FORAGING STRATEGIES AND FACILITATIVE INTERACTIONS AMONG COMMON (*STERNA HIRUNDO*) AND ROSEATE TERNS (*S. DOUGALLII*) IN THE NORTHWEST ATLANTIC OCEAN

By

HOLLY FRANKLIN GOYERT

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree of Doctor of Philosophy,
The City University of New York

2013

This manuscript has been read and accepted for the Graduate Faculty in Biology
in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

Date

Chair of Examining Committee
Dr. Richard R. Veit
College of Staten Island

Date

Executive Officer
Dr. Laurel A. Eckhardt

Dr. Lisa L. Manne
College of Staten Island

Dr. Jennifer Basil
Brooklyn College

Dr. Mark E. Hauber
Hunter College

Dr. Jennifer Arnold
Penn State University, Berks Campus

Dr. William A. Montevecchi
Memorial University of Newfoundland

Supervisory Committee

The City University of New York

Abstract

FORAGING STRATEGIES AND FACILITATIVE INTERACTIONS AMONG
COMMON (*STERNA HIRUNDO*) AND ROSEATE TERNS (*S. DOUGALLII*)
IN THE NORTHWEST ATLANTIC OCEAN

By Holly F. Goyert

Advisor: Richard R. Veit

Marine resources are characteristically patchy and concealed beneath the surface of a "featureless" ocean, which makes facilitative species interactions especially advantageous to seabirds. My research addresses how behavioral mechanisms accommodate prey availability, or more specifically, how common (*Sterna hirundo*) and roseate terns (*S. dougallii*) locate and access food when it is not easily detectable. I study their foraging behavior and ecology from pre- to post-breeding, offshore in the pelagic realm (chapter 1), around the colony (chapter 2), and in nearshore waters (chapter 3). My first chapter tests the hypothesis that, as broadly-ranging seabirds, common and roseate terns forage over habitat where marine mammals and predatory fish help to find and access prey. I quantify the spatial association among foraging terns, tunas, dolphins, and their habitat, using Bayesian hierarchical models, and tests of behavioral community interactions. Facilitation explains how terns benefit from subsurface predators through local enhancement and commensal relationships: foraging tunas improve the detection and availability of prey by signaling their presence, and driving them to the surface. Chapter 2 evaluates the link between resource utilization and foraging strategy, measured by nest provisioning and patterns among foraging routes or feeding flocks. I propose that the opportunistic generalists, common terns, depend more on social cues than the specialists, roseate terns, which rely more heavily on spatial memory to find predictable prey. The results support this and suggest that increased breeding and foraging success in roseate terns relates to higher quality and abundance in their preferred prey, sandlance (*Ammodytes* spp.); in contrast, common terns seem to endure prey limitation through their use of local enhancement. In my third chapter, I hypothesize that habitat variability and prey availability predict interspecific differences in tern foraging. Behavioral tests and density-surface models, with distance sampling, show that foraging common and roseate terns respond positively to the distribution and abundance of each other and their preferred prey. Clearly, common and roseate terns use conspecifics, heterospecifics and subsurface predators to encounter prey via facilitation: such interactions create dynamic hotspots that need to be considered in an ecosystem approach to marine spatial planning.

Acknowledgements

I offer my sincere gratitude to Dick Veit, for providing me with the guidance, opportunity, and support, over the past six years, to pursue questions that have fundamentally intrigued and fulfilled me at personal and professional levels. A special thanks to Carolyn Mostello, who stepped in at a critical moment to provide me with professional support: access to Bird Island, logistical and staff assistance, and invaluable counsel that stems from her profound knowledge of terns. I genuinely appreciate Lisa Manne who, through her mastery and eloquent teaching, provided the encouragement and inspiration to transform statistical tedium into the drive for quantitative rigor. I thank all my committee members for helping to provide direction in my career path, by contributing their time, expertise, commentary, advice, and show of interest: in addition to those aforementioned, Jenny Basil, Mark Hauber, Jennifer Arnold, and Bill Montevecchi. I appreciate additional feedback from Ian Nisbet, Jeff Spendelow, John Verzani, Jochen Albrecht, Aaron Owen, and Jennifer Costello, as well as administrative assistance from Josephine Caputo and Joan Reid. Thank you to Sarah Luecke-Flaherty, who kindled my wholehearted appreciation of terns through her enthusiasm and dedication. I would also like to express gratitude towards Marie Caroline-Martin, for being supportive and considerate throughout the journey. My loving thanks to Bryce Geyer, for his commitment to being my steadfast island, comfort in creating a home for me to nest in, adaptability throughout all of our migrations, patience enduring my long absences in the field, fortitude in weathering the tempest, and integrity in encouraging my aspirations. I am grateful for my family members, whom I admire for their strength, reliability, and inspiration: my mom for encouraging me from the very beginning, my sister, Wendy, for exemplifying how to pursue a meaningful lifestyle and career of marine stewardship, and my brother, Johnny, for challenging me with passion and reason. My

thanks to Rachel Messer, for her friendship and pledge to humanity: I will strive to devote as much towards biodiversity.

The offshore surveys described in chapter 1 were funded by the Bureau of Ocean Energy Management (BOEM), and the CUNY graduate program provided additional support. Jon Hare, Jerry Prezioso, and Mike Jech of the NOAA NEFSC Oceanography and Ecosystem Surveys Branches provided the opportunity to participate as a volunteer seabird observer aboard the offshore EcoMon and Herring Surveys; I additionally thank them and colleagues for helping to boost ship's morale aboard the Gordon Gunter, FSV Pisces, FSV Henry B. Bigelow, and FRV Delaware II, especially Cristina Bascuñan and Tamara Holzwarth-Davis. I appreciate the input from those who helped to collect data at sea, in particular: Marie Martin, Tim White, Tom Johnson, Chris Vogel, Kris Winiarski and Ellen Jedrey. I am grateful for Beth Gardner's modeling advice, Chris Jackson's assistance troubleshooting BUGS, along with Andrew Thomas and Tim Handley. Jim Manning at NOAA provided shipboard along-track oceanographic data. Andrew Gilbert assisted with ArcGIS data processing and generated the tool used to calculate species densities at sea. Eugene Dedits offered support in accessing the CUNY College of Staten Island High Performance Computing Center. I acknowledge further feedback from Brian Kinlan, Chris Elphick, Adam Wilson, Alain Zuur, Dave Fournier, Hans Skaug, Ben Bolker, Simon Wood, Evan Cooch, Carl Safina, and two anonymous reviewers.

The Bird Island research described in chapter 2 was supported by The Nuttall Ornithological Club Blake Fund, which covered costs for the assistant, housing, and logistics in 2011, and the Norcross Wildlife Foundation A.V. Stout Fund, which supplied funding for boat transportation in 2010. Thank you to my assistant, Margo Servison, and volunteer Lainga Tong, who both helped to observe over five times as many tern foraging departures in 2011 than in

2010. The MDFW crew (Joanna Hatt, Bird Island manager 2009) also offered logistical support, and the town of Marion harbormasters granted access to the lighthouse and provided aid. I also acknowledge feedback from four anonymous reviewers.

Jeremy King, Vinnie Manfredi, and Matt Camisa at the Massachusetts Division of Marine Fisheries (MADMF) allowed me the opportunity to participate as a volunteer seabird observer aboard the inshore bottom trawl surveys, and they also provided requested data. I thank them and Mark Szymanski for sharing their thorough understanding of fish habits and identification, along with some great laughs; thanks also to Carl Rhodes and the crew of the RV Gloria Michelle for accommodating me. With regard to distance sampling guidance, I am especially grateful to Kris Winiarski for supplying useful resources, and I deeply appreciate Dave Miller’s helpfulness and receptivity to my inquiries on density-surface modeling.

Dedication

I dedicate this dissertation to my migratory family:

Bryce, Mom, Johnny, Wendy,

and the loving memory of my father.

Table of Contents

List of Tables

List of Figures

Overview

The ocean is a “featureless” and dynamic environment, where marine resources tend to aggregate into temporarily superabundant prey patches (‘bait balls’): such patterns may mediate facilitation, where top predators exploit each other to reveal the otherwise inconspicuous prey concealed beneath the sea surface (Lack 1946; Langham 1968; Dunn 1972; Au & Pitman 1986; Poysa 1992; Buckley 1997; Hacker & Gaines 1997; Ramos 2000). Facilitation is a type of Allee effect: a mutualism where individuals benefit from the presence of neighbors through positive density-dependence (Berec 2010). Although positive and negative species interactions may occur jointly, mutualisms tend to get overlooked by the literature, because competition may override facilitation when resources are limited (Safina 1990a, b; Bruno et al. 2003). Conversely, facilitation may eclipse competition as long as prey remain available (Lack 1946; Langham 1968; Dunn 1972; Au & Pitman 1986; Poysa 1992; Buckley 1997; Hacker & Gaines 1997; Ramos 2000). Conventionally, the patchy distribution of marine resources results from bottom-up trophic cascades of phytoplankton, zooplankton and forage fish, that attract top predator assemblages (Lamb 1964; Haney 1986b; Shealer 2001; Frederiksen et al. 2006), producing feeding frenzies among seabirds and subsurface marine predators (Ashmole & Ashmole 1967; Evans 1982; Au & Pitman 1986; Skov et al. 1995; Camphuysen & Webb 1999; Jaquemet et al. 2004; Hebshi et al. 2008); these likely involve two facilitative mechanisms: local enhancement and commensalism. Local enhancement is a type of observational learning, or social facilitation, where individuals use visual cues from foraging neighbors to locate unpredictable prey (Roberts 1941; Thorpe 1951; Pallaud 1984; Poysa 1992; Buckley 1997; Goodenough et al. 2001; Davoren et al. 2003; Grunbaum & Veit 2003; Silverman et al. 2004; Elliott et al. 2009a; Weimerskirch et al. 2010; Fauchald et al. 2011). Commensalism is a type of mutualism, where seabirds benefit facultatively from marine mammals or predatory fish that drive prey up to the surface; it is assumed that cetaceans and tunas gain nothing from the interaction, although possible that diving seabirds also help to signal prey and direct fish downwards (Ashmole & Ashmole 1967; Au & Pitman 1986). Marine birds may choose alternative foraging strategies over facilitation, depending on the detectability or availability of prey. When environmental conditions (i.e. fog) compromise visual cues, seabirds may resort to magnetic orientation or route-based foraging—the latter can involve spatial memory, an advanced cognitive process that is adaptive for navigation (Shettleworth 1998; Bonadonna et al. 2003; Ricklefs 2004). Spatial memory more likely profits species that specialize on specific, persistent prey, as compared to facilitation, which rewards more opportunistic seabirds that consume diverse prey and readily join feeding frenzies (Davoren et al. 2003; Elliott et al. 2009a; Weimerskirch et al. 2010).

My research assesses how common (*Sterna hirundo*) and roseate terns (*S. dougallii*) use facilitation or memory to forage, and how differences between them relate to differences in their prey utilization, particularly prey specificity and availability. This is important because it speaks to how top predators in marine communities differentially respond to ecological flux (chapter 1), how advanced cognition relates to resource utilization in the natural environment (chapter 2), and how facilitative interactions may alleviate limitations in resource availability (chapter 3). Two basic questions frame the theme of this thesis: (1) how do terns locate and access food when it is not easily detectable? And, (2) how do differences in breeding success relate to differences in foraging strategies? I present original documentation of tern spatial patterns offshore in the pelagic realm of the Northwest Atlantic Ocean (chapter 1), near the colony (chapter 2), and inshore, within Massachusetts state waters (chapter 3); chapter 2 covers the breeding season (June-July), while chapters 1 and 3 examine the pre- or early-breeding and post-breeding seasons. Chapter 1 implements Bayesian hierarchical modeling and tests of behavioral community interactions to address the hypothesis that common and roseate terns forage over habitat where they interact with subsurface predators. Local enhancement and commensalism explain the positive spatial association among foraging terns and tunas. Dolphins, sea surface temperature, depth, and distance to shore also contribute to pelagic tern distribution and abundance. These results demonstrate that common and roseate terns are broadly-ranging seabirds, and share life history traits with their pelagic relatives, Arctic (*S. paradisaea*) and sooty terns (*Onychoprion fuscatus*). Although there exists anecdotal evidence of researchers and fishers following terns to find tuna schools (Erdman 1967; Grimes 1977), and common and/or roseate terns feeding on fish pursued by tunas (Dunn 1972; Britton & Brown 1974; Oro 1995), this study is the first to quantify the degree of association and recognize the mechanism behind it as potentially facilitative. In chapter 2, I predict tern foraging strategies from differences in their resource utilization, by analyzing chick provisioning and correlations among commuting trajectories between breeding and feeding grounds. I test the hypothesis that common terns, as generalists, forage more socially than roseate terns, which are specialists that remember where to fish for predictable, high quality prey. My observations support this, and suggest that terns deliver larger prey to their chicks after longer foraging trips, consistent with central-place foraging theory (Orians & Pearson 1979). The findings also indicate how responsive roseate terns are to interannual fluctuations in the availability of their preferred prey, outperforming common terns in feeding proficiency, during years of abundance. Having the flexibility to choose between facilitation and memory may allow terns to overcome foraging constraints, and respond appropriately to such anthropogenic threats as climate change and overfishing. Chapter 3 evaluates the hypothesis that habitat and prey availability relate directly to the behavior, distribution and abundance of common and roseate terns. I assess density-surface models with distance sampling, and behavioral tests of tern interactions with each other and sampled prey. The results point to conspecifics, heterospecifics, principal prey species, depth, primary productivity, and sea surface temperature as significant covariates in tern spatial patterns. In other words, terns search for fish over productive habitat, and increase their chances of encountering prey by congregating with other foraging terns. The foraging behavior and ecology of roseate terns is especially dependent on other tern flocks and their preferred prey, sandlance (*Ammodytes* spp.).

Common and roseate terns are excellent subjects for comparative research on foraging behavior and ecology in the field, since they suit studies that account for phylogeny (being sister species, Bridge et al. 2005) and shared study sites (breeding and feeding grounds). Like other colonial seabirds, common and roseate terns are central-place foragers during the breeding season, and pelagic during other parts of the year (Kirkham 1986; Dänhardt et al. 2011). Colony-based study design is useful for assessing route-based foraging (chapter 2), especially since the North American breeding population of roseate terns is divided amongst few islands that support a dominant proportion of the continental subspecies (*S. d. dougallii*, Gochfeld et al. 1998). While breeding studies govern the literature, published observations of offshore tern foraging habits are sparse (Powers 1984; Haney & Stone 1988), which reflects the practical difficulties of tracking terns at sea, and contributes to the misconception that they are “coastal waterbirds”. Although band resightings and geolocator tracks have demonstrated the capacity for terns to travel efficiently and at length during the post-breeding season and migration (Shealer & Kress 1994; Egevang et al. 2010; Spendelow et al. 2010; Nisbet et al. 2011), terns are too small (under 150 g) to equip high-resolution tracking transmitters, at present (Wikelski et al. 2007; Burger & Shaffer 2008). Only shipboard surveys (chapters 1 and 3) provide data on interactions among terns, other marine predators, and their prey, as gauged by their offshore behaviors, numbers, locations, and habitats (Camphuysen et al. 2004; Camphuysen & Garthe 2004). Because terns are more conspicuous than other ocean-dwelling species of their foraging guild, such as cetaceans, they act as good ecosystem and fisheries indicator species (Furness & Camphuysen 1997; Camphuysen & Webb 1999; Furness & Tasker 2000; Diamond & Devlin 2003; Jaquemet et al. 2004; Le Corre & Jaquemet 2005; Jaquemet et al. 2007; Monticelli et al. 2007; Einoder 2009; Dänhardt & Becker 2011a).

This dissertation provides clear evidence that facilitation is advantageous to common and roseate terns. These species rely on subsurface predators (chapter 1), and each other (chapters 2 and 3), to detect and access food through local enhancement and facultative commensalism. That is not to say that intra- or inter-specific tern competition is absent, rather, that the benefits and incidence of facilitation eclipse competition when marine resources are characteristically dynamic, patchy, and transiently superabundant (chapters 1-3). Alternatively, the “misfortune” of prey limitation, which may accompany environmental instability or ecological cycles, could allow competition to overpower facilitation. As a result, roseate terns, which are well-adapted to specialize on sandlance using memory, may resort to local enhancement to update their feeding strategies, but may also suffer from unpredictability in the availability of their preferred prey (chapters 2-3). Common terns are more likely to adjust to a volatile climate through their flexibility and opportunism. Yet, if they are to endure the depletion of Northwest Atlantic tuna populations that results from overexploitation (Fromentin & Powers 2005; Safina & Klinger 2008; Lotze & Worm 2009), then they face the challenge of adopting alternative strategies from facilitation (chapter 1). Documenting the sensitivity of terns to the presence of other predators (tunas, conspecifics, heterospecifics, chapters 1-3), and to the availability of prey (chapter 3), is crucial to understanding how significant a role starvation may play in the mortality of adults and their offspring (chapter 2). By following the relative availability of sandlance, herring, and even tuna, managers may be able to explain a portion of the uncertainty concerning interannual changes in productivity and survival of terns. This could ultimately impact conservation through proper integration into management, especially for the U.S. population of roseate terns, which is federally "endangered" and continues to decline; common terns have recovered since the end of the 20th century millinery trade, and are listed as "special concern" pursuant to the Massachusetts Endangered Species Act (Mostello 2012). Beyond providing more complete data on common and roseate tern life histories, this thesis reveals how they interact with their community of marine predators and prey. Not only do terns serve as good indicators, but they may also contribute to consumption impacts on highly valued commercial fish through top-down processes (Monaghan 1992; Hunt & McKinnell 2006; Frederiksen et al. 2007; Overholtz & Link 2007). Monitoring the offshore foraging distribution, abundance, and associations of terns, subsurface predators, and their prey, is a high priority for marine spatial planning in the NW Atlantic: such data are necessary to forecast the future impacts of permanent wind facilities, or to designate marine protected areas, in the interest of vulnerable species like roseate terns

(Camphuysen et al. 2004; Kress & Hall 2004; Ehler & Douvere 2009; Burger et al. 2011; Maclean et al. 2013). Species interactions may identify more irregular areas of high resource use than can be predicted merely by habitat. Therefore, managers need to consider an ecosystem approach that accounts for the dynamic nature of the marine processes that shape community hotspots.

Chapter 1. Offshore: Facilitative interactions among the pelagic community of temperate migratory terns, tunas, and dolphins

Co-authors: Richard R. Veit, Lisa L. Manne, College of Staten Island, CUNY

Abstract

We studied the influence of foraging facilitation on the marine community of top pelagic predators off the northeastern United States. We treat common (*Sterna hirundo*) and roseate terns (*S. dougallii*) as ecosystem indicator species, since they are conspicuous and highly sensitive to environmental influence. This research documents the offshore behavior and ecology of these seabirds, which is a little-understood but predominant part of their life cycle. Few rigorous tests examine the effect of interspecific competition on seabird distributions, though many papers note the importance of habitat suitability. We hypothesize that tern foraging is strongly affected by facilitation: defined as positive interactions among multiple taxa (birds, fish, mammals), where individuals use foraging neighbors for improved prey detection or availability. We used spatiotemporal-structured Bayesian hierarchical models to test for the association of common and roseate terns with aggregations of tunas and cetaceans (large, easily-detected subsurface marine predators), and with standard oceanographic parameters. High tern abundance corresponded to relatively high tuna densities, low dolphin densities, high sea surface temperatures, shallow water, and proximity to shore. The fact that terns foraged in the presence of tunas or high densities of dolphins supports our hypothesis that the mechanism behind this spatial association involves positive interspecific interactions (attraction). We propose that terns, as opportunistic seabirds, use facilitation to locate and access prey. This study reveals the large impact that dynamic interspecific interactions can have in structuring communities, and focuses

attention on the need for implementation of community-based ecosystem approaches in marine spatial planning.

Introduction

Marine resources are unique in their characteristically aggregated quality, where the relatively superabundant nature of ephemeral patches can mediate facilitative interactions across multiple taxa (Lack 1946; Au & Pitman 1986; Poysa 1992; Buckley 1997; Ramos 2000). There are widely-known examples of mutualisms (especially of mixed-species foraging flocks, Farine et al. 2012), but their role in marine systems has generally been undervalued. Pelagic seabirds have the exceptionally difficult task of targeting prey concealed beneath the sea surface, which makes facilitation advantageous. Feeding frenzies have been described for highly pelagic tern species associating with subsurface predators, predominantly sooty terns (*Onychoprion fuscatus*) with tunas and Arctic terns (*S. paradisaea*) with cetaceans (Ashmole & Ashmole 1967; Evans 1982; Au & Pitman 1986; Skov et al. 1995; Camphuysen & Webb 1999; Jaquemet et al. 2004; Hebshi et al. 2008). Two mechanisms behind such interactions have been identified as facilitative: (1) commensalism, where subsurface predators increase accessibility to food by pushing prey up to the surface (Ashmole & Ashmole 1967; Au & Pitman 1986); or (2) local enhancement (LE), where cues from foraging neighbors attract heterospecifics to feeding assemblages (Poysa 1992; Buckley 1997; Silverman et al. 2004; Fauchald et al. 2011). Analysis of spatial association among marine predators at sea could reveal two alternatives to facilitation (i.e. positive interactions): (1) negative, competitive interactions (involving “suppressors”, Camphuysen & Webb 1999); or (2) lack of interaction around shared resources (indifference). Foraging overlap could possibly indicate competition between subsurface predators and terns if resources are limited (Poysa 1992). Yet, the opportunity to exploit heterospecifics in pursuit of unpredictable, high density prey (i.e. LE, Silverman et al. 2004; Elliott et al. 2009a; Fauchald et al. 2011), may offer enough benefits to minimize competition costs (Poysa 1992). This research offers a novel approach to quantifying facilitative foraging interactions, by supplementing spatial models with behavioral statistics across multiple taxa. We hypothesize that, as broadly-ranging seabirds, common and roseate terns forage over pelagic habitat where they interact positively with marine mammals and predatory fish, for improved prey detection (local enhancement) and availability (commensalism).

We analyzed four years of shipboard surveys conducted on the northeastern U.S. continental shelf (up to 350 km offshore). Common (*Sterna hirundo*), and roseate terns (*S. dougallii*) spend two thirds of their life cycle away from the colony, yet little is known about their behavior and ecology while they forage at sea (Gochfeld et al. 1998; Nisbet 2002). Most mixed-species tern flocks in the temperate Northwest Atlantic region are dominated by common and roseate terns, yet published observations are sparse, especially for the latter species (Powers 1984). Arctic terns appear rarely, therefore we avoid characterizing their habits. As conspicuous apex predators that breed in the Northwest Atlantic, terns serve as good fisheries and ecosystem indicators (Furness & Tasker 2000; Jaquemet et al. 2004; Hyrenbach et al. 2006; Monticelli et al. 2007; Dänhardt & Becker 2011a). Unfortunately, the relatively small size of terns constrains tracking technology to coarse resolution (Egevang et al. 2010; Nisbet et al. 2011) or reduced spatial extent (Perrow et al. 2011); in contrast, shipboard surveys provide a precise, real-time, high resolution, non-invasive, and spatiotemporally extensive view of the surrounding behavioral and ecological influences on offshore tern foraging behavior and ecology (Camphuysen &

Garthe 2004). Hierarchical abundance models allow us to evaluate simultaneous tern associations with habitat and multiple taxa, at a large spatial extent and fine-scale resolution, while accounting for both tern counts and zeroes, survey effort (offset), and a nested spatiotemporal structure; thus, they are more informative than traditional occurrence or occupancy models (Oppel et al. 2012).

We aim to identify direct interactions of terns with top predators, in the context of the determinants of trophic productivity (Ashmole & Ashmole 1967). Our method uniquely quantifies community associations together with environmental variables so that we may ask (1) what oceanographic parameters best characterize tern habitat, and (2) to what degree terns associate with subsurface marine predators. Our first question addresses whether terns select marine habitats based on common oceanographic parameters. In the Northeast Atlantic, common and roseate tern abundance correlates positively with sea surface temperature (SST) and negatively with chlorophyll-α concentration (an index of primary productivity), distance to shore, and depth (Amorim et al. 2009). Terns are piscivorous, and although their abundance may correlate with that of phytoplankton (Amorim et al. 2009), it is not a direct food source, therefore we expected primary productivity to serve as only a weak predictor of tern abundance. Sooty terns, after all, forage successfully in some of the most oligotrophic waters in the world, benefiting from convergence zones with high SST (Hyrenbach et al. 2006) as well as subsurface predators that provide access to prey (Au & Pitman 1986; Jaquemet et al. 2004). Common and roseate terns spend August through April away from their colonies, and dedicate roughly a quarter of their lifecycle to post-breeding dispersal, when adults are capable of traveling over 500 km/day to feed fledglings and stage for migration (Shealer & Kress 1994; Nisbet et al.

2011). Yet, the overrepresentation of foraging studies in neritic breeding habitat has led to the assumption that these “coastal waterbirds” adhere in close proximity to the coastline (Gochfeld et al. 1998; Nisbet 2002; Perrow et al. 2011); we assert that, as broadly-ranging seabirds, they occupy the pelagic niche shared with their relatives, Arctic and sooty terns.

Our second question addresses whether terns cue in on subsurface predators: although inshore studies during the breeding season suggest that predatory fish may improve common and/or roseate tern foraging (Safina & Burger 1988; Shealer 1996) and inevitably their reproductive success (Ramos 2000), narrow focus on interference competition has predominated over tests of facilitation (Safina 1990a; Monticelli et al. 2006). Furthermore, the degree of an association with tunas has not been previously quantified. Sooty terns, pelagic tropical residents, have demonstrated facilitative foraging relationships with tunas and cetaceans that push shared prey to the surface (Ashmole & Ashmole 1967; Au & Pitman 1986). Accordingly, our main objective is to determine the significance of associations with subsurface marine predators as drivers of common and roseate terns’ offshore distribution. We propose that facilitative interactions surmount the influence of both habitat and competition on the foraging strategies of common and roseate terns in the pelagic realm. We suspect that terns cue on the presence of tunas and cetaceans to find food (local enhancement), and then rely on commensal relationships for access to those prey.

Methods

Data

We conducted ship-based surveys aboard NOAA NEFSC (National Oceanic and Atmospheric Administration: Northeast Fisheries Science Center) research vessels from May-

June and August-October 2006-2009: the Ecosystems Monitoring Survey (EcoMon), and the Atlantic Herring Acoustic Survey (Supplementary material, Appendix 1.1). Survey tracks between randomly stratified stations crossed the continental shelf from Cape Hatteras to George's Bank and the Gulf of Maine. Each observer alternated, either one or two hour watches, to collect data continuously from sunrise to sunset, sampling a forward quadrant off one side of the vessel, while the ship was underway at 7-12 knots on average. We entered data using the program dLOG3 (R.G. Ford Consulting Co. 2009), which logs time and GPS coordinates along the ship track. Observations included species, counts of individuals, behavior, distance and angle (from the observer) of each sighting, and weather conditions; at times of high activity, we substituted the 300 m strip transect for a distance-sampled line transect method (Tasker et al. 1984). We categorized tern behaviors as resting (sitting, rafting), foraging (feeding, diving, milling/circling), and travelling (flying along a uniform path), adapted from Camphuysen and Garthe (2004). Detectable subsurface predator behaviors included swimming, feeding (e.g. for tuna, signature turbulence and identifiable dorsal fins), jumping, porpoising, and blowing. Standard oceanographic data were simultaneously logged by NOAA along the ship track using hull-mounted sensors: fluorescence (a measure of chlorophyll concentration in parts per million, PPM), SST (°C), and salinity (parts per thousand, PPT). Bathymetry data (depth in meters) were available online from GEBCO (GEBCO_08 Grid 2009, http://www.gebco.net). We used ArcGIS Desktop 9.3 (ESRI 2009) to extract bathymetric raster data, calculate tern distance to shore, and spatially join the seabird and oceanographic survey data. We pooled common and roseate terns to best represent mixed-species flocks of indistinguishable individuals (including "unidentified" species, which may have incorporated a very small number of Arctic terns, Table 1.4). We calculated densities of terns, tunas and dolphins (count/km^2) for a 300 m strip along 1 km segments; each sampling unit was a "cell" 1 km long by 300 m wide (0.3 km^2). We used counts of whales sighted at any distance in the analysis (encounter rate, count/km), since they are visible to birds at a much greater range.

While typical of the oceanic abundance and distribution of seabird species, the nature of the data requires special handling methods as an alternative to classical approaches. The dataset is large (N > 10,000), non-negative (count data), zero-inflated, overdispersed (variance >> mean), spatially/temporally autocorrelated, and skewed (non-normal), with a majority of low values and occasional ecologically-important "outliers" (isolated large feeding flocks/schools are of special interest). We largely address these issues using (1) a spatiotemporal-structured Bayesian hierarchical framework with Markov chain Monte Carlo (MCMC) implementation to model habitat and community-level spatial associations, and (2) non-parametric tests of community-level behavioral associations among terns, tunas, and dolphins. We conducted all analyses and produced supporting figures using R version 2.15.0 (R Development Core Team 2012).

Habitat and community associations

To test for associations among tern counts, marine habitat, and density of subsurface marine predators within 0.3 km^2, we divided data into "spring" (pre-/early-breeding season, May-Jun., mid-Atlantic to New England, Figure 1.1a) and "fall" (post-breeding, Aug.-Oct., New England, Figure 1.1b); see Table 1.3 for more details. These subsets allowed us to investigate seasonal processes more efficiently, and reduce the impact of missing values. We ran spatiotemporal-structured zero-inflated negative binomial generalized linear mixed models

(ZINB GLMM), using the package “R2WinBUGS” (Sturtz et al. 2005) to access WinBUGS Version 1.4.3 (Lunn et al. 2000) via R. The negative binomial distribution is most appropriate in handling non-negative response values, skew, and overdispersion; by using a size parameter of one, the distribution qualified as a “geometric” case (Zuur et al. 2009). Modeling zero-inflation with a random effect and spatial correlation structure additionally helped to account for overdispersion (Zuur et al. 2012). We scaled covariates by subtracting their means and dividing by their standard deviation, to generate unrelated sample chains (Zuur et al. 2012).

The spatiotemporal structure in the models incorporated survey date as a random effect (Zuur et al. 2009), and a measure of spatial correlation (Zuur et al. 2012). To verify the choice of scale, we cross-correlated terns with tuna and dolphin density, to establish at what patch size they overlapped; then we determined tern neighborhood size by calculating the distance lag above which positive spatial autocorrelation dropped to insignificance (functions "acf" and "ccf" in R). We used this value to set the weights of an intrinsic conditional autoregressive (CAR) correlation structure, which made up the model’s residual term (Thomas et al. 2004; Saracco et al. 2010). See Appendix 1.1 for more detail.

To assess collinearity in explanatory variables (habitat, species densities), we calculated pair-wise Spearman rank correlation coefficients (Figures 1.2 and 1.3) and generalized variance inflation factors (GVIF), retaining variables with a GVIF of 2 or less (Zuur et al. 2012). Prior to analysis, we omitted all records for any tested parameter with missing values. We discarded fluorescence from the “fall” data entirely, because it was highly correlated with SST. We thus began model selection for the ZINB CAR GLMM with the following predictors: fluorescence (spring only), SST, salinity, depth, distance to shore, tuna density, dolphin density, and number of whales (Table 1.2). The final dataset retained a survey effort of 3,712 km in the "spring" and 8,715 km in the "fall"; roughly 200 "spring" hours and over 450 "fall" hours (for which there were more surveys but shorter daylight).

For model selection, we used a backwards stepwise approach, beginning with a "beyond optimal" model and subsequently eliminating weak predictors (Zuur et al. 2009), starting with one of each pair of collinear explanatory variables until all covariates were significant (Table 1.2) We did not rely heavily on Deviance Information Criterion (DIC) validation of best-fit models (lower values being better, analogous to other information criteria, Zuur et al. 2012), since weak effects of most covariates offered few comparable final models.

The selected models include two parts: a count process and a binomial process. The number of terns (*Y*) for each observation *i* are negative-binomial distributed with mean μ_i, and probability of false zero π:

$$Y_i \sim ZINB(\mu_i, \pi)$$

The count process in the "spring" model utilizes a logistic link function with mean μ_i, and parameters α (the intercept) and β (the coefficient for each covariate), and a log-transformed offset term: the transect area of each sampling unit (in square meters, averaging 300,000 m^2):

$$log(\mu_i) = \alpha + offset(LogTransectArea_i) + \beta_1 \times SST_i + \beta_2 \times Depth_i + \beta_3 \times Dolphins_i + a_i + \varepsilon_i$$

The random effect (a_i) allows for a different intercept for each date, which we assume is normally distributed with a mean 0 and variance σ^2_{Date} (Zuur et al. 2012):

$$a_i \sim N(0, \sigma^2_{Date})$$

The spatial residual term (ε_i) imposes CAR correlation structure (specifically, car.normal) on the response variable (Thomas et al. 2004; Saracco et al. 2010; Zuur et al. 2012):

$$\varepsilon_i \sim N(0, \sigma^2_{Spatial})$$

The binary process comprises the second part of the equation, is zero-inflated utilizing a logit link, and follows a Bernoulli distribution with probability 1-π (the true/structural zeroes), where π is the probability of false (sampling/statistical) zeroes (Zuur et al. 2012):

$$logit(\pi) = \gamma_1$$

We also considered models that included covariates, a random effect (a_i), and spatial residual term (ε_i), in both the count and binary processes. All models included an offset, in the count process only. Please see Appendix 1.1 for additional details of the implementation of the ZINB CAR GLMM.

The final "fall" model is:

$$Y_i \sim ZINB(\mu_i, \pi)$$

$$\log(\mu_i) = \alpha + offset(LogTransectArea_i) + \beta_1 \times Distance_i + \beta_2 \times Tunas_i + a_i + \varepsilon_i$$

$$a_i \sim N(0, \sigma^2_{Date})$$

$$\varepsilon_i \sim N(0, \sigma^2_{Spatial})$$

$$\text{logit}(\pi) = \gamma_1$$

Behavioral associations

To analyze foraging associations, we drew records from the complete dataset of eight surveys (Table 1.3) that noted tern behaviors per 1 km (0.3 km^2) bin (N = 537 tern groups made up of N = 3,277 tern individuals). Due to the non-normality of the data, we used a series of non-parametric tests in R to analyze tern behaviors within and between taxa. We used a Kruskal-

Wallis test to determine the dominant behavior of tern groups, with a Bonferroni adjustment for multiple pairwise comparisons. We tested the relationship between dolphin densities and individual tern behaviors with Wilcoxon-Mann-Whitney rank sum.

Results

Consistent with typical seabird data, tern counts were aggregated; the variance: mean ratio was much greater than one (presence only: “spring” = 80.0, “fall” = 99.6; including absences: “spring” = 86.6, “fall” = 110.1), supporting the use of the negative binomial distribution to model an overdispersed response variable (Zuur et al. 2009). “Fall” log tern and tuna densities were cross-correlated at 0-1 km lag distances (2 km patch sizes, Figure 1.5). Of the five surveys in the “fall”, tunas were only sighted in eight survey legs, three legs of which showed significant cross-correlation ($p < 0.05$) between absolute tern and tuna density (untransformed) for 1-3 km patch sizes. These neighborhood sizes verify that it was appropriate to bin data into 1 km segments for the purposes of modeling fine-scale cross-taxa associations. Tern counts were significantly autocorrelated in the “spring” up to 2 km and in the “fall” up to 4 km (Figure 1.6). These values are a close match to those reported by Amorim et al. (2009), and to the distance of 4.5 km at which birds are likely to be recruited to foraging flocks at sea, as calculated by theoretical models (Haney et al. 1992). The lack of autocorrelation in “spring” and “fall” Pearson residuals demonstrates that the 4 km neighborhood used for the CAR models sufficiently accounted for autocorrelation in the response variable (Figure 1.6).

In the “spring” ZINB CAR GLMM (N = 3,712; 20 groups (dates); DIC = 27,813), three variables were strong (significant) predictors of tern counts; for model fit, refer to Figure 1.7. Higher tern counts were more likely to be observed at higher sea surface temperatures and over shallower water (note that we gave depth negative values for better graphical representation). The negative correlation coefficient with dolphins indicates that, when terns are present, their numbers are inversely related to pod densities; in other words, few individuals may associate with sparse-to-dense dolphins, unlike large tern flocks that may dissociate from dolphins altogether (Table 1.1a, Figure 1.1a).

During the post-breeding season, observers positively identified tern species on the north edge of George's Bank: four roseate terns > 100 km offshore, including one 237 km east of Cape Cod, Massachusetts (MA), and several common terns at distances of up to 350 km, dispelling the notion that common terns are more restricted than roseate terns in their offshore ventures (Gochfeld et al. 1998; Nisbet 2002). The high correlation between fluorescence and SST in the "fall" data (Pearson's product-moment correlation coefficient: $t = 46.9$, $df = 2496$, $P < 1e\text{-}15$, 95% confidence interval $r = 0.66 - 0.70$; Figure 1.4) justified the removal of fluorescence from the dataset prior to analysis (see Figures 1.2 and 1.3 for other correlation coefficients between variables in the final datasets). In the "fall" ZINB CAR GLMM (N = 8,715; 78 groups (dates); DIC = 442,931), two variables significantly predicted tern counts; for model fit, refer to Figure 1.7. Higher tern counts were more likely to be observed over larger, more concentrated densities of tunas, closer to shore (Table 1.1b, Figure 1.1b). One model showed a weak positive correlation between tern counts and dolphin densities (contrary to the strong inverse effect in the "spring"), but this relationship was insignificant at the 5% level, therefore we removed dolphins from the final "fall" model.

Behavioral data revealed that exclusively foraging terns (not travelling or resting) associated with tunas (tuna densities present at foraging tern individuals: mean ± variance = 91.1

± 21,331.6, range = 3.3 – 333.3). Foraging terns also associated with significantly higher densities of dolphins than did travelling terns; no terns rested in association with dolphins (Wilcoxon-Mann-Whitney rank sum test: W = 1170283, $P < 1e\text{-}15$, Figure 1.8b). Significantly higher counts of terns foraged than either travelled or rested, in other words, larger groups were more likely to be foraging than traveling or resting (Kruskal-Wallis: $\chi^2 = 70.7$, df = 2, $P < 1e\text{-}15$; Pairwise comparisons using Bonferroni adjustment: foraging-resting $P < 0.01$, foraging-travelling $P < 1e\text{-}11$, Figure 1.8a). Together, these results from Figure 1.8 (a, b) suggest that higher densities of foraging terns associated with higher densities of dolphins, compared to resting or traveling terns.

Discussion

The most important findings were the significant spatial and behavioral associations among foraging common and roseate terns, and subsurface predators: tunas and dolphins. The patterns of tern distribution and associations differed for the “spring” and “fall” models. In the “spring”, with the onset of the breeding season, higher densities of terns were found over shallow water and high SST (2009), which likely reflects their rapid, direct migratory return from wintering grounds over warm coastal waters (Nisbet et al. 2011). Alternatively, terns follow warm-core Gulf Stream eddies that protrude into the cold Labrador Current on the Northwest Atlantic continental shelf edge (Hunt & Schneider 1987). Common and/or Arctic terns have been sighted at such features, where convergent circulation produces ephemeral, dynamic and oligotrophic filaments of warm, downwelled water that abut upwelled cold-core masses (Haney 1986a). Sharp gradients in SST and/or chlorophyll concentration conventionally initiate bottom-up processes where vertical mixing increases superficial nutrient load, providing ideal conditions for primary and secondary productivity (Hyrenbach et al. 2006). The presence of plankton then attracts higher trophic levels, including top predators such as terns and dolphins or tunas (Ashmole & Ashmole 1967; Au & Pitman 1986; Jaquemet et al. 2004; Walli et al. 2009). While SST was positively correlated with chlorophyll concentration in the "fall", no such relationship existed in the "spring", neither did we find a strong effect of primary productivity, contrary to other findings (Amorim et al. 2009). A theoretically indirect relationship between phytoplankton and forage fish may not be recognizable at such a fine scale due to spatial and temporal lag, or trophic mismatch (Hunt & Schneider 1987; Grémillet et al. 2008), implying that terns rely on a more effective mechanism to find prey: namely, subsurface predators. The inverse spatial relationship between terns and dolphin densities in the "spring" model suggests that smaller flocks of terns may associate with large dolphin pods whereas larger flocks may dissociate from dolphins; one possible explanation for this is that many of the dolphin observations occurred in deep water, far from high tern densities (Figure 1.1). Alternatively, terns prefer to forage with tunas (see below for further discussion), of which there are few sightings off New England in the "spring", likely because they spawn elsewhere (Walli et al. 2009). This leaves cetaceans, with which Arctic terns have been known to associate (Evans 1982; Camphuysen & Webb 1999), particularly dolphins during their migration in the Northeast Atlantic (Skov et al. 1995).

In the "fall", when both tunas and dolphins were abundant, terns associated with high densities of tunas, likely in synchrony with fall migration, when bluefin tuna (*Thunnus thynnus*) more frequently visit foraging grounds off the New England shelf (Walli et al. 2009). Here, tunas and terns likely target overlapping prey species such as Atlantic herring (*Clupea harengus*) and sandlance (*Ammodytes spp.*), which dominate their diets during the summer months (Gochfeld et al. 1998; Nisbet 2002; Walli et al. 2009). Given that our study unveils the under-appreciated pelagic range of common and roseate terns (Figure 1.1), the locations of feeding areas relative to survey effort may explain the increased sightings of terns closer to shore in the “fall”. The fact that terns foraged when in the presence of tunas and relatively high densities of dolphins provides substantial evidence of their attraction to subsurface predators, supporting our hypothesis that the mechanism behind the spatial association involves opportunistic, positive, facilitative interactions. Furthermore, the combined evidence that terns associated with these subsurface predators at a scale of 0.3 km^2 (in the “spring” and “fall” models), and cross-correlated with them inside 3 km neighborhoods, indicates a response to fine-scale and ephemeral foraging patches. The lack of an effect of whales on tern densities may have been due to scale: although whales are conceivably visible to terns at much greater distances than smaller subsurface predators, the detection of terns across such a vast range is limited. It is unclear why common and roseate terns seem to prefer tunas over dolphins, as do sooty terns (Au & Pitman 1986; Jaquemet et al. 2004). This association could result from (1) a tighter overlap between tern and tuna prey (Ashmole & Ashmole 1967); (2) the behavioral match between foraging terns and visible tunas that predominantly feed at the surface (Jaquemet et al. 2004), since dolphins feed more heavily at greater depths (Scott et al. 2012); or even (3) tern avoidance of intensified prey disruption, or interference competition (Safina 1990a) in the presence of dolphin pods. Both facilitative and competitive components characterize species interactions (Stachowicz 2001), where competition occurs at larger habitat scales and facilitation at local patch scales (Fauchald et al. 2011). While interspecies competition affects tern foraging success (Safina & Burger 1988; Safina 1990a; Monticelli et al. 2006), we argue that facilitative interactions may override its influence on the spatial co-occurrence of terns, tunas and dolphins, given the relatively superabundant, ephemeral nature of resource patches in the pelagic realm (Lack 1946; Au & Pitman 1986; Poysa 1992; Shealer 1996; Buckley 1997; Ramos 2000). Sooty terns have a tight relationship with tunas, as “near-obligate commensals” (Au & Pitman 1986), akin to common and roseate terns, which appear to be “facultative commensals”. We believe that the opportunistic nature of terns leads them to associate with suitable habitat until they come across subsurface predators that improve prey detectability: either dolphins or, preferably, high density schools of tunas, at which point they resort to facilitative interactions with tunas for increased accessibility.

Our research introduces the first documentation of common and roseate terns statistically associating with tunas and dolphins, which presents important ecological ramifications. First and foremost, given the interdependence of taxa that rely on facilitation (Stachowicz 2001), decreases of one component predator species may impact others. Thus, the decline in Atlantic tuna populations that results from overfishing (Lotze & Worm 2009) poses potential challenges to the conservation of terns. Whereas common terns have largely recovered from decimation due to the millinery trade, the U.S. population of roseate terns is federally listed as “Endangered” owing to recent declines (Nisbet 2002; Amaral & Saliva 2010). Therefore, as bluefish (*Pomatomus saltatrix*) have been termed “keystone competitors” with common and roseate terns during the breeding season (Safina 1990a), we propose to consider tunas of the Northwest Atlantic as “keystone facilitators” (Stachowicz 2001). Second, the dependence of terns on SST revealed by this study raises the question as to how the community will adapt to fluctuating changes in climate, particularly concerning roseate terns, since limited phenotypic plasticity and feeding specialization can set constraints on adaptability (Grémillet & Boulinier 2009). Third, the predominance of roseate tern adult mortality during the nonbreeding season remains unexplained, therefore identifying the pelagic distribution of terns jointly with their community trophic interactions will help to inform restoration projects and recovery efforts (Gochfeld et al. 1998; Nisbet 2002). Last, and of latest relevance, evaluating "hot spots" where terns are likely to aggregate at sea precedes appropriate management of offshore wind facility development to establish risks and prevent migratory hazards (Amaral & Saliva 2010). Our study highlights the dual ecological value of common and/or roseate terns in the Northwest Atlantic. Not only do they serve both as good fisheries and ecosystem indicators (Furness & Tasker 2000; Monticelli et al. 2007; Dänhardt & Becker 2011a), but they also impact their community by acting as initiators in multi-species feeding associations (Camphuysen & Webb 1999). As conspicuous benefactors and beneficiaries to their community structure, common and roseate terns are uniquely poised to present crucial information to umbrella conservation efforts in the Northwest Atlantic. We emphasize the dynamic nature of the marine processes that shape hotspots of focal species, and recommend a community-based ecosystem approach in marine spatial planning for the purpose of designating protected areas.

Tables

Table 1.1. Offshore tern habitat and community model summary, by season.

Each predictor shows significance in these final "spring" (a) and "fall" (b) generalized linear mixed models (GLMM), given the confidence intervals (2.5% and 97.5%) that do not include zero. The mean and standard deviation (SD) refer to the coefficients, and indicate the nature of the relationship (positive or negative) between the response variable (terns) and covariates. Abbreviations denote sea surface temperature (SST), random effect (RE), conditional autoregressive (CAR) correlation structure, effective sample size ('N.eff'), and the deviance calculated from the zero-inflated negative binomial (ZINB) distribution ('dev'), as opposed to the "deviance" based on the NB distribution (WinBUGS, 2004; Zuur et al. 2012).

node	term	mean	SD	2.50%	median	97.50%	n.eff
(a) "Spring"							
alpha	intercept	-1.33	1.54	-4.63	-0.89	1.07	9
beta[1]	SST	0.93	0.20	0.45	0.96	1.25	10
beta[2]	Depth	0.90	0.15	0.60	0.89	1.20	72
beta[3]	Dolphins	-1.21	0.87	-3.41	-0.94	-0.15	14
sigma.date	RE	2.23	0.42	1.56	2.17	3.19	2700
sigma.spatial	CAR	0.28	0.25	0.01	0.21	0.81	5
dev		7.17E+09	1.12E+10	4.08E+07	4.13E+09	4.75E+10	10
deviance		1850	291.50	1303	1912	2183	6
(b) "Fall"							
alpha	intercept	-0.55	2.59	-4.54	-0.24	3.56	4
beta[1]	Distance	-1.03	0.16	-1.33	-1.05	-0.74	12
beta[2]	tunas	0.21	0.10	0.07	0.19	0.41	300
sigma.date	RE	2.55	0.30	2.02	2.52	3.20	55
sigma.spatial	CAR	1.07	0.58	0.07	1.13	1.96	24
dev		5.55E+22	1.58E+24	7.64E+08	3.91E+12	5.55E+21	21
deviance		4769	966.90	3582	4490	6735	34

Table 1.2. Offshore tern habitat and community model selection by season, and seasons combined.

The best models selected from the candidate set are shown in bold, and indicate: the final selected models 1a (“spring”) and 2a (“fall”), the number of observations (n), number of model parameters (Param.), mean coefficient and significance of each covariate (* $p < 0.05$, shaded in gray), and the deviance information criterion (DIC) value, based on the negative binomial distribution (Zuur et al. 2012). Covariates for habitat (columns at left) include: sea surface temperature (SST), fluorescence (chlorophyll concentration, ‘Chl’), salinity (‘Sal’), depth, and distance to shore (‘Dist’). Community covariates (columns at right) include: tuna or dolphin density (‘Dolph’), and number of whales per km (‘Whl’). The ‘x’ indicates parameters that were not tested (i.e. not included in the data), the ‘-’ indicates covariates that were not considered as predictors in the models shown (i.e. they were not significant in more complex models). We used a backwards stepwise approach, where the weak effects of most covariates offered few comparable final models; e.g. the second-best models (1b and 2b) had non-significant predictors. Models 3a and 3b summarize analyses across both seasons, combined, for which the dataset included fluorescence, and thereby excluded 11,009 observations with missing data – we chose not to report on these models, since they are not representative of the complete dataset, and have relatively poor fit.

				Habitat			• Covariates •			Community		
Model	Seasons	N	Param.	SST	Chl	Sal	Depth	Dist	Tuna	Dolph	Whl	AIC
1a	**Spring**	**3,712**	**3**	**0.93***	**-**	**-**	**0.90***	**-**	**-**	**-1.21***	**-**	**27,813**
1b	Spring	3,712	3	0.64*	-	-2.95	-	-	-	-0.20*	-	42,636
2a	**Fall**	**8,715**	**2**	**-**	**x**	**-**	**-**	**-1.03***	**0.21***	**-**	**-**	**442,931**
2b	Fall	8,715	3	-	x	-	-	-1.12*	0.20*	0.09	-	444,778
3a	**Combined**	**6,208**	**3**	**-**	**-**	**-0.24***	**0.38***	**-**	**0.14***	**-**	**-**	**124,194**
3b	Combined	6,208	3	0.73*	-	-	-	-0.74*	0.13*	-	-	127,114

Table 1.3. 2006-2009 offshore survey dates.

Two Ecosystems Monitoring (EcoMon) Surveys, each extending from the mid-Atlantic (Cape Hatteras) to the Gulf of Maine / George’s Bank, composed the “spring” data. Five surveys made up the “fall” data: one EcoMon and four Atlantic Herring Hydroacoustic Surveys (shaded gray). A survey “leg” refers to a spatiotemporally-delimited track either west or east of the longitude 71°W (Buzzards Bay, Massachusetts, Figure 1.1a). “Fall” data did not include the 2009 EcoMon Survey due to their missing salinity values. Therefore, lack of a yearly replicate for the southwesterly leg of the “fall” 2008 EcoMon gave reason for its exclusion as well, thereby restricting “fall” analysis to New England waters (Figure 1.1b). For analyzing tern behavioral associations, data incorporated all surveys, and excluded records without tern behaviors.

Cruise Code	Survey	Season	Year	Start Date	End Date
DEL0615	Herring	“Fall”	2006	19-Sep	28-Sep
DEL0706	EcoMon	“Spring”	2007	23-May	3-Jun
DEL0710	Herring	“Fall”	2007	14-Oct	25-Oct
DEL0808	EcoMon	“Fall”	2008	17-Aug	28-Aug
DEL0809	Herring	“Fall”	2008	4-Sep	9-Oct
DEL0905	EcoMon	“Spring”	2009	28-May	10-Jun
DEL0909	EcoMon	“Fall”	2009	17-Aug	28-Aug
DEL0910	Herring	“Fall”	2009	12-Sep	15-Oct

Table 1.4. Occurrence, count, and density of tern species across all offshore surveys.

Occurrence indicates the number of groups observed, counts enumerate individuals, and density is calculated from counts divided by sampling unit area (0.3 km^2, on average). For a list of Northwest Atlantic tuna and cetacean species, see: NMFS (2013) and Wynne et al. (1999).

Species	Occurrence	Count	Density (count/km^2)
Common	341	1567	5283.8
Roseate	32	141	470.0
Arctic	31	64	213.9
Unidentified	149	2672	9727.1
Total	553	4444	15694.7

Figures

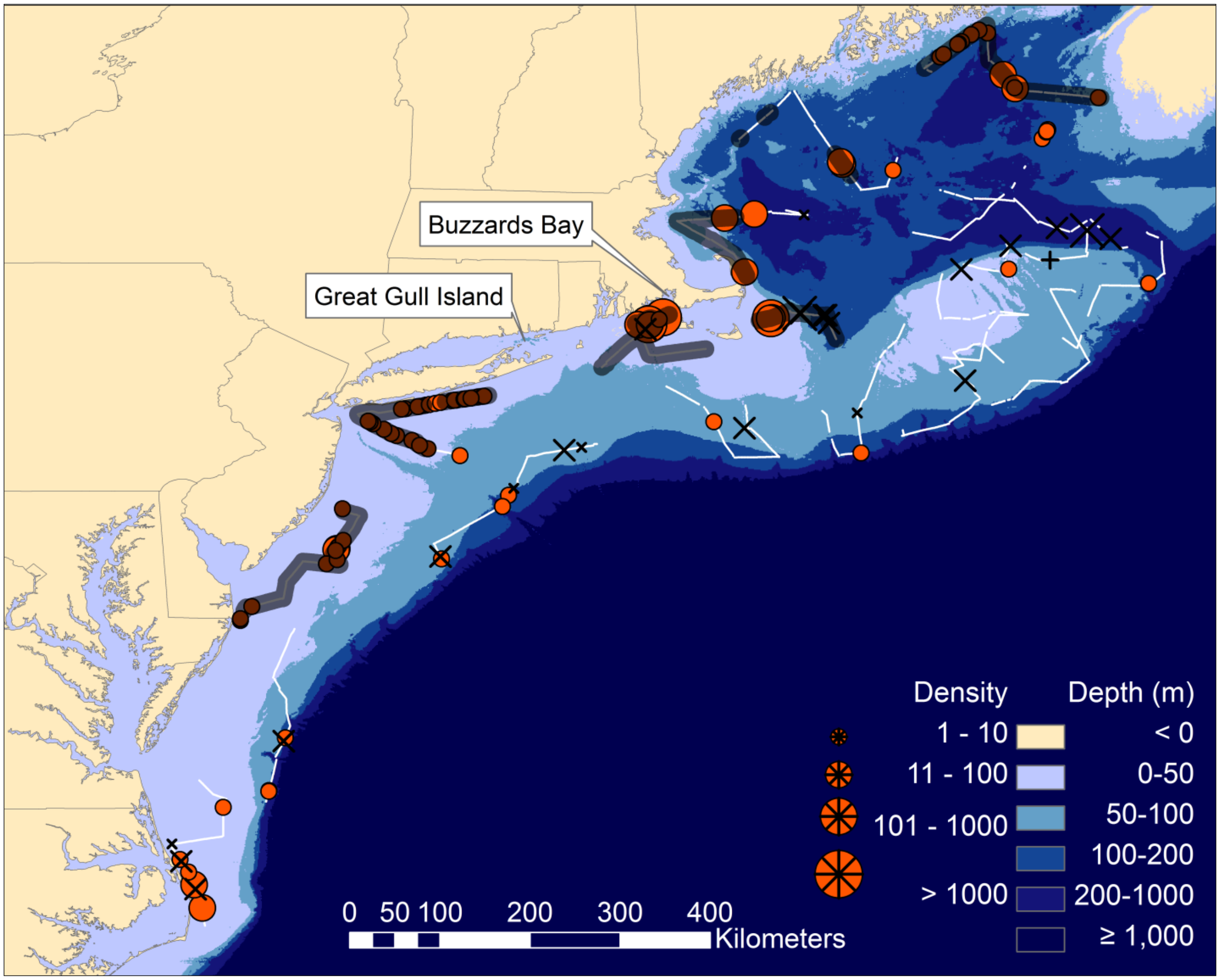


Figure 1.1 **(a)**

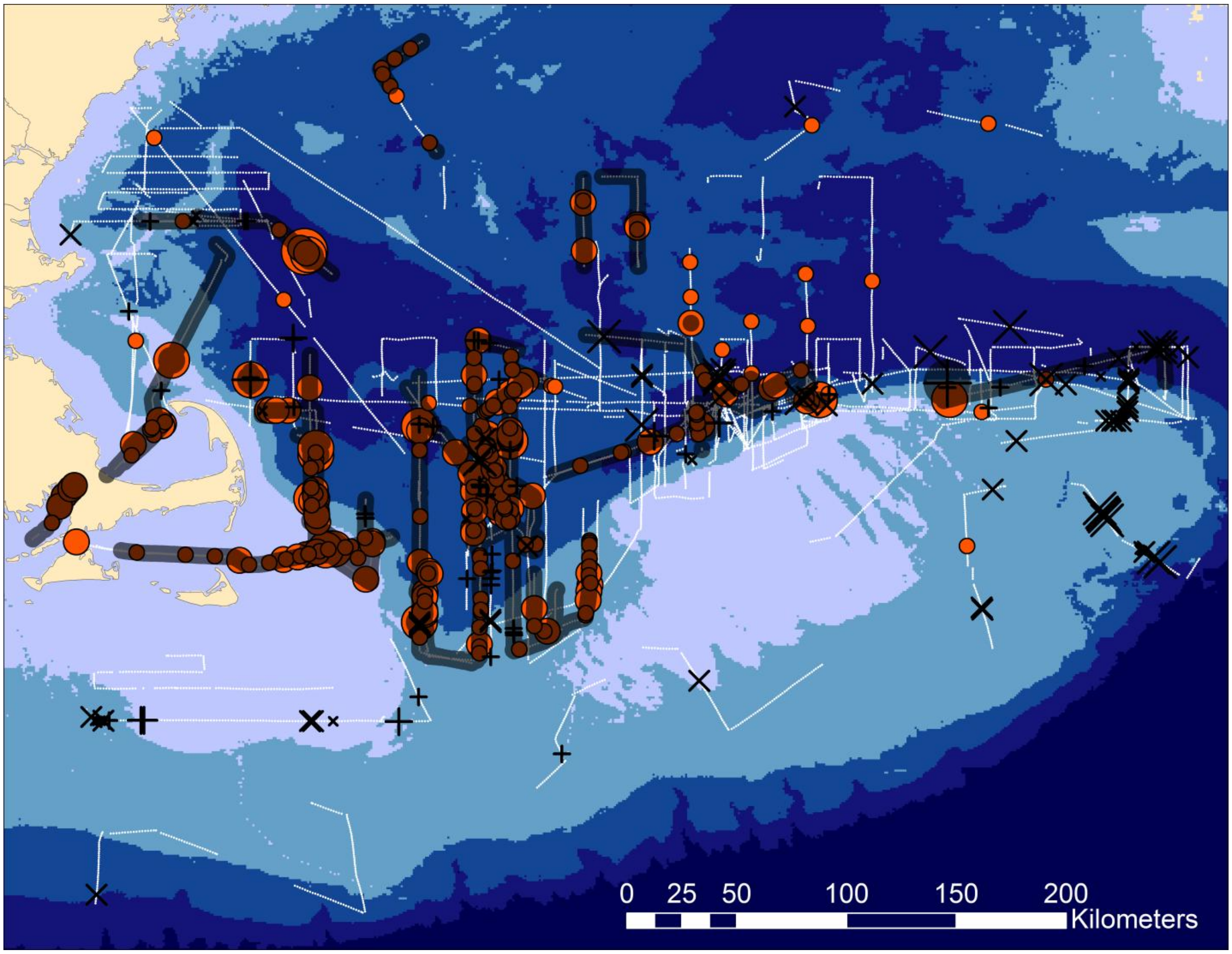


Figure 1.1 **(b)**

Figure 1.1. Observed and fitted distribution of terns during the offshore surveys, with observed tunas and dolphins, by season.

2006-2009 “spring” (a) and “fall” (b) cruise tracks, indicating observed and fitted absences, are shown in white. Orange circles represent observed tern density (count/km^2), and darkly shaded circles (equally scaled) represent fitted densities ≥ 0.5 terns/km^2 (fitted counts standardized by sampling area). Tuna densities are shown as “+” and dolphin densities as “×”. Size of points is relative to the density scale legend (count/km^2), shown in (a). Text boxes (a) point to the two largest shared breeding grounds of both common and roseate terns in North America: Great Gull Island, New York and Buzzards Bay, Massachusetts, USA—which includes Bird, Ram, and Penikese Islands.

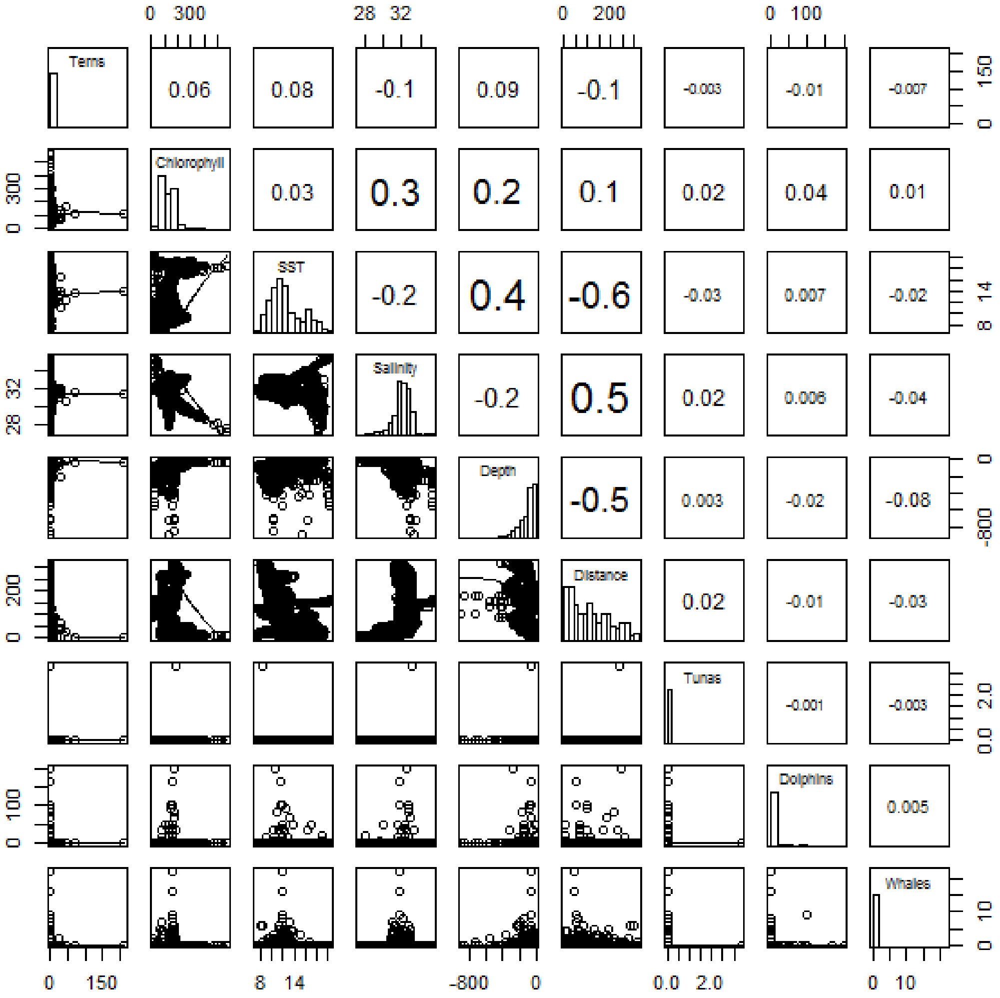


Figure 1.2. Relationships between terns and predictors in the “spring” model.

This “pairplot” (package “AED”, Zuur 2010) shows histograms of each variable on the diagonal, pair-wise Spearman rank correlation coefficients (font size proportional to value), and scatterplots with a LOESS smoother, axes labeled alternately (x at top or bottom, y at left or right). The response of pooled common and roseate terns, against the covariates considered for the “spring” model, is shown in the left column and top row (N = 3,712). The variables considered as covariates were: chlorophyll (fluorescence, parts per million), sea surface temperature (SST, °C), salinity (parts per thousand), depth (m), distance to shore (km), tuna density (per km^2), dolphin density (per km^2), and number of whales per km.

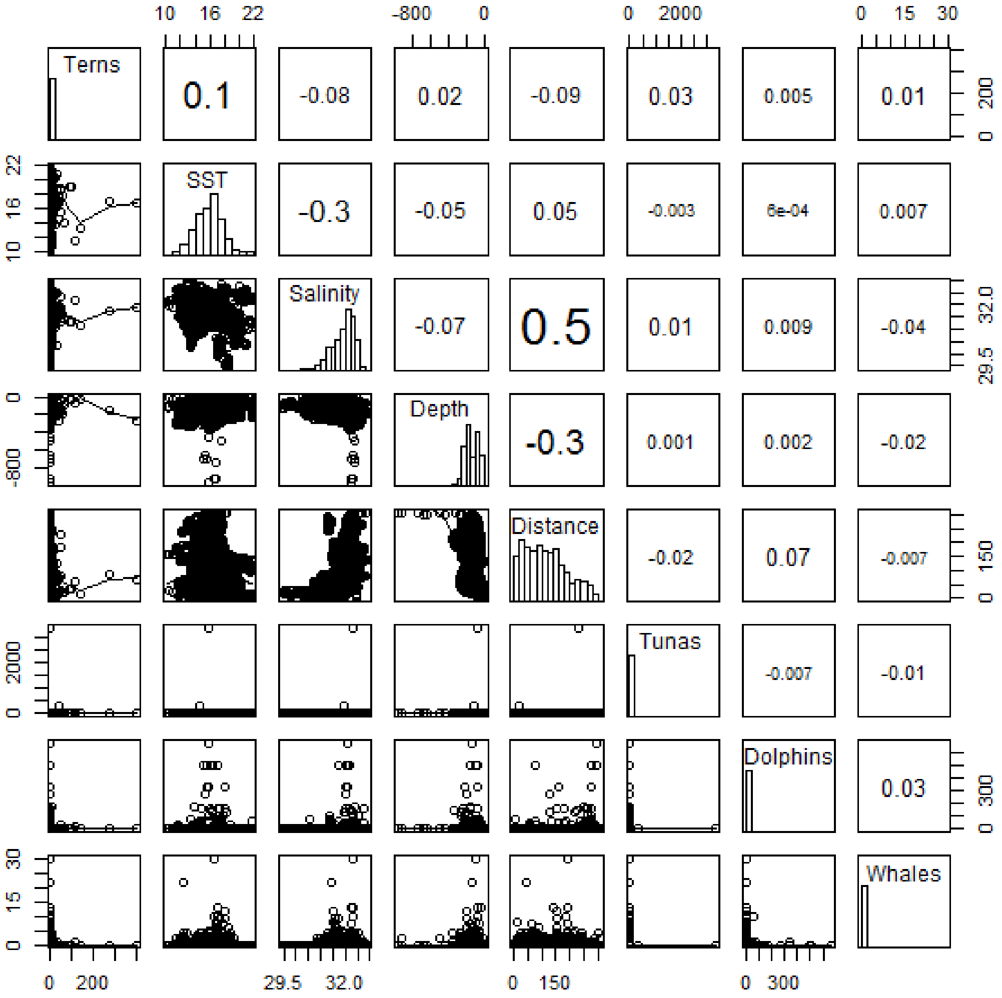


Figure 1.3. Relationships between terns and predictors in the “fall” model.

This “pairplot” (package “AED”, Zuur 2010) shows histograms of each variable on the diagonal, pair-wise Spearman rank correlation coefficients (font size proportional to value), and scatterplots with a LOESS smoother, axes labeled alternately (x at top or bottom, y at left or right). The response of pooled common and roseate terns, against the covariates considered for the “fall” model, is shown in the left column and top row (N = 8,715). The variables considered as covariates were: sea surface temperature (SST, °C), salinity (parts per thousand), depth (m), distance to shore (km), tuna density (per km^2), dolphin density (per km^2), and number of whales per km.

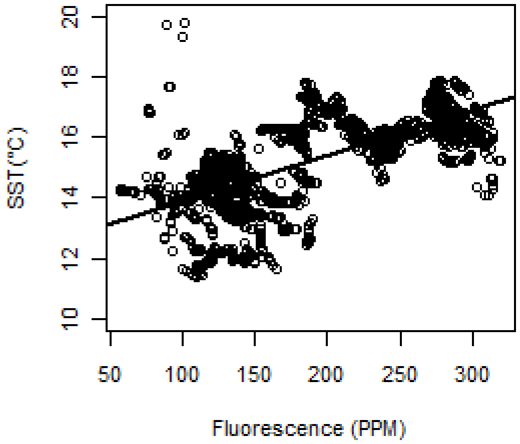


Figure 1.4. Relationship between chlorophyll concentration and sea surface temperature (SST).

This scatterplot of SST against fluorescence (parts per million) in the "fall" shows a line slope corresponding to the Pearson's product-moment correlation coefficient. Due to the high collinearity, we removed fluorescence from "fall" data for modeling purposes.

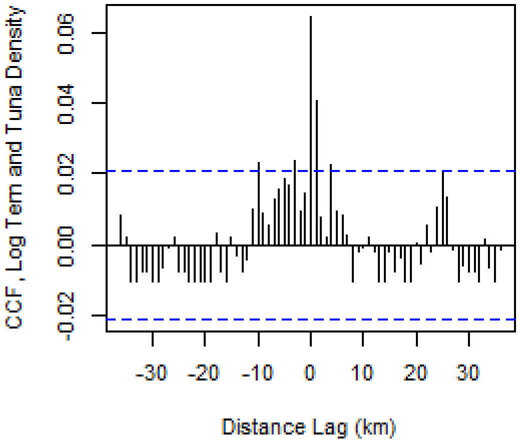
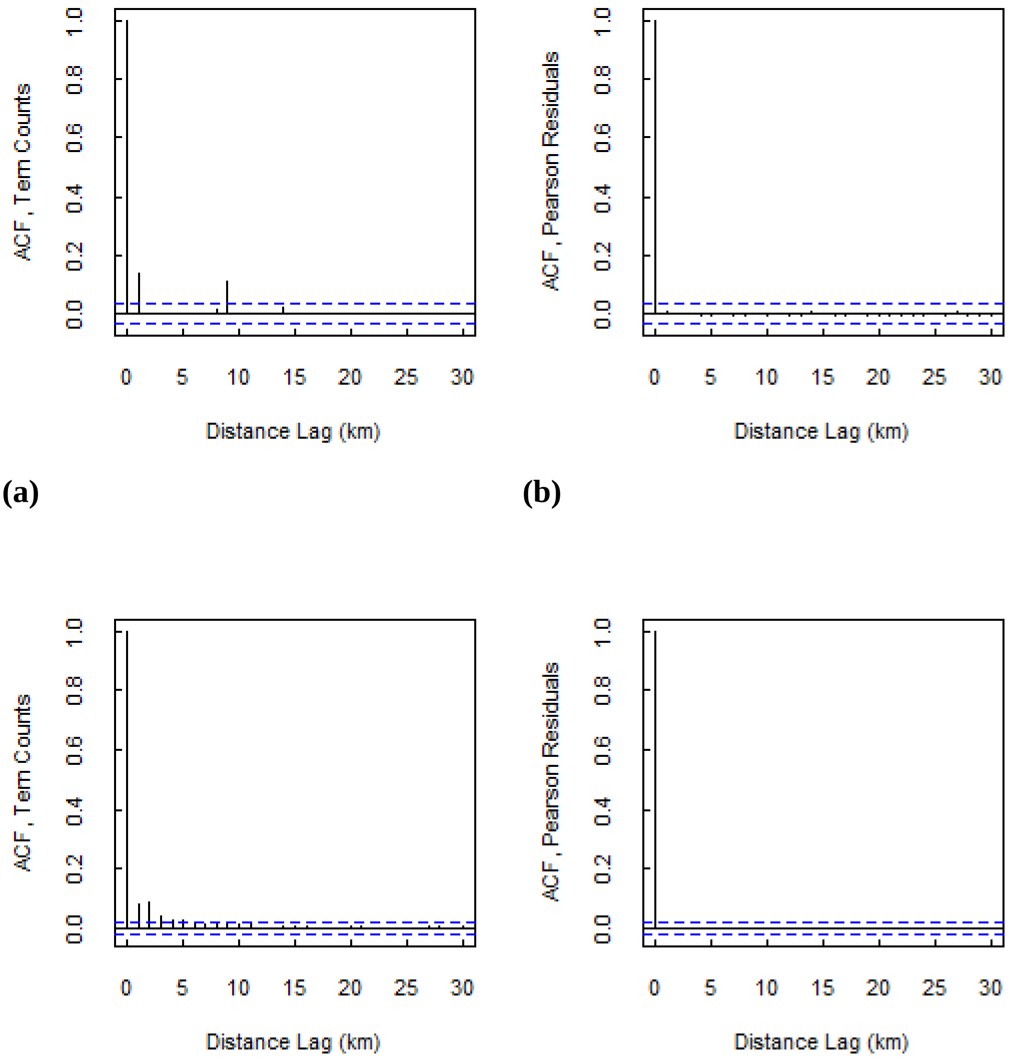


Figure 1.5. Spatial overlap between tern and tuna densities.

The cross-correlation function (CCF), with 95% confidence intervals (dotted line), shows significantly cross-correlated 0-1 km lag distances (2 km patch sizes) of "fall" log tern and tuna densities.

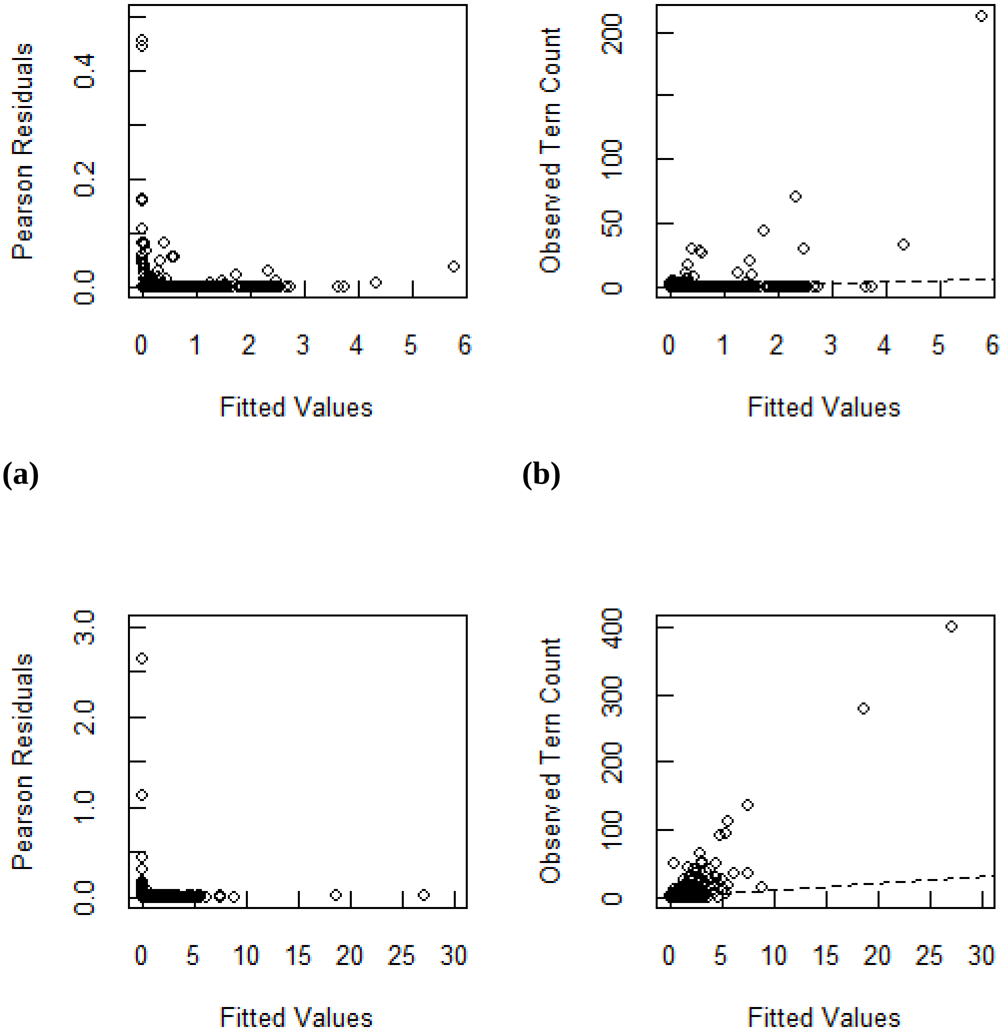


(a) **(b)**

(c) **(d)**

Figure 1.6. Spatial autocorrelation, as accommodated in the selected models.

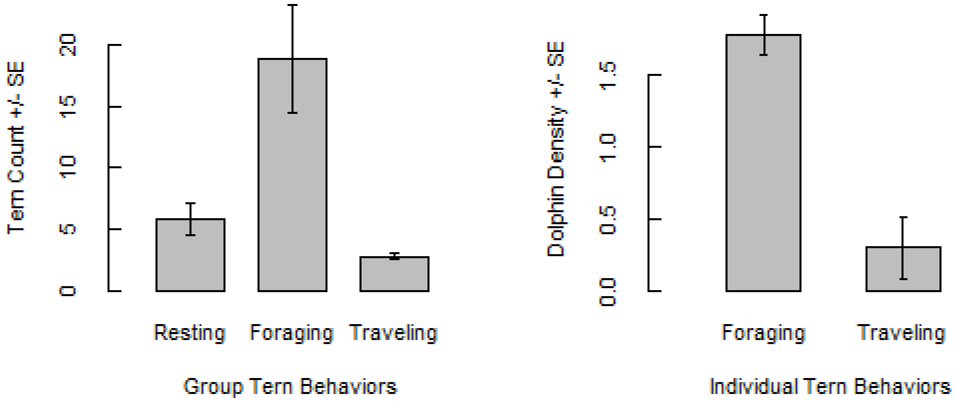
The autocorrelation function (ACF), with 95% confidence intervals (dotted line), shows significant autocorrelation at distance lags up to 2 km in “spring” tern counts (a) and 4 km in “fall” tern counts (c). The lack of autocorrelation in “spring” (b) and “fall” (d) Pearson residuals demonstrates that the model sufficiently accounted for autocorrelation in the response variable (no distance lags have a correlation value that is significantly greater than zero).



(a) **(b)**

(c) **(d)**

Figure 1.7. Relationship between values of the response variable, model fit, and residuals. Pearson residuals and observed tern counts are plotted against the models' fitted values for "spring" (a, b) and "fall" data, omitting the outlying fitted value of 6.84E+14 (c, d). Dotted line represents where observed and fitted tern counts would be equal, indicating model underestimation of the ecologically-important outliers (isolated large feeding aggregations).



(a) **(b)**

Figure 1.8. Behavioral associations among terns and dolphins.

High densities of foraging terns associated with high densities of dolphins: at the 1km (0.3 km^2) scale, flocks of foraging terns were significantly larger (i.e. more dense) than groups of resting or traveling terns (a), and foraging tern individuals associated with significantly higher densities of dolphins (b) than did travelling terns (no terns rested near dolphins). Bars indicate standard errors (SE). The expansive post-breeding range of common and roseate terns that we document challenges previous notions that they are constrained to roosting onshore (Gochfeld et al. 1998; Nisbet 2002), and this is supported by novel evidence of them resting on the water during migration (our at-sea observations and Nisbet et al. 2011).

Supplementary Material

Appendix 1.1. Details on methods of preliminary analyses, model structure and implementation.

We conducted preliminary analyses using the package MCMCglmm (Hadfield 2010), with an offset, random effect (date), and zero-inflated Poisson distribution—this aided in model selection, with respect to the treatment of explanatory variables. The lack of an autocorrelation term in this zero-inflated negative binomial generalized linear mixed model (ZINB GLMM) means that it gives a reasonable estimate of parameter effects, while unveiling non-significant variables through its inflation of type I errors (Hawkins et al. 2007). SST gradient over 1 km (frontal strength) emerged as insignificant; hence, we did not consider it in the final models. Additionally, to ensure that we were not abandoning a critical variable by discarding fluorescence from “fall” data, we conducted model selection across both seasons, combined: this dataset included fluorescence, and excluded observations that contained missing values (Table 1.2, models 3a and 3b). The ZINB CAR (intrinsic conditional autoregressive) GLMM fit poorly to the mere 6,208 observations, subset from 17,217, which amounted to less than half of the total N = 12,427 for the final spring and fall models.

In those final models, we rectified violation in the assumption of independence by incorporating spatiotemporal structure—to avoid type I errors—and accounting for collinearity—to reduce type II error rates (Zuur et al. 2010). For temporal structure, we chose date as a random effect, since it is nested within surveys, aiming to (1) allow spatially-overlapping survey “legs” to be treated as distinct, (2) accommodate overnight gaps in data transects, and (3) remove interdependence between neighboring points at short lags (Zuur et al. 2009). We used a car.normal spatial structure for the residual term, which requires three matrices: adjacency (neighbor identity), number (neighbor count), and unnormalized weights—calculated using the neighborhood distance of 4 km (Figure 1.6) in package “spdep” (Besag et al. 1991; Thomas et al. 2004; Saracco et al. 2010; Bivand et al. 2012; Saracco et al. 2012). We accounted for collinearity by ensuring quantities of two or less in the generalized variance inflation factors (GVIF) values of all covariates considered in initial models (Zuur et al. 2010).

We ran the final models in WinBUGS Version 1.4.3 (a Windows program for Bayesian inference Using Gibbs Sampling, Lunn et al. 2000), assessing significance of covariates after 100,000 iterations (those where the 95% confidence interval did not span zero), storing every 100th realization (the thinning rate) to reduce auto-correlation in the three chains, and setting burn-in at 10,000 samples.

Chapter 2. Colony: Foraging specificity and prey utilization: evaluating social and memory-based strategies in seabirds

Abstract

Seabirds modify their foraging tactics in response to the predictability of resources, indicating behavioral plasticity. Those species that depend on persistent food resources function largely on memory-based foraging strategies, while others use observational learning to locate prey opportunistically. Based upon extensive field observations, I hypothesized that roseate terns (*Sterna dougallii*), dietary specialists, rely more heavily on spatial memory to pursue specific prey at predictable feeding areas, whereas common terns (*S. hirundo*), prey generalists, depend more on observational learning by foraging in mixed-species flocks. I tested this prediction using direct species-comparisons of chick-provisioning rates and analyses of the patterns among bearings of commuting trajectories between the shared, mixed-species breeding colony, foraging sites, and feeding flocks. Common tern flight paths correlated positively with conspecific and heterospecific foraging aggregations, demonstrating local enhancement, a form of observational learning. Roseate terns bypassed those nearby feeding flocks and displayed fidelity to the southeast of the colony, thus dedicating more effort to memory-based foraging and less to social cues. With respect to nest provisioning, roseate terns were responsive to interannual fluctuations in the availability of preferred prey, outperforming common terns in years of abundance. To varying degrees, both species likely use memory of previously successful trips to search for food, until presented with the opportunity to exploit facilitative feeding assemblages to more rapidly encounter dense prey. This study elucidates the link between foraging strategy and resource

utilization, where cognitive flexibility has the potential to offset constraints in prey availability and specificity.

Introduction

Marine birds have the challenging task of targeting inconspicuous patches of prey beneath the dynamic, but “featureless” (Bonadonna et al. 2003), sea surface. Being able to predict prey availability using memory (Davoren et al. 2003; Weimerskirch et al. 2010), or alternatively, to exploit social cues that signal unpredictable, transitory food patches, may be adaptive to assure foraging success in the face of ecological uncertainties (Erwin 1977; Wittenberger & Hunt 1985; Waltz 1987; Gotmark 1990; Buckley 1997; Irons 1998; Weimerskirch 2007; Fauchald 2009). Spatial memory is a specialized cognitive process adaptive for navigation (Shettleworth 1998; Ricklefs 2004). Local enhancement (LE, Roberts 1941; Thorpe 1951) is a form of observational learning or social facilitation (Pallaud 1984; Goodenough et al. 2001), where individuals use foraging neighbors as cues to locate unpredictable prey (Poysa 1992; Davoren et al. 2003; Grunbaum & Veit 2003; Silverman et al. 2004; Elliott et al. 2009a; Weimerskirch et al. 2010). LE usually occurs at remote feeding assemblages, in contrast to colony-based information centers (IC) where individuals exchange information on promising foraging locations (Ward & Zahavi 1973; Waltz 1987). The cognitive capacity for exercising memory-based foraging tactics in combination with social learning has been described as observational spatial memory (OSM) in corvids (jays and ravens), which remember locations of cached food identified by other individuals (Bednekoff & Balda 1996a; Bednekoff & Balda 1996b; Balda & Kamil 2006; Scheid & Bugnyar 2008). It is possible that ecological, social, and physiological constraints, such as habitat and feeding specialization, act as selective forces in refining spatial memory (Yoerg 2001; Balda & Kamil 2006), and that environmental complexity and/or social facilitation lead to aptitude for observational learning (Seed et al. 2009).

Foraging strategies may range according to the degree of feeding specificity across species, where specialists that depend on a memory-based strategy choose to use spatial memory, and generalists that rely on a more social strategy opt for tactics such as observational learning or information exchange (Balda & Kamil 2006; Elliott et al. 2009a). Common (*Sterna hirundo*) and roseate terns (*S. dougallii*) are piscivorous seabirds that share breeding grounds and exposure to the same marine resources and colony-based social interactions, yet they differ in foraging habits (Gochfeld et al. 1998; Nisbet 2002). In the Northwest Atlantic, Roseate terns are specialists on sandlance (*Ammodytes* spp., Figure 2.6), an epipelagic fish that is slender enough for chicks to digest at considerable length (Kirkham 1986; Safina et al. 1990; Heinemann 1992; Rock et al. 2007). In contrast, common terns are opportunistic generalists that exploit unpredictable, heterogeneous, and ephemeral prey patches, which makes them prime candidates for LE (Erwin 1977) and information exchange (Waltz 1987). This study directly compares common and roseate terns to examine the link between foraging strategies and resource utilization, in the context of prey specificity and availability (Table 2.1). I evaluate three foraging tactics through analysis of flight patterns: 1) memory, 2) LE, and 3) the collective use of memory and information exchange, inferring the process of OSM through the pattern that I label "observational spatial persistence" (OSP): where the exchange of social information on the location of feeding areas reinforces foraging fidelity. These data serve to test the hypothesis that seabirds exhibit OSP to varying degrees, where feeding specialists (roseate terns) strongly depend on memory to pursue predictable prey, and opportunists (common terns) rely more heavily on LE to encounter diverse, ephemeral resource patches; see Figure 2.1 for study design (Davoren et al. 2003; Elliott et al. 2009a; Weimerskirch et al. 2010). I infer prey utilization from chick provisioning observations, where prey composition represents degree of feeding specialization, prey length presents an index of quality, and time between deliveries provides a measure of tern effort, given that energy delivery varies with prey composition (Barrett et al. 2007). Prey availability is calculated from sampled fisheries data that overlaps spatially and temporally with the study's extent (see methods and chapter 3). This information allows me to assess the prediction that specialized species dedicate more effort to selecting higher quality, persistent prey than their generalist counterparts, assuming that slower provisioning rates result from traveling farther to better habitat for larger fish (Dunn 1972). Terns are single-prey loaders, therefore this hypothesis is compatible with the main principle of central-place foraging theory (CPFT, Orians & Pearson 1979), that longer forage trips yield better returns: individuals accommodate the increased expense by selecting larger prey for their chicks. My expectation is that the foraging constraints placed on roseate terns (i.e. prey restrictions and reduced dependence on social cues) accompany a set of refined cognitive skills that allow them to profit from the pursuit of more suitable prey.

Methods

Study Site

Bird Island, Marion, Massachusetts (MA), USA (Figure 2.2a) supports one of just three large breeding colonies for common and roseate terns in North America: the 937 pairs of roseate terns in 2011 comprised 30% of the entire breeding population of the endangered subspecies (*S.*

d. dougallii, Mostello 2012). The islet is approximately 100 m in diameter and contains a centrally-located lighthouse with a viewing platform that offers a 360° panorama of Buzzards Bay through eight windows, each framing one 45° sector at 37 feet above sea level. The relatively small size and protected status of terns constrains the efficacy, precision, and spatial coverage of available tracking devices (Nisbet et al. 2011; Perrow et al. 2011); therefore this project's design implements an observational approach, which minimizes disturbance of the study subjects. Data collection involved the use of binoculars, with observations entered directly into a computer in the field, backed up with voice recordings.

Foraging Routes

As central-place foragers when provisioning chicks, breeding terns provide the opportunity to test for correlations among the direction of commuting trajectories between the colony and feeding grounds (Kirkham 1986). To log "population-level" foraging routes for June-July 2009-2011, I tallied the number of departures and returns of common and roseate tern adults from the Bird Island lighthouse, and counted the number of individuals in mixed-species feeding flocks, for five minutes in each of eight consecutive 45° sectors. Previous studies of common terns (Becker et al. 1993; Burness et al. 1994), Sandwich terns (Gotmark 1990) and other larids (Racine et al. 2012) have shown that paths are direct between the colony and foraging sites; since Bird Island is situated alone, terns are not likely to be diverted by shoreline. By limiting observations to within 100-500 m of the lighthouse, I quantified definitive departures and origins of return, by sector: the near-island boundary eliminated confusion from circuitous routes taken to avoid kleptoparasitism. Additionally, I excluded the few instances that courses traversed across the field of view instead of towards and away from the island. Two to three 40-minute scans of simultaneous departures and returns were scheduled at varying times throughout the day. Sets of 16 scans were randomized by starting sector and sequence (clockwise or counterclockwise). Occasional overnight visits allowed for the extension of sampling hours to dawn and dusk. With assistance in 2010-2011, I observed individual flight paths from blinds for one-hour stints, distinguishing nest adults with markings outfitted by outside projects (see next section for more details). We conducted these 1-h “individual-level” stints either alternately or in synchrony with the coinciding 40-min “population-level” scans. Nearby weather stations provided data online: at hourly intervals from BUZM3 at the mouth of Buzzards Bay (2009-2011), and every 5-10 min from the more representative KMAMARIO3 at the Marion inner harbor (2010-2011, unavailable in 2009).

The analysis of commuting trajectories is based on the following assumptions: 1. returns originate from the direction of successful foraging sites, given that most returning individuals carry prey destined for chicks (a pilot study confirmed that the low incidence of adults with apparently absent prey turned out to be carrying small, undetectable invertebrates); 2. departure directions denote choice of foraging tactic based on endogenous or exogenous cues (i.e., memory versus social information). First, a correlation among successive departure angles of marked individuals suggests that terns choose where to forage based on memory of where they have predictably found food. Second, OSP involves a significant, positive correlation among or between species in their directions of departure (individual or population) and population flights (departures or returns); “individual-level” OSP refers to marked individuals, otherwise it is “population-level”. I also test whether OSP occurs on the scale of minutes (“within scan”) or if it lasts hours: between scans that occur either on the same day (“within day”) or on consecutive days (“between day”). Last, LE is recognizable within a scan, when directions of population departures or returns correlate positively with the bearings of visible mixed-species feeding flocks. See Figures 2.1 and 2.3 for depictions of these tests.

The package “circular” (Agostinelli & Lund 2011) served to analyze all circular data in R (R Development Core Team 2012). I calculated circular Pearson’s product moment correlation coefficients for mean angles of individual, population, and wind directions by scan, and for successive individual departures. The Wallraff two-sample test determined whether population tracks were significantly different from each other in angular dispersion (angular distance to sample means), which is a circular version of the Kruskal-Wallis chi-squared test (nonparametric tests were appropriate since trajectories did not follow a circular normal, or Von Mises, distribution according to the Watson F-test). Construction of graphics involved the package “ggplot2” (Wickham 2009).

Nest Provisioning

Observations of prey deliveries to unfledged chicks presented information on dietary composition and feeding rate, across three breeding seasons, June-July 2009-2011. With the help of an assistant, I observed chick-provisioning in approximately 15 study nests per 1-h stint, from behind a blind, with binoculars, at least once per day per species, when conditions allowed. Nest plots chosen for viewing were highly visible, close to a permanent blind (within 10 m), and with discernible adults; fences pre-installed around common tern nests by the Massachusetts Division of Fisheries & Wildlife (MDFW), following Nisbet and Drury (1972), aided in identification of individuals and their nests. Additionally, common and roseate tern adults and young had markings (bands and/or dye) applied during studies conducted by others (Tims et al. 2004;

Spendelow et al. 2008). We removed obstructing vegetation prior to the stint, to assist in island management and prevent obscurity of chicks. Stint observations of individual study nests lasted until chicks fledged (less than a month later), at which point other nests, based on the stated criteria, served as replacements; this longitudinal design allowed for consistent sampling of chick age distribution. I recorded the category and length of any prey item delivered to a nest. Prey categories (species or family) were identifiable by attributes such as color, body shape, tail shape, and rigidity. Prey lengths were estimated to 0.25 adult bill lengths, measured to gape. Results are reported in relative bill lengths, which is more precise than converting to absolute bill lengths, since common and roseate tern culmens have the same range of 3.4-3.9 cm (Gochfeld et al. 1998; Nisbet 2002). For each year of data, I calculated prey composition, size (relative bill length), provisioning rate per nest (number of prey delivered per nest, per h) and per capita (per nest, per chick, per h), and time from an individual's departure to delivery for the subsample of completed forage trips that we observed within a 1-h stint in 2010-11. For an index of regional prey availability by year, I averaged the mid-May abundance of sandlance (*A. dubius*), herring (Atlantic herring, *Clupea harengus*, plus other clupeids) and anchovy (bay, *Anchoa mitchilli* or striped, *A. hepsetus*, plus rainbow smelt, *Osmerus mordax*, due to the slight possibility of confusion) into 30 "cells" of 225 km^2 each, sampled using the inshore bottom trawl data provided by the Massachusetts Division of Marine Fisheries (chapter 3).

Results

Foraging Routes

At the population-level, common terns dispersed in all directions around Bird Island, averaging southeast where roseate terns concentrated (Figure 2.4): the Wallraff rank sum test showed that dispersion from their mean was significantly higher for departures of common (mean ± standard deviation [SD] = 119.4° ± 2.1, N = 12,284) than roseate terns (138.0° ± 1.1, N = 3,606), $\chi^2 = 951.2$, *df* = 1, p < 0.001; and for returns of common (mean ± SD = 133.4° ± 2.1, N = 10,148) than roseate terns (144.8° ± 1.3, N = 3,467), $\chi^2 = 852.9$, *df* = 1, p < 0.001. At the individual-level (Figure 2.5), common terns departed to the northeast on average (24.1° ± 1.6, N = 204 departures of 61 individuals, similarly to Kirkham 1986, when they departed northerly), and roseate terns to the south (185.2° ± 1.5, N = 92 departures of 43 individuals). Measured winds prevailed from the SW and NE, averaging SE (Figure 2.2b). Within 40-min population scans, common terns flew against mean measured winds, for both departures (*r* = 0.26, p = 0.0025) and returns (*r* = -0.23, p = 0.0093); this is possible given the high variation among scans, in wind and/or flight directions. Note that the directions of wind bearings refer to their origin, as with return flight directions, whereas departure directions refer to their destination—this explains the positive relationship among departures into winds that originate from the same sector; conversely, a negative relationship between wind and returns indicates that they originate from different source sectors. There was no significant overall effect of winds on roseate tern routes.

Table 2.2 (diagramed in Figure 2.3) details results for the tests of correlation among flight directions and feeding flocks, between or within 1-h individual-level stints (2010-2011) and 40-min population-level scans (2009-2011), across all sampled years. First, as a test of memory-based foraging, successive departures greater than a day apart were significantly (positively) correlated for both common (*r* = 0.26, p = 0. 014) and roseate tern individuals (*r* = 0.52, p = 0.0042), yet successive departures that fell within only a day of each other were significantly correlated exclusively for roseate individuals (*r* = 0.89, p = 0.0077, Table 2.2), suggesting that roseate terns rely on both short- and long-term memory. Similarly, in the subsample of successive departures that occurred within a 1-h stint, all roseate terns headings (n = 13 for seven individuals) fell within 90° of each other except for a single case, in contrast to the 15% of obtuse headings by almost one third of common terns (n = 47 for 22 individuals); such divergence indicates that common terns are more exploratory. As a test of individual-level OSP, individual roseate departures correlated with coincident population-level common ($r = 0.31$, $p = 0.0022$) and roseate ($r = 0.41$, $p < 0.001$) departures. With respect to tests of population-level OSP, common and roseate departures ($r = 0.45$, $p < 0.001$) and returns ($r = 0.45$, $p < 0.001$) were significantly correlated within scans. Population-level common departures were positively correlated between scans within the same day ($r = 0.47$, $p = 0.0026$). Both population-level roseate departures ($r = 0.47$, $p = 0.010$) and returns ($r = 0.55$, $p = 0.0019$) were correlated within the day. From one day to the next, only returns were correlated for population-level common ($r = 0.39$, $p = 0.0060$) and roseate terns ($r = 0.31$, $p = 0.043$). Last, common terns associated with nearby feeding flocks, demonstrating LE, whereas roseate terns evaded those aggregations. The travel directions of common terns (population-level) and the mean bearing of mixed-species tern foraging assemblages were positive correlated, within-scans: they returned from the vicinity of feeding flocks that included both common ($r = 0.79$, $p = 0.0051$) and roseate terns ($r = 0.93$, $p = 0.017$); they also demonstrated an affinity for interspecific associations, departing in the direction of roseate flocks ($r = 0.84$, $p = 0.024$). In contrast, roseate tern departures correlated *negatively* with feeding aggregations of both common ($r = -0.55$, $p = 0.047$) and roseate terns ($r = -0.58$, $p = 0.044$), implying avoidance.

Nest Provisioning

Consistent with the values from previous studies in the Northwest Atlantic (Kirkham 1986; Safina et al. 1990; Heinemann 1992; Tims et al. 2004), sandlance was the dominant prey delivered both to roseate tern chicks in all years, comprising an average of 70% of prey deliveries, and to common tern chicks in 2009-2010 (up to 40%); the next most numerous prey were herring (primarily Atlantic herring) then anchovy, which incurred the most noticeable interannual variations (Table 2.3, Figure 2.7). All years combined, the proportions of sandlance, herring, and anchovy were significantly different for each tern species: $\chi^2 = 87.0$, $df = 2$, $p < 0.001$. “Other” prey consisted most commonly of Atlantic silverside (*Menidia menidia*), cunner (*Tautogolabrus adspersus*), hake (silver, *Merluccius bilinearis*, red, *Urophycis chuss*, or spotted, *U. regia*), and butterfish (*Peprilus triacanthus*). Common terns delivered invertebrates such as shrimp (sand, *Crangon* spp., or grass, *Palaemonetes* spp.). Unknowns were items either too small, delivered too quickly for identification, or obscured from view. The Shannon-Wiener/Weaver Diversity Index (base = 10) confirmed that common terns (2.9) have a more diverse diet than roseate terns (2.6).

There were significant effects on prey size (Figure 2.8) by tern species ($t_{973.3} = -5.9$, $p < 0.001$), year ($F_{2,\,1012} = 120.7$, $p < 0.001$), and prey category ($F_{2,\,1012} = 95.2$, $p < 0.001$). In the first two years, roseate terns delivered significantly longer sandlance than did common terns ($\mu = 1.9 > 1.8$ in 2009, $p < 0.05$); compared to 2009, significantly shorter sandlance were delivered in 2011 by both roseate ($\mu = 1.3$, $p < 0.001$) and common terns ($\mu = 1.4$, $p < 0.001$). 2011 was the only year during which sandlance showed underrepresentation in common tern deliveries (Table 2.3), and showed no significant size difference from the other main prey, nor between the two tern species (Figure 2.8). The relationship between sandlance length and energy content is nonlinear, such that longer sandlance have a disproportionally higher energy content characterized by increased lipid: protein ratios (Hislop et al. 1991; Robards et al. 1999). Hislop et al. (Table 1, 1991) reports that the caloric value (kJ/g^{-1} dry weight) of sandlance is higher than that of equally-long Atlantic herring: herring = 18.55 and sandlance = 21.87 calories at 6.5 cm length; herring = 19.50 and sandlance = 22.12 calories at 7.5 cm length. These values correspond to mean absolute lengths of prey deliveries by terns, calculated from the upper range of their bill lengths (Table 2.5). For example, in 2009, roseate terns with a 3.9 cm bill delivered approximately 7.4 cm sandlance, versus 5.9 cm herring; based on the energy values reported by Hislop et al., this would indicate that roseate terns made deliveries of sandlance with approximately 20% more energy value than those of herring. Similarly, the evidence that roseate terns delivered significantly longer fish to their chicks, than common terns, translates to those fish being significantly higher in quality (Figure 2.8). 2009 was a noticeably good year for sandlance quality, and according to the abundance data, it was also a good year for sandlance availability: the effect of year was linked to prey abundance ($F_{2, 234} = 4.5$, $p < 0.05$, Figure 2.9), where there were significantly more sampled sandlance in 2009 ($\mu = 220.5$) than in the two later years ($\mu = 46.5$ in 2010 and 15.4 in 2009, $p < 0.05$); please refer to Figure 2.10 for the distribution of sampled prey abundance. These trends in prey availability mirrored annual roseate tern productivity at Bird Island (number of chicks fledged per pair, Table 2.4), as reported by Mostello (2010, 2011, 2012).

Departure directions of all tern species were significantly different among the four dominant prey types delivered to chicks at the end of each forage trip ($F_{3, 89} = 4.0$, $p < 0.001$):

deliveries of sandlance and herring occurred after individuals traveled south (mean ± SD = 202.5 ± 2.2 and 185.3 ± 2.0, respectively), whereas anchovies were delivered after westerly departures (286.3 ± 2.2), and shrimp after northerly common tern departures (352.0 ± 0.6); these directions were significantly different between sandlance and shrimp for common terns ($\chi^2 = 6.8$, $df = 1$, $p < 0.01$). A circular-linear regression showed that significantly longer prey were delivered after departures to the south (mean = 160°; coefficient = 0.93, log-likelihood = 4.2, p = 0.0034).

Nest provisioning rates of common terns were significantly higher than those of roseate terns in 2009 ($t_{44.1} = 2.9$, $p < 0.01$) and 2011 ($t_{48.9} = 2.0$, $p < 0.05$). Per capita provisioning rates (by chick), were slightly higher in common than roseate terns, only for 2009 ($t_{44.2} = 2.5$, $p < 0.05$), yet see Figure 2.11 for all three years combined. There was no significant difference in interspecific provisioning rates for 2010. Average forage trip times (n = 77 trips by 33 common terns and 37 trips by 20 roseate terns) were greater for roseate (20 min) than common terns (17 min), though this difference was not significant ($t_{76.3} = -0.95$, $p = 0.35$). A simple linear regression of prey length against forage trip time showed a positive association in common terns (coefficient = 0.011, $R^2 = 0.1$, $p = 0.0043$). Roseate terns that foraged to the southerly quadrant (135°-225°) had significantly longer forage trip times than those that departed to the northeast quadrant (0-90°, averaging 20 min vs. 9 min, $t_{17.3} = 3.0$, $p = 0.008$), whereas common terns showed no significant difference.

Discussion

As expected, common and roseate terns demonstrated observational spatial persistence to varying degrees: roseate terns foraged primarily southeast of Bird Island for sandlance, relying more heavily on a spatial memory-based strategy than on social tactics, versus common terns, which committed more to observational learning (LE) than memory, on the short term. Additionally, memory-based tactics superseded information exchange in roseate terns: individuals' successive departures were significantly correlated, without influence from population-level returns (similarly to murres, *Uria* spp., in response to persistent resources, Davoren et al. 2003). The significant correlation between all tern individuals' successive departures greater than a day apart suggests that common terns likewise use memory, but on the longer-term, especially since they evidently ignore social information from population departures or returns. Nevertheless, both tern species demonstrated short-term population-level OSP by departing in the same direction during consecutive same-day (not day-to-day) population scans. In this case, it is not possible to isolate memory-based tactics, as with the individual-level successive departures, since terns may be following each other. With regard to population-level returns, roseate terns consistently traveled from the same sector scan-to-scan, suggesting that the location of successful foraging grounds was persistent: a basic condition for employing memory. Furthermore, neither common nor roseate departures correlated with returns from previous scans, therefore it appears more important to remember prior departures of the day than prior returns. A possible explanation is that the tendency for common terns to fly into the wind could lead to departure directions that are slightly offset from the returning sector: if terns travel in adjacent upwind sectors towards their final destinations (personal observations and Heinemann 1992), then previous departure bearings override returns as appropriate directions of reference for future departures. This study showed no consistent effect of wind direction on roseate terns, which could be due to its variability, negligible impact relative to the species' foraging site tenacity, or to a minor role of differential strength where heavier winds potentially have more impact than lighter winds. Development of safe, high-resolution, continuous tracking devices, appropriate for these small, protected terns, is necessary to record precise behaviors during foraging trips (Wikelski et al. 2007).

As predicted, common terns were more opportunistic than roseate terns, exploiting social foraging cues on the short-term. Departures of common terns (individual or population-level) never correlated significantly with any population-level returns, suggesting that they are not relying on an information center and are more exploratory than roseate terns. Their flight directions (Figures 2.4 and 2.5) plainly illustrate the tendency to frequent all sectors at significantly more dispersed, obtuse angles than roseate terns: as generalists, their food may be geographically ubiquitous but less persistent in availability. This could also explain why common terns departed in the direction of visible roseate tern flocks, appearing to exploit them through LE, which is a short-term, opportunistic tactic (especially given competitive advantage, Duffy 1986; Safina 1990a); murres similarly respond to unpredictable resources through their use of LE, without an IC (Davoren et al. 2003; Elliott et al. 2009a). Common and roseate terns may indeed use each other as guidance when sharing a mutual resource, given their population-level OSP displayed by significant positive correlations between interspecific departures or returns within scans. Yet, it is difficult to discern how roseate terns treat social information. The significant positive correlation between their individual departures and coincident population-level departures, conspecific and heterospecific, suggests that they follow other terns to feeding grounds, but alternatively this is a circumstance of their preference for the southeast. Exercising the capacity to choose between observational learning and spatial memory (e.g. via cognitive plasticity) would presumably liberate roseate terns from the constraints of foraging specialization. Yet, their apparent avoidance of feeding flocks (perhaps to evade competition at high densities, Duffy 1986; Safina 1990a) provides compelling evidence that roseate terns may elect to ignore social signals and instead frequent their favored grounds. This supports the hypothesis that memory is the leading mechanism behind roseate tern foraging fidelity to the southeast.

Prey utilization in roseate terns seems to echo their foraging strategy: overlapping with common terns yet distinctly more specific. As expected, they delivered proportionally over twice as many sandlance as common terns, which had a more diverse diet; they also offered significantly longer sandlance to chicks than did common terns, but did so less rapidly (i.e. from greater distances, as predicted by central-place foraging theory). Slower provisioning rates could be related to greater search times, but also lower chick demands, or less efficient foraging techniques. The latter option is the least plausible, since roseate terns have greater flight speeds than common terns, and have comparable situation-dependent capture rates (Gochfeld et al. 1998; Nisbet 2002). The former two explanations are more likely, given that roseate terns delivered fishes with overall higher energy content than common terns: this may incur a benefit to chicks that offsets costs of increased foraging effort, where the two are interrelated. The suggestion that individuals deliver larger prey to their chicks after longer foraging trips is consistent with central-place foraging theory (Orians & Pearson 1979; Shealer 1998; Burke & Montevecchi 2009; Elliott et al. 2009b). CPFT also explains why common terns retrieved longer prey when they spent more time traveling (farther). Yet, compared to roseate terns, common terns feed chicks at relatively short intervals, likely as a result of nearshore foraging preferences (within 3 km of land, Lack 1968; Erwin 1977; Perrow et al. 2011). Roseate terns seem to travel farther (Dunn 1972) to reliable foraging grounds in the south (possibly 20-30 km from Bird Island, Heinemann 1992), where they spend more time foraging, and to where departures of both tern species result in deliveries of longer sandlance and herring. It is possible that roseate terns travel faster to farther destinations, and even catch up to common terns, resulting in no significant difference between the time length of their foraging trips. Ultimately, roseate terns appear to allocate more effort towards the pursuit of higher quality prey, when they can predict the distribution of those prey. The increased probability of encountering longer sandlance at more distant but reliable feeding grounds may outweigh the costs of limitations inherent to foraging specialization. The ability to accomplish this through the use of memory would clearly be adaptive to the species, given their foraging specificity, whereas it may not be as important to common terns, which have more flexibility to seek out quality over a greater range. With respect to common terns, the social benefits of local enhancement should outweigh the costs of their reduced feeding proficiency: they may not deliver as high quality fish to their chicks, but are more resilient to variability in prey abundance.

Interannual fluctuations in prey specificity resembled those of availability (Safina et al. 1990), and productivity (Table 2.4, courtesy of Mostello 2012). 2011 was a poor sandlance year with respect to dietary composition, prey size, and availability. Roseate terns did not compensate for reduced prey quality with faster per capita provisioning rates, and consequently experienced their lowest productivity of the three years, even lower than common terns. Thus, their specialization on sandlance acts in their favor during years of bounty, when they outperform common terns, but to their detriment otherwise; it is a likely contributor to their population instability. The abundance of sandlance and Atlantic herring populations in the NW Atlantic historically shows inverse trends; sandlance has decreased since the late 1980s, while herring has rebounded since the 1990s (Overholtz et al. 2000). Decreases in prey abundance have negatively impacted the breeding success of common and roseate terns in the past (Safina et al. 1988), and led to population declines (Szostek & Becker 2012). Reductions in the length and mass of older Atlantic herring (Overholtz et al. 2004) have also prompted common tern dietary shifts from herring to sandlance (Diamond & Devlin 2003). At Bird Island two decades ago, roseate terns fished for sandlance that were generally shorter than herring from the northeast of Bird Island. Since then, it seems that herring quality has deteriorated and the distribution of sandlance has shifted southeast, where a larger area of marine habitat provides more feeding opportunities (Figure 2.2, personal observations and Heinemann 1992). High sensitivity to sandlance is likely a limiting factor contributing to the population decline of roseate terns in the U.S., since their listing as endangered in 1987 (Nisbet & Spendelow 1999), especially given that common terns have largely recovered from the 20th century tern population demise (Mostello 2012).

This study elucidates the relationship between resource specialization and cognitive advancement in roseate terns (Balda et al. 1996; Balda & Kamil 2006), highlighting that spatial memory and/or observational learning (LE) are more valuable to both tern species than strictly information exchange, consistent with mounting evidence (Wittenberger & Hunt 1985; Gotmark 1990; Buckley 1997; Irons 1998; Davoren et al. 2003). For example, Sandwich terns (*Thalasseus sandvicensis*) demonstrate LE (Gochfeld & Burger 1982) as a more advantageous and ubiquitous form of social exchange than an information center (Gotmark 1990). Similarly, gulls appear to ignore the social information available at their nests (Racine et al. 2012). Reliance on memory has factored into explanations for common terns' ability to return to breeding sites following long-distance migration from South America (Becker et al. 2008), and to assess food availability based on previous experience (Safina & Burger 1988) or environmental cycles (i.e. tides, Becker et al. 1993). Evidently, roseate terns show more foraging site-fidelity than common terns: they seem to revisit the southeast by means of spatial memory. As dietary and habitat specialists, they likely endure selective pressures in response to changes in resources or the environment, which drive proficiency in the recognition of predictability. Annual experiences in learning where to find persistent sources of sandlance in the NW Atlantic may have further reinforced their aptitude for spatial memory (Irons 1998; Davoren et al. 2003; Weimerskirch 2007; Elliott et al. 2009a; Grémillet & Boulinier 2009; Weimerskirch et al. 2010). Evidence of OSP, comparable to observational spatial memory in the highly "intelligent" corvid family (Bednekoff & Balda 1996a; Bednekoff & Balda 1996b), supports the hypothesis that both common and roseate terns are relying on a combination of advanced cognitive mechanisms to forage for food. Other generalist and opportunistic seabird species, murres and Northern gannets (*Sula bassana*) demonstrate flexibility in memory and LE, suggesting that both processes serve to handle environmental change (Davoren et al. 2003; Elliott et al. 2009a; Montevecchi et al. 2009). At coarse spatial and temporal scales, terns likely use spatial memory (Becker et al. 1993) to return to known "hot spots", then optionally switch to LE to search for prey patches more opportunistically (Erwin 1977), at a finer resolution (Davoren et al. 2003). Yet, the tendency for roseate terns to evade heterospecific feeding flocks calls into question their adaptability to unpredictable (rapid or extreme) changes in sandlance distribution. Ideally, cognitive plasticity would enable them to learn new prey locations (e.g. from other terns) and update their memories, allowing them to compensate for their reduced phenotypic plasticity (feeding specialization). To address this, future research should assess how common and roseate terns alter their foraging strategies in the absence of sandlance, for example at their wintering grounds in South America. This study establishes the link between resource utilization and foraging strategy, and emphasizes the need for incorporating cognitive flexibility into understanding the behavioral and ecological response of a study species to its natural environment; such information is applicable to population research and management alike, and may provide remarkable insight into nonhuman aptitude (Regular et al. 2013).

Tables

Table 2.1. Predicting foraging strategy and tactics from prey utilization, in the context of prey specificity and availability.

If roseate terns pursue specific prey items that highly dominate their diet and are highly predictable in their availability, then it would be adaptive to use a highly memory-based strategy to revisit feeding hotspots, with spatial memory as the tactic of choice. Because roseate terns (gray shading) have a diet that is low in diversity, and low in transience (high in persistence), then they are less likely to use a social or facilitative strategy. Common terns rely on prey that are low in dominance and low in predictability, therefore, they are less likely to use spatial memory. Instead, they select a highly diverse set of patchy, highly transient prey, and thereby benefit from the use of a highly social strategy for opportunistic foraging on facilitative cues (e.g. local enhancement). In other words, if terns can't remember where the food is, then they may turn to others for clues.

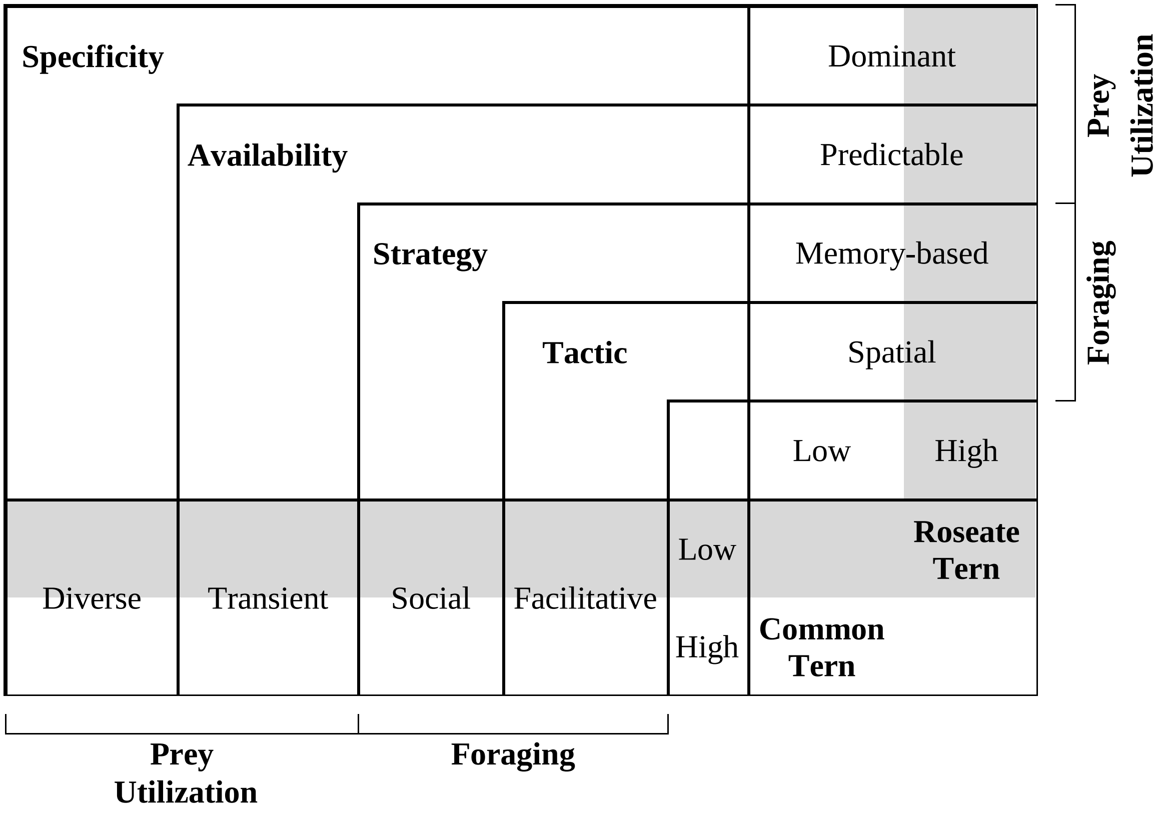


Table 2.2. Circular correlation tests of foraging strategy hypotheses, using mean angles of flight directions, and bearings of tern flocks. Significant Pearson's product moment correlation coefficients (*r*, in bold: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) among departures, returns, and/or feeding flocks, with sample sizes (n), indicate common (CT) and roseate tern (RT) use of memory, local enhancement (LE), or observational spatial persistence (OSP), during 40-min population scans and 1-h individual stints, at increasing scales: "within scan" observations are separated by minutes, "within day" by hours, and "between day" by one night (noted with a gap). See Figure 2.3 for a visual depiction of these flight patterns.

					Individual Stints		Population Scans											
					Within Day		Within Scan				Within Day				Between Day			
					Departures		Departures		Returns		Departures		Returns		Departures		Returns	
					CT	RT	CT	RT	CT	RT	CT	RT	CT	RT	CT	RT	CT	RT
OSP	Individual Stints 2010-2011	Departures	CT	***r***	0.11		-0.12	0.039	-0.067	0.063								
				n	47		204	204	204	204								
			RT	***r***		**0.89****	**0.31****	**0.41*****	-0.13	-0.15								
				n		13	92	92	92	92								
	Population Scans 2009-2011	Departures	CT	***r***				**0.45*****	0.10		**0.47****				0.19			
				n				127	127		43				51			
			RT	***r***						**0.29****		**0.47***				0.20		
				n						127		43				51		
		Returns	CT	***r***						**0.45*****	0.12		0.31		0.079		**0.39****	
				n						127	43		43		51		51	
			RT	***r***								0.28		**0.55****		0.23		**0.31***
				n								43		43		51		51
LE		Flocks	CT	***r***			-0.086	**-0.55***	**0.79****	0.069								
				n			13	13	13	13								
			RT	***r***			**0.84***	**-0.58***	**0.93***	0.20								
				n			8	8	8	8								
					Memory													

Table 2.3. Prey composition (proportion) of nest provisioning at Bird Island, 2009-2011. Proportions indicate the relative number of prey delivered to chicks by common (CT) and roseate terns (RT), from June-July, by year (N). See Figure 2.7 for corresponding pie charts.

	2009		2010		2011	
	CT	RT	CT	RT	CT	RT
sandlance	0.41	0.87	0.31	0.64	0.17	0.57
herring	0.16	0.08	0.27	0.28	0.20	0.18
anchovy	0.05	0.02	0.01	0.00	0.20	0.13
shrimp	0.10	0.00	0.04	0.00	0.09	0.00
other	0.12	0.01	0.10	0.00	0.04	0.00
unknown	0.16	0.02	0.27	0.08	0.30	0.12
N =	385	245	169	88	359	169

Table 2.4. Productivity (number of chicks fledged per pair) at Bird Island, 2009-2011. These values provide interannual comparisons of breeding success, courtesy of the Massachusetts Division of Fisheries & Wildlife (Mostello 2010, 2011, 2012).

	2009	2010	2011
CT	1.14	0.65	1.43
RT	1.44	1.33	1.23

Table 2.5. Absolute prey length values calculated from length relative to bill range (cm).

Absolute prey length values (bold) are calculated by multiplying bill length range (cm, left column, Gochfeld et al. 1998; Nisbet 2002) by relative prey length (estimates from observations, top row). The lower and upper observed ranges are given in 0.25 increments, the mean prey lengths in 0.1 increments. The bottom three rows indicate which columns correspond to mean relative prey lengths for sandlance ('Sl') and herring ('Hg') in 2009 or across all 3 years (yr) for common terns (CT) and/or roseate terns (RT, shaded gray). Sandlance and herring delivered by roseate terns in 2009 are highlighted in bold, for comparison to energy values reported by Hislop et al. (1991).

	Relative prey length														
	Lower range				Mean							Upper range			
Bill length (cm)	0.50	0.75	1.00	1.25	1.30	1.40	1.50	1.60	1.70	1.80	1.90	2.00	2.25	2.50	2.75
3.4	**1.7**	**2.6**	**3.4**	**4.3**	**4.4**	**4.8**	**5.1**	**5.4**	**5.8**	**6.1**	**6.5**	**6.8**	**7.7**	**8.5**	**9.4**
3.5	**1.8**	**2.6**	**3.5**	**4.4**	**4.6**	**4.9**	**5.3**	**5.6**	**6.0**	**6.3**	**6.7**	**7.0**	**7.9**	**8.8**	**9.6**
3.6	**1.8**	**2.6**	**3.5**	**4.4**	**4.7**	**5.0**	**5.4**	**5.8**	**6.1**	**6.5**	**6.8**	**7.2**	**8.1**	**9.0**	**9.9**
3.7	**1.8**	**2.6**	**3.5**	**4.4**	**4.8**	**5.2**	**5.6**	**5.9**	**6.3**	**6.7**	**7.0**	**7.4**	**8.3**	**9.3**	**10.2**
3.8	**1.8**	**2.6**	**3.5**	**4.4**	**4.9**	**5.3**	**5.7**	**6.1**	**6.5**	**6.8**	**7.2**	**7.6**	**8.6**	**9.5**	**10.5**
3.9	**1.8**	**2.6**	**3.5**	**4.4**	**5.1**	**5.5**	**5.9**	**6.2**	**6.6**	**7.0**	**7.4**	**7.8**	**8.8**	**9.8**	**10.7**
	Absolute prey length (cm)														
Year					3 yr	2009	**2009**	3 yr	3 yr	2009	**2009**				
Tern					CRT	CT	**RT**	CT	RT	CT	**RT**				
Prey					Hg	Hg	**Hg**	Sl	Sl	Sl	**Sl**				

Figures

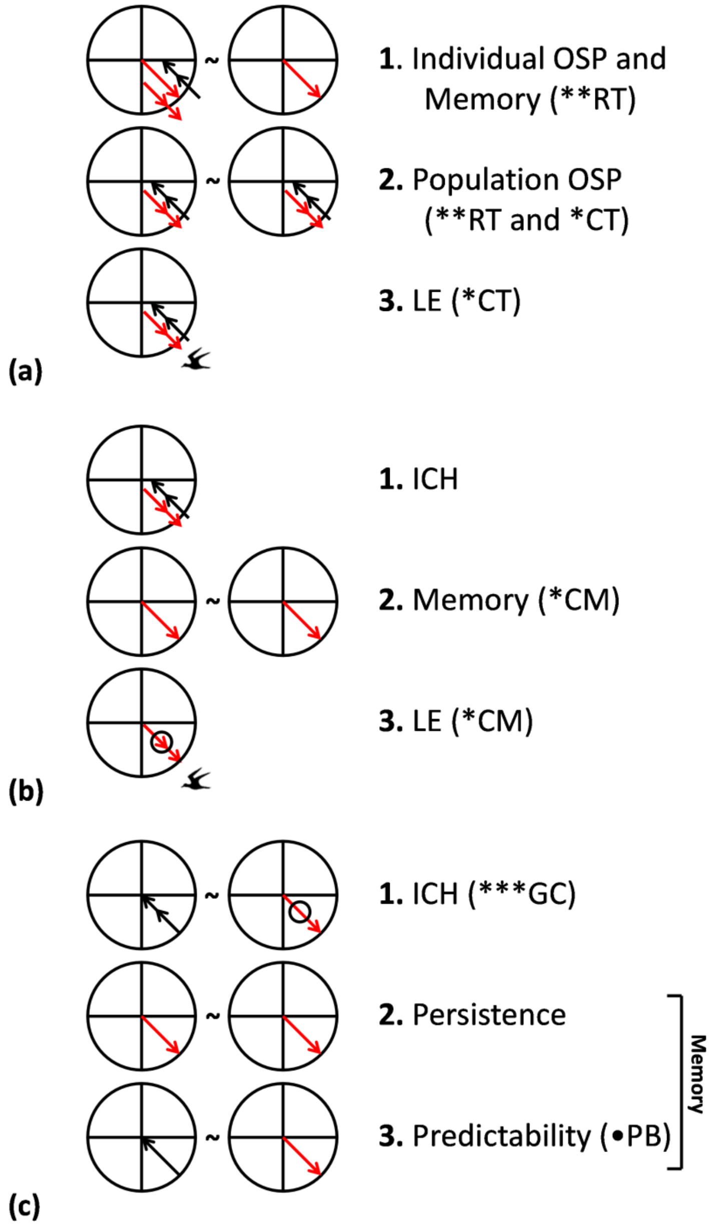


Figure 2.1. Comparative study design to test foraging strategy hypotheses from correlations among flight directions and bearings of species aggregations.

Positively-correlated angles of individual and population-level departures and returns, and bearings of species aggregations, are consistent with study hypotheses of foraging strategy, in (a) three seasons at Bird Island, (b) Davoren et al. (2003) and (c) Weimerskirch et al. (2010). Axes denote cardinal directions on a compass (large black circles), with colony location at the center. Black arrows: returns; red arrows: departures; single arrows: mean directions of marked individuals; multiple arrows: mean directions of the sampled population; bird in flight: mixed-species feeding assemblages; small black circle: the location at the perimeter of the colony where pursuit-diving seabirds land on the water prior to departure. Rows define the tested hypotheses, and columns represent sampling periods: either 1-h stints observing marked individuals, or 40-min scans of the population. Correlation tests were conducted on commuting trajectories within sampling periods (left column of a, and b.1) and across consecutive sampling periods ('~' indicates within and/or among days, from left to right). Significant correlations (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, • $p = 0.05$) are shown for study species: RT = roseate tern (*Sterna dougallii*), CT = common tern (*S. hirundo*), CM = common murre (*Uria aalge*), GC = Guanay cormorant (*Phalacrocorax bougainvillii*), PB = Peruvian booby (*Sula variegata*). At Bird Island, significant positive correlations between: (a.1) individual departures and population departures or returns show reliance on individual-level observational spatial persistence (OSP, a combination of social and memory-based tactics); successive departures of marked individuals demonstrate heavier dependence on spatial memory than information exchange, as was found in roseate terns; (a.2) population departures and returns within scans, between scans within a day, or between scans on consecutive days, provide evidence for population-level OSP, as with both roseate and common terns; (a.3) bearings of feeding flocks and mean directions of population departures or returns within a scan illustrate local enhancement (LE) as shown in common terns; see Figure 2.3 for more detail. According to Davoren et al. (2003): (b.1) a negative correlation between the mean direction of returns and departures, within a scan, contradicts the information center hypothesis (ICH) in murres; (b.2) a positive correlation between successive departures of marked individuals demonstrates memory-based tactics; and (b.3) murres use local enhancement from the vantage point of a "splashdown area", where they land prior to joining mixed-species feeding assemblages. According to Weimerskirch et al. (2010), positive correlations between: (c.1) population returns and bearings of a “compass raft”, from which Guanay cormorants depart for social foraging trips, support an IC; (c.2) successive individual departures display persistence, a memory-based tactic; and (c.3) individual returns with immediate departures provide evidence that Peruvian Boobies use memory-based tactics to search for predictable (not persistent) resources.

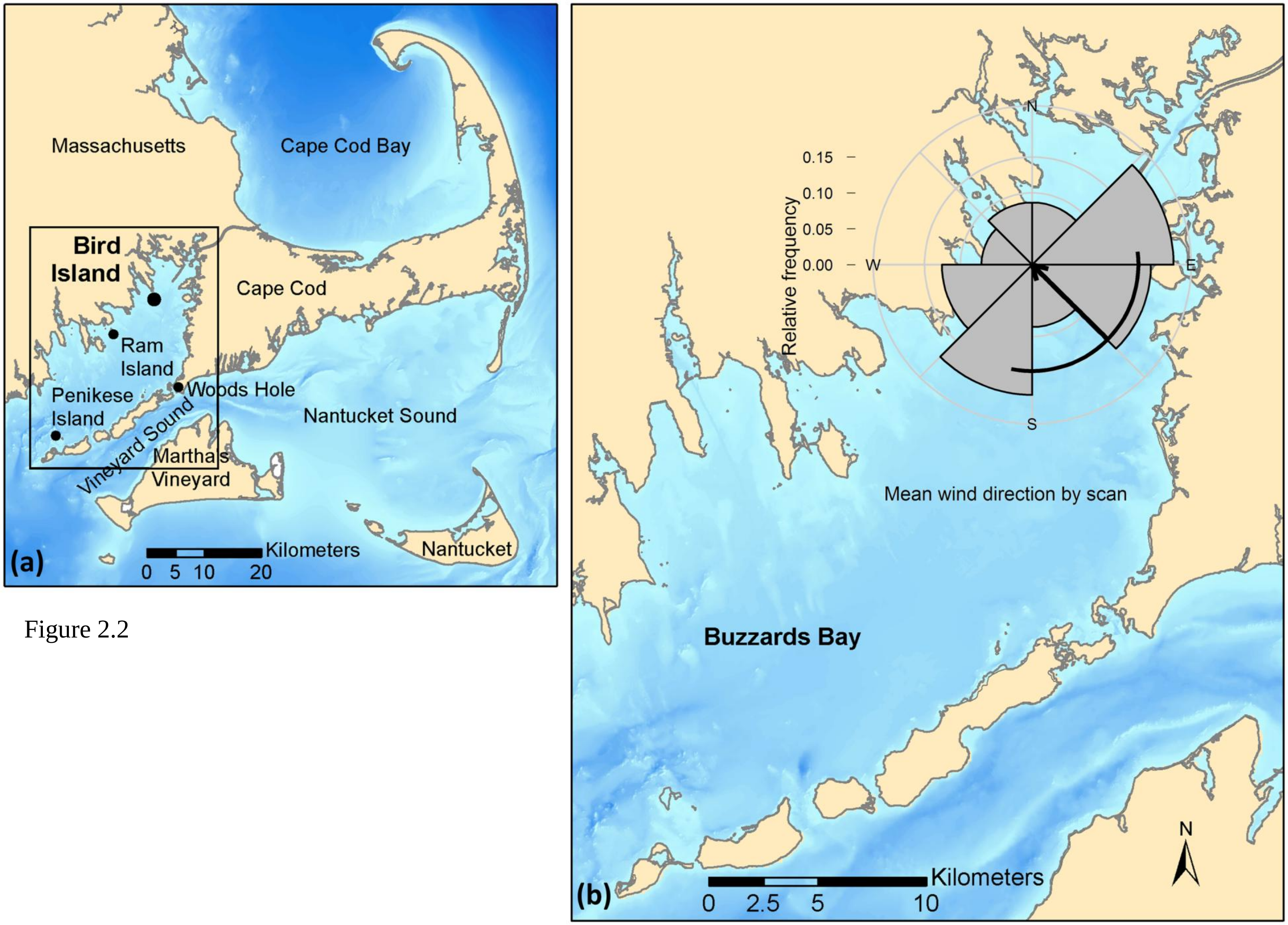

Massachusetts
Cape Cod Bay
Bird Island
Cape Cod
Ram Island
Penikese Island
Woods Hole
Nantucket Sound
Vineyard Sound
Martha's Vineyard
Nantucket
(a)
Kilometers
0 5 10 20
0.15
0.10
0.05
0.00
Relative frequency
N
W
E
S
Mean wind direction by scan
Buzzards Bay
(b)
Kilometers
0 2.5 5 10
N

Figure 2.2

Figure 2.2. Wind directions at the study site.

(a) One of the largest shared breeding grounds of both common and roseate terns in North America: Buzzards Bay, Massachusetts, USA—which includes Bird, Ram, and Penikese Islands. (b) Buzzards Bay magnified: rose diagram (circular frequency histogram) of mean wind direction for all population-level scans, at Bird Island. The black arrow represents the mean, and the black arc represents the 95% confidence interval. Data were sourced from the mouth of Buzzards Bay via NOAA weather station BUZM3 (2009), and from Marion inner harbor via KMAMARIO3 (2010-2011). These maps were produced using ArcGIS (ESRI 2012), with land feature and bathymetry data layers from the online Office of Geographic Information (MassGIS).

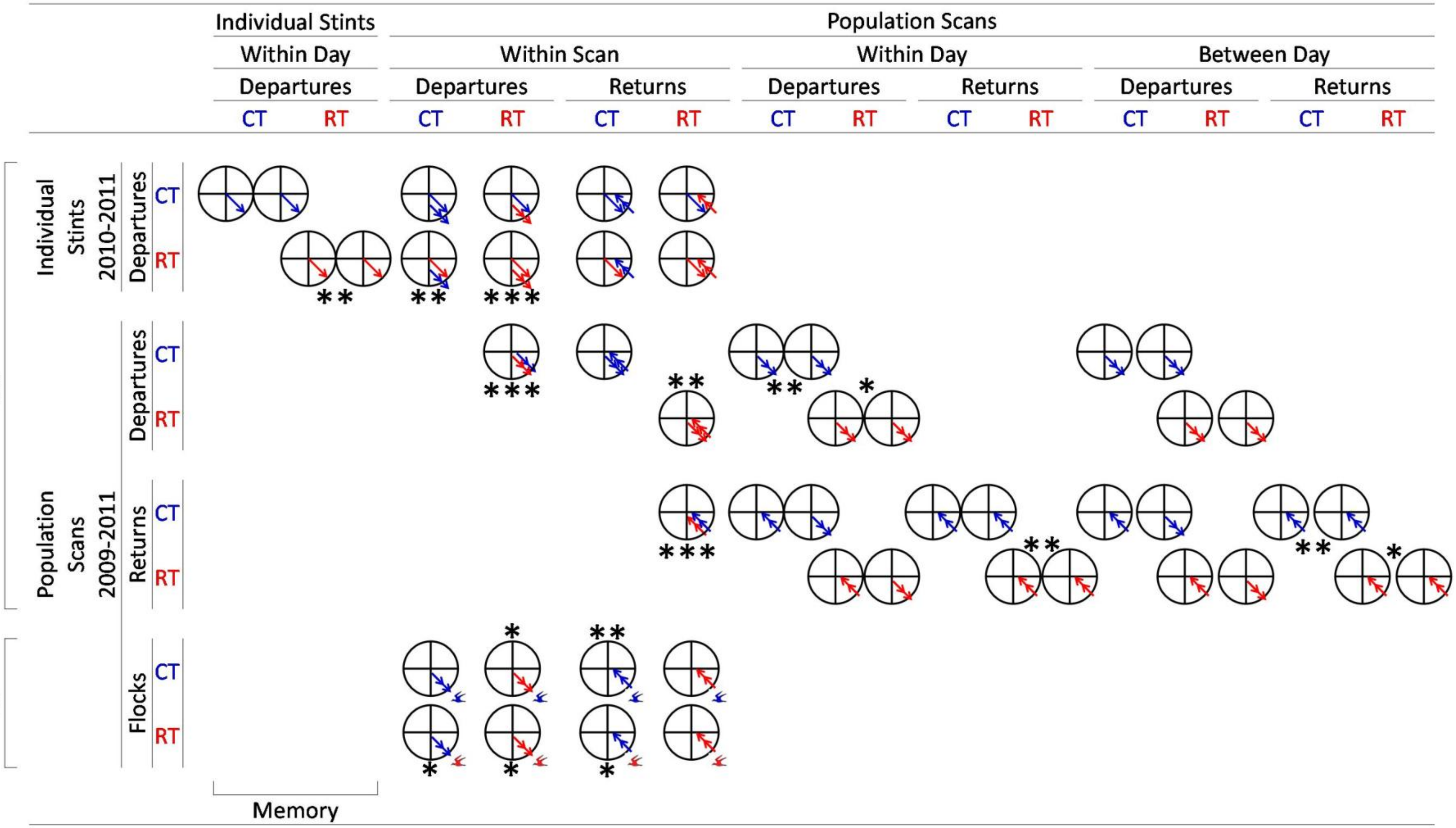
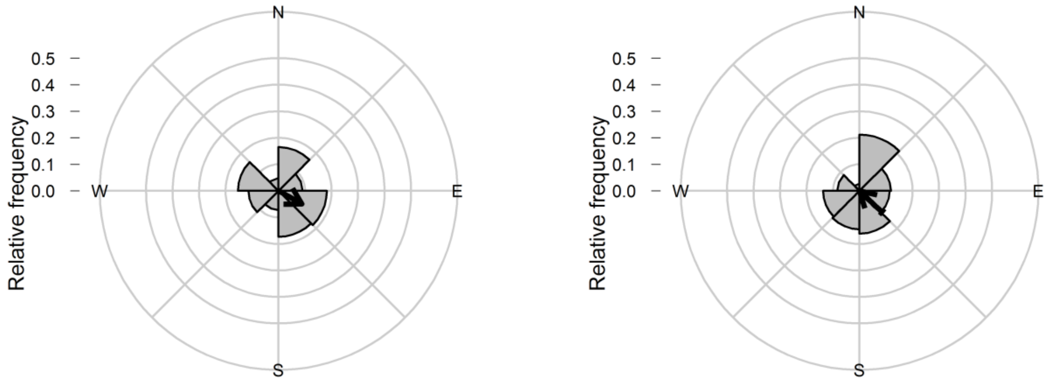


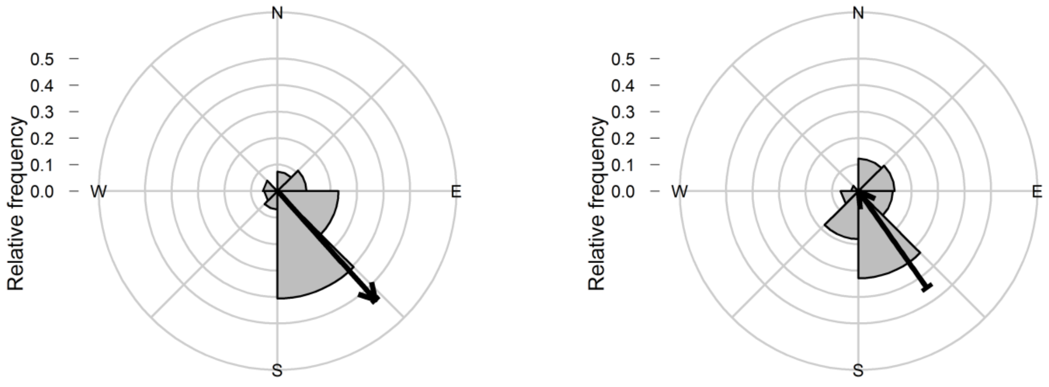
Figure 2.3. Depiction of Table 2.2 to visualize correlations in flight patterns, for tests of foraging strategy hypotheses.

Significant circular correlation coefficients (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) among theoretical angles of departure or return (single arrows – marked individuals, double arrows – population), and feeding flocks (tern in flight) indicate common (CT, blue) and roseate tern (RT, red) use of memory, local enhancement (LE), or observational spatial persistence (OSP), during 40-min population scans and 1-h individual stints: “within scan” observations are separated by minutes, “within day” by hours, and “between day” by one night. Axes denote cardinal directions on a compass, with Bird Island at the center. See Figure 2.1 for more details.



CT population departures
(a)

CT population returns
(b)



RT population departures
(c)

RT population returns
(d)

Figure 2.4. Directions and relative frequencies of population-level routes to and from Bird Island during the 2009-2011 breeding seasons, observed from the lighthouse.

The black arrow represents the mean direction, with a narrow 95% confidence interval arc, calculated by simple bootstrap using the concentration parameter kappa for a von Mises distribution, for: (a) common tern (CT) departures (N = 12,284), (b) common tern returns (N = 10,148), (c) roseate tern (RT) departures (3,606), and (d) roseate tern returns (3467).

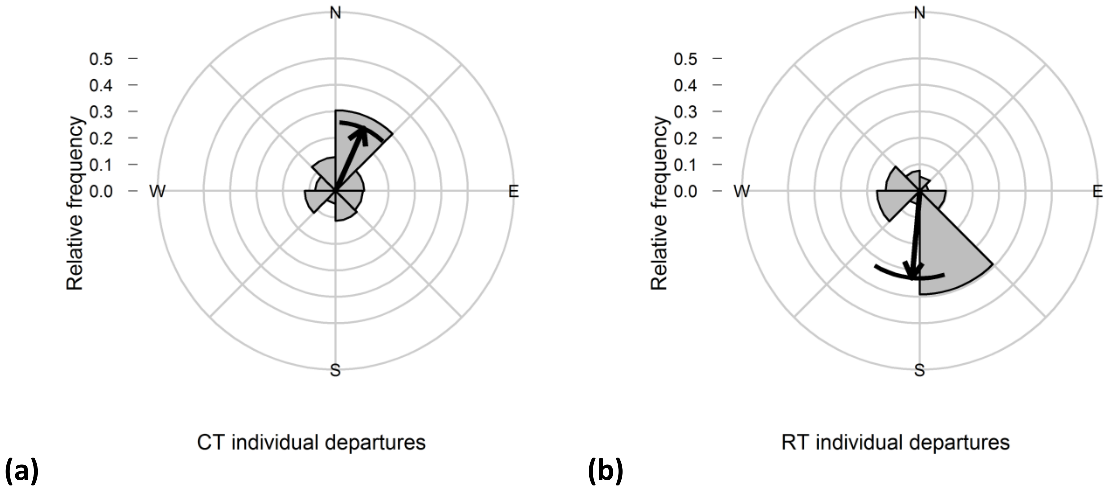


Figure 2.5. Relative frequencies of individual-level departures from Bird Island during the 2010-2011 breeding seasons, observed from blinds.

The black arrow represents the mean direction, with a 95% confidence interval arc, for: (a) common terns (CT, N = 204 departures of 61 individuals) and (b) roseate terns (RT, N = 92 departures of 43 individuals).

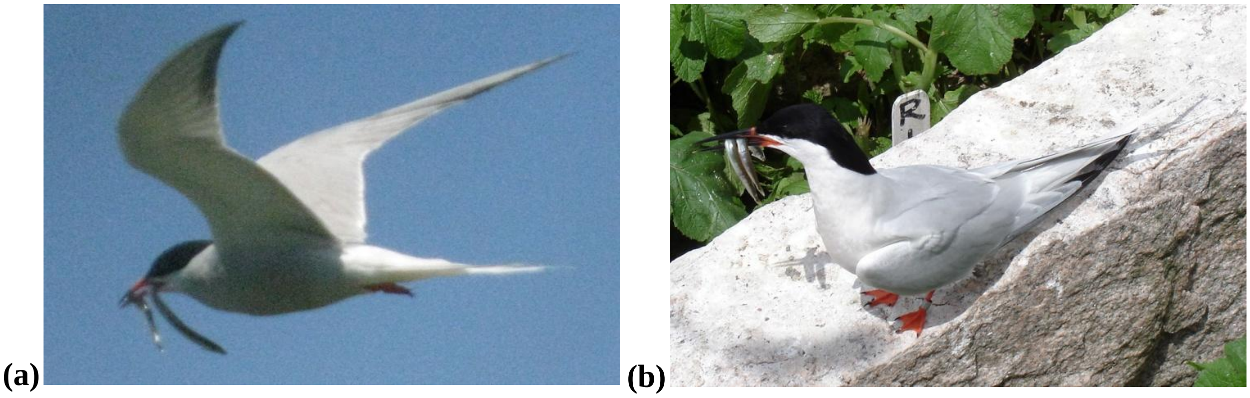


Figure 2.6. Images of a common and roseate tern carrying sandlance.

A common tern with sandlance (a), photo by Bryce Geyer, and roseate tern with two sandlance (b), a rare photo-documented event since terns are generally single-prey loaders (credit: Holly Goyert).

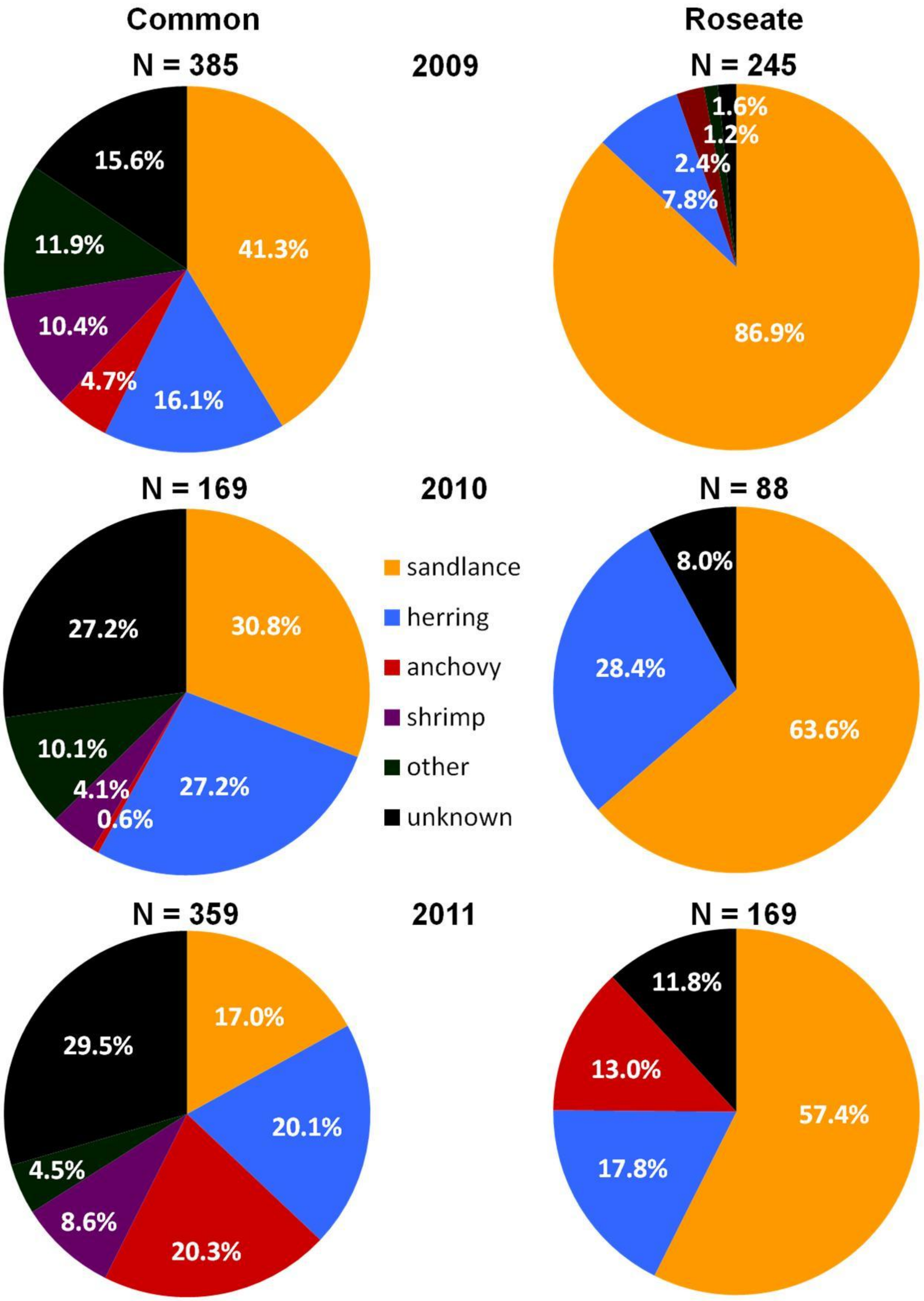


Figure 2.7. Prey composition (percentile) of nest provisioning at Bird Island, 2009-2011. Percentages indicate the relative number of prey delivered to chicks by common (left) and roseate terns (right), from June-July, by year (N). See Table 2.3 for proportions.

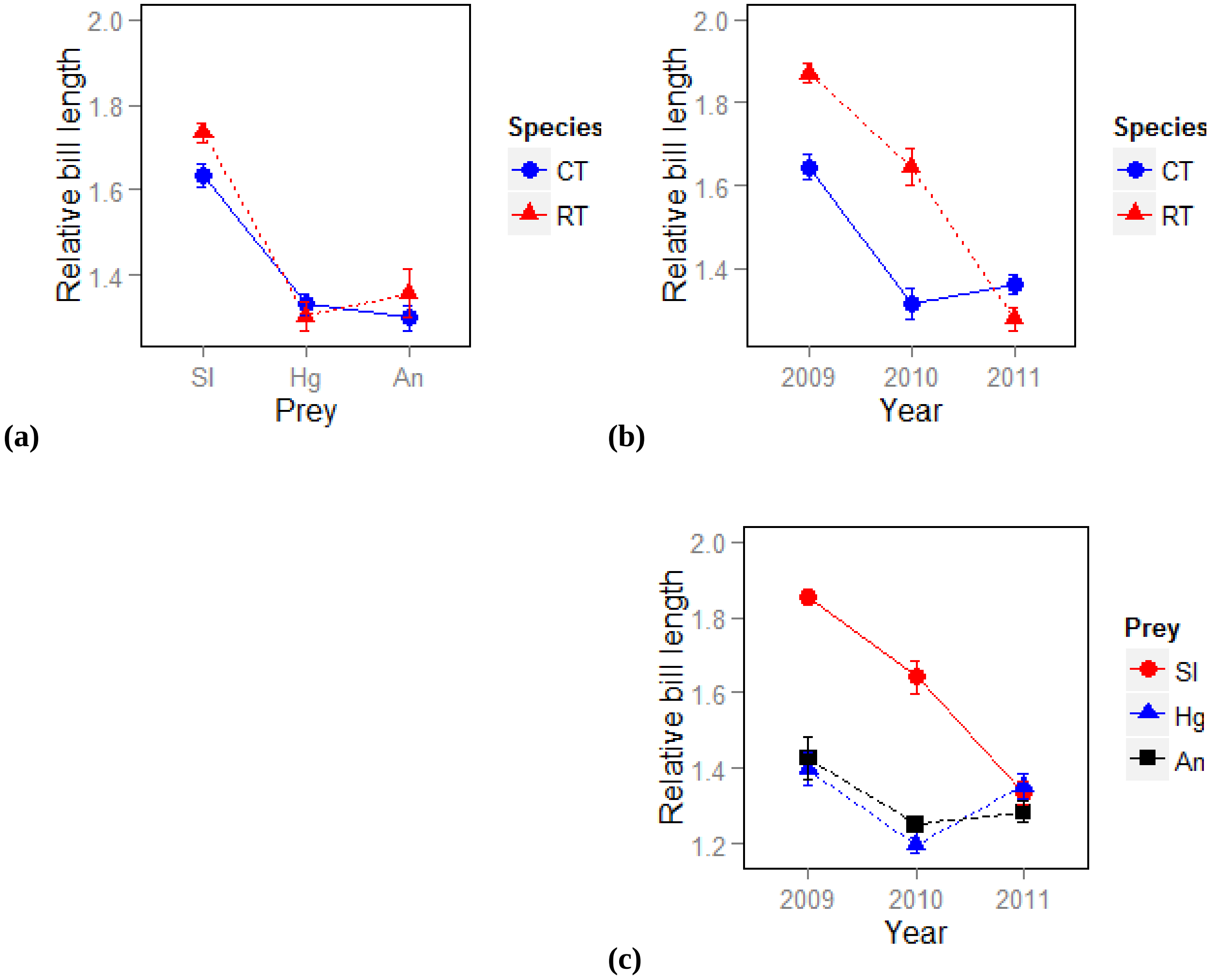


Figure 2.8. Size of the three dominant fish delivered to chicks, by tern species, year, and prey category.

Roseate terns (RT) delivered longer sandlance (‘Sl’), especially in 2009-2010. For the three years combined, (a) roseate terns delivered sandlance ($\mu = 1.7$) that were significantly longer than those delivered by common terns (CT, $\mu = 1.6$, $p < 0.05$), and significantly longer than herring (‘Hg’) or anchovy (‘An’) delivered by either tern species ($p < 0.001$). More specifically, there was a significant interaction of year with (b) tern species ($F_{2, 1012} = 31.9$, $p < 0.001$) and with (c) prey category ($F_{4, 1012} = 11.2$, $p < 0.001$). In the first two years, roseate terns delivered significantly longer sandlance than did common terns ($p < 0.05$); compared to 2009, significantly shorter sandlance were delivered in 2011 by both roseate and common terns ($p < 0.001$). Points and bars indicate mean ± standard error.

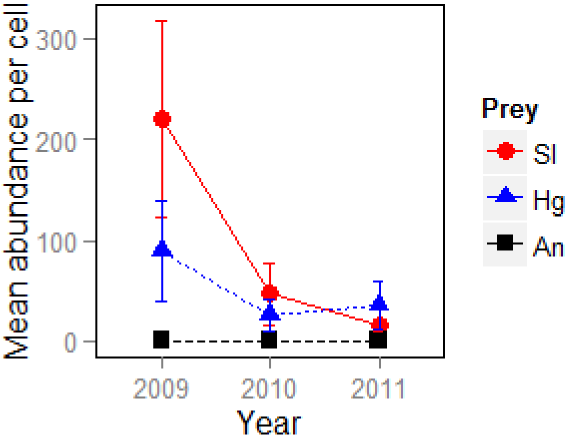


Figure 2.9. Sampled spring abundance of the three dominant prey categories by year.

Sandlance ('Sl') was significantly more abundant in 2009 than in 2010-2011 ($p < 0.05$). There was a significant effect on abundance (average number at length per 15 km x 15 km cell) by prey category ($F_{2, 234} = 4.1$, $p < 0.05$) and year ($F_{2, 234} = 4.5$, $p < 0.05$). Anchovy ('An') abundance was negligible, as they are more common in the fall. Points and bars indicate mean ± standard error, herring = 'Hg'.

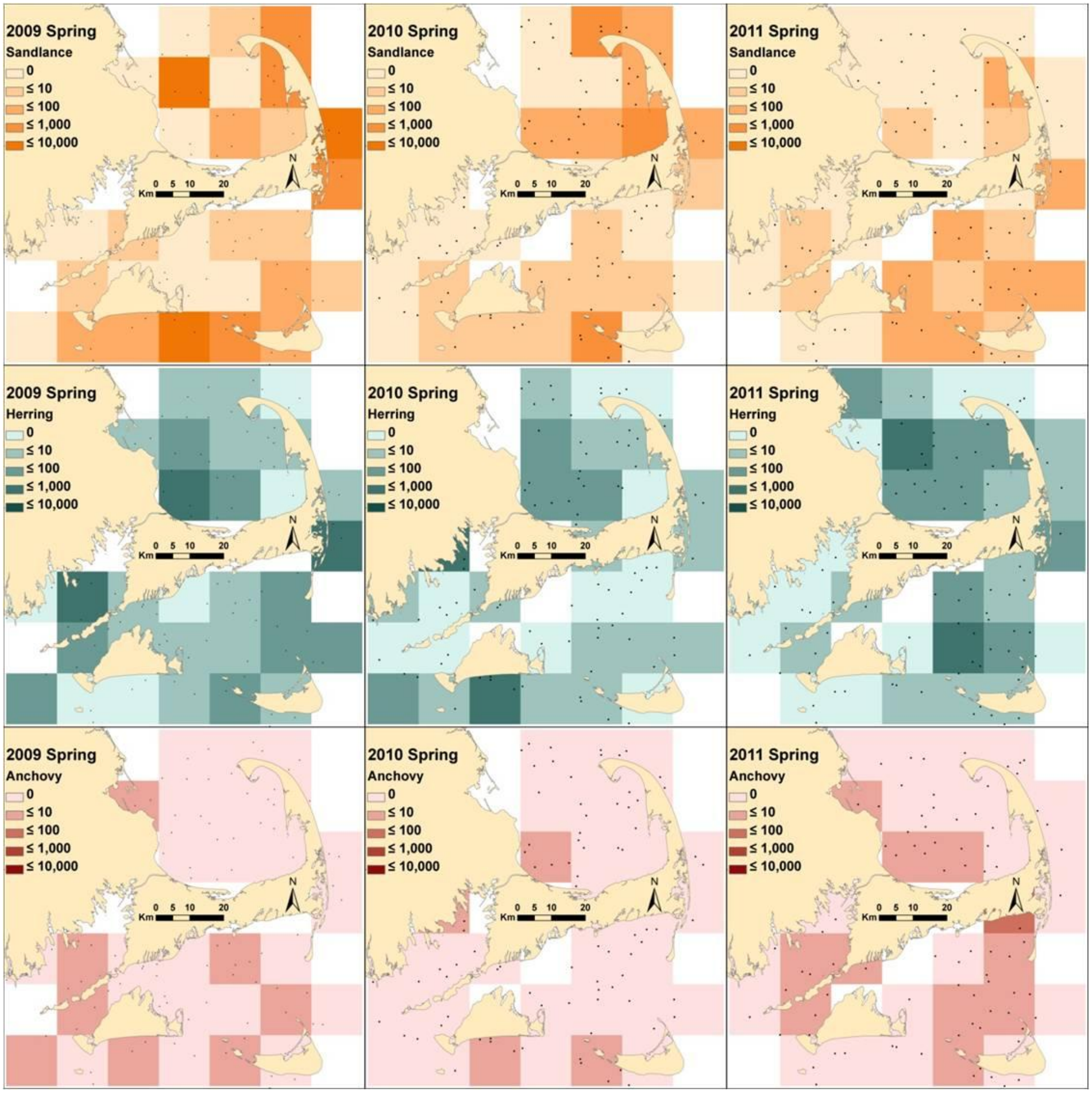


Figure 2.10. Sampled spring distribution of the three dominant prey categories by year.

The study region shows Cape Cod, Massachusetts, during three surveys: spring of 2009 (left) – 2011 (right). The square grid (with 15 km x 15 km cells) shows counts at length of sandlance, herring, and anchovy, interspersed with black dots representing prey sampling stations. White cells indicate missing data (areas of no survey coverage); see chapter 3 methods for more details.

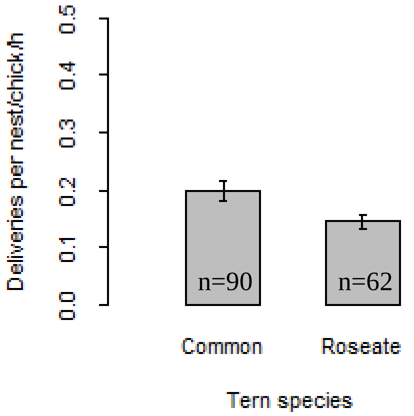


Figure 2.11. Per capita chick provisioning rates by tern species.

Across all years combined, provisioning rates of common terns (number of prey delivered per hour) were significantly higher than those of roseate terns, both by nest ($t_{146.7} = 3.5$, $p < 0.001$), and by chick ($t_{148.4} = 2.6$, $p = 0.010$, above, mean ± standard error bars).

Chapter 3. Inshore: The relationship among prey availability, habitat and the foraging behavior, distribution, and abundance of common (*Sterna hirundo*) and roseate terns (*S. dougallii*)

Abstract

The behavior, distribution and abundance of seabirds relates to their ecological niche, changing in response to habitat variability and prey availability. To quantify these influences on the foraging strategies of common (*Sterna hirundo*) and roseate terns (*S. dougallii*), I implemented density-surface models with distance sampling, using remotely-sensed habitat covariates. I collected tern and prey data aboard inshore trawl surveys, selecting the three dominant regional prey categories: sandlance (Northern, *Ammodytes dubius*), herring (primarily Atlantic, *Clupea harengus*), and anchovies (*Anchoa* spp.). The size of tern flocks, the abundance of sandlance and herring, water depth, chlorophyll concentration, and sea surface temperature significantly predicted common and roseate tern spatial patterns. Roseate tern foraging showed especially close links to sandlance abundance. Identifying the direct relationship between prey association and tern foraging is essential to understanding species-specific differences in their response to environmental instability. This study demonstrates that terns provide each other with cues to the presence of prey; therefore, the conservation and management of roseate terns depends not only on the availability of sandlance, but also on the ecology of common terns.

Introduction

The direct impact of prey availability on the spatial distribution and abundance of top marine predators is difficult to quantify, and although essential for conservation (Safina & Burger 1988; Diamond & Devlin 2003; Dänhardt & Becker 2011a), such information is sparse in the literature (Heinemann 1992; Shealer & Kress 1994; Einoder 2009; Williams et al. 2009). Behavioral and ecological factors together affect prey availability, conventionally through bottom-up processes in the marine realm (Hunt & Schneider 1987; Frederiksen et al. 2006; Grémillet et al. 2008): habitat influences resource predictability, and this, in turn, drives interspecific differences in prey utilization (Davoren et al. 2003; Weimerskirch 2007; Elliott et al. 2009a; Weimerskirch et al. 2010). I hypothesize that habitat variability and prey availability predict interspecific differences in the foraging of seabirds, and directly relate to the behavior, distribution and abundance of common (*Sterna hirundo*) and roseate terns (*S. dougallii*).

Numerous studies in the Northwest Atlantic indicate that roseate terns are feeding specialists on sandlance (*Ammodytes* spp.), and common terns are opportunistic generalists (Safina et al. 1990; Heinemann 1992; chapter 2, Gochfeld et al. 1998; Nisbet 2002; Rock et al. 2007), yet these accounts fall short of testing how terns respond directly to changes in the availability of their prey. The foraging strategies of common and roseate terns are highly responsive to patterns of prey availability, such that roseate terns seem to use memory to pursue persistent prey (similarly to murres, *Uria* spp. Davoren et al. 2003), and have better breeding success during years of high sandlance abundance (chapter 2). Common terns, on the other hand, appear more resilient to prey variability, through their use of local enhancement: they use social cues from conspecifics or heterospecifics to exploit unpredictable patches (chapter 2, as with murres, Davoren et al. 2003; Elliott et al. 2009a). I collected data from shipboard surveys to measure the effect that habitat, forage fish, and mixed-species tern flocks have on the feeding behavior and ecology of common and roseate terns at sea. To assess the ecological context of trophic interactions between terns and their prey, I use standard oceanographic parameters: bathymetry, sea surface temperature (SST), and chlorophyll concentration, an index of primary productivity (chapter 1). I selected sandlance (Northern, *A. dubius*), herring (primarily Atlantic, *Clupea harengus*), and anchovies (*Anchoa* spp.) to represent the dominant three prey items delivered to chicks at the primary breeding grounds in the state of Massachusetts (MA), USA (chapter 2, Kirkham 1986; Safina et al. 1990; Tims et al. 2004). These are neritic or epipelagic baitfish that are recognized as important to other top predators in the Northwest Atlantic, including humans: while sandlance and anchovies may be fished passively, they are not targeted commercially, nor are they regulated like Atlantic herring (Robins & Ray 1986; Bigelow & Schroeder 2002). Consequently, these forage fish experience short (interannual) and long-term (decadal) fluctuations in their distribution and abundance, resulting from consumptive impacts, fisheries pressure, and climate change (Overholtz et al. 2000; Overholtz & Link 2007; Lucey & Nye 2010; Nye et al. 2013). Moreover, sandlance are notoriously difficult to sample, due to their slender body shape, burrowing habits, and irregular distribution in the water column (Robards et al. 2000; Dänhardt et al. 2011). Unreliable patterns in fish behavior can complicate the generally positive relationship between the availability of prey and their abundance or distribution (Dänhardt & Becker 2011b), yet trawl surveys provide one systematic method of predicting the spatial patterns of sandlance and other important fish species (Garrison et al. 2002; Nye et al. 2013). This study addresses the sensitivity of common and roseate terns to their habitat and principle prey, to assess their performance as ecological and fisheries indicator species, for both bottom-up (Furness & Camphuysen 1997; Camphuysen & Webb 1999; Furness & Tasker 2000; Diamond & Devlin 2003; Jaquemet et al. 2004; Le Corre & Jaquemet 2005; Jaquemet et al. 2007; Monticelli et al. 2007; Einoder 2009; Dänhardt & Becker 2011a) and top-down processes (Monaghan 1992; Hunt & McKinnell 2006; Frederiksen et al. 2007; Overholtz & Link 2007).

Methods

Data collection

Two outside sources supplemented my seabird observation data: 1) bottom trawl catch results, and 2) online geographic information system (GIS) marine data layers. I joined the NOAA Research Vessel Gloria Michelle during the Massachusetts Division of Marine Fisheries (MADMF) Resource Assessment Bottom Trawl Survey, in May 2010, Sep 2010, and May 2011. For the duration of the cruise (approximately two weeks), I continuously recorded data on all species while in transit; I followed established protocols from the offshore surveys (chapter 1), using distance sampling along line transects but resorting to 300 m strip transects during occasional bursts of high densities (Tasker et al. 1984; Thomas et al. 2010). NOAA and MADMF employees deployed an otter trawl net at stations that were randomly stratified by region and depth in MA state waters: each tow was standardized to 20 min at 2.5 knots (King et al. 2010). I assisted in sorting, processing, and entering the catch results into their computer system. They provided me with a subset of data that I selected to represent the availability of dominant tern prey species, by composition and size: the number of sandlance, herring, and anchovy individuals, no longer than 15 cm. These categories included the following species, in order of decreasing biomass: sandlance: Northern sandlance; herring: Atlantic herring, alewife

(*Alosa pseudoharengus*), blueback herring (*A. aestivalis*), American shad (*A. sapidissima*), and Atlantic menhaden (*Brevoortia tyrannus*, negligible in biomass); anchovy: bay anchovy (*Anchoa mitchilli*) and striped anchovy (*A. hepsetus*), with rainbow smelt (*Osmerus mordax*) to account for the slight possibility of being mistaken for anchovies. To access marine habitat data, I downloaded raster layers into ArcGIS: a) 30 m bathymetry for MA and adjacent federal waters from the online Office of Geographic Information (MassGIS), and b) remotely-sensed data from the National Aeronautics and Space Administration's (NASA) Aqua satellite using Duke's Marine Geospatial Ecology Tools (Roberts et al. 2010): 4 km monthly daytime SST (JPL PO.DAAC MODIS Global Level 3) and chlorophyll-a (GSFC OceanColor Level 3 Standard Mapped Image). These covariates made up eight data layers: 1) depth (m); 2) SST (°C); 3) chlorophyll-a concentration ('Chl', mg/m^3); counts at length of 4) sandlance ('Sl'), 5) herring ('Hg'), and 6) anchovy ('An'); and total number of 7) common and mixed terns ('CMT') or 8) roseate and mixed ('RMT') terns. CMT and RMT are mutually exclusive as covariates (depending on which species is treated as a response variable), therefore, only seven covariates could be analyzed at one time; "mixed" refers to mixed species flocks of common and roseate terns that were difficult to distinguish at farther distances (e.g. 500 m).

The proper spatial scale for analysis fit the following criteria: large enough to accommodate autocorrelation (due to continuous tern sampling) and to minimize the number of covariate cells with missing data (attributable to discrete prey sampling), yet small enough to prevent diluting predictions with missing data, for example by projecting onto land. The spatial dispersion of bottom trawl stations largely determined the optimal resolution: 15 km x 15 km raster cells (225 km^2). Therefore, I aggregated covariate values by mean (depth, SST, chlorophyll, number of fish by species), and tern abundance by sum, into this grid resolution. 30 cells made up the total study area (6750 km^2), but data coverage varied slightly by parameter and survey. I calculated the length of track lines within each cell to determine transect effort.

Data analysis

Distance sampling computes the detection probability of study subjects from their observed range (perpendicular distance to a line transect), for the purpose of evaluating population abundance (Thomas et al. 2010; Gjerdrum et al. 2012). Density-surface modeling (DSM, Miller et al. 2013a) implements distance sampling to determine the relationship among the spatial distribution of population abundance and covariates. I used the package “dsm” (Miller et al. 2013b) in R (R Development Core Team 2012), which integrates two components (a two-stage approach) to model the effect of habitat covariates on the distribution and abundance of terns. First, DSM relies on the package “Distance” (Miller 2012) to perform Conventional Distance Sampling (CDS), or alternatively, with the addition of one covariate (visibility), Multiple Covariate Distance Sampling (MCDS): these engines fit a detection function (Figure 3.2) onto the observed tern counts. The detection probabilities (P) are then used to calculate abundance over the sampled area (N, Table 3.2), as well as estimated abundance over the entire study area. The second DSM component runs a generalized additive model (GAM) on the sampled data cells (n, Table 3.1), fitting abundance (N, Table 3.2) to covariates; next, by projecting the results over modified covariate values that span the entire study area, the user may predict population distribution and abundance (of terns, Table 3.2).

Model selection involved testing combinations of a limited number of parameters (depending on the degrees of freedom in each GAM), given the seven possible covariates. I evaluated four model categories defined by the response variable and number of surveys analyzed: 1) common, roseate, and mixed terns (‘CRMT’) over all three surveys (62 possible combinations of a maximum of five parameters, given six possible covariates), 2) common terns (‘CT’) over all three surveys (126 combinations of six parameters given seven optional covariates; no roseate terns were identified in the fall 2010 survey), 3) common terns in the two spring surveys (56 combinations of four parameters, given six covariates), 4) roseate terns (‘RT’) in the two spring surveys (56 combinations). Additionally, models varied by distribution (Poisson or negative binomial), and distance sampling engine (CDS or MCDS). I used a backwards stepwise approach, starting with the “beyond optimal” models (e.g. seven covariates, six parameters), then subsequently dropping one parameter. Once all covariates in the models resulted as significant ($p < 0.05$), I compared nested models with likelihood ratio tests and selected those with the lowest AIC (Akaike’s Information Criterion) scores (Wood 2006; Zuur et al. 2012). There was no need to account for autocorrelation in the models, since the 15 km grid scale properly accommodated for spatial autocorrelation, rendering it insignificant; Moran’s I values were computed with the midpoint coordinates of each cell using package “ncf” (Bjornstad 2009). To determine the effect of sampled prey numbers on the comparative behavior of each tern species in the spring, I classified behaviors into foraging (feeding, milling) and not foraging (traveling, resting), then used a two-factor analysis of variance (ANOVA) and Tukey's multiple comparisons.

Results

The GVIF values of all covariates were less than two, indicating sufficient independence to allow that all combinations be assessed in the models (Figure 3.1). The distribution of the response variables (histograms, Figure 3.1) illustrates that the Poisson and negative binomial families were indeed more appropriate for analysis than a Gaussian curve. For the DSM, the study area (and prediction grid) consisted of 30 data cells, but the total number of sampled data cells (n, Table 3.1) was less than 90 for all three surveys, and n < 60 for the two spring surveys, due to missing data (survey coverage or data availability). The four selected density-surface models (Table 3.1) differed from the other candidate models chiefly in habitat covariate influences (SST versus chlorophyll or depth); only in the case of roseate terns did prey covariates have a distinct effect on model selection. Model 10 had an AIC value did not differ significantly from its nested model (Table 3.1); given that model 10 was more complex (with the addition of one prey parameter, herring, to accompany sandlance), the likelihood ratio test evaluated it as significantly better (Johnson & Omland 2004). The combination of a negative binomial distribution with MCDS produced best-fit models only for roseate terns—although there were few three- or four-parameter candidate models that showed significance in all covariates, they had especially low AIC values; these unique properties reflect the low incidence of roseate tern observations relative to common terns at sea. Overall, distance sampling resulted in well-fit density-surface models (high explained deviance, Table 3.1), and reasonable estimations of common tern abundance over the survey area, yet it over-inflated roseate tern abundance estimates, compared to the censused MA breeding population size (Table 3.2).

Sandlance was the only covariate that influenced all four selected models (Table 3.1), demonstrating its strong effect on common and roseate tern distribution and abundance. While model 10 suggests that roseate terns have an inverse relationship with sandlance, model 2 suggests otherwise: common, roseate, and mixed terns were likely to be observed at high and low values of sandlance (Figure 3.4). There were clear differences between seasons, notably that no roseate terns were observed in the fall 2010, which was characterized by higher SST and more anchovies (Figure 3.3); this seasonal increase in anchovy availability is supported by the positive correlation between this prey category and SST (Figure 3.1). In the spring, common terns (model 8, Table 3.1) were likely to be found in higher numbers where intermediate SST, 8-10 °C, characterized the habitat (Figure 3.4). Of the selected four models, only in model 8 did SST emerge as a significant predictor, stronger than depth or chlorophyll (note that I assigned depth a negative value, and it was positively correlated with SST and chlorophyll, such that shallow water embodied higher values). Additionally, this model singly excluded bathymetry, suggesting that SST may sufficiently account for variation in depth, given their co-dependence. Overall, higher counts of common and roseate terns were likely to occur where waters were shallow, less than 40 m deep, with variable sandlance abundance, and sampled herring numbers that reached 200 per cell (Figure 3.4). The distribution of sandlance and herring (Figure 3.3) appeared to follow colder water than anchovies, as supported by a negative correlation with SST (Figure 3.1). Models 2 and 6 suggest that, across the three surveys, common terns, and apparently roseate terns, were positively influenced by chlorophyll concentration above 4 mg/m^3 (with a peak at 6 mg/m^3); since both seasons were analyzed in these two models, the effect of primary productivity is attributable to the fall. Unmistakably, heavily influenced are both tern species by the presence of other tern flocks, conspecific and heterospecific: common terns aggregate with any number of roseate and mixed terns (RMT > 100, model 6; RMT < 100, model 8); roseate terns assemble with intermediate counts of common and mixed terns (CMT 50-300, model 10).

In the two spring surveys, common tern individuals (mean: μ = 19.1) were observed over areas with significantly higher numbers of sampled herring than roseate terns (μ = 8.7): $t_{121.0}$ = 3.7, p < 0.001 (n = 1863, Figure 3.6), however there was no significant relationship between their foraging behavior and sampled herring numbers (Figure 3.7b). As for sandlance, the interaction between tern species and behavior was significant ($F_{1,\ 1863}$ = 47.1, p < 0.001), where individual foraging roseate terns (μ = 59.6) were observed over areas with significantly higher numbers of sampled sandlance (p < 0.01) than were foraging common terns (μ = 21.1), and non-foraging common (μ = 19.0) or roseate terns (μ = 5.9). Individual foraging and non-foraging common terns were found over significantly more sandlance than non-foraging roseate terns; all other behavioral group comparisons of sandlance and herring were insignificant (Figure 3.7).

Discussion

This research demonstrates a clear relationship between prey availability and the foraging behavior, distribution, and abundance of common and roseate terns. While colony-based studies have described herring and sandlance as important for the provisioning of chicks (chapter 2), I found that adults depend on the distribution and abundance of their principal prey. Sandlance availability is a key determinant of roseate tern foraging behavior and ecology, in Massachusetts and, likely, the NW Atlantic. Such information highlights the need to assess the health of forage fish populations through proper management of commercial fisheries stocks (e.g. herring), or designation of Marine Protected Areas (i.e. sandlance habitat) for the protection of endangered species (roseate terns).

Sandlance distribution and abundance was the primary predictor of tern foraging among all covariates—flocks of other terns were secondary. The inconsistencies in the positive effect of sandlance on common and roseate terns likely had more to do with unreliability in sampling than in occurrence (given that sandlance can be available to terns even when sampling indicates otherwise, Dänhardt et al. 2011). The prevalence of sandlance and herring in the spring (Figure 3.3) fits their profile as colder-water species, as compared to anchovies (Garrison et al. 2002; Lucey & Nye 2010). I suspect that this places a temporal constraint on roseate tern migration, explaining their phenology: why they stage earlier than common terns. During their pre-migratory dispersal they may pursue adult sandlance that move offshore (Robards et al. 2000), which would explain the lack of roseate terns observed inshore during September. The surveys overlapped spatially and temporally with tern breeding habits, therefore the utility of shallower water may relate to good coastal fishing habitat, where terns exploit tidal patterns (Heinemann 1992; Becker et al. 1993). Habitat strongly affected common terns seasonally, where SST has a greater impact in the spring, and chlorophyll in the fall. Primary productivity (chlorophyll) showed greater importance in this study than in chapter 1, likely due to an inshore coastal effect, and the use of a larger scale to account for spatiotemporal lag in bottom-up trophic interactions that attract fish to plankton (Hunt & Schneider 1987; Grémillet et al. 2008). The behavioral relationship between foraging roseate terns and sandlance illustrates that terns may signal the presence of prey, which supports the notion that they rely on each other to find food. The social aggregation of common and roseate terns with flocks of conspecifics and heterospecifics provides unequivocal evidence of local enhancement.

The advantage of using density-surface modeling was its performance at determining the distribution of terns (Figure 3.5); the disadvantage was its inflated abundance predictions. The nature of seabird distributions likely explains why the GAM and distance sampling contribute to over-inflation in abundance estimation. First, seabird aggregation patterns produce large counts at few covariate values, resulting in high fitted values, as predicted by the GAM (personal communication, David Miller). Second, the problem may be inherent to using distance sampling with a biological population such as seabirds (e.g. as opposed to whales, which presumably have a lower detection probability since they are below the surface). For example, a mean detection probability of 25% (as in model 2), is low for an experienced seabird observer scanning the 300-500 m range, and 2% detection of roseate terns (model 10) is artificially low. MCDS seemed to over-compensate for attributing lack of visibility to sparse observations of roseate terns, by estimating high abundance from low detection probability; low detection should have matched more closely to low abundance. However, MCDS did allow for exceptional fit in roseate terns (provided the appropriate distribution family), resulting in a suitably-complex model that retained biologically-meaningful variation instead of favoring parsimony-induced fit (Johnson & Omland 2004). Given its strengths and weaknesses, DSM qualified as an effective method of estimating seabird distribution and relative abundance, yet users need to exercise caution in making over-estimated predictions of absolute abundance, especially with respect to the management of roseate terns.

This study calls into question whether the foraging tactics of roseate terns will deviate in response to global climate change and fisheries pressure. It is possible that the reduction of top predators to accompany global warming may contribute to relative increases in some of the pelagic forage fish of interest to terns (Nye et al. 2013). Shifts in SST and primary productivity would presumably accompany a redistribution of prey, to which common terns could likely respond. If roseate terns are competent at detecting prey availability, independently of SST and primary productivity, as the spring model suggests, then they may be able to keep pace with an increasingly northerly distribution of sandlance (Lucey & Nye 2010). They would be required to update their short-term memory on feeding locations (chapter 2), and local enhancement would improve their chances of success. However, if roseate terns strictly rely on long-term memory, then it is possible that rapid, unpredictable changes in sandlance distribution could result in prey limitation and allow tern competition to overpower the benefits and incidence of facilitative interactions (Safina & Burger 1988). If the distribution of sandlance were to extend far beyond the primary breeding grounds of roseate terns in New York and MA, then these highly philopatric species could either expend too much energy traveling longer distances between the colony and foraging areas, causing chicks to starve, or they would have to endure nesting displacement, as they often have in the past (Gochfeld et al. 1998; Nisbet 2002). Prey depletion has compromised the breeding success of common and roseate terns in the past (Safina et al. 1988), and contributed to population declines (Szostek & Becker 2012). Since the 1990s, herring stocks in the NW Atlantic have generally followed a slowly increasing trend, in contrast to sandlance abundance, which has been on the decline since the late 1980s (Overholtz et al. 2000). Roseate terns were federally listed as endangered in 1987, and their populations currently show no improvement, therefore, further research should assess whether their productivity mirrors long-term historical trends in sandlance, to address the extent to which prey sensitivity may limit their potential for population recovery (Nisbet & Spendelow 1999)—especially given that common terns have largely rebounded over the past few decades (Mostello 2012). It is important that we better understand not only where common and roseate terns consistently forage across years, but how they will respond to changes in prey availability. The miniaturization of enhanced tracking devices (Burger & Shaffer 2008) should be able to provide a means for future studies to better quantify tern utilization of foraging habitat; such information is essential to advancing the conservation and management of these protected species. Furthermore, the demonstrated sensitivity of common and especially roseate terns to habitat and prey availability (this study and chapter 2) classifies them as good ecosystem and fisheries indicator species (Einoder 2009); the measured response of terns to their environment may serve to identify the threats and safeguards facing the less conspicuous members of their trophic community, such as tunas and cetaceans (chapter 1).

Tables

Table 3.1. Density-surface model selection.

The best models selected from the candidate set are shown in bold (with significant predictors shaded in gray), and indicate: the response variable, number of surveys analyzed, number of data cells sampled (n), distribution family (negative binomial: ‘Neg Bin’), type of distance sampling used in the detection (Detect.) function – either conventional (CDS) or multiple covariate distance sampling (MCDS), number of model parameters (Param.), significance of each covariate (*** p < 0.001, ** p < 0.01, * p < 0.05), the explained deviance (Dev.), and the Akaike’s information criterion (AIC) value. Covariates for habitat (columns at left) include: sea surface temperature (SST), chlorophyll concentration (‘Chl’), and depth. Prey covariates (middle columns) include: anchovy (‘An’), herring (‘Hg’), and sandlance (‘Sl’). Other tern covariates (columns at right) include: common and mixed terns (‘CMT’) or roseate and mixed (‘RMT’) terns. The ‘x’ indicates parameters that were not tested (i.e. not included in the data), the ‘-’ indicates covariates that were not considered as predictors in the models shown (i.e. they were not significant in more complex models).

							Habitat			Prey			Other terns			
Model	Response	Surveys	n	Family	Detect.	Param.	SST	Chl	Depth	An	Hg	Sl	CMT	RMT	Dev.	AIC
1	CRMT	3	55	Poisson	CDS	5	***	-	***	**	***	***	x	x	94.2%	360
2			**52**	**Poisson**	**CDS**	**4**	-	***	***	-	***	***	**x**	**x**	**95.4%**	**333**
3			52	Poisson	CDS	3	***	***	***	-	-	-	x	x	83.9%	520
4	CT	3	52	Poisson	CDS	5	***	***	-	***	-	***	x	***	96.5%	297
5			52	Neg Bin	CDS	5	-	*	***	-	*	**	x	*	48.3%	373
6			**52**	**Poisson**	**CDS**	**4**	-	***	***	-	-	***	**x**	***	**98.5%**	**266**
7			52	Neg Bin	MCDS	4	-	***	***	-	-	***	x	***	88.5%	674
8		2 - spr	**39**	**Poisson**	**CDS**	**4**	***	-	-	**x**	*	***	**x**	***	**99.8%**	**223**
9			37	Poisson	CDS	3	-	***	***	x	-	***	x	-	92.6%	274
10	RT	2 - spr	**40**	**Neg Bin**	**MCDS**	**4**	-	-	*	**x**	**	*	***	**x**	**95.3%**	**209**
11			40	Neg Bin	MCDS	3	-	-	***	x	-	***	***	x	92.5%	208

Table 3.2. Sampled, estimated, predicted, and actual abundance of two species of tern in Massachusetts, USA.

Distance sampling abundance calculations of common, roseate, and/or mixed terns (‘CRMT’) across 2 or 3 surveys, as compared to density-surface model predictions (Predicted Abund.), are referenced to 2010-2011 mean Massachusetts (MA) breeding population sizes (right column, calculated from Mostello 2011; 2012). For each cluster of tern observations (Obs.), the detection function (Figure 3.2) computes detection probabilities (P) over the distance range. These (p) are used to calculate the estimated abundance (Estim. Abund.) of tern clusters and individuals (Individs.) over the entire study area (6750 km^2), based on the percentage of area covered by the sampled abundance of terns (N). The density-surface models (see Table 3.1) fit N to the covariates, then predict abundance over the study area, based on the average of those covariates across surveys.

					Sampled		Expected	Estim. Abund.			Predicted	Mean
Response	Surveys	Obs.	Range	Mean p	Abund. (N)	Area	Cluster size	Cluster	Individs.	Model	Abund.	MA pop.
CRMT	3	390	0-500	25.7%	1,517.5	10.4%	3.8	14,643.2	55,043.2	2	1.15E+33	35,736
CT	3	344	0-300	36.0%	956.9	6.2%	3.5	15,389.5	53,818.0	6	1.17E+06	32,984
CT	2 - spr	334	0-300	35.3%	944.9	4.4%	3.5	21,585.1	75,871.1	8	2.80E+213	32,984
RT	2 - spr	30	0-300	2.0%	1,493.6	4.4%	2.3	34,116.7	78,026.8	10	8.95E+82	2,752

Figures

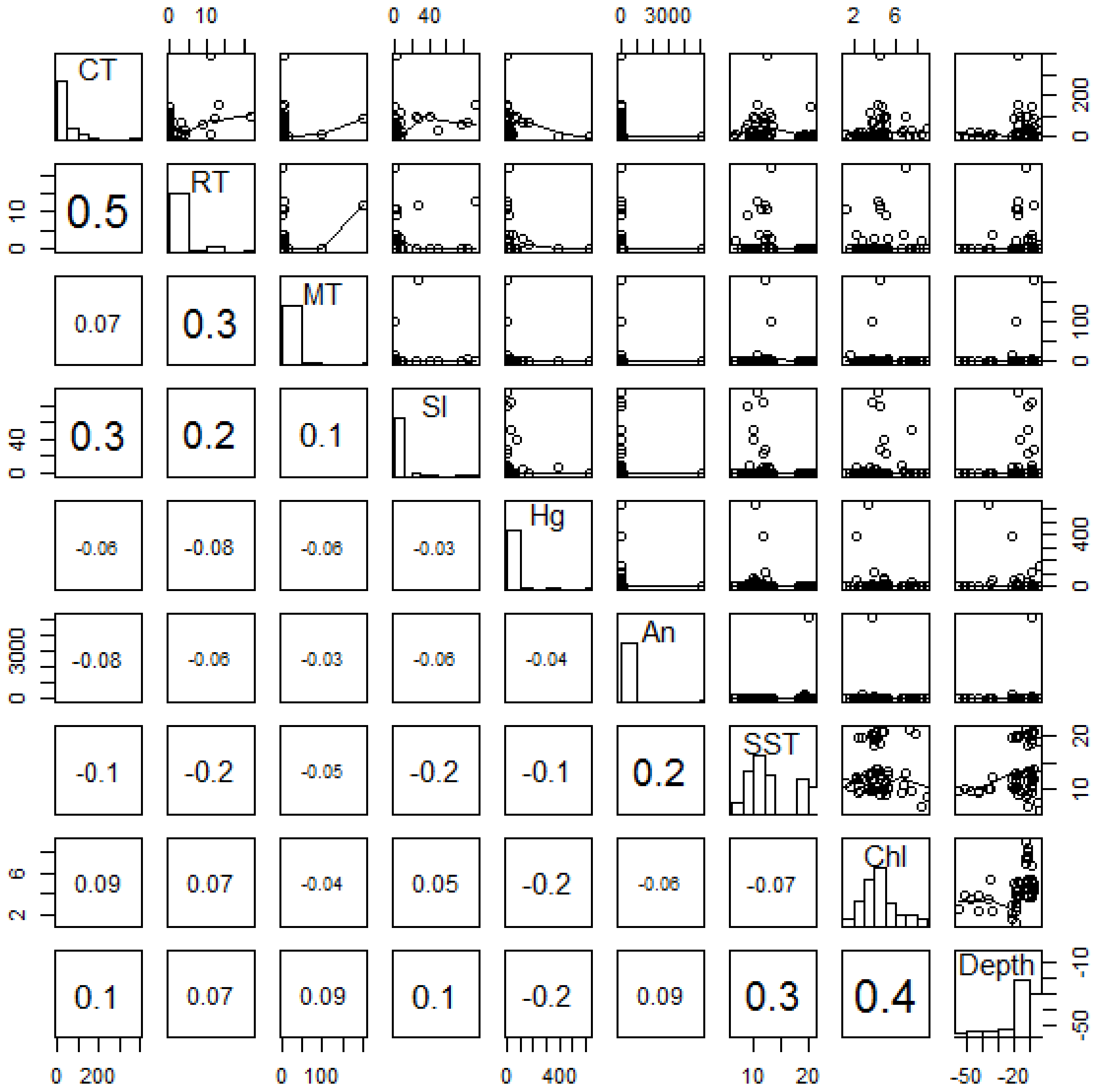
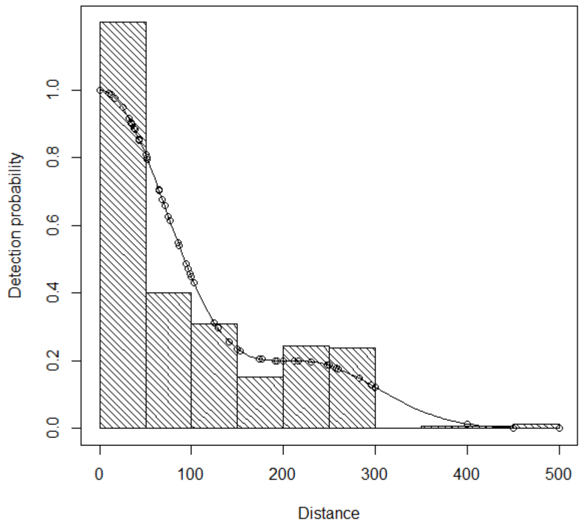
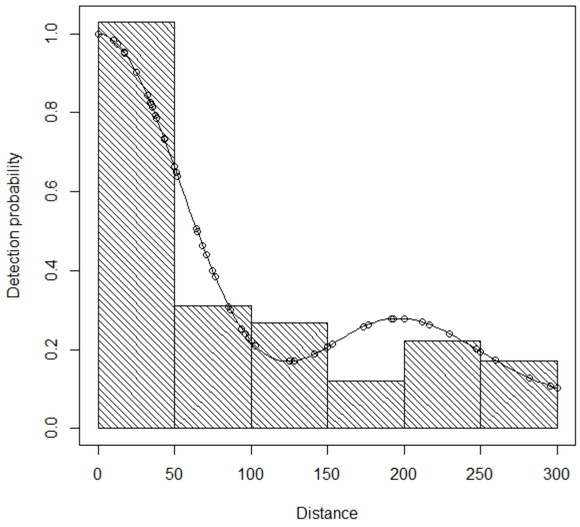


Figure 3.1. Relationships among the response variables and covariates across all three inshore surveys.

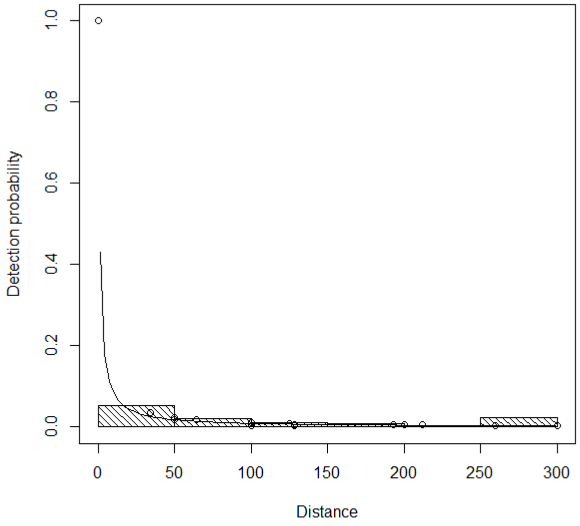
This “pairplot” (Zuur et al. 2012) shows histograms of each variable on the diagonal, pair-wise Spearman rank correlation coefficients (font size proportional to value), and scatterplots with a LOESS smoother, axes labeled alternately (x at top or bottom, y at left or right). The response variables are in the top rows and left columns (n = 52): common (‘CT’), roseate (‘RT’), or mixed terns (‘MT’); prey covariates are sandlance (‘Sl’), herring (‘Hg’), and anchovy (‘An’) and habitat covariates are sea surface temperature (SST), chlorophyll concentration (‘Chl’), and depth.



(a)



(b)



(c)

Figure 3.2. Detection function plots.

Detection probabilities of (a) common, roseate, and mixed terns across all three surveys using conventional distance sampling (CDS); and across the two spring surveys: (b) common terns (CDS) and (c) roseate terns, using visibility in multiple covariate distance sampling (MCDS).

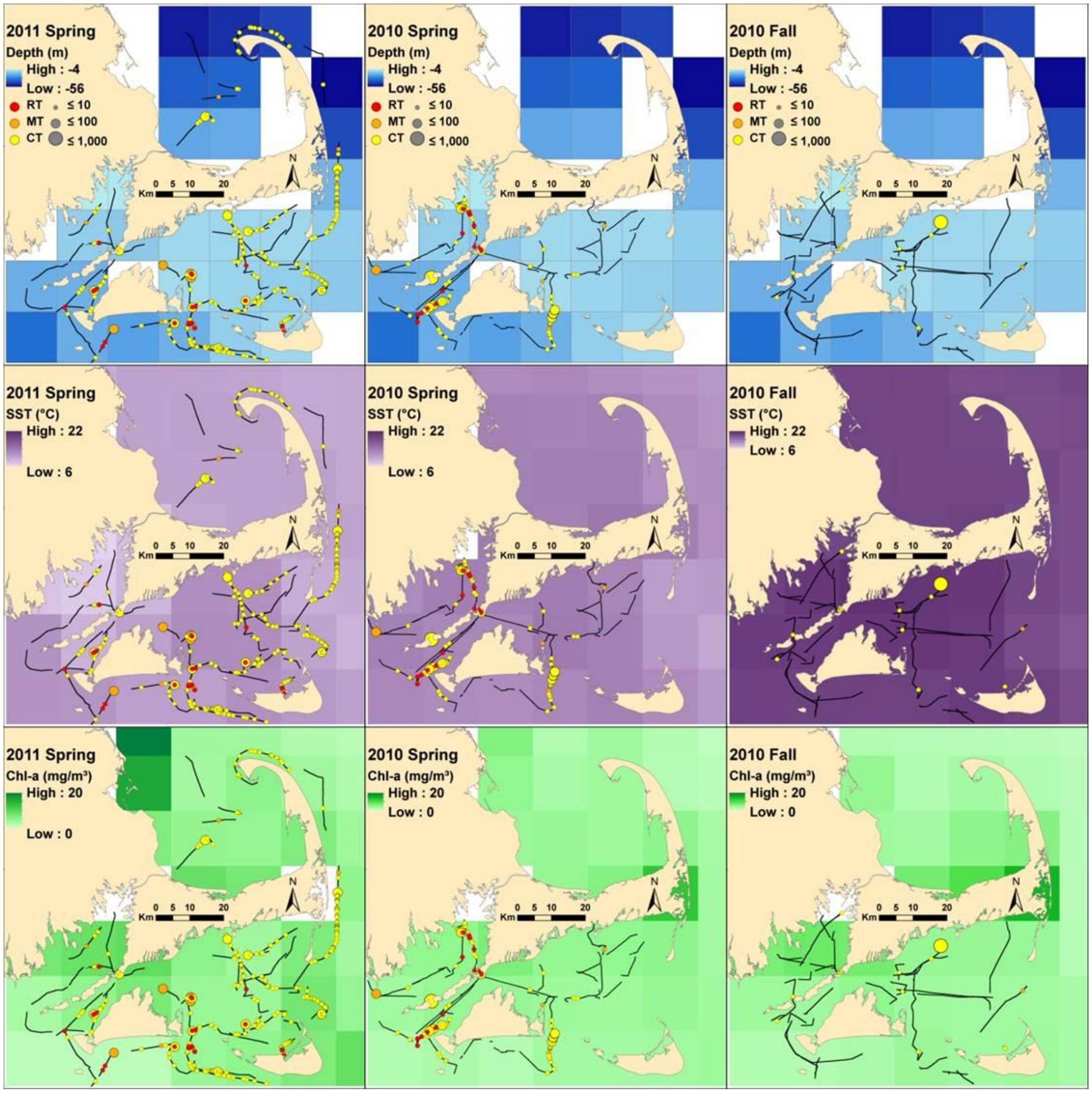

2011 Spring
Depth (m)
High : -4
Low : -56
RT
≤ 10
MT
≤ 100
CT
≤ 1,000
0 5 10 20
Km
N
2010 Spring
Depth (m)
High : -4
Low : -56
RT
≤ 10
MT
≤ 100
CT
≤ 1,000
0 5 10 20
Km
N
2010 Fall
Depth (m)
High : -4
Low : -56
RT
≤ 10
MT
≤ 100
CT
≤ 1,000
0 5 10 20
Km
N
2011 Spring
SST (°C)
High : 22
Low : 6
0 5 10 20
Km
N
2010 Spring
SST (°C)
High : 22
Low : 6
0 5 10 20
Km
N
2010 Fall
SST (°C)
High : 22
Low : 6
0 5 10 20
Km
N
2011 Spring
Chl-a (mg/m³)
High : 20
Low : 0
0 5 10 20
Km
N
2010 Spring
Chl-a (mg/m³)
High : 20
Low : 0
0 5 10 20
Km
N
2010 Fall
Chl-a (mg/m³)
High : 20
Low : 0
0 5 10 20
Km
N

Figure 3.3 (**a**)

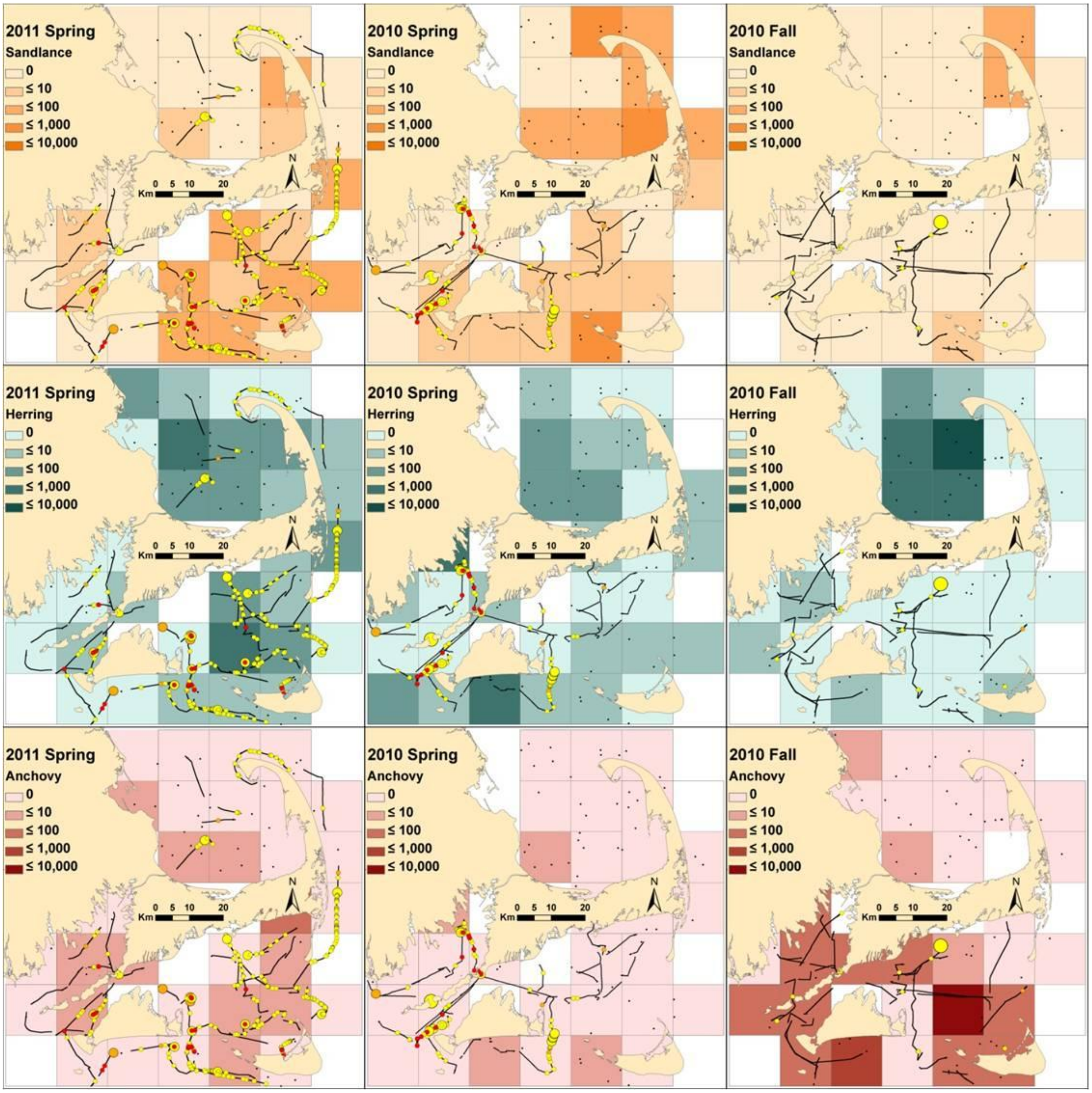
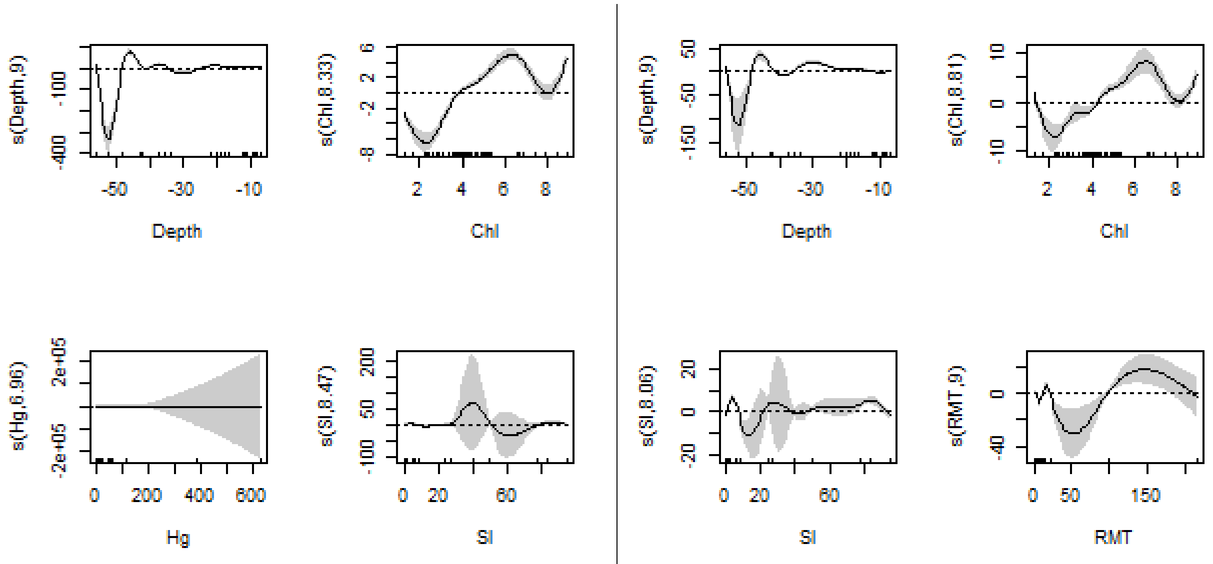


Figure 3.3 **(b)**

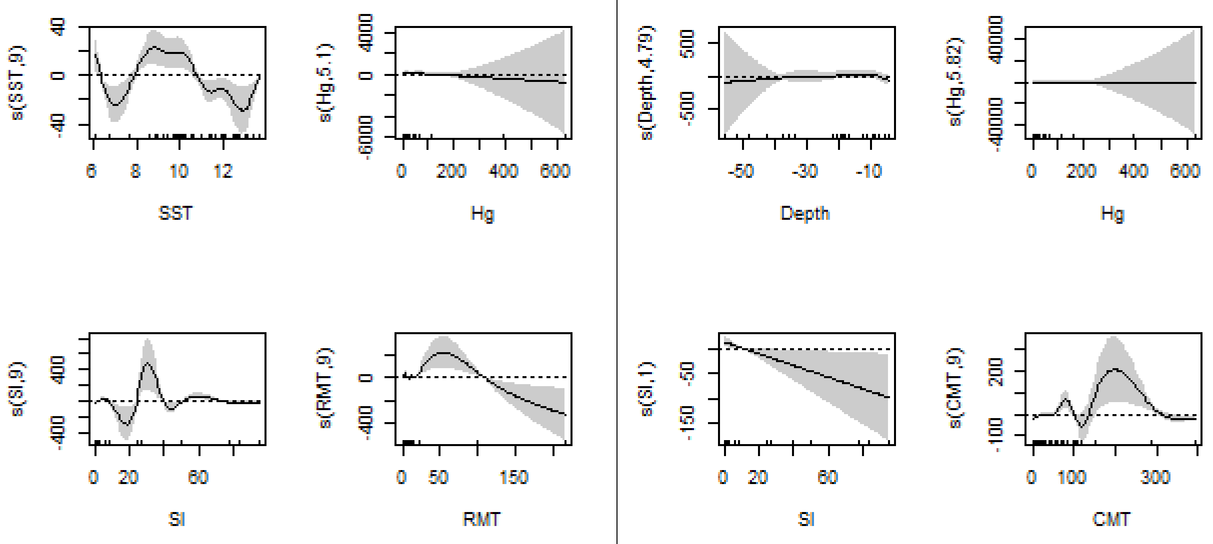
Figure 3.3. Tern habitat and prey covariate data layers for the three inshore surveys.

The study region shows Cape Cod, Massachusetts, USA, during the spring 2011 (left), spring 2010 (center) and fall 2010 (right). The transect effort (black line), is overlapped by counts of observed common, roseate, and mixed terns (circles), and interspersed with prey sampling stations (black dots). Habitat covariate layers (a): depth, sea surface temperature (SST) and chlorophyll concentration; and prey covariate layers (b): counts at length of sandlance, herring, and anchovy. Bathymetry, top row (a), delineates the 30 sampled grid cells (each 15 km x 15 km) used in the density-surface modeling; white cells indicate missing covariate data.



(a) Model 2: all common, roseate, mixed terns

(b) Model 6: common terns (3 surveys)

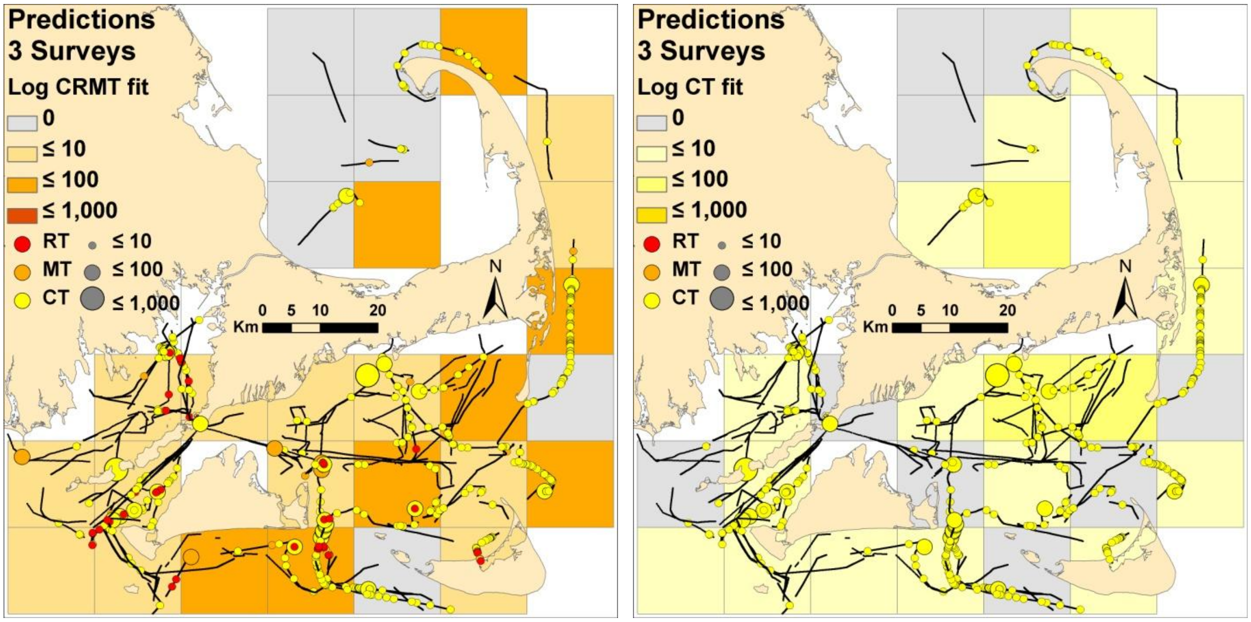


(c) Model 8: common terns (2 spring surveys)

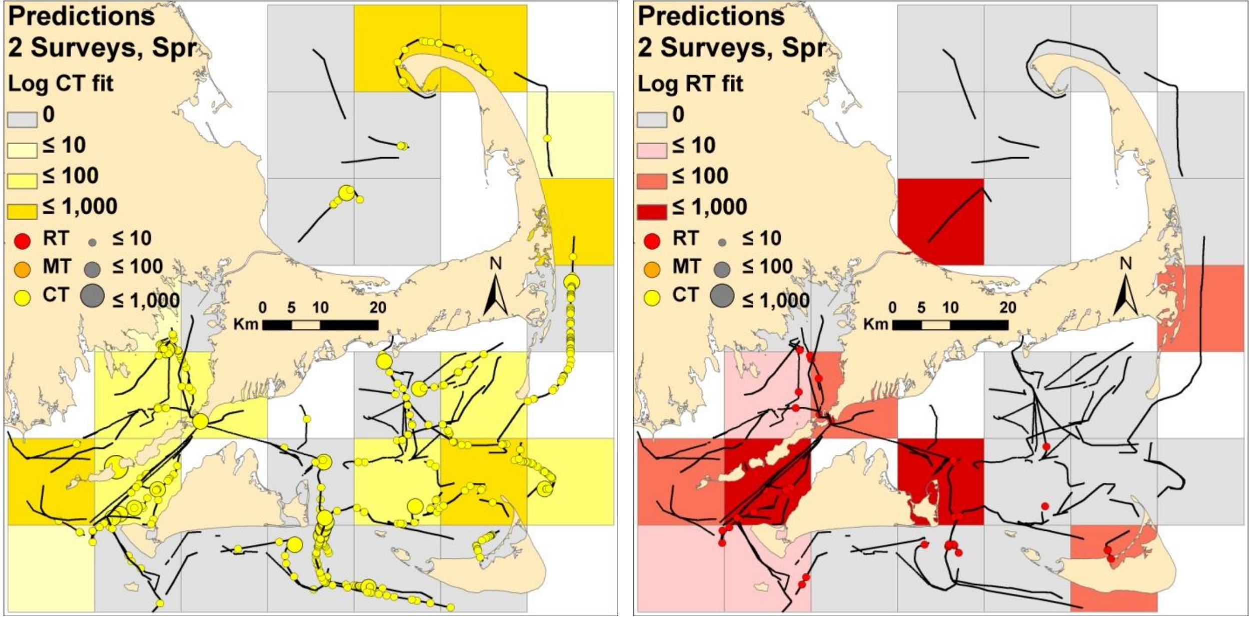
(d) Model 10: roseate terns (2 spring surveys)

Figure 3.4. GAM plots of the four selected models.

The y-axes show the effects of the covariates (x-axes) on the response variables (fitted tern abundance); all three surveys: (a) common, roseate, and mixed terns (Model 2), (b) common terns (Model 6); two spring surveys: (c) common terns (Model 8), and (d) roseate terns (Model 10). Shaded areas demarcate the standard error bounds (confidence bands), and dotted lines delineate where y = 0. Habitat covariates are sea surface temperature (SST), chlorophyll concentration (‘Chl’), and depth; prey covariates are anchovy (‘An’), herring (‘Hg’), and sandlance (‘Sl’); other tern covariates are common and mixed terns (‘CMT’) or roseate and mixed (‘RMT’) terns.



(a) Model 2 **(b)** Model 6



(c) Model 8 **(d)** Model 10

Figure 3.5. Predicted tern distribution and abundance, in Massachusetts waters.

The study region shows Cape Cod, Massachusetts, with observed (circles) and fitted (square grid) common, roseate, and/or mixed terns, based on predictions from the four selected models over the corresponding covariates, averaged across either all three surveys: (a) common, roseate, and mixed terns (Model 2), (b) common terns (Model 6); or the two spring surveys: (c) common terns (Model 8), and (d) roseate terns (Model 10). The black line represents transect effort, white cells indicate missing covariate data (resulting in n = 28 for all four predictive grids), and the tern fit values correspond to each grid cell (the log of abundance per 225 km^2).

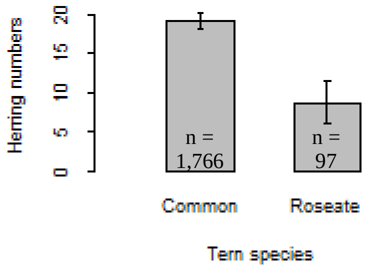
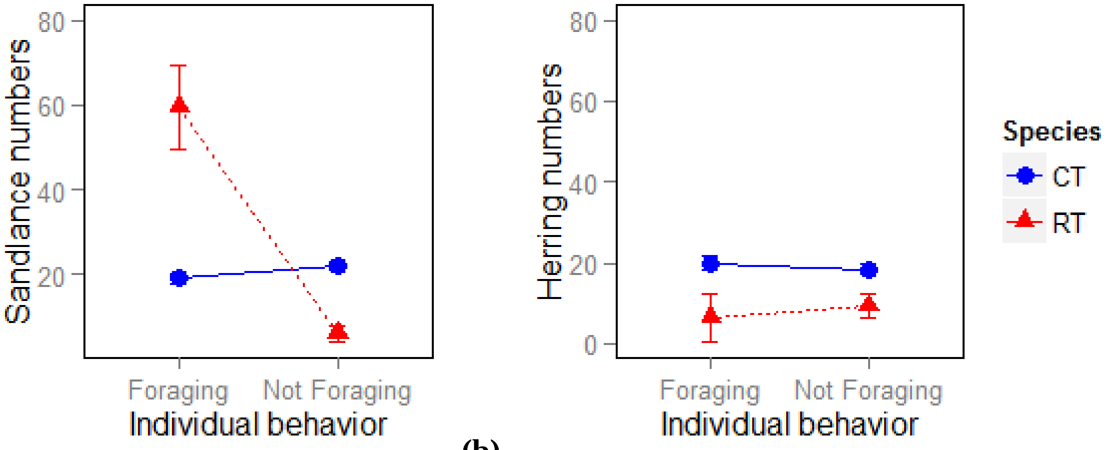


Figure 3.6. Mean herring numbers by tern species across the two spring inshore surveys.

Individual common terns (mean: μ = 19.1) were observed over areas with significantly higher numbers of sampled herring than were roseate terns (μ = 8.7): $t_{121.0} = 3.7$, $p < 0.001$ (N = 1863, mean ± standard error bars). However, comparisons between behavioral groups of tern species were not significant for herring (Figure 3.7b).



(a) **(b)**

Figure 3.7. Mean prey numbers by tern species and behavior across the two spring inshore surveys.

The interaction between tern species and behavior (a) was significant ($F_{1, 1863} = 47.1$, $p < 0.001$), where individual foraging roseate terns (RT, μ = 59.6) were observed over areas with significantly higher numbers of sampled sandlance ($p < 0.001$) than were foraging common terns (CT, μ = 21.1), and non-foraging common (μ = 19.0) and roseate terns (μ = 5.9), with mean ± standard error bars. Individual foraging and non-foraging common terns were found over significantly more sandlance than non-foraging roseate terns ($p < 0.01$); all other behavioral group comparisons of (a) sandlance and (b) herring were non-significant. Bars indicate standard errors.

Literature Cited

Agostinelli, C. & Lund, U. (2011) R package 'circular': Circular statistics. Version 0.4-3.

Amaral, M. & Saliva, J. E. (2010) Caribbean roseate tern and North Atlantic roseate tern (*Sterna dougallii dougallii*): 5-year review: Summary and evaluation. U.S. Fish and Wildlife Service, Concord, New Hampshire.

Amorim, P., Figueiredo, M., Machete, M., Morato, T., Martins, A. & Serrão Santos, R. (2009) Spatial variability of seabird distribution associated with environmental factors: A case study of marine important bird areas in the Azores. *ICES Journal of Marine Science* **66**: 29-40.

Ashmole, N. P. & Ashmole, M. J. (1967) *Comparative feeding ecology of sea birds of a tropical oceanic island*. Peabody Museum of Natural History, Yale University, New Haven.

Au, D. W. K. & Pitman, R. L. (1986) Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *The Condor* **88**: 304-317.

Balda, R. & Kamil, A. (2006) The ecology and life history of seed caching corvids. In: *Animal spatial cognition: Comparative, neural, and computational approaches* (Brown, M. F. & Cook, R. G., eds), available online. www.pigeon.psy.tufts.edu/asc/.

Balda, R. P., Kamil, A. C. & Bednekoff, P. A. (1996) Predicting cognitive capacity from natural history: Examples from four species of corvids. *Current Ornithology* **13**: 33-66.

Barrett, R. T., Camphuysen, K., Anker-Nilssen, T., Chardine, J. W., Furness, R. W., Garthe, S., Huppop, O., Leopold, M. F., Montevecchi, W. A. & Veit, R. R. (2007) Diet studies of seabirds: A review and recommendations. *ICES Journal of Marine Science* **64**: 1675-1691.

Becker, P. H., Ezard, T. H. G., Ludwigs, J. D., Sauer-Gürth, H. & Wink, M. (2008) Population sex ratio shift from fledging to recruitment: Consequences for demography in a philopatric seabird. *Oikos* **117**: 60-68.

Becker, P. H., Frank, D. & Sudmann, S. R. (1993) Temporal and spatial pattern of common tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* **93**: 389-393.

Bednekoff, P. A. & Balda, R. P. (1996a) Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour* **52**: 833-839.

Bednekoff, P. A. & Balda, R. P. (1996b) Social caching and observational spatial memory in pinyon jays. *Behaviour* **133**: 807-826.

Berec, L. (2010) Impacts of foraging facilitation among predators on predator-prey dynamics. *Bulletin of Mathematical Biology* **72**: 94-121.

Besag, J., York, J. & Mollie, A. (1991) Bayesian image restoration, with two applications in spatial statistics. *Annals of the Institute of Statistical Mathematics* **43**: 1-59.

Bigelow, H. B. & Schroeder, W. C. (2002) *Fishes of the Gulf of Maine*. Woods Hole Oceanographic Institution. http://www.gma.org/fogm/.

Bivand, R., and contributors, Altman, M., Anselin, L., Assunção, R., Berke, O., Bernat, A., Blanchet, G., Blankmeyer, E., Carvalho, M., Christensen, B., Chun, Y., Dormann, C., Dray, S., Halbersma, R., Krainski, E., Legendre, P., Lewin-Koh, N., Li, H., Ma, J., Millo, G., Mueller, W., Ono, H., Peres-Neto, P., Piras, G., Reder, M., Tiefelsdorf, M. & Yu, D. (2012) spdep: Spatial dependence: Weighting schemes, statistics and models. R package version 0.5-46.

Bjornstad, O. N. (2009) ncf: Spatial nonparametric covariance functions. R package version 1.1-3.

Bonadonna, F., Benhamou, S. & Jouventin, P. (2003) Orientation in "featureless" environments: The extreme case of pelagic birds. In: *Avian migration* (Berthold, P., Gwinner, E. & Sonnenschein, E., eds). Springer, Berlin. pp. 367-377.

Bridge, E. S., Jones, A. W. & Baker, A. J. (2005) A phylogenetic framework for the terns (sternini) inferred from mtdna sequences: Implications for taxonomy and plumage evolution. *Molecular Phylogenetics and Evolution* **35**: 459-469.

Britton, P. L. & Brown, L. H. (1974) The status and breeding behaviour of East African lari. *Ostrich* **45**: 63-82.

Bruno, J. F., Stachowicz, J. J. & Bertness, M. D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* **18**: 119-125.

Buckley, N. J. (1997) Spatial-concentration effects and the importance of local enhancement in the evolution of colonial breeding in seabirds. *American Naturalist* **149**: 1091-1112.

Burger, A. E. & Shaffer, S. A. (2008) Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *Auk* **125**: 253-264.

Burger, J., Gordon, C., Lawrence, J., Newman, J., Forcey, G. & Vlietstra, L. (2011) Risk evaluation for federally listed (roseate tern, piping plover) or candidate (red knot) bird species in offshore waters: A first step for managing the potential impacts of wind facility development on the Atlantic outer continental shelf. *Renewable Energy* **36**: 338-351.

Burke, C. M. & Montevecchi, W. A. (2009) The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology* **278**: 354-361.

Burness, G. P., Morris, R. D. & Bruce, J. P. (1994) Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male common terns (*Sterna hirundo*). *Canadian Journal of Zoology* **72**: 1243-1251.

BUZM3. (2009-2011) National Oceanic and Atmospheric Administration (NOAA) National Data Buoy Center (NDBC). http://www.ndbc.noaa.gov/station_history.php?station=buzm3.

Camphuysen, C. J., Fox, A. D., Leopold, M. F. & Petersen, I. K. (2004) Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K., Royal Netherlands Institute for Sea Research, Texel.

Camphuysen, C. J. & Garthe, S. (2004) Recording foraging seabirds at sea: Standardised recording and coding of foraging behaviour and multi-species foraging associations. *Atlantic Seabirds* **6**: 1-32.

Camphuysen, C. J. & Webb, A. (1999) Multi-species feeding associations in North Sea seabirds: Jointly exploiting a patchy environment. *Ardea* **87**: 177-198.

Dänhardt, A. & Becker, P. (2011a) Herring and sprat abundance indices predict chick growth and reproductive performance of common terns breeding in the Wadden Sea. *Ecosystems* **14**: 791-803.

Dänhardt, A. & Becker, P. H. (2011b) Does small-scale vertical distribution of juvenile schooling fish affect prey availability to surface-feeding seabirds in the Wadden Sea? *Journal of Sea Research* **65**: 247-255.

Dänhardt, A., Fresemann, T. & Becker, P. (2011) To eat or to feed? Prey utilization of common terns (*Sterna hirundo*) in the Wadden Sea. *Journal of Ornithology* **152**: 347-357.

Davoren, G. K., Montevecchi, W. A. & Anderson, J. T. (2003) Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecological Monographs* **73**: 463-481.

Diamond, A. W. & Devlin, C. M. (2003) Seabirds as indicators of changes in marine ecosystems: Ecological monitoring on Machias Seal Island. *Environmental Monitoring and Assessment* **88**: 153-175.

Duffy, D. C. (1986) Foraging at patches: Interactions between common and roseate terns. *Ornis Scandinavica* **17**: 47-52.

Dunn, E. K. (1972) Studies on terns with particular reference to feeding ecology. Ph.D. Thesis, Univ. of Durham, Durham, UK.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. & Silk, J. R. D. (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration.

Proceedings of the National Academy of Sciences of the United States of America **107**: 2078-2081.

Ehler, C. & Douvere, F. (2009) Marine spatial planning: A step-by-step approach toward ecosystem-based management. Intergovernmental Oceanographic Commission and Man and the Biosphere Programme. IOC Manual and Guides No. 53, ICAM Dossier No. 6, Paris: UNESCO.

Einoder, L. D. (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* **95**: 6-13.

Elliott, K. H., Bull, R. D., Gaston, A. J. & Davoren, G. K. (2009a) Underwater and above-water search patterns of an Arctic seabird: Reduced searching at small spatiotemporal scales. *Behavioral Ecology and Sociobiology* **63**: 1773-1785.

Elliott, K. H., Woo, K. J., Gaston, A. J., Benvenuti, S., Dall'Antonia, L. & Davoren, G. K. (2009b) Central-place foraging in an Arctic seabird provides evidence for storer-ashmole's halo (l'approvisionnement à partir d'un nid central chez un oiseau de mer de l'arctique fournit une preuve du halo de storer-ashmole). *Auk* **126**: 613-625.

Erdman, D. S. (1967) Sea birds in relation to game fish schools off Puerto Rico and the Virgin Islands. *Caribbean Journal of Science* **7**: 79-85.

Erwin, R. M. (1977) Foraging and breeding adaptations to different food regimes in three seabirds: The common tern, *Sterna hirundo*, royal tern, *Sterna maxima*, and black skimmer, *rynchops niger*. *Ecology* **58**: 389-397.

ESRI (2012) ArcGIS desktop 10.0. Environmental Systems Research Institute, Redlands, California, U.S.A.

Evans, P. G. H. (1982) Associations between seabirds and cetaceans: A review. *Mammal Review* **12**: 187-206.

Farine, D. R., Garroway, C. J. & Sheldon, B. C. (2012) Social network analysis of mixed-species flocks: Exploring the structure and evolution of interspecific social behaviour. *Animal Behaviour* **84**: 1271-1277.

Fauchald, P. (2009) Spatial interaction between seabirds and prey: Review and synthesis. *Marine Ecology Progress Series* **391**: 139-151.

Fauchald, P., Skov, H., Skern-Mauritzen, M., Hausner, V. H., Johns, D. & Tveraa, T. (2011) Scale-dependent response diversity of seabirds to prey in the North Sea. *Ecology* **92**: 228-239.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C. & Wanless, S. (2006) From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* **75**: 1259-1268.

Frederiksen, M., Furness, R. W. & Wanless, S. (2007) Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. *Marine Ecology Progress Series* **337**: 279-286.

Fromentin, J. M. & Powers, J. E. (2005) Atlantic bluefin tuna: Population dynamics, ecology, fisheries and management. *Fish and Fisheries* **6**: 281-306.

Furness, R. W. & Camphuysen, K. (1997) Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* **54**: 726-737.

Furness, R. W. & Tasker, M. L. (2000) Seabird-fishery interactions: Quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* **202**: 253-264.

Garrison, L. P., Michaels, W., Link, J. S. & Fogarty, M. J. (2002) Spatial distribution and overlap between ichthyoplankton and pelagic fish and squids on the southern flank of Georges Bank. *Fisheries Oceanography* **11**: 267-285.

Gjerdrum, C., Fifield, D. A. & Wilhelm, S. I. (2012) Eastern Canada seabirds at sea (ecsas) standardized protocol for pelagic seabird surveys from moving and stationary platforms. Canadian Wildlife Service, Atlantic Region.

Gochfeld, M. & Burger, J. (1982) Feeding enhancement by social attraction in the Sandwich tern. *Behavioral Ecology and Sociobiology* **10**: 15-17.

Gochfeld, M., Burger, J. & Nisbet, I. C. T. (1998) Roseate tern (*Sterna dougallii*). In: *The birds of North America* (Poole, A., ed). Cornell Lab of Ornithology, Ithaca, NY.

Goodenough, J., McGuire, B. & Wallace, R. A. (2001) *Perspectives on animal behavior*. John Wiley & Sons, Inc., New York.

Gotmark, F. (1990) A test of the information-center hypothesis in a colony of Sandwich terns *Sterna sandvicensis*. *Animal Behaviour* **39**: 487-495.

Grémillet, D. & Boulinier, T. (2009) Spatial ecology and conservation of seabirds facing global climate change: A review. *Marine Ecology Progress Series* **391**: 121-137.

Grémillet, D., Lewis, S., Drapeau, L., Van Der Lingen, C. D., Huggett, J. A., Coetzee, J. C., Verheye, H. M., Daunt, F., Wanless, S. & Ryan, P. G. (2008) Spatial match–mismatch in the benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology* **45**: 610-621.

Grimes, L. G. (1977) A radar study of tern movements along the coast of Ghana. *Ibis* **119**: 28-36.

Grunbaum, D. & Veit, R. R. (2003) Black-browed albatrosses foraging on Antarctic krill: Density-dependence through local enhancement? *Ecology* **84**: 3265-3275.

Hacker, S. D. & Gaines, S. D. (1997) Some implications of direct positive interactions for community species diversity. *Ecology* **78**: 1990-2003.

Hadfield, J. D. (2010) MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software* **33**: 1-22.

Haney, J. C. (1986a) Seabird affinities for Gulf Stream frontal eddies: Responses of mobile marine consumers to episodic upwelling. *Journal of Marine Research* **44**: 361-384.

Haney, J. C. (1986b) Seabird segregation at Gulf Stream frontal eddies. *Marine Ecology Progress Series* **28**: 279-285.

Haney, J. C., Fristrup, K. M. & Lee, D. S. (1992) Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scandinavica* **23**: 49-62.

Haney, J. C. & Stone, A. E. (1988) Seabird foraging tactics and water clarity: Are plunge divers really in the clear? *Marine Ecology Progress Series* **49**: 1-9.

Hawkins, B. A., Diniz-Filho, J. A. F., Mauricio Bini, L., De Marco, P. & Blackburn, T. M. (2007) Red herrings revisited: Spatial autocorrelation and parameter estimation in geographical ecology. *Ecography* **30**: 375-384.

Hebshi, A. J., Duffy, D. C. & Hyrenbach, K. D. (2008) Associations between seabirds and subsurface predators around Oahu, Hawaii. *Aquatic Biology* **4**: 89-98.

Heinemann, D. (1992) Foraging ecology of roseate terns breeding on Bird Island, Buzzards Bay, Massachusetts. USFWS, Manomet, MA.

Hislop, J. R. G., Harris, M. P. & Smith, J. G. M. (1991) Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *Journal of Zoology* **224**: 501-517.

Hunt, G. L., Jr. & Schneider, D. C. (1987) Scale-dependent processes in the physical and biological environment of marine birds. In: *Seabirds: Feeding ecology and role in marine ecosystems* (Croxall, J. P., ed). Cambridge University Press, Cambridge. pp. 7-41.

Hunt, J. G. L. & McKinnell, S. (2006) Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. *Progress in Oceanography* **68**: 115-124.

Hyrenbach, K. D., Veit, R. R., Weimerskirch, H. & Hunt, G. L. (2006) Seabird associations with mesoscale eddies: The subtropical Indian Ocean. *Marine Ecology Progress Series* **324**: 271-279.

Irons, D. B. (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* **79**: 647-655.

Jaquemet, S., Le Corre, M. & Quartly, G. D. (2007) Ocean control of the breeding regime of the sooty tern in the southwest Indian Ocean. *Deep-Sea Research Part I: Oceanographic Research Papers* **54**: 130-142.

Jaquemet, S., Le Corre, M. & Weimerskirch, H. (2004) Seabird community structure in a coastal tropical environment: Importance of natural factors and fish aggregating devices (FADs). *Marine Ecology Progress Series* **268**: 281-292.

Johnson, J. B. & Omland, K. S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution* **19**: 101-108.

King, J. R., Camisa, M. J. & Manfredi, V. M. (2010) Massachusetts Division of Marine Fisheries trawl survey effort, list of species, and bottom temperature trends, 1978-2007., MADMF.

Kirkham, I. R. (1986) Comparative foraging and breeding habits of Arctic and common terns. Ph.D. Thesis, Dalhousie Univ., Halifax, Nova Scotia.

KMAMARIO3. (2010-2011) Weather Underground. http://www.wunderground.com/weatherstation/WXDailyHistory.asp?ID=KMAMARIO3.

Kress, S. W. & Hall, C. S. (2004) Tern management handbook: Coastal northeastern United States and Atlantic Canada. U.S. Department of the Interior, Fish and Wildlife Service, Hadley, MA.

Lack, D. (1946) Competition for food by birds of prey. *Journal of Animal Ecology* **15**: 123-129.

Lack, D. L. (1968) *Ecological adaptations for breeding in birds*. Methuen, London.

Lamb, K. D. A. (1964) Sea birds at the confluence of the Gulf Stream and the Labrador Current east of New York. *Sea Swallow* **16**.

Langham, N. P. E. (1968) The comparative biology of terns, *Sterna spp.* Ph.D. Thesis, Univ. of Durham, Durham, UK.

Le Corre, M. & Jaquemet, S. (2005) Assessment of the seabird community of the Mozambique channel and its potential use as an indicator of tuna abundance. *Estuarine, Coastal and Shelf Science* **63**: 421-428.

Lotze, H. K. & Worm, B. (2009) Historical baselines for large marine animals. *Trends in Ecology & Evolution* **24**: 254-262.

Lucey, S. & Nye, J. (2010) Shifting species assemblages in the Northeast US continental shelf large marine ecosystem. *Marine Ecology Progress Series* **415**: 23-33.

Lunn, D. J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS - a Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing* **10**: 325-337.

Maclean, I. M. D., Rehfisch, M. M., Skov, H. & Thaxter, C. B. (2013) Evaluating the statistical power of detecting changes in the abundance of seabirds at sea. *Ibis* **155**: 113-126.

MassGIS. (2013) Office of Geographic Information, Commonwealth of Massachusetts, Information Technology Division. http://www.mass.gov.

Miller, D. L. (2012) Distance: A simple way to fit detection functions to distance sampling data and calculate abundance/density for biological populations. Version 0.7.1.

Miller, D. L., Burt, M. L., Rexstad, E. A. & Thomas, L. (2013a) Spatial models for distance sampling data: Recent developments and future directions. *Methods in Ecology and Evolution*: doi: 10.1111/2041-210X.12105.

Miller, D. L., Rexstad, E., Burt, L., Bravington, M. V. & Hedley, S. (2013b) dsm: Density surface modelling of distance sampling data. Version 2.0.1. http://github.com/dill/.

Monaghan, P. (1992) Seabirds and sandeels: The conflict between exploitation and conservation in the northern North Sea. *Biodiversity and Conservation* **1**: 98-111.

Montevecchi, W. A., Benvenuti, S., Garthe, S., Davoren, G. K. & Fifield, D. (2009) Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. *Marine Ecology Progress Series* **385**: 295-306.

Monticelli, D., Ramos, J. A. & Pereira, J. (2006) Habitat use and foraging success of roseate and common terns feeding in flocks in the Azores. *Ardeola* **53**: 293-306.

Monticelli, D., Ramos, J. A. & Quartly, G. D. (2007) Effects of annual changes in primary productivity and ocean indices on breeding performance of tropical roseate terns in the western Indian Ocean. *Marine Ecology Progress Series* **351**: 273-286.

Mostello, C. S. (2010) Inventory of terns, laughing gulls, and black skimmers nesting in Massachusetts in 2009. MDFW, Natural Heritage and Endangered Species Program (NHESP), Westborough, MA.

Mostello, C. S. (2011) Inventory of terns, laughing gulls, and black skimmers nesting in Massachusetts in 2010. MDFW, NHESP, Westborough, MA.

Mostello, C. S. (2012) Inventory of terns, laughing gulls, and black skimmers nesting in Massachusetts in 2011. MDFW, NHESP, Westborough, MA.

National Marine Fisheries Service. (2013) A guide to the tunas of the western Atlantic ocean. Noreast Media, LLC. http://www.noreast.com/tuna/tunapage2.cfm.

Nisbet, I. C. T. (2002) Common tern (*Sterna hirundo*). In: *The birds of North America* (Poole, A., ed). Cornell Lab of Ornithology, Ithaca, NY.

Nisbet, I. C. T. & Drury, W. H. (1972) Measuring breeding success in common and roseate terns. *Bird-Banding* **43**: 97-106.

Nisbet, I. C. T., Mostello, C. S., Veit, R. R., Fox, J. W. & Afanasyev, V. (2011) Migration and winter quarters of five common terns tracked using geolocators. *Waterbirds* **34**: 32-39.

Nisbet, I. C. T. & Spendelow, J. A. (1999) Contribution of research to management and recovery of the roseate tern: Review of a twelve-year project. *Waterbirds* **22**: 239-252.

Nye, J. A., Gamble, R. J. & Link, J. S. (2013) The relative impact of warming and removing top predators on the Northeast US large marine biotic community. *Ecological Modelling* **264**: 157-168.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A. F., Miller, P. I. & Louzao, M. (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation* **156**: 94-104.

Orians, G. H. & Pearson, N. E. (1979) On the theory of central place foraging. In: *Analysis of ecological systems* (Horn, D. J., Mitchell, R. D. & Stairs, G. R., eds). Ohio State University Press, Columbus. pp. 155-177.

Oro, D. (1995) Audouins gulls *Larus audouinii* associate with subsurface predators in the mediterranean sea. *Journal fur Ornithologie* **136**: 465-467.

Overholtz, W. J., Jacobson, L. D., Melvin, G. D., Cieri, M., Power, M., Libby, D. & Clark, K. (2004) Gulf of Maine - Georges Bank Atlantic herring complex, 2003. Northeast Fisheries Science Center.

Overholtz, W. J. & Link, J. S. (2007) Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977–2002. *ICES Journal of Marine Science* **64**: 83-96.

Overholtz, W. J., Link, J. S. & Suslowicz, L. E. (2000) Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. *ICES Journal of Marine Science* **57**: 1147-1159.

Pallaud, B. (1984) Hypotheses on mechanisms underlying observational learning in animals. *Behavioural Processes* **9**: 381-394.

Perrow, M. R., Skeate, E. R. & Gilroy, J. J. (2011) Visual tracking from a rigid-hulled inflatable boat to determine foraging movements of breeding terns. *Journal of Field Ornithology* **82**: 68-79.

Powers, K. D. (1984) Pelagic distributions of marine birds off the northeastern United States. U.S. Dept. of Commerce, NOAA Technical Memorandum NMFS–F/NEC–27.

Poysa, H. (1992) Group foraging in patchy environments: The importance of coarse-level local enhancement. *Ornis Scandinavica* **23**: 159-166.

R Development Core Team (2012) R: A language and environment for statistical computing. Version 2.15.0. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Racine, F., Giraldeau, L. A., Patenaude-Monette, M. & Giroux, J. F. (2012) Evidence of social information on food location in a ring-billed gull colony, but the birds do not use it. *Animal Behaviour* **84**: 175-182.

Ramos, J. A. (2000) Characteristics of foraging habitats and chick food provisioning by tropical roseate terns. *Condor* **102**: 795-803.

Regular, P. M., Hedd, A. & Montevecchi, W. A. (2013) Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Animal Behaviour* **86**: 545-552.

Ricklefs, R. E. (2004) The cognitive face of avian life histories: The 2003 Margaret Morse Nice lecture. *Wilson Bulletin* **116**: 119-133.

Robards, M. D., Anthony, J. A., Rose, G. A. & Piatt, J. F. (1999) Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. *Journal of Experimental Marine Biology and Ecology* **242**: 245-258.

Robards, M. D., Willson, M. F., Armstrong, R. H. & Piatt, J. F. (2000) Sand lance: A review of biology and predator relations and annotated bibliography. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Roberts, D. (1941) Imitation and suggestion in animals. *Bulletin of Animal Behaviour* **1**: 11-19.

Roberts, J., Best, B., Dunn, D., Treml, E. & Halpin, P. (2010) Marine geospatial ecology tools: An integrated framework for ecological geoprocessing with ArcGIS, python, R, matlab, and c++. Environmental Modelling & Software 25. 1197-1207. http://mgel.env.duke.edu/mget.

Robins, C. R. & Ray, G. C. (1986) *A field guide to Atlantic coast fishes: North America*. The Peterson Field Guide Series, Houghton Mifflin Company, New York, NY.

Rock, J. C., Leonard, M. L. & Boyne, A. W. (2007) Foraging habitat and chick diets of roseate tern, *Sterna dougallii*, breeding on country island, Nova Scotia. *Avian Conservation and Ecology* **2**: 4. http://www.ace-eco.org/vol2/iss1/art4/.

Safina, C. (1990a) Bluefish mediation of foraging competition between roseate and common terns. *Ecology* **71**: 1804-1809.

Safina, C. (1990b) Foraging habitat partitioning in roseate and common terns. *Auk* **107**: 351-358.

Safina, C. & Burger, J. (1988) Ecological dynamics among prey fish, bluefish, and foraging common terns in an Atlantic coastal system. In: *Seabirds and other marine vertebrates: Competition, predation, and other interactions* (Burger, J., ed). Columbia University Press, New York, NY. pp. 95-173.

Safina, C., Burger, J., Gochfeld, M. & Wagner, R. H. (1988) Evidence for prey limitation of common and roseate tern reproduction. *Condor* **90**: 852-859.

Safina, C. & Klinger, D. H. (2008) Collapse of bluefin tuna in the western Atlantic. *Conservation Biology* **22**: 243-246.

Safina, C., Wagner, R. H., Witting, D. A. & Smith, K. J. (1990) Prey delivered to roseate and common tern chicks; composition and temporal variability. *Journal of Field Ornithology* **61**: 331-338.

Saracco, J., Royle, J., DeSante, D. & Gardner, B. (2012) Spatial modeling of survival and residency and application to the monitoring avian productivity and survivorship program. *Journal of Ornithology* **152**: 469-476.

Saracco, J. F., Royle, J. A., DeSante, D. F. & Gardner, B. (2010) Modeling spatial variation in avian survival and residency probabilities. *Ecology* **91**: 1885-1891.

Scheid, C. & Bugnyar, T. (2008) Short-term observational spatial memory in jackdaws (*Corvus monedula*) and ravens (*Corvus corax*). *Animal Cognition* **11**: 691-698.

Scott, M., Chivers, S., Olson, R., Fiedler, P. & Holland, K. (2012) Pelagic predator associations: Tuna and dolphins in the eastern tropical Pacific ocean. *Marine Ecology Progress Series* **458**: 283-302.

Seed, A., Emery, N. & Clayton, N. (2009) Intelligence in corvids and apes: A case of convergent evolution? *Ethology* **115**: 401–420.

Shealer, D. A. (1996) Foraging habitat use and profitability in tropical roseate terns and Sandwich terns. *Auk* **113**: 209-217.

Shealer, D. A. (1998) Size-selective predation by a specialist forager, the roseate tern. *Auk* **115**: 519-525.

Shealer, D. A. (2001) Foraging behavior and food of seabirds. In: *Biology of marine birds* (Schreiber, E. A. & Burger, J., eds). CRC Press, New York, NY. pp. 137-177.

Shealer, D. A. & Kress, S. W. (1994) Postbreeding movements and prey selection of roseate terns at Stratton Island, Maine. *Journal of Field Ornithology* **65**: 349-362.

Shettleworth, S. J. (1998) Cognition, evolution, and the study of behavior. In: *Cognition, evolution, and behavior*. Oxford University Press, New York. pp. 3-47.

Silverman, E. D., Veit, R. R. & Nevitt, G. A. (2004) Nearest neighbors as foraging cues: Information transfer in a patchy environment. *Marine Ecology Progress Series* **277**: 25-35.

Skov, H., Durinck, J., Danielsen, F. & Bloch, D. (1995) Co-occurrence of cetaceans and seabirds in the Northeast Atlantic. *Journal of Biogeography* **22**: 71-88.

Spendelow, J. A., Hines, J. E., Nichols, J. D., Nisbet, I. C. T., Cormons, G., Hays, H., Hatch, J. J. & Mostello, C. S. (2008) Temporal variation in adult survival rates of roseate terns during periods of increasing and declining populations. *Waterbirds* **31**: 309-319.

Spendelow, J. A., Mostello, C. S., Nisbet, I. C. T., Hall, C. S. & Welch, L. (2010) Interregional breeding dispersal of adult roseate terns. *Waterbirds* **33**: 242-245.

Stachowicz, J. J. (2001) Mutualism, facilitation and the structure of ecological communities. *BioScience* **51**: 235-246.

Sturtz, S., Ligges, U. & Gelman, A. (2005) R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software* **12**: 1-16.

Szostek, K. & Becker, P. (2012) Terns in trouble: Demographic consequences of low breeding success and recruitment on a common tern population in the german Wadden Sea. *Journal of Ornithology* **153**: 313-326.

Tasker, M. L., Hope-Jones, P., Dixon, T. & Blake, B. F. (1984) Counting seabirds at sea from ships: A review of methods and a suggestion for a standardized approach. *Auk* **101**: 567-577.

Thomas, A., Best, N., Lunn, D., Arnold, R. & Spiegelhalter, D. (2004) Geobugs user manual. Version 1.2. http://www.mrc-bsu.cam.ac.uk/bugs.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R., Marques, T. A. & Burnham, K. P. (2010) Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* **47**: 5-14.

Thorpe, W. H. (1951) The learning abilities of birds. *Ibis* **93**: 252-296.

Tims, J., Nisbet, I. C. T., Friar, M. S., Mostello, C. & Hatch, J. J. (2004) Characteristics and performance of common terns in old and newly-established colonies. *Waterbirds* **27**: 321-332.

Walli, A., Teo, S. L. H., Boustany, A., Farwell, C. J., Williams, T., Dewar, H., Prince, E. & Block, B. A. (2009) Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. *PLoS ONE* **4**.

Waltz, E. C. (1987) A test of the information center hypothesis in 2 colonies of common terns, *Sterna hirundo*. *Animal Behaviour* **35**: 48-59.

Ward, P. & Zahavi, A. (1973) The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis* **115**: 517-534.

Weimerskirch, H. (2007) Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II -Topical Studies in Oceanography* **54**: 211-223.

Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C. & Goya, E. (2010) Use of social information in seabirds: Compass rafts indicate the heading of food patches. *PLoS ONE* **5**: e9928.

Wickham, H. (2009) Ggplot2: Elegant graphics for data analysis. Springer, New York. http://ggplot2.org/.

Wikelski, M., Kays, R. W., Kasdin, N. J., Thorup, K., Smith, J. A. & Swenson, G. W. (2007) Going wild: What a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology* **210**: 181-186.

Williams, C. T., Whittam, B. & Purvis, M. (2009) The nearshore distribution of terns and other seabirds in relation to industrial project development in Stormont Bay, Nova Scotia. Bird Studies Canada, Atlantic Region.

Wittenberger, J. F. & Hunt, G. L., Jr. (1985) The adaptive significance of coloniality in birds. In: *Avian biology*, Vol. 8 (Farner, D., King, J. & Parkes, K., eds). Academic Press, New York. pp. 1-78.

Wood, S. N. (2006) *Generalized additive models: An introduction with R*. Chapman & Hall/CRC, New York, NY.

Wynne, K., Schwartz, M. & Mix, G. (1999) *Guide to marine mammals & turtles of the U.S. Atlantic & Gulf of Mexico*. Rhode Island Sea Grant, University of Rhode Island, Narragansett, RI.

Yoerg, S. I. (2001) *Clever as a fox: Animal intelligence and what it can teach us about ourselves*. Bloomsbury. Distributed by St. Martin's Press, New York.

Zuur, A. F. (2010) AED: Data files used in mixed effects models and extensions in ecology with R (Zuur et al. 2009). R package version 1.0. http://www.highstat.com/book2.htm.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**: 3-14.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, NY.

Zuur, A. F., Saveliev, A. A. & Ieno, E. N. (2012) *Zero inflated models and generalized linear mixed models with R*. Highland Statistics, Ltd., Newburgh, UK.