Assessing the Importance of Frontal Zones on the Distribution of Upper Trophic Level Predators off Cape Hatteras

by

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Masters project submitted in partial fulfillment of the
requirements for the Master of Environmental Management degree in
the Nicholas School of the Environment and Earth Sciences of
Duke University
2006

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Abstract

Effective conservation of upper trophic level marine predators requires a comprehensive understanding of their distributions and of the underlying biological and physical processes that drive these distributions. We investigated the spatial distributions of marine mammals and seabirds off Cape Hatteras, NC, in relation to positions of the shelf break and Hatteras Front system. We conducted transect surveys with synoptic, fine-scale oceanographic sampling in August 2004, and derived the daily position of the Hatteras Front from temperature, salinity, and pressure data collected by a scanfish. To account for the correlated and autocorrelated nature of the environmental data, we assessed the influence of the Front on species distributions using a suite of Mantel's tests. Pure partial Mantel's results show that marine mammal distribution over all survey days was influenced by salinity. Results of the daily Mantel's tests show that no one variable consistently influenced the distribution of marine mammals. Pure partial Mantel's results show that seabird distribution over all survey days was influenced by depth, distance from shelf break, fluorescence, and space. The significance of space indicates that another variable or variables with spatial structure influenced the distribution of seabirds but were not tested. Results of the daily Mantel's tests show that different combinations of environmental variables influenced the distribution of seabirds on different days. However, one variable consistently influenced seabird distribution – fluorescence. These findings enable consideration of spatially explicit approaches to the conservation of marine mammals and seabirds and other upper trophic level predators in this region.

Keywords: marine mammal distribution; seabird distribution; spatial analysis; Hatteras Front

Introduction

In the ocean, variables such as temperature, salinity, and density do not vary gradually with horizontal or vertical distance. Large regions with small horizontal gradients are bounded by narrow regions with large horizontal gradients (Mann and Lazier 1996). These regions of intense gradients are called oceanic fronts. An important influence on the transport of nutrients and biota into or out of the euphotic zone, frontal zones can drive the formation of prey patches (Mann and Lazier 1996).

Oceanic fronts vary in size and duration of existence. Tidal fronts are ephemeral, typically only a few kilometers long, and separate waters that may differ by only 1-2 °C (Mann and Lazier 1996). Fronts associated with western-boundary currents, such as the Gulf Stream, are thousands of kilometers long, occur over long periods of time, and exhibit temperature changes of 10 °C in the upper water layers (Mann and Lazier 1996). In between is a category of fronts only recently described in the literature – persistent mesoscale fronts. Mesoscale fronts (10s to 100s km) orient across isobaths and occur in regions where coastal water masses converge alongshelf. For example, on the continental shelf and slope near Cape Hatteras, NC, Middle Atlantic Bight shelf water and South Atlantic Bight shelf water converge from opposite directions. Both water masses have significantly different origins and large differences in their temperature-salinity (T-S) characteristics (Flagg et al. 2002; Savidge and Bane 2001). This convergence gives rise to strong alongshelf gradients in temperature, salinity, and density – a feature known as the Hatteras Front.

Upper trophic level marine predators, including marine mammals and seabirds, are not uniformly distributed across the world's oceans. These species aggregate along frontal systems and bathymetric gradients on broad spatial scales (Hastie et al. 2004), but little is understood about the relative importance of these two habitat features, especially where they overlap in time and space (Haney and McGillivary 1985; Haney 1986a; Haney 1986b; Selzer et al. 1988; Baumgartner 1997; Davis et al. 1998; Davis et al. 2002). Additionally, uncertainty exists over the extent to which variability in the strength and location of oceanographic fronts influences the distribution of these predators. This uncertainty makes it difficult to discriminate between changes in populations due to natural environmental variability and changes due to anthropogenic impacts (Hyrenbach et al. 2000).

Marine organisms live at a variety of temporal and spatial scales that mirror their trophic levels. For instance, small plankton have life spans of several months and travel relatively short distances, whereas large marine predators – such as marine mammals and seabirds – have life spans of decades and travel vast distances. However, even large marine predators tend to concentrate certain activities over localized regions and for short periods of time. For example, many marine mammals undertake long annual migrations, but return seasonally to confined foraging areas (Read and Westgate 1997; Mate et al. 1999; Baumgartner et al. 2003). Albatrosses range over ocean basins, but forage in comparatively small areas for extended periods of time (Hyrenbach et al. 2002). Usually interpreted as the result of foraging decisions made at meso- (10s to 100s km) and fine-scales (1 to 10 km), we assume that these distribution patterns occur because highly mobile animals remain near a prey patch until the patch is no longer energetically beneficial to the animal (Stephens and Krebs 1986).

Much of the information on the relationship between distributions of upper trophic level predators and hydrographic and bathymetric gradients at synoptic spatial and temporal scales has been anecdotal; the goal of the present study was to determine empirically whether a significant correlation exists between the distribution of marine mammals and seabirds and hydrographic and bathymetric gradients in the region of the Hatteras Front. I hypothesize that the front itself will significantly influence the distribution of marine mammals and seabirds at a daily time scale.

Methods

Study Area

The Hatteras Front is the boundary between the southward flowing Middle Atlantic Bight shelf water and the ambient South Atlantic Bight shelf water (Figure 1). The Hatteras Front coincides with the Gulf Stream seaward of the continental slope. This dynamic coastal system has horizontal and vertical components that meander spatially and temporally, creating one of the most oceanographically complex areas off the eastern United States (Stefansson et al. 1971).

Data Collection

Marine mammal and seabird distribution data and fine-scale synoptic oceanographic data were collected from 1-August to 14-August, 2004, on the 40-meter research vessel, *R/V Cape Henlopen*. A trackline grid was surveyed five times over the course of the cruise. Observers conducted a visual watch from the bridge of the *R/V Cape Henlopen* for marine mammals and seabirds during all daylight hours while the ship was underway (speed > 5 knots), and in a sea state less than Beaufort 5. When weather permitted, oceanographic was collected data 24 hours per day. All sighting, environmental, and positional data were recorded on a laptop running WinCruz, an event-driven program that records sighting and effort data on ship line-transect surveys (Holland 1996).

Data Collection: Marine Mammals

Marine mammal sighting data were collected following Hiby and Hammond (1989) and Palka (1995), and modified when necessary to allow for continuous oceanographic sampling. Three observers rotated through one hour periods of scanning, data recording, and rest. The primary on-watch observer scanned from 90^o abeam to the bow of the ship on the non-glare side, from the near-field out to the horizon with "naked eyes" and 7x hand-held binoculars. The secondary observer (data recorder) recorded effort, sighting, and environmental data, and actively scanned from 90^o abeam to the bow opposite the primary observer when environmental conditions and sighting rate allowed. When the data recorder was actively scanning, her effort was recorded as well. Only sightings made by observer(s) on-watch from 90^o abeam to the bow, without input or cues from others, were recorded as *on-effort* sightings. All other sightings (sightings made past 90^o abeam by on-effort observer, sightings made by others) were entered as *off-effort* sightings and were not used in the analysis.

Sighting information collected for marine mammals included:

- relative angle from the bow of the ship
- reticle from 7x binoculars (distance) (Lerczak and Hobbes 1998)
- lowest taxon identification (to species when possible)
- school size count ("best, high, low" of two observers on watch) and percentage of species if the sighting was of mixed species

Data Collection: Seabirds

Seabird sighting data were collected following Gould and Forsell (1989) and BIOMASS Working Party on Bird Ecology (1992), and modified when necessary to allow for continuous oceanographic sampling. Observers only recorded seabirds if they were within 300 meters of the ship and within the primary observer's scanning swath. To determine distance to the seabird, observers used personal rangefinders (BIOMASS Working Party on Bird Ecology 1992). Observers took great care to observe ship-following behavior to avoid double counting any birds. Most seabirds rest on the water after foraging, so observers also recorded *sitting* and *flying* activities to determine if foraging had recently occurred.

Environmental Observations and Position Data

Observers updated environmental observations at every observer rotation and when a change in the weather altered viewing conditions. Environmental factors included Beaufort sea state, wind speed (knots), true wind direction, swell height (feet), swell direction (magnetic), horizontal and vertical sun position and visibility (nautical miles). Positional data were automatically entered in WinCruz from a handheld Garmin GPS unit linked to the laptop. Positional data included ship's speed (knots), ship's heading (magnetic), latitude, longitude and local time.

Oceanographic Data Collection

Dr. Glen Gawarkiewicz of the Woods Hole Oceanographic Institution (WHOI) and Dr. Dana Savidge of Skidaway Institute of Oceanography developed and implemented the oceanographic sampling design for this survey. Because hydrographic transects that use typical shelf station spacing (~10 km) are inadequate to resolve the position of the front, and the required number of CTD (conductivity/temperature/depth) casts to obtain higher horizontal resolution would compromise the synoptic nature of the sections and reduce the time available to make the repeat crossing needed to record frontal evolution, we towed a Danmark/Chelsea Scanfish MKII undulating CTD sensor (scanfish) 24 hours per day when weather permitted. To resolve the daily position of the Hatteras Front, the scanfish undulated between the surface and 150 meters when in deep water, and between the surface and 3 meters of the bottom in water shallower than 150 meters. The *R/V Cape Henlopen* was also equipped with a ship-mounted Acoustic Doppler Current Profiler (ADCP) that averaged current velocities over 15 minutes at 7m, 15m, 20m, 25m, and 35m depths. The scanfish and ship-mounted ADCP typically render horizontal resolution of about one kilometer after processing (Munchow et al. 1992; Gawarkiewicz et al. 2001). This resolution is adequate to sample the Hatteras Front (Glenn and Ebbesmeyer 1994; Gawarkiewicz et al. 1996; Savidge 2002). To determine the daily position of the Hatteras Front, Dr. Gawarkiewicz mapped temperature, salinity, and fluorescence data in MatLab 7.0.1 using the objective mapping technique described in LeTraon (1990).

Spatial Sampling

I compared occurrence patterns (presence/absence) of marine mammals and seabirds to hydrographic and ecological variables (e.g., depth, slope of seafloor, distance from shore, distance from shelf break, distance from front, temperature, salinity, and fluorescence). Due to Hurricane Alex and mechanical disruptions during the survey period, we only obtained four days of synoptic animal sighting and oceanographic data.

To address the spatial nature of our data, I constructed databases of marine mammal and seabird sightings, trackline effort, and all environmental and physical variables in ArcGIS 9.1 (Environmental Systems Research Institute, Inc.). All databases were projected into Universal Transverse Mercator Zone 18 North (North American Datum 1983).

To describe the environment where marine mammals or seabirds were not observed, I generated pseudo-absence points. First, I determined effective sighting distance for marine mammals (2 km) by calculating the greatest perpendicular sighting distance to the trackline. This distance was then used to create an on-effort buffer area around the trackline. In turn, I generated pseudo-absence points in the on-effort buffer area using the *Generate Random Points* tool in the ArcGIS 9.1 extension, Hawth's Tools (http://www.spatialecology.com/htools/tooldesc.php). Seabird sightings were collected within a 300 meter strip, so I also buffered on-effort sections of the trackline with a 300 meter buffer and generated pseudo-absence points in this buffer for seabirds.

To estimate depth, I downloaded a 3-arc second bathymetry grid from the National Geophysical Data Center website (http://www.ngdc.noaa.gov/mgg/coastal/coastal.html). I calculated slope by running a 3x3 standard deviation focal window on the bathymetry grid. Distance grids for distance from shore, shelf break, and front were produced using Euclidean distance. I defined the shelf break as the 100 meter isobath.

After analyzing the oceanographic data, Dr. Gawarkiewicz resolved the position of the Hatteras Front as the 34 practical salinity unit (psu) contour at 30 meters depth. Frontal positions in a GIS are usually determined by calculating areas with a high rate of change in a hydrographic parameter, but Dr. Gawarkiewicz's definition of the front was the result of his expert knowledge of the area and analysis of the scanfish data. Additionally, Dr. Gawarkiewicz's definition allowed us to work at a higher spatial resolution than traditional methods. I created 2x2 km grids of the objectively mapped temperature, salinity, and fluorescence fields in ArcGIS 9.1. All grids of oceanographic variables were created from the 30 meter depth profiles to be consistent with the position of the Hatteras Front. I sampled all environmental grids at each marine mammal and seabird on-effort sighting, and each marine mammal and seabird pseudo-absence point.

<u>Statistical Analyses</u>

Inherent in ecological data are correlation and autocorrelation. All environmental variables exhibit a degree of correlation with each other. For example, as distance from shore increases, depth typically increases. Autocorrelation reflects the effect of space. When the value of a variable at one location provides some knowledge of its value at another location, the variable is autocorrelated. That is, the similarity between values depends on their separation distance. In cases where autocorrelation occurs, parametric statistics are not a valid option because the assumption of independence is violated. To determine the degree of correlation amongst environmental variables, I performed Pearson's correlation coefficient tests on all the environmental variables.

Mantel's tests are non-parametric regressions that overcome some of the problems noted above. In Mantel's tests, dependent and independent variables are transformed into distance or dissimilarity matrices that summarize pairwise similarities among sample locations (Mantel 1967). Mantel's tests assess whether environmental variables affect observed spatial patterns while accounting for correlation among the variables and autocorrelation (Mantel 1967; Legendre and Fortin 1989; Legendre and Legendre 1998). Using a series of Mantel's tests I assessed which variables had the highest correlation value with the observed distributions of marine mammals and seabirds.

As described in Schick and Urban (2000) and Urban et al. (2002), simple Mantel's tests look at the effect of one variable on species distribution. I used simple Mantel's tests to investigate the effect of each variable on marine mammal and seabird distribution, and to investigate the effect of space (autocorrelation) on each variable. Partial Mantel's tests address a more specific question: What is the effect of each variable on species distribution given that the variables have spatial structure and are correlated with one another? (Schick and Urban 2000). For example, in the case of assessing the influence of fluorescence and depth on seabird distribution, a partial Mantel's test controlling for the effect of space and distance explains the effect fluorescence has on seabird location given that depth is spatially autocorrelated and correlated with fluorescence.

Because of small sample sizes, I did not test for environmental influence on individual marine mammal or seabird species distributions. I assessed all marine mammals as one guild and all seabirds as one guild.

I ran simple and partial Mantel's tests for all marine mammal and seabird data combined over the four days. I then ran daily Mantel's tests on marine mammal and seabird sighting data. All statistical analyses were conducted in SPlus 6.1.

Results

Marine Mammal and Seabird Distributions and Effort

Figure 2 depicts trackline effort and marine mammal and seabird sightings from all survey days. Table 1a summarizes the marine mammal sightings, in which bottlenose dolphins were observed most frequently (39.6%). Table 1b summarizes the seabird sightings, in which unidentified storm petrels were observed most frequently (46.8%).

Environmental Variables

As noted above, the strongest and most persistent signal of the Hatteras Front was 34 psu at 30 meters depth (Glen Gawarkiewicz, personal communication). Over the four days assessed, the position of the front varied (Figure 3).

Pearson's correlation coefficient tests

Marine Mammals

Environmental variables were correlated with each other in 16 (57%) of the 28 possible combinations associated with sightings of marine mammals (Table 2a). The significant ($p < 0.05$) relationships were: 1) as depth increased, temperature and salinity decreased, and distance from front increased; 2) as slope of the seafloor increased, temperature and salinity increased; and 3) as distance from shore increased, salinity increased.

Seabirds

Environmental variables were correlated with each other in 25 (89%) of the 28 possible combinations associated with sightings of seabirds (Table 2b). The significant ($p < 0.05$) relationships were: 1) as depth increased, temperature and salinity decreased, and distance from front and fluorescence increased; 2) as slope increased, temperature and salinity increased, and distance from front and fluorescence decreased; 3) as distance from shore increased, temperature and salinity increased, and distance from front and fluorescence decreased; and 4) as distance from shelf break increased, temperature decreased, and distance from front increased.

Mantel's tests

Marine Mammals

Simple Mantel's results for the marine mammal observations show that all environmental variables except for slope of the seafloor and the distribution of marine mammals were significantly autocorrelated (Table 3a, column 2). The partial Mantel's results suggest that marine mammal distribution was influenced by the static physical variables only (Table 3a, column 3). But when spatial autocorrelation and correlation were controlled for, salinity was the only variable that significantly influenced the distribution of marine mammals (Table 3a, column 4).

Daily Mantel's tests show that no one variable consistently influenced the distribution of marine mammals (Table 4). Distance from shelf break, distance from front, and temperature significantly influenced marine mammal distribution on August 5^{th,}, while slope of the seafloor influenced marine mammal distribution on August 5th and 9th (Table 4).

Seabirds

Simple Mantel's results for the seabird observations show that all environmental variables and the distribution of seabirds were autocorrelated (Table 3b, column 2). Partial Mantel's results suggest that temperature, salinity, and fluorescence influenced seabird distribution (Table 3b, column 3). But when spatial autocorrelation and correlation were controlled for, the effect of space, depth, distance from shelf break, temperature, and fluorescence significantly influenced seabird distribution (Table 3b, column 4). The significance of space indicates that another variable or variables with spatial structure influenced seabird distribution but were not tested.

The results from the daily Mantel's tests show that different combinations of environmental variables influenced the distribution of seabirds on different days (Figure 5). However, one variable consistently influenced seabird distribution – fluorescence (Table 5). Additionally, distance from front was significant on August 5th and 9th and marginally non-significant on August 11th. On August 10th, distance from shelf break was marginally non-significant. On all other days distance from shelf break was not significant (Table 5, column 4). On August 10th, the front meandered almost directly over the shelf break (Figure 3, Aug 10th).

To test for a temporal trend in the influence of fluorescence on seabird distribution I evaluated the confidence limits generated from bootstrapping the pure partial Mantel's correlation coefficient. There was no significant temporal trend in the influence of fluorescence on seabird distribution (Figure 6).

Discussion

The results did not support my hypothesis that the distribution of marine mammals is significantly influenced by the Hatteras Front at a daily time scale, but there was some support for the influence of the Front on the distribution of seabirds. No environmental variable consistently influenced marine mammal distribution. Seabird distribution was influenced by the Front on three of the four days assessed, and fluorescence consistently influenced seabird distribution. It is interesting that distance from front was not a significant influence on the distribution of marine mammal at a daily time scale. However, Mantel's tests assume linear relationships, so if the relationship between the Front and the species distributions is not linear, then Mantel's tests will not capture the relationship.

Several aspects of my survey design may have swayed my results. Results from spatial analyses are highly dependent on the spatial and temporal scales at which the data are collected. Patterns in species distributions can be overlooked if the scale at which the data are collected is too small, or patterns can be smoothed over if the scale is too large (Levin 1992). The small number of marine mammal sightings in a relatively small survey area may have produced an incomplete pattern of species distribution. If the scale at which I collected the data was too small, the Mantel's tests would not determine any significant relationships between the environmental variables and the distribution of marine mammals. Future studies off Cape Hatteras should include areas further from the Front to increase the spatial scale.

Observers only collected sighting data during daylight hours, which may have introduced a diurnal bias. For example, pilot whales may prefer nocturnal foraging because their preferred prey, long-finned squid (*Loligo pealei*), ascends in the water column at night (Gannon et al. 1997). Observations of pilot whales accounted for approximately 25% of the marine mammal sightings. Due to the large daily variation in the position of the Front, and the possibility that pilot whales were foraging at night, the pilot whales observed could have been completely unassociated with foraging activities even if they were associated with the Front itself.

My results suggest that the distribution of seabirds is influenced by fluorescence. Fluorescence is the luminescence caused by the absorption of radiation at a particular wavelength. Due to the wavelength used to measure fluorescence, this environmental variable is a proxy for chlorophyll. Chlorophyll can account for up to 65% of plankton biomass (Lohrenz et al. 2002; personal communication Veronica Lance, Duke Marine Laboratory). My analysis indicates that chlorophyll concentrations in the area consistently influenced seabird distribution. Seabirds are upper trophic level marine predators, and, as such, are likely responding to aggregations of plankton and small fish which, in turn, are responding to concentrations of chlorophyll. I did not collect seabird prey data, but we did collect ADCP data which provides information on plankton and fish biomass. To better understand the relationship between fluorescence and the distribution of seabirds, I am analyzing the backscatter data and will incorporate it in another suite of spatial analyses.

Although not consistent over all days tested, distance from front was shown to influence seabird distribution on three days. On the one day distance from front was not significant (August 10th), distance from shelf break was marginally non-significant. Additionally, the front meandered almost directly over the shelf break on August 10th. As the two variables occupied the same geographic space, Mantel's tests were not able to separate the relationships between the Front and seabird distribution, and the shelf break and seabird distribution. It is likely that the Hatteras Front consistently influenced seabird distribution at the spatial and temporal scale we examined.

The influence of the Front on seabird distribution may seem counter-intuitive when one considers that we described the Front at 30 meters depth and that most of the seabird sightings were not sightings of deep diving species (approximately 47% of seabird sightings were of unidentified storm petrels, which forage at the water's surface). Additionally, the vertical distribution of the front differs from the horizontal distribution due to entrainment of the Middle Atlantic and South Atlantic Bight waters into the Gulf Stream (Glen Gawarkiewicz personal communication). To determine if these vertical displacements affected the results, I am in the process of determining surface fluorescence values. Once surface fluorescence is determined, I will calculate chlorophyll concentrations. Additionally, I am calculating frontal positions from fluorescence gradients to determine if there is a relationship between fluorescence fronts and seabird distribution.

In this study, I described a suite of analytical techniques that provide an effective test of observed species distribution in the face of potentially confounding variables. Mantel's tests are only exploratory analysis tools, but my preliminary results provide quantitative information on the spatial and temporal scales of marine mammal and seabird distributions.

Acknowledgements

I would like to especially thank Dr. Gawarkiewicz and Dr. Savidge for allowing me to join their research cruise. Their collaboration on this project was essential. I would like to thank my advisor, Dr. Andrew Read, and my *secondary advisor* Dr. Pat Halpin for their support and guidance. I would like to thank Dr. Dean Urban, Caroline Good, Leigh Torres, and Dr. Ari Friedlaender for their statistical assistance, insights, and comments on my master's project. Danielle Waples, Lynne Williams, and Leigh Torres gave copious amounts of moral support and commented liberally on drafts of this paper – my sanity would not have survived without them. Thank you. I particularly owe a debt of gratitude to Jason Roberts. He always took time out of his busy schedule to fix whatever computer or software glitch arose (and there were many), and constantly humored me by listening to all of my far-fetched ideas. Thank you.

I would also like to thank my family for all their support, encouragement, and understanding.

This research was partially supported by the *Predictive Spatial Analysis of Marine Mammal Habitats* project funded by the Strategic Environmental Research and Development Program, and the *Digital Archive of Marine Mammal/Bird/Turtle Data for the Ocean Biogeographic Information System* project funded by the Alfred P. Sloan Foundation.

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Table 1a

Number and percent of marine mammal species sighted while on-effort.

Common Name	Species Name	# of *on-effort* sightings	% of total sightings
Bottlenose dolphin	*Tursiops truncatus*	21	39.6
Risso's dolphin	*Grampus griseus*	1	1.9
Pilot whales	*Globicephala ssp.*	13	24.5
Striped dolphin	*Stenella coeruleoalba*	1	1.9
Atlantic spotted dolphin	*Stenella frontalis*	1	1.9
Cuvier's beaked whale	*Ziphius cavirostris*	3	5.7
unidentified *Stenella* ssp.		2	3.8
unidentified dolphin		10	18.9
unidentified small dolphin		1	1.9
Total		53	100

Table 1b

Number and percent of seabird species sighted while on-effort.

Common Name	Species Name	# of *on-effort* sightings	% of total sightings
Manx shearwater	*Puffinus puffinus*	1	0.4
Audubon's shearwater	*Puffinus lherminieri*	5	2.2
Cory's shearwater	*Calonetris diomedea*	10	4.3
Greater shearwater	*Puffinus gravis*	14	6.1
Leach's storm petrel	*Oceanodrama leucorhoa*	7	3.0
Wilson's storm petrel	*Oceanites oceanicus*	5	2.2
unidentified shearwater		36	15.6
unidentified petrel		10	4.3
unidentified sorm petrel		108	46.8
unidentifed gull		12	5.2
small tern		9	3.9
unidentified bird		14	6.1
Total		231	100

Table 2a

The Pearson linear correlation coefficients (*r*) among environmental variables for marine mammals. Significant correlation coefficients are in bold font ($p < 0.05$), degrees of freedom = 86.
dpth = depth, slp = slope of seafloor, dtsh = distance from shore, dtshbk = distance from shelf break, dtft = distance from front, th = temperature, sal = salinity, flr = fluorescence.

Marine Mammals

	dpth	slp	dtsh	dtshbk	dtft	th	sal
dpth	1						
slp	**-0.3557**	1					
dtsh	**-0.8712**	**0.3180**	1				
dtshbk	**-0.5931**	**-0.2121**	**0.4575**	1			
dtft	**0.3996**	-0.1963	**-0.4530**	-0.1434	1		
th	**-0.2776**	**0.2385**	0.1278	-0.0999	-0.0903	1	
sal	**-0.3739**	**0.3196**	**0.2488**	-0.0092	-0.0530	**0.9466**	1
flr	0.1198	-0.1197	0.0637	0.1408	0.0019	**-0.9044**	**-0.8462**

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Table 2b

The Pearson linear correlation coefficients (*r*) among environmental variables for seabirds. Significant correlation coefficients are in bold font ($p < 0.05$), degrees of freedom = 377.
dpth = depth, slp = slope of seafloor, dtsh = distance from shore, dtshbk = distance from shelf break, dtft = distance from front, th = temperature, sal = salinity, flr = fluorescence.

Seabirds

	dpth	slp	dtsh	dtshbk	dtft	th	sal
dpth	1						
slp	**-0.4338**	1					
dtsh	**-0.8336**	**0.4604**	1				
dtshbk	**-0.2362**	**-0.2959**	**-0.1672**	1			
dtft	**0.3348**	**-0.3573**	**-0.4934**	**0.2528**	1		
th	**-0.4488**	**0.2864**	**0.3690**	**-0.1269**	**-0.1841**	1	
sal	**-0.5686**	**0.3397**	**0.4916**	-0.0652	**-0.1724**	**0.9285**	1
flr	**0.2496**	**-0.1237**	**-0.0710**	0.0273	0.0553	**-0.8469**	**-0.7719**

Table 3a

Mantel's results for combined marine mammal observations. Column 1 ($r_{(mm*e)}$): regression of variables on marine mammal distribution. Column 2 (r(mm or e|s)): test of spatial autocorrelation for each variable and marine mammal distribution. Column 3 ($r_{(mm*e|e)}$): partial Mantel's test of the influence of each variable on marine mammal distribution controlling for spatial autocorrelation. Column 4 ($r_{(mm*e|e*s)}$): pure partial Mantel's test of the influence of each variable on marine mammal distribution controlling for spatial autocorrelation and correlation with other variables. The first value in column 4 is the effect of space on marine mammal distribution controlling for all environmental variables. ns = not significant

	Column 1		**Column 2**		**Column 3**		**Column 4**	
Overall	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Marine mammal distribution			ns				ns	
Depth	0.041	0.031	0.386	0.001	0.035	0.039	ns	
Slope of seafloor	0.031	0.038	ns		0.030	0.045	ns	
Distance from shore	0.035	0.021	0.606	0.001	0.028	0.021	ns	
Distance from shelf break	ns		0.387	0.001	ns		ns	
Distance from front	ns		0.299	0.001	ns		ns	
Temperature	ns		0.547	0.001	ns		ns	
Salinity	ns		0.439	0.001	ns		0.034	0.018
Fluorescence	ns		0.527	0.001	ns		ns	

Table 3b

Mantel's results for combined seabird observations. Column 1 ($r_{(mm*e)}$): regression of variables on seabird distribution. Column 2 (r(mm or e|s)): test of spatial autocorrelation for each variable and seabird distribution. Column 3 ($r_{(mm*e|e)}$): partial Mantel's test of the influence of each variable on seabird distribution controlling for spatial autocorrelation. Column 4 ($r_{(mm*e|e*s)}$): pure partial Mantel's test of the influence of each variable on seabird distribution controlling for spatial autocorrelation and correlation with other variables. The first value in column 4 is the effect of space on seabird distribution controlling for all environmental variables. ns = not significant

	Column 1		**Column 2**		**Column 3**		**Column 4**	
Overall	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Seabird distribution			0.067	0.001			0.036	0.001
Depth	0.025	0.002	0.434	0.001	ns		0.013	0.011
Slope of seafloor	0.011	0.011	0.093	0.002	ns		ns	
Distance from shore	ns		0.744	0.001	ns		ns	
Distance from shelf break	ns		0.389	0.001	ns		0.008	0.036
Distance from front	0.018	0.001	0.351	0.001	ns		ns	
Temperature	0.105	0.001	0.413	0.001	0.085	0.001	0.035	0.001
Salinity	0.082	0.001	0.323	0.001	0.064	0.001	ns	
Fluorescence	0.077	0.001	0.363	0.001	0.057	0.001	0.057	0.001

Table 4

Mantel's results for daily marine mammal observations. Column 1 ($r_{(mm*e)}$): regression of variables on marine mammal distribution. Column 2 (r(mm or e|s)): test of spatial autocorrelation for each variable and marine mammal distribution. Column 3 ($r_{(mm*e|e)}$): partial Mantel's test of the influence of each variable on marine mammal distribution controlling for spatial autocorrelation. Column 4 ($r_{(mm*e|e*s)}$): pure partial Mantel's test of the influence of each variable on marine mammal distribution controlling for spatial autocorrelation and correlation with other variables. The first value in column 4 is the effect of space on marine mammal distribution controlling for all environmental variables.
ns = not significant

	Column 1		**Column 2**		**Column 3**		**Column 4**	
5-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Marine Mammal distribution			ns				ns	
Depth	ns		0.624	0.001	ns		ns	
Slope of seafloor	0.257	0.042	0.510	0.003	0.2179	0.034	0.326	0.014
Distance from shore	0.2756	0.022	ns		ns		ns	
Distance from shelf break	0.2756	0.022	ns		0.2585	0.031	0.285	0.023
Distance from front	0.1682	0.045	0.721	0.001	ns		0.208	0.020
Temperature	ns		0.581	0.001	ns		0.147	0.049
Salinity	ns		0.694	0.001	ns		ns	
Fluorescence	ns		0.225	0.058	ns		ns	

9-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Marine Mammal distribution			ns				ns	
Depth	0.341	0.026	ns		0.331	0.001	ns	
Slope of seafloor	0.753	0.024	ns		0.757	0.033	0.760	0.030
Distance from shore	ns		0.592	0.010	0.341	0.001	ns	
Distance from shelf break	ns		ns		ns		ns	
Distance from front	ns		0.800	0.011	ns		ns	
Temperature	ns		0.830	0.002	ns		ns	
Salinity	ns		0.619	0.020	ns		ns	
Fluorescence	ns		0.680	0.009	ns		ns	

10-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Marine Mammal distribution			ns				ns	
Depth	ns		0.494	0.001	ns		ns	
Slope of seafloor	ns		ns		ns		ns	
Distance from shore	ns		0.613	0.001	ns		ns	
Distance from shelf break	ns		0.355	0.001	ns		ns	
Distance from front	ns		0.266	0.001	ns		ns	
Temperature	ns		0.574	0.001	ns		ns	
Salinity	ns		0.374	0.001	ns		ns	
Fluorescence	ns		0.431	0.001	ns		ns	

11-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Marine Mammal distribution			ns				ns	
Depth	ns		0.587	0.001	ns		ns	
Slope of seafloor	ns		ns		ns		ns	
Distance from shore	ns		0.744	0.001	ns		ns	
Distance from shelf break	ns		0.403	0.001	ns		ns	
Distance from front	ns		0.522	0.001	ns		ns	
Temperature	ns		0.456	0.001	ns		ns	
Salinity	ns		0.402	0.003	ns		ns	
Fluorescence	ns		0.412	0.001	ns		ns	

Table 5

Mantel's results for daily seabird observations. Column 1 ($r_{(mm*e)}$): regression of variables on seabird distribution. Column 2 (r(mm or e|s)): test of spatial autocorrelation for each variable and seabird distribution. Column 3 ($r_{(mm*e|e)}$): partial Mantel's test of the influence of each variable on seabird distribution controlling for spatial autocorrelation. Column 4 ($r_{(mm*e|e*s)}$): pure partial Mantel's test of the influence of each variable on seabird distribution controlling for spatial autocorrelation and correlation with other variables. The first value in column 4 is the effect of space on seabird distribution controlling for all environmental variables. ns = not significant

	Column 1		**Column 2**		**Column 3**		**Column 4**	
5-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Seabird distribution			0.164	0.001			0.040	0.047
Depth	0.239	0.001	0.705	0.001	0.177	0.001	ns	
Slope of seafloor	0.078	0.009	0.208	0.001	0.046	0.021	ns	
Distance from shore	ns		0.849	0.004	ns		ns	
Distance from shelf break	ns		0.129	0.000	ns		ns	
Distance from front	0.042	0.037	0.769	0.001	ns		0.059	0.009
Temperature	0.271	0.001	0.559	0.001	0.219	0.001	0.117	0.002
Salinity	0.253	0.001	0.685	0.001	0.196		ns	
Fluorescence	0.144	0.002	0.196	0.001	0.116	0.003	0.116	0.002

9-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Seabird distribution			0.053	0.035			ns	
Depth	ns		0.312	0.001	ns		ns	
Slope of seafloor	ns		0.219	0.001	ns		ns	
Distance from shore	ns		0.650	0.001	ns		ns	
Distance from shelf break	ns		0.469	0.001	ns		ns	
Distance from front	0.041	0.035	0.594	0.001	ns		0.035	0.045
Temperature	0.092	0.004	0.576	0.001	0.075	0.004	0.033	0.025
Salinity	0.036	0.021	0.466	0.001	ns		ns	
Fluorescence	0.072	0.003	0.377	0.001	0.056	0.004	0.056	0.007

10-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Seabird distribution			0.139	0.001			0.068	0.001
Depth	0.048	0.003	0.465	0.001	ns		ns	
Slope of seafloor	0.049	0.005	0.070	0.005	0.039	0.004	0.017	0.044
Distance from shore	ns		0.748	0.001	ns		ns	
Distance from shelf break	ns		0.348	0.001	ns		0.018	0.053*
Distance from front	0.081	0.001	0.229	0.001	0.051	0.002	ns	
Temperature	0.213	0.001	0.393	0.001	0.174	0.001	ns	
Salinity	0.197	0.001	0.207	0.001	0.174	0.001	0.061	0.001
Fluorescence	0.164	0.001	0.487	0.001	0.111	0.001	0.111	0.001

11-Aug-04	$r_{(mm*e)}$	p value	$r_{(mm\ or\ e\|s)}$	p value	$r_{(mm*e\|s)}$	p value	$r_{(mm*e\|e*s)}$	p value
Seabird distribution			ns				ns	
Depth	ns		0.603	0.001	ns		ns	
Slope of seafloor	ns		0.130	0.002	ns		ns	
Distance from shore	ns		0.764	0.001	ns		0.011	0.100
Distance from shelf break	ns		0.290	0.001	ns		ns	
Distance from front	ns		0.535	0.001	0.022	0.026	0.015	0.058*
Temperature	0.016	0.050	0.312	0.001	ns		ns	
Salinity	0.017	0.049	0.295	0.001	0.015	0.049	ns	
Fluorescence	0.018	0.047	0.356	0.001	0.015	0.049	0.016	0.039

*marginally non-significant

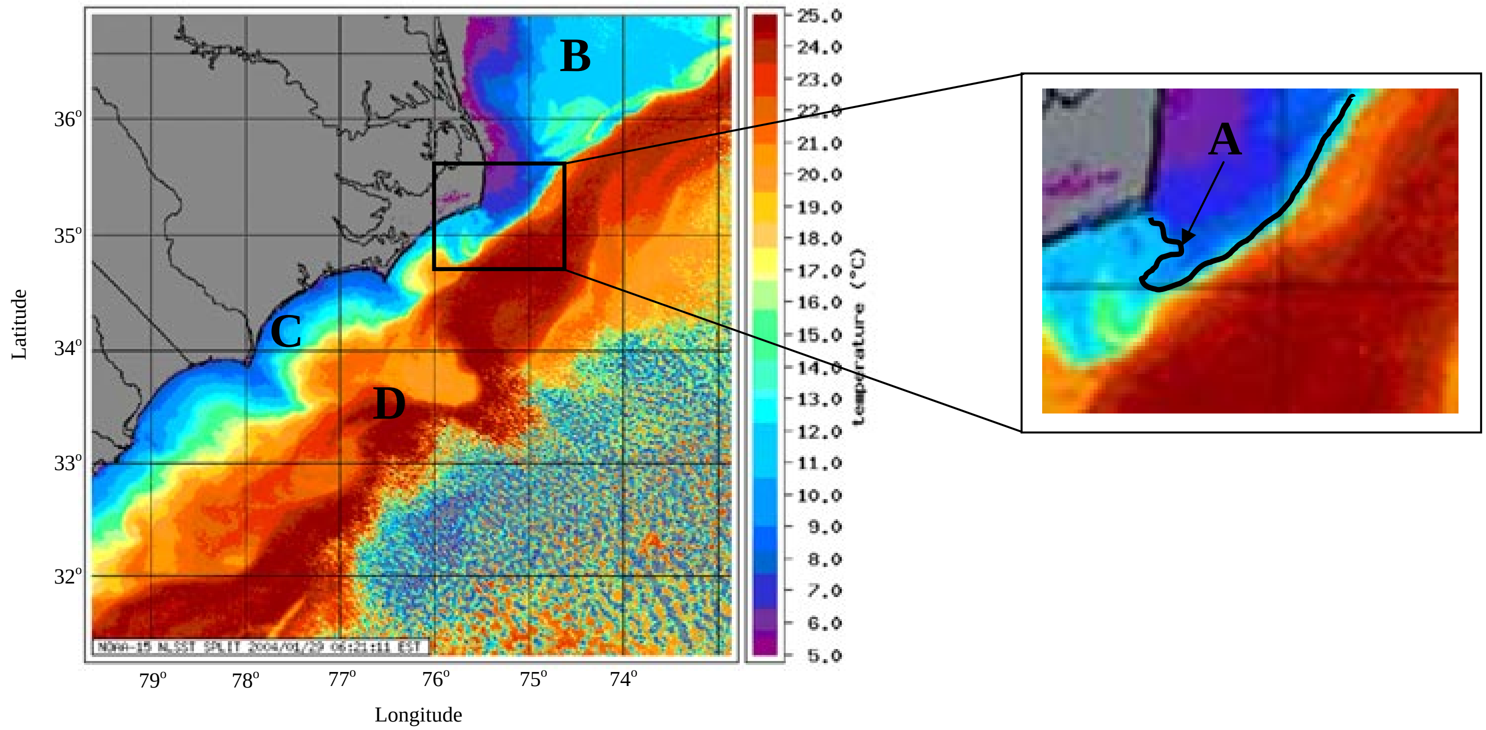

Figure 1
A satellite image of sea surface temperature showing a sharp thermal gradient over the continental shelf off Cape Hatteras. The Hatteras Front (A) is formed by the convergence of southward flowing Middle Atlantic Bight continental shelf water (B) and northward flowing South Atlantic Bight continental shelf water (C). The Hatteras Front is also influenced by the Gulf Stream (D). http://www.whoi.edu/science/PO/hatterasfronts/index.html

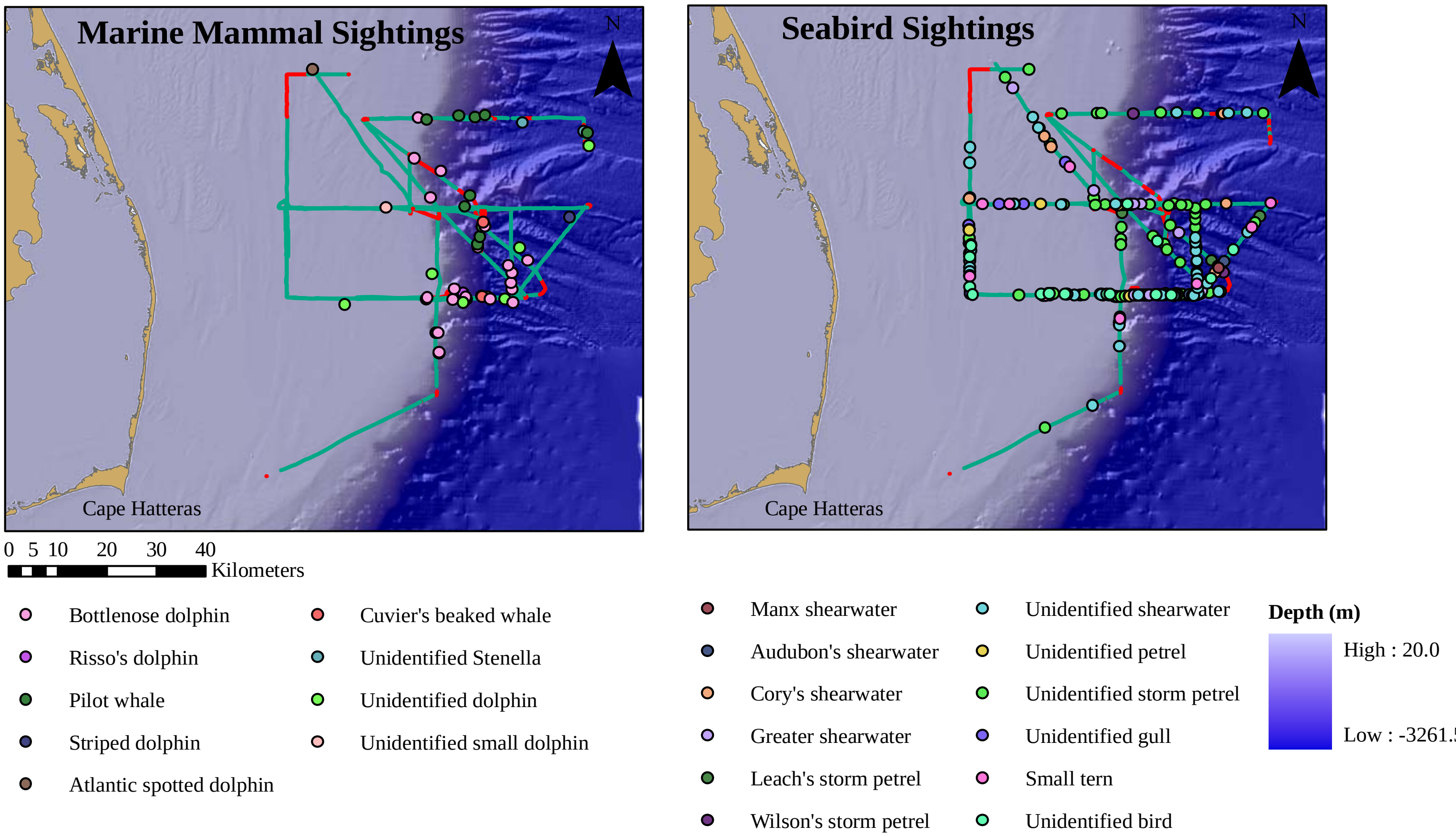

Figure 2
All on-effort marine mammal and seabird observations overlaid on a bathymetry grid. Lines represent ship's tracklines color coded by effort. Green lines = on-effort. Red lines = off-effort.

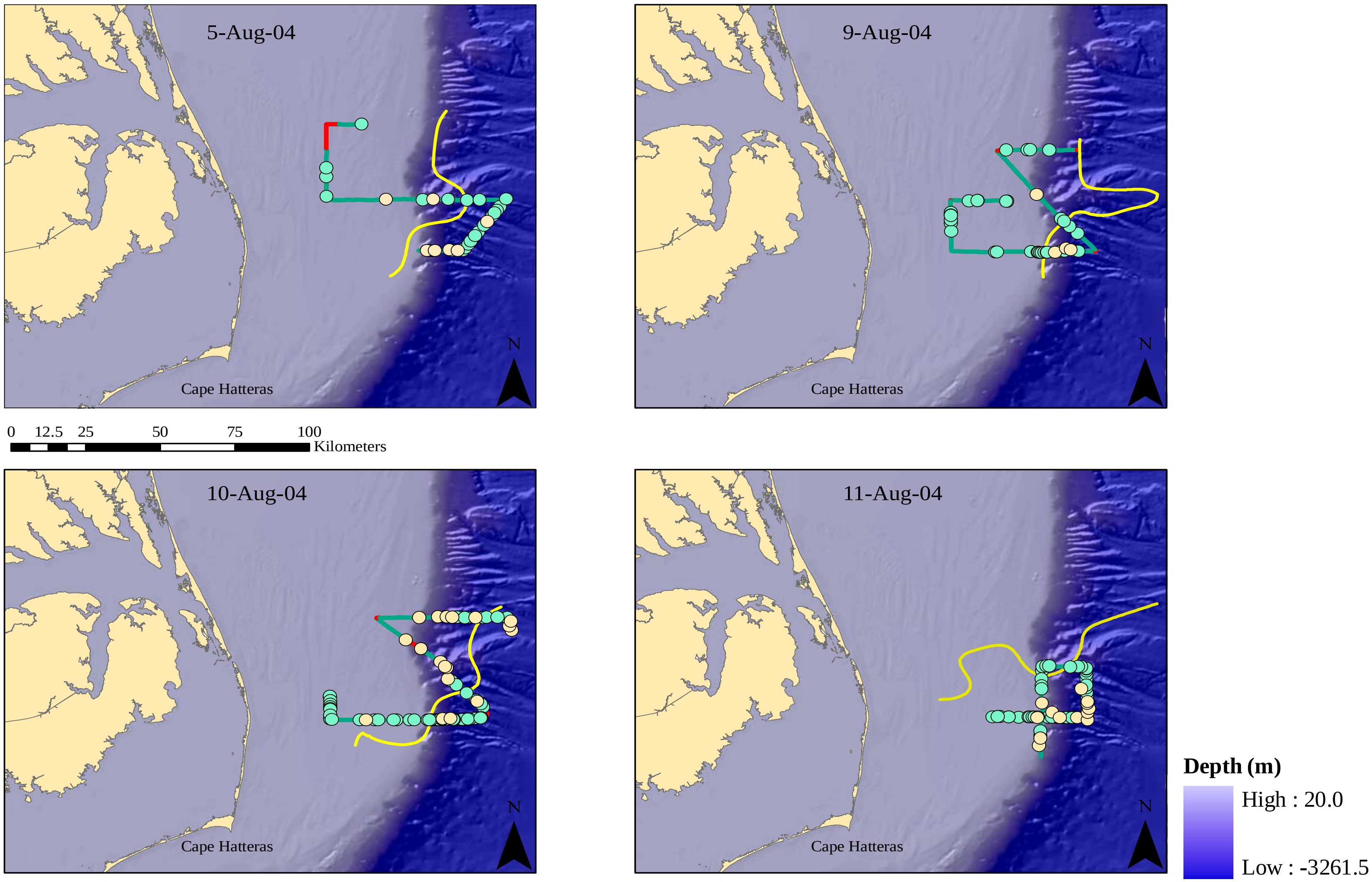

Figure 3
Daily observations of marine mammals (beige dots) and seabirds (green dots) overlaid on a bathymetry grid. The yellow line is the position of the Hatteras Front. Ship's tracklines are color-coded by effort: green = on-effort; red = off-effort.

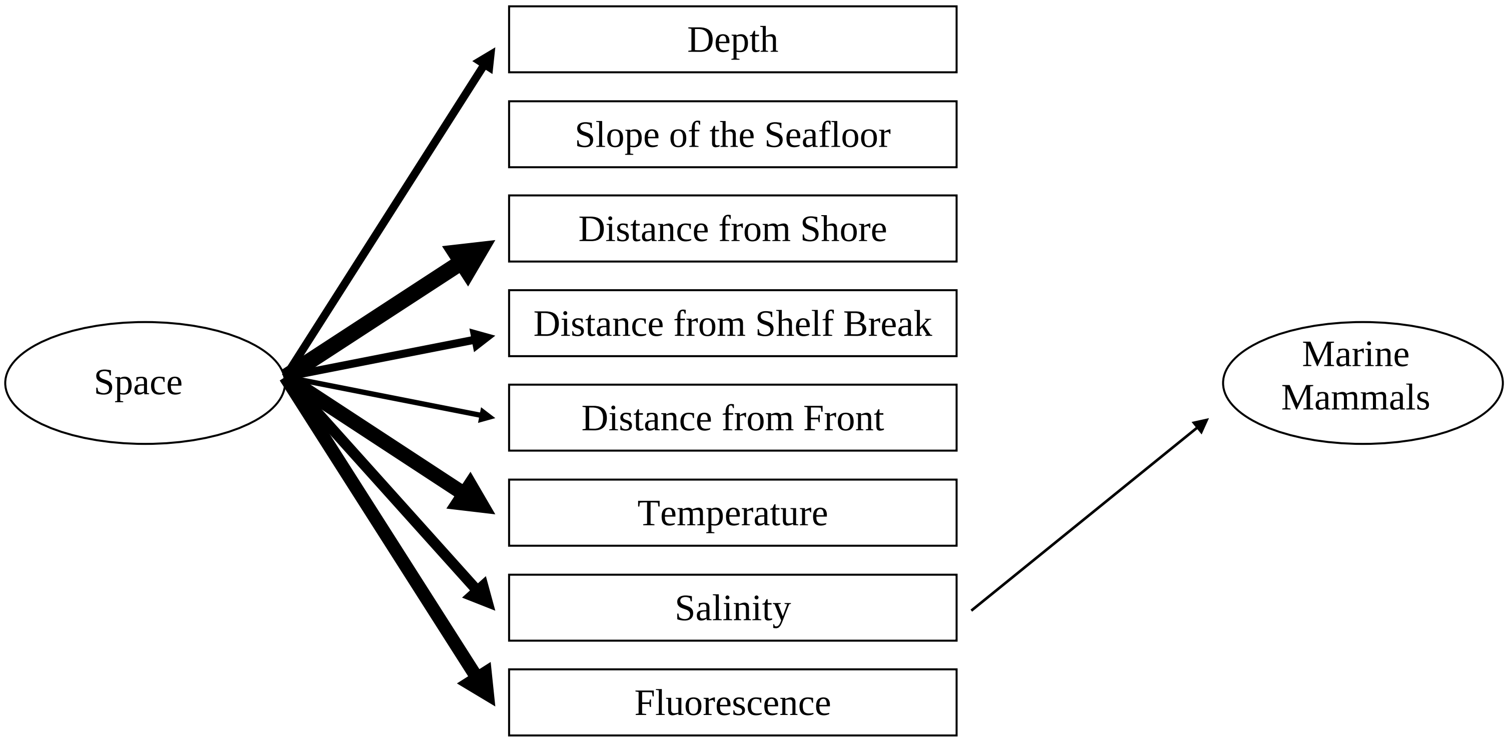

Figure 4
Results from simple and pure partial Mantel's tests on marine mammal observations presented as a path diagram. Arrows represent a significant effect and thickness represents the strength of the correlation . Arrows from *Space* to an environmental variable indicate spatial structure. The arrow from *Salinity* to *Marine Mammals* indicates an influence of salinity on marine mammal distribution when autocorrelation and correlation are taken into account.

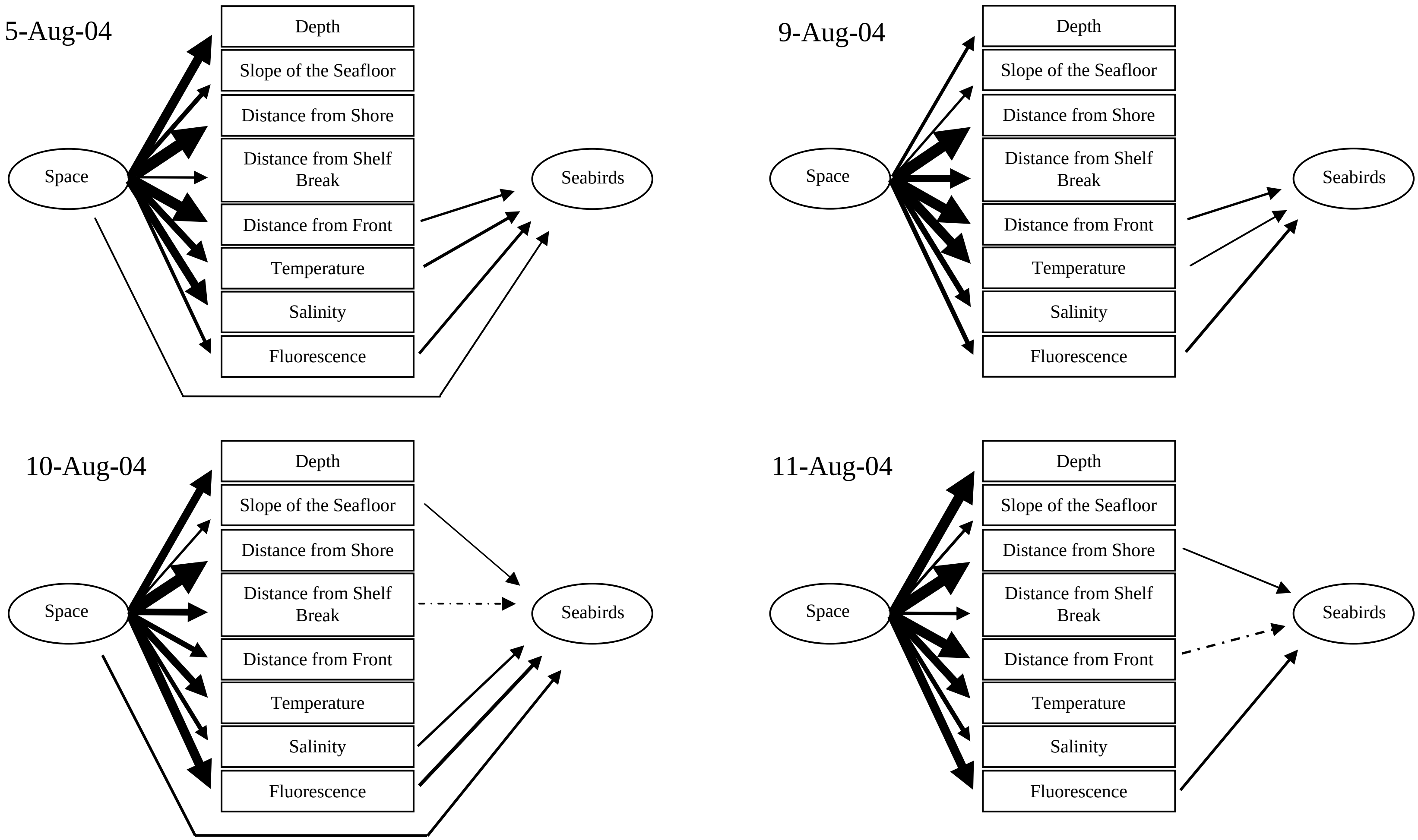

Figure 5

Results from simple and pure partial Mantel's tests on daily seabird observations presented as a path diagram. Arrows represent a significant effect and thickness represents the strength of the correlation . Arrows from *Space* to an environmental variable indicate spatial structure. Arrows from an environmental variable to *Seabirds* indicate an influence on seabird distribution when autocorrelation and correlation are taken into account. Marginal results are represented with a broken line.

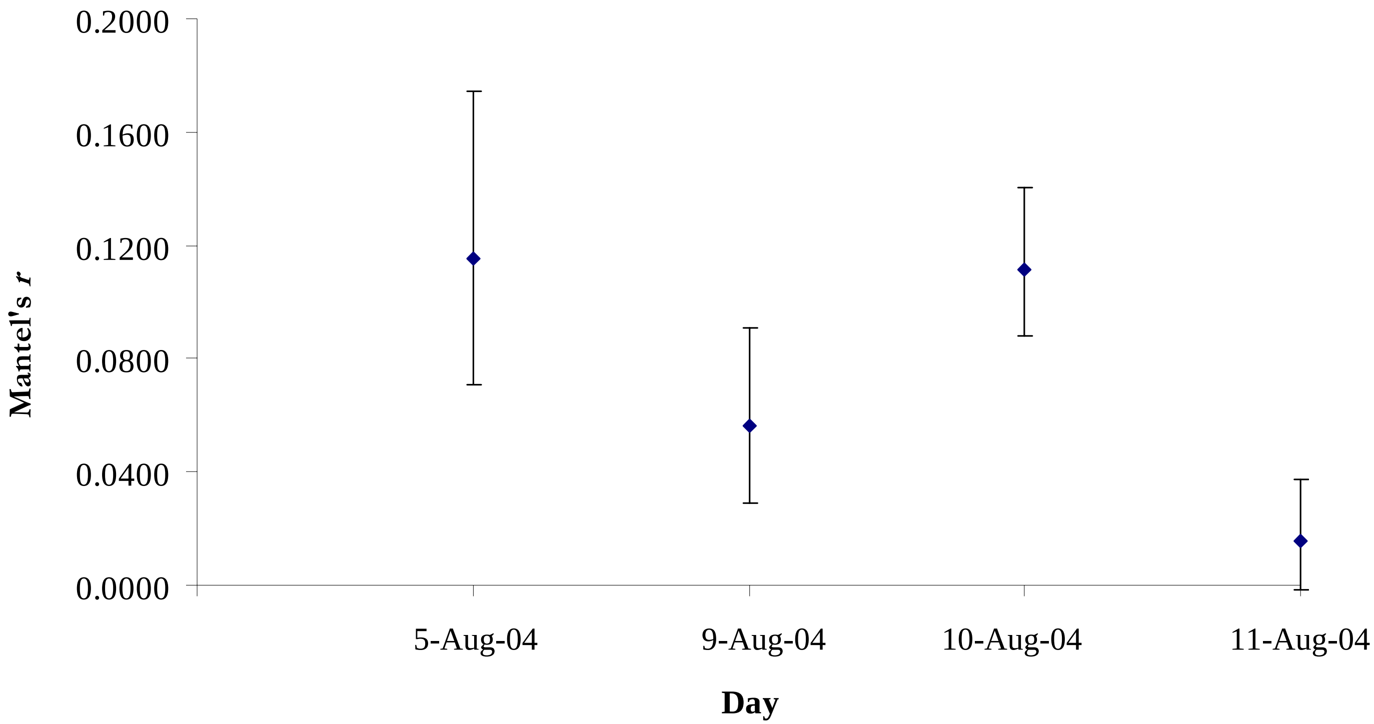

Figure 6
Daily pure partial Mantel’s correlation coefficient (*r*) of fluorescence and seabird distribution.
Confidence intervals were determined from 10,000 bootstrap iterations.