Seabird Foraging in Dynamic Oceanographic Features

by

Lesley Helen Thorne

University Program in Ecology
Duke University

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Dr. Doug Nowacek

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor of Philosophy in the University Program in
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ABSTRACT

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Abstract

Oceanographic features, such as fronts, eddies, and upwellings, provide important foraging areas for marine predators. These areas serve as important "hotspots" of marine life, by aggregating weakly swimming lower and mid-trophic level species which, in turn, attract foraging predators. Despite the importance of these dynamic features, we lack a comprehensive understanding of how they create foraging habitat for seabirds and other marine predators. In the first part of this dissertation, I review current knowledge of how seabirds use oceanographic features with an emphasis on developing a more mechanistic understanding of these features, and identify important considerations for future studies. I use the findings of this review to inform two field research projects in the Bay of Fundy, Canada and Onslow Bay, North Carolina. In these two projects, I examined seabird abundance and distribution in relation to oceanographic features that occur at different spatial and temporal scales. In the first project, I examined foraging habitat of red-necked phalaropes (*Phalaropus lobatus*) in relation fine-scale tidal forcing near the Brier Island ledges in the Bay of Fundy. This research demonstrated the importance of biophysical interactions in creating phalarope habitat, and characterized red-necked phalarope habitat in both space and time. In Onslow Bay, I investigated the effects of Gulf Stream fronts and eddies on the abundance and distribution of seabirds using both remotely sensed and *in* *situ* data. I used fisheries acoustics surveys to investigate prey distribution within Gulf Stream frontal eddies. I then developed habitat models for the six most commonly sighted species or species groups (Cory's shearwaters, *Calonectris diomedea*; greater shearwaters (*Puffinus gravis*; Wilson's storm-petrel, *Oceanites oceanicus*; Audubon's shearwaters, *Puffinus lherminieri*; black-capped petrels, *Pterodrama hasitata*; and red and red-necked phalaropes, grouped together as *Phalaropus* spp.) using multivariate modeling techniques. Gulf Stream frontal eddies influenced the abundance and distribution of seabirds in Onslow Bay, although frontal features were not as important in predicting seabird habitat as demonstrated in previous studies in the South Atlantic Bight. Prey availability in Gulf Stream frontal eddies was highest in eddy cold core regions, particularly in those regions close to the Gulf Stream. Taken together, the results of my dissertation: underscore the importance of conducting standardized surveys to assess dynamic environmental variables; demonstrate the use of multivariate methods to examine seabird foraging in relation to oceanographic features; emphasize the need to evaluate both prey distributions and physical regimes within oceanographic features at depth; and highlight the importance of temporal aspects of oceanographic features, such as the persistence and age of the features, when assessing the role that these features play in creating seabird foraging habitat.

Dedication

For my parents, Susan and Guy.

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General introduction

Background

Physical processes play an important role in structuring biological patterns in marine environments (Mann and Lazier 1996). Due to the close coupling of physics and biology in marine ecosystems (Legendre and Demers 1984, Steele 1985, 1998), oceanography is an important determinant of the distribution of marine organisms at lower trophic levels (e.g., Haury et al. 1978, Legendre and Demers 1984, Mackas et al. 1985), and thus has important effects on the availability of food resources for upper trophic level animals (e.g., Brown and Gaskin 1988, Hunt 1997, Ladd et al. 2005). Consequently, understanding the effects of oceanographic processes is critical to improving our understanding of the foraging ecology of marine predators that must search for prey in an extremely dynamic patchy environment, often over very large spatial scales.

Oceanographic features, such as fronts, eddies, and upwellings, are dynamic marine habitats that create aggregations of low and mid-trophic level species and thus create foraging habitats for marine predators (e.g., Alldredge and Hamner 1980, Hamner and Hauri 1981, Franks 1992, St. John et al. 1992, Rankin et al. 1994, Rodhouse et al. 1996, Griffin 1999, Johnston et al. 2005a,b). However, the underlying processes controlling biological patterns within many of these systems remain unclear, and few comprehensive studies of these systems have been conducted to date. The study of food web dynamics within oceanographic features has the potential to add substantially to our understanding of trophic exchange in marine ecosystems. Studies of these systems can be used to identify and predict "hotspots" of marine productivity and important habitats for marine organisms of concern.

There are many challenges in conducting quantitative and comprehensive studies of oceanographic features in relation to the habitat of marine predators. Marine habitats are dynamic in both space and time (e.g., Steele 1985, Barry and Dayton 1991), and physical processes affect biological phenomena at a variety of spatial and temporal scales (Haury et al. 1978). In order to identify and understand links between biological patterns and the processes driving these patterns, particularly those connecting oceanography with mid- and upper trophic levels, physical and biological patterns must be examined at appropriate scales (Haury et al. 1978, Legendre and Demers 1984). In addition, linking physical parameters with patterns in seabird abundance and distribution requires knowledge of both physical processes and biological patterns occurring at multiple trophic levels, which presents further challenges to sampling efforts. For these reasons, it is important to use appropriate survey designs in order to capture and account for variation in the physical environment. Careful survey design is particularly important because studying both physical patterns and organisms occurring throughout the food web in marine systems is inherently expensive due to requirements of ship time and expensive technological equipment. Long-term sampling programs are required in order to assess how changes to the physical environment affect biological patterns, and sampling designs must consider the feasibility of long-term surveys in offshore regions that are difficult and expensive to observe.

Several important technological advances have improved our ability to sample physical and biological patterns in marine systems in recent years. These include the ability to record fine-scale biological and physical measurements continuously and in real time (Mann and Lazier 1996). However, these advances, or the appropriate or quantitative analysis of the data resulting from these advances, have not been fully realized in studies of the pelagic habitats of seabird species. Improvements in statistical modeling and analysis software (e.g., Guisan 2000) have allowed the effects of a number of environmental predictors on seabird habitat to be evaluated simultaneously. Studies of marine predator habitat use in oceanographic features have rarely taken advantage of these techniques; few have quantitatively assessed the effects of these features and processes on habitat, while very few have taken a process-oriented approach (Tremblay et al. 2009). A more quantitative approach is required to improve our understanding of trophic transfer within these systems.

Seabirds are often used as indicators of the status of marine systems and stocks of their prey species (e.g., Bost and le Moho 1993, Bost et al. 1994, Einoder 2009), and changes in seabird prey have been observed in response to oceanographic influences and associated regime shifts in marine food webs (Montevecchi and Myers 1996). As such, trends in the abundance, distribution and habitat use of seabirds can be used to identify and assess changes in marine systems. Before we can understand these trends, we must first improve our understanding of the factors driving seabird habitat use.

Outline of dissertation

This dissertation explores the role of oceanographic features in creating dynamic foraging habitat for seabirds. Many studies have discussed physical features and processes and their effects on seabird foraging habitat (reviewed in Chapter 1), but most of these studies have been descriptive. It is necessary to examine directly the links between physical processes and low and mid-trophic level organisms so that we can better understand the effects of oceanographic processes on seabird abundance and distribution.

My research builds on previous knowledge of seabirds and oceanographic features, and focuses on particular research areas and techniques that have been lacking in previous studies. Specifically, my dissertation seeks to review our knowledge of the role of physical oceanographic features in enhancing foraging opportunities for seabirds; to quantitatively assess seabird foraging habitat in oceanographic features occurring at different spatial and temporal scales; and to provide concrete suggestions for future research directions and sampling efforts.

I employ an interdisciplinary approach to investigate how physical fields within oceanographic features relate to the distribution of both seabirds and their prey, and to inform future sampling efforts in this field. Complex trophic linkages in these features may obscure relationships between seabirds and ocean physics (Daunt et al. 2006), and thus studies of seabird habitat use in oceanographic features should be coupled with studies of their prey species. I conducted surveys of prey fields within oceanographic features at two different sites, representing physical processes occurring over different spatial and temporal scales: the Brier Island ledges in the Bay of Fundy, Canada and Gulf Stream regions of Onslow Bay, North Carolina.

Research on the foraging habitat of red-necked phalaropes (*Phalaropus lobatus*) in the Bay of Fundy provides an example of the biological effects of a fine-scale oceanographic feature under extreme tidal influences. This research presents an example of the importance of considering oceanographic processes when sampling critical habitats of marine predators, and indicates the need to develop standardized approaches that reflect local physical processes within long-term sampling programs.

In contrast, my studies in Onslow Bay examined relationships between seabirds and a number of habitat variables, including Gulf Stream fronts and eddies, and shelf breaks. In this research, I examined the distribution and habitat use of multiple seabird species. Multi-species assessments of seabirds, including studies of birds foraging in different parts of the water column and on different prey species and trophic levels, are important to understanding links between seabirds and oceanographic features. Such assessments help to provide a more complete picture of seabird habitat use within a particular system, because species foraging in different locations or at different trophic levels often exhibit different responses to changes in the physical environmental (Montevecchi et al. 2006). Seabirds using different foraging strategies, or species feeding on different prey species, have been found to target different water masses, different parts of oceanographic features, or different oceanographic features altogether (Haney 1986a, Hunt 1997, Daunt et al. 2006). A different number of trophic linkages separates planktivorous and piscivorous seabirds from ocean physics, and consequently the associations between seabirds and oceanographic processes, and the strength of those associations, may differ among these types of seabird (Daunt et al. 2006).

My dissertation is divided into four chapters. In the first chapter, I review our current knowledge of how oceanographic features create enhanced foraging opportunities for seabirds in pelagic environments. The biological effects of these features in relation to seabird prey and seabird foraging habitat are reviewed in this chapter, with a particular focus on the importance of providing a more mechanistic understanding of the dynamics of oceanographic features. I critically assess the research that has been conducted to date, and make suggestions for future research in this field. Chapter 2 emphasizes the use of quantitative studies and prey studies in seabird studies in an assessment of red-necked phalarope habitat use at a tidally-driven upwelling in the Bay of Fundy. In particular, this chapter focuses on the significance of spatial and temporal scale in quantifying relationships between seabirds and oceanography. Chapter 3 provides an example of the use of repeated standardized survey techniques and multivariate analysis techniques to assess seabird habitat in relation to dynamic oceanography. In this chapter, I analyze seabird distribution relative to a suite of environmental predictors using Classification and Regression Trees (CARTs) and Maximum Entropy modeling techniques in order to characterize seabird habitat in Onslow Bay, North Carolina. Lastly, in Chapter 4 I use a combination of *in situ* measurements and satellite-derived datasets to examine seabird habitat use relative to Gulf Stream frontal eddies and to provide a preliminary assessment of prey distributions within these features.

In summary, this research identifies, defines and predicts important seabird foraging habitat in relation to oceanographic features in two different study sites using quantitative and multivariate analyses, and provides guidelines for future efforts to examine seabird habitat and to sample biological patterns in dynamic marine environments.

Chapter 1: From pattern to process: a critical review of the literature linking seabirds and oceanographic features

Abstract

Many studies have demonstrated relationships between the distribution of foraging seabirds and oceanographic features, but we lack a comprehensive understanding of how these physical features facilitate trophic exchange and create foraging habitat for seabirds. Elucidating the effects of physical oceanographic processes on trophic exchange is a critical step in improving our understanding of food web dynamics in marine systems. Moving towards more mechanistic studies of trophic interactions within oceanographic features would provide important progress in this respect, and is a critical step in identifying the factors driving pelagic seabird habitat. This chapter critically reviews our current knowledge of the effects of oceanographic features on the distribution and behavior of seabirds, with the goal of moving from correlation to causation and increasing our predictive capacity. I review past studies that have related seabirds to a variety of oceanographic features, examining sampling and analytical techniques, and aspects of scale. I provide examples of seabird studies to date that have furthered our knowledge of biophysical interactions within oceanographic features and propose future directions for research in this field. In particular, I

emphasize the importance of considering the temporal and spatial scale of the features examined and the techniques used to sample these features, and highlight the importance of working closely with biological and physical oceanographers in order to further our understanding of the processes occurring within ocean ecosystems.

1. Introduction

Oceanographic features, such as fronts, eddies, upwellings, and convergence zones, can affect plankton and weakly swimming nekton directly through physical forcing (Alldredge and Hamner 1980, Hamner and Hauri 1981, Franks 1992, St. John et al. 1992, Rankin et al. 1994), or indirectly by attracting mid-trophic level predators to aggregations of their prey (Rodhouse et al. 1996, Maravelias and Reid 1997). As such, these features are important foraging areas for many top predator species (Griffin 1999, Mendes et al. 2002, Johnston et al. 2005a, b). Seabirds, in particular, aggregate at many different oceanographic features, including fronts (e.g., Schneider 1982, Kinder et al. 1983, Haney and McGillivary 1985a, b, Brown 1988a, b, Ainley et al. 1998, Spear et al. 2001), eddies (e.g., Haney 1986a, b, 1987b, Weimerskirch et al. 2004, Hyrenbach et al. 2006), features resulting from seamount effects (Haney et al. 1995), deep or steep thermoclines (Ribic and Ainley 1997, Ribic et al. 1997), and regions of localized upwelling (Haney 1985b, Brown and Gaskin 1988). Several authors have indicated a need to understand the biophysical processes creating and sustaining regions of enhanced biomass relative to seabird habitat in order to understand the importance of these areas in the transfer of energy up the food chain, and to understand their effects on the population dynamics of seabirds (e.g., Schneider 1990, Nel et al. 2001, Hyrenbach et al. 2002, Hyrenbach 2006).

In order to generate a more mechanistic understanding of the processes underlying the observed patterns of seabird distribution, it is important to understand how ocean physics drives the formation of enhanced foraging opportunities within various oceanographic features. Understanding how biophysical forcing affects seabird foraging behavior is a critical prerequisite to predicting seabird habitat and identifying and managing areas of conflict with human interests (Gonzalez-Solis and Shaffer 2009). Despite the recognized importance of these features, we lack a comprehensive understanding of how oceanographic dynamics create foraging habitat for seabirds. This is a classic ecological problem of understanding the processes underlying observed biological patterns, which must be accomplished before it is possible to derive explanatory relationships and prediction.

Seabirds are highly mobile, searching for prey over very large spatial scales, but their foraging efforts occur at smaller, and occasionally very fine, spatial scales (Brown 1988, Jouventin and Weimerskirch 1990, Weimerskirch et al. 2004). Wakefield et al.

(2009) note that pelagic seabirds differ from most other marine predators because the medium that most seabirds travel through (air) is different from that in which they forage (water). As such, seabirds exhibit rapid dispersal speed compared to those of their prey, and can respond rapidly to spatial variation in prey (Russell et al. 1992), and, presumably, to physical changes in their foraging habitat. Breeding seabirds are central place foragers, placing spatial and temporal constraints on the extent and duration of foraging trips (e.g., Weimerskirch et al. 1993, Shaffer et al. 2003).

We currently have only a rudimentary understanding of the biophysical interactions occurring within oceanographic features, and how these interactions play out at different temporal and spatial scales to affect seabird habitat. An improved understanding of the biophysical coupling and trophic mechanisms at work in these systems is required to determine their importance in the energy transfer up the food chain and to the population dynamics of top predators (e.g., Schneider 1990, Hunt and Schneider 1987, Nel et al. 2001, Johnston et al. 2005a,b, Hyrenbach et al. 2006). This requires that studies include sampling efforts focused on physical dynamics, lower and mid-trophic level species, as well as foraging seabirds. Conducting such comprehensive studies within oceanographic features is challenging and expensive, particularly within dynamic systems. Nevertheless, our understanding of these features and their importance to foraging seabirds has improved markedly, in part due to technological developments (Ballance et al. 2006). In recent years, several technological and methodological improvements have created new opportunities for investigating seabird-habitat relationships at a variety of scales. Recent advances in telemetry, oceanography, fisheries acoustics and remote sensing technologies, together with the development and use of appropriate statistical methods, are of particular importance in understanding links between seabirds and the biophysical environment (Tremblay et al. 2009).

Previous review papers investigating the effects of the physical environment on seabird abundance, distribution and habitat use have focused on specific regions of the ocean (e.g., Schneider et al. 1987, Dunnet et al. 1990, Hunt 1991, Veit and Braun 1984, Hunt 1997, Croxall and Wood 2002, Ballance et al. 2006, Bost et al. 2009), or examined the effects of the physical environment more generally, rather than focusing specifically on oceanographic features (Hunt and Schneider 1987, Tremblay et al. 2009). A few papers have focused on specific features (Schneider 1990, Stirling et al. 1997). Tremblay et al. (2009) note that of the environmental factors evaluated in seabird-environment studies, the contribution of environmental factors describing oceanographic structure (i.e., reflecting oceanographic features that might affect prey availability) is very small (4.8%). This highlights the need to better understand seabird habitat in the context of oceanographic features and the importance of summarizing our knowledge in this field to date in order to inform future studies.

The objective of the current paper is to provide a review of current knowledge of seabird use of oceanographic features in reference to trophic exchange and biophysical coupling, as assessed in peer-reviewed literature, at a variety of spatial and temporal scales. In particular, I seek to examine development in this field since Hunt and Schneider's (1987) review, which provides an important summary of seabird habitat use in relation to oceanography (though not oceanographic features specifically) up to the date of that review, and provides a baseline against which to compare progress in this field. This review focuses on developing a more mechanistic understanding of oceanographic features by examining biophysical interactions within these features, and emphasizes the importance of doing so in order to increase our predictive capacity for modeling seabird habitat relative to these systems. I highlight the issue of spatial and temporal scale, both of the oceanographic features themselves and of the physical and biological data used to investigate seabird-environment relationships, and emphasize the importance of scale when making suggestions to direct future studies.

For the purposes of this paper, an oceanographic feature is defined as a physical oceanographic phenomenon distinguishable from the surrounding environment, based on gradients in physical properties, and which has measurable effects on organisms and/or biological processes.

2. *Approach*

To compile a list of studies published in peer-reviewed journals that directly assessed relationships between seabirds and specific oceanographic features, I conducted a literature search using the approach of Tremblay et al. (2009). I searched the Web of Science database with the key word "seabird" along with relevant key words, which in this case included the following: front, eddy, gyre, oceanograph*, geostrophic, boundary, Gulf Stream, Kuroshio, Oyashio, Benguela, Canary, Azores, Peru, Humboldt, Bonney, Costa Rica Dome, Transition Zone Chlorophyll Front, seamount, headland, island wake, jet, plume, tide, warm core ring, cold core ring, upwelling, shelf break, Langmuir, shear, physical, ice, convergence, divergence, and current. These search terms were generated from oceanographic features discussed in Hunt and Schneider (1987), with the addition of several similar or related features not mentioned in that text that are known to be important foraging areas for marine predators (e.g., Bonney upwelling, Transition Zone Chlorophyll Front; Bayliss et al. 2008, Polovina et al. 2001). Studies published before July 2010 were included in the analysis.

Within the studies identified using the approach outlined above and references therein, I focused on studies investigating direct effects of oceanographic features on seabird foraging habitat through physical forcing or enhanced local productivity. I did not include studies focused on long term changes to oceanographic features (i.e., climate) or systems unless these studies also included an analysis of the physical or biological properties of the feature relative to seabird foraging habitat (i.e., effects at the event scale, or the time scale at which biophysical interactions within the features would be expected to affect foraging habitat). Other review papers and non-peer-reviewed literature were not included in the analysis due to the emphasis herein on comparing methodologies, sampling designs, and analyses, which are often not included at an appropriate level of detail in review papers or in publications such as book chapters. In addition, studies investigating seabird distribution relative to water masses or habitat variables that could not be used to identify a specific oceanographic feature (e.g., raw sea surface temperature or chlorophyll-a measurements rather than gradients in these properties that could be used to identify fronts) were also excluded.

The approach of Tremblay et al. (2009) provides several important considerations for evaluating studies of seabird-habitat relationships, and I applied metrics used in that paper to the more specific goal of investigating seabird habitat use relative to oceanographic features. These include evaluating how the number of publications on this subject has changed through time, an analysis of the statistical techniques used to evaluate seabird-habitat relationships, and a comparison of the number of ship-based vs. telemetry studies of seabirds for specific features. Initially, I examined trends in publication over time and the general location of the studies conducted (Figure 1). I categorized the following oceanographic phenomena: bathymetric features; vertical clines (thermocline or pycnocline); eddies; fronts; frontal regions; gyres; ice-related features (e.g., ice edge, ice cover); internal waves; plumes; tidal features (e.g., tidal currents, tidal jet); or upwellings. I distinguished fronts from frontal zones, such as the Antarctic Polar Front or the sub-tropical convergence, which I considered to be zones of interaction between different water masses that are fairly stationary in space and time (see Kostianoy and Nihoul 2009). Several studies investigated multiple features; in these cases I included each of the features in the analysis. I discuss advances in research for each of these types of oceanographic features, and highlight findings that advance our understanding of trophic transfer within these systems or improve our predictive capacity of seabird foraging habitat.

I then investigated issues of scale, sampling and analysis to assess the approaches used in previous studies of seabirds and oceanographic features. I categorized oceanographic features according to spatial scale and temporal persistence. I used the following categories to define spatial scale: fine (1- 10 km); meso (10- 200 km); large (200- 1000 km); macro (1000- 3000 km); and mega (> 3000 km). These categories were adapted from Hunt and Schneider's (1987) review to reflect the definition of meso-scale features typically used in the oceanographic literature (e.g., Kinder et al. 1980, Doney et al. 2003). I categorized features based on the greatest spatial scale evident from their description. For example, the front studied by Jahncke et al. (2005) showed widths of approximately 10 to 45 km in different sampling locations, but the front appeared to occur along the length of the 50 m isobath (over a distance of more than 1000 km), so I considered this to be a macro-scale feature. I categorized temporal persistence as described in Wakefield et al. (2009): features in a steady state show little to no change through time (e.g., the Polar Front), while features with a characteristic periodicity change at a predictable time scale (e.g., tidal fronts), and episodic features (e.g., eddies formed by Gulf Stream meanders) are more transient through time.

I also determined the research approaches used by individual studies: ship-based surveys or telemetry techniques to identify seabird foraging areas; quantitative analyses (defined as the use of statistical analyses to examine trends in seabird abundance, distribution or movements relative to physical or biological characteristics of the oceanographic features); oceanographic surveys; prey surveys; measurements in the vertical dimension (any measurements of physical or biological properties at depth); and analyses of microhabitats within oceanographic features (any habitats defined within the study that occurred at a finer spatial scale than the feature being investigated, e.g., eddy cold core vs. warm filament within a Gulf Stream frontal eddy). I further categorized oceanographic surveys according to the means of data collection (*in situ* methods using independent instrumentation, *in situ* measurements using species-mounted instrumentation, or remotely sensed data), and determined whether surveys of prey were either qualitative or quantitative. Quantitative prey surveys estimated the biomass of prey in the water column; diet analyses were considered to be qualitative estimates of prey in the oceanographic features being investigated. In addition, I evaluated the spatial and temporal scale of the physical or prey surveys and the extent of the shipboard surveys or seabird tracks relative to the scale of the feature being investigated.

To examine trends in the methods and analyses used in studies of seabirds and oceanographic features, I used all studies identified using the above criteria. I discuss studies of seabird habitat use in different types of oceanographic features, and then indicate several themes that should be considered in moving from descriptive studies towards research addressing causation. Using examples of important progress made to date, I make suggestions for how seabird research could achieve a more mechanistic understanding of these systems.

3. Studies of seabirds and oceanographic features

Using the criteria described above, I identified a total of 117 studies of seabirds and oceanographic features published in peer-reviewed journals using the Web of

Science database. More studies were conducted in polar (51) and temperate regions (38) than in tropical oceans (27; one telemetry study was global in extent).

Recent advances in satellite remote sensing technologies and modeling techniques (e.g., Joint and Groom 2000, Zainuddin et al. 2006, Miller 2009) and telemetry techniques (Phillips et al. 2007a, Hart and Hyrenbach 2009) have allowed insights into the effects of oceanographic features on foraging seabirds at a global scale. The data supplied by these technologies have profoundly improved our ability to identify and sample oceanographic features used by foraging seabirds. The number of studies examining seabirds and specific oceanographic features has increased steadily in each decade, with approximately half of the studies occurring in the last decade (Table 1). The use of these data types to improve our understanding of these systems will be discussed in further detail below.

Nearly a third of the features examined by studies in the literature search were fronts (Figure 2a). A number of studies also examined seabirds in relation to frontal regions, upwellings, eddies, ice cover and ice edge regions, and bathymetric features, but few studies investigated the effects of gyres, internal waves, tidal features, vertical gradients (thermoclines, haloclines or pycnoclines), and freshwater plumes. Observed patterns of seabird habitat use in relation to each of these types of features are reviewed in the following sections. Discussions are limited to studies that make important contributions to our understanding of the importance of oceanographic features to seabird foraging habitat or to our knowledge of food web dynamics within these systems. In particular, understanding how different seabird species with different prey preferences and foraging strategies vary in their use of oceanographic features is a key component of understanding the biological effects of these features.

3.1 Fronts

Ocean fronts are areas of high horizontal physical gradients, typically temperature or salinity, which are formed by the meeting of two water masses. Fronts are ubiquitous oceanographic features that occur at a variety of scales and are often easy to identify remotely, thus facilitating sampling and analysis. Many studies have found that fronts are regions of enhanced biomass, and the physical processes leading to this local enhancement vary widely within different frontal systems (e.g., tidal fronts, topographic fronts, estuarine fronts, water mass fronts, upwelling fronts; Franks 1992, Olson 1994, Mann and Lazier 1996). The effects of both physical forces and physiological processes combine to result in concentrations of biomass at fronts (Franks 1992).

Many seabird species have been found to be positively associated with fronts, both in ship-based (e.g., Brown 1978, Kinder et al. 1983, Haney 1985a; Haney and

McGillivary 1985a,b, Abrams and Miller 1986, Mehlum et al. 1988, Haney 1989, Veit and Hunt 1992, Decker and Hunt 1996, Hunt et al. 1996, Hunt and Harrison 1990, Skov and Durinck 1998, O'Driscoll 1998, Ainley et al. 2005, DiGiacomo et al. 2002, Grémillet et al. 2006, Louzao et al. 2009) and telemetry studies (e.g., Charrassin and Bost 2001, Suryan et al. 2006, Cotte et al. 2007). Relationships between fronts and foraging seabirds have been demonstrated at a range of scales. Convergence and divergence fronts or fronts produced by the interaction of tidal currents with local bathymetric features can affect foraging seabirds at fine scales (e.g., Brown and Gaskin 1988, Hunt et al. 1998). Examples of meso-scale fronts included tidal and sea surface temperature fronts identified from satellite imagery (e.g., Begg and Reid 1997, Cotte et al. 2007, Louzao et al. 2009). Gulf Stream and mid-shelf fronts affect the distribution of seabirds at large scales (e.g., Haney 1985a, Haney and McGillivary 1985a, b), while macro-scale fronts associated with the continental shelf also influence the distribution of foraging seabirds (e.g., Veit and Hunt 1991, Jahncke et al. 2005).

Several studies examining multiple species found that some seabirds were associated with fronts while others were not (Veit and Hunt 1991, Begg and Reid 1997, Hoefer 2000, Ladd et al. 2005, O'Hara et al. 2006, Camphuysen 2007). In some cases, the differential use of fronts as foraging habitat has been linked to the distribution of prey. For example, Hunt et al. (1998) and Russell et al. (1999) found that prey species were aggregated differentially in a frontal system and that least, crested, and parakeet auklets (*Aethia pusilla*, *A. cristatella*, and *A. psittacula*, respectively) were separated spatially reflecting the relative distributions of their prey. Begg and Reid (1997) found some evidence for spatial partitioning by species within a front in the Irish Sea and suggested that this partitioning was facilitated by the use of different foraging strategies.

Seabird species may also partition resources by exploiting different fronts or features. For example, Schneider et al. (1982) found that northern fulmars (*Fulmarus glacialis*) and fork-tailed storm-petrels (*Oceanodroma furcata*) were associated with the shelf break front in the Bering Sea while murres (*Uria* spp.) and shearwaters (*Puffinus* spp.) were associated with a shallow front on the continental shelf. In a study by Ladd et al. (2005), surface feeding species were associated with tidal features or Langmuir circulation, while short-tailed shearwaters foraged at fronts and sub-surface feeders were observed in turbulent, well-mixed areas. Ainley et al. (2005) found that different seabird species were significantly associated with one of three different fronts within the California Current. Within these features, species also exhibited preferences for different sides of the fronts (cooler, more saline waters inshore vs. warmer, less saline waters offshore).

Schneider et al. (1987) found that seabird abundance was greater at stronger flow gradients than at weaker flow ones, and that the strength of the surface flow gradients had a greater effect on seabird abundance than the presence of a front. Thus, studies of seabird prey under a variety of gradients would be useful in understanding patterns of seabird abundance. A flow gradient of a given strength (dependent on the swimming speed of the prey species) may be required to aggregate seabird prey, or increasing flow gradients may aggregate increasingly higher densities of prey, while seabirds show a threshold response to prey density, as observed in other marine predators (Piatt and Methven 1992, Hines et al. 1997, Sims 1999). These observations indicate that a description of both oceanographic features and prey fields is critical to understanding the interplay between physical and biological factors and their influence on seabird foraging.

3.2 Frontal regions

Frontal zones were distinguished from fronts as zones of interaction between water masses that are fairly stationary in space and time. Frontal regions can create regions of enhanced biomass (e.g., Laubscher et al. 1993, Detmer and Bathmann 1997, Moore et al. 1999), though some studies suggest that multiple meso-scale effects occur within these larger frontal regions (e.g., Brown and Landry 2001). Frontal regions have important effects on seabird abundance, distribution and foraging behavior, as well as providing important migratory stopover sites. These conclusions have been demonstrated using both ship-based (Ainley and Jacobs 1981, Griffiths et al. 1982, Abrams 1985, Pakhomov and McQuaid 1996, Guinet et al. 1997, Spear et al. 2001, van Franecker et al. 2002, Woehler et al. 2006, Hyrenbach et al. 2006, 2007) and telemetry methods (Jouventin et al. 1994, Rodhouse et al. 1996, Bost et al. 1997, Hull et al. 1997, Waugh et al. 1999, Koudil et al. 2000, Charrassin and Bost 2001, Gauthier-Clerc et al. 2002, Catry et al. 2004, Shaffer et al. 2009, Egevang et al. 2010). Apart from the studies by Spear et al. (2001) and Egevang et al. (2010), all studies of seabird distribution in relation to frontal zones were conducted in relation to the three mega-scale Southern Ocean circumpolar features: the subtropical; sub-Antarctic; and Antarctic Polar fronts, which I highlight in this section.

Ship-based studies have demonstrated high densities of seabirds at the Antarctic Polar Front (APF; Griffiths et al. 1982, Pakhomov and McQuaid 1996, van Franeker et al. 2002, Woehler et al. 2006) and telemetry studies, in combination with diet analyses or surveys of seabird prey, have shown the importance of this frontal region to foraging seabirds (Jouventin et al. 1994, Rodhouse et al. 1996, Bost et al. 1997, Guinet et al. 1997, Hull et al. 1997, Waugh et al. 1999, Koudil et al. 2000, Charrassin and Bost 2001, Gauthier-Clerc et al. 2002, Catry et al. 2004, Shaffer et al. 2009). For example, studies of telemetered grey-headed albatross (*Thalassarche chrysostoma*), conducted in conjunction with prey surveys, indicated the presence of a cephalopod prey community in the APF similar to that exploited by these albatrosses (Rodhouse et al. 1996). The authors suggest that eddies and other meso-scale features associated with the APF provide predictable foraging areas for grey-headed albatrosses. The APF is also important to foraging king penguins (*Aptenodytes patagonicus*); these birds increase their food intake within the APF and their foraging range is affected by annual variability in the position of the APF (Bost et al. 1997). Charrassin and Bost (2001) suggested that king penguins used the APF in summer and foraged further south when prey became less accessible in the autumn and winter. Guinet et al. (1997) found that both the sub-Antarctic Front and the APF provided important foraging areas for king penguins, and suggested that the sub-Antarctic Front provides reliable but less accessible prey, while the APF has a seasonally abundant and accessible prey base. Gauthier-Clerc et al. (2002) found that food provisioning in king penguins during hatching is influenced by the predictability of the position of the APF, indicating the importance of this feature to the foraging habitat and reproductive success of this species.

As with fronts, several studies found that the importance of frontal regions to seabirds varied among species. Waugh et al. (1999) found that grey-headed albatrosses foraged primarily at the APF while black-browed albatrosses (*Thalassarche melanophrys*) spent a much lower proportion of their time foraging in this region. Hyrenbach et al. (2006) found that wedge-tailed shearwaters (*Puffinus pacificus*), sooty terns (*Onychoprion* *fuscatus)* and bridled terns (*Onychoprion anaethetus*) were associated with a convergence zone, while great-winged petrels (*Pterodroma macroptera*)were not. As with fronts, there is evidence that these differences in the habitat use of different seabird species were driven by underlying differences in the foraging ecology of these species and the distribution of their prey. In the Eastern Tropical Pacific, Spear et al. (2001) found that planktivorous species were associated with the Equatorial Front while piscivores were more abundant in waters of the North Equatorial Countercurrent. van Franeker et al. (2002) found that planktivorous seabirds were associated with fine-scale gradients within the APF while fish- and squid-eating seabirds were not. However, at a broader scale, increases in all seabird densities were observed in APF. The authors suggested that the effects of the APF were diffused in space and time for upper trophic level predators due to time lags between responses of different trophic levels and to variability in the APF. Pakhomov and McQuaid (1996) note the importance of prey availability, rather than solely physical parameters, to predicting seabird distributions (see also Gremillet et al. 2008). This is logical, since it is the availability of prey, rather than a particular physical parameter, that influences seabird fitness. To better understand the links between the foraging ecology of different seabird species and the hydrographic processes occurring at frontal regions, we need to better understand how physical factors affect the availability and species composition of prey in horizontal, vertical and temporal dimensions. Examining these patterns within broad scale frontal regions initially may be useful in informing finer-scale studies of smaller gradients occurring within these larger systems.

3.3 Rings and eddies

Oceanic eddies are rotating water masses that are typically formed from meanders of strong fronts such as the Gulf Stream front. Larger, longer-lived eddies, such as those shed from the Gulf Stream north of Cape Hatteras which persist for approximately one year, are often termed "rings" (Olson 1991). Eddies serve important functions in many marine systems, enhancing upwelling and bringing nutrients into the euphotic zone, thus stimulating primary production (Yoder et al. 1981, Lee et al. 1981, Kimura et al. 1997, McGillicuddy et al. 1998, Muraleedharan et al. 2007) and creating important sources of food for mid- and upper trophic levels (e.g., Atkinson and Targett 1983, Haney 1986a, b, Lobel and Robinson 1986, 1988). These features can have profound influences on ocean productivity; as an example, episodic upwelling produced by eddies is thought to supply a significant fraction of the nutrients required to sustain primary productivity in the subtropical ocean (McGillicuddy et al. 2007).

Eddies affect seabird abundance and distribution in a variety of settings. Studies in the North Atlantic (Haney 1986a, b, 1987a, 1989), the North Pacific (Yen et al. 2006), the Gulf of Mexico (Ribic et al. 1997), the Indian Ocean (Weimerskirsch et al. 2004, Hyrenbach et al. 2006, Kai et al. 2009), the South Atlantic Ocean (Camphuysen 2007) and the Southern Ocean (Nel et al. 2001, Cotte et al. 2007) demonstrated associations between seabirds and meso-scale eddies, while one study found that seabirds were associated with a large-scale eddy (a warm core ring) in the North Atlantic (Haney 1987b).

Eddies appear to have differential effects on seabird species; some species are more abundant within eddies while other species are not (Haney 1987b, Ribic et al. 1997, Hyrenbach et al. 2006, Yen et al. 2006). In two of these studies, negative associations were observed between eddies and seabird species (Ribic et al. 1997, Yen et al. 2006). Ribic et al. (1997) found that at certain times of the year, herring gulls (*Larus smithsonianus*), laughing gulls (*Larus atricilla*) and terns (*Sterna* spp.) were more likely to be found outside than inside eddies. Yen et al. (2006) found that black-footed albatrosses, Leach's storm-petrels (*Oceanodroma leucorhoa*) and red phalaropes (*Phalaropus fulicarius*) were positively associated with eddies, but northern fulmars, dark shearwaters (sooty and short-tailed shearwaters (*Puffinus tenuirostris*)) and red-necked phalaropes avoided these features.

Eddies can affect productivity in different ways; upwelling of nutrient-rich waters occurs at the centre of cold core (cyclonic) rings and eddies and is associated with increased primary and secondary productivity (Ring Group 1981, Yoder et al. 1981, 1983, Atkinson and Target 1983). The situation in warm core rings and eddies is more complicated; down-welling occurs in the centre of warm core (anti-cyclonic) rings and eddies, where nutrient-depleted waters are typically observed. However, warm core eddies can be associated with increased productivity through complex mixing and flow mechanisms (Yentsch and Phinney 1985, McCarthy and Nevins 1986). Seabirds appear to respond differently to warm and cold core eddies. Several studies have found that seabirds are positively associated with cold core eddies (Haney 1986a, b, 1987a, 1989, Cotte et al. 2007), while seabird responses to warm core eddies appear to be more complex. Haney (1987b) found that overall seabird abundance in a Gulf Stream warm core ring was much higher than seabird abundance in the Sargasso Sea, but was slightly lower than values in slope and shelf waters. Audubon's shearwaters (*Puffinus lherminieri*) were the only species that were significantly more abundant within the warm core ring. Ribic et al. (1997) found that pomarine jaegers (*Stercorarius pomarinus*) were the only species that were more likely to be observed within the warm core eddies observed during the winter. Yen et al. (2006) found that black footed albatrosses and red phalaropes were associated with anti-cyclonic eddies in the California Current system, while Leach's storm-petrels were associated with both cold and warm core eddies. Camphuysen (2007) found that great winged and Leach's storm-petrels were associated with both cold and warm core eddies. Rodhouse et al. (1996) suggested that squid associated with warm core rings in the Southern Ocean could provide predictable foraging areas for foraging grey-headed albatrosses.

Studies of seabird habitat use relative to eddies and rings have suggested that seabirds may target the edges of these features. Weimerskirch et al. (2004) found that great frigatebirds (*Frigata minor*) appeared to be associated with the edges of cold core eddies in the Mozambique Channel. Grey-headed albatrosses in the southern Indian Ocean also appear to feed at the edge of both warm and core eddies (Nel et al. 2001). Camphuysen (2007) suggested that great-winged petrels and Leach's storm-petrels were particularly abundant at the interfaces between warm and cold core eddies. Kai et al. (2009) found that great frigatebirds in this region tracked Lagrangian coherent structures, which can be used to detect transport barriers, vortex boundaries and filaments in the physical environment. Our understanding of seabird associations with eddy edges would be enhanced with studies of prey distributions within these features.

Zooplankton and fishes are accumulated at the edges of these eddies, or just outside of them (Olson and Backus 1985, Froneman and Perissonotto 1996, Lima et al. 2002). This may explain the confounding results of studies investigating seabird associations with warm core eddies; analyses of seabirds relative to fronts associated with the margins of eddies would be particularly useful in this regard. Increased productivity in the eddy core of cyclonic eddies has been documented in a number of studies (e.g., Ring Group 1981, Lobel and Robinson 1988, Zimmerman and Biggs 1999, Ressler and Jochens 2003, Gasca 2003). However, the size and abundance of various prey species can differ between core regions of eddies and outside waters features (Ring Group 1981) and between the core and periphery of cold core eddies (Lobel and Robison 1988, Huntley et al. 2000). Thus, seabird preference for particular prey species could explain their associations with the edges, rather than the core, of cyclonic eddies. Haney (1986a) found that seabird species were segregated by water mass within Gulf Stream frontal eddies and suggested that the preference for different water masses was influenced by the feeding strategies of the birds. These findings highlight the importance of considering micro-habitats and conducting concurrent prey surveys within oceanographic features.

Eddies and rings can persist for days to months, and the age of eddies and rings (the amount of time elapsed since their formation) are likely of great importance to the biological associations within these features and their use as foraging habitat for seabirds. The age of Gulf Stream frontal eddies is significantly correlated with species diversity and richness, while trends in species composition data suggested that the relative abundance of plankton- and nekton-feeding seabirds decreased and increased, respectively, with eddy age (Haney 1989). Phenological prey studies of Gulf Stream frontal eddies have not been conducted to date, but studies of longer-lasting Gulf Stream cold core rings have indicated that important changes occur in the prey field of these features through time. The abundance, species composition and depth distribution of zooplankton and fish in Gulf Stream cold core rings change as these features age (Ortner et al. 1978, Wiebe and Boyd 1978, Backus and Cradduck 1982), which likely influences foraging opportunities for seabirds. Patterns of seabird habitat use in oceanic eddies should be considered relative to both the spatial and temporal dimensions of these features.

3.4 Upwellings

Upwellings occur when nutrients from deep waters are brought into the euphotic zone. This upwelling of nutrients, along with stratification of the water column causing phytoplankton to be retained in the euphotic zone, is central to high biological productivity in marine systems (Mann and Lazier 1996). In coastal upwelling systems, strong seasonal winds cause a net movement of water offshore, causing surface water to be replaced by deeper, nutrient-rich water. Studies have examined seabirds foraging in upwelling regions, at fine-scales (Brown and Gaskin 1988), meso-scales (Haney 1985b), and within large coastal upwelling systems (e.g., Brown 1978, Duffy 1989, Leopold 1993, Oedekoven et al. 2001, Becker and Besseinger 2003, Burger 2003, Weichler et al. 2004, Ainley et al. 2005, 2009, Yen et al. 2006, Gremillet et al. 2008, Ronconi and Burger 2008, Zavalga et al. 2008, Magalhães et al. 2008, Peery et al. 2009). Ship and land-based observations (Brown 1979, Haney 1985b, Mercier and Gaskin 1985, Brown and Gaskin 1988, Duffy 1989, Leopold 1993, Oedekoven 2001, Becker and Besseinger 2003, Burger 2003, Weichler et al. 2004, Ainley et al. 2005, 2009, Vilchis et al. 2006, Yen et al. 2006, Ronconi and Burger 2008), and telemetry techniques (Gonzalez-Solis et al. 2007, Gremillet et al. 2008, Zavalga et al. 2008, Magalhaes et al. 2009, Peery et al. 2009) have been used to examine seabird associations with upwelling at various scales.

Several studies have demonstrated important effects of upwelling regions on seabird foraging behavior. Becker and Beissenger (2003) found that marbled murrelets (*Brachyramphus marmoratus*) were able to forage closer to their nesting habitat during periods of intense upwelling. Cory's shearwaters (*Calonectris diomedea*) exploited upwelling areas during long foraging trips, which are typically used to replenish energy reserves of adult birds after using short trips to procure food for their chicks (Magalhães et al. 2009). Peery et al. (2009) found that variation in the intensity of upwelling had important influences on the foraging behavior of marbled murrelets over short time scales.

Predictable upwelling regions can create important foraging habitat for seabirds during migrations. In the Bay of Fundy, localized tidally-induced upwelling produces aggregation of prey items in surface waters that are exploited by red-necked phalaropes at a migratory stop-over site (Mercier and Gaskin 1985). Brown and Gaskin (1988) found that fine-scale upwelling and convergences were the primary factor driving the pelagic abundance and distribution of phalaropes in the Bay of Fundy. However, the specific mechanism of prey aggregation in these studies has not been identified to date. Similarly, a telemetry study demonstrated the importance of upwelling systems (Canary, Benguela and Brazilian Currents) to the wintering habitat of Cory's shearwaters (Gonzalez-Solis et al. 2007).

As observed with other oceanographic features, seabird species differ in their use of upwelling areas. Brown (1979) examined seabird distributions in the Senegal upwelling and found differences in species composition between zones of upwelling. Yen et al. (2006) found that black-footed albatrosses, Leach's storm-petrels and red phalaropes were associated with the California Current, while Cook's petrels (*Pterodroma cookii*), dark shearwaters and red-necked phalaropes were more prevalent away from the Current. In the Eastern Tropical Pacific (ETP), Leach's and wedge-rumped storm-petrels (*Oceanodroma tethys*) appear to be associated with upwelling regions while wedge-tailed shearwaters and Juan Fernandez petrels (*Pterodroma externa*) are associated with areas of low productivity and tropical surface waters, respectively (Vilchis et al. 2006). Haney (1985b) suggested that band-rumped storm-petrels occurring off the coast of the southeastern United States may use patchy, localized upwellings more frequently than other storm-petrel species in this region. Differences in the upwelling areas used by red and red-necked phalaropes in the Bay of Fundy were associated with differences in their prey species; red-necked phalaropes foraged on larger copepods in the north-west of the Bay, while red phalaropes foraged in areas with lower concentrations of smaller copepods further to the south (Brown and Gaskin 1988).

The results of these studies stress the importance of considering both physical and biological factors when investigating seabirds relative to upwelling processes. Ainley et al. (2009) found that when models included prey data, physical factors (distance to upwelling front) became less important in explaining seabird occurrence. Ainley et al. (2005) found that micronekton and zooplankton were more abundant in waters along the inshore edge of the upwelling in the California Current. The authors suggest that the presence of more recently upwelled water at this location was responsible for this region of enhanced productivity, which resulted in increased prey availability and hence seabird abundance.

3.5 Ice edges, ice cover and icebergs

Many studies have examined the importance of ice cover to seabird demography, survival, and breeding schedules, particularly in the context of climate change (e.g., Croxall et al. 1992, Fraser et al. 1992, Barbraud et al. 2000, Wilson et al. 2001, Croxall et al. 2002, Gaston et al. 2005, 2009, Olivier et al. 2005, Laidre et al. 2008). In addition, a number of studies have related ice cover or extent to general patterns of seabird diet or distribution (e.g., Cline et al. 1969, Ainley et al. 1978, 1984, Chaulk et al. 2007). Studies of foraging seabirds in relation to sea ice have been primarily conducted in the Antarctic, where seasonal sea ice plays a pivotal role in the annual cycle of Antarctic krill (*Euphausia superb*; Daly 1990), an important prey species for seabirds and many other predators in the Southern Ocean. Hunt (1991) went so far as to suggest that ice cover is the most important physical feature influencing seabird habitat in the Southern Ocean. Several studies have examined distributions of foraging seabirds in relation to particular ice features, such as ice edges, icebergs, and ice-associated fronts that are thought to create patches of enhanced productivity. These studies have included ship-based surveys (Bradstreet 1979, 1980, 1982, Ainley and Jacobs 1981, Bradstreet and Cross 1982, Plotz et al. 1991, Ainley et al. 1994, Smith 2007, Beaulieu et al. 2010) and telemetry studies (Bost et al. 2004, Egevang et al. 2010).

The "ice edge" is contained within the Marginal Ice Zone (MIZ), a region forming the interface between the open sea and pack ice that is an important foraging area for seabirds, both in the Arctic (e.g., Mehlum 1990, Hunt et al. 1996) and in the Southern Ocean (Hunt 1991). In the Arctic, under-ice habitat provides refuge and foraging opportunities for seabird prey, e.g. Arctic cod (*Boreogadus saida*; Bradstreet 1980, 1982) and thus seabirds foraging at the ice edge have increased accessibility to prey items that are associated with under-ice habitats (Hunt 1991). As such, ice edges are important physical features structuring the food web in the Arctic, and provided enhanced foraging opportunities for seabirds and other marine predators (Bradstreet and Cross 1982; Gaston et al. 2009). In the Canadian High Arctic, Bradstreet (1979) found that thick-billed murres (*Uria lomvia*) were associated with ice edges and occurred in higher densities on offshore ice edges than on coastal ice edges. Black guillemots (*Cepphus grille*) were associated with ice edges and with cracks in land-fast ice, but showed no preference for coastal or offshore ice edges. Bradstreet (1980) studied murre and guillemot diets in relation to habitat use at offshore and coastal ice edges and found that the species composition of the diets differed between the two species and between coastal and offshore ice edge habitats. These two species foraged in different parts of the water column at ice edges. Ice edges were also found to be important foraging areas for northern fulmars in Arctic regions (Bradstreet 1982, McLaren 1982). The MIZ appears to influence the distribution of short-tailed shearwaters during the summer breeding season as they follow its retreat (Woehler et al. 2006).

The mechanism by which the MIZ creates enhanced foraging opportunities for seabirds and the spatial extent of these effects differs in the Southern Ocean. The melting of the pack ice in the spring and summer in the Southern Ocean stratifies the water column seaward of the pack ice, which initiates plankton blooms and generates trophic effects that can extend far beyond the ice edge (Smith and Nelson 1985). These ice edge blooms provide an important source of food for krill, creating enhanced aggregations of prey seaward of the ice edge (Daly and Macaulay 1991, Brierley et al. 2002). Several studies have evaluated the importance of ice edge habitats to foraging seabirds in the Antarctic. Ainley et al. (1998) found that foraging snow petrels (*Pagodroma nivea*) were associated with the ice edge, while Ainley and Jacobs (1981) observed peaks in the density of surveyed seabirds occurred at the ice edge (Ainley and Jacobs 1981, Plotz et al. 1991). Ainley et al. (1994) found that proximity to ice edge was an important habitat variable for: Antarctic prions (*Pachyptila desolata*); diving (*Pelecanoides* spp.), Kerguelen (*Lugensa brevirostris*), blue (*Halobaena caerulea*), and cape petrels (*Daption capense*); chinstrap penguins (*Pygoscelis antarcticus*); and southern giant fulmars (*Macronectes giganteus*). Veit and Hunt (1991) found that individual seabird species were associated with ice edge, although overall seabird abundance was not. These authors found that aggregations of snow petrels were observed at the ice edge more often than would be expected at random, and aggregations of Arctic terns (*Sterna paradisaea*) also appeared to be associated with the ice edge. The MIZ provides important foraging habitat for Arctic Terns, constituting the main wintering region for this species (Egevang et al. 2010). King penguins used the MIZ more than other regions of ice cover and travelled more slowly through the MIZ, indicating the importance of this habitat as a foraging area (Bost et al. 2004). These authors suggest that during the winter, myctophid fish may be more abundant in the MIZ than in the polar frontal zone, where the penguins forage during the summer, and that the MIZ provides a predictable feeding area during times of low food availability in the polar frontal zone.

At a fine scale, icebergs and ice floes can enhance primary production and concentrate krill, supporting aggregations of seabirds (Daly 1990, Smith et al. 2007, Schwarz and Schodlock 2009). Smith et al. (2007) found that seabird abundance and the number of seabird species observed was significantly greater closer to icebergs than farther away.

3.6 Bathymetric features

Bathymetric features, such as continental shelf breaks, banks, seamounts and canyons can influence local oceanography and influence primary and secondary productivity (Dower and Mackas 1996, Holm-Hansen et al. 2005). Independent of seabird research, many studies have evaluated the processes creating aggregations of zooplankton and fish relative to these features (e.g., Werner et al. 1993, Townsend and Pettigrew 1996, Genin 2004). Several studies have suggested that bathymetric features have important effects on seabird foraging habitat, using ship-based surveys (Schneider et al. 1982, Plotz et al. 1991, Coyle et al. 1992, Hay 1992, Haney 1995, Hunt et al. 1996, Burger 2003, Parrish and Zador 2003, Yen et al. 2004, 2005, Ribic et al. 2008) and telemetry (Egevang et al. 2010, Paiva et al. 2010).

Haney et al. (1995) found that seabird density and biomass were elevated in the vicinity of the Fieberling Guyot seamount in the North Pacific and suggested that changes in the deep-scattering layer were responsible for creating enhanced foraging habitat for seabirds. Several studies (e.g., Ainley and Jacobs 1991, Haney and McGillivary 1985b) observed peaks in bird density at the fronts associated with the shelf break, while Woehler et al. (2006) found that the foraging distribution of short-tailed shearwaters was not related to the shelf break in the Southern Indian Ocean. In coastal California, Yen et al. (2004) found that distance to the shelf break and the Cordell Bank seamount were important predictors of Cassin's auklet distribution and that auklets showed increased aggregation at this seamount over several years.

Seabirds are also associated with other underwater topographic features, including canyons and banks. Yen et al. (2005) found that fork-tailed storm-petrels were associated with steep topography and that in some years Cassin's auklets were associated with an underwater bank. This study showed that bathymetric complexity was among the most important predictors of seabird habitat in the coastal ecosystem.

Both the Agadir canyon and an area with underwater banks and seamounts near the northwestern African continental shelf appeared to be important foraging areas for Cory's shearwaters (Paiva et al. 2010). Burger (2003) found that prey densities were highest at the edges of the Juan de Fuca Canyon and suggested that proximity to the canyon was an important habitat variable for seabirds. Plotz et al. (1991) found that the abundance of Antarctic petrels, snow petrels, and Adelie penguins (*Pygoscelis adeliae*) was higher in pack ice in the Maud Rise region in the Weddell Sea, which is considered to be a productive region creating large krill aggregations under the sea ice. Distance to the Marguerite Trough was an important habitat variable for Adelie penguins (Ribic et al. 2008), a region along the Mid-Atlantic Ridge serves as a stopover region for Arctic terns and sooty shearwaters during both northward and southward migrations (Egevang 2010, Hedd and Montevecchi unpubl.). In the Bay of Fundy, strong tidal flows occurring over steep bottom topography is thought to cause aggregations of prey in surface waters, creating foraging habitat for seabirds (Braune and Gaskin 1982, Brown and Gaskin 1988).

Few studies of seabirds in relation to bathymetric features have included surveys of prey distribution. The seamount studied by Haney (1995) was not associated with significant prey enhancement, though observations from Multiple Opening and Closing Environmental Sensing System (MOCNESS) tows suggested that seamount effects may have influenced the prey species and the size of prey occurring over the seamount. Coyle et al. (1992) found that the highest densities of thick-billed and common murres typically occurred in close proximity to the highest densities of prey, and suggested a submarine ridge likely played a role in creating these prey aggregations.

Overall, few studies of seabirds have directly addressed the physical effects of bathymetric features. To tease apart the effects of bathymetric features from those of other habitat factors, studies should be directed at determining how physical and biological processes are affected by the presence of bathymetric features, and how this in turn affects foraging seabirds. Alternatively, one could compare oceanographic processes, prey density and the distribution of seabirds in areas where bathymetric features are present and absent. In particular, synoptic oceanographic, prey and seabird studies are needed to determine how bathymetric features affect the aggregation of seabird prey.

3.7 Vertical gradients

The depth and location of vertical gradients play an important role in structuring plankton and fish distributions (e.g., Denman and Gargett 1983, Mackas et al. 1985, Cooney 1989, Olla and Davis 1990, Swartzman et al. 1994, Gray and Kingsford 2003). Vertical gradients often distinguish the habitats of seabirds with different diving abilities or prey species (e.g., Haney 1991, Ballance et al. 1997, Ribic et al. 1997b, Oedekoven et al. 2001, Spear et al. 2001, Vilchis et al. 2006, Ainley et al. 2009). Haney (1991) found that the vertical structure of the water column has different effects on the distribution of alcid species. Auklet distribution was more strongly related to pycnocline depth, thickness, and strength than that of larger alcids, likely due to restricted diving abilities affecting the accessibility of prey at different depths. The author suggests that larger auklets were not associated with the pycnocline due to a reliance on larger or benthic prey species not associated with this gradient. In the Southern Ocean, king penguins were found to forage below the thermocline, suggesting that prey was aggregated below the surface mixed layer (Charrassin and Bost 2001), though the oceanographic processes leading to this aggregation were not investigated. Balance et al. (1997) found that thermocline depth was an important predictor in discriminating between the three main flocks of seabirds observed, and suggest that competition and energetic constraints associated with flight costs determine flock structure in regions of low vs. high productivity. These studies emphasize the need to understand the effects of oceanographic processes on the prey species and foraging habitats of seabirds with different foraging strategies, flight capabilities and diving depths.

3.8 Tidal features

Foraging seabirds are often associated with tidally-driven oceanographic features. This finding has been demonstrated using both ship-based (Decker and Hunt 1996, Hunt et al. 1996, Begg and Reid 1997, Durazo et al. 1998, Slater 2003, Zamon 2003, Jahncke et al. 2005, Ladd et al. 2005) and telemetry techniques (Grémillet et al. 2006). Most studies did not investigate temporal trends of habitat use at these features, although a few found that temporal components of these features were important factors. Zamon (2003) related counts of seabirds to the tidal phase and noted that the probability of encountering prey was associated with tidal phase in a narrow pass in the San Juan Islands. However, the mechanism by which tidal jets created regions of increased prey for foraging seabirds in this region was unclear. In the Bay of Fundy, Braune and Gaskin (1982) found that numbers of feeding birds and availability of their prey (insects, euphausiids, fishes) were related to tidal phase, likely due to interactions of strong tidal currents with bathymetry. In a nearby study area, Mercier and Gaskin (1985) found no significant difference in numbers of phalaropes or their prey between tide phases and suggested local topography allowed plankton to be aggregated during both ebb and flood tides. Further studies would be useful in determining the mechanism of prey aggregation in this study area and how biophysical interactions affect the availability of different prey species.

In many cases, the mechanism responsible for observed tidal effects on seabird abundance and distribution has not been investigated. For example, Brown and Gaskin (1988) hypothesized that interaction between tidal currents and shallow ledges could create local regions of upwelling, leading to dense aggregations of prey for foraging phalaropes, but this hypothesis has not been tested (see Chapter 2). Additional studies elucidating the mechanisms responsible for tidal effects on marine predators and their prey would be useful in furthering our understanding of these features and their importance to marine predators.

3.9 Other oceanographic features

Internal waves are sub-surface waves that occur over small spatial and temporal scales. Stevick et al. (2008) found that internal waves, along with euphausiid behavior, caused euphausiids to be aggregated in surface swarms near a shallow bank in the Gulf of Maine, and that shearwaters and storm-petrels were associated with this bank. Conversely, the distribution of gulls and gannets was not affected by the presence of the bank. Haney (1987c) found that seabirds were associated with crests of internal waves off of the coast of North Carolina, but no seabirds were observed within troughs. This relationship was significant for black-capped petrels, Audubon’s shearwaters and pomarine jaegers. The mechanism responsible for this trend of increased seabird abundance at wave crests is unclear, as studies of prey in internal waves have shown increased prey aggregations at wave troughs (e.g., Zeldis and Jillet 1982, Lennert-Cody and Franks 1999). Thus, further research is needed to understand the biophysical coupling at internal waves and the effects of these features on foraging seabirds.

Other types of oceanographic features are likely important to foraging seabirds. For example, Ribic et al. (1997) found that terns were associated with a freshwater plume in the Gulf of Mexico, an area of low salinity and high productivity. Island wakes, generated by strong flow around islands, can aggregate zooplankton and nekton (Alldredge and Hamner, 1980, Wolanski and Hamner, 1988, St. John et al., 1992), creating important foraging habitat for marine mammals (Johnston et al. 2005a, Johnston and Read 2007). These features likely have similar effects on foraging seabirds, but have not been examined in detail relative to distributions or tracks of foraging seabirds.

4. Moving from correlation toward causality and prediction

This review of seabird habitat relative to different types of oceanographic features highlights several themes that are important to consider as we move from descriptive studies towards research that provides causation and prediction. These themes are relevant to seabird habitat use in all types of oceanographic features, and are thus reviewed here together.

4.1 Sampling methods

Sampling methods significantly affect the extent to which inference of underlying processes can be made. While several studies I reviewed (25) did not include any measurements of the physical environment, more than half (63) used *in situ* oceanographic sampling. Remote sensing was the next most common means of oceanographic sampling (42 studies), while very few researchers used species-mounted instruments to sample the physical environment (3). Several studies used more than one method of sampling the physical environment (16), with the majority of these studies (11) having been conducted within the last decade. This suggests that seabird biologists are moving towards sampling plans that will allow the physical mechanisms underlying patters of seabird habitat use to be analyzed.

Studies examining physical processes alone are unlikely to characterize the habitat of foraging seabirds in an adequate manner. Seabird species differ in their use of oceanographic features, and there is spatial partitioning within features among species. The heterogeneous distribution of prey species relative to physical forces is likely an important factor structuring these patterns of differential habitat use, highlighting the importance of including measurements of prey in studies relating predators to oceanographic features. Hunt and Schneider (1987) noted that at the time of their review paper, very few seabird studies included surveys of prey. Sampling prey has become more common (43), but most studies I reviewed (74) did not attempt to measure the distribution or density of prey. Sampling both the physical environment and prey distributions within oceanographic features is critical to developing a more mechanistic understanding of the importance of oceanographic features to seabirds. However, few studies conducted both quantitative prey and oceanographic surveys (24). Many studies (66) sampled only the physical environment without providing quantitative estimates of prey; very few (4) included quantitative prey estimates but no oceanographic sampling.

Previous studies of seabird habitat use within oceanographic features which measure both oceanography and prey distributions at depth provide important examples for how this approach can be used to further our knowledge of how physical mechanisms affect prey distributions of foraging seabirds. For example, Hunt et al. (1998) show that crested, least, and parakeet auklets show species-specific patterns, foraging in regions of shallow passes in the Aleutian Islands that are upstream, downstream, and on top of the passes, respectively. Spatial differences in the location of the different prey species of these auklets (euphausiids, copepods, and fish/ invertebrates, respectively) were found to drive this pattern of differential habitat use. Increased tidal speed was associated with an increase in the number of auklets foraging in the passes. Concurrent physical oceanographic, fisheries acoustics and MOCNESS tows allowed both physical and biological patterns within these systems to be evaluated simultaneously and at depth. The results of this study represent an important step forward in understanding specifically how, where and when physical processes affect seabird prey distributions and affect seabird foraging habitat within oceanographic features. The authors present the hypothesis that the strength of physical processes likely drives the extent of zooplankton patchiness. This presents the next step in research within this system, and an important step in studies of seabird habitat in relation to oceanographic features more broadly: connecting physical oceanographic processes with distributions of seabird prey species. While biological oceanographers have made substantial progress in understanding how biophysical interactions within different oceanographic features structures biological patterns (e.g., Alldrege and Hamner 1980, Wolanski and Hamner 1988, Tremblay and Sinclair 1992, Genin 2004), our understanding of how the effects of these interactions are transferred up the food web to foraging seabirds could be improved. Working closely with physical and biological oceanographers in conducting studies of seabirds in oceanographic features could be useful in this respect.

Other studies making important contributions to our knowledge of seabird habitat emphasize the importance of conducting the synoptic surveys outlined above. A series of studies by Haney (1986a,b, 1989) furthered our knowledge of seabird habitat use in relation to ocean eddies. Synoptic *in situ* and satellite measurements, and previous physical and biological oceanographic studies investigating these features (e.g., Legeckis 1979, Lee et al. 1981, Yoder et al. 1981) allowed an understanding of the physical mechanisms at work within these eddies. These studies demonstrated the importance of these features to the abundance and distribution of seabirds in the South Atlantic Bight, and suggested that seabirds with different foraging behaviors use different foraging habitats within these features. However, prey surveys were not included in these pioneering studies. It is difficult to interpret the patterns of habitat use by different seabird species without first understanding how these eddies affect the distributions of their prey, and thus studies evaluating prey distributions represent the next step in studies of seabirds and Gulf Stream frontal eddies (see Chapter 4).

The methods used to sample prey and oceanography also have important implications for the extent to which studies can address mechanistic questions. For example, relying on measurements of primary productivity will likely not describe nor allow prediction of habitat for seabirds that forage at several trophic levels above phytoplankton (Grémillet et al. 2008). In addition, seabirds likely use visual and olfactory cues to locate sub-surface processes from above the surface (Nevitt 2000, Nevitt et al. 2004). Thus, relying only on surface-based methods may not be an appropriate means of identifying oceanographic anomalies, especially for diving birds when prey are aggregated at depth. Investigating the biological and physical dynamics of oceanographic features in three dimensions is necessary to clearly elucidate their effects on foraging seabirds (Burger 2003, Daunt et al. 2006, Hyrenbach et al. 2006). Less than half of the studies reviewed sampled prey or oceanographic parameters in the vertical dimension (50); 21 studies included prey surveys in the vertical dimension. Forty papers used oceanographic methods that included measurements at depth (e.g., CTD casts); 3 included species-mounted measurements in the vertical dimension; and 14 included more than one of these methods to sample prey or oceanography in the vertical dimension.

Sampling in the vertical dimension appears to be more common in investigations of smaller-scale features. Of the 14 studies that investigated fine-scale features, 10 included vertical samples of prey or oceanography. This was true for 24 of the 49 studies of meso-scale features, 4 of the 13 large-scale features, 13 of the 33 macro-scale features, and 6 of the 24 mega-scale features. Regardless of the scale of feature, measuring physical and biological properties in the vertical dimension is critical to understanding the processes occurring within oceanographic features and their importance to trophic transfer. In future studies, quantitative estimates of oceanography and prey in three dimensions, particularly when examining features with a large spatial extent, would provide important contributions in this respect.

The studies of Haney (1991), Hunt et al. (1998) and Russell et al. (1999) emphasized the utility of conducting studies of both oceanography and prey distributions at depth in order to understand the habitat use of diving seabirds. These studies indicated that distributions of different seabird prey species were aggregated in different parts of the water column, and that both the distribution of prey species and the diving abilities of different auk species were important in predicting their foraging habitat. A study by Jahncke et al. (2005) demonstrated the importance of both including measurements at depth and of conducting seabird studies that evaluate both primary productivity and lower trophic level species in order to understand how physical effects are transferred up the food web. By examining frontal structure, primary productivity and euphausiid distributions at a front in the Bering Sea, this study demonstrated that seabird foraging habitat in this system is dependent on the availability of nutrients at depth and on the aggregation of zooplankton. This approach demonstrates how we can advance our understanding of trophic transfer within oceanographic features.

Of the 117 studies analyzed in the present study, 89 used ship-based surveys, 29 used telemetry techniques, and 1 included both techniques. Telemetry studies have become much more frequent in recent years, as decreases in tag size and cost have allowed deployments on a large number of seabirds (Table 1). Louzao et al. (2009) discuss the importance of combining ship-based and telemetry data to gain an improved understanding of seabird habitat, but to date these data types have rarely been integrated. Studies working towards integrating these data types are currently being conducted (e.g., B. Montevecchi, pers. comm.) and will provide an important means of improving our knowledge of pelagic seabird habitat use.

4.2 Scale of measurements

The sampling effort of studies examining seabirds and oceanographic features must reflect the scale of the processes occurring within these features (Hunt and Schneider 1987), particularly due to the heterogeneous, scale-dependent nature of the marine environment (Ashmole 1971). In addition, although the *spatial* scale of patterns is typically considered in sampling plans, the *temporal* scale of sampling efforts has received little attention.

Continuous sampling of the water column is critical to evaluating bio-physical relationships within fine-scale features, or to evaluating fine-scale processes that might occur within larger-scale features. When data are collected using continuous sampling and surveys are designed appropriately, patterns and processes can be examined at multiple scales. Continuous sampling has become increasingly feasible in recent years with advances in sampling and data processing technologies. However, only 21 studies used techniques that continuously sampled the water column (17 and 11 studies investigated prey and oceanography continuously and at depth, respectively, while 7 studies did both). Acoustic Doppler Current Profilers (ADCPs) and fisheries acoustics techniques were used in many studies to examine the physical environment and the prey field at depth and in real time (Harrison et al. 1990, Decker and Hunt 1996, Hunt et al. 1996, Rodhouse et al. 1996, Russell et al. 1999, Burger 2003, Vliestra et al. 2005, Zamon 2003, Ainley et al. 2005, Jahncke et al. 2005, Ladd et al. 2005, Ribic et al. 2008, Stevick et al. 2008). The simultaneous deployment of these instruments has been used infrequently (e.g., Coyle et al. 1992, Hunt et al. 1998, Becker and Beissenger 2003, Ainley et al. 2005, 2009), but would provide an improved understanding of the biophysical links structuring these systems.

Most studies investigating fine-scale features (8 of 14) included continuous data, but only two sampled both prey and physical fields continuously. At larger scales, few studies included continuous measurements of the water column (8 of 49 meso-scale features; 2 of 13 large-scale features; 7 of 33 macro-scale features; and 1 of 24 mega-scale features), likely because it is less tractable to conduct *in situ* physical measurements over very large spatial scales. Only three studies included sampling designs devised to assess physical processes or prey fields at multiple spatial scales.

In many studies of seabirds and oceanographic features, the resolution of sampling measurements could better reflect the scale of the feature being investigated.

Several studies investigated features at different scales but did not vary their sampling plans to reflect the scale of these features. In addition surveys conducted at a scale that is fine enough to allow us to examine the patterns occurring within oceanographic features, rather than simply identifying where the features occur, would allow a the processes occurring within oceanographic features to be examined.

A study by van Franeker et al. (2002) in the APF demonstrates how hierarchical sampling can be used to examine how oceanographic processes affect seabird species foraging on different trophic levels at different scales. The authors suggest that there is a "gradual spatio-temporal diffusion" of the effects of the APF on organisms at increasingly higher trophic levels, highlighting the importance of both temporal and spatial scale in examining seabird habitat use within oceanographic features. Ainley et al. (2009) conducted surveys at different scales to examine both fine-scale and meso-scale processes, which provided important inferences on the importance of habitat factors occurring at different scales (see below).

Importantly, few studies discussed sampling methods relative to the temporal scale of the oceanographic features being investigated. For many features, temporal aspects of the measurements could have important effects on the patterns observed in the study. For example, the conclusions drawn from a study that had a high spatial resolution of sampling but which used data collected within a time period of a few days would provide observations that might be relevant to that time period only. Patterns observed within studies of tidal features conducted only during a spring or neap tide, for example, might be exaggerated or lessened during the opposite tidal phases. Such scenarios could have important implications for animals that require prey densities of a certain threshold to forage efficiently. These results highlight the importance of considering not only the spatial scale but also the temporal scale of variation. In addition, assessing the scale of the feature in advance would allow the feature to be sampled appropriately to illustrate oceanographic processes underlying patterns in seabird habitat use.

4.3 Spatial scale of oceanographic features

Many of the discussed types of oceanographic features exploited by foraging seabirds occur at a variety of spatial scales. The scale of foraging habitats can have important effects on the foraging behavior of predators (Morrison et al. 2010); seabirds adjust the scale of their foraging movements depending on the environment being exploited (Pinaud and Weimerskirch 2005). In addition, the mechanisms responsible for aggregating seabird prey and creating foraging opportunities likely occur at different scales within oceanographic features of different spatial dimensions. Future studies could use spatial techniques such as Mantel's tests to explicitly address the effects of the scales of these features on seabird foraging.

Ainley et al. (2009) conducted a multivariate analysis to examine the relative importance of different variables to seabird habitat in the northern California Current in two different years, and found interesting patterns regarding the spatial scale of processes influencing seabird habitat. During a food-rich year, meso-scale oceanographic features were the most important factors explaining seabird occurrence, while smaller-scale patterns of prey abundance were the most important explanatory factors during a food-poor year. The authors highlight the need for more information on the spatio-temporal ambits of different seabird species in order to better understand habitat use, and emphasize the need for further study of species interactions at meso-scale and finer scales at which important interactions occur.

Most of the oceanographic features identified for the purposes of this review paper were meso-scale features, while fewer studies investigated fine-, large-, mega- and macro-scale features (Figure 2b). Particular features and regions appeared to have been studied intensively and have contributed substantially to the literature. For example, of the 25 mega-scale features studied, 19 occurred in the Southern Ocean and 14 of these studies investigated seabird relationships with the Polar Front. Studies of fine-, meso-, large- and macro-scale features typically investigated several types of oceanographic features in a variety of locations.

Studies that have directly assessed the effects of the size of oceanographic features in relation foraging seabirds suggest that size has important effects on the use of these features. Haney (1985a) found that longer mid-shelf fronts along the southeastern U.S. coast attracted greater numbers of phalaropes and that the size of Gulf Stream frontal eddies was positively related to overall seabird abundance, biomass, and energy requirements (Haney 1986b). These results suggest that larger features were more attractive, potentially because larger features were either easier to detect, or because they supported higher densities or greater overall biomass of prey.

Further studies of oceanographic features that occur at a variety of scales, including studies directly assessing the influence of scale using spatial analysis techniques, could be used to address the issue of scale-dependent patterns of habitat use. Studies evaluating processes within the same feature at multiple scales would be particularly helpful in understanding the mechanisms driving the formation of seabird foraging habitat and how these mechanisms vary with scale.

4.4 Temporal persistence and predictability of oceanographic features

Temporal aspects of oceanographic features, such as their predictability and persistence, have important implications in terms of their use and importance as seabird habitat. Most of the oceanographic features studied in conjunction with seabird foraging were in a steady state or had a characteristic periodicity; far fewer were episodic (Figure 2c). Features in a steady state or with a characteristic periodicity are easier to sample, while episodic features, particularly those that are short-lived, are difficult to locate and study. However, it is unclear whether the large number of studies showing relationships between seabirds and consistent or regularly recurring features was due to a sampling bias or whether seabirds might target these features because they were more predictable.

The temporal persistence of a spatially predictable prey field is an important determinant of the foraging patterns of central place foraging seabirds (Davoren et al. 2003a, b), and several studies have suggested the importance of predictability to seabird foraging habitat (e.g., Schneider et al. 1987, Brown and Gaskin 1988, Irons 1998). The predictability of foraging opportunities created by oceanographic features has however not been assessed in detail. Some seabird species have also developed mechanisms allowing them to forage successfully in unpredictable environments (Gauthier-Clerc et al. 2002, Weimerskirch et al. 2004). Understanding temporal patterns in the physical mechanisms underlying patterns of seabird prey would elucidate the role of predictability in seabird foraging habitat, and could be used to better predict areas of seabird foraging habitat in both space and time. Conducting analyses of environmental variables evaluated over multiple time scales would be particularly useful in understanding the temporal scale at which oceanographic features influence seabird habitat. For example, Suryan (2010) suggest that examining the anomalies in chlorophyll distributions over multiple years provides a means of evaluating the persistence of hotspots, and is important to understanding primary and tertiary productivity in relation to seabird habitat. Examining anomalies analyzed at a variety of temporal scales could provide an informative means of evaluating temporal trends in oceanographic features functioning as seabird habitat.

It is important to note that while the predictability of most of the features examined in this review could be identified as being in a steady state, having a characteristic periodicity, or being episodic, it was often unclear whether the feature persisted for hours, days, weeks, or months. The temporal persistence of oceanographic features has significant implications for the formation of prey aggregations and is thus of enormous importance to their significance as foraging areas. Oceanographic features that act to aggregate prey through physical forcing of prey items are typically dependent on local current regimes and thus affect prey distributions over short time scales (e.g., several hours; Braune and Gaskin 1982, Zamon 2003). Features that enhance primary productivity and successively increase productivity at higher trophic levels typically influence seabird prey over longer spatial scales; in these features, time lags typically exist between increases in primary and secondary productivity (Vinogradov 1981, Croll et al. 2005). Depending on the trophic level of the seabird (e.g., plankivores vs. piscivores), prey aggregations may be formed over time scales of several weeks or months.

Studies of other marine predators at a variety of time scales provide suggestions for how future seabird surveys could further incorporate issues of temporal habitat trends. Evaluating seasonal trends in oceanographic regimes and prey distributions allowed Croll et al. (2005) to determine that there was a three to four month lag between increases in primary productivity in Monterey Bay and peak densities of blue whale prey (euphausiids). Studies of cetacean habitat use have suggested that due to lagged effects of oceanographic processes on the abundance of fish and squid, the inclusion of time-lagged data may increase the predictive power of habitat models (Soldevilla 2008). Similarly, studies of seabirds in relation to oceanographic and environmental variables could consider time-lagged data in future studies.

Ignoring the temporal persistence of the features can influence the observed patterns of association between seabirds and oceanographic features. As a result, biophysical interactions within these features might be observed to be more or less pronounced depending on the feature's persistence. Haney (1989) assessed the persistence of fronts in relation to phalarope habitat use in the South Atlantic Bight and found that the abundance of phalaropes declined in years when the persistence of mid-shelf front was lower. This illustrates that patterns of seabird habitat use over short time periods should consider the effects of persistence over a longer time scale; in this case, the effects of fronts on phalarope abundance and distribution might appear to be weaker during years of decreased persistence. In many cases, observed differences in the spatial scale of predator responses could be mediated by differences in temporal scale that have not been addressed to date. For example, spatial trends observed by van Franeker et al. (2002), in which planktivorous seabirds responded to physical frontal gradients at smaller spatial scales than seabirds at higher trophic levels, may also have occurred in the temporal dimension. Time lags between responses of different trophic levels may cause planktivorous seabirds to be correlated with oceanographic features at shorter time scales than seabirds feeding at higher trophic levels. These examples illustrate that temporal persistence is an important factor that should be given more attention in future research.

4.5 Analytical techniques

Early studies of seabirds and oceanographic features were typically descriptive. Hunt and Schneider (1987) found that studies using statistics to assess the amount of variation in patterns of seabird habitat use in relation to physical regimes had not been widely used, while descriptive studies were far more common. The authors note the importance of quantitative studies in understanding the importance of oceanography to seabird distribution. In this review, quantitative analyses (70) were more common than qualitative approaches, but a considerable number of the quantitative studies (47) linked seabirds and oceanographic features in a qualitative fashion. The number of quantitative studies has increased through time (Table 1), although the proportion of studies including quantitative analyses is only slightly higher in the most recent decade than in the first time period of studies I reviewed. Though the use of quantitative studies appears to have increased since Hunt and Schneider's review, there is still a need to move away from descriptive studies towards quantitative hypothesis-driven, spatially-explicit studies of seabirds in relation to oceanographic features that address issues of scale.

Tremblay et al. (2009) noted that, in spite of the spatial nature of the data, few studies examining seabird-habitat relationships have used spatially-explicit analysis techniques. The results of this review suggest that many studies examined autocorrelation in seabird data in order to conduct analyses at an appropriate spatial scale and satisfy assumptions of independence (e.g., Hunt et al. 1996, Ribic et al. 1997, 2008, Ainley et al. 1998, 2005, 2009, van Franeker et al. 2002, Yen et al. 2004, 2006, Vliestra et al. 2005, Suryan et al. 2006, Hyrenbach et al. 2006, 2007). However, I found only two studies (O'Driscoll 1998, Ribic et al. 2008) that conducted analyses of seabirds in relation to biological or physical variables in oceanographic features using spatially explicit techniques, such as Ripley's K, Mantel's tests or wavelet analyses. Wakefield et al. (2009) noted that many quantitative analyses of seabirds compare oceanographic regions (e.g., by depth) that are human-defined and may be of limited biological relevance to the birds themselves. These authors suggest that using oceanographic phenomena, such as examining depth classes in terms of stratified vs. mixed water, might be a more appropriate means of integrating oceanographic data into models of seabird habitat use. Similarly, in studies of specific oceanographic features, more objective methods could be used to identify oceanographic features. For example, edge detection tools can provide a more objective means of identifying fronts than arbitrarily selected gradient values used to indicate a front.

Hierarchical analyses have rarely been used in studies of seabirds and oceanographic features, but this approach could be used to effectively address issues of scale (e.g., Schick et al. 2008). Studies using a hierarchical approach to correlate seabirds with oceanographic features have shown that results vary depending on scale (van Franeker et al. 2002, Pinaud and Weimerskirch 2005). As discussed above, many studies included sampling techniques that continuously sampled oceanographic or prey data, but few analyzed these data in a spatial framework. Continuous data collected over a large spatial scale could be analyzed over bins of different sizes to examine effects of spatial scale, for example using a variogram (e.g., Simard and Lavoie 1999). Multivariate Mantel's tests could be used to examine spatial patterns in multivariate data (e.g., García-Charton and Pérez-Ruzafa 2001).

The analysis of seabird telemetry data in relation to oceanographic features could be improved by the use of state space models (e.g., Jonsen et al. 2005, Schick et al. 2008). These models allow foraging areas to be identified objectively from animal telemetry data using robust statistical techniques, and allow estimates of error to be assessed directly (Jonsen et al. 2003). Given the increasing number of telemetry studies evaluating seabirds in relation to oceanographic features (Table 1), the use of objective and quantitative means of identifying foraging areas from telemetry data is particularly important.

5. Conclusions

Levin (1992) noted that identifying the mechanisms responsible for observed patterns in ecology is critical to prediction and understanding. Accordingly, studies of seabirds and oceanographic features are moving from identifying descriptive links between birds and physical factors towards a more mechanistic understanding of these relationships, a transition which is necessary in order to improve our predictive abilities. There are many challenges associated with conducting such research, including the costs of ship time, tag deployments and equipment required to sample the physical and biological environment. Logistical issues are inherent in studies of far-ranging, patchily-distributed seabirds that are often inaccessible to researchers except during breeding periods and constraints in the distance or duration of ship-based cruises or tag deployments can limit the scale or extent of sampling efforts. Studies that provide new insight into the mechanics of oceanographic features and their importance as foraging habitat will require detailed consideration of scale in sampling plans, including preliminary surveys to assess sampling scales for comprehensive studies, and interdisciplinary collaboration between physical and biological oceanographers and seabird biologists. Burger (2003) notes that accurate predictions of the distribution of seabirds will not be possible until we gain a better understanding of the interactions between bathymetry, physical forces, seabirds and their prey.

This review has highlighted several specific areas of research that would help to develop a more process-oriented understanding of the importance of oceanographic features as habitat for foraging seabirds. Foremost among these are studies including an assessment of the distribution of prey (in three dimensions). Differential use of habitat by species is difficult to interpret without an understanding of the mid-trophic levels that link seabirds with these physical processes. In particular, differences in the vertical distribution of seabird prey have important implications for the availability of prey to seabird species using different foraging strategies.

To date, many studies of seabirds and oceanographic features have relied exclusively on surface characteristics of oceanographic features, and particularly on satellite-derived sea surface temperature (SST) images. Such surface measurements are useful to identify oceanographic features, but they provide little information on the processes occurring at depth which structure prey distributions in the water column and thus influence the distribution of foraging seabirds.

Scale in both temporal and spatial dimensions is a critical factor when considering seabird-environment relationships (Hunt and Schneider 1991, Ballance et al. 2006, Wakefield et al. 2009). The spatial extent of oceanographic features and processes is often discussed relative to their importance as seabird foraging habitat, but could be assessed directly in the future (e.g., Haney 1985a, 1986b). The temporal dimension of these features has received less attention. The temporal and spatial scale of sampling efforts is critical to demonstrating links between the physics and the biology in these features.

Small-scale processes within oceanographic features would allow for a better understanding of the effects of oceanographic features on seabird distributions, as several authors have noted previously (e.g., Hyrenbach et al. 2006, Kai et al. 2009). Species are often segregated within oceanographic features; differences in the horizontal and/or vertical distribution of prey between these “microhabitats” are likely responsible for such observed differences (Hunt et al. 1998, Russell et al. 1999, Ladd et al. 2005). Elucidating how oceanographic processes aggregate different prey species would allow us to understand how microhabitats within oceanographic features are formed. Fine-scale sampling would be useful in this respect; this would allow processes occurring within features to be detected in addition to the location of the overall feature. Hierarchical sampling designs, allowing patterns to be assessed at multiple scales, could address this goal. Spatially-explicit analysis techniques would allow the effects of scale to be evaluated directly.

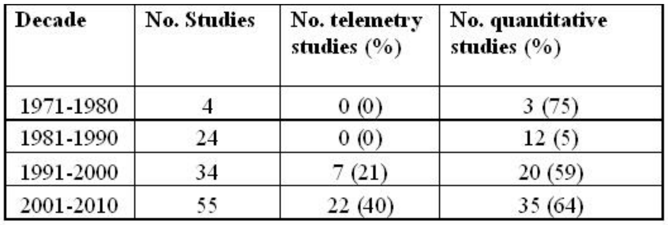
Lastly, concurrent measurements of physical forces and biological variables at different trophic levels are necessary in order to elucidate trophic effects of oceanographic features and understand patterns of habitat use of marine predators.

Due to technological advances in recent years, the synoptic collection of large quantities of both oceanographic and prey data in real-time is now feasible. Future studies of seabirds and oceanographic features should include measurements of ocean physics, and the distribution of prey (zooplankton and fish) in the vertical dimension concurrent with seabird observations.

Studies of seabirds and oceanographic features to date have made important progress in understanding the ecological succession linking physical processes with aggregations of zooplankton and fish and with distributions and movements of foraging seabirds. However, there is still considerable work to be done in this respect, and specific hypotheses regarding prey aggregation within oceanographic features from previous studies (e.g., Hunt et al. 1998, Zamon 2003, Brown and Gaskin 1988, Haney 1986) provide important starting points for future studies investigating biophysical interactions in relation to seabird habitat.

The physical marine environment plays a key role in structuring seabird habitat at a variety of scales (Hunt and Schneider 1987). Understanding how physical processes drive patterns in seabird abundance and distribution and that of their prey is critical to understanding how seabirds use the world’s oceans and to understanding the factors driving trophic exchange in marine systems. Studies within oceanographic features provide an important means of doing so, allowing relationships between dynamic oceanographic processes and biological patterns to be assessed at a number of trophic levels.

Table 1: Number of studies of seabirds in relation to oceanographic features by decade.



Decade	No. Studies	No. telemetry studies (%)	No. quantitative studies (%)
1971-1980	4	0 (0)	3 (75)
1981-1990	24	0 (0)	12 (5)
1991-2000	34	7 (21)	20 (59)
2001-2010	55	22 (40)	35 (64)

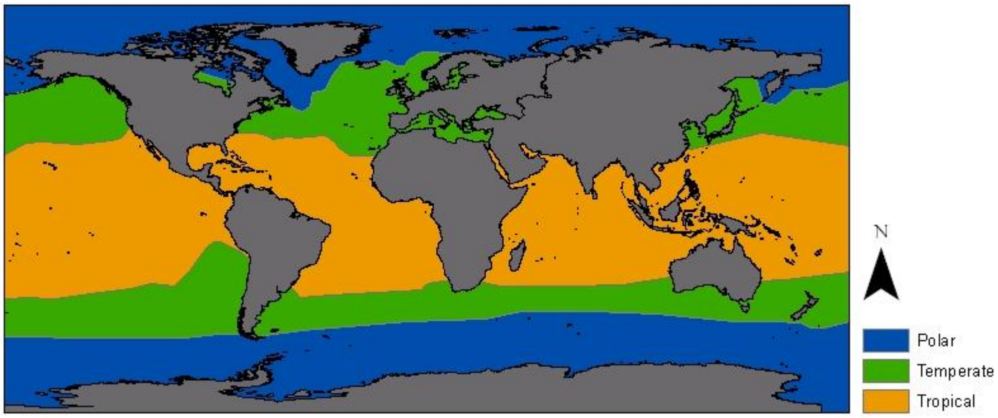


Figure 1: Polar, temperate and tropical regions of the ocean used in the analysis. Regions were adapted from Hall (1964), as follows: polar, < 10°C; temperate, 10-18°C; and tropical, > 18°C.

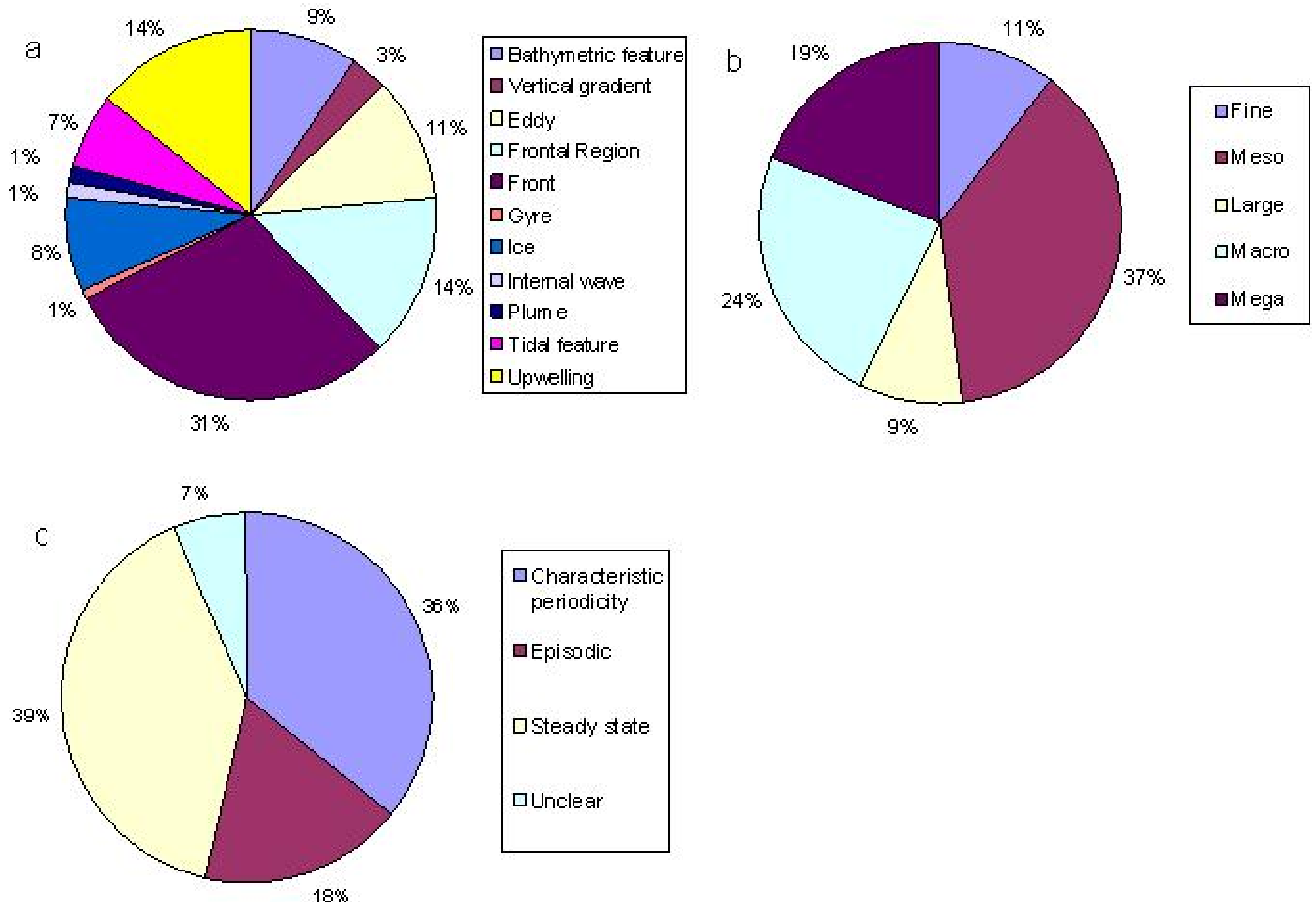


Figure 2: Oceanographic features investigated in studies of seabirds and oceanographic features, categorized by: a. Type of oceanographic feature; b. Scale of feature; and c. temporal persistence of feature.

Chapter 2: A quantitative assessment of red-necked phalarope foraging habitat in the Bay of Fundy, Canada: the importance of considering biophysical dynamics at a fine scale

Abstract

The abandonment of a long-time migratory stop-over area by more than one million red-necked phalaropes (*Phalaropus lobatus*) in the western Bay of Fundy during the mid-1980s has raised concern regarding the species' status in North America. It has been hypothesized that this decline was caused by a reduction in the availability of the prey of red-necked phalaropes, which are constrained to feed at the ocean surface. However, there has been no quantitative examination of long-term trends in prey abundance, nor of the effects of fine-scale oceanographic features on their distribution. I demonstrate the importance of biophysical interactions in structuring phalarope habitat in a foraging area in the Bay of Fundy by sampling both biological and physical aspects of the environment and integrating these observations into multivariate models. Strong tidal currents interact with steep bathymetric gradients to enhance vertical mixing, creating relatively dense aggregations of stage CV *Calanus finmarchicus* copepods at fine temporal and spatial scales. Such quantitative descriptions of marine habitats are possible only when a rigorous sampling design is employed at appropriate spatial and

temporal scales. This is particularly important in highly dynamic systems, such as the Bay of Fundy, and when results are of relevance to the management of species at risk.

1. Introduction

Red-necked phalaropes (*Phalaropus lobatus*) are small shorebirds that breed in the Arctic and spend their non-breeding months at sea. Phalaropes are obligate surface feeders, foraging on prey items in the top 10 cm of the water column (Hohn 1968; Dodson and Eger 1980). Phalaropes are known for a spinning behavior in ponds on their Arctic breeding grounds which brings their prey to the surface (Haney and Stone 1988; Obst *et al*. 1996). In other seasons, however, these birds must rely on fine-scale oceanographic features to aggregate prey at the surface of their marine habitat (Brown 1978; Haney 1985a; DiGiacomo *et al*. 2002). After the breeding season concludes in late summer, phalaropes leave the Arctic and migrate south. During this migration, many birds feed at a migratory stop-over site in the highly productive waters of the Bay of Fundy (Brown and Gaskin 1988).

Researchers documented the ecology, diet and energetic requirements of migratory red-necked phalaropes in the Bay of Fundy during the 1980s (Brown and Gaskin 1988, 1989; Mercier and Gaskin 1985). These studies described two foraging areas in the Bay of Fundy: one between Campobello and Deer Islands (Head Harbour

Passage) and the other along the northwestern coast of Nova Scotia (the Brier Island ledges; Figure 3). Red phalaropes (*Phalaropus fulicarius*) were also reported at Brier Island, although at one or two orders of magnitude less than red-necked phalaropes. The latter species fed primarily on a single copepod species, *Calanus finmarchicus*, and their distribution was closely associated with areas of high *C. finmarchicus* density, particularly fifth copepedite (stage CV) copepods. During the late summer, this copepod stage is in diapause and thus contains high concentrations of lipids (Hirche 1996). These copepods are typically observed at depths of 90-140m in the Bay of Fundy during daylight, although some individuals migrate to surface waters during nighttime (Baumgartner et al. 2003). Phalaropes are visual predators (Mercier 1983) and so must depend dependent on physical oceanographic forces to bring their prey to surface waters during daylight hours.

Since these studies were conducted in the early 1980s, aerial surveys have reported drastic declines in the numbers of red-necked phalaropes in eastern Canada (Morrison *et al*. 2001). Of particular concern is the abandonment of the Head Harbour Passage migratory stop-over area, where as many as one to two million red-necked phalaropes were observed in late summer during the 1970s and early 1980s (Vickery 1978; 1979; 1981; Mercier and Gaskin 1985). The number of red-necked phalaropes using the Head Harbour area declined rapidly during the mid-1980s and birds have been absent since 1990 (Brown *et al*. 2005). Unpublished data collected by the Canadian Wildlife Service in 2002 suggested that the density of *Calanus finmarchicus* in surface waters in the Head Harbour region was approximately ten times lower than that reported by Brown and Gaskin (1989), while the density of smaller copepod species (*e.g.*, *Acartia* spp. and *Eurytemora* spp.) were approximately twice as high (J. Chardine, Canadian Wildlife Service, pers. comm.).

Declines in the abundance of the primary prey of red-necked phalaropes may, therefore, have been a factor in their abandonment of the Head Harbour foraging area. A considerable proportion of the North American population of red-necked phalaropes uses the Bay of Fundy as a staging ground during their fall migration (Mercier 1983), so the decline of phalaropes observed in Head Harbour likely has important population-level implications. Small numbers of red-necked phalaropes continue to be observed at Brier Island, but there is no evidence that large numbers of phalaropes moved to another staging area, prompting widespread concern over the status of this species in North America (Donaldson *et al*. 2000; Morrison *et al*. 2001; Brown *et al*. 2005).

Consumption of lipid-rich prey in the Bay of Fundy plays an important role in the energy balance of these birds during migration. Mercier (1985) estimated that red-necked phalaropes accumulated between 40 and 45% of their body mass in the Bay of Fundy before continuing their southward migration, highlighting the importance of this area to the energetic budget of migrating phalaropes. The wintering area of red-necked phalaropes has not been fully described, but it has been suggested that the birds may overwinter in the Humboldt Current (Mercier 1983), although some red-necked phalaropes are observed in the South Atlantic Bight during winter (Haney 1985a; L.H. Thorne and A.J. Read, unpublished observations).

Understanding how biophysical interactions influence the availability of red-necked phalaropes in the Bay of Fundy is critical to determining how, when and where foraging habitat is created for these birds in this migratory stop-over. Before we can understand the effects of broad oceanographic influences, such as the North Atlantic Oscillation, we must first assess how the physical environment structures prey aggregations within foraging areas. It has long been understood that fine-scale oceanographic features are responsible for making *Calanus finmarchicus* available in surface waters, but early studies in the Bay of Fundy did not quantify the occurrence or effects of these features. Brown (1980) and Brown and Gaskin (1988) developed, but did not quantitatively assess, hypotheses regarding the oceanographic processes responsible for the observed patterns of phalarope and plankton distribution. No studies of the pelagic habitat use of red-necked phalaropes in Eastern North America have been published in peer-reviewed journals since their decline in the mid-1980s, so these early hypotheses have yet to be addressed. It is particularly important to describe the foraging habitat of phalaropes in quantitative terms today, so that we may determine the factors that influence phalarope demography.

In the present study, I describe the mechanism by which phalarope prey are aggregated in surface waters at Brier Island and compare the prey field currently available to foraging phalaropes with historical observations. The specific objectives are to: (1) determine the abundance, species and stage composition of copepods currently observed at Brier Island; (2) assess how physical oceanography at the Brier Island ledges structures the prey field of red-necked phalaropes at fine spatial and temporal scales; and (3) examine patterns of phalarope habitat use in relation to these biophysical habitat variables.

2. *Methods*

2.1 Study area

The Brier Island ledges are located at the outer reaches of the Bay of Fundy, with Northwest Ledge occurring approximately 5 km north and west of Brier Island in southwestern Nova Scotia (Figure 3). Steep bottom topography exists around the ledges and depths increase rapidly to the west of the ledges from approximately 10 m over Northwest Ledge to more than 200 m in the Grand Manan Channel, over a horizontal distance of less than 3 km. I focused my sampling efforts here, rather than in Head

Harbour, because phalaropes are still observed in this area and because historical data on foraging phalaropes and their prey exist for this location. The sampling was conducted primarily over the Northwest Ledge.

2.2 Oceanographic sampling

I conducted oceanographic surveys on nine survey days between August 16 and September 6, 2007 on both the ebb and flood tide phases. I designed box transects to cover a variety of habitats over and beyond the ledges and repeatedly sampled the same locations through time (as in Johnston and Read 2007; Figure 3). I sampled sea surface temperature (SST) and current speeds at depth using a 300 kHz RDI Workhorse Sentinel acoustic Doppler current profiler (ADCP) with bottom tracking capability. The ADCP was deployed over the side of a 12-m boat and the transducer head was positioned 1 m below the water's surface. Survey speed did not exceed 2.6 m s^{-1}. The ADCP was set to ping as fast as possible; data were averaged over one min intervals and collected in 4-m bins with a maximum of 60 bins, reflecting the deepest regions surveyed. I collected data using VmDas software and visualized the observations in VmDas and WinADCP and imported them into a GIS to overlay the ADCP data with bathymetry, plankton and phalarope data. A new ADCP file was created for each box transect, to avoid having multiple measurements from a given location.

I sampled zooplankton concurrent with ADCP surveys and followed the general sampling design of Brown and Gaskin (1989), so that I could compare the data with their observations. I employed a net with a 363-μm mesh size attached to a metal ring with a diameter of approximately 0.5 m. This mesh size was larger than that (243-μm) used by Brown and Gaskin, but was sufficiently fine to sample the copepod species they sampled (> 500 μm). The tows lasted for 5 min at a speed of approximately 1 m s^{-1}, during which the net was half submerged in the water. The net was occasionally lifted to avoid floating rockweed. I preserved samples in buffered formalin and transferred them to 70% ETOH for counting and identification. Copepods were counted, sexed and identified to species and life stage using a stereo microscope. All species identifications were verified by Dr. Pat Tester at the National Oceanographic and Atmospheric Administration Southeast Fisheries Science Center Laboratory in Beaufort, NC. Plankton samples were divided using a Folsom plankton splitter to produce sub-samples of approximately 250 individuals. Abundance was calculated as the number of copepods per m^3 by calculating the volume of water passing through the net from the tow length, the net diameter (assuming that half of the cross-sectional surface area of the net was submerged, as described above), the direction and speed of the boat and that of the measured current. After counts and identifications were conducted, I oven-dried the samples and weighed them using a balance with an accuracy of 0.0001 g.

2.3 Phalarope Surveys

Visual surveys were used to estimate the abundance, species composition and behavior of phalaropes observed at the Brier Island ledges. Phalaropes in the Bay of Fundy occur in large, ephemeral feeding flocks. As a result, modified survey methods are required to acquire accurate estimates of abundance and species composition. Two observers conducted visual surveys from approximately 6 m above the water on clear days with a Beaufort sea state of less than four during nine survey days in early August and mid-September, 2007. Data on the location, species composition, behavior (sitting, flying, feeding at the surface, or feeding in weed mats) and abundance of phalaropes were collected. Tracks were initiated at the north or south end of the ledges, and were conducted across the ledges using a saw-tooth pattern until birds were observed. To obtain accurate counts, I decreased speed when flocks of phalaropes were encountered and the boat was maneuvered alongside the flocks. In late summer, red and red-necked phalaropes are in non-breeding plumage and can be difficult to distinguish. I also collected oceanographic data concurrent with phalarope surveys on four survey days (see below).

2.4 Analysis

I interpolated depth estimates from ADCP surveys to provide a comprehensive bathymetry for the study area. Continuous coverages of SST, average current speed and depth were produced by interpolating short-term averaged (1 min) in ArcGIS 9.2 using Kriging interpolation in the Spatial Analyst extension. The depth coverage was used to generate a continuous coverage of distance to the 20 m depth contour, used as a metric of distance to the shallow regions of Northwest Ledge. SST and depth coverages were used to create grids of SST and depth gradients using the slope function in Spatial Analyst. All interpolated coverages had a pixel size of 50 m.

I assessed the spatial autocorrelation of individual zooplankton tows using a Moran's I correlogram (Legendre and Legendre 1998). Moran's I indicates the degree of spatial autocorrelation of data and can be used to determine whether significant autocorrelation is present. Negative values of Moran's I indicate segregation, while positive values indicate aggregation (Fortin et al. 1989). I used a lag distance of 250 m for 20 lags and a Bonferroni correction to allow for multiple testing, and assessed significance using Monte Carlo randomization tests for 1500 simulations using the Excel add in Rook Case (Sawada 1999, Louzao et al. 2006). To assess autocorrelation, I used plankton samples collected during phalarope surveys rather than using data collected during box transects. Box transects repeatedly surveyed the same area through time, these surveys would therefore include multiple measurements at one given location at different times, thus causing confounding temporal effects. Autocorrelation was assessed for all dependent variables (see below).

I used Generalized Linear Models (GLMs) to assess relationships between copepod abundance and the following predictor variables: SST, SST gradient, daily SST anomaly (*i.e.*, deviance of a given SST measurement from the daily mean SST), distance to 20 m contour, depth gradient, current speed and tide phase (flood vs. ebb). Since this analysis aimed to capture the effects of current speed and bathymetry on surface distributions of copepods that are typically observed at depths of approximately 100 m, the current speed throughout the water column was used in this analysis.

GLMs are extensions of linear regression models that relax assumptions about linear relationships and allow data from a range of different probability distributions and data containing non-constant variance structures to be modeled (Hastie and Tibshirani 1990). Counts and dry mass values of zooplankton tows were used as dependent variables along with *Calanus finmarchicus* as a proportion of total copepods, using the volume of the tow as an offset (Qian 2009) to account for differences in mass or abundance due to increased water flow. To assess *Calanus finmarchicus* as a proportion of total copepods, the number of *Calanus finmarchicus* was used as the dependent variable, while both water volume and the total number of copepods were used as model offsets. I assessed the normality of counts and dry mass values using q-q plots and Anderson-Darling normality tests. I employed a Gaussian distribution to evaluate dry mass values, which were log-transformed to meet assumptions of normality.

Copepod count data were analyzed using a negative binomial distribution due to over-dispersion of the data. For all GLM models, I conducted variable selection using stepwise regression model selection to determine the model with the lowest Akaike Information Criterion value (AIC; Akaike 1973, 1974). Goodness of fit was assessed using adjusted D^2 values (equivalent to the R^2 in least-square models; Guisan and Zimmerman 2000). Non-significant values were stripped from the final model. To examine the temporal structure of the copepod data, I assessed the relationship between volume-corrected copepod counts and tidal phase (hours since low tide). I used a Mantel's correlogram (Legendre and Fortin 1989) to examine autocorrelation among zooplankton tows in different temporal bins using a Bonferroni correction to account for multiple tests.

To accurately assess the abundance of phalaropes on the ledges, phalarope surveys were conducted from one end of the ledge to the other so that given regions of the ledge were not surveyed repeatedly. Conversely, the oceanographic box transect surveys were designed to repeatedly survey a given area through time. Therefore, I did not obtain synoptic estimates of phalarope abundance, behavior or distribution during box transect surveys of fine-scale oceanography. However, as noted above, I collected oceanographic data concurrent with phalarope surveys on four survey days when oceanographic box transects were not conducted, yielding 82 sightings of phalaropes, representing more than 13,000 birds, with concurrent oceanographic data. Using this data set, I used Classification and Regression Trees (CARTs, Breiman *et al*. 1984) to analyze the behavioral state of phalaropes (feeding on the water *vs*. not feeding on the water) relative to oceanographic predictor variables. CART models define multivariate habitat envelopes based on a number of environmental variables. In the case of categorical data, data are categorized into presence and absence categories based on recursive binary splits of the environmental data into increasingly homogenous partitions. The resulting trees were pruned based on misclassification rates to avoid over-fitting of the model.

I conducted all statistical analyses in the R statistical package (version 2.9) using the "MASS", "tree" and "ecodist" packages to construct GLMs, CARTs and Mantel's correlograms, respectively.

3. Results

I conducted 133 plankton tows on the Brier Island ledges. The minimum time between zooplankton tows was 15 min and there was no significant spatial autocorrelation between individual tows (Moran's I correlogram; $p > 0.05/20$ for all distance lags for total dry biomass, total *Calanus finmarchicus*, total stage CV *C. finmarchicus*, and *C. finmarchicus* as a proportion of total copepods, respectively). Thus, individual tows were considered to be independent at the scale at which they were collected and were used as the sample unit for the GLM models.

The mean species composition of zooplankton tows in the present study and those conducted by Brown and Gaskin (1989) in the months of August and September are shown in Table 2. Overall, *Calanus finmarchicus* made up an average of 54% of copepod species collected in the present study. There was a high degree of variation between samples, as indicated by the large standard deviation values, so any general trends among weeks were swamped by variation at a finer temporal scale. For example, *C. finmarchicus* ranged from 4.5 to 95.5% of copepods and from 0.01 to 200.6 individuals m^{-3} and dry biomass of plankton samples ranged from 0.01 to 13.8 mg m^{-3}. I was unable to statistically compare these data with historical observations because only mean values, without estimates of error, were provided in the previous studies. In addition, the small sample sizes in previous studies make it difficult to conduct meaningful comparisons. Due to the large variation in abundance and biomass, I examined trends in *C. finmarchicus* through time using maximum observed values. The maximum observed proportion of *C. finmarchicus* (proportion of total copepods per tow) and stage CV *C. finmarchicus* (proportion of *C. finmarchicus* in the fifth copepedite stage) generally increased from mid August to early September, although the maximum abundance of stage CV *C. finmarchicus* (no m^{-3}) peaked in late August (Figure 4).

It was not possible to compare the biomass values with those from previous studies due to methodological differences in calculating the volume of water passing through the plankton net during a tow. In the present study, I accounted for boat speed as well as current speed in calculating water volume, but historical estimates of volume considered boat speed but not current speed. Currents in this area exhibit a huge variation throughout the tidal cycle (see below), so this is an important consideration when attempting to make quantitative comparisons. I measured current speeds at the Brier Island ledges from 0.053 to 1.94 m s^{-1}. During the flood tide, the direction of current flow over the ledges was primarily to the northeast, although the direction varied considerably over the ledges. In particular, plots of mean current vectors during the flood tide showed that the current direction on the northernmost part of the ledges had a stronger eastward component than currents on other regions of the ledge (Figure 5). Due to the steep bathymetric gradients to the west of Northwest Ledge, water advected onto the ledge in this region would pass over a steeper bathymetric gradient than that on other parts of the ledge.

I analyzed models using daily SST anomalies and SST values as predictor variables separately to determine which was the better predictor of surface plankton because these terms provided different means of examining the importance of temperature and were highly correlated (Pearson's correlation, r=0.74). SST was a better predictor of plankton abundance and dry biomass. GLMs showed a significant interaction between SST and current speed, which is evident when examining plots of SST and temperature at a given location on the ledges through time (Figure 6a). Current speeds also appeared to be highest over the ledges than in deeper waters. Variables included in the optimal models predicting total *Calanus finmarchicus* and stage CV abundance and dry biomass of plankton tows are shown in Table 3, together with adjusted D^2 values. Distance to the 20-m contour, current speed, SST and tidal phase were important predictors of the abundance of *C. finmarchicus* in surface waters. Similarly, distance to the 20-m contour, current speed and SST were significantly correlated with the abundance of stage CV *C. finmarchicus*. Distance to the 20-m contour was the only significant predictor of total dry biomass of plankton and *C. finmarchicus* as a proportion of total copepods. For all measures of plankton abundance, distance to the 20-m contour was negatively correlated with plankton abundance. Current speed was positively correlated with the abundance of stage CV and total *C. finmarchicus* and SST was negatively correlated with these variables (Figure 6b). More *C. finmarchicus* were observed during the flood than ebb tide phase. Adjusted D^2 values for the models were relatively high for total and stage CV *C. finmarchicus* (0.52 and 0.49, respectively), suggested that approximately half of the observed variation in these measures were explained by the model. The adjusted D^2 values of the dry plankton biomass and proportion of *C. finmarchicus* models were lower (0.20 and 0.06, respectively), but these models were constructed using only distance to the 20-m contour.

Distance to the 20-m contour was an important predictor value in the GLM models, so I used this parameter to examine the spatial and temporal extent of the effects of the ledges on surface plankton concentrations. Plots of the number of *Calanus finmarchicus* m^{-3} vs. distance to the 20-m contour suggested that I would expect to observe measurable effects of the physical environment on the abundance of zooplankton at the surface at distances of 1100 m from the ledges (defined by the 20-m contour). To examine whether this distance appropriately captured patterns in the abundance of *C. finmarchicus*, I compared the abundance of *C. finmarchicus* collected at locations both within and beyond 1100 m of Northwest Ledge (Figure 7). Next, I examined temporal patterns in the abundance of *C. finmarchicus* in surface waters on Northwest Ledge. Since I was interested in the temporal structure of the data associated with local phenomena on the Brier Island ledges, I examined the temporal structure of plankton samples collected within 1100 m of the 20-m depth contour. Temporal autocorrelation within 1100 m of the ledge was observed at time lags of approximately 6 and 12 h (Mantel's correlogram; *p* values of 0.05 and 0.04, respectively); however, autocorrelation was not significant after a Bonferroni correction was applied to account for multiple testing (Figure 8).

Given the observed relationship between current speed and surface concentrations of *Calanus finmarchicus* and zooplankton biomass, I expected that broader temporal trends in current speed would also have important effects of the abundance of *C. finmarchicus* in surface waters. Figure 9 shows the maximum observed abundance of total *C. finamarchicus* and stage CV *C. finmarchicus* relative to the average tidal amplitude at Brier Island (determined from tidal charts for Wesport, NS). Maximum tidal amplitude peaked in the week of August 25-31, as did the maximum abundance of total *C. finamarchicus* and stage CV *C. finmarchicus* in surface waters.

A CART describing oceanographic factors relative to the behavioral state of phalaropes (feeding on the water *vs*. not feeding on the water) showed that phalaropes were feeding more than 4.2 h after low tide in regions and during periods when current speeds were greater than 0.40 m s^{-1}. The CART had a misclassification error rate of 12.5, indicating that approximately 87% of phalarope behavioral states were classified correctly, and explained 30.8% of the variance in phalarope behavioral states. The residual mean deviance of the model was 0.69.

Figure 10 shows the abundance of red, red-necked and unidentified phalaropes by survey date. A large proportion of phalaropes could not be identified to species level during surveys, but the abundance of red-necked phalaropes decreased after early August. The largest number of red-necked phalaropes observed was 5,616 on August 1.

The number of red phalaropes generally increased throughout the survey period, reaching a maximum of 6,457 birds on the last survey day (September 14).

4. Discussion

Stage CV *Calanus finmarchicus*, which typically occur at depths of approximately 100 m in the Bay of Fundy, are physically forced into surface waters at the Brier Island ledges because of interactions between strong tidal currents and steep bathymetric gradients. The abundance and biomass of zooplankton in surface waters at Brier Island are positively correlated with current speed and proximity to shallow ledges. Significant negative interactions between current speed and SST indicate that local upwelling occurs during periods of high current speed, particularly on the flood tide. The models for abundance of total and stage CV *C. finmarchicus* explained more than twice the variation as the model of dry biomass. Dry biomass includes all species, which includes several species present in surface waters that are less affected by the sub-surface processes aggregating *C. finmarchicus* at the Brier Island ledges.

I was unable to compare the results with historical estimates of dry zooplankton biomass and species composition due to disparities in sampling designs and the high level of variability observed between samples. However, estimates of species composition could provide important data against which to make future comparisons, provided that samples are sampled at an appropriate spatial and temporal scale. I observed a high degree of variation in species composition, especially when these samples were analyzed at the temporal scale of the historical data set (Table 2). In addition, models suggested that proximity to the 20-m contour had a significant negative relationship on *Calanus finmarchicus* as a proportion of total copepods, indicating that more *C. finmarchicus* were found closer to the ledge. Thus, the location of samples collected relative to the ledge is an important factor to consider during future sampling efforts.

The abundance of zooplankton in the Bay is influenced by immigration from both the Gulf of Maine and the Scotian Shelf (Fish and Johnson 1937; Kulka *et al*. 1982; Roff 1983). Thus, it is possible to consider an alternate hypothesis that *Calanus finmarchicus* are aggregated in surface waters in the Gulf of Maine or on the Scotian Shelf, and are then transported into the Bay of Fundy during the flood tide. Under this scenario, distributions of *C. finmarchicus* would be expected to be associated with tidal phase, but the composition of samples would be similar both over and away from the ledge. However, distance to ledge (represented by the 20 m depth contour) was a significant predictor of plankton abundance and biomass and *C. finmarchicus* as a proportion of total copepods, suggesting local effects on plankton abundance, species composition and biomass associated with the ledge. Further, an examination of plankton abundance and distribution collected throughout the tidal cycle demonstrated marked differences in the abundance of *C. finmarchicus* at locations on and off the ledge. Samples collected over the ledge showed an increase in the abundance of *C. finmarchicus* during the mid-flood tide, as well as a small increase during the mid-ebb tide, while samples collected off of the ledge were much lower throughout the tidal cycle. This demonstrates the local effect of the ledges on the abundance of surface *C. finmarchicus* concentrations.

Calanus finmarchicus data showed patterns of autocorrelation at temporal scales of approximately 6 and 12 h, indicating a tidally-driven pattern in the abundance of this species in surface waters. I emphasize that the physical mechanism influencing the distribution of *C. finmarchicus* is one of direct tidal forcing and physical advection. This differs from the mechanism of prey aggregation in many oceanographic features, in which increases in primary productivity are followed by time-lagged effects at successive trophic levels of the food web (*e.g.,* Croll *et al.* 2005). The effects of biophysical interactions appeared to be most pronounced within 1100 m, but continuous sampling would be required to assess the spatial dimensions of plankton patches. Optical plankton counters would be useful in further assessing plankton patch dynamics in this area.

The GLM models indicated that zooplankton abundance increased during the flood tide phase. During this tide phase the northwestern part of the ledge was dominated by a stronger eastward flow than elsewhere and waters passing through this region pass over a very steep bathymetric gradient. This results in stronger vertical mixing than during the ebb tide. In addition, this causes a convergence of strong tidal currents on this part of the ledge. Both of these factors likely lead to increased densities of zooplankton in surface waters. Though examining this pattern in more detail would involve a more standardized sampling plan than that used in the present study, a visual examination of the data suggest that plankton concentrations may be higher along the northwest region of the ledge.

Many previous studies have found increased densities of zooplankton caused by flow over steep bathymetric gradients (discussed in Genin 2004), although I am unaware of studies demonstrating bio-physical links at the fine spatial and temporal scale observed in the present study. The physical regime on Georges Bank has been particularly well studied. Strong tidal currents flowing over steep bathymetric gradients produce a well-mixed area over the bank (*e.g.*, Flagg, 1987; Perry *et al*. 1993) and complex dynamics, including high variability in mixing during the tidal cycle and the breaking of internal waves (Loder *et al*. 1992; 1993). Coupled bio-physical models indicate that tidal forcing over the bank results in elevated zooplankton concentrations (Franks and Chen

1996). These authors note the difficulties associated with sampling such a dynamic feature, particularly since enhanced vertical mixing and horizontal gradients are formed for only a brief period. Similar fine-scale bio-physical models would be useful in better understanding the mechanisms controlling zooplankton abundance in surface waters at the Brier Island ledges.

Brown and Gaskin (1989) found significant differences in phalarope abundance and zooplankton biomass between control sites and localized upwelling or convergence zones at Brier Island and suggested that tidal currents were important in structuring the surface plankton community in these features. Furthermore, Brown (1980) suggested that tidal currents interacting with the ledges created regions of upwelling immediately above the ledges, which then drift downstream and create convergence streaks, where weed mats are aggregated, as they sink. The results support these hypotheses and demonstrate that strong tidal currents generate plankton-rich upwelling regions above the ledges at fine temporal and spatial scales.

Surface zooplankton distributions in the Head Harbour region were likely the result of similar dynamic oceanographic processes created by strong tidal currents, as described by Smith *et al.* 1984. During the early 1980s, zooplankton samples collected at Head Harbour contained high densities of *Calanus finmarchicus* during both ebb and flood tide phases. Physical forcing in the Bay of Fundy is dominated by large semidiurnal tides (Smith et al. 1984), but zooplankton samples from Head Harbour were not analyzed at a fine enough temporal scale to make comparisons with the results presented here. For example, Mercier (1983) compared surface distribution of zooplankton between the flood and ebb tide phases, but did not examine temporal variation within these tidal phases.

It is difficult to draw quantitative comparisons between the observations and historical samples, but I draw attention to temporal differences in the proportions of *Calanus finmarchicus* observed in zooplankton samples from this area. For example, the mean proportion of total copepods comprised by *C. finarchicus* was 54% in surface waters at Brier Island during August and early September in the present study. Similar estimates from Brown and Gaskin (1989) from the same months during the late 1970s and early 1980s were typically below 20% at Brier Island and higher than 85% in Head Harbour. I do not have enough information to be able to tease apart the factors responsible for this variation, but they may have been significant factors in the observed changes of patterns of habitat use exhibited by red-necked phalaropes in the Bay of Fundy. *C. finmarchicus* is an important component of the Bay of Fundy ecosystem and is an important determinant of the population dynamics of several other marine predators that exploiting the productive waters of this region during summer months (Greene and Pershing 2004).

The CART model indicated that phalaropes were likely to forage after mid-flood in regions and during times of mid- to high current velocity (> 0.40 m s^{-1}). Visual examination of *Calanus finmarchicus* abundance relative to tidal phase (e.g., Figure 6b and Figure 7) suggests that this species was more abundant during the early flood tide phase. This apparent temporal mismatch between phalarope habitat use and copepod abundance over the ledges could be associated with the location and local depletion of prey patches. Individual phalaropes may locate profitable foraging patches during the mid-flood tide, and draw aggregations of multiple birds after the patches are located. Large numbers of feeding phalaropes could deplete prey resources in surface waters, particularly if episodic tidal effects create only short pulses of zooplankton in surface waters.

Oceanographic processes in other locations within the Bay of Fundy also create dynamic foraging habitat for phalaropes. Phalaropes likely move between different foraging patches over different tidal phases. For example, phalaropes were observed to feed on weed “slicks”, likely associated with convergence fronts (Brown 1980), south of Brier Island during low tide, when convergence between in- and out-flowing tidal currents would be expected. Similarly, observations of foraging phalaropes from aerial survey data suggest that these birds are associated with bathymetric gradients and features in the Grand Manan basin (R. Hunnewell, unpublished observations).

Evaluating surface zooplankton distributions in these areas would provide a more complete picture of the prey field currently available to foraging phalaropes. Ongoing bay-wide aerial and boat-based surveys in this region by the University of New Brunswick and the Manomet Center for Conservation Science will provide a more comprehensive picture of present-day phalarope abundance habitat use within the Bay of Fundy.

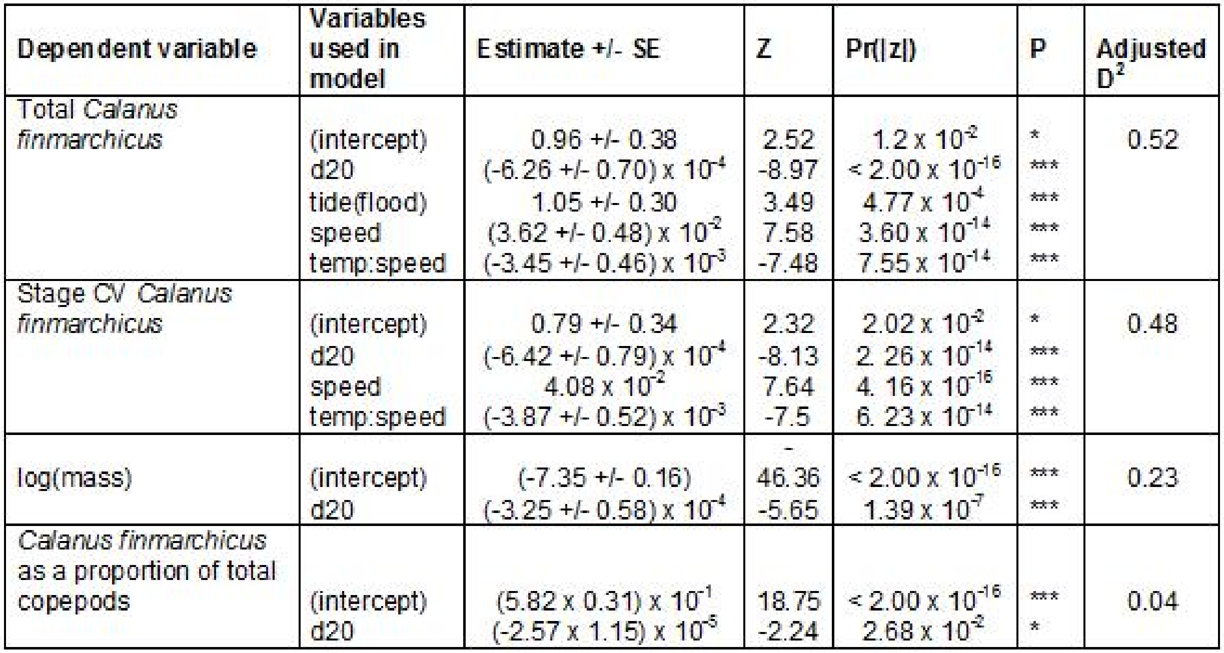
The southward migration of red-necked phalaropes occurs during a period of high availability of stage CV *Calanus finmarchicus* in certain surface waters of the Bay of Fundy. The density and energy content of CV *C. finmarchicus* in the Bay of Fundy are low in the early summer months, increase in the late summer and peak in September and October (Michaud and Taggart 2007). In the past, red-necked phalaropes were observed in the Bay of Fundy from early August to mid-September (Mercier 1983). We do not know whether or not the timing of migration has changed in the Bay of Fundy since the 1980s, highlighting the need for basic information on the habitat use of red-necked phalaropes. The development of tags allowing the movements of red-necked phalaropes to be tracked over large distances would be helpful in elucidating the broader-scale habitat use, seasonal movements, energy budgets and population trends of this species.

In conclusion, the present study documents the zooplankton prey field available to phalaropes foraging in the Brier Island region of the Bay of Fundy and demonstrates the importance of physical forcing in structuring the foraging habitat of this species at fine spatial and temporal scales. At broader scales, I observed high variation in the density of surface zooplankton samples due to the extremely dynamic nature of this area, demonstrating the need for careful survey design and methods. This is particularly important so that we can accurately assess the potential drivers of the demography of red-necked phalaropes.

Table 2: Mean species composition and stages of *Calanus finmarchicus* as a proportion of total copepods collected plankton tows conducted on the Brier Island ledges during August and September. Standard deviations are shown for the present study, while data were not available to calculate this information from Brown and Gaskin (1989). * See text for discussion of methodological differences in calculations. Abbreviations are as follows: C.fin = *Calanus finmarchicus*; *Centro*. sp = *Centrapages* sp.; Oith. sp. = *Oithona* sp.

	No. tows	Average mg m^{-3}*	Total copepods	*C. fin.*	*Acartia sp.*	*Pseudo. sp.*	*Centro. sp.*	*Anom sp.*	*Oith. sp.*	Other copepods	Stage CV *C .fin.*	Adult *C. fin.*
Present study												
August 13-19	36	1.0 +/- 0.8	20633	61.9 +/- 23.9	17.9 +/- 19.1	5.8 +/- 9.1	6.3 +/- 7.3	7.0 +/- 19.6	0.1 +/- 0.53	0.9 +/- 1.5	21.2 +/- 12.17	22.7 +/- 14.9
August 25-31	36	2.1 +/- 3.4	144900	51.8 +/- 26.8	16.8 +/- 22.9	20.8 +/- 16.6	5.4 +/- 4.9	1.4 +/- 2.8	0 +/- 0	3.8 +/- 6.8	23.8 +/- 15.3	17.2 +/- 13.9
September 1-6	60	0.7 +/- 1.1	66372	50.1 +/- 25.4	18.5 +/-20.74	15.3 +/- 16.2	11.6 +/- 10.8	3.4 +/- 5.0	0 +/- 0	1.2 +/- 6.8	20.1 +/- 14.9	17.4 +/- 13.4
TOTAL	132	1.15 +/- 2.1	231905	53.8 +/- 25.7	17.9 +/-20.77	14.2 +/- 15.7	8.5 +/- 9.1	3.9 +/- 6.9	0 +/- 0.3	1.8 +/- 4.0	21.4 +/- 14.3	18.8 +/- 14.0
Brown and Gaskin (1989)												
August 13-20, 1975	11	2.6	3593	20.7	43.3	32.0	1.4	0.5	0.2	1.9	N/A	N/A
August 21-29, 1975	8	1.0	2443	2.3	64.1	26.7	2.6	0.7	1.3	2.3	N/A	N/A
August 25-31, 1976	12	6.6	8934	6.1	4.1	62.6	18.9	2.6	0.8	4.9	N/A	N/A
September 1 and 15, 1976	3	4.5	1727	3.4	10.1	36.9	44.9	1.2	2.3	1.2	N/A	N/A
August 18, 1977	7	2.6	2941	24.4	28.1	34.3	1.9	1.0	1.6	8.7	N/A	N/A
August 16-21, 1978	12	1.8	1291	81.6	6.2	5.1	0.8	5.1	0.0	1.0	N/A	N/A

Table 3: Variables included in best fit models for total *Calanus finmarchicus*, stage CV *C. finmarchicus*, dry plankton biomass and *C. finmarchicus* as a proportion of total copepods. Models were offset with water volume to account for differences in flow between samples. To examine *C. finmarchicus* as a proportion of total copepods, the model used the total number of *C. finmarchicus* individuals and was offset by the total number of copepods in addition to water volume. Abbreviations are as follows: d20 = distance to 20 m contour; tide = tidal state (flood vs. ebb); speed = current speed; temp = sea surface temperature.



Dependent variable	Variables used in model	Estimate +/- SE	Z	Pr(|z|)	P	Adjusted D^2
Total *Calanus finmarchicus*	(intercept)	0.96 +/- 0.38	2.52	1.2×10^{-2}	*	0.52
	d20	$(-6.26 +/- 0.70) \times 10^{-4}$	-8.97	$< 2.00 \times 10^{-16}$	***	
	tide(flood)	1.05 +/- 0.30	3.49	4.77×10^{-4}	***	
	speed	$(3.62 +/- 0.48) \times 10^{-2}$	7.58	3.60×10^{-14}	***	
	temp:speed	$(-3.45 +/- 0.46) \times 10^{-3}$	-7.48	7.55×10^{-14}	***	
Stage CV *Calanus finmarchicus*	(intercept)	0.79 +/- 0.34	2.32	2.02×10^{-2}	*	0.48
	d20	$(-6.42 +/- 0.79) \times 10^{-4}$	-8.13	2.26×10^{-14}	***	
	speed	4.08×10^{-2}	7.64	4.16×10^{-16}	***	
	temp:speed	$(-3.87 +/- 0.52) \times 10^{-3}$	-7.5	6.23×10^{-14}	***	
log(mass)	(intercept)	(-7.35 +/- 0.16)	-46.36	$< 2.00 \times 10^{-16}$	***	0.23
	d20	$(-3.25 +/- 0.58) \times 10^{-4}$	-5.65	1.39×10^{-7}	***	
Calanus finmarchicus as a proportion of total copepods	(intercept)	$(5.82 \times 0.31) \times 10^{-1}$	18.75	$< 2.00 \times 10^{-16}$	***	0.04
	d20	$(-2.57 \times 1.15) \times 10^{-5}$	-2.24	2.68×10^{-2}	*	

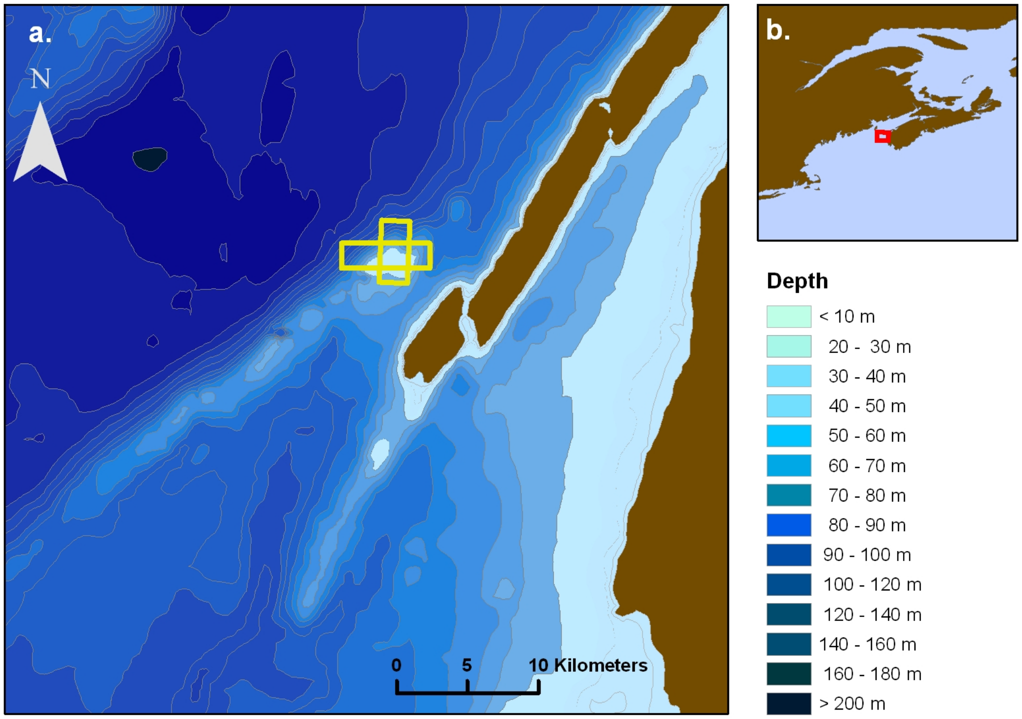


Figure 3a. Example of box transects (as indicated by the yellow boxes) used for oceanographic surveys relative to the bathymetry surrounding the Brier Island ledges. Study efforts focused on Northwest Ledge. b. Location of the study site within Atlantic Canada.

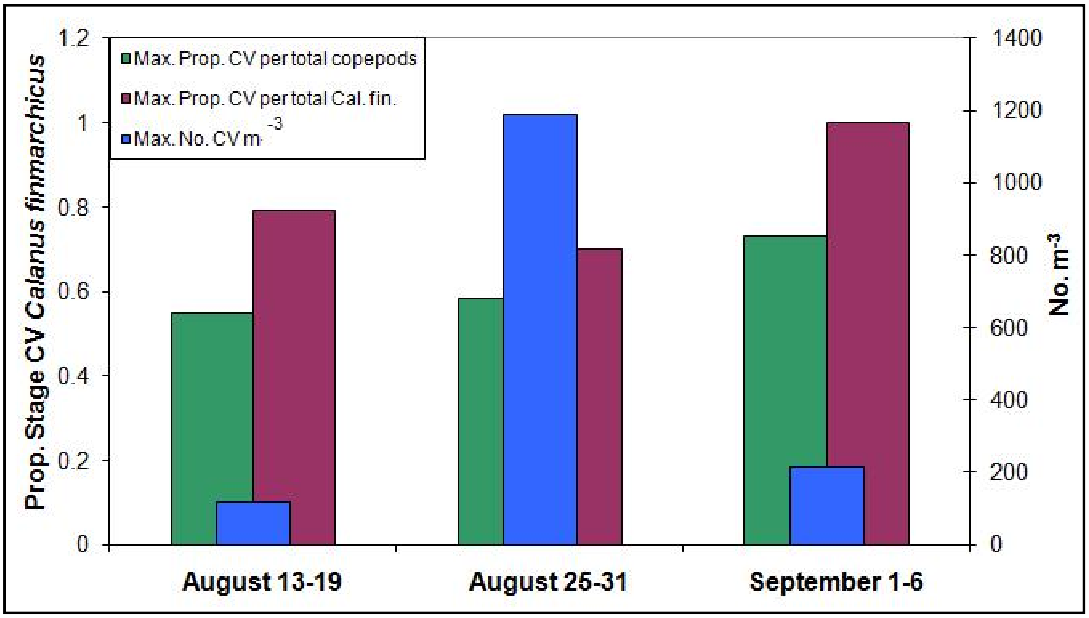


Figure 4: Maximum proportion and biomass of stage CV *Calanus finmarchicus* by survey week. CV is shown both as a proportion of total copepods and as a proportion of total *C. finmarchicus* (indicated as Cal. fin.).

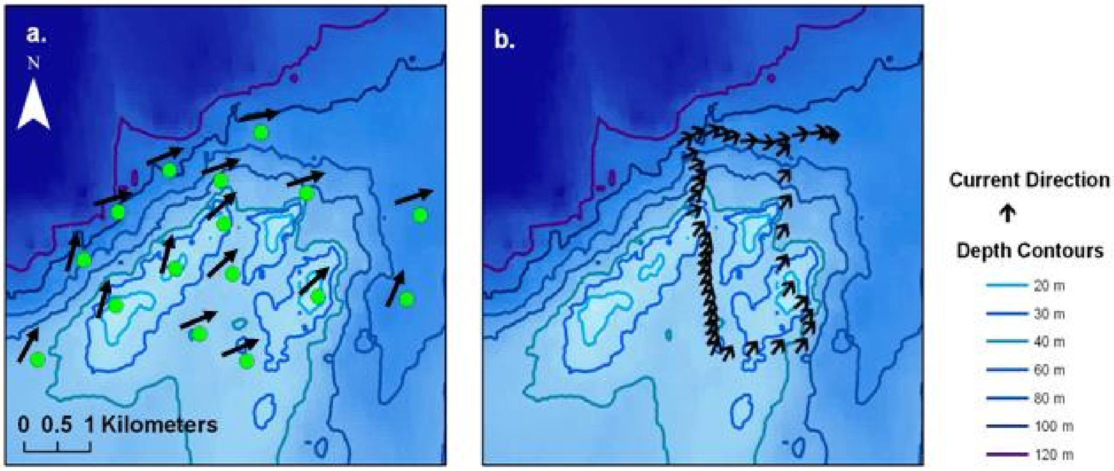


Figure 5: a. Mean direction of flow during flood tide at the indicated sample points, as calculated using circular statistics (current measurements taken 1 h before slack high and 1 h after slack low were excluded). b. Example of current direction during the mid-flood tide showing a shift in current direction towards the east at the north part of Northwest Ledge.

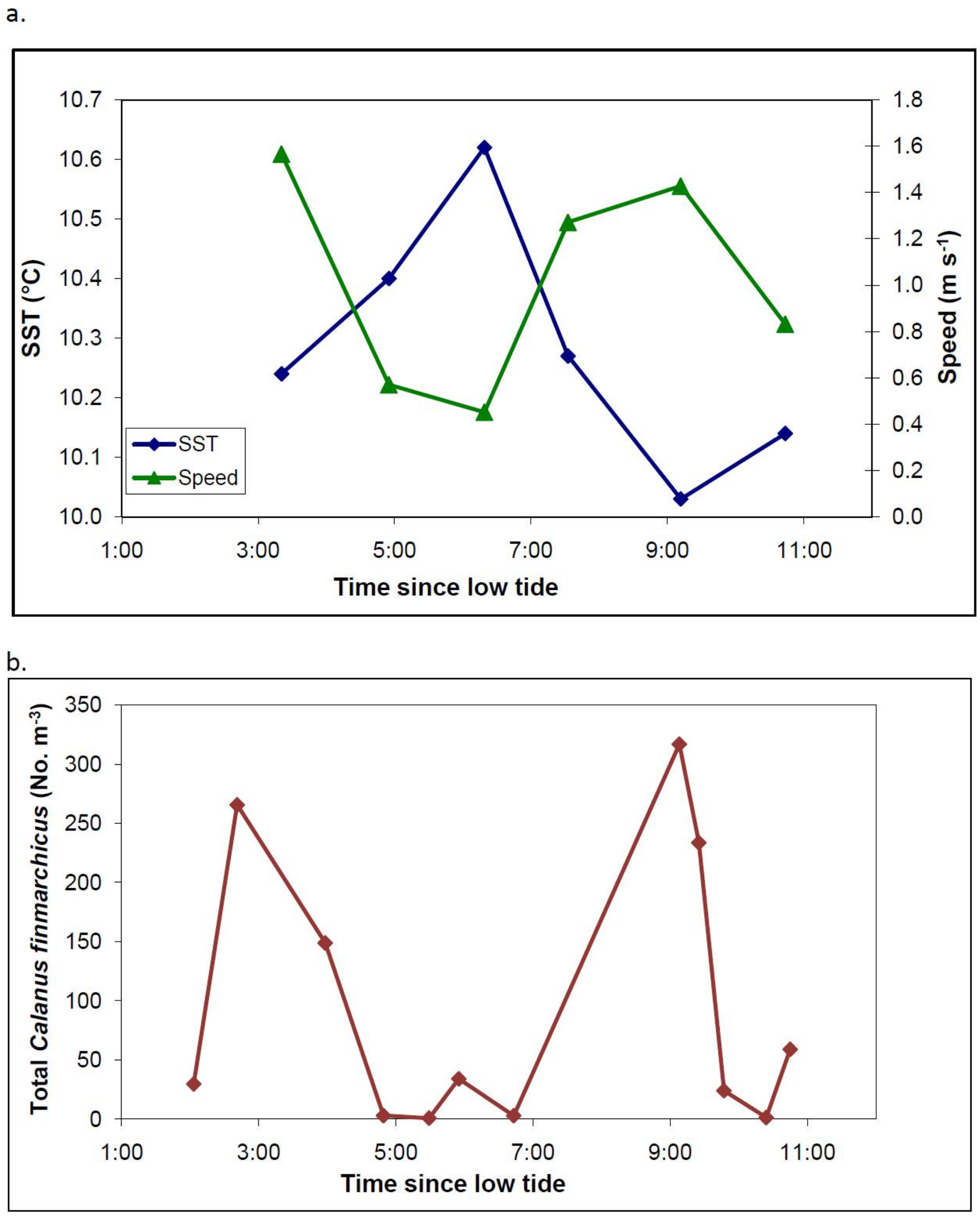


Figure 6: a. Example of the relationship between SST and speed relative to time of tidal cycle (sampled at a central point on Northwest Ledge with a depth of 30 m on August 30, 2007). Note that current speeds measured at this location during slack high tide were > 0.40 m s^{-1}. Current speeds measured in other locations during slack high tide reached approximately 0.05 m s^{-1}. b. The abundance of total *Calanus finmarchicus* is shown relative to time since low tide for the same day.

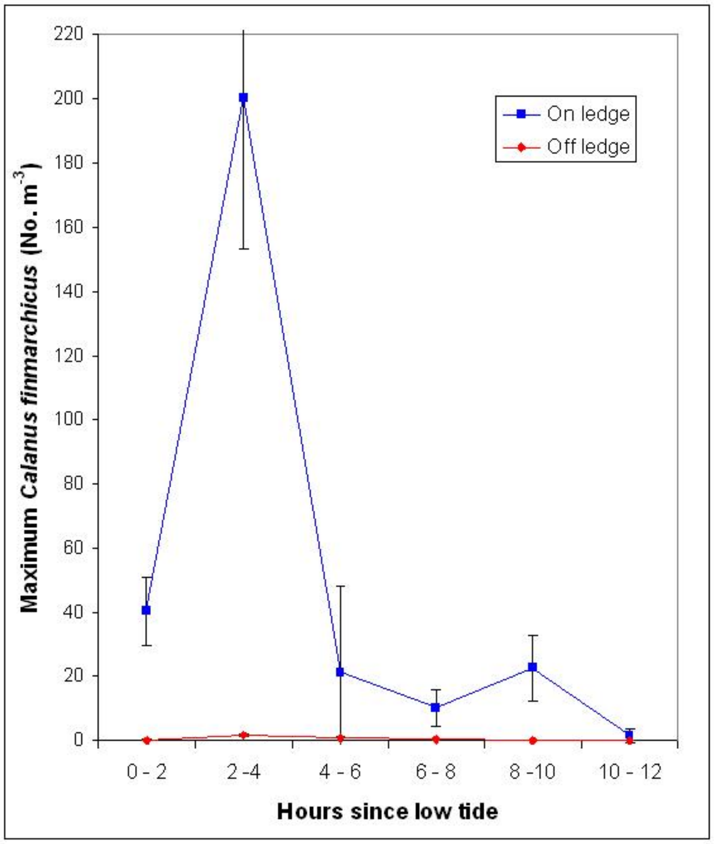


Figure 7: Average *Calanus finmarchicus* abundance (No. m^{-3} +/- standard deviation) by tidal phase on Northwest Ledge (within 1100 m of the 20 m depth contour) and off of Northwest Ledge.

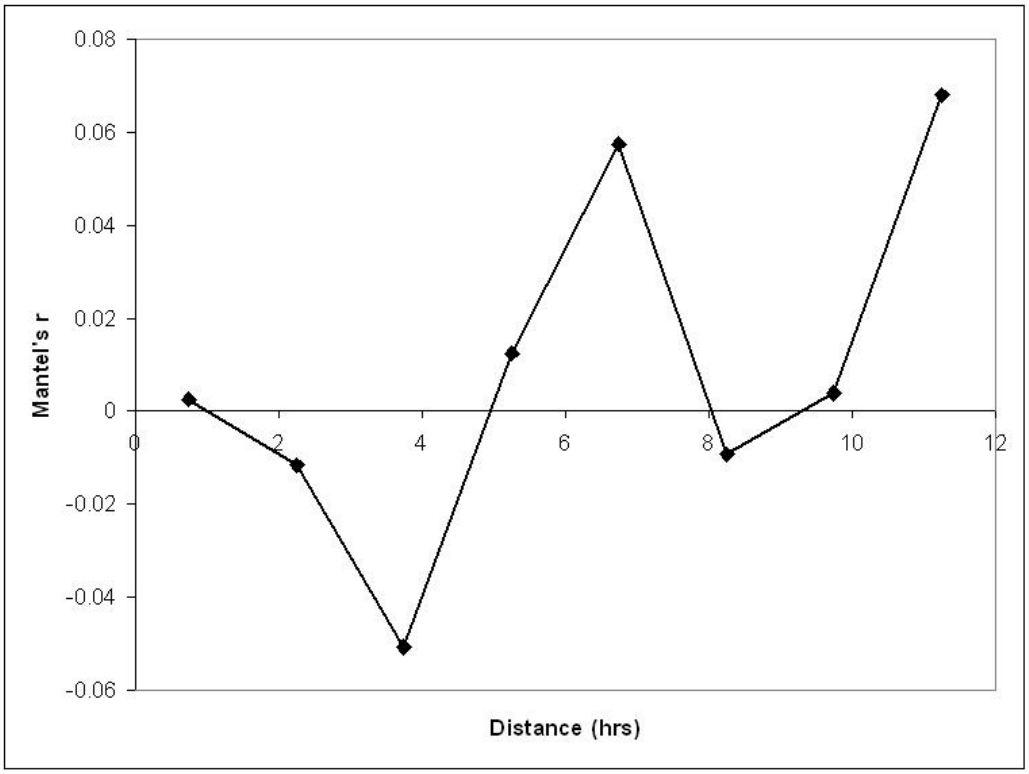


Figure 8: Mantel's correlogram assessing similarity in total *Calanus finmarchicus* abundance (No. m^{-3}) relative to tidal phase (time since low tide) at the Brier Island ledges. Positive autocorrelation at temporal lags of approximately 6 and 12 h relative to tidal cycle was not significant after a Bonferroni correction was applied, but suggests strong tidal effects on plankton abundance.

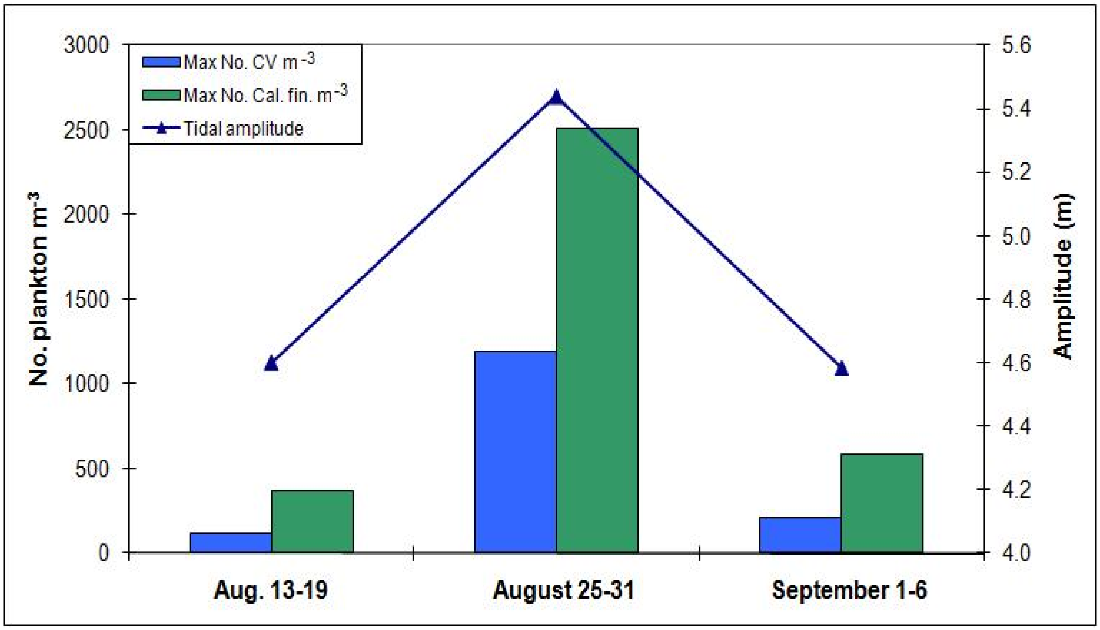


Figure 9: Maximum abundance of total *Calanus finmarchicus* and stage CV *C. finmarchicus* by survey week relative to tidal amplitude at the Brier Island ledges.

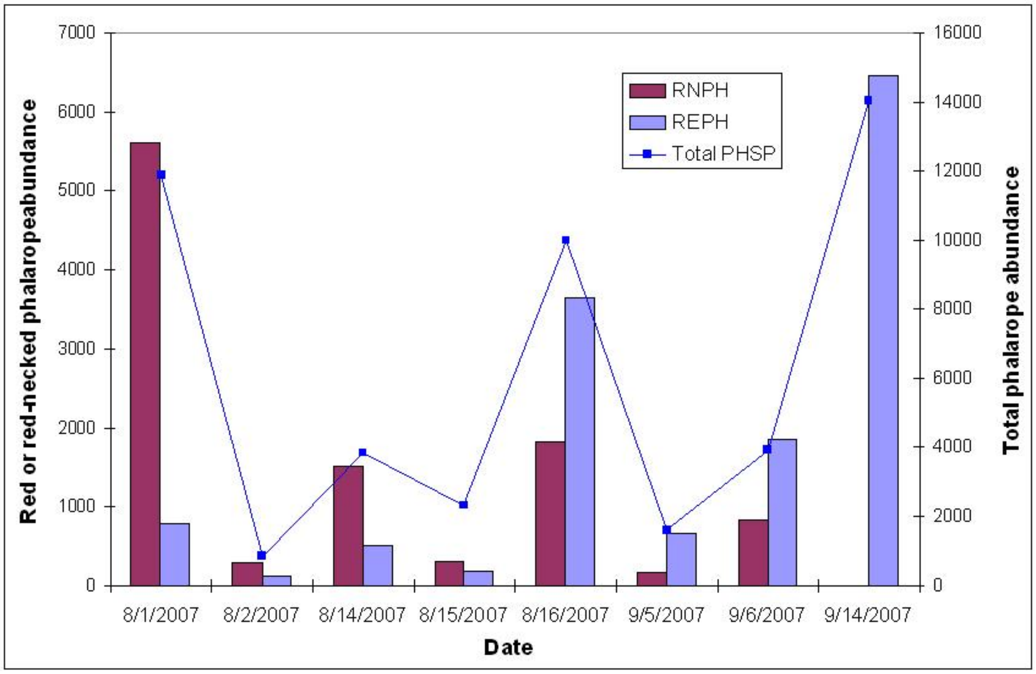


Figure 10: Phalaropes observed at the Brier Island ledges by species and date. Note that while many more unidentified phalaropes than identified phalaropes were observed, red-necked phalaropes (*Phalaropus lobatus*) were observed less frequently with time and red phalaropes (*Phalaropus fulicarius*, REPH) were observed more frequently with time. PHSP indicates the total number of phalaropes observed (*Phalaropus* spp.; both identified and unidentified phalaropes).

Chapter 3: Predictive habitat models of seabird abundance and distribution in Onslow Bay, North Carolina

Abstract

The Gulf Stream has important physical and biological effects on coastal and shelf waters in the South Atlantic Bight (SAB). In the 1980s, a suite of studies examined the influence of dynamic Gulf Stream features on the distribution of seabirds off the SAB, but no quantitative studies have been conducted in this area since then. The present study evaluates the habitat use of seabirds in Onslow Bay, North Carolina over a two and a half year period. Physical habitat features were described using remotely sensed data and *in situ* observations made during boat-based surveys. Multivariate techniques were used to examine the relative importance of multiple environmental predictor variables, representing both dynamic and fixed factors, to seabird habitat. Low seabird densities were observed in Onslow Bay, though densities were comparable to those observed further south in the SAB. Maximum entropy modeling techniques produced robust habitat models for five of the six most commonly observed species or species groups. Frontal features in Onslow Bay were less important habitat features than in previous studies in the SAB; potential explanations for this discrepancy are discussed. At least one dynamic variable (sea surface temperature, distance to front, or water mass, defined as Gulf Stream, eddy cold core, eddy warm filament, or shelf waters) was an important predictor of habitat for each seabird species evaluated. Black-capped petrel (*Pterodrama hasitata*) habitat occurred over the outer continental shelf, inshore of the Gulf Stream, and in cold core regions of Gulf Stream frontal eddies. Audubon's shearwaters (*Puffinus lherminieri*) were found to prefer medium depths in regions of the outer shelf close to the inshore shelf break, and were associated with cold core regions of Gulf Stream frontal eddies. Cory's shearwaters (*Calonectris diomedea*) used waters of the outer continental shelf that are influenced by the Gulf Stream, and cold core regions of GSFEs appear to provide important habitat for the species. Phalaropes (*Phalaropus* spp.) used shelf waters with cooler sea surface temperatures that are relatively close to frontal features, while Wilson's storm-petrels used offshore habitats close to the inshore shelf break, particularly those located within Gulf Stream waters. These results demonstrate the importance of dynamic habitat variables to seabird habitat in the SAB, and highlight the use of multivariate techniques in assessing seabird habitat in dynamic environments.

1. Introduction

The Gulf Stream is the dominant flow component along the outer continental shelf of the South Atlantic Bight (SAB; Atkinson et al. 1983, Lee et al 1989) and has important biological effects within this region. In particular, dynamic features associated with the Gulf Stream stimulate primary production on the continental shelf

(Lee et al. 1981, Yoder et al. 1981, Lohrenz et al. 1993). Previous research off the coast of Georgia and southern South Carolina has demonstrated significant associations between seabirds and two types of fronts: mid-shelf fronts, formed seasonally at 20-40 m between October and March; and Gulf Stream fronts (Haney 1985a, Haney and McGillivary 1985a,b). Cory's shearwaters (*Calonectris diomedea*) were significantly more abundant at Gulf Stream fronts during summer and fall (Haney and McGillivary 1985a), and mid-shelf fronts created important foraging habitat for wintering phalaropes (Haney 1985a). The abundance of seabirds was highest when mid-shelf fronts were present and birds were aggregated within 10 km of these fronts (Haney and McGillivary 1985b). Gulf Stream frontal eddies create episodic upwelling in the SAB (e.g., Yoder et al. 1981), which provides important habitat for foraging seabirds (e.g., Haney 1986a,b; discussed in more detail in Chapter 4).

Previous studies of seabird habitat use in the SAB were restricted to southern regions (Florida, Georgia and the southern reaches of South Carolina). Very few studies have evaluated seabird habitat use further north in the SAB (Haney 1987, Lee 1987), and I am not aware of any relevant seabird research in the SAB since these studies were conducted in the mid-1980s. Furthermore, these studies did not assess the relative importance of frontal features to seabird habitat in relation to other habitat characteristics. Studies evaluating seabird habitat use of particular oceanographic features in relation to other habitat factors are expensive since they require repeated surveys of a given area over a long period. However, such studies provide a more complete picture of the role of oceanographic features in creating foraging habitat for seabirds, and are necessary to assess changes in seabird habitat use through time.

The present study examines seabird abundance and distribution in Onslow Bay, North Carolina in relation to physical features of habitat. In particular, I examine the importance of sea surface temperature (SST) fronts in the context of other relevant physical habitat factors.

2. *Methods*

2.1 Study site

Onslow Bay lies within the SAB, between Cape Lookout and Cape Fear, North Carolina (Figure 11). A small, narrow front separates the Gulf Stream from shelf waters south of Cape Hatteras (Pietrafesa et al. 1985). This front, which forms along the western edge of the Gulf Stream, is among the most energetic frontal regions in the world (Olson et al. 1994). The Gulf Stream meanders, causing daily variation in its distance from shore and, as a result, SST in any particular location can show considerable variation over a few days (e.g., Webster 1961, Stegmann and Yoder 1996). The mid-shelf fronts that are present further south in the SAB (Haney and McGillivary 1985a) may be obscured in Onslow Bay, where these fronts often join with the Gulf Stream front (Govoni and Spach 1999).

The continental shelf drops off steeply off the coast of North Carolina, with deep waters (> 1000 m) occurring within 100 km of the coast in the northernmost regions of Onslow Bay (Figure 11). This is in contrast to further south in the SAB, where the 1000 m depth contour is located more than 350 km offshore. The bathymetric characteristics of this region likely exert different biological effects than those observed further south in the SAB. In addition, Gulf Stream fronts investigated during previous research (Haney and McGillivary 1985b) were coincident with the 200 m shelf break, making it difficult to distinguish between the effects of the shelf break and those of frontal features. Meanders of the Gulf Stream become more pronounced further north in the SAB (Bane and Brooks 1979). Consequently, the Gulf Stream front often occurs well away from the 200 m shelf break in Onslow Bay (Figure 12), allowing the effects of these two features to be evaluated separately.

2.2 Seabird surveys in Onslow Bay

Seabird surveys were conducted within a 74 km by 83 km (40 nm by 45 nm) study site in Onslow Bay between June, 2007 and September, 2009. Seabird abundance, distribution and species composition were assessed using ship-based surveys over cross-shelf transects 74 km (40 nm) in length (Figure 11). Each transect began approximately 50 to 70 km offshore and extended past the shelf break and into Gulf Stream waters. These transects were designed to assess the abundance of marine mammals and sea turtles in a proposed Navy training range, but presented the opportunity to conduct regular, standardized seabird surveys across a range of physical habitat gradients.

Seabird surveys were conducted aboard one of two observation platforms (12- and 13-m sport-fishing boats) at a speed of 5 m s^{-1}. All seabirds observed within a 90 degree bow-beam arc within 300 m of the starboard side of the ship were recorded by a dedicated seabird observer sitting approximately 5 m above the water (Tasker et al. 1984). Surveys were conducted in Beaufort sea states of 0-3 to omit biases associated with poor sighting conditions produced by rough seas. SST was recorded from a hull-mounted temperature sensor every 15 min to ground-truth boundaries of water masses observed from remotely sensed data. Four trained and experienced observers conducted seabird surveys, with one seabird observer (the author) conducting most (77%) surveys. Two observers conducted surveys on only a single day, so it was not possible to make quantitative comparisons because error estimates could not be determined for these observers. I compared sightings per km^2 of effort for the main observer to those of all of the other observers combined using a Wilcoxon test, using only summer surveys to reduce any bias associated with seasonal effects. To investigate seasonal trends the year was divided into seasons as follows: Summer, June to August; Fall, September to November; Winter, December to February; and Spring, March to May (as in Haney and McGillivary 1985a).

Seabird observations were made using a Sony digital voice recorder to allow for continual scans of the strip transect during survey effort (i.e., so the observer could continue looking at the water rather than having to write or type the data as it was collected). Observations were later transcribed for analysis. For each seabird sighting, a waypoint was taken using a handheld Garmin GPS, and the species identification, number and behavior of birds (sitting, flying, or feeding) was recorded. Species identifications were made to the lowest taxonomic level possible. When positive identifications could not be made to the species level with certainty, species were lumped into species groups (e.g., unidentified storm-petrel, unidentified phalarope). Few ship-following birds were observed, but any birds that were associated with the survey vessel, such as white-tailed tropicbirds (*Phaethon lepturus*), were noted. Due to the low density of birds in the study area (see below), many of the difficulties associated with counting large numbers of seabirds (reviewed in Tasker et al. 1984) were not an issue in the present study.

2.3 Satellite oceanography

Daily satellite images of SST were used to identify Gulf Stream and shelf waters, as well as the location of the Gulf Stream and mid-shelf fronts. Advanced Very High Resolution Radiometer (AVHRR) data from the National Oceanographic and Atmospheric Administration (NOAA) Polar-Orbiting Environmental Satellites (POES) provide SST data at a resolution of 1 km, and these data were used to describe the boundaries of oceanographic features whenever possible. However, interference from cloud formations, which form frequently over the Gulf Stream, often rendered POES data unusable in the study area. Geostationary Operational Environmental Satellites (GOES) provide lower resolution data (8 km pixels), but provide measurements every 30 min, which allows cloud motions to be resolved (Legeckis 1978). GOES satellite data were used to detect SST fronts using the Cayula-Cornillon fronts tool in the Marine Geospatial Ecology Tools package for ArcGIS (Roberts et al. 2010; available at http://code.env.duke.edu/projects/mget), which uses the single edge detection algorithm developed by Cayula and Cornillon (1992).

Shipboard measurements of SST, measured every 15 min, were used in combination with satellite images of SST to identify the presence of GSFEs during seabird surveys. Shipboard SST measurements were interpolated in ArcGIS 9.2 using Kriging interpolation in the Spatial Analyst extension with a pixel size of 100 m. GSFEs were identified from satellite images of SST (see discussion of GOES and POES images above). GSFEs comprise a cold water core surrounded by warm Gulf Stream waters to the east and by a warm filament to the west (see further discussion in Chapter 4). SST values of these water masses varied seasonally, but water masses were distinguished based on spatial variation in SST signatures observed in ship-based and satellite measurements. Surface temperature measurements between water masses within

GSFEs differ by approximately 1°C, though temperature differences are much greater at depth (Glenn and Ebbesmeyer 1994). Seabird habitat use relative to frontal features and eddy habitat was also evaluated in a multivariate framework (see description of habitat models below).

2.4 Spatial autocorrelation in seabird data

Spatial autocorrelation in seabird distribution was assessed using the Moran's I coefficient to determine the spatial scale at which sampling bins could be considered to be independent for spatial analyses. Moran's I indicates the degree of spatial autocorrelation of data and can be used to determine whether significant autocorrelation is present. Negative values of Moran's I indicate segregation, while positive values indicate aggregation (Fortin et al. 1989). Survey transects were divided into 1 km grid cells and spatial autocorrelation was assessed at a lag distance of 4 km for 20 lags. Moran's I values were compared with those produced from 1500 Monte Carlo simulations to assess significance using a modified Bonferroni correction for multiple testing (Legendre and Fortin 1989; Louzao et al. 2006). Moran's I calculations and Monte Carlo simulations were conducted using the Excel add-in Rookcase (Sawada 1999). Spatial autocorrelation for each species was assessed separately using the survey day with the largest number of sightings for that species. The scale of autocorrelation was then used to determine the scale of the sampling grid used in further analyses.

2.5 Seabird habitat models

Habitat models were developed for frequently observed seabird species using both dynamic and fixed physical habitat variables. These variables were assessed in a GIS using ArcGIS version 9.2 and included: SST; distance to SST front; distance to “inshore” and “offshore” shelf breaks (defined below); distance to land; depth; and water mass (Gulf Stream, eddy cold core, warm filament, and shelf waters). The “inshore” and “offshore” shelf breaks were defined as the 200 m and 1000 m contours, respectively. Steep bathymetric gradients occur near these depth contours (see Figure 11). Transect lines crossed the inshore shelf break, but did not reach the offshore shelf break, so distance to the offshore shelf break is only an indicator of proximity to deep water habitats, rather than a metric of the importance of this shelf break. The Euclidean distance tool in the Spatial Analyst extension of ArcGIS was used to create continuous rasters of distance to front, distance to land, and distance to inshore and offshore shelf breaks. The UTM projection was used to produce accurate distance measurements within Onslow Bay (Banergee 2005).

Classification and Regression Trees (CARTs) and Maximum Entropy modeling techniques were used to evaluate habitat factors characterizing seabird habitat in Onslow Bay. These techniques were selected because they: can incorporate interactions between predictor variables; allow the use of both continuous and categorical variables;

make no assumptions about the relationships between independent and dependent variables or between predictor variables; and allow non-linear relationships to be evaluated. CARTs are multivariate recursive partitioning techniques that can be used to define habitats based on a number of environmental predictor variables (Breiman et al. 1984). When categorical data are used (e.g., presences vs. absences), a classification tree is produced which categorizes data based on binary splits of environmental data into increasingly homogenous partitions. Grid cells in which no seabirds were observed were used as pseudo-absences for the CART analysis. The results of the autocorrelation indices were used to inform the size of the survey grid used in CART analyses. The "tree" package was used to build and assess CART models in the R Statistical Software package (version 2.9). Over-fitting of CART models was avoided by using misclassification costs to "prune" the trees and produce an optimal tree, and models were assessed using cross-validation (Bradford et al. 1998).

Seabird habitat was also assessed using Maximum Entropy (Maxent) techniques, which determine the distribution of maximum entropy, or that which is closest to uniform, to estimate the target distribution in question. In determining the maximum entropy distribution, the model is constrained to produce expected values that match the empirical average (Phillips et al. 2004, 2006). Maxent is a presence-only modeling technique, using data from species occurrences to build the model and presenting the results relative to background data representing available habitat. Maxent performs well compared to other presence-only modeling techniques and to models using both presence and absence data (Elith et al. 2006). Seabirds are highly mobile, so locations where seabird species are not observed do not necessarily represent true absences, and thus presence-only modeling techniques are particularly useful in assessing the habitat of these species. In addition, Maxent performs well with small sample sizes, making this a useful technique for examining distributions of rare or sparsely distributed species (Hernandez et al. 2008, Wisz et al. 2008). Bias in survey effort in certain areas can be accounted for by applying the same bias to the background data used to develop Maxent models (Phillips et al. 2009). Thus, the 8000 background points used in the Maxent model were restricted to dates and locations that had been surveyed during standardized seabird surveys in Onslow Bay. The Maxent program, version 3.3.1 (available from http://www.cs.princeton.edu/~schapire/maxent), was used to build Maximum Entropy models. To test the performance of the model, 25% of the sightings were set aside and used as test samples.

Maxent provides both threshold-dependent and threshold-independent measures of model outputs. Threshold-independent assessments are provided using the Area Under the Curve (AUC) metric of the Receiving Operator Characteristic (ROC) curve (Fielding and Bell 1997). In a ROC curve, all sensitivity values (true positives) are plotted on the y-axis against 1 – specificity (false positive) values on the x-axis. The AUC value provides a threshold-independent metric of overall accuracy, and ranges between

0.5 and 1.0. Values of 0.5 indicate that scores of specificity and sensitivity do not differ, while scores of 1.0 indicate that the distributions of the scores do not overlap (Fielding and Bell 1997). AUC values were evaluated as in Hosmer and Lemeshow (1989): < 0.5 represented no discrimination; 0.7 to 0.8 indicated an acceptable discrimination; 0.8 to 0.9 indicated an excellent discrimination; and > 0.9 represented outstanding discrimination. Threshold-dependent assessments of the model were provided using one-tailed binomial tests that determined whether the model predicted the test localities significantly better than a random prediction with the same fractional predicted area. Thresholds of 5 and 10 were applied (Waltari et al. 2007), and the performance of the model was assessed using the extrinsic omission rate and the proportional predicted area by applying a one-tailed binomial test to determine whether test locations were predicted significantly better than random. The extrinsic omission rate is the fraction of test localities that occur on pixels that are not predicted to be suitable for the species, while the proportional predicted area is the fraction of pixels that are predicted to be suitable habitat (Phillips et al. 2006).

3. Results

3.1 Seabird surveys in Onslow Bay

A total of 1458 seabirds were recorded over the 939 km^{-2} surveyed on 44 days. More surveys were conducted during summer; few surveys were conducted during the winter when high seas and poor sighting conditions precluded surveys. There was no significant difference in sightings per unit effort (SPUE) between the primary observer and other observers ($p > 0.8$). Overall SPUE was 1.5 birds km^{-2} and was highest in the winter, lower in the fall and spring, and lowest in the summer (Figure 13). Haney and McGillivary (1986a) observed similar patterns in coastal waters off Georgia, with high SPUE observed in winter, intermediate values of SPUE observed during fall and low SPUE in spring and summer. In the present study, winter sightings were dominated by phalaropes and one sighting of many Bonaparte's gulls (*Larus philadelphia*). Due to the relatively low survey effort during winter, these sightings had a considerable effect on the total SPUE for that season.

Twenty-four species were observed during surveys (Table 4). Seabirds with the highest relative abundance were Cory's shearwater (*Calonectris diomedea*; observed on 29 survey days), greater shearwaters (*Puffinus gravis*; 20 days), Wilson's storm-petrel (*Oceanites oceanicus*; 21 days), Audubon's shearwaters (*Puffinus lherminieri*; 23 days) and black-capped petrels (*Pterodrama hasitata*; 13 days). These five species comprised 62% of the total number of identified seabirds. It is difficult to identify phalaropes to species at sea (particularly in non-breeding plumage), so red and red-necked phalaropes (*Phalaropus fulicarius* and *P. lobatus*) were grouped into *Phalaropus* spp., which also showed a high relative abundance and were observed on 10 survey days. The habitat use of phalaropes and the other five species was investigated in a multivariate framework. A large number of common terns (*Sterna hirundo*) were observed in the study site, but the species was only observed on four survey days, with one sighting contributing more than 90% of the total number observed throughout the study. Thus, this species was not included as one of the focal species for further investigations of habitat use.

Seasonal trends in the observations of these species groups in Onslow Bay are shown in Figure 14. Phalaropes were observed in large numbers in the winter, and were also recorded frequently in spring (primarily in March). Small numbers of phalaropes were also observed in summer and fall. There are no published records of the species composition of phalaropes in Onslow Bay, but records from the Cape Hatteras National Seashore indicate that red phalaropes are common from September to April. Red-necked phalaropes are frequently observed between May and October, with fewer observations occurring in June and July (Fussel et al. 1990). However, both red and red-necked phalaropes have been observed in shelf waters off the coast of Georgia in large numbers during winter months, as well as during fall (Haney 1985a). Thus, the phalaropes observed during winter months may have been either species.

Cory's shearwaters were primarily observed in fall and also in summer, consistent with previous observations in North Carolina (Fussel et al. 1990). Greater shearwaters were observed less frequently than Cory's shearwaters and typically occurred during spring and summer, with small numbers observed during fall.

Wilson's storm-petrels and Audubon's shearwaters were observed during winter, spring and summer, with small numbers observed during fall. The high relative abundance of Audubon's shearwaters in winter differed from observations near Cape Hatteras, where these seabirds are rarely observed during winter. However, all winter observations of Audubon's shearwaters occurred on a single day in February, 2009. Black-capped petrels were observed in the spring, summer and fall, with no sightings occurring during winter. Black-capped petrels occur in North Carolina waters year-round (Fussel et al. 1990) and the lack of records for this species in winter months was likely due to low survey effort.

3.2 Spatial autocorrelation in seabird data

Wilson's storm-petrels were spatially autocorrelated at a scale of 8 km ($p < 0.05/20$ using a Bonferroni correction), while no significant spatial autocorrelation was observed for the other focal seabird species at spatial distances less than 8 km. Consequently, models were analyzed using a 10 km grid (i.e., seabird counts within 10 km grid cells were analyzed relative to environmental variables measured at the centroid of each grid cell) for Wilson's storm-petrels, and a 4 km grid for all other species since no autocorrelation was observed for other species at this distance.

3.3 Seabird habitat models

Observations for each species (presences) used in the habitat models were restricted to dates with clear GOES satellite images when all variables, including distance to front and water mass (e.g., Gulf Stream vs. shelf), could be identified simultaneously. This eliminated 10 survey days. After the remaining sightings were binned to account for autocorrelation, the total number of observations available to develop models was 32 for Black-capped petrels; 38 for Audubon's shearwaters; 87 for Cory's shearwaters, 59 for greater shearwaters; 19 for *Phalaropus* spp. and 29 for Wilson's storm-petrels. The seasonal distribution of the remaining surveys was uneven, but was similar to that of the overall survey effort (see Figure 13); the number of surveys by season was 19 for summer, 7 for fall, 2 for winter, and 6 for spring, respectively.

Mid-shelf fronts were not observed frequently in Onslow Bay and were certainly less prevalent than in other areas of the SAB. For example, Haney (1985a) found that the pelagic distribution of wintering phalaropes was closely associated with mid-shelf fronts, but we did not observe mid-shelf fronts within the study area on any of the days when phalaropes were present during winter surveys. Figure 15 shows frontal features identified using the edge detection tool used in the present study relative to survey transects and phalarope sightings on March 13, 2008. Note that while mid-shelf fronts are observed further south in the SAB using this tool, the Gulf Stream front appears to have coalesced with the mid-shelf front in Onslow Bay, as has been noted previously

(Govoni and Spach 1999), and that phalarope sightings were located close to the Gulf Stream front.

CART models for Audubon's shearwaters, Cory's shearwaters, black-capped petrels, Wilson's storm-petrels and phalaropes showed low misclassification error rates (0.066, 0.10, 0.036, 0.092, and 0.0020, respectively). However, this low misclassification rate was driven by correctly predicted absences; many of the species presences were misclassified. CART models for greater shearwaters did not distinguish between habitat and non-habitat for this species. Due to the resulting low specificity of the models (0.14, 0.43, 0.52, 0.31, and 0.63 for Audubon's shearwaters, Cory's shearwaters, black-capped petrels and Wilson's storm-petrels and phalaropes, respectively) and the inability to distinguish between habitat and non-habitat for greater shearwaters, CART models were not used to further investigate seabird habitat use.

Maximum entropy models performed well in predicting seabird habitat for five of the six species groups. For black-capped petrels, threshold-dependent tests indicated that the model predicted test localities significantly better than random (p-values of binomial tests for thresholds 5 and 10 were all << 0.001; Table 5). The AUC values were 0.96 and 0.86 for training and test localities, respectively, which provided "outstanding" and "excellent discrimination" based on our interpretation of AUC values (see above). A jackknife of regularized training gain for black-capped petrels indicated that distance to the offshore shelf break and depth were the most important predictor variables, followed by distance to land, distance to inshore shelf break, and SST. Distance to front and water mass were weak predictors of black-capped petrel habitat (Figure 16). Figure 17 shows model gain in relation to the different habitat variables after interactions between habitat variables have been accounted for. Model gain was highest at low distances to the offshore shelf break, deep depths, intermediate distances to the inshore shelf break, intermediate temperature values, and large distances from land. Model gain was highest for cold core eddy regions, but there was no relationship between model gain and distance to front.

For Audubon's shearwaters, the prediction of test localities was significantly better than random based on threshold-dependent tests for thresholds of 5 and 10 (p values < 0.05; Table 5). AUC values of 0.78 and 0.77 for training and test data, respectively, represented acceptable discrimination. Jackknife tests of regularized training gain indicated that distance to offshore shelf break and depth were the most important variables influencing the model, and distance to land and distance to the inshore shelf break were also important predictor variables (Figure 18). SST, distance to front and water mass were only weak predictors. Relationships between model gain and habitat variables indicated that intermediate distances to offshore shelf break and intermediate depths, large distances from land and low to intermediate distances to inshore shelf break were associated with increased model gain. Low to intermediate temperatures showed higher values of model gain, while water mass and distance to front had little effect on model gain, with slightly higher values occurring within Gulf Stream waters and at low distances from fronts (Figure 19).

Threshold-dependent tests demonstrated that the Maxent model predicted test localities significantly better than random for Cory's shearwaters at thresholds of 5 and 10 ($p < 0.05$), while threshold-independent tests showed AUC values of 0.78 and 0.73 for training and test points, respectively (Table 5). These AUC values represented an acceptable level of discrimination by the model. SST was the most important predictor variable, as indicated by jackknife tests of regularized training gain, with the highest values of model gain occurring at intermediate to high values of SST (Figure 20). Water mass, distance to land, distance to front and depth were moderate contributors to the overall model gain, while distance to inshore and offshore shelf breaks were weaker predictors of Cory's shearwater habitat. Model gain was highest for eddy cold core regions, intermediate depths, and low distances to land, and was slightly higher at low distances to fronts and large distances from inshore and offshore shelf breaks (Figure 21).

Maxent models performed very well in predicting Wilson's storm-petrel habitat, with threshold-dependent tests showing that test data were predicted significantly better than random ($p < 0.01$; Table 5). AUC values for training and test data were 0.88 and 0.92, showing excellent and outstanding discrimination, respectively. Distance to land and depth were the best predictors of Wilson's storm-petrel habitat, followed by

SST and distance to inshore and offshore shelf breaks. Water mass and distance to front were weak habitat predictors (Figure 22). Increased model gain was associated with intermediate to high distances from land, low to intermediate depths, intermediate to high SSTs, low to intermediate distances to inshore and offshore shelf breaks, Gulf Stream waters, and low to intermediate distances to fronts (Figure 23).

The Maxent model predicted test locations significantly better than random ($p < 0.05$) for phalaropes at thresholds of 5 and 10, while AUC values for training and test data offered outstanding discrimination (0.95 and 0.90, respectively). Jackknife tests of regularized training gain showed that SST was the best predictor of phalarope habitat, followed by water mass, distance to inshore and offshore shelf breaks and distance to front. Distance to land and depth were weaker predictors of phalarope habitat (Figure 24). Increased model gain indicated that phalarope habitat was observed at lower values of SST, large distances to inshore and offshore shelf breaks, shelf waters, as well as waters of the eddy cold core, low to intermediate values of distance to front, intermediate values of distance to land, and shallow depths (Figure 25).

Maxent models performed poorly in predicting greater shearwater habitat. Threshold-dependent tests indicated that models did not perform significantly better than random at predicting test locations for thresholds of 5 and 10 (Table 5), while the AUC for the test data (0.65) was lower than the “acceptable” cut-off of 0.70 and was considerably lower than that for the training data (0.82). The model suggested that SST, distance to front, and distance to land were important predictor variables, while water mass, distance to inshore and offshore shelf breaks and depth were weak predictors (Figure 26). Model gain was higher for intermediate to high SSTs, low distances to front, and high distances from land (Figure 27). Model gain showed little response to the remaining habitat variables, though model gain for Gulf Stream, eddy cold core and shelf waters, short distances to offshore shelf break, intermediate distances to inshore shelf break and intermediate depth values appeared to be slightly higher.

4. Discussion

Maximum entropy models generally performed well in predicting seabird habitat, while CART models were unable to adequately distinguish habitat from non-habitat. CART models rely on pseudo-absences to compare habitat to non-habitat; pseudo-absences were generated in the presence study from grid cells along transect lines in regions where no seabirds were observed. Seabirds are highly mobile predators, covering large distances in short periods of time (e.g., Jouventin and Weimerskirch 1990, Weimerskirch et al. 2004). Consequently, the pseudo-absences used to generate CART models may not have accurately represented regions were seabirds were not present. For example, seabirds may not have been observed in a given grid cell when the survey vessel transited through that cell, but could have occupied the grid cell just after the vessel had passed by. Maxent models use only environmental variables at locations where seabirds are observed to build the model, so problems associated with pseudo-absences were avoided using this modeling technique.

These results highlight the importance of considering dynamic physical oceanographic variables in habitat analyses and of analyzing seabird habitat using multivariate techniques. There is considerable fine-scale temporal variation in the location of the Gulf Stream (e.g., Stegmann and Yoder 1996) and it is, therefore important to consider the physical environment at a daily level. At least one dynamic variable (SST, distance to front, or water mass) was an important predictor of habitat for each seabird species. In addition, the results of this study provide important habitat data on seabirds using the outer continental shelf and Gulf Stream regions of offshore waters of North Carolina, where few standardized seabird surveys have been conducted. Recent records of seabirds off the coast of North Carolina have primarily come from pelagic bird watching cruises that use chum to attract birds to the boat (B. Patteson, pers. comm.). Conducting standardized surveys in a variety of oceanographic habitats and over extended periods is critical to determining the abundance of different seabird species and to understanding the factors driving the distribution of seabirds.

Overall trends of habitat use can be taken from the Maxent habitat models for each species in Onslow Bay. Black-capped petrels were found over the outer continental shelf, inshore of the Gulf Stream (as indicated by a preference for moderate SST values) and cold core regions of Gulf Stream frontal eddies. The importance of Gulf Stream frontal eddies to the at-sea habitat of this species was first described by Haney (1987). Audubon's shearwaters prefer medium depths in regions of the outer shelf close to the inshore shelf break. Audubon's shearwaters are a tropical species, but the model predicted that they prefer relatively cool SSTs. The outer shelf of North Carolina is unique in that warm waters of the Gulf Stream occur immediately adjacent to cold waters of the shelf, and the temperature differential between these water masses is particularly high during winter months. All sightings of Audubon's shearwaters in cooler waters (< 25 °C) occurred on days when Gulf Stream frontal eddies were present. Thus, Audubon's shearwaters were likely exploiting enhanced prey aggregations in cooler eddy regions during these sightings in relatively cold water regions (see Chapter 4). Cory's shearwaters used waters of the outer continental shelf that are influenced by the Gulf Stream, and cold core regions of GSFEs appear to provide important habitat for the species even when other habitat factors are considered. Phalaropes used shelf waters with cooler SSTs that are relatively close to frontal features, while Wilson's storm-petrels used offshore habitats close to the inshore shelf break, particularly those located within Gulf Stream waters. These findings present important quantitative data on the habitat use of these seabirds in the South Atlantic Bight.

The inability of Maxent models to characterize greater shearwater habitat suggests that habitat factors other than those measured in the present study are important features of the habitat of this species. Few studies have examined the at-sea habitat use of greater shearwaters in detail, so it is difficult to suggest which environmental factors may be of importance to the habitat of this species. Ronconi et al. (2010) found that the regions used by tagged greater shearwaters differed markedly in environmental characteristics, diving behavior, and foraging locations. In the present study, it is possible that fine-scale fronts not considered in this analysis may represent an important habitat factor for greater shearwaters (see below).

The results of this study suggest that seabird density in Onslow Bay is quite low. The mean SPUE of 1.5 birds km^{-2} is within the range of values presented by Haney and McGillivary (1985a) for waters off the coast of Florida and Georgia, though the seasonal maximum (winter) value observed in the present study (6.04 birds km^{-2}) was considerably lower than that observed in this previous study (13.66 birds km^{-2}). However, Haney and McGillivary (1985a) conducted surveys closer inshore and evaluated the effects of mid-shelf fronts occurring at depths of approximately 20-40 m. Inner shelf regions of the SAB show relatively high productivity (Yoder et al. 1987). Waters of the mid- and outer shelf of North Carolina within the SAB show relatively low productivity (Barnard et al. 1997); subsurface waters in these regions are low in nutrients, and thus vertical mixing within these regions does not stimulate high productivity (Yoder 1985). Rather, upwelling produced by winds and by Gulf Stream frontal eddies (see Chapter 4) produce episodic regions of high productivity within the outer shelf in this region of the SAB (Verity et al. 1993). Thus, the regions surveyed by

Haney and McGillivary (1985a) likely represented inshore regions of higher productivity, while surveys in the present study were conducted in regions characterized by lower and episodic productivity. Overall, the seabird densities observed in this study and previously by Haney's published work represent relatively low bird densities in comparison to highly productive regions or oceanographic features of the world's oceans. For example, Schneider (1992) observed large seabird aggregations at fronts in the Bering Sea, with densities ranging from 7 to 3600 birds km^{-2} in the vicinity of bird aggregations.

The species composition of species observed in Onslow Bay was similar to that observed by Haney (1986a,b,c). However, as a result of the more inshore distribution of the survey effort in his published work, several coastal species (e.g., *Larus* species; royal terns, *Sterna maxima*) were observed that were not observed in the present study. In addition, Haney occasionally observed large numbers of masked boobies (*Sula dactylatra*) off the coasts of South Carolina and Georgia (J.C. Haney, pers. comm.), but this species was not observed in the present study.

Seasonal trends in species composition were similar to those observed previously near Cape Hatteras (Lee 1987, Fussel et al. 1990) and further south in the SAB (Haney and McGillivary 1985a). High seabird densities were observed in the winter in both the present study and in Haney and McGillivary (1985a). Eddy- and wind-induced upwelling on the outer shelf of the South Atlantic Bight is high during unstratified winter months (Yoder et al. 1981, Ryan and Yoder 1996), and the highest chlorophyll concentrations occur between approximately November and March. Seasonal changes in river runoff and wind stress are likely responsible for these patterns (Barnard et al. 1997). While high chlorophyll concentrations primarily occur inshore, high chlorophyll concentrations extend into mid- and outer shelf waters from November through February, coinciding with the peak in seabird SPUE observed in these regions in the present study. High chlorophyll concentrations decrease by summer, when regions of high productivity are limited to inshore regions and regions near shoals (Barnard et al. 1996). These patterns of productivity match well with observed patterns of seabird SPUE (Figures 13 and 14). The effects of these seasonal patterns of physical forcing and primary productivity on mid-trophic level organisms is less clear and requires further study in order to understand how variability in oceanographic processes transfers to higher trophic levels. For example, SST fronts may have lagged effects on productivity and upper trophic level studies. While examining chlorophyll distributions relative to SST fronts, Ryan and Yoder (1996) found that in some cases, SST fronts appeared to have delayed effects on biological patterns. Time-lagged effects of fronts merit further investigation in studies of seabird distribution relative to frontal features in the SAB.

The large number of unidentified phalaropes observed during winter months highlights the need to understand the species composition of phalarope flocks present in coastal waters of the southern United States during winter. The wintering habitat of red-necked phalaropes migrating along the coast of eastern North America is unknown (Bent 1927, Hayman et al. 1986), but the SAB is not considered to provide wintering habitat for red-necked phalaropes, which have been presumed to winter off the coast of Peru (Haney 1985a).

Few previous studies of seabirds in relation to oceanographic features have used a multivariate approach, so it is difficult to compare the relative importance of habitat factors with the published literature. Fronts are known to have significant effects on seabird abundance and distribution (Haney and McGillivary 1985a,b), although they were generally not an important predictor of seabird habitat in the present study. Mid-shelf fronts are prominent features off the coast of Georgia and Florida during winter months (e.g., Haney and McGillivary 1985a). These fronts occur less frequently and often join with the Gulf Stream front further north in the South Atlantic Bight (e.g., Govoni and Spach 1999). My results concur with this finding. During the limited number of winter surveys, it appeared that the mid-shelf front had coalesced with the Gulf Stream front in this region and that seabirds such as phalaropes were associated with the Gulf Stream front. However, the mid-shelf was still distinct from the Gulf Stream front further south in the SAB (Figure 15). These differences in frontal features could have important implications for seabird habitat use in different regions of the SAB.

In previous research off the coasts of Georgia and South Carolina (Haney and McGillivary 1985b), Gulf Stream fronts were contiguous with the 200 m shelf break, which may have modulated frontal processes (Ryan and Yoder 1996). Bathymetric features, such as shelf breaks, seamounts and regions of steep bathymetric gradients can have important effects on local oceanography and prey distributions, and can create foraging habitat for seabirds (e.g., Coyle et al. 1992, Haney et al. 1995, Hunt et al. 1996; reviewed in Chapter 1). Interactions between fronts and the shelf break in the southern SAB may have created enhanced foraging opportunities for seabirds. For example, Haney and McGillivary (1985b) observed feeding aggregations of hundreds of Cory's shearwaters at Gulf Stream fronts off the coast of Florida and Georgia, but no feeding aggregations of this size were observed during surveys in Onslow Bay over the two and a half year survey period.

Bathymetric features (distance to inshore and offshore shelf breaks) were important predictors in habitat models of several seabird species. Distance to the offshore shelf break was the most important predictor of black-capped petrel habitat, with petrels observed closer to this shelf break. The survey transects did not cross this shelf break, so it is unclear whether this result represents an effect of the shelf break itself, or (perhaps more likely) that is merely a reflection for an affinity to deep-water habitats. Audubon's shearwaters were associated with the inshore shelf break, with regions in close proximity to the shelf break comprising habitat for this species.

Audubon's shearwaters are the deepest diving of the species evaluated here, foraging by pursuit diving (del Hoyo et al. 1992) at depths of up to 35 m (Burger 2001). Regions of enhanced primary productivity, together with relatively high zooplankton and larval fish densities, are associated with shelf break fronts (e.g., Herman et al. 1981, Munk et al. 1985). Thus, Audubon's shearwaters may be more able to exploit prey aggregations occurring at depth near the shelf break than other seabird species which feed in surface or near-surface regions.

The means by which frontal features are identified could have important influences on the observed relationships between seabird distribution and SST fronts. An edge detection tool was used to identify SST fronts, which provides a consistent and objective means of identifying these features. Previous studies of seabirds and fronts derived from satellite images of SST have not clearly articulated how the location of SST fronts were defined. For example Haney and McGillivary (1985b) included no explanation of how Gulf Stream fronts were identified. Discrepancies between methods used to identify fronts could lead to differences in observed habitat relationships. Nevertheless, the response of seabirds to these features observed in Haney and McGillivary (1985a,b) was considerably larger than that observed in the present study (see above).

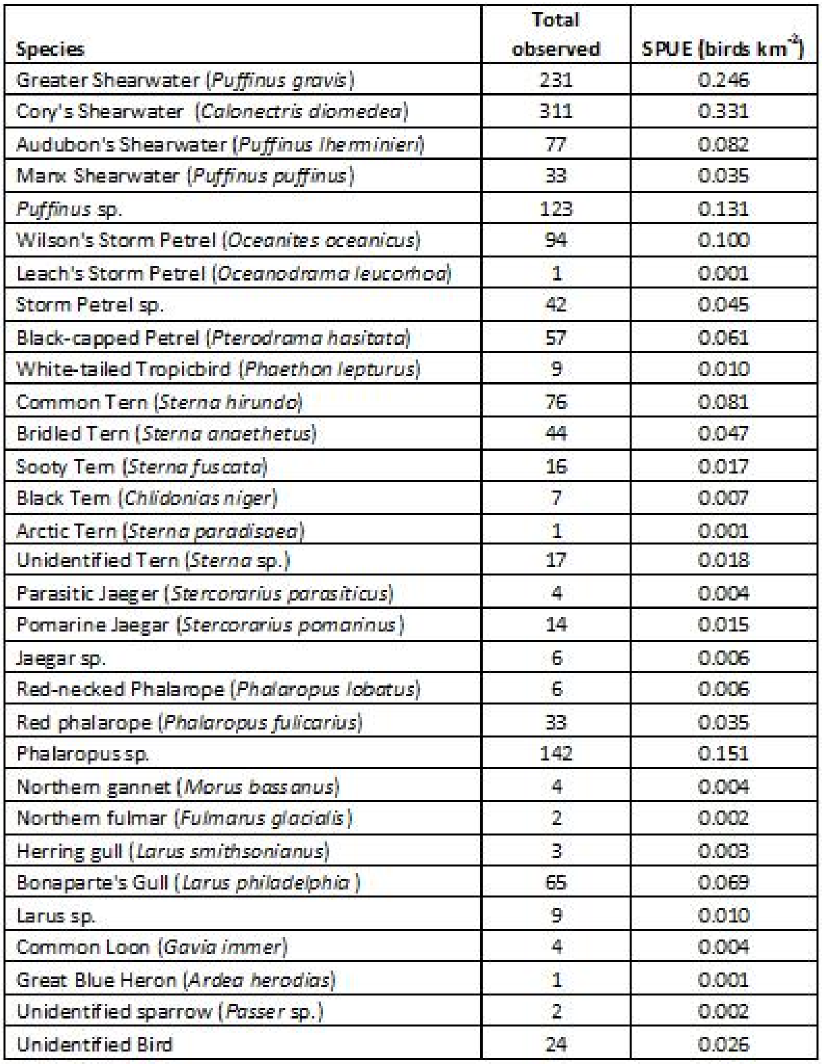
The distribution of seabird prey may be controlled by physical processes occurring at a relatively fine spatial scale (van Franeker et al. 2002). Fine-scale fronts would not be captured using edge detection of satellite images, while the temporal resolution of SST sampling during the present study (15 min, representing a distance of 4.5 km) was insufficient to detect fine-scale fronts. Observations of variation in SST during survey transects indicated rapid changes in SST over short spatial scales that would not be captured by data measured at this frequency. Continuous measurements of sea surface temperature during surveys would be useful in order to evaluate the effects of fine-scale fronts.

In addition, other important habitat features, such as *Sargassum* mats, would also not be detected using the methods of the present study. *Sargassum* mats can be formed by fine-scale features such as Langmuir circulation and convergence fronts, and are known to have important effects on seabird abundance (Haney 1986c). Haney suggested that zooplankton and fish associated with these *Sargassum* mats allowed seabirds to forage efficiently on these mats. In the present study, *Sargassum* mats observed during survey transects appeared to be associated with increases in the density of bridled terns and phalaropes, but the location and extent of these mats were difficult to assess quantitatively while traveling at survey speed (10 knots). Satellite images have been used to evaluate the movements of *Sargassum* mats (Gower and King 2008), and this technology presents the opportunity to evaluate this habitat variable in relation to seabird habitat in the future. Issues of cloud cover continue to be a problem for habitat analyses relying on satellite data.

The habitat models developed in this study demonstrate that at-sea seabird habitat may be quantified using a suite of environmental predictor variables, and that Maxent is an appropriate model to use for quantifying highly mobile and sparsely distributed species. Surveys conducted repeatedly in a given area over a long temporal period are important to determining seabird-habitat relationships in dynamic areas, although the present study included few surveys during winter months. This is particularly evident from surveys conducted in Onslow Bay, where low densities of seabirds required a large number of surveys to obtain adequate observations in order to parameterize habitat models. The results of this study provide important information for species of conservation concern including the endangered black-capped petrel, for which there are few recent published observations of pelagic habitat use. Evaluating the abundance habitat use of this species is important to understanding trends in the species through time, and requires regular monitoring in offshore waters that are not easily accessible by small boats. Concerns regarding the status of red-necked phalaropes due to declines in the abundance of the species at a staging area in the Bay of Fundy (see Chapter 2) highlight the importance of assessing phalarope habitat use in the SAB in more detail. Future studies could use a modified sampling design, closing on flocks of feeding phalaropes to assess species composition, as is frequently done for marine mammal surveys (e.g., Kinzey et al. 2000).

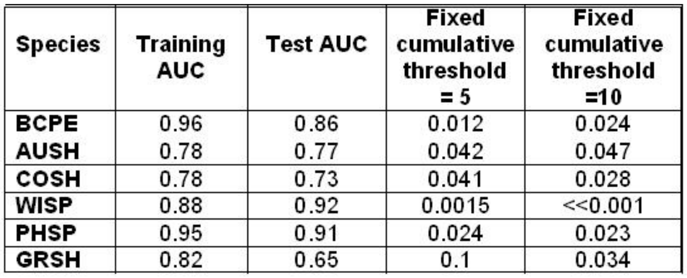
Proposals for offshore wind energy in Onslow Bay (e.g., Apex Wind Energy 2010) highlight the need to improve our understanding of seabird habitat use within this region, and within the SAB more broadly. Long-term observations are needed to provide baseline values of seabird densities against which future values can be compared. The results of the present study will be useful in this respect. However, dedicated seabird transects, beginning further inshore and continuing into deeper waters than those surveyed in the present study, are needed to more fully address seabird habitat in both coastal and deep water offshore environments.

Table 4: Bird species observed during seabird surveys in Onslow Bay between June, 2007 and July, 2009. SPUE = sightings per unit effort.



Species	Total observed	SPUE (birds km^{-2})
Greater Shearwater (*Puffinus gravis*)	231	0.246
Cory's Shearwater (*Calonectris diomedea*)	311	0.331
Audubon's Shearwater (*Puffinus lherminieri*)	77	0.082
Manx Shearwater (*Puffinus puffinus*)	33	0.035
Puffinus sp.	123	0.131
Wilson's Storm Petrel (*Oceanites oceanicus*)	94	0.100
Leach's Storm Petrel (*Oceanodrama leucorhoa*)	1	0.001
Storm Petrel sp.	42	0.045
Black-capped Petrel (*Pterodrama hasitata*)	57	0.061
White-tailed Tropicbird (*Phaethon lepturus*)	9	0.010
Common Tern (*Sterna hirundo*)	76	0.081
Bridled Tern (*Sterna anaethetus*)	44	0.047
Sooty Tern (*Sterna fuscata*)	16	0.017
Black Tern (*Chlidonias niger*)	7	0.007
Arctic Tern (*Sterna paradisaea*)	1	0.001
Unidentified Tern (*Sterna* sp.)	17	0.018
Parasitic Jaeger (*Stercorarius parasiticus*)	4	0.004
Pomarine Jaegar (*Stercorarius pomarinus*)	14	0.015
Jaegar sp.	6	0.006
Red-necked Phalarope (*Phalaropus lobatus*)	6	0.006
Red phalarope (*Phalaropus fulicarius*)	33	0.035
Phalaropus sp.	142	0.151
Northern gannet (*Morus bassanus*)	4	0.004
Northern fulmar (*Fulmarus glacialis*)	2	0.002
Herring gull (*Larus smithsonianus*)	3	0.003
Bonaparte's Gull (*Larus philadelphia*)	65	0.069
Larus sp.	9	0.010
Common Loon (*Gavia immer*)	4	0.004
Great Blue Heron (*Ardea herodias*)	1	0.001
Unidentified sparrow (*Passer* sp.)	2	0.002
Unidentified Bird	24	0.026

Table 5: Model parameters for Maxent habitat models of seabird species observed in Onslow Bay. AUC = Area Under Curve (see text); BCPE = black-capped petrel; AUSH = Audubon's shearwaters; COSH = Cory's shearwaters; WISP = Wilson's storm-petrels; GRSH = greater shearwater; PHSP = phalarope species (*Phalaropus* sp.).



Species	Training AUC	Test AUC	Fixed cumulative threshold = 5	Fixed cumulative threshold =10
BCPE	0.96	0.86	0.012	0.024
AUSH	0.78	0.77	0.042	0.047
COSH	0.78	0.73	0.041	0.028
WISP	0.88	0.92	0.0015	<<0.001
PHSP	0.95	0.91	0.024	0.023
GRSH	0.82	0.65	0.1	0.034

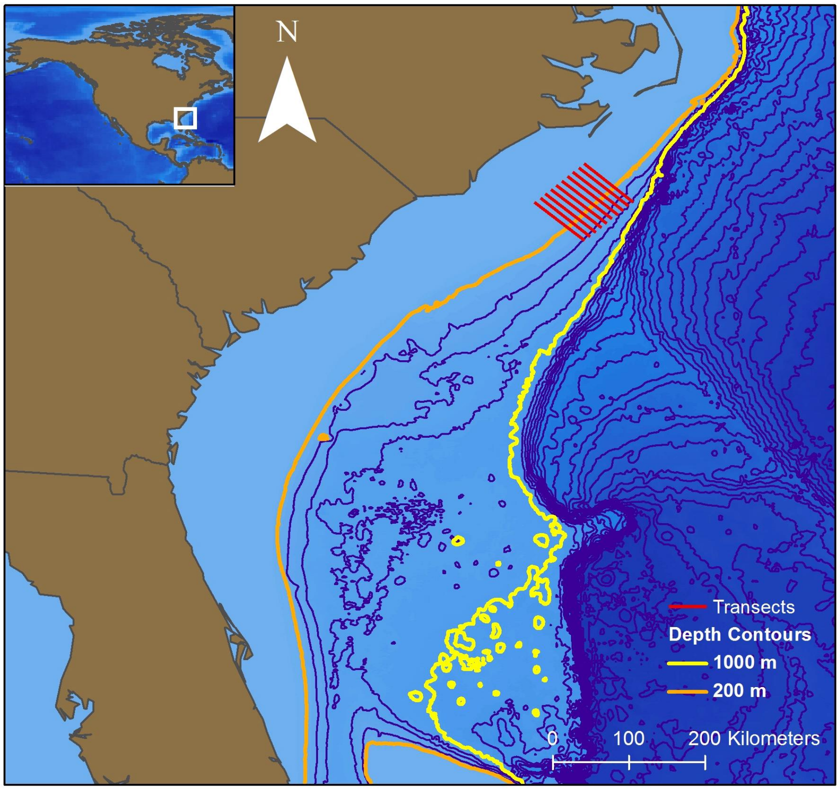


Figure 11: Location of the study site and survey transects (indicated by red lines) within Onslow Bay, North Carolina relative to bathymetry along the southeastern coast of the United States. Depth contours at 200 m intervals are shown in blue, while yellow depth contours represent the 200 m and 1000 m contours, respectively.

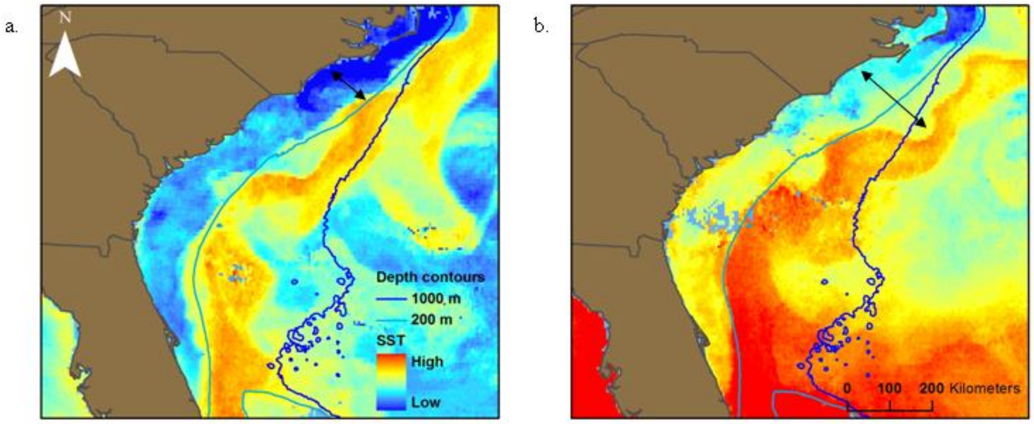


Figure 12: Variability in the location of the Gulf Stream front relative to the coastline (indicated with black arrows) and the 200 m depth contour in Onslow Bay, North Carolina shown for April 29 and July 16, 2009, respectively.

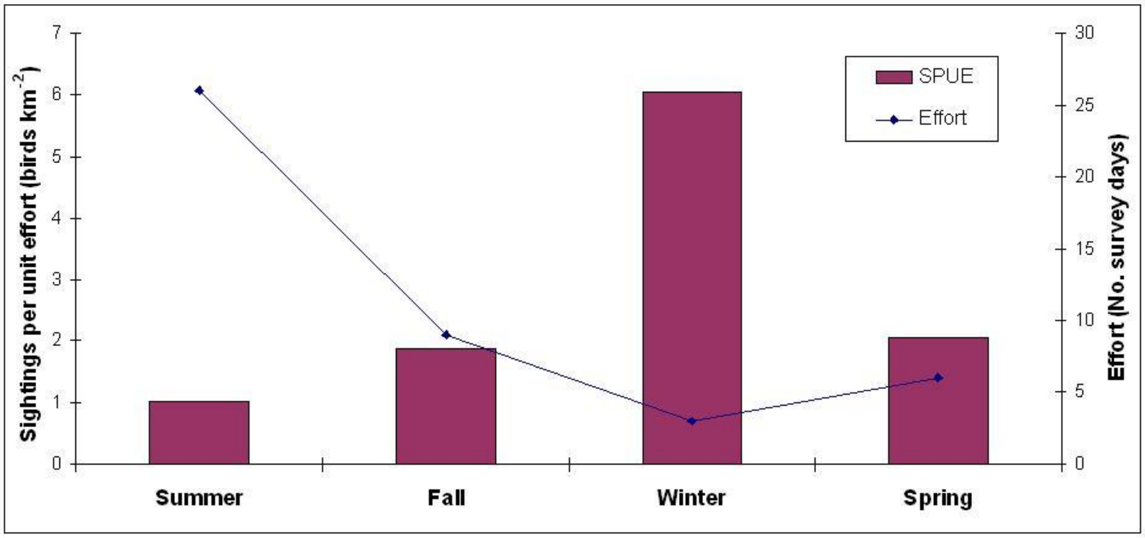


Figure 13: Seabird sightings per unit effort (birds km^{-2}) and number of survey days in Onslow Bay by season.

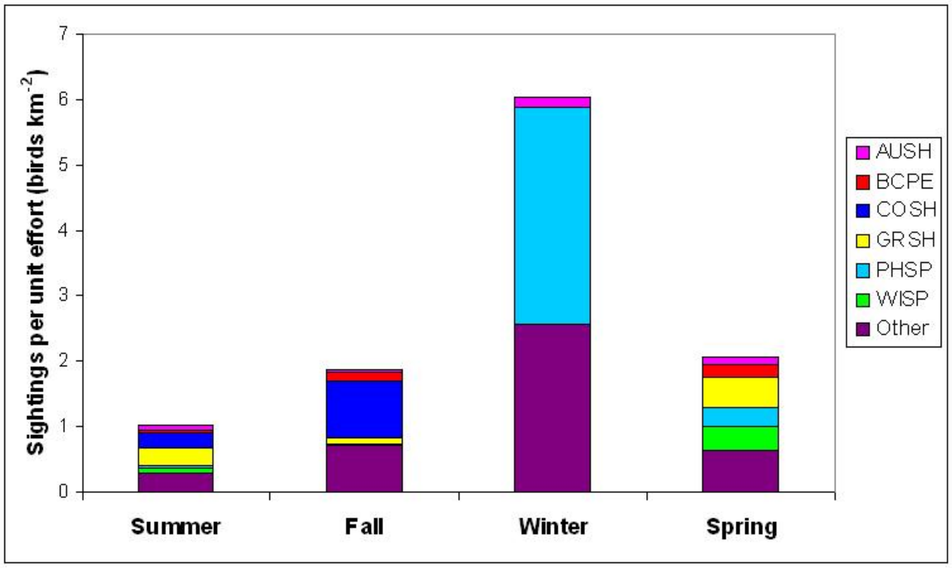


Figure 14: Seasonal trends in sightings per unit effort (birds km^{-2}) for the six most common species or species groups of seabird observed in Onslow Bay. AUSH= Audubon's shearwater; BCPE= black-capped petrel; COSH= Cory's shearwater; GRSH= greater shearwater; PHSP= *Phalaropus* spp.; WISP= Wilson's storm-petrel; Other= seabird species other than the above six most common species or species groups.

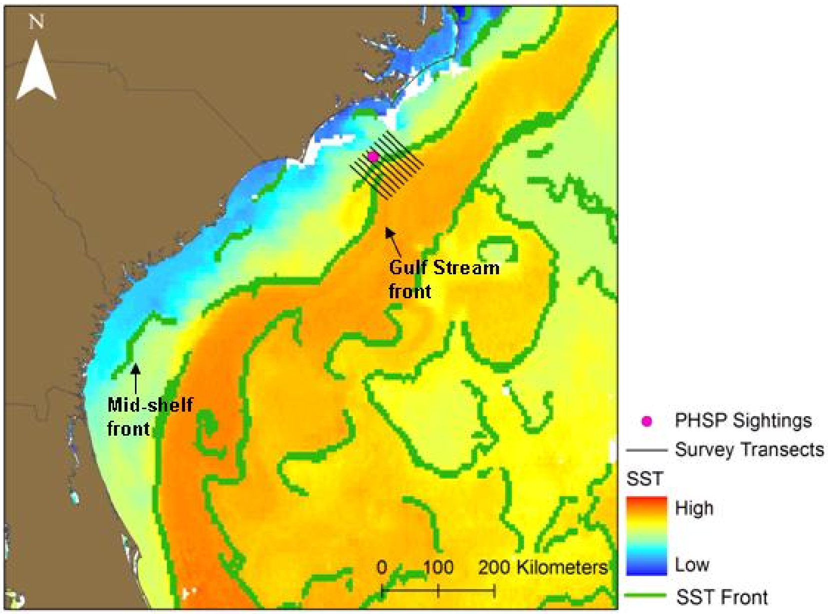


Figure 15: Example of sea surface temperature fronts calculated using the MGET edge detection tool relative to survey transects and phalarope sightings on March 13, 2008. Note that no mid-shelf front was detected in Onslow Bay at this time, though mid-shelf front.

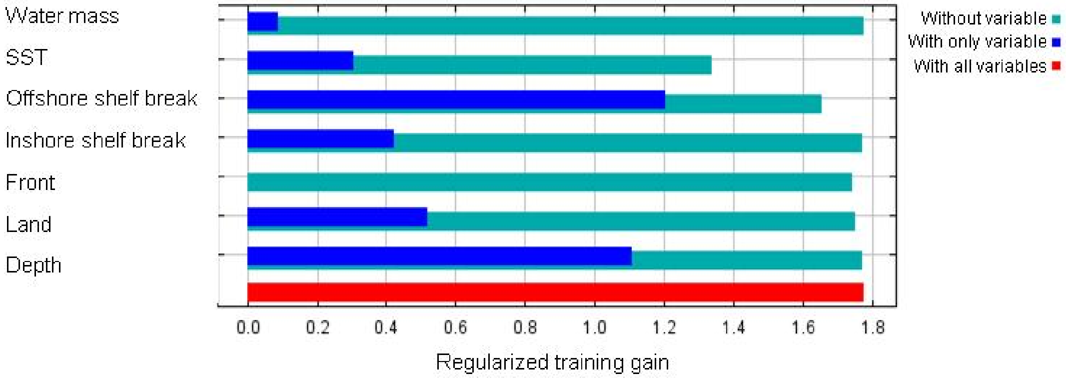


Figure 16: Jackknife test of regularized training gain for the Maxent model of black-capped petrel habitat. Variables are as follows: Water mass = Gulf Stream, cold core, warm filament or shelf waters; SST = sea surface temperature (°C); Inshore shelf break = distance to inshore shelf break (m); Offshore shelf break = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

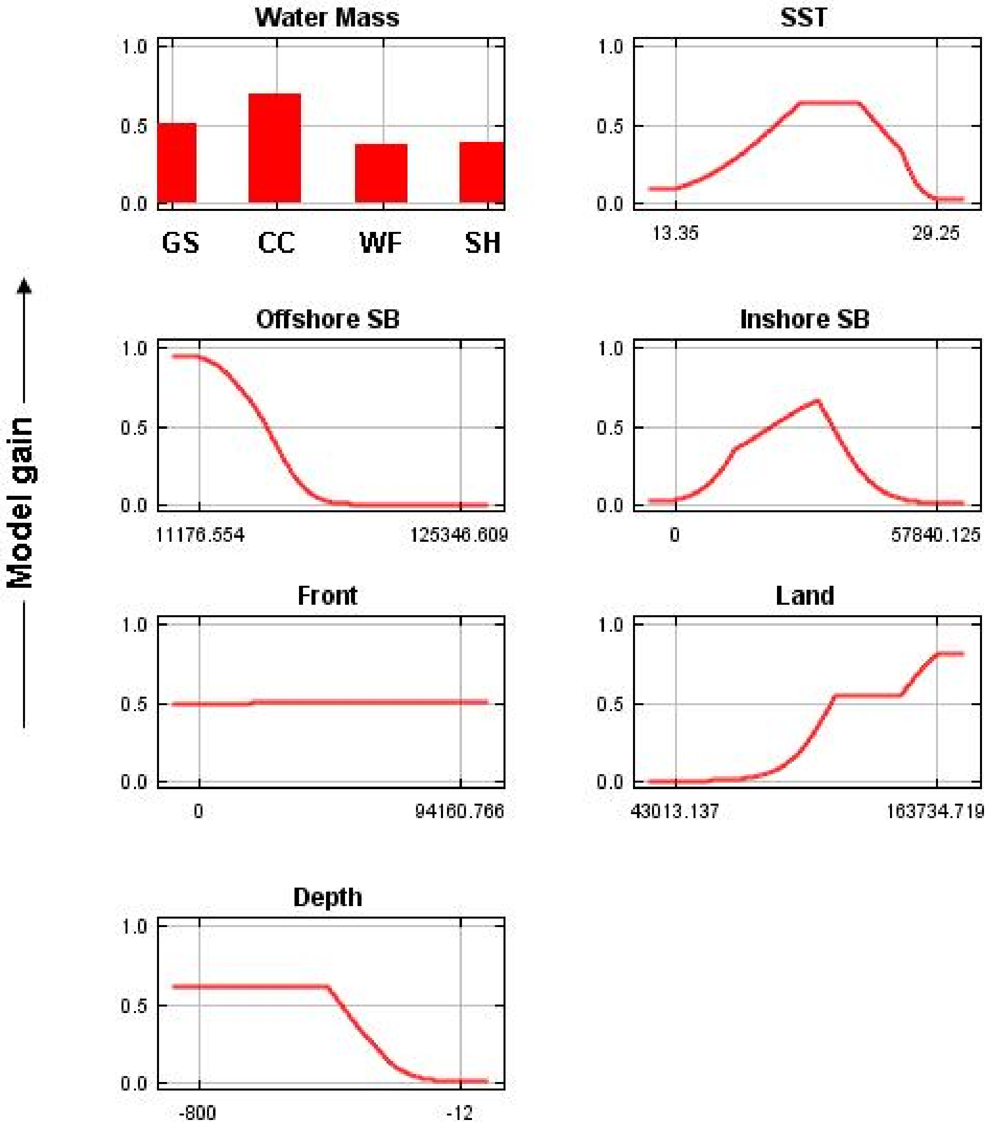


Figure 17: Relationship between model gain and habitat variables for black-capped petrel habitat. Variables are as follows: Water mass, GS = Gulf Stream, WF = eddy warm filament, CC = eddy cold core, SH = shelf waters; SST = sea surface temperature (°C); Inshore SB = d distance to inshore shelf break (m); Offshore SB = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

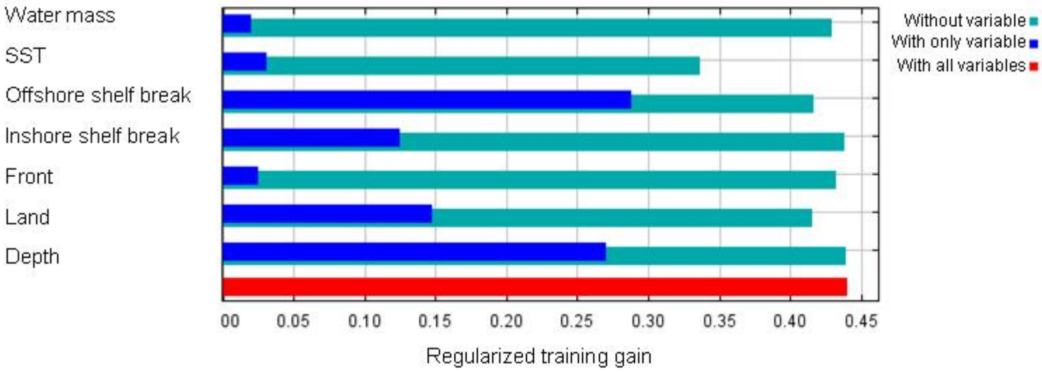


Figure 18: Jackknife test of regularized training gain for the Maxent model of Audubon's shearwater habitat. Variables are as follows: Water mass = Gulf Stream, cold core, warm filament or shelf waters; SST = sea surface temperature (°C); Inshore shelf break = distance to inshore shelf break (m); Offshore shelf break = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

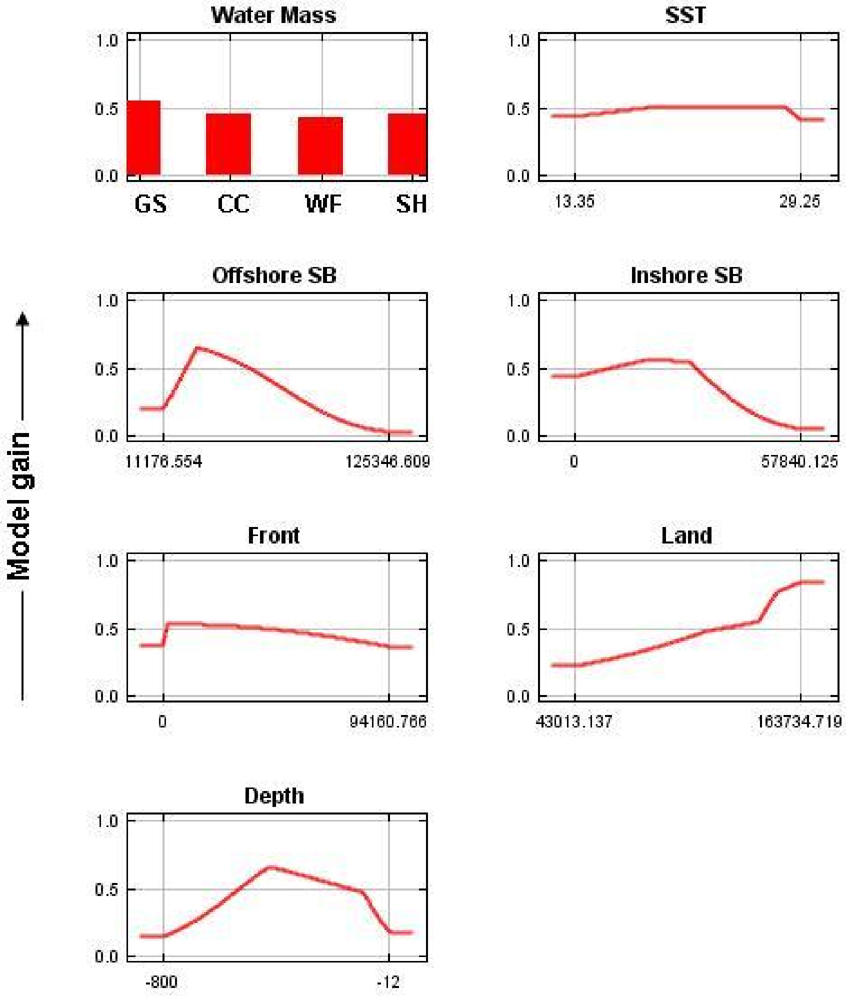


Figure 19: Relationship between model gain and habitat variables for Audubon's shearwater habitat. Variables are as follows: Water mass, GS = Gulf Stream, WF = eddy warm filament, CC = eddy cold core, SH = shelf waters; SST = sea surface temperature (°C); Inshore SB = distance to inshore shelf break (m); Offshore SB = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

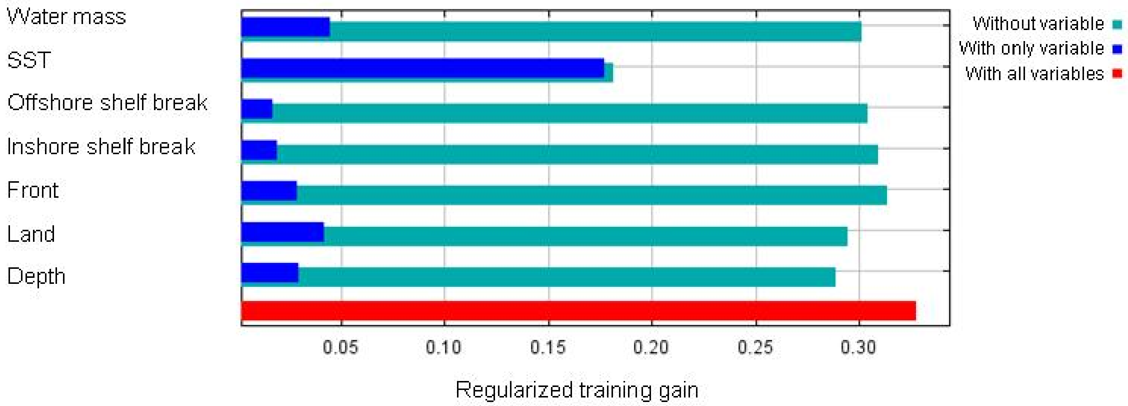


Figure 20: Jackknife test of regularized training gain for the Maxent model of Cory's shearwater habitat. Variables are as follows: Water mass = Gulf Stream, cold core, warm filament or shelf waters; SST = sea surface temperature (°C); Inshore shelf break = distance to inshore shelf break (m); Offshore shelf break = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

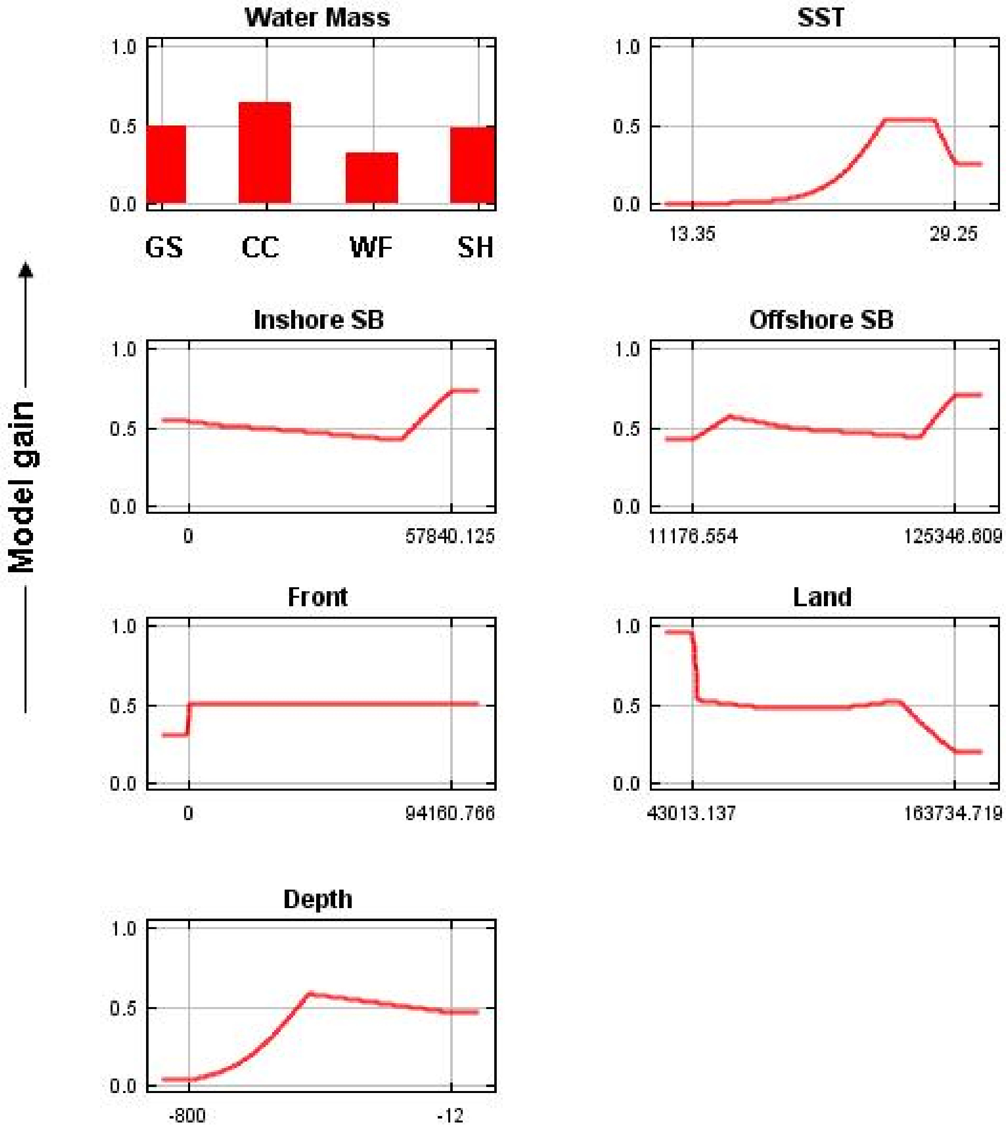


Figure 21: Relationship between model gain and habitat variables for Cory's shearwater habitat. Variables are as follows: Water mass, GS = Gulf Stream, WF = eddy warm filament, CC = eddy cold core, SH = shelf waters; SST = sea surface temperature (°C); Inshore SB = distance to inshore shelf break (m); Offshore SB = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

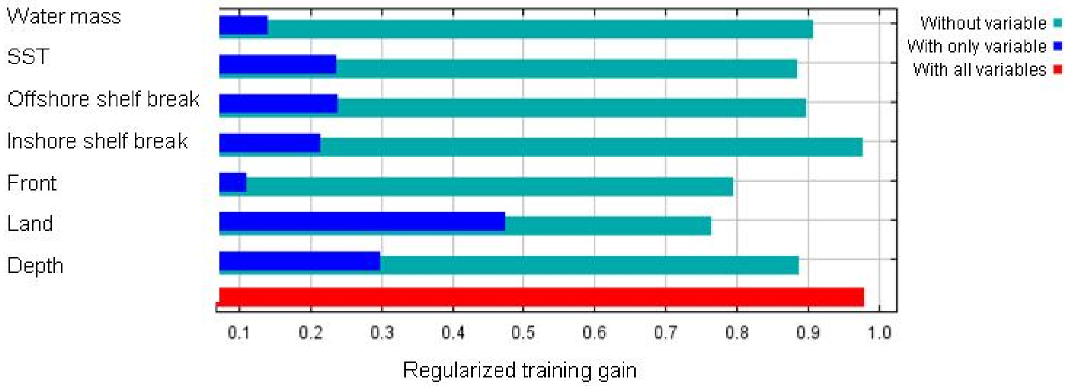


Figure 22: Jackknife test of regularized training gain for the Maxent model of Wilson's storm-petrel habitat. Variables are as follows: Water mass = Gulf Stream, cold core, warm filament or shelf waters; SST = sea surface temperature (°C); Inshore shelf break = distance to inshore shelf break (m); Offshore shelf break = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

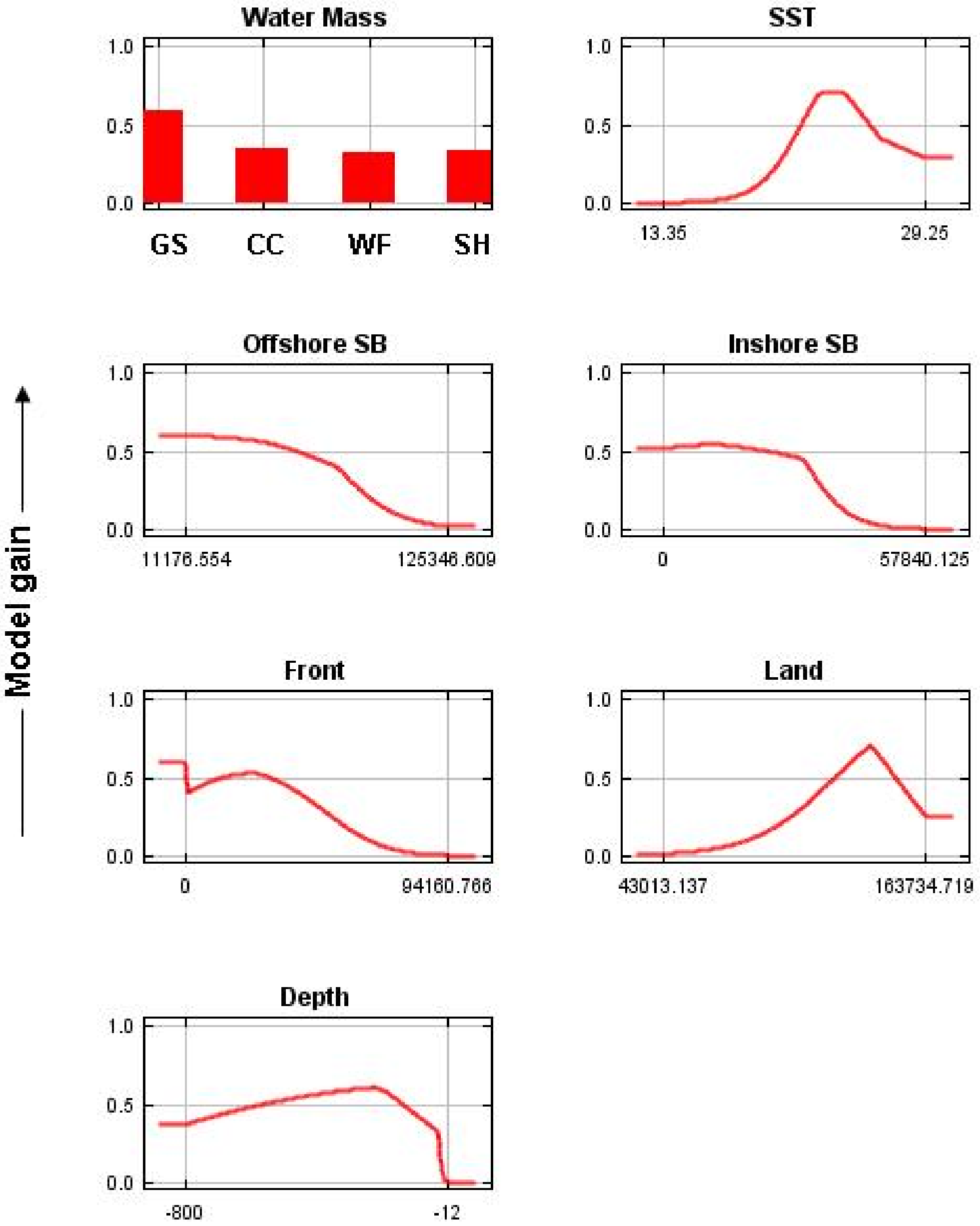


Figure 23: Relationship between model gain and habitat variables for Wilson's storm-petrel habitat. Variables are as follows: Water mass, GS = Gulf Stream, WF = eddy warm filament, CC = eddy cold core, SH = shelf waters; SST = sea surface temperature (°C); Inshore SB = distance to inshore shelf break (m); Offshore SB = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

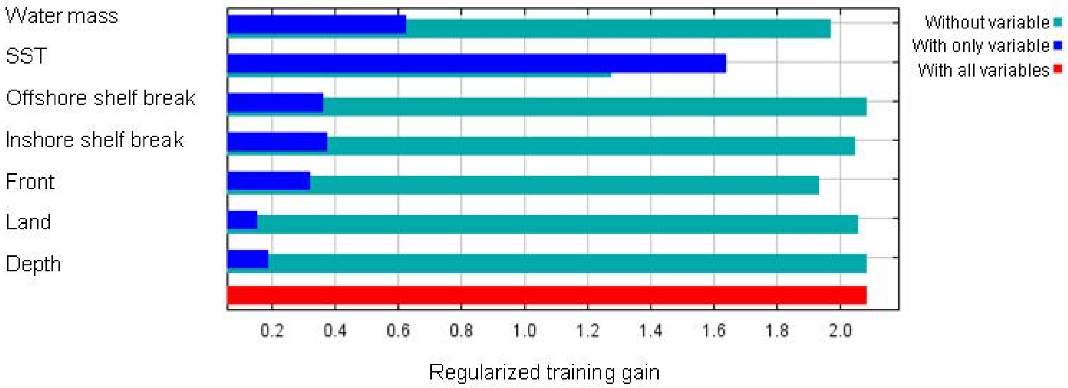


Figure 24: Jackknife test of regularized training gain for the Maxent model of phalarope habitat. Variables are as follows: Water mass = Gulf Stream, cold core, warm filament or shelf waters; SST = sea surface temperature (°C); Inshore shelf break = distance to inshore shelf break (m); Offshore shelf break = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

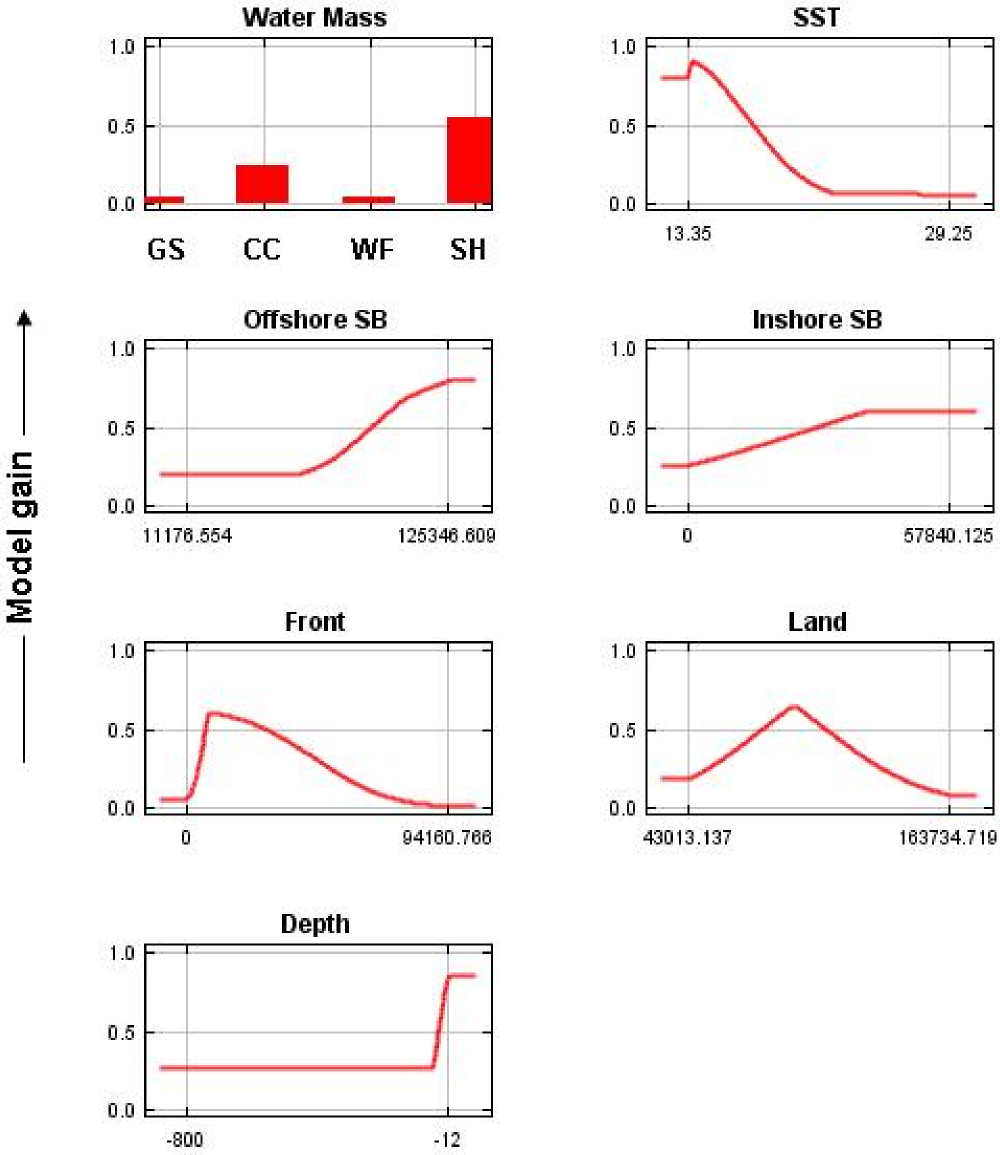


Figure 25: Relationship between model gain and habitat variables for phalarope habitat. Variables are as follows: Water mass, GS = Gulf Stream, WF = eddy warm filament, CC = eddy cold core, SH = shelf waters; SST = sea surface temperature (°C); Inshore SB = distance to inshore shelf break (m); Offshore SB = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m): Depth (m).

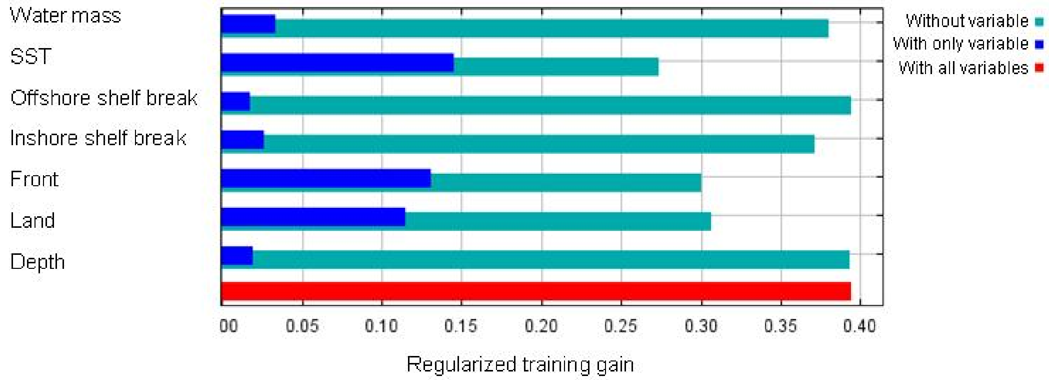


Figure 26: Jackknife test of regularized training gain for the Maxent model of greater shearwater habitat. Variables are as follows: Water mass = Gulf Stream, cold core, warm filament or shelf waters; SST = sea surface temperature (°C); Inshore shelf break = distance to inshore shelf break (m); Offshore shelf break = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m); Depth (m).

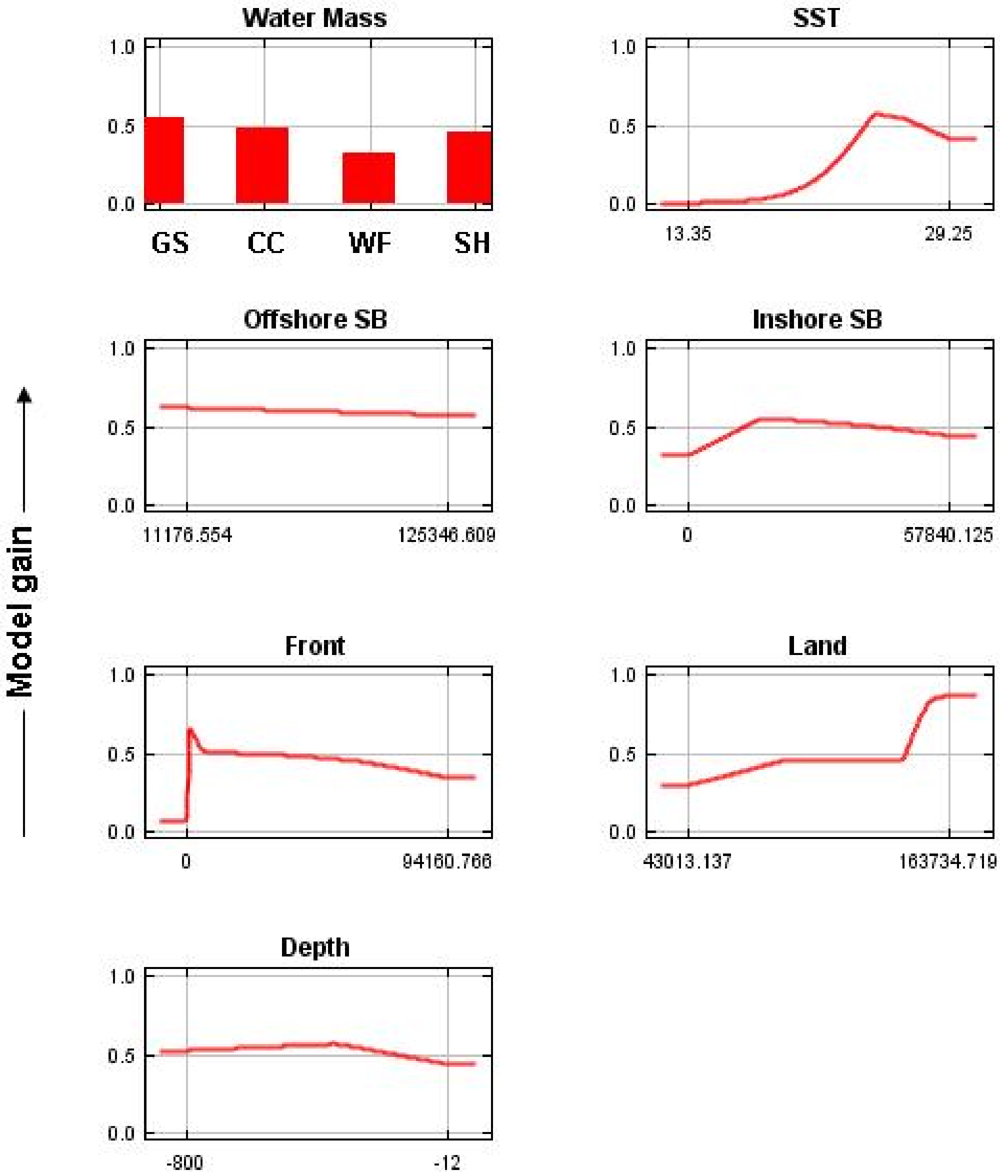


Figure 27: Relationship between model gain and habitat variables for greater shearwater habitat. Variables are as follows: Water mass, GS = Gulf Stream, WF = eddy warm filament, CC = eddy cold core, SH = shelf waters; SST = sea surface temperature (°C); Inshore SB = distance to inshore shelf break (m); Offshore SB = distance to offshore shelf break (m); Front = distance to front (m); Land = distance to land (m): Depth (m).

Chapter 4: Gulf Stream frontal eddies affect the fine-scale distribution of seabirds

Abstract

I conducted seabird surveys within Gulf Stream frontal eddies in Onslow Bay, North Carolina, on 11 days between June 2007 and August 2009. Fish and squid-eating seabirds (black-capped petrels, *Pterodrama hasitata*; Cory's shearwaters, *Calonectris diomedea*; Audubon's shearwaters, *Puffinus lherminieri*; Manx shearwaters, *Puffinus puffinus*; and bridled terns, *Onychoprion anaethetus*) were more abundant in the eddy cold core while smaller, planktivorous Wilson's storm-petrels (*Oceanites oceanicus*) were evenly distributed throughout the eddy regions. Preliminary acoustic surveys were conducted across Gulf Stream frontal eddies using a 38 kHz Simrad EK-60 transducer with an over-the-side-mount from a 12-m sportfishing vessel. Survey transects were conducted across all eddy regions (Gulf Stream, cold core, warm filament and shelf waters) in two eddies during the fall of 2009. Data from these preliminary surveys suggested that the abundance of near-surface prey was higher in eddy cold core regions than in waters of the Gulf Stream, eddy warm filament and shelf. The increased prey availability within eddy cold core regions likely drives the higher densities of fish and squid-eating seabirds observed within cold core eddy regions. The even distribution of planktivorous seabirds observed throughout the different eddy regions suggests that oceanographic processes within Gulf Stream frontal eddies have different effects on the

distribution of zooplankton in surface waters. In summary, this study presents preliminary data characterizing the effects of Gulf Stream frontal eddies on mid-trophic level organisms, and demonstrates the effects of these features on the fine-scale distribution of seabirds off the coast of North Carolina.

1. Introduction

Many studies have demonstrated the importance of oceanographic features to foraging seabirds (reviewed in Chapter 1). However, few studies have investigated the mechanisms of prey aggregation within oceanographic features, and studies linking upper trophic level species to ocean physics have largely excluded investigations of zooplankton and forage fish (Haney 1986a,b, 1987a,b, Weimerskirch 2004, Johnston et al. 2005a,b, Hyrenbach 2006). These gaps in our knowledge of oceanographic features make it difficult to demonstrate links between physical forces and seabirds.

Seabirds exploit oceanographic features, such as tidal fronts or upwellings, that are predictable over short spatial and temporal scales (e.g., Mercier 1985, Gaskin and Brown 1988, Hunt et al. 1998; Ch. 2), as well as features that are less predictable in space and time (e.g., Haney 1985a, Haney and McGillivary 1985, Haney 1987b, Nel et al. 2001, Hyrenbach et al. 2006). It is particularly challenging to study dynamic oceanographic features because the location of a particular feature often cannot be predicted before it has formed, making it difficult to design and carry out standardized surveys. However, episodic features, such as eddies, or fronts that migrate seasonally, are important components of the foraging habitat of some seabird species (Haney 1985a,b, 1987b, Bost et al. 1997, Gauthier-Clerc et al. 2002, Hyrenbach et al. 2006, Charrassin and Bost 2007), so it is important to improve our understanding of these features. In oligotrophic regions, where prey availability is limited, dynamic oceanographic features may be particularly important foraging habitat for seabirds.

Several oceanographic features in the oligotrophic waters of the South Atlantic Bight (SAB) have been found to influence seabird abundance and distribution. Gulf Stream Frontal Eddies (GSFEs; discussed in more detail below) act as "nutrient pumps," advecting nutrients onto the continental shelf, thus stimulating production within this region (Yoder et al. 1981, Lee et al. 1991). Upwelling within the cold core stimulates primary production (Yoder et al. 1981) and is believed to initiate a "succession of biological responses" (Lee et al. 1991). However, the responses to this increased productivity at middle and upper trophic levels are not well understood.

GSFEs have important influences on seabird abundance and distribution in the SAB (Haney 1986a). Seabirds with different foraging behaviors have different affinities for frontal eddies. Haney's research indicated that aerial foragers, such as bridled terns and black-capped petrels, are associated with nutrient-poor waters of the warm filament and Gulf Stream, respectively, while species that forage on the ocean's surface - shearwaters (*Puffinus gravis* and *Calonectrijs diornedea*) and storm-petrels (*Oceanites* *oceanicus* and *Oceanodroma castro*) - are observed in the cold upwelled water of eddy cores (Haney 1986a). An increased knowledge of prey aggregation within GSFEs is necessary for understanding seabird habitat use relative to GSFEs. In addition, seabird habitat use relative to GSFEs has not been investigated since the early 1980s, and has never been investigated off the coast of North Carolina, where the bathymetry differs from regions farther south in the SAB (see Chapter 3). Dimensions of GSFEs also vary between the southern and northern SAB (see below), highlighting the importance of investigating the effects of these features in North Carolina.

The present study examines seabird abundance and distribution in relation to GSFEs in Onslow Bay, North Carolina, and presents preliminary results of the distribution of prey biomass within GSFEs.

2. *Methods*

2.1 Study site

The oceanographic characteristics of Onslow Bay, North Carolina, are presented in Chapter 3. GSFEs often occur during offshore meanders of the Gulf Stream (Yoder et al. 1981). These cyclonic cold core eddies are formed by the protrusion of warm water into shelf waters, which then encloses a ring of colder water (Figure 28; e.g., Lee et al. 1981, 1991). Cross-shelf dimensions of GSFEs are approximately 30-50 km, while along-shelf dimensions vary greatly, ranging from roughly 50-100 km south of Jupiter, Florida, to 100-200 km off the coast of Charleston, South Carolina, and reaching as much as 300 km in length between Charleston and Cape Hatteras (Legeckis 1979, Lee et al. 1981). GSFEs propagate north with the Gulf Stream at speeds of approximately 40 cm s^{-1}, and have a period of approximately 2-14 days (Legeckis 1979).

GSFEs differ from the larger and longer-lasting cold core rings that are formed north of Cape Hatteras because the cold water of the cold core originates from nutrient-rich water upwelled from deep in the Gulf Stream rather than from cooler waters of the continental shelf (Mann and Lozier 1996). Thus, GSFEs play an important role in advecting nutrients onto the continental shelf and stimulating production within this region (Yoder et al. 1981).

2.2 Seabird abundance and distribution in relation to Gulf Stream frontal eddies

Seabird survey methodology is described in Chapter 3, along with methods used to identify GSFEs during survey transects. Briefly, daily sea surface temperature (SST) measurements from boat-based surveys and satellite images were used to identify GSFEs. Data from Advanced Very High Resolution Radiometer (AVHRR) data from the National Oceanographic and Atmospheric Administration (NOAA) Polar-Orbiting Environmental Satellites (POES) have a high resolution (1 km) and were used whenever clear images of Onslow Bay were available. When POES images were unusable due to cloud cover, Geostationary Operational Environmental Satellites (GOES), which provide lower resolution data (8 km pixels), were used to identify eddies. When eddies were present within the study area, sea surface temperature measurements recorded every 15 min during boat-based survey transects were used to identify the location of Gulf Stream (GS), cold core (CC), warm filament (WF) and shelf (SH) waters within and adjacent to GSFEs. At the surface, the temperature of water masses within GSFEs differs by approximately 1°C, though these differences are much greater at depth (Glenn and Ebbesmeyer 1994).

I examined differences in seabird habitat use by eddy water mass using the methods of Haney (1986a) to allow for comparisons with previous studies in the South Atlantic Bight. The total number of birds and the number of the most frequently observed species of seabird were assessed in the Gulf Stream, cold core, warm filament and shelf waters, and were compared to the number of sightings expected given the total amount of effort in each water mass if distribution across water masses was uniform. The expected and observed seabird counts were compared using a chi-squared test.

2.3 Preliminary acoustic surveys of Gulf Stream frontal eddies

A pilot study investigated the availability of prey biomass within GSFEs in Onslow Bay and examined how the distribution of biomass at depth differed between the different eddy regions. Fisheries acoustic surveys were conducted from a 12-m sportfishing boat using an over-the-side-mount modified from Hench et al. (2000)

containing a 38 kHz split-beam Simrad transducer. The transducer was located 1 m below the water surface, and survey speed was maintained at approximately 2.5 m s^{-1}. Echo intensity was measured at a frequency of 1 ping s^{-1} and a pulse width of 256 μs. A 38.1 mm tungsten carbine sphere of known target strength (-42.04 dB; Parker-Parker-Stetter et al. 2007) was used to calibrate the echosounder every three weeks during acoustic surveys. A threshold of -90 dB was used to collect acoustic data to filter noise and exclude unwanted targets; data were integrated over 1-m depth bins (Parker-Stetter et al. 2007, Hazen et al. 2009). A 5-m near-surface zone was excluded from analysis due to near-field effects of the transducer (Parker-Stetter et al. 2007), and the bottom of the water column was automatically detected and was hand-corrected in Echoview 4.7.

Satellite images of sea surface temperature were used to locate GSFEs prior to sampling, and shipboard measurements of sea surface temperature and expendable bathythermograph (XBT) probes were used to determine the boundaries of water masses within the eddies. GOES satellite images, in combination with boat-based measurements of sea surface temperature, were sufficient to identify water masses within Gulf Stream frontal eddies during seabird surveys, but due to their lower resolution, GOES satellite images alone often did not provide an appropriate resolution to accurately identify the location of these water masses to inform sampling efforts (i.e., to sample across different eddy habitats). Thus, I used POES satellite images exclusively to identify and localize GSFEs and to determine the location of sampling transects (see Figure 29).

I quantified acoustic biomass in GS, CC, WF and SH waters of GSFEs and adjacent waters. Due to limitations of the survey vessel speed, the dynamic nature of GSFEs (moving through Onslow Bay in approximately three days), and the offshore location of the eddies (e.g., boundaries between GS and CC waters occurring as far as 140 km offshore), entire GSFEs could not be sampled in one continuous transect on a given survey day. Thus, survey transects were designed to sample specific regions of GSFEs, with portions of two eddy habitats (e.g., GS and CC) typically surveyed on a given survey day. Ocean data view (ODV) software was used to produce temperature contours from XBT casts in GSFEs. After the removal of bad data regions due to missed pings or interference from boat noise, fisheries acoustics data were integrated in 1-m depth bins during transects within each eddy region in Echoview 4.7. The results were expressed as values of Nautical Area Scattering Coefficient (NASC, MacLennan et al. 2002).

3. *Results*

3.1 Seabird abundance and distribution in relation to Gulf Stream frontal eddies

The extent of a typical GSFE was larger than the largest scale of spatial autocorrelation observed in the seabird data (8 km; see Chapter 3), so I compared seabird habitat use between different eddy regions. Mean sightings per unit effort (SPUE) for the GS, CC and WF were 1.18, 2.31 and 0.28 sightings per km^2, respectively. The mean SPUE in shelf waters on days when eddies were present was 3.87 sightings per km^2. However, this value was highly influenced by a large aggregation of Bonaparte's gulls (*Larus philadelphia*) and phalaropes (*Phalaropus* spp.) observed on one survey day (the only day on which Bonaparte's gulls were observed). This observation was considered to be an outlier and was removed from the analysis. These SPUE values are slightly lower than the observations of Haney (1986), who found 2.91-16.35 birds km^{-2} within waters of the eddy CC, 0.16-3.07 birds km^{-2} in WF waters, and 0.15-1.51 birds km^{-2} within non-eddy regions.

Eleven GSFEs were surveyed in Onslow Bay. Six species of seabirds were observed frequently in GSFEs (>10 sightings on days when eddies were present): Audubon's shearwaters, Cory's shearwater, Manx shearwaters, Wilson's storm-petrels, black-capped petrels, and bridled terns. Together these species made up 80% of the total number of seabirds observed on days when eddies were present.

The abundance of these six focal species was assessed relative to eddy water mass to examine seabird habitat use within GSFEs. For all but one of these six species (Wilson's storm-petrels), there were significant differences between observed numbers of seabirds and expected numbers (derived assuming uniform seabird distribution across water masses). Audubon's shearwaters, Cory's shearwaters, Manx shearwaters, black-capped petrels and bridled terns (*Onychoprion anaethetus*) were more abundant within the eddy CC than in GS, WF or SH waters. There was no significant difference in the number of Wilson's storm-petrels among water masses (Table 6).

3.2 Preliminary acoustic surveys in Gulf Stream frontal eddies

Fisheries acoustic surveys were conducted within GSFEs on five days in the summer and fall of 2009 (Table 7). Figure 30 shows an example of temperature contours at depth within a GSFE sampled on October 1, 2009. The domed temperature contours indicate local upwelling within the GSFE, while the more pronounced doming at depths of approximately 200-400 m indicates the larger temperature differential between CC and adjacent water masses at depth, consistent with previous observations of GSFEs (Glenn and Ebesmeyer 1994).

Fisheries acoustic surveys were conducted within different regions of GSFEs (GS, CC, WF and adjacent SH waters) on each survey day, with survey transects designed to sample multiple regions each day. However, due to logistical constraints, GS, CC and WF regions were sampled on only two survey days, while the SH region was only sampled on one of these survey days (Table 7). Variability in the abundance and distribution of biomass between days made it difficult to conduct comparisons of eddy regions among GSFEs surveyed on different days. In addition, the location of the eddy cold core relative to the shelf and shelf break varied considerably among days (Table 7 shows the minimum and maximum depth of the eddies surveyed), which likely has important consequences for aggregation of nekton within GSFEs, thereby making it difficult to compare biomass at depth between days. As a result, only data from the two survey days on which all eddy regions were sampled (September 24 and October 22, 2009) will be discussed herein. Table 8 shows the survey effort in each eddy region during these two survey days.

Figure 31 shows biomass as a function of depth within the GS, CC and WF on September 24, 2009, and in these eddy regions as well as in SH waters on October 22, 2009, respectively. On September 24, the eddy cold core extended to a depth of 80 m and GS waters were surveyed to depths of 150 m. GS waters showed a layer of acoustic backscatter at a depth of approximately 80 m. Two regions within the eddy cold core were sampled, one close to the WF (CC 1), and one closer to the GS (CC 2). These two cold core regions showed different trends in the distribution of biomass. Close to the GS, the CC showed higher acoustic backscatter in the top 40 m of the water column. Close to the WF, the CC showed acoustic backscatter similar to that observed in the WF, in which acoustic biomass was considerably lower than that observed at similar depths in the CC near the GS. These findings suggest that prey availability may be higher in CC regions near the GS than in CC regions near the WF.

On October 22, the cold core of the eddy extended to a depth of approximately 500 m. Acoustic sampling was focused within the top 240 m of the water column; deep-water prey biomass was not of interest in the present study, which focused on prey biomass relative to seabird foraging in the upper 35 m of the water column. However, analyzing prey biomass at depths greater than 35 m (i.e., 35 to 240 m) allowed differences in the distribution of biomass to be compared between regions. GS waters showed low acoustic biomass throughout the water column, while the CC showed peaks in acoustic backscatter at depths of 90, 130 and 190 m, and relatively high acoustic backscatter within the top 40 m of the water column, which extended into near-surface waters. The WF and SH waters showed lower acoustic backscatter in near-surface waters, though a layer of acoustic backscatter was observed in SH waters at a depth of approximately 30 m. On both of these survey days, the distribution of biomass in the upper 40 m of the CC suggests that more prey was available to seabirds in near-surface waters of the CC. However, the differences in the distribution of biomass between the two days, and the observed difference in biomass within different regions of the CC on September 24, indicate that further surveys are required to generate the statistical power needed to better understand the effect of GSFEs on distributions of seabird prey.

4. Discussion

Seabird abundance differed among regions within GSFEs. With the exception of Wilson's storm-petrels, all commonly observed seabirds within GSFEs were more abundant within the CC than would be expected if seabirds were uniformly distributed among water masses. Total seabird abundance was also greater within the CC.

Preliminary acoustic studies within GSFEs suggested that prey availability in surface or near-surface waters is likely higher within the CC than in other eddy regions. Similarly, waters of the WF appeared to show a higher density of biomass in surface or near-surface waters than those in the GS (Figure 31). Thus, increased prey availability within eddy cold core regions likely drives the higher densities of fish and squid-eating seabirds observed within cold core eddy regions.

The results of this study were similar to those of Haney (1985, 1986a) who found significantly higher seabird abundance within CC regions. There were, however, significant differences in habitat use by water mass for Cory's shearwaters (more birds in the CC), black-capped petrels (observations in the CC and GS waters, but not in SH or WF waters) and bridled terns (all observations occurred within the WF; Haney 1986a). Audubon's shearwaters were observed in all eddy regions and were more abundant within the CC, although the difference was not significant. Haney found no significant difference in the habitat use of Wilson's storm-petrels between eddy regions when all eddy regions were compared, though the species appeared to be more abundant within the eddy CC.

Haney (1986b) suggested that seabird densities were higher near frontal boundaries between eddy water masses, which could explain the observed discrepancies between the present results and those in previous studies. Proximity to frontal boundaries within eddies may be an important metric to include in assessing seabird abundance within GSFEs, rather than simply examining eddy water mass. Location within the CC appeared to influence patterns of prey biomass within this region, with higher densities occurring in surface waters close to the Gulf Stream in comparison to waters close to the WF (Figure 31a). This supports Haney's (1986b) assertion that seabirds were more abundant close to the front between the Gulf Stream and CC due to frontal effects on prey distributions in these regions.

Due to the small differences in sea surface temperature at the surface of GSFEs in comparison to those observed at depth (Glenn and Ebesmeyer 1994), it can be difficult to discriminate between water masses within GSFEs using sea surface temperature alone. To investigate biological patterns within GSFEs, future studies should quantify the location of frontal boundaries using oceanographic measurements at depth rather than simply using sea surface temperature measurements, as in the present study and in the studies of Haney and colleagues. This is particularly important since sub-surface mechanisms are responsible for the aggregation of nutrients and, presumably, plankton or weakly swimming nekton within GSFEs (see below), highlighting the need for measurements of oceanographic properties at depth to be used in order to characterize fronts within these oceanographic features.

Haney (1985a) suggested that differences in habitat use within Gulf Stream frontal eddies among different seabirds were directly related to the foraging strategies of these species. It is important to characterize the distribution and type of prey within

GSFEs to shed light on the effects of GSFEs on species using different foraging strategies; it is difficult to understand how or why differences between different species exist without first understanding the effects of GSFEs on prey distributions.

In the present study, limited acoustic data within Gulf Stream frontal eddies were obtained due to speed limitations of the survey vessel, which made it difficult to reach and adequately sample offshore regions of GSFEs within a single survey day, and due to the low speed required to sample using the over-the-side mount for the fisheries acoustics transducer. In addition, interference from boat noise made fisheries acoustics data unusable at higher sampling speeds (more than approximately 2.5 ms^{-1} through the water). This was particularly problematic in regions of rapid current speeds within the GS, where little progress along a linear cross-shelf transect could be made without increasing boat speed. Difficulties in assessing regions within GSFEs while on the water complicated efforts to obtain adequate data in each of the eddy regions. Further prey data collected in continuous transects across GSFEs are necessary before acoustic backscatter in different depth bins can be quantitatively correlated with relevant environmental variables such as eddy water mass, fronts separating water masses, and vertical gradients (see Hazen and Johnston 2010 for a comparable analysis at a broad spatial scale).

Previous studies of GSFEs suggest that these features are important sources of nutrients for plankton production (Flierl and Davis 1983), while zooplankton studies within a remnant of a GSFE CC mass showed a unique mid-shelf assemblage of zooplankton (Deibel 1985). Further, these studies indicated that little mixing had occurred between the shelf waters and this remnant CC based on the species composition of the CC. Previous acoustic studies and concurrent prey tows across the Gulf Stream front have suggested that size classes of nekton differ within waters of the Gulf Stream and the continental shelf, with larger acoustic scatterers observed in slope waters in comparison to Gulf Stream waters (Nero et al. 1990). Such data are not available for the different regions of GSFEs, but differences in prey species, or size classes of prey species, observed in different parts of GSFEs could have important effects on seabirds foraging in these features.

In the present study, surface-feeding birds that feed primarily on fish or squid were associated with CC eddy regions. Black-capped petrels feed on fish, invertebrates, and squid and feed by dynamic soaring and surface or aerial dipping (Ashmole 1971, Clapp et al. 1982, Haney 1987a, Lee 2000), while Cory's shearwaters feed by surface seizing on fish and squid (Ashmole et al. 1971, Clapp et al. 1982, Granadeiro et al. 1998). Bridled terns feed on squid and small surface-schooling fish by aerial seizing (Clapp et al. 1982, de Silva 1985, Hulsman and Langham 1985, Kohno and Kishimoto 1991), while Manx shearwaters feed on squid and fish by plunge diving (Brown et al. 1978, Brooke 1990, Furness 1994). Audubon's shearwaters, which feed on fish, squid and crustaceans by pursuit diving or plunging, pattering or surface seizing (del Hoyo et al. 1992), can dive to depths as high as 35 m (Burger 2001). These four species were primarily observed in eddy CC regions, where fisheries acoustics studies suggested that availability of larger prey items was higher. Wilson's storm-petrels that feed primarily on small crustaceans using aerial dipping (Ashmole 1971, Croxall et al. 1988) were observed throughout all eddy habitats.

Small acoustic targets produce more acoustic scattering at high frequencies, while the frequency has less of an effect on large targets (Simmonds and MacLennon 1992). Thus, concentrations of the small zooplankton prey items of storm-petrels would not be detected by the 38 kHz transducer used in this study. In addition, due to ring-down effects of the transducer (i.e., near-surface noise associated with near-field transducer effects), prey abundance within the top 5 m of the water column was not assessed (e.g., Gal et al. 1999; Parker-Parker-Stetter et al. 2007). Assessing surface distributions of prey, and investigating the distribution of smaller prey items, is particularly important to understanding the habitat use of Wilson's storm-petrels within GSFEs. Future studies should use surface tows to evaluate surface distributions of prey within GSFEs. In addition, transducers of different frequencies can be used to assess distributions of prey species of different sizes (Jech and Michaels 2006, Korneliussen et al. 2008), and the use of multiple frequencies would allow for further discrimination of prey within GSFEs. Smaller prey species, such as zooplankton, would be best assessed with high frequency transducers (e.g., Brierley et al. 1998), and this would allow the mechanisms of prey aggregation to be related to physical oceanographic processes at depth. Using multiple frequencies in future studies would be particularly beneficial since differences in prey species between water masses or frontal regions may play an important role in influencing the species composition of seabirds foraging within GSFEs. Previous studies in the Bering Sea (Hunt et al. 1998, Russell et al. 1999) have shown that different prey species are aggregated upstream and downstream of frontal regions, and that seabirds with preferences for different prey species are segregated accordingly. Frontal boundaries within GSFEs may have similar effects, with different prey species being aggregated on inshore (CC) and offshore (GS) regions of the front. In addition to using surface tows and multiple acoustic frequencies, further studies of the prey field in this region should investigate prey abundance and distribution on days when no eddies are present to compare typical prey distributions in this region, and to identify effects that can be attributed to GSFEs specifically.

In the present study, oceanographic surveys within GSFEs were conducted by day from a small boat so that sampling efforts within GSFEs could be initiated on short notice as these features approached the study site. This created several sampling constraints, such as limited time within the study area, and interference from boat noise at relatively slow sampling speeds due to the over-the-side mount of the transducer. In addition, the requirement that multiple transducers be placed in close proximity on an over-the-side mount caused interference between fisheries acoustics transducers and an

Acoustic Doppler Current Profiler (ADCP), which was intended to allow for the measurement of eddy currents at depth but could not be used for this reason. As a result, surveys focused solely on prey mapping and concurrent measurements of currents and prey distributions were not obtained. The use of large research vessels with hull-mounted acoustic instruments, allowing for sampling over longer temporal periods, would be advantageous in future investigations of GSFEs. However, since GSFEs are episodic and it is difficult to predict when these features will occur in a given study area, the use of large, expensive research vessels could be difficult. Recent efforts to survey GSFEs aboard large research vessels were unsuccessful due to limited ship time, poor weather and the reliance on satellite images to detect these features, which are often hampered by cloud formations over the Gulf Stream (D. Hyrenbach, pers. comm.). Studies of the mechanics of GSFEs in relation to seabird habitat require that oceanographic regimes, prey distributions and seabird abundance and distribution be assessed simultaneously. Future studies investigating the dynamics of GSFEs would require a larger research vessel for several weeks. Since GSFEs occur at a frequency of approximately one every 2 to 14 days, persisting for one to three weeks and moving northward at a rate of approximately 20 km/day (Lee et al. 1981; Glenn and Ebesmeyer 1994), a three week study period should allow at least one GSFE to be identified studied, and followed and surveyed over several days as it traveled north with the Gulf Stream. Previous oceanographic surveys have successfully examined the physical dynamics of

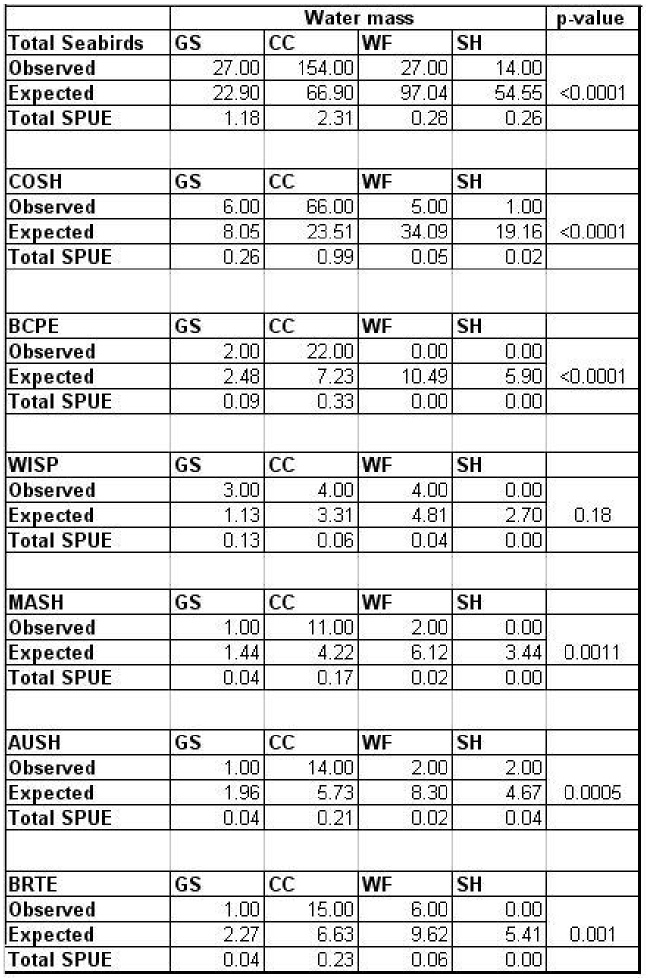
GSFEs using a similar sampling design (e.g., Glenn and Ebesmeyer 1994a,b), though these studies did not include assessments of biological patterns. Other studies investigating the physical oceanography of GSFEs employed moored instruments to examine changes in oceanographic processes in a given location through time (e.g., Lee et al. 1981). A similar approach, using transducers measuring both physical oceanography and prey distributions, would be extremely useful in elucidating biophysical interactions within GSFEs. Moored fisheries acoustics transducers have been used to investigate patterns in fish distributions in other study sites (e.g., Guillard et al. 2004, Brierley et al. 2006), and this sampling approach would be particularly useful in dynamic GSFEs which are otherwise very difficult to locate and sample. Moored transducers would also allow any lagged effects of GSFEs on zooplankton and fish distributions to be assessed at a given location.

Lagged effects of oceanographic features on biological patterns in the SAB and elsewhere have been well documented (e.g., Ryan and Yoder 1996, Croll et al. 2005, Soldevilla 2008). GSFEs likely have important effects on upper-level predators other than seabirds. In particular, cetaceans have been associated with eddies and rings at a variety of scales (e.g., Waring et al. 1992, 1993, Griffin et al. 1999, Biggs et al. 2005), and the ability to forage at depth would allow cetaceans to exploit prey aggregations in regions that are not accessible to most seabird species. The use of moored fisheries acoustics instruments along with concurrent boat-based seabird or cetacean surveys or deployments of passive acoustic monitoring devices to examine patterns of cetacean habitat use (e.g., Wiggins and Hildebrand 2007) would allow the effects of GSFEs on multiple trophic levels and different marine predator species to be assessed.

In spite of the challenges associated with sampling dynamic oceanographic features, the importance of understanding biophysical mechanics within these features becomes particularly clear when considering their influences on ocean productivity. For example, episodic eddy-driven upwelling is thought to supply a significant fraction of the nutrients required to sustain primary productivity of the subtropical ocean (McGillicuddy et al. 2007). Since GSFEs are important drivers of primary productivity in coastal regions of the SAB (Lee et al. 1981, Yoder et al. 1981, 1983), understanding how their mechanics affect organisms throughout the food chain is particularly important to improving predictions of biological productivity.

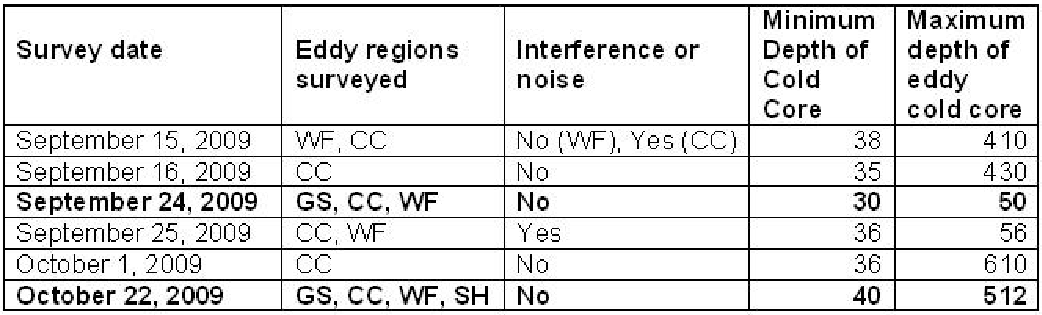
This study used both *in situ* and remotely sensed data to examine trends in seabird habitat use within dynamic GSFEs over multiple years. Seabird surveys demonstrated the effects of these features on the fine-scale distribution of seabirds off the coast of North Carolina. Preliminary data presented here suggest that the effects of Gulf Stream frontal eddies on mid-trophic level organisms likely drove the observed differences in seabird habitat use within GSFEs.

Table 6: Observed numbers of seabirds in different water masses on days when Gulf Stream frontal eddies were observed relative to numbers expected given the amount of survey effort in each region assuming uniform seabird distribution between water masses. P-values indicate significance using a Chi-squared test to compare observed and expected seabird abundance in different eddy regions (Haney 1986a). GS = Gulf Stream; CC = eddy cold core; WF = eddy warm filament; SH = shelf waters; COSH = Cory's shearwaters; BCPE = black-capped petrels; WISP = Wilson's storm-petrels; MASH = Manx shearwaters; AUSH = Audubon's shearwaters; BRTE = bridled terns.



	Water mass				p-value
Total Seabirds	GS	CC	WF	SH	
Observed	27.00	154.00	27.00	14.00	<0.0001
Expected	22.90	66.90	97.04	54.55	
Total SPUE	1.18	2.31	0.28	0.26	
COSH	GS	CC	WF	SH	
Observed	6.00	66.00	5.00	1.00	<0.0001
Expected	8.05	23.51	34.09	19.16	
Total SPUE	0.26	0.99	0.05	0.02	
BCPE	GS	CC	WF	SH	
Observed	2.00	22.00	0.00	0.00	<0.0001
Expected	2.48	7.23	10.49	5.90	
Total SPUE	0.09	0.33	0.00	0.00	
WISP	GS	CC	WF	SH	
Observed	3.00	4.00	4.00	0.00	0.18
Expected	1.13	3.31	4.81	2.70	
Total SPUE	0.13	0.06	0.04	0.00	
MASH	GS	CC	WF	SH	
Observed	1.00	11.00	2.00	0.00	0.0011
Expected	1.44	4.22	6.12	3.44	
Total SPUE	0.04	0.17	0.02	0.00	
AUSH	GS	CC	WF	SH	
Observed	1.00	14.00	2.00	2.00	0.0005
Expected	1.96	5.73	8.30	4.67	
Total SPUE	0.04	0.21	0.02	0.04	
BRTE	GS	CC	WF	SH	
Observed	1.00	15.00	6.00	0.00	0.001
Expected	2.27	6.63	9.62	5.41	
Total SPUE	0.04	0.23	0.06	0.00	

Table 7: Dates of oceanographic surveys, showing eddy regions surveyed, interference or noise in acoustic data, and minimum and maximum depth of the eddy cold core (m). Entries in bold show data used to compare prey biomass at depth between eddy regions. GS= Gulf Stream; CC= eddy cold core; WF= eddy warm filament; SH = shelf waters.



Survey date	Eddy regions surveyed	Interference or noise	Minimum Depth of Cold Core	Maximum depth of eddy cold core
September 15, 2009	WF, CC	No (WF), Yes (CC)	38	410
September 16, 2009	CC	No	35	430
September 24, 2009	**GS, CC, WF**	**No**	**30**	**50**
September 25, 2009	CC, WF	Yes	36	56
October 1, 2009	CC	No	36	610
October 22, 2009	**GS, CC, WF, SH**	**No**	**40**	**512**

Table 8: Linear survey effort for each eddy region surveyed on September 24, 2009 and October 22, 2009. GS= Gulf Stream; CC= eddy cold core; WF= eddy warm filament; SH= shelf waters.

Date	GS	CC	WF	SH
September 24, 2009	12.5 km	10.1 km	8.6 km	9.1 km
October 22, 2009	6.2 km	29.7 km	4.3 km	N/A

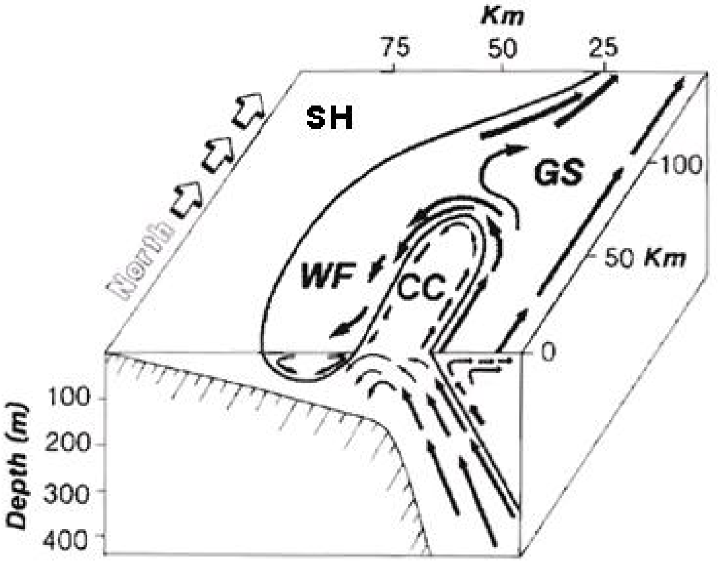


Figure 28: Schematic diagram of a Gulf Stream frontal eddy from Haney (1986a). Arrows represent circulation patterns. GS= Gulf Stream; CC= eddy cold core; WF= eddy warm filament; SH= shelf waters.

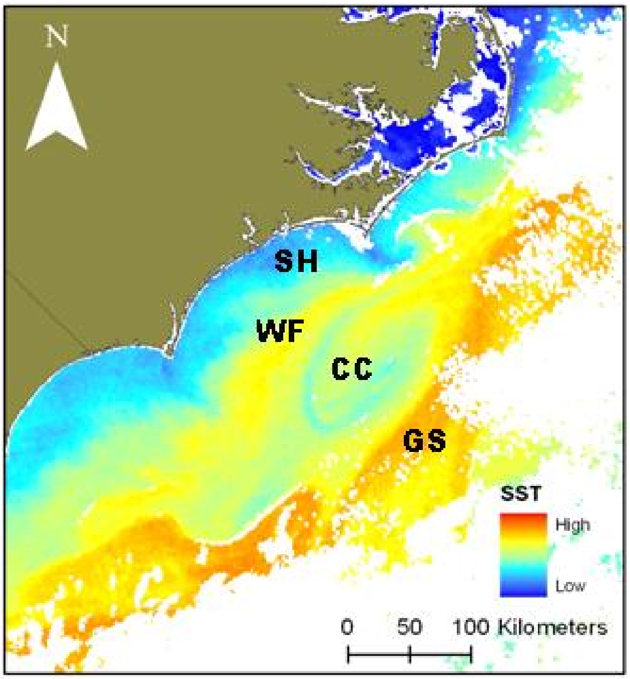


Figure 29: A large Gulf Stream frontal eddy sampled in Onslow Bay on October 1, 2009, showing the location of the different eddy regions. GS= Gulf Stream; CC= eddy cold core; WF= eddy warm filament; SH= shelf waters.

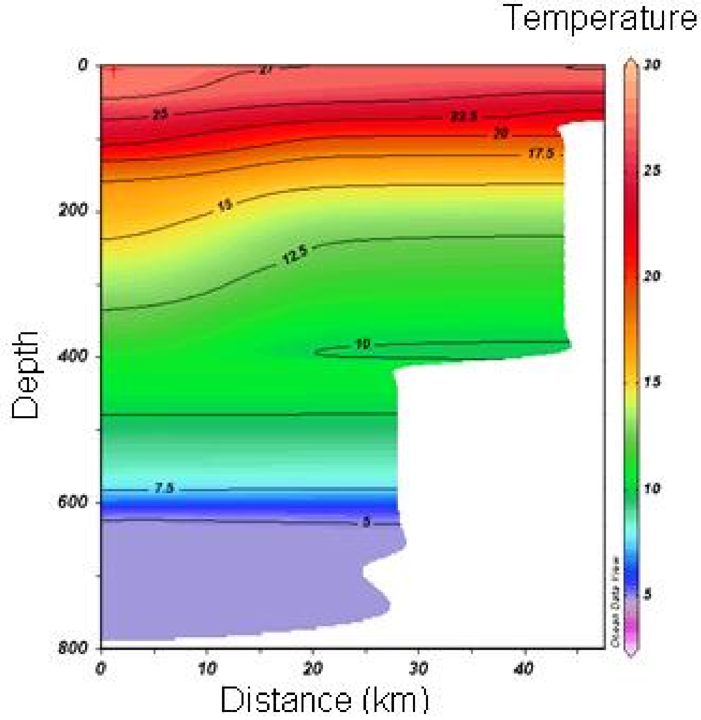


Figure 30: Temperature profiles at depth within a Gulf Stream frontal eddy produced from ecasts. Domed temperature contours at depth indicate the presence of the eddy cold core, while blank areas indicate bottom topography.

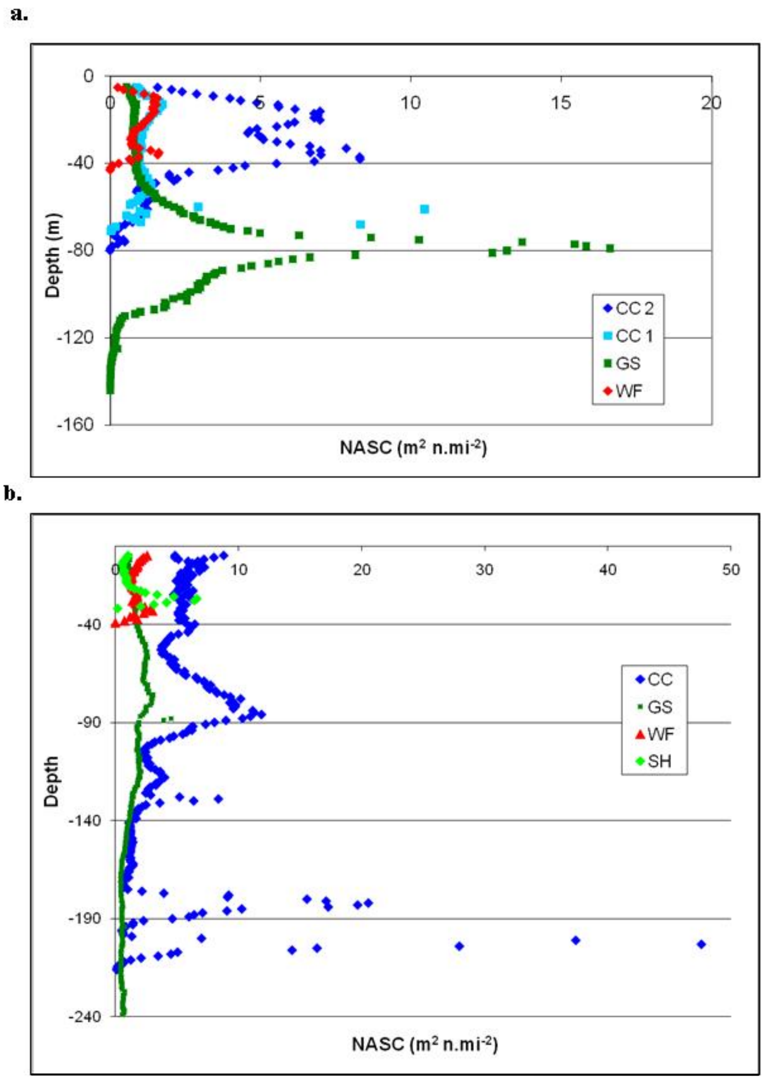


Figure 31: Abundance of prey biomass at depth within different regions of Gulf Stream frontal eddies sampled on (a) September 24 and (b) October 22, 2009. Prey biomass in near-surface waters (e.g., top 40 m) was highest in eddy cold core regions, though variability in prey biomass was observed within the CC (a). GS = Gulf Stream; CC = eddy cold core; WF = eddy warm filament; SH = shelf waters.

General conclusion

Importance of assessing relationships between seabirds and oceanographic features

Many previous studies have emphasized the importance of seabirds as indicator species of marine systems (Ricklefs et al. 1984, Croxall et al. 1988, Bost et al. 1994, Montevecchi and Myers 1995, Diamond and Devlin 2003, Piatt et al. 2007). If we wish to predict, rather than document, the effects of changes to marine environments, we must understand how physical factors drive seabird habitat use. Oceanographic features create foraging opportunities for seabirds by aggregating prey (Chapter 1), thus presenting appropriate focal regions in which to study oceanographic aspects of seabird habitat. Understanding the dynamics of these features is critical to: understanding seabird habitat; predicting the occurrence of seabird habitat in space and time; and predicting how changes to the physical environment will affect seabird habitat, as well as marine ecosystems more broadly.

The results of my dissertation elucidate the importance of understanding biophysical interactions within oceanographic features that occur at vastly different scales, and demonstrate how seabird habitat can be identified and predicted using a suite of environmental predictor variables. Together, these studies highlight the importance of conducting repeated standardized surveys in order to understand the effects of dynamic habitat variables, and demonstrate the utility of spatial analyses and quantitative methods to improving our understanding of seabird habitat use within oceanographic features. The effects of oceanographic features are often evaluated without considering confounding influences from other habitat factors, and the multivariate approach used in the present studies demonstrates how the relative importance of individual oceanographic variables can be evaluated. Investigations of seabird-oceanography relationships within this dissertation also highlight the importance of incorporating prey studies in order to directly assess how oceanographic features influence foraging seabirds. Lastly, these studies provide quantitative assessments of the at-sea habitat of several seabird species, including two species of conservation concern, the endangered black-capped petrel and the red-necked phalarope (not currently designated as threatened or endangered, but the abandonment of a long-time migratory stopover has caused concern for the species in eastern North America).

The results of my dissertation provide several considerations for the sampling and analysis of future studies of how oceanographic features influence seabirds.

Future directions

Determining links between biological patterns and the processes driving these patterns requires that physical and biological parameters be examined at appropriate scales (Haury et al. 1978, Legendre and Demers 1984). Spatial scale is often considered in seabird studies, but temporal scale is equally important and is often ignored (Chapters 1 and 2). Future studies should carefully consider temporal aspects of oceanographic features, such as the persistence and age of the features (e.g., Haney 1989), when assessing the role that they play in creating seabird habitat.

Our understanding of the mechanics of oceanographic features and their importance to trophic exchange is currently limited by a lack of knowledge of biophysical interactions throughout the food web. Important progress has been made in this respect in studies of foraging seabirds (e.g., Hunt et al. 1998, Russell et al. 1999, Jahncke et al. 2005), but this field of research would benefit from direct assessment of the influence of physical forces on lower and mid-trophic level organisms. Without this knowledge, studies of seabird habitat use in relation to oceanographic features must rely on indirect inferences. By omitting consideration of seabird prey, we limit our ability to understand specifically how and why these features create important foraging habitat. Interdisciplinary studies, involving collaborations between oceanographers and seabird biologist to investigate the biophysical dynamics of oceanographic features, are needed to more fully understand the influence of oceanographic features on food web dynamics. More comprehensive studies of these systems would allow predictive modeling of their biological effects, a goal that is particularly important in light of the potential for long-term, climate-driven change to the physical marine environment (IPCC 2004).

Knowledge of seabird habitat use in relation to the dynamics of oceanographic features in the vertical dimension has improved (e.g., Hunt et al. 1998, Russell et al. 1999, Charassin and Bost 2001), but should be investigated more widely. To date, most studies investigating the biological influence of oceanographic features have only examined surface characteristics of these features from satellite images. Relying only on surface-based methods may not accurately identify oceanographic features, especially when organisms may be aggregated at depth. Information regarding the sub-surface mechanism by which mid-trophic level organisms are aggregated at these features is limited (Haney and McGillivary 1985), and aggregation within these features is likely heterogeneous. Biomass is thought to be aggregated within smaller features, such as fine-scale thermal fronts at the periphery of eddies (Hyrenbach et al. 2006). The results of preliminary fisheries acoustics surveys within Gulf Stream frontal eddies support this assertion (Chapter 4). Investigating the biological and physical dynamics of oceanographic features in three dimensions is necessary to clearly elucidate their effects on trophic exchange (Hyrenbach et al. 2006). Remote sensing data are readily available and frequently used, so a comparison of remotely sensed and boat-based surveys could provide important information elucidating how well the ecological processes occurring within oceanographic features can be evaluated from satellite data.

The biological effects of oceanographic features have important implications for trophic transfer in marine systems. An improved understanding of the biophysical coupling in these systems is required to determine the extent to which, and the mechanisms through which, oceanographic features influence the transfer of energy through the food web and the population dynamics of upper trophic level species. The importance of understanding biophysical mechanics of oceanographic features is particularly clear when considering their vast influences on ocean productivity. As an example, episodic eddy-driven upwelling is thought to supply a significant fraction of the nutrients required to sustain primary productivity of the subtropical ocean (McGillicuddy et al. 2007). Thus, determining how physical factors drive the productivity of these features is an important step in increasing our ability to predict primary and secondary productivity in marine ecosystems. My dissertation provides concrete suggestions for improving our knowledge of biophysical interactions within oceanographic features to reduce uncertainty and improve prediction.

Lastly, predictable oceanographic features represent important habitats that could be used as focal areas for long-term monitoring studies. Identifying and elucidating changes to physical or biological patterns is a key goal of long-term monitoring studies, and detailed preliminary studies assessing biological and physical patterns represent in an important first step in studying biophysical processes within oceanographic features. However, integrating small-scale observations with large scale patterns in marine systems remains a challenge (Dayton and Tegner 1984). Long term monitoring that reflects small-scale variation at a number of sites over a broad geographic area could provide an important means of addressing this challenge.

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Publications

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Thorne, L.H. and A.J. Read (*In review*) A quantitative assessment of red-necked phalarope *(Phalaropus lobatus*) foraging habitat in the Bay of Fundy, Canada: the importance of considering biophysical dynamics at a fine scale.

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