HABITAT ASSOCIATION AND SPATIAL DISTRIBUTION OF PROCELLARIIFORM SEABIRDS ALONG THE CONTINENTAL SHELF OF THE NORTHEAST OF THE UNITED STATES AND THE SOUTHEASTERN CANADA: RELATIONSHIPS TO PREY AND OTHER TOP PREDATORS

BY

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ABSTRACT

Habitat association and spatial distribution of Procellariiform seabirds along the continental shelf of the northeast of the United States and southeastern Canada: Relationships to prey and other top predators

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In the first chapter, I compare habitat association among seven species within the order of Procellariiform seabirds that includes shearwaters, storm-petrels and northern fulmars (*Fulmarus glacialis*) along the northeastern continental shelf of the United States and southeastern Canada (Northwest Atlantic). Environmental factors such as bathymetry, sea-surface temperature (SST), chlorophyll concentration, and frontal features affected seabird densities and influenced their distribution. My model suggested that some species could be influenced by changes to large-scale hydrographic features and that all species will not respond equally to potential climatic fluctuations. In the second chapter, I focus on the northeast Georges Bank and Jeffreys Ledge regions of the Gulf of Maine, recording the presence of marine predators during four hydroacoustic surveys. The primary objective of these surveys was to make annual assessments of the pre-spawning stock of Atlantic herring (*Clupea harengus*). I explain the interannual variability of top predators (seabirds, dolphin, whale) using a general additive model that included environmental parameters and fish acoustic index to understand the possible reasons of this variability, including: 1) the effect of environmental predictors on top predators and prey; 2) piscivorous marine predator abundance correlated to fish acoustic biomass index data; and 3) the effect of fishing vessel density effect on marine predators. All predators and Atlantic herring were affected by oceanographic variables; northern gannet (*Sula bassana*) by fish density, as well. There were also spatial overlap between fishing vessels, humpback whales (*Megaptera novaeangliae*), great shearwaters (*Puffinus gravis*) and herring gulls (*Larus argentatus*). This study shows the importance of accounting for multiple environmental parameters in order to understand the variability of marine predators abundance in highly productive areas such as Georges Bank, in addition to assess spatiotemporal overlap between aggregated predator and prey for improving fisheries management. Finally, in the third chapter, I examine the foraging associations between Procellariiform seabirds and one species of Pelecaniform (northern gannet), dolphins, whales, and two species of tuna along the continental shelf. The general linear model results suggested seasonality in aggregation types. Great shearwater density increased with humpback and fin whales (*Balaenoptera physalus*) in the summer, and shifted to common dolphin (*Delphinus delphis*) in the fall.

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"When you realize the value of all life, you dwell less on what is past and concentrate more on the preservation of the future."

Dian Fossey (1932-1985)

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INTRODUCTION

The Northwest Atlantic is an evolving ecosystem and rapid hydrographic changes could have serious consequences on zooplankton, fish, and squid abundances, which are the dominant prey of marine predators, including seabirds, marine mammals, and predatory fish. Seabirds are considered ecological indicators at sea, as they are often highly visible and feed directly upon these prey species (Piatt & Sydeman, 2007). This dissertation is composed of three chapters. In Chapter 1, my objectives were 1) to determine the relation between Procellariiform seabird abundance and environmental variables, and 2) to assess at the species level which variables might be the most important predictors. In Chapter 2, my goal was 1) to measure the effect of environmental predictors on top predators and Atlantic herring density which could explain their interannual variability, and 2) to examine if piscivorous marine predator abundance was correlated to fish acoustic biomass index data. In Chapter 3, my aim was to investigate associations between Procellariiform and one Pelecaniform seabirds with subsurface predators along the northeast continental shelf. This introduction will describe the oceanographic, geographic and species context of the work to follow. I compared habitat associations among seven Procellariiform seabird species within the order that includes shearwaters, storm-petrels, and northern fulmars (*Fulmarus glacialis*). Procellariiform seabirds spend most of their life foraging at sea (Nevitt, 2000). They are highly pelagic and we do not know enough about their association with oceanographic variables or how the fluctuations will affect the seabirds. Many petrels, albatrosses, and shearwaters are endangered in many part of the world (Birdlife international, 2004). Models could help to predict how these seabirds will respond to hydrographic feature changes and where they will be found in greatest abundance. This study showed that Procellariiform seabirds were influenced by changes in hydrographic features, and that all species do not respond equally to potential climatic fluctuations. I analyzed data collected from the R/V *Delaware II* between 2006 and 2009 along the continental shelf of the northeastern United States and southeastern Canada. I modeled habitat association using a zero-altered negative binomial fitted with generalized additive model (GAM). This conditional, two-step (not mixture) model has rarely been used for seabird study, but I selected this method to overcome the zero count and overdispersion in my data count (Yee, 2010; Peron, 2010). Differences in habitat association among species were found. Three predictors had the most effect on species abundance: sea-surface temperature (SST) and frontal features such as SST front intensity, and distance to chlorophyll fronts. These models suggested that most species abundance declined with increasing SST. Cory's shearwater (*Calonectris diomedea*) might be able to adapt to warmer conditions. Procellariiformes did not respond equally to hydrographic fluctuations.

Seabird phenology

Seven species of Procellariiformes regularly occur along the East Coast of the United States; only three species breed on the East coast of North America: Leach's storm-petrel (*Oceanodroma leucorhoa*) (Hedd & Montevecchi, 2006), northern fulmar (Mallory et al., 2008), and Manx shearwaters (*Puffinus puffinus*) (Roul, 2010). Others are highly migratory species that spend the winter in the Northwest Atlantic. The continental shelf of the northeastern United States and southeastern Canada represents one of the most important wintering and migrating grounds for all these seabirds (Powers & Van Os, 1977; Brown et al., 1981; Huettmann & Diamond, 2000). Sooty shearwaters (*Puffinus griseus*) are ubiquitous, whereas great shearwaters (*Puffinus gravis*) have a more restricted range between the Atlantic and Indian Oceans (Brown, 1981; Shaffer et al., 2006). Great shearwaters and sooty shearwaters fly to the Northwest Atlantic to reach the most productive waters (Power & Van Os, 1977; Ronconi et al., 2010; Hedd et al., 2012). Sooty shearwaters wintering in the North Atlantic could be part of several subpopulations (Passavy, 2011). Manx shearwater colonies are largely based around Europe, from the islands of the United Kingdom to the Canaries (Onley & Scofield, 2007), but some recent colonies have been established in North America between Newfoundland, Labrador, Gulf of Saint-Lawrence, Gulf of Maine and Massachusetts (Bierregaard et al., 1975; Onley & Scofield, 2007). Cory's shearwaters are also Northern Hemisphere breeders, but their colonies are located around the Azores and Canary Island (Navarro & Gonzales- Solis, 2009). They breed between May and June, and winter in several parts of the Atlantic Ocean. Wilson's storm-petrel (*Oceanites oceanicus*) breeds on sub-Antarctic islands and Antarctica. They winter in the Northwest Atlantic (Brown, 1988; Quillfeldt et al., 2010). Leach's storm-petrel is widespread in the Northern Hemisphere. They incubate on islands from southern Labrador to Massachusetts (Sibley & Monroe, 1990) and winter off West Africa (Warham, 1990). Fulmars breed throughout the North Atlantic and North Pacific, ranging from Japan to the United Kingdom (Mallory & Forbes, 2005; Van Franeker & Luttik, 2008). The North American population has been increasing over the past 100 years (Stenhouse & Montevecchi, 1999).

Geological and Physical Environment of the northeast of the United States and southeastern Canada

The bathymetry in this region is heterogeneous, ranging from flat, sandy bottoms, such as Nantucket shoals, to more complex topography, such as Jeffreys Ledge, Georges Bank, Great South Channel, and Hudson Canyon (Sherman, 1988). The study area is bordered in the south by the Gulf Stream and the slope of the continental shelf, which drops from 1000 meters depth to about 4000 meters in areas such as the Gulf of Maine (Northeast channel), separating the mainland from the deep waters of the Atlantic (Fautin et al., 2010). The continental slope gradient varies considerably from Canada to the southeast United States, as does the temperature profile of the water. Cold, deep water flows south from the Labrador Sea and surrounds the continental slope. The Gulf Stream brings warmer waters north from the Gulf of Mexico onto the southeast shelf of the United States (Atkinson et al., 1983; Sherman et al., 1996). Finally, the Labrador Current and the Gulf Stream meet over the edge of the Grand Bank and turn into a thermohaline circulation (Druon et al., 2009). The continental shelf is influenced by a semi-permanent atmospheric pressure system: the Icelandic Low and the Azores High (Fogarty, 2007). Both the Icelandic Low and the Azores High vary in magnitude, a phenomenon known as the North Atlantic Oscillation (NAO) (Visbeck et al., 2001). When the Icelandic Low decreases and when the Azores High increases, the NAO is in a positive phase. This creates an increase in north winds and precipitation over southeast Canada, the east coast of the United States, and northwest Europe (Hurrell & Van Loon, 1997). When the NAO index becomes negative, hydrographic conditions change. There are fewer west winds and fewer storm systems, the east coast of the United States and northwestern Europe become drier, and water temperatures warm Labrador and Newfoundland. These phases of the NAO last between 7 and 10 years and greatly influence the entire marine ecosystem (Ottersen et al., 2001). Over the past 180 years, the index has shifted back and forth from negative to positive values (Hurrell et al., 2001). The northeastern United States and southeastern Canadian continental shelf experienced a gradual warming with interannual variability over the past 50 years. Sea-surface temperatures increased about 1.08°C between 1957 and 2006 (Belkin, 2009).

Physical environment of Georges Bank and Jeffreys Ledge

The Gulf of Maine is one of the most productive areas for seabirds along the continental shelf of the northeastern United States. This area also represents one of the most highly productive fishing grounds for the United States and Canada (Bubier & Rieser, 1986; Pudden & Vanderzwaag, 2007), and as a result has been the focus of geopolitical pressures since the mid-1970's (Kaye, 2008). Georges Bank is a complex and highly productive oceanographic system (Link et al., 2008). On a large scale, this bank is part of a very long coastal current system that flows south from Labrador to the Mid-Atlantic Bight (Chapman & Beardsley, 1989). Cold coastal water enters the Gulf of Maine from the Scotian Shelf and warmer water enters through the Northeast Channel (Townsend et al., 2004; Johnson et al., 2011). These two water masses mix in a cyclonic movement that slows or reverse during winter (Brown & Irish, 1992). The tidal current, interacting with bathymetry, turns in a circular manner and moves along the southern flank of the Bank (Pringle & Franks, 2001). Permanent hydrographic fronts south of the Bank separates the shelf water from offshore water and water movements on the Bank are dominated by strong tides and wind associated with storms (Flagg, 1987; Chen et al., 2003). Furthermore, warm-core Gulf Stream rings influence the water circulation along the southern edge of the bank (Myers & Drinkwater, 1989). Georges Bank has experienced some of the North Atlantic's largest changes in sea-surface temperature and the North Atlantic experiences the second highest amplitude variations in interannual surface pressure patterns (NAO) (Wallace & Gutzler, 1981; Gordon et al., 1992). These variations have a period of about seven years (Hurrell et al., 2001) and are associated with wind strength, SST anomalies, and changes in water masses, Labrador Sea water formation, and ice coverage. This also drives fluctuations in abundance of some species, such as cod (Ottersen et al., 2001; Brander, 2010). Jeffreys Ledge is a long, complex, shallow area, 54 kilometers long that stretches from Rockport, Massachusetts, to the southeast of Cape Elizabeth, Maine. It is characterized by depths between -45 and -150 meters. The bottom substrate is a mixture of rock, sand, gravel, and mud (Weinrich et al., 2000).

Hydrographic changes and ecological consequences

These hydrographic fluctuations affect the availability and range of many fish and invertebrates (Fogarty et al., 2007). Sea-surface temperature changes predict shifts in distribution of many marine communities (Perry et al., 2005). Species temperature preferences plus habitat requirements will determine the extent of potential distributional changes. Climate change may strongly influence plankton and fish life cycle, distribution, abundance, and responses to other trophic levels (Perry et al., 2005). Changes in prey distribution or abundance might lead to negative impacts within predator populations. Studies have demonstrated the consequences of hydrographic changes on breeding populations of seabirds and other marine animals (Gaston & Smith, 2001; Cjerdrum et al., 2003; Sandvik et al., 2005; Simmonds & Isaac, 2007), such as reproductive failure. Consequences have been observed on foraging predators, as well (Montevecchi & Myers, 1997). For example, during the 1982-83 El Niño-Southern Oscillation (ENSO) event in the Pacific, spawning market squid (*Loligo opalescens*) left the southern California area, followed by the short-finned pilot whales (*Globicephala macrorhynchus*) that normally prey on them (Shane, 1995) (Shane, 1995). As waters warm, it is suggested that many species will shift poleward, reducing the global range for species that are adapted to cold water (Righton et al., 2010). Veit et al. (1997) showed a 94% decline of sooty shearwaters over the California Current between 1987 and 1994. This decline is negatively correlated with an increase in SST. They also found that there was a nine-month lag in response by shearwaters to changing temperatures. Sooty shearwater is the most abundant seabird species of the California Current in summer (Briggs & Chu, 1986). Using the time series from California Cooperative Oceanic Fisheries Investigations (CALCOFI) cruises, Roemmich (1992) showed a temperature increase of 0.8°C of the upper 500 meters between 1950 and 1982. Sooty shearwaters feed principally on *Euphausia Pacifica* and warming temperatures have been accompanied by a 70% decline in zooplankton abundance (Roemmich & McGowan, 1995; Veit et al., 1996). Veit et al. (1996) did not expect seabirds to respond immediately to changing SST. The decline of sooty shearwater populations is also consistent with slowed growth of resident sooty shearwaters in the northern part of the California Current. Seabirds have also been declining due to the reduction of prey species in their wintering ground (Ainley et al., 1995; Shaffer et al., 2006).

Foraging niche Overlap

Differences in Procellariformes foraging niches can be ambiguous. Several species overlap while at sea (Pinaud & Weimerskirch, 2007). Niche segregation is considered an interspecific or intraspecific microevolution factor (Rayner et al., 2011). This speciation process will result in adaptive radiation for many species of pelagic birds (Warham, 1996; Futuyama, 1998). For example, grey-headed albatross (*Diomedea chrysostoma*) and black-browed albatross (*Diomedea melanophrys*) are sympatric species—both seabirds breed in mixed colonies, but display distinct foraging strategies and diets (Waugh et al., 2000). When their foraging distributions overlap, interspecific competition between these two populations could potentially increase (Arata et al., 2004). Satellite tracking data suggest that black-browed albatrosses breeding on Diego Ramirez islands (Drake Passage) forage over neritic waters in five-day trips with alternate longer trips over oceanic waters. In contrast, the grey-headed albatross breeding on the same islands display different feeding behavior, foraging over oceanic waters (Arata et al., 2004). On Diego Ramirez Island between 2001 and 2003, grey-headed albatrosses fed mainly on species associated with the Antarctic Polar Front during the chick-rearing period, whereas black-browed albatross consumed benthopelagic species. Great shearwaters and sooty shearwaters were also observed in the same geographic areas at the same time in the Northwest Atlantic, but there are few chances that these species are competing, since they exhibit slight differences in diet (Brown et al., 1981). In southeastern Canada, great shearwaters eat more squid and mackerel (*Scomber scombrus*), while sooty shearwaters consume more Atlantic herrings and crustaceans (Brown et al., 1981). Also, they do not migrate simultaneously—sooty shearwaters arrive in the Northwest Atlantic a few weeks earlier and their range is larger than that of great shearwaters (Hedd et al., 2012). Finally, both species possess different morphological structures and diving abilities. Archival tags and Time-Depth Recorder results suggested that Sooty shearwaters dive deeper than great shearwaters (Shaffer et al., 2006; Ronconi et al., 2010). Great shearwater dove mostly around two meters (n=2); the deepest was about 18 meters (Ronconi et al., 2010). Sooty shearwaters (n=19) were equipped with archival tags in the Pacific Ocean; the mean depth was about 14 meters and the maximum depth was about 68 meters (Shaffer et al. 2006)

Response to hydrographic changes

As previously described, the NAO might affect prey and predators distribution in the Northwest Atlantic. Foraging seabirds do not respond equally to changes in hydrographic features (Thompson & Ollason, 2001; Barbraud & Weimerskirch, 2003; Weimerskirch et al., 2012). Most migratory species are vulnerable to rapid environmental changes, and species are expected to show variation in their capacity to respond to fluctuations in abiotic and biotic factors (Berteaux et al., 2004). The degree of behavioral plasticity is difficult to assess, but is required to understand how species will respond to their environment (Gremillet & Charmantier, 2010). My objectives were to: 1) determine the relationship between Procellariiform seabird abundance and environmental variable; and 2) assess at the species level which variables might be the most important predictors. Some species within the same order might respond very differently, which could lead to negative consequences in their population dynamics (Guilford et al., 2008; Louzao et al., 2006). Understanding habitat association, foraging ecology, and spatial distribution will help determine which species might be at risk or which might be at an advantage in changing environmental conditions (Rivalan et al., 2010; Weimerskirch et al., 2012).

Seabird Procellariiform range expansion

Northern fulmars have seen their breeding range increase dramatically over the past 200 years in the western North Atlantic (Stenhouse & Montevecchi, 1999). The breeding range of the northern fulmar expanded southward between 1800 and 1900 from the Arctic to boreal regions in the eastern North Atlantic (Fischer, 1952). The expansion was a result of a large increase in the Icelandic population (Fischer, 1952). It has been suggested that this expansion had been facilitated by 2 major causes: 1) fulmar successful exploitation of offal discarded by whaling and fishing vessels; and 2) correlation to changes in hydrographic features (Brown, 1970). The increasing abundance of fulmars in the Northwest Atlantic could be due to same reasons, as factory trawler fishing intensified on the Newfoundland and Labrador Banks in the 1950's (Stenhouse & Montevecchi, 1999). The increase in fisheries activities may have interacted synergistically with oceanographic features to contribute to range expansion (Brown, 1970; Camphuysen & Garthe, 1997). The extension of nesting fulmars appears to have been related to the intensification of ice conditions associated with colder weather patterns in the first half of twentieth century. This may have increased the flow of the Labrador Current and reduced water temperatures both in the Gulf of Saint Lawrence and off eastern Newfoundland from 1972 to 1976. Mallory et al. (2008) used satellite tags to show that northern fulmars were also observed over cooler waters during their winter migration. These findings are consistent with reports from shipboard surveys (Salomonsen, 1965; Brown, 1970), which showed fulmars had a preference for waters between 3.5 and 7°C (Hatch & Nettleship, 1998).

Foraging behavioral plasticity

Along the eastern United States, the first official sightings of Cory's shearwaters were off the coast of Alabama in 1973 and in the Gulf of Mexico in 1975 (Pulich, 1982). Since then, the number of occurrences of Cory's shearwaters increased in the southeastern and northeastern United States. Pulich (1982) suggested a relationship between their distribution and water fronts over the South Texas continental shelf. Large numbers of the shearwaters subspecies *Calonectris diomedea borealis* crossed the Atlantic in mid-summer, then moved up to the East Coast of the United States in the fall and congregating off New England and Canada (Shy, 1982) before returning to eastern Atlantic waters. Dias et al. (2010) supported this observation after analyzing geolocator data from 74 different migrations, including 14 birds from Selvagem Grande Island, that were tracked for more than one non-breeding season between 2006 and 2008. These seabirds showed a remarkable capacity to change winter destinations between years. In 2006 and 2007, 11 other Cory's shearwaters from Berlenguas (Azores) and 25 from Selvagens (Azores), two different colonies, were tagged with geolocators to follow them during the wintering period (Catry et al., 2011). All individuals adjusted their foraging strategies to their winter locations as a response to local food resource availability (Catry et al., 2011). Cory's shearwaters present a high degree of behavioral plasticity toward their environment, and might be more flexible than other species in overcoming environmental changes (Dias et al., 2010). Some Cory's shearwaters returned to the same wintering grounds, others shifted to the eastern South Atlantic or to the Indian Ocean (Dias et al., 2010). *Calonectris diomedea borealis* from separate breeding islands showed a difference in selection of foraging sites (Paiva et al., 2010a; Paiva et al., 2010b). During long trips, some populations foraged above shallow waters and areas with a high concentration of chlorophyll-a and low SST, while another population fed primarily over seamounts and frontal zones (Paiva et al., 2010b).

Survivorship and consequences on population demography

Finally, about 61% of the variation in Cory's shearwater adult survival could be explained by the Southern Oscillation Index fluctuations. These results were obtained by modeling adult survival using banding methods, capture and recapture (Jenouvrier et al., 2009). Hurricanes and storms in La Nina years may also increase adult mortality for Cory's shearwaters during winter months. The North Atlantic Oscillation may affect seabird mortality directly (wind) or indirectly (prey availability). Studies have showed that these effects are indirect rather than direct (Harris et al., 2005; Gremillet & Boulinier, 2009).

In Chapter 2, I discuss how environmental variables and abundance of prey influenced the interannual variability of marine predators in a complex hydrographic system such as the Georges Bank and Jeffreys Ledge regions of the Gulf of Maine in the Northwest Atlantic. First, I analyzed how environmental variables are related to the most abundant top predator densities and to an important prey: the Atlantic herring. Next, I examined how an acoustic index of

Atlantic herring related to top predator abundance. In addition, I included an additional top predator density (fishing boats) from 2007 to 2009 to determine if fishing vessel density could influence the abundance of other top predators. All predators were affected by oceanographic variables explaining at least some variability from year to year. One was also influenced by the fish density. This study shows the importance of accounting for multiple parameters in order to understand the variability of marine predator abundance in highly productive areas such as Georges Bank. My model also includes marine predators that are either finished breeding, such as northern fulmars (Garthe et al., 2004) or northern gannet (*Sula bassana*) (Garthe et al., 2003), or are ready to return to their respective breeding ground, such as great shearwater (Cuthbert, 2005), as well as humpback whales (*Megaptera novaeangliae*) (Rosenbaum et al., 2009).

Atlantic herring ecology

The Jeffreys Ledge and Georges Bank regions are critically important areas for Atlantic herring (*Clupea harengus*), which are the primary forage fish for many top predators. Atlantic herring is also considered a keystone species in the Northwest Atlantic (Overholtz & Link, 2007). Herring are small baitfish that school in coastal waters and are considered a major food resource for several top predators (Nøttestad et al., 1996; Tyrrell et al., 2008). They feed on zooplankton, mostly copepods (Johnson et al., 2011), and are consumed by various species, including humans, marine mammals, fish, and seabirds. In the western North Atlantic, they range from Labrador to Cape Hatteras, where spring and autumn spawning populations support major commercial fisheries (Kanwit & Libby, 2009). In United States waters, herring from the Gulf of Maine and Georges Bank are managed as a single stock complex with two spawning populations. Herring deposit demersal eggs in areas with strong tidal currents (Stevenson & Knowles, 1988). The larval stage of fall-spawned herring in the Gulf of Maine last to 4 to 8 months. Currents affect the pelagic larvae near the spawning site. Atlantic herring were extremely abundant in waters of the northeast United States around 1960 and were fished intensively. Their population collapsed between 1960 and 1980 due to overfishing (Overholtz & Link, 2007). Today, Atlantic herring populations have recovered, but ecosystem managers must take into account marine predators other than humans (Read & Brownstein, 2003).

Foraging strategy of marine predators

Marine mammals use several foraging strategies to detect their prey, from vision to echolocation (Perrin et al., 2009). Odontocete cetaceans use echolocation, a foraging technique not used by baleen whales. Although most fish cannot detect echolocation, clupeid fish, such as herring, can (Popper et al., 2004). One of the challenges for foraging cetaceans is to locate dense patches of prey in order to satisfy their huge metabolic requirements (Brodie, 1978; Piatt et al., 1989). If a whale detects dispersed prey, they might compensate by fishing in groups or emitting bubbles to regroup the schools (Tyack, 1997). Seabirds, however, are highly mobile, and can cue on other top predators from above the water (Silverman et al., 2004). In order to increase their foraging success, all predators try to find patches of prey with high density (Fauchald, 2009). In order to survive, prey must move away from high-density predators to reduce their risk of mortality. Pelagic birds are extremely mobile and move over long distances at relatively low energetic cost, though they have a constant energy demand. The relation between seabirds and prey patches can be either strong or weak, but most studies find that the relationships become stronger as the geographic spatial scale increases (Fauchald, 2009). The spatial pattern of seabirds and their prey is also dependent on environmental factors and hydrographic properties (Planque et al., 2011).

Many top predators tend to congregate while feeding on fish schools or zooplankton swarms since subsurface predators can push unreachable prey to the surface (Burger, 1988; Burger, 2004; Ballance, 2007). For two weeks in September, Atlantic herring congregate in dense, pre-spawning schools along the northeast edge of Georges Bank and Jeffreys Ledge at a depth of about 150 to 200 meters (Lazzari & Stevenson, 1992; Maravelias et al., 2000; Jech & Michaels, 2006). These aggregations are primarily available to marine mammals or predatory fishes that can dive deep enough to access these schools. This is particularly true for marine predators such as humpback whales, common dolphin (*Delphinus delphis*), or tuna. These predators can also facilitate food access for seabirds by pushing prey to the surface when foraging (Evans, 1982). In order to feed, seabirds such as gannets plunge dive about 20 meters beneath the surface (Garthe et al., 2000) and great shearwaters can reach 18 meters deep (Ronconi et al., 2010). Northern gannets plunge- dive directly above schools (Garthe et al., 2000) and have been seen during acoustic observation in the North Sea to reach a mean depth of 19.7 meters (Brierley & Fernandez, 2001). In response, Atlantic herring have also developed strategies to avoid predation, such as remaining deeper in turbid waters or school dilution (Axelsen et al., 2001). Bluefin tuna (*Thunnus thynnus*) is a major apex predator. Near the beginning of 1970, herring and tuna were both relatively abundant and herring consumption was relatively high as well. Around 1980, herring and tuna have both seriously declined due to overexploitation. With the passage of the Magnuson Fishery Conservation Act (1976-1977), distant-water fleets were not allowed in United States waters, and the abundance of herring stocks increased. Fisheries managers need more quantitative data to understand the role of herring in relation to other predators (Read & Brownstein, 2003; Overholtz & Link, 2007). As previously mentioned, many seabirds are known to forage in association with other marine predators (Burger, 1988). In

Chapter 3, I examined if there is association of Procellariiform (including shearwater, northern fulmar, and storm-petrel) and one Suliform seabird (northern gannet), with subsurface predators such as dolphin, whales, and tuna along the continental shelf of the northeast United States and southeast Canada. I used a zero-altered negative binomial general linear model (GLM) to investigate associations. Great shearwater density increased with humpback whales and fin whales in the summer; and increased with common dolphins in the fall. Great shearwaters are the most abundant species of shearwaters until November along the continental shelf of the northeast United States, and are ready to return to the Southern Hemisphere at this time of the year (Brown et al., 1981; Powers et al., 1983). These seabirds are most likely taking the opportunity to feed commensally over dolphin pods in order to accumulate fat reserves and begin their southern migration. Feeding over tuna schools might be costly energetically since these predatory fish are fast swimmers and their feeding frenzies harder to follow.

Foraging associations

Seabirds primarily consume fish, squid, plankton, or offal from fishing vessels. Whales and dolphins drive many of these preys to the surface (Evans, 1982). Evans (1982) defined the association between seabirds and cetaceans as an "intentional movement made by seabirds towards a cetacean or the converse and also a prolonged presence of individuals from both taxonomic groups together". More often, however, the association is reported as an extended presence together of individuals from different taxonomic groups. The most well-known association is that of tropical seabirds, dolphins, and schools of tuna, which drive smaller fishes to the surface (Ashmole & Ashmole, 1967). One association commonly reported in the Northwest Atlantic is that of the humpback whale and a variety of seabirds, particularly great shearwaters and northern gannets (Perkins & Whitehead, 1977). Humpback whales off the Newfoundland coast feed mainly on spawning capelin (*Mallotus villosus*), which also forms an important part of the diet of Atlantic puffins (*Fratercula arctica*), common guillemots (*Uria aalge*), and kittiwakes (*Rissa tridactyla*) (Brown & Nettleship, 1983). Some cetaceans, as well as humpback whales, may use a variety of methods to feed on different prey, either deep diving to feed on plankton swarms or taking schooling fish both at depth and close to the surface (Evans, 1982). Dolphins, whales, and tuna generally forage in highly productive waters (Piatt et al., 1989; Allen et al., 2001; Xavier et al., 2011). Marine mammals, and predatory fish play a top-down role, the effect of which has yet to be measured (Baum & Worm, 2009). Removal of sub-surface predators such as Atlantic bluefin tuna could impact the foraging ecology of other marine predators (Block et al., 2011). Parkinson’s petrel (*Procellaria parkinsoni*) is regularly associated with two dolphin species: the melon-headed whale (*Peponocephala electra*) and the false killer whale (*Pseudorca cradissens*). This seems to be an important foraging relationship for these seabirds. In fact, the association between Parkinson’s petrels and other species of dolphins occurs when these two particular mammal species are present as well (Pitman & Ballance, 1992). Parkinson’s petrel was not observed over large feeding aggregations, but took advantage of the feeding behavior of melon-headed whales and false killer whales. When feeding, these mammals dismember their prey below the surface; Parkinson’s petrel can easily dive to feed on pieces. All Procellariiform species feed at sea on a variety of fish, cephalopods and invertebrates, either socially or alone (Warham, 1996). Over a long period of time, these seabirds have evolved specialized foraging strategies, great flying capabilities, and an ability to dive underwater and have developed a unique olfactory system (Nevitt, 2000; Bonnadona et al., 2006; Shaffer et al., 2006; Ronconi et al., 2010). Dietary segregation between the species seems also to depend on differences in foraging techniques (Martin & Prince, 2001), but little is understood about sensory systems of these seabirds and how they affect foraging strategies.

Procellariiform foraging strategy and relation to other predators

Procellariiform seabirds have an acute sense of smell (Cunningham & Nevitt, 2011). When petrels are foraging at sea, they use odors as cues to detect prey. Procellariiformes are able to detect dimethyl sulfide (DMS), compound related to phytoplankton in productive waters (Grubb, 1972; Nevitt, 1999). Birds use smell on a large scale, but on finer scales, they use area restricted search (ARS) to locate their prey (Nevitt & Veit, 1999; Pinaud & Weimerskirch, 2007) and cue to other animals. Seabirds can also use a second foraging strategy, local enhancement (LE), in which they increase their turning rate around prey patches or other individuals (Veit, 1999; Grünbaum & Veit, 2003), such as other seabirds or subsurface predators. Sakamoto et al. (2009) deployed an airborne camera on black-browed albatross. Images recorded show the albatross feeding by actively following closely killer whales (*Orcinus orca*). Finding marine mammals or predatory fishes represents an important foraging strategy for these seabirds. Sooty shearwaters cross large geographic areas especially over the Pacific Ocean where primary productivity is low (Shaffer et al., 2009; Raymond et al., 2010). They were also found to dive more than expected (Kuroda, 1954; Burger, 2001; Shaffer et al., 2009) and feed over predatory fish schools (Jackson, 1988). Streaked shearwaters (*Calonectris leucomelas*) migrate up to 5400 kilometers from Japan (where they breed) to wintering areas in the tropics. They winter around Papua New Guinea in areas of low productivity, but with a high density of skipjack tunas (*Katsuwanus pelamis*). Data from bio-loggers showed that streaked shearwaters landed more frequently at dawn and dusk when the predatory fish was the most active (Yamamoto et al., 2008). In general, Procellariiform seabirds forage in productive fishing grounds around the world (Delord et al., 2010; Uhlmann & Jeschke, 2011). These seabirds fish where the resources are available in large quantity, and easily accessible.

Overlap of feeding aggregations and commercial fisheries: risk of bycatch increase, and consequences of apex predator removal

Major issues regarding interactions of seabird with commercial fisheries have arisen over the past decades in many places. The most common species being killed worldwide are albatrosses, shearwaters, and petrels (Anderson et al., 2011). We must understand the degree of overlap between highly productive foraging grounds and commercial fisheries areas (Uhlmann, 2003; Delord et al., 2010) in order to assess the possibility of bycatch, and meanwhile understanding how apex predator removal will influence the seabird foraging populations. White-chinned petrels (*Procellaria aequinoctialis*) were tracked around Kerguelen Island, where petrels and fisheries vessels are also commonly found together (19% of the seabirds were found in the vicinity of boats) (Delord et al., 2010). Seventeen of 22 albatross species are under threat because of bycatch capture level, and seven other seabird Procellariformes species are also endangered (Anderson et al., 2011). Sooty shearwaters and short-tailed shearwaters (*Puffinus tenuistris*) are often killed as incidental bycatch, threatening the breeding population. Bycatch risks depend on spatial and temporal overlap between fishing boats and seabird distribution (Uhlmann, 2003). Seabirds are obviously attracted by fisheries activities and the offal left behind commercial fishing boats, but most importantly the birds were feeding in the same areas because of the high primary productivity found there, and were consequently overlapping with other subsurface predators. For seabirds, foraging association is perhaps the most important strategy used to deal with complicated oceanic ecosystems in several ocean basins. Most foraging aggregations described in the literature are based in equatorial waters, where productivity is relatively low and sea-surface temperature is high (tropical waters are defined as about 23°C or warmer) (Ashmole, 1971; Ballance & Pitman, 1992). These interactions are critical for seabirds to access food resources and overcome primary productivity issues (Pitman & Ballance, 1992). Pierroti (1988) has studied feeding associations in the Northwest Atlantic, where it was not so obvious that marine mammals and seabirds interact. Some aggregations were observed, but statistical results were not found significant. Finally, I included another species of seabirds: the northern gannet. Gannets are Pelecaniform seabirds. They feed also on fish or squids, but they use a different foraging strategy since they are plunge-diving. They are also abundant seabirds along the continental shelf of the northeastern United States, and associations with marine mammals have been previously demonstrated (Davoren et al., 2010).

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HABITAT ASSOCIATION OF PROCELLARIIFORM SEABIRDS ALONG THE NORTHEASTERN CONTINENTAL SHELF OF THE UNITED STATES AND SOUTHEASTERN CANADA

CHAPTER 1

HABITAT ASSOCIATION OF PROCELLARIIFORM SEABIRDS ALONG THE NORTHEAST CONTINENTAL SHELF OF THE UNITED STATES AND SOUTHEASTERN CANADA

Abstract: Ecosystem changes will influence the foraging ecology and distribution of Procellariiform seabirds. Shearwaters, fulmars, and storm-petrels are abundant species found in the Northwest Atlantic. I analyzed data collected over nine shipboard surveys between 2006 and 2009 along the northeast continental shelf of the United States and the southeastern Canada. I modeled habitat association for seven seabird species and five environmental covariates using a zero-altered negative binomial fitted with generalized additive model. Differences in habitat association among species were found, but one major variable affected seabird density: sea-surface temperature (SST). Cory's shearwater (*Calonectris diomedea*) density was positively correlated with SST in the study area while other species density was negatively correlated. Procellariiformes will not respond equally to hydrographic fluctuations. Modeling habitat association will help to predict how seabirds might respond to a continuously changing ecosystem, and to assess their foraging behavioral plasticity. Since pelagic seabirds are spending most of their existence in the marine environment, we must understand the underlying hydrographic interactions on species ecology.

INTRODUCTION

Environmental changes trigger contrasting responses among seabird species (Gremillet & Boulinier, 2009; Moe et al., 2009; Peron et al., 2010; Weimerskirch et al., 2012). Procellariiform seabirds spend most of their lifetime at sea and have to face complex ecosystem changes (Hatch, 1990; Phillips, 2005; Shaffer et al., 2006). Evaluating habitat association for migrating species, not central place foragers remains a difficult task (Louzao et al., 2006; Pinet et al., 2009; Adams & Flora, 2010; Hedd et al., 2012). Migratory birds are vulnerable to fast environmental changes and species will not respond equally to them (Berteaux et al., 2004). There are 3 possible scenarios: 1) seabirds shift their foraging range north when food resources become less available due to hydrographic fluctuations (Veit et al., 1996; Wynn et al. 2007); 2) individual species adapt to continuous evolving environment, exhibit a higher behavioral foraging plasticity (Dias et al., 2011; Weimerskirch et al., 2012); 3) seabirds unable to face ecosystem changes (Louzao et al., 2006). Procellariiformes forage on preys directly influenced by environmental conditions such as fish, squids or zooplankton (Grubb, 1972; Weimerskirch, 1988; Cherel et al., 2006; Barrett et al., 2006). Some explanatory variables have been identified as factors such as Sea Surface Temperature (SST) (Veit et al., 1997;Guinet et al., 1998; Baduini, 2003), Sea Surface Salinity (SSS) (Ribic & Ainley, 1997; Ainley, 2005), bathymetry (Spear et al., 2001; Pinaud et al., 2005), Chlorophyll concentration (Baduini & Hyrenbach, 2003; Raymond, 2010; Fauchald et al.,2011), thermal fronts (Bost et al., 2009).

Effect of temperature change on the marine ecosystem, and Procellariiform seabirds

Climate change may strongly influence marine prey distribution and abundance (Perry et al., 2005). Seabirds are considered '*ecological indicators*' since they are visible and feed directly on fishes and invertebrates (Piatt & Sydeman, 2007). Fast changes in abundance and prey distributions have a negative impact on seabird populations (Sandvick et al., 2005). Between 1987 and 1994, sooty shearwaters declined 94 percent over the California Current (Veit et al, 1997). This decline was negatively correlated with warming SST and consistent with increase of sooty shearwaters in the northern part of the California Current, suggesting a change in population dynamic (Ainley et al., 1995; Spear & Ainley, 1999; Oedekoven et al., 2001). It has been suggested that Procellariiform seabirds will not respond equally to hydrographic fluctuations (Thompson & Ollason, 2001; Barbraud & Weimerskirch, 2006; Weimerskirch et al., 2012). Seven species of this seabird order forage along the northeast continental shelf, and southeastern Canada. The northeast continental shelf of the United States has been experiencing a gradual warming with interannual variability these past 50 years. SST increased about 1.08°C from 1957 to 2006 (Belkin, 2009). Our main objectives were: 1) to determine the relation between Procellariiform seabird abundance and environmental factors over our study area; 2) to assess at the species level which parameter might be the most important density predictors. Northern fulmar (*Fulmarus glacialis*), Cory's shearwater (*Calonectris diomedea*), great shearwater (*Puffinus gravis*), Manx shearwater (*Puffinus puffinus*), sooty shearwater (*Puffinus griseus*), Wilson's storm-petrel (*Oceanites oceanicus*) and Leach's storm-petrel (*Oceanodroma leucorrhea)* were included in my model. Understanding habitat association at the species level will help to determine which ones might be at higher risk, or which one might be advantaged (Rivalan et al., 2010; Weimerskirch et al., 2012).

MATERIAL AND METHODS

Study area

Seabird data were collected along the continental shelf extending from Nova Scotia (45°N; 63°W) to Cape Hatteras (35°N; 75°W) in the Northwest Atlantic. The bathymetry of the continental shelf in this region is heterogeneous, ranging from flat, sandy bottom, such as Nantucket shoals to more complex topography, such as Jeffreys Ledge, Georges Bank, Great South channel, and Hudson Canyon (Sherman, 1988). The study area (about 310,000 km^2) is bordered in the south by the Gulf Stream and the slope of the continental shelf, which drops from 1000 meters depth to about 4000 meters in areas such as the Gulf of Maine (Northeast Channel) separating the mainland from the deep waters of the Atlantic (Fautin et al., 2010). The continental slope gradient varies considerably from Canada to the Southeast United States, as does the temperature profile of the water. Cold, deep water flows south from the Labrador Sea and surrounds the continental slope. The Gulf Stream brings warmer waters north from the Gulf of Mexico (Atkinson et al., 1983; Sherman et al., 1996). The Labrador Current and the Gulf Stream meet over the edge of the Grand Bank and turn into a thermohaline circulation influencing climatic changes over the Northwest Atlantic. The northeast continental shelf experienced a gradual warming with interannual variability these past 50 years. SST increased about 1.08°C between 1957 and 2006 (Belkin, 2009). Climate and weather patterns in the northeast of the United States and the southeast Canada are influenced by two major, semi-permanent atmospheric pressure systems; a phenomenon known as the North Atlantic Oscillation (NAO) (Visbeck et al., 2001; Fogarty, 2007). These fluctuations of the NAO last between 7 and

10 years, having strong consequences on ecosystems. The NAO index has been shifting from negative to positive over the past 180 years (Hurrell & Van Loon, 1997; Hurrell et al., 2001).

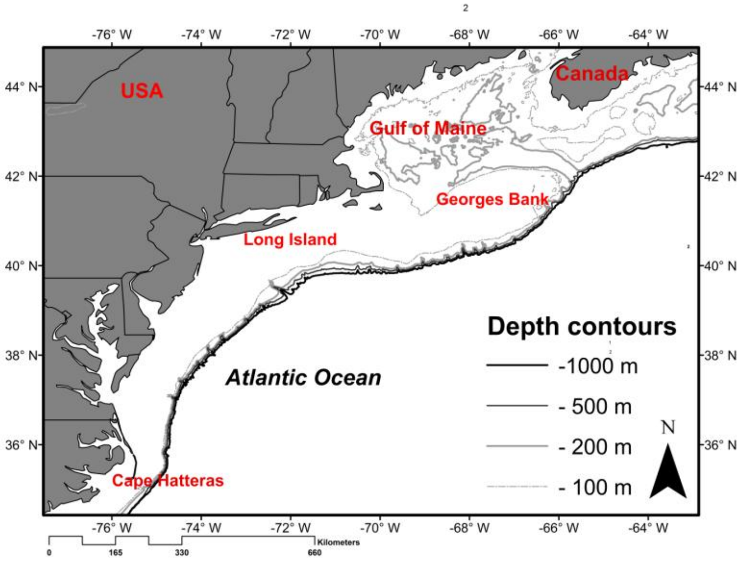


Fig.1: The northeast continental shelf

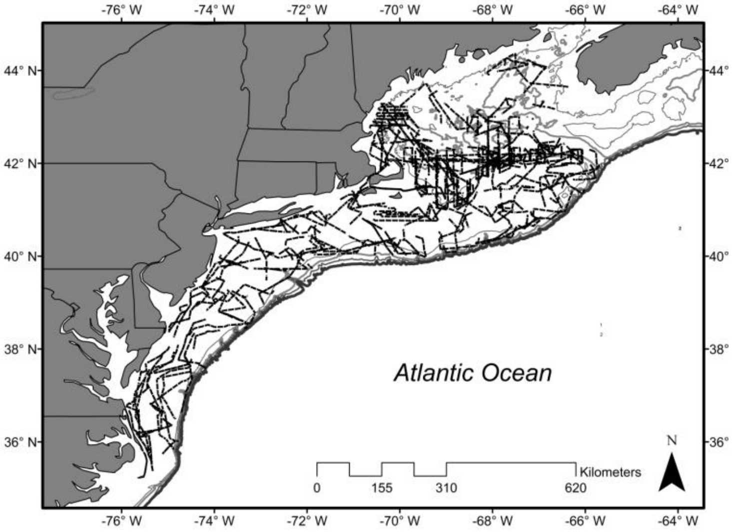


Fig.2: Surveys tracks from 2006 to 2009 along the northeast continental shelf of the United States and the southeastern Canada. Nine surveys were included.

Data collection: Seabird survey protocol

From 2006 to 2009: four years of surveys, we participated to nine shipboard surveys on the NOAA's R/V *Delaware II* (Fig.2). The cumulative area sampled for seabirds was about 19148 km^2 and 1299 effort hours (Table 2). The survey effort was unequal between the 4 years of our study (Table 5), and seabird density highly variable (Table 4 and 5). In 2006, we sampled only over Georges Bank and Jeffreys Ledge (Gulf of Maine). Between 2007 and 2009, we sampled the entire northeast continental shelf. We observed respectively 101 hours in 2006, 284 hours in 2007, 330 hours in 2008 and finally, 584 hours in 2009. One observer from the flying bridge continuously counted all seabirds flying in a 90° zone on one side of the ship using a combination of strip and line transect methods with distance sampling (Camphuysen & Garthe, 2004). The survey protocol assumed a 300 meters strip-width where all birds are being detected (Tasker et al., 1984; Hyrenbach et al., 2007; Ronconi & Burger, 2009). Behavior of seabirds, plumage, size, weather, sea state, observer ability or change in density influence detection probability (Barbraud & Thiebot, 2009). All these variables have been recognized as issues for seabird counts from shipboard platforms (Tasker et al., 1984; Hyrenbach et al., 2007). Coefficient of detection or correction factors might be applied in theory, but evaluating the specific reasons behind detection differences is nearly impossible. All seabirds entering the observation strip are counted once. Some species are more likely to be attracted by the vessel presence than others and will follow the ship. This behavior pattern is recognized by experienced observers, and those individuals identified as 'ship followers' were excluded from our density estimation. Transects were conducted from sunrise to sunset while the ship was moving at about 10 knots. Data were entered in real time. Observers entered data directly onto a laptop computer with the software D-Log2 and D-Log3 (©*Glenn Ford Consultant agency*). All data were processed using the software ESRI ArcView 9.3.1 and 10(©ESRI). Seabird densities were calculated with the *Seabird* tool (© USGS- Gilbert A.).

Table 1: Seabird species

Species code	**Common name**	**Scientific name**	**Total count**	**Mean density (km^2)**
NOFU	Northern fulmar	*Fulmarus glacialis*	4123	0.77
COSH	Cory's shearwater	*Calonectris diomedea*	2714	0.46
GRSH	great shearwater	*Puffinus gravis*	22073	4.67
MASH	Manx shearwater	*Puffinus puffinus*	121	0.03
SOSH	Sooty shearwater	*Puffinus griseus*	5262	1.43
WISP	Wilson's storm-petrel	*Oceanites oceanicus*	15712	2.43
LESP	Leach's storm-petrel	*Oceanodroma leucorhoa*	3859	0.72

Table 2: Summary effort surveys (2006- 2009)

Name survey	**Date**	**Effort hours**	**Area sampled (km^2)**
Atlantic herring survey	18 to 28 September 2006	101	1160
Ecosystem Monitoring Survey	22 May to 7th June 2007	149	2049
Atlantic herring survey	14 to 25 October 2007	135	1346
Ecosystem Monitoring Survey	14 to 26 August 2008	150	2413
Atlantic herring survey	15 to 24 September 2008	180	3361
Ecosystem Monitoring Survey	29 January to 12 February 2009	115	1483
Ecosystem Monitoring Survey	28 May to 10 June 2009	181	2587
Ecosystem Monitoring Survey	17 to 28 August 2009	138	1877
Atlantic herring survey	21 September to 02 October 2009	150	2872
TOTAL		**1299**	**19148**

Table 3: seabird count per year (km^2)

Species code	2006	2007	2008	2009	Total
NOFU	2	1948	38	473	4123
COSH	0	4	594	2148	2746
GRSH	2174	7028	5477	7394	22073
MASH	10	24	38	31	103
SOSH	15	3704	16	1527	5262
WISP	81	5817	1013	8584	15495
LESP	360	1211	705	1560	3836

Table 4: seabird density per year (km^2)

Species code	2006	2007	2008	2009	Total
NOFU	0.006	2.00	0.032	0.84	0.77
COSH	0	0.001	0.11	1.049	0.46
GRSH	6.59	7.17	3.37	4.12	4.67
MASH	0.030	0.033	0.022	0.050	0.030
SOSH	0.05	3.83	0.007	1.70	1.43
WISP	0.25	5.21	0.18	1.70	2.43
LESP	1.11	1.23	1.44	0.89	0.72

Table 5 : Effort survey per year

Year	Effort survey (km)
2006	1575
2007	4453
2008	6029
2009	12596

Environmental covariates

Seabird occurrence and then density are related to specific oceanographic features that constrain prey distribution (Selzer & Payne, 1988). I examined the effect of five oceanographic variables that influenced the density and behavior of marine prey. SST is considered one of the most important regulators of marine organism distribution, influencing their behavior and limiting their distribution (Pinet, 1992; Montevecchi & Myers, 1997; Drinkwater, 2005). Temperature control chemical reactions, which regulate in turn the development of organisms at the bottom of the trophic ladder. Then, bathymetric features affect water column mixing, and create local conditions that increases primary productivity (presence of fronts or eddies) along bank edges, shelf break or canyons. Shallower waters are generally warmer because of the sunlight penetration, and consequently increase primary productivity. Seabirds are highly correlated to oceanic or continental shelf bathymetric features (Hyrenbach et al, 2000). Higher chlorophyll concentration is an indicator of biological productivity and attracts marine predators. Seabird Procellariiform feed on higher trophic level organism who feeds directly on phytoplankton (Baduini & Hyrenbach, 2003). Finally, we included both chlorophyll and SST frontal intensity. Chlorophyll and thermal fronts are not always coincident (Stegmann & Ullman, 2004; Gould & Arnone, 2004). Fronts can either increase primary productivity, zooplankton communities and food availability or in contrast can be repulsive to some species due to a strong SST or physico - chemical gradient (Clapp et al., 1982; Olson et al., 1994). Seabirds can respond quite differently behaviorally to the intensity or biochemical nature (Jahncke et al., 2005; Bost et al., 2009; Thorne, 2010). Predictor variables included were: depth (m) (DEPTH), chlorophyll concentration (mg/-m^3) (CHLORO), SST (°C) (SST), intensity of SST fronts (count of fronts detected over a five-day window across a 1.25 x1.25 km spatial window) (INTFRONTSST), intensity of chlorophyll front (count of fronts detected over a 5-day window across a 1.25x1.25 km spatial window) (INTFRONTCHLORO). Fronts, sea-surface temperature and chlorophyll concentration were derived from AHVRR satellite images. Frontal data were extracted using the Marine Geospatial Ecology Tools (MGET), which is an implementation of the single-day Cayulla-Cornillon front algorithm (Ullman, 2000; Roberts et al., 2010). To minimize the effects of cloudiness, we used five-day composites of SST and chlorophyll, representing five day median at a spatial scale of 1.25x1.25 km. Values obtained for chlorophyll and SST frontal intensities and distance were based on the number of cells within the spatial window that contained a front (Roberts et al., 2010). Sea-surface temperature was also collected continuously on the vessel using the flow-through system. Depth contours were extracted from General Bathymetric Chart of the Oceans (GEBCO).

Table 6: Environmental variable summary

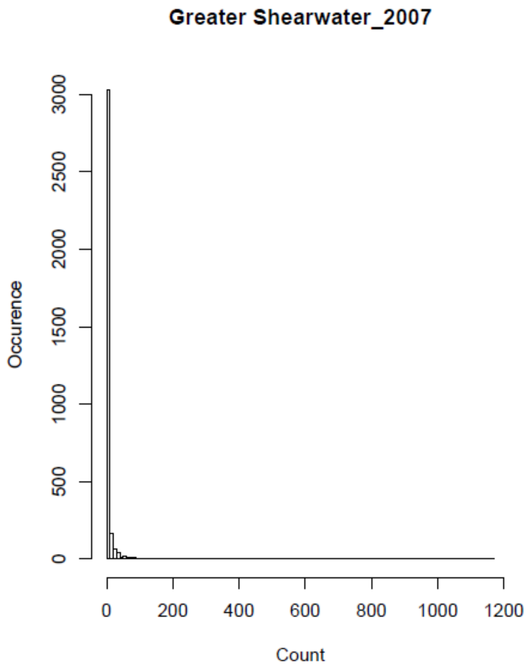
Variable	**Definition**	**Unit**
DEPTH	Depth	m
CHLORO	Chlorophyll concentration	mg/m^3
SST	Sea Surface Temperature	°C
INTFRONTCHLORO	Intensity Chlorophyll fronts	Count of fronts detected over a five-day window across a 1.25x1.25 km spatial window
INTFRONTSST	Intensity SST fronts	Count of fronts detected over a five-day window across a 1.25x1.25 km spatial window

Statistical Modeling

Seabird density was used as the response variable, and calculated from survey lines segmented at 1 km interval bins. My datasets included a large number of zeroes (Table.7; Fig.2). In ecological studies, datasets are often considered zero-inflated, meaning that these data contains a larger proportion of zeros than expected (Barry & Welsh, 2002). ‘Zero’ abundance is considered a common event in the fisheries (Yee, 2010), bycatch studies (Minami et al., 2007; Gilman et al., 2008; Winter et al., 2011), marine mammal and seabird surveys (Ver Hoef & Jansen, 2007; Peron et al., 2010). Observation of a very high number of seabirds is rare (Clarke et al., 2003). Zero counts are valuable information but excessive number of zeros will create over-dispersion or under-dispersion (Podlich et al., 2002; Yee, 2009). I selected the zero-altered negative binomial distribution, instead of zero-inflated negative binomial distribution used previously (Peron et al., 2010). For the zero-altered negative binomial method aka hurdle, two-step, truncated or delta F, zeros came from a single source, whereas for zero-inflated, three origins are possible: 1) seabirds not detected by observer, 2) seabirds not present at the time of observation but habitat is good, and 3) seabirds not seen because the habitat is inappropriate (Zuur et al., 2009). My model includes two steps. In the first step, the presence/ absence was modelled and in the second step, the ‘positive count’ was modelled using a truncated probability distribution (endorsing the role of hurdle for positive values) (Mullahy, 1986; Zuur et al., 2009; Yee, 2010). This method identify that the underlying reasons determining seabird presence can be different from the ones determining the abundance (Potts & Elith, 2006; Heinanen et al., 2008) The negative binomial distribution allows over-dispersion in the positive part of the count data. Finally, a generalized additive model (GAM) was fitted to the hurdle model (Hastie & Tibshirani, 1986). GAM allows for nonlinear relationships and effects between the response and multiple explanatory variables and use non-parametric regressions to investigate relationships between environmental covariates and response variables such as seabird density (Hastie & Tibshirani, 1986; Wood, 2006; Heinanen et al, 2008). GAM is a method for data exploration or predictive modeling (Wood, 2006). In this study, GAM was used as an exploratory method to examine the relationships between seabird density and environmental covariates. I selected the package VGAM available in the statistical calculation R CRAN program (Yee, 2010; ©R Development Core Team 2011). VGAM computed the maximum likelihood estimates of models and distributions. GAM coefficients were summarized by species. Smoothing parameters relationships between environmental predictors and seabird abundance were represented using non-parametric regressions. This regression analysis shows the average value of a response variable (seabird density) as function of a predictor (environmental covariate). Each plot represents the variable response in relation to the probability (natural logarithm of the odds) of the species occurrence in the model. The x-axis is defined by the observed values of the predictor (harsh marks). Values above zero on the y-axis mean that the environmental predictor value have more than average effect on species density. The solid line is the smoothed response curve. Dashed lines indicate the approximate 95% confidence intervals around the covariate main effects and the degree of freedom (DF= 2). The non-parametric regression uses the vector cubic smoothing spline.

Table 7: Proportion of zero count in dataset

Species code	% zero dataset
NOFU	92
COSH	95
GRSH	76
MASH	99
SOSH	95
WISP	90
LESP	95



Number of zero occurrences in dataset: Example of great shearwater 2007.

RESULTS

The seven species displayed contrasting responses to the effect of each environmental predictor. The most abundant species observed between 2006 and 2009 were great shearwaters (n = 22073) and Wilson's storm-petrels (n = 15495). We counted 4123 northern fulmars, 5262 sooty shearwaters, 3836 Leach's storm-petrels, 2747 Cory's shearwaters and 103 Manx shearwaters respectively.

Model selection

After comparing Akaike Information Criterion (AIC) values for each species and between 5 models (zero altered Poisson, zero inflated Poisson, zero altered negative binomial, zero inflated negative binomial, and negative binomial), I kept the zero altered negative binomial. This method demonstrated the lowest AIC scores; however, the zero altered Poisson showed the second lowest AIC values. Several environmental covariates might affect densities but only predictors showing statistical significant relationships (p-value < 0.05) were the one selected. To rank the most parsimonious model and keep the best explanatory model, we first performed a stepwise regression both sides with data permutation for model variable selection using the MASS package (©R Development Core Team; Venable & Ripley, 2002). I selected the model with the lowest AIC score and with p-values <0.05 in the second part of the model (positive count). AIC values are higher since our statistical method includes all counts (including zero). The fittest models are displayed for each species. The model selected is presented below in **bold**.

Table 8: model selection for northern fulmar

Final model selected	DF	AIC	Log likelihood model
DEPTH + SST	**7**	**14901.32**	**-7436.65**
DEPTH + INTFRONTCHLORO	7	15770.59	-7878.29
DEPTH + CHLORO	7	15779.15	-7882.57

Table 9: model selection for Cory's shearwater

Final model selected	DF	AIC	Log likelihood model
DEPTH + SST	**7**	**10437.85**	**-5211.85**
DEPTH + INTFRONTSST	7	10535.52	-5260.52

Table 10: model selection for great shearwater

Final model selected	DF	AIC	Log likelihood model
SST + CHLORO + INTFRONTSST	**7**	**47786.55**	**-23884.27**
SST + CHLORO	7	47821.35	-23903.67
SST + INTFRONTSST	7	47844.43	-23915.21

Table 11: model selection for Manx shearwater

Final model selected	DF	AIC	Log likelihood model
SST + CHLORO	**7**	**1309.583**	**-647.79**
CHLORO	5	1325.515	-657.75
DEPTH + SST	7	1343.214	-664.60

Table 12: model selection for sooty shearwater

Final model selected	DF	AIC	Log likelihood model
SST + INTFRONTCHLORO	**7**	**10031.38**	**-5008.68**
DEPTH + INTFRONTCHLORO	7	10763.40	-5374.70
DEPTH	5	10789.93	-5389.96

Table 13: model selection for Wilson’s storm-petrel

Final model selected	DF	AIC	Log likelihood model
DEPTH + SST + CHLORO	**7**	**19797.61**	**-9889.80**
SST + CHLORO	7	19816.88	-9991.43
DEPTH + SST	7	19824.98	-9905.48

Table 14: model selection for Leach’s storm-petrel

Final model selected	DF	AIC	Log likelihood model
SST + INTFRONTSST	**7**	**10971.52**	**-5478.782**
SST	5	10980.06	-5484.530
DEPTH + INTFRONTSST	7	11194.35	-5590.17

Model validation

I evaluated the performance of each model using k-fold cross validation (Li et al., 2011). Cross validation addresses over-fitting problems. When Over fitting happen, the model includes either more variables than required or not enough of them (Zuur, 2009). The dataset was divided into *k* equal-size subsets and the cross validation repeated 10 times (*k*= 10) (Wenger & Olden, 2012). One of the k subsets was used as a "test" dataset, while the other *k*-1 datasets were used for "training" purposes. The mean square error (MSE) between the "training" and "test" datasets were computed. Finally, best fit models were selected based on the lowest AIC score and difference between the "training" and "test" mean square error (Table 15).

Table 15: Training and errors MSE from zero altered negative binomial model (10 fold cross-validation)

Species	fit model #	Model	AIC	Log model likelihood	Training error MSE	Test error average MSE
NOFU	1	**DEPTH + SST**	**14901.32**	**-7436.65**	**217.51**	**217.67**
	2	DEPTH + INTFRONTCHLORO	15770.59	-7878.29	217.60	217.63
	3	DEPTH + CHLORO	15779.15	-7882.57	218	218.60
COSH	1	**DEPTH + SST**	**10437.85**	**-5211.85**	**50.06**	**50.08**
	2	DEPTH + INTFRONTSST	10535.52	-5260.52	50.06	50.07
GRSH	1	**SST + CHLORO + INTFRONTSST**	**47786.55**	**-23884.27**	**2642**	**2644**
	2	SST + CHLORO	47821.35	-23903.67	2667.23	2667.27
	3	SST+ INTFRONTSST	47844.43	-23915.06	2639	2640
MASH	1	**SST + CHLORO**	**1309.583**	**-647.79**	**0.32**	**0.31**
	2	CHLORO	1325.515	-657.75	0.28	0.28
	3	DEPTH + SST	1343.214	-664.60	0.26	0.27
SOSH	1	**SST + INTFRONTCHLORO**	**10031.38**	**-5008.68**	**1556**	**1556.95**
	2	DEPTH + INTFRONTCHLORO	10763.40	-5374.70	1562.91	1562.50
	3	DEPTH	10789.93	-5389.96	1562.79	1562.19
WISP	1	**SST + DEPTH + CHLORO**	**19797.61**	**-9889.80**	**896.89**	**896.59**
	2	SST + CHLORO	19816.88	-9991.43	897.69	897.25
	3	DEPTH + SST	19824.98	-9905.48	895.45	895.28
LESP	1	**SST + INTFRONTSST**	**10971.52**	**-5478.78**	**209.98**	**209.86**
	2	SST	10980.06	-5484.53	209.91	209.84
	3	DEPTH + INTFRONTSST	11194.35	-5590.17	213.75	213.63

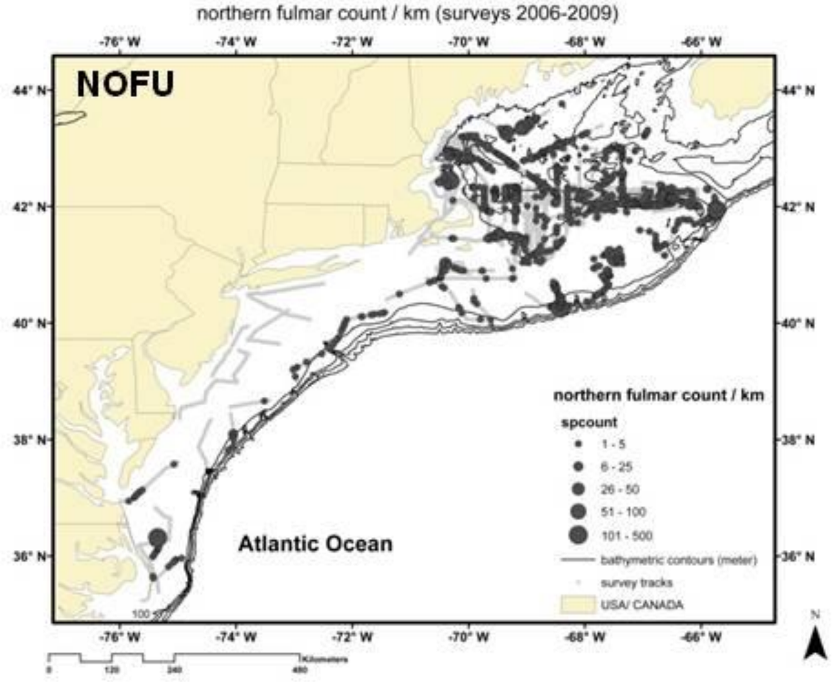


Fig.3: Distribution of northern fulmars between 2006 and 2009.

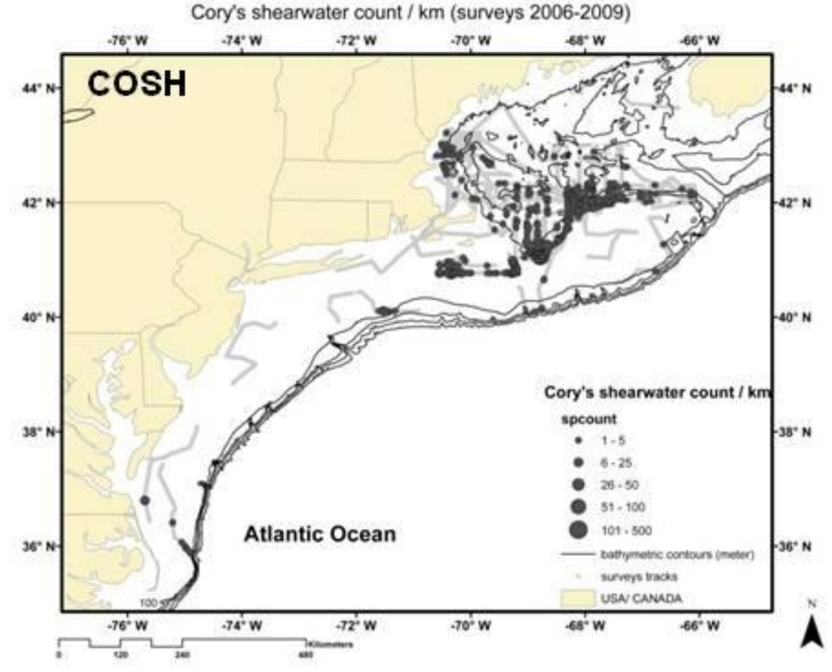


Fig.4: Distribution of Cory's shearwaters between 2006 and 2009.

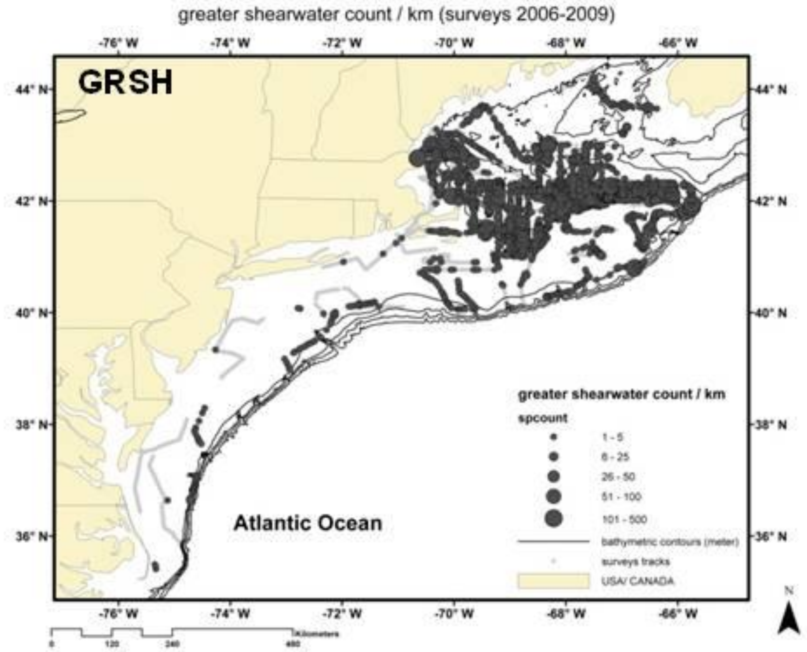


Fig.5: Distribution of great shearwaters between 2006 and 2009.

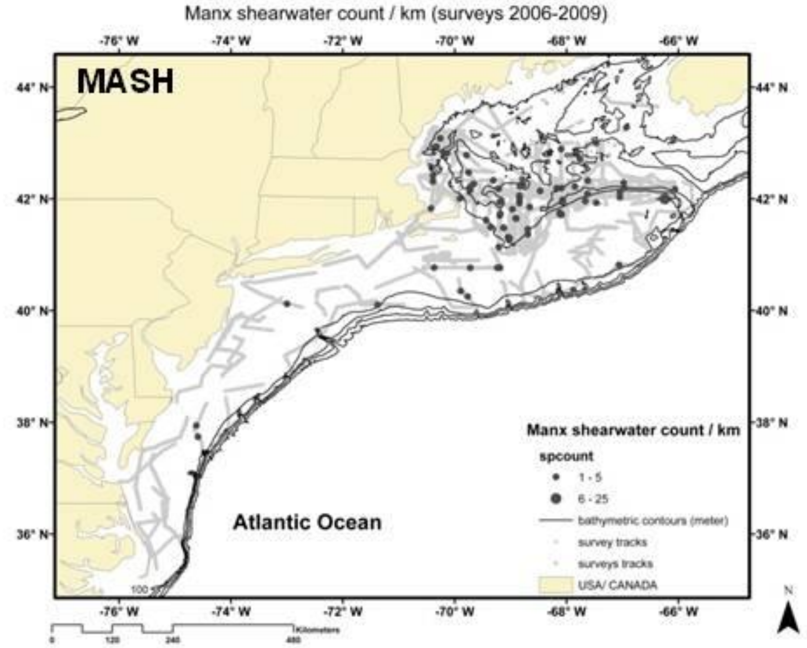


Fig.6: Distribution of Manx shearwaters between 2006 and 2009.

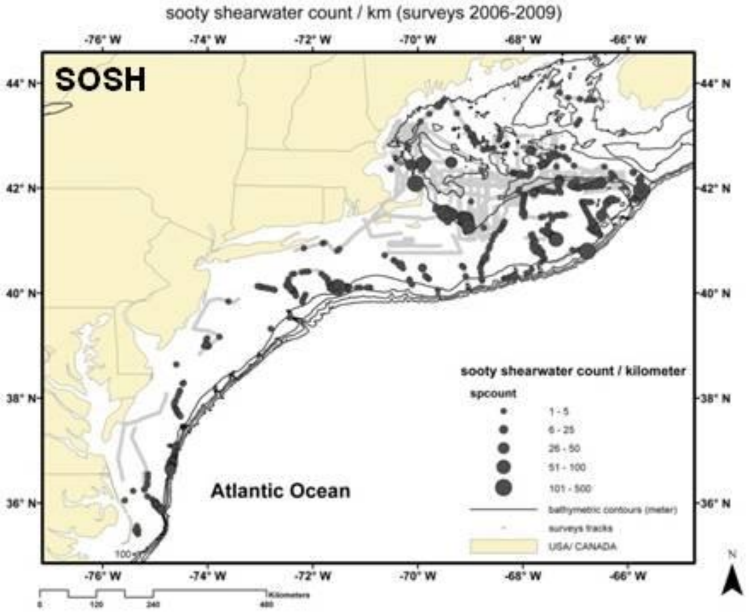


Fig.7: Distribution of sooty shearwaters between 2006 and 2009.

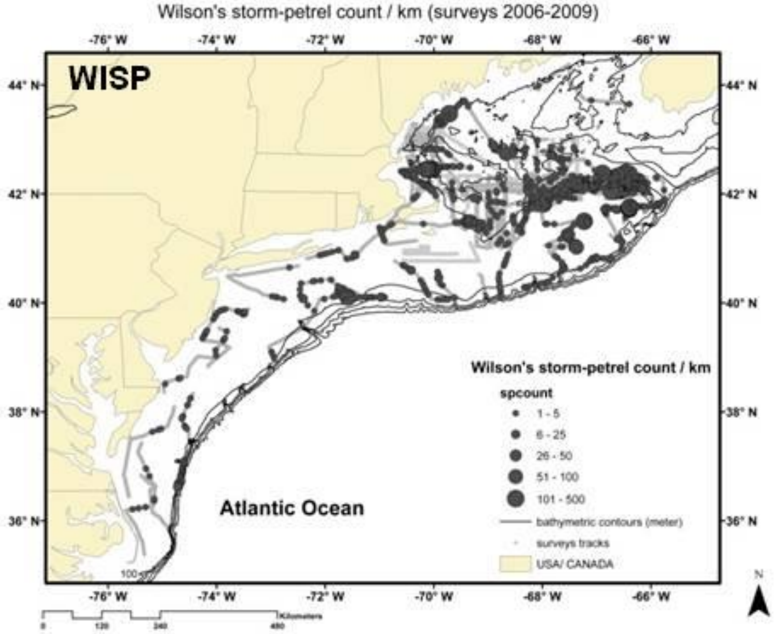


Fig.8: Distribution of Wilson's storm-petrels between 2006 and 2009.

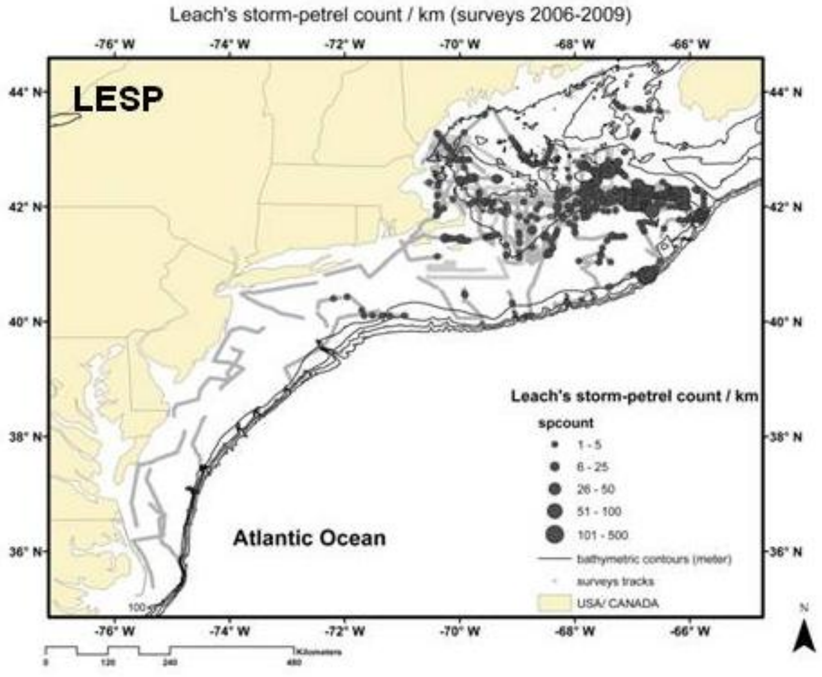


Fig.9: Distribution of Leach's storm-petrels between 2006 and 2009.

Northern fulmar (NOFU)

The density of northern fulmar was variable with peaks in 2007 and 2009 (Fig.10). They were the most abundant in 2007 and 2009. The model DEPTH + SST was the most parsimonious (AIC=14901.32) (Table 16). Fulmars were more abundant between and -100 m and -170 m (Fig.11) (Estimate= -0.003; SE= 0.001; P< 0.001; CI= [0.002; 0.004]. The density was also affected by SST; they were more abundant in temperatures between 2 and 10°C, and were negatively correlated with increasing SST (Estimate= -0.139; SE= 0.011; p< 0.001; CI= [-0.160; -0.118]) (Fig.12).

Table 16: Parameter estimates for NOFU (log likelihood: -7443.661; DF=7)

Step 1: Zero hurdle model coefficient					
Parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	2.374	0.171	<**0.001**	2.044	3.704
DEPTH	0.003	0.0009	<**0.001**	0.002	0.004
SST	-0.139	0.006	<**0.001**	-0.150	-0.128
Step 2: Count model coefficient (truncated with negative binomial)					
Parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	4.374	0.206	<**0.001**	2.044	3.704
DEPTH	0.003	0.001	<**0.005**	0.002	0.004
SST	-0.139	0.011	<**0.001**	-0.160	-0.118

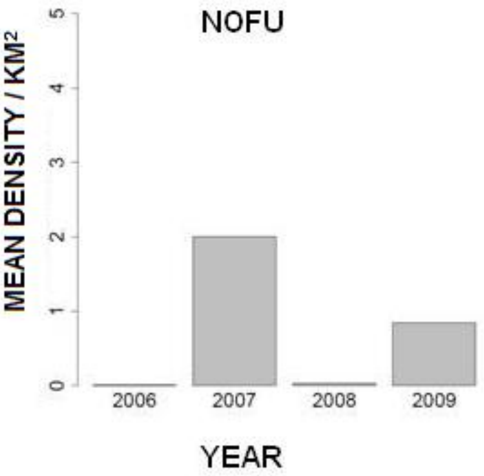


Fig. 10. Northern fulmar mean density/ km ^{2} over 4 years.

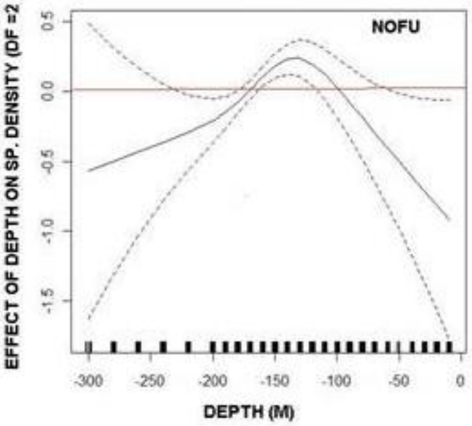


Fig.11. Effect of covariate depth on northern fulmar density.

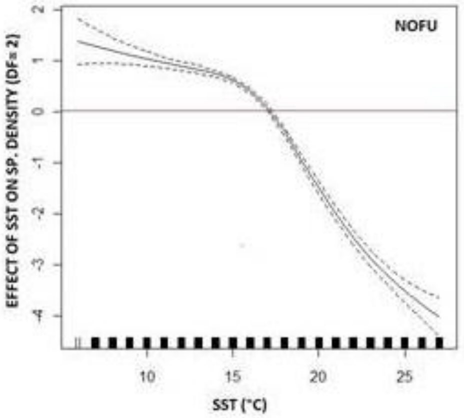


Fig.12. Effect of covariate SST on northern fulmar density.

Cory’s shearwater (COSH)

Cory’s shearwaters were not observed in 2006. The species density increased abruptly between 2008 and 2009 (Fig.13). The model DEPTH + SST was the most parsimonious (AIC= 10437.85) (Table 17). The highest density was observed in depths over -150 m (Fig.14) (Estimate = -0.003; SE= 0.001; p< 0.001; CI= [-0.004; -0.002]. Their density was negatively correlated with shallower bathymetry. COSH density was negatively correlated with SST elevation, with an optimal thermal range between 14 and 22°C (Fig.15) (Estimate= -0.065; SE= 0.009; P< 0.001; CI= [-0.082; -0.048].

Table 17: Parameter estimates for COSH (log likelihood: -5211.94; DF=7)

Step 1: Zero hurdle model coefficient (logit link)					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-6.389	0.250	**<0.001**	-6.879	-5.899
DEPTH	-0.011	0.001	**<0.001**	-0.012	-0.011
SST	-0.091	0.009	**<0.001**	-0.108	-0.074
Step 2: Count model coefficient (truncated with negative binomial) (log link)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	2.006	0.250	**<0.001**	1.516	2.496
DEPTH	-0.003	0.001	**<0.001**	-0.004	-0.002
SST	-0.065	0.009	**<0.001**	-0.082	-0.048

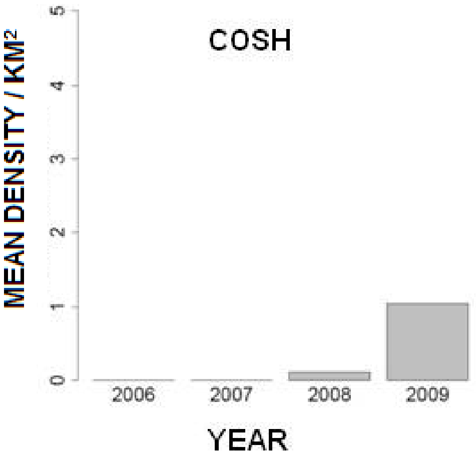


Fig.13. Cory's shearwater mean density/ km^2 over 4 years.

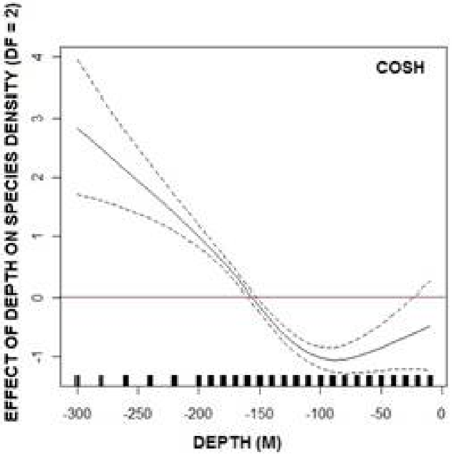


Fig.14. Effect of covariate depth on Cory's shearwater density.

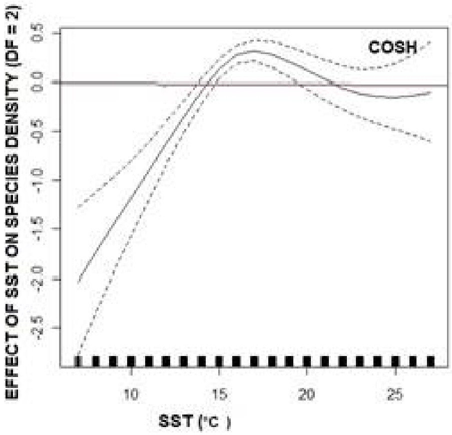


Fig.15. Effect of covariate SST on Cory's shearwater density.

Great shearwater (GRSH)

Great shearwaters were the most abundant species along the northeast continental shelf, and their density was higher in 2006 and 2007 (Fig.16). The model SST + CHLORO + INTFRONTSST was the most parsimonious (Table 18) (AIC= 47786.55). Their density was negatively correlated to SST increase. Their abundance was the highest between 7 and 17 °C (Estimate = -0.106; SE= 0.010; p< 0.001; CI= [-0.125; -0.087] (Fig.17). The model suggested that GRSH density was positively correlated with primary productivity (Estimate = 0.102; SE= 0.010; P< 0.001; CI= [0.083; 0.121]) (Fig.18). They were also observed in higher number in SST frontal areas, but negatively correlated to higher intensity (Estimate= -1.186; SE= 0.021; P<0.001; CI= -1.227; -1.145) (Fig.19)

Table 18: Parameter estimates for GRSH (log likelihood: -23884.27; DF=9)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	0.940	0.085	**<0.001**	0.774	1.106
SST	-0.130	0.005	**<0.001**	-0.139	-0.121
CHLORO	0.030	0.006	**<0.001**	0.019	0.041
INTFRONTSST	-0.065	0.012	**<0.001**	-0.088	-0.042
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	3.991	0.161	**<0.001**	3.676	4.306
SST	-0.106	0.010	**<0.001**	-0.125	-0.087
CHLORO	0.102	0.010	**<0.001**	0.083	0.121
INTFRONTSST	-1.186	0.021	**<0.001**	-1.227	-1.145

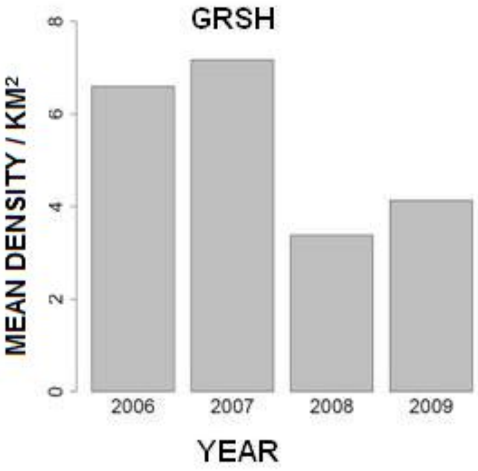


Fig.16. Great shearwater mean density / km^2 over 4 years.

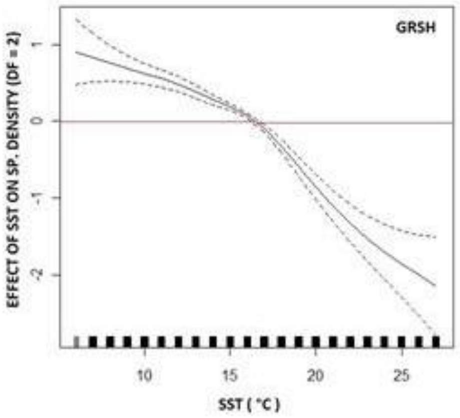


Fig.17. Effect of covariate SST on great shearwater density.

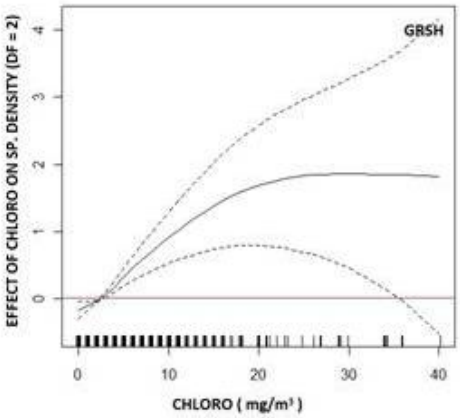


Fig.18. Effect of covariate chlorophyll concentration on great shearwater density.

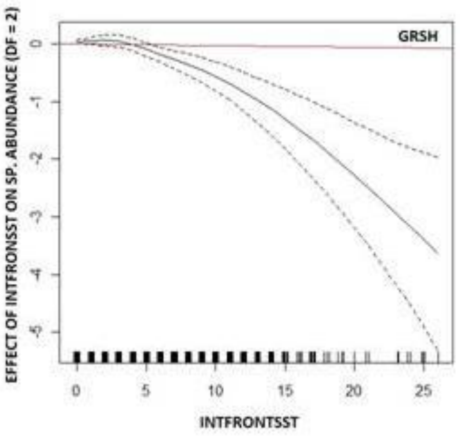


Fig.19. Effect of covariate SST front intensity on great shearwater density.

Manx shearwater (MASH)

Manx shearwater was the least abundant species over the four years of study, but their density slowly increased (Fig.20). The model the most parsimonious was SST + CHLORO (AIC= 1309.583) (Table 19). Manx shearwaters were found in water between 7 and 17°C, and their density was negatively correlated with higher temperature (Estimate= -0.095; SE= 0.022; P<0.001; CI= [-0.116; -0.074]) (Fig.21). MASH density was positively correlated with primary productivity (Estimate= 0.096; SE= 0.011; P< 0.001; CI= [0.075; 0.117]) (Fig.22).

Table 19: Parameter estimates for MASH (log likelihood: -647.79; DF=7)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-4.471	0.590	**<0.001**	-5.621	-3.321
SST	-0.034	0.036	**>0.05**	-0.077	0.009
CHLORO	0.004	0.047	**>0.05**	-0.088	0.096
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	2.699	0.333	**<0.001**	2.047	3.351
SST	-0.095	0.022	**<0.001**	-0.116	-0.074
CHLORO	0.096	0.011	**<0.011**	0.075	0.117

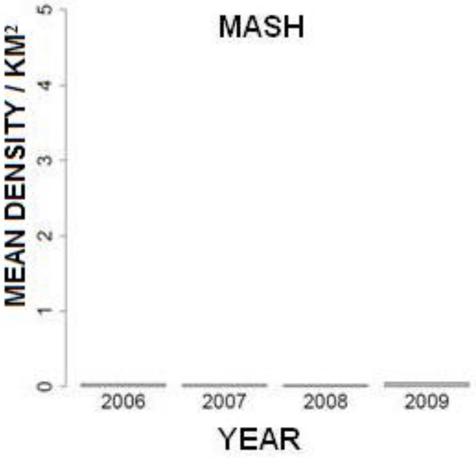


Fig.20. Manx shearwater mean density / km^2 over 4 years.

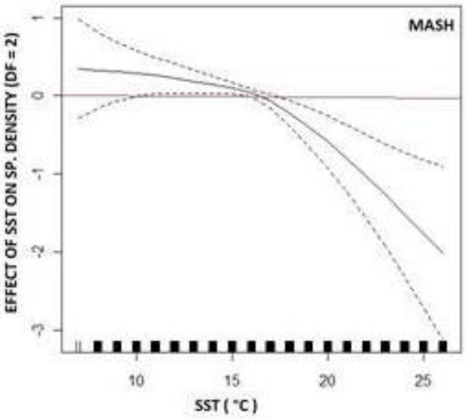


Fig.21. Effect of covariate SST on Manx shearwater density.

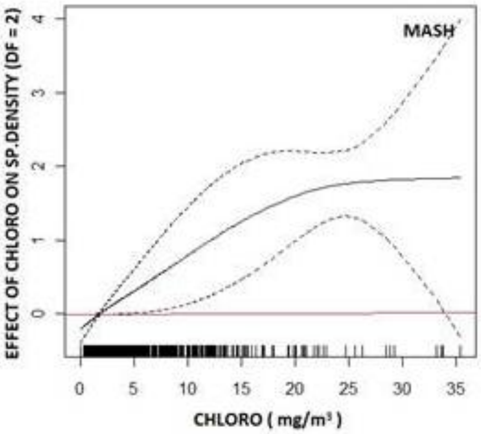


Fig.22. Effect of covariate chlorophyll concentration on Manx shearwater density.

Sooty shearwater (SOSH)

Sooty shearwater density was also variable, with highest peaks in 2007 and 2009 (Fig.23). The model SST + INTFRONTCHLORO was the most parsimonious (AIC= 10031.38) (Table 20). Sooty shearwater density was negatively correlated with SST. They were observed in higher numbers between 7 and 17°C (Estimate = -0.087; SE= 0.028; p< 0.001; CI= [-0.141; -0.033] (Fig.24). SOSH density was negatively correlated to chlorophyll frontal area, and found in lesser intense frontal areas (Estimate= -0.219; SE= 0.066; P<0.001; CI= [-0.348; -0.090]) (Fig.25).

Table 20: Parameter estimates for SOSH (log likelihood: -5008.689; DF=7)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-3.077	0.380	**<0.001**	-3.821	-2.333
SST	0.358	0.021	**<0.001**	0.307	0.665
INTFRONTCHLORO	0.026	0.045	**>0.05**	-0.062	0.114
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	3.579	0.377	**<0.001**	2.841	4.317
SST	-0.087	0.028	**<0.005**	-0.141	-0.033
INTFRONTCHLORO	-0.219	0.066	**<0.005**	-0.348	-0.090

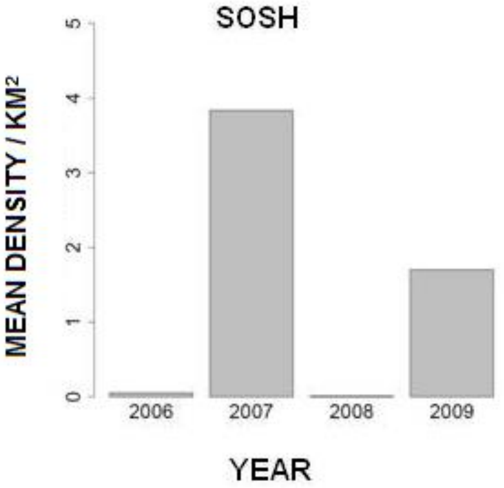


Fig.23. Sooty shearwater mean density/ km^2 over 4 years.

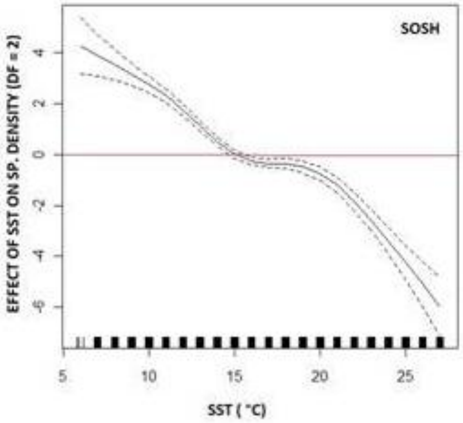


Fig.24. Effect of covariate SST on sooty shearwater density.

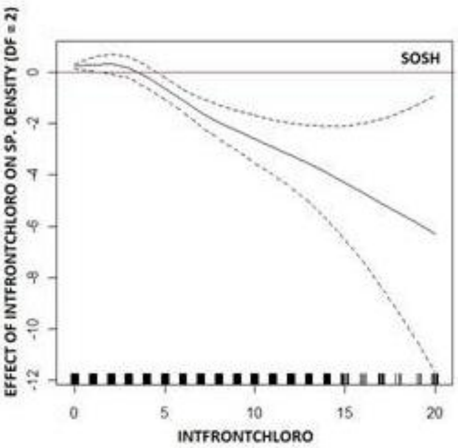


Fig.25. Effect of covariate chlorophyll front intensity on sooty shearwater density.

Wilson’s storm-petrel (WISP)

Wilson’s storm-petrel density fluctuated over the four years with peaks in 2007 and 2009 (Fig.26). The model DEPTH + SST + CHLORO was the most parsimonious (AIC= 19797.61) (Table 21). WISP were more abundant in depth lesser than -150 m (Estimate= 0.005; SE= 0.001; P<0.001; CI= [0.0049; 0.0051]) (Fig.27). WISP density was negatively correlated to SST. This species was found in higher abundance between 7 and 14°C (Estimate = -0.127; SE= 0.010; P< 0.001; CI= [-0.146; -0.107]) (Fig.28). WISP density was positively correlated with primary productivity (Estimate = 0.0005; SE= 0.0008; p< 0.001; CI= [0.000; 0.0150]) (Fig.29).

Table 21: Parameter estimates for WISP (log likelihood: -9889.80; DF=9)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-1.046	0.474	**<0.05**	-1.966	-0.126
DEPTH	0.003	0.001	**<0.05**	0.002	0.004
SST	0.045	0.013	**<0.005**	0.020	0.070
CHLORO	-0.050	0.043	**>0.05**	-0.134	0.034
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	3.867	0.252	**<0.001**	3.374	4.360
DEPTH	0.005	0.001	**<0.001**	0.0049	0.0051
SST	-0.127	0.010	**<0.001**	-0.146	-0.107
CHLORO	0.0005	0.0008	**<0.001**	0.000	0.0150

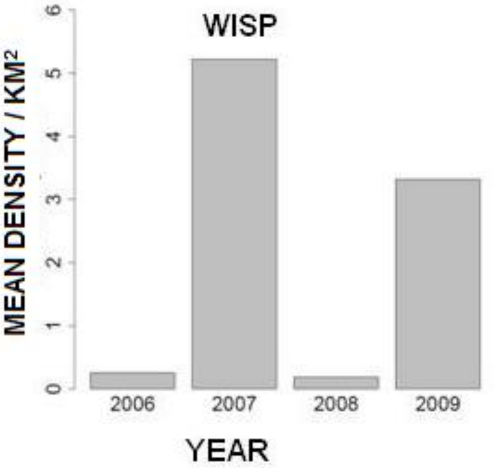


Fig. 26. Wilson's storm-petrel density mean / km^2 over 4 years.

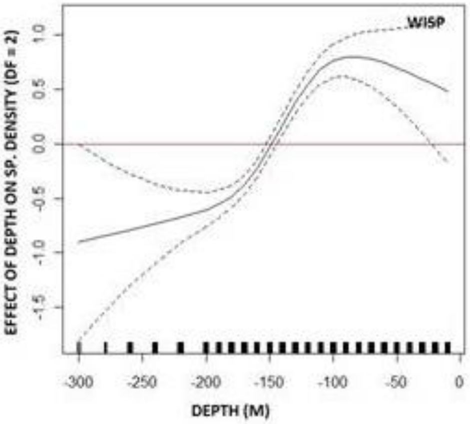


Fig.27. Effect of covariate depth on Wilson's storm-petrel density.

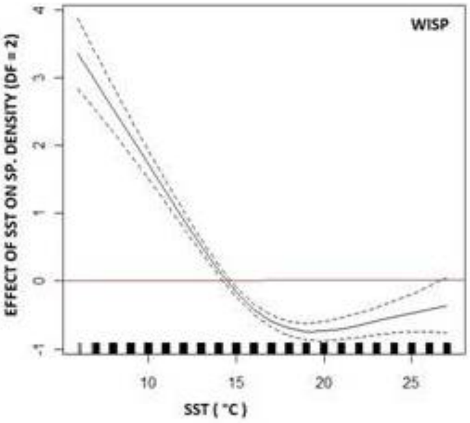


Fig.28. Effect of covariate SST on Wilson's storm-petrel density.

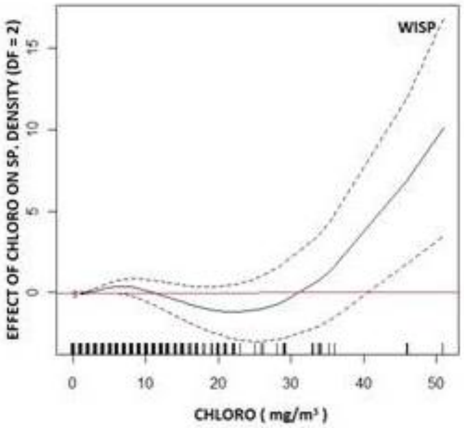


Fig.29. Effect of covariate chlorophyll concentration on Wilson's storm-petrel density.

Leach’s storm-petrel (LESP)

Abundance of Leach’s storm-petrel was the lowest in 2008 (Fig.30). The model SST + INTFRONTSST was the most parsimonious (AIC= 10971.52) (Table 22). LESP density was negatively correlated with SST. Higher densities were observed in temperatures between 8 and 16°C (Estimate = -0.143; SE= 0.018; p<0.005; CI= [-0.178; -0.108]) (Fig.31). This latter species was negatively correlated with SST frontal intensity (Estimate = -0.100; SE= 0.026; p<0.001; CI= [-0.150; -0.050]) (Fig.32).

Table 22: Parameter estimates for LESP (log likelihood: -5478.78; DF=7)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-0.735	0.165	**<0.001**	-1.058	-0.412
SST	-0.155	0.011	**<0.001**	-0.176	-0.134
INTFRONTSST	-0.036	0.015	**>0.05**	-0.065	-0.070
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	4.078	0.299	**<0.001**	3.492	4.664
SST	-0.143	0.018	**<0.001**	-0.178	-0.108
INTFRONTSST	-0.100	0.026	**<0.001**	-0.150	-0.050

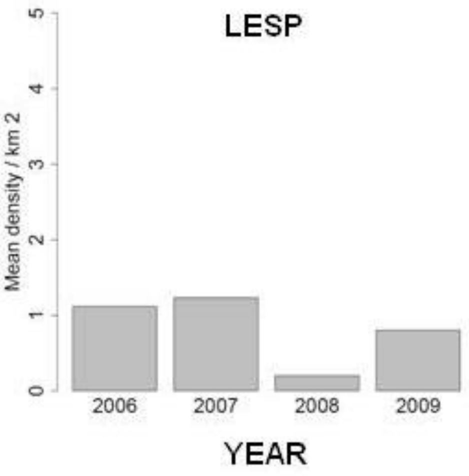


Fig.30. Leach's storm-petrel mean density / km^2 over 4 years.

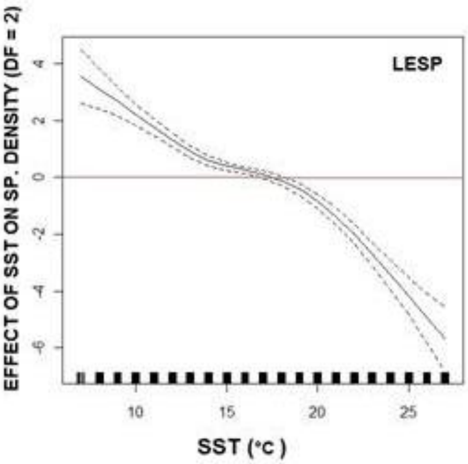


Fig. 31. Effect of covariate SST on Leach's storm-petrel density.

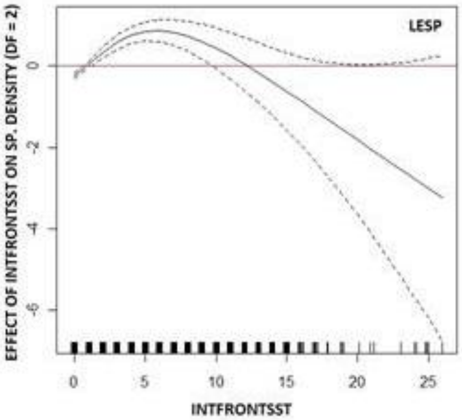


Fig.32. Effect of covariate SST front intensity on Leach's storm-petrel density.

Effect of environmental covariates summary

Effect of depth on species density*:* The model suggested that NOFU, COSH and WISP densities were highly correlated with bathymetry. The model suggested that NOFU were found between -100 and -170 m (Fig.11) (Estimate= 0.003; SE= 0.001; P<0.001; CI= [0.002; 0.004]. COSH were observed in high abundance between over -150 m (Estimate= -0.003; SE= 0.001; p<0.001; CI= [-0.004; -0.002] (Fig.14). WISP density was highest below -150 m, and dropped drastically between -150 and -100 m (Estimate= 0.005; SE= 0.001; P<0.001; CI= [0.0049; 0.0051] (Fig.27).

Effect of SST on species density: The SST covariate affected all seabird species (Table 23). Models of NOFU (Estimate= -0.139; SE= 0.006; p<0.001; CI= [-0.150; -0.128] (Fig. 12), GRSH (Estimate= -0.106; SE= 0.010; p< 0.001; CI= [-0.125; -0.008] (Fig.17), MASH (Estimate= 0.095; SE= 0.022; P<0.001; CI= -0.116; -0.074) (Fig.21), SOSH (Estimate = -0.087; SE= 0.028; p<0.001; CI= [-0.141; -0.033] (Fig.24), WISP (Estimate= -0.127; SE= 0.010; p< 0.001; CI= [-0.146;-0.107]) (Fig.28), LESP (Estimate= -0.100; SE= 0.026; p< 0.001; CI= [-0.150; -0.050]) (Fig.31). GRSH and SOSH were observed in highest abundance in temperature between 13 and 17°C, NOFU in SST between 2 and 15°C. Models showed that LESP were observed in higher number between 8 and 16°C and WISP between 6 and 14°C. COSH density was negatively correlated to SST, but these species was found in higher number between 15 and 22°C (Fig.16).

Table 23: SST range with highest densities by species

Species	Temperature range (°C)
Northern fulmar	2-15
Cory’s shearwater	15-22
Great shearwater	6-16
Manx shearwater	7-17
Sooty shearwater	6-15
Wilson’s storm-petrel	6-14
Leach’s storm-petrel	5-17

Effect of chlorophyll concentration on species density: The variable primary productivity was strongly correlated to GRSH density (Estimate= 0.102; SE= 0.010; P<0.001; CI= [0.083; 0.121]) (Fig.18), MASH (Estimate= 0.096; SE= 0.011; P<0.001; CI= [0.075; 0.117] (Fig.22) and WISP (Estimate= 0.0005; SE= 0.0008; P< 0.001; CI= [0.000; 0.0150]) (Fig. 29).

Effect of SST fronts intensity on species density: GRSH (Estimate= -1.186; SE= 0.021; P< 0.021; CI= [-1.227; -1.145]) (Fig.19) and LESP (Estimate= -0.100; SE= 0.026; P<0.001; CI= -0.150; -0.050]). Both species density was negatively correlated with SST front intensity.

Effect of chlorophyll front intensity on species density: SOSH density was also negatively correlated with intensity of chlorophyll fronts (Estimate= -0.219; SE= 0.066; P<0.001; CI= [-0.348; -0.090]) (Fig.25).

Discussion

I investigated the effect of five environmental covariates on the density of seven Procellariiform species from 2006 to 2009 along the northeast continental shelf of the United States and southeastern Canada. Density of these seabird fluctuated. I suggest some possible underlying conditions. Also, one environmental covariate affected the abundance of all species: sea-surface temperature.

Interannual seabird density variation

Northern fulmar, great shearwater, sooty shearwater and Wilson's storm-petrel mean densities were highest in 2007; whereas Cory's shearwater density increased abruptly in 2009 (Table 3 and 4). Numerous reasons could be proposed to explain interannual density variation; 1) Climate variability strongly influences seabird population dynamics during their breeding period, and during non- breeding periods (Saether et al., 2006); 2) Prey biomass may increase or decrease due to climate regime shifts (Veit et al., 1997, Rose, 2005b); 3) Fish discard may increase local food resources (Phillips et al., 2009); 4) Surveys do not cover the same exact strata and sampling effort survey can differ annually.

1. Climate fluctuation can directly or indirectly influence bird populations. Population size is strongly correlated to climate variation during the non-breeding period. Individual survival rate is being determined by climate patterns (*Tub hypothesis*) and the breeding success is directly related to the weather conditions, influencing recruitment in the population (*Tap hypothesis*). For seabirds, large scale climatic phenomena, including NAO or ENSO are associated to time lags in the population dynamic responses (Jenouvrier et al., 2009; Saether & Engen, 2010).

2. Prey biomass fluctuates with climate regime shifts (Montevecchi & Myers, 1997; Veit et al., 1997). In the Northwest Atlantic, the diet of northern fulmar, great shearwater and sooty shearwater is composed in large proportion of species considered ‘Cold water fish’ species such as Capelin or mackerel (Brown et al., 1981; Phillips et al., 1999; Cherel et al., 2001). Capelin are distributed in northern oceans, in temperatures ranging from -1 to 14°C but spawning sites, migration and feeding areas can shift quickly as a function of water temperature (Rose, 2005b). Atlantic herring or mackerel abundance is also negatively correlated to water temperature (Rose, 2005b). The limiting factors are either temperature or plankton distribution: their principal food resource (Rose, 2005a). Marine Predators need to either find capelin aggregations located northward (Rose, 2005b), or feed on other species available due to the regime shift. Cory’s shearwater density has been increasing abruptly in 2009 along the northeast continental shelf.

This seabird breeds in the Azores and on Mediterranean islands (Granadeiro et al., 1998). Stomach contents analyses collected in 1994 during the breeding period suggested that they feed on small schooling fish such as saury (*Scomberesox saurus*) (5%), trumpet fish (*macrorhamphosus sp.)* (40%), boarfish (*Capros aper*) (46%), horse mackerel (*Trachurus Trachurus*) (5%) (Granadeiro et al., 1998). A similar field study conducted in 2005 showed that adult breeders fed mostly on Blue Jack mackerel (*Trachurus picturatus*) (72%), trumpet fish (15%) and boarfish (9%) (Xavier et al., 2011). There appears to be temporal variation in Cory’s shearwater diet in function of their locations, environmental conditions and fisheries practices (Granadeiro et al., 1998; Paiva et al., 2010). In the meantime, abundance of “warm water” fish species has been increasing in the Northwest Atlantic (Montevecchi & Myers, 1997; Rose, 2005b). Saury abundance has been increasing in southeastern Canadian waters and the Gulf of Maine. Saury overall abundance is poorly known in our study area (Pohle et al., 1992). They are mostly found in temperate to warmer waters in the Atlantic Ocean, and range from Newfoundland to North Carolina. Other species such as boarfishes have been increasing in the Bay of Biscay (From 0.3% in 1973 to 16% in 2000) (Blanchard & Wandermeisch, 2005). Similar observations have been made in the Celtic sea and offshore Galicia more recently (Hussy et al, 2011; O'Donnell et al., 2012). These examples demonstrate how fish community variations might influence seabird densities on regional and range scale. Cory's shearwater may have benefitted of the proliferation of "warm water" fish species in the study area. These birds are highly adapted to feed over "*warmer water species*". It has been demonstrated that some opportunistic seabird species overcome oceanographic changes quicker than others, by adapting their diet to new feeding scenarios. For example, Northern gannet populations have been increasing in the Northwest Atlantic whereas Black-legged kittiwake (*Rissa tridactyla*) breeding productivity was negatively correlated to warmer temperatures (Montevecchi & Myers, 1997; Frederiksen et al., 2007). Sooty shearwater in the California current shifted their distribution due to lack of resources during a warming period (Veit et al., 1997). Wilson's storm-petrels feed on zooplankton. It has been previously demonstrated that the relation between zooplankton/chlorophyll concentration can be rather complex. It has also been suggested that zooplankton was positively correlated to SST, with the result that a warming ocean might be beneficial to some plankton communities (Richardson & Schoeman, 2004). Wilson's storm-petrel density is strongly correlated to crustaceans, while Leach's storm-petrel target primarily small fish. In Newfoundland, Leach's storm-petrel feed on myctophyds (87%), and on crustaceans (amphipods, euphausiids, isopods and copepods) (Hedd et al., 2009). In a study conducted on Wilson's storm-petrel in South Georgia, they fed the chicks with a diet composed at 98% of crustaceans (amphipods, copepods, and euphausiids) and only 1% of myctophids

(Croxall et al., 1988).These difference in diet might explain some of the interannual density fluctuations observed in this study.

3. Fisheries practices influence seabird density on a regional scale (Bartumeus, 2010). Species such as northern fulmar or great shearwater are positively correlated to fish discards (Camphuysen & Garthe, 1997; Valeiras, 2003). Bycaught immature great shearwater numbers have been increasing in the Gulf of Maine (Martin & Shield, unpublished data). Finally, northern fulmar populations have been expanding in the Northwest Atlantic (Stenhouse & Montevecchi, 1999). It has been suggested that their range expansion, and population increase was indeed related to climate variability, in synergy with an increasing amount of fisheries discards (Thompson & Ollason, 2001).

4. The total survey effort has been increasing between 2006 and 2009 (Table 5) but did not cover the same exact sampling areas along the northeast continental shelf. Density differences might also be explained to some extent by variations in survey effort.

Oceanographic variable effect on seabirds

Depth

Oceanic bathymetry affects water circulation, influencing its physical and chemical properties, which enhance productivity and concentrate prey. Physical processes related to shallow, deep, or heterogeneous topography affect fish or zooplankton availability for seabirds. Seabirds are highly correlated to oceanic or continental shelf bathymetric features (Hyrenbach et al, 2000). Northern fulmars were more abundant between -50 and -110 meters. Other studies showed that fulmars were also related to bathymetric features in Eastern Canada but forage over a large range of depths as a function of prey availability (Huttmann & Lock, 1997). Bathymetry also affected density of Cory's shearwater. This species was found in greater abundance over -150 meters. Other previous models showed that Cory's shearwater density was influenced by topography, such as steep bathymetry gradient or continental shelf edge. During their breeding period, Cory's shearwaters forage in oceanic waters around seamounts near the Azores (where the primary productivity is higher), but they were also highly correlated to inshore waters (< 30 m) (Amorim et al., 2009). Cory's shearwater is highly correlated to a combination of oceanographic features, all of which enhanced local productivity (Louzao et al., 2009). Wilson's storm-petrel density was also natively associated with bathymetry, and was observed in greater densities in water less than -150 m. Other studies previously suggested that depth was a predictor of their abundance in the Gulf of Maine and along the northeast continental shelf of the United States (Pittman & Huettmann, 2006; Thorne, 2010).

Sea-surface temperature

All species were affected by SST. The density of Cory's shearwaters along the northeast coast of the United States increased abruptly between 2008 and 2009. It was suggested that this fluctuation might be directly related to the NAO fluctuations (Veit, *pers.comm.*). Density estimates between 1979 and 1988 showed that their abundance was relatively low, but exhibited a sudden increase between 1979 and 1980 (Schneider & Heinemann, 1986). Cory's shearwater might benefit from a warming environment compared to others species (Dias et al., 2010). From 2006 to 2009, 14 Cory's shearwaters fitted with geolocators on Selvagem Grande showed that these birds shifted location from one year to another (South Atlantic to Northwest Atlantic, Western to East Atlantic, Benguala to Alguhlas Currents) (Dias et al., 2010). They also adapt their foraging strategies according to food availability over their post-breeding winter dispersal (Catry et al., 2011). Both Manx shearwater and northern fulmar densities have been increasing along the northeast coast of the United States over the past 50 years (Lee, 1995; Stenhouse & Montevecchi, 1999). Manx shearwater was more abundant in temperatures between 7 and 17°C, a range that can be classified as temperate. They have been also observed between 1975 and 1989 along the southeast continental shelf of the United States in a wide range of water temperature between 7 and 23°C (Lee, 1995). Northern fulmars are considered 'cold water' species (Brown, 1970; Camphuysen & Garthe, 1997; Hatch & Nettleship, 1998; Stenhouse & Montevecchi, 1999) and were more abundant in water between 2 and 17°C (with optimum between 2 and 10°C). If SST continues to increase as predicted along the continental shelf of the northeastern United States, the foraging distribution of this species might be affected (Friedland & Hare, 2007). Great and sooty shearwaters responded similarly to SST: their highest densities were observed between 6 and 17°C. Both species migrate from the Southern Hemisphere, where they breed on Subtropical and Subantarctic Islands. Sooty shearwaters are observed earlier in the Northwest Atlantic than great shearwaters (Hedd et al., 2012), migrating to the Northern hemisphere in early April, to become the most abundant Procellariiform seabird along the northeast coast of North America between May and October (Brown et al., 1975; Brown et al., 1988). Both species share similar diets with a large prey overlap (Brown et al., 1981). My model support previous results demonstrating that great shearwater and sooty shearwater were more likely adapted to forage in a wide range of temperatures (Shaffer et al., 2006; Shaffer et al., 2009; Ronconi et al., 2010; Hedd et al., 2012), but locally, over the northeast continental shelf, their density might decrease with increasing SST. In the California Current, sooty shearwater abundance declined 94 percent during a period of ocean warming between 1987 and 1994 (Veit et al., 1997). Leach’s storm-petrel was found in greater abundance between 5 and 17°C, as well, while Wilson’s storm-petrel was observed in larger numbers between 6 and 14°C. The latter species density was at its lowest between 15 and 22°C. Leach’s storm-petrel breeds from Newfoundland to Massachusetts (North America), while the Wilson’s storm-petrel migrates from and breeds in sub-Antarctic and Antarctic waters (Brown, 1988).

Primary productivity

Great shearwater, Manx shearwater and Wilson’s storm-petrel were highly positively correlated to chlorophyll concentration. Their density was higher over areas rich in chlorophyll. Procellariiform seabirds have an acute sense of smell (Cunningham & Nevitt, 2011) and use their olfactory system on a large scale to locate their prey (Nevitt & Veit, 1999; Pinaud & Weimerskirch, 2007). Procellariiformes are able to detect dimethyl sulfide (DMS), compound related to phytoplankton in productive waters (Grubb, 1972; Nevitt, 1999). Previous studies showed that great shearwaters, Manx shearwaters and Wilson’s storm-petrels forage in highly productive waters (Brown et al., 1981; Stone et al., 1995; Lee, 1995; Begg & Read, 1997; Ronconi et al., 2010; Quillfeldt et al., 2010).

SST and chlorophyll front intensity

Frontal zones and their relationships to seabirds can be rather complex (Spear et al., 2001; Bost et al., 2009). On a large scale, the relationship between seabird abundance and frontal features are more obvious that at a fine scale (Bost et al., 2009). In the study area, several types of fronts were identified, including upwelling zones, estuarine frontal zones, tidal fronts, shelf break fronts, and eddies. Frontal zones generally increase primary productivity, and then enhance food availability. When these fronts become intense, they can also be repulsive to zooplankton and fish because they create strong SST or salinity gradients (Clapp et al., 1982; Olson et al., 1994). Some species are observed closer to upwelling; whereas others will be located further away (Schollaert et al., 2004). Also, the relationship between chlorophyll and thermal fronts is not always coincident (Stegmann & Ullman, 2004; Gould & Arnone, 2004). Some seabird species are highly dependent on frontal features, but respond quite differently to their intensity or biochemical nature (Jahncke et al., 2005; Bost et al., 2009; Thorne, 2010). My model suggested a negative correlation between Leach's storm-petrel and SST frontal intensity along the continental shelf. These seabirds are generally attracted to frontal areas (Veit, 1996; Spear et al., 2001; Niizuma, 2008). Sooty shearwater density was also negatively correlated to chlorophyll front intensity. They were observed in frontal zones, but of lesser intensity. Sooty shearwaters overwinter in the Northern Hemisphere and breed in sub-Antarctic islands. During their migration, they rely on productive oceanographic features to find prey (Shaffer et al., 2006; Raymond et al., 2010; Hedd et al., 2012).

All Procellariiformes seabirds along the continental shelf were largely influenced by the same major factor: SST—but do not respond equally to all of them. Cory's shearwater density increased over 4 years, of the study. The model suggested that they were observed over 15°C; the other species might be more vulnerable to hydrographic changes. This model has also some limitations. Only four years of surveys are included, and more oceanographic variables could have been included to explain seabird density. This model was also data-driven, and suggested trends along the continental shelf of the northeastern United States and southeastern Canada. However, performing these types of models with large numbers of observations could also be valuable to assess specific behavioral response (such as foraging distributional shifts).

Conclusion

In general, the model showed that there are differences between habitat associations among species. This study highlighted the importance of covariates such as SST, chlorophyll concentration, and frontal features on seabird density over the continental shelf. Species such as northern fulmar, great shearwater, Manx shearwater, sooty shearwater, Wilson's storm-petrel, and Leach's storm-petrel are adapted to a large range of SST, but their abundance could decline if fish and zooplankton communities shift from colder to warmer species. Cory's shearwater was negatively correlated to SST over 15°C in the study area. This species might be able to face a changing ecosystem as previously suggested (Dias et al., 2010). The model also showed some limitations, such as relating the highest abundance of seabird to spatial distribution. It was not used for prediction, but as exploratory method. The main purpose of my zero-altered (hurdle) negative binomial GAM model was to show trends in our data and to identify differences in habitat association among species. These models could certainly improve with additional data and explanatory variables. Modeling species-specific habitat associations is required to understand population foraging ecology or distribution changes over time and to predict how seabirds might respond to climatic events and global climate change. Also, from a conservation point of view (Marine Protected Areas creation / habitat prediction for endangered species) or to assess spatial conflicts with offshore wind turbines, physical or biological oceanographic variables (such as wind direction) should be considered. Finally, habitat association models should be related to demographic models, tracking studies, seabird bycatch rates, and other habitat models done in other part of the world, such as the Patagonian shelf or European waters.

-II-

CAN WE CORRELATE ENVIRONMENTAL PREDICTORS AND PRE-SPAWNING ATLANTIC HERRING ABUNDANCE INDEX TO EXPLAIN INTERRANNUAL VARIABILITY OF TOP PREDATOR DENSITY IN GEORGES BANK AND JEFFREYS LEDGE REGIONS IN THE NORTHWEST ATLANTIC?

CHAPTER 2

CAN WE CORRELATE ENVIRONMENTAL PREDICTORS AND PRE-SPAWNING ATLANTIC HERRING ABUNDANCE INDEX TO EXPLAIN INTERANNUAL VARIABILITY OF TOP PREDATOR DENSITY IN GEORGES BANK AND JEFFREYS LEDGE REGIONS OF THE NORTHWEST ATLANTIC?

Abstract: Pre-spawning Atlantic herring (*Clupea harengus*) and marine predators overlap spatially and temporally in the Gulf of Maine every fall. Top predator abundance fluctuates on Georges Bank and Jeffreys Ledge region, which are recognized as historical spawning grounds for a keystone species, the Atlantic herring. I analyzed seabird, cetacean, and tuna observation data and acoustic index collected during four annual hydroacoustic shipboard surveys conducted each fall between 2006 and 2009 to assess pre-spawning assessment stock. I investigated: 1) if environmental covariates had an effect on predator and Atlantic herring density; 2) if herring abundance could explain the interannual variability of top predators in the study area; and 3) if fishing vessel density influenced marine predator density. Habitat association for nine species was modelled, as well as their relation to Atlantic herring acoustic index using a zero-altered negative-binomial fitted with generalized additive model (GAM). My model showed that species responded differently to environmental parameters. Great black-backed gull (*Larus marinus*) and tuna (*Tuna sp*.) did not show statistically significant relationships with the selected variables. Humpback whale (*Megaptera novaeangliae)* and common dolphin (*Delphinus delphis*) were influenced primarily by high primary productivity. Seabirds such as northern fulmar (*Fulmarus* *glacialis*), great shearwater (*Puffinus gravis*), and herring gull (*Larus argentatus*) density were influenced by SST. Northern gannet (*Sula bassana*) density increased in areas of higher herring acoustic index. Finally, using a general linear model (GLM), we found that commercial fishing vessel density affected species such as humpback whale (*Megaptera novaeangliae*), great shearwater *(Puffinus gravis)*, and herring gull (*Larus argentatus*), suggesting overlap with commercial fisheries.

INTRODUCTION

Modeling marine ecosystems can be relatively complex because so many trophic levels have to be considered (Overholtz & Link, 2007; Davoren et al., 2008; Hunsicker et al., 2011). Atlantic herring is a major food resource for many predators such as seabirds, marine mammals, predatory fishes and humans in the Northwest Atlantic (Read & Brownstein, 2003). This keystone species collapsed between 1960 and 1970 due to overfishing (Overholtz, 2006; Overholtz & Link, 2007; Tyrell et al., 2011). Since then, the population has recovered since but ecosystem managers must incorporate other marine predators in future fisheries management and stock assessments (Read & Brownstein, 2003). It has been previously suggested that degree of interaction between aggregated predator and fish stock has been an underestimate (Croxall, 1987). Climatic fluctuations, in addition to overfishing will modify all trophic levels. A rising sea-surface temperature (SST) predicts shifts in the distribution of marine communities (Montevecchi & Myers, 1997; Perry et al., 2005; Jonshon et al., 2011). The northeast continental shelf of the United States has been experiencing a gradual warming with interannual variability these past 50 years. SST increased about 1.08°C from 1957 to 2006 (Belkin, 2009). In addition, the region's ecosystem is influenced by the North Atlantic Oscillation (NAO), which changes phases every 7 to 10 years (Hurrell & Van Loon, 1997; Ottersen et al., 2001). The objective of my study was to understand how environmental variables affect foraging variability by top predators and a major prey species on Georges Bank and Jeffreys Ledge over a period of four years and whether a species such as Atlantic herring could influence the interannual variability of top predator abundance. Our study includes marine predator species in their non-breeding season such as northern fulmar (*Fulmarus glacialis*) (Garthe et al., 2004) and northern gannet (Nettleship et al.,1984), as well as other species preparing to return to their respective breeding grounds, such as great shearwater (*Puffinus gravis*) (Cuthbert, 2005) and humpback whales (Rosenbaum et al., 2009). During this period in the Northern Hemisphere, seabirds are not central-place foragers (Burke & Montevecchi, 2009). Northern gannet, northern fulmar, great black-backed gull (*Larus marinus*) and herring gull (*Larus argentatus*) winter along the northeast continental shelf (Schneider & Heinemann, 1996). Our main objectives were to investigate: 1) if environmental covariates had an effect on predator and pre-spawning Atlantic herring density; 2) if Atlantic herring abundance could explain the interannual variability of top predators in the study area; and 3) if fishing vessel density influenced marine predator density. My models included the most abundant marine predators in the fall: humpback whale (*Megaptera novaangliae*), common dolphin (*Delphinus delphis*), northern gannet (*Sula bassana*), northern fulmar (F*ulmarus glacialis*), great shearwater (*Puffinus gravis*), great black-backed gull (*Larus marinus*), herring gull (*Larus argentatus*), and tuna *(Thunnus thynnus and Thunnus albacores*), as well as Atlantic herring abundance (*Clupea harengus*) and commercial fishing boat density (for 2007, 2008, and 2009).

Atlantic herring (Clupea harengus)

Atlantic herring is a baitfish about 30 to 35 centimeters in length that schools in coastal waters (Nøttestad et al., 1996). *Clupea harengus* range from Labrador to Cape Hatteras, where spawning populations support major commercial fisheries. They perform extensive vertical migrations throughout the water column that could be linked to time of the day, light intensity, water turbidity, tidal currents, food resources and presence of predators (Blaxter, 1985; Axelsen et al., 2001; Haslob et al., 2009). During their pre-spawning period, herring migrate to their breeding ground, where they aggregate deeper in the water column than usual to avoid predation (Maravelias, 2000; Jech & Stroman, 2012). Herring schools swim fast and stop feeding for almost two weeks. At dusk, only small and dense aggregations migrate vertically to the euphotic zone (Jech & Stroman, 2012). Atlantic herring were extremely abundant in waters of the northeast United States and southeastern Canada waters around 1960. They were fished intensively until the stock collapsed in the 1970’s due to overexploitation (Stephenson, 1990). The northwest stock has recovered and is increasing (Read & Brownstein, 2003; Overholtz & Link, 2007). There are concerns about continued fishery management because predators such as seabirds, marine mammals, and piscivorous fish are not completely included in stock assessments (Read & Brownstein, 2003; Tyrrell et al., 2011). Most consumption model on Georges Bank have been considering energy flux, but not direct interactions or spatiotemporal overlap between predators and preys (Croxall, 1987; Overholtz, 2006; Tyrrell et al. 2008; Curry et al., 2011).

MATERIALS AND METHODS

Study area

Top predator data were collected in the Gulf of Maine, along the northeast edge of Georges Bank (41°12′ 36″N; 67°22′51”9W) and Jeffreys Ledge (43°01’66 “N; 70°16’ 66”72’W) (Fig.1). Georges Bank is a 240 kilometer-long submerged extension of the North American continent, and Jeffreys Ledge a 54 kilometer-long shallow glacial deposit (Emery & Uchupi, 1965; Weinrich et al., 2000). Georges Bank is a highly productive system and part of a very long coastal current system that flows south from Labrador to the Mid-Atlantic Bight (Chapman & Beardsley, 1989; Link et al., 2008). Colder water enters the Gulf of Maine from the Scotian Shelf and warmer water comes through the Northeast Channel. Tidal currents turn circularly along the southern flank of the Bank (Pringle & Franks, 2001; Townsend et al., 2004; Johnson et al., 2011). Permanent hydrographic fronts along the southern edge of the Bank separates the shelf from offshore waters (Flagg, 1987). Georges Bank has experienced some of the North Atlantic's largest SST changes related to the North Atlantic Oscillation (NAO) (Gordon et al., 1992). NAO phases partially explain the variability within some fish stocks in the northwest Atlantic (Rogers, 1984; Ottersen et al., 2001; Drinkwater, 2005; Fogarty, 2008; Brander, 2010). Jeffreys Ledge is recognized as critically important area for Atlantic herrings spawning.

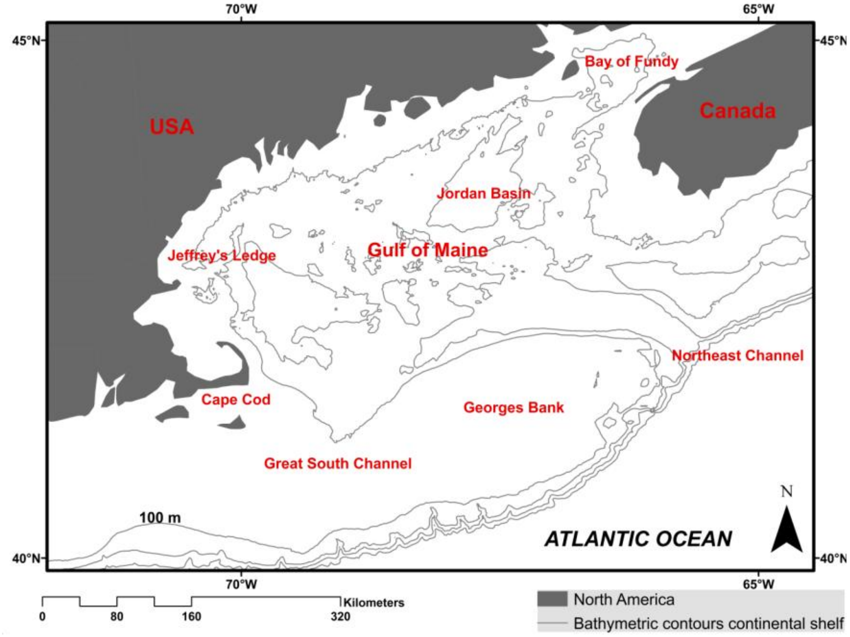


Fig.1: Study area

Data collection: seabird survey protocol

We participated in four shipboard surveys on the National Oceanic and Atmospheric Administration's (NOAA) research vessel *Delaware II* in 2006, 2007, 2008, and 2009. The primary objective of the National Marine Fisheries Service (NMFS) surveys was to make annual assessments of the pre-spawning stock of Atlantic herring. The cumulative area sampled for top-predator was about 8739 square kilometers over 566 effort hours (Table 1). One observer from the flying bridge continuously counted all predators in a 90° zone on one side of the ship using a combination of strip and line transect methods (Camphuysen & Garthe, 2004). All seabirds and other animals were detected in a 300 meters strip-width using distance sampling (Tasker et al., 1984; Hyrenbach et al., 2007; Ronconi & Burger, 2009). Many parameters influence detection probability such as predator behavior, size, weather, sea state, observer experience, and change in density (Barbraud & Thiebot, 2009). All these parameters have been recognized as issues for seabird counts from shipboard platforms (Tasker et al., 1984; Hyrenbach et al., 2007). Coefficient of detection or correction factors might be applied in theory, but evaluating the specific reasons behind detection differences is nearly impossible. All animals entering the observation strip were counted once. Some species are more likely to be attracted by the vessel presence than others and will follow the ship. This behavior pattern is recognized by experienced observers and those individuals identified as 'ship followers' were excluded from our density estimation. Transects were conducted from sunrise to sunset while the ship was moving at about 10 knots. Observers entered data in real time directly onto a laptop computer with the software D-Log2 and D-Log3 (©Glenn Ford Consultant agency). All data were processed using the software ArcView 9.3.1 and 10 (©ESRI). Seabird densities were calculated with the Seabird tool (©USGS- Gilbert A.).

Table 1 : Survey effort summary

Survey name	Survey date	Hours effort	Area sampled km^2
Atlantic herring survey (leg II)	18 to 28 September 2006	101	1160
Atlantic herring survey (leg II)	14 to 25 October 2007	135	1346
Atlantic herring survey (leg I,II,III)	15 to 24 September 2008	180	3361
Atlantic herring survey (leg I,II,III)	21 September to 02 October 2009	150	2872
TOTAL		**566**	**8739**

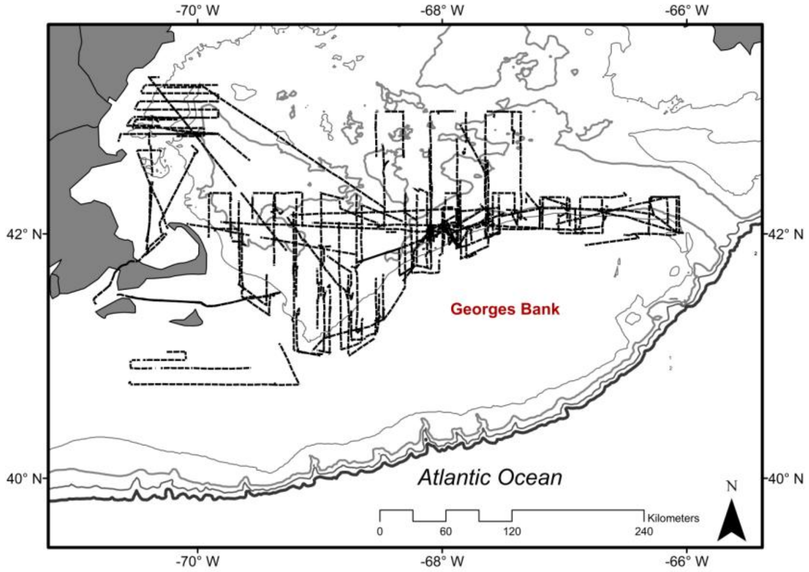


Fig.2. Surveys transects in Georges Bank and Jeffreys Ledge regions

Top predator variables

I focused on the most abundant piscivorous predators on the study area in the fall. Species included were Humpback whale, common dolphin, northern fulmar, great shearwater, great-black backed gull, herring gull and yellowtail and bluefin tuna. Some species demonstrated high density variability from one year to another (Table 3 and 4).

Table 2: species variables

Species	**Common name**	**Scientific name**	**family**
HUWH	humpback whale	*Megaptera novaangliae*	Mysticeti
CODO	common dolphin	*Delphinus delphis*	Delphinidae
NOGA	northern gannet	*Sula bassana*	Sulidae
GRSH	great shearwater	*Puffinus gravis*	Procellariidae
NOFU	Northern fulmar	*Fulmarus glacialis*	Procellariidae
GBBG	Great- black backed gull	*Larus marinus*	Laridae
HERG	Herring gull	*Larus argentatus*	Laridae
TUNA	Yellowtail and bluefin tuna	*Thunnus thynnus & Thunnus albacores*	Scombridae

Table 3: predator count per year (km^2)

Species code	**2006**	**2007**	**2008**	**2009**	**Total**
HUWH	68	10	104	52	234
CODO	140	32	172	132	476
NOGA	4	106	97	479	686
GRSH	2174	2781	4794	5595	15344
NOFU	2	973	12	321	1308
GBBG	588	436	1580	2168	4772
HERG	224	589	1853	1518	4184
TUNA	3	12	14	1163	1192

Table 4: predator density per year (km^2)

Species code	**2006**	**2007**	**2008**	**2009**	**Mean total**
HUWH	0.20	0.02	0.11	0.06	0.10
CODO	0.40	0.08	0.17	0.16	0.20
NOGA	0.01	0.25	0.14	0.60	0.25
GRSH	6.59	7.12	5.20	6.56	6.37
NOFU	0.006	2.55	0.01	0.36	0.73
GBBG	1.75	1.13	1.65	2.29	1.70
HERG	0.68	1.52	1.91	1.86	1.50
TUNA	0.01	0.03	0.01	1.33	0.34

Atlantic herring acoustic index: response variable and covariate

Multi-frequency, 18, 38, and 120 kHz, acoustic data were collected using a SIMRAD EK500 through 2008 and a SIMRAD EK60 from 2009 to present (Jech & Michaels, 2006; Jech & Stroman, 2012). The EK500 and EK60 operated hull-mounted split-beam transducers with beam widths of 10, 12, and 7 degrees for the 18, 38, and 120-kHz echo sounders, respectively. The systems were calibrated using the standard target method (Foote et al., 1987) prior to each survey. Acoustic data were post-processed using Myriax ECHOVIEW© software (v5+). Acoustic echograms were examined for Atlantic herring and total areal backscatter (s_A, NASC, m^2 nm^{-2}) was used to estimate relative areal fish density along survey transects. Because of the large range of s_A (0 to 262 144), we transformed the herring acoustic data index into a ranking system from 0 to 11 (INDEX) (Table 3). Acoustic data were collected continuously but only those data collected from sunrise to sunset concurrent with top-predator data were analyzed.

Table 5: Acoustic signal index interval and transformation ranks

Acoustic signal index interval m^2 nm^{-2}	Index Rank from smallest to highest density
0	0
1-128	1
128- 256	2
256- 512	3
512- 1,024	4
1,024- 2,048	5
2,048- 4,096	6
4,096- 8,192	7
8,192- 16,384	8
16,384- 32,768	9
32,768- 65,536	10
65,536- 262,144	11

Environmental covariates

Seabird occurrence and then density are related to specific oceanographic features that constrain prey distribution (Selzer & Payne, 1988). I examined the effect of five oceanographic variables that influenced the density and behavior of marine prey. SST is considered one of the most important regulators of marine organism distribution, influencing their behavior and limiting their distribution (Pinet, 1992; Montevecchi & Myers, 1997; Drinkwater, 2005). Temperature control chemical reactions, which regulate in turn the development of organisms at the bottom of the trophic ladder. Then, bathymetric features affect water column mixing, and create local conditions that increases primary productivity (presence of fronts or eddies) along bank edges, shelf break or canyons. Shallower waters are generally warmer because of the sunlight penetration and consequently more productive. Seabirds are highly correlated to oceanic or continental shelf bathymetric features (Hyrenbach et al, 2000). Higher chlorophyll concentration is an indicator of biological productivity and attracts marine predators. Seabird Procellariiform feed on higher trophic level organism who feeds directly on phytoplankton (Baduini & Hyrenbach, 2003). Finally, we included both chlorophyll and SST frontal intensity. Chlorophyll and thermal fronts are not always coincident (Stegmann & Ullman, 2004; Gould & Arnone, 2004). Fronts can either increase primary productivity, zooplankton communities and food availability or in contrast can be repulsive to some species due to a strong SST or physico-chemical gradient (Clapp et al., 1982; Olson et al., 1994). Seabirds can respond quite differently behaviorally to the intensity or biochemical nature (Jahncke et al., 2005; Bost et al., 2009; Thorne, 2010). Predictor variables included were: depth (m) (DEPTH), chlorophyll concentration (mg/-m^3) (CHLORO), sea-surface temperature (°C) (SST), intensity of SST fronts (count of fronts detected over a five-day window across a 1.25 x1.25 km spatial window) (INTFRONTSST), intensity of chlorophyll front (count of fronts detected over a 5-day window across a 1.25x1.25 km spatial window) (INTFRONTCHLORO). Fronts, sea-surface temperature and chlorophyll concentration were derived from AHVRR satellite images. Frontal data were extracted using the Marine Geospatial Ecology Tools (MGET), which is an implementation of the single-day Cayulla-Cornillon front algorithm (Ullman, 2000; Roberts et al., 2010). To minimize the effects of cloudiness, we used five-day composites of SST and chlorophyll, representing five day median at a spatial scale of 1.25x1.25 km. Sea-surface temperature was also collected continuously on the vessel using the flow-through system. Depth contours were extracted from General Bathymetric Chart of the Oceans (GEBCO).

Table 6: Environmental variable summary

Variable	Definition	Unit
DEPTH	Depth	m
CHLORO	Chlorophyll concentration	mg/m^3
SST	Sea Surface Temperature	°C
INTFRONTCHLORO	Intensity Chlorophyll fronts	Count of fronts detected over a 5-day window across a 1.25x1.25 km spatial window
INTFRONTSST	Intensity SST fronts	Count of fronts detected over a 5-day window across a 1.25x1.25 km spatial window)

Statistical Modeling

Species density was used as the response variable, and calculated from survey lines segmented at 1 km interval bins. My datasets included a large number of zeroes (Table 8). In ecological studies, datasets are often considered zero-inflated, meaning that these data contains a larger proportion of zeros than expected (Barry & Welsh, 2002). ‘Zero’ abundance is considered a common event in the fisheries (Yee, 2010), bycatch studies (Minami et al., 2007; Gilman et al., 2008; Winter et al., 2011), marine mammal and seabird surveys (Ver Hoef & Jansen, 2007; Peron et al., 2010). Observation of a very high number of seabirds is rare (Clarke et al., 2003). Zero counts are valuable information but excessive number of zeros will create over-dispersion or under-dispersion (Podlich et al., 2002; Yee, 2009). I selected the zero-altered negative binomial distribution, instead of zero-inflated negative binomial distribution used previously (Peron et al., 2010). For the zero-altered negative binomial method aka hurdle, two-step, truncated or delta F, zeros came from a single source, whereas for zero-inflated, three origins are possible: 1) seabirds not detected by observer 2) seabirds not present at the time of observation but habitat is good, and 3) seabirds not seen because the habitat is inappropriate (Zuur et al., 2009). My model includes two steps. In the first step, the presence/ absence was modelled and in the second step, the ‘positive count’ was modelled using a truncated probability distribution (endorsing the role of hurdle for positive values) (Mullahy, 1986; Zuur et al., 2009; Yee, 2010). This method identify that the underlying reasons determining seabird presence can be different from the ones determining the abundance (Potts & Elith, 2006; Heinanen et al., 2008). The negative binomial distribution allows over-dispersion in the positive part of the count data. Finally, a generalized additive model (GAM) was fitted to the hurdle model (Hastie &

Tibshirani, 1986). GAM allows for nonlinear relationships and effects between the response and multiple explanatory variables and use non-parametric regressions to investigate relationships between environmental covariates and response variables such as seabird density (Hastie & Tibshirani, 1986; Wood, 2006; Heinanen et al, 2008). GAM is a method for data exploration or predictive modeling (Wood, 2006). In this study, GAM was used as an exploratory method to examine the relationships between seabird density and environmental covariates. I selected the package VGAM available in the statistical calculation R CRAN program (Yee, 2010; ©R Development Core Team 2011). VGAM computed the maximum likelihood estimates of models and distributions. GAM coefficients were summarized by species. The coefficients statistically significant are presented in **bold**. Smoothing parameters relationships between environmental predictors and seabird abundance were represented using non-parametric regressions. This non parametric regression analysis shows the average value of a response variable (seabird density) as function of a predictor (environmental covariate). Each plot represents the variable response in relation to the probability (natural logarithm of the odds) of the species occurrence in the model. The x-axis is defined by the observed values of the predictor. Values above zero on the y-axis mean that the environmental predictor value have more than average effect on species density. Each mark on the x-axis represents an observation with this value. The solid line is the smoothed response curve. Dashed lines indicate the approximate 95% confidence intervals around the covariate main effects and the degree of freedom (DF= 2). The non-parametric regression uses the vector cubic smoothing spline.

Table 7: Proportion of zero occurrence in dataset

Species code	Proportion 0 (%)
HUWH	99
CODO	99
NOGA	96
GRSH	70
NOFU	93
GBBG	86
HERG	87
TUNA	99

RESULTS

1) EFFECT OF ENVIRONMENTAL PREDICTORS ON SPECIES ABUNDANCE

Model selection

After comparing Akaike Information Criterion (AIC) values for each species, and in between models (zero altered Poisson, zero inflated Poisson, zero altered negative binomial, zero inflated negative binomial, and negative binomial), I kept the zero altered negative binomial. This method demonstrated the lowest AIC scores; however, the zero altered Poisson was the second best fitting method. Both methods: zero altered negative binomial, and zero altered Poisson agreed on the best final fit models. Several environmental covariates might affect densities but only predictors showing statistical significant relationships (p-value < 0.05) were the one selected. Many environmental parameters might affect animal densities but only predictors statistically significant were selected. To rank the most parsimonious model and choose the best explanatory model, we first performed a stepwise regression both sides with data permutation for model variable selection using the MASS package (©R Development Core Team; Venables & Ripley, 2002). We selected the model with the lowest AIC score, and all statically significant variables included ($P < 0.05$) for positive count. For species such as humpback whale and common dolphin: only one model was statistically significant (chlorophyll concentration); for great black-backed gull and tunas, no variables selected were significant. The fittest model selected is presented in **bold.**

Table 8: model selection for HUWH

Model selected	DF	AIC	Log likelihood model
CHLORO	**5**	**2020.837**	**-1005.418**

Table 9: model selection for CODO

Model selected	DF	AIC	Log likelihood model
CHLORO	**5**	**873.200**	**-431.200**

Table 10: model selection for NOGA

Model selected	DF	AIC	Log likelihood model
DEPTH + CHLORO + INDEX	**7**	**5009.152**	**-2576.679**
DEPTH + CHLORO	7	5015.469	-2585.660
INTFRONTCHLORO	5	5022.077	-2595.540

Table 11: model selection for NOFU			
Model selected	DF	AIC	Log likelihood model
DEPTH + SST	**7**	**7242.002**	**-3614.045**
SST	5	7248.647	-3619.320
DEPTH	5	7892.970	-3941.485

Table 12: model selection for GRSH			
Model selected	DF	AIC	Log likelihood model
SST	**5**	**32867.22**	**-16428.610**
CHLORO	5	32875.88	-16432.445
INDEX	5	32916.40	-16453.200

Table 13: model selection for HERG			
Model selected	DF	AIC	Log likelihood model
SST + INTFRONTCHLORO	**7**	**14695.68**	**-7362.930**
SST	7	14706.17	-7348.083
CHLORO + INTFRONTCHLORO	7	14722.62	-7354.311

Table 14: model selection for Atlantic herring			
Model selected	DF	AIC	Log likelihood model
DEPTH + CHLORO + INTFRONTSST	**7**	**22943.77**	**-11462.89**
DEPTH + CHLORO	7	22978.63	-11482.32
CHLORO + INTFRONTSST	7	23030.84	-11508.42

Model validation

I evaluated the performance of each model using k-fold cross validation (Li et al., 2011) (Table 16). Cross validation addresses over-fitting problems. When Over fitting happen, the model includes either more variables than required or not enough of them (Zuur, 2009). The dataset was divided into *k* equal-size subsets and the cross validation repeated 10 times (*k*= 10) (Wenger & Olden, 2012). One of the k subsets was used as a "test" dataset, while the other *k*-1 datasets were used for "training" purposes. The mean square error (MSE) between the "training" and "test" datasets were computed. Finally, best fit models were selected based on the lowest AIC score and difference between the "training" and "test" mean square error.

Table 15: Training and errors MSE from the zero altered negative binomial model K fold cross - validation

Species	Fit Model	Model	AIC	Log model likelihood	Training error MSE	Test error MSE
HUWH	**1**	**CHLORO**	**2020.83**	**-1005.41**	**31.48**	**32.25**
CODO	**1**	**CHLORO**	**873.20**	**-431.20**	**19.23**	**19.25**
NOGA	1	**DEPTH + CHLORO + INDEX**	**5009.15**	**-2576.67**	**3.65**	**3.65**
	2	DEPTH + CHLORO	5015.46	-2585.66	3.65	3.65
	3	INTFRONTCHLORO	5022.07	-2595.54	3.66	3.66
NOFU	1	**DEPTH + SST**	**7242.00**	**-3614.04**	**15.42**	**15.40**
	2	SST	7248.64	-3619.32	15.42	15.39
	3	DEPTH	7892.97	-3941.48	16.16	16.15
GRSH	1	**SST**	**32867.22**	**-16428.61**	**978.92**	**977.92**
	2	CHLORO	32875.88	-16432.44	982.41	979.83
	3	INDEX	32916.40	-16453.20	979.89	979.02
HERG	1	**SST + INTFRONTCHLORO**	**14695.68**	**-7362.93**	**311.76**	**311.48**
	2	SST	14706.17	-7348.08	311.87	311.57
	3	CHLORO + INTFRONTCHLORO	14722.62	-7354.62	337.31	347.05
HERRING	1	**SST + INTFRONTSST**	**22943.77**	**-11462.89**	**1004.08**	**1004.08**
	2	SST	22978.63	-11482.32	1004.21	1004.22
	3	DEPTH + INTFRONTSST	23030.84	-11508.42	1003.36	1003.38

Humpback whale (HUWH)

Humpback whale density mean was the highest in 2006 (Fig.3). The model the most parsimonious was CHLORO (AIC= 2020.837) (Table 16). Humpback whales density was positively correlated with chlorophyll concentration (Estimate = 0.027; SE= 0.013; p< 0.05; CI= [0.025; 0.052]) (Fig.4).

Table 16: Parameter estimates for HUWH (log likelihood: -1005.418; DF=5)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-4.341	0.108	**<0.001**	-4.552	-4.130
CHLORO	0.061	0.025	**<0.05**	-0.037	0.159
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	1.800	0.066	**<0.001**	1.671	1.929
CHLORO	0.027	0.013	**<0.05**	0.025	0.052

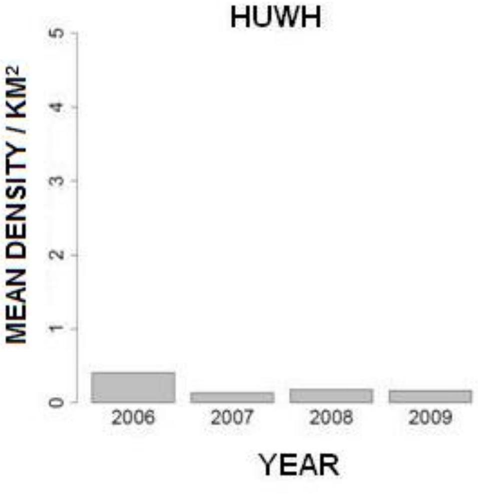


Fig.3. Humpback whale mean density/km² over 4 years.

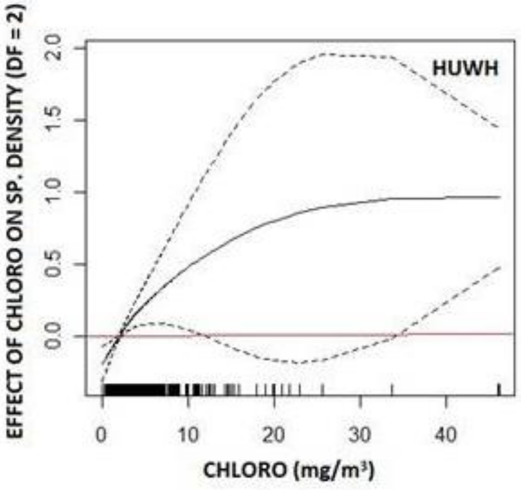


Fig.4. Effect of covariate chlorophyll concentration on humpback whale density.

Common dolphin (CODO) Common dolphin density was also the highest in 2006 (Fig.5). The model the most parsimonious was CHLORO (AIC=873.200) (Table 17). CODO density was positively correlated with chlorophyll concentration (Estimate = -0.349; SE= 0.120; P< 0.005; CI= [-0.584; -0.114]) (Fig.6).

Table 17: Parameter estimates for CODO (log likelihood: -431.600; DF=5)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-5.566	0.186	<0.001	-5.930	-5.202
CHLORO	0.071	0.037	**>0.05**	-0.001	-0.143
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	4.570	0.353	<0.001	3.979	5.261
CHLORO	-0.349	0.120	**<0.005**	-0.584	-0.114

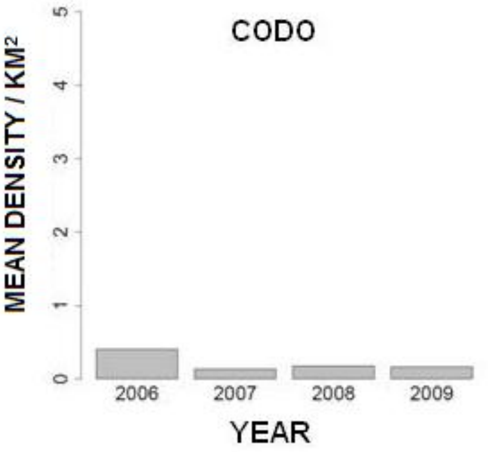


Fig.5. Common dolphin mean density / km² over 4 years.

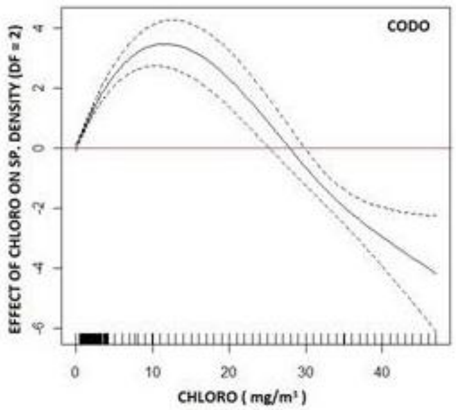


Fig.6. Effect of covariate chlorophyll concentration on common dolphin density.

Northern gannet (NOGA): Northern gannet density increased in 2007 and 2009 (Fig.7). The most parsimonious model was DEPTH + CHLORO+ INDEX (AIC=5009.152) (Table 18). NOGA density was negatively correlated with shallower depth, but positively correlated with depth between -150 and -200 m (Estimate = -0.002; SE=0.001; p<0.05; [CI= -0.003; -0.001]) (Fig.8). NOGA density was positively correlated with higher chlorophyll concentration (Estimate= 0.072; SE= 0.032; P< 0.05; CI= [0.010; 0.134] (Fig.9). Finally, the species abundance was positively correlated with Atlantic herring index ranks (Estimate = 0.048; SE= 0.028; p< 0.05; [CI= 0.003; 0.093] (Fig.10).

Table 18: Parameter estimates for NOGA (log likelihood: -2576.67; DF=7)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-3.107	0.220	<0.001	-3.538	-2.676
DEPTH	0.001	0.001	**>0.05**	0.000	0.002
CHLORO	0.098	0.018	**<0.001**	0.063	0.133
INDEX	0.064	0.027	**<0.05**	0.012	0.116
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	1.094	0.274	**<0.001**	0.557	1.631
DEPTH	-0.002	0.001	**<0.05**	-0.003	-0.001
CHLORO	0.072	0.032	**<0.05**	0.010	0.134
INDEX	0.048	0.023	**<0.05**	0.003	0.093

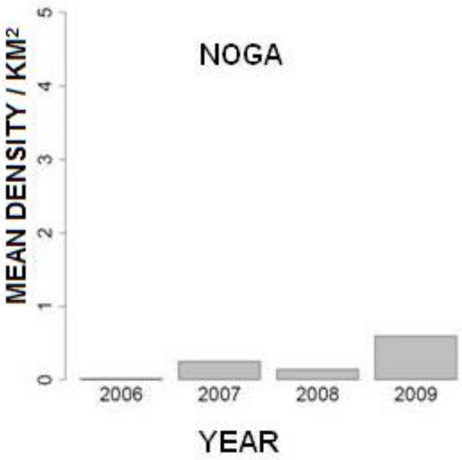


Fig.7. Northern gannet mean density / km^2 over 4 years.

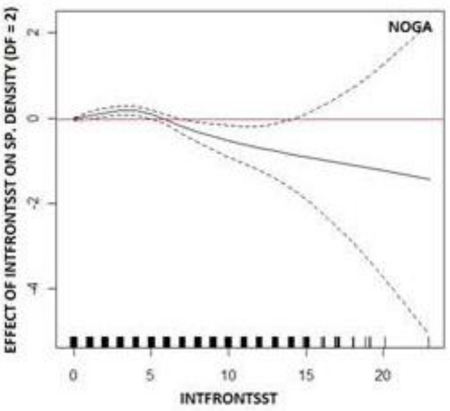


Fig.8. Effect of covariate SST front intensity on northern gannet density.

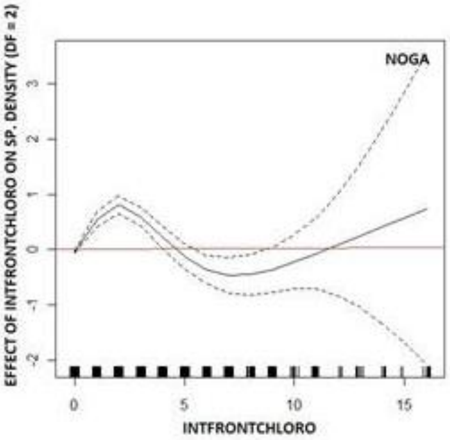


Fig.9. Effect of covariate chlorophyll front intensity on northern gannet density.

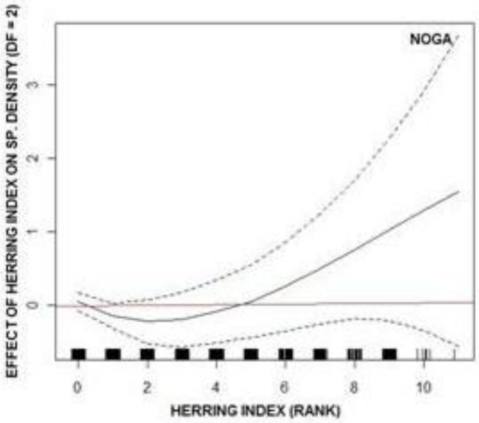


Fig.10. Effect of covariate herring index on northern gannet density.

Northern fulmar (NOFU): Northern fulmars were most abundant in 2007 and 2009 (Fig.8). The following model was selected: DEPTH + SST (AIC= 7242.089) (Table 19). NOFU was positively correlated with bathymetry. The species density was the highest between -130 and -220 meters (Estimate = 0.003; SE= 0.001; $p< 0.05$; CI= [0.002; 0.004]) (Fig. 12). Species density was negatively correlated with SST (Estimate = -0.145; SE= 0.033; $p<0.001$; CI= [-0.209; -0.081) (Fig.13).

Table 19: Parameter estimates for NOFU (log likelihood: -3614.045; DF=7)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	9.019	0.568	**<0.001**	7.909	10.129
DEPTH	-0.002	0.001	**<0.05**	-0.003	-0.001
SST	-0.801	0.036	**<0.001**	-0.871	-0.731
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	4.617	0.571	**<0.001**	3.498	5.736
DEPTH	0.003	0.001	**<0.05**	0.002	0.004
SST	-0.145	0.033	**<0.001**	-0.209	-0.081

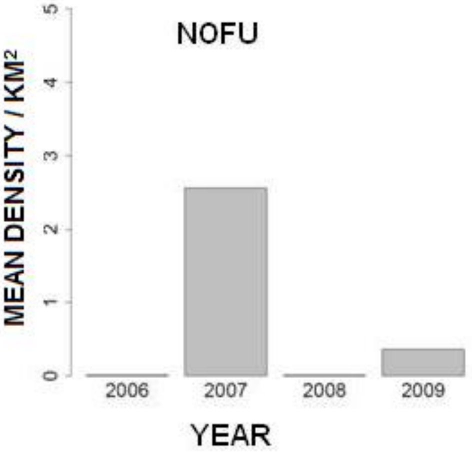


Fig.11. Northern fulmar mean density / km^2 over 4 years.

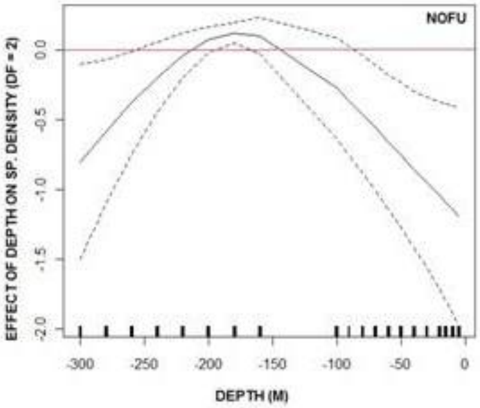


Fig.12. Effect of covariate depth on northern fulmar density.

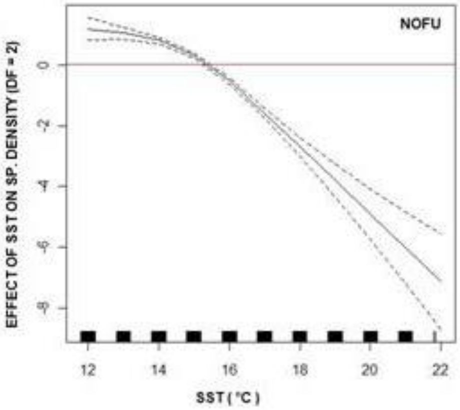


Fig.13. Effect of covariate SST on northern fulmar density.

Great shearwater (GRSH): Great shearwater density remained stable over the study area (Fig.14). The model selected was SST (AIC=32867.22) (Table 20). Their density was negatively correlated with SST. Great shearwater was found in greatest number between 13 and 17°C in the study area (Estimate = -0.046; SE= 0.022; P<0.001; CI= [-0.089; -0.003]) (Fig.15).

Table 20: Parameter estimates for GRSH (log likelihood: -16428.61; DF=5)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	1.125	0.231	**<0.001**	0.673	1.577
SST	-0.116	0.014	**<0.001**	-0.143	-0.089

Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	3.368	0.356	**<0.001**	0.673	1.577
SST	-0.046	0.022	**<0.001**	-0.089	-0.003

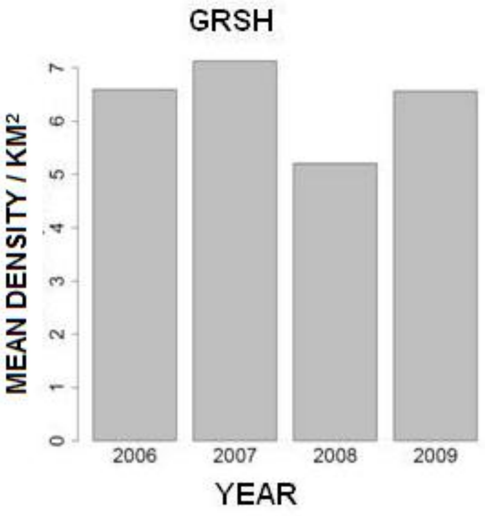


Fig.14. Great shearwater mean density / km^2 over 4 years.

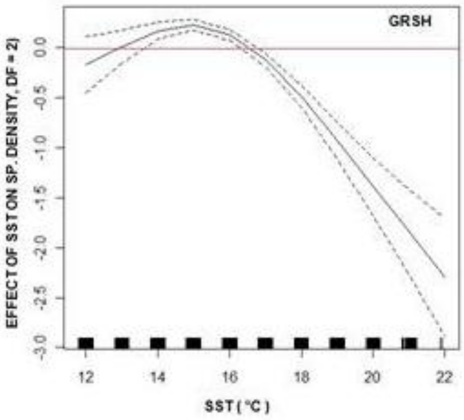


Fig.15. Effect of covariate SST on great shearwater density.

Great black-backed gull (GBBG)

Great black-backed gull density increased over the four surveys in the study area (Fig.16). No model was statistically significant.

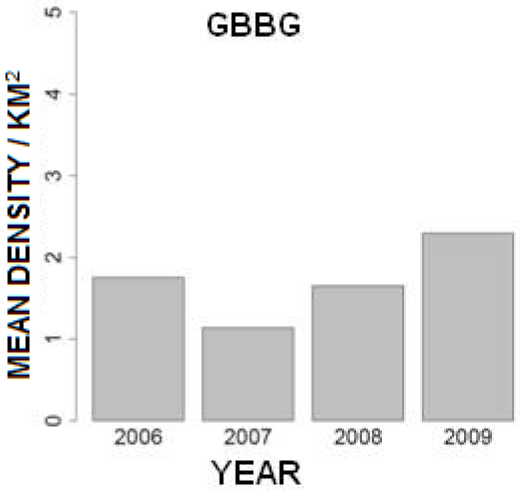


Fig.16. Great black-backed gull mean density / km^2 over 4 years.

Herring gull (HERG)

Herring gull density increased over the four surveys (Fig.17). The most parsimonious model was SST + INTFRONTCHLORO (AIC=14695.68) (Table 21). Herring gull density was negatively correlated with SST (Estimate= -0.078; SE= 0.028; P< 0.005; CI= [-0.132; -0.024]) (Fig.18). HERG density was negatively correlated with chlorophyll front intensity; this species was more abundant in area of lesser frontal intensity (Estimate = -0.078; SE= 0.028; p< 0.005; CI= [-0.132; -0.024] (Fig.19).

Table 21: Parameter estimates for HERG (log likelihood: -7362.93; DF=7)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-1.847	0.032	**<0.001**	-1.909	-1.785
SST	0.122	0.022	**<0.001**	0.079	0.165
INTFRONTCHLORO	-0.080	0.022	**<0.001**	-0.123	-0.037
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	3.508	0.446	**<0.001**	2.634	4.382
SST	-0.078	0.028	**<0.005**	-0.132	-0.024
INTFRONTCHLORO	-0.094	0.033	**<0.005**	-0.158	-0.030

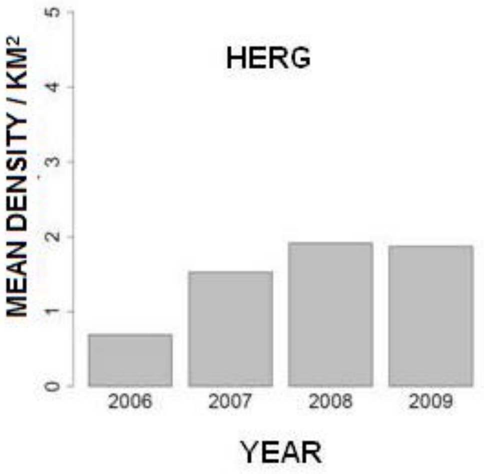


Fig.17. Herring gull mean density / km^2 over 4 years.

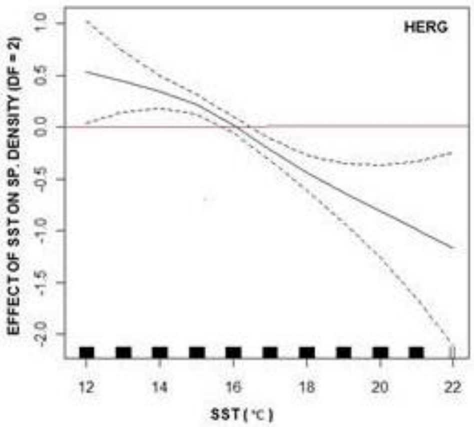


Fig.18. Effect of covariate SST on herring gull density.

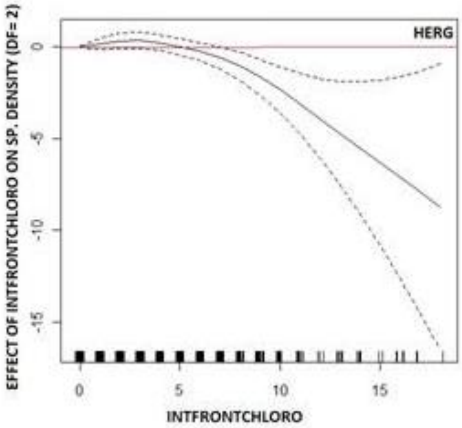


Fig.19. Effect of covariate chlorophyll front intensity on herring gull density.

Tuna

Tuna density increased abruptly in 2009 (Fig.20). No models found statistically significant.

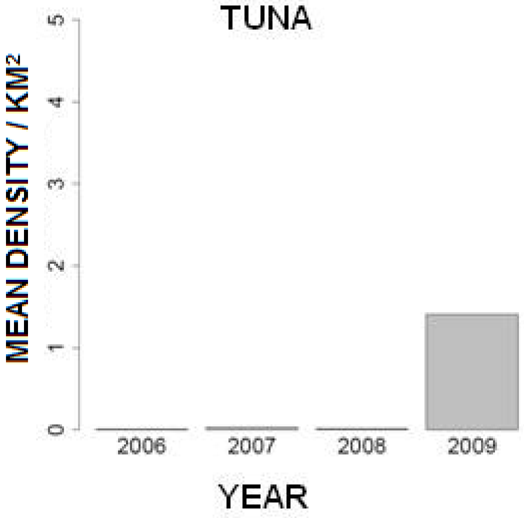


Fig.20. Tuna mean density / km^2 over 4 years.

Atlantic herring (HERRING)

The most parsimonious model was DEPTH + CHLORO + INTFRONTSST (AIC= 22943.77) (Table 22). Atlantic herring density was higher in depths between -120 and -200 meters with a peak at -150 meters (Fig.21) (Estimate= -0.005; SE= 0.0008; P< 0.001; CI= [-0.065; -0.0035]. The model suggested that Atlantic herring index was positively correlated with primary productivity (Estimate= -027; SE= 0.0013; p< 0.005; CI= [-0.052; -0.002] (Fig.22). Atlantic herring density was negatively correlated with SST frontal intensity (Estimate= -2.069; SE= 0.395; P< 0.01; CI= [-2.839; -1.299]) (Fig.23).

Table 22: Parameter estimates for HERRING (log likelihood: -11462.89; DF=7)

Step 1: Zero hurdle model coefficient					
parameter	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	0.737	0.102	**<0.001**	0.538	0.936
DEPTH	0.003	0.0004	**<0.001**	-0.002	0.008
CHLORO	-0.255	0.019	**<0.001**	-0.292	-0.218
INTFRONTSST	0.0002	0.008	**>0.05**	-0.014	0.0152
Step 2: Count model coefficient (truncated with negative binomial)					
	Estimate	Std Error	P value	Lower CI	Upper CI
intercept	-2.004	0.398	**<0.001**	-2.784	-1.224
DEPTH	-0.005	0.0008	**<0.001**	-0.065	-0.0035
CHLORO	-0.027	0.013	**<0.005**	-0.052	-0.002
INTFRONTSST	-2.069	0.013	**<0.005**	-0.052	-0.002

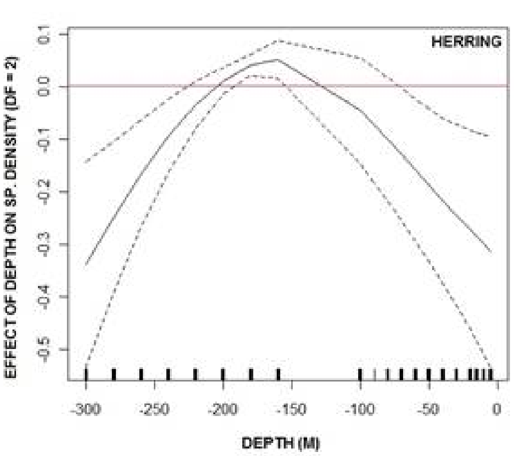


Fig.21. Effect of covariate depth on Atlantic herring index.

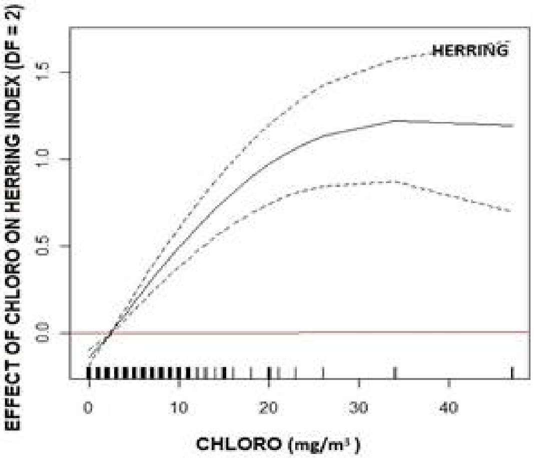


Fig.22. Effect of covariate chlorophyll concentration on Atlantic herring index.

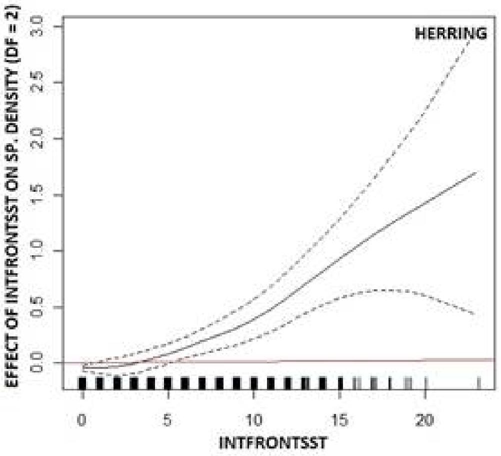


Fig.23. Effect of covariate SST front intensity on Atlantic herring index.

Environmental variables effect on species density summary

Effect of depth on species density: Depth affected NOGA density (Estimate= -0.002; SE= 0.001; $P<0.05$; CI= [-0.003; -0.001]) (Fig.8), NOFU (Estimate= 0.003; SE= 0.001; $P< 0.001$; CI= [0.002; 0.004]) (Fig.12) and Atlantic herring (Estimate= -0.005; SE= 0.0008; $P< 0.001$; CI= [-0.065; -0.0035]) (Fig.21). NOGA density was negatively correlated with bathymetry, but their density was higher between -150 and -200 m. NOFU were found more abundant between – 140 m and – 220 m. Finally Atlantic herring was also found more abundant in depth between -125 m and – 200 m (with highest ranks about - 160 m).

Effect of SST on species density: SST was negatively correlated with NOFU density (Estimate= -0.145; SE= 0.033; $P<0.001$; CI= [-0.209; -0.081]) (Fig.13), GRSH density (Estimate= -0.046; SE= 0.022; $P< 0.001$; CI= [-0.089; -0.003] (Fig.15) and HERG (Estimate= -0.078; SE= 0.028; $P< 0.005$; CI= [-0.132; -0.024] (Fig.18).

Effect of chlorophyll concentration on species density: HUWH density (Estimate= 0.027; SE= 0.013; $P<0.05$; CI= [0.025; 0.052]) (Fig.4) and CODO density (Estimate= -0.349; SE= 0.120; $P< 0.005$; CI= [-0.584; -0.114]) (Fig.6) were negatively correlated to primary productivity, NOGA (Estimate= 0.072; SE= 0.032; $P< 0.05$; CI= 0.010; 0.134])(Fig.9) and Atlantic herring (Estimate= -0.027; SE= 0.013; $P< 0.005$; CI= [-0.052; -0.002]) (Fig.22) were positively correlated with chlorophyll concentration.

Effect of frontal feature intensity on species density: Atlantic herring density was positively correlated with SST frontal activity (Estimate= -2.069; SE= 0.395; P<0.001; CI= [-2.839; -1.299]) (Fig.23). Herring gull density was negatively correlated with chlorophyll front intensity (Estimate= -0.094; SE= 0.033; P< 0.005; CI= [-0.158; -0.030] (Fig.19).

Effect of Atlantic herring index rank on species density: The model suggested that this predictor had an effect on two species. NOGA density was positively correlated with Atlantic herring ranks ((Estimate NB= 0.025; SE= 0.024; p> 0.05; [CI= -0.022; 0.072] (Fig. 10)

2) EFFECT OF FISHING BOAT DENSITY ON SPECIES ABUNDANCE

Commercial fishing vessels were also counted during our surveys in 2007 (Fig. 60), 2008 (Fig.61), and 2009 (Fig.62). However, we were unable to collect data on their precise fishing activities. Their density increased over 3 years (Fig.24). Separate models using a zero- altered negative binomial general linear model (GLM) were performed for these three consecutive years to examine commercial fishing boat density on species abundance along with environmental parameters. We showed that the fishing vessel density increased over three years in the study area (Fig.23). Fishing boat density was positively correlated with humpback whale density (Estimate= 0.643; SE=0.086; P<0.001; CI= [0.475; 0.811]) (Fig.25), great shearwater (Estimate= 0.137; SE= 0.048; P< 0.005; CI= [0.043; 0.231]) (Fig.26) and herring gull (Estimate= 0.198; SE= 0.043; P< 0.001; CI= [0.114; 0.282]) (Fig.27). All these species were observed in higher number around fishing boats. The GLM statistical coefficients for the step 2 of the model (estimate negative binomial) are summarized (Table 23). The statistical significant results are presented in **bold**.

Table 23: Parameter estimate negative binomial for fishing boat density effect on species density (tuna not included)
Step 2 GLM zero- altered NB – Positive Count model

species	Parameter	Log-likelihood model	DF	Estimate	Std. Error	p-value	Lower CI	Upper CI
HUWH	intercept	**-736.500**	5	-4.363	0.103	<0.001	-4.564	-4.162
	fishing boat			**0.643**	**0.086**	**<0.001**	**0.475**	**0.811**
CODO	intercept	-316.246	5	-5.595	0.190	>0.05	-5.967	-5.223
	fishing boat			-0.025	0.236	>0.05	-0.487	0.437
NOGA	intercept	-2443.89	5	1.870	0.056	>0.05	1.761	1.979
	fishing boat			-0.084	0.081	>0.05	-0.242	0.074
NOFU	intercept	-3780.69	5	2.003	0.034	<0.001	1.937	2.069
	fishing boat			0.111	0.052	>0.05	0.010	0.212
GRSH	intercept	**-13974.8**	5	2.604	0.041	<0.001	2.524	2.684
	fishing boat			**0.137**	**0.048**	**<0.005**	**0.043**	**0.231**
GBBG	intercept	-6992.60	5	2.130	0.062	<0.001	2.050	2.210
	fishing boat			0.081	0.045	>0.05	-0.007	0.169
HERG	intercept	**-6780.8**	5	2.229	0.053	<0.001	2.126	2.332
	fishing boat			**0.198**	**0.043**	**<0.001**	**0.114**	**0.282**

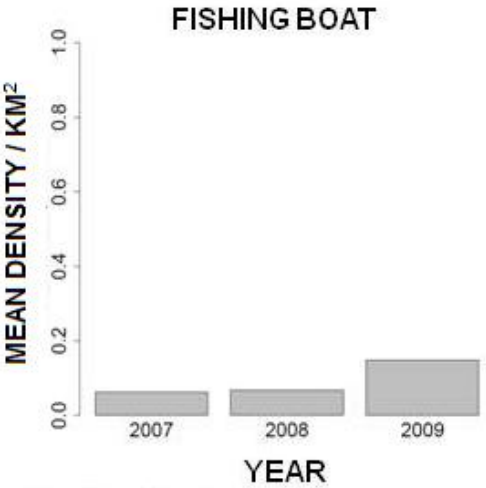


Fig.24. Fishing boat mean density / km^2 over 3 years.

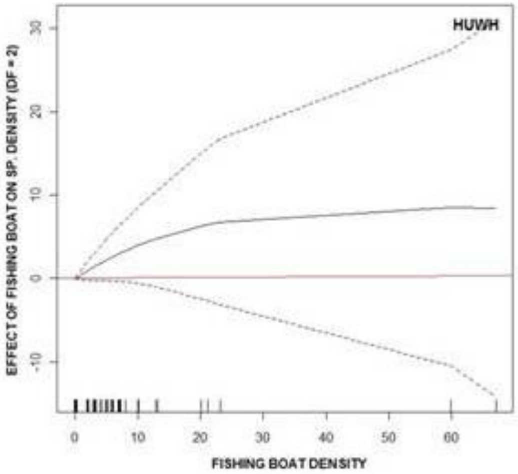


Fig.25. Effect of fishing boat density on humpback whale density.

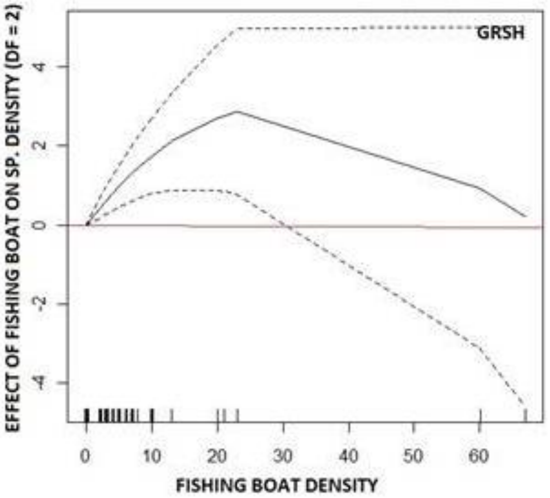


Fig.26. Effect of fishing boat density on great shearwater density.

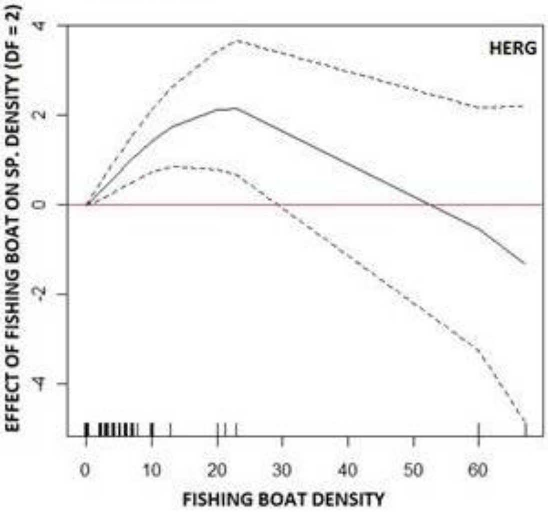


Fig.27. Effect of fishing boat density on herring gull density.

DISCUSSION

The objective of this study was to determine if we could correlate environmental predictors and pre-spawning Atlantic herring (*Clupea harengus*) abundance to explain interannual variability of top predator density in the Georges Bank and Jeffreys Ledge regions of the Northwest Atlantic. Using a negative binomial zero-altered GAM, we showed that both environmental parameters and Atlantic herring index do influence the interannual variability of top predators on Georges Bank and Jeffreys Ledge.

SST

Marine animals forage on preys directly influenced by environmental conditions such as fish, squid or zooplankton (Grubb, 1972). Our models suggested that northern fulmar, great shearwater and herring gulls were influenced by SST. Previous studies suggested that fulmar density decreased with increasing temperature. Northern fulmar is associated with colder waters (Brown, 1970; Camphuysen & Garthe, 1997; Stenhouse & Montevecchi, 1999). If SST continues to increase as predicted along the northeast continental shelf, the foraging distribution of these species might be affected on a longer term. Herring gull density was negatively correlated with SST. Correlation between their abundance and SST in the Gulf of Maine has been previously shown using only presence data models (Pittman & Huettmann, 2006). Herring gull population has been decreasing, and indirect SST effect on breeding populations has been measured as well (Massaro et al., 2000; Rome & Ellis, 2004). In Newfoundland, between 1998 and 1999, Capelin (*Mallotus villosus*) arrived late due to changes in hydrographic conditions. Herring gulls predated more juvenile kittiwake (*Rissa tridactyla*) during these two years (Massaro et al., 2000).

Hydrographic features influence on gulls foraging ecology in the open ocean is still poorly understood (Skov & Durinck, 2001), and more is actually known about how these birds are attracted to fishery offal and fishing vessels (Camphuysen,1995; Garthe et al, 1996). Great shearwaters are the most abundant Procellariiform seabird between May and October along the northeast coast of North America (Brown et al., 1975; Brown et al., 1988). In the fall, great shearwaters are ready to migrate to their colonies in the Southern Hemisphere. Our model supports previous results demonstrating that great shearwater were more likely adapted to forage in a wide temperature range (Ronconi et al., 2010) but locally, over the northeast continental shelf, their density is negatively correlated with SST.

Bathymetry

Depth affected northern gannet, northern fulmars and Atlantic herring. Northern gannet density was negatively correlated with bathymetry. This species was observed in higher number between -140 m and -200 m. Previous studies showed that gannets concentrated their fishing activity around bathymetric features increasing primary production (Hamer et al., 2000). Northern fulmar density was the highest in depth between -140 and – 220 m. Other studies showed that fulmars were also related to bathymetric features in Eastern Canada but forage over a large range of depths in function of availability of preys (Huttmann & Lock, 1997). Atlantic herring was found in higher density between -125 and -200 m, with a peak at -150 m. The pre-spawning aggregation remains between -100 to -200 m deep (Maravelias et al., 2000; Jech & Michaels, 2006).

Chlorophyll concentration

The relation between top predators and chlorophyll concentration is considered indirect; they do not eat phytoplankton but consume animals who feed on phytoplankton (Baduini & Hyrenbach, 2003). Chlorophyll concentration affected humpback whale, common dolphin, northern gannet densities, and Atlantic herring index. All these species were positively correlated with primary productivity. Northern gannets are attracted to areas of high chlorophyll concentration, and shift of foraging locations in relation to productivity (Garthe et al, 2007; Montevecchi et al, 2009; Votier et al., 2010; Grecian et al., 2011). Since northern gannet density increased over the four surveys years, we suggest that Georges Bank and Jeffreys Ledge represent an important future foraging destination for this species. Other studies previously showed that cetaceans were positively correlated to chlorophyll *a* level. Previous models suggested that humpback whale and common dolphin density were strongly correlated to primary productivity (MacLeod et al., 2007; Rosa, 2010; Visser et al. 2011; Rosa et al., 2012). *Clupea harengus* was more abundant in areas rich in chlorophyll *a*, results that are supported by previous studies (Vikebø et al., 2012). Pre-spawning herring swim in dense schools in deeper waters without feeding for almost two weeks. Low visibility, swimming deeper in the water column, and schooling aid in predator avoidance (Maravelias et al., 2000; Axelsen et al., 2001). If herring stay in high-productivity surface waters at the edge of the bank, it helps confuse predators. Another explanation is that spawning adult herring need to feed quickly in order to recover after spawning. They migrate again vertically, feeding in smaller and denser schools to avoid intense predation from surface feeders (Fauchald, 2009). Finding them in areas rich in chlorophyll concentration might be explained by several survival processes for mature adults, as well as larvae development (Sinclair & Tremblay, 1984).

Frontal features

Frontal zones and their relation to seabirds and other marine predators are indeed a complex one (Bost et al., 2009). Fronts can either increase primary productivity, zooplankton communities and food availability, or on contrary, can be lethal or repulsive to some species by presenting a strong SST or saline gradient (Olson et al., 1994). Several types of fronts have been identified: upwelling zones, estuarine frontal zones, tidal fronts, shelf break fronts and eddies, are a few. This study did not take into account the physical properties of fronts. Many questions regarding the biological response to fronts still need to be answered (Olson, 1994; Schneider, 1982). Oceanographers are trying to determine if the Gulf Stream plays the role of barrier, or exchange zone (Bower et al., 1985; Schollaert et al., 2004), or the relationship between chlorophyll and thermal fronts, since they are not always coincident (Stegmann & Ullman, 2004). On a large scale, relationship between seabird abundance and frontal features is more obvious than at a fine scale (Bost et al., 2009). The model suggested that herring gull density was negatively correlated to chlorophyll front intensity. They were found in larger number in areas of lesser frontal activity. Gulls might be correlated to tidal fronts around Georges Bank and Jeffreys Ledge regions, since these areas are relatively shallow, with heterogeneous bathymetry creating water mixing that enhance primary productivity (Garthe, 1997; Hunt et al, 1999). Atlantic herrings are positively correlated with SST frontal features. My model support previous studies (Misund et al., 1997; Lacoste et al., 2001). Vertical mixing along frontal areas might assist larvae development. Circular water movement such as those in gyres or caused by tidal currents will retain herring larvae in ideal conditions. Moreover, adults can also feed in these areas before or after the pre-spawning period (Stewart & Arnold, 1994).

Atlantic herring

Georges Bank and Jeffreys Ledge are historical spawning grounds for Atlantic herring (Read & Brownstein, 2003; Overholtz & Link, 2007). Atlantic herring index ranked from 0 to 11 represents the biomass acoustic density from 1 to 262 144 m^2/nm. *Clupea harengus* stop feeding at the end of August and aggregate in dense, fast-swimming schools (Lazzari & Stevenson, 1992; Fauchald, 2009). Pre-spawning schools remain between -100 and -200 meters deep in the water column to avoid surface predation (Maravelias et al., 2000; Jech & Stroman, 2012). The model suggested that northern gannet density was positively correlated with Atlantic herring index. *Clupea harengus* compose one of the largest diet proportions of northern gannet in the Northwest Atlantic (Montevecchi & Myers, 1987; Overholtz & Link, 2007; Garthe et al. 2007). Northern gannets are considered 'visual foragers' and do not feed nocturnally (Garthe et al, 1999; Mallory et al., 2009). They are also generalist and opportunist, traveling where resources are predictable (Montevecchi et al., 2009; Pettex et al., 2010), and their population and distribution have been increasing since 1900 in the Northwest Atlantic (Montevecchi & Myers, 1997). The model suggested that northern gannet density increased with index rank between 5 and 11. When these seabirds spot large prey aggregations, they can plunge dive up to -24 meters directly over the school; one of the dominant preys along their range is *Clupea harengus* (Montevecchi & Myers, 1997; Garthe et al., 1999; Brierley & Fernandez, 2001). In order to capture their prey, gannets can surface dive, plunge-dive and pursuit-dive (Ropert-Coudert et al., 2008). When plunge-diving, they do gain momentum, can propel themselves underwater using their wings and extend their diving time. If these seabirds dive from 40 meters for example, they can reach up to -24 m by swimming underwater. Consequently, they are certainly more efficient over fish schools than other seabirds. If fish aggregations surface in the first 10 meters or over shallower banks, northern gannets are probably able to spot them and plunge-dive immediately. Atlantic herring represent a large part of the diet of great shearwaters in the Northwest Atlantic as well (Brown,1981; Montevecchi, 2009; Davoren et al., 2010). This shearwater can dive up to 18 meters by pursuit diving; meaning that the offshore pre-spawning Atlantic herrings are not directly accessible to this species (Ronconi et al., 2010). Northern fulmars and herring gulls are only superficial divers (Hobson & Welsh, 1991; Garthe & Furness, 2001). There are three possibilities for how these predators might be obtaining food resources: 1) Cetaceans, tunas, or fishing boats could help to access food sources by pushing fish to the surface (Evans, 1982; Hudson & Furness, 1988; Hebshi et al., 2008); 2) Seabirds are feeding on other available prey since herring are schooling in deep waters with a euphotic zone rich in chlorophyll, and around frontal zones; 3) A small number of Atlantic herring migrate vertically at night to reach the euphotic zone (Jech & Stroman, 2012).

Effect of commercial fishing vessels

The model suggested humpback whale, great shearwater and herring gull densities were positively correlated with fishing boat density in the 2007, 2008 and 2009 surveys. These results suggested spatio-temporal overlap with commercial fishing vessels. Other studies have previously showed overlap between whales and fish spawning locations using real time data (Piatt et al., 1989; Nøttestad et al., 2002). Great shearwaters and herring gulls are opportunistic feeders, which are also found in higher density around fishing fleets (Garthe, 1997; Tuck et al., 2011). Great shearwater is also abundantly bycaught in many parts of the Atlantic Ocean (Tuck et al., 2011), and is today under monitoring.

This study suggested that interannual variability of seabirds, marine mammals and Atlantic herring might be possibly explained by oceanographic features such as SST, bathymetry, primary productivity, chlorophyll and thermal frontal zones. Atlantic herring index, in synergy with environmental parameters influenced northern gannet in Georges Bank and Jeffreys Ledge regions. Also, future studies should include other fish or zooplankton acoustic index since Atlantic herrings are not the only prey. More predators such as fin whale *(Balaenoptera physalus)*, minke whales (*Balaneoptera physalus*), or Atlantic white-sided dolphin (*Lagenorhynchus acutus*) should also be incorporated. However, we should attempt to understand species-specific interactions, since predators do not show the same relation strength to prey. Also, predator density fluctuates annually and these density variations should be modeled with dynamic fisheries consumption models (Curry et al., 2011). Finally, models for Atlantic herring habitat association can be complex (Maravelias et al. 2000; Maravelias, 2001). Our study area represents a remarkable breeding location due to the high chlorophyll concentration and frontal features around pre-spawning grounds. Environmental variables should also be also considered as part of stock assessments for predators and preys. These models should be performing annually to understand the different possible response to environmental variables or prey biomass.

CONCLUSION

Environmental variables such as SST, bathymetry, and chlorophyll concentration affected both predator and prey density on Georges Bank and Jeffreys Ledge. My model suggested that northern gannet density increased in the study area, and was correlated to Atlantic herring index. These opportunistic seabirds foraged over the larger fish aggregations. Fishing vessels influence humpback whale, great shearwater and herring gull densities, and suggests a spatiotemporal overlap with commercial fisheries. Annual top predator density estimation and behavioral interactions on a spawning site such as Georges Bank should be incorporated in future fisheries management models.

Fig.28. Whale count/ km and herring index 2006

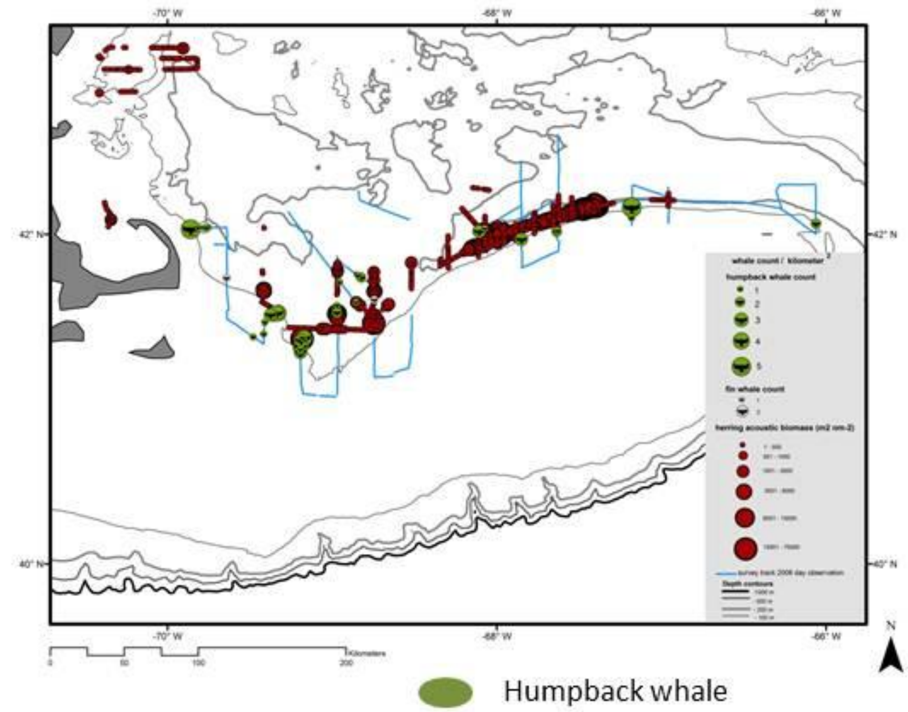


Fig.29. Whale count/ km and herring index 2007

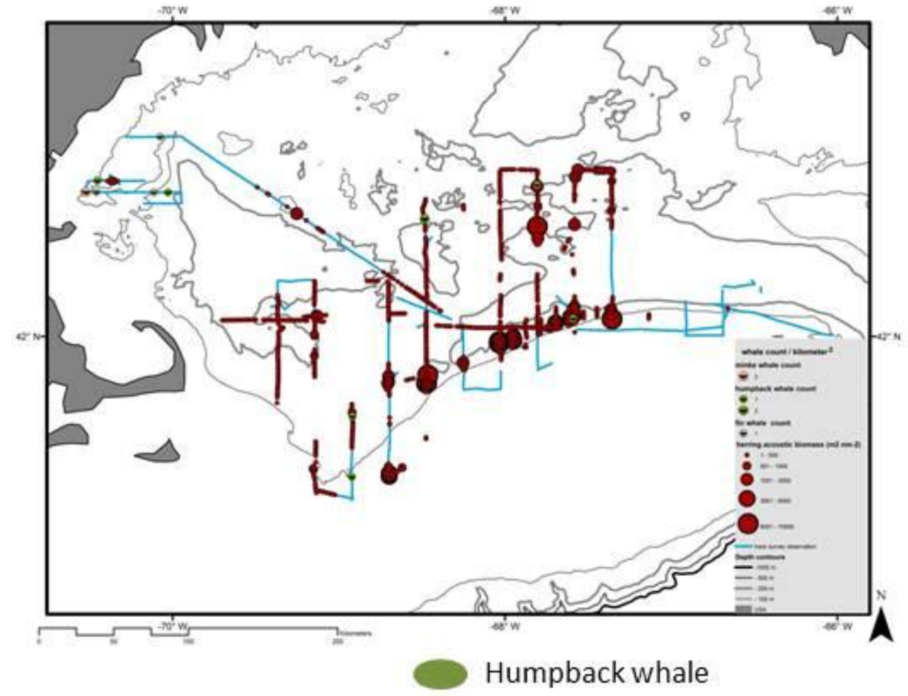
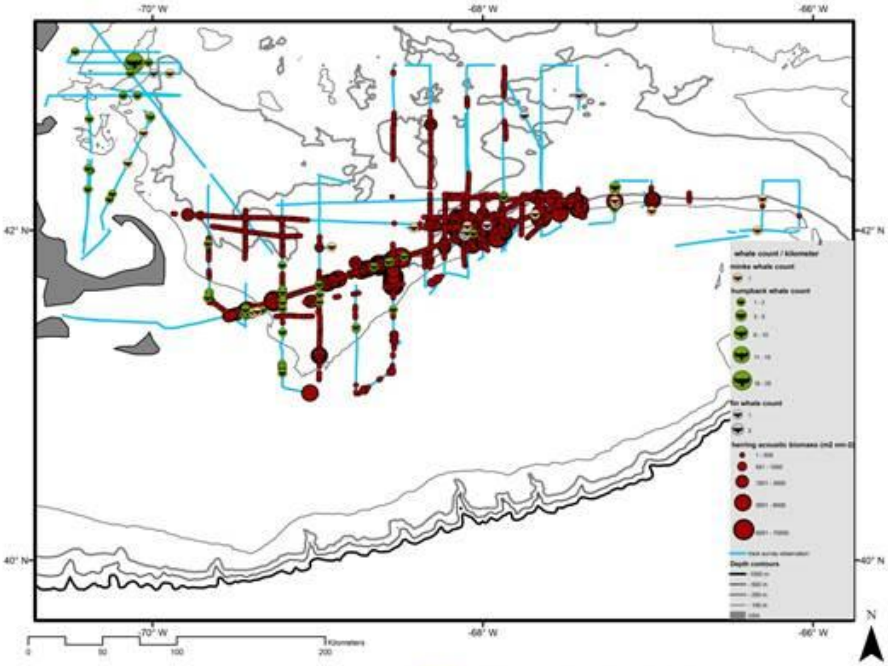
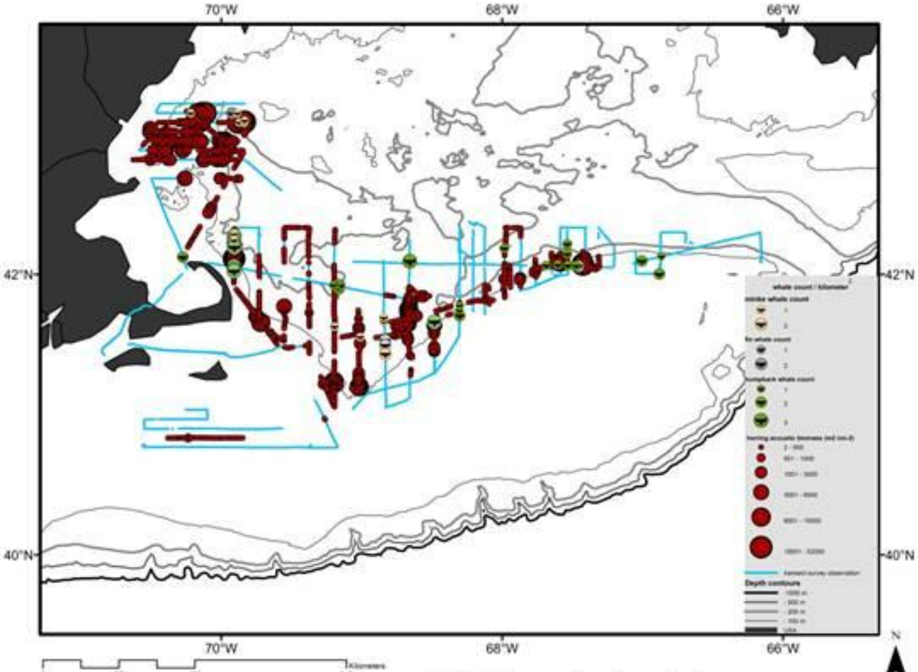


Fig.30. Whale count/ km and herring index 2008



● Humpback whale

Fig.31. Whale count/ km and herring index



● Humpback whale

Fig.32. Dolphin count/ km and herring index 2006

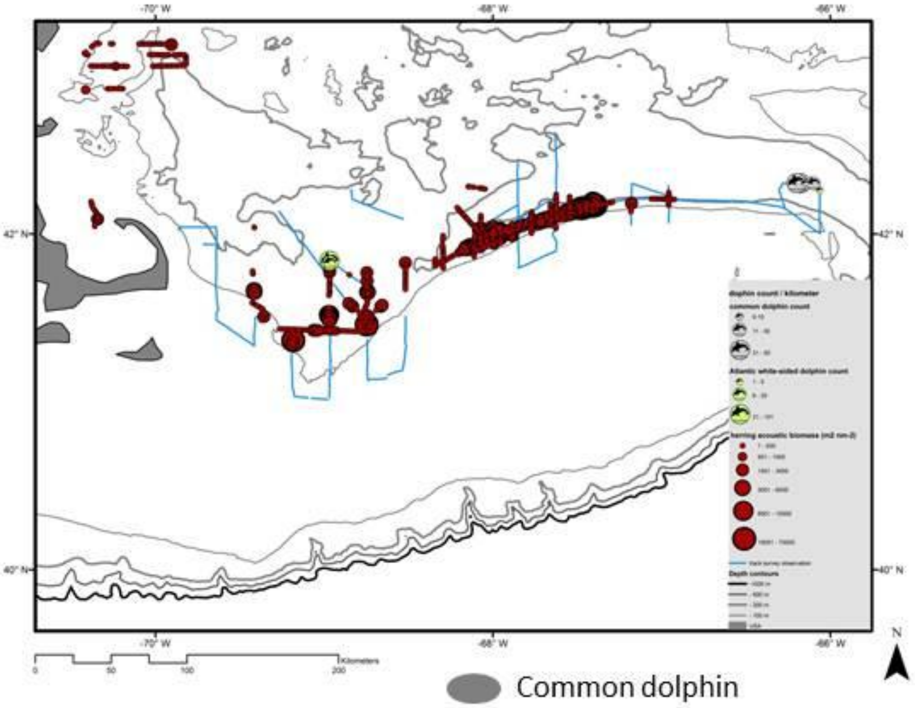


Fig.33. Dolphin count/ km and herring index 2007

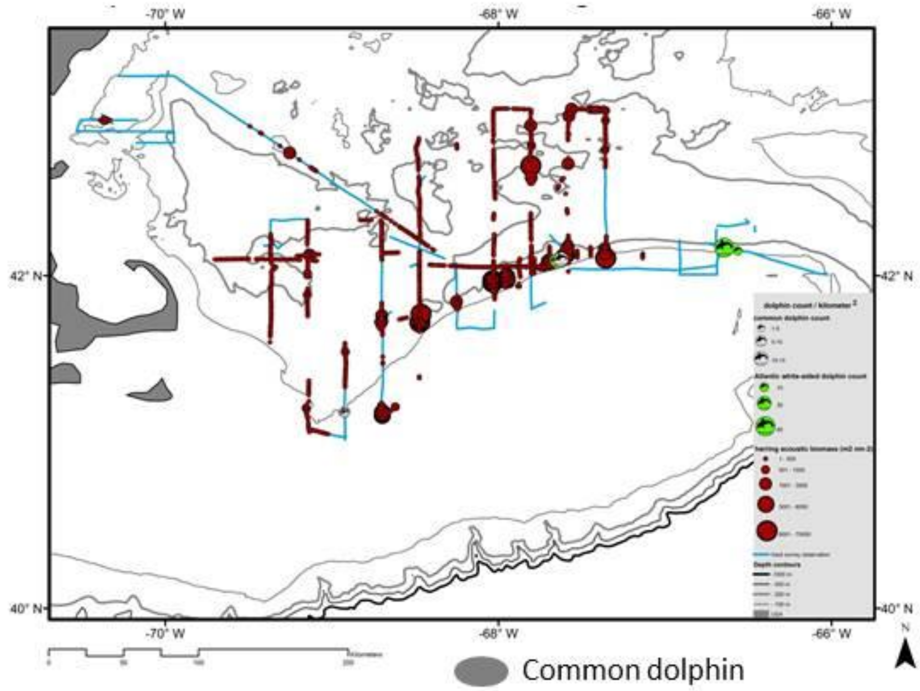


Fig.34. Dolphin count/ km and herring index 2008

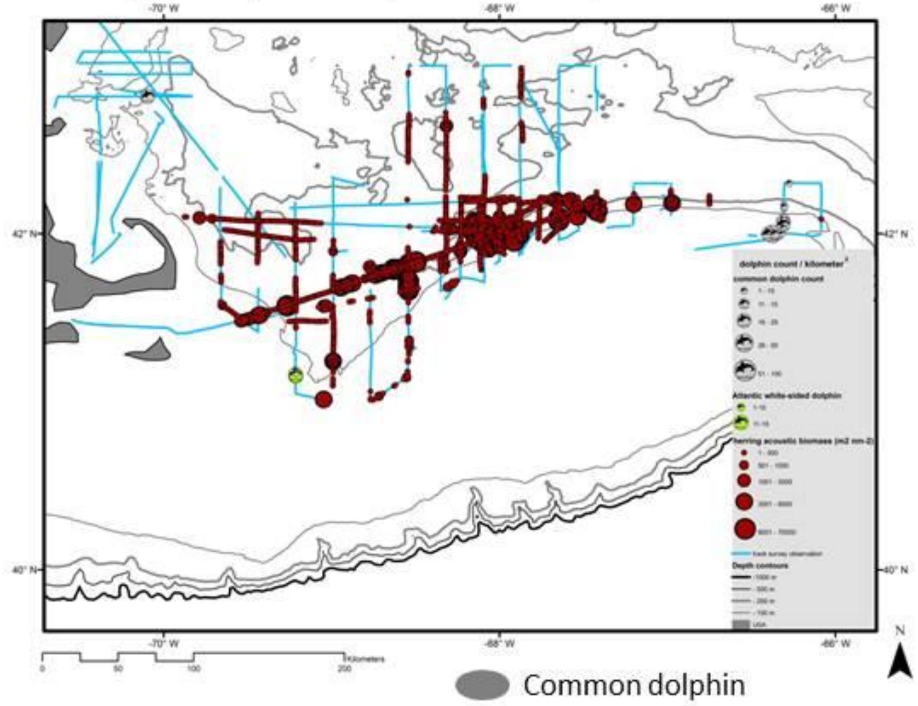


Fig.35. Dolphin count/ km and herring index 2009

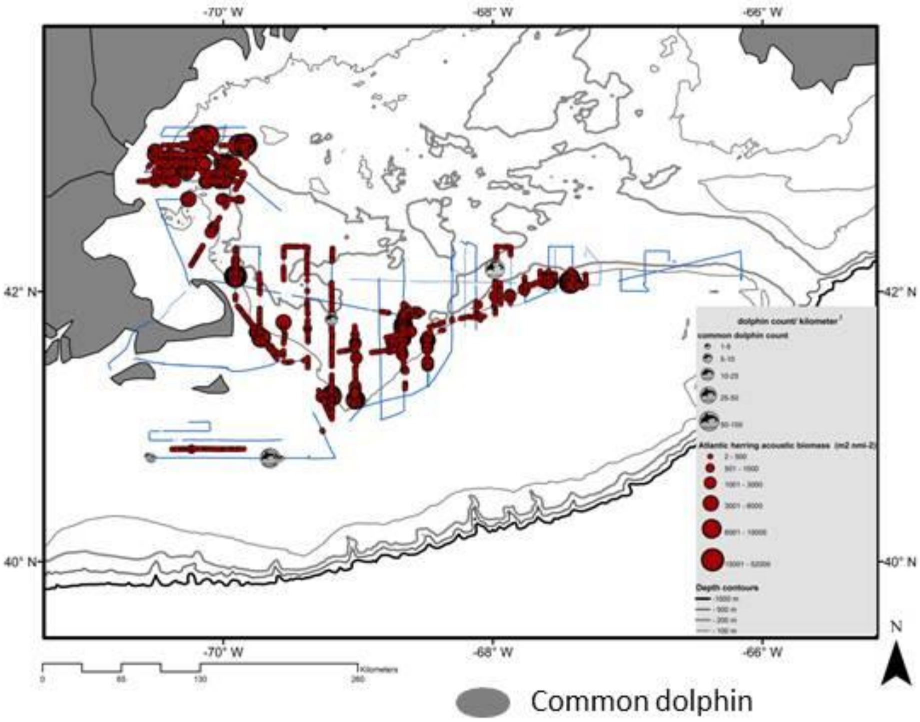


Fig.36. northern gannet count/ km and herring index 2006

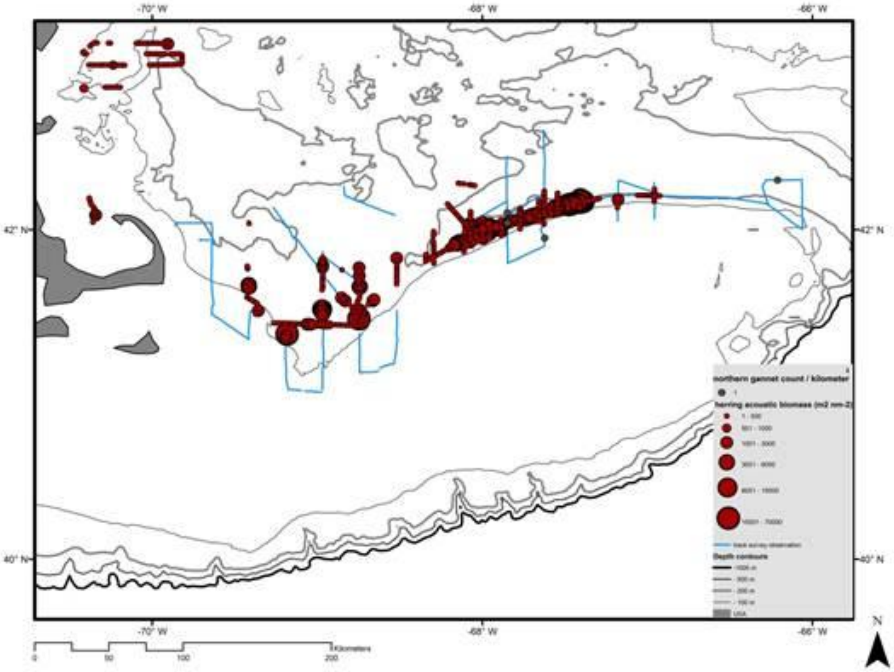


Fig.37.northern gannet count/ km and herring index 2007

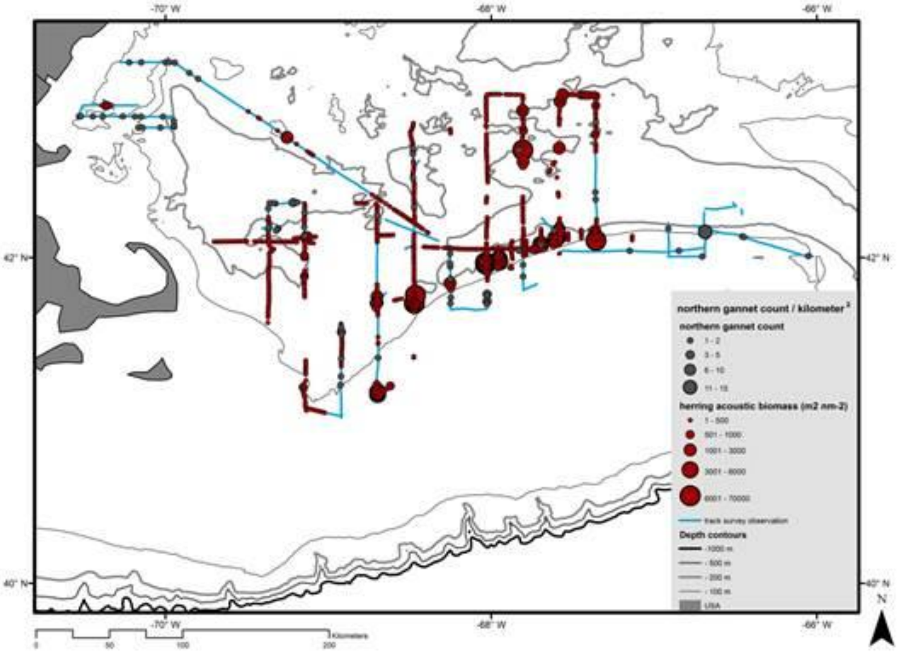


Fig.38. northern gannet count/ km and herring index 2008

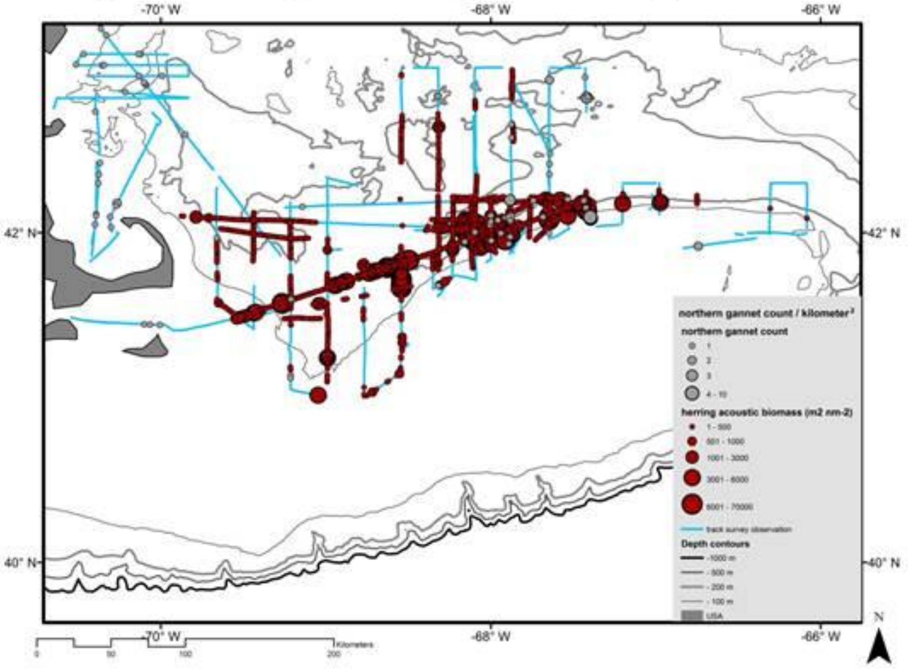


Fig.39. northern gannet count/ km and herring index 2009

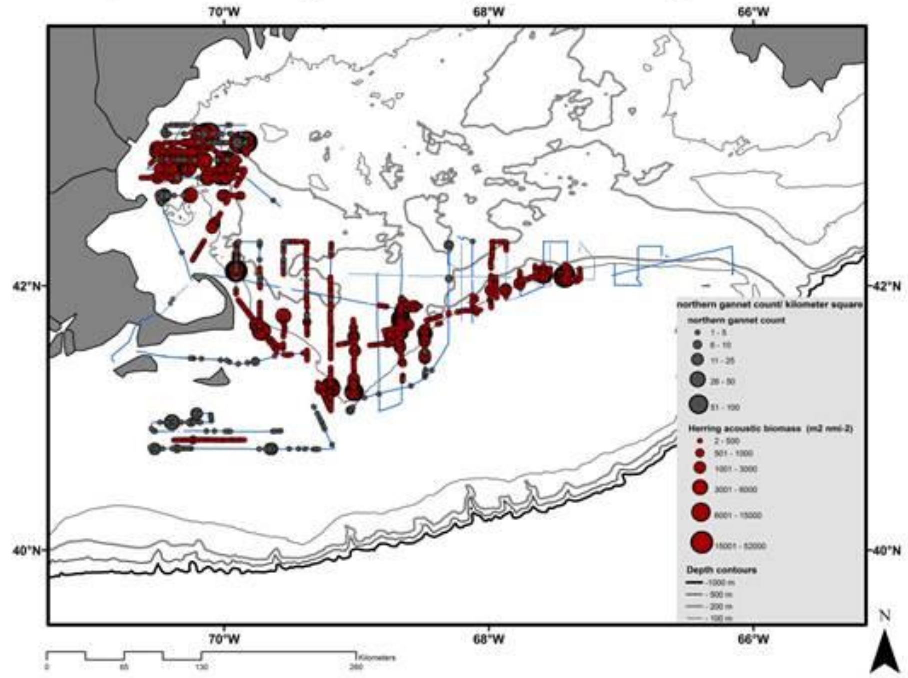


Fig.40. northern fulmar count/ km and herring index 2006

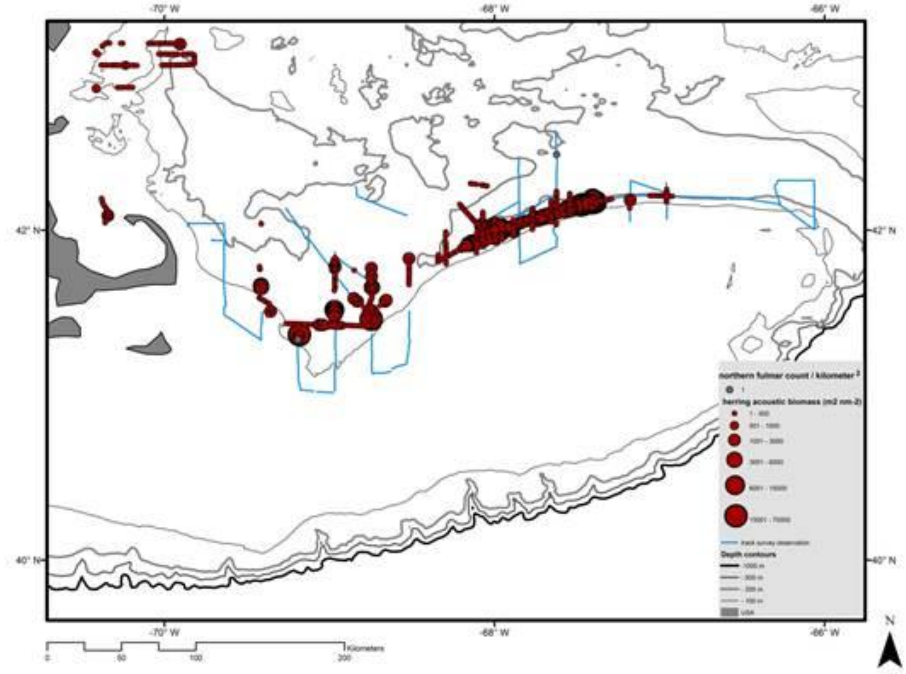
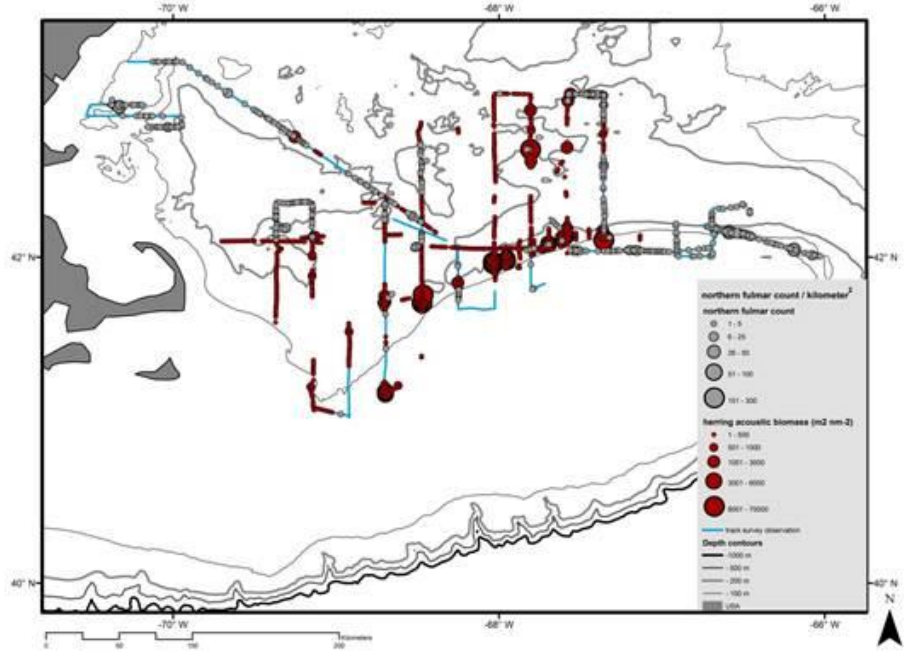


Fig.41. northern fulmar count/ km and herring index 2007



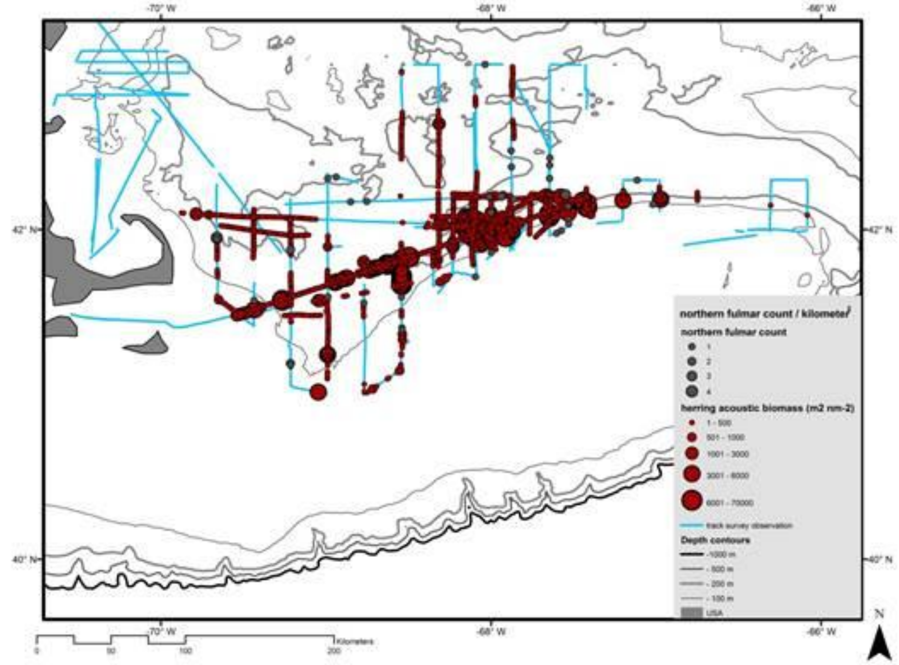


Fig.42. northern fulmar count/ km and herring index 2008

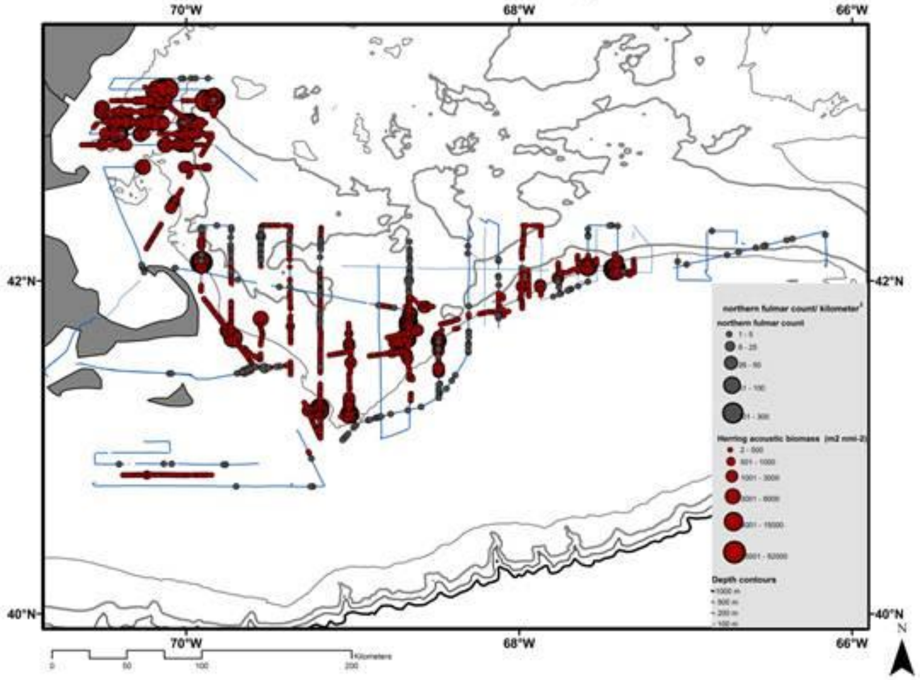


Fig.43. northern fulmar count/ km and herring index 2009

Fig.44. great shearwater count/ km and herring index 2006

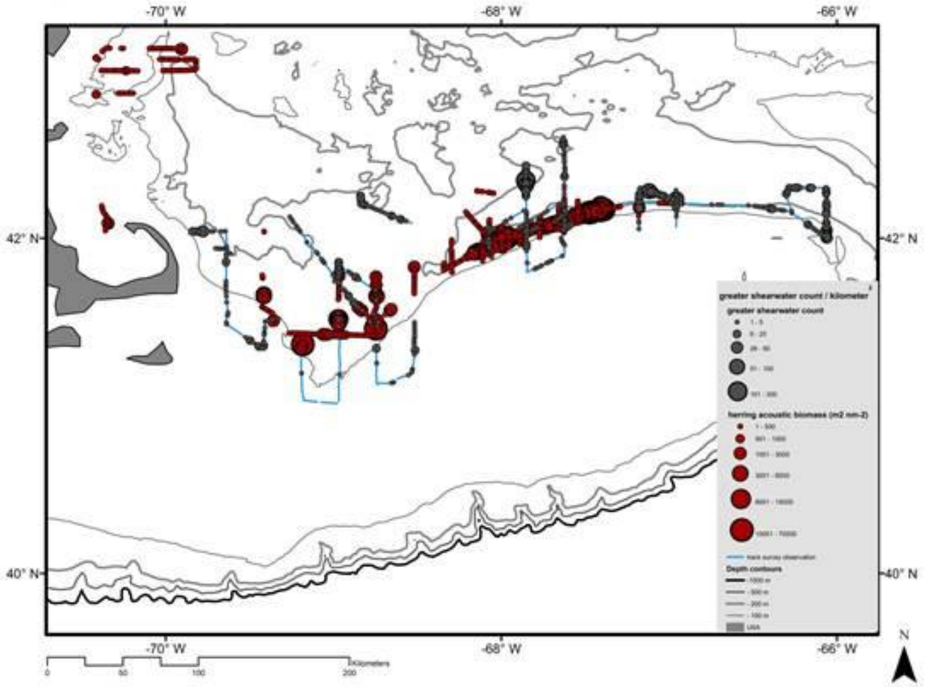


Fig.45. great shearwater count/ km and herring index 2007

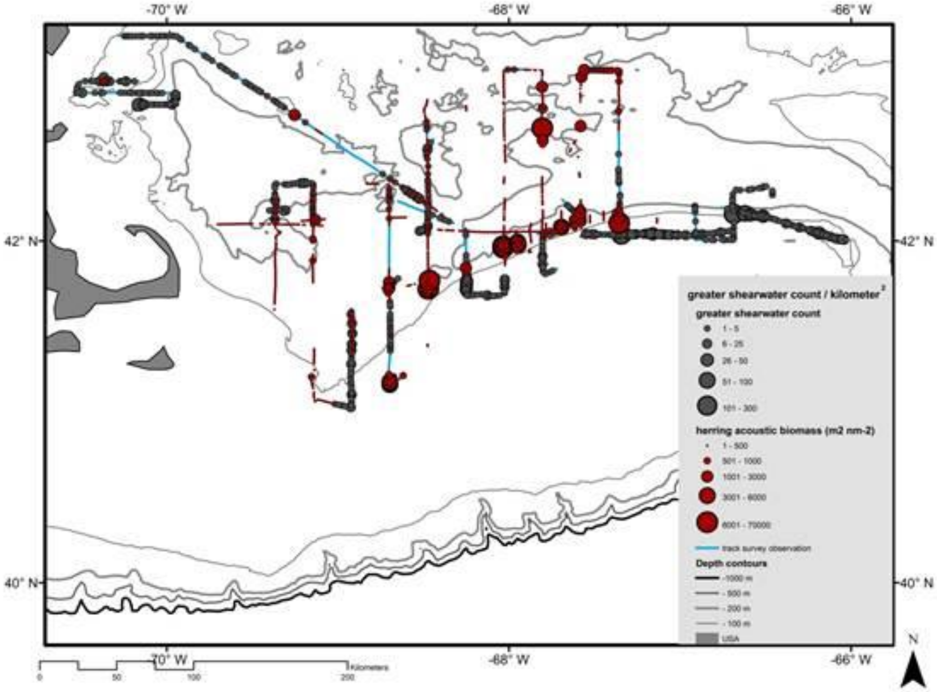


Fig.46. great shearwater count/ km and herring index 2008

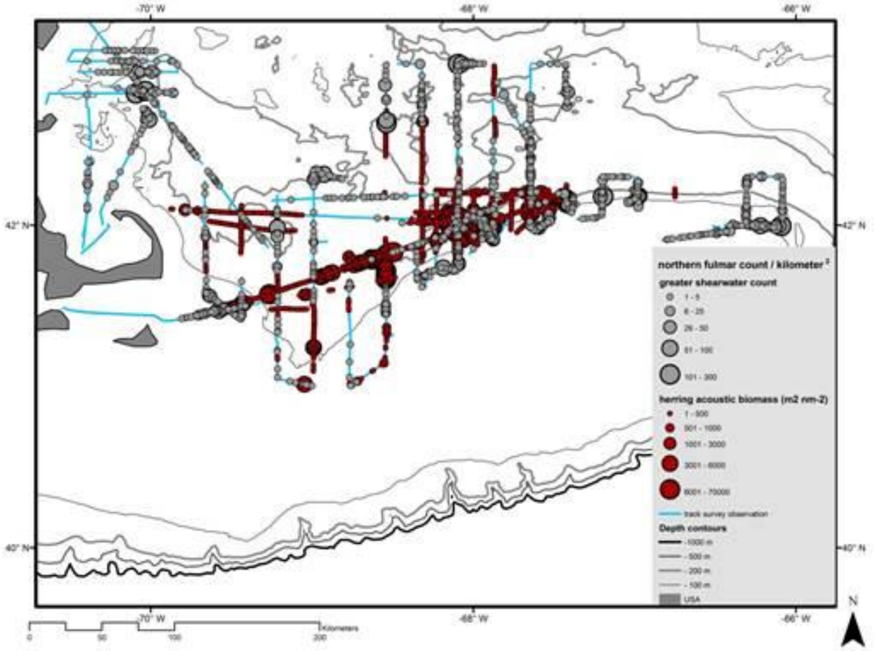


Fig.47. great shearwater count/ km and herring index 2009

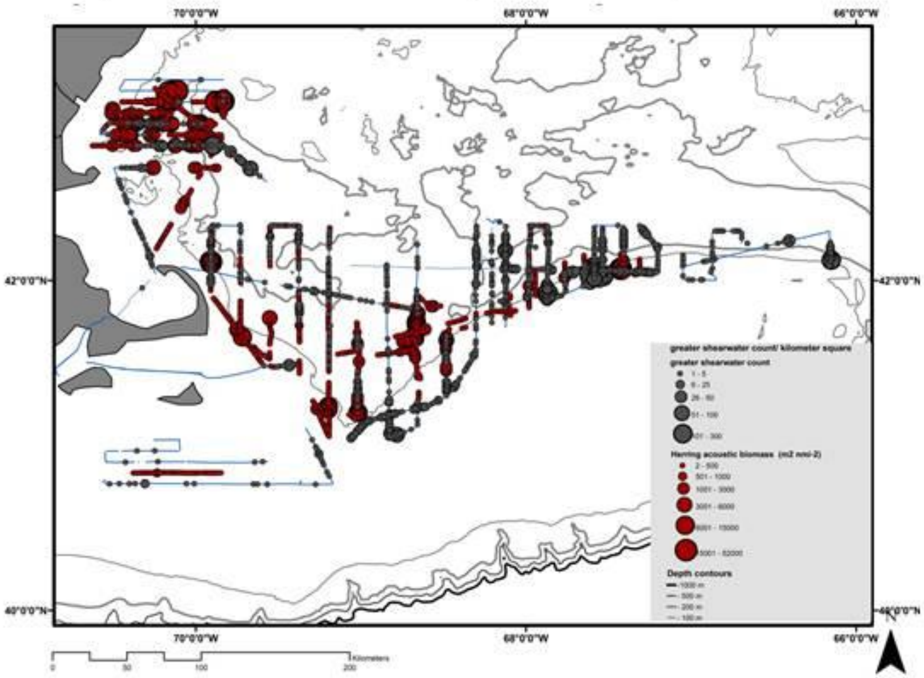


Fig.48. great black-backed gull count/ km and herring index 2006

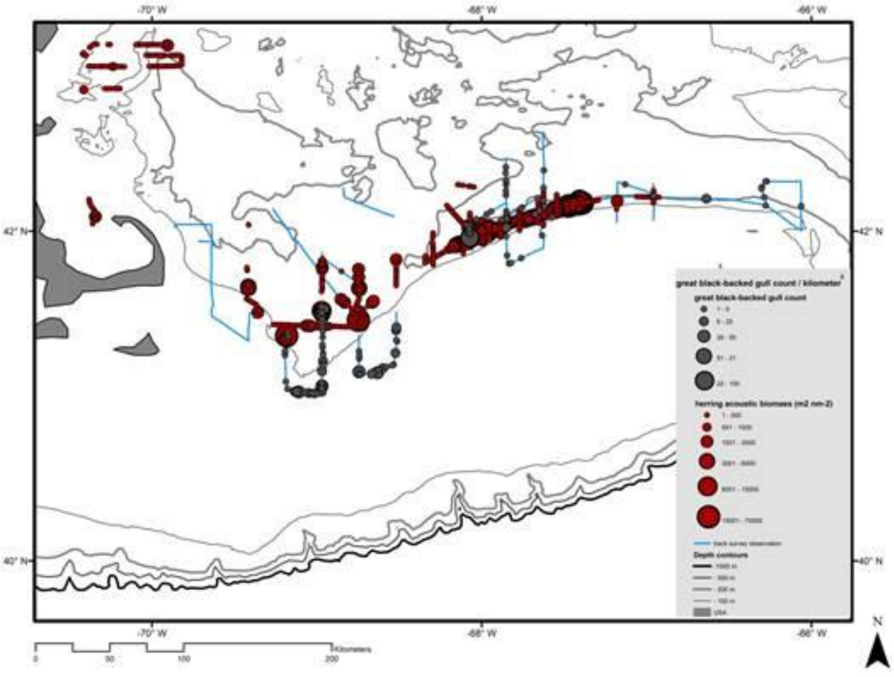


Fig.49. great black-backed gull count/ km and herring index

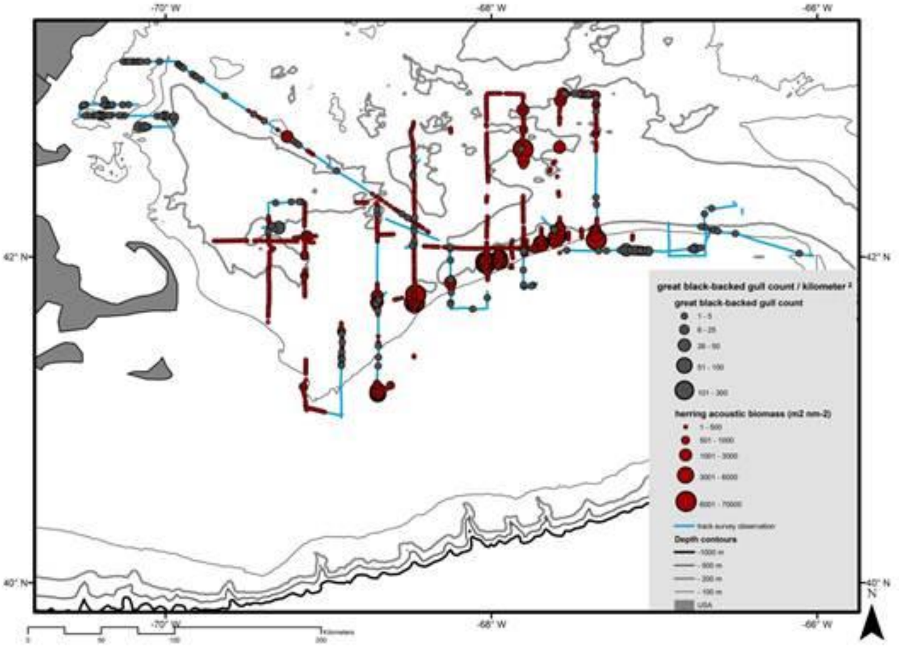


Fig.50. great black-backed gull count/ km and herring index 2008

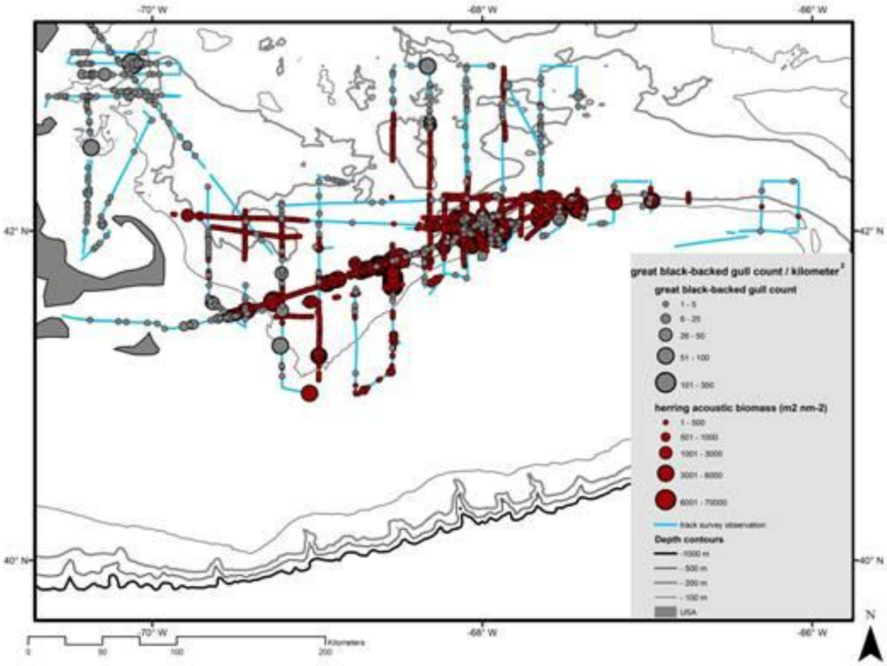


Fig.51. great black-backed gull count/ km and herring index 2009

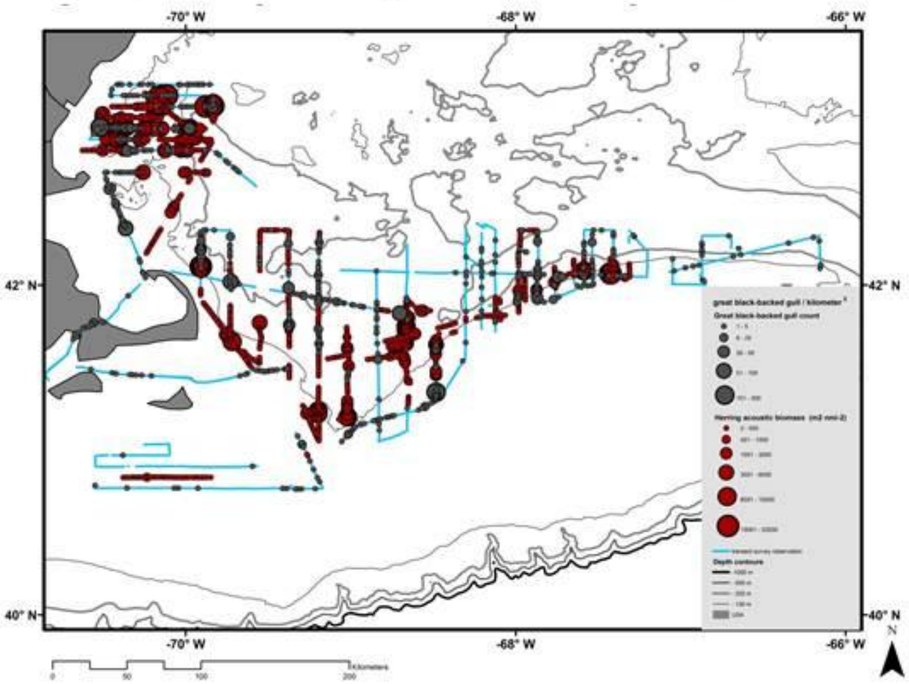


Fig.52. herring gull count/ km and herring index 2006

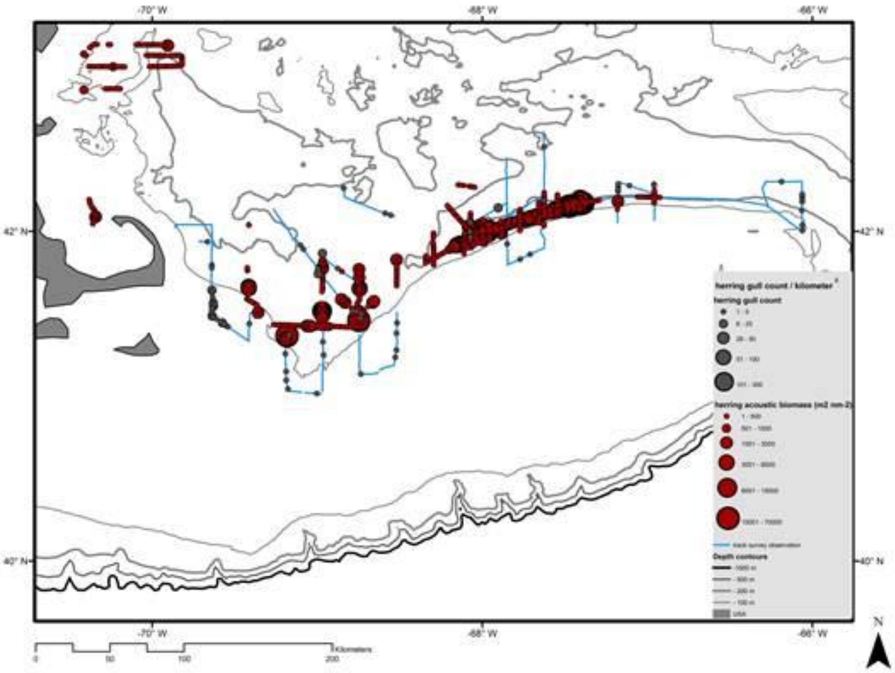


Fig.53. herring gull count/ km and herring index 2007

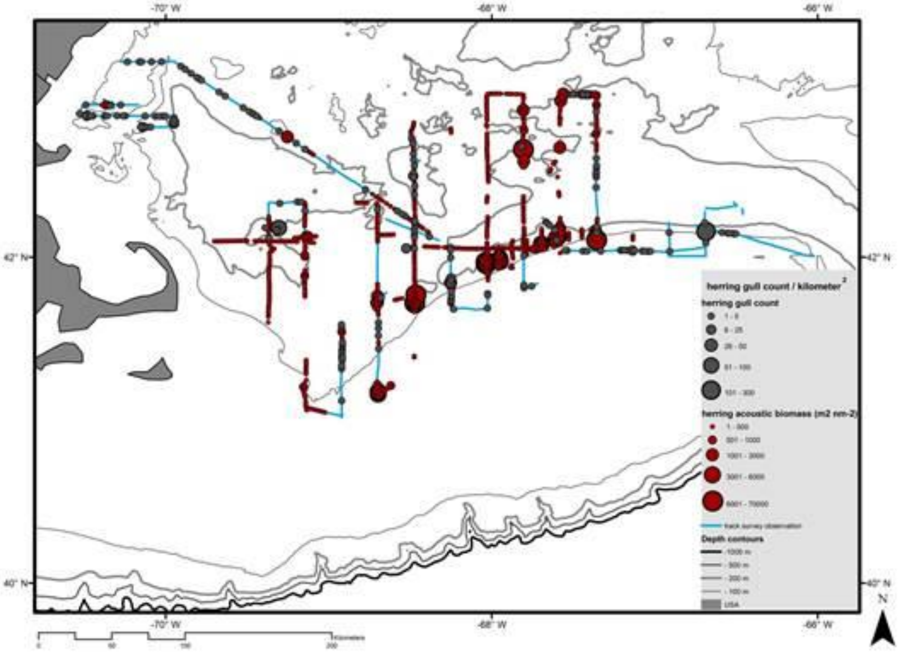


Fig.54. herring gull count/ km and herring index 2008

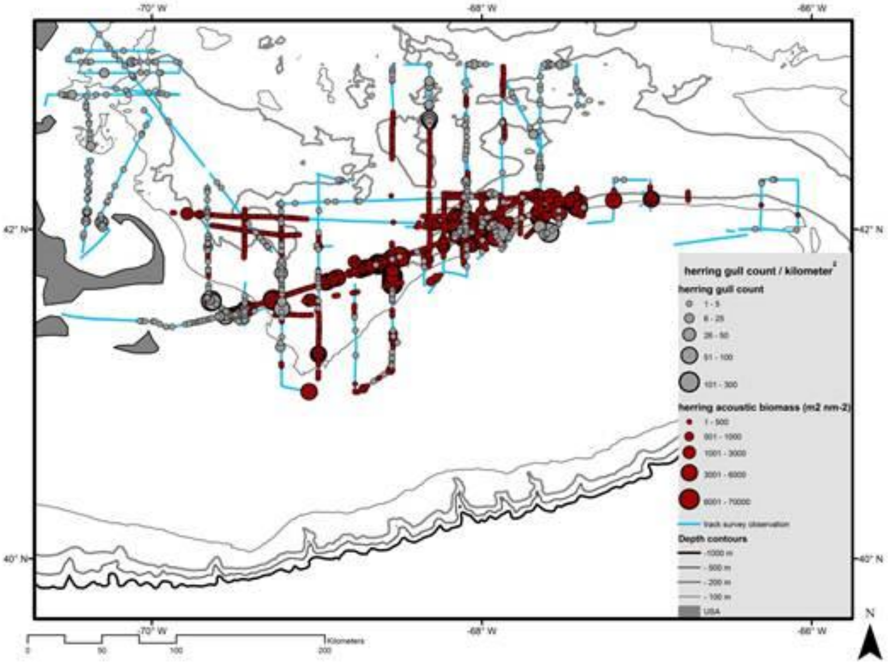


Fig.55. herring gull count/ km and herring index 2009

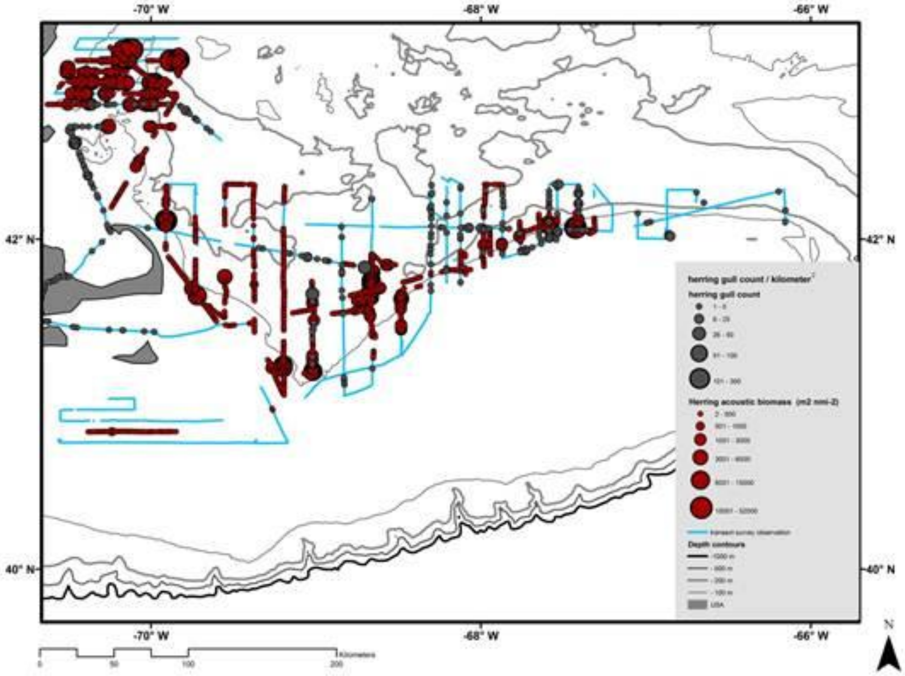


Fig.56. tuna count/ km and herring index 2006

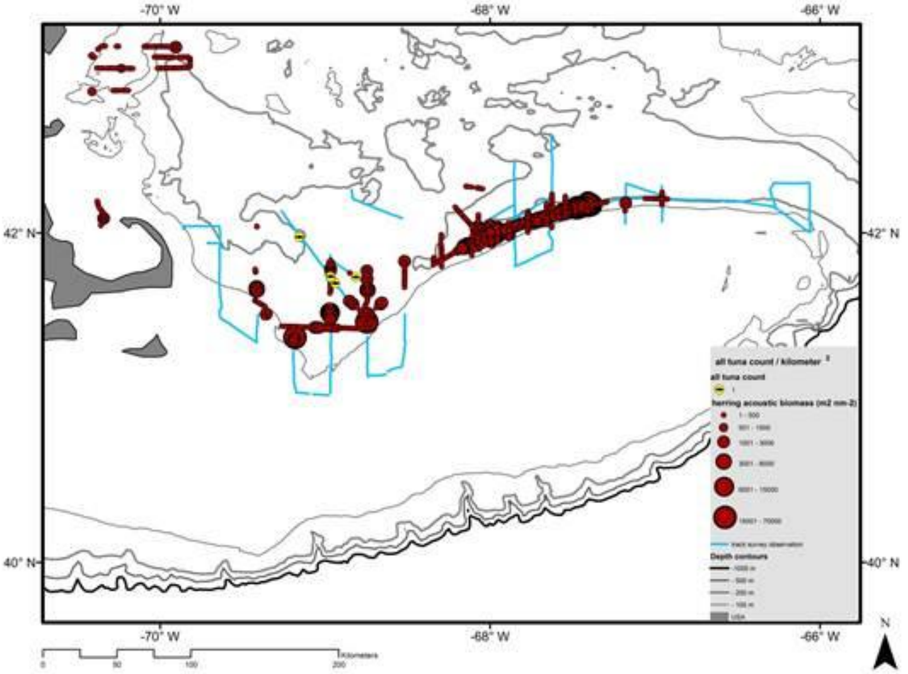


Fig.57. tuna count/ km and herring index 2007

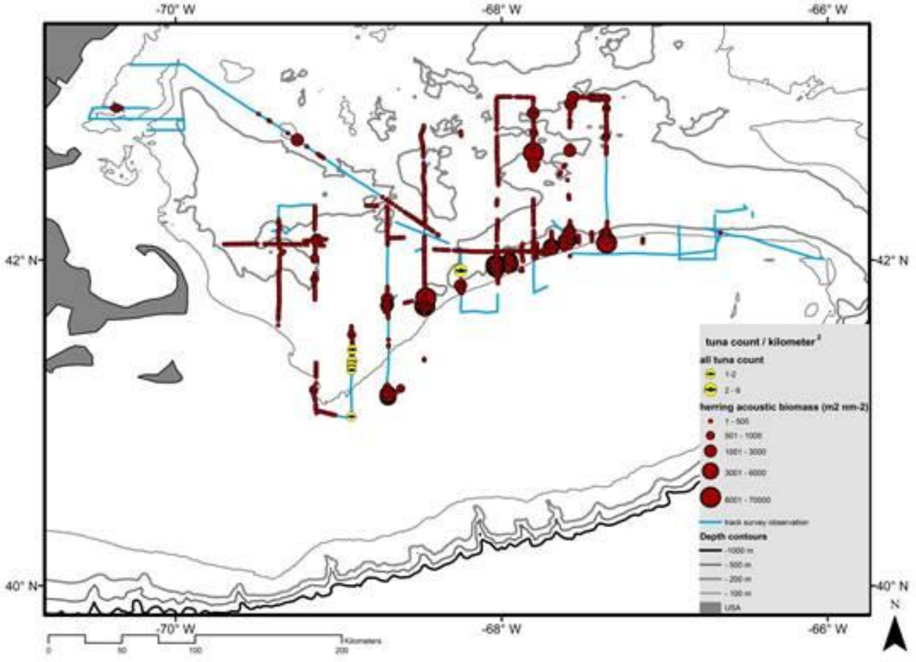


Fig.58. tuna count/ km and herring index 2007 08

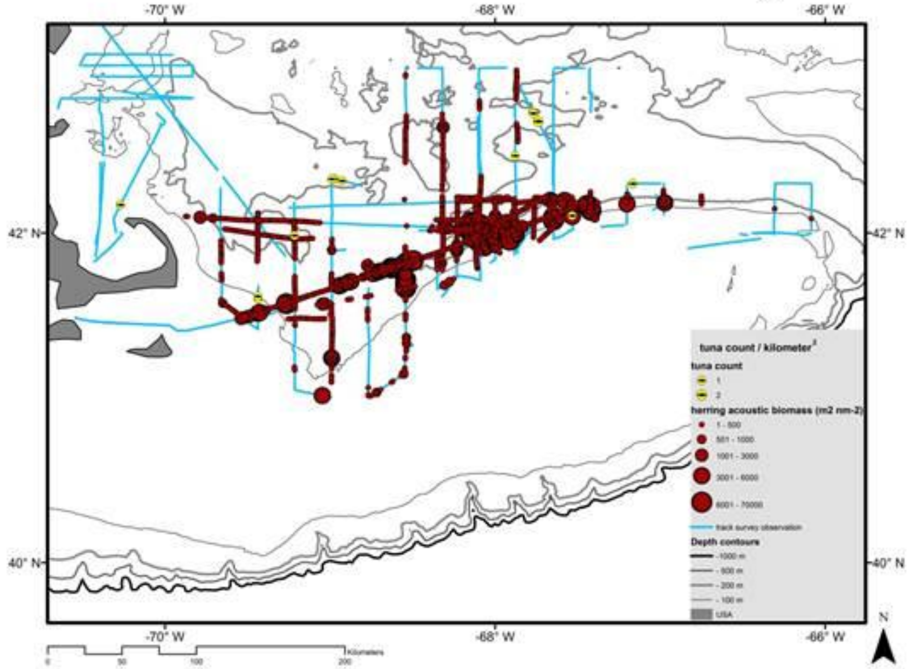
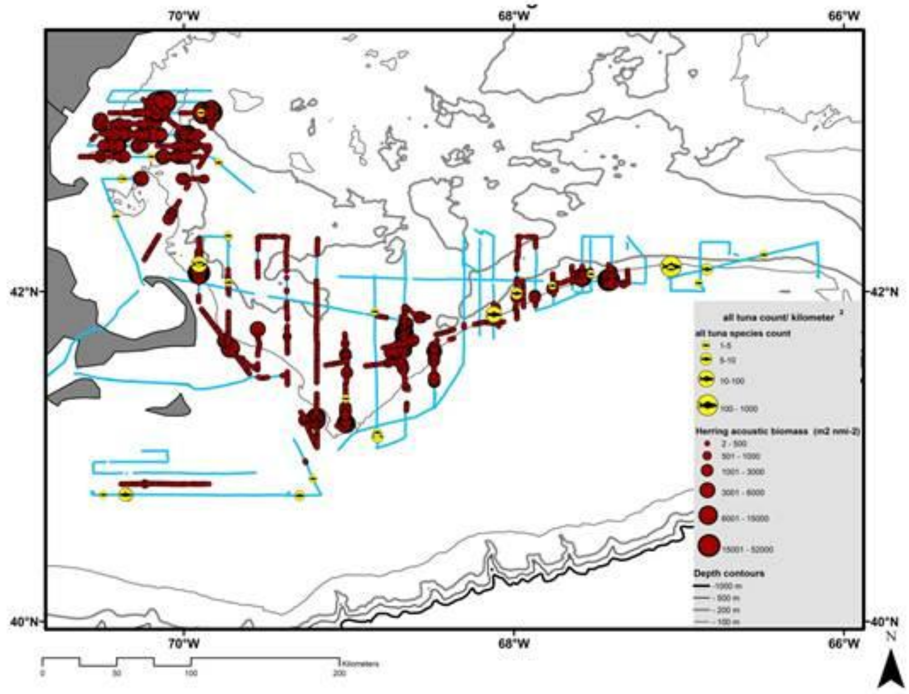


Fig.59. tuna count/ km and herring index



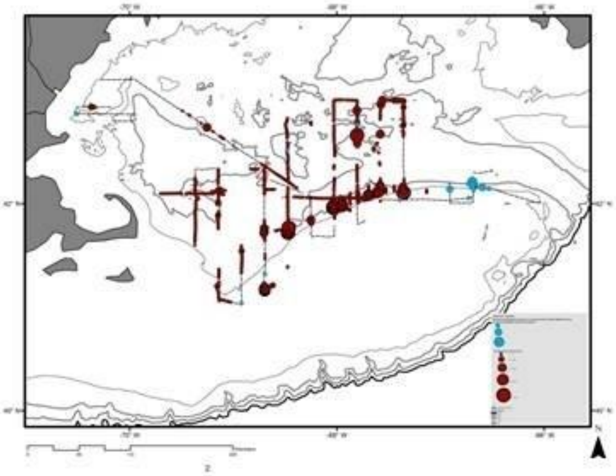


Fig. 60. Commercial fishing vessel count / km and herring acoustic index 2007.

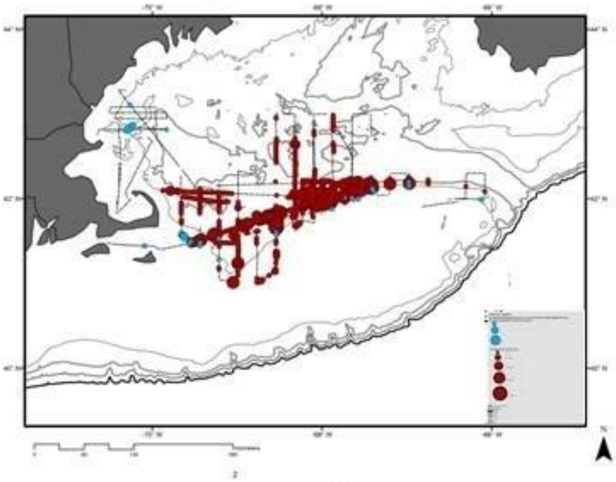


Fig. 61. Commercial fishing vessel count / km and herring acoustic index 2008.

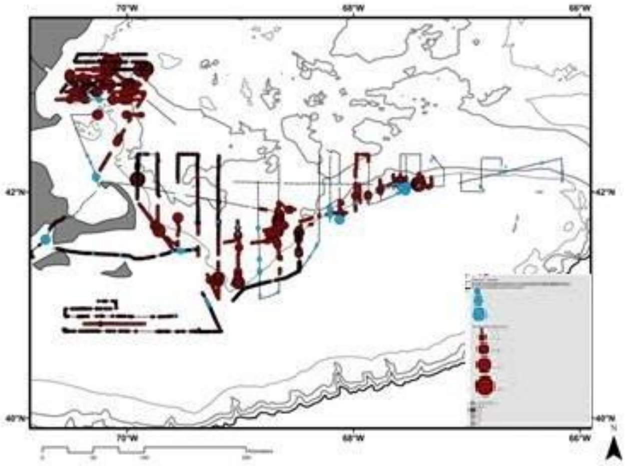


Fig. 62. Commercial fishing vessel count / km and herring acoustic 2009.

-III-

CAN WE IDENTIFY FORAGING ASSOCIATIONS OF PROCELLARIIFORM AND PELECANIFORM SEABIRDS WITH OTHER SUBSURFACE PREDATORS ALONG THE NORTHEASTERN OF UNITED STATES AND SOUTHEASTERN CANADA CONTINENTAL SHELF? IF SO, COULD WE DISTINGUISH SEASONALITY IN FREQUENCY, AND TYPE OF ASSOCIATION ?

CHAPTER 3

CAN WE IDENTIFY FORAGING ASSOCIATIONS OF PROCELLARIIFORM AND PELECANIFORM SEABIRDS WITH OTHER SUBSURFACE PREDATORS ALONG THE NORTHEASTERN OF UNITED STATES AND SOUTHEASTERN CANADA CONTINENTAL SHELF? IF SO, COULD WE DISTINGUISH SEASONALITY IN FREQUENCY AND TYPE OF ASSOCIATION ?

ABSTRACT: Procellariiform and Pelecaniform seabirds are often seen co-occurring with other marine predators in the Northwest Atlantic. Shearwaters forage over marine mammals and tuna schools using local enhancement (LE) in many oceans, but multispecies aggregation studies are sporadic along the northeast continental shelf of the United States and southeastern Canada. Using a Zero-altered (hurdle) negative binomial general linear model (GLM), we looked for aggregations among seven species of seabirds and subsurface predators during nine surveys from 2006 to 2010. This model suggested that great shearwater (*Puffinus gravis*) density was positively correlated to humpback whale (*Megaptera novaeangliae*) and fin whale (*Balaenoptera physalus*) density during summer and to common dolphins (*Delphinus delphis*) in the fall. Great shearwaters also feed commensally over whales and dolphin pods. This study highlights the importance of understanding foraging associations and their seasonality along the continental shelf to detect eventual “foraging hotspots”, and of understanding seabird foraging ecology throughout the year.

INTRODUCTION

Procellariiform seabirds and northern gannets are considered opportunistic feeders (Brown, 1981; Montevecchi & Myers, 1997; Nevitt et al., 2004). Procellariiform seabirds consume primarily fish, squid, plankton, or offal from fishing vessels (Brown, 1981; Granadeiro et al., 1998; Lipinski & Jackson, 2009); northern gannets (*Sula bassana*) principally feed on fish (Montevecchi & Myers, 1997). A multi-species association has been defined as a deliberate movement made by seabirds towards a cetacean, or the inverse, and as a prolonged presence together of individuals from both taxonomic groups (Evans, 1982). Interspecific associations have been well described between tropical seabirds, dolphins, and tuna schools, which drive smaller fishes to the surface (Ashmole & Ashmole, 1967; Pitman & Balance, 1992; Hebshi et al., 2008). In the Northwest Atlantic, humpback whales (*Megaptera novaeangliae*) have been found aggregate feeding on capelin with several seabird species particularly great shearwaters, northern gannets, Atlantic puffins (*Fratercula arctica*), common guillemots (*Uria aalge*), and kittiwakes (*Rissa tridactyla*) (Brown, 1983). Humpback whales may feed using a variety of strategies upon different preys, either deep diving to feed on plankton swarms, or taking schooling fish at depth and close to the surface (Friedlaender et al., 2009). When humpback whales are feeding on Atlantic herring (*Clupea Harengus*), individuals will dive deeply in line, surfacing more than 100 meters from the diving site, and can push prey toward the surface (Perkins & Whitehead, 1977).

I looked for associations between seabirds (Procellariiform and Pelecaniform) and cetaceans and predatory fish. It is important to remember that a statically significant joint presence of seabirds and subsurface predators does not enable us to distinguish whether one derives benefit from the other, or whether they are attracted independently to a common prey that they may locate by other means (Pierroti, 1988). Procellariiformes have evolved specific foraging strategies: great flying capabilities and an ability to dive underwater (Shaffer et al., 2006; Ronconi et al., 2010). Dietary segregation among the species seems also to depend on differences in foraging techniques (Martin & Prince, 2001). Shearwaters have efficient vision to enable visual pursuit of active prey below the surface and a sophisticated olfactory system (Nevitt et al., 1995; Martin & Prince, 2001; Cunningham et al., 2011). Seabirds detect smells on a large scale when using area-restricted research foraging strategy (ARS), but at a fine scale, they use local enhancement (LE) to cue on the presence of other animals, including other seabirds or subsurface predators, and their feeding activity (Nevitt & Veit, 1999). Spotting marine mammals and predatory fishes is an important foraging strategy for these seabirds (Sakamoto et al., 2009). Many Procellariiformes are known to forage in association with other marine predators such as whales, dolphins, and tuna, which drive prey to the surface (Evans, 1982; Pitman & Ballance, 1992; Yamamoto et al., 2008). During their migration, sooty shearwaters (*Puffinus griseus*) cross large geographic areas over the Pacific Ocean, where primary productivity is low, and dive more than expected to feed over predatory fish schools (Burger, 2001; Uhlmann, 2003; Shaffer et al., 2009; Raymond et al., 2010; Block et al., 2011).

Apex predator decline and species foraging overlap

In the Northwest Atlantic, dolphins, whales, and tuna generally forage in highly productive waters (Piatt et al., 1989; Allen et al., 2001; Xavier et al., 2011). Apex predators play a top-down role, but their effect on other species has never been measured (Baum & Worm, 2009; Block et al., 2011). For example, stocks of Atlantic bluefin tuna (*Thunnus thynnus)* have been overexploited, with the possibility of collapse in the Northwest Atlantic. This decline might affect the population of seabirds foraging in association with these top predators (Nevitt & Veit, 1999; Bjordnal et al., 2006; Xavier et al., 2011). Seabirds are also attracted by commercial fishing activity. Spatial overlap between fisheries, seabirds, and subsurface predators has become a major concern worldwide (Lewinson et al., 2004; Delord et al., 2010). Issues regarding fatal interactions between seabirds and commercial fisheries have arisen the past decades in many parts of the world. The most common species being killed are albatrosses, shearwaters, and petrels (Anderson et al., 2011). Understanding these interactions might help address bycatch issues in the future, and determining "feeding hotspots" (Nur et al., 2011). For migrating seabirds, foraging associations are perhaps one of the most effective behavioral strategies for coping with marine ecosystems such as in equatorial regions that have low productivity (Pittman & Ballance, 1992). However, studying offshore foraging aggregations represents a statistical challenge. Pierroti (1988) has been studying feeding associations in the Northwest Atlantic. Nevertheless, it was not so obvious that marine mammals and seabirds interact. Some aggregations were observed, but statistical results were not found significant.

MATERIAL AND METHODS

Study area

Seabird data were collected along the continental shelf of eastern North America extending from Nova Scotia (45°N; 63°W) to Cape Hatteras (35°N; 75°W) in the Atlantic Ocean. The bathymetry of the continental shelf in this region is heterogeneous, ranging from flat, sandy bottom, such as Nantucket shoals, to more complex topography, such as Jeffreys Ledge, Georges Bank, Great South channel, and Hudson Canyon (Sherman, 1988). The study area is bordered in the south by the Gulf Stream and the slope of the continental shelf, which drops from 1000 meters depth to about 4000 meters in areas such as the Gulf of Maine (Northeast Channel) separating the mainland from the deep waters of the Atlantic Ocean (Fautin et al., 2010). The continental slope gradient varies considerably from Canada to the southeast United States, as does the temperature profile of the water. Cold, deep water flows south from the Labrador Sea and surrounds the continental slope; the Gulf Stream brings warmer waters north from the Gulf of Mexico onto the southeast shelf of the United States (Atkinson et al., 1983; Sherman et al., 1996). The Labrador Current and the Gulf Stream meet over the edge of the Grand Bank and turn into a thermohaline circulation influencing heat transport and climatic changes over the Northwest Atlantic. Gyre circulation in the Gulf of Maine and nutrients from large estuaries maintain strong primary productivity year-round (Druon et al., 2009).

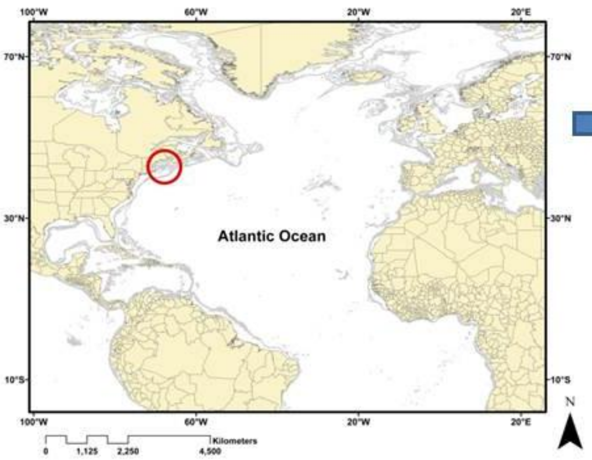


Fig.1. The northeast continental shelf location (red circle) in the northwest Atlantic.

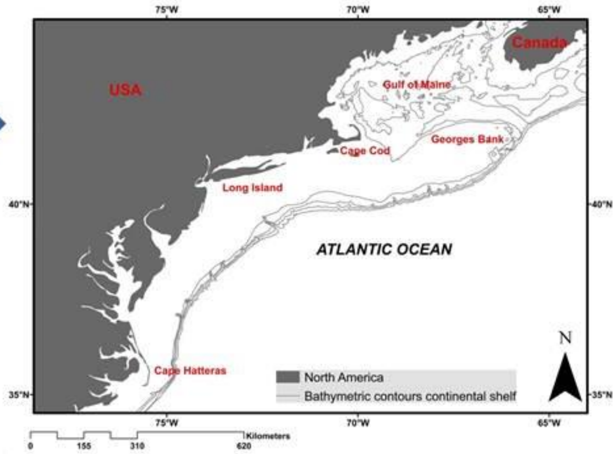


Fig.2. Detail of the northeast and southeastern continental shelf.

Data collection: Seabird survey protocol

From 2006 to 2010, we participated in nine shipboard surveys on the National Oceanic and Atmospheric Administration research vessel *Delaware II*. The cumulative area sampled for seabirds covered 28,440 square kilometers and totaled 1,314 effort hours (Table 1). One observer on the flying bridge continuously counted all seabirds and subsurface predators flying or swimming in a 90° zone on one side of the ship using a combination of strip and line transect methods (Camphuysen et al., 2004). The survey protocol used sampling distance. All seabirds were counted within a 300 meter strip-width (Tasker et al., 1984; Hyrenbach et al., 2007; Ronconi & Burger, 2009). Several parameters influence data collection, including animal behavior, plumage, coloration, size, weather, sea state, observer ability, and change in density influence detection probability (Barbraud & Thiebot, 2009). All these factors have been recognized as issues for seabird counts from shipboard platforms (Tasker et al., 1984; Hyrenbach et al., 2007). Coefficient of detection or correction factors might be applied in theory, but evaluating the specific reasons behind detection differences is difficult because so many parameters are involved. All animals entering the observation strip were counted once. Some species are more likely to be attracted by the vessel presence than others and will follow the ship. This behavior pattern is recognized by experienced observers, and those individuals identified as 'ship followers' were excluded from our density estimation. Transects were conducted from sunrise to sunset while the ship was moving at about 10 knots. Observers entered data in real time directly onto a laptop computer with the software D-Log2 and D-Log3 (©*Glenn Ford*

Consultant Agency). All data were processed using the software ArcView 9.3.1 and 10 (©ESRI). Seabird densities were calculated with the *Seabird* tool (©USGS, Gilbert A.).

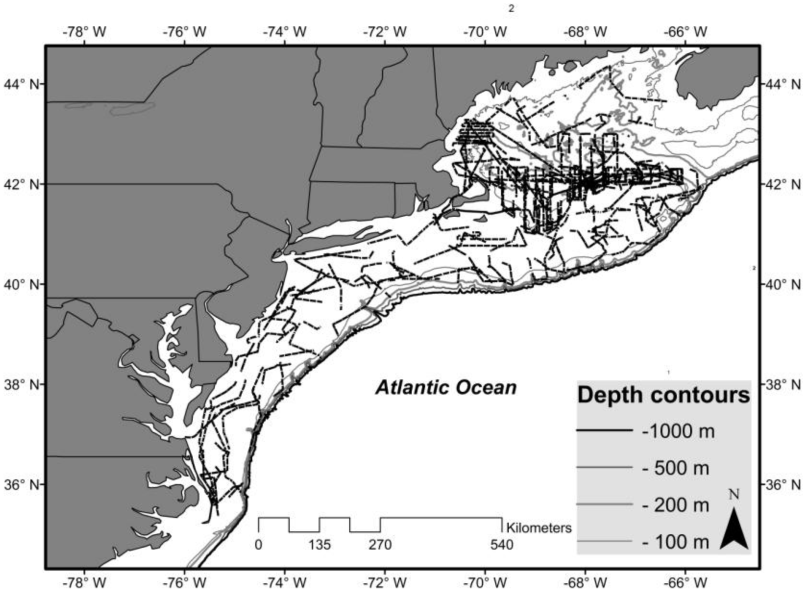


Fig.3. Transects along the continental shelf (9 surveys between 2006 and 2010)

Table 1: Summary effort surveys

Survey name	Survey dates	Hours observation	Area sampled (km^2)
Atlantic herring survey	18 to 28 September 2006	101	1160
Ecosystem Monitoring Survey	14 to 26 August 2008	150	2413
Atlantic herring survey	15 to 24 September 2008	180	3616
Ecosystem monitoring survey	28 May to 10 June 2009	181	4022
Ecosystem Monitoring Survey	17 to 28 August 2009	138	4012
Atlantic herring survey	21 September to 02 October 2009	150	3079
Ecosystem monitoring survey	3 to 19 November 2009	132	3100
Ecosystem monitoring survey	26 May to 09 June 2010	160	4010
Ecosystem monitoring survey	11 to 21 November 2010	122	3028

Variable selection

1) *Seabirds*

Seabird and subsurface predator abundances were used as the response variable and calculated from survey lines segmented at 1 kilometer interval bins. I included one Pelecaniform species, northern gannet, and six species of Procellariiform seabirds: northern fulmar (*Fulmarus glacialis*), Cory's shearwater (*Calonectris diomedea*), sooty shearwater, great shearwater, Leach's storm-petrel (*Oceanodroma leucorhoa*) and Wilson's storm-petrel (*Oceanites oceanicus*). Only seabirds displaying foraging behavior, such as milling, feeding, diving, plunge diving, or pattering, were included in the analysis. Shearwaters and northern fulmars are able to see beneath the surface, and dive to pursue or retrieve prey; sooty shearwaters and great shearwaters are efficient divers (Brown et al., 1981; Garthe & Furness, 2001; Shaffer et al., 2006; Ronconi et al., 2010). Northern gannets plunge dive and can also pursuit dive when they identify feeding resources (Lewis, 2004). Wilson's storm-petrels generally hover and patter above the water in order to collect zooplankton, invertebrates, fish eggs, or larvae, unlike Leach's storm-petrel, which displays a more erratic, bouncing flight when foraging (Whiters, 1978; Veit et al., 1996).

Table 2: Seabird species

Order	**Common name**	**Scientific name**
Pelecaniform	Northern gannet	*Sula bassana*
Procellariiform	Northern fulmar Cory's shearwater Sooty shearwater Northern fulmar Leach's storm-petrel Wilson's storm-petrel	*Fulmarus glacialis* *Diomedea calonectris* *Puffinus griseus* *Fulmarus glacialis* *Oceanodroma leucorhoa* *Oceanites oceanicus*

2) *Subsurface predators*

I first examined the effect of three predictor variables on the abundance of seven seabird species over five years and three seasons: spring, summer, and fall. Predictor variables included were merged by subgroups: whale, dolphin, and tuna (Table 3). Next, I performed the same model analysis with subsurface predator species.

Table 3: Subsurface predators

Name	Species	Scientific name
WHALE	Humpback whale	*Megaptera novaeangliae*
	Fin whale	*Balaenoptera physalus*
	Sei whale	*Balaenoptera borealis*
	Minke whale	*Balaenoptera acurostrata*
	Right whale	*Eubalaena glacialis*
	sperm whale	*Physeter macrocephalus*
	Unidentified whale	
DOLPHIN	Harbor porpoise	*Phocoena phocoena*
	Atlantic white-sided dolphin	*Lagenorhynchus longirostris*
	Common dolphin	*Delphinus delphis*
	Bottlenose dolphin	*Tursiops truncatus*
	Spotted dolphin	*Stenella frontalis*
	Pilot whale	*Globicephala sp.*
	Unidentified dolphin	
TUNA	Atlantic Bluefin tuna	*Thunnus thynnus*
	Yellow fin tuna	*Thunnus albacores*
	Unidentified tuna	*Thunnus sp.*

Table 4: Species count and zero proportion in dataset

Species/ subgroups	Cumulative density	% frequency	% zero in dataset	mean density/ km^2
Wilson's storm-petrel	41677	23.52	96.89	1.44
Great shearwater	23598	23.52	96.65	0.82
Northern gannet	8024	8	96.08	0.27
Sooty shearwater	6700	6.68	99.13	0.23
Northern fulmar	6408	6.38	99.13	0.22
Leach's storm-petrel	5087	5.07	99.17	0.17
Cory's shearwater	2334	2.32	99.21	0.08
dolphin	5293	5.27	99.01	0.18
whale	902	0.89	98.37	0.09
tuna	267	0.26	99.87	0.03

Statistical modeling

Seabird density was used as the response variable and calculated from survey lines segmented at 1 kilometer interval bins. In marine and fisheries studies, datasets often contain a larger proportion of zeros than expected (Minami et al., 2007; Ver Hoef & Jansen, 2007; Gilman et al., 2008; Yee, 2010; Peron et al., 2010). Observation of a very large number of marine animals is rare (Clarke et al., 2003). Excessive zeros will create over-dispersion or under-dispersion (Table 4) (Podlich et al., 2002; Yee, 2009). After performing an Akaike information criterion (AIC) as model selection between quasi-Poisson, Poisson, and negative binomial, we selected the best-fit model, which is the zero-altered negative binomial distribution. For the zero-altered method, zeros arise from a single source, whereas for zero-inflated, three origins are possible: 1) seabirds not seen by observers; 2) seabirds not observed, but habitat is good; and 3) seabirds not seen because the habitat is inappropriate (Zuur et al., 2009). We were not able to explain the reasons for seabird absence (zero probability). Our model includes two steps. In the first step, I modeled the zero probability. In the second step, I modeled the ‘positive’ (non-zero) observations using a truncated probability distribution endorsing the role of hurdle for positive values (Mullahy, 1986; Zuur et al., 2009; Yee, 2010). The negative binomial distribution allows over-dispersion in the positive part of the count data. Finally, I selected a generalized linear model (GLM) because it can extend linear or logistic regressions to non-normal response distribution. It can also explain the relationship between an observed response variable and a number of covariates (in our case subsurface predators). The GLM also allows for linear transformation or combination of multiple dependent variables (Nelder & Wedderburn, 1972). I selected the VGAM package available in the statistical calculation program R CRAN (Yee, 2010; ©R Development Core Team 2011). VGAM computed the maximum likelihood estimates of models and distributions and GLM coefficients were summarized by species. Smoothing parameter relationships between environmental predictors and seabird abundance were represented using non-parametric regressions. This regression analysis shows the average value of a response variable (seabird density) as function of a predictor (environmental covariate). Each plot represents the variable response in relation to the probability of species occurrence in the model on a log scale. The x-axis indicates observed values of the predictor, with each mark representing an observation. Values above zero on the y-axis indicate that the environmental predictor values have more than average effect on species density. The x-axis is equal to the values for each covariate, and the y-axis is a contribution of the smoother to the fitted values. The solid line is the smoothed response curve, and dashed lines indicate the approximate 95% confidence intervals around the covariate main effects and the degree of freedom (DF= 2). The non-parametric regression uses the vector cubic smoothing spline.

RESULTS

In the first part, the overall seabird density with abundance of dolphin, whale, and tuna were modeled; meaning that all seasonal datasets were incorporated. Next, I modeled by species. Only statistically significant results are included in the following tables. P-values appear **in bold** (p<0.05, p<0.005 and p<0.001). The model suggested that whale and dolphin density was correlated to great shearwater density (Estimate=-0.190; SE=0.062; P<0.005; CI=[-0.31; -0.07] (T.5) (Table 6). During the summer season, great shearwater density was positively correlated with humpback whales (Estimate=-0.645; SE=0.296; P<0.05; CI=[-1.225; -0.065]) (Table 7) and fin whales (Estimate=-1.184; SE=0.409; P<0.001; CI=[-1.984; -0.384]) (Table 8). Great shearwater observations also increased with the number of dolphins in the fall (Estimate=0.049; SE=0.017; P<0.05; CI=[0.016; 0.082]) (Table 9) and were associated with common dolphins (Estimate=0.099; SE=0.030; P<0.05; CI=[0.041; 0.157]) (Table 10). The model suggested seasonality in feeding aggregations. Procellariiform seabirds were associated with whales during the summer and shifted to dolphin pods in the fall.

Table 5: Estimates for great shearwater and whale (All SEASONS)
(AIC: 1944.426; log likelihood: -967.213; DF=5)

Step 1: Zero hurdle model coefficient						
parameter	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	2.659	0.157	16.906	**<0.001**	2.359	2.959
WHALE	0.459	0.090	-5.094	**<0.001**	-0.779	-0.289
Step 2: Count model coefficient (truncated with negative binomial)						
	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	2.945	0.165	17.829	**<0.001**	2.625	3.265
WHALE	-0.190	0.062	-3.041	**<0.005**	-0.31	-0.07

Table 6: Estimates for great shearwater and whale (SUMMER)

(AIC: 1949.543; log likelihood: -969.771; DF=5)

Step 1: Zero hurdle model coefficient						
parameter	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	3.292	0.140	23.132	**<0.001**	3.022	3.562
WHALE	-0.737	0.245	-3.003	**<0.005**	-1.217	-0.257
Step 2: Count model coefficient (truncated with negative binomial)						
	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	2.683	0.171	15.687	**<0.001**	2.348	3.018
WHALE	-0.173	0.067	-2.554	**<0.05**	-0.304	-0.042

Table 7: Estimates for great shearwater and humpback whale (SUMMER)

(AIC: 1966.101; log likelihood: -978.050; DF=5)

Step 1: Zero hurdle model coefficient						
parameter	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	3.188	0.138	23.05	**<0.001**	2.918	3.458
HUWH	-3.913	2.680	-1.46	>0.05	-9.165	1.337
Step 2: Count model coefficient (truncated with negative binomial)						
	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	2.652	0.165	15.99	**<0.001**	2.331	2.973
HUWH	-0.645	0.296	-2.180	**<0.05**	-1.225	-0.065

Table 8: Estimates for great shearwater and Fin whale (SUMMER)

(AIC: 1965.757; log likelihood: -977.878; DF=5)

Step 1: Zero hurdle model coefficient						
parameter	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	3.195	0.135	23.517	**<0.001**	2.931	3.459
FIWH	-4.462	3.239	-1.378	>0.05	-10.802	1.878
Step 2: Count model coefficient (truncated with negative binomial)						
	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	2.672	0.164	16.266	**<0.001**	2.351	2.993
FIWH	-1.184	0.409	-2.894	**<0.05**	-1.984	-0.384

Table 9: Estimates for great shearwater and dolphin (FALL)

(AIC: 24298.24; log likelihood: -12144.12; DF=5)

Step 1: Zero hurdle model coefficient						
parameter	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	-8.485	5.744	-1.477	>0.05	-19.735	2.795
DOLPHIN	-0.765	3.865	-0.025	>0.05	-8.340	6.810
Step 2: Count model coefficient (truncated with negative binomial)						
	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	0.550	0.028	19.057	**<0.001**	0.496	0.604
DOLPHIN	0.049	0.017	2.815	**<0.05**	0.016	0.082

Table 10: Estimates for great shearwater and Common dolphin (FALL)

(AIC: 24287.98; log likelihood: -12138.99; DF=5)

Step 1: Zero hurdle model coefficient						
parameter	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	-8.948	8.721	-1.026	>0.05	-26.038	8.142
WHALE	0.180	0.172	1.052	>0.05	-0.157	0.517
Step 2: Count model coefficient (truncated with negative binomial)						
	Estimate	Std Error	Z value	P value	Lower CI	Upper CI
intercept	0.549	0.028	19.070	**<0.001**	0.495	0.603
WHALE	0.099	0.030	3.235	**<0.05**	0.041	0.157

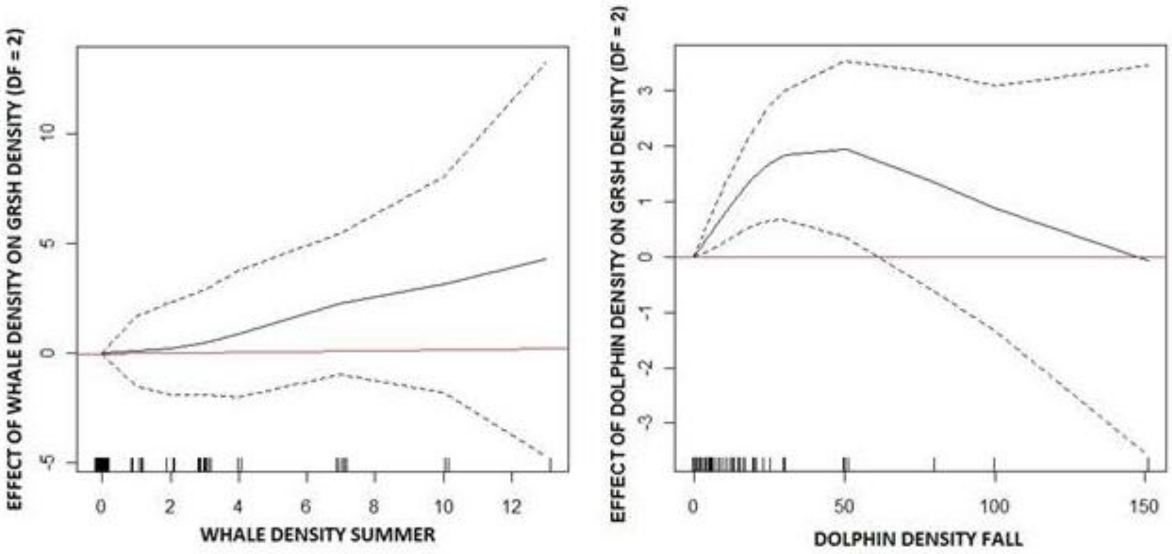


Fig. 4 & Fig.5: Effect of whale density (summer) and dolphin density (fall) on great shearwater density using non- parametric logistic regression. The x-axis represents the values for each covariate, and the y-axis is the contribution of the smoother to the fitted values. The solid line is the smoothed response curve. Dashed lines indicate the approximate 95% confidence intervals around the covariate main effects and the degree of freedom (DF= 2).

DISCUSSION

Models suggested that the density of foraging great shearwater in the study area was positively correlated with whale density (humpback and fin) in the summer and common dolphins during the fall. Our results are supported by previous studies (Perkins & Whitehead, 1977; Evans, 1982; Payne et al., 1986; Pierroti, 1988). Great shearwaters are opportunistic feeders, and the most abundant species of shearwaters along the continental shelf of the northeast United States from May to November (Brown et al., 1981). In the fall, great shearwaters can be seen in large numbers before they return to the Southern Hemisphere (Brown et al, 1980; Ronconi et al., 2010). The total abundance of humpback whales and fin whales is the highest in spring and summer along the northeastern United States and southeastern Canada (Payne et al., 1986; Hain et al., 1992). Whales feed mostly on schooling fishes such as Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes sp*.), Capelin (*Mallotus villosus*) or euphausiids (Evans, 1982; Piatt et al., 1989). One of the most important feeding corridors in the Gulf of Maine for whales and great shearwaters is the Great South Channel (Powers, 1983; Payne et al., 1986; Hain et al., 1992). Since great shearwaters need to feed extensively prior beginning their migration to Tristan da Cunha Island groups, they might be taking advantage of commensal feeding in the productive Northwest Atlantic. Great shearwater will cross lower productivity equatorial waters when migrating and might feed commensally by following dolphins and predatory fish. Great shearwaters might be shifting to feed over dolphin pods in the fall because humpback and fin whales dive deeper, forcing seabirds to wait in order to retrieve food. Whales might be surfacing minutes after the dive at the same location or further away. As a result, great shearwaters have three options: 1) sitting on the water and constantly checking for cetaceans to return, 2) milling to spot the cetaceans (using Local Enhancement strategy), or 3) finding another opportunity. It has been showed previously that other shearwaters deliberately follow dolphins that are feeding or travelling pods in the Atlantic and Pacific Ocean (Evans, 1982; Martin, 1986; Au & Pitman, 1986; Pittman & Balance, 1992; Hebshi et al., 2008). Observers have also identified species such as Cory's shearwaters in the Azores feeding over blue jack mackerel (*Trachurus picturatus*) and trumpet fish (*Aulostomus maculatus*) that were pushed to the surface by subsurface predators such as dolphins and tuna (Clua & Grosvalet, 2001). Interspecific aggregations might be an important part of the feeding ecology of shearwaters (Xavier et al., 2011). Along the northeast continental shelf, dolphins might be: 1) sharing the same habitat as shearwaters and consequently found more often in multi-species aggregations; or 2) feeding on similar prey as seabirds, leaving available remains on the surface (Au & Pittman, 1986; Skov et al., 1995). The results were not significant between seabirds and tuna. Tuna are fast swimmers that feed on smaller fishes at the surface during the day (with peak feeding activity for Atlantic bluefin tuna during transition light times). As a result, seabirds have to be extremely fast and mobile to take advantage of these transient feeding frenzies (Lutcavage et al., 2000), potentially making the energy cost high when following tuna schools (Au & Pittman, 1986). Since tuna are highly migratory along the northeast continental shelf, it might be more difficult for shearwaters to follow these fast aggregations (Walli et al., 2009). We did not observe large numbers of great shearwaters feeding over tuna schools; overall, few individuals were following, milling, and diving in a hectic manner. This study also revealed some limitations. First, more surveys are needed in order to increase the sample size during different seasons of the year. Aggregations are rare statistical events in offshore waters (>30 m). Most of the studies done on foraging associations were highly significant for inshore waters or in areas with a steep bathymetric gradient (Pittman & Ballance, 1982; Davoren et al., 2010). Foraging observations between seabirds, marine mammals and predatory fishes can be observed regularly from fishing boats used for recreation or during whale watching trips. We suggest that future studies should be done during marine mammal surveys or any surveys related to cetacean research (including whale watching trips). Marine mammal scientists generally approach animals for identification or to perform biopsies and are able to stop the ship to make further observations or break the transect line. In our case, we were generally not approaching associations or moving away because we were in constant motion following specific transects lines and was only able to stop occasionally. Second, I made the choice to include only Procellariiform and one species of Pelecaniform (the northern gannet), since I was mainly interested in how these seabirds interact with subsurface predators. Other species might are more likely to be found feeding in multi-species aggregations with by subsurface predators such as terns (Jaquemet et al., 2005; Anderwald et al., 2011).

CONCLUSION

I modeled Procellariiform seabirds and northern gannet feeding associations using a zero-altered negative binomial GLM along the continental shelf of the northeastern United States and the southeastern Canada. Great shearwater was positively correlated to whales (humpback and fin) during the summer and shifted to dolphins (common dolphin) during the fall. Great shearwaters are the most abundant species of shearwaters until November along the continental shelf of the northeastern United States and are preparing to migrate back to the Southern Hemisphere at this time of the year (Brown et al., 1981; Powers et al., 1983). As a result, this species is most likely taking opportunity to feed commensally over subsurface predators in order to accumulate fat reserves and begin their southern migration. Feeding over tuna schools might be costly energetically since tuna are fast swimmers and their transient feeding frenzies harder to follow. This study suggests that great shearwater is an opportunistic seabird which might rely more than expected on multi-species feeding aggregations along the continental shelf, but also over the Atlantic Ocean.

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