PATTERNS OF MARINE BIRD BIODIVERSITY AND HABITAT USE IN THE GULF OF MAINE

By

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ABSTRACT

Vessel surveys of birds at sea provide important information about marine ecology and food webs. The Gulf of Maine and Scotian Shelf are productive habitats for seabirds that breed in both the Northern and Southern Hemispheres. I examined seabird vessel survey data from the 1980s through the 2000s in these areas during summer. My objective was to understand changes in seabird distributions, abundances, diversity and aggregations. Nonbreeding Southern Hemisphere species far outnumbered locally breeding species. Modeled habitat relationships for the dominant species showed that trans-equatorial Great Shearwaters (Puffinus gravis) were found in colder, deeper waters off the coast. A comparison of habitat use by Leach's Storm-Petrels (Oceanodroma leucorhoa) and trans-equatorial migrant Wilson's (Oceanites oceanicus) showed Leach's Storm-Petrels closer to temperature fronts, but in lower chlorophyll density areas, while Wilson's Storm-Petrels had no relationship to fronts or chlorophyll densities, but were seen in deeper more oceanic waters. Overall seabird numbers increased from the 1980s to the 2000s and species composition changed. Audubon's Shearwaters (Puffinus lherminieri), Common Terns (Sterna hirundo), and Atlantic Puffins (Fratercula arctica) increased significantly, and Sooty Shearwaters (Puffinus griseus) declined significantly. Average taxonomic distinctness, a diversity measure used to indicate relatedness of a group of species, increased, showing greater distinctness (decreased relatedness) among seabirds studied. High species diversity, densities of seabirds, and endangered species use, e.g. Roseate Terns, identified key areas, such as the Jordan Basin, that warrant further investigation.

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Chapter 1 General Introduction

Seabirds are highly mobile energy-demanding top predators that exploit predictable and ephemeral productive habitats in marine ecosystems (Hunt 1990). They are sensitive to changes in the marine environment from human exploitation of oceanic resources, pollution, and climate change. They respond rapidly to environmental change and their conspicuousness and vulnerability to both oceanographic and anthropogenic changes make them robust bio-indicators of the ocean environment (Schneider and Heinemann 1996). They can indicate the state of the food webs that support top predators (Davoren et al. 2003a) as well as the levels of pollution or toxic chemicals in the ocean environment (Blais et al. 2005, Goodale et al. 2008).

Seabird at-sea survey data are used to capture patterns of seabird distribution and diversity (e.g. Brown 1986). At-sea surveys can also be used to detect changes in the seabird community structure and to assess changes in seabird populations (Veit et al. 1997, Mallory et al. 2006). To evaluate risks posed by environmental influences, studies that link the ecology of seabirds at sea to the biophysical marine environment are needed (Gonzáles-Solís and Shaffer 2009).

A wealth of multi-species data on diversity, distribution, seasonal changes and the abundance of seabirds were collected from vessel surveys in the Gulf of Maine during the 1970s to the early 1990s. These data were collected to supply basic information on the ecology and distributions of seabirds in Atlantic Canada as a response to growing public concern with both seabird and general environmental health (Brown et al. 1975). After a hiatus of more than a decade, seabird surveys were resumed in 2006 in Atlantic Canada by the Canadian Wildlife Service (CWS). The recent survey data can be used as baseline data for contemporary and historic comparisons of seabird distributions, diversity and community assemblages (Huettmann and Diamond 2006, Gjerdrum et al. 2012). Comparisons of recent and archived survey data are being used to highlight and evaluate changes in biodiversity, abundance, distribution, and aggregations. Owing to ocean climate change, anthropogenic activity at sea, as well as changes in terrestrial breeding habitat, the relative diversity and numbers of birds using the marine ecosystem has changed during recent decades (Nisbet et al. 2013).

In this thesis, I examined the summer diversity and distributions of seabird species in the Gulf of Maine. I built models using biophysical environmental features to examine the relationships between seabird species and their habitat. I interrogated seabird diversity using and comparing a battery of diversity indices. I compared the recent surveys with those of previous decades to assess changes. I highlighted important marine areas, consider environmental risks for birds at sea and identified research gaps and opportunities that warrant further study.

1.1. Study Site

This study is focused on the Gulf of Maine, including Georges Bank and southern portions of the Scotian Shelf (Figure 1.1). The Labrador Current brings cold fresh waters from the Arctic to the Scotian Shelf, which is also influenced by the warm, salty Gulf Stream waters from the south. The Gulf of Maine and Scotian Shelf have broad continental shelves with year round fluxes and tidal mixing of nutrient-rich deep waters and winter convective mixing that replenish surface nutrients. These physical processes facilitate an extensive spring plankton bloom (Townsend et al. 2004) which creates a highly productive environment that supports large populations of local breeders and non-breeding migrant seabirds during summer (Brown 1986, Nisbet et al. 2013).

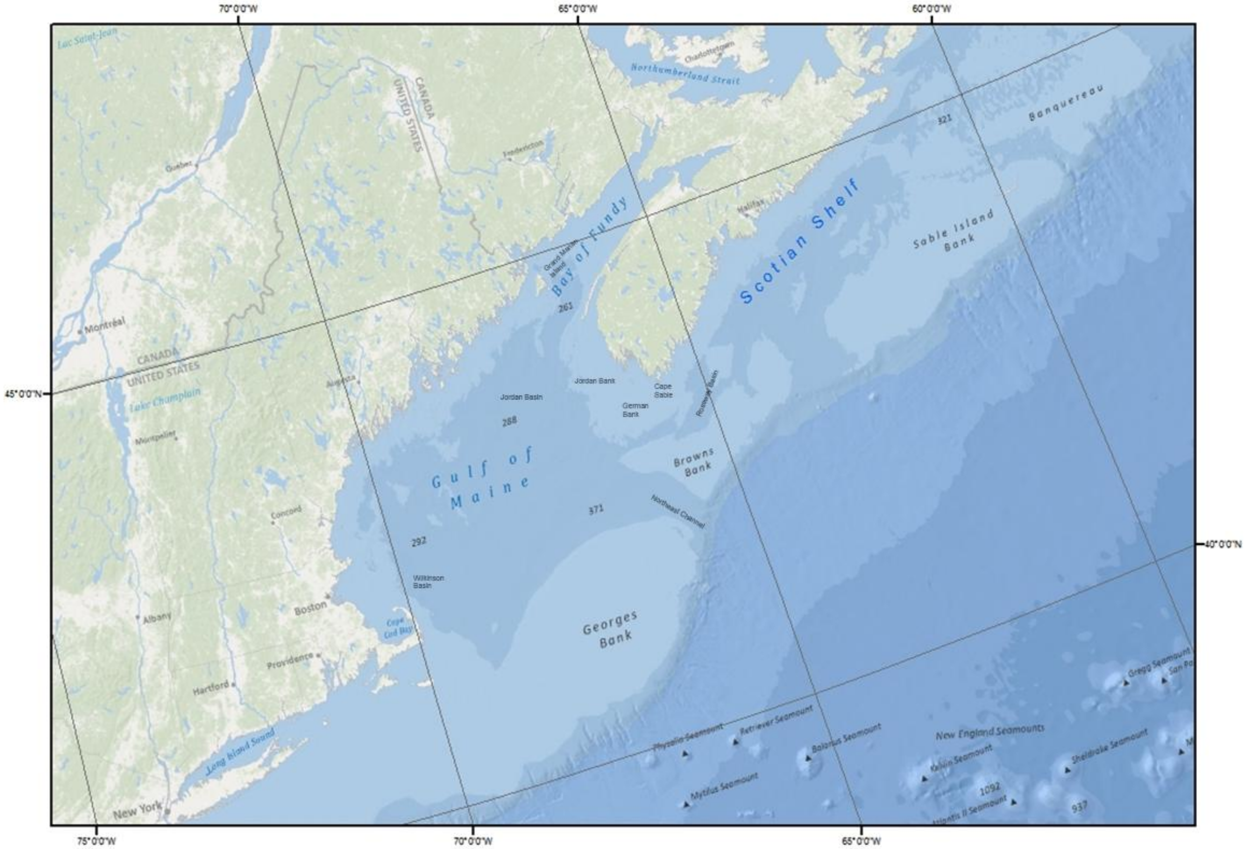

Figure 1.1: The study area for this thesis is the Gulf of Maine, including the Bay of Fundy, Georges Bank, and the Scotian Shelf.

Global climate change is likely influencing seabird populations in the Gulf of Maine (Nisbet et al. 2013). Elsewhere, for example, warming water trends have been associated with declines of Sooty Shearwaters (Puffinus griseus) in the California Current and increases in Northern Gannets (Morus bassanus) in Newfoundland (Veit and Montevecchi 2006).

In the Gulf of Maine changes in water mass are associated with the North Atlantic Oscillation (NAO) oceanographic index. The NAO is an oscillation of wintertime surface atmospheric pressure systems over the Icelandic (low) and the subtropical Atlantic (high), and operates on a decadal scale (Townsend et al. 2004). The index is measured as a difference relative to a long term mean, and the oscillations drive an oceanographic response that affects the shelf waters in the Northwest Atlantic. In low or negative NAO years with small north-south pressure differences, the Labrador Current can travel further southward as far as the New York Bight because the north wall of the Gulf Stream warm waters is displaced to the south, while in high or positive years, the Labrador Current only reaches as far south as the Laurentian Channel (Townsend et al. 2004). These fluctuations influence not only water temperatures, but also the regional nutrient fluxes. The thermal and nutrient changes influence many taxa in the North Atlantic ecosystem, including the food web supporting seabirds in the Gulf of Maine (Drinkwater et al. 2003).

1.2 Seabirds and Ocean Habitat

Many environmental habitat variables influence the distributions of seabirds (Huettmann and Diamond 2006). Temperature or chlorophyll fronts are often areas of higher marine productivity and biomass, due either to increased local primary production and/or prey transport to fronts by convergence (Schneider 1982, Bost et al. 2009). Cory's Shearwaters (Calonectris diomedea), for example, aggregate at Gulf Stream hydrographic fronts in the South Atlantic Bight that are associated with enhanced food availability because the water is well mixed with organisms retained by the convergence zone of the shear front (Haney and McGillivary 1985). Areas where birds aggregate are indicative of biodiversity hotspots for animals beyond marine birds (Louzao et al. 2009, Davoren 2013). Other physical factors that influence seabird distributions include thermocline depth and chlorophyll density (Ballance et al. 1997), ice and water column stratification (Hunt 1990), sea surface temperature, seabed slope, depth, distance from the coast (Amorim et al. 2009), persistent chlorophyll anomalies (Suryan et al. 2012), and prey abundance and conspecific behaviour (Davoren et al. 2003b). In my study, I interrogated seabird distributional data in relation to several habitat variables: sea surface temperature, chlorophyll density, water depth, bathymetric slope, distance to SST front, distance from the coast, and distance to the 1000-m isobath.

1.3 Biodiversity

Studying species diversity, or species richness, over time provides insight into the persistence and dynamics of species aggregations (Hamilton 2005). Persistence or stability can reflect the resiliency of an ecosystem to recover following disturbance. In theory, species-rich communities have more animals with varying traits and therefore a greater capability for recovery following perturbation, and can maintain productivity and resiliency (Mace et al. 2005). Diversity has been linked to ecosystem functioning, though others argue that diversity is important in itself, not as something to protect solely for humans' sake (Hamilton 2005).

Top predators such as seabirds often aggregate in biodiversity hotspots, indicating oceanic habitats that hold particular value for conservation (Worm et al. 2005, Montevecchi et al. 2012, Davoren 2013). Knowledge of such important habitat sites can influence identifications of important oceanic hotspots and designations of Marine Protected Areas (MPAs), through understanding which animals use the area and the scale at which effective protection could be implemented (Yorio 2009).

There are many ways to measure and to index biodiversity. In studies with uneven sampling using different methods over decades, such as the sampling used in my thesis, comparing changes in diversity over time can be challenging as several assumptions for using diversity measures are not met. Similar studies are difficult to find and often are based on terrestrial systems (LaSorte and Boecklen 2005). I opted to explore several different methods to compare changes in seabird diversity in the Gulf of Maine on a decadal time scale to assess what type of information each could provide.

One way to compare surveys with different effort is to use species accumulation curves (Hurlbert 1971). This method involves tallying species observed at survey locations, site by site, until reaching the final observation sites. The gradually increasing number of sites and species are drawn as a curve illustrating the relationship between numbers of species and sites surveyed. Bootstrapping can be used to obtain an average relationship over many random iterations. There are several methods to do this, which include examining observations by individuals instead of by sites, but this is not recommended for organisms such as seabirds that are unevenly distributed in the environment. Because seabirds are patchily distributed, I used a site-based approach (Hunt 1990).

Diversity metrics reflect the variety of species in an area or ecosystem. Despite the non-linear relationship between species counted and effort, many studies today still use simple effort-adjusted species counts, or metrics based on the number of species observed to assess diversity (Hurlbert 1971, Magurran and McGill 2011). It is often the case that the more effort spent surveying an area, the more species are observed, to a point. This influence of effort is well illustrated in the species accumulation curves, which increase rapidly at first, then less so, until they reach an asymptote, as illustrated in Chapter 3 and in Hurlbert (1971).

Species relationships also warrant consideration in biodiversity indices. For instance, an aggregation of five species could be composed of all species from the same family, or they could be from several orders, but the species count would not reflect those differences. A diversity metric called taxonomic distinctness can be used to assess this issue by measuring an aggregation’s relative relatedness, or distinctness, in terms of the species’ taxonomic backgrounds (Clarke and Warwick 1998). While taxonomic distinctness is influenced by the sampling effort, an average of the taxonomic distinctness across all species observed in the sample is not. This makes it a good choice to measure diversity in areas where there are many different levels of sampling effort (LaSorte and Boecklen 2005) or even lists of taxonomic samples that were collected over long periods (Peat et al. 2007).

1.4 Thesis Objectives

The goal of my thesis was to examine the diversity and distribution of seabirds in the Gulf of Maine during summer (June through September). I focused on this period as it as was a data set to which I made direct contributions, and because it provided a tractable data set that avoided some complexities of well-known and important seasonal cycles in the Northwest Atlantic (Burke et al. 2012). I assessed how diversity has changed on a decadal scale from the 1980s to the present, and how oceanographic factors influence seabird distribution. My research objectives were: 1) to assess how seabirds distribute themselves in the Gulf of Maine based on habitat influences and by foraging and breeding guilds and 2) to assess decadal changes in seabird diversity in the Gulf of Maine from the 1980s to 2010.

In Chapter 2, I examined the abundances of different seabird species and mapped the distributions of foraging and breeding guilds. I modeled habitat features for the numerically dominant species, the Great Shearwater (Puffinus griseus), a trans-equatorial migrant, and I compared the habitat association of two related storm-petrel species, the Wilson’s Storm-Petrel (Oceanites oceanicus) which breeds in the southern hemisphere and the Leach’s Storm-Petrel (Oceanodroma leucorhoa) which breeds in the Gulf of Maine to see how these species distribute themselves within the environment and share or partition habitat. I also examined the endangered and threatened seabird species observed on surveys in the Gulf of Maine and mapped them to illustrate areas that could be important to these species. These studies focused on the seabird data collected by the Canadian Wildlife Service (CWS) from 2006 to 2010, though I used seabird distribution data from previous surveys (PIROP and Manomet) for the endangered species study, as endangered and threatened species are encountered much less frequently in surveys.

In Chapter 3, I examined different aspects and indices of diversity on a decadal time scale, which incorporated both the recent survey data collected by CWS and data collected within the same regions from 1980 to 1990. Evaluating changes in diversity can be difficult when survey effort varies. The more a region is surveyed, the more species are recorded, but the relationship between survey effort and number of species observed is not linear (Clarke and Warwick 1998). I analyzed the seabird data using several methods of measuring diversity in a study area, and discussed the results obtained through the different methods, in order to best address my research objective of understanding diversity changes in the Gulf of Maine.

The ultimate aim of this study is to provide up to date information on summer seabird distributions in the Gulf of Maine and to examine the changes in diversity. Findings can be used to help inform management plans, which is important because many climatic and anthropogenic influences affect Gulf of Maine ecosystems (Nisbet et al. 2013). Over-fishing has shifted food webs and at times depleted the food sources for seabirds which indirectly impacted their breeding success (Tasker et al. 2000). Seabirds are regularly caught in gillnet, long-line and trawl fisheries (Montevecchi 2002, Moore et al. 2008, Regular et al. 2013). The levels at which birds are caught in the Atlantic are impacting seabird populations (Regular et al. 2013), and many of the birds caught are shearwaters that breed in the Southern Hemisphere making the potential population impacts difficult to discern (Moore et al. 2008). Oil spills are deadly for seabirds, and oil development in the Gulf of Maine is ongoing (Lotze and Milewski 2004). Climate change also will impact seabirds, though the specific nature of that impact is as yet uncertain (Grémillet and Boulinier 2009). Modeling changes in the abiotic aspects of the Gulf of Maine can help explain changes in the spatial dynamics of seabirds. Knowledge of the seabirds using the area is important for adequate understanding of and protection from anthropogenic impacts, for mitigation in case of an environmental disaster (e.g. oil spill), for understanding influences of climate changes, and to document changes in seabird populations over time.

Chapter 2 Vessel surveys reveal distributions and habitat relationships of marine birds in the Gulf of Maine

2.1 Introduction

Seabirds are conspicuous top-predators whose movements, foraging behaviour, and survival are influenced by oceanographic features and environmental changes, making them useful bio-indicators (Piatt et al. 2007). In order to understand these seabird signals we need to explore and document their relationships to their environment. In this chapter I documented current distributions of seabirds in the Gulf of Maine and examined the relationships to habitat for several species.

The Gulf of Maine is a well-studied region where the Canadian Wildlife Service's PIROP (Programme intégré de recherches sur les oiseaux pélagiques) and Manomet Bird Observatory programs were used to systematically survey seabirds from 1969 to 1992. These surveys were initiated to assess influences of anthropogenic changes to the environment, in particular the effects that oil spills, pesticides, and fisheries could have on seabirds. They aimed to document and map the distributions of birds in Atlantic Canada as a baseline for future comparisons, as at the time information on seabird distributions at sea was sparse and data were not collected systematically (Brown et al. 1975). The surveys terminated in 1992. Huettmann and Diamond (2006) reexamined these data to explore the importance of patch sizes of predators and prey, and the influences scale can have on the analysis of spatial datasets. They also used the data to explore the relationships between seabird species and habitat variables, finding different groups of seabirds were linked to specific water bodies defined by sea surface salinity, sea surface temperature, or depth, and that most species interacted with the environment on larger scales than 1 degree of latitude and longitude (Huettmann and Diamond 2006).

The need for more surveys in Atlantic Canada was identified after studies of seabird interactions with offshore oil and vessel-based oil pollution revealed negative impacts, risks, and the importance of monitoring (Weise et al. 2001, Weise and Robertson 2004). Subsequently surveys were conducted to, from and briefly at oil platforms on the Grand Bank of Newfoundland to document seabird diversity in relation to oil extraction activities, from 1999 to 2003 (Burke et al. 2005, 2012). Further surveys were carried out throughout Atlantic Canada's waters in November 2004 following the Terra Nova oil spill on the Grand Bank (Wilhelm et al. 2007). The paucity of seabird data in the spill area indicated a need for reinstating surveys, which were begun in 2006 by the Canadian Wildlife Service (CWS; Fifield et al. 2009). The surveys focused on the Grand Bank and Scotian Shelf but also covered the eastern Canadian waters of the Gulf of Maine (Gjerdrum et al. 2012).

In this study, I examined the CWS vessel surveys from 2006 to 2010 to evaluate the current status of seabirds in the Gulf of Maine from June through September. I focused on this time period to match the study period to my fieldwork experience, and to avoid the complexities of seasonal signals (e.g. Burke et al. 2005). The analysis provides a benchmark for comparison to survey data in previous decades, as well as a baseline for environmental and anthropogenic changes in the coming decades.

The specific objectives of the study were to 1) determine the dominant seabird species in the Gulf of Maine during summer and identify their habitat usage, 2) compare the characteristics (foraging mode, migrant, local breeding) of seabirds in the Gulf and distribution differences among these groups, 3) examine differences in the distributions and habitat use of Wilson's (Oceanites oceanicus) that breed in the Southern Hemisphere compared to the closely related locally breeding Leach's Storm-Petrels (Oceanodroma leucorhoa) bound by central place foraging constraints to learn more about differences between similar breeding and non-breeding birds, and 4) list species of concern within the study region and map observations of federally endangered species to identify areas used by endangered species.

I used mapping techniques to examine the habitat use of different groups and species of seabirds within the Gulf of Maine. To gain a better understanding of the different avian groups in the Gulf of Maine, I mapped the distributions of the dominant species and also mapped where different seabird assemblages (foraging guilds and migrant versus local species) were distributed. As noted by Regular et al. (2013), for example, anthropogenic impacts influence seabirds differently depending on their foraging methods; diving species are more commonly caught in gill nets, so removing the nets caused an increase in abundance of diving birds, while surface-foraging birds experienced a decline through a decrease in food availability from discards. Surface-feeding seabirds such as gulls are also often more sensitive to ocean climate change than are divers that can forage in three dimensions rather than two (Montevecchi 1993). I integrated and discussed the findings from these analyses to gain a clear understanding of seabird use of marine habitat in the Gulf of Maine.

2.2 Methods

2.2.1 Study Area

The study area is the Gulf of Maine, the southern portion of the Scotian Shelf, and northern edge of Georges Bank (Figure 2.1). The Gulf of Maine extends from Cape Cod, Massachusetts to southwestern Nova Scotia. Georges and Browns Banks form a semi-enclosed area, with the greater than 300 m deep Northeast Channel providing a deep-water exchange corridor. Tidal mixing, seasonal cycles, and varying influxes of cold, fresh waters from the Scotian Shelf all influence the biological productivity of the Gulf (Townsend et al. 2004).

The Scotian Shelf is a wide shelf with many deep basins and channels. Waters from the Gulf of St. Lawrence and the Labrador Current make the Scotian Shelf waters fresh and cold. Deeper continental slope waters also rise up from beyond the shelf edge. Frontal dynamics, tidal mixing, and upwelling all have influences on the biological productivity (Townsend et al. 2004). Both the Scotian Shelf and the Gulf of Maine are biologically productive habitats for large numbers of seabirds throughout the summer season.

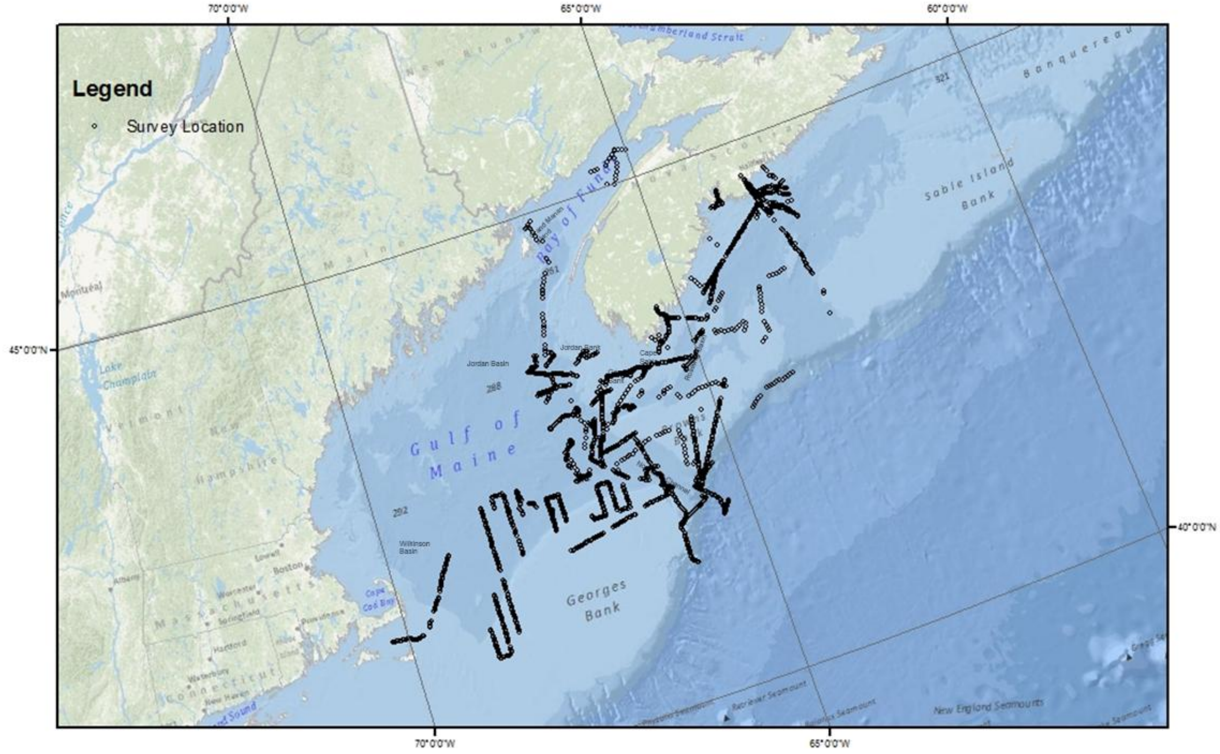

FIGURE 2.1 Survey locations in the Gulf of Maine, Scotian Shelf and Georges Bank regions from CWS surveys in June to September of 2006 to 2010. Circles indicate the starting locations of 5-min transects.

2.2.2 Survey Data Collection

Seabird survey data were collected on programmed laptops from the bridges of ships of opportunity along strip transects 300 m wide and either 5 or 10-min long with vessel speeds of 4

- 19 knots (Gjerdrum et al. 2012). For this study the survey period examined was restricted to June through September. At the start of each 5-min transect the date, time, start and end positions, course, speed, weather, visibility and sea conditions were recorded. Birds were identified to species or lowest possible taxon and geo-referenced based on the start location of the survey period. Each bird was recorded in a distance category (0-50 m, 50-100 m, 200-300 m), along with number of birds, species associations, behaviours (flying, sitting on water, foraging), flight direction and when possible age class and moult. Snapshot methods were used to record flying birds at regular intervals depending on ship speed, so as to not inflate the numbers of flying birds counted (Tasker et al. 1984). For more details on the methods see Gjerdrum et al. (2012). A subset of these variables was used in this study (species, location information, date information, numbers of birds, distance) due to the study's focus on broad-scale patterns of habitat use.

2.2.3 Data Analysis

For this analysis only birds that were seen within the 300 m transect were included. Both birds that were flying through the transect and birds that were on the water were analyzed, but not birds following the ship. Flying birds were only included when they were counted during the once a minute "snapshots" of effort (Gjerdrum et al 2012). Surveys from June through September of 2006 to 2010 were included. Survey locations are shown in Figure 2.1, and kernel densities of survey effort in Figure 2.2.

Kernel densities are used to analyze the intensity with which different areas are used within a larger study area, transforming a pattern of points into a density estimate (Wood et al. 2000). It is a non-parametric approach to assess animal movement throughout the study environment and to high or low use areas (Pinaud and Weimerskirch 2002). A density estimate is evaluated for each intersection of a grid with grid sized defined by the user. The density estimate is calculated based on an algorithm, or the kernel function, which specifies which grid locations are included and how they are weighed (Wood et al. 2000). The technique used here is the bivariate normal kernel, which weighs locations based on the bivariate Gaussian distribution and has a maximum at the individual grid point being processed (Wood et al. 2000). Kernel density functions were used throughout the study to measure densities of birds within the study area using different specified search radii and cell sizes.

Survey effort was concentrated in the Canadian waters of the Gulf of Maine and off the Scotian Shelf, with effort especially high near Halifax as most cruises originated there. Figure 2.2 shows clear gaps in survey effort in the western Gulf of Maine and the Bay of Fundy. Most of the surveys were offshore, except for a portion along the banks of Nova Scotia. As the surveys were conducted on ships of opportunity, the seabird observers did not choose study locations. The uneven survey distribution influenced our results, and interpretation of seabird distributions address the intensity of survey effort in the area in question. Vessel survey data were examined using ArcMap version 10.0 Geographic Information System (GIS).

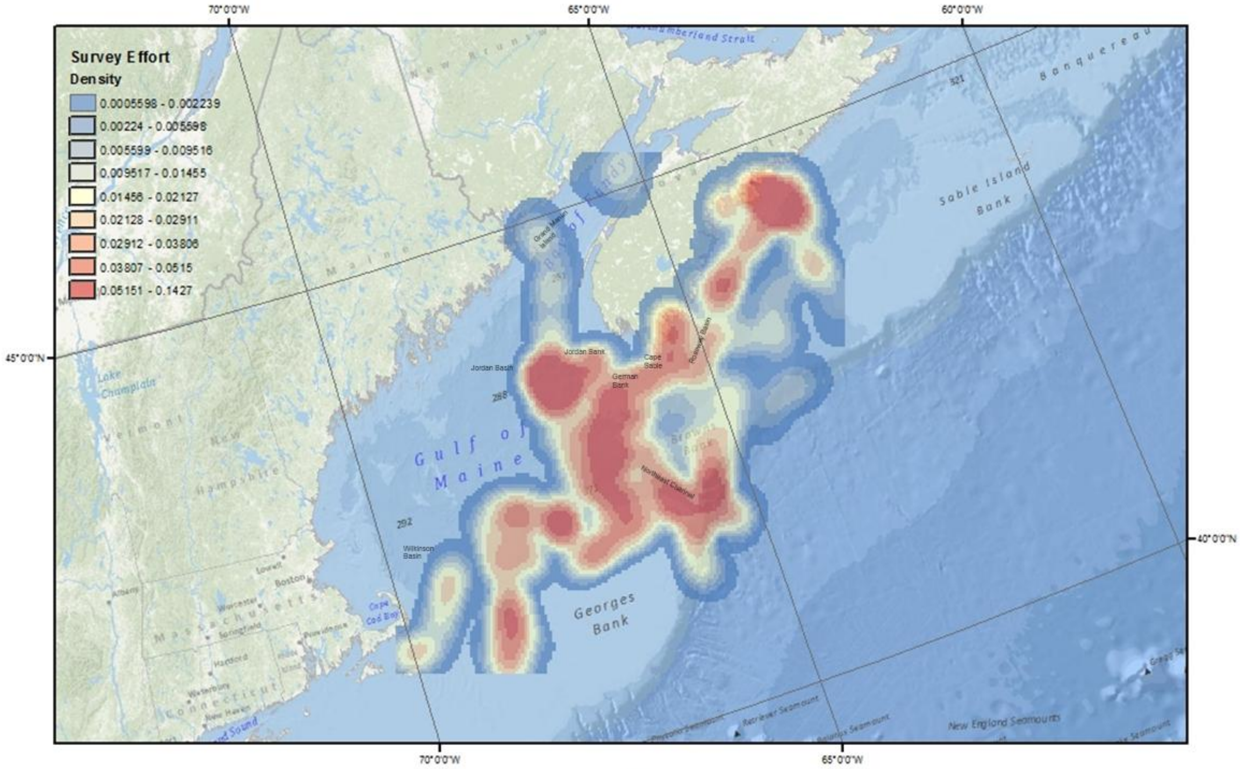

FIGURE 2.2 Kernel density of survey effort in the Gulf of Maine, on the Scotian Shelf, and Georges Bank regions from CWS seabird vessel surveys in June to September of 2006 to 2010. Kernel density search radius was 30 km. Units were surveys per kilometer.

As a method to examine aggregations of seabirds I examined most numerous (dominant) seabird species, and how different groups of birds were distributed within the environment. Dominant seabird species were determined by comparing total numbers of birds recorded on all transects. General foraging ecology dynamics were examined by classifying birds as diving or surface foragers using information from species accounts in the Birds of North America (e.g. Huntington et al. 1996) or Harrison (1983) when no Birds of North America account was available (e.g. Great Shearwaters). Species that are both diving and surface-feeders (e.g. shearwaters) were classified as divers because they have the capability to access parts of the water column which strictly surface feeders (e.g. gulls, terns) do not. Numbers of species seen of each type were calculated, as well as number of individuals observed.

Seabirds were then classified as breeding or non-breeding seabirds in the summer in the Gulf of Maine. Non-breeding birds from the Arctic and from the Southern Hemisphere were included. Numbers of species seen of each type were calculated, as well as number of individuals observed. I constructed kernel density maps of seabird groups in ArcGIS 10.0. The groups of birds were: local breeding divers, local breeding surface-foragers, migrant divers, migrant surface-feeders. Kernel density maps for each group had a 30 km search radii and 3 km cell size. The kernels were weighted by birds observed per linear km for each transect length. I used the metric birds per linear km to enable comparisons to earlier surveys presented in later chapters and because these data were not corrected for variation in detectability. To control for survey effort, the bird kernel density maps were divided by the survey effort kernel density map of the same size and search radius. Similar storm-petrel species were examined more closely for their summer distributions. The distributions of Leach's and Wilson's Storm-Petrels were mapped in the study area, and distance from the coastline was calculated to compare their habitat associations. The degree of spatial overlap between the two species was examined in ArcGIS. Percent kernel densities for Leach's and Wilson's Storm-Petrels were mapped using a smaller cell size of 1 km and search radius of 15 km. The overlay between the 50, 80, 90, 95 and 100 % polygon kernel densities were calculated using the Overlay tool in ArcGIS. The index of niche overlap was calculated following Ronconi (2008) as:

$$\text{Area Overlap (species A and B)} / \text{Total Area (species A + B)} = \text{Niche Overlap}$$

Total area was calculated using the union of the two species' 100% kernel densities.

Habitat models were built for Great Shearwaters, Leach's and Wilson's Storm-Petrels. These three species were chosen for habitat modeling because they were dominant species in the summer in the Gulf of Maine (Great Shearwaters) or because their potential differences in habitat use could provide interesting information related to differences between locally breeding and seasonally migrant species distributions (Storm-Petrels). Habitat variables are found in Table 2.1. Habitat features were chosen based on past studies showing their influence on seabird distributions. Fronts can attract marine birds (Schneider 1982, Bost et al. 2009), so distance to fronts was included to see whether these specific birds were attracted to them. Chlorophyll density can be used as an indicator of productivity (Ballance et al. 1997), and warmer or cooler waters can influence productivity, as well as define habitats both for seabirds and their forage fish (Amorim et al. 2009, Watanuki and Ito 2012), and therefore both were included in this study. Slope and depth have been found to correlate with seabird distributions (Amorim et al. 2009) and can influence seabird habitat choices. Distance to shore was included as well to see if animals were influenced by proximity to land (Amorim et al. 2009). The 1000 m isobath was used to examine possible relationships between seabird species and the continental slope, which has been found to be important for explaining Wilson's Storm-Petrel distributions (Powers 1983). Some of the habitat variables are potentially correlated, so correlation tests were run to ensure no highly correlated variables were included in the same model.

Habitat feature rasters were developed and sampled using ArcGIS 10 and Marine Geospatial Ecology Tools (MGET) (Roberts et al. 2010). Mean monthly sea surface temperature (SST) and chlorophyll density data were downloaded from the Ocean Color database online http://oceancolor.gsfc.nasa.gov/. The SST front was calculated using the Cayula-Cornillon fronts tool in MGET, which makes use of the Cayula-Cornillon sea surface temperature edge detection algorithm (Cayula and Cornillon 1992).

Species-specific habitat use was interrogated using presence and absence of species as the seabird counts were not corrected for differences in detectability of seabirds. Generalized Linear Models were built using a binomial distribution with a clog-log link, which is used if you have many zero counts (Zuur et al. 2009). A chi test for single term deletions was used to strengthen the model by testing results if variables are dropped (Zuur et al. 2009). Model selection was based on low Akaike Information Criterion (AIC) values and presence of significant covariates. Variables that were correlated above 40% were not included in the same models. Resulting models were examined using variograms to assess the errors for spatial autocorrelation. Model associations were significant at the $p < 0.05$ level.

TABLE 2.1 Environmental variables used for seabird habitat modeling.

Layer	Source and Information
Sea surface temperature (SST) (°C)	Nighttime AquaMODIS mean monthly, 9 km resolution
Chlorophyll Concentration (CHL) (mg/m^3)	AquaMODIS mean monthly, 9 km resolution
Distance to SST front (m)	Cayula-Cornillion fronts in ArcGIS Raster – MGET tool, ArcGIS Distance tool
Depth of the sea floor (m)	GEBCO global 30 arc-second grid
Bathymetric Slope (°)	Slope function in ArcGIS Spatial Analyst
Distance from the coastline (m)	ArcGIS Distance tool
Distance to the 1000 m isobath (m)	ArcGIS Distance tool

Federal and state/provincial lists of endangered or at risk bird species were examined for the United States, (Maine, New Hampshire, Massachusetts), and for Canada (Nova Scotia, New Brunswick), which are all the land regions surrounding the Gulf of Maine. Species that were observed within the study region were checked for their status in these different states, provinces and countries, and listed in a table (Nisbet et al. 2013). In order to have a more complete study of the region, I included species within the data set from the 1970s through 1990s as well as data from 2006 to 2010. The older data set is discussed at length in Chapter 3. This is a broader dataset than that used in Chapter 3 to allow for a more thorough examination of endangered species present in the Gulf of Maine. Information on species status was obtained from Nisbet et al. (2013) and at the following government websites:

http://www.maine.gov/ifw/wildlife/species/endangered_species/state_federal_list.htm
http://www.wildlife.state.nh.us/Wildlife/Nongame/endangered_list.htm
http://www.mass.gov/dfwele/dfw/nhesp/species_info/mesa_list/mesa_list.htm
http://www.wildspecies.ca/

2.3 Results

2.3.1 Species Diversity

Vessel survey counts of seabirds in the Gulf of Maine and southern Scotian Shelf resulted in records of 12,050 birds from 29 species. Six species of Procellariidae were seen, and Great Shearwaters were by far the most numerous of these (95%) and the most abundant species overall with 5,753 birds observed, or 47.7% of total seabirds surveyed (Table 2.2, Figure 2.3). Sooty and Cory’s Shearwaters were the second and third most abundant of the Procellariidae (Table 2.2). Scolopacidae (Red, Red-necked and unidentified Phalaropes) were the next most abundant avian group with 4,054 or 34% of total birds recorded (Table 2.2). Hydrobatidae

(Wilson's, Leach's and unidentified Storm-Petrels, Table 2.2) were the next most abundant with 1,141 observed (9% of total bird count, Table 2.2).

TABLE 2.2 Seabird diversity and abundance based on ECSAS vessel surveys in the Gulf of Maine in June through September 2006-2010. Seabirds are presented taxonomically and grouped for higher taxonomic analysis. Number of birds observed is shown in birds per linear km, with 4932.5 km surveyed for the total study area and period. Family group totals include all birds identified to species and those identified to higher taxonomic levels. Birds identified only to higher taxa levels are included as separate line items as well, where needed.

Common Name	Scientific Name	Bird Count	Birds per Linear Km	Feeding Strategy	Breeding Resident
Northern Fulmar	*Fulmarus glacialis*	48	0.0097	Surface	No
Cory's Shearwater	*Calonectris diomedea*	68	0.0138	Diving	No
Great Shearwater	*Puffinus griseus*	5753	1.17	Diving	No
Sooty Shearwater	*P. griseus*	163	0.033	Diving	No
Manx Shearwater	*P. puffinus*	14	0.0028	Diving	No
Audubon's Shearwater	*P. lherminieri*	3	0.0006	Diving	No
Procellariidae	**Total Species: 6**	**6049**	**1.227**	**-**	**-**
Wilson's Storm-Petrel	*Oceanites oceanicus*	439	0.089	Surface	No
Leach's Storm-Petrel	*Oceanodroma leucorhoa*	486	0.0985	Surface	Yes
Unidentified Hydrobatidae		216	0.0438	-	-
Hydrobatidae	**Total Species: 2**	**1141**	**0.231**	**-**	**-**
Northern Gannet	*Morus bassanus*	124	0.0251	Diving	No

Sulidae	**Total Species: 1**	**124**	**0.0251**	**-**	**-**
Double-crested Cormorant	*Phalacrocorax auritus*	55	0.0112	Diving	Yes
Great Cormorant	*Phalacrocorax carbo*	1	0.0002	Diving	Yes
Phalacrocoracidae	**Total Species: 2**	**56**	**0.011**	**-**	**-**
Red-necked Phalarope	*Phalaropus lobatus*	44	0.0089	Surface	No
Red Phalarope	*P. fulicarius*	46	0.0093	Surface	No
Unidentified Phalarope Spp.		3964	0.804	-	-
Scolopacidae	**Total Species: 2**	**4054**	**0.822**	**-**	**-**
Black-legged Kittiwake	*Rissa tridactyla*	1	0.0002	Surface	No
Laughing Gull	*Leucophaeus atricilla*	3	0.0006	Surface	Yes
Ring-billed Gull	*Larus delawarensis*	1	0.0002	Surface	Yes
Herring Gull	*L. argentatus*	180	0.0365	Surface	Yes
Lesser Black-backed Gull	*L. fuscus*	2	0.0004	Surface	Yes
Great Black-backed Gull	*L. marinus*	285	0.0578	Surface	Yes
Unidentified Laridae		5	0.001	-	-
Laridae	**Total Species: 6**	**477**	**0.0967**	**-**	**-**
Common Tern	*Sterna hirundo*	40	0.0081	Surface	Yes
Arctic Tern	*S. paradisaea*	12	0.0024	Surface	Yes
Unidentified		20	0.0041	-	-

Sternidae

Sternidae	**Total Species: 2**	**72**	**0.015**	**-**	**-**
Great Skua	*Stercorarius skua*	2	0.0004	Surface	No
South Polar Skua	*S. maccormicki*	9	0.0018	Surface	No
Pomarine Jaeger	*S. pomarinus*	20	0.0041	Surface	No
Stercorariidae	**Total Species: 3**	**31**	**0.0062**	**-**	**-**
Dovekie	*Alle alle*	1	0.0002	Diving	No
Common Murre	*Uria aalge*	1	0.0002	Diving	No
Razorbill	*Alca torda*	1	0.0002	Diving	Yes
Black Guillemot	*Cepphus grille*	18	0.0036	Diving	Yes
Atlantic Puffin	*Fratercula arctica*	20	0.0041	Diving	Yes
Unidentified Alcid		3	0.0006	-	-
Alcidae	**Total Species: 6**	**46**	**0.0093**	**-**	**-**

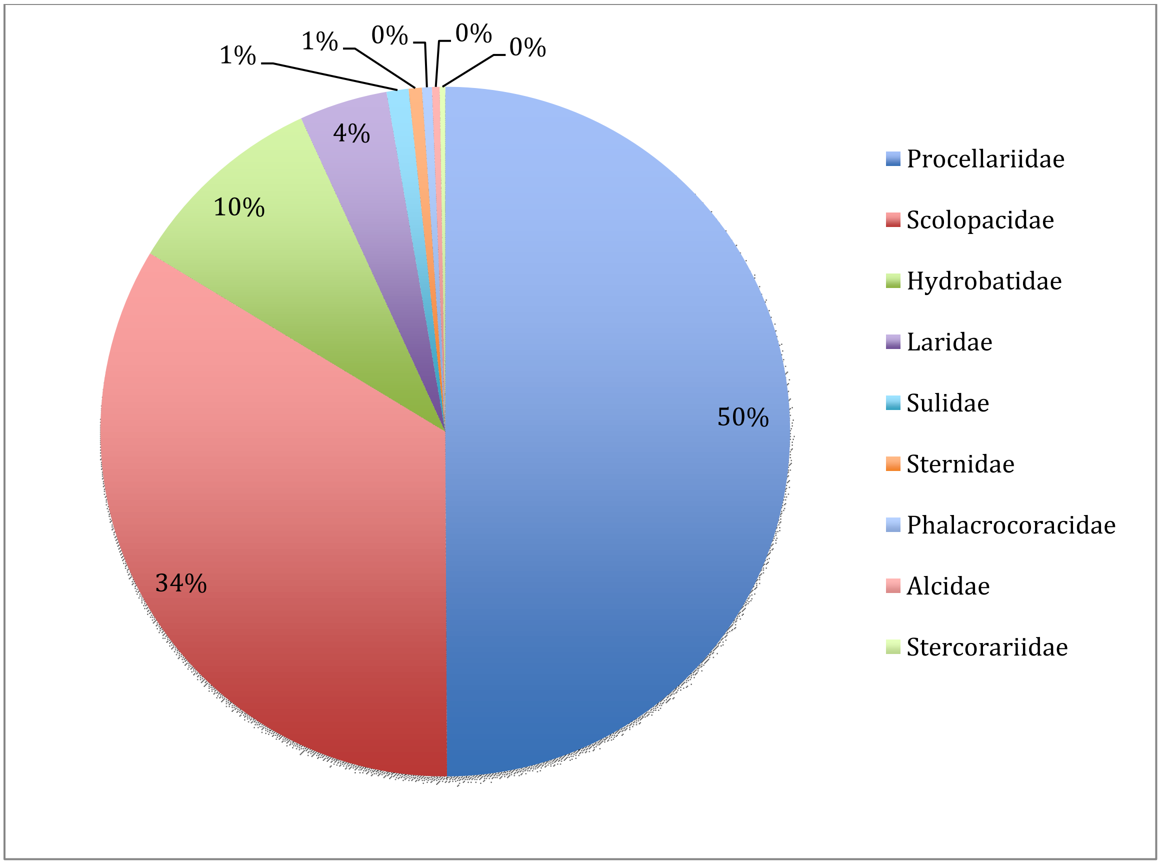

FIGURE 2.3 Seabird species composition by number in the Gulf of Maine based on ECSAS vessel surveys from June to September of 2006-2010. Taxonomic groups are shown in order of abundance.

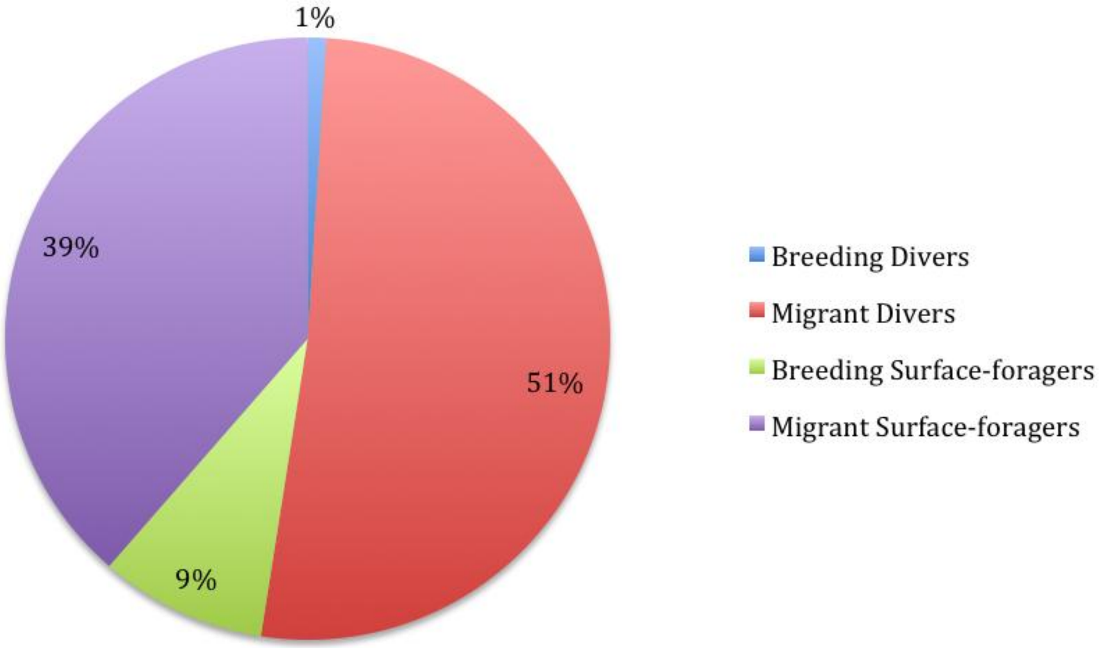

FIGURE 2.4 Seabird species composition observed during summer in the Gulf of Maine 2006-2010, categorized by breeding and foraging group.

2.3.2 Feeding and Breeding Guilds

General feeding ecology classifications revealed that migrant birds, both surface-feeding and diving, dominated the study area, with a paucity of breeding birds (Figure 2.4). Migrant birds composed the most numerous species and the most birds in the Gulf of Maine during summer. There were 8 species of migrant non-breeding diving birds, and 8 species of non-breeding surface-feeding birds, while among locally breeding birds there were 5 diving species and 8 surface-feeding species. The two most numerous groups were the migrant divers and migrant surface-feeders (Figure 2.4). The different feeding and breeding groups were found in different locations and concentrations. Breeding divers were observed inshore in Nova Scotia, with higher concentrations near Halifax, Cape Sable and the Bay of Fundy (Figure 2.5A).

Migrant divers were seen in high concentrations in more offshore environments, with notable high density areas in the Jordan Basin, Roseway Basin, German Bank, the Bay of Fundy and some on Georges Bank (Figure 2.5B). Locally breeding surface-feeding birds are more dispersed than the other seabird groups, with some higher concentrations in the Bay of Fundy, which may be due to the Leach's Storm-Petrel distributions (Figure 2.5C). The migrant surface-feeding birds were very concentrated in the vicinity of German Bank (Figure 2.5D).

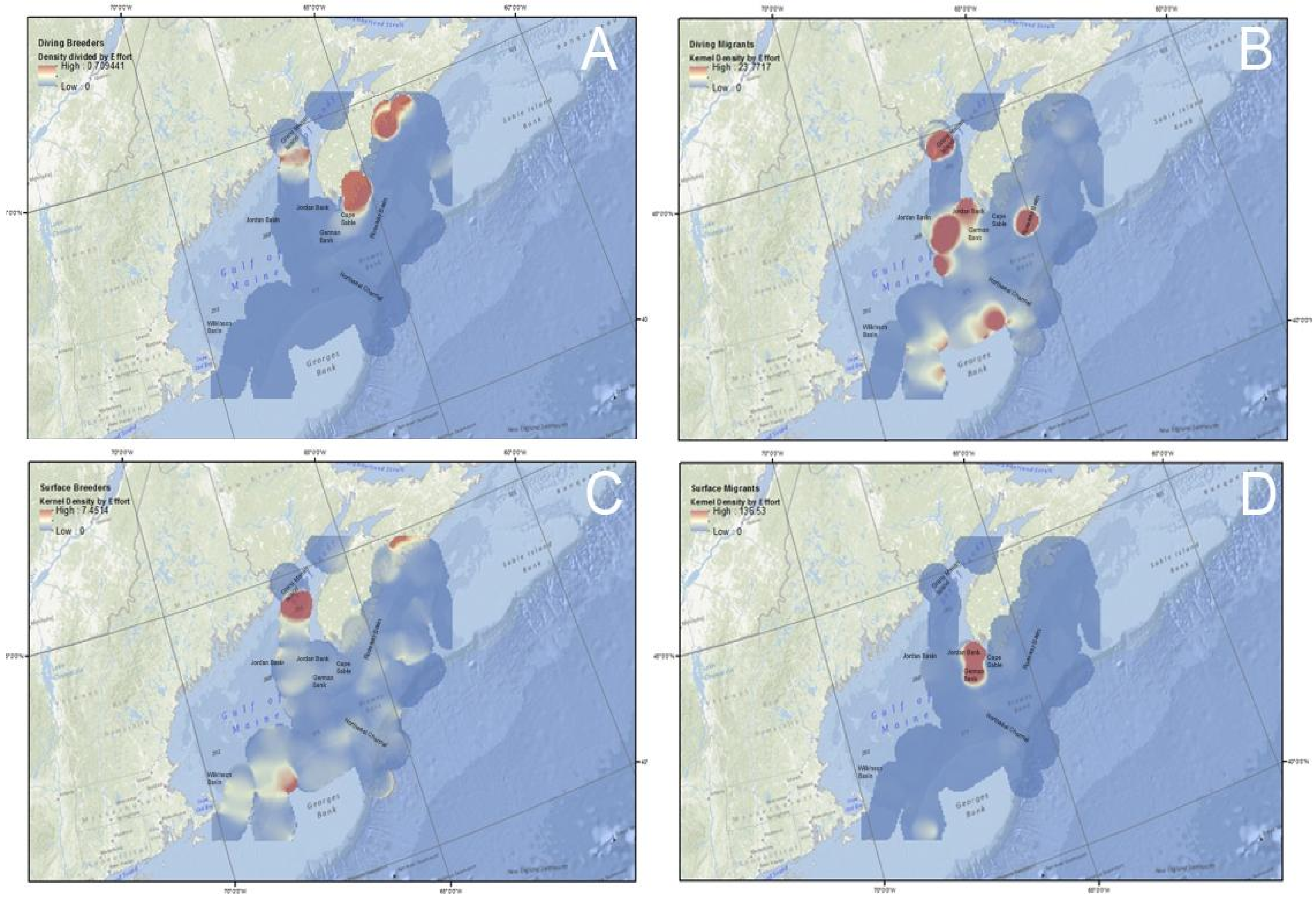

FIGURE 2.5 Effort correct kernel density maps of bird groups using the Gulf of Maine based on ECSAS seabird vessel survey data. Maps illustrate: A) locally breeding, diving foraging birds, B) migrant non-breeding, diving, foraging birds, C) locally breeding, surface foraging birds, and D) migrant non-breeding, surface foraging birds. Units are birds per kilometer surveyed.

2.3.3 Storm-Petrel Comparison

The highest densities of Wilson's Storm-Petrels were in the Jordan Basin, whereas the highest densities of Leach's Storm-Petrels were near Grand Manan Island in the Bay of Fundy (Figure 2.6). Both species were widely dispersed in low numbers throughout the study region, though their highest abundances were found in different locations in the Gulf of Maine (Figure 2.6). Area of overlap of the two species was calculated at different kernel densities (Table 2.3). At the higher percent kernel densities, the two species did share greater niche overlap (Table 2.3). Areas where they overlap at these higher levels include the Roseway Basin, the Northeast Channel, the German Bank, and portions of the Scotian Shelf. The percent overlap at the 50% kernel density level is less than 1% of the total area. Areas at the 50% level of overlap are the Jordan Basin and the entrance of the Northeast Channel (Figure 2.7).

TABLE 2.3: Spatial overlap between Wilson's and Leach's Storm-Petrels in vessel surveys from June to September of 2006-2010 in the Gulf of Maine. Total kernel density is 47394.3 km^2.

Kernel Density	Area of Overlap (km^2)	Percent Niche Overlap
50	391.1	0.083
80	2520.0	5.32
90	4883.8	10.30
100	20683.7	43.64

2.3.4 Habitat Selection

Habitat variables that were correlated at higher than 40% were excluded from the same models. Strongly correlated variables were depth and slope (r = 0.52), distance to front and distance to coast (r = 0.48), slope and distance to the 1000 m isobath (r = 0.43), and distance to the coast and distance to the 1000 m isobath (r = 0.47). Habitat models revealed differences in the parameters that influence distributions of seabird species (Table 2.4). Great shearwaters were found in areas with lower temperatures, in deeper waters further from the coast, and showed a decreasing relationship over both months and years (Binomial GLM, SST $p \leq 0.05$ estimate -7.837e-2; Depth x Distance to the coast $p \leq 0.01$, 2.210e-8; factor Month ≤ 0.05; factor Year $p \leq 0.001$, df = 2767, AIC: 3019.6).

Storm-Petrel species showed differences between the habitat features influencing their distributions (Table 2.4). Leach's Storm-Petrels were found in areas with lower chlorophyll densities, closer to temperature fronts, and increased over the months surveyed (Binomial GLM, CHL $p \leq 0.001$ estimate -1.226; Distance to front $p \leq 0.001$ estimate -1.029e-5; factor Month $p \leq 0.05$, df = 2627, AIC: 1247.3). Wilson's Storm-Petrels, however, had no relationship to chlorophyll densities or fronts, but were seen in deeper waters that were further from the coast and decreased over months, but increased over years surveyed (Binomial GLM, factor Month ≤ 0.001; factor Year ≤ 0.001; Depth x Distance to the coast $p \leq 0.05$ estimate 4.561e-8, df = 2627, AIC: 1170.8).

TABLE 2.4: Significant associations for seabird species distributions in the Gulf of Maine from generalized linear models with binomial error structures and a clog-log link. Great Shearwaters (GRSH), Leach's Storm-Petrels (LESP), and Wilson's Storm-Petrels (WISP). An increase is indicated with (+), a decrease with (-), and no significant change with 0.

Species	SST	CHL	Depth	Distance to Coast	Distance to Front	Month	Year	Depth * Distance to Coast
GRSH	-	0	-	+	0	-	-	+
LESP	0	-	0	0	-	+	0	0
WISP	0	0	-	+	0	-	+	+

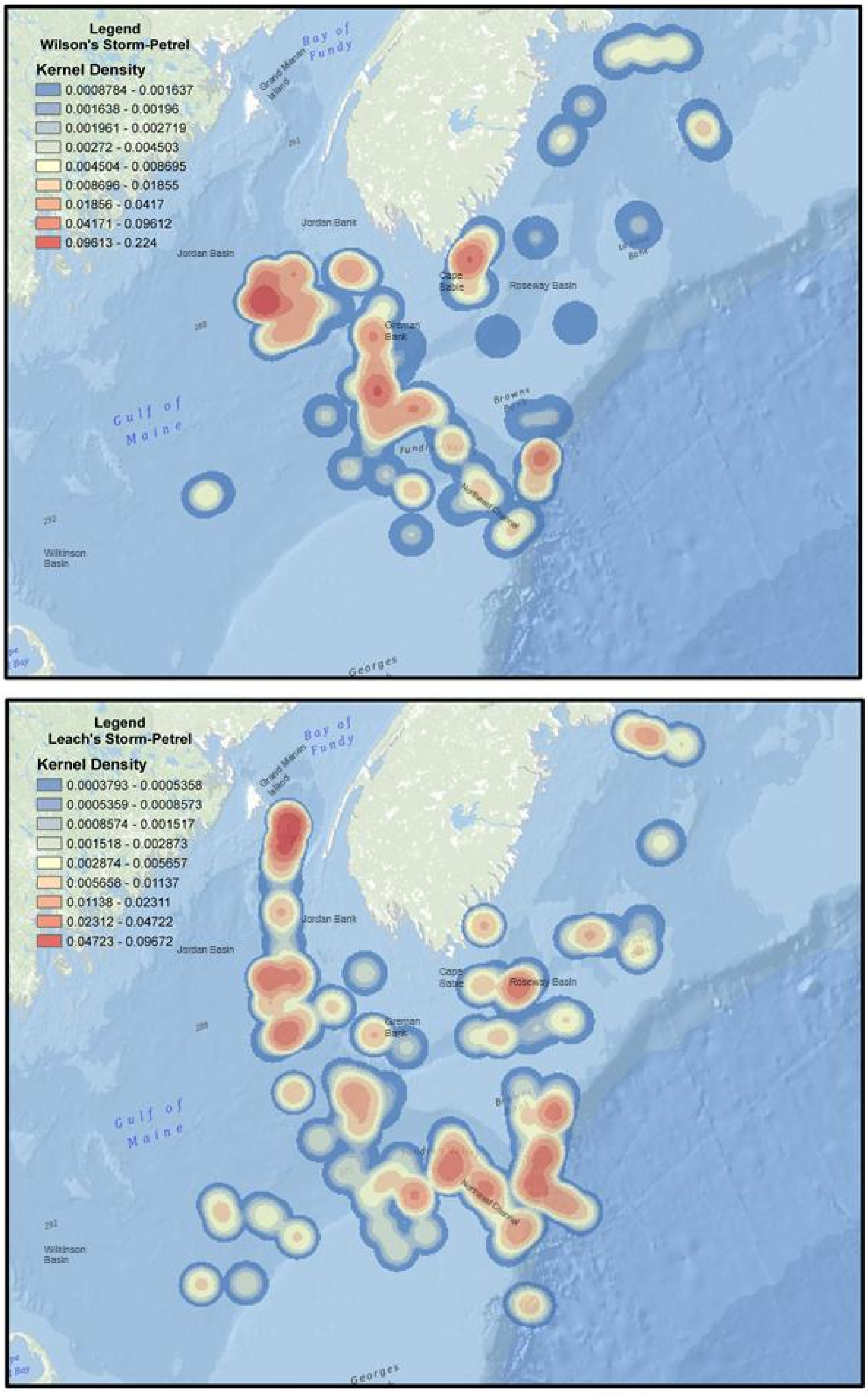

FIGURE 2.6: Kernel densities for Leach's and Wilson's Storm-Petrel sightings during June to September vessel surveys from 2006-2010. Densities are based on counts of birds in vessel surveys. Search radius is 15 km. Units are birds per kilometer.

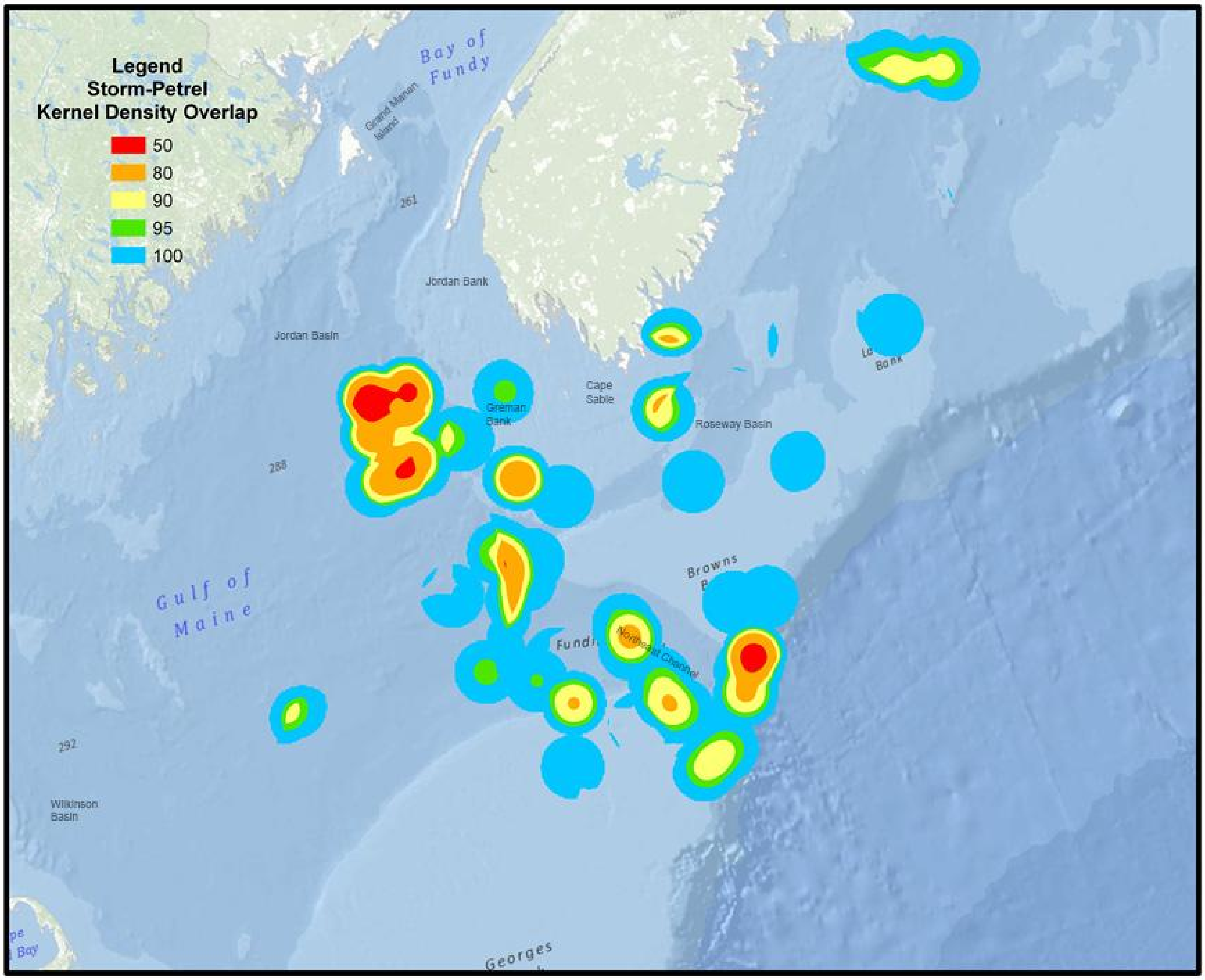

FIGURE 2.7: Kernel density overlap between Wilson's and Leach's Storm-Petrel distributions. Overlap is shown at 50, 80, 90, 95, and 100% kernel densities for each species. Kernel densities are based on vessel surveys from June to September 2006-2010.

2.3.5 Endangered Species

The Roseate Tern is listed as Federally Endangered or At Risk in every region examined (Table 2.5). Leach's Storm-Petrels are listed as Endangered in Massachusetts, but are not listed elsewhere in the region. Arctic Terns and Common Terns are both listed at medium to lower levels of risk, as are Atlantic Puffins and Razorbills. Great Cormorants are listed at medium risk levels as well. Phalarope species, Black-legged Kittiwakes and Wilson's Storm-Petrels are all listed at lower levels of potential risk. Lower level risk species were seen in a fairly even distribution throughout the study area (Figure 2.8). Medium and lower risk species were grouped together for ease of comprehension in the map. Roseate Terns were observed in the older data, between 1969 and 1985 during the PIROP and Manomet surveys discussed in Chapter 3 (Figure 2.8) but not in the more recent surveys. They were observed inshore in Cape Cod, the Bay of Fundy near Grand Manan Island, and inshore in Nova Scotia by St. Margaret's Bay and provincial parks south of Halifax. Wilson's and Leach's Storm-Petrels were widely distributed throughout the study area, and were the most common of the threatened and endangered species. Arctic and Common Terns were seen predominantly in the inshore areas near Halifax and the southern tip of Nova Scotia, as well as Cape Cod and off of Georges Bank. Great Cormorants were observed inshore on Nova Scotia, and Black-Legged Kittiwakes in the Bay of Fundy, inshore in Nova Scotia, and off Georges Bank. Red and Red-necked Phalaropes were both observed inshore off of Southern Nova Scotia, though Red Phalaropes were also observed off of Georges Bank. Razorbills were observed in the Bay of Fundy, and Atlantic Puffins were as well, in addition to being found south of Nova Scotia.

TABLE 2.5: Species of special concern in the Gulf of Maine region listed in taxonomic order. The list includes species listed by Maine (ME), New Hampshire (NH), and Massachusetts (MA) in the United States, and by Nova Scotia (NS) and New Brunswick (NB) in Canada. Each country has its own system of designated risk, as do the states. ME and NH indicate designations of Endangered and Threatened, MA indicates Endangered, Threatened and Species of Concern, and NS and NB list At Risk, May be at Risk, and Sensitive. Each of these systems moves from more or less at risk. Species designations by region are displayed below. Animals listed in bold are also federally Endangered or At risk.

Species	ME	NH	MA	NS	NB
Wilson's Storm-Petrel					Sensitive
Leach's Storm-Petrel			Endangered		Sensitive
Great Cormorant	Threatened			Sensitive	
Red Phalarope				Sensitive	Sensitive
Red-necked Phalarope				Sensitive	Sensitive
Black-legged Kittiwake				Sensitive	
Common Tern		Threatened	Species of concern	Sensitive	Sensitive
Arctic Tern	Threatened		Species of concern	May be at risk	May be at risk
Roseate Tern	**Endangered**	**Endangered**	**Endangered**	**At risk**	**At risk**
Razorbill	Threatened			Sensitive	
Atlantic Puffin	Threatened			Sensitive	Sensitive

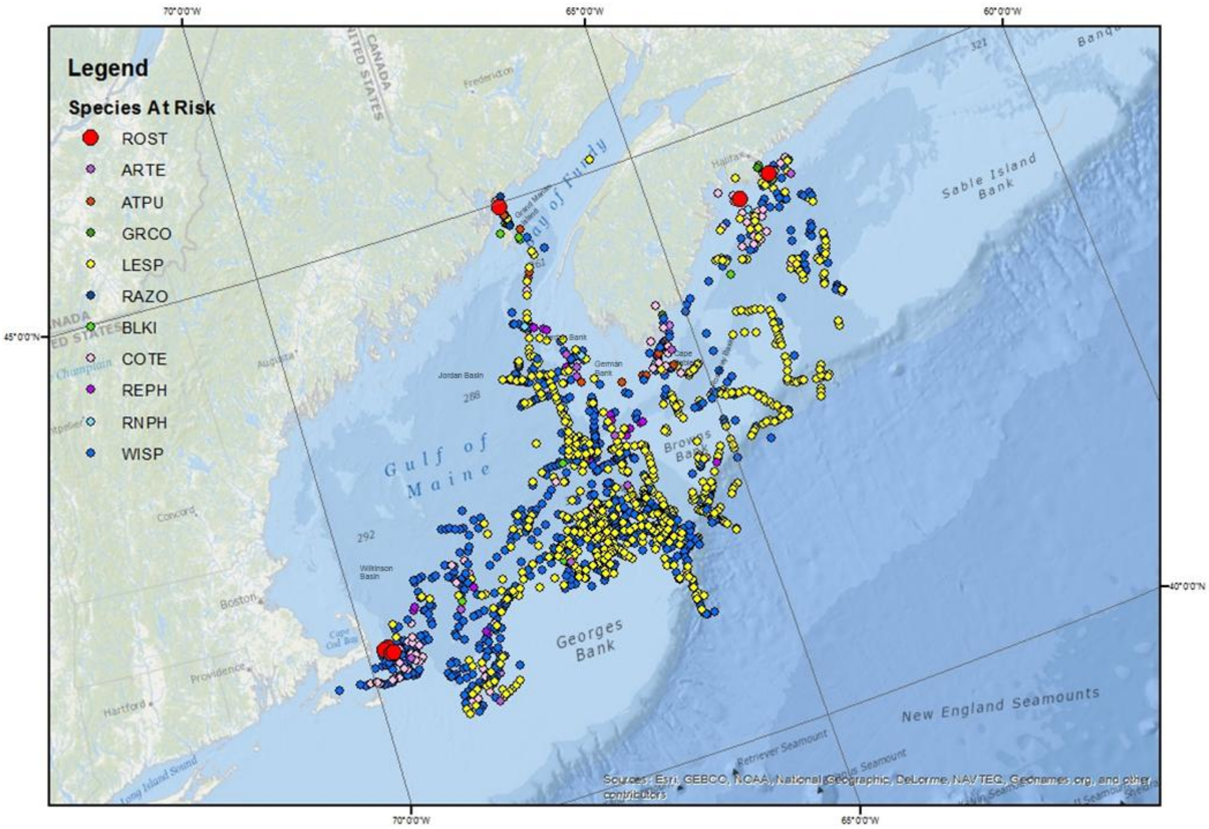

Figure 2.8 Locations of species of special concern in the study area. Roseate Tern is listed as endangered in Maine, New Hampshire, and Massachusetts and federally for the United States, and as At risk in Nova Scotia and New Brunswick and federally for Canada. Observations of Roseate Terns are indicated by large red dots. No observations were made of Roseate Terns in the study area for ECSAS data set discussed in this chapter, these seven observations occurred between 1969 and 1985 during the PIROP and Manomet surveys discussed in Chapter 3. Locations of other species are presented as well.

2.4 Discussion

2.4.1 Species Abundance and Diversity

Survey results revealed that Southern Hemisphere breeding Great Shearwaters were the most numerous species in the study area (Table 2.2). Other studies have also found that non-breeding offshore species numerically dominate the breeding resident populations in the Gulf of

Maine (Schneider and Heinemann 1996). Great Shearwaters breed at the Tristan da Cunha archipelago and most migrate to the Northern Hemisphere for the Southern Hemisphere's winter (Harrison 1983). Great Shearwaters range over most of the North Atlantic pelagic zone during the austral winter, feeding primarily on fish, krill and squid (Ronconi et al. 2010b). While they do use much of the North Atlantic for wintering grounds, millions feed in the Gulf of Maine, making it part of their feeding ground networks (Brown et al. 1975).

Phalarope species were the next most abundant group observed, and these birds are also nonbreeding migrants through the area. Both species of Phalaropes nest in the Arctic and move through the Gulf of Maine prior to their breeding season in the spring, and return after their breeding season before migrating to tropical (Red-necked Phalarope; Rubega et al. 2000) and southern temperate and sub-tropical oceans (Red Phalarope; Tracy et al. 2002). Red Phalaropes have been found to remain in large flocks in the Bay of Fundy until October (Brown et al. 1975). Other migrant birds used the Gulf of Maine during the study period as well, with many Wilson's Storm-Petrels observed as well as other species of shearwaters, South Polar and Great Skuas, Black-legged Kittiwakes, Northern Gannets, and birds that are more commonly seen in the winter months in the study area, Dovekies and Thick-billed Murres (Brown et al. 1975). While the Gulf of Maine is just one of their many stops along the way to and from breeding sites, each location is important for providing food to fuel those migrations, and the physical properties of the Gulf of Maine create a productive environment to support many species of birds (Brown 1986).

These non-breeding, numerically dominant species are not tied to foraging near breeding colonies (i.e. not restricted to central-place foraging; Weimerskirch 2007) like breeding birds are in the Gulf of Maine (Garthe et al. 2009). Studies of where the migrant species forage could reveal important biodiversity sites. Great Shearwaters on Georges Bank accounted for 40% of the total energy flux to birds, primarily in June and July (Schneider et al. 1987), making them the dominant avian predator in summer. The same study found less flux to Northern Fulmars (17%), Herring Gulls (12%) and Great Black-backed Gulls (12%). Changes in seabird species diversity can result in different energy flux today, though the dominant species in the summer remains the Great Shearwater. Great and Sooty Shearwaters have been found to move throughout the North Atlantic following increased concentrations of euphausiids and smaller fish and squids (Brown et al. 1981, Hedd et al. 2012).

Locally breeding birds were found throughout the study area in smaller numbers. Herring and Great Black-backed Gulls were commonly seen, with fewer Laughing, Lesser Black-backed and Ring-billed Gulls observed. Common and Arctic Terns were observed, as well as locally breeding alcid species, specifically Atlantic Puffins, Razorbills and Common Murres. These are all species that breed in the region, though some portions of their populations are comprised of non-breeders.

2.4.2 Feeding and Breeding Guilds

Similar numbers of species from the four groups were observed but migrant birds dominate both the diving and surface-feeding guilds in terms of numbers of birds observed. The migrant birds were observed in different locations within the system, however, depending on their feeding methods. Highest concentrations of the surface-feeding migrant birds were found inshore on the German Bank, while the diving birds were found in high concentrations both inshore and offshore. Locally breeding birds also showed distributional differences depending on their feeding methods, with divers found inshore, and surface-feeders dispersed throughout the inshore and offshore environments. These differences in their distributions can be attributed both to the different prey and foraging tactics, and to the differences between the restricted foraging environments of locally-breeding birds compared to non-breeding birds that are unrestricted in their use of foraging locations (Garthe et al. 2009). Studies that incorporate prey distributions are better able to model the drivers behind species distributions, such as the close relationship between capelin distributions and Common Murres in Newfoundland (Davoren et al. 2003a). The distributions of the migrant species show high concentrations in the German Bank area, indicating this area as a high use location for migrant birds during summer.

Examining the locally breeding seabirds shows that there were more gulls observed than auks and terns (Table 2.2). Seabirds have been drastically reduced from anthropogenic pressures from market hunting and over-exploitation for eggs and feathers during the late 19th and early 20th centuries but have rebounded since adequate and enforced protections were put in place (Montevecchi and Tuck 1987, Nisbet et al. 2013). There are other reasons for the dominance of gulls. Gulls take advantage of fisheries discards and human refuse, which also accounts for their great increase in the 20th century (Howes and Montevecchi 1993). These seabirds often breed near one another in mixed colonies (Burger 1981), and while gulls, terns, and auks exploit some of the same prey (though use different mechanisms to forage), auk and tern eggs, chicks and adults are often targeted directly by gulls (Finney et al. 2003, Donehower et al. 2007). Terns forage closer to shore, and inshore surveys were limited and not close to many of their breeding colonies in Maine, which is likely the main reason for the lower numbers of terns observed. Additionally, the core breeding ranges for auks are further north, which likely contributes to the lower numbers observed.

Differences in diving and surface-feeding bird species populations to fishing pressures have been noted in Newfoundland (Regular et al. 2013). Surface-feeding birds have declined recently as an easily available food resource – fisheries discards – was drastically reduced during eastern Canadian fishery closures (Regular et al. 2013). Distributions of the feedings guilds are different due to the fact that they are foraging for different resources, as diving birds are able to access resources unavailable to surface feeding birds. Untangling differences between populations of different seabird species and guilds is complicated, and can be aided by studies such as this one that documents decadal population change. Abundances of guilds of surface-feeding breeding birds have been used as indicators of marine environmental health in Scotland, in particular for the health of specific prey items (Parsons et al. 2008).

2.4.3 Storm-Petrel Comparison

The similar storm-petrel species provided an interesting comparative study between a resident breeder (Leach's Storm-Petrel) and a Southern Hemisphere breeder (Wilson's Storm-Petrel). The two species forage for similar foods, small crustaceans and fish (Croxall et al. 1988, Huntington et al. 1996, Quillfeldt et al. 2005, Hedd et al. 2009) but have different foraging constraints. In theory, Leach's Storm-Petrels are restricted to returning to their colonies (central-place foraging), while Wilson's are not tied to breeding sites. Interestingly, like other studies we found Leach's foraging offshore in cooler, deeper waters (Huntington et al. 1996, Hedd et al. 2009). When density was considered, however, more Leach's Storm-Petrels were observed inshore, particularly near Grand Manan Island in the Bay of Fundy. Wilson's Storm-Petrels showed high densities south of the Jordan Basin. These distributional differences may reflect different prey preferences (Quillfeldt et al. 2005, Hedd et al. 2009) or could be evidence for niche partitioning. My habitat models indicate different factors influencing the distributions of the two storm-petrel species (Ronconi 2008). The overlap of the highest density areas of the two species was small and restricted to the Jordan Basin and Northeast Channel. In Newfoundland, Leach's Storm-Petrels forage on myctophids in deep slope and channel water masses, and the same preference may be found in the Gulf of Maine (Hedd et al. 2009).

2.4.4 Habitat

The three procellarid species examined for habitat relationships responded in a variety of ways to the environmental variables. The two non-breeding species, Wilson's Storm-Petrels and Great Shearwaters, showed the most similar relationships to habitat variables. Both were found close to deep-water offshore areas, suggesting that these areas play an important role in their habitat. From previous research involving vessel surveys in Newfoundland, it is evident that Leach's Storm-Petrels forage in deep water at least in that region (Hedd et al. 2009), but this was not the case in for this study. It is probable however that more intensive studies beyond the shelf would have led to encountering more Leach'st Storm-Petrels, changing their habitat model. Great Shearwaters and Wilson's Storm-Petrels both showed no relationship to chlorophyll densities, whereas Leach's Storm-Petrels had a negative relationship with chlorophyll. Other studies have reported the lack of a relationship between mean chlorophyll densities and bird densities, and some avian species that do not have a strong relationship with chlorophyll densities have been found to have a significant relationship with persistent high densities of chlorophyll (Suryan et al. 2012). Great Shearwaters had a negative relationship to sea surface temperature, indicating that they were distributed in areas with colder water. Huettmann and Diamond (2006) used linear models to examine habitat relationships and found that storm-petrels showed the best linear fit with sea surface temperature across all scales examined. Leach's Storm-Petrels were found closer to temperature fronts, which are likely areas of increased productivity and prey availability (Schneider 1982), but neither storm-petrel species showed a relationship with water temperature in this study. Differences in the distributions and habitat preferences for the three species may be due to in part to Leach's being unable to use their "ideal" habitat, and instead must travel back to the colony to care for offspring, as in central-place foraging (Garthe et al. 2009), though one might also expect parents to have the greatest pressures for high-quality nutritious prey. Recent tracking studies have illustrated, however, that Leach's Storm-Petrels travel much further than expected for foraging during the breeding season, off the shelf for over a thousand kilometers (Pollet et al 2014). It is likely that the limited scope of the survey area influenced the habitat results in this study for the storm-petrels, as their ideal habitat off the shelf was not surveyed.

Seabirds are patchily distributed over preferred habitat and are concentrated where the water column is unstable (Brown 1986). Oceanographic fronts, the edges of continental shelves, and restricted zones such as the tide-rips in the Bay of Fundy are all areas where seabird species aggregate (Brown 1986, Ronconi 2010a). Wilson's Storm-Petrels were found to be most common over the shelf-break on Georges Bank, which was represented here by the 1000-m isobath (Brown 1986). Satellite tracked Great Shearwaters have been found to spend the bulk of their time in the Gulf of Maine in areas with strong tidal upwellings, in particular the southern portion of the Bay of Fundy, Brown's Bank, German Bank, and George's Bank (Ronconi 2010a). These are areas that were important for migrant diving foraging birds in this study, like Great Shearwaters (Figure 2.5). No relationship was found with the shelf break in this study, but the habitat was not thoroughly sampled. Amorim et al.'s (2008) models of Cory's Shearwater distributions were not highly explanatory due to the fact that their study area didn't encompass the entire range of the shearwaters, which could be a problem with my study as well.

2.4.5 Species at risk

Roseate Terns breed on the coast of Cape Cod, Maine, and eastern Nova Scotia, and all of the summer observations of these birds were made close to breeding colonies. No recent observations (2006-2010) were made in the study area during summer. Roseate Terns are at risk from pollution, habitat degradation, including inter-annual variation in sandlance availability (Goyert 2013) and are also at risk of collision with inshore and offshore wind turbines during the breeding and migratory seasons (Burger et al. 2011). Protection in offshore areas near colonies, not just on the colonies, could be important for maintaining and increasing populations of these endangered species (Goyert 2013). Other threatened and endangered species were distributed widely throughout the study area. The most observed of these were Wilson's and Leach's Storm-Petrels, whose distributions have been detailed above. Arctic and Common Terns were both found predominantly in areas which were found to be important to Roseate Terns in the historical data examined (Figure 2.8).

2.4.6 Overview

During summer in the Gulf of Maine the seabird aggregations were numerically dominated by trans-equatorial migrant Great Shearwaters. They were associated with deeper water offshore habitats. Examining species group distributions revealed some differences in habitat use. Migrant diving and surface feeding birds dominated the area. Locally breeding divers were concentrated inshore, while the surface-feeding local breeders were dispersed throughout the study area. The two groups of migrant birds overlapped in areas of high density off of the German Bank, with diving birds found in high concentrations elsewhere as well. Compared to the diving birds, surface-feeding birds are less likely to be affected by gillnet bycatch and are more likely to be caught on long-lines.

Both storm-petrel species were widely dispersed throughout the region, though they did not share areas of highest abundance. Different habitat features influenced the two species, with Leach's Storm-Petrels in areas closer to fronts with lower chlorophyll densities, while Wilson's were in deeper waters further from the coast. Wilson's distribution was more similar to the migrant Great Shearwaters than to the more closely related Leach's Storm-Petrels. This finding lends some support for the constraints of central place foraging theory mentioned above (Hedd et al. 2009).

A number of Endangered and At Risk birds occur widely in the Gulf of Maine. Any developments made in the Gulf of Maine must consider the seabird inhabitants, and the risks developments may have (Croxall et al. 2012, McFarlane-Tranquilla et al. 2013).

Determining where seabirds are distributed throughout the marine environment is essential for understanding their habitat and trophic interactions. Kernel density maps of different seabird groups reveal different high use areas, and distribution maps of species can reveal additional important areas for key species (e.g. Hedd et al. 2011, McFarlane-Tranquilla et al. 2013). This information is key for minimizing the risks anthropogenic pressures carry for marine animals and their habitats (Hedd et al. 2011). Shearwaters, along with other pelagic seabirds, are threatened by bycatch – it is their greatest threat offshore in foraging areas (Croxall et al. 2012). While it is difficult to study the impacts of bycatch, recent work has shown that the removal of gill nets in Newfoundland has led to an increase in alcid numbers in breeding colonies (Regular et al. 2013). Portions of the Gulf of Maine overlap with fisheries, and the coast and shelf areas of eastern Canada have been found to be important area of high overlap between fisheries and marine birds (Karpouzi et al. 2007). Oil and gas development is ongoing in the Gulf of Maine and on the Scotian Shelf and has had large negative impacts on seabirds at sea

(Schneider and Heinemann 1996, Weise et al. 2001, Fifield et al. 2009), with the major threat being well failure (e.g. Deepwater Horizon in the Gulf of Mexico, Montevecchi et al. 2011). The Jordan Basin is not currently a site for oil exploration in Canada. For some of the most abundant birds, however, the Jordan Basin is highlighted as an area with high bird densities. This is an area that could be considered for protection, perhaps as a designation as an Important Bird Area (IBA). Further analyses should incorporate studies of how birds relate to the habitat in this specific area, compared to other regions in the Gulf of Maine.

Alternative energy developments such as wind and tidally-generated power are increasing and pose new risks for migrating land birds and seabirds. These risks include collisions with the turbine base and blades, destruction of underwater habitat for prey, displacement from feeding areas, and increased energy expenditure (Goodale and Divoll 2009). Knowledge of important areas for seabirds can minimize the impact of these energy developments on seabirds, by proper siting of wind farms or oil development in less populated areas of the ocean.

Chapter 3 Decadal Changes in Seabird Diversity of the Gulf of Maine

3.1 Introduction

In this chapter, I assess the diversity of seabirds in the Gulf of Maine during the summer and how that diversity has changed on a decadal time scale. I explore several of the many different methods available to examine diversity.

The Gulf of Maine is a region used heavily by breeding and by non-breeding seabirds (Schneider and Heinemann 1996), and studying changes in seabird diversity over time can indicate decadal shifts in species composition that reflect the environmental variation and change. Identifying locations of top predator diversity hotspots can help clarify links between seabirds, multi-species interactions and ocean habitat (Montevecchi et al. 2012). Biodiversity increases the capacity of ecosystems to adapt to environmental change and maintain productivity and resiliency (Mace et al. 2005). Measures of taxonomic distinctness, or the average taxonomic path length (evolutionary distance) between species observed in the study area, can also be used to determine levels of ecosystem functioning and to test the effects of a disturbance on a community (Warwick and Clarke 1998). Studying the diversity of top predators improves understanding of food webs and of the lower trophic levels that support them (Louzao et al. 2011).

It is important to monitor seabird numbers and distributions at sea, because as shown in Chapter 2 many non-breeding birds use the area and monitoring at colonies is inapplicable to them (Schneider and Heinemann 1996). Studies of seabirds through tracking have greatly advanced understanding the behavioural and movement ecology of birds at sea (Frederiksen et al. 2011, Hedd et al. 2012, Montevecchi et al. 2012), yet vessel survey data yield the most information on seabird diversity, population distributions, and densities.

The Gulf of Maine and Scotian Shelf are productive ocean habitats due in part to cross-isobath fluxes of high nutrient waters and winter mixing (Townsend et al. 2004). These productive areas, as explained in greater depth in Chapter 1, are used extensively by both breeding and non-breeding seabirds from the Northern and Southern Hemispheres (Brown et al. 1986). Seabirds are highly visible top predators that reflect food webs and ecological processes (Grémillet and Charmantier 2010). Accordingly, climatic and anthropogenic change can have profound direct and indirect effects on seabird populations (e.g. Regular et al. 2013), with indirect effects mainly through changes in oceanographic processes and subsequent changes in availability of prey (Grémillet and Boulinier 2009). Substantial ecosystem changes have occurred over time in the physical water properties, from both climate and human influences (Mountain and Kane 2010). Groundfish fisheries have been overexploited by decades of fishing with management practices limited by social and economic variables, which impacts the entire Gulf of Maine ecosystem (Acheson and Gardner 2011). A major decrease in salinity occurred in the 1980s and 1990s, as well as significant changes in the zooplankton community structure during the same period (Mountain and Kane 2010). Changes in the salinity and zooplankton communities could impact seabird distributions and prey availability, i.e. where and how they are able to find their food.

Many stressors are associated with the dense coastal populations of humans in the Gulf of Maine. Human threats include alterations of the coastal hydrologic regime and human land use, organic and toxic materials such as oil spills, and intensive fishing pressure (Schneider and Heinemann 1996, Peterson et al. 2003, Nisbet et al. 2013). Marine birds are caught and drowned in fishing nets, trawls and longline gear, and this has only gotten worse with technological advances in fishing methods (Montevecchi 2002, Regular et al. 2013). Marine birds can be affected by more ecologically friendly human use as well, such as wind energy developments (Garthe and Hüppop 2004, Nisbet et al. 2013). By identifying areas that are important for seabirds, we can work to protect these areas by enforcing best practices for anthropogenic uses (Davoren 2013). For example, best practices with offshore wind development include field research to generate spatial data with which to build models of avoidance of hotspots and low use areas, siting properly to minimize impacts to marine birds, and monitoring of impacts after construction and any adaptive management as needed (Dolman and Simmonds 2010).

This chapter documents the changes in species richness, evenness, abundance, taxonomic distinctness, and taxonomic variability of the seabirds that use the Gulf of Maine. Specific attention is directed at distributional shifts of seabird diversity hotspots. In this chapter, I analyze Canadian Wildlife Service data from standardized surveys conducted during June to September from 2006 to 2010 (Gjerdrum et al. 2012) to assess locations of high seabird diversity. I contrast these findings with seabird surveys completed from 1980 to 1990 in decadal assessments of changes in seabird diversity. In addition, identified diversity hotspots are indicated and recommended for considerations of potential protective status to help maintain biodiversity, productivity, and to help prevent further ecosystem impacts. Data information gaps are also indicated and suggestions for future research target areas are offered.

3.2 Methods

3.2.1 Study Area

The Gulf of Maine, the southern portion of the Scotian Shelf and the northern edge of Georges Bank comprised the study area (Figure 3.1). The Gulf of Maine has high biological productivity - in the offshore, primary productivity averages 270 gC m-2 yr-1 (Townsend et al. 2004). As a comparison, the Grand Banks offshore of Newfoundland average 200 gC m-2 yr-1

(Townsend et al. 2004). The high productivity is due to tidal mixing, seasonal cycles, and influxes of cold, fresh, nutrient-rich water from the Scotian Shelf through the Northeast Channel, as well as warm surface shelf waters (Townsend et al. 2004). The Scotian Shelf is a broad shelf with deep basins and channels and is similarly influenced by tidal mixing, frontal dynamics, and influxes of cold fresh water from the North. Chapter 1 provides further details.

3.2.2 Data Collection

ECSAS (2006 - 2010)

Seabird survey data were collected in strip transects 300 m wide of 5 or 10-min duration with vessel speeds of 4 - 19 knots from the bridges of ships of opportunity. GPS location was recorded at the start and end of each transect, as well as the distance traveled (Gjerdrum et al. 2012). For the study area and time period, average line length was 1.77 km, and average velocity 10.08 knots. At the start of each 5-min survey the date, time, course, speed, weather, visibility and sea conditions were recorded. Birds were identified to species or lowest possible taxa and for each flock a distance category (0-50 m, 50-100 m, 200-300 m), number of birds, species associations, behaviours, age, moult, sex and flight direction were recorded when possible. Flying birds were counted once each minute instead of constantly in order to not inflate the numbers of flying birds (Tasker et al. 1984). For details on the methods see Gjerdrum et al. (2012). A subset of these variables (species, number, location) was used in this study to look at broader context changes over decades.

PIROP (1966 - 1992)

The Programme Intégré de Recherches sur les Oisaux Pelagiques (PIROP) is a database with counts of seabirds in Eastern Canada and the Arctic from 1966 to 1992 (Brown et al. 1975, Brown 1986). Surveys were conducted in 10-min intervals onboard ships of opportunity, mostly with unlimited transect width and survey areas, and cannot be standardized to density estimates (Brown 1986). Flying birds were sampled continuously which can inflate the number of seabirds counted, providing a measure of seabird “flux” rather than presence (Gjerdrum et al. 2012). This will likely cause a higher count of flying birds in the PIROP dataset compared to the current data.

Manomet (1980 - 1988)

The Manomet Bird Observatory in the Gulf of Maine conducted seabird surveys between 1980 and 1988 as part of a long-term monitoring project to assess the abundance and distribution of seabirds, as well as cetaceans and sea turtles in shelf and shelf-edge waters off the Northeastern US (Pittman and Huettmann 2006) using a 300 m band transect (Tasker et al. 1984). The surveys focused in large part on Georges Bank (Powers 1983). As in the PIROP surveys, flying birds were sampled continuously, which can inflate the number of seabirds counted (Tasker et al. 1984, Spear et al. 1992, Gjerdrum et al. 2012).

Temporal Coverage

The survey period examined in this study was the summer, defined here as June through September to limit the influence of seasonal changes in the data set and more closely match my study periods. To examine changes over time, the surveys were partitioned in to three 5-year time blocks with similar spatial coverage: 1980-1984, 1985-1990, and 2006-2010. No surveys were conducted in the study area in 1989. Extremely few surveys were run in the 1990s and coverage in the Gulf of Maine from 1968 - 1979 was substantially lower and restricted spatially to Canadian waters and therefore was not included in this analysis. Figure 3.1 illustrates the changes in temporal survey effort.

Spatial Coverage

All surveys within the area of 40º x 45.5º N latitude, -63º x -71º W longitude were extracted from the database. The PIROP and Manomet survey data were restricted to points within 20 km of an ECSAS survey to ensure similar areas were covered for comparisons. This was undertaken to keep the survey areas as similar as possible for comparative purposes. This spatial restriction resulted in excluding the 60% of the PIROP and Manomet survey points which were located further from the more recent ECSAS survey locations. Survey points were plotted inside a 50 x 50 km grid cell for analysis. Survey coverage was restricted to area grid cells with coverage from all three time periods (Figure 3.1).

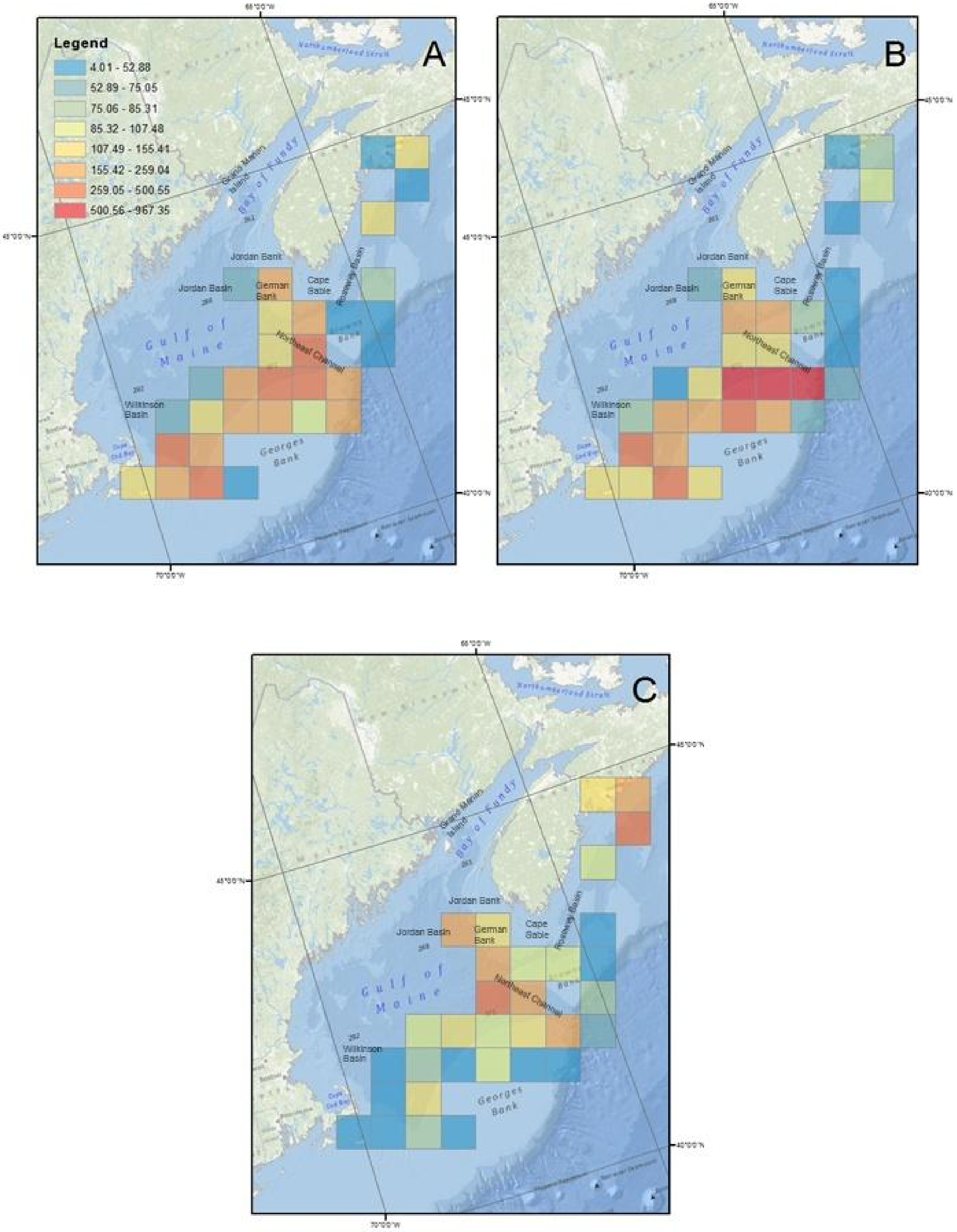

Figure 3.1: Maps of survey effort (linear km surveyed) in 50 x 50 km grid cells used in the seabird diversity study for the periods: A) 1980-1984, B) 1985-1990, C) 2006-2010. Warmer colours indicate more linear kilometers surveyed within the cell.

3.2.3 Species Observed

The numbers of individual birds counted in the study area were divided by total linear kilometers surveyed to control for effort across time periods. Each 5-year segment was totaled individually. Both the individual species observed and the groupings of species into higher taxonomic levels were totaled. The higher taxonomic level totals include birds observed that were only identified to family or genus, while species totals are only birds that were identified to species. The rankings of different species were noted, as were the changes in taxonomic groups over time.

3.2.4 Spatial Diversity Calculations

Besides the number of animals using the area, different diversity measures contribute other information to assessments of seabird ecology. Species richness can be a valuable tool for comparing systems, as can evenness or the extent to which any given species is dominating the system (Humphries et al. 1995). All of these measures, however, are highly dependent on sampling effort, which can lead to misleading results with unequal sampling between study areas or times (Clarke and Warwick 1998), as we have with this study. Differences in spatial coverage and survey times increase the chance of seeing new species, but not in a linear fashion, which makes standardizing by area surveyed or sampling effort ineffective and inaccurate (Gotelli and Colwell 2001, O'Hara 2005). One of the assumptions for analyses of commonly used diversity indices is a random distribution of animals in the environment (Flather 1996), which is not true of seabirds at sea, as illustrated in Chapter 2. Average taxonomic distinctness and variability, which are not influenced by sampling effort, were used in this study as additional measures of diversity and are explained in detail below (Clarke and Warwick 2001). These diversity measures are based on taxonomic relatedness of species observed. Additionally, rarefied species richness allows for comparisons between survey periods with the same effort because you can examine the richness at the same level of effort between different time periods, as is explained in detail below (Clarke and Warwick 2001).

3.2.5 Species Richness from Species Accumulation Curves

Sample-based species accumulation curves of birds per linear kilometer were drawn with bootstrapping techniques using PRIMER (Clarke and Gorley 2006). Curves were re-drawn 1,000 times from the data and average curves were based on these iterations. For data sets with patchy distributions of subjects the sample-based species accumulation curves are more precise for modeling than individual-based curves because they consider only incidence and not abundance of species. Individual-based rarefaction curves ignore patchiness and overestimate expected richness for rarefied samples, as they assume a random distribution of species in the samples. Sample-based curves, on the other hand, provide a realistic estimate of the number of species to be found in sets of real-world samples (Colwell et al. 2004). Simple species number was also used in this analysis, explained below.

Species accumulation curves were drawn for 5-year samples of species richness within the entire study area. The 5-year samples (1980-1984, 1985-1990, 2006-2010) were chosen to allow for comparisons between the older and more recent data with rarefaction curves. The curves can compensate for differences in numbers of surveys conducted because you can compare different time periods by looking at the same effort per number of surveys conducted. Areas surveyed more frequently will yield higher numbers of species and individuals detected, so species accumulation curves were drawn for the entire survey area (Figure 3.1). Bootstrapping was used to draw the species accumulation curves because their shape depends on the order of accumulated samples. Hence, species accumulation curves were drawn and re-drawn randomly to ensure that each time new species were added different orderings of species were taken into account; an average of these 1,000 bootstrapped curves provides a robust estimate of the species accumulation for a given area.

Estimates of total species richness can be used to correct observed species richness by adding a term based on species observed only once or twice in the survey sample. Estimates were made using the first order Jackknife using the Species Accumulation Curves tool in PRIMER (Clarke and Gorley 2006). The estimator is useful to approximate total species richness in an incompletely sampled community. To reduce uncertainty in estimates of species richness, Walther and Moore (2005) recommend using Jackknife 1 to reduce potential bias and increase accuracy of estimates based on extensive comparisons of richness estimators.

The first Jackknife estimates the number of species missing from the sample using frequencies of species found in the collection of sites. The first order jackknife for abundance data is:

$$S_P = S_O + f_1$$

where S_P is the extrapolated richness in the pool, S_O is the observed number of species in the collection, and f_1 is the number of species observed once (Gotelli and Colwell 2011).

The asymptote of a species accumulation curve indicates the estimate for species richness in a given collection. Changes in the rate of accumulation, or the shape of the curve, are of interest because they reflect the relative abundance (evenness) of species, and the spatial distribution of the species (Flather 1996). The rate of accumulation of species declines when the proportion of relatively rare species increases, and when individuals are more clumped in their environment. In terrestrial ecosystems Flather (1996) found that landscapes with more agriculture and urban land uses accumulated species more slowly than landscapes with more natural habitats, showing that areas impacted more heavily by humans have slower accumulation rates. Rarefaction curves that do not reach an asymptote indicate inadequate survey coverage of the area, and differences between curves for observed and estimated richness can indicate under sampling (Brown et al. 2011).

3.2.8 Diversity Measures

Species richness (R), abundance (A), evenness (J'), average taxonomic distinctness ($\Delta+$), and average taxonomic variability ($\Lambda+$) were calculated for individual 50 x 50 km grid cells over the three periods using PRIMER's DIVERSE tool (Clarke and Gorley 2006).

Species richness refers to the number of species observed within the grid cell. $R = s$ where s = number of species observed.

Abundance is the number of animals seen in a grid cell during the survey period. $A = n$ where n = the number of animals observed.

Evenness refers to Pielou's evenness, which uses the Shannon Diversity index to measure how even or uneven an assemblage is. Evenness is a calculation of the contribution of each species to the overall number of individuals in an assemblage (Mulder et al. 2004). The evenness calculation is based on the formula:

$$J' = H'/H'\text{max}$$

where $H' = -\sum_{i=1}^{R} pi \ \ln pi$ and pi is the proportion of individuals belonging to the ith species in the dataset, and H'max is the maximum of H' or $H'\text{max} = -\sum_{i=1}^{s} \frac{1}{s} \ln \frac{1}{s}$. The values for this measure range from 0, where all individuals are from one species, and 1, where multiple species are present in equal abundance. Numbers closer to 0 indicate large differences in species evenness, with one or two species dominating the numbers of animals observed and the rest of the species represented by few individuals; numbers approaching 1 indicate more evenness in species diversity, with each species represented by close to the same number of individuals (Mulder et al. 2004).

Higher taxonomic distinctness values indicate species are on average less closely related and more distinct from one another, and low values indicate species are more closely related and less distinct. Taxonomic distinctness provides an understanding of the taxonomic diversity of a system and can allow for comparisons between areas with different sampling intensity (Clarke and Warwick 1998). Lower taxonomic distinctness can indicate a greater vulnerability to loss of species because the available species composition is more restricted (Clarke and Warwick 1998). Taxonomic distinctness (Δ*) is modified to decrease some of the dependence of Δ on the species abundance distribution. Taxonomic distinctness can also be used for presence/absence data in the form of average taxonomic distinctness (Δ+). In this study, I used Δ+, which is a measure of the average path length, or taxonomic distance, between any two individuals drawn at random from the data. Taxonomic distinctness is calculated by summing the total path lengths between species on a taxonomic tree, and dividing by the number of paths (Clarke and Warwick 2001). The distinctness values for different aggregations or time periods can be compared using an ANOVA. Average taxonomic distinctness (Δ+) is a form of Simpson's Diversity Index constructed to test the probability that two individuals taken at random from the full set are from the same species. Taxonomic distinctness incorporates taxonomic relatedness in this measure (Warwick and Clarke 1995).

$$\Delta + = \left[\Sigma\Sigma_{\mathrm{i}<j}\mathrm{w}_{\mathrm{ij}}\right]/[\frac{m(m-1)}{2}]$$

where m is the number of species in the study and wij is the weight (path length) given to the taxonomic relationship between species i and j.

Average taxonomic variability (Λ+) is a measure of the unevenness of the taxonomic diversity, to see if taxa are over- or under-represented (Clarke and Warwick 2001). Higher values indicate that there is more variation in the taxonomic tree structure, and lower values indicate less variation. Taxonomic variability is the variance of the paths connecting species and indicates the degree of unevenness of a taxonomic tree. Average taxonomic variability is independent of sample size.

Both taxonomic distinctness and taxonomic variability calculations were based on weighted branch lengths between species (Table 3.1; Clarke and Warwick 2001). These weights were calculated based on the taxonomic distinctness of the master taxonomy list used for the analysis (Clarke and Warwick 1999) which includes all birds observed over all surveys and time periods within 40 x 45.5 N latitude, -63 x -71 W longitude. The weights that were given to a step, i.e. a movement from species to genus, were defined as proportional to the percentage by which taxon richness decreases at that step (Clarke and Warwick 1999). These weights help highlight distances between species and genera, rather than families and orders, as there are fewer of the higher taxonomic categories observed overall (Table 3.1).

Diversity data results are only included for cells with greater than 3 species across all periods, because when fewer than 3 species are observed, calculations of Δ+, Λ +, and J’ resulted in errors. Therefore this portion of the study deals with a more restricted area compared to the sections concerning species occurrence and species accumulation curves. Grid cells included in this section are illustrated in Figure 3.6.

Table 3.1: Richness of different taxon levels observed in the master taxonomy of the Gulf of Maine study region during the summer, and the weight assigned to that branch length for the study.

Taxon	Richness	Weight
Species	46	19.01
Genus	25	45.65
Family	9	68.78
Order	4	100
Class	1	100

3.2.9 Statistical Analysis

Simple linear models were built to test the change in seabird abundance over the three time periods based on higher taxonomic groups and individual species groups. Pearson's correlation coefficients and dot charts were used to examine the influence of individuals counted and survey effort on each diversity measure. To allow for different variances, generalized least square methods were used. The VarIdent variance structure was used to allow for different variances by time period in the R package nlme by adding variance covariates for the variance of the residuals (Pinheiro et al. 2011). Scatter plots with 95% contours were constructed to test for survey locations with significantly low or high taxonomic distinctness and variability measures. Values of taxonomic distinctness were plotted on 50 x 50 km grid cells to highlight areas with the highest values, and the species composition of these high taxonomic distinctness areas was examined for the three periods.

I built general linear models to determine changes in the diversity within each individual grid cell over time. Models were built to examine changes over time for each diversity measurement, and I examined the slope coefficients to see if they were positive or negative (LaSorte and Boecklen 2005). I then calculated the percentage of positive coefficients over all grid cells for an indication of overall changes in each diversity measurement. The correlations between the model slope coefficients of different diversity measurements for individual grid cells were tested to see if any relationships exist between trends in diversity measures for individual cells – if, for instance, grid cells with increases in species richness also had increases in species evenness.

3.3 Results

3.3.1 Species Observed and Changes

Total survey lengths varied among the three time periods: 1980-1984 5,529.8 km; 1985-1990 6,042.2 km; 2006-2010 4,720.9 km. There were differences in temporal coverage for months surveyed between the three time periods (Table 3.2) The abundances of taxonomic groups and species varied through the different periods (Tables 3.3 and 3.4). Shearwaters, phalaropes and auks showed a trend to an increase (Table 3.3, Figure 3.2), with the auks, primarily Atlantic Puffins, and phalaropes increasing markedly from the 1980s through the 2000s. No significant changes were detected among the three time periods for the higher taxa levels (Table 3.3). Overall, numbers of birds observed increased, with the highest total number of birds observed per km surveyed in 2006-2010 (0.40 birds per km, compared to 0.34 for 1980-1984 and 0.30 for 1985-1990). Storm-petrel species exhibited a decrease over time, while gulls, terns, skuas and jaegers fluctuated through the three periods (Table 3.3).

Table 3.2 Transects completed by month for the three 5-year time periods.

Years	June	July	August	September
1980-1984	630	184	551	139
1985-1990	389	29	750	628
2006-2010	7	414	570	755

Table 3.3: Seabirds observed during surveys from the three periods adjusted for effort. Abundance among the surveys is controlled for effort by dividing birds counted by the total linear km surveyed (5529.8 km 1980-1984; 6042.2 km 1985-1990; 4720.9 km 2006-2010). This table includes birds identified to species and birds identified to higher taxonomic levels. Overall trend between 1980-1984, and 1985-1990 and 2006-2010 is indicated as an increase (+) or decrease (-) in observed species abundance. Percent change calculations were made comparing 2006-2010 and the earliest period, 1980-1984. No significant changes were found

Taxa	1980-1984	1985-1990	2006-2010	Change	% Change
Puffinus and *Calonectris* spp.	0.127	0.129	0.182	+/+	43%
Hydrobatidae	0.118	0.09	0.088	-/-	-25%
Scolopacidae	0.001	0.004	0.019	+/+	1800%
Laridae	0.056	0.051	0.062	-/+	11%
Sternidae	0.006	0.01	0.007	+/-	17%
Sterrcorariidae	0.004	0.007	0.004	+/-	0%
Alcidae	0.0004	0.001	0.005	+/+	1150%
Total All Taxa	0.337	0.303	0.395	-/+	17%

Table 3.4: Abundance of birds (birds/linear km) observed during surveys from the time periods, by species. The numbers of birds included are only for those identified to the species level. Abundance between the surveys is controlled for effort by dividing birds counted by the total linear km surveyed (5529.9 km 1980-1984; 6042.2 km 1985-1990; 4720.9 km 2006-2010). Overall change is indicated as an increase (+) or decrease (-) in observed species abundance, with the change from period 1 to 2 first, and then the change from 2 to 3. One star (*) indicates significance at the 0.10, three (***) indicate significance at the 0.01 level.

ID to Species	1980-1984	1985-1990	2006-2010	Change
Northern Fulmar	0.0199	0.0081	0.0085	-/+
Cory's Shearwater	0.015	0.018	0.01	+/-
Great Shearwater	0.08	0.084	0.162	+/+
Sooty Shearwater	**0.029**	**0.018**	**0.007**	**-/- *****

Manx Shearwater	0.0027	0.0023	0.0023	-/+
Audubon's Shearwater	**0**	**0.0002**	**0.0004**	**+/+ ***
Wilson's Storm-Petrel	0.068	0.061	0.036	-/-
Leach's Storm-Petrel	0.049	0.021	0.04	-/+
Northern Gannet	0.0045	0.0013	0.0148	-/+
Double-crested Cormorant	0	0.0003	0.004	+/+
Great Cormorant	0	0.00017	0.0002	+/+
Wilson's Phalarope	0	0.0002	0	+/-
Red-necked Phalarope	0.0004	0.0005	0.0034	+/+
Red Phalarope	0.0004	0.0012	0.0047	+/+
Black-legged Kittiwake	0.0005	0.001	0.0002	+/-
Laughing Gull	0.0016	0.0013	0.0006	-/-
Ring-billed Gull	0	0	0.0002	0/+
Herring Gull	0.018	0.02	0.025	+/+
Iceland Gull	0.0002	0	0	-/0
Lesser Black-backed Gull	0.0002	0	0.0004	+/-
Great Black-backed Gull	0.035	0.029	0.036	-/+
Least Tern	0	0.0002	0	-/+
Roseate Tern	0.0002	0.0005	0	+/-
Common Tern	**0.0036**	**0.004**	**0.0045**	**+/+ ***
Arctic Tern	0.0007	0.001	0.0009	+/-
Royal Tern	0.0002	0	0	-/0
Great Skua	0.0002	0.001	0.0004	+/-
South Polar Skua	0	0.0003	0.0013	+/+
Pomarine Jaeger	0.0025	0.002	0.0025	-/+
Parasitic Jaeger	0.00072	0.00066	0	-/-
Dovekie	0.0002	0.0005	0.0002	+/-
Common Murre	0.00018	0.00017	0.00021	-/+
Thick-billed Murre	0	0	0.0002	0/+

Razorbill	0	0	0.0002	0/+
Black Guillemot	0	0	0.001	0/+
Atlantic Puffin	**0**	**0.0002**	**0.002**	**+/+ ***

Great Shearwaters were the numerically dominant seabird species throughout all periods, and have exhibited a non-significant trend to an increase (Table 3.4). Great Shearwaters made up a higher percentage of the birds observed in the current surveys (44%) compared to earlier periods (24% 1980-1984, 30% 1985-1990). Wilson's Storm-Petrels were the second most abundant species, close behind Great Shearwaters in 1980-1984. The numbers of Wilson's Storm-Petrels decreased from 20% to 10% of the birds observed, while the abundance of Leach's Storm-Petrels remained about the same. Some individual species increased or decreased significantly over time (Table 3.4). Sooty Shearwaters showed a significant decline throughout the decades, dropping from 9% to 2% of birds observed (Table 3.4). Common Terns, Atlantic Puffins, and Audubon's Shearwaters all showed slightly significant increases over time (Table.3.4).

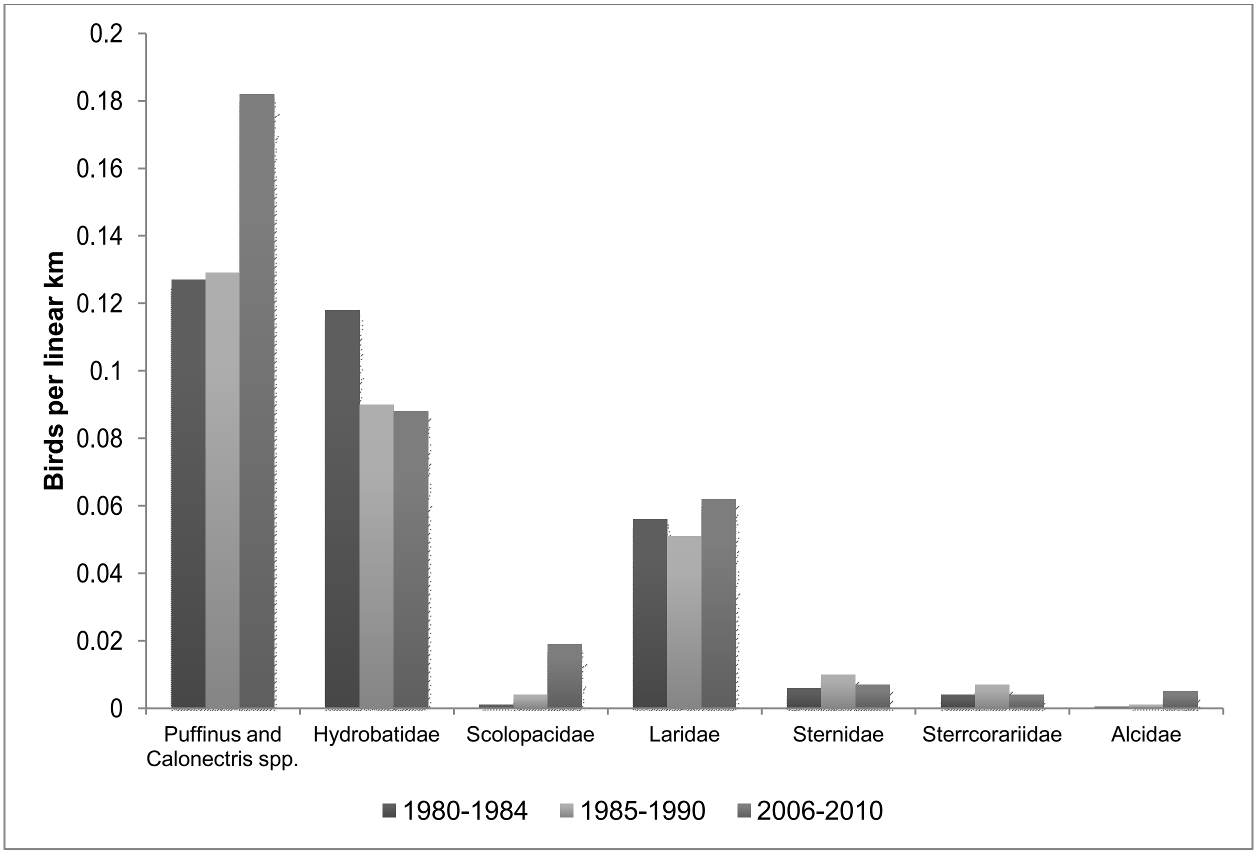

Figure 3.2: Seabirds observed during the three periods by higher taxonomic group.

3.3.2 Rarefied Species Richness

Site-based rarefaction curves show the highest diversity of birds in 1985-1990 (Figure 3.3). The curves account for differences in number of sites sampled. None of the observed species accumulation curves reached an asymptote, though they were close. This signals that further surveying would still reveal more species in the Gulf of Maine during summer and that the additional species are rare. All species accumulation curves increased rapidly, indicating an even species abundance distribution (Gotelli and Colwell 2011). When I compared the rarefied estimates for the same number of surveys (n = 579, lowest number of surveys from 1980-1984, Table 3.5), the highest number of species was observed in 1985-1990. Estimates of extrapolated species richness, or the total number of species, including unobserved species, are different for the three periods, with the highest estimated species values found during 1985-1990 (Table 3.5, Figure 3.4).

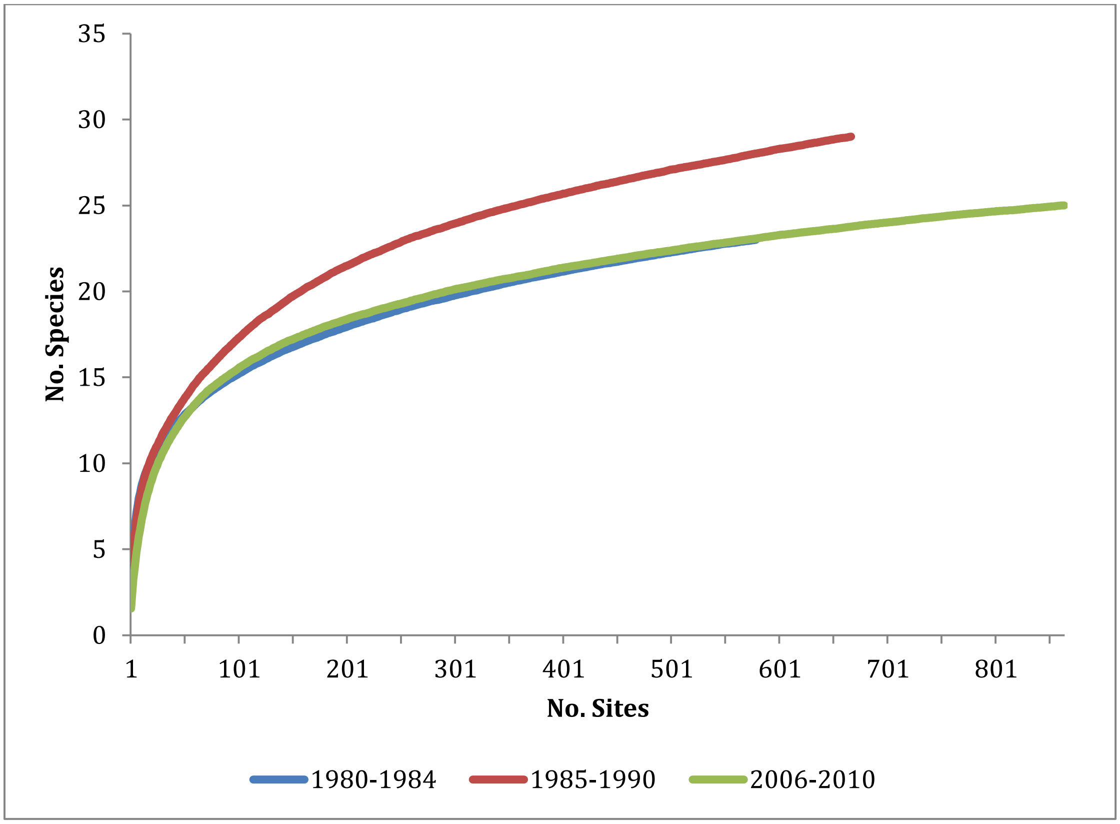

Figure 3.3: Observed species accumulation over increasing surveys conducted for the three periods, 1980-1984, 1985-1990, and 2006-2010.

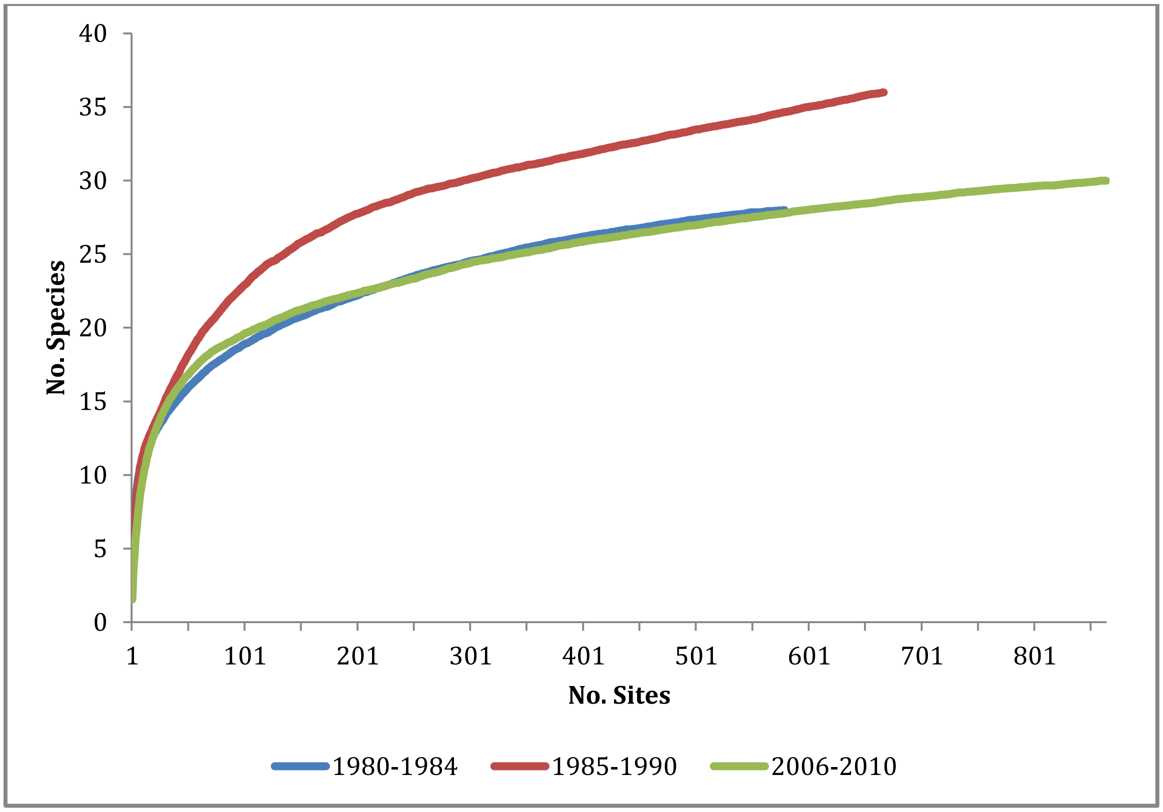

Figure 3.4: Jackknife 1 estimates of species accumulation over increasing survey effort for the three periods, 1980-1984, 1985-1990, and 2006-2010.

Table 3.5: Estimates of extrapolated species richness including unseen or unobserved species. The estimate of Jackknife 1 does not include an error estimate. Jackknife 1 estimates are estimates of total species richness for all surveys during the survey area and each period.

Survey Period	Total Species Observed	Total No. Surveys	No. Species Observed at 579 Surveys	Jackknife 1 Estimate
1980-1984	23	579	23 ± 0	28
1985-1990	29	678	28 ± 1	36
2006-2010	26	879	23 ± 1	30

3.3.3 Diversity Measures

The different diversity measures show varying levels of correlations to the number of individuals observed (Figure 3.5). Correlation between number of individuals observed and species richness is strongly positive (Pearson's $r = 0.41$, $p = 0.003$, $n = 75$), and species evenness is strongly negatively correlated with number of individuals (Pearson's $r = -0.49$ $p < 0.001$, $n = 75$). Neither average taxonomic distinctness nor average taxonomic variability were significantly correlated with the number of individuals observed. These correlations suggest that species richness and evenness were both influenced by how many individuals were observed, while average taxonomic distinctness and variability were not.

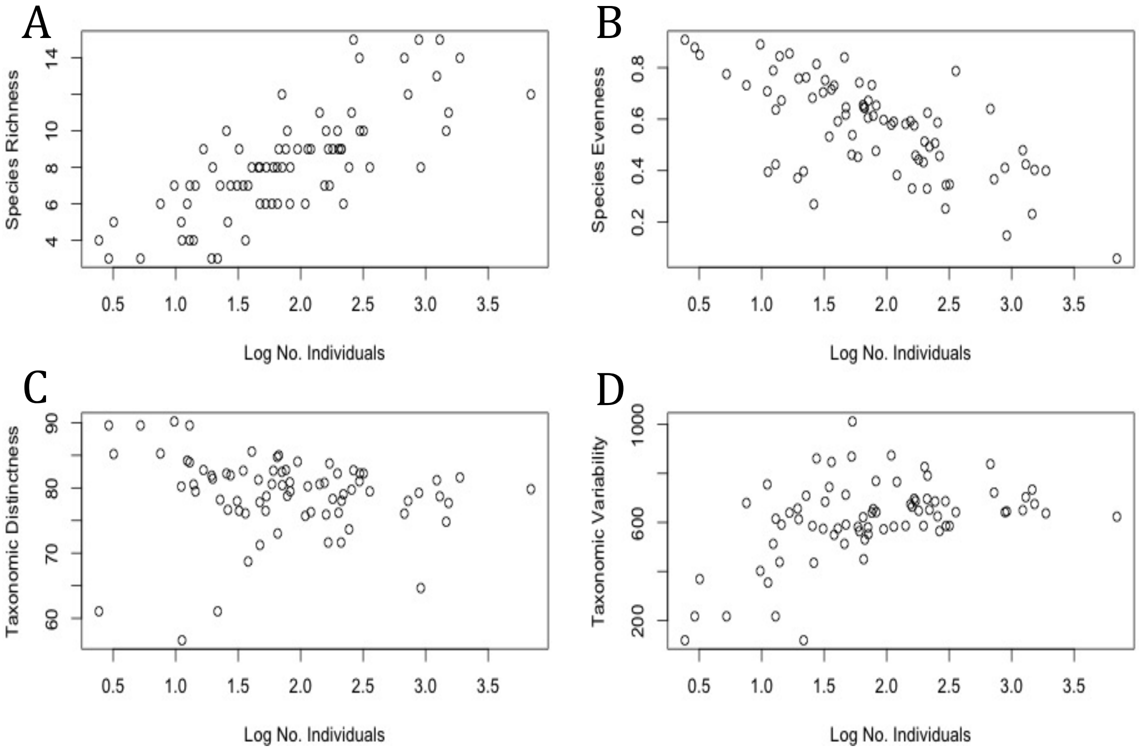

Figure 3.5: Correlations between number of individuals and a) species richness, b) species evenness, c) taxonomic distinctness, and d) taxonomic variability. Number of individuals is presented on a natural log scale.

No significant differences were found among the periods for species richness, abundance, evenness, or average taxonomic variability ($t > 1.7109$, $p > 0.05$, $n = 25$). A linear model revealed significant differences in taxonomic distinctness in 1985-1990 compared to 1980-1984 (t = 2.54, p = 0.013, n = 25). Model validation, however, showed problems with heterogeneity of the residuals, so a generalized least square model was fitted with a variance structure to allow for unequal variances between categorical variables. There was a significant improvement in model fit from the general linear mode to the generalized least square model (AIC 477.3 to 475.3, p = 0.05). This test showed a significant difference between 1980-1984 and 1985-1990 (t = 2.87, p = 0.005), but 2006-2010 was not different from either of the other two periods. This means that taxonomic distinctness increased significantly between the earlier two time periods, but the time period 2006-2010 was not significantly higher or lower than those prior. Table 3.6 presents average measures across grid cells for the three time periods.

Table 3.6: **Average species richness (S), abundance (N), evenness (J'), Shannon's Diversity (H'), average taxonomic diversity ($\Delta+$), and average taxonomic variability ($\Lambda+$) over the three time periods.**

Metric	1980-1984	1985-1990	2006-2010
S	8.58	8.83	7.42
N	296.08	526.69	154.46
J'	0.58	0.61	0.52
H'	1.19	1.24	0.99
$\Delta+$	77.02	80.97	78.73
$\Lambda+$	605.67	629.49	595.25

The ellipse plots for taxonomic distinctness versus taxonomic variability did not show any points deviating from expected values or points outside of the 95% confidence intervals in funnel plots based on the total bird taxonomy (Clarke and Warwick 1998). Taxonomic distinctness values varied within the grid cells over time (Figures 3.6 and 3.7, Table 3.6). The northern portion of the Georges Bank was an area of high taxonomic distinctness, as was the

Roseway Basin, while the Northeast Channel showed an overall decrease. An area northwest of the Georges Bank, called the Wilkinson Basin, showed a dramatic increase as well. This area is in deeper waters than the other areas that showed high increases.

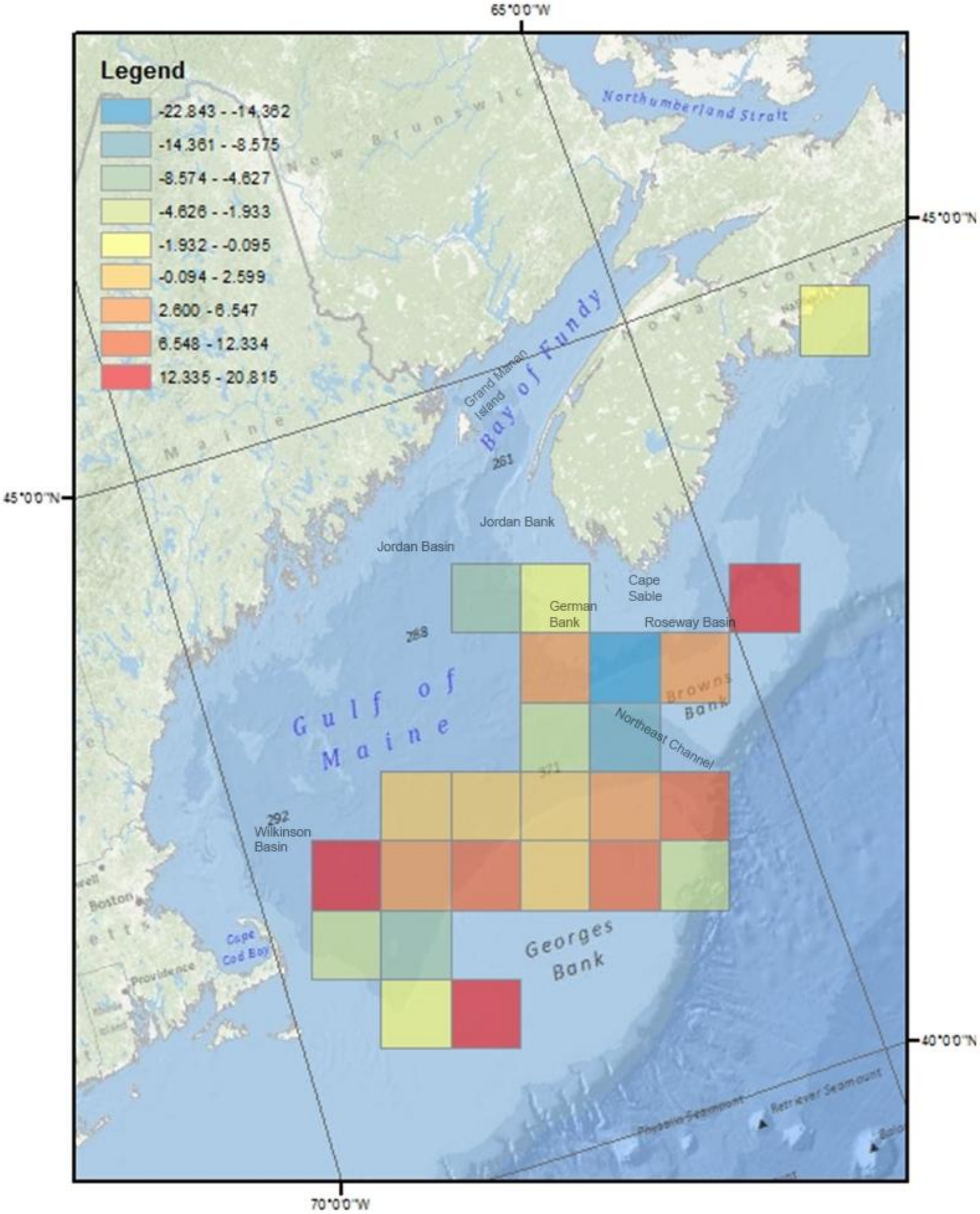

Figure 3.6: Changes in taxonomic distinctness values (or mean branch lengths between species observed) from 1980-1984 to 2006-2010.

Comparisons of four grid cells over time reveal what changes in taxonomic distinctness mean in terms of species observed (Table 3.7). Grid cell 21, or the Wilkinson Basin, increased in taxonomic distinctness from 1980-1984 to 2006-2010. In the early 1980s the area was dominated by shearwaters, fulmars and storm-petrels, with a single gull species, while in the 2000s Great Shearwaters, Northern Gannets, Red-necked Phalaropes, Pomarine Jaegers, Great Black-backed and Herring Gulls were observed, illustrating a shift from a predominately Procellariidae family to observed species from more varied taxa. Simply assessing changes in species number would show a drop from 7 to 6 species, but taxonomic distinctness is more informative in indicating the importance of species that are driving the increase in taxonomic distinctness, as some managers may not find a change from a variety of Procellariidae to a mix of other species the most desirable (Veit pers. comm.).

Slope coefficients of diversity measures over time show that most individual grid cells declined over the three periods in: species richness (68% negative slopes), species abundance (68%), species evenness (66%), and taxonomic variability (66%). More grid cells increased in taxonomic distinctness over the three periods (60% positive slopes). There were no significantly correlated relationships between the different diversity measures' slope coefficients over time, except for a negative correlation found between average taxonomic distinctness and number of species observed in a cell.

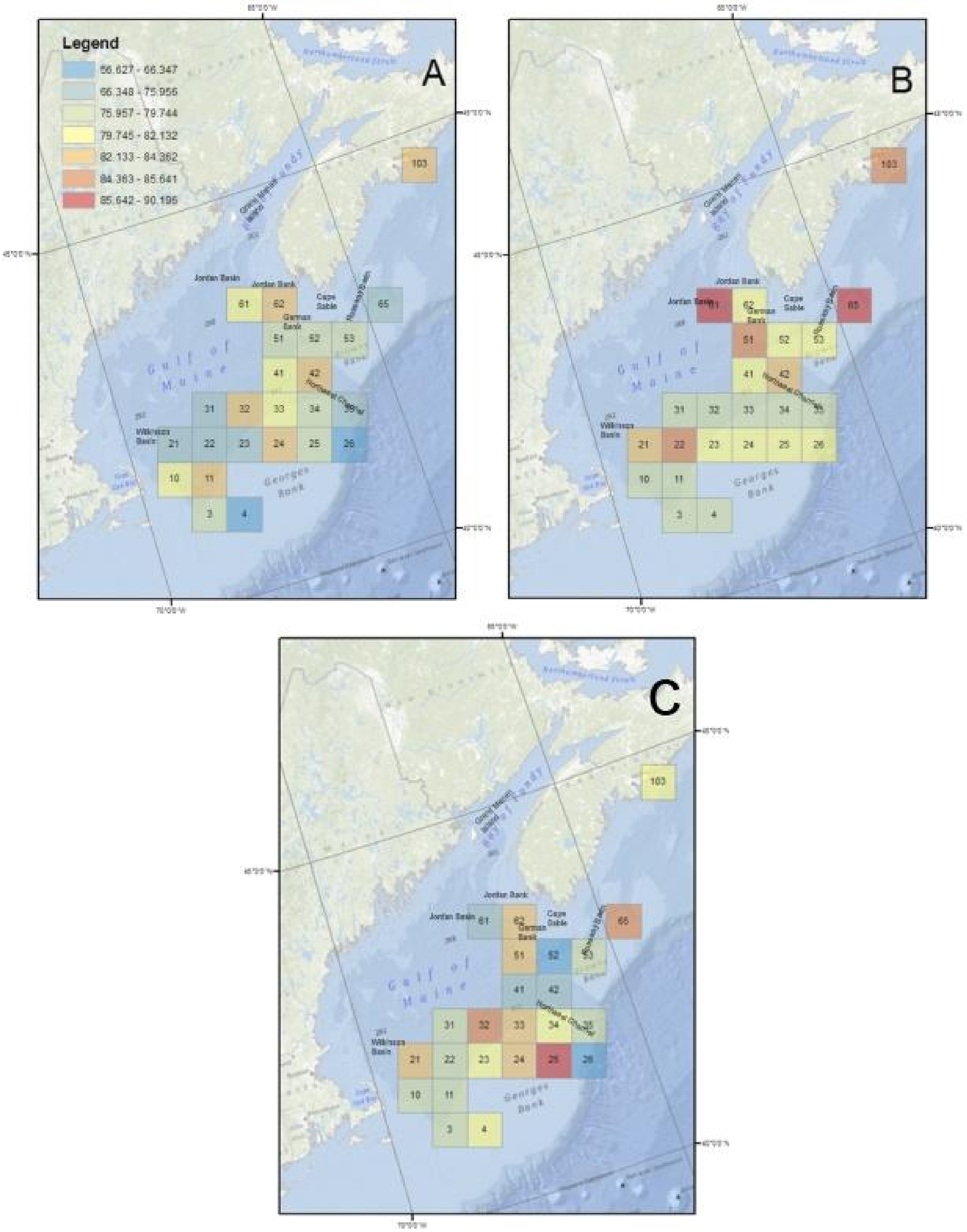

Figure 3.7: Temporal changes in average taxonomic distinctness values, or average taxonomic branch length between observed species during A) 1980-1984, B) 1985-1990, and C) 2006-2010. Numbers inside the grid cells indicate the unique ID for that cell.

Table 3.7: Comparisons of species observed in grid cells with an increase or decrease in taxonomic distinctness between 1980-1984 and 2006-2010. To relate cell numbers to locations refer to Figure 3.8.

Cell numbers	**21 – Increase**		**65 – Increase**		**4 – Increase**		**52 - Decrease**	
Years	**80-84**	**06-10**	**80-84**	**06-10**	**80-84**	**06-10**	**80-84**	**06-10**
Great Shearwater	x	x	x	x	x	x	x	x
Sooty Shearwater	x		x				x	x
Cory's Shearwater	x					x		
Northern Fulmar	x		x		x		x	
Wilson's Storm-Petrel	x		x	x	x		x	x
Leach's Storm-Petrel	x		x	x	x		x	x
Northern Gannet		x						
Red-necked Phalarope		x						
Red Phalarope							x	
Pomarine Jaeger		x					x	
Parasitic Jaeger								
Great Black-backed Gull	x	x	x				x	
Herring Gull		x		x			x	
Arctic Tern						x		
Common Murre						x		

3.4 Discussion

3.4.1 Changes in Species Composition

My first objective for this thesis was to ascertain how seabirds distribute themselves throughout the environment. I achieved this through mapping distributions of seabird guilds, modeling habitat of some dominant species, and examining distributions of endangered and threatened species. The abundance of birds in the Gulf of Maine has increased since 1980 (Table 3.4). Studies of Georges Bank and the Gulf of Maine have shown that major changes occurred between the 1980s and 1990s, with decreasing salinity, shifts in zooplankton community structure, and increases in cod and haddock abundance and survival (Mountain and Kane 2010).

My study documents additional changes to the Georges Bank and Gulf of Maine ecosystem with regard to seabirds. While species richness, abundance of birds, evenness, and taxonomic variability showed no significant changes, there was a significant increase in taxonomic distinctness. This was due to differences in species composition driving the changes in taxonomic distinctness, with a greater variety of species occurring in the 1985-1990 years. These changes could be related to changes in the environment, increased species movement or even better observer familiarity with rare and unusual species; more thorough modeling is needed to assess these potential relationships.

Several species have exhibited changes that have altered the seabird species composition in the Gulf of Maine. Auk and phalarope densities have shown recent increases, and storm-petrel species have decreased. The recent increase in phalaropes is likely indicative of a distributional shift from the Bay of Fundy where they were formerly very highly abundant and aggregated during late summer and autumn (Brown 1986, Nisbet et al. 2013). There is not adequate survey coverage over the periods to evaluate changes within the Bay of Fundy directly. Red-necked Phalaropes suffered a severe decline since the 1880s, but may be recovering based on numbers recorded on spring migrations (Nisbet et al. 2013). Leach’s Storm-Petrels are difficult to census as they are nocturnal and breed in burrows, but it is estimated that around 40,000 pairs breed in the Gulf of Maine, and recent censuses have indicated potentially declining numbers (Nisbet et al. 2013). Estimates of Wilson’s Storm-Petrel numbers are even less well known.

Higher abundances of Razorbills in the Gulf of Maine (White et al. 2011, Nisbet et al. 2013) are likely due to growing North American breeding populations (Chapdelaine et al. 2001).

Atlantic Puffin observations have increased greatly since the earlier period, which could also reflect a population increase due to successful reintroduction and expansion (Kress and Nettleship 1988), reductions in bycatch mortality (Regular et al. 2013), or changes in their distribution at sea.

A significant decrease in the number of Sooty Shearwaters was observed (Nisbet et al. 2013). These changes may have resulted from declines in fishery discards rather than colony declines (Schneider and Heinemann 1996). Sooty Shearwaters have declined in the Pacific, based on evidence from vessel surveys in the California Coastal Current system (Veit et al. 1997) and colony declines in New Zealand (Jones 2000). The decline was considered to be due in part to a decrease in prey availability in the California Current (Veit and Montevecchi 2006). In a recent tracking study Sooty Shearwaters from the Falkland Islands traveled offshore to Newfoundland and the Mid-Atlantic Ridge without stopping in the Gulf of Maine during spring migration (Hedd et al. 2012). The decline in Sooty Shearwaters in the Gulf of Maine could be due to a distributional shift, rather than a population decline, though there is no other information at present to bring to bear on these possibilities.

Comparisons to other studies of Gulf of Maine seabirds showed changes in the abundance of different species from 1978 to 1988, including marked declines in shearwater species (Schneider and Heinmann 1996). Declines were also noted among Northern Fulmars, Great Black-backed and Herring Gulls. These changes were attributed to decreased availability of discards from trawlers, as these are all species that scavenge at ships (Regular et al 2013). Differences between our assessments of changes are likely due to differences in survey areas and time periods. More recent assessments by Nisbet et al. (2013) indicate increases in Razorbills and Atlantic Puffins, decreases in the gulls as well Roseate and Arctic Terns and Great Cormorants, and inconclusive trends in the shearwater species.

Some of the recent changes noted could be due to differences in survey methodology that have also changed since the 1980s. During the early 1980s, observers counted all birds sighted as well as all flying birds. In 1984, the transect width was restricted to 300 meters, and all birds flying and on the water were counted within the transect. In the 2000s, the transect width was still 300 meters, but observers only counted flying birds periodically on "snapshot" counts (Gjerdrum et al. 2012). These differences could account for some of the results of this study by artificially inflating the numbers of birds before the 2000s, though the results here show an increase in the later time period, not a decrease as would be expected for the change in methods. Differences could also be influenced by the timing of when surveys were completed (Table 3.2). Surveys in September could pick up more immature birds and fledglings, or different species moving through the area, compared to surveys in June.

3.4.2 Changes in Diversity

Considering each of these diversity measures helps to capture different aspects of diversity that would likely be missed if only a single measure was used (La Sorte and Boecklen 2005). Rarefaction curves and estimates of species abundance indicate a peak in species abundance during 1985-1990. A comparison of the number of species at the same survey effort for the three periods showed the same increase in species. Thus, there appears to have been an increase in species richness in the late 1980s, followed by a recent decline. None of the curves reached an asymptote, indicating species were possibly missing from the observations due to inadequate sampling. To assess which species could have been missed, I examined the USGS database of seabirds observed in the coastal Atlantic shelf (O'Connell et al. 2009). These data include surveys conducted by American seabird observers from 1978 to 2009 which are not included in the ECSAS dataset used here (O'Connell et al. 2009). Sixteen species were found in the database within the study area that were not found in any of the years in the data examined in this thesis. These species include Band-rumped Storm-Petrel, Long-Tailed Jaeger, and Common Loon. This result indicates that species accumulation curves can be useful to indicate if an area has been surveyed enough to observe all the species.

Of the different diversity measures tested the only one that showed a significant change was average taxonomic distinctness. Average taxonomic distinctness indicated a significant increase during 1985-1990, though there was no significant change in 2006-2010 (see also Nisbet et al. 2013). Average taxonomic distinctiveness and variability measures did not correlate with the number of animals observed, while both species evenness and richness were correlated with the number of animals observed. Taxonomic distinctness has been found to relate to conservation value in terrestrial bird assemblages, while simple species richness did not show the same relationship (von Euler and Svensson 2001). Hence, taxonomic distinctiveness is a useful way to measure biodiversity, specifically to measure the variety of organisms living in an area (Mace et al. 2005).

It must be emphasized that my application of the taxonomic distinctness metric to ephemeral seabird assemblages is not used to assess structural community relationships but rather to simply detect changing species groupings. In this study as in others, average taxonomic distinctness increased when areas had species from different families, instead of only species from the same family or genus. For example, an area such as cell 52 near the Northeast Channel that had observations of several shearwaters and storm-petrels along with gulls, jaegers, fulmars and phalaropes was more distinct in 1980-84 than in the 2000s when it had observations of only shearwaters and storm-petrels. Whether either assemblage suggests higher conservation value can be questioned, considering that these are temporary feeding aggregations compared to the more stationary land bird communities studied in the references cited. In particular, seabird assemblages formed entirely of tubenoses may have the highest need for conservation because of the severe threats that most of these species face (Furness 2003, Croxall et al. 2012). There is high overlap between fisheries and seabird foraging distributions in the Gulf of Maine and on the eastern Canadian shelf (Karpouzi et al. 2007). Conservation needs for foraging assemblages of seabirds could be quite different from what a taxonomic distinctness index suggests, though its use in indicating changes in species assemblages is informative. Additionally, taxonomic distinctness can be used to indicate changing quality of a habitat through changes in the species composition, which might be detectable before it becomes obvious in other ways (von Euler and Svensson 2001). In consideration of all of these factors, I recommend continued but qualified use of taxonomic distinctness in future marine bird diversity studies.

Changes in individual grid cells over time showed decreases in all diversity measures except for average taxonomic distinctness. This result indicates that different diversity measures can be used to detect changes in different aspects of diversity, showing the value of using multiple measures (La Sorte and Boecklen 2005). Decreases in species abundance, richness, evenness and taxonomic variation over time for individual cell comparisons were different from the changes observed in the study area as a whole. Correlations between the diversity slope coefficients indicate that the areas that showed increases in taxonomic distinctness also have fewer animals. For this study when areas had more individuals present they were less taxonomically distinct, which is likely related to observations of large single species aggregations or those of more closely related species.

The increases in taxonomic distinctiveness shown in Table 3.5 are generally indicative of shifts from mostly members of Procellaridae to a more diverse mix of species. As this study shows it is important to check specific changes in taxonomic distinctness, because different species often have different conservation needs.

3.4.3 Next Steps

Relating changes in diversity to, for example, fishing activity over time, could illustrate some human impacts on marine birds. Relating diversity measurements to environmental features would also provide information about habitat change, and how seabirds respond to dynamic environmental conditions. More intensive studies of the Northern Georges Bank could help determine if portions should be considered for conservation attention. The Roseway Basin, an important area for North Atlantic Right Whales, was designated as a conservation area in 1993. I found the Roseway Basin to be an area of increasing taxonomic distinctness, both before and after it was designated as a conservation area. Measures that were taken to protect North Atlantic Right Whales may also be benefitting the seabirds. Designating the area as an Important Bird Area could benefit seabirds and help conserve this taxonomically diverse habitat. Large important bird areas can benefit from best-practice management of extractive and exploitative activities (Lascelles et al. 2012). Satellite telemetry studies in the Gulf of Maine indicated similar summer and autumn hotspots of Great and Sooty Shearwaters in German Bank and George's Bank, as well as the Bay of Fundy and Brown's Bank, adjacent to the Roseway Basin (Ronconi 2010a).

My study highlights uneven sampling of the Gulf of Maine. The Bay of Fundy has been surveyed to a very limited extent by the CWS in recent years and not in areas that allow for direct comparisons to earlier survey data. The central and US coastal regions of the Gulf of

Maine are also inadequately represented in these vessel survey data sets. Collaboration with US researchers to combine their American-focused and restricted surveys with Canadian surveys would increase understanding of wider changes in seabird species composition in the Gulf of Maine, Georges Bank, and regions further south. Studies that incorporate surveys throughout broad regions can detect seabird distributional shifts, or population declines (Veit et al. 1997). Combining boat based surveys with tracking studies could provide more information on residency within hotspots found in surveys (Louzao et al. 2009), indicate risks that species are exposed to (McFarlane-Tranquilla et al. 2013), and could provide a biological basis for habitat models similar to those presented here. Additionally, proposals for Marine Protected Areas from groups of scientists or organizations are more likely to be well received by policy makers, making collaboration among researchers in the same areas even more important (Lascelles et al. 2012). Continued qualified use of the taxonomic distinctness measure is encouraged, for as demonstrated, this measure can be used as an index to detect changes in species composition of areas and diversity that could otherwise go unobserved.

Chapter 4 General Discussion

Seabirds spend the bulk of their life in the marine environment where they exploit a variety of habitats and are exposed to many risks. Historically in the Gulf of Maine opportunistic vessel surveys provided baseline information about where seabirds were distributed at sea (Brown et al. 1975, Brown 1986). In summer hundreds of thousands of seabird breed in the Gulf of Maine (Nisbet et al. 2013) while millions migrate to the Gulf from the Arctic or from the Southern Hemisphere to use the region in their non-breeding season as a wintering area or a stopover site (Brown 1986, Nisbet et al. 2013). Non-breeding migrant birds are more numerous than breeding birds at sea, as they are in the Gulf of St. Lawrence (Cairns et al. 1991).

The Gulf of Maine has been a major commercial fishing area for centuries, it is crossed by major shipping lanes, and offshore energy developments are ongoing (Nisbet et al. 2013). Additionally, climate change is ongoing in the Gulf of Maine. Some changes have been rapid and unforeseen with consequences that are difficult to predict, such as increased frequency of extreme precipitation events, which are decreasing primary productivity through light limitation by stabilizing the water column and through massive influx of detritus from river discharges (Balch et al. 2012). Since the 1980s, decreases in surface layer salinity due to increased inflow of low salinity surface waters from the Scotian Shelf are causing changes in the zooplankton community (Mountain and Kane 2010). All of these factors create new conditions and stresses in the Gulf of Maine which affect seabird foraging conditions and habitat.

This thesis investigated changes in diversity and distribution of the seabird species that have occurred in the Gulf of Maine over a decadal scale since the 1980s. It examined the at-sea distributions of birds in the Gulf of Maine, and identified locations of high diversity, abundance, and the presence of rare species.

4.1 Seabirds of the Gulf of Maine

During summer non-breeding migrant seabird species from the Southern Hemisphere and the Arctic outnumber breeding species in the Gulf of Maine by a factor of 10. This may be similar to patterns seen in large mid-latitude gulfs in eastern North America (e.g. see Cairns et al. 1991 for a similar pattern in the Gulf of St. Lawrence).

Specifically, Great Shearwater was the numerically dominant seabird throughout the study periods. The Great Shearwater uses the Gulf of Maine as a wintering site during its non-breeding season. Brown (1986) and Schneider and colleagues (1987) also found the Great Shearwater to dominate the avian community on Georges Bank. Sooty Shearwaters appear to have declined. Surveys in the eastern Pacific found declines in Sooty Shearwaters that were early indications of colony declines (Veit et al. 1997, Jones 2000). At least some of the Sooty Shearwaters that come to the Gulf of Maine originate in the Falkland Islands, where the Sooty Shearwater colonies are not known to be in decline. More likely, this is evidence of a distributional shift further north to waters off Newfoundland (Hedd et al. 2012).

The number of phalaropes has increased in the study area. This also is due to a distributional shift, as phalaropes were formerly found in high numbers within the Bay of Fundy (Brown and Gaskin 1988, Nisbet et al. 2013) but have been recently observed more on the Scotian Shelf. This present comparative study did not include the Bay of Fundy due to inadequate survey coverage between the two time periods. Further surveys, especially ones that include the Bay of Fundy, will help reveal more details about phalarope distributions and changes in their preferred habitats.

The results of this study also confirm increases in auks in the Gulf of Maine, as reported elsewhere (Chapdelaine et al. 2001, White et al. 2011, Nisbet et al. 2013). Auks have been recovering following former decades of hunting pressure and closure of the eastern Canadian gill-net fisheries and the removal of thousands of gill-nets that imposed very considerable by-catch mortality (Montevecchi 2002, Regular et al. 2013).

Mapping the federally Endangered Roseate Tern distribution showed the importance of foraging areas in the vicinity of breeding colonies at Cape Cod, the Bay of Fundy and south of Halifax. The absence of records of Roseate Terns in the more recent data could be indicative of population decreases or distributional shifts. Goyert (2013) has shown the Roseate Terns from colonies in Buzzard's Bay at Cape Cod forage consistently at persistent offshore sites, which was not found in this study with less intensive surveys or in some cases no surveys of their foraging areas. Protection at breeding colonies could help maintain breeding populations of this endangered species, but the protection may be ineffective without further protection at sea. Breeding success at colonies suggests that mortality during the non-breeding period may be the greatest population threat (Goyert 2013). Other state and provincially listed species were encountered in the surveys, with Wilson's and Leach's Storm-Petrels the most common of them and the two most widely distributed. Other species were distributed in predominantly inshore areas. Any developments in the Gulf of Maine must include more intensive studies of that region in order to protect federally, state, and provincially listed species.

4.2 Habitat Relationships and Important Areas in the Gulf of Maine

The habitats that seabirds exploit in the marine environment are often more ephemeral and much more difficult to discern compared to habitats of terrestrial birds. Yet seabirds read cues in their environment well and use certain areas of the sea at different times. This thesis showed several relationships between seabirds and their marine habitats. Specific habitat models showed that locally breeding and visiting migrant species relied on different features of the marine environment, owing in large part to the breeders being more coastally concentrated by their central place foraging constraints. This was particularly apparent when examining diving species, with locally breeding divers concentrated inshore along Nova Scotia and the Bay of Fundy, and migrant divers further from the shore near oceanic features that would concentrate their prey.

The comparison between Wilson's and Leach's Storm-Petrels distributions was revealing as it illustrated the different habitat requirements of two closely related species. The two species were likely drawn to different habitats while foraging for different prey (Huntington et al. 1996, Hedd et al. 2009). The differences in habitat use might also be due in part to Leach's not being able to use their "ideal" habitat, because of the constraints of central-place foraging (Garthe et al. 2009), though breeding Leach's Storm-Petrels forage many hundreds of kilometers from massive colonies in Newfoundland (Hedd 2013 pers. comm.). Interestingly, the two tube-nosed Southern Hemisphere migrant species exhibited the most similar habitat requirements; both Wilson's Storm-Petrels and Great Shearwaters were found in deeper water areas further from the coast. Leach's Storm-Petrels were found further inshore, closer to temperature fronts, which were likely areas of high productivity (Schneider 1982). No relationship was found for water depth for Leach's Storm-Petrels, unlike Hedd et al. (2009) who found birds consistently distributed in deeper waters off Newfoundland. Leach's Storm-Petrels were the only species examined that were found closer to SST fronts. It was expected that other species would also show such associations, as many studies have found birds closely linked to fronts (Schneider 1982, Haney and McGillivary 1985, Bost et al. 2009). Wind-driven fronts tend to be ephemeral, and intermittent vessel surveys no doubt miss many of these.

While seabirds occur throughout the Gulf of Maine, their densities are disproportionally distributed. High densities of seabirds occurred consistently in the Jordan Basin and the mouth of the Bay of Fundy. The Jordan Basin, Georges Bank, and the Roseway Basin had high taxonomic distinctness, and the Roseway Basin was also an area of high density of diving birds in particular. While listed species were observed throughout the study area, federally endangered Roseate Terns were observed offshore of Cape Cod, north of Grand Manan Island, and southwest of Halifax during the PIROP and Manomet surveys (Figure 3.8), and more recently south and east off Cape Cod by Goyert (2013). Goyert (2013) found Roseate Terns over 100 km offshore from Cape Cod on Georges Bank, in addition to areas around their breeding colonies on Cape Cod. Further studies of areas used by Roseate Terns in Canadian waters are needed to ensure adequate protection of their foraging areas at sea, especially if they are making use of areas offshore of Nova Scotia that have not yet been noted.

4.3 Conclusions

The Gulf of Maine is dominated by non-breeding migrant species during summer primarily by Great Shearwaters, along with Red and Red-necked Phalaropes. Habitat models built for Great Shearwaters and Wilson's Storm-Petrels were more similar than those for Leach's Storm-Petrels, suggesting that the two migrant species cue in on similar habitat features. Diversity has not changed greatly since the 1980s, though the species composition has changed, with the more recent data being more taxonomically distinct. As well, more scarce migrants and vagrants are being recorded due to the increasing numbers of surveys taking place (Nisbet et al. 2013). The Roseway Basin was an area with high taxonomic distinctness, with high densities of locally breeding and migrant diving foraging birds.

Increasing anthropogenic and climactic pressures are increasing risks for birds at sea. Protection of seabirds in colonies helps conserve populations but land-based protection is not enough as seabirds spend most of their lives at sea. The analysis and integration of several different variables used in this thesis can help highlight important offshore areas and habitats for conservation consideration. High diversity areas and changes in diversity over time can be detected with different metrics (e.g. taxonomic distinctness) that account for taxonomic relatedness in species aggregations. Integrating measurements of seabird diversity and density and the locations of listed species as I have here aids in understanding the roles top predators play in marine ecosystems and in developing effective management plans.

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