	spr aut	0.034 0.329*	-0.010° 0.796°	0.005	0.700 0.290	0.15 1.16	30 36
Silver hal	ke spr aut	0.015° 0.869°	0.008*	0.013 0.019	0.541 0.420	0.38	30 36
Red hake	spr	0.036*	-0.006*	0.002	0.780	0.08	30
	aut	0.903	-0.414*	0.039	0.251	1.36	36

Table 2. cont.

Prey	Season	Intercept(a)	Slope (b)	<u>R²</u>	Prob	<u>F</u>	<u>n</u>	
Whitesided dolphin								
Loligo	sp: aut		-0.050* -0.016	0.100 0.210	0.096 0.004°	2.96 9.30	30 36	
Illex	sp: aut		-0.213* -0.023*	0.045 0.079	0.258 0.096	1.33 2.93	30 36	
Butterfis	sh spi aut		-0.078* -0.018	0.083 0.146	0.123 0.021*	2.54 5.93	30 36	
Herring	sp: au		0.128* -0.001*	0.031	0.349 0.978	0.91 0.00	30 36	
Mackerel	sp:		-0.092* -0.037*	0.021 0.000	0.440 0.611	0.61 0.26	30 36	
Sandlance	sp:		0.307 -0.017*	0.232 0.008	0.007° 0.609	8.47 0.27	30 36	
Silver ha	ake spi au		-0.038* 0.022*	0.013 0.149	0.550 0.020*	0.37 5.93	30 36	
Red hake	sp: au		-0.040* 0.009*	0.005 0.010	0.701 0.570	0.15 0.33	30 36	
	•		Pilot whal	<u>e</u>				
Loligo	sp au		-0.004* -0.016*	0.003 0.022	0.784 0.387	0.08 0.77	30 36	
Illex	sp au		0.294 0.071°	0.323 0.075	0.001* 0.106	13.33 2.76	30 36	
Butterfis	sh sp au		-0.004* -0.023*	0.000 0.025	0.880 0.349	0.02 0.90	30 36	
Herring	sp au		-0.049* 0.005*	0.017 0.000	0.496 0.940	0.48 0.01		
Mackerel	sp au		-0.013* 0.016*	0.002 0.000	0.835 0.945	0.04 0.00		
Sandlanc	e sp au		-0.032* 0.198	0.009 0.104	0.611 0.055	0.26 3.96		
Silver h	ake sp au		0.055 -0.004	0.099	0.091 0.908	3.07 0.01		
Red hake	sp		0.075° 0.018°	0.069 0.004	0.161 0.721	2.07 0.13		

Table 2. cont.

Prey	Season	Inte	ercept(a)	Slope (b)	<u>R</u> ²	Prob	<u>F</u>	<u>n</u>
				Fin whale				
Loligo	sp		0.016 0.019	-0.002* -0.004*	0.025 0.092	0.406 0.073	0.71	30 36
Illex	sr		0.015 0.004*	-0.012* 0.007*	0.022 0.054	0.439 0.172	0.62 1.95	30 36
Butterfis	sh sr a		0.016° 0.017	-0.004 -0.004*	0.037 0.069	0.310 0.121	1.07 2.54	30 36
Herring	s <u>r</u> aı		0.005 0.010	0.022* 0.003*	0.129 0.004	0.051 0.704	4.16 0.15	30 36
Mackerel	sṛ		0.016 0.011	-0.010° -0.005°	0.036	0.316	1.04	30 36
Sandlance	e s <u>p</u> aı	or it	0.013 0.006*	0.000* 0.023	0.000 0.118	0.997 0.040*	0.00 4.56	30 36
Silver ha		or it	0.023 0.011	-0.005* 0.000*	0.035	0.322 0.935	1.01	30 36
Red hake		pr it	0.017° 0.009°	-0.004* 0.001*	0.007	0.651 0.832	0.21 0.05	30 36

^{*} Significant at (P < 0.05).

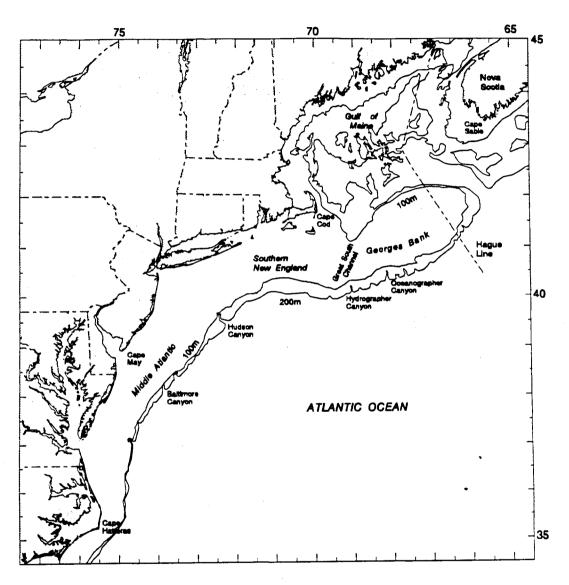


Figure 1. Northeast USA shelf.

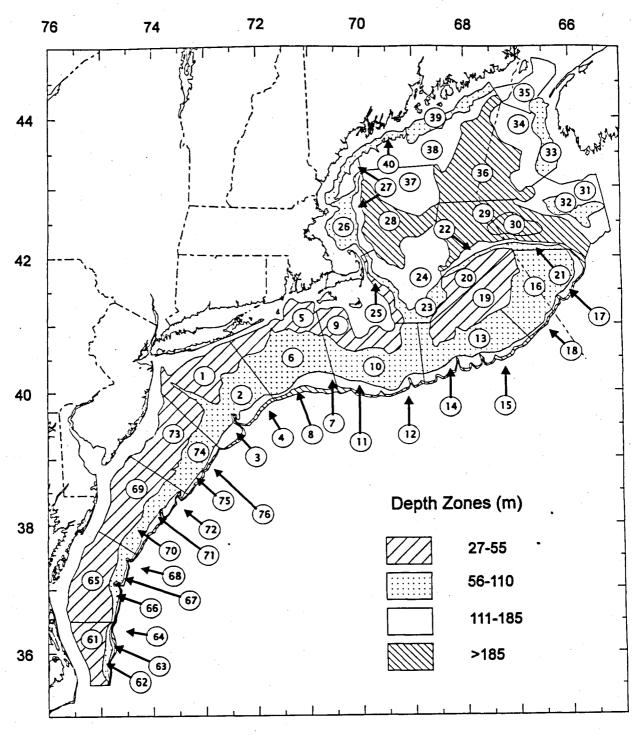
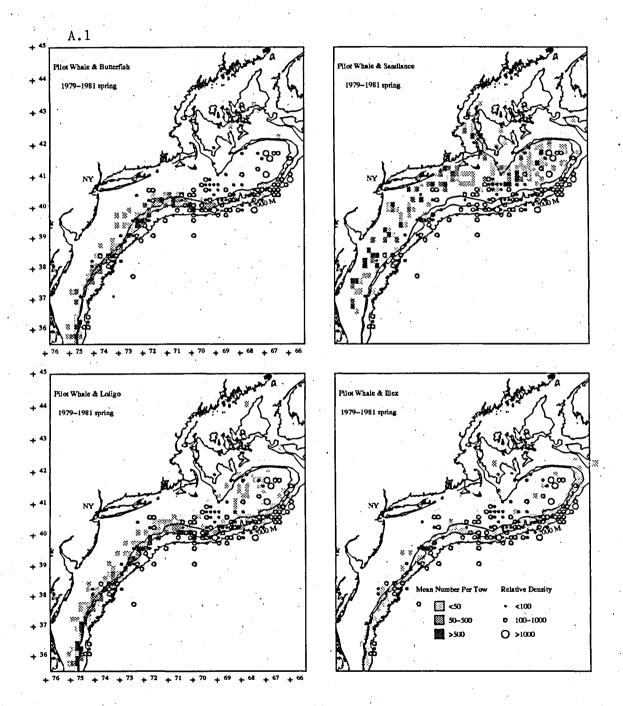
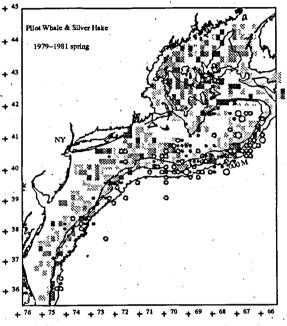


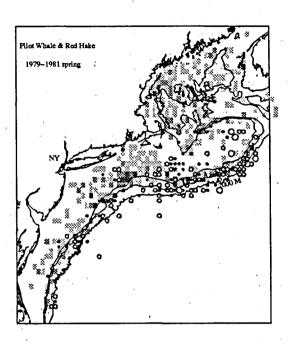
Figure 2. Location of the Northeast Fisheries Science Center research vessel sampling strata.

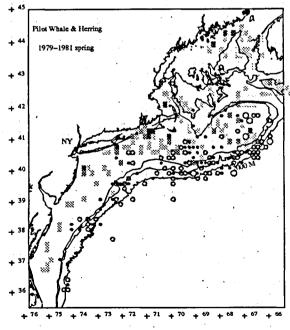
- A.1. Pilot whale overlap with butterfish, sand lance, Loligo and Illex, 1979-81 spring.
- A.2. Pilot whale overlap with silver hake, red hake, herring and mackerel, 1979-81 spring.
- A.3. Pilot whale overlap with butterfish, sand lance, Loligo and Illex, 1979-81 autumn.
- A.4. Pilot whale overlap with silver hake, red hake, herring and mackerel, 1979-81 autumn.
- A.5. Common dolphin overlap with butterfish, sand lance, Loligo and Illex, 1979-81 spring.
- A.6. Common dolphin overlap with silver hake, red hake, herring and mackerel, 1979-81 spring.
- A.7. Common dolphin overlap with butterfish, sand lance, Loligo and Illex, 1979-81 autumn.
- A.8. Common dolphin overlap with silver hake, red hake, herring and mackerel, 1979-81 autumn.
- A.9. Whitesided dolphin overlap with butterfish, sand lance, Loligo and Illex, 1979-81 spring.
- A.10. Whitesided dolphin overlap with silver hake, red hake, herring and mackerel, 1979-81 spring.
- A.11. Whitesided dolphin overlap with butterfish, sand lance, Loligo and Illex, 1979-81 autumn.
- A.12. Whitesided Dolphin overlap with silver hake, red hake, herring and mackerel, 1979-81 autumn.
- A.13. Bottlenose dolphin overlap with butterfish, sand lance, Loligo and Illex, 1979-81 spring.
- A.14. Bottlenose dolphin overlap with silver hake, red hake, herring and mackerel, 1979-81 spring.
- A.15. Bottlenose dolphin overlap with butterfish, sand lance, Loligo and Illex, 1979-81 autumn.
- A.16. Bottlenose dolphin overlap with silver hake, red hake, herring and mackerel, 1979-81 autumn.
- A.17. Fin whale overlap with butterfish, sand lance, Loligo and Illex, 1979-81 spring.
- A.18. Fin whale overlap with silver hake, red hake, herring and mackerel, 1979-81 spring.
- A.19. Fin whale overlap with butterfish, sand lance, Loligo and Illex, 1979-81 autumn.
- A.20. Fin whale overlap with silver hake, red hake, herring and mackerel, 1979-81 autumn.

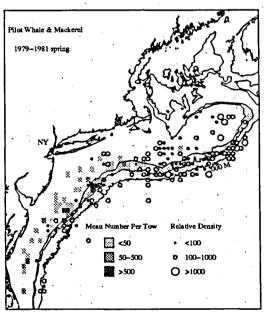


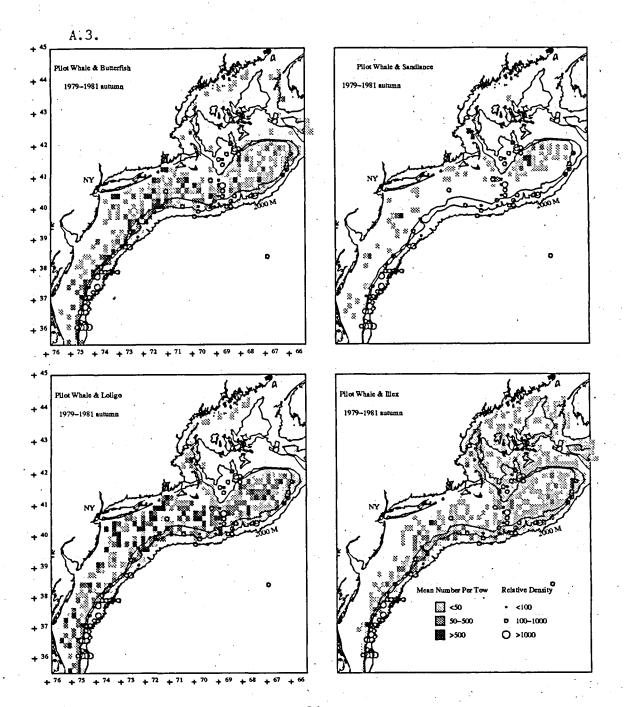


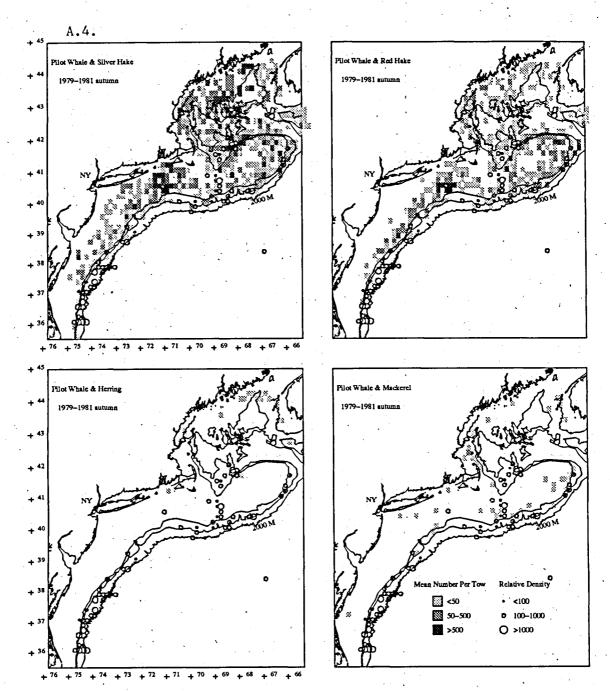


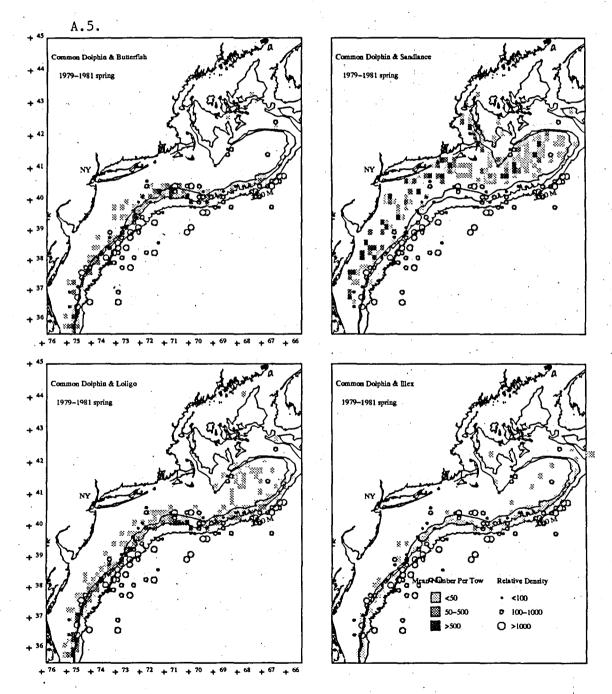


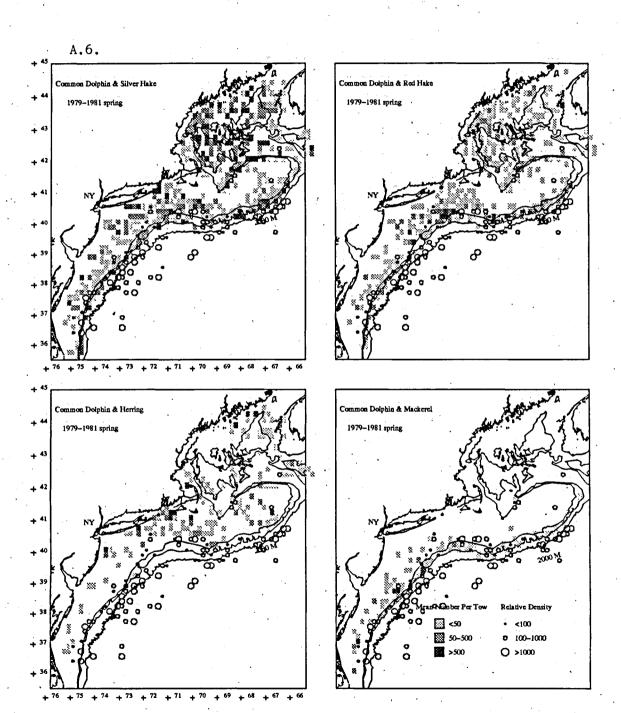


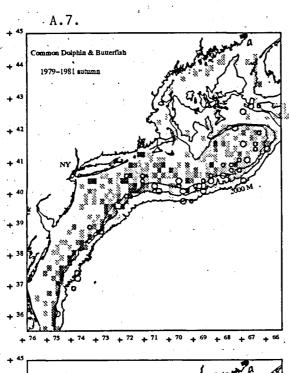


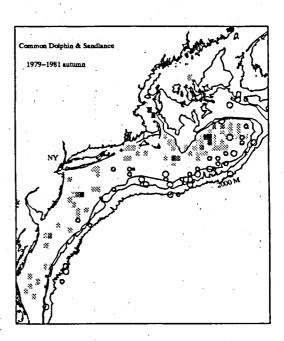


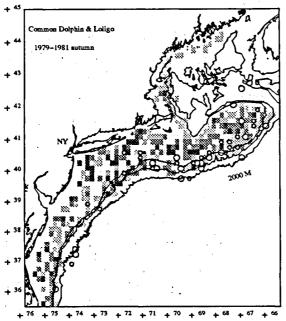


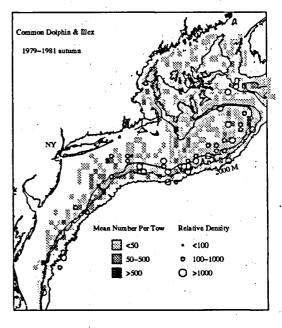


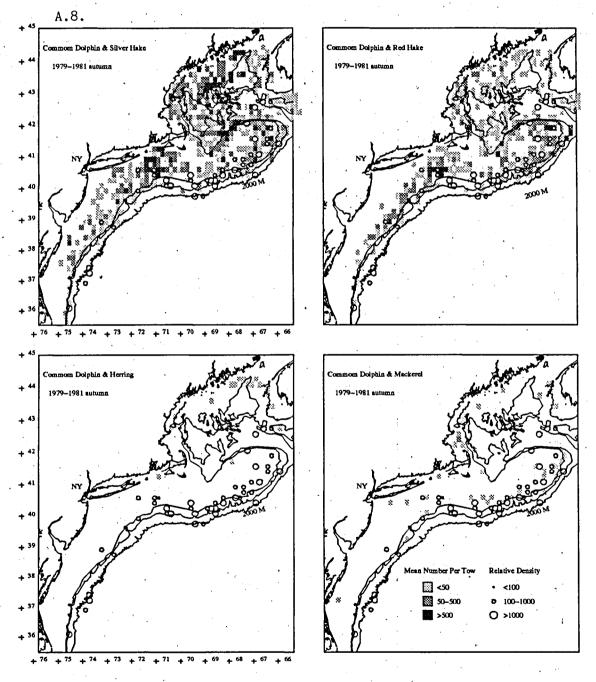


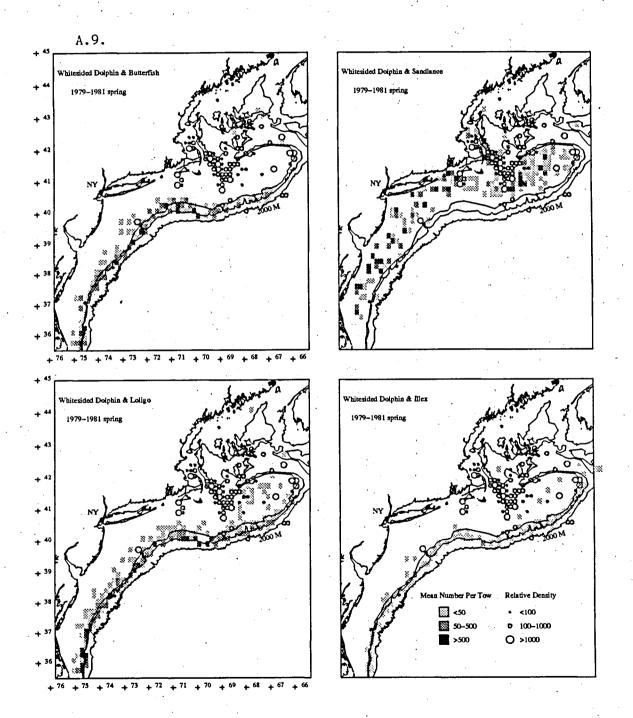


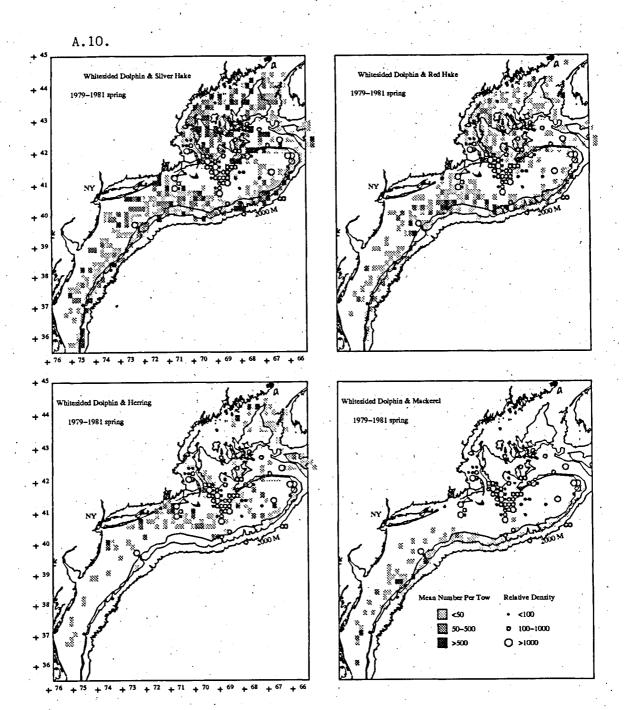


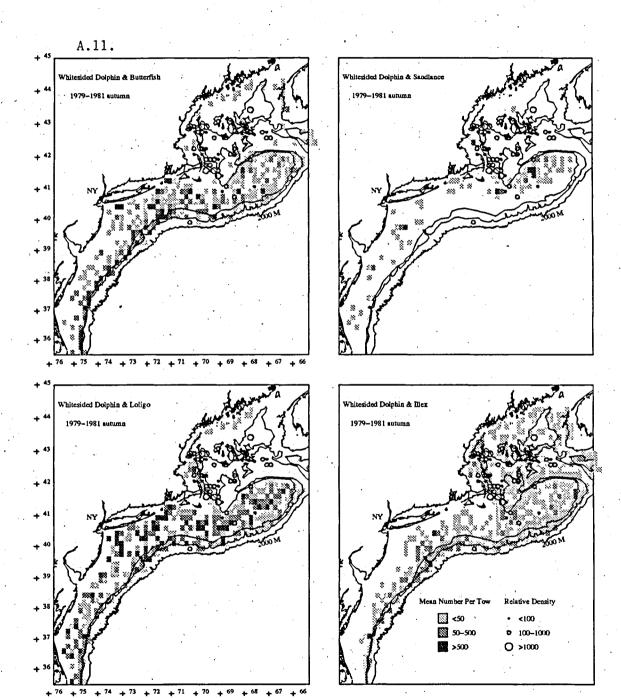


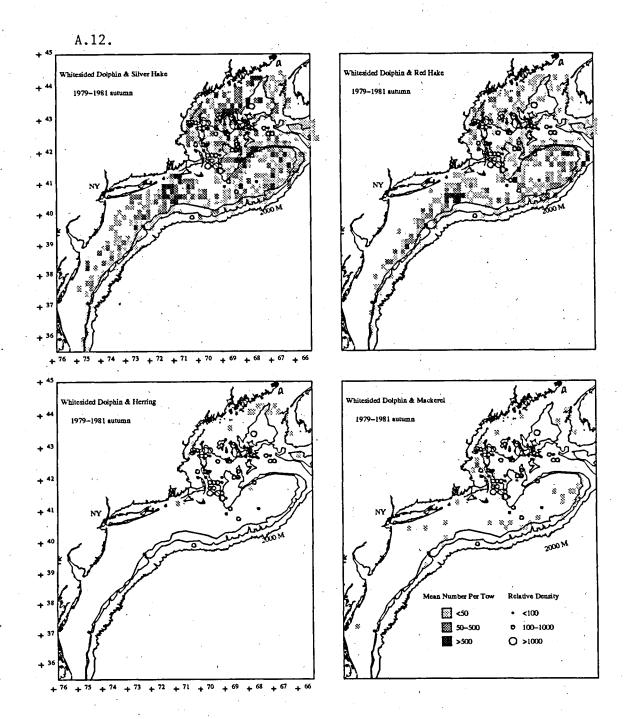


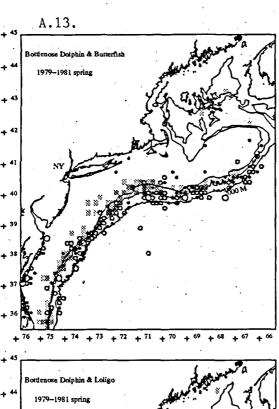




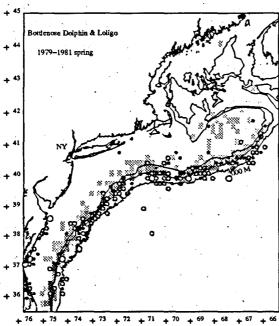


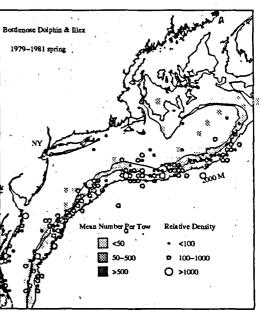




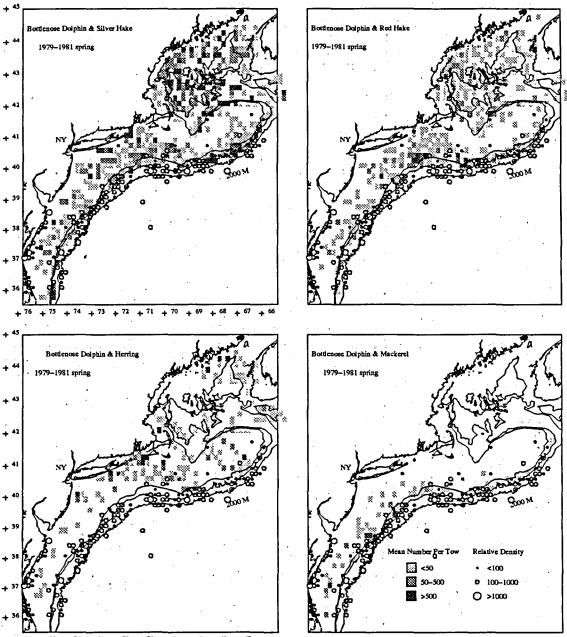


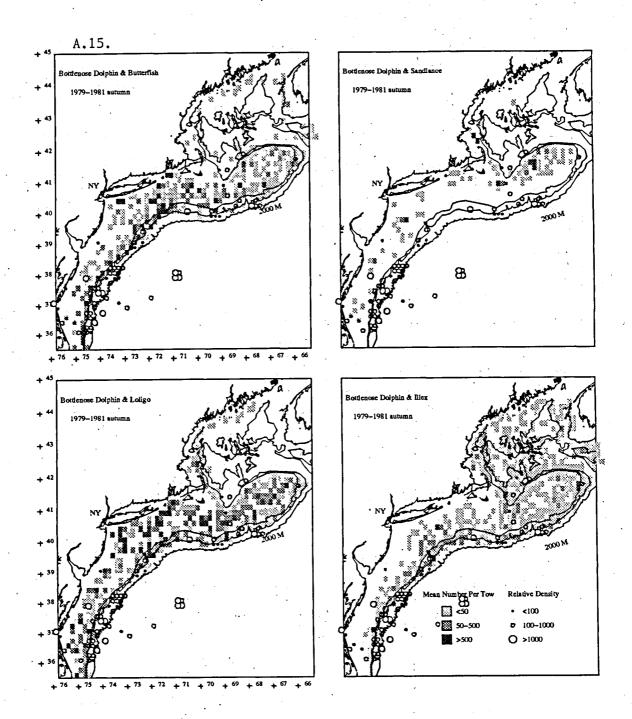


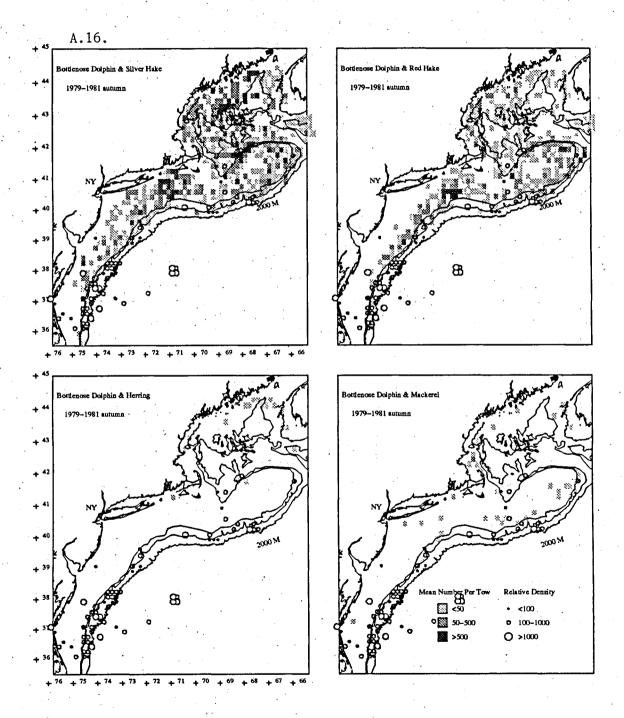


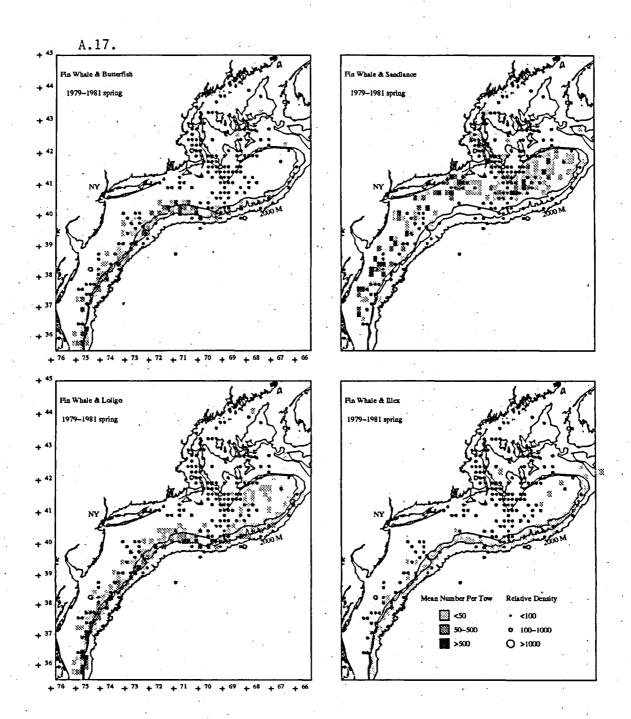


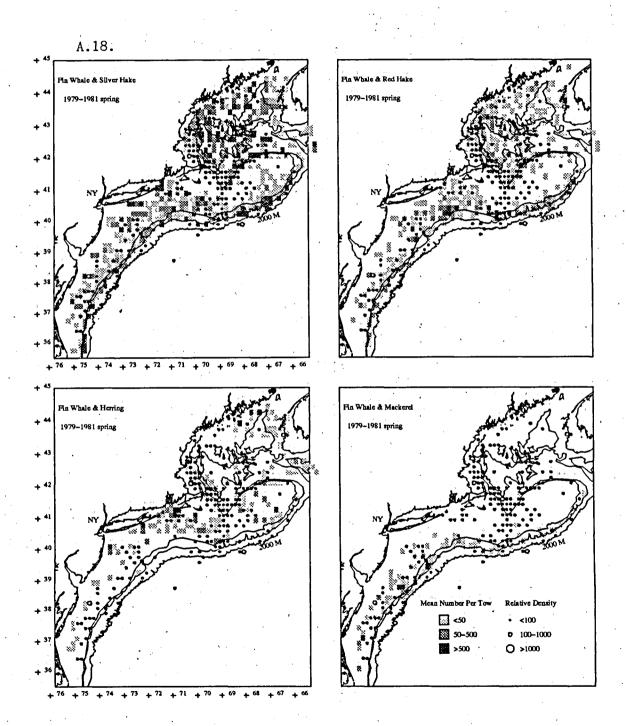


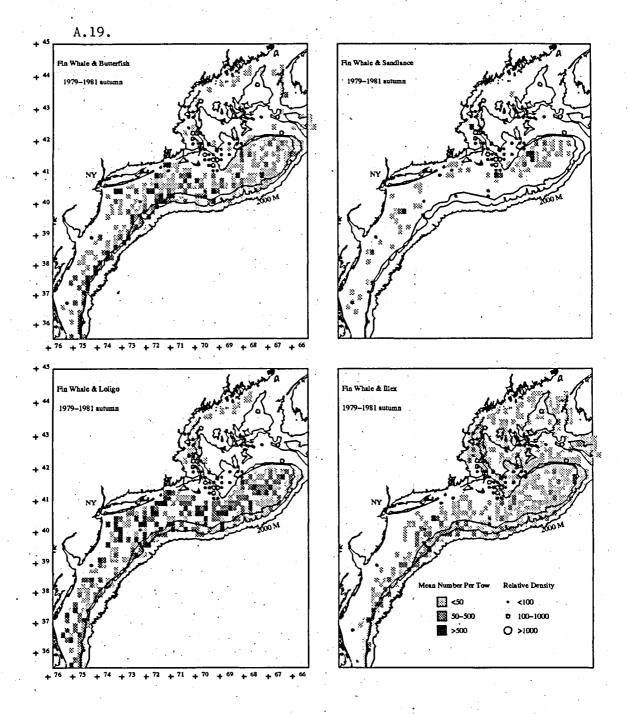


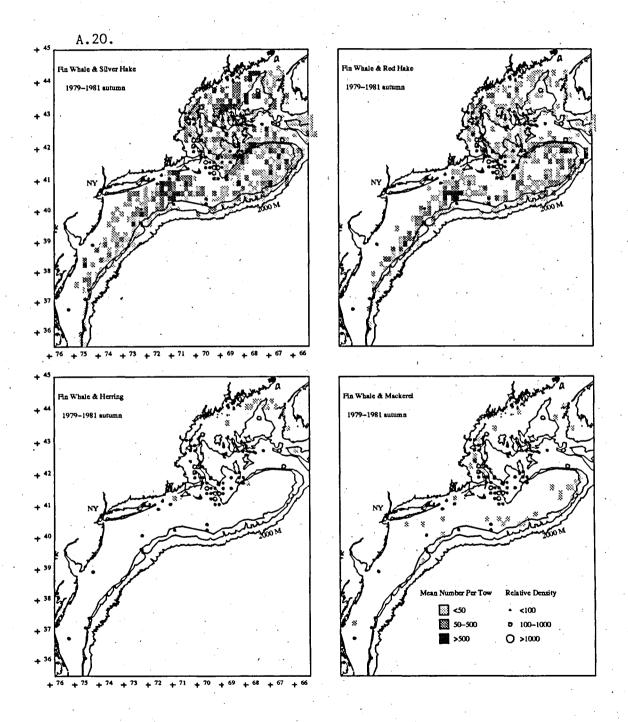












Appendix B. Bottom trawl survey abundance indices (ln + 1 number per tow), kilometers of marine mammal searching effort, and cetacean sightings per kilometer by cruise, season, and strata set.

cru'st se bu	hr il lo	mk rh	sl sh	km	fw	pw b	d cd wd	fw/km pw/km	bd/km cd/km wd/km
8303 1 1 2.17 0. 8402 1 1 2.82 0. 8502 1 1 2.85 0. 8603 1 1 3.41 0. 8702 1 1 2.77 0. 8206 1 2 2.65 0. 8306 1 2 4.12 0. 8405 1 2 3.99 0. 8508 1 2 3.48 0. 8508 1 2 2.76 0.	00 0.45 4.63 00 0.87 4.69 00 0.38 5.06 02 0.48 4.67 00 1.93 3.36 00 2.00 4.97 00 2.54 3.41 00 1.69 3.64 00 2.41 4.28	0.13 0.49 0.20 0.70 0.65 0.67 0.92 0.57 0.49 0.38 0.08 0.08 0.00 0.08 0.00 1.14 0.00 0.14	0.00 1.81 0.00 2.10 0.00 2.51 0.00 2.43 0.01 0.98 0.00 0.47 0.00 0.43 0.00 1.70 0.00 0.61	323.00 192.90 294.70 519.80 318.30 258.50 298.10 328.60 411.30	12 1 0 2 1 0 2 0 0 0 1 3		59 0 0 0 0 0 38 4 0 0 0 25 0 0 0 0 0 0 25 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0.003 0.000 0.000 0.000 0.002 0.023 0.000 0.000 0.008 0.000 0.000 0.033 0.000 0.297	0.009 0.024 0.000 0.285 0.000 0.000 0.285 0.000 0.000 0.326 0.000 0.000 0.326 0.000 0.008 0.096 0.073 0.008 0.096 0.073 0.000 0.000 0.097 0.000 0.537 0.000 0.000 0.537 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
8303 2 1 0.72 0. 8402 2 1 1.19 0. 8502 2 1 1.53 0. 8603 2 1 2.22 0. 8702 2 1 0.67 0. 8206 2 2 0.00 0. 8306 2 2 0.17 0. 8405 2 2 0.98 0. 8508 2 2 0.69 0. 8606 2 2 0.53 0.	00 0.03 2.52 04 0.50 3.07 00 0.36 2.28 00 1.05 0.99 00 2.01 0.38 00 0.80 0.49 00 1.22 2.14 00 1.00 1.79 00 0.38 0.25	0.00 1.53 1.66 1.35 0.00 2.06 0.00 1.69 0.00 0.28 0.00 1.27 0.00 0.85 0.13 1.60	0.04 2.26 0.00 2.45 0.00 3.84 0.07 3.39 0.00 0.85 0.00 1.57 0.00 2.62 0.00 2.79	50.90 40.20 100.40 78.20 218.00 15.30 123.60 144.50 92.50	0 1 1	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0.000 0.000 0.000 0.000 0.000 0.793 0.101 0.651 0.000 0.000 0.002 0.000 0.002 0.000	0 0.000 0.220 0.00
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8206 5 2 1.57 0. 8306 5 2 2.58 0. 8405 5 2 0.51 1.	10 0.00 0.00 87 0.00 0.00 82 0.00 0.00 10 0.00 0.00 45 1.53 1.65 27 0.45 1.84 73 0.93 1.13 96 0.97 3.28 14 0.97 1.89	0.00 0.41 0.24 0.38 0.09 0.87 0.00 0.97 0.22 1.95 0.06 1.70 0.07 2.00 0.059 2.73	0.73 0.72 0.62 1.56 0.10 1.71 0.73 1.11 1.20 2.74 0.19 3.40 0.47 3.73 0.33 2.91	71.20 94.00 78.70 182.80 117.30 157.40 137.00 92.10		0 0 0 0 132 0 0 133 0 0 51	6 25	0.029 0.000 0.000 0.000 0.117 0.000 0.051 0.000 0.071 0.72 0.009 0.000 0.013 0.210 0.000 0.000 0.000 0.55	0 0.000 0.000 1.372 0 0.000 0.044 0.184 0 0.000 0.000 0.421 0 0.000 0.000 0.106 0 0.000 0.000 0.064 2 0.000 0.000 0.000 0 0.000 0.000 0.000 0 0.000 0.000 0.000 0 0.000 0.000 0.000 0 0.000 0.000 0.000
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¹ cru = cruise, st = strata set, se = season (1=spring, 2=autumn), bu = butterfish, hr = Atlantic herring, il = illex, lo = loligo, mk = mackerel, rh = red hake, sl = sand lance, sh = silver hake, km = kilometers searched, fw = fin whale, pw = pilot whale, bd = bottlenose dolphin, cd = common dolphin, ws = whitesided dolphin.