12-2012

Life History Variation of Common Terns in the Gulf of Maine

Jeffery Bryant Kimmons
University of Arkansas, Fayetteville

Recommended Citation

Kimmons, Jeffery Bryant, "Life History Variation of Common Terns in the Gulf of Maine" (2012). *Theses and Dissertations*. 641.
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LIFE HISTORY VARIATION OF COMMON TERNS IN THE GULF OF MAINE

LIFE HISTORY VARIATION OF COMMON TERNS IN THE GULF OF MAINE

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

By

Jeffery Bryant Kimmons
Drury University
Bachelor of Arts in Biology, 1998
Missouri State University
Master of Science in Biology, 2003

December 2012
University of Arkansas

ABSTRACT

Life history is the inheritable rules that determine energy and time allocation towards different competing functions in the energy budget of an organism. Reproductive effort varies as organisms make reproductive decisions based on available energy. Factors influencing life histories are those that change energy and time budgets such as diet, competition, and environmental conditions.

Common tern (*Sterna hirundo*) life history phenotypes vary between islands in the Gulf of Maine. Common terns on offshore islands (>10km from mainland) and nearshore islands (5 to 10km from mainland) lay smaller clutches, hatching chicks with slower growth rates than common terns on inshore islands (<5km from mainland). Previous research suggests differences are due to offshore colonies consuming lower quality prey than inshore terns. Common tern diets on different islands were determined by carbon and nitrogen stable isotopes in juvenile feathers and observations of prey deliveries to juveniles by adults. Common terns on offshore islands were feeding low quality euphasiids (*Meganyctiphanes norvegica*) and had a depleted nitrogen signature relative to inshore islands feeding on fish.

Common terns could be competing with other tern species. Offshore island colonies contain arctic (*Sterna paradisaea*) and common terns, inshore and nearshore colonies contain common and roseate (*Sterna dougallii*) terns. Competition was determined by overlap of carbon and nitrogen stable isotopes in juvenile feathers and Morisita’s index of dietary overlap for observed prey deliveries by adults to juveniles. Competition could exist between arctic and common terns on Matinicus Rock, an offshore island, and common and roseate terns on Outer Green Island, an inshore colony and Eastern Egg Rock, a nearshore island.

Decreased temperatures between islands also forces chicks to expend more energy for thermoregulation instead of growth. Thermoregulatory costs between offshore and inshore islands were measured using copper models representing tern chicks. Thermoregulatory costs were higher on offshore islands relative to inshore islands.

Common tern phenotype plasticity in the Gulf of Maine was mainly due to diet. Consistent cooler temperature on offshore colonies also influences energy dedicated to growth in juveniles. Competition may limit energy budgets, but possible competition could be seen on all island types.

This dissertation is approved for

Recommendation to the
Graduate Council

Dissertation Director:

Dr. Kimberly G. Smith

Dissertation Committee:

Dr. Steven J. Beaupre

Dr. Gary R. Huxel

Dr. Ian C. T. Nisbet

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ACKNOWLEDGMENTS

I thank the following organizations for providing funding for this study: Arkansas Audubon Society Trust and the Nisbet Research Grant. I thank the staff and volunteers of National Audubon Society's Seabird Restoration Program for assistance with feather collection and feeding observations, especially island supervisors – Noel Dodge, Suzanne Dodge, Christina Donehower, Johanna Hiscock, Katie Kauffman, Matt Klostermann, Alison Kocek, Juliet Lamb, Pam Loring, Matt Martinkovic, Ellen Peterson, Lauren Scopel, Paula Shannon, Emily Tupper, and Carlos Zavalaga. I thank Scott Hall and Steve Kress for mentorship on the field sites. I thank the University of Arkansas Stable Isotope Laboratory Staff for analyses and advice – Erik Pollock and Tom Millican. I thank Elisha Ott for assistance in preparing isotope specimens. I thank the Biological Sciences office staff for all clerical support, especially Wanda Parr and Nancy Welsh.

I thank present and former members of the Smith Lab and fellow graduate students for their support and encouragement, especially Christy Slay, Mike Slay, Jason Luscier, James Van Dyke, Melissa Pilgrim, Sara Wittenberg, Lara Douglas, Joe Agugliaro, and Jason Ortega. I thank the University of Arkansas for support through my graduate assistanceship and Jeanne McLachlin for support for any student related problems in the Human Physiology Labs.

I especially thank Steve Beaupre, Gary Huxel, Ian Nisbet, and Kimberly Smith for their advice, editing, and use of their laboratory facilities. Finally I thank Amanda Lightcap for her help on islands and in the lab, and my mother, Lula Kimmons, for her continuous support.

DEDICATION

This work is dedicated to the memory of John Kimmons, whose commitment to veterinary medicine and hard work gave me a platform to build my interests in the sciences.

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CHAPTER 1. INTRODUCTION

Life histories are genetic rules that interact with environmental conditions to produce characteristics of a population (Dunham et al. 1989). Life history will determine how energy is allocated to competing functions within an energy budget (Cody 1966; Gadgil and Bossert 1970; Drent and Daan 1980). Functions, such as reproductive effort, are determined by available resources (Stearns 1976). Energy budgets are limited. If not enough energy is acquired then portions of a budget have to be decreased or an organism may not survive (Bryant 1979; Nur 1988).

Energy budgets can be balanced with reproductive trade-offs that allow an organism to maximize current reproduction under particular environment conditions (Stearns 1989; Roff 1992). Energy can be conserved by limiting reproductive effort, growth rates, or maturing later in life (Drent and Daan 1980). Reproductive effort is the amount of energy and nutrients devoted to offspring throughout reproduction (Stearns 1976).

Birds, as determinate growers, are limited in reproductive trade-offs to egg size, clutch size, or number of clutches within a season (Lack 1968). Variation among reproductive traits is mainly a result of food availability during each stage of reproduction (Martin 1987). However traits can also fluctuate depending on other environmental factors besides foraging resources (Schew and Ricklefs 1998).

Although seabird life history characteristics are strongly influenced by prey availability (Kitaysky et al. 2000), many seabirds have the ability to change their life history phenotypes in different environmental conditions. Some seabirds are known to change parental effort during different stages of reproduction to compensate for low prey availability (Uttley et al. 1994) and extreme temperatures (Nisbet 1982; Klaassen 1994; Klaassen et al. 1994) impacting chick energy budgets. Additional parental effort is only used to compensate for poor resources rather than to gain additional resources in areas with better foraging (Zador and Piatt 1999). Life history phenotypes appear to be set by foraging resources available to these birds, but instead birds are choosing not to forage for additional resources.

Seabirds, such as common terns (*Sterna hirundo*), display reproductive trade-offs in various environmental conditions among different locations (Nisbet 2002; Becker and Ludwigs 2004). Common terns only lay one clutch per year (Hays 1984) therefore reproductive trade-offs are concentrated to one event. A lot of energy can be saved by manipulating this single clutch as a large portion of female's energy budget is dedicated to clutch formation (Wiggins and Morris 1987; Wendeln 1997).

Common terns have the ability to expand their clutch size if they want. Female common terns lay additional eggs to replace eggs lost from a nest within a week of initial laying (Nisbet 1978; Arnold et al. 1998; Wendeln et al. 2000; Becker and Zhang 2010). However increasing clutch size may not increase overall productivity if a tern pair cannot support additional offspring in a particular environment (Langham 1972). Common tern reproductive effort is limited during other reproductive stages than egg production.

Explanations of common tern life history plasticity are focused primarily on food. Common terns arrive on their breeding sites after an extensive migration (Austin 1953; Nisbet et al. 2011), forcing terns to rely on exogenous resources to fuel reproduction (Pearson 1968). Life history phenotypes have been correlated to many factors influencing foraging success. Common tern foraging success is influenced by age (Nisbet 1973; Nisbet et al. 1984), experience (Nisbet 1983; Arnold et al. 2004), body condition (Nisbet 1973; Wendeln and Becker 1996; Wendeln 1997; Wendeln and Becker 1999; Becker et al. 2001), prey availability (Hall et al. 2000; Schwemmer et al. 2009; Danhardt et al. 2011), and weather (Dunn 1972, 1973, 1975). Factors influencing foraging success may account for most variation within a single colony (Massias and Becker 1990; Hall and Kress 2004), but foraging success may not be the same factors influencing phenotypes among colonies (Nisbet et al. 1984).

A unique situation has been created to view life history phenotype variations between different common tern colonies in the Gulf of Maine. National Audubon Society's Seabird Restoration Program (SRP) has restored seven tern nesting islands along the Maine coast. Life history phenotype variation has been observed among islands based on their distance from the mainland. Common terns on offshore islands (>10km from mainland) and nearshore islands (5 to 10km from mainland) lay small clutches that hatch chicks with slower growth rates, reaching a smaller asymptotic mass before fledging than common terns on inshore islands (<5km from mainland; Hall and Kress 2004).

The goal of my research is to determine proximate causes for life history phenotype variation in common terns among SRP islands. Phenotype variation in the Gulf of Maine metapopulation is not likely due to genetic variation among locations (Burson 1990). Although many factors could exist that would influence tern energy budgets on various islands, I specifically will test 1) dietary, 2) competition, and 3) thermoregulatory cost differences among SRP islands. Previous work by Hall and Kress (2004) indicate dietary differences as the cause for variation on SRP islands. Terns on offshore islands have been observed delivering a higher percentage of invertebrates to the nest than inshore islands (Hall et al. 2000). Offshore terns may also be traveling farther to forage than inshore terns (Hall and Kress 2004).

Dietary differences among SRP islands will be determined by observations of prey deliveries and stable isotopes. Common tern adults carry prey perpendicular in their mouths back to the nest allowing for identification of prey species and size. Carbon and nitrogen stable isotopes have been used to determine seabird diets (ex. Hobson 1987; Hobson et al. 1994; Minami et al. 1995; Bearhop et al. 2006) and specifically diets of common terns (Hobson et al. 2000; Nisbet et al. 2002; Charette 2005). $\delta^{13}C$ and $\delta^{15}N$ enrich as organisms forage in higher trophic levels allowing for trophic level comparisons between islands (Deniro and Epstein 1978; Wada et al. 1987; Fry 1988; Hobson and Welch 1992).

There are several advantages to using stable isotopes to determine tern diets on SRP islands. Isotope analysis will allow for identification of unidentified fish, which is one disadvantage of using observations alone (Barrett 2007; Danhardt et al. 2011). Analysis of assimilated diet can be done with non-invasive tissue sampling when using tissue such as feathers. Stable isotopes show assimilated diet overtime in which a sampled tissue was grown (Hobson and Clark 1992; Bearhop et al. 2002) allowing for diet to be assessed for juveniles as they develop in individual breeding colonies.

A major principle behind SRP's restoration efforts is to maximize tern population size in the Gulf of Maine. Terns foraging close to their breeding colonies (Duffy 1986; Becker et al. 1993) could limit foraging resources, influencing life history phenotypes (Ashmole 1963). To assess possible competition associated with SRP islands I will use Morisita's index of dietary overlap modified by Horn (1966; Diamond 1982) and use stable isotopes of carbon and nitrogen to compare assimilated diets between arctic (*Sterna paradisaea*), common, and roseate (*Sterna dougallii*) terns on islands containing multiple species. Carbon and nitrogen stable isotopes show assimilated diets over time, and possibly feeding locations as carbon isotopes can enrich if terns are feeding in areas closer to the mainland (Rau et al. 1982; Goericke and Fry 1994; Cherel et al. 2000; Nisbet et al. 2002). Although Morisita's index values and stable isotopes do not directly show competition, there will be a higher probability for competition between species in a specific colony if there is high observed dietary overlap and similar carbon and nitrogen stable isotope signatures.

Although food may be contributing more to phenotype variation among SRP islands (Martin 1987), other factors, such as thermoregulation, could be taking away energy and time from tern juveniles and adults. Terns in colder environments will expend more energy thermoregulating when not being brooded (Visser and Ricklefs 1993; Klaassen 1994). To determine differences in thermoregulation among tern colonies I will use copper models to compare thermoregulatory costs on inshore and offshore colonies. To calculate thermoregulatory costs, operative temperatures will be measured using models that represent six day old tern chicks. Operative temperature is the temperature an organism due to convection, conduction, and radiation (Bakken 1976). Operative temperatures will be applied in Klaassen's (1994; 1995) equations for estimating thermoregulatory cost. If operative temperatures are lower on offshore colonies relative to inshore colonies, then offshore thermoregulatory costs will be greater than on inshore colonies. Higher thermoregulatory costs could limit growth rate of offshore chicks relative to inshore chicks, assuming that brooding time and diet is the same between inshore and offshore colonies (Klaassen 1994, Klaassen et al. 1994)

Life history plasticity among SRP island terns has a large impact as it determines which islands will be sources or sinks for the Gulf of Maine common tern metapopulation. Determining overall influence of diet, competition, and energy for thermoregulation on reproductive phenotypes of common terns among colonies will give a better understanding of how multiple factors play a role in life history expression between locations. As life history influences energy and time budgets, multiple factors need to be assessed to determine how life histories are being expressed in separate locations.

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CHAPTER 2. REPRODUCTIVE LIFE HISTORY PLASTICITY IN COMMON TERNS IN THE GULF OF MAINE: A STABLE ISOTOPE APPROACH

ABSTRACT

Life history plasticity occurs among common tern (*Sterna hirundo*) colonies in the Gulf of Maine. Variations in life history have been observed as increased clutch size, higher growth rate, and asymptotic mass for chicks on inshore islands (<5 km from mainland) relative to nearshore (5 to 10 km) and offshore islands (>10 km). To determine if energy inputs are driving this life history phenomenon, common tern diet was monitored from 2005 to 2007 on National Audubon Society Seabird Restoration Program islands. Common tern diet was determined by observations of adult prey deliveries to chicks as well as carbon and nitrogen stable isotope analyses of 16-18 day old juvenile feathers. Carbon and nitrogen feather signatures were compared to prey items dropped in the colony and collected from juveniles at the nest to determine juvenile diet. Common terns on inshore islands were observed consuming a higher percentage of fish, hake and herring, than terns on offshore islands. Offshore island terns were observed consuming more invertebrates than inshore islands. Feather nitrogen values were most deplete in offshore common tern juveniles during all three years. Depleted nitrogen values on offshore islands indicate offshore terns were feeding at a lower trophic level than terns nesting closer to the mainland. Dropped prey collected in colonies had similar carbon and nitrogen values for many common fish species, including invertebrates, preventing more precise diet estimations. Reproductive phenotypes on offshore islands were probably due to decreased energy to parents and offspring as common terns were specializing on invertebrates. Common terns on inshore islands had higher quality diets which gave them more energy to dedicate to reproduction.

INTRODUCTION

Life histories govern phenotypes produced due to the environmental influence on an organism's genetic makeup. Different organismal responses to environmental conditions during various stages of life lead to differences in populations. Organisms with greater genetic variability produce a wider variety of phenotypes depending upon energy availability to competing categories of an organism's energy budget. Life histories determine energy allocations to competing functions, allowing organisms to redistribute energy to stay within energy budget limits (Cody 1966; Gadgil and Bossert 1970; Drent and Daan 1980). Operating beyond energy budget decreases future survivorship (Bryant 1979; Nur 1988).

Costly events such as reproduction require organisms to make trade-offs to maintain within an energy budget in environments without high food availability (Drent and Daan 1980; Stearns 1989). Determinate growers, such as birds, display a wider variety of reproductive trade-offs as they possess less competing categories in their energy budgets relative to non-determinant growers, such as reptiles (Schluter et al. 1991). Tradeoffs balance energy budgets between current costs of reproduction and survival (Stearns 1989; Dijkstra et al. 1990; Roff 1992; Niewiarowski and Dunham 1994). Allocable energy for different functions is affected by location due to foraging time and available food supply (Lack 1954) or through density dependent factors influencing competition (Ashmole 1963).

Even with increased flexibility for tradeoffs, birds vary in their ability to allocate energy within energy budgets. Common reproductive trade-offs within birds include variations in egg size, clutch size, and chick growth rate (Lack 1968). Variation in egg and clutch size allows for initial adjustment of reproductive effort prior to laying. Reproductive effort is also adjusted after hatch for nidicolous birds relying on parental care, influencing juvenile growth rate.

Seabirds, such as common terns (*Sterna hirundo*), are good models to observe reproductive trade-offs. Common terns have little leeway in their energy budgets as they expend three to six times their basal metabolic rate per day during while feeding chicks (Gailbraith et al. 1999). Such high energy demands causes common terns to allocate energy to reproduction based on environmental sources available around the colony instead of from storage (Pearson 1968). Common terns have a short foraging range causing resources dedicated to reproduction to be obtained from foraging locations near their breeding colonies (Duffy 1986; Becker et al. 1993). Reproductive decisions made by common terns are based mostly on available energy resources around their breeding colonies (Pearson 1968; Hobson et al. 2000; Ezard et al. 2007). This relationship between energy availability and reproductive output is apparent as common terns display many different reproductive phenotypes within and between different breeding locations (Nisbet 2002; Becker and Ludwigs 2004).

Variation in phenotypes by common terns are impacted by environmental resources and not solely genetic variability between locations. Although common terns nesting on islands in northern and northeast North America exhibit high nest site fidelity, initial nest site selection may not be in their natal colony (Dittmann et al. 2005). Dispersal from the natal colony creates gene flow among colonies resulting in genetic similarity among colonies (Burson 1990). When forced to change breeding locations common terns are known to change reproductive output becoming similar to individuals at the new breeding colony overtime (C. Scott Hall per. comm..). Therefore life history variation in common terns is influenced by adult performance and their surrounding environment not just genetic constraints.

Without genetic constraints, a strong relationship exists between common tern foraging success and reproductive life history phenotype. Common terns consume fish and to a lesser extent crustacean and mollusks in freshwater and marine environments depending on the location of their breeding colony (Pearson 1968; Hopkins and Wiley 1972; Lemmetyinen 1976; Courtney and Blokpoel 1980; Safina et al. 1990; Hall et al. 2000). Breeding ranges for common terns extend from freshwater lakes to oceanic islands (Nisbet 2002). Terns nesting on islands close to the mainland are known to forage along the coastline (Nisbet 1983; Duffy 1986; Safina et al. 1988). It is suspected that terns nesting farther from the mainland on offshore islands travel to coastal areas to feed as well (Hall and Kress 2004).

In terns, reproductive phenotypes for a pair are influenced by male performance during the three reproductive stages; courtship, incubation, and brooding. During courtship, females acquire materials for egg production from male food deliveries (Nisbet 1973). Females have the greatest mass gain during courtship as the entire clutch is formed before laying (Wendeln and Becker 1996). Male provisioning is positively correlated with clutch size and body mass making male performance directly related to female output (Nisbet 1973; Wendeln 1997). Males continue to provide for females during incubation. After chicks hatch, females brood chicks until chicks can thermoregulate while males forage for both females and chicks (Wiggins and Morris 1987). Females require a high amount of protein during egg production while chicks require a high protein diet throughout their development (Lilja 1997). Males preferentially deliver higher quality food back to the nest, if available (Danhardt et al. 2011). Absence of proper nutrition at any stage of reproduction could decrease clutch size or chick growth rates.

Male ability to provide for females and offspring is determined by their foraging success. Common tern foraging success is influenced by age (Nisbet 1973; Nisbet et al. 1984), experience (Nisbet 1983; Arnold et al. 2004), body condition (Nisbet 1973; Wendeln and Becker 1996; Wendeln 1997;

Wendeln and Becker 1999; Becker et al. 2001), and prey availability (Hall et al. 2000; Schwemmer et al. 2009; Danhardt et al. 2011). However other influences can restrict common tern reproductive output beyond foraging success alone.

Variation in clutch characteristics may not be based solely on energy available to females during clutch formation. Females are using male courtship feedings to acquire materials for egg production. Male performance during this time may function as a tool for mate selection as well. Females could be using performance to judge a males ability to provide during later stages of reproduction (Nisbet 1973). Common terns rarely produce two clutches in a season (Hays 1984), limiting reproduction to be a typically single event for a pair. Females are choosing to limit the clutch size produced as they can lay additional eggs to replace those lost from the nest within a week of initial laying period (Nisbet 1978; Arnold et al. 1998; Wendeln et al. 2000). Indirectly, females are being influenced further by environmental characteristics of a colony location as it too will have an impact on male foraging performance being viewed by the female.

As females have the ability to adjust reproductive output, environmental characteristics of a given colony may play a larger role in determining life history characteristics. Many parameters that influence life history characteristics are evaluated within breeding colonies, but rarely are factors investigated among colonies. Clutch size, clutch mass, and chick growth rate fluctuate between different populations. Factors such as age and body condition that are considered to be influential within a colony may not be the sole reason for variation among colonies (Nisbet et al. 1984). Reproductive differences between colonies have emphasized prey availability, foraging locations, time between prey deliveries, competition for shared resources, and differences in parental foraging behavior (Hunt 1972; Hunt et al. 1986; Lewis et al. 2001; Falk et al. 2002; Davoren and Montevecchi 2003; Hall and Kress 2004). These factors all have an impact on foraging success and are influenced by environmental characteristics of foraging habitat around colonies and not solely male condition.

Reproductive phenotype variations have been observed on seven islands managed by National Audubon Society’s Seabird Restoration Program (SRP) along the Gulf of Maine coast (Hall and Kress 2004). Variations in life history have been observed as increased clutch size, and higher growth rate and asymptotic mass for chicks on inshore islands (<5 km from mainland) relative to nearshore (5 to 10 km) and offshore islands (>10 km; Hall and Kress 2004). Life history phenotype differences were originally attributed to energy availability as foraging rate for nearshore and offshore islands was lower relative to inshore islands (Hall and Kress 2004). Prey quality may also be playing a role as offshore and nearshore island adults are delivering lower quality prey items back to chicks, such as sticklebacks and euphasiids (Braune 1987; Massias and Becker 1990; Hall et al. 2000). Prey variation in chick diet has been determined using nest observations from blinds described by Hall et al. (2000). However nests are only being observed at peak foraging times throughout the day (Hall et al. 2000).

The objective of this study was to determine dietary differences of common terns on seven islands managed by SRP by combining nest observations and stable isotopes of carbon and nitrogen. Carbon and nitrogen stable isotopes have been used to determine dietary sources within marine birds (Hobson 1987, 1990; Mizutani et al. 1990; Hobson and Welch 1992; Rau et al. 1992; Hobson et al. 1994; Minami et al. 1995; Forero et al. 2002) and specifically with common terns (Hobson et al. 2000; Nisbet et al. 2002). Common tern adult diet was estimated using juvenile feather carbon and nitrogen values. Assimilated diet of chicks closely represents diet assimilated by adults (Nisbet et al. 2002). Evaluating chick diets using feathers is a less destructive tissue to sample and represents assimilated diet during the time period in which feathers are grown (Hobson 1999).

If common terns on offshore and nearshore islands are feeding on lower quality prey than common terns on inshore islands, offshore and nearshore terns should have a more deplete nitrogen, and to a lesser extent, carbon values than inshore common terns (Hobson et al. 1994). Decreases in growth rate due to starvation can influence deposition of nitrogen, but not carbon, isotopes in feathers during formation (Hobson et al. 1993). , siblings with varying growth rates were tested for differences in delta carbon and nitrogen. As offshore and nearshore colonies have a decreased growth rate due to diet, isotope deposition needs to be examined in common terns to be sure nitrogen signatures in feathers are due to diet and not starvation. Therefore carbon and nitrogen isotopes were compared between siblings with varying growth rates to determine isotope deposition varies with consumption.

METHODS

Field Sites

Common terns nest on seven islands managed by National Audubon Society's Seabird Restoration Program (SRP). Islands are grouped into three categories based on distance away from the mainland; inland, nearshore, and offshore islands.

<u>Inland Islands</u> (< 5 km for mainland)

Three islands are considered inland islands; Stratton Island, Jenny Island, and Pond Island National Wildlife Refuge (Figure 1). Stratton Island (SI) is a 12.2 ha island located in Saco Bay, ME. Jenny Island (JI) is a 1 ha. island in eastern Casco Bay, ME. Pond Island National Wildlife Refuge (PINWR) is a 4 ha island located 0.8 km from Popham Beach State Park on the Kennebec River, ME. All inland island colonies contain mostly common terns with less than 50 pairs of arctic (*Sterna paradisaea*) and roseate (*S. dougallii*) terns.

<u>Nearshore Island</u> (5-10 km from mainland)

The two nearshore islands monitored by SRP are Outer Green Island and Eastern Egg Rock (Figure 1). Outer Green Island (OGI) is a 2.2 ha island 8 km east of Portland, ME in Casco Bay. Eastern Egg Rock (EER) is a 2.8 ha island located at the mouth of Muscongus Bay, ME. Outer Green Island contains mostly common terns with less than 50 pairs of arctic and roseate terns. Eastern Egg Rock is also dominated by common terns but contains a larger amount of other seabirds. Approximately 100 pairs each of arctic and roseate terns as well as a large colony of atlantic puffins (*Fratercula arctica*) and black guillemots (*Cepphus grille*) nest on EER.

<u>Offshore Islands</u> (> 10 km from mainland)

The two offshore islands overseen by SRP are Matinicus Rock National Wildlife Refuge and Seal Island National Wildlife Refuge (Figure 1). Matinicus Rock National Wildlife Refuge (MRNWR) is a 12 ha island located 35 km from southeastern Rockland, ME. Seal Island National Wildlife Refuge (SINWR) is a 26.3 ha island located 38 km from southeast Rockland, ME. Both MRNWR and SINWR support large breeding colonies of arctic and common terns.

Feeding Observations

Common terns carry fish perpendicular in their bills which allows for the identification of prey as they feed nidicolous offspring. Feeding observations were performed on six or seven nests at a time from a single observation blind. Single and multiple egg nests were selected for observations. At hatch, chicks were banded with a federal band for identification. Chicks were color marked for identification during feedings using different colored markers for each nest. Siblings were marked on different positions on their bodies for identification. Common terns have asynchronous hatching so chick hatch order is identified using A, B, or C with the A chick being hatched first.

Chicks were monitored until 21 days after hatch. Each nest was monitored for 12 hours each week with 4-three hour periods. Observation periods were performed either in morning or evening hours when feeding mainly occurs. Observers were trained to identify fish to species and invertebrates to general types, such as amphipods and isopods. Observers were trained to identify common prey items such as herring (*Clupea harengus*), hake (*Urophycis tenuis*), sandlance (*Ammodytes americanus*), butterfish (*Poronotus triacanthus*), 3-spinned stickleback (*Gastecosteus aculeatus*), lumpfish (*Cyclopterus lumpus*), and euphasiid (*Meganyctiphanes norvegica*). Observers determined the species of prey delivered to a specific chick, as well as prey item size relative to the parent tern's bill length. Lengths were recorded in quarter bill length intervals.

Feeding observations were not made during weather conditions that resulted in wet vegetation, such as rain, fog, and heavy morning dew. Researchers did not enter the wet tern colony when an abundance of young chicks less than four days old were present to ensure parents were not scared off of the nest, wetting chicks too young to thermoregulate. After a majority of chicks were older than four days, observations could be made in wet conditions except for rain.

Feather Collection

Juvenile feathers were used to determine isotope composition relative to their diet. Feathers were collected from juveniles used in feeding observation and in growth monitoring plots. Growth monitoring plots were fenced areas containing 15 or more nests used to obtain daily morphometric measurements. On all islands, feathers were collected from A chicks. Two body contour feathers were removed from the breast and stored in plastic bags on days 16 to 18 after hatch in June and July of 2005 through 2007 breeding seasons.

Prey Collection

Potential prey items in a tern chick's diet were collected on multiple islands to relate isotopically to tern feathers. Prey items were collected as accidental drops by terns into the colony, when chicks did not consume prey at the nest, or by active removal of prey from chicks by researchers. Prey items were only collected if the body appeared fresh and had not dried out. All prey items were stored in plastic bags and frozen in liquid nitrogen until they could be transported back to the mainland.

Isotope Analysis

Feathers used for carbon and nitrogen isotope analyses were selected randomly from sampled chicks. Feathers were washed in a 2:1 chloroform methanol solution to remove oil and debris, and allowed to dry for 48 hours before analysis. Barbules were removed along the entire rachis with scissors to insure isotopes were sampled over the entire period of feather formation.

Prey items collected on the islands were kept frozen until analysis. Frozen prey had all foreign debris removed and rinsed in water before vacuum drying. Dried prey items were homogenized using a WiggleBug®.

Both feathers and prey items were weighed and packaged in tin capsules for analysis at the University of Arkansas Stable Isotope Laboratory. Isotopes of carbon and nitrogen for both feathers and prey items were analyzed using a CE Instruments NC2500 elemental analyzer with a Finnigan Delta Plus isotope ratio mass spectrometer with machine error less than 0.2 for both carbon and nitrogen. Delta values (δX) were obtained from each analysis by comparison with an element-specific standard where: δX ‰ = [(R sample/R standard) – 1] x 1000 (Deniro and Epstein 1978). R sample and R standard refer the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Peedee Belemite is the carbon standard and atmospheric nitrogen is the nitrogen standard used for isotope comparison.

Population Parameters

Population size for common terns was measured on inshore and nearshore islands by counting all nests on each island and subtracting arctic and roseate tern nests. Counted nests were identified with wooden markers. Markers were used as part of a mark and recapture calibration with a Lincoln Index to obtain a calibration factor for missed nests.

Offshore islands with larger populations of arctic terns prevented a direct count of common tern nests. Instead a percentage of common and arctic terns was produced by identifying each species on nests from a blind in a particular area. The total number of nests was subdivided using the percent of each tern species.

Clutch size and productivity for each island was determined by following nests in productivity plots and feeding studies. Productivity is the number of chicks from each nest that survived to fledging. Nests were followed at least for 15 days or until chicks were presumed to have fledged.

Statistical Analysis

Adult prey deliveries to chicks were calculated by combining number of prey items by prey size, resulting in a volume measurement based on bill length. Percent observed diet volume is displayed for prey items that occur greater than 5% on multiple islands. Percent observed chick diet volume was compared among different island types, inshore, nearshore, and offshore, using Repeated Measures (PROC GLM SAS). Repeated Measures was performed with a heterogeneous autoregressive covariance structure and island specific tern average isotope values repeating between years. F-values were reported from Pillai's Trace. Comparisons of carbon and nitrogen values for common tern feathers among the seven islands for 2005 to 2007 was determined using a MANOVA (PROC MIXED SAS). If the model determined there was a difference between colonies, a Tukey-Kramer test was used to show where differences occurred (SAS).

RESULTS

Diet Observations

Although common terns have a broad diet, only a few prey items made up a majority of common tern diet during this study. Prey items consistently absent from multiple colonies and comprising less than 5% of prey deliveries were not included. From 2005 to 2007, terns on inshore and nearshore islands fed a high percent of fish whereas diet of terns on offshore islands were generally higher in euphasiids.

There was a significant higher-order interaction between prey species and year indicating that prey were not consistent among years (Pillai's Trace; $F_{16,72}$ =5.64; p<0.001). Prey species were also significantly different among inshore, nearshore, and offshore islands (F_8=25.07; p<0.001).

In 2005, prey deliveries observed were dominated by hake (Figure 2). Herring was fed on inshore and nearshore islands in small percentages, but was not observed on offshore islands (Figure 2). Sandlance was mainly fed on inshore islands and occurred rarely on nearshore and offshore islands (Figure 2). Other fish species were observed in low quantities except for rock eels (*Pholis gunnellus*) only observed on EER (9%) in 2005. Euphasiids were observed on offshore islands in greater quantities and were rarely observed on nearshore and inshore islands except for PINWR (Figure 2).

Overall, a decrease was observed in hake and an increase in other fish species in 2006. Hake still comprised a large percentage of prey deliveries on most islands (Figure 3). Herring feedings increased on all islands (Figure 3). Sandlance was only observed on inshore islands and offshore islands in low amounts (Figure 3). Other fish species had low frequencies on all islands. Euphasiids were fed in greatest quantities on offshore islands and only in trace amounts on inshore islands (Figure 3).

In 2007, hake remained the dominant prey item in almost all colonies followed by herring and sandlance. Percent hake was similar to observations in 2006 (Figure 4). Percent herring decreased in all colonies from 2006, but still comprised a large portion of tern diet on most islands (Figure 4). Sandlance feedings were observed on all islands (Figure 4). Euphasiids continued to be rare on all islands except for SINWR (Figure 4).

Isotope Analysis

In 2005, average feather values for each colony shared similar patterns of carbon and nitrogen by location with offshore islands more deplete and inshore islands more enriched in carbon and nitrogen. Juvenile feather carbon showed a 2‰ enrichment between offshore, SINWR and MRNWR, and inshore islands, PINWR and JI (Figure 5). Inshore islands, PINWR and JI, were enriched in $\delta^{13}C$ by 1‰ relative to nearshore islands, EER and OGI (Figure 5). A similar pattern also existed for $\delta^{15}N$ in 2005 with inshore islands enriched by 1.5 to 2‰ relative to offshore islands, with the exception of SI (Figure 5). Nearshore islands were only enriched by 0.5 to 1‰ relative to offshore islands (Figure 5).

There was a significant difference in tern carbon and nitrogen among inshore, nearshore, and offshore islands in 2005 (Pillai's Trace; $F_{12,194}$ =17.74; p<0.0001). A Tukey-Kramer test showed that carbon differences were found between three groups. Group 1 was JI and PINWR, 2 was OGI, EER, and SI, and 3 was SINWR and MRNWR (Figure 5). Nitrogen differences separated islands into multiple groups. Group 1 was JI and PINWR, group 2 was PINWR and EER, group 3 was EER, OGI, and SI. Nitrogen signatures for MRNWR and SINWR were significantly different from all other islands (Tukey-Kramer; Figure 5).

Tern dietary items collected in 2005 separated into two different groups by carbon values. Butterfish and hake were depleted in carbon relative to herring, euphasiids, and lumpfish. All dietary items were similar in nitrogen with delta values near 10‰ (Figure 6).

In 2006 there was an overall island effect of juvenile feathers between islands (Pillai's Trace; $F_{12,186}$ = 40.46; p<0.0001). For carbon, islands separated into three groups. PINWR juvenile feathers remained more enriched in carbon (Figure 7). Inshore, nearshore, and offshore island carbon signatures followed with JI, OGI, and SINWR (Figure 7). Islands most deplete in carbon were SI, EER, and MRNWR (Figure 7). Nitrogen values were enriched around 1‰ for inshore, and nearshore islands relative to offshore islands (Figure 7). Carbon was more enriched on PINWR, OGI, and JI followed by EER and SI (Figure 7). Nitrogen was depleted at SINWR and MRNWR (Figure 7).

Tern dietary items in 2006 clustered into a few different groups similar to 2005 (Figures 6 and 8). Butterfish and hake were still deplete in carbon relative to herring (Figure 8). $\delta^{15}N$ was similar for butterfish, hake, and herring around 10‰ (Figure 8). Stickleback was had a similar carbon value as butterfish and hake, but an enriched nitrogen signature relative to all other fish (Figure 8).

Differences in chick feather $\delta^{13}C$ and $\delta^{15}N$ with growth rate were tested in 2007. Stratton Island A and B chicks feathers were analyzed between nests with similar and different growth rates. There was no significant difference between $\delta^{13}C$ (paired t-test; t_9 =1.25; p=0.2442) or $\delta^{15}N$ (paired t-test; t_9 =0.53; p=0.6065) of sibling feathers with different or similar growth rates (Figure 9).

For all of the islands in 2007, there was an overall island effect for $\delta^{13}C$ and $\delta^{15}N$ in juvenile tern feathers (Pillai's Trace; $F_{12,176}$ = 11.38; p<0.0001). Carbon separated into three groups, but no pattern emerged by island location. Carbon was most enriched on PINWR followed by SINWR, EER, JI, and OGI (Figure 10). Carbon signatures on SI and MRNWR did overlap with all islands except PINWR (Figure 10). Nitrogen feather signatures also separated into three groups. Nitrogen was most enriched on JI and OGI (Figure 10). Eastern Egg Rock and MRNWR were similar to OGI (Figure 10). Nitrogen was most depleted in SINWR, PINWR, and SI (Figure 10). Stratton Island was also similar to MRNWR and EER (Figure 10).

Tern dietary items in 2007 had similar relationships as seen in 2006 between butterfish, hake, and herring. Butterfish and hake were more depleted in $\delta^{13}C$ than herring (Figure 11). Sandlance $\delta^{13}C$ was similar to herring (Figure 11). All prey in 2007 had similar $\delta^{15}N$ around 10‰ except for lumpfish. Lumpfish was enriched in both $\delta^{13}C$ and $\delta^{15}N$ (Figure 11).

Population Parameters

Common tern population on each island fluctuated during 2005 to 2007. Population fluctuation should be attributed to redistribution of common terns among islands. Predation by gulls on tern nests in 2007 on SINWR is responsible for a large decrease in nests counted in 2006 (Table 1). Common terns deserting SINWR caused an increase in nests on MRNWR and EER (Table 1).

Average inshore common tern clutch size during 2005 to 2007 was larger than average offshore common tern clutch size (Table 1). Average nearshore common tern clutch size was larger on OGI than on EER (Table 1). Average clutch size on OGI was as large as or larger than average inshore clutch size (Table 1).

Average productivity for common terns was generally higher on inshore islands from 2005 to 2007 relative to nearshore or offshore common tern colonies (Table 1). Productivity on PINWR in 2007 was lower than previous years due to high predation (Table 1). Productivity was higher on EER and OGI in 2007 relative to the two previous years.

DISCUSSION

Dietary data from observations and stable isotopes both indicate higher consumption of euphasiids on offshore islands relative to inshore and nearshore islands. Euphasiids occupy a lower trophic level, depleting δ^{15}N of common terns consuming euphasiids relative to other prey items (Fry 1988; Hobson et al. 1994; Jarman et al. 1996; Sydeman et al. 1997; Dunton 2001; Becker et al. 2007). Feeding observations indicated larger consumption of euphasiids for both MRNWR and SINWR in most years causing δ^{15}N values to be lower on offshore islands relative to most other islands. Offshore chicks being fed at a lower trophic levels indicate that adults are feeding at a lower trophic level as well (Nisbet et al. 2002; Danhardt et al. 2011).

Seabird diets with a high percent of low quality food may be influencing reproductive characteristics on offshore islands. Clutch size and productivity was consistently lower on offshore islands relative to inshore islands. Lower quality foods, such as invertebrates, have less protein and digestible mass which could cause a decrease in growth and development of juvenile terns (Dahdul and Horn 2003). A lack of high quality prey items being delivered to chicks on offshore islands indicates less high quality prey items available for adult consumption (Danhardt et al. 2011). Adults foraging at lower trophic levels will have less energy to dedicate for egg production thus decreasing clutch size on offshore islands relative to nearshore and inshore islands (Winkler and Walters 1983).

The exact composition of tern diet could not be estimated using δ^{13}C and δ^{15}N to generate a mixing model. Not enough consistent variability was observed between carbon and nitrogen for different prey items to distinguish among prey sources. Although preconceived differences led to the application of carbon and nitrogen stables isotopes in the Gulf of Maine (Charette 2005; Fry 2006), delta values obtained for herring and hake were too similar preventing a distinction between major dietary components of terns (Phillips and Gregg 2003; Bond and Diamond 2011). Values obtained for euphasiids also had more enriched δ^{13}C and δ^{15}N than prior dietary studies (Fry 1988; Hobson et al. 1994; Jarman et al. 1996; Sydeman et al. 1997; Dunton 2001; Becker et al. 2007). Euphasiid isotope signatures were similar to other prey items preventing a model from distinguish among euphasiids, hake, and herring. However if euphasiids displayed a similar relationship to other studies of a more deplete δ^{13}C and δ^{15}N relative to fish (e.g. Becker et al. 2007) then δ^{13}C enrichment observed on SINWR and MRNWR in 2006 and SINWR in 2007 would have been caused by an increase in fish consumption by tern chicks.

Inshore common terns could have more energy for reproduction as stable isotopes and dietary observations show terns consuming a higher quality diet than offshore and most nearshore islands. An inshore island, PINWR or JI, was more enriched in $\delta^{15}N$ throughout the study. A nearshore island, OGI, also had enriched $\delta^{15}N$ tern feathers in 2006 and 2007. Feeding observations showed terns on PINWR, JI, and OGI consumed more fish, hake, herring, and sandlance, than other islands. Even though these islands have been classified differently, PINWR, JI, and OGI are all located within foraging distance of Casco Bay, Maine. Resources within a particular bay could be dominated by higher quality prey for foraging (Shealer and Kress 1994).

Inshore, PINWR, and nearshore, SI, island terns had depleted $\delta^{15}N$ signatures close to both offshore islands in 2007. However feeding observations for PINWR and SI do not show a large consumption of euphasiids as observed on SINWR. Nitrogen feather signatures could be being depleted by other prey items, such as sandlance. Although sandlance had a similar $\delta^{15}N$ value to hake and herring, other tern species consuming large percentages of sandlance had similar $\delta^{15}N$ signatures to PINWR and SI common tern juveniles (Chapter 3).

Variability seen on PINWR could be caused by decreased prey availability in 2007. Commercial landings of hake and herring were lower in 2007 relative to 2005 and 2006 (http://www.maine.gov/dmr/commercialfishing/historicaldata.htm). Decreased prey availability may have caused inshore island birds to change their diet. Delivery of different prey species could be missed as feeding observations were conducted consistently during a particular time of day (Safina et al. 1990). A decrease in prey availability could also have forced common terns to forage in more freshwater environments which are more $\delta^{15}N$ depleted (France 1994).

Although nitrogen signatures of inshore nesting terns may be affected by freshwater signature, it is unlikely that offshore terns are also showing an enriched $\delta^{13}C$ associated with foraging in freshwater. Differences between marine and freshwater foraging have been previously determined by subsequent $\delta^{13}C$ enrichment of foraging in a freshwater environment relative to marine (Hobson and Welch 1992; France 1995). A 2‰ $\delta^{13}C$ enrichment occurred in SINWR common terns from 2005 to 2006. An increase in foraging distance from SINWR, thus foraging effort, has been suggested as a plausible explanation for a decrease in parental energy for offshore common terns (Hall and Kress 2004). However $\delta^{13}C$ enrichment on SINWR in 2006 and 2007 is probably due to increased fish delivered to offspring as observed hake and herring consumption increased in 2006 and these fish are more enriched in $\delta^{13}C$ than euphausids. Common terns do have the ability to forage for over large distances (Erwin 1977), but generally forage around their breeding colony (Duffy 1986; Becker et al. 1993). Offshore terns also do not have decreased provisioning rates which would occur with greater foraging distances relative to other colonies (Hall and Kress 2004). As lower quality euphasiids are the most available prey to SINWR adults (Danhardt et al. 2011), it would be a poor strategy for a central forager to travel long distances for such a low energetic return (Orians and Pearson 1979).

Nitrogen signatures can show relative trophic levels but $\delta^{15}N$ can vary depending on nutritional status of a bird. Body condition in chicks has been related to enrichment in $\delta^{15}N$ when chicks are nutritionally stressed (Hobson et al. 1993). A nutritional stress should also decrease juvenile tern growth rates (Dahdul and Horn 2003). However no differences were found in $\delta^{13}C$ or $\delta^{15}N$ between A and B chicks with different growth rates relative to pairs with similar growth rates. There was also no observed enrichment in $\delta^{15}N$ on offshore islands foraging on low quality prey relative to inshore islands.

Decreased energy on nearshore and offshore islands has resulted in decreased clutch size and productivity relative to inshore islands. Reproductive plasticity displayed by common terns in the Gulf of Maine shows their ability to adapt to different environmental conditions. This has allowed managers to use a wide variety of islands to aid in restoring the common tern population in the Gulf of Maine. However, offshore island common tern colonies have now become a sink for the metapopulation in the Gulf of Maine. Offshore colonies have a consistently larger population size than inshore colonies. Greater clutch size and productivity on inshore islands results in inshore island common tern colonies being a source for the metapopulation as offspring from inshore colonies eventually move to offshore tern colonies. Although offshore colonies have decreased foraging resources, offshore tern colonies may be more attractive than inshore islands due to their larger size or decreased predation relative to inshore tern colonies.

ACKNOWLEDGMENTS

I thank the following organizations for providing funding for this study: Arkansas Audubon Society Trust and the Nisbet Research Grant. I thank the staff and volunteers of National Audubon Society's Seabird Restoration Program for assistance with feather collection and feeding observations, especially island supervisors – Noel Dodge, Suzanne Dodge, Christina Donehower, Johanna Hiscock, Katie Kauffman, Matt Klostermann, Alison Kocek, Juliet Lamb, Pam Loring, Matt Martinkovic, Ellen Peterson, Lauren Scopel, Paula Shannon, Emily Tupper, and Carlos Zavalaga. I thank Scott Hall and Steve Kress for mentorship on the field sites. I thank the University of Arkansas Stable Isotope Laboratory Staff for analyses and advice – Erik Pollock and Tom Millican. I thank Elisha Ott for assistance in preparing isotope specimens. I especially thank Steve Beaupre, Gary Huxel, Ian Nisbet, and Kimberly Smith for their advice and editing.

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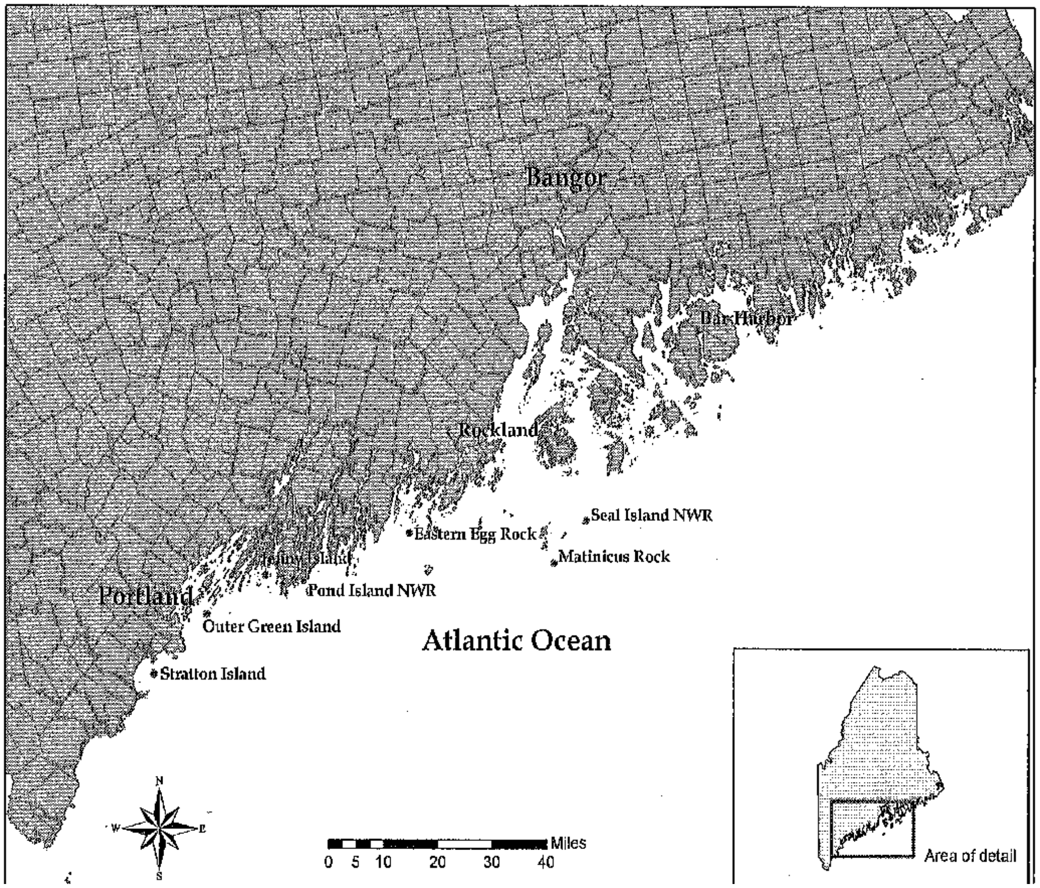

Figure 1. Islands managed by National Audubon Society's Seabird Restoration Program in the Gulf of Maine. Inshore islands (<5km from mainland) include Stratton, Jenny, and Pond Islands. Nearshore islands (5 to 10km from mainland) include Outer Green Island and Eastern Egg Rock. Offshore islands (>10km from mainland) include Matinicus Rock National Wildlife Refuge and Seal Island National Wildlife Refuge.

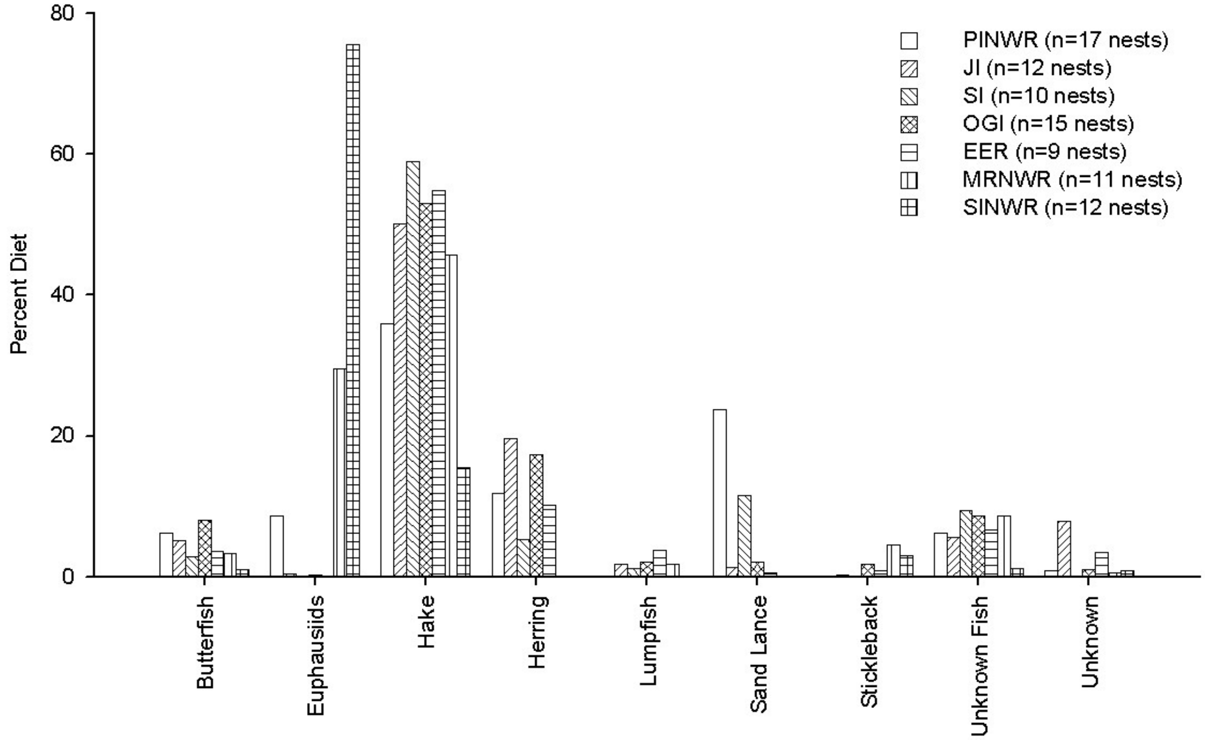

Figure 2. Common tern observed diet in 2005 is listed as inshore to offshore islands from left to right for each prey category. Diets on most islands were dominated by hake. Offshore islands had a higher percentage of euphasiids than nearshore and inshore islands.

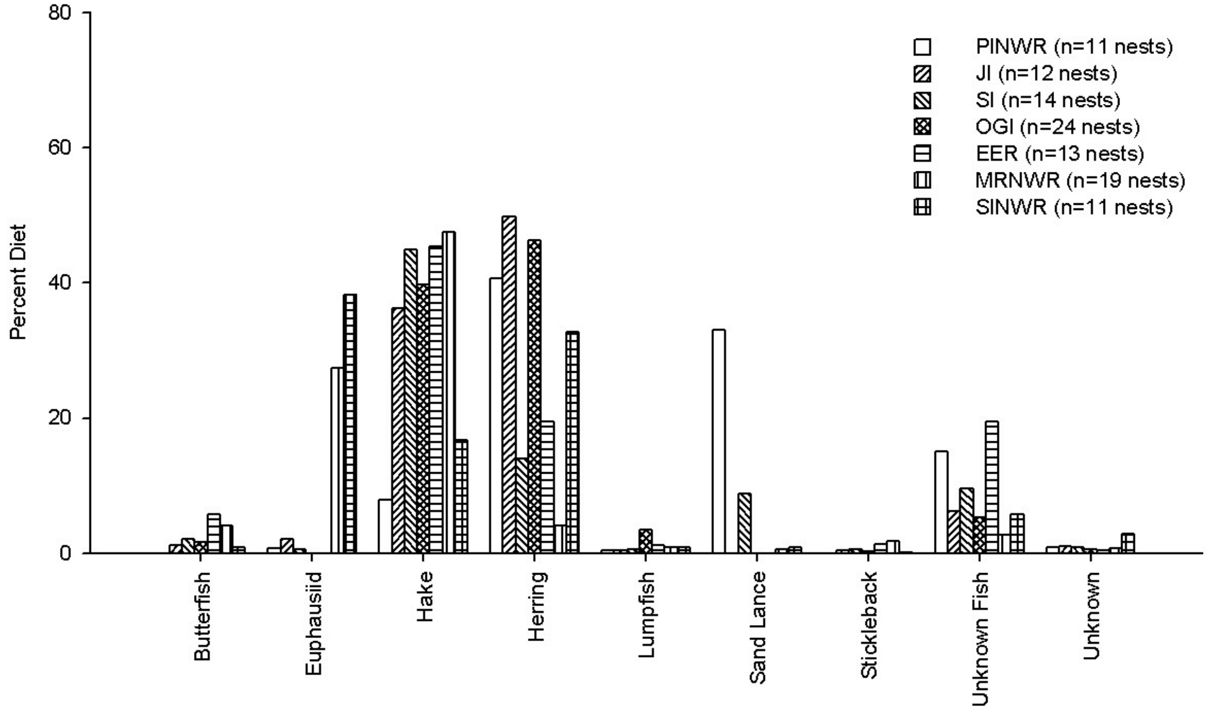

Figure 3. Common tern observed diet in 2006 is listed as inshore to offshore islands from left to right for each prey category. Herring was more abundant causing diets on most islands to be a mixture of hake and herring. Euphasiids were still observed as a major component of offshore colony diets.

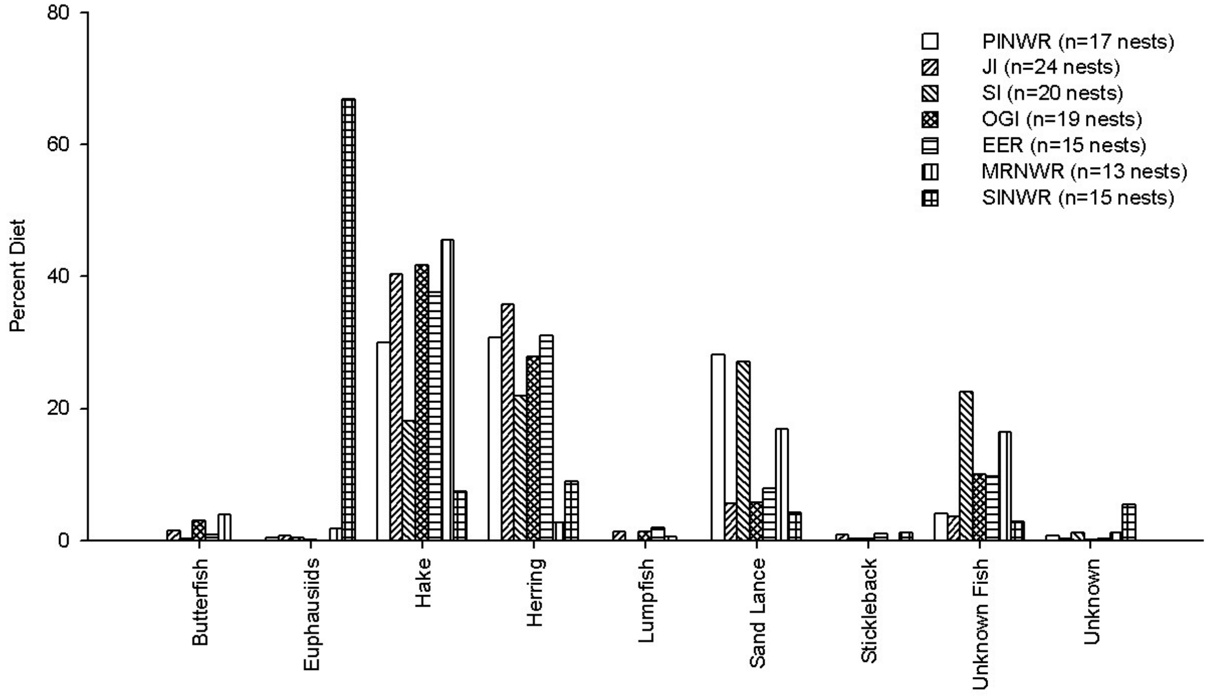

Figure 4. Common tern observed diet in 2007 is listed as inshore to offshore islands from left to right for each prey category. Hake and herring were observed more frequently on most islands. Terns on inshore islands, PINWR and SI, were also observed feeding sandlance. Diet on SINWR continued to be dominated by euphasiids.

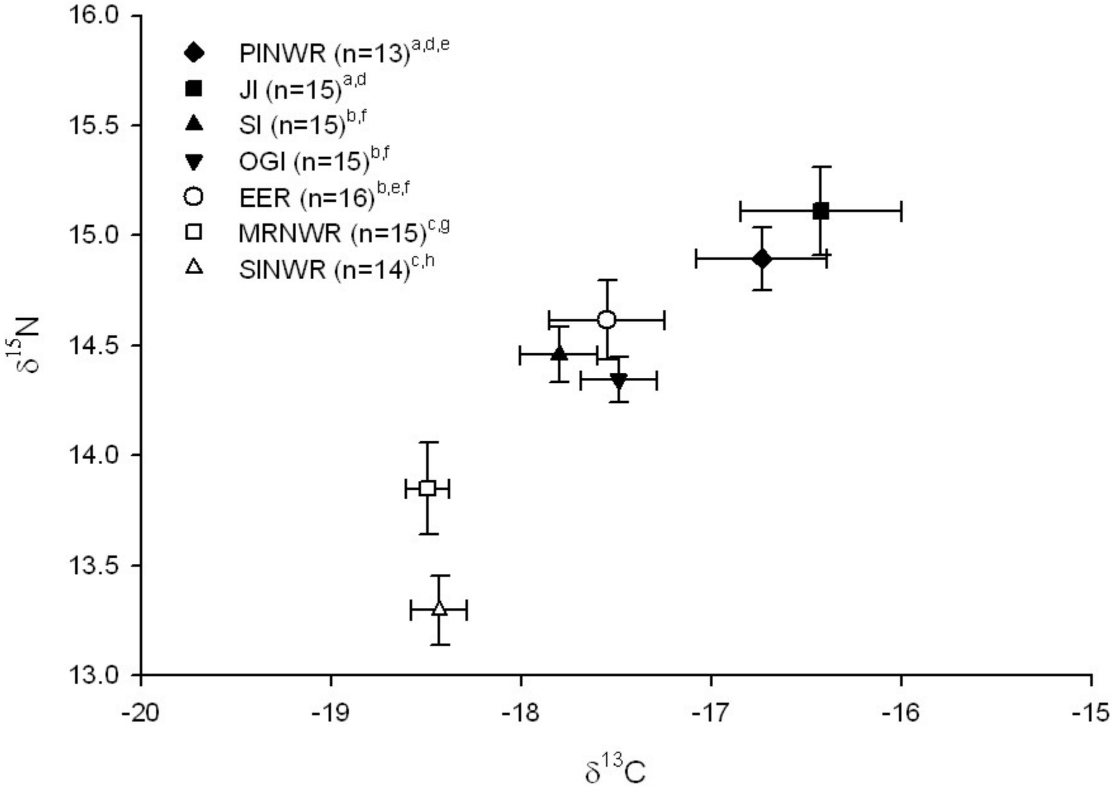

Figure 5. Mean δ^{13}Carbon and δ^{15}Nitrogen signatures (± 2SE) of juvenile Common Tern feathers in 2005. Islands sharing the same letters were not significantly different in δ^{13}Carbon (a, b, or c) and δ^{15}Nitrogen (d, e, f, g, or h). Offshore islands, MRNWR and SINWR, were more deplete in δ^{13}Carbon and δ^{15}Nitrogen than nearshore and inshore islands. Inshore islands, PINWR and JI, were more enriched in δ^{13}Carbon and δ^{15}Nitrogen than nearshore and offshore islands.

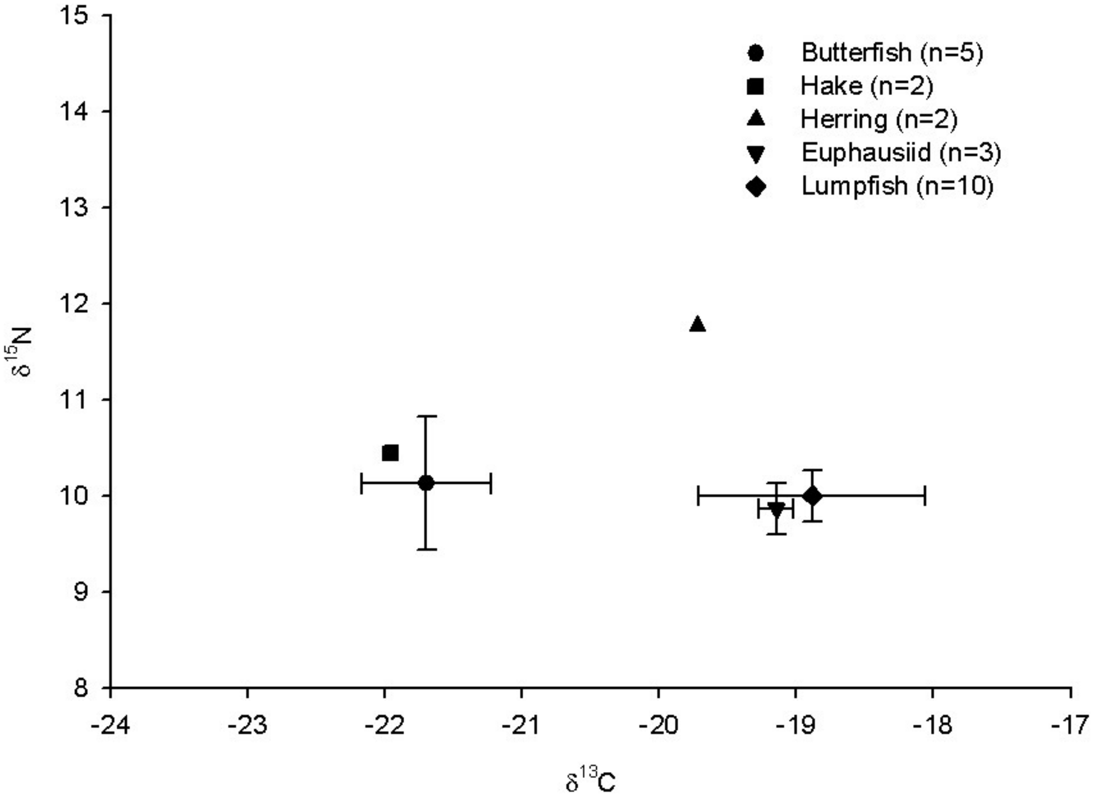

Figure 6. Mean δ^{13}Carbon and δ^{15}Nitrogen signatures (± 2SE) of tern dietary items in 2005. All prey drops had overlapping δ^{15}N values, but separated into two groups based on δ^{13}C. Butterfish and hake were more deplete in δ^{13}C than euphasiids, herring, or lumpfish.

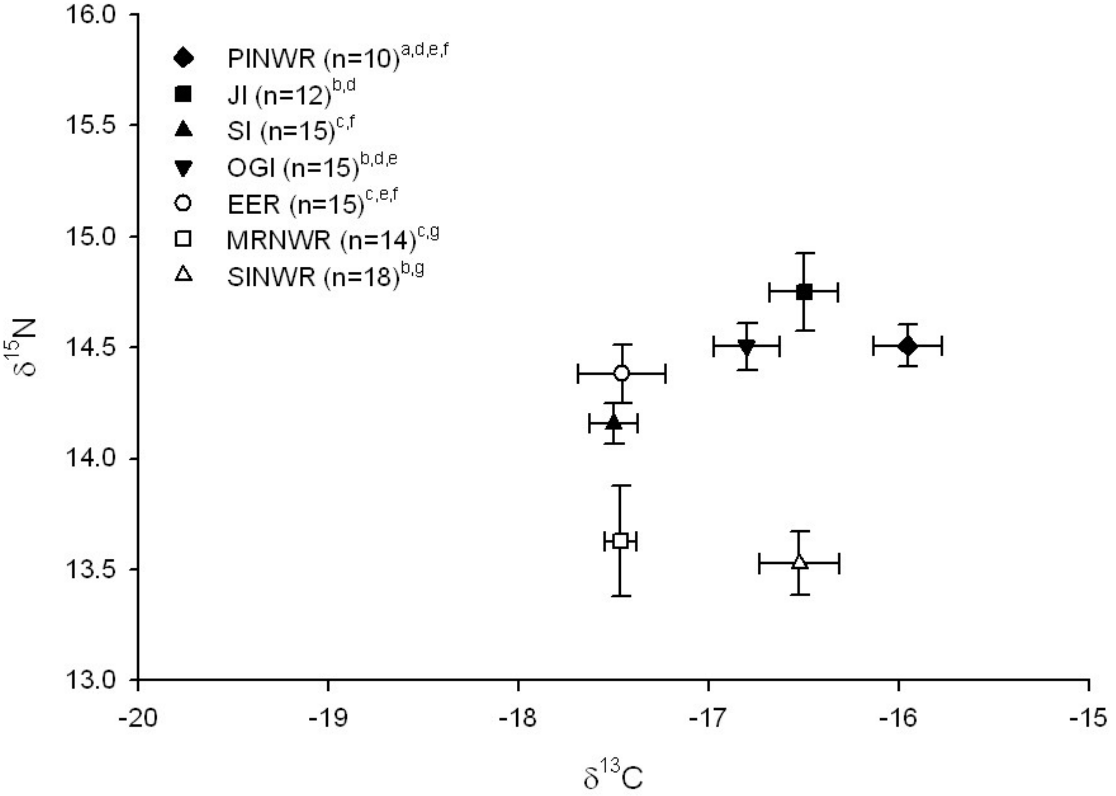

Figure 7. Mean δ^{13}Carbon and δ^{15}Nitrogen signatures (± 2SE) of juvenile Common Tern feathers in 2006. Islands sharing the same letters were not significantly different in δ^{13}C (a, b, or c) and δ^{15}N (d, e, f, g, or h). Carbon was more enriched on PINWR relative to other islands. Offshore islands were more deplete in δ^{15}N, but not δ^{13}C.

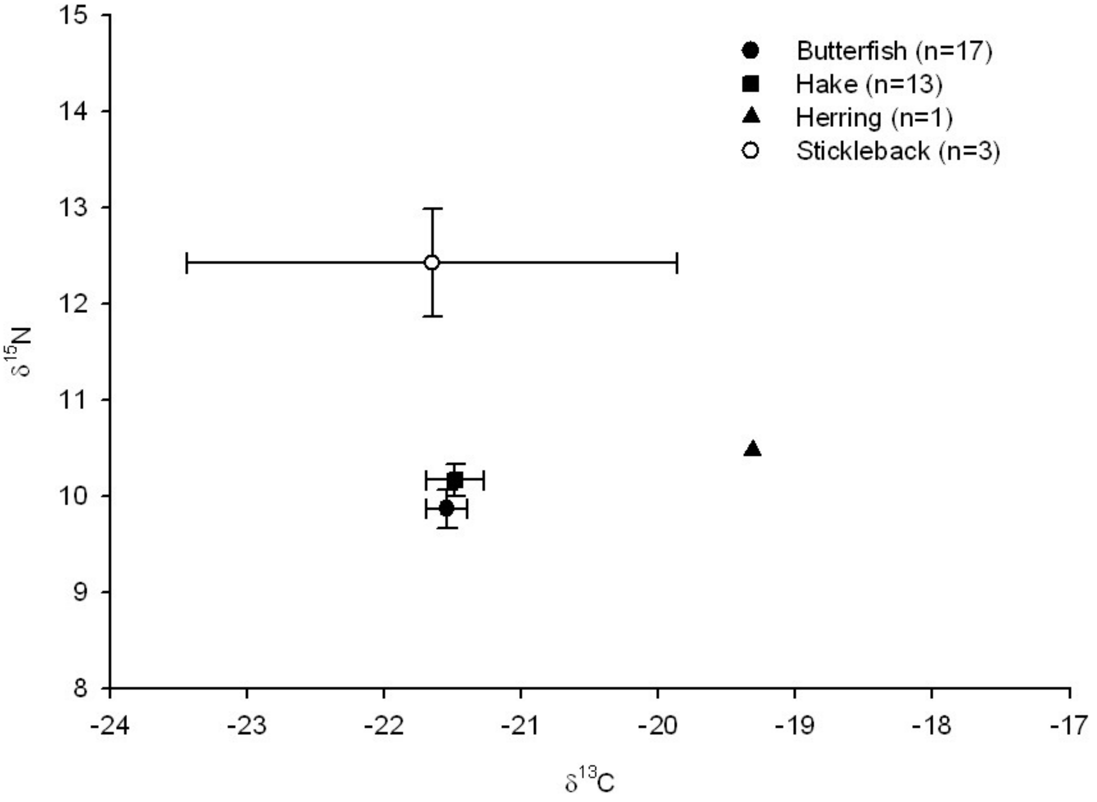

Figure 8. Mean δ^{13}Carbon and δ^{15}Nitrogen signatures (± 2SE) of tern dietary items in 2006. Herring was enriched in δ^{13}C while stickleback was enriched in δ^{15}N.

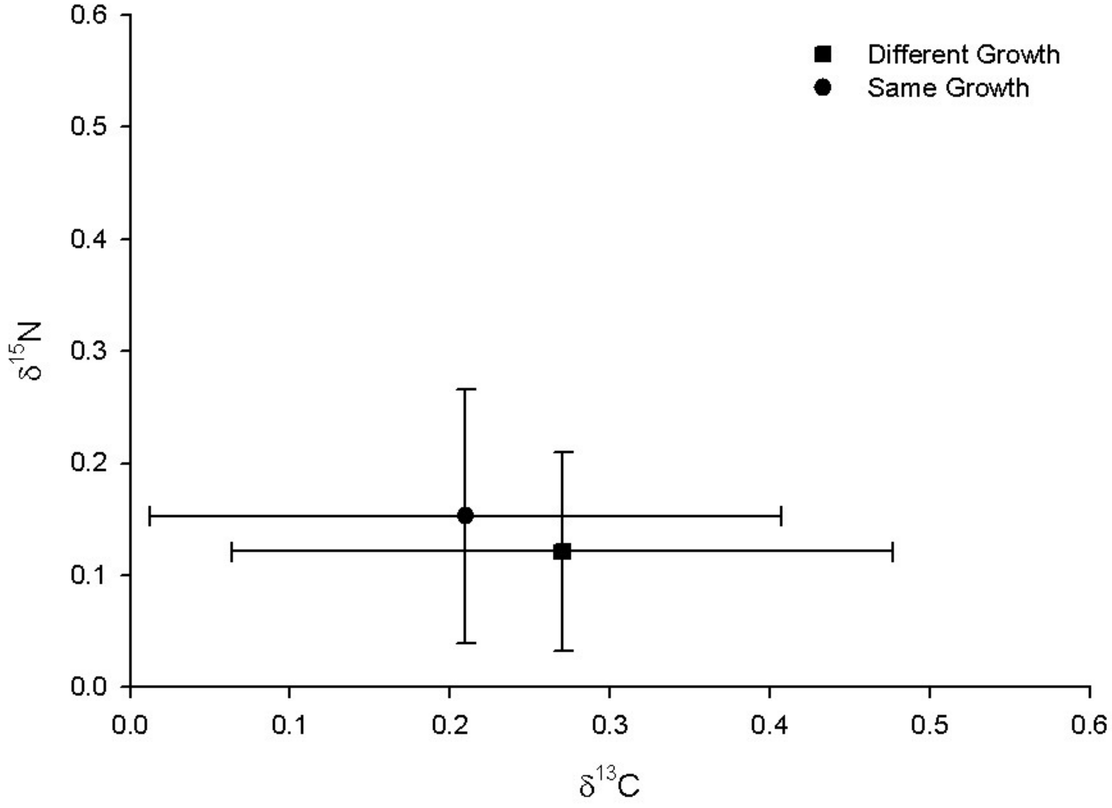

Figure 9. Differences in mean δ13Carbon and δ15Nitrogen (± 2SE) between A and B pairs in 2007 on SI. There were no significant differences in δ13C or δ15N between sibling pairs with or without growth rate differences.

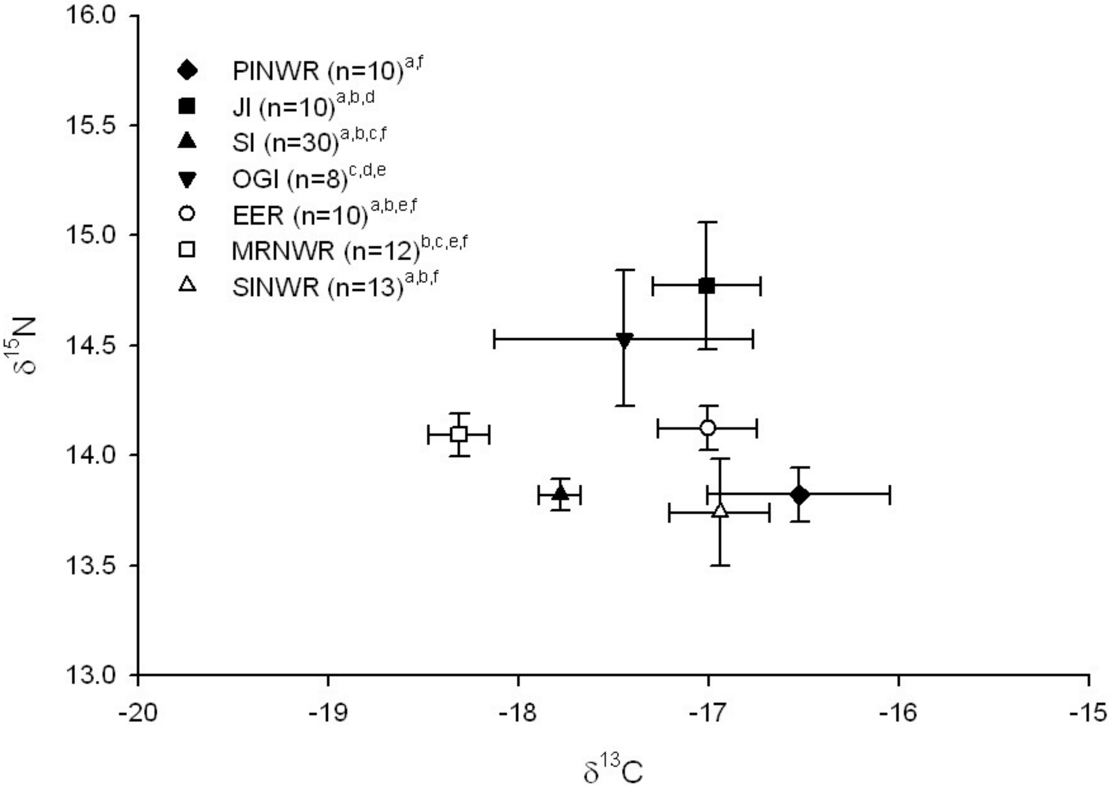

Figure 10. Mean δ^{13}Carbon and δ^{15}Nitrogen signatures (± 2SE) of juvenile Common Tern feathers in 2007. Islands sharing the same letters are not different in δ^{13}C (a, b, or c) and δ^{15}N (d, e, or f). Islands that were more enriched in δ^{15}N were closer to the mainland. No overall pattern was present for δ^{13}C. Inshore islands were enriched in δ^{13}C, but not all offshore islands were depleted in δ^{13}C.

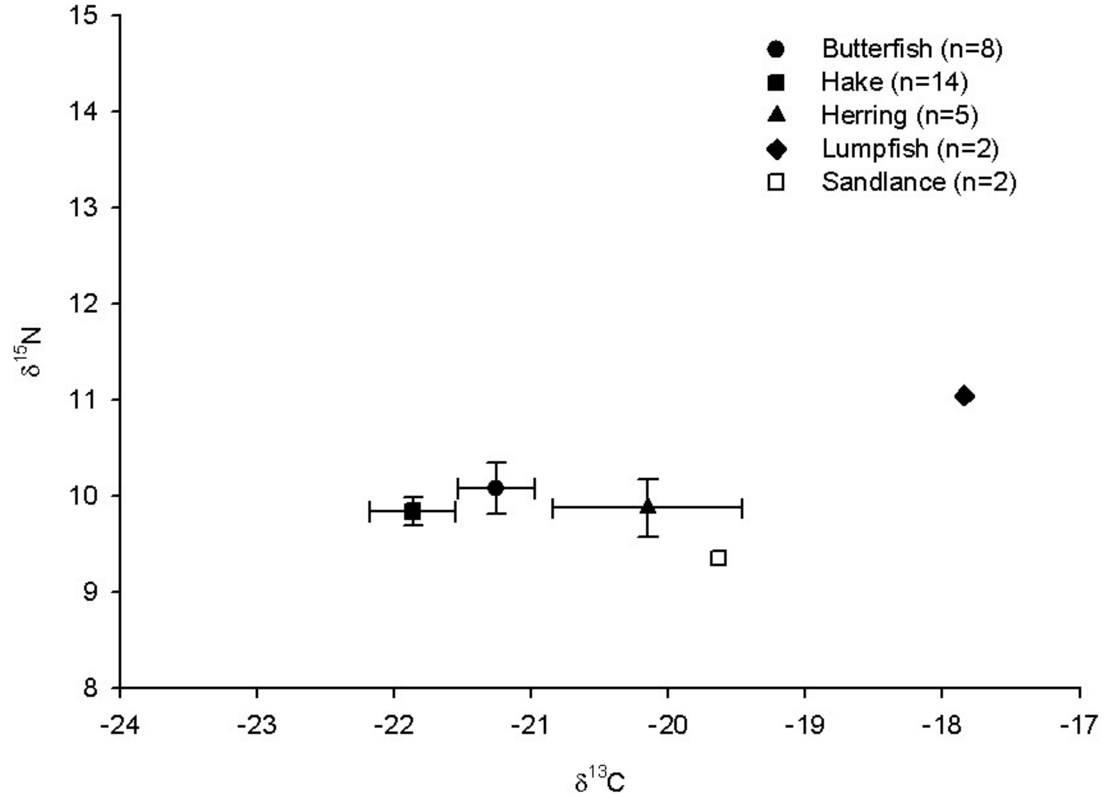

Figure 11. Mean δ^{13}Carbon and δ^{15}Nitrogen signatures (± 2SE) of prey drops in tern colonies in 2007. Butterfish and hake were more deplete in $\delta^{13}C$ than herring and sandlance. All prey had similar $\delta^{15}N$ except for lumpfish which was enriched in both $\delta^{13}C$ and $\delta^{15}N$.

Island	Year	Total nests	Clutch size	Productivity	n
PINWR	2005	324	2.47	1.09	32
PINWR	2006	484	2.28	0.40	36
PINWR	2007	316	2.50	2.03	30
JI	2005	532	2.20	1.00	25
JI	2006	589	2.47	1.05	43
JI	2007	684	2.35	1.67	51
SI	2005	156	2.20	1.02	49
SI	2006	673	2.68	1.00	50
SI	2007	752	2.55	1.79	67
OGI	2005	971	2.22	0.67	54
OGI	2006	732	2.35	1.13	75
OGI	2007	936	2.48	1.71	57
EER	2005	758	2.01	0.59	69
EER	2006	763	2.11	0.64	84
EER	2007	1206	2.04	1.18	67
MRNWR	2005	243	1.77	0.64	44
MRNWR	2006	292	1.80	0.70	40
MRNWR	2007	663	1.72	0.48	46
SINWR	2005	1220	1.79	0.57	74
SINWR	2006	1726	2.01	0.93	84
SINWR	2007	1004	1.87	0.66	53

Table 1. Population parameters of common terns on National Audubon Society's Seabird Restoration Program Islands. Data from SRP final reports and Gulf of Maine Seabird Working Group.

CHAPTER 3. COMPETITION BETWEEN ARCTIC, COMMON, AND ROSEATE TERNS ON MANAGED ISLANDS IN THE GULF OF MAINE USING STABLE ISOTOPES AND MEASURES OF DIETARY OVERLAP

ABSTRACT

Terns have coevolved to occupy different spaces within breeding colonies. However management of these species has created large populations to maximize tern numbers. National Audubon Society's Seabird Restoration Program has restored several islands in the Gulf of Maine. Common terns nest on all islands. Arctic terns nest on islands farther from the mainland, Seal Island National Wildlife Refuge (MRNWR), and Eastern Egg Rock (EER). Roseate terns nest on islands closer to the mainland, EER, Outer Green Island (OGI), and Stratton Island (SI). Competition was estimated using stable isotopes of carbon and nitrogen in juvenile tern feathers, Morisita's index of dietary overlap, and statistical analyses of most abundant prey items observed in tern diets. Tern diets were determined by observing prey deliveries by adults to juveniles in the nest. If terns had high dietary overlap and similar carbon and nitrogen values, then there is a higher probability of competition existing between tern species. Nitrogen isotopes in feathers were similar in tern comparisons on each island indicating that terns at each location were foraging at the same trophic level. Less competition was occurring between arctic, common, and roseate terns on EER and common and roseate terns on SI in 2007. Terns in both locations had low dietary overlap and different carbon signatures. High dietary overlap and similar carbon and nitrogen signatures occurred between arctic and common terns on MRNWR and common and roseate terns on OGI. Competition could be higher between terns in those colonies. Overall comparisons show higher dietary overlap and similar isotope signatures between common and roseate terns relative to arctic and common terns. Competition should be higher for common and roseate terns as they travel to the coastline to feed while arctic terns feed farther from the coastline.

INTRODUCTION

Restoration and protection of specific islands for tern breeding has established large numbers of terns into a few historic breeding colonies. Terns are displaced from breeding areas by a variety of gull species (Nisbet 1973b). Restoration techniques employed by National Audubon Society have recreated large breeding colonies by limiting gull nesting in the Gulf of Maine (Kress 1983). As a result, Audubon colonies are occupied by 2 to 3 tern species, arctic (*Sterna paradisaea*), common (*S. hirundo*), and roseate (*S. dougalii*) terns (Kress 1983). Although space has been made available, terns are forced to select breeding colonies that may not match the criteria of their traditional breeding grounds (Burger and Lesser 1978, 1979).

Criteria for tern breeding colonies are best described by their nesting and foraging habitats. Although common terns have more flexible nesting requirements than arctic or roseate terns, all three species primarily nest on islands in the Gulf of Maine (Gochfeld et al. 1998; Hatch 2002; Nisbet 2002). Beginning at courtship, terns focus efforts on foraging in specific areas (Nisbet 1977, 1983). Common and roseate terns are known to forage closer to the mainland in shallower waters than arctic terns (Duffy 1986; Safina et al. 1988; Gochfeld et al. 1998; Rock et al. 2007). However common terns are not restricted to nesting on colonies close to the mainland as roseate terns are (Hall and Kress 2004). Terns with differences in preferred foraging habitat will cause tern species to have different preferred diets. Common terns forage in a wider variety of habitats consume a higher diversity of fish and invertebrates relative to arctic and roseate terns that are more specialized on fish (Hopkins and Wiley 1972; Lemmetyinen 1976; Chapdelaine et al. 1985; Safina et al. 1990; Gochfeld et al. 1998; Hall et al. 2000; Robinson et al. 2001; Hatch 2002; Rock et al. 2007).

Terns nesting in managed colonies have evolved to nest on the same islands. Colonies are partitioned by terns to prevent competitive exclusion (Lack 1971). Each species has different nesting requirements which minimize nesting overlap in the breeding colony (Gochfeld et al. 1998; Hatch 2002; Nisbet 2002).

As interspecific competition for breeding space may not be high, competition could be intense in other areas of tern breeding ecology, such as foraging. Terns occupying the same breeding colonies are known to consume similar diets (Hopkins and Wiley 1972; Hall et al. 2000). Common and roseate terns forage together in mixed flocks (Duffy 1986; Safina 1990a, b; Shealer and Burger 1993). Depending upon the colony location and community interactions, a tern species may be at a competitive disadvantage when foraging with other tern species (Safina 1990a; Shealer and Burger 1993; Shealer 1996). Preferred foraging environment does play a role in foraging success compared with a closely related competitor (Safina 1990b) or between different locations (Nisbet 1977).

Breeding colony location determines which foraging habitats are available and the type of prey that can be obtained there (Hulsman 1987). Terns with similar diets have a greater chance for negative interactions with other tern species in the same colony (Hopkins and Wiley 1972). Arctic, common, and roseate terns are also similar in body and bill size which increases competition as they are foraging for similar sized prey (Ashmole 1968; Hulsman 1987). Increased competition around seabird islands increases pressure on food resources depending on the range and territory of the tern species (Ashmole 1963; Ricklefs 1977). Food availability impacts how reproductive life history characteristics, such as clutch size, are displayed at a particular colony location (Nisbet 1973a, 1978; Safina et al. 1988; Monaghan et al. 1992; Suddaby and Ratcliffe 1997). Competition affects on food supply could be displayed differently depending on the species involved (Nisbet and Cohen 1975).

However terns located together at the same colony with similar diets are not required to be foraging competitors (Rock et al. 2007). Assuming that foraging resources are not unlimited (Pearson 1968), arctic, common, and roseate terns of similar size still have morphological and behavioral differences that could reduce competition between species (Duffy 1986). Both arctic and common terns dive height and times of immersion are lower than that of roseate terns (Dunn 1972). Differences in dive characteristics may be attributed to longer wings of roseate terns (Duffy 1986). The ability of terns to exploit other areas of their environment, such as foraging depth, decreases competition.

Decreased foraging competition also occurs as terns forage at varying distances and directions from a shared breeding colony (Duffy 1986; Rock et al. 2007). Arctic and roseate terns are known to forage farther away from the colony than common terns (Duffy 1986; Robinson et al. 2001). Multiple tern species have been observed to return with prey to a colony from different directions (Hopkins and Wiley 1972; Uttley et al. 1989).

Preferences for particular foraging conditions could decrease competition for communal foraging tern species. Common terns have greater foraging success than roseate terns at higher wind speeds (Dunn 1972). Increased wind aids common terns in hovering and provides additional cover from fish that are close to the surface (Dunn 1973). Increased wind may also help common terns forage better than arctic terns as arctic terns prefer to hunt in waters with higher transparency (Lemmetyinen 1976).

The goal of this study was to determine if foraging overlap exists in tern colonies managed by National Audubon Society Seabird Restoration Program in the Gulf of Maine. National Audubon Society has created island colonies at various distances from the mainland along the Maine coast. Islands close to the mainland are occupied by common and roseate terns, such as Stratton (SI) and Outer Green (OGI) Islands. Islands far from the mainland contain common and arctic terns, such as Matinicus Rock (MRNWR) and Seal Island National Wildlife Refuges (SINWR). Eastern Egg Rock (EER), an island located at an intermediate distance, has breeding colonies of all three species.

To determine foraging competition between terns located in the same colonies I used a combination of direct observations of parents provisioning young and stable isotope analysis of carbon and nitrogen. Tern chicks were used as an indirect measure for foraging resources available to adults. Tern adults deliver prey to chicks that are readily available to parents on the foraging grounds (Danhardt et al. 2011). Adults carry prey back to the colony perpendicular to their bills allowing for prey species and size to be determined. Carbon and nitrogen stable isotope have been used to determine dietary sources in marine birds (Hobson 1987, 1990; Mizutani et al. 1990; Hobson and Welch 1992; Rau et al. 1992; Hobson et al. 1994; Minami et al. 1995; Hobson et al. 2000; Forero et al. 2002; Nisbet et al. 2002). Assimilated juvenile diet was determined by analyzing isotopes in juvenile feathers representing prey fed by parents to offspring while feathers are developing (Hobson 1999). Adults and offspring consuming the same prey will cause adults to have assimilated diets similar to offspring assimilated diets (Nisbet et al. 2002). Using stable isotopes and dietary observations I specifically tested; to what extent does tern diets delivered to offspring on the same islands overlap? Do terns deliver a similar amount of common prey items to offspring on the same islands? Is the overall assimilated diet, represented in juvenile tern feathers, similar between tern species on the same islands?

METHODS

Feeding Observations

Feeding observations were preformed during summer from 2005 to 2007 on a group of nests in view from observations blinds. Two blinds were dedicated to each species on each island, except for roseate terns on OGI in 2007 and arctic terns on EER in 2005 and 2007 in which only one blind was used. Six to 7 nests were observed from each blind. Single and multiple egg clutches were selected for observations. Specific nests were identified by banding chicks with a federal band and color marking for identification. Nests were monitored for 12 hours each week during 4-3 hour periods until 21 days after chicks hatched. Observations were performed either in morning or evening when feeding mainly occurs. Observers were trained to identify fish to species and invertebrates to general types, such as amphipods and isopods. Prey size was measured relative to the parent tern's bill length. Lengths were recorded in quarter bill length intervals.

Feeding observations were made in good weather conditions. Researchers did not enter the colony in weather resulting in wet vegetation, such as rain, fog, and heavy morning dew. This prevented flushing parents from nests and subsequently wetting young chicks before they could thermoregulate.

Feather Collection

Feather collections were made from juveniles used in feeding and growth observation plots. Growth observation plots were 15 or more nests in designated area monitored to obtain morphometric growth data. Feathers from all species were collected from first hatched juveniles designated as "A" chicks. Second hatched "B" chicks of common terns were also sampled in 2007. Two body contour feathers were removed from the breast and stored in plastic bags on days 16 to 18 after hatch. Samples were collected from common and arctic terns in 2005 to 2007. Roseate terns, a federally endangered species, were only sampled in 2007.

Prey Collection

Prey items consumed by tern chicks were collected on multiple islands to relate isotopically to tern feathers. Prey items were collected as accidental drops by adult terns into the colony, when chicks did not consume prey at the nest, or by active removal of prey from chicks by researchers. Prey items were only collected if the specimen appeared fresh and had not dried out. All prey items were stored in plastic bags and frozen in liquid nitrogen until they were transported back to the mainland.

Isotope Analysis

Individuals used for isotopic analysis of feather carbon and nitrogen were selected at random using a random number generator as not all samples were analyzed. Feathers were washed in a 2:1 chloroform methanol solution to remove oil and debris. Feathers were allowed to dry for 48 hours before analysis. Barbules were removed along the entire rachis with scissors to insure isotopes were sampled over the complete period of feather formation.

Prey items collected on the islands were kept frozen until analysis. Frozen prey had all foreign debris removed from the surface and rinsed in water before vacuum drying. Dried prey items were homogenized using a WiggleBug.

Both feathers and prey items were weighed and packaged in tin capsules for analysis at the University of Arkansas Stable Isotope Laboratory. Carbon and nitrogen isotopes for both feathers and prey items were analyzed using a CE Instruments NC2500 elemental analyzer with a Finnigan Delta Plus isotope ratio mass spectrometer with machine error less than 0.2 for both carbon and nitrogen. Delta values (δX) were obtained from each analysis by comparison with an element-specific standard where: δX ‰ = [(R sample/R standard) – 1] x 1000 (Deniro and Epstein 1978). R sample and R standard refer the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Statistical Analysis

Differences in carbon and nitrogen isotope signatures were determined using MANOVA. Isotopic signatures were compared within each island for each year. Dietary overlap between tern species on each island was determined using Diamond's (1982) approach of measuring dietary overlap in seabirds which includes Horn's (1966) modification of Morisita's Index:

$$C = \frac{2\sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2}$$

where *s* is the number of prey categories and *i* is the number of times a prey category is represented in species *x* and species *y*. Prey items were separated into different size classes based on tern bill length size estimates. All fraction bill length estimates were rounded to the next whole bill length.

An ANCOVA (SPSS) was used to determine differences in the most commonly fed prey item size classes between tern species on each island. A MANCOVA (SPSS) was used to determine if differences existed between individual prey item size classes between tern species. Hours of observation was used as the covariate for ANCOVA and MANCOVA analyses.

RESULTS

Isotope Analysis

Carbon and nitrogen delta values for common and arctic terns at SINWR differed in carbon signature only in 2006 and 2007. Carbon and nitrogen tern feather signatures were similar for common and arctic terns in 2005 (MANOVA Wilks' Lambda $F_{2,26}$=0.86; p=0.4345; Figure 1). In 2006, common and arctic terns had similar $\delta^{15}N$ values, but arctic terns were more depleted in $\delta^{13}C$ than common terns (MANOVA Wilks' Lambda $F_{2,30}$=15.83; p<0.001; Figure 1). A similar pattern was observed in 2007 as common tern $\delta^{15}N$ values were the same as $\delta^{15}N$ values in arctic terns, but arctic terns were more depleted in $\delta^{13}C$ than common terns (MANOVA Wilks' Lambda $F_{2,14}$=20.30; p<0.0001; Figure 1).

Matinicus Rock National Wildlife Refuge showed similar carbon and nitrogen delta values between common and arctic terns for most years. A significant difference was found between MRNWR tern signatures in 2006 (MANOVA Wilks' Lambda $F_{2,27}$=6.65; p=0.0045) with arctic terns more depleted in $\delta^{13}C$ than common terns (Figure 2). No differences were found between common and arctic terns in 2005 (MANOVA Wilks' Lambda $F_{2,27}$=0.30; p=0.7426) or 2007 (MANOVA Wilks' Lambda $F_{2,17}$=2.05; p=0.1596; Figure 2).

Eastern Egg Rock terns had similar signatures in 2006, but 2005 and 2007 values were different among some tern species. Common and arctic tern nitrogen signatures were similar in 2005, but $\delta^{13}C$ values were significantly different (MANOVA Wilks' Lambda $F_{2,22}$=9.54; p=0.0010; Figure 3). Common and arctic terns in 2006 had similar carbon and nitrogen signatures (MANOVA Wilks' Lambda $F_{2,27}$=2.30; p=0.1195; Figure 3). In 2007, a significant difference was found when all three species were compared (MANOVA Wilks' Lambda $F_{4,60}$=17.25; p<0.0001). Common and roseate terns had similar $\delta^{13}C$ signatures (Tukey-Kramer p=0.6485). Common and roseate tern $\delta^{13}C$ signatures were more enriched than arctic tern $\delta^{13}C$ (Tukey-Kramer $p<0.0001$; Figure 3). Roseate tern $\delta^{15}N$ signature was more depleted than arctic (Tukey-Kramer $p<0.0001$; Figure 3) and common tern $\delta^{15}N$ (Tukey-Kramer $p=0.0052$; Figure 3).

Common and roseate terns were only sampled on OGI and SI in 2007. Common and roseate terns on OGI were not significantly different in $\delta^{13}C$ or $\delta^{15}N$ signatures (MANOVA Wilks' Lambda $F_{2,11}=1.27$; $p=0.3190$; Figure 4). However common and roseate terns on SI had significantly different $\delta^{13}C$ and $\delta^{15}N$ signatures (MANOVA Wilks' Lambda $F_{2,40}=28.41$; $p<0.0001$; Figure 5).

Morisita's Index

Arctic and common terns had a high Morisita's Index value on SINWR in 2005 (arctic tern n=18 nests; common tern n =12 nests; C=0.91), 2006 (arctic tern n=19 nests; common tern n=12 nests; C=0.98), and 2007 (arctic tern n=18 nests; common tern n=12 nests; C=0.98; Table 1). Terns on SINWR had a high percentage of euphasiids in all years and a low percentage of hake (Figures 6, 7, and 8). Herring was also observed in arctic and common tern deliveries in 2006 on SINWR (Figure 7).

On MRNWR, arctic and common terns had a high Morisita's Index value in 2005 (arctic tern n=16 nests; common tern n=11 nests; C=0.90) and 2007 (arctic tern n=16 nests; common tern n=13 nests; C=0.87), but low values in 2006 (arctic tern n=16 nests; common tern n=13 nests; C=0.06; Table 1). Euphasiids and hake made up a majority of prey deliveries in 2005 and 2006 (Figures 9 and 10). Hake dominated diets of both terns in 2007 (Figure 11). Low overlap in 2006 occurred as at least 25% more dietary categories were observed as well as an increase in unshared dietary categories relative to other years (Table 1; Figures 9, 10, and 11).

Morisita's index values were higher for arctic and common terns on EER in 2005 (arctic tern n=6 nests; common tern n=12 nests; C=0.96) relative to 2006 (arctic tern n=7 nests; common tern n=14 nests; C=0.20) and 2007 (arctic tern n=7 nests; common tern n=15 nests; C=0.57; Table 1). Common and arctic terns were feeding mostly hake in 2005 and 2006, but increased herring deliveries in 2007 (Figures 12, 13, and 14). Overlap values were higher for roseate terns (n=13 nests) in 2007 between arctic (C=0.62) and common (C=0.69) terns relative to arctic and common tern overlap (Table 1; Figure 14). Roseate terns had a diet mainly of hake with very little herring (Figure 15).

Common (n=18 nests) and roseate (n=4 nests) terns on OGI had high overlap (C=0.89) in 2007 (Table 1). Terns on OGI were consuming hake, herring, and sandlance (Figure 15). Common (n=21 nests) and roseate (n=14 nests) terns on SI had a lower overlap (C=0.61) in 2007 (Table 1). Terns on SI consumed herring and sandlance, but only common terns were observed consuming hake (Figure 16).

Dietary Observation Statistical Analysis

For dietary observations on SINWR in 2005, five major prey groups were compared between arctic (n=20 terns) and common terns (n=20 terns), euphasiid size 1, euphasiid size 2, hake size 1, hake size 2, and hake size 3. There was no difference between major prey items of arctic and common terns (ANCOVA; F_1=0.493; p=0.484) although there was a higher-order interaction between tern species and prey items (ANCOVA; F_4=2.960, p=0.021).

Six major prey groups were compared between arctic (n=22 terns) and common terns (n=15 terns) on SINWR in 2006, euphasiid size 1, euphasiid size 2, hake size 1, hake size 2, herring size 2 and herring size 3. There was a significant difference between arctic and common tern diets (ANCOVA; F_1=4.740; p=0.031). Individual prey size class comparisons also indicate that a difference exists between arctic and common tern prey groups (MANCOVA; Pillai's Trace; $F_{6,29}$=7.179; p<0.001). Between subjects effects indicated the difference existing between terns in herring size 3 (F_1=23.252; p<0.001).

Four major prey groups were compared on SINWR in 2007 for arctic (n=18 terns) and common terns (n=12 terns), euphasiid size 1, euphasiid size 2, hake size 1, and hake size 2. There was no significant difference between arctic and common tern diets (ANCOVA; F_1=1.109; p=0.295).

Five major prey groups were compared on MRNWR in 2005 between arctic (n=23 terns) and common terns (n=16 terns), amphipod size 1, euphasiid size 1, euphasiid size 2, hake size 1, and hake size 2. A significant difference was found between arctic and common tern diets (ANCOVA; F_1=4.457; p=0.036). However no difference was found for individual comparisons of the major prey items between arctic and common terns (MANCOVA; Pillai's Trace; $F_{6,31}$=1.180; p=0.343).

Six major prey groups were compared on MRNWR in 2006 between arctic (n=21 terns) and common terns (n=20 terns), amphipod size 1, euphasiid size 1, euphasiid size 2, hake size 1, hake size 2, and hake size 3. There was a higher-order interaction among tern species and prey items (ANCOVA; F_5=2.705; p=0.021). There was no significant difference between arctic and common tern diets (ANCOVA; F_1=0.309; p=0.579).

Seven major prey groups were compared on MRNWR in 2007 between arctic (n=15 terns) and common terns (n=16 terns), amphipod size 1, hake size 1, hake size 2, hake size 3, sandlance size 1, sandlance size 2, and sandlance size 3. There was no significant difference between major prey items for arctic and common terns (ANCOVA; F_1=3.703; p=0.056).

Arctic (n=6 terns) and common tern (n=9 terns) comparisons on EER in 2005 include seven major prey groups, hake size 1, hake size 2, hake size 3, hake size 4, herring size 1, herring size 2, and herring size 3. There was a significant higher-order interaction among tern species and major prey items (ANCOVA; F_6=3.300; p=0.006). There was no significant difference between arctic and common tern diets (ANCOVA; F_1=0.920; p=0.340.

Six major prey groups were compared on EER in 2006 between arctic (n=5 terns) and common terns (n=23 terns), hake size 1, hake size 2, hake size 3, herring size 1, herring size 2, and herring size 3. There was no significant difference between overall comparison of arctic and common tern diets (ANCOVA; F_1=3.618; p=0.059). Individual comparisons of prey groups between tern species did show a significant difference (MANCOVA; Pillai's Trace; $F_{6,20}$=7.400; p<0.001). Between subject tests indicated prey group differences between arctic and common terns for hake size 1 (F_1=20.843; p<0.001), hake size 3 (F_1=7.051; p=0.014), and herring size 2 (F_1=4.611; p=0.042).

Roseate terns (n=12 terns) were added to the comparison among arctic (n=11 terns) and common terns (n=27 terns) on EER in 2007 for 4 major prey groups, hake size 1, hake size 2, herring size 2, and sandlance size 2. There was a higher-order interaction among tern species and major prey items (ANCOVA; F_6=2.567; p=0.021). There was a significant difference among tern diets (ANCOVA; F_2=7.731; p=0.001). Individual comparison of prey groups among tern species showed there was a significant difference (MANCOVA; Pillai's Trace; $F_{8,88}$=3.551; p=0.001). Between subject effects show that significant differences specifically existed among terns for herring size 2 (F_2=8.367; p=0.001) and sandlance size 2 (F_2=4.974; p=0.011).

Seven prey groups were compared on OGI in 2007 between common (n=37 terns) and roseate terns (n=4 terns), hake size 1, hake size 2, hake size 3, herring size 2, sandlance size 1, sandlance size 2, and sandlance size 3. There was a higher-order interaction between tern species and prey groups (ANCOVA; F_6=6.426; p<0.001). There was a significant difference between tern species diets (ANCOVA; F_1=16.924; p<0.001) and a significant difference between individual prey group comparisons for tern species (MANCOVA; Pillai's Trace; $F_{7,32}$=10.411; p<0.001). Between subject effects indicate differences existed between terns for hake size 1 (F_1=6.594; p=0.014), sandlance size 1 (F_1=19.454; p<0.001), sandlance size 2 (F_1=48.450; p<0.001), and sandlance size 3 (F_1=13.682; p=0.001).

Four prey groups were compared on SI in 2007 between common (n=48 terns) and roseate terns (n=10 terns), hake size 2, herring size 2, sandlance size 2, and sandlance size 3. There was a significant higher-order interaction among tern species and prey groups (ANCOVA; F_3=23.807; p<0.001). There was no significant difference between terns diets for the four prey groups (ANCOVA; F_1=0.091; p=0.763). There was a significant difference when comparing individual prey groups between arctic and common terns (MANCOVA; Pillai's Trace; $F_{4,52}$=11.756; p<0.001). Between subject effects indicated a significant difference between hake size 2 (F_1=12.664; p=0.001), herring size 2 (F_1=18.463; p<0.001), sandlance size 2 (F_1=16.697; p<0.001), and sandlance size 3 (F_1=5.264; p=0.026).

DISCUSSION

Dietary overlap values do not directly show competition between two species (Diamond 1982). However there is a higher probability for species to be competitors if they are consuming the same diet at the same location. Therefore high overlap values between tern species that have similar carbon and nitrogen signatures have a higher probability of being competitors than low overlap values with different isotope signatures. Separation of both index and isotope values appeared to only occur on EER and SI in 2007. Arctic terns had a depleted carbon signature relative to both common and roseate terns on EER.

On SI, common tern carbon signature was depleted relative to roseate terns. However significant differences in major prey items consumed by terns on both EER and SI were only found on EER in 2007.

Nitrogen signatures for all tern species were similar in all comparisons. Only carbon varied in each tern comparison within a specific year. Variation in carbon signatures among tern species could represent several things. Carbon enrichment occurs as organisms feed at higher trophic levels (Deniro and Epstein 1978; Fry 1988). However feeding at higher trophic levels would also cause a subsequently larger enrichment in nitrogen (Wada et al. 1987; Fry 1988; Hobson and Welch 1992), a phenomenon not seen among terns in this study.

Carbon enrichment can also occur as terns forage on different prey items within a specific trophic level (Hobson et al. 1994). Carbon enrichment of juveniles due to a dietary difference would be observed in prey deliveries by adults. Dietary differences would be represented by a decrease in overlap between terns. Lower overlap coupled with different carbon signatures were observed between arctic terns and common and roseate terns on EER as well as common and roseate terns on SI in 2007.

Carbon enrichment with high dietary overlap can occur as terns consume similar prey in different locations that have different primary producers, such as plankton versus terrestrial plants (Hobson 1987, 1990). Terns foraging in more offshore environments will have a depleted carbon signature relative to inshore feeding terns (Hobson et al. 1994). Separation in carbon signatures with high dietary overlap occurred on EER in 2005 and SINWR in 2006 and 2007. On both islands arctic terns were more depleted in carbon than common or roseate terns. Arctic terns are known to forage farther from the mainland than common and roseate terns (Duffy 1986; Safina et al. 1988; Gochfeld et al. 1998; Rock et al. 2007).

High overlap values and similar carbon and nitrogen signatures occurred at some point on most islands. However high overlap values and isotope signatures consistently occurred on MRNWR and OGI. Statistical analyses disagreed with dietary overlap and isotope signatures as terns on MRNWR in 2005 and OGI in 2007 consumed significantly different amounts of major prey items. Arctic and common terns on MRNWR also had significantly different carbon and nitrogen signatures in 2006, but differences in either isotope were not separated enough to show a trophic shift (Deniro and Epstein 1978, 1981) or differences in foraging location (Hobson and Welch 1992).

There was not a consistent relationship between dietary overlap and covariate analysis of major prey items in tern diets. Morisita's index accounts for the number of prey categories that overlap among species and the frequency of prey in each category. Covariate analysis was specifically testing differences among small numbers of major prey items and was not accounting for differences among the twenty or more categories among tern species. As these two techniques of observing diets did not agree in many comparisons shows how terns have adapted to competition in the colony. Significant differences in diet on MRNWR (2005), SINWR (2006), and OGI (2007) show terns feeding different amounts of major prey items when tern diets had high dietary overlap values.

Common and roseate terns had consistently higher overlap values and similar isotope signatures relative to comparisons of arctic and common terns. Arctic and common terns had separation in overlap values, carbon signatures, or both on EER and SINWR while common and roseate terns only varied on SI. Common and roseate terns could be subjected to higher levels of competition than arctic and common terns when sharing the same breeding habitat. Higher overlap values and similar isotope signatures between common and roseate terns could be due to a preference for foraging along the coastline. Less competition could be occurring between arctic terns relative to common and roseate terns as arctic terns have a preference foraging in offshore waters (Hall et al. 2000).

The impact of competition on managed seabird colonies in Maine is unknown as populations are influenced by multiple environmental factors. Tern populations are influenced by other environmental factors, such as predation and weather. As managers restore new tern colonies they need to consider how location will impact species interactions. Nearshore islands located between foraging habitat types for different tern species may decrease foraging competition as seen on EER.

ACKNOWLEDGEMENTS

I thank the following organizations for providing funding for this study: Arkansas Audubon Society Trust and the Nisbet Research Grant. I thank the staff and volunteers of National Audubon Society's Seabird Restoration Program for assistance with feather collection and feeding observations, especially island supervisors – Noel Dodge, Suzanne Dodge, Christina Donehower, Johanna Hiscock, Katie

Kauffman, Matt Klostermann, Alison Kocek, Juliet Lamb, Pam Loring, Matt Martinkovic, Ellen Peterson, Lauren Scopel, Paula Shannon, Emily Tupper, and Carlos Zavalaga. I thank Scott Hall and Steve Kress for mentorship on the field sites. I thank the University of Arkansas Stable Isotope Laboratory Staff for analyses and advice – Erik Pollock and Tom Millican. I thank Elisha Ott for assistance in preparing isotope specimens. I especially thank Steve Beaupre, Gary Huxel, Ian Nisbet, and Kimberly Smith for their advice, editing, and use of laboratory space and equipment.

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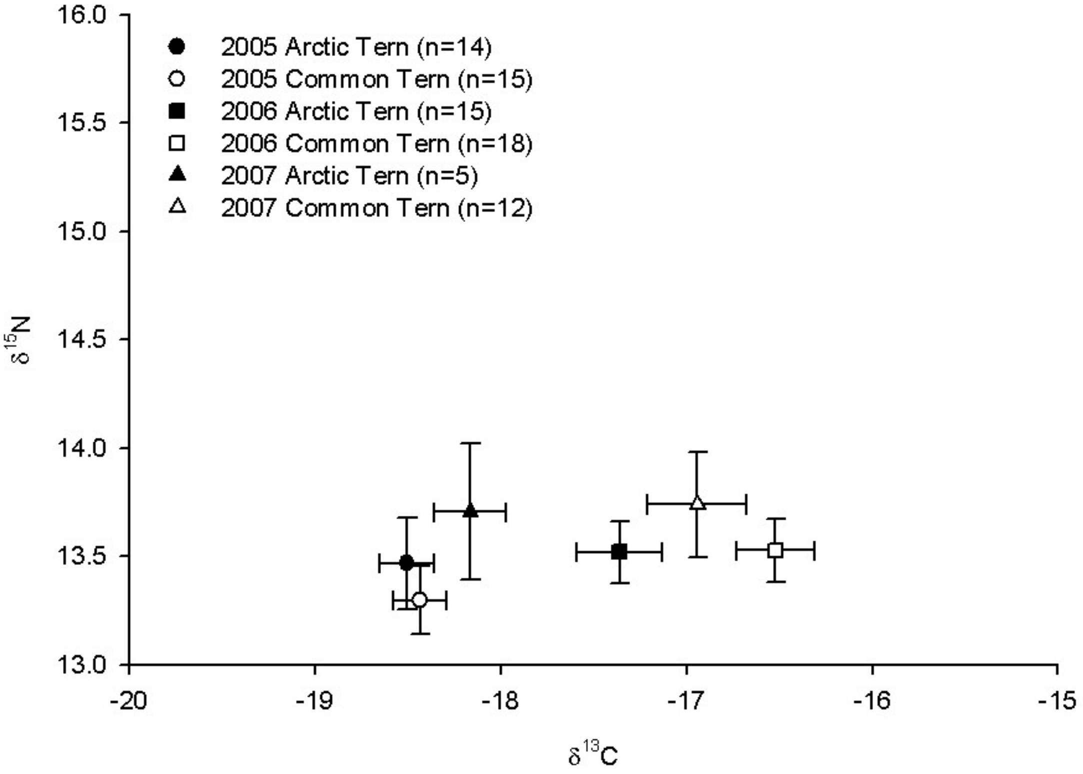

Figure 1. Arctic and common terns on Seal Island National Wildlife Refuge had similar carbon and nitrogen signatures in 2005. Nitrogen signatures were also similar in 2006 and 2007 but terns differed in δ^{13}C values. Values presented are means±2SE.

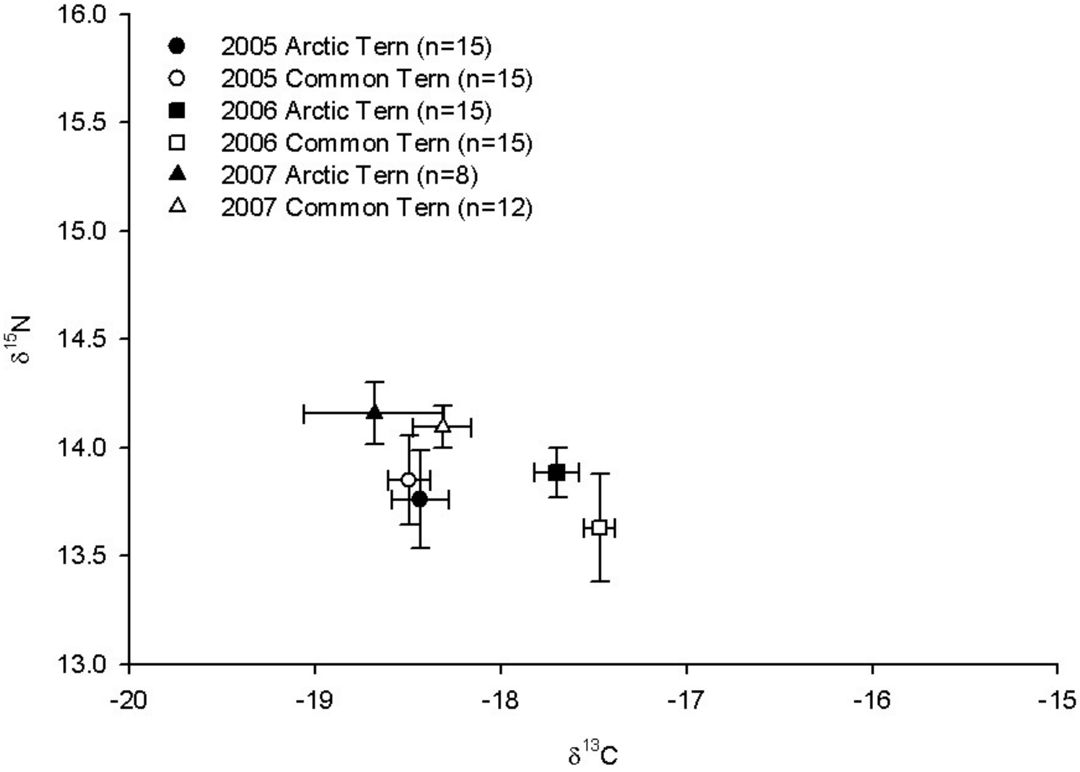

Figure 2. Matinicus Rock National Wildlife Refuge arctic and common terns had similar carbon and nitrogen signatures each year. Values presented are means±2SE.

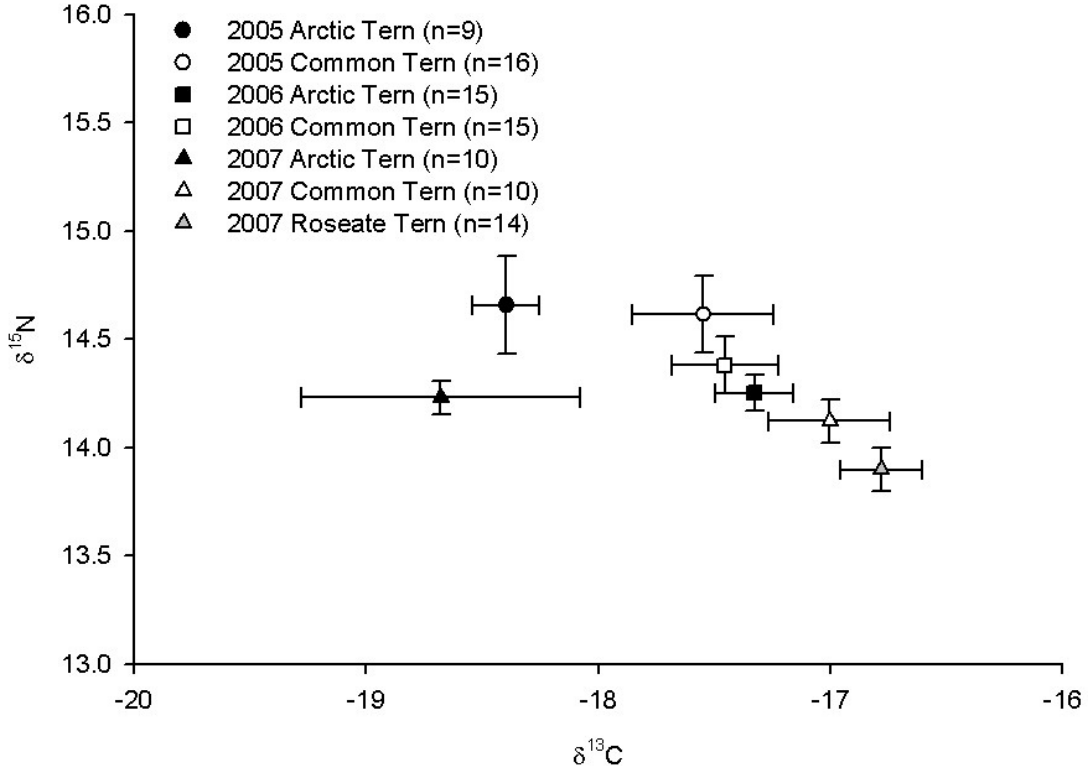

Figure 3. Eastern Egg Rock arctic and common terns had different carbon signatures in 2005 and 2007. Roseate terns also differed in carbon signatures from arctic terns, but not common terns. Values presented are means±2SE.

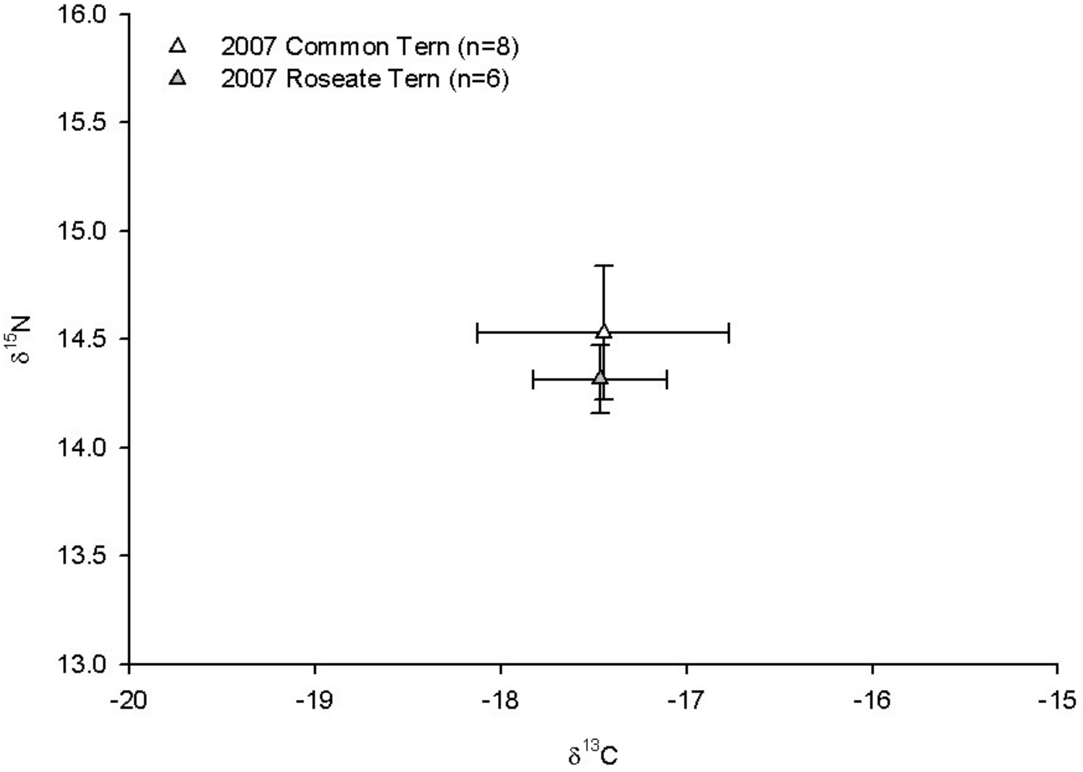

Figure 4. Outer Green Island common and roseate tern isotope signatures were similar in 2007. Values presented are means±2SE.

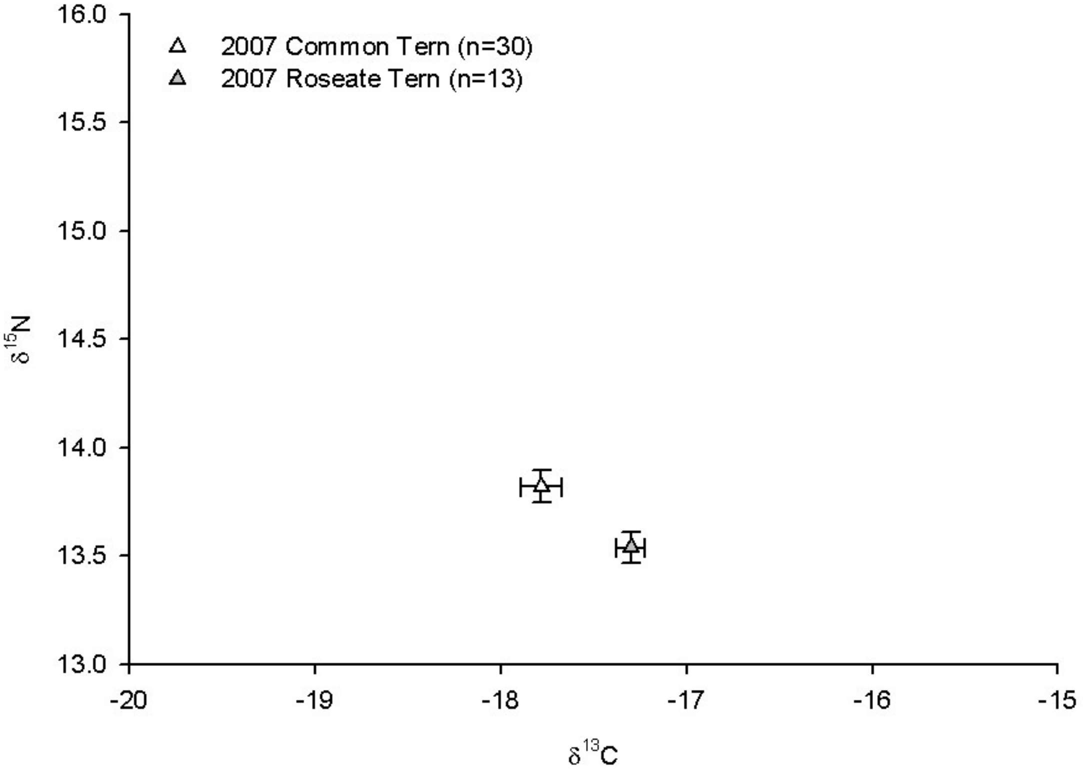

Figure 5. Stratton Island common and roseate terns had different carbon signatures in 2007. Values presented are means±2SE.

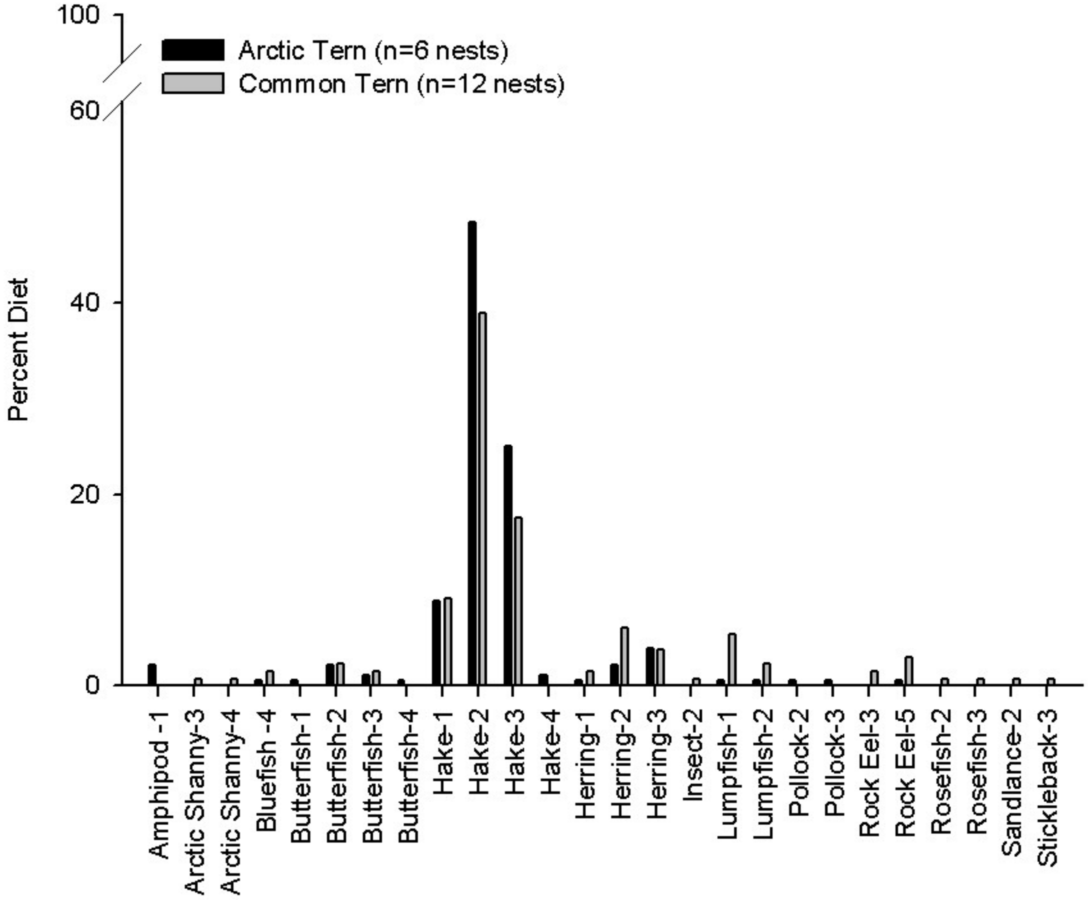

Figure 6. Arctic and common terns on Seal Island National Wildlife Refuge had high overlap (C=0.91) in 2005. Tern diets were mainly size 1 euphasiids and sizes 1 and 2 hake.

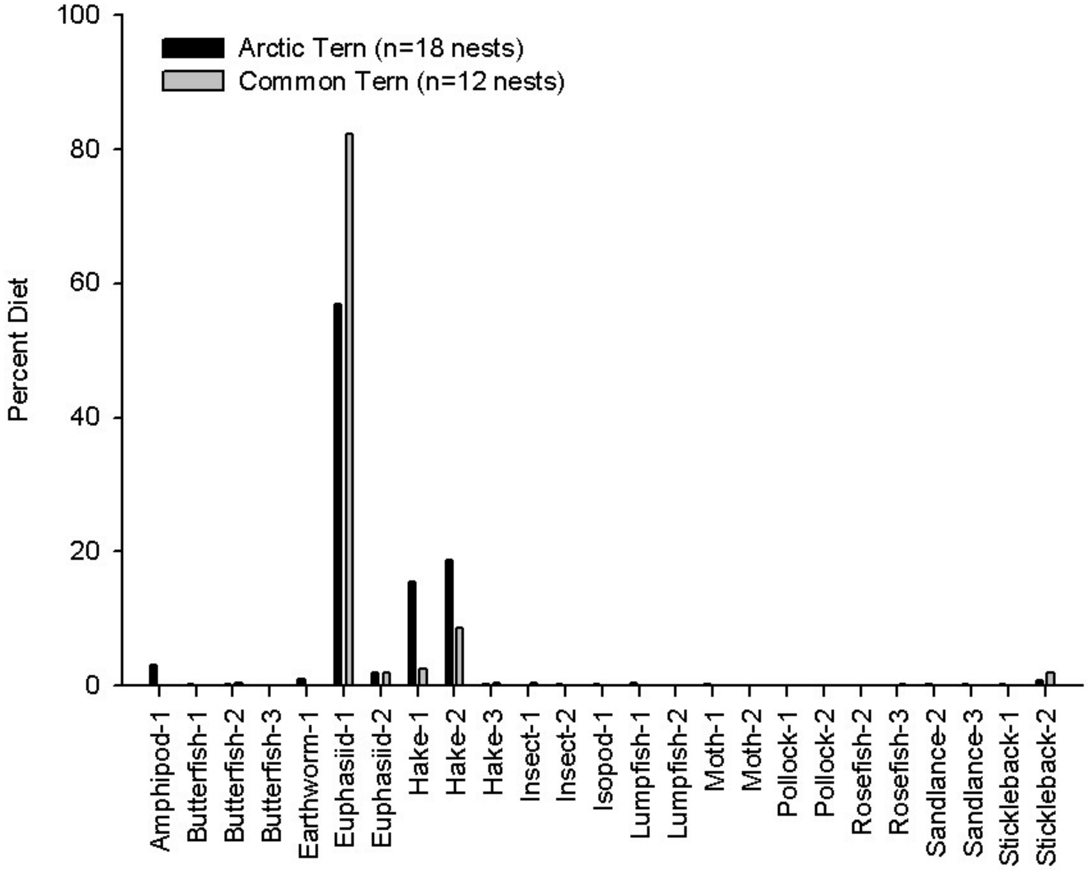

Figure 7. Arctic and common terns had a high overlap (C=0.98) on Seal Island National Wildlife Refuge in 2006. Tern diets included sizes 1 and 2 for euphasiids and hake and sizes 2 and 3 of herring.

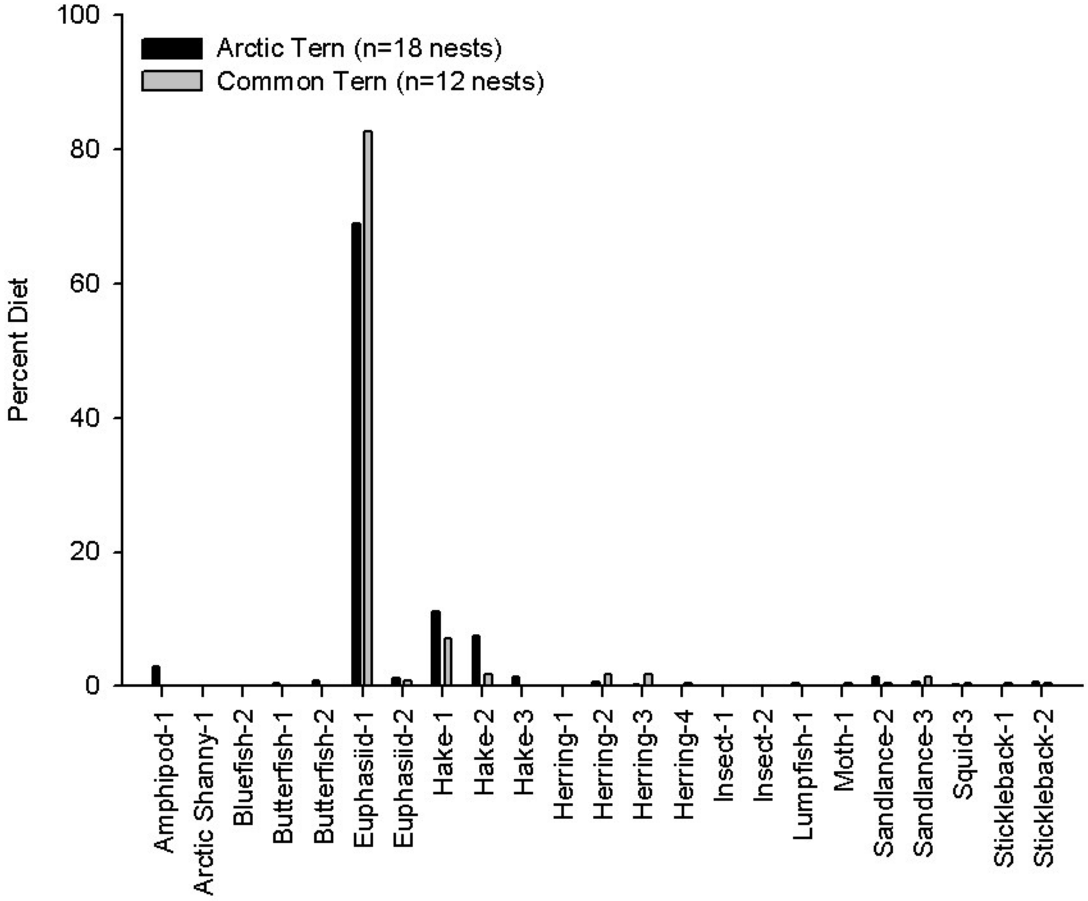

Figure 8. Arctic and common terns had a high overlap (C=0.98) on Seal Island National Wildlife Refuge in 2007. Tern diets were composed of size 1 euphasiids and sizes 1 and 2 hake.

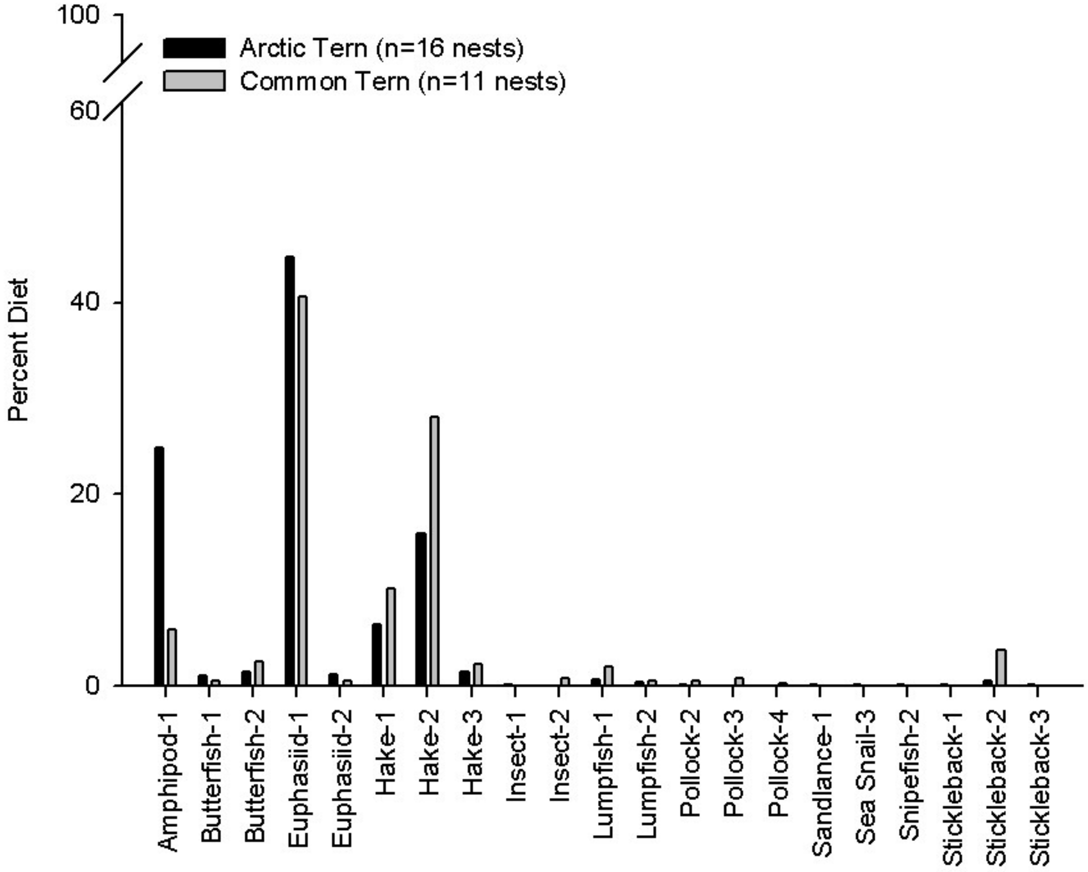

Figure 9. Arctic and common terns had high overlap (C=0.90) on Matinicus Rock National Wildlife Refuge in 2005. Terns had similar diets of size 1 amphipods and euphasiids, and size 1 and 2 hake.

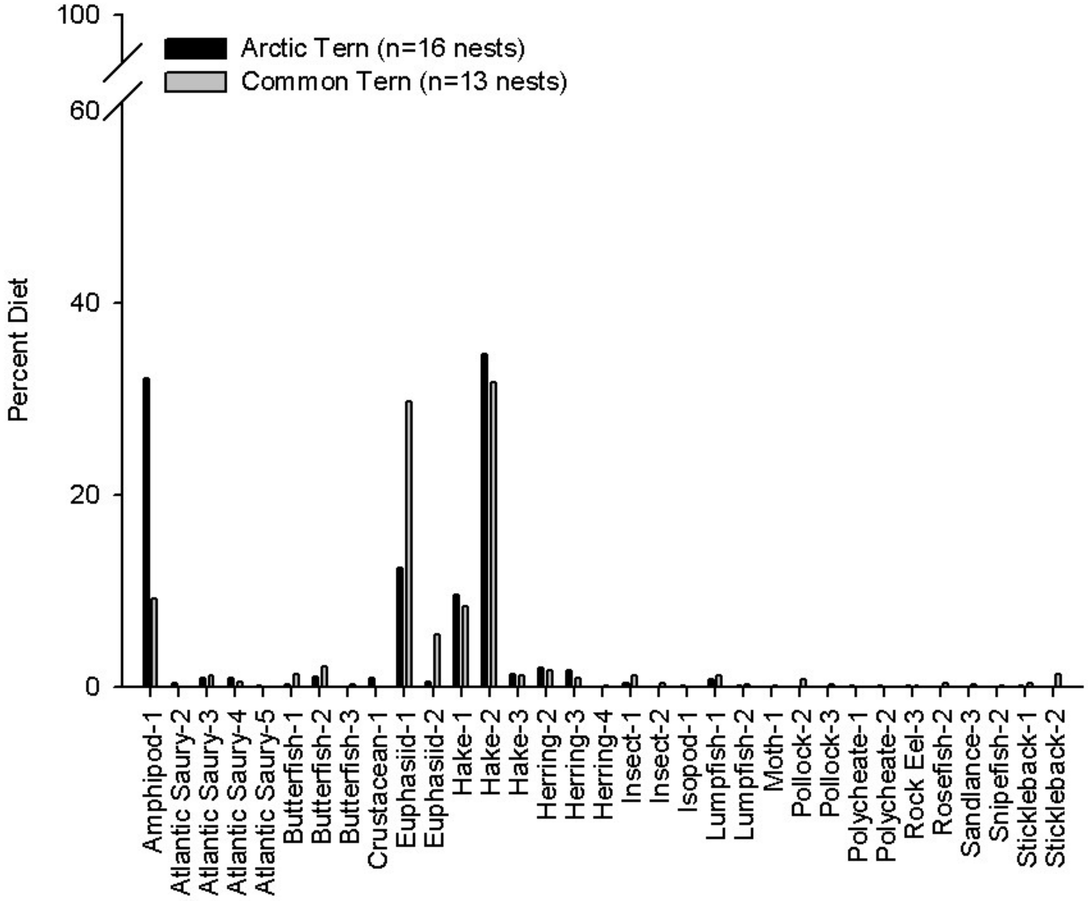

Figure 10. Arctic and common terns had a low overlap (C=0.06) on Matinicus Rock National Wildlife Refuge in 2006. Low overlap was a result of an additional 12 categories observed and an increase in diet categories not shared between species.

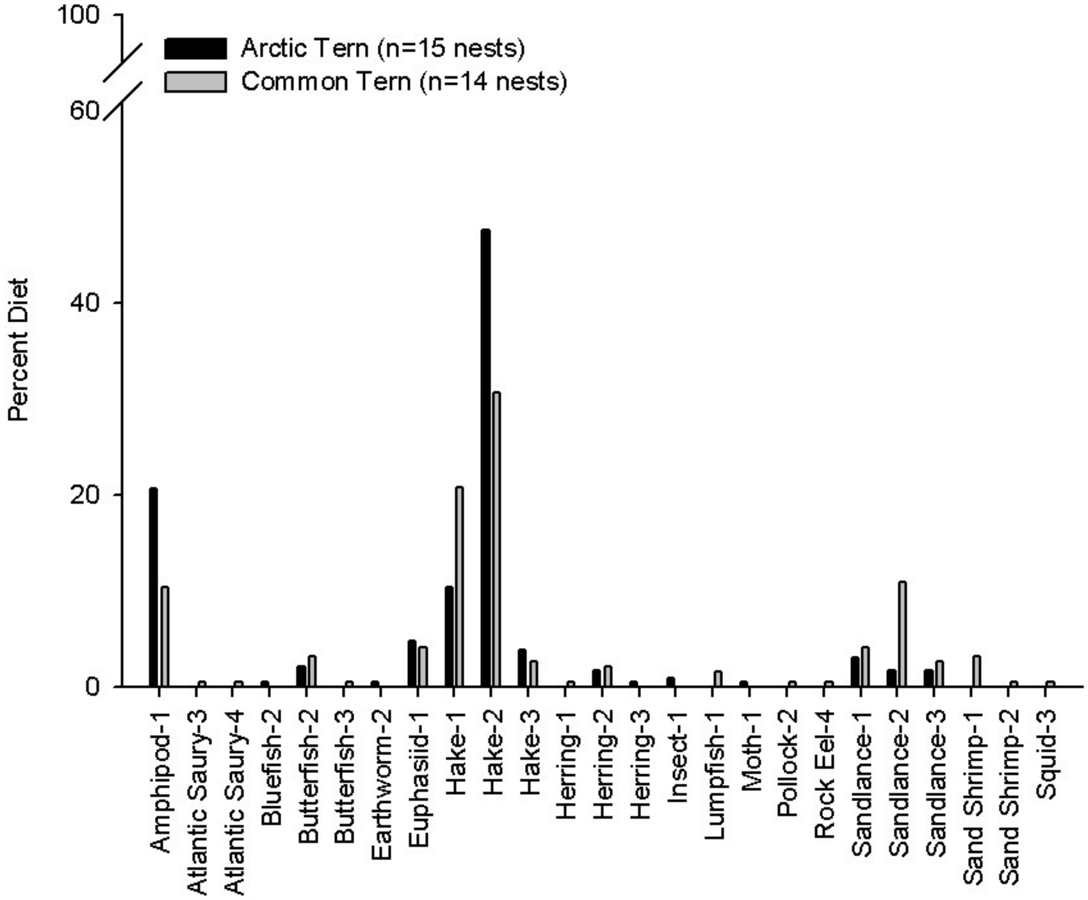

Figure 11. Arctic and common terns had high overlap (C=0.87) on Matinicus Rock National Wildlife Refuge in 2007. Terns consumed similar diets of size 1 amphipods and euphasiids and size 1 and 2 hake.

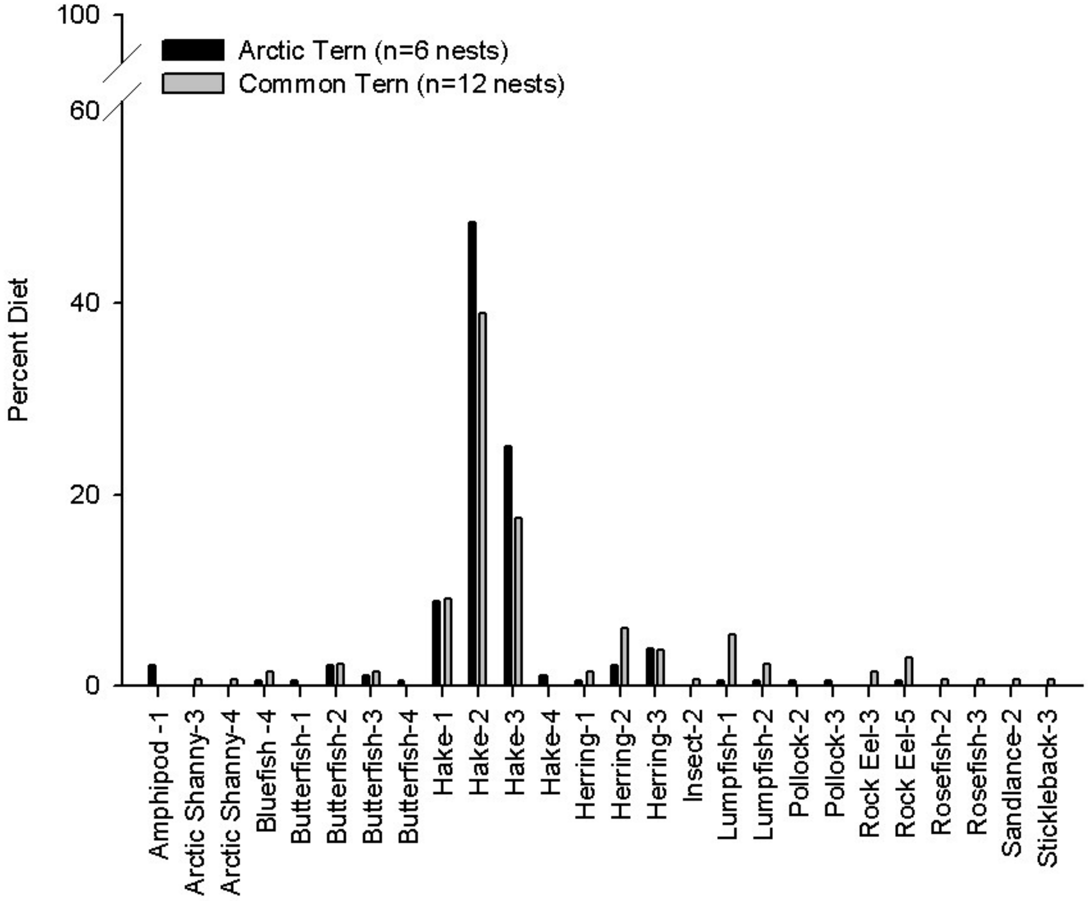

Figure 12. Arctic and common terns had high overlap (C=0.96) on Eastern Egg Rock in 2005.

Tern diets were mostly size 1, 2, and 3 hake.

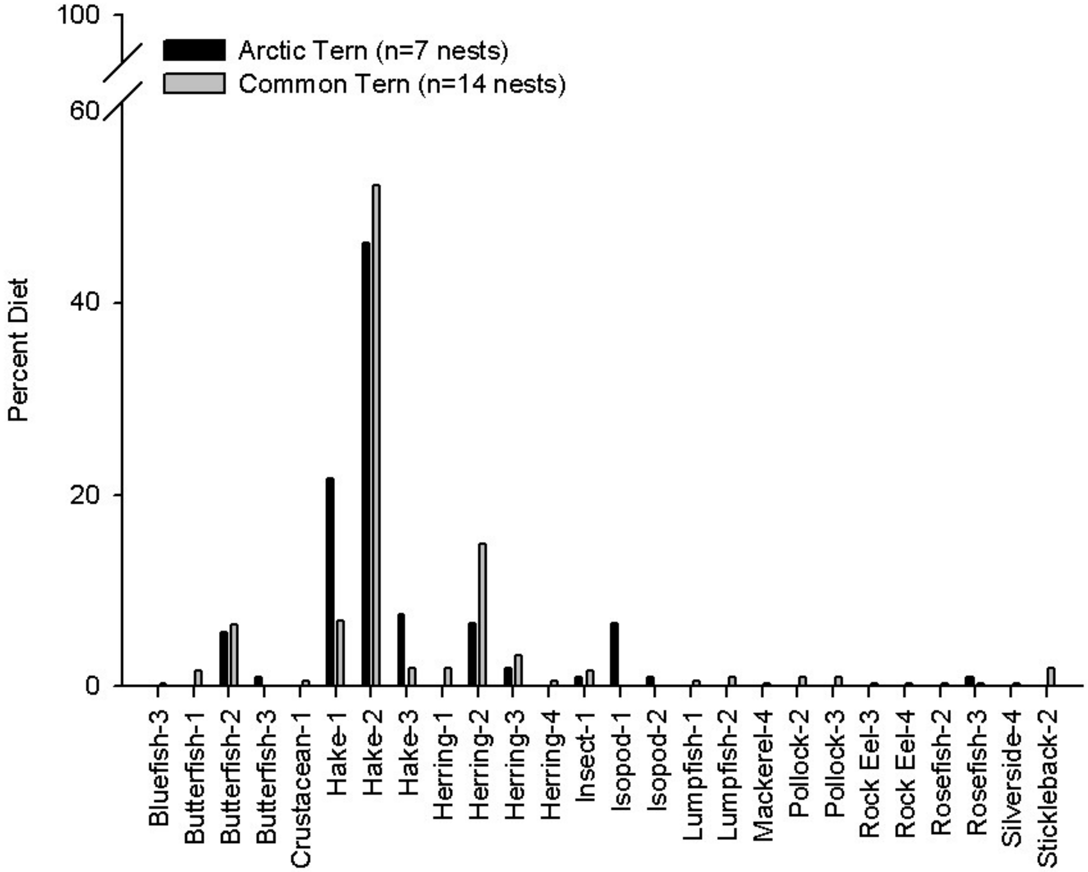

Figure 13. Arctic and common terns had low overlap (C=0.20) on Eastern Egg Rock in 2006. Fifty percent of both tern diets were size 2 hake, while sharing very little of other dietary categories.

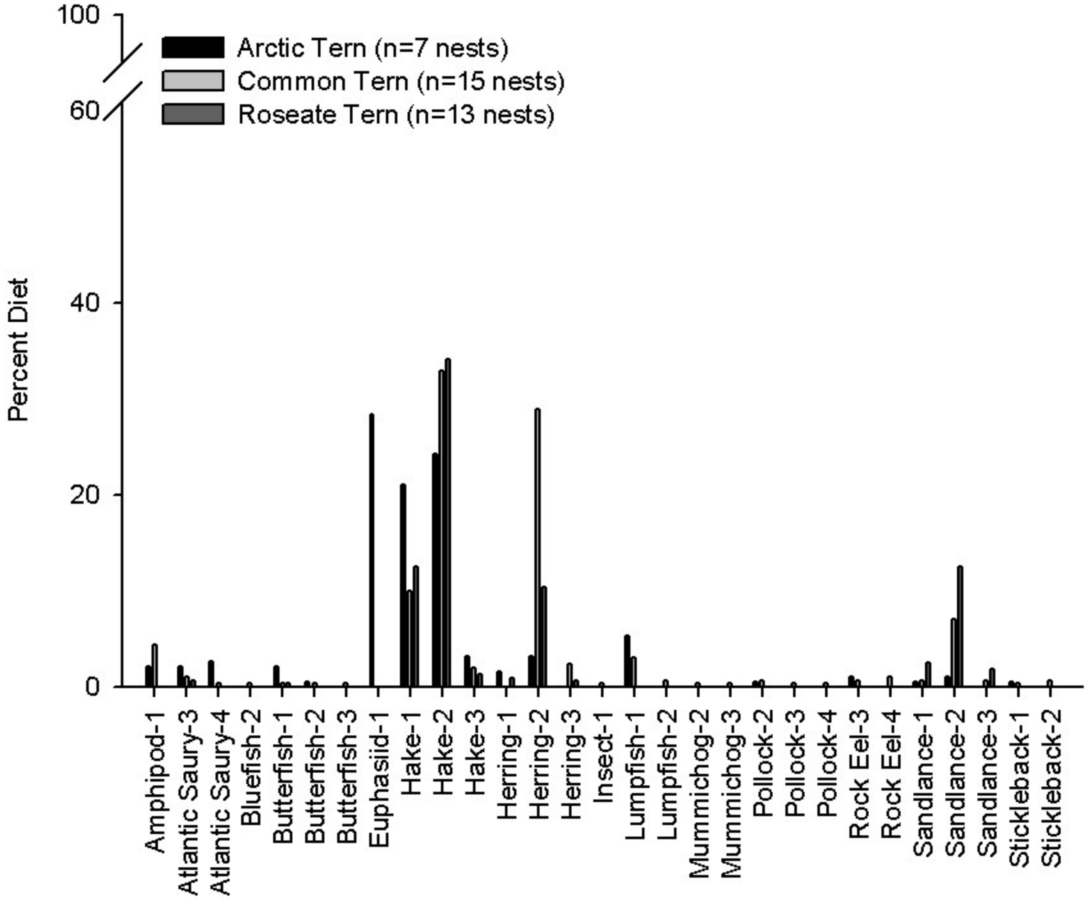

Figure 14. Arctic, common, and roseate terns all had medium overlap on Eastern Egg Rock in 2007. Comparisons between arctic and common terns (C=0.57), arctic and roseate terns (C=0.62), and common and roseate terns (C=0.69) showed a diet overlap in size 1 and 2 hake.

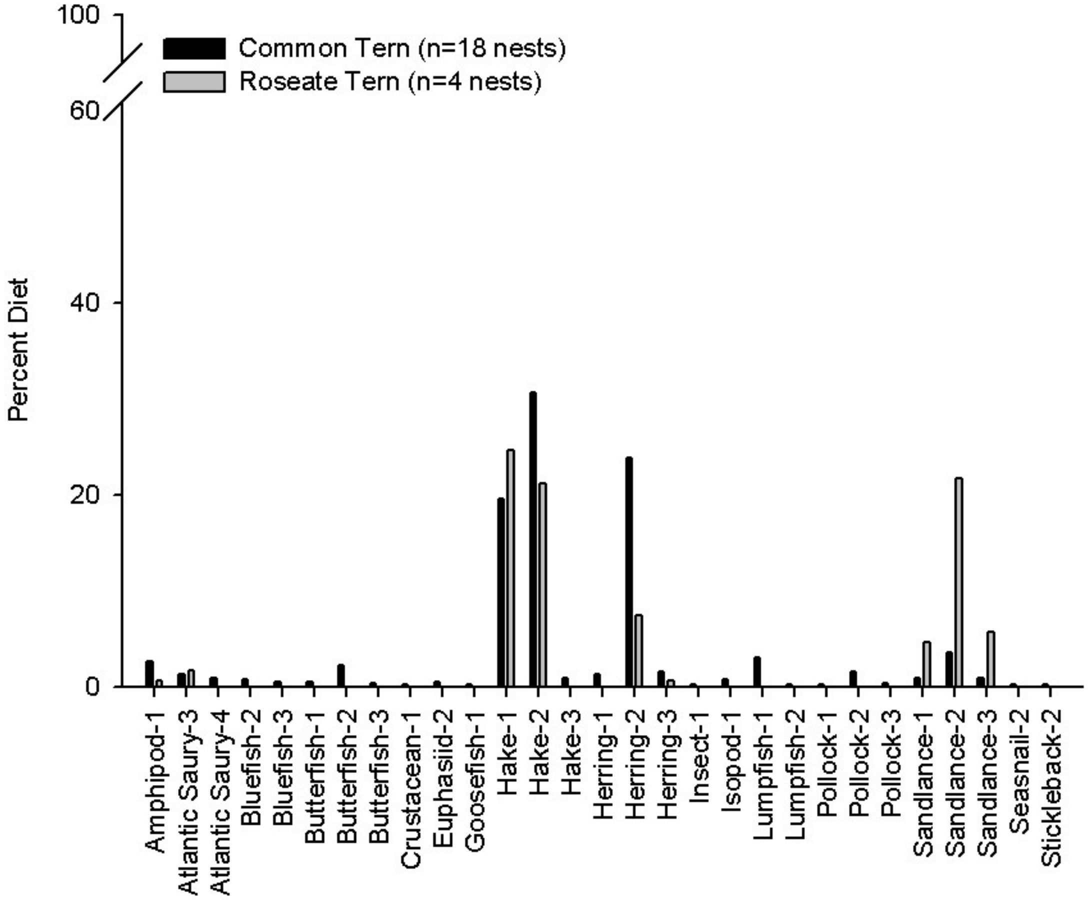

Figure 15. Common and roseate terns had high overlap (C=0.89) on Outer Green Island in 2007. Terns shared diets of size 1 and 2 hake and size 2 herring.

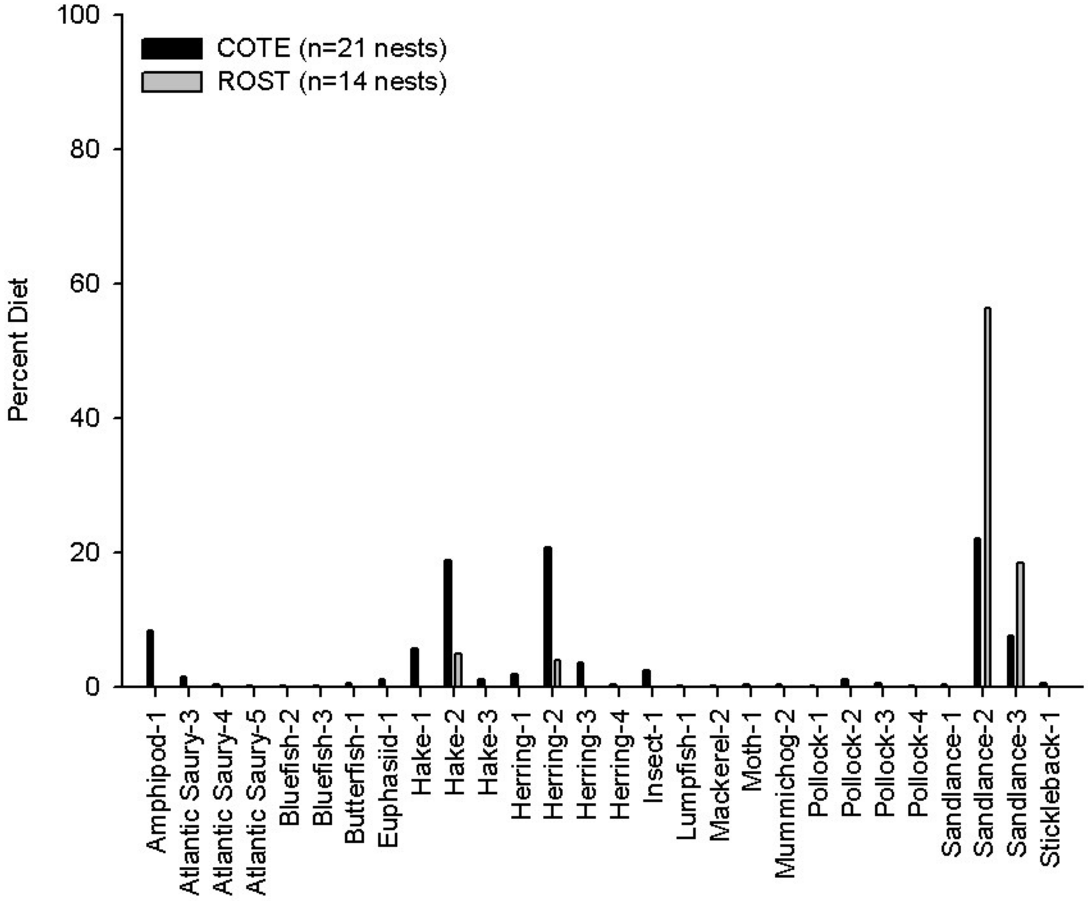

Figure 16. Common and roseate terns had a medium overlap (C=0.61) on Stratton Island in 2007. Terns shared diets of size 2 herring and size 2 and 3 sandlance.

Island	Year	Species Comparison	Index Value	Dietary Catagories
SINWR	2005	Arctic and Common terns	0.91	25
MRNWR	2005	Arctic and Common terns*	0.90	21
EER	2005	Arctic and Common terns	0.96	26
SINWR	2006	Arctic and Common terns*	0.98	25
MRNWR	2006	Arctic and Common terns	0.06	33
EER	2006	Arctic and Common terns	0.20	26
SINWR	2007	Arctic and Common terns	0.98	23
MRNWR	2007	Arctic and Common terns	0.87	25
EER	2007	Arctic and Common terns*	0.57	29
EER	2007	Arctic and Roseate Terns*	0.62	29
EER	2007	Common and Roseate terns*	0.69	28
OGI	2007	Common and Roseate terns*	0.89	29
SI	2007	Common and Roseate terns	0.61	28

Table 1. Morisita's index values were high for most comparisons. Lowest index values were seen between arctic and common terns in 2006 on Matinicus Rock National Wildlife Refuge and Eastern Egg Rock. Medium index values were found between arctic, common, and roseate terns on EER in 2007 as well as common and roseate terns on SI in 2007. Significant differences determined by ANCOVA between tern diet observations are indicated by *.

CHAPTER 4. LIFE HISTORY PLASTICITY IN COMMON TERNS: EFFECT OF THERMOREGULATORY COSTS IN DIFFERENT COLONIES.

ABSTRACT

Life history phenotypes vary among common terns (*Sterna hirundo*) nesting on National Audubon Society's Seabird Restoration Program islands in the Gulf of Maine. Offshore tern colonies (>10km from mainland) have a smaller clutch, hatching chicks that exhibit slower growth rates than inshore tern colonies (<5km from mainland). Variations among colonies are often viewed as a result of dietary differences impacting energy budgets. However other environmental factors such as temperature differences also have an impact on energy budgets. To test energy differences among locations, operative temperatures were measured using copper models representing young tern chicks in tern colonies on Stratton Island (SI), an inshore island, and Seal Island National Wildlife Refuge (SINWR), an offshore island, in June and July 2009. Operative temperatures were used to calculate thermoregulatory costs by Klaassen's (1994; 1995) equations on tern thermoregulation. National Oceanic and Atmospheric Administration weather stations were used to collect wind speed, ambient and water temperatures near inshore and offshore colonies. Operative, ambient, and water temperatures were consistently higher on SI than SINWR even with higher precipitation on SI than SINWR in 2009. Thermoregulatory costs were greater on SINWR than SI. Despite variation in precipitation among the last four years, ambient and water temperatures were consistently higher for inshore than offshore buoys. Decreased temperature for common tern chicks on SINWR cause chicks to have higher thermoregulatory costs than SI chicks when chicks are not being brooded by parents. Although rate of prey delivery is similar between inshore and offshore tern colonies, offshore colonies are known to deliver lower quality prey items than inshore colonies. Diet has been suggested as a cause for reproductive differences among adults in separate colonies. Tern chicks on offshore islands may further compensate for energy losses due to thermoregulatory costs by decreasing growth rates relative to inshore islands chicks.

INTRODUCTION

Life histories influence characteristics of a population by determines how energy is allocated to competing functions in an individual's energy budget (Cody 1966; Gadgil and Bossert 1970; Drent and Daan 1980; Dunham et al. 1989). Resources dedicated from an energy budget for reproductive effort (Stearns 1976) and parental effort (Low 1978) are determined by life history as well. Expending more energy foraging, producing offspring, and for body maintenance than energy acquired from the environment will decrease future survivorship (Bryant 1979; Nur 1988).

Energy for reproduction is rationed between different activities, adjusting productivity in different environments. Tradeoffs associated with different reproductive traits allow parental effort to be adjusted to maximize current reproduction while not jeopardizing future reproduction (Stearns 1989; Dijkstra et al. 1990; Roff 1992). Without tradeoffs adults would have to sacrifice body reserves to maintain reproductive output and decrease parental survivorship (Martin 1987).

The widest variety of tradeoffs can be seen in reproduction and growth of reptiles and amphibians as they can change energy allocation to reproduction and growth (Congdon et al. 1982). As birds are determinate growers, tradeoffs can be best observed during reproduction. For birds, common reproductive tradeoffs are the size and number of eggs produced as well as growth rate of juveniles (Lack 1968). Egg size is influenced by decisions made early in egg production. Egg composition determines initial resources for growth and development which is important for precocial and semi-precocial chicks. Clutch size is often used in evaluating life histories as it shows a discrete reproductive product. In some species, clutch size can fluctuate based on environmental resources (Ricklefs 1977). Growth rate also fluctuates depending on environment and foraging resources available to parents (Schew and Ricklefs 1998)

Lack's (1947) life history theory states that birds use all available resources for reproduction to maximize productivity. However birds limit reproductive expenditures during different stages of reproduction by limiting parental effort. Reproductive output in seabirds is influenced by prey availability (Kitaysky et al. 2000). As prey availability decreases in an area, some seabirds compensate behaviorally by increasing effort (Uttley et al. 1994). Increased foraging effort by parents are seen only in colonies that have become limited in resources and not used by parents to gain additional resources in areas with good foraging success (Zador and Piatt 1999). Parents are choosing not to overexert themselves to raise their offspring. Parents are sacrificing current reproduction to keep material in reserve for future reproductive events (Drent and Daan 1980).

Some seabirds, such as common terns (*Sterna hirundo*), have enough genetic variability to adjust clutch size and egg size with varying parental effort (Nisbet 2002). Laying only one clutch per season

(Hays 1984) limits common terns in tradeoffs made at any one time. Common tern females can save energy by adjusting materials in a clutch as it requires a lot of energy dedicated to clutch formation at one time (Wiggins and Morris 1987; Wendeln 1997).

Common tern females could lay more eggs if they choose. Common terns are not expanding their clutches due to a lack of resources to form eggs. Common tern females lay additional eggs to replace eggs lost from a nest within a week of initial laying period (Cody 1966; Nisbet 1978; Arnold et al. 1998; Wendeln et al. 2000; Becker and Zhang 2010).

Common terns may not maximize productivity by producing more eggs. Common terns lay up to 3 eggs in a clutch that hatch asynchronously (Nisbet 2002; Becker and Ludwigs 2004). The last egg laid is usually the smallest of the entire clutch and its probability for survival is lower than its siblings (Nisbet 1973; Gochfeld 1977; Bollinger 1994). The youngest chick often dies as parents lack the ability to provide for them (Langham 1972). The youngest chick's role may not be to expand productivity, rather as insurance in case an older sibling perishes (Nisbet and Cohen 1975). Tern chicks often die due to cold and wet weather (Nisbet 2002).

Other factors beyond insurance also play a role in adjusting reproductive effort dedicated to egg formation. Variations in life history phenotypes are influenced to a higher extent by food availability during each stage of reproduction (Martin 1987). Common terns can lay larger clutches in better food years (Safina et al. 1988). Females derive materials to form clutches during male courtship feedings (Nisbet 1977). However differences observed in courtship feedings do not always result in differences in clutch size (Moore et al. 2000). As previously discussed, females do not dedicate all resources to egg production. Courtship feedings allow females to adjust clutch size based on their mate's foraging success, showing his ability to provide for future offspring (Nisbet 1973; Wendeln and Becker 1996; Wendeln 1997).

Variation in reproductive phenotype of common terns may relate more to foraging success. Common terns arrive on their breeding sites after an extensive migration (Austin 1953; Nisbet et al. 2011). Terns use most of their reserves during migration, depleting energy reserves for reproduction (Pearson 1968) causing tern reproductive output to be directly related to their foraging success. Foraging success of common terns is known to be influenced by age (Nisbet 1973; Nisbet et al. 1984), experience

(Nisbet 1983; Arnold et al. 2004), body condition (Nisbet 1973; Wendeln and Becker 1996; Wendeln 1997; Wendeln and Becker 1999; Becker et al. 2001), prey availability (Hall et al. 2000; Schwemmer et al. 2009; Danhardt et al. 2011), and weather (Dunn 1972, 1973, 1975). Differences in foraging success lead to changes in life history phenotypes within a breeding colony (Martin 1987; Nisbet 2002).

Differences in reproductive phenotypes between colonies could be caused by other factors than those that influence life history variation within a single colony (Nisbet et al. 1984). Differences in a species life history between locations could be caused by genetic differences that have evolved in separate populations. Terns breeding in a similar region belong to a metapopulation made of smaller populations (Spendelow et al. 1995; Schippers et al. 2009). Although terns generally return to prior breeding colonies (Spendelow et al. 1995) genetic diversity between islands within a region should be similar as juveniles are initially selecting nesting sites away from their natal colony (Dittmann et al. 2005).

Without genetic differences among colonies, life history phenotypes will be closely linked to local environmental conditions. Environmental conditions around a colony will include foraging opportunities and other environmental factors influencing tern energy budgets. Although common terns can travel a large distance to forage, they are considered to have a short foraging range making them rely on resources close to breeding sites (Duffy 1986; Becker et al. 1993). This forces reproductive decisions influencing reproductive phenotypes to be based on resources around breeding colonies (Pearson 1968; Hobson et al. 2000; Ezard et al. 2007). Being able to locate food close to the nesting colony is essential for common tern reproductive success (Courtney and Blokpoel 1980).

Comparisons among colonies attribute differences mainly to foraging success. Populations farther from food sources expend additional energy foraging, leaving less energy for reproduction (Hunt 1972; Davoren and Montevecchi 2003; Hall and Kress 2004). Larger seabird colonies could create food shortages with increased competition relative to smaller colonies (Ashmole 1963; Ricklefs 1980; Lewis et al. 2001). Weather conditions also influence foraging success among colonies (Massias and Becker 1990; Frank 1992).

Weather can also have a more direct impact on reproductive phenotypes. Colder temperatures will require birds to expend more energy thermoregulating. Temperature has an impact on resting metabolism and growth rate of juveniles (Klaassen and Drent 1991). For species such as common terns that display a range of growth rates between locations (Klaassen et al. 1992), growth rates will be influenced as environmental costs increase. Chicks in colder environments have higher costs for thermoregulation relative to birds in warmer environments (Klaassen 1994). Decreasing growth rate can save energy for a chick to survive (Klaassen et al. 1989a; Klaassen et al. 1992; Klaassen 1994).

A unique situation has been created in the Gulf of Maine to view reproductive plasticity among different common tern colonies. National Audubon Society's Seabird Restoration Program has restored 7 nesting islands along the Maine coast. Different reproductive phenotypes have been observed among islands based on their distance from the mainland. Common terns nesting on offshore islands, greater than 10km from the mainland, and nearshore islands, between 5 and 10km from mainland, lay smaller clutches, hatch chicks that have decreased growth rates, and reach a lower asymptotic mass than common terns nesting on inshore islands, less than 5km from mainland (Hall and Kress 2004). Life history differences between colonies have been attributed to foraging differences between colonies with outer islands delivering lower quality prey items than inshore islands (Hall et al. 2000; Hall and Kress 2004).

The goal of this study was to measure operative temperatures among colonies to determine how much environmental temperatures are influencing energy budgets between inshore and offshore islands. Operative temperatures show the temperature that an organism would be with only conduction, convection and radiation (Bakken 1976). Thermoregulatory costs can be calculated using operative temperatures, estimates of basal metabolic rate, and thermal conductivity for tern chicks (Klaassen 1994). Tern chicks will expend more energy as ambient temperature moves away from chick body temperatures if chicks are not brooded (Klaassen et al. 1989b; Klaassen 1994). Therefore I specifically asked; are thermoregulatory costs of tern chicks were higher on offshore islands relative to inshore tern colonies?

METHODS

Operative temperature models were constructed as copper spheres setting atop a copper shaft (Walsberg and Weathers 1986; Klaassen 1994). Copper models were constructed to represent a 6 day old chick that is beginning to thermoregulate (Klaassen et al. 1989b). Copper was electroplated onto 35mm diameter wax spheres on 20 mm copper tubing with 20 mm diameter. Models were painted blonde on top with black stripes and black numbers and gray on the lower sphere and shaft. A DS19216-

F5 thermochrom I-button was suspended inside the sphere. I-buttons were set to record temperature within 0.5°C every 21 minutes starting on 15/6/2009 to 16/7/2009. Models were placed adjacent to random common tern nests on an inshore island, Stratton Island (SI), and an offshore island, Seal Island National Wildlife Refuge (SINWR; Figure 1).

Models were calibrated to non-thermoregulating chicks using a taxidermic mount of a 6 days old chick. Chick core temperature was measured with a HH-25TC Omega thermometer connected to a wire thermocouple inserted into its abdomen through its cloaca. A copper model containing an I-button was placed beside a taxidermic model for calibration. A calibrating factor was determined as the average difference between taxidermic and copper models. The average calibration was added to copper model data.

Operative temperatures were used to calculate thermoregulatory costs in the following equation: $Eth = h(T_b - T_e) - BMR$; where h is thermal conductance, T_b is tern body temperature, T_e is operative temperature, and BMR is basal metabolic rate (Klaassen 1994). Thermal conductance was calculated by $h = 1.28M^{-0.502}(0.71)$ where M is chick mass (Klaassen 1994; Klaassen 1995). Chick mass represented by the models was 35g therefore $h=0.153\ mlO_2g^{-1}h^{-1}{}^{\circ}C^{-1}$. T_b for tern chicks was assumed to be 39°C (Klaassen 1994). Basal metabolic rate was calculated by $BMR = (1.17 + 0.038M + 10^{-4})(-2.365)(M^2)(0.71)$ where M is chick mass of 35g (Klaassen 1994; Klaassen 1995). BMR was $1.57\ mlO_2g^{-1}h^{-1}$. $Eth = 0$ if $h(T_b - T_e) < BMR$.

Model temperature and thermoregulatory costs were analyzed using repeated measures (SAS Proc Mixed) with a heterogeneous autoregressive covariance structure and time repeating. Model temperatures and thermoregulatory costs were averaged per hour and separated into day and night temperatures to reduce data size for analysis. Day and night measurements on SI and SINWR were determined by sunrise and sunset times in Portland, ME, and Rockland, ME respectively. High and low temperatures were also analyzed using repeated measures (SAS Proc Mixed) with a heterogeneous autoregressive covariance structure and time repeating.

Precipitation measurements were obtained daily on SI and SINWR. A rain gauge was checked once daily at 0600, recording precipitation to 0.1 inches. Precipitation measurements were used to identify storm events that could impact model temperatures.

Buoy data between June 15 and July 17 were obtained from Portland, ME buoy (Station 44007), Central Maine Shelf buoy (Station 44032), and Matinicus Rock, ME lighthouse (Station MISM1) for 2007 through 2009 was collected from NOAA's National Data Buoy Center (www.ndbc.noaa.gov). Four previous years were obtained for comparison as 2009 had an above average year of rainfall. Ambient and water temperatures were collected hourly by buoys and averaged per day for comparisons. Ambient temperatures were collected by all three buoys, while water temperatures were only collected by Portland, ME and Central Maine Shelf buoys.

RESULTS

Daytime model temperatures fluctuated in daily unison on SI and SINWR (Figure 2). Daytime model temperatures were warmer on SI than SINWR. Mean daytime model temperature on SI (n=360) was 28.0°C (±0.42 2SE; Figure 2). Mean daytime model temperature on SINWR (n=360) was 25.7°C (±0.36 2SE; Figure 2). Repeated measures for daytime temperatures showed a higher-order interaction effect between islands and days (Proc Mixed, $F_{29,638}$=131.75, p<0.0001). A significant difference also existed in daytime temperatures between islands (Proc Mixed, $F_{1,22}$=54.07, p<0.0001) and days (Proc Mixed, $F_{29,638}$=58.42, p<0.0001).

Nighttime model temperatures were cooler on SINWR than SI. Mean nighttime temperature on SI (n=360) was 23.0°C (±0.13 2SE; Figure 3). Mean nighttime temperature on SINWR (n=360) was 21.0°C (±0.11 2SE; Figure 3). Repeated measures for nighttime temperatures showed a significant higher-order interaction effect between islands and days (Proc Mixed, $F_{29,638}$=103.63, p<0.0001). A significant difference also existed in nighttime temperatures between islands (Proc Mixed, $F_{1,22}$=402.20, p<0.0001) and days (Proc Mixed, $F_{29,638}$=90.57, p<0.0001).

Daily high model temperatures were greater on SI than SINWR. Mean high model temperature on SI (n=360) was 34.5°C (±0.81 2SE) while SINWR (n=360) was 32.0°C (±0.71 2SE; Figure 4). There was a higher-order interaction effect for high temperatures between islands and day (Proc Mixed, $F_{27,594}$=23.75, p<0.0001). There was a significant difference in high temperatures between islands (Proc Mixed, $F_{1,22}$=12.15, p<0.0021) and days (Proc Mixed, $F_{27,594}$=67.88, p<0.0001).

Daily low model temperatures were lowest on SINWR than SI. Mean low model temperature on SI (n=360) 22.0°C (±0.16 2SE) and on SINWR (n=360) was 20.2°C (±0.11 2SE; Figure 5). Low model temperatures also showed a high order interaction effect between islands and days (Proc Mixed, $F_{27,594}$=35.03, p<0.0001). Low temperatures were significantly different between islands (Proc Mixed, $F_{1,22}$=491.81, p<0.0001) and days (Proc Mixed, $F_{27,594}$=114.36, p<0.0001).

Thermoregulatory costs calculated from operative temperatures were higher for SINWR terns than SI terns (Figures 6 and 7). There was a significant effect of island on average daily thermoregulatory costs ($F_{1,22}$=513.20, p<0.0001) and a higher-order interaction for average daily thermoregulatory costs between island and date ($F_{27,594}$=67.73, p<0.0001). There was also a significant effect of island on average daytime thermoregulatory costs ($F_{1,22}$=219.49, p<0.0001) with SINWR terns having a higher thermoregulatory cost than SI terns (Figure 6). Daytime thermoregulatory costs did have a higher-order interaction between island and date ($F_{27,594}$=58.42, p<0.0001). Nighttime thermoregulatory costs were also significantly greater on SINWR relative to SI ($F_{1,22}$=626.30, p<0.0001; Figure 7) with a higher-order interaction between island and date ($F_{27,594}$=60.48, p<0.0001).

Precipitation was higher on SI than SINWR (Figure 8). Mean daily precipitation on SI (n=28) was 0.4 inches (±0.26 2SE) and on SINWR (n=28) average precipitation was 0.3 inches (±0.18 2SE). Total precipitation was higher on SI (11.6 inches) than SINWR (7.7 inches).

Buoy ambient and water temperatures in 2009 were greater at Portland, ME (Station 44007) than buoys farther from the mainland (Figure 8). Portland, ME buoy (n=28) had a mean ambient temperature of 14.49°C (±0.57 2SE). Offshore buoys had cooler ambient temperatures with Central Maine Shelf (Station 44032; n=28) averaging 12.67°C (±0.52 2SE) and Matinicus Rock, ME (Station MISM1; n=11) averaging 11.67°C (±0.50 2SE). Buoy water temperatures were also warmer at Portland, ME (n=28; 13.90°C ±0.51 2SE) than Central Maine Shelf (n=28; 11.63°C ±0.52 2SE).

Buoy wind speeds in 2009 were similar between Portland, ME and Central Maine Shelf (Figure 9). Comparisons could only be made during June as the Portland, ME buoy stopped collecting data in July. Portland, ME (n=14) averaged wind speeds of 4.01m/s (±1.12 2SE). Central Maine Shelf (n=14) averaged wind speeds of 5.11m/s (±1.07 2SE).

Historical buoy data shows that Portland, ME had warmer ambient and water temperatures relative to Central Maine Shelf and Matinicus Rock, ME. In 2005, Portland, ME (n=28) had an ambient temperature of 15.33°C (±0.97 2SE) while Central Maine Shelf (n=28) was 13.15°C (±0.73 2SE) and

Matinicus Rock, ME was 12.75°C (±0.85 2SE; Figure 10). Average water temperature in 2005 for Portland, ME (n=28) was 14.13°C (±0.65 2SE) and Central Maine Shelf (n=28) was 11.89°C (±0.54 2SE; Figure 11).

Overall ambient and water buoy temperatures were warmer in 2006 for both inshore and offshore buoys. Average ambient temperature in Portland, ME (n=28) was 17.54°C (±0.29 2SE), on Central Maine Shelf (n=28) was 16.03°C (±0.57 2SE), and on Matinicus Rock, ME (n=28) was 15.59°C ±0.65 2SE; Figure 12). Water temperature was 16.20°C (±0.40 2SE) in Portland, ME (n=28) and 14.78°C (±0.52 2SE) on Central Maine Shelf (Figure 13).

In 2007, July ambient and water temperatures were similar at inshore and offshore locations, but June temperatures were greater for inshore than offshore buoys. Average ambient temperatures were still greater in Portland, ME (n=28; 15.78°C ±0.44 2SE) than Central Maine Shelf (n=27; 14.53°C ±0.46 2SE) or Matinicus Rock, ME (n=28; 14.24°C ±0.48 2SE; Figure 14). Even though Portland, ME waters were warmer than Central Maine Shelf in June, average water temperatures were similar for Portland, ME (n=28; 13.80°C ±0.33 2SE) and Central Maine Shelf (n=27; 13.11°C ±0.58 2SE; Figure 15).

Weather in 2008 returned to the previous relationship with Portland, ME having warmer ambient and water temperatures than offshore buoys. Ambient temperatures were again greater in Portland, ME (n=28; 16.51°C ±0.61 2SE) than Central Maine Shelf (n=28; 15.04°C ±0.70 2SE) and Matinicus Rock, ME (n=28; 15.02°C ±0.73 2SE; Figure 16). Water temperatures had increased as well in Portland, ME (n=28; 15.79°C ±0.34 2SE) relative to Central Maine Shelf (n=28; 13.42°C ±0.63 2SE; Figure 17).

DISCUSSION

Thermoregulatory costs were greater for tern chicks on SI than terns on SINWR. Thermoregulatory costs show the impact that operative temperature may have on tern energy budgets among islands. Operative daytime and nighttime temperatures of common tern chicks were higher on Stratton Island than Seal Island National Wildlife Refuge. High and Low operative temperatures were also warmer on Stratton Island for most of June and July with only a few occurrences where temperatures were similar to Seal Island.

Tern chicks exposed to cooler temperatures on offshore islands have higher thermoregulatory costs. Chicks on offshore islands will need to spend more energy themoregulating than chicks on inshore islands. Higher thermoregulatory costs could decrease energy for growth in tern chicks assuming larger chicks had the same relationship with temperature as young chicks represented by copper models (Klaassen 1994). Less energy for growth may result in decreased growth rate, a phenomenon observed by Hall and Kress (2004) on offshore islands.

Higher thermoregulatory costs of offshore island tern chicks could be offset by parental care. Brooding chicks decreases chick energy loss by 40 up to 80% (Klaassen 1994; Klaassen et al. 1994). When chicks are brooded in offshore colonies they will save energy that could be dedicated to growth. Although brooding time was not measured, provisioning rates between inshore and offshore island terns are similar (Hall and Kress 2004). Assuming provisioning rates represents tern parental effort among colonies, inshore and offshore terns could be brooding chicks for the same amount of time. Therefore offshore tern chicks may not be brooding longer to compensate for differences in temperature among locations.

Ambient and water temperatures recorded by buoys in the Gulf of Maine in 2009 were also higher around inshore islands relative to offshore islands. Buoy temperatures in Portland, Maine were consistently warmer than temperatures on the Central Maine Shelf and Matinicus Rock, Maine. Temperatures around the Central Maine Shelf and Matinicus Rock, away from the mainland, were similar. Although copper models were only placed on inshore and offshore islands, similarities between Central Maine Shelf and Matinicus Rock buoys show that environmental conditions on nearshore islands would be similar to offshore islands instead of inshore islands. Phenotypes of common terns nesting on nearshore islands are similar to terns on offshore islands (Hall and Kress 2004) even though nearshore island diets are similar to inshore islands (Hall et al. 2000). Decreased temperatures and subsequent increases in thermoregulatory costs could be why life history phenotypes on nearshore colonies are more similar to offshore colonies than inshore colonies.

Storm events in 2009 were responsible for decreasing temperatures throughout the Gulf of Maine. Storms were also responsible for large fluctuations in operative temperatures on both islands by decreasing solar input (Klaassen et al. 1989a). Storm events produced more rain on inshore islands, but wind speeds were similar for inshore and offshore buoys. Assuming microhabitat between islands has a minimal impact on operative temperatures (Robinson et al. 2001), forced convection would be similar between the two locations causing differences between locations to be due to radiation and conduction.

Warmer ambient and water temperatures in Portland, Maine relative to offshore buoys are a consistent through time. In the four years prior, 2005 and 2007 buoys showed similar temperatures as observed in 2009. All three years had above normal storm events decreasing temperatures equally for both inshore and offshore buoys. Fewer storms occurred in 2006 and 2008 allowing for more solar input and increased temperatures for both inshore and offshore buoys.

Warmer temperatures may not be entirely advantageous for tern chicks. Higher temperatures cause terns on inshore islands to expend more energy cooling than terns on offshore islands (Murphy 1985; Klaassen et al. 1989b). Unheated models show operative temperatures increasing above tern body temperature several times in 2009. Tern chicks have a difficult time surviving in temperatures above the mid 30°C (Nisbet 1982). Higher temperatures have killed tern chicks over 10 days old and severely dehydrated chicks 9 days old and younger (Nisbet 1982). Parents help cool chicks by brooding and occasionally use belly-soaking before incubating chicks on hot days (Nisbet 1982). In years with less storm events, such as 2006 and 2008, should have more hot days than 2009. Heat stress could cause terns to leave nutrient rich inshore islands for cooler nearshore and offshore tern colonies. Heat stress could be an additional reason why terns disperse to offshore islands even though offshore colonies are a sink for the common tern metapopulation in the Gulf of Maine (Chapter 2).

Although temperatures are playing a role in which phenotypes are displayed among colonies, foraging differences are probably the dominant cause of phenotypic variation between inshore and offshore islands (Martin 1987). Offshore islands are considered euphasiid specialists delivering a higher percentage of krill than inshore islands (Hall et al. 2000). Low energy prey items, such as krill, would require offshore islands to have a higher provisioning rate than inshore islands to meet energy needs of chicks (Hall and Kress 2004). As provisioning rates are similar between inshore and offshore colonies (Hall and Kress 2004), both foraging and temperature differences will result in offshore island terns having less energy for reproduction and growth relative to inshore islands.

ACKNOWLEDGEMENTS

I thank the Arkansas Audubon Society Trust for providing funding for this study. I thank the staff and volunteers of National Audubon Society's Seabird Restoration Program for assistance with feather collection and feeding observations, especially island supervisors – Matt Klostermann, Pam Loring, and Lauren Scopel. I thank Scott Hall and Steve Kress for mentorship on the field sites. I especially thank Steve Beaupre, Gary Huxel, Ian Nisbet, and Kimberly Smith for their advice, editing, and use of laboratory space and equipment.

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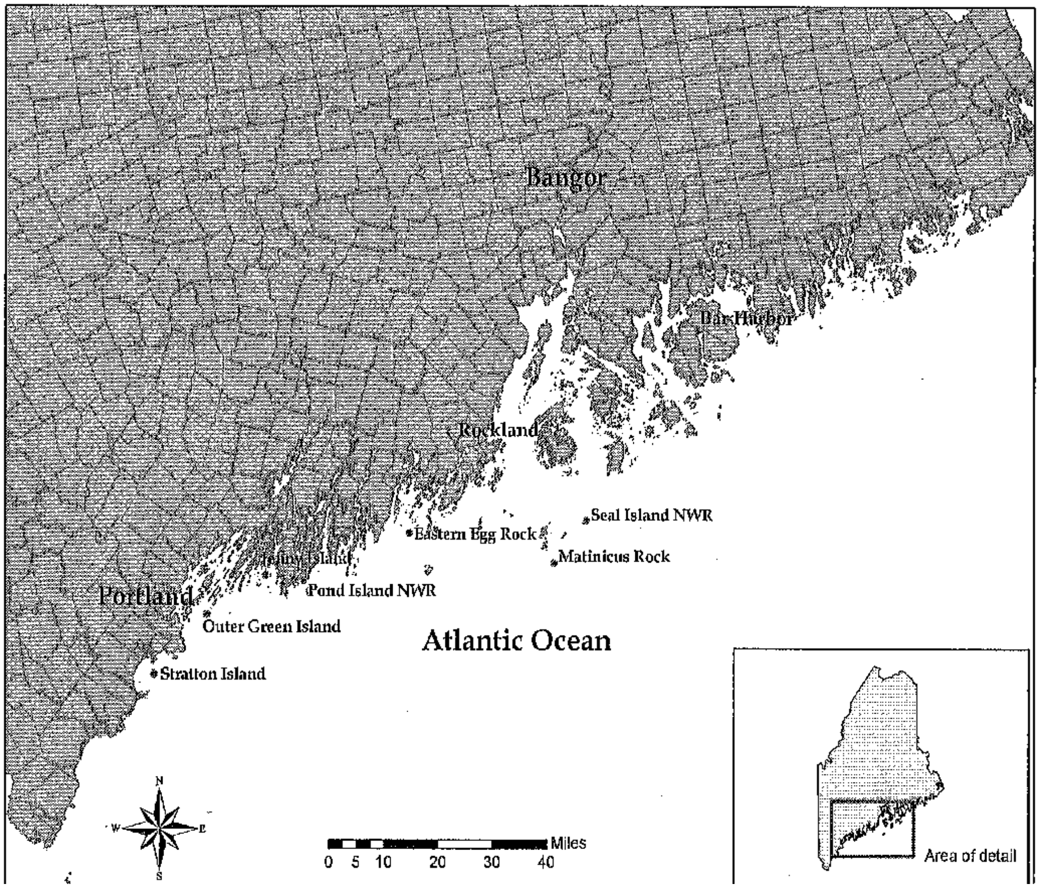

Figure 1. Islands managed by National Audubon Society's Seabird Restoration Program in the Gulf of Maine. Temperature models were located on Stratton Island, an inshore colony, and Seal Island National Wildlife Refuge, an offshore colony.

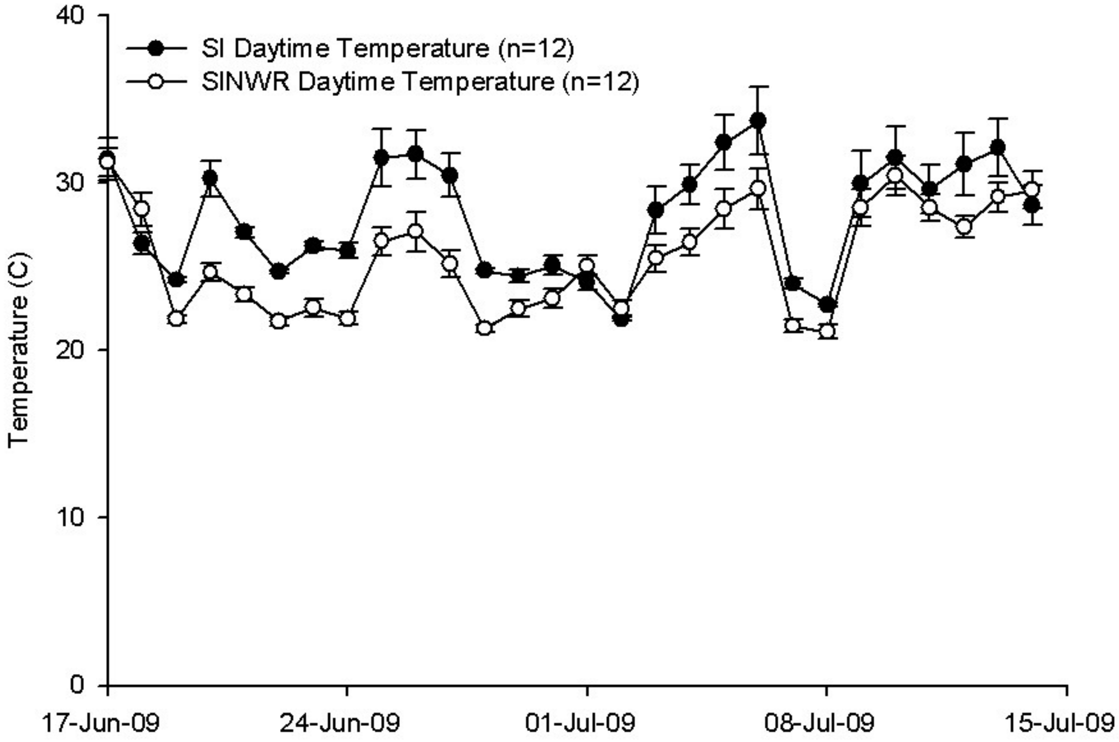

Figure 2. Mean daytime operative temperatures were consistently higher on SI than SINWR. Error bars represent 2 standard error.

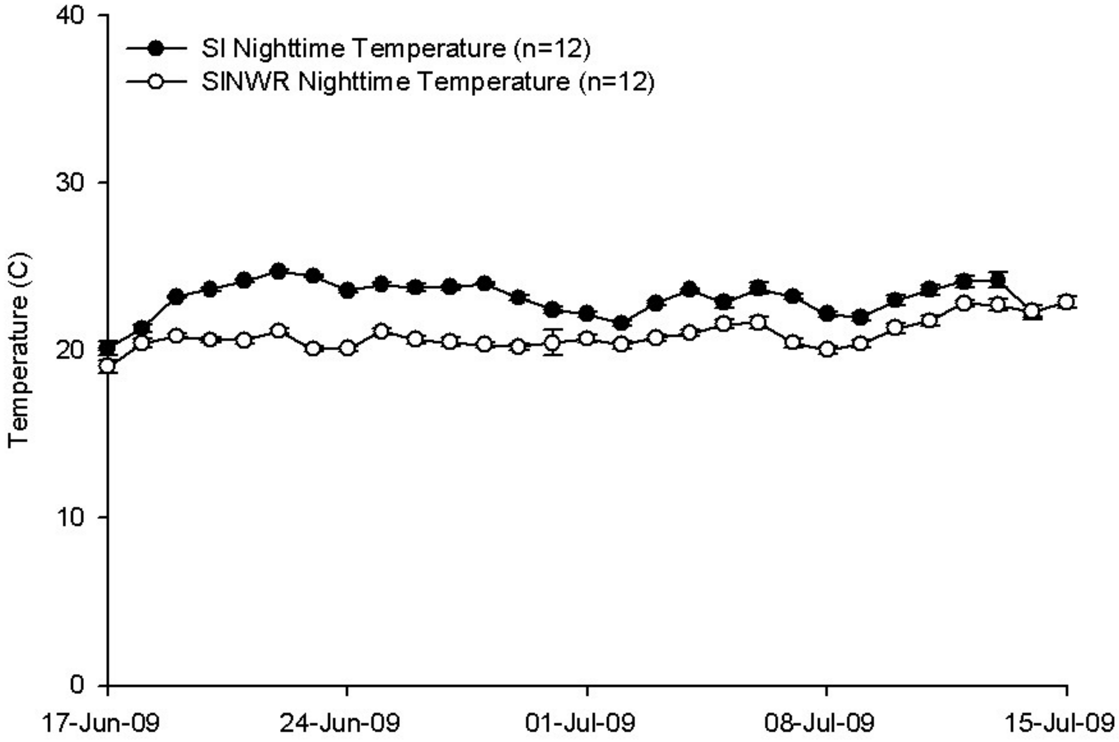

Figure 3. Mean nighttime operative temperatures were consistently higher on SI relative to SINWR. Error bars represent 2 standard error.

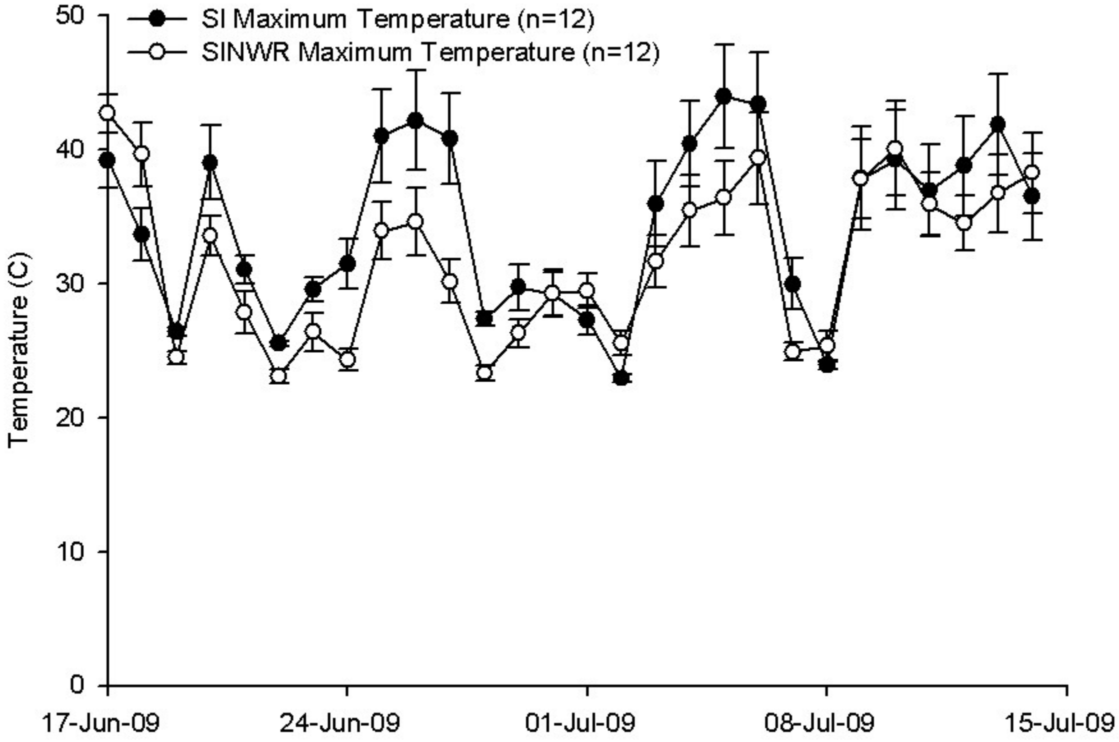

Figure 4. A majority of high operative temperatures were greater on SI relative to SINWR.

Values presented are mean high temperatures ± 2 standard error bars.

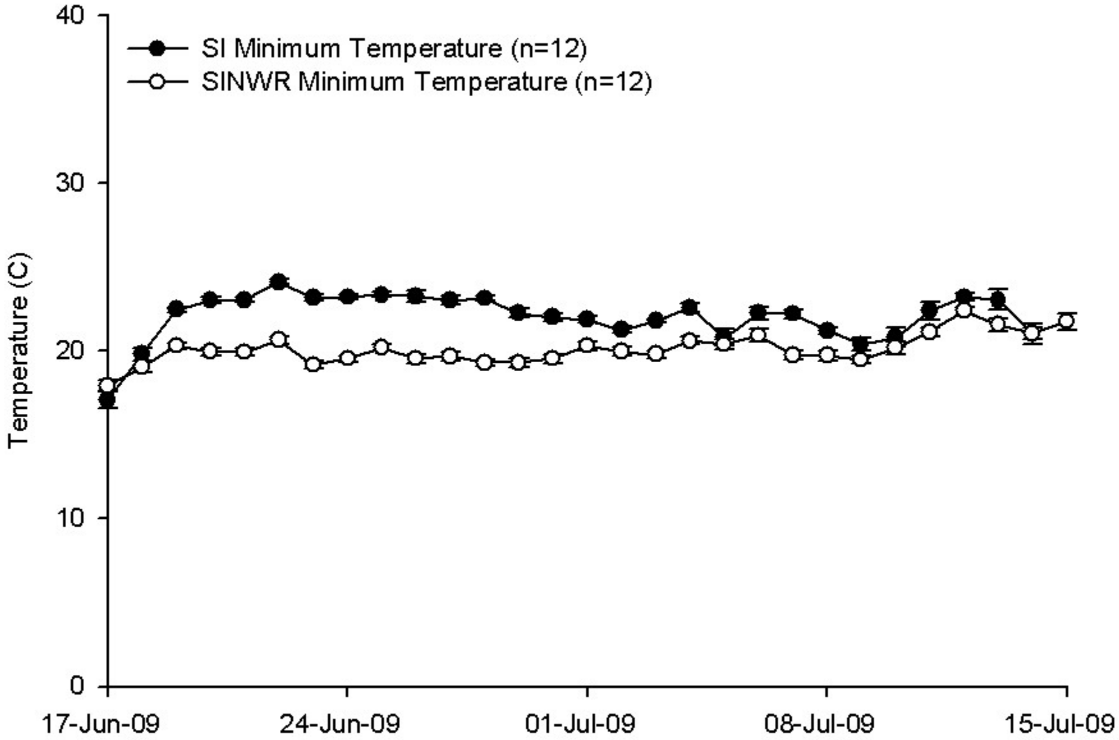

Figure 5. Mean low operative temperatures were greater on SI relative to SINWR. Error bars represent 2 standard error.

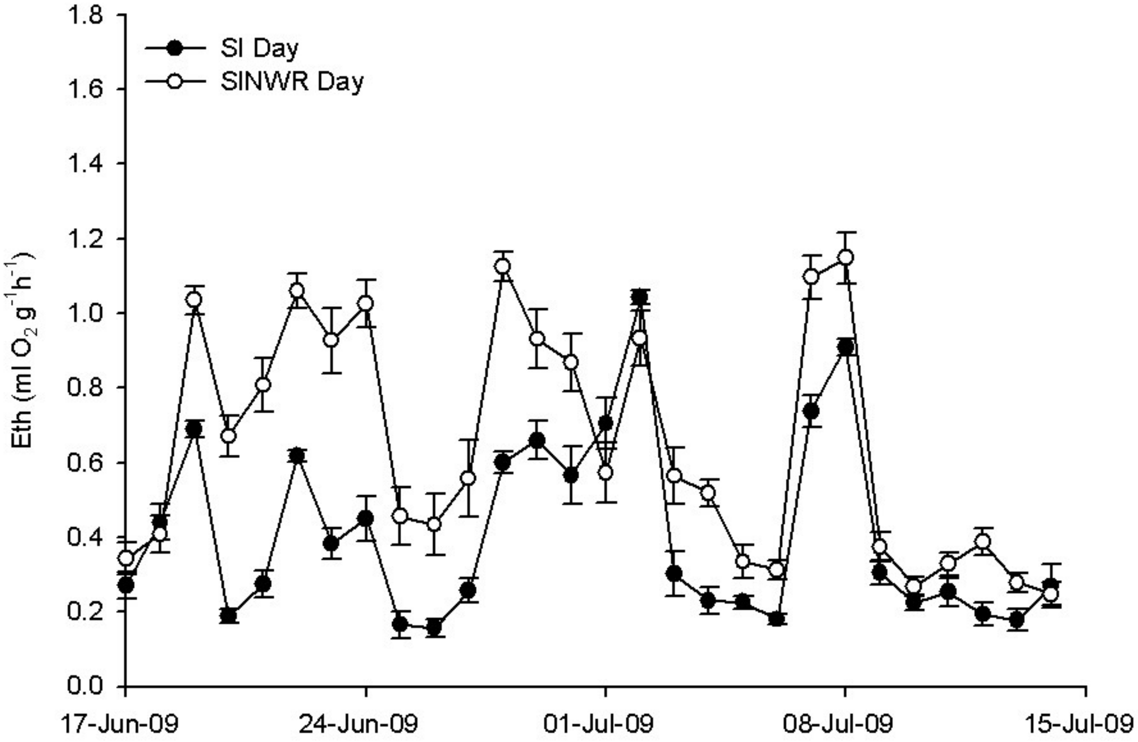

Figure 6. Thermoregulatory costs during the day were significantly higher on SINWR than SI ($F_{1,22}$=219.49, p<0.0001). Values represented are daily mean costs ± 2SE.

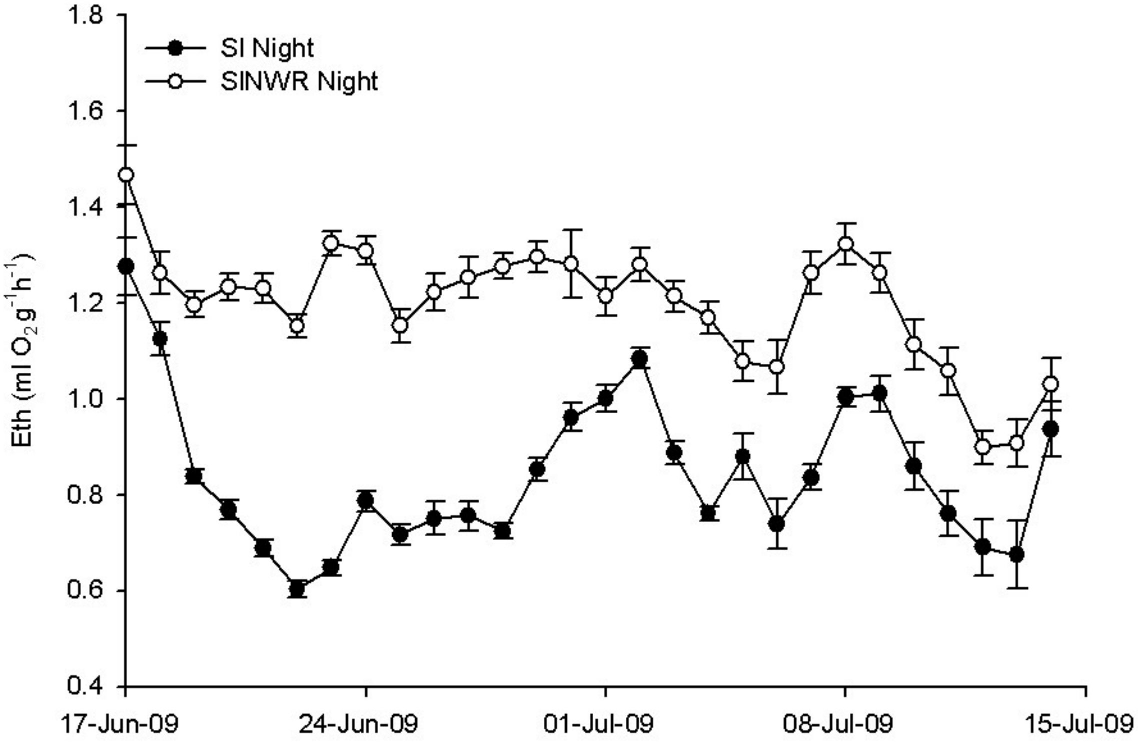

Figure 7. Thermoregulatory costs during the night were significantly higher on SINWR than SI ($F_{1,22}$=626.30, p<0.0001). Values represented are daily mean costs ± 2SE.

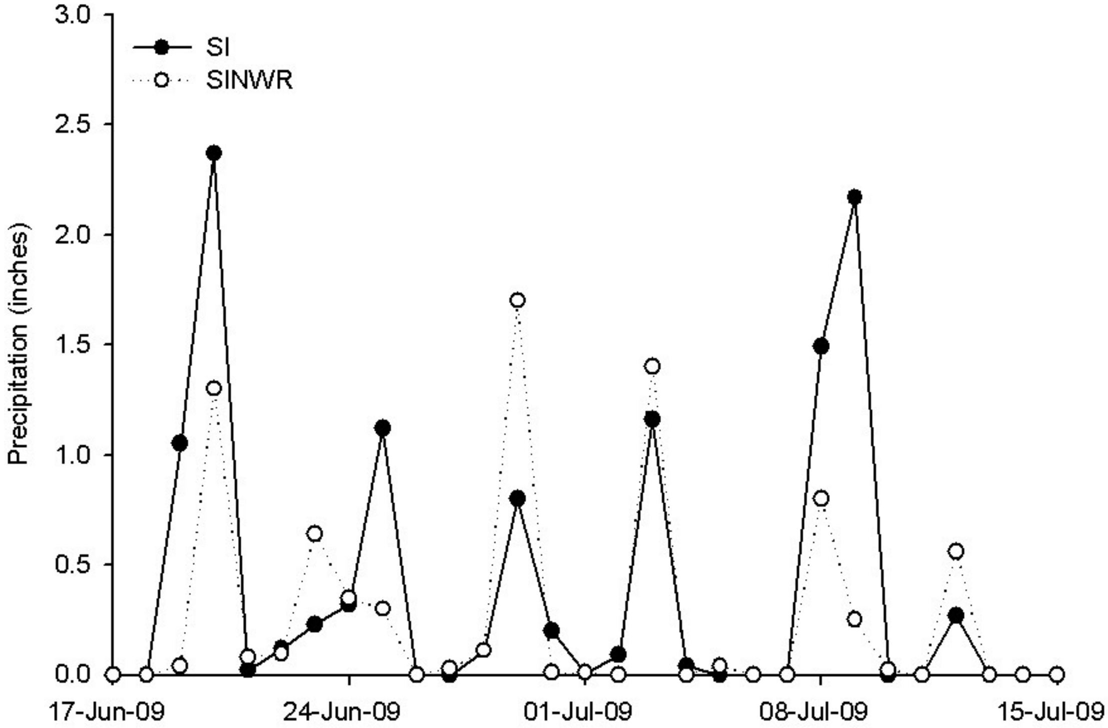

Figure 8. Storm events on SI and SINWR observed as precipitation abundance. Total precipitation was greater on SI than SINWR.

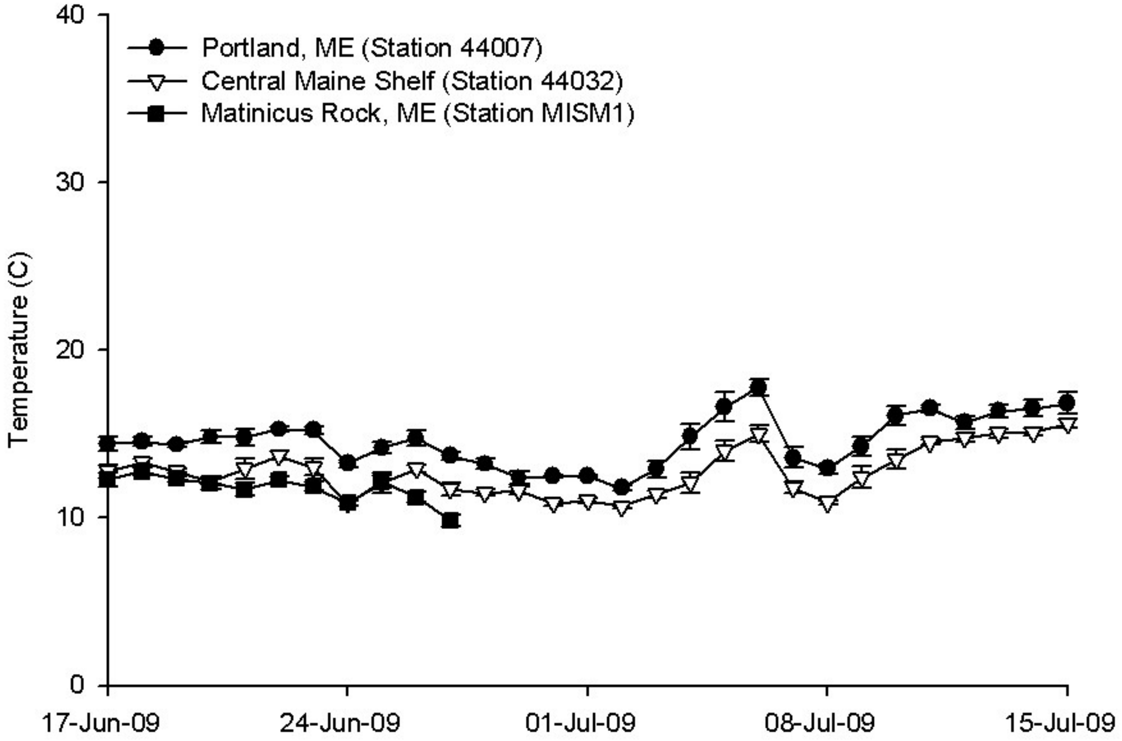

Figure 9. Buoy mean ambient temperatures in 2009 were greater near Portland, ME relative to offshore buoys of Central Maine Shelf and MRNWR lighthouse. Error bars represent 2 standard error.

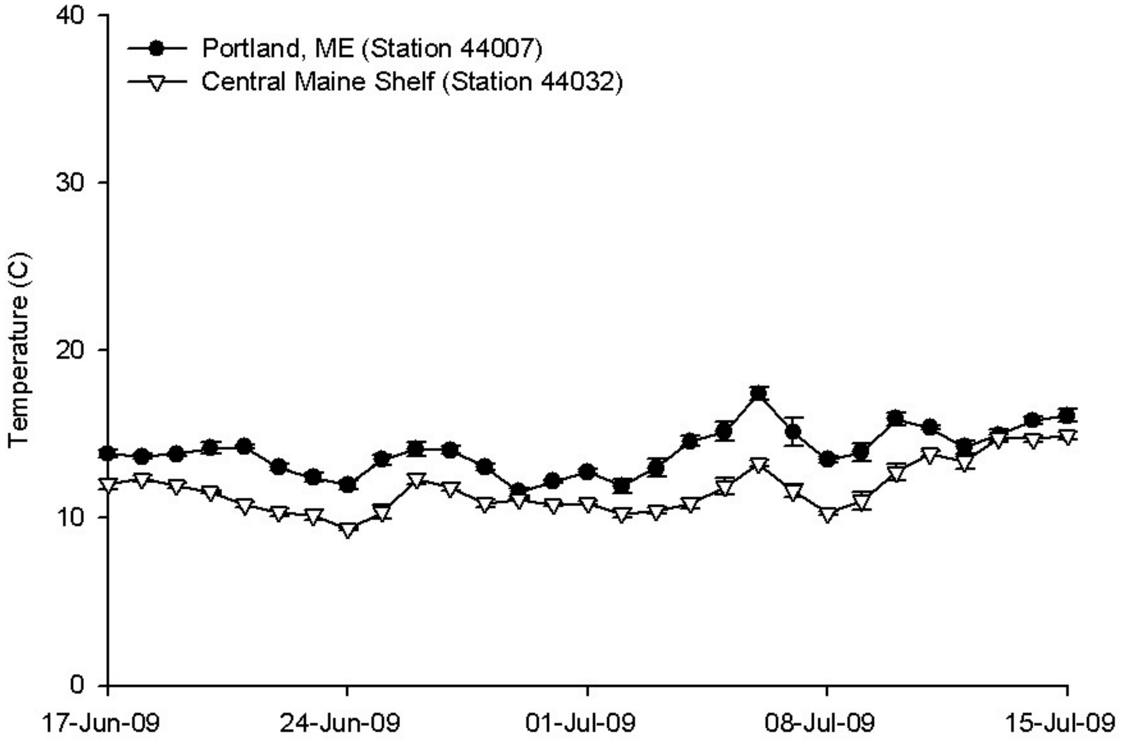

Figure 10. Buoy mean water temperatures in 2009 were greater around Portland, ME relative to Central Maine Shelf. Error bars represent 2 standard error.

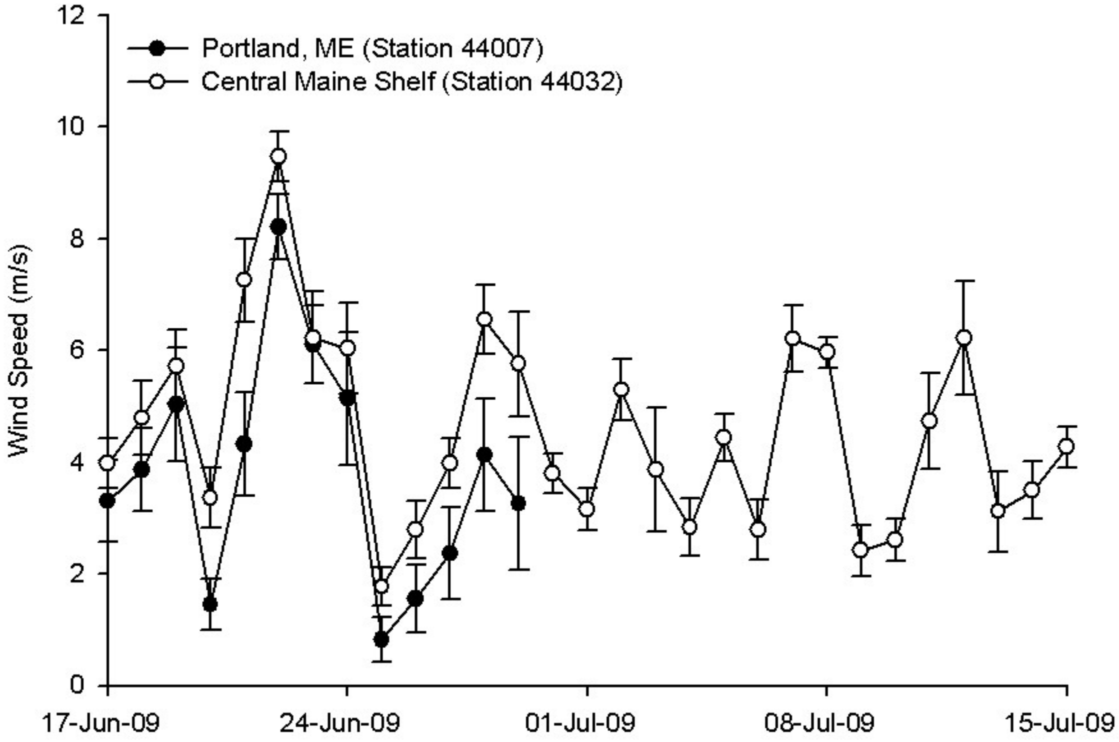

Figure 11. Mean wind speeds were similar between inshore and offshore buoys. Error bars represent 2 standard error.

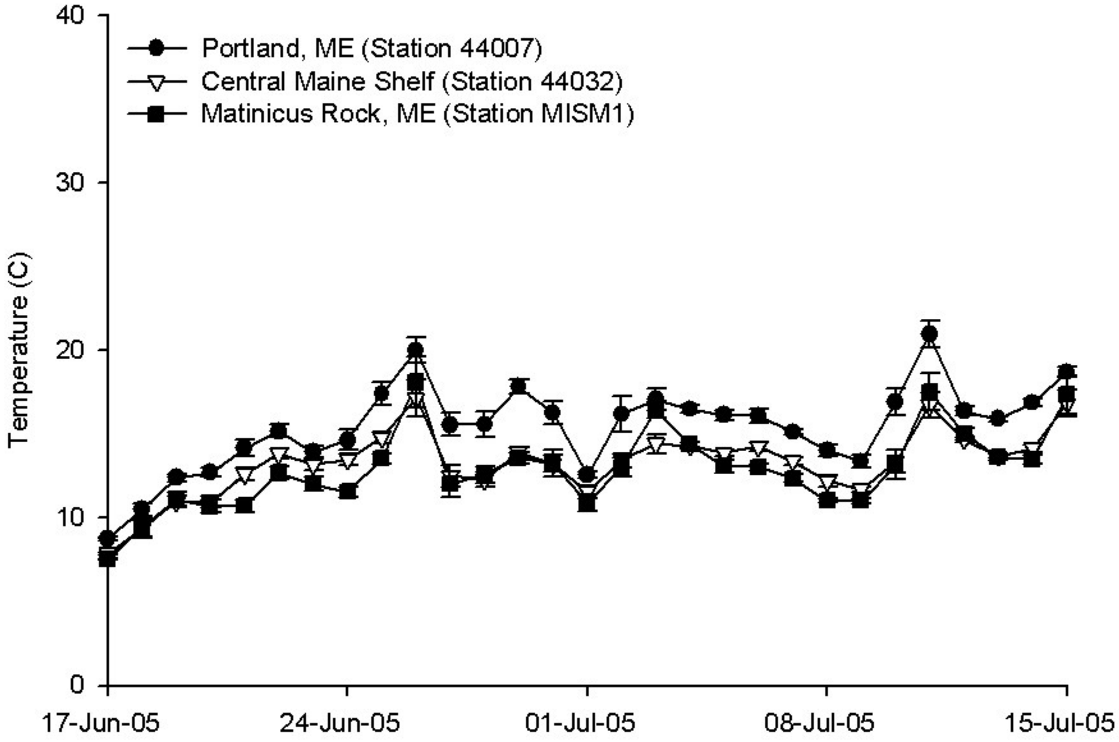

Figure 12. Buoy mean ambient temperatures in 2005 were similar to relationships observed in 2009. Highest average temperatures were in Portland, ME relative to offshore buoys of Central Maine Shelf and Matinicus Rock, ME. Error bars represent 2 standard error.

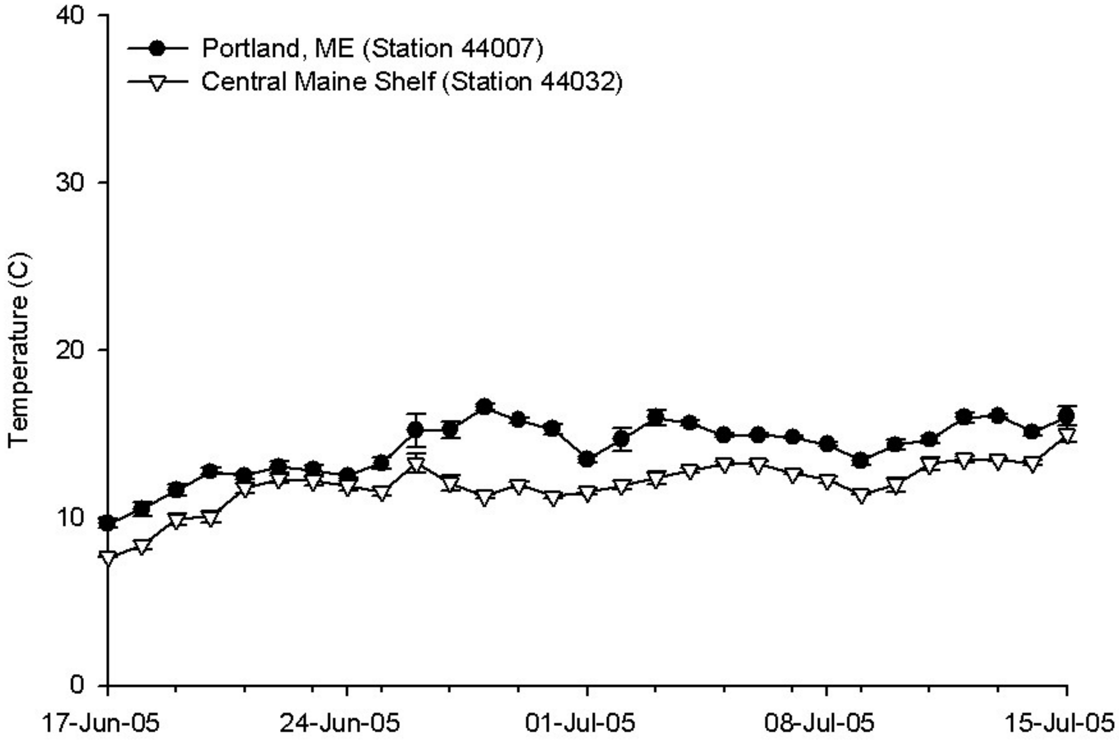

Figure 13. Mean water temperatures in 2005 were also similar to relationships observed in 2009. Portland, ME waters were warmer than Central Maine Shelf. Error bars represent 2 standard error.

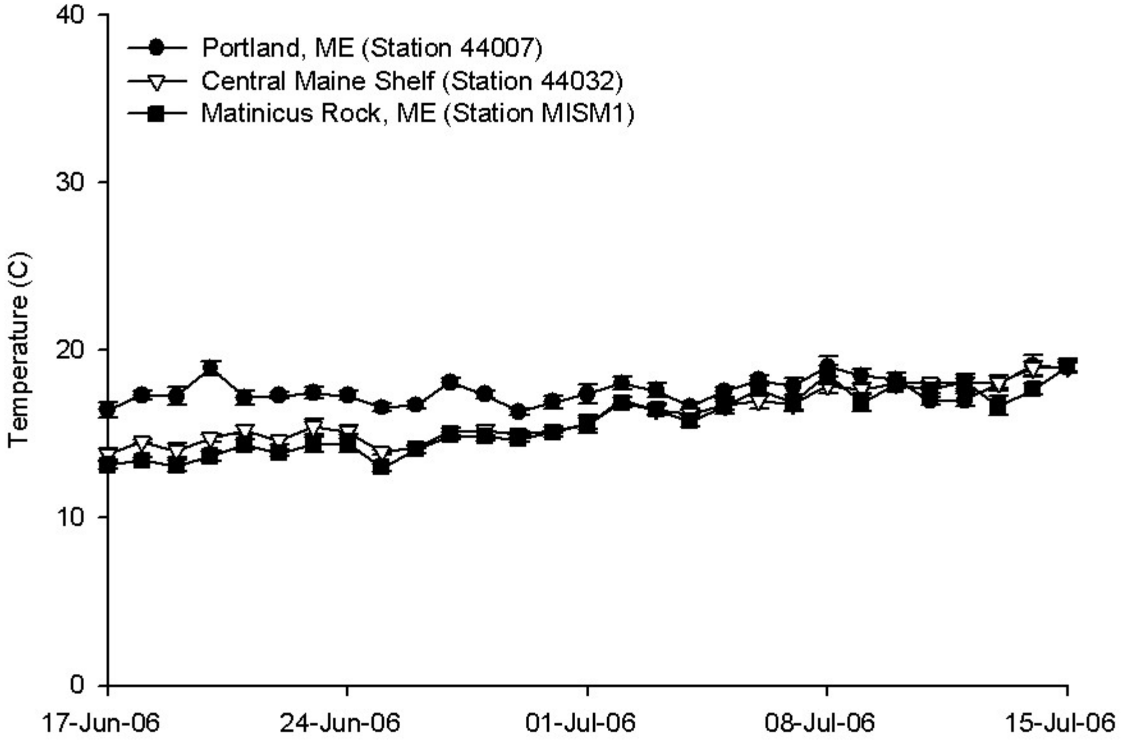

Figure 14. Buoy mean ambient temperatures in 2006 show that Portland, ME was warmer than Central Maine Shelf or Matinicus Rock, ME for June and most of July. Error bars represent 2 standard error.

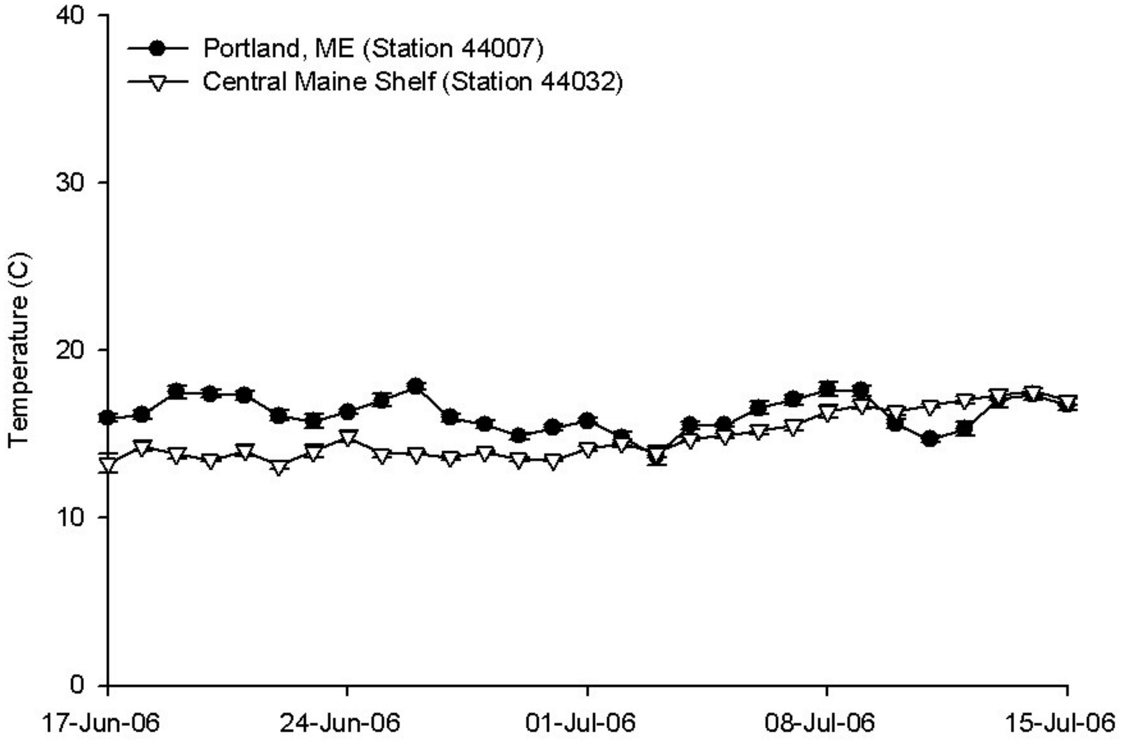

Figure 15. Buoy mean water temperatures in 2006 were warmer in Portland, ME than Central Maine Shelf for June and most of July. Error bars represent 2 standard error.

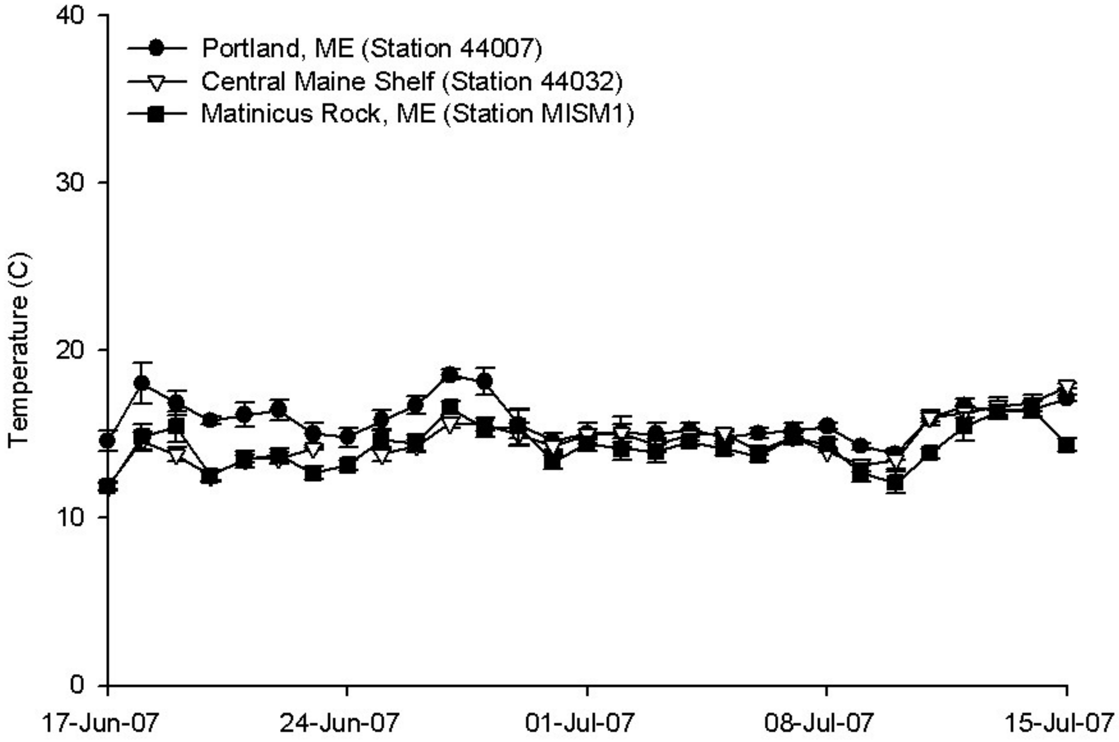

Figure 16. Buoy mean ambient temperatures in 2007 deviate from previous temperature patters. Portland, ME had warmer temperatures in June relative to offshore buoys. Ambient temperatures in July were similar between all three locations. Error bars represent 2 standard error.

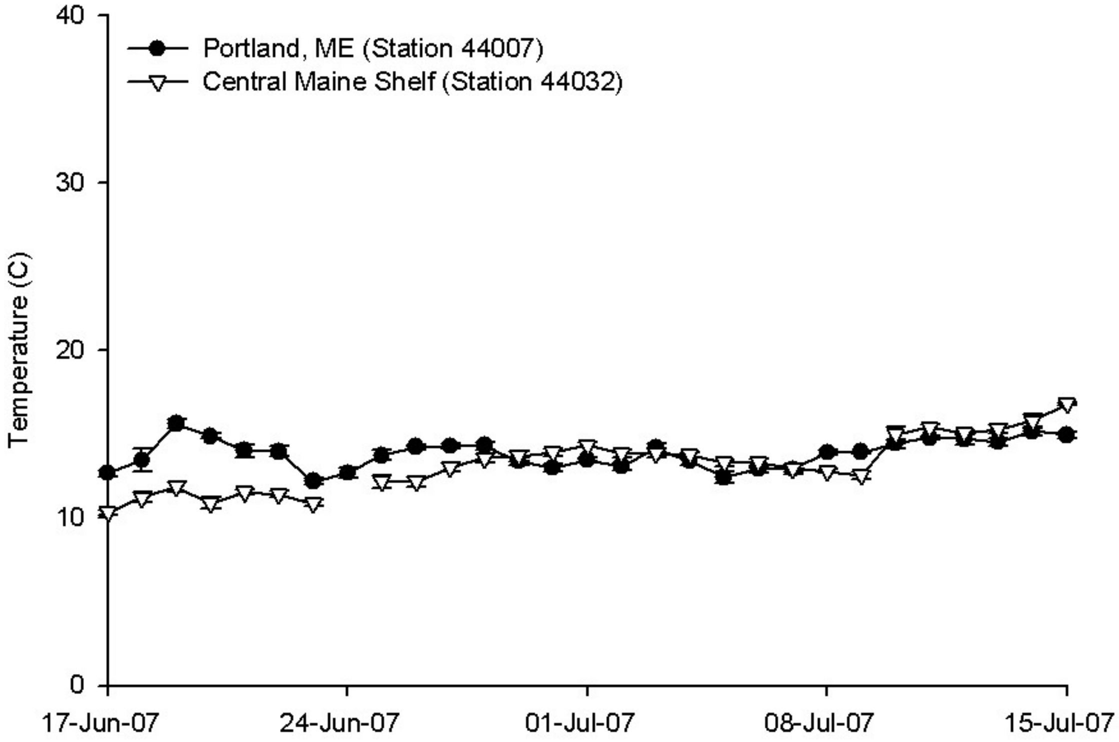

Figure 17. Buoy mean water temperatures in 2007 show that Portland, ME had similar temperatures to Central Maine Shelf except for a short period in early June. Error bars represent 2 standard error.

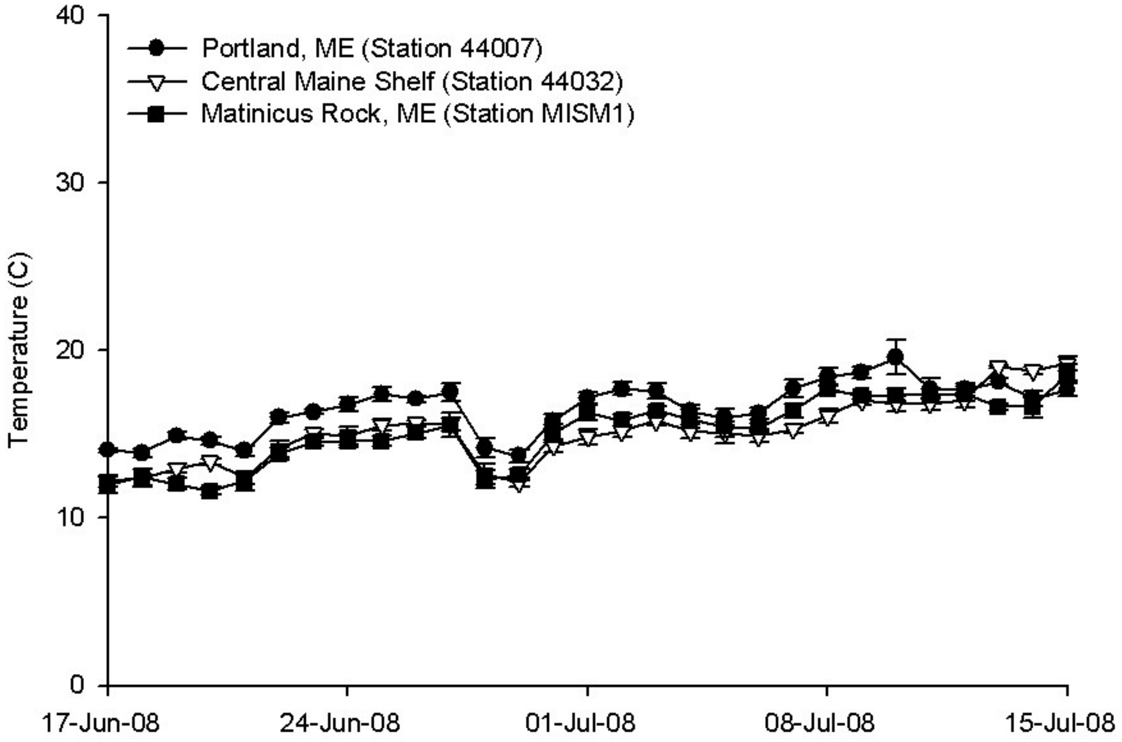

Figure 18. Buoy mean ambient temperatures in 2008 return to previous relationship where Portland, ME is warmer than Central Maine Shelf or Matinicus Rock, ME. Error bars represent 2 standard error.

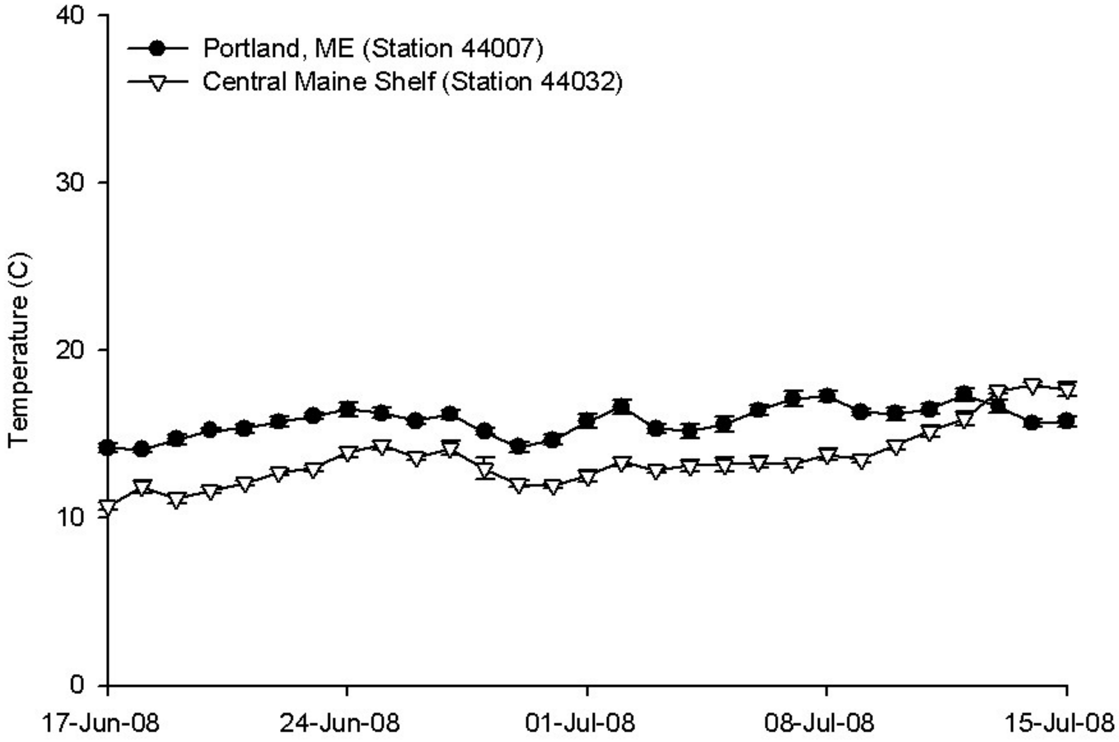

Figure 19. Buoy mean water temperatures in 2008 also returned to the previous relationship where Portland, ME waters are warmer than Central Maine Shelf. Error bars represent 2 standard error.

CHAPTER 5. CONCLUSION

In summary, variations in common tern (*Sterna hirundo*) life history phenotypes on National Audubon Society's Seabird Restoration Program islands in the Gulf of Maine are due to both diet and other environmental factors influencing tern colonies. Common terns in offshore and nearshore colonies lay smaller clutches that hatch chicks with slower growth rates reaching a lower asymptotic mass than terns on inshore islands. Reproductive tradeoffs represent an energy conservation strategy on offshore island terns relative to terns on inshore islands due to increased thermoregulatory costs and higher consumption of lower quality prey items. Common terns on nearshore islands show similar reproductive tradeoffs to offshore islands which may also indicate an energy conservation strategy. Ambient and water temperatures around nearshore islands were similar to offshore islands which could represent higher thermoregulatory costs for terns on nearshore islands relative in inshore colonies. However tern diets on nearshore islands were similar to diets of terns nesting on inshore islands.

During the 2005 to 2007 breeding seasons, common terns in offshore colonies were feeding on lower quality prey items than nearshore and inshore islands. Nitrogen stable isotope signatures of juvenile common tern feathers were depleted on offshore islands, Seal Island National Wildlife Refuge (SINWR) and Matinicus Rock National Wildlife Refuge (MRNWR), relative to most nearshore and inshore islands throughout this study. Depleted nitrogen signatures indicated that offshore islands were foraging at a lower trophic level than inshore and nearshore islands (Hobson et al. 1994). Prey deliveries by adults to juveniles also indicated that offshore terns were foraging on a lower trophic level consuming more invertebrates relative to nearshore and inshore island terns. Inshore tern colonies foraging on high quality fish, hake and herring, have more energy for clutch production, increasing clutch size or creating greater female confidence in males to provide for future offspring (Nisbet 1973). Increased fish on inshore islands also increased growth rates of inshore juveniles. Chicks had more energy and protein to dedicate to tissue production (Becker and Ludwigs 2004).

Nearshore common tern chicks also received higher quality prey than offshore island terns. Feeding observations showed more fish being delivered to juveniles on nearshore islands, Eastern Egg Rock (EER) and Outer Green Islands (OGI). Nitrogen stable isotope signatures indicated that nearshore terns were foraging at a higher trophic level than terns on offshore islands. Although nearshore terns have a higher quality diet, their reproductive phenotypes are similar to offshore than inshore nesting terns

(Hall and Kress 2004). The overall amount of prey delivered to offspring could be different between nearshore and inshore tern colonies as nearshore terns had a slower provisioning rate than inshore terns (Hall and Kress 2004). Other factors that could also be playing a role in determining energy available for reproduction on nearshore tern colonies are competition and thermoregulatory expenses.

Competition may be influencing energy budgets on nearshore islands. Increased foraging for similar resources close to nearshore colonies would decrease fish stocks, decreasing energy availability, and influencing life history phenotypes (Ashmole 1963). Highest Morisita's Index values of dietary overlap and overlapping carbon and nitrogen signatures were between common and arctic (*Sterna paradisaea*) terns on MRNWR and between common and roseate (*Sterna dougallii*) terns on OGI. Eastern Egg Rock containing all tern species had the lowest Morisita's Index values. Carbon and nitrogen signatures were similar for common and roseate terns on EER. Common and roseate terns differed in carbon signatures from arctic terns on EER. By this assessment, competition between common and roseate terns would be greater on OGI and EER relative to Stratton Island (SI), an inshore island. Common and roseate terns on nearshore islands may be more likely to follow one another to feed as both species feed along the coastline (Nisbet 2002). Common and roseate terns on inshore islands could be moving in different directions away from the colony to specific foraging grounds as inshore islands are close to the coastline (Safina 1990).

It is unknown how consistent competition is on nearshore islands between common and roseate terns as roseate tern feathers were only collected in 2007. Morisita's index values and stable isotope signatures of tern feathers only represent the probability for competition to exist. If prey were abundant in foraging areas where terns were feeding, similar diets would not represent competition (Diamond 1982).

Nearshore tern energy budgets could also be limited by other environmental factors forcing common tern chicks to thermoregulate more than inshore island chicks. Thermoregulatory costs determined from operative temperatures of young tern chicks collected on an offshore island, SINWR, and an inshore island, SI, were higher on offshore islands relative to inshore islands. Offshore island tern chicks spent more energy thermoregulating than inshore tern chicks if chicks were not being brooded (Klaassen 1994). Brooding was not measured among colonies, but provisioning rates, here representing foraging parental effort, are similar between inshore and offshore colonies (Hall and Kress 2004). Extra energy for tern chick thermoregulation in offshore colonies would come from sacrificing energy and structural components for higher growth rate.

Temperatures experienced on nearshore colonies were closer to offshore islands than inshore islands. Buoy ambient temperatures from the Central Maine Shelf were cooler than ambient temperatures reported by the Portland, ME buoy. Central Maine Shelf ambient temperatures were the same as temperatures on MRNWR, an offshore island. Central Maine Shelf represents temperatures on nearshore islands as it is located a short distance away from EER. Cooler ambient temperatures on nearshore and offshore colonies are due to cooler water temperatures relative to waters around inshore colonies.

Cooler temperatures caused thermoregulatory costs to be higher on offshore islands relative to inshore islands. As nearshore islands experienced cooler temperatures similar to offshore islands, thermoregulatory costs on nearshore islands should be higher than on inshore islands. Increased energy expenditure for nearshore chicks could be responsible for decreased growth rates. Decreased temperatures could also cause adults to thermoregulate more, decreasing energy for parental effort on nearshore islands. However this is speculation based on ambient temperatures as operative temperature models represent the mass of young tern chicks.

Higher temperatures on inshore islands have a negative impact as well. Adult and juvenile terns experience heat stress as temperatures in the colony rise above 30°C (Nisbet 1982). Temperatures above 30°C can injure and kill tern chicks (Nisbet 1982). Operative temperatures were higher on inshore islands relative to offshore islands therefore terns on inshore islands are more likely to experience heat stress than terns on offshore islands.

Higher temperatures are not the only things that have a negative impact on the nearshore island productivity. One environmental variable that was not accounted for between different islands was predation. Predation is higher on inshore islands relative to nearshore and offshore islands (Hall and Kress 2004). Predation pressure may have an indirect impact on life histories forcing terns to change time budgets, influencing energy budgets (Martin 1995; Ricklefs and Wikelski 2002). Historically mammals, such as mink (*Neovison vison*), have produced heavy predation pressure removing both adults and juveniles. Mink swim between islands to reach seabird colonies therefore normally effecting colonies closer to the mainland.

As gull populations increase, they are becoming a more common predator of tern juveniles and adults (Donehower et al. 2007). Gull predation is not confined to inshore islands as herring (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) are found on all islands managed by the Seabird Restoration Program. It is unknown if there is a life history impact due to gull predation in the Gulf of Maine. However with gulls on all islands the predation pressure may be equal within all colonies.

Reproductive phenotypes of common terns on all Seabird Restoration Program islands are influenced by multiple environmental factors, such as diet, thermoregulatory costs, and competition. Variation in reproductive output based on energy differences among common tern colonies in the Gulf of Maine may explain why inshore colonies represent sources and offshore colonies form sinks for the Gulf of Maine metapopulation. Common tern productivity is greater on inshore islands as inshore terns may have more energy to spend on parental effort, increasing clutch size and growth in chicks. However competition, predation, and heat stress encourages dispersal away from inshore colonies. Offshore island tern colonies have less energy for reproduction relative to inshore colonies due to increased thermoregulatory costs and lower quality diets. The safer, more predictable environment on offshore islands encourages adults to immigrate to offshore colonies. Tradeoffs made by common terns to reproduce in offshore environments decrease productivity relative to inshore islands.

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