Finding the "Arctic" in the Arctic Tern: breeding biology and diet across the latitudinal range of an iconic seabird

by

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DEDICATION

To Josh, who is always there for me, and who has been infinitely patient.
ABSTRACT

As climate change progresses in the Arctic, it is essential to have tools to warn of changing ecosystems. Arctic Terns are seabirds suitable as indicators of ecosystem health. Their breeding ecology has been studied intensively at low latitudes, but little at Arctic breeding sites. I studied the breeding ecology of Arctic Terns in High Arctic Canada, comparing them to those in Boreal Canada to determine if knowledge from low-latitude studies may be applied to Arctic populations. The Arctic population responded in predictable ways to presence of predators and lack of food, but had fewer predators and apparently higher functional food availability than the Boreal population. The Arctic population was generally more successful; however, I found each study differed from others in their oceanographic zones. I therefore concluded that because these birds show high phenotypic plasticity, responses at accessible temperate colonies cannot be used to infer responses in High Arctic colonies.
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Chapter 1: Introduction

Seabirds and the effects of climate change

Marine birds are among the apex predators in ocean ecosystems, with approximately 10 million pairs representing 28 species breeding in the Canadian Arctic each summer (Mallory and Fontaine 2004). Many aspects of their breeding ecology are known to be affected by environmental factors, and consequently, they have been recognized as effective indicators of the condition of marine ecosystems (Cairns 1987, Montevecchi 1993, Diamond and Devlin 2003, Piatt et al. 2007a, Mallory et al. 2010).

Many of these environmental factors are in flux as climate change progresses, particularly in the Arctic. Average air temperature north of 60° is predicted to increase between 2 and 9°C by 2100 and sea-ice cover, having reached its lowest extent three times since 1979 in 2007, 2008, and 2010 (National Snow and Ice Data Center 2010), is expected to decrease up to 33% by 2080 (Anisimov et al. 2007). There is an increased flow of freshwater into the Arctic Ocean from rivers as a result of glacial- and snow-melt, and in recent years there has been evidence of more snow and ice loss than previously predicted. This rapid melting had led to a positive feedback loop of less albedo and a further increase in warming and melting (eg. Holland and Bitz 2003). Concurrent with these events, marked increases in erosion and industrial activities (shipping traffic, mineral and oil exploration and exploitation, and commercial fishing) are taking place in the Arctic, all of which will directly or indirectly affect seabird populations (Arctic Climate Impact Assessment 2005).
The level of pollution will rise and the chances of toxic spills will increase as industrial activities in the Arctic proceed; invasive organisms that may alter the food web could be introduced through ballast-water flushing (Arctic Climate Impact Assessment 2005). As the summer sea-ice edge retreats, the ice-associated marine organisms dependent on the ice edge such as copepods, amphipods and Arctic Cod (*Boreogadus saida*), will move with it (Anisimov et al. 2007). Since breeding seabirds are central-place foragers (they must return to their nest after each foraging period; eg. Baird 1991, Ropert-Coudert et al. 2004), should this productive edge move out of the range of foraging trips from seabird colonies, we may expect a reduction in marine bird breeding productivity (Arctic Climate Impact Assessment 2005, Gaston et al. 2005b). The annual phytoplankton bloom initiated by the increased light penetrating the surface of the ocean in the spring break-up of sea-ice begins a trophic pulse that carries through to breeding seabirds (Sakshaug and Slagstad 1992). Earlier break-up of sea-ice has already led to a change in fish communities in Hudson Bay (Gaston et al. 2003), and has also resulted in a timing mismatch between Arctic seabirds (Gaston et al. 2009b) and other marine functional groups on which they prey. This mismatch not only leaves seabirds without appropriate prey during the breeding season, but also decreases the efficiency of energy transfer through the food web up to the level of the seabirds (Edwards and Richardson 2004). Warmer temperatures could also lead to increased risks of algal blooms, and possible higher parasite loads (Arctic Climate Impact Assessment 2005, Anisimov et al. 2007); it has already caused some Arctic seabirds to abandon their nests, and caused unusual mortality in adults (Gaston et al. 2002). Furthermore, with increased fishing, the
food web may become quite altered with possibly large consequences for seabird populations.

Because seabirds are long-lived with low annual reproduction, evidence of the effect of climate change in the Arctic is predicted to show itself indirectly in much the same manner as other ecosystem changes do (e.g. Piatt et al. 2007a), such as a shift of southern-edge breeders toward the north (Gaston et al. 2005a), changes in phenology of breeding seabirds in the Arctic (Gaston et al. 2009b), and changes in breeding productivity (Arctic Climate Impact Assessment 2005). Anticipated food-web changes allow us to predict that foraging behaviour and diet will also change. Studies are already showing that phenology is shifting to an earlier start of the breeding season at some Arctic seabird colonies, (Gaston et al. 2005a) as well as at other colonies further south (Møller et al. 2006, 2009, Irons et al. 2008, Wanless et al. 2009). Typically the melting of local sea ice, and thus availability of seabird prey, and the breeding phenology of seabirds are synchronised. But in at least one study of Arctic-breeding seabirds, this synchrony has already been shown to be broken (termed an "ecological mismatch"; Gaston et al. 2009b). Knowledge of the breeding biology and foraging ecology of seabirds at different stages of their breeding cycle in these areas is critical to enable wildlife managers to most effectively guide human activities around colonies to ensure breeding populations are minimally affected. This is especially important considering the top trophic position that seabirds occupy in the Arctic food web; in this role, they play a pivotal part in the functioning of the ecosystem (Estes et al. 2011).
At present, studies on the breeding biology of seabirds in the Arctic have focused largely on Thick-billed Murres (*Uria lomvia*; Falk et al. 2000, Gaston et al. 2005a, Hipfner et al. 2005) and Dovekies (*Alle alle*; Harding et al. 2008, Wojczulanis-Jakubas et al. 2009, Wojczulanis-Jakubas et al. 2011), which are diving birds with access to food in a three-dimensional environment. Recent High Arctic research has also focused on Northern Fulmars (*Fulmarus glacialis*), which are predominately surface feeders, but which travel long distances from the colony to acquire food (at least 175 km; Mallory and Forbes 2007). In contrast, Arctic Terns (*Sterna paradisaea*) are High Arctic breeders that are two-dimensional feeders, with access to food from a very limited depth at the surface of the ocean. These seabirds are also more closely tied to their breeding colony during the breeding season than Northern Fulmars (Black 2006). The very little information about two-dimensional feeders within the High Arctic is limited largely to counts of individuals at a colony, and some contaminant work (Braune 2007, Gaston et al. 2009a). Because they are more restricted in their feeding ranges both in distance from the colony and vertically in the water column, surface-feeders like terns may provide earlier indications of changes in the marine environment than seabirds with larger foraging ranges. The reason for this is simple: they have fewer foraging options compared to species with large foraging ranges (e.g., terns cannot pursue hard-to-reach prey like divers, nor can they travel vast distances like long-distance foragers).

However, because many seabirds exhibit significant phenotypic plasticity that may preclude their use as indicators of marine ecosystem change (some breeding parameters in some species are not strongly tied to environmental factors, while other parameters
are strongly linked but at varying times and locations; see Grémillet and Charmantier 2010), it is important that traits that are flexible are identified within each seabird species being considered as an indicator.

Arctic Terns: global seabirds with local influence

Arctic Terns, small seabirds of the gull and tern family (Laridae), have a global distribution, making the longest known annual migrations of any species by migrating from their breeding areas in the northern hemisphere to the Southern Ocean surrounding Antarctica, where they spend the boreal winter (Egevang et al. 2010). During the boreal summer, they have a circumpolar breeding distribution covering a wide range of latitudes: between 84°N on the coasts of Greenland and 42°N on the eastern coast of North America (Hatch 2002). In all breeding regions, they are concentrated in colonies ranging from a few pairs to as many as 25,000 pairs in Iceland (Birdlife International 2010), with their global population estimated to be 1-2 million pairs (Hatch 2002). In North America, the largest colonies can reach 2000 pairs along the eastern coast (Kress and Hall 2002, Diamond and Devlin 2003, Gaston et al. 2009a). From these breeding colonies, adult terns must depart to find prey for themselves and their young. Their foraging trips are typically within 10 to 30 kilometres of the colony (Hatch 2002, Black 2006, Rock et al. 2007).

In addition to their role as predators in marine systems, terns, like other seabirds, contribute to the base of the food web through the deposition of guano on and around
the colony. As it washes into the surrounding environment, guano adds otherwise limiting nitrogen and phosphorus, permitting an increase in primary production, thus helping to maintain a complex local marine community (Zelickman and Golovkin 1972, Bosman et al. 1986, Michelutti et al. 2010). Collectively, Arctic Terns have a significant influence on localized marine communities during their breeding season.

**Current knowledge**

The importance of Arctic Terns to local ecosystems has previously been recognised, and there have been many studies of their breeding biology, foraging ecology, and behavioural ecology, among others, which have provided us with a great deal of knowledge about the species. The vast majority of these studies have focused on colonies in temperate regions in the Boreal oceanographic zone (waters extending south from the Scotian Shelf in the Atlantic Ocean, south of the Low Arctic oceanographic zone where polar and non-polar ocean waters mix in the upper 200-300m; Dunbar 1953), near or at the southern extent of their breeding range (e.g. Pettingill 1939, Hawksley 1957, Lemmetyinen 1973a, b, c, Monaghan et al. 1989, 1992, Uttley 1992, Amey 1998, Hall et al. 2000, Robinson and Hamer 2000, Paquet 2001, Black 2006, Devlin 2006, Minich 2007, Rock et al. 2007, Devlin et al. 2008, Gaston et al. 2009a, Schwemmer et al. 2009). Little research has focused on colonies in the Low or High Arctic oceanographic zones, despite the fact that these regions encompass the heart of the breeding range of these seabirds (Birdlife International 2011). Further, the great majority of the studies in the Arctic have been conducted in Europe, not North America
(e.g. Bengtson 1971, Lemmyinen 1972, Klaassen et al. 1989, Węsławski et al. 1994, 2006, Østnes et al. 1997, Egevang 2010, Egevang et al. 2010) and since the currents around the European colonies are vastly different than those in the Canadian High Arctic, the marine environment is potentially much different as well. Of the few studies conducted in North America: a) one was in a freshwater environment (Hobson et al. 2000); b) a second, though informative and comparing breeding Arctic Terns in the Canadian Arctic to those in other areas, was largely descriptive and based on one incomplete season (Drury 1960); and c) a third concentrated on partitioning of foraging habitat with co-nesting gulls, and did not study the breeding biology of the terns (Abraham and Ankney 1984). Two others were conducted in the Low Arctic (Boekelheide 1980, Kirkham 1986). Further, only three studies on this species were undertaken at colonies located in High Arctic waters (Węsławski et al. 1994, 2006, Levermann and Tottrup 2007, Egevang 2010, Egevang et al. 2010), and these were in Europe. Only one study (Kirkham 1986) made direct comparisons between Arctic Terns breeding at different latitudes; this again took place in the Low Arctic, was conducted over one season, and was concerned with foraging behaviour and nesting. As a result, there is a major gap in knowledge about the breeding ecology and diet of these birds in the High Arctic of Canada which clearly needs to be addressed in light of the rapid changes unfolding in the Arctic.

To gain a better understanding of the breeding biology and diet of Arctic Terns in the Canadian High Arctic, to determine what differences may exist between Arctic- and Boreal-breeding populations, and to help quantify the phenotypic plasticity of Arctic Terns across a large portion of its latitudinal range, I conducted a study focusing on
breeding ecology and diet of Arctic Terns on a small island in the High Arctic of Nunavut, Canada, with no official name (hereafter called Nasaruvaalik Island), where approximately 500-600 pairs of Arctic Terns nest in two colonies separated by about 1.5 km. I compare these terns with those nesting near the southern edge of their breeding range of coastal North America on Machias Seal Island, New Brunswick in the Gulf of Maine, and more generally compare the knowledge of Arctic Terns breeding in High Arctic and Boreal sites.

**Objectives**

The primary objective of this thesis was to compare the breeding and foraging ecology of Arctic Terns breeding in the High Arctic with those breeding in the Boreal oceanographic zone at Machias Seal Island. To do this, I measured the breeding phenology, success, chick feeding and growth rates, and adult morphometrics of the Arctic Terns breeding on Nasaruvaalik Island, Nunavut. For this colony, I also examined Arctic Tern diet through the trophic positions and niche width of pre-laying and incubating adults, and chicks during chick-rearing, using stable-isotope analyses. I determined if any of these breeding and diet parameters differed from published results elsewhere in the Arctic. Arctic Terns breeding at Nasaruvaalik Island migrate across extensive stretches of sea ice to nest at this isolated site, presumably because of small polynyas (open areas of water surrounded by sea ice, typically key sites for wildlife; Stirling 1997) that provide feeding areas throughout the pre-breeding and breeding season. With the paucity of published works regarding the breeding biology and diet of
terns nesting in the High Arctic, an investigation of breeding near polynyas offers a unique comparison to breeding ecology elsewhere in the species’ range.

Of the many aspects of breeding ecology I compared between the Arctic colony and temperate ones, I predicted differences in only a few. First, and most obviously, I expected that the timing of the onset of breeding of the Arctic Terns in the north would be much later than those of the south. Egg-laying is dependent on availability of suitable nesting locations made accessible by snowmelt (Lack 1933, Abraham 1986, Stenhouse et al. 2001), as well as melting of sea-ice and the resultant availability of prey as the spring phytoplankton bloom pulses upward through the food web (Gaston et al. 2005b, Mallory and Forbes 2007, Laidre et al. 2008). Consequently, delayed melting at higher latitudes means that the timing of breeding should be later at such locations.

Second, I predicted that body size of adult Arctic Terns breeding in the north will be larger than those in the south, based on Bergmann's rule, which predicts that homeotherm body size increases with increasing latitude (Meiri and Dayan 2003).

Third, I predicted that the Arctic Terns in the High Arctic would have higher chick feeding rates per day and exhibit less of a diel pattern to their chick feeding compared to terns in southeastern Canada. The High Arctic experiences 24 hours of daylight during the breeding season, so foraging Arctic Terns are not restricted by the length of day, unlike those in the southern parts of their breeding range. Some other High Arctic seabirds forage throughout the full 24 hours of daylight; during the breeding season in
the High Arctic, Thick-Billed Murres forage during the 'night' as well as the 'day' (Falk et al. 2000, Mehlum et al. 2001). Since Arctic-breeding birds have a shorter period of time in which to complete their breeding cycle, they may compensate for this constraint by taking advantage of the available 24-hour daylight period to increase their energy intake.

**Thesis structure**

This thesis was written in the Articles format. Chapter 1 provides a background to the work, and Chapter 5 provides a general discussion; neither are independent from the thesis. Chapters 2, 3 and 4 are data chapters to be submitted as scientific articles to journals. All of these articles will be co-authored with Dr. Mark L. Mallory and Dr. Antony W. Diamond. I conducted the field work at the High Arctic site and resultant lab work, analyzed the data and wrote the manuscripts. The original idea for the research was provided by Dr. Mallory and refined by all three co-authors; advice and editing of the manuscript was provided by Drs. Diamond and Mallory; data from Machias Seal Island were provided by Dr. Diamond.

Chapters 2 and 3 focus, respectively, on the breeding biology and the diet of Arctic Terns nesting on Nasaruvaalik Island, Nunavut. Chapter 4 compares the breeding biology of the terns of Nasaruvaalik Island to those of Machias Seal Island, New Brunswick and, more generally, to colonies in the three oceanographic zones in which they breed: High Arctic, Low Arctic and Boreal. Chapter 5 is a discussion of key
findings in Chapters 2, 3 and 4, tying together my findings about the breeding biology and diet of Arctic Terns in Canada's High Arctic, and how they compare to breeding Arctic Terns in other zones.

**Literature cited**


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Chapter 2: Breeding biology of Arctic Terns in Canada's High Arctic

Abstract

There have been many studies of Arctic Terns near the southern part of their breeding range, but there is no knowledge about these birds breeding in the unique environment of the Canadian High Arctic. I studied the breeding biology of Arctic Terns at Nasaruvaalik Island, Nunavut over four summers. In this period, terns experienced a great deal of interannual variability, with the first two years being good breeding years, and the latter two years being poor years. This variability appears to be driven by predators and food availability. Despite this variability, the colony at Nasaruvaalik Island is a more productive colony than others in the High Arctic oceanographic zone, likely because it has few land predators and is situated near many polynyas.

Introduction

The breeding range of Arctic Terns (*Sterna paradisaea*) extends from 84°N in coastal Greenland south to 42°N on the eastern coast of North America (Hatch 2002), with the majority of their breeding population within the Subarctic through High Arctic marine zones (Salomonsen 1965, Birdlife international 2004). Despite this, most research on these birds has focused on colonies in temperate regions of the Boreal marine zone (e.g., Hawksley 1957, Lemmetyinen 1973b, Gaston et al. 2009a). Seabirds are generally recognized as sensitive indicators of marine ecosystem conditions (Cairns 1987, Diamond and Devlin 2003), but we currently lack knowledge about the breeding
ecology of many species of seabirds in the High Arctic of Canada, making their utility as indicators limited. To date, only two studies of Arctic Terns have been conducted in High Arctic Europe (Węsławski et al. 1994, 2006, Egevang 2010, Egevang et al. 2010) and only one in the High Arctic of North America (Boekelheide 1980).

Because species may differ in their breeding ecology in different parts of their range (Mallory et al. 2008c), it is important to evaluate whether knowledge gathered from studies elsewhere can be extrapolated to the Canadian Arctic. Basic knowledge about the ecology of Arctic-breeding seabirds is particularly urgent at a time when climate change, which disproportionately affects higher latitudes (Arctic Climate Impact Assessment 2005), is advancing. Rapidly increasing temperatures in the Arctic are expected to affect seabirds through changes to the food web as warming waters promote more algal blooms, increased possibilities of parasitism (Anisimov et al. 2007) and ecological mismatches throughout the food web (Gaston et al. 2005b). They will also be threatened by anthropogenic stressors such as shipping traffic, oil spills, and fishing as increases in Arctic resource exploration and exploitation occur (Arctic Climate Impact Assessment 2005, Arctic Council 2009).

Receding sea-ice will take with it the marine organisms dependent on the ice such as Arctic Cod (*Boreogadus saida*), which are often major prey for many seabirds. If the ice edge recedes out of reach of foraging trips for seabirds, which are central-place feeders in the breeding season (e.g., Baird 1991), their productivity will likely decrease (Arctic Climate Impact Assessment 2005). Decreasing productivity is one of the anticipated indirect ways that the effects of climate change will first be seen in seabirds, due to their
long life spans and low annual fecundity (Arctic Climate Impact Assessment 2005). Breeding phenology is already starting to change in some Arctic seabirds (Gaston et al. 2005a). Furthermore, without understanding the variability of seabird breeding between seasons, their use as indicators of change is limited (Durant et al. 2009, Grémillet and Charmantier 2010).

To further understand the ecology of Arctic Terns in Canada's High Arctic, I spent four field seasons studying their reproductive ecology at a colony on a small island in Nunavut and compared these results to those from colonies elsewhere in the High Arctic. I also examined the variability of several breeding parameters of this species among the four seasons, encompassing periods of high and low productivity. This study expands upon previous knowledge about this pan-Arctic species, which currently is based largely on temperate colonies in North America and Europe, and is the only study to examine interannual variability of the species at a single High Arctic colony.

**Methods**

**Study Site**

The study site was located on Nasaruvaalik Island, Nunavut (75°49.5'N, 96°18.8'W; Figure 2-1), a low, crescent-shaped 3 km by 1 km gravel reef marked by large historical beach ridges on the low-lying north and south crescent tips of the island. Vegetation is sparse, dominated by scattered clumps of purple saxifrage (Saxifraga oppositifolia) outside the tern colonies. The low-lying south end is covered in a thin layer of moss and
lichen, with thicker moss and grasses around the shallow ponds. The north end is largely vegetation-free, with sparsely scattered lichen and saxifrage, and some moss and grass carpets by the ponds. There are two Arctic Tern colonies on the island; the main colony is at the south end of the island, and the second, less populated and less dense colony approximately 1.5 km to the north, with the sloping island centre rising to about 30m above sea level. I focused my work on terns in the south colony, which has an area of approximately 0.15 km$^2$.

Two small bird-observation blinds (1.2 x 1.2 x 1.2m and 2.4 x 1.2 x 1.2m) were located on a particularly high beach ridge that bisects the south colony longitudinally. From these, several nests could be observed using binoculars and scopes, though few nest contents could be recorded. Although many researchers elevate their blinds to help increase observation effectiveness, this was not possible on this island, as the wandering, curious Polar Bears (*Ursus maritimus*) would destroy supports beyond repair in a short time. The colony was monitored during the breeding seasons of 2007 - 2010 from mid-June through mid-August, except for 2009, when researchers departed at the end of July. The 2007 season was exploratory.
Nest Initiation

In 2007, most work was conducted from the blinds to establish whether the colony would tolerate human presence. The terns did not appear to be affected by our intrusions, so in 2008, we began in-colony monitoring. To establish nest initiation dates, the south colony was visited daily. Once nesting behaviour was evident (birds sitting...
with chests low in nest cups with tail and wings angling upward), we made a thorough daily search of the colony for new nests beginning at approximately 1300h in 2008, 0930h in 2009 and 2010. In 2009 I established a study plot containing about 100 nests, encompassing most habitat types found within the colony including the periphery and the centre to ensure no bias with regard to nest location in the colony (Coulson 1968, Anotolos et al. 2006). This plot was the only section of the colony searched for new nests in 2009 and 2010, but otherwise the methods from 2008 to 2010 were unchanged. Each nest was marked with an individually numbered nest stake 1m away from the nest in a direction stipulated by the nest number to avoid the possibility that a potential predator would learn to associate a nest marker with a nest (i.e. stakes were not always in the same direction from the nest). Geographic coordinates were recorded with a Garmin eTrex handheld GPS unit.

*Nest monitoring and breeding phenology*

Nest monitoring began the day each nest was found. Because few nest contents were visible from the blinds, we revisited each nest containing only 1 egg daily until either a second egg was laid, or five successive days had passed; Arctic Terns generally do not lay more than two eggs north of 70°N, and have no more than a five-day lag between each laid egg (Hatch 2002). Though this regime minimized disturbance to the colony, it was at the risk of missing late-laid eggs. However since only one second egg was found to be laid after the five days had passed, it can be assumed that this occurrence was very rare. Eggs were labelled A or B (first- and second-laid eggs respectively) with a non-
toxic permanent marker, and length and breadth measured with a dial calliper ± 0.01 mm.

In 2008 100 nests, for which the nest initiation date and laying order of the eggs within the nest were known, were selected randomly by nest number to monitor further for hatching and chick growth rates. In 2009 and 2010, this activity was restricted to the nests within the plot.

After 20 days of incubation, daily visits to nests resumed and continued until hatching (Arctic Terns generally incubate for 21-23 days; Hatch 2002). Once hatched and dry, chicks were banded with a numbered stainless steel band on one leg and a year-specific colour band on the opposite leg. Nests were checked daily until all chicks were hatched and banded, and to assess growth rates (described below).

Chick growth rates

Though it is common in most tern studies to fence nests to ensure chicks can be found (Nisbet and Drury 1972, Bond et al. 2007a, Egevang 2010), this was not practical in this colony since inter-nest distances were large and a great deal of fencing would be required. More importantly, regular visits by polar bears intent on examining the research gear meant that anything larger than a nest stake but smaller than the blinds was damaged beyond repair within a week. A search of a portion of monitored nests (in 2008) or the entire monitoring plot (2009, 2010) was conducted every three days. Banded chicks were weighed with a Pesola spring scale and 'unflattened' wing chord.
(Pyle 1997) was measured with an end-stopped wing ruler. This continued until fledging or researcher departure.

**Chick feeding rates**

Nests were observed from within the two blinds in the south colony. Researchers watched one or two nests continuously over 3-4 hours, recording the time when an adult brought food to the nest, the size of the prey item(s) in relation to the length of the adult's bill, how many items were brought, and the type of prey (fish or invertebrate, but including more detail if possible). To allow comparison with southern colonies that experience darkness in summer, nocturnal hours were considered those hours after sunset (21:00) and before sunrise (5:30) in July and August such as at a temperate colony off the coast of New Brunswick, Canada (Machias Seal Island – see Chapter 4). Feeding watches were planned to rotate through the 24-hours, but nocturnal watches were under-sampled due to poor weather, and wide nest spacing restricted our ability to watch multiple nests at once. Feeding watches were conducted in 2007 and 2008 only.

**Adult body condition and morphometrics**

Adults were captured on their nests using bownets in all years, timed to coincide with the incubation period between seven days after nest initiation and prior to the date of hatching, the period with a reduced risk of parental abandonment (Kania 1992). In 2007
through 2009, tern eggs were replaced with artificial eggs during trapping to minimize potential damage from adults jumping in panic when caught. In 2010, real eggs were left in the nest during trapping to reduce trapping time; no eggs were lost to breakage by the terns during trapping. Adults were targeted arbitrarily, but nests selected for monitoring were excluded from capture attempts to avoid any potential effects of repeated visitation. Once captured, adults were weighed with a 300g Pesola spring scale, measured and banded using numbered stainless steel bands. Measurements of length of culmen, head + culmen, bill depth at gonys and diagonal tarsus were taken using dial or digital callipers (to the nearest 0.01mm), and a stopped wing rule was used to measure natural ('unflattened') wing chord (wrist to tip of tenth primary), and the central (fork), 5th and outer (tail streamer) retrices.

**Predators**

In all years, the number of avian predators observed each day was recorded; these included Parasitic Jaegers (*Stercorarius parasiticus*), Pomarine Jaegers (*S. pomarinus*), Long-tailed Jaegers (*S. longicaudus*), Glaucous Gulls (*Larus hyperboreus*), Peregrine Falcons (*Falco peregrinus*), Gyrfalcons (*F. rusticolus*) and Common Ravens (*Corvus corax*). Comparisons of mean daily number of predators were made among years using data during the pre-breeding and incubation periods only, since these are the only periods when researchers were on the island every year. Mammalian predators (polar bears and Arctic foxes, *Alopex lagopus*) were not included in counts because their effects on the terns at this site were negligible. They occurred infrequently, and when
bears were noticed, researchers moved rapidly to chase them from the island. Though the single fox at the site in 2009 could not be chased from the island, its influence was minimal (see Discussion).

Statistical analyses

Nests, eggs and predators

Calendar dates were converted to ordinal days, with 1 January marking day 1. To test for differences in incubation period within nests, paired Wilcoxon rank sum tests were used. For comparisons of nest initiation and incubation periods between nests and years, analyses of variance (ANOVA) with Tukey post-hoc test comparisons were performed unless the data did not meet parametric assumptions, in which case Kruskal-Wallis rank-based tests with Dunn's multiple comparisons were used. To compare incubation period in relation to nest initiation date, egg incubation period was divided up into categories (in number of days, <21, 21-21.5, 22-22.5, 23+), and nest initiation date centred on each annual mean as the dependent variable was compared using a Kruskal-Wallis test followed by Dunn's multiple comparisons.

Additional clutch data were available from surveys of the island from 2002 through 2006 inclusive (Mallory and Gilchrist 2003, Mallory unpublished data). Because these data were acquired during surveys lasting only one day, it is possible they may contain incomplete clutches and thus underestimate clutch size. However, because each survey was conducted well into the predicted incubation period of the terns when most clutches
would likely be complete, I used these data to compare to data collected in 2007-2010. Analyses of clutch size, hatching success and predator data were conducted using generalized linear models with a binomial logit link, negative binomial, or quasibinomial link function, followed either by comparisons of Wald's 95% confidence intervals, where non-overlapping 95% CI's were considered significant, or by Tukey's multiple comparison tests.

Avian predator data were tested in three ways:

- overall: data were pooled across pre-breeding and incubation for broad season-wide comparisons among years
- pre-breeding: data from the period before average nest initiation in each year were compared among years
- incubation: data gathered during incubation were compared among years

Neither nest success nor fledging success could be determined, largely because our inability to maintain fences meant that we could not reliably relocate chicks.

Egg sizes were compared by first converting measurements, taken in millimetres, to an index of egg volume using the equation

\[
\text{Volume index} = \frac{\text{length} \times \text{breadth}^2}{1000}
\]

as used in several seabird studies (e.g., Davis 1975, Gaston et al. 2005b, Sorensen et al. 2009). Some studies include a scalar as well (e.g., 0.00048*length*breadth²; Suddaby and Ratcliffe 1997) but the reason for this is not well-documented. However, as long as
all values are being treated equally, they are comparable and the scalar is not important (Davis 1975).

To identify differences between volume indices of A and B eggs within nests, paired t-tests or Wilcoxon signed rank sum tests were used. For non-paired, between-year comparisons, Mann-Whitney or Kruskal-Wallis tests were used, the latter followed by Dunn's multiple comparison tests.

To determine if there was a trend of change in egg volume with later lay dates, I centred nest initiation dates on annual means to remove any differences among years. I then regressed A egg volume indices against centred lay dates, first pooling all data among all years, and then conducted individual regressions within each year.

*Chick growth and feeding*

The linear growth period in Arctic Terns is reported to be between four and 14 days old (Hatch 2002), between days five and 15 (Bond et al. 2006) or even days four and 15 (Robinson and Hamer 2000). Ages of chicks whose exact hatching date was unknown were estimated using measurements of known-age chicks between days zero and five. Linear growth rates of weight (g/day) and wing length (mm/day) between days four to 14 and days five to 15 were determined using the slope of the regression line in that period for each chick.
The total number of feeds/hour/nest was calculated for each nest, as well as subsets for diurnal and nocturnal hours. For chick growth and feeding rates, recorded in two years only, *t*-tests were used to assess differences between years when data followed parametric assumptions, and Mann-Whitney rank sum tests when they did not.

*Adult body condition*

To compare adult terns among years, I attempted to calculate an index of body condition following Peig & Green (2009). In brief, this is a non-ratio method of scaling the weight of each individual that includes finding a linear body measurement that correlates with weight. Of the nine body measurements taken (culmen, head, bill depth, tarsus, wing chord, three tail measurements and weight; see Appendix A) only three were retained to test for use as a scalar of weight. Head length and bill depth predict sex in temperate-breeding members of Arctic Terns (Devlin et al. 2004) and tail measurements vary with age (Voelker 1997). Since the sex and age of most of my study birds were unknown, I chose to eliminate these parameters. Of those that remained (culmen, tarsus and wing chord), none correlated strongly with body weight: the strongest correlation was between ln(wing) and ln(weight) (*n*=345, *r*²=0.089, β=0.85, *p*<0.001). Despite the statistical significance of the relationship, the correlation explained only 9% of the variation in the data, which I considered negligible. Attempting to correct body weight for structural size using this method was therefore not possible, and since ratio scalars of weight are inappropriate (Green 2001), body weight itself was used as a proxy of body condition of the terns (Monaghan et al. 1992). Weight from only the first capture of
multiple-recaptured terns was used to eliminate pseudoreplication. Comparisons of weight were made among years using a one-way ANOVA followed by multiple comparison $t$-tests using the Holm-Sidak method of family-wise error rate correction.

**High Arctic colony comparisons**

I compared breeding parameters of terns nesting at Nasaruvaalik Island to other High Arctic colonies for which there are published data. Clutch size was the only parameter for which there were adequate data from multiple colonies. For sites with data from multiple years (Sand Island, Greenland and Nasaruvaalik Island), clutch size was pooled among years to incorporate annual variation within each site. A one-way ANOVA was used to determine differences among sites, followed by multiple comparison $t$-tests using the Holm-Sidak method of family-wise error rate control. Sources of these data are noted in Appendix A. Clutch size was also pooled among all colonies except Nasaruvaalik and the mean of annual means at Nasaruvaalik was calculated to enable comparison between Nasaruvaalik and the mean for the High Arctic zone. A $t$-test was used to compare zonal mean of means to Nasaruvaalik mean of means.

Egg volume indices were compared between Nasaruvaalik and Sand Islands using an index based on the study by Suddaby and Ratcliffe (1997). I used this rather than the previously described index because Sand Island researchers reported their egg volumes in this manner (Egevang 2007, Egevang et al. 2008) and did not give the length and breadth data for A and B eggs separately. A mean weighted on the number of eggs
measured in each year was taken of the means and standard deviations on Sand Island and compared to the site mean for Nasaruvaalik Island using a *t*-test.

All analyses were performed using R (R Development Core Team 2011) or Sigmaplot 11 (Systat Software 2008).

Unless otherwise noted, values are reported as mean ± one standard error. Medians and 25th and 75th quartiles are reported for those data that were analysed using non-parametric tests. Except where noted, differing letters above bars on graphs or alongside rows in tables denote significant differences, while bars or rows with the same letters are not significantly different. Numbers within bars, boxes or alongside points are sample sizes, and error bars represent ± 95% confidence intervals, unless described otherwise. For all tests, alpha was set at 0.05.

**Results**

*Nests: initiation and incubation period*

Arctic Terns spent similar amounts of time incubating A and B eggs in any year (all *V*<503, all *p*>0.05) but for consistency, only A eggs were compared among years. First egg incubation periods in 2008 and 2009 were similar to each other, but in 2010, terns spent significantly longer incubating their eggs (Table 2-1; *H*<sub>2</sub>=22.1, *p*≤0.001; 2008:2010, *Q*=4.5, *p*<0.05; 2009:2010, *Q*=3.3, *p*<0.05). Incubation periods recorded in
2009 were biased toward early nesters since researchers left the island prior to the estimated hatching date of half the eggs.

Table 2-1: Incubation period for Arctic Terns at Nasaruvaalik Island in 2008 and 2009 were similar, while 2010 was significantly longer than both 2008 and 2009. Rows sharing a letter are not significantly different.

| Terns initiated nests significantly earlier in 2009 compared to both 2008 and 2010 (Table 2-2; $H_2=36.4$, $p≤0.001$; 2008:2009, $Q=5.9$, $p<0.05$; 2010:2009, $Q=4.7$, $p<0.05$). |

Table 2-2: Arctic Tern nest initiation on Nasaruvaalik Island in 2009 was earlier than 2008 and 2010. Rows sharing a letter are not significantly different.
Comparing nest initiation date to incubation periods among years, later nesters tended to have a shorter incubation period than those that initiated their nests earlier (Figure 2-2; $H_3=10.2, p=0.017$; <21 days vs. 23+ days: $Q=2.9, p<0.05$).

Figure 2-2: Median centred nest initiation dates for Arctic Tern first-laid eggs (A eggs) from 2008-2010 on Nasaruvaalik Island show that eggs laid later in the season were incubated for a significantly shorter period than those laid earlier. Bars show 25\textsuperscript{th} and 75\textsuperscript{th} percentiles, numbers beside bars are sample sizes. Different letters atop points indicate significant differences.
From 2002 - 2010, terns nesting at Nasaruvaalik Island had a mean clutch size of 1.8 ± 0.01 eggs (n=893). Clutch sizes were similar from 2003 – 2008, but in 2009 and 2010, clutches were significantly smaller than the other years, and similar to each other. The apparently lower tern clutch size in 2002 did not differ significantly from any other year (Figure 2-3; Wald's $\chi^2=0.8$; non-overlapping 95% confidence intervals are considered significantly different). Terns laid similar clutch sizes in 2002 and 2007, but because information from only 25 nests was collected in 2002, the variance is higher in that year, possibly obscuring actual similarities or differences in that year. Clutch sizes in 2009 were biased toward early nests because researchers departed prior to the end of the breeding season.
Hatching success decreased significantly across the three years in which it was measured, with 2008 having the highest hatching success, followed by 2009, and then an abrupt drop in 2010 (Table 2-3; 2008-2009: $z=-3.3$, $p=0.003$; 2008-2010: $z=-8.2$, $p<0.001$; 2009-2010: $z=-4.9$, $p<0.001$.

Figure 2-3: Arctic Terns at Nasaruvaalik Island in 2009 and 2010 had significantly lower clutch sizes than all other years except 2002. Bars show means, and lines show 95% confidence intervals. Numbers at the top of bars depict sample size, and bars sharing letters are not significantly different.
Table 2-3: Arctic Tern hatching success at Nasaruvaalik Island declined among all years in which it was measured. Hatching success reported for 2009 was limited to early-nesters and was not the final hatching success, so may be biased high. Years with different letters in the right column are significantly different.

**Hatching success**

<table>
<thead>
<tr>
<th>Year</th>
<th>Proportion hatched</th>
<th>lower 95% CI</th>
<th>upper 95% CI</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>0.95</td>
<td>0.90</td>
<td>0.98</td>
<td>104 a</td>
</tr>
<tr>
<td>2009</td>
<td>0.78</td>
<td>0.66</td>
<td>0.87</td>
<td>45 b</td>
</tr>
<tr>
<td>2010</td>
<td>0.36</td>
<td>0.29</td>
<td>0.44</td>
<td>111 c</td>
</tr>
</tbody>
</table>

*Eggs*

Egg-laying order was unknown in 2007, so comparisons of paired, known-order eggs did not include that year. A eggs were significantly larger than B eggs in 2008 and 2010, but not in 2009 (Figure 2-4).
Volume indices of A eggs were no different from single-egg clutches in any year ($U=772$ to $5178$, all $p>0.14$), so A eggs and single-egg clutches (both first-laid eggs) were pooled to assess differences in volume indices among years. Terns nesting in 2009 laid significantly larger first eggs than those in 2008 or 2010 (Figure 2-5), but there was no difference between volume index of first-laid eggs in 2008 and 2010. B-eggs showed no significant differences among years.

Figure 2-4: Tests of paired Arctic Tern A and B eggs show that B eggs were significantly smaller in both 2008 and 2010 at Nasarvuallik Island, but not in 2009 (2008: $z=-3.5$, $p<0.001$; 2010: $z=-3.1$, $p=0.002$). 2007 eggs were not included in this analysis because order of laying was unknown in that year. Asterisks above sets of bars indicate significant differences; numbers between bars indicate sample size (number of nests). Bars show medians, lines are 25th and 75th quartiles.
To enable comparisons with 2007 when laying order was unknown, volume indices of all eggs were pooled within each year to compare overall mean egg volume index among years. Terns laid eggs that were similar in size in 2007 and 2009, and in 2008 and 2010, but those laid in 2007 and 2009 were significantly larger than those laid in 2008 and 2010 (Figure 2-6).

Figure 2-5: First egg volume of Arctic Terns at Nasaruvaalik Island was significantly greater in 2009 than both 2008 and 2010 ($H_s=9.524, p=0.009$; 2009-2008: $Q=2.8, p<0.05$; 2009-2010: $Q=2.8, p<0.05$). Bars show medians, lines are 25th and 75th quartiles. Numbers on top of bars show sample size, and bars sharing letters are not significantly different.
Within and across years, regressions of egg volume indices against centred lay dates showed that there was no significant relationship between timing of egg-laying and the size of egg. This lack of relationship held when analysed overall, and in any one year.

**Chick growth rates**

Chick growth was calculated only in 2008 and 2010. Linear growth rates between days four to fourteen and five to fifteen showed no differences in weight or wing length, so
hereafter, growth from days five to fifteen was used to enable comparison to other colonies. Rate of weight increase of chicks was significantly higher in 2008 than in 2010 ($U_{4,13}=3.5, p=0.01$). Chicks on average decreased in weight in 2010 between days five and fifteen, while those in 2008 increased (Figure 2-7). Wing growth rates did not differ between years.

![Figure 2-7: Arctic Tern chicks on Nasaruvaalik Island in 2010 decreased in weight until adults abandoned the colony shortly after hatching. Rate of weight change is significantly different between the years, as shown by different letters above lines. Bars show medians, lines are 25th and 75th quartiles, numbers above bars show sample size.](image-url)
Chick feeding rates

Chick feeding watches were conducted only in 2007 and 2008, owing to the truncated 2009 season and the collapse of the colony in 2010 shortly after hatching. Pooling all times of day, tern chicks were fed at similar rates in 2007 and 2008 overall (Table 2-4 $U_{10,22}=69.0$, $p=0.10$), during diurnal feeding only (Table 2-4; $U_{9,19}=60.0$, $p=0.22$), and during nocturnal feeding (Table 2-4; $t_5=1.7$, $p=0.15$). Diurnal and nocturnal data from both years were therefore pooled before testing for differences between diurnal and nocturnal feeding rates. No differences were observed between diurnal and nocturnal feeding rates (Table 2-5; $U_{7,28}=71.0$, $p=0.27$). However, the lack of significant difference between diurnal and nocturnal feeding is likely due to the few nocturnal observation periods, which led to a low power to detect a difference (difference in means=1.7, power=0.08, $n_1=7$, $n_2=28$). Were there more observation periods, a difference between diurnal and nocturnal feeding may have been apparent.

In 2007 several chick watches contained extreme values, wherein adults were observed obtaining food for chicks immediately off the colony. This produced extremely high feeding rates (~20 feeds/nest/hour). Removing these extreme values did not alter test results significantly.
Adult weight

Adult Arctic Terns had similar body weights during incubation in 2007 and 2008 and in 2009 and 2010, but weight was significantly greater in the first two years than in the latter (Figure 2-8; $F_{3}=23.3$, $p<0.001$; 2007-2009: $t_{143}=4.7$, $p<0.001$; 2007-2010: $t_{278}=7.2$, $p<0.001$; 2008-2009: $t_{67}=4.2$, $p<0.001$; 2008-2010: $t_{202}=5.1$, $p<0.001$).
Predators

There were significantly fewer avian predators observed daily throughout the 2007 season compared to 2008 and 2010 (Figure 2-9; 2007-2008: $z=2.6, p=0.045$; 2007-2010: $z=8.8, p<0.001$). Overall predator numbers were similar in 2008 and 2009, while 2010 had significantly higher numbers of predators than any other year (Figure 2-9; 2008-2010: $z=6.2, p<0.001$; 2009-2010: $z=7.3, p<0.001$). One day in 2010 contributed an extreme value (70 predators in one day) which exerted leverage on the generalized linear model, however, removal of this value yielded similar results.

Figure 2-8: Body weight of adult incubating Arctic Terns at Nasaruvaalik Island was significantly lower in 2009 and 2010 compared to 2007 and 2008. Bars show means ± 95% CI. Numbers above bars show sample size, and bars with different letters are significantly different.
Numbers of avian predators present during pre-breeding were similar in 2007 and 2009, but significantly higher in both 2008 and 2010 (Figure 2-9; 2008-2007, \( z=4.0, p<0.001 \); 2008-2009: \( z=-3.6, p=0.002 \); 2010-2007: \( z=4.9, p<0.001 \); 2010-2009: \( z=4.4, p<0.001 \)).

Similar numbers of predators were observed during pre-breeding in 2008 and 2010.

During incubation, avian predators were far more numerous in 2010 than in any other year (\( p<0.001 \)). Predator numbers during incubation were similar in 2008 and 2009, as they were 2007 and 2008, but 2007 had fewer avian predators during incubation than 2009 (\( p=0.045 \)).
High Arctic colony comparisons

Arctic Terns laid larger clutches on Nasaruvaalik Island than at Sand Island, Greenland ($t_{1054}=5.794$, $p<0.001$), but otherwise Nasaruvaalik clutch sizes did not differ

Figure 2-9: At the Nasaruvaalik Island Arctic Tern colony, 2007 had the fewest visits from avian predators overall, and 2010 the highest. During pre-breeding, 2008 and 2010 had similar numbers of avian predators on the island, while many more visited the island during incubation in 2010 than all other years. Bars show means ± 95% CI. In this graphic, different letters within each pane indicate significant differences. Numbers above bars show sample sizes (# days observed).
significantly from other High Arctic sites. However, the mean clutch size at Nasaruvaalik Island was significantly higher than the High Arctic zone mean (Table 2-6; $t_{13}=-2.571, p=0.023$).

Table 2-6: Mean of annual mean Arctic Tern clutch sizes at Nasaruvaalik Island as well as the mean of annual means from other studies in the High Arctic zone. Sources of these data are noted in Appendix A.

<table>
<thead>
<tr>
<th></th>
<th>Clutch size mean of means ± SE</th>
<th>$n^\dagger$</th>
</tr>
</thead>
<tbody>
<tr>
<td>High Arctic</td>
<td>1.6 ± 0.04</td>
<td>6</td>
</tr>
<tr>
<td>Nasaruvaalik Island</td>
<td>1.8 ± 0.05</td>
<td>9</td>
</tr>
</tbody>
</table>

$^\dagger$ sample size for High Arctic mean is the number of sites; for Nasaruvaalik, it is the number of years

Terns at Nasaruvaalik Island laid larger eggs than terns on Sand Island (Table 2-7; $t_{1377}=4.7, p<0.001$; Egevang 2007, Egevang et al. 2008). Statistical comparisons of chick growth rates could not be made as data from Sand Island lack measures of variance (Table 2-8).

Table 2-7: Arctic Tern egg volume index was significantly higher at Nasaruvaalik Island compared to Sand Island, as depicted by different letters in the right column.

<table>
<thead>
<tr>
<th></th>
<th>Egg volume index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>Nasaruvaalik Island</td>
<td>16.79 ± 0.04</td>
</tr>
<tr>
<td>Sand Island</td>
<td>16.32 ± 0.09</td>
</tr>
</tbody>
</table>
Discussion

By conducting the first multi-year study of Arctic Tern reproductive ecology in the Canadian Arctic, I was able to generate novel baseline information on breeding parameters of this species in the core of the tern breeding range in Canada, similar to studies in other countries and regions (e.g., Pettingill 1939, Hawksley 1957, Bengtson 1971, Lemmytyinen 1972, 1973a, b, Chapdelaine et al. 1985, Egevang 2010). Moreover, I found marked differences in adult body condition, clutch size, nest initiation dates, incubation periods, hatching success, chick growth rates and predator numbers among years. I provide some interpretation of factors that may explain this interannual variation below.

Breeding and feeding: Effects of predators and food resources

Arctic Terns on Nasaruvaalik Island made attempts to breed in all four years of this study, as they have every year since at least 2002 when visits to the island began.

### Table 2-8: Arctic Tern chick weight and wing growth rates on Nasaruvaalik Island (2008 and 2010 combined) and Sand Island (reported for 2008 only). Measures of variance were not available for the Sand Island data.

<table>
<thead>
<tr>
<th></th>
<th>Weight growth (g/day)</th>
<th>Wing growth (mm/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SE</td>
<td>n</td>
</tr>
<tr>
<td>Nasaruvaalik Island</td>
<td>5.32 ± 1.51</td>
<td>18</td>
</tr>
<tr>
<td>Sand Island</td>
<td>5.99</td>
<td></td>
</tr>
</tbody>
</table>


(Mallory and Gilchrist 2003), and there is evidence Arctic Terns have nested on Nasaruvaalik Island for at least 100 years (Michelutti et al. 2010). However 2009 and 2010 proved to be poor breeding years for the terns, with the lowest clutch sizes of all recorded years, and the lowest hatching success and chick growth rates occurring in 2010 immediately prior to a complete colony failure. In that year, adults in both the north and south colonies abandoned the colony after several days of high wind, snow and sleet shortly after the start of chick-hatching in the first week of August. During this storm at least one Peregrine Falcon visited the colony, as was evident by the carcasses of a few adult terns that stayed on their nests and one 2-week old Sabine's Gull (Xema sabinii) chick. Though it would seem that this storm may have been the cause of abandonment in 2010, I do not believe this to be the case. When the storm occurred, few chicks had hatched, and since eggs may be left exposed for periods of cooling without killing the embryos (Bennett and Dawson 1979), the terns should have been able to return to incubating and continue the season even if the visiting falcon forced them to leave their nests for a period during the storm. The abandonment was likely a culmination of a very poor season for the terns in this year, which will be discussed in detail below. This island-wide abandonment was unrelated to human disturbance: although the south colony was visited daily and studied intensively, the north colony was visited only weekly or on alternate weeks in 2009 and 2010. Furthermore, Arctic Tern breeding effort and success increased again in 2011, despite similar levels of human activity in the colony (Mallory pers. comm.).

Arctic Tern colonies, like those of all seabirds, go through good years and bad. These fluctuations may be related to many factors, but the two most frequently invoked are the
presence of predators (Lemmetyinen 1973a, Levermann and Tottrup 2007, Wojczulanis-Jakubas et al. 2008) and food availability (e.g., Lemmetyinen 1972, 1973b, Monaghan et al. 1989, 1992, Avery et al. 1992, Suddaby and Ratcliffe 1997, Votier et al. 2008). Both of these factors influenced the reduced reproductive success of the terns in 2009 and 2010, depicted in Figures 2-10 and 2-11. Weather may have been an additional contributing factor in 2010. Because it is more difficult for adults to find food in stormy weather, heavy rains early in chick-rearing will cause widespread failure in tern colonies due to exposure and starvation (Power 1964, Becker and Specht 1991). However at Nasaruvaalik, the 2010 storm took place before most chicks had hatched, and those that had hatched were already dying, apparently from starvation.

Figure 2-10: Several aspects of Arctic Tern breeding ecology at Nasaruvaalik Island are affected by food availability, which here is represented by the weight of adult terns. These parameters are also influenced by high numbers of predators on the island in 2010. Points show means ± 95% CI, numbers beside points are sample sizes.
The number of avian predators observed on Nasaruvaalik Island was low from 2007-2009. These years were in contrast to the 2010 season, during which I recorded an average of 13 avian predators per day on the island throughout the season, reaching a peak of 70 during a day of poor weather. Notably however, during the pre-breeding portion of the season, 2008 and 2010 had similar numbers of avian predators seen daily, with both years significantly higher than 2007 and 2009. However 2010 was the only year in which the number of predators on or over the island continued to increase throughout the incubation period, leading to a average of 18.5 predators daily in that
period. I speculate that the reason for these higher numbers in 2010 may be widespread low food availability in the region (see below).

Despite the presence of one Arctic Fox on the island in 2009, few tern nests \((n=6)\) were depredated. It is likely that the fox used alternate prey, notably eggs from the approximately 300 Common Eider \((Somateria mollissima)\) and several Long-Tailed Duck \((Clangula hyemalis)\) nests. As a result, the terns did not appear to be disturbed by this land predator, and did not exhibit the same alarm behaviour observed in 2010. Also surprising was though Polar Bears frequented the colonies, they were not observed depredating tern nests, nor were eggs or nests missing after any of the bears passed through the colony.

Food availability could not be sampled directly in this study, but inferences can be made. Body weight of adult terns during incubation was approximately 8\% lower in 2009 and 2010 compared to 2007 and 2008. During their long migrations, Arctic Terns use energy reserves obtained in the wintering grounds to maintain their body condition (Agius 2008), and must replenish these reserves on arrival at the breeding colony. Though it is possible that the lower body weights of the terns in 2009 may be a carry-over effect from their wintering grounds, more likely it is indicative of low food resources at the breeding colony on arrival (Monaghan et al. 1989, Wendeln 1997, Gaston et al. 2005b). Supporting this are my qualitative observations of courtship feeding during pre-breeding: in 2007 and 2008, 5+ cm polychaete worms were brought to the colony frequently, but in 2009 and 2010, courtship prey was smaller \((<2\text{ cm})\) and limited in quantity.
The high chick mortality in 2010, even prior to the poor weather, suggests poor food availability. Chicks in this year were frequently found dead beside their nests a few days after hatching, externally unharmed and sometimes with the attending parent still incubating the remaining egg. This implies that the chicks had lived as long as their yolk sac reserves had lasted, but that the parents were unable to feed them enough to sustain them thereafter.

Breeding terns exhibited responses consistent with negative effects of predator presence or low food availability in almost every aspect of breeding ecology that was measured. Later nest initiation dates in 2008 and 2010 are likely due to the increased number of avian predators seen in both years prior to nest initiation. An increased presence of predators during the pre-breeding portion of the season may cause seabirds to delay the onset of laying, or forgo breeding entirely (Boekelheide 1980, Levermann and Tottrup 2007).

The longer incubation period in 2010 compared to all other years was likely a result of high numbers of predators during incubation and lack of food in that year. Incubation can be extended when predators are present (Boekelheide 1980). The predators at the colony kept terns off their nests repeatedly throughout incubation. Our qualitative observations of colony-wide flushing ('panic flights'; Hatch 2002) noted that terns were far more likely to flush from their nests even when a predator was not in sight in 2010. Frequent flushing occurred most often immediately after a falcon came through the colony; this species is a potential predator of nesting adults rather than just nest contents. Terns were also kept away from nests as their foraging trips became longer.
with the decrease in food availability. Several nests were apparently abandoned for several days, only to have an adult return to incubate, possibly after replenishing its reserves. This apparent inability to locate food near the colony may have been exacerbated by the advanced ice-melt also observed in 2010, estimated to be 2 - 3 weeks earlier than the three previous years. As terns are surface-feeders, prey must be close the surface to be accessible, and ice, especially over shallow water as it is around Nasaruvaalik Island, is an ideal platform around which terns centre their feeding activities. Currents passing under ice cause prey to be swept from the underside of it, making prey available to terns in ice-associated currents (Hunt 1991a, b); these visible currents were often sites of intense tern foraging activity around the island. Fewer ice platforms around the colony would make successful near-colony foraging difficult for the terns. Early removal of sea-ice also led to low prey availability and reduced fledging success of Arctic Terns at Cooper Island, Alaska (Boekelheide 1980).

Particularly related to low food availability in the latter 2 years of the study, clutch size declined in 2009 and remained low in 2010. A decrease in clutch size occurs when females are in poor body condition (e.g., Suddaby and Ratcliffe 1997). Though statistically clutch size in 2002 was similar to 2009 and 2010, this may be a function of low sample size and high variance in that year. However, lower clutch sizes in 2002 could also be a result of exceptionally late break up of sea ice; this caused reduced breeding success in a nearby seabird colony (Gaston et al. 2005b). Because recurrent polynyas around Nasaruvaalik Island allow terns access to potential prey items (Mallory and Fontaine 2004, Hannah et al. 2009), late sea-ice break up in 2002 would not have physically restricted access to prey, but may have delayed the seasonal plankton bloom
and associated trophic pulse up the food web (Laidre et al. 2008), leading to lower prey availability during pre-breeding and lower female body condition prior to egg-formation.

Hatching success is another breeding parameter that was affected by both low food availability and increased predation. Hatching success declined from 2008 to 2009, however we observed no evidence of predation in 2009 other than six nests that were presumably eaten by the Arctic Fox, and no behavioural changes in the adults akin to those we saw in 2010. It is likely that adults faced with nutritional stress abandoned their nests. It should be noted that the hatching success in 2009 was likely even lower than reported because it was biased towards early nests: researchers left the island prior to the end of anticipated incubation periods for 51% of nests in that year, and early nests tend to have higher overall success rate (e.g., Nisbet 1978, Anotolos et al. 2006). In 2010, there was a larger decrease in hatching success. As might be expected from the higher numbers of predators, many nests were depredated during the incubation period. Additionally, parents may have provided insufficient heat, since they left their nests for longer periods in this year, presumably on extended foraging trips or as a result of panic flights, causing the exposed, developing embryo to die. The final cause of the widespread hatching failure in 2010 was the entire abandonment of the colony before many chicks hatched.

Chick growth rates were obviously affected by the lack of food in 2010. Only four chicks from the 2010 plot lived to be measured twice in the linear growth period of five to fifteen days. Given that Klaassen et al. (1994) found that a 30% reduction in food to
Arctic Terns led to a 50% drop in growth rate, a decrease in weight gain when food availability is low is not surprising. It is also similar to what has been noted in other Arctic Terns that are confronted with poor food resources (Lemmetyinen 1972, Suddaby and Ratcliffe 1997), Common Terns (*Sterna hirundo*) fed on poor quality food (Massias and Becker 1990) and Caspian Terns (*Hydroprogne caspia*) fed restricted diets (Lyons and Roby 2011). The wing growth rate of Arctic Terns at Nasaruvaalik Island did not appear to differ between 2008 and 2010, however my power to detect a difference was low due to low sample size and high variation among the chicks in each year. This variation among chicks may be derived from the differences in growth rate between the chicks that survived to fledge and those that did not. Chicks which ultimately die within the colony may grow at a slower rate than those that fledge successfully (e.g., Watanuki 1988), however my sample size was such that I could not exclude any chicks and still compare growth rates among years. Though wing growth rates are not usually affected by decreased food availability (Lack 1968), chicks will have limited wing growth rates when food supplies are very low (Cairns 1987, Phillips et al. 1996, Lyons and Roby 2011).

Chick feeding observations were made in 2007 and 2008 only, and no differences were found between the years, nor between diurnal and nocturnal feeding. My power to detect differences between years or time-of-day feeding rates was low, attributable to low sample size and highly variable chick feeding rates. However, since removing the extreme feeding rates and retesting gave the same results, the likelihood that there were no real differences between 2007 and 2008 overall chick feeding rates is great. As these
two years were similar in the number of predators present and their inferred food availability, this is expected.

Despite my inability to state conclusively that there were no differences between diurnal and nocturnal feeding rates, it is clear that terns in the Canadian High Arctic do forage throughout the 24-hour period. This supports my prediction that terns experiencing 24 hours of daylight would exhibit less of a diel foraging pattern than terns that experience a dark night, as is seen in other high latitude seabirds (Barrett et al. 1997, Mehlum et al. 2001), including terns (Boekelheide 1980). Terns often have high foraging success during rapid tidal movements and vary their foraging behaviour with the tidal cycle (Baird and Moe 1978, Frick and Becker 1995, Schwemmer et al. 2009; but see Paquet 2001). Though we did not gather tidal rhythm data at the site, in our observations of feeding, terns formed the largest feeding flocks immediately offshore of the colony when tidal currents were moving fast and upwellings were visible. They congregated either in the lee of multiyear ice or at edges of the island where currents wrapped around the land. These locations contained upwellings from either the sea floor or from the undersides of chunks of multiyear ice, which host more under-ice fauna than young ice (Lonne and Gabrielsen 1992). Optimal foraging conditions at this site therefore likely occur during periods of fast tidal currents that bring prey to the surface.
High Arctic colony comparisons

The comparisons with other High Arctic tern colonies suggest that, despite the inclusion of two poor breeding years, Nasaruvaalik Island is a good site for breeding Arctic Terns compared to other sites within the High Arctic. This may explain why it has been occupied for at least 100 years. Part of the reason for the quality of the site likely lies in the nearby polynyas to the north in Queen's Channel and Penny Strait as well as near Dundas Island and to the south at Karluk Brooman (Hannah et al. 2009). The latter are within 30 - 35 km of the island, which is similar to known foraging distances of some breeding terns elsewhere (Black 2006) though not others (Rock et al. 2007). Two smaller polynyas immediately north and south of Nasaruvaalik Island were also open in mid-June in all four years of this study, when all of the ice between Cornwallis and Nasaruvaalik Islands was unbroken (pers. obs.). For many Arctic-nesting seabirds, ice plays a major role in the timing of breeding, and years of thick ice or late ice break-up can negatively affect entire breeding seasons (Boekelheide 1980, Gaston et al. 2005b, Mallory and Forbes 2007) because birds cannot access prey items, or thick ice or late break-up results in late phytoplankton blooms, in turn delaying increases in all associated potential prey items for seabirds (Laidre et al. 2008). Polynyas are known to be important resources for seabirds for these reasons (Stirling 1980, 1997, Mallory and Gilchrist 2005). At Nasaruvaalik Island, no ice-related changes in the onset of laying were apparent; the polynyas ensure that the terns have access to prey items on arrival and throughout the season, which is especially important at this site given the absence of terrestrial prey sources, especially at the start of the season. Although we do not know if there are fish-sustaining ponds on nearby islands, there are none on Nasaruvaalik, and
insects do not emerge from Nasaruvaalik ponds until the end of June around the same time as the onset of laying.

The quality of Nasaruvaalik Island as a High Arctic breeding location is also related to predation pressure. In four years of study at Sand Island, Greenland, Arctic foxes constrained the ability of Arctic Terns to reproduce in two of the years (Egevang and Frederiksen 2011). Fox predation on that island may also be the cause of variable laying locations there. Despite similar numbers of nests in both years, 2008 tern nests were concentrated in the centre of the island, whereas 2007 nests were dispersed (Egevang 2010). The concentration in 2008 may have occurred as the terns formed a denser colony to facilitate colony-wide defence. This is markedly different from Nasaruvaalik Island, where, since at least 2002 and reaching as far back as 100 years in the south colony (Michelutti et al. 2010), terns have confined their nests to the two colonies at either end of the island, while the approximately 300 Common Eiders nested largely outside the tern colony. The presence of these sea ducks is likely a large reason for the low fox- and bear-related predation experienced by the terns at Nasaruvaalik. Because terns exert a vigorous colony defence (Hatch 2002), the fox likely stayed away from the colony because of the availability of larger eider clutches and eggs that could be acquired with less physical risk. At Sand Island in 2007, only 10-15 common eider and one or two long-tailed duck nests were reported, while in 2008, the number of eider nests increased to around 100. However, even 100 eider nests, roughly a third of what has been found on Nasaruvaalik Island, may not have been enough to dissuade foxes from depredating tern nests, especially if the terns are not concentrated into annual distinct colony locations.
Seabird breeding phenology has already been documented as shifting in relation to climate change in the last 30 years (Møller et al. 2006, 2009, 2010, Gaston et al. 2009b, Wanless et al. 2009). Thus, recently-collected data (e.g., this study) that will serve as a baseline for future monitoring of a species may already differ from a baseline that would have been established based on observations collected more than 30 years ago; this is often termed a 'shifting baseline' (e.g., Pinnegar and Engelhard 2008). Since effects of climate change have been documented for these past 30 years, data collected now will not reflect the state of pre-climate change breeding biology of Arctic Terns in the High Arctic. Nonetheless, in the absence of earlier baseline data, it is important to establish current, 'typical' parameters of reproductive ecology as soon as possible, however shifted they may be (Mallory et al. 2010), to enable documenting and modelling future changes. This study has increased our knowledge of Arctic Terns breeding in High Arctic environments, and provides the base for future monitoring of Canadian High Arctic terns. It will allow future use of this species as a bioindicator of the marine health of the region (e.g., Montevecchi 1993, Diamond and Devlin 2003, Piatt et al. 2007a) as climate change continues and as human activities become increasingly pervasive throughout the Canadian High Arctic archipelago. It may allow mitigation or avoidance of negative consequences of human stressors on the marine environment and ground-nesting seabirds themselves.

This study has shown that Arctic Terns breeding on Nasaruvaalik Island experience high reproductive success in most years, although diminished success or complete
reproductive failure may also occur. It has also demonstrated the high degree of interannual variability in the indicators of reproductive success of these birds. When one measure of success, clutch size, is compared across nine years and to other colonies with their High Arctic zone, it seems that the Nasaruvaalik Island colony is a particularly good one for terns. Nesting alongside polynyas on a small island that rarely attracts mammalian predators probably explains much of this pattern. This study has therefore added to knowledge of the importance of polynyas to breeding wildlife in the Arctic.

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Chapter 3: Diet of Arctic Terns in the Canadian High Arctic: stable isotopes reveal temporal specialization and income breeding

Abstract

The diet of seabirds affects all aspects of their breeding ecology, but little is known of the diet of Arctic Terns breeding in the High Arctic of Canada. Using stable isotopes, I compared the diet of these seabirds across the breeding season and between seasons at High Arctic Nasaruvaalik Island, Nunavut. I found that the trophic position of incubating adults dropped and trophic niche width expanded in a year of poor breeding success. I found that pre-breeding adults have a wider trophic niche than incubating adults and chicks. I also confirmed that, similar to Arctic Terns breeding elsewhere, these High Arctic terns rely on nutrients gathered near the colony for egg formation.

Introduction

The diet of seabirds during the breeding season affects all aspects of their breeding ecology, from clutch size and egg volume, to hatching success, chick growth rates and overall reproductive success (e.g., Cairns 1987, Sydeman et al. 1991, Suddaby and Ratcliffe 1997). Consequently, factors that influence the availability or quality of prey for seabirds will indirectly influence seabird reproduction. Global warming is affecting polar regions more rapidly than other areas of the globe, altering the timing and distribution of sea-ice cover which influences the ability of Arctic seabirds to find and
access prey (Arctic Climate Impact Assessment 2005). As the climate changes, we are beginning to see that seabird reproduction, until recently timed to match peak prey availability (Laidre et al. 2008), is becoming mismatched (Moline et al. 2008, Gaston et al. 2009b).

Currently, much of our knowledge about seabirds in the Arctic comes from studies of pursuit-diving Thick-billed Murres (*Uria lomvia*: Falk et al. 2000, Gaston et al. 2005a, Hipfner et al. 2005), Dovekies (*Alle alle*: Harding et al. 2008, Wojczulanis-Jakubas et al. 2009, 2011), or surface-feeding Northern Fulmars (*Fulmarus glacialis*: Mallory and Forbes 2007, Mallory et al. 2008b, 2008c). Like all breeding seabirds, fulmars are central-place foragers (Stephens and Krebs 1986), but they are able to forage at distances greater than 200 km from the colony because they are able to store prey for later regurgitative feeding to chicks (Mallory et al. 2008a). As a result, these three species have greater access to prey than two-dimensional surface-feeders that feed prey directly to chicks, or "direct-feeders". These seabirds cannot pursue increasingly unavailable prey to depths, and cannot fly long distances from the colony in search of surface prey. Surface-feeding, near-colony foragers are therefore less buffered against changes in prey availability and may provide earlier indications of changes in the ocean than pursuit-divers and long-distance foragers (Furness and Camphuysen 1997). Though some studies have described some aspects of the diet of surface-feeding seabirds in the High Arctic (Węsławski et al. 1994), none have described the diet of these birds during different parts of the breeding season.
To further understand the diets of surface-feeding "direct-feeders" in the High Arctic, I studied Arctic Terns (*Sterna paradisaea*) at a colony approximately 130 km northwest of Resolute Bay, Nunavut, Canada. These birds are small, ground-nesting seabirds that are surface-feeders, able to plunge-dive to no more than 50 cm below the surface (Hatch 2002). During the breeding season, they are restricted to feeding within 35 km of their breeding colony (Black 2006). I studied diet of these birds using stable isotopes of nitrogen (\(\delta^{15}N\)), and in some cases carbon (\(\delta^{13}C\)), examining trophic positions and niche width of adults during pre-laying and incubation, as well as chicks fed by parents at the colony. Furthermore, as the diet of seabirds immediately prior to breeding affects their ability to reproduce successfully (Sorensen et al. 2009), I assessed allocation of nutrients for egg formation to determine if these nutrients are acquired near or far from the colony. I also wished to determine the source of nutrients for egg formation to enable comparisons of the pre-breeding diet of the females to that in other parts of the breeding season, as described below.

I used stable isotope analysis for several reasons. First, Arctic Tern adults consume their prey away from the colony, so it is not possible to observe from land what adults eat directly, nor is it practical to observe terns on the water given the wide areas over which terns may forage. Second, though the diet of the chicks can be observed more readily from blinds, in this colony where the nests are not close together, few nests can be observed in enough detail to correctly identify each prey item brought to the chicks. Solutions to these problems are outlined in detail in both Barrett et al. (2007) and Duffy and Jackson (1986); however for this study, stable-isotope analysis was the best method for investigating the diet of these birds.
Differences in the relative abundances of stable isotopes in the tissues of a study subject were recognized over thirty years ago as being derived from the diet (Deniro and Epstein 1978, 1981). Since then there have been numerous seabird studies involving stable isotope ratio analyses (e.g., Hobson 1993, Barrett et al. 2007, Inger and Bearhop 2008, Bond and Jones 2009). This approach relies upon lighter isotopes being metabolised preferentially over heavier ones at each level of a food chain, especially nitrogen, in which the relative abundance of uncommon $^{15}$N to the very common $^{14}$N increases in a predictable manner from prey to consumer. The stable-nitrogen isotope ratios of an organism, when compared to the base of the local food web, can therefore be used to identify the trophic position of the organism in a food web (Vander Zanden and Rasmussen 1999). The ratio of heavy to light carbon isotope changes very little through trophic positions, so carbon is not useful for trophic analyses (Deniro and Epstein 1978, Hobson and Welch 1992). However, since carbon isotope ratios closely resemble the diet at any position in the food web, they thus reflect the primary producers of a system. Carbon isotopes may therefore be used to determine whether organisms derive their nutrients from marine vs. terrestrial origins, or inshore vs. offshore food webs (Hobson and Welch 1992, Hobson et al. 1994).

Niche width can be assessed using variance of isotopic ratios within groups to identify 'isotopic' niche width, as described in detail by Bearhop et al. (2004) and Newsome et al. (2007). To summarize, niche width as explored through stable-isotope variance can have multiple interpretations: high variance within a population could indicate a broad niche width for every individual within the population, or it could indicate that the population is composed of many individuals all specialising on different prey items. Regardless, a
large isotopic variance of a population indicates the population as a whole uses many different prey resources and is, collectively, a generalist (though it may be composed of individuals which are specialists and those that are generalists). On the other hand, a population with narrow isotopic variance indicates that all members are specializing on prey items of similar isotopic composition. Comparing variances of isotopic ratios among groups and in comparison to the base of the web, or simply their potential prey, can provide information about differences in their foraging niche. Hereafter, "niche width" refers to this isotopic proxy for diet breadth, one important component of a species’ ecological niche.

Stable isotopes of nitrogen or carbon can also be used to determine the degree to which a population uses exogenous or endogenous resources in egg formation (Hobson et al. 2000, Hobson 2006, Bond and Diamond 2010). Much like comparing isotopic ratios of a consumer to those of potential prey items to determine which are most likely to have comprised the diet of the consumer, one can compare the isotopic signatures of eggs to a source that reflects the local isotopic signatures and one that reflects the diet of the bird near or at the wintering site (provided of course that these signatures are different). If the egg is formed from exogenous resources, the isotopic signature of the egg should closely match the local food source. If it is formed using endogenous resources, the egg signature will more closely match resources at the wintering site. This approach has been used to demonstrate, for example, that many birds previously thought to rely exclusively on endogenous reserves for egg formation are actually using a mix of endogenous and exogenous sources (Gauthier et al. 2003), while others have a heavier
reliance on exogenous reserves for egg formation (Bond et al. 2007b, Bond and Diamond 2010).

My objective is to describe the diet of Arctic Terns during different stages of their breeding season, and to explore interannual variation in diet at a High Arctic colony in Canada. The study provides dietary information about a species that forages in a two-dimensional, colony-restricted foraging range in the High Arctic.

**Methods**

*Study site*

The study site was located on Nasaruvaalik Island, Nunavut, approximately 130 km northwest of Resolute Bay, Nunavut, as described in Chapter 2.

*Sample collection*

I collected samples from 31 adult Arctic Terns in 2008 and 23 in 2009 when they were caught for banding, no earlier than one week into incubation, as described in Chapter 2. Four to five breast feathers were collected to use as an indicator of winter diet; since Arctic Terns grow body feathers at their wintering grounds (Pyle 2008), and feathers are isotopically inert once grown (Pearson et al. 2003, Inger and Bearhop 2008), breast feathers contain the isotopic signature of the wintering grounds. Blood was collected by
pricking the brachial vein with a 27-gauge needle and collecting approximately 150µl of blood in heparinised capillary tubes (Gaunt et al. 1999). Within five hours, I spun the blood in a microhematocrit centrifuge for 5 minutes to separate the plasma from the red blood cells (Howlett 2000). Each portion was placed in separate microcentrifuge tubes and kept frozen; this does not affect the stable isotopes within a sample (Bosley and Wainright 1999, Bugoni et al. 2008). I used the 2008 plasma for determining the extent to which these terns use exogenous resources for egg formation. I used plasma from both years to determine the trophic positioning and niche width of adults during incubation. This was possible because plasma isotope ratios turn over within a few days to one week (Hobson and Clark 1993, Pearson et al. 2003, Inger and Bearhop 2008). In 2007, whole blood was collected from terns collected throughout the breeding season for another study, but it was not separated into its constituent parts prior to freezing. Unlike the fast turnover of plasma, whole blood turns over isotopically in 2-4 weeks (Hobson and Clark 1992a). This means that whole blood collected during early incubation will reflect the diet of the birds during the pre-breeding portion of the season, or possibly even migration. However, whole blood sampled during the last week of incubation and chick-rearing will reflect the same period as plasma collected from incubating birds in 2008 and 2009.

I collected blood samples from 25 chicks at their last handling immediately prior to fledging in 2008, as described for adults. Chick plasma was used to assess trophic position and niche width of chicks.
Eggs were collected in 2008 as described in Akearok et al. (2010) to assess nutrient allocation to egg formation by Arctic Terns at this colony; in this year, laying order was known, and whole clutches were collected. In 2007, all eggs were collected from nests of terns whose parents were collected for another project, but laying order in 2007 was unknown. If these terns are similar to other populations and can be considered 'income' breeders (deriving the nutrients for their eggs locally; Hobson et al. 2000, Bond and Diamond 2010), their eggs should reflect the diet of the female at the breeding colony prior to nest initiation. Thus, eggs were also used to ascertain the pre-breeding trophic position and niche width of adult females in 2007 and 2008.

Finally, to determine the $\delta^{15}$N and $\delta^{13}$C values of the base of the local marine food web and obtain the $\delta^{15}$N and $\delta^{13}$C values from potential prey species, plankton tows were conducted once in 2008 and twice in 2009 by pulling a 200µm net through the top 30-50cm of water immediately offshore of the south colony at a lead in the ice. Resulting samples contained in seawater were frozen at -20°C in individual sealed plastic bags (Whirl-paks) until separated in the lab (Lovvorn et al. 2005). Dropped and regurgitated prey (Arctic cod *Boreogadus saida*, polychaete worms and unidentified amphipods) were recovered from within the colony, and frozen in Whirl-paks.

*Sample analyses*

Blood samples were dried in an oven at 60°C for 12-24 hr, or freeze-dried for 6-12 hr. To remove potential contaminants (including preen oils) from surfaces, I triple-washed
feathers in a 0.25M NaOH solution, rinsed with distilled, deionised water (Bearhop et al. 2000, 2002, Catry et al. 2008, Ramos et al. 2009) and dried them in the 60°C oven.

Plankton tow samples were separated by hand into groupings by standard size classes (<1mm, 1-1.9mm, 2-4.9mm and >5mm; Landry et al. 2008, Hannides et al. 2009, Koppelmann et al. 2009), type (calanoid copepods, harpacticoid copepods, and amphipods: Gammarus sp., Onisimus sp., Themisto sp.) and collection date. Resulting groups were freeze-dried in glass vials.

Tissues containing high amounts of lipids are depleted in $^{13}$C (McConnaughey and McRoy 1979, Ricca et al. 2007). Because the amount of lipids in tissues varies among individuals or tissue type, comparing high lipid-content tissues to each other or to non-lipid-containing tissues is inaccurate (McConnaughey and McRoy 1979, Hobson 1995). To “lipid-normalize” tissues, McConnaughey and McRoy (1979) recommended any tissues with a carbon to nitrogen ratio greater than 4.0 be lipid-extracted. The only tissues containing enough lipids to warrant extraction were tern eggs and Arctic cod. Eggs were homogenized, and Arctic cod was filleted to obtain muscle tissue. Both were freeze-dried and ground, and lipids were removed using 2:1 chloroform:methanol rinses based on a modified Bligh and Dyer (1959) method. Both tissue types were dried in the oven at 60°C after lipid-extraction. Lipid-extraction has a negligible effect on stable-nitrogen isotopes (Hobson 1995, Bearhop et al. 2002, Charette 2005, Ricca et al. 2007).

I ground all samples except feathers into a homogenous powder using a mortar and pestle and weighed it into tin cups for analysis; the range of dry weight of sample required was 0.200 – 0.240mg. The distal tips of cleaned feathers were cut with scissors.
into small pieces and weighed into the tin cups. All tissue samples, except the 2008 egg samples, were analysed by the Stable Isotopes in Nature Laboratory (SINLAB) at the University of New Brunswick. The 2008 eggs were analysed at the University of Ottawa G.G. Hatch Stable Isotope Laboratory. At both labs, samples were combusted in an elemental analyzer, and gases were sent to the isotope-ratio mass spectrometer using a continuous flow interface. Similar standardization procedures are used at both labs, including internal repeats and international standards, reported in Table 3-1. Data are reported as differences in isotopic ratios, for which the units are parts per thousand (or per mil; ‰) compared to Pee Dee Belemnite (PDB or V-PDB; 2 interchangeable scales) for carbon, and atmospheric nitrogen (AIR) for nitrogen, according to the following equation:

$$\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{std}}} - 1 \right) \times 1000$$

where $\delta X$ is the isotope of interest (in this case, $\delta^{15}$N or $\delta^{13}$C), \(R\) is the ratio of the abundance of the heavy to the light isotope ($^{15}$N/$^{14}$N or $^{13}$C/$^{12}$C), with $R_{\text{sample}}$ being the ratio within the given sample, and $R_{\text{std}}$ the ratio of heavy to light isotope within the international standard.
Table 3-1: Isotopic values for International Atomic Energy Agency (IAEA) and internal standards used at the University of New Brunswick’s SINLAB and the University of Ottawa's G.G. Hatch Stable Isotope Laboratory to assess accuracy and precision of results obtained from stable isotope analyses.

<table>
<thead>
<tr>
<th>International standard</th>
<th>δ$^{13}$C (‰)</th>
<th>δ$^{15}$N(‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SINLAB</td>
<td></td>
<td></td>
</tr>
<tr>
<td>IAEA-CH6</td>
<td>-10.4 ± 0.06</td>
<td>-</td>
</tr>
<tr>
<td>IAEA-CH7</td>
<td>-31.88 ± 0.10</td>
<td>-</td>
</tr>
<tr>
<td>IAEA-N1</td>
<td>-0.40 ± 0.10</td>
<td></td>
</tr>
<tr>
<td>IAEA-N2</td>
<td>-20.47 ± 0.35</td>
<td></td>
</tr>
<tr>
<td>G.G. Hatch Stable</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isotope Laboratory</td>
<td></td>
<td></td>
</tr>
<tr>
<td>IAEA-CH6</td>
<td>-10.4</td>
<td></td>
</tr>
<tr>
<td>NBS-22</td>
<td>-29.91</td>
<td></td>
</tr>
<tr>
<td>USGS-40</td>
<td>-26.24</td>
<td>-4.52</td>
</tr>
<tr>
<td>USGS-41</td>
<td>37.76</td>
<td>47.57</td>
</tr>
<tr>
<td>IAEA-N1</td>
<td>-0.4</td>
<td></td>
</tr>
<tr>
<td>IAEA-N2</td>
<td>20.3</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Internal standard</th>
<th>δ$^{13}$C (‰)</th>
<th>δ$^{15}$N(‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SINLAB</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acetanilide</td>
<td>-27.63 ± 0.10</td>
<td>-1.98 ± 0.16</td>
</tr>
<tr>
<td>Nicotinamide</td>
<td>-34.20 ± 0.08</td>
<td>-1.79 ± 0.13</td>
</tr>
<tr>
<td>bovine liver</td>
<td>-18.72 ± 0.15</td>
<td>7.20 ± 0.17</td>
</tr>
<tr>
<td>small-mouth bass</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Micropterus dolomieu)</td>
<td>-23.26 ± 0.09</td>
<td>12.49 ± 0.10</td>
</tr>
<tr>
<td>G.G. Hatch Stable</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isotope Laboratory</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C-51 Nicotiamide</td>
<td>-22.95</td>
<td>0.07</td>
</tr>
<tr>
<td>C-52 mix of ammonium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>sulphate and sucrose</td>
<td>-11.94</td>
<td>16.58</td>
</tr>
<tr>
<td>C-54 caffeine</td>
<td>-34.46</td>
<td>-16.61</td>
</tr>
<tr>
<td>C-55 glutamic acid</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(blind standard)</td>
<td>-28.53</td>
<td>-3.98</td>
</tr>
</tbody>
</table>
Statistical analyses

Trophic position

Trophic position in this context is used not to indicate distinct levels at which each group of terns may be feeding, but as a continuum. Trophic positions of terns were calculated according to the equation developed by Vander Zanden and Rasmussen (1999) and modified by Post (2002):

$$TP_{\text{consumer}} = \lambda + \frac{(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{base}})}{\Delta n}$$

where $TP_{\text{consumer}}$ is the trophic position of the individual, $\Delta n$ is the average diet to tissue discrimination factor for the food web under study, $\delta^{15}N_{\text{consumer}}$ is that of the individual, $\delta^{15}N_{\text{base}}$ is that of the sample species chosen to represent the base of the food web, and $\lambda$ is its trophic position. In many cases when the true base is not obtainable, calanoid copepods are used to represent the 'base' of the food web, occupying the primary consumer trophic position, since they incorporate and integrate the various signals from the primary producers which are likely to change rapidly throughout the day and season (Fisk et al. 2001, Hoekstra et al. 2003, Falk-Petersen et al. 2009). Unfortunately, the smallest size-class of calanoid copepods yielded too little nitrogen to derive an accurate reading of their $\delta^{15}N$ values; only the larger (>5mm) size-class provided sufficient mass for reliable determination of nitrogen isotope content. However, some calanoid copepods are omnivores, and larger individuals would have larger prey, thus likely occupying a higher trophic position than those in a smaller size class (Hobson et al.)
I therefore used the smallest two size classes of harpacticoid copepods to represent primary consumers; they consume phytoplankton and bacteria as well, and in the Arctic are commonly sympagic (Kern and Carey 1983, Gradinger et al. 1999). Small harpacticoid copepods are therefore appropriate to use as a base, since Arctic cod and other small potential prey items of Arctic Terns are often ice-associated (e.g., Węsławski et al. 1994). The value used for Δn, the average discrimination factor for this system, was 3.8‰, as established for the North Water Polynya, which is relatively close to my study site (Hobson and Welch 1992). Prior to conversion to trophic position, δ^{15}N values were corrected for tissue-specific discrimination factors by subtracting the tissue-tissue discrimination factor differences from each value, thus eliminating the effect of tissue between the breeding stages of the individuals compared (Table 3-2). These discrimination factors are derived from non-Arctic Tern species which may affect the accuracy of the results (Bond and Diamond 2011), but are the best currently available. Trophic positions were then compared among years and breeding stages using a Kruskal-Wallis rank sum test followed by Dunn's multiple comparisons. Trophic positions could not be calculated for 2007 because plankton tows were not conducted in that year, so the base of the web was unknown.

**Niche width**

To evaluate differences in niche width, Fligner-Killen tests of equal variance were first performed on δ^{15}N values, followed by F-tests of equal variances. To compare variances
among years, values from whole blood sampled in the last week of incubation and chick-rearing in 2007 were pooled prior to equal-variance tests.

These variance comparisons depend on the prey items themselves maintaining consistent isotopic variance. Finding differences in isotopic variance between groups sampled at different times could indicate merely that there has been a shift in the variance of the prey base, rather than true differences in trophic niche width. Because all of my samples are reflective of the pre-breeding and breeding periods, which extend across approximately two months, I assumed that the prey base had consistent variance over that time, and therefore isotopic niche width as determined by variance in $\delta^{15}$N can be considered a true proxy of trophic niche width.

Nutrient allocation

The extent to which terns at this colony are income or capital breeders was established using the Bayesian mixing model SIAR (Stable Isotope Analysis in R; Parnell et al. 2010). This modeling application takes into account different discrimination factors between tissues, and it allows researchers to determine what proportion of the nutrients for egg formation came from endogenous reserves or exogenous sources. The differences between tissue discrimination factors had to be determined to use this model; this was done by gathering appropriate diet-tissue discrimination factors from the literature, and using the differences between the diet-tissue discrimination factors as the tissue-tissue discrimination factors (as described in Bond and Diamond 2010; Table 3-
2). In 2007 and 2008, feathers were used as a proxy of adult tern winter diet, and blood as a proxy of the local, breeding colony diet. Whole blood from the collected terns of 2007 was again used, limited to the blood taken during late incubation and chick-rearing to ensure that isotopic turnover had occurred and the blood was thus reflective of local isotopic sources. Plasma taken during incubation was used to represent the local diet in 2008. Because feathers were not collected in 2009, nutrient allocation tests could not be completed for that year. To test for potential differences between male and female incubating adults, isotopic ratios of known-sex birds were compared using a MANOVA for δ¹⁵N and δ¹³C of each tissue type in 2007. Unfortunately, blood from the 2008 season was contaminated during sample preparation, compromising the carbon analysis. Therefore, only nitrogen isotopes were used in the 2008 comparisons. A t-test was used to check for potential differences in δ¹⁵N between male and females within each tissue type in 2008. Because males and females showed no differences, males, females and unknown-sex birds were pooled in each year.

Analyses were conducted in R (R Development Core Team 2011) or Sigmaplot 11 (Systat Software 2008). For all tests, alpha = 0.05. In Tables and Figures, different letters represent significantly different test results. Numbers within bars or alongside points are sample sizes.
Table 3-2: Differences in discrimination factor ($\Delta^{15}N$, $\Delta^{13}C$) between tissue types that were used as proxies for breeding colony nutrients (plasma) and wintering ground nutrients (feather), to adjust for tissue type prior to trophic position calculations, and to determine nutrient allocation to eggs. Diet-tissue fractionation values are the means reported for each tissue in the literature. As discrimination factors vary greatly with species and size of individuals (McCutchan et al. 2003), the studies listed below were chosen because they contained discrimination factors for closely-related species of similar size to Arctic Terns. Egg values are not common, so I used what was available for a seabird and landbirds. Tissue-tissue fractionation values are the differences of the mean discrimination factor for each tissue type.

### Diet-tissue fractionation values

<table>
<thead>
<tr>
<th>Tissue</th>
<th>$\Delta^{15}N$</th>
<th>$\Delta^{13}C$</th>
<th>Literature source</th>
<th>Species derived from</th>
</tr>
</thead>
<tbody>
<tr>
<td>whole blood</td>
<td>+3.00</td>
<td>+0.50</td>
<td>Hobson and Clark 1992, Ogden et al. 2004</td>
<td>Ring-billed Gull (<em>Larus delawarensis</em>), Dunlin (<em>Calidris alpime</em>)</td>
</tr>
<tr>
<td>plasma</td>
<td>+3.30</td>
<td>+0.50</td>
<td>Ogden et al. 2004</td>
<td>Dunlin (<em>Calidris alpime</em>)</td>
</tr>
<tr>
<td>feather</td>
<td>+3.00</td>
<td>+0.20</td>
<td>Hobson and Clark 1992</td>
<td>Ring-billed Gull (<em>Larus delawarensis</em>)</td>
</tr>
<tr>
<td>albumen</td>
<td>+4.12</td>
<td>+0.86</td>
<td>Hobson 1995, Polito et al. 2009</td>
<td>as above</td>
</tr>
<tr>
<td>lipid-free homogenized egg†</td>
<td>+3.93</td>
<td>+0.42</td>
<td>†</td>
<td>†</td>
</tr>
</tbody>
</table>

†calculated from diet-tissue fractionation values of lipid-free yolk and albumen, above, using the weighted average of each tissue-type in tern eggs, as reported in Ostnes et al. (1997)

### Tissue-tissue fractionation values

<table>
<thead>
<tr>
<th>Tissue pairing</th>
<th>$\Delta^{15}N$</th>
<th>$\Delta^{13}C$</th>
</tr>
</thead>
<tbody>
<tr>
<td>lipid-free homogenized egg – feather</td>
<td>+0.93</td>
<td>+0.22</td>
</tr>
<tr>
<td>lipid-free homogenized egg – plasma</td>
<td>+0.63</td>
<td>-0.08</td>
</tr>
<tr>
<td>whole blood – plasma</td>
<td>+0.30</td>
<td></td>
</tr>
<tr>
<td>whole blood - lipid-free homogenized egg</td>
<td>+0.93</td>
<td></td>
</tr>
</tbody>
</table>
Results

In 2007, I obtained 16 whole blood, 12 egg, and 36 feather samples for isotope analysis. In 2008, 24 chick plasma, 31 adult plasma, 35 egg, and 33 feather samples were collected, and in 2009, I collected 23 samples of adult blood plasma for analysis (Table 3-3).

Table 3-3: Stable isotope ratios for Arctic Tern tissues used in this study to determine trophic positions, niche width and nutrient allocation at Nasaruvaalik Island. These values are uncorrected for tissue-tissue discrimination factors.

<table>
<thead>
<tr>
<th>Year</th>
<th>Tissue Type</th>
<th>δ¹⁵N (‰) Mean ± SE</th>
<th>n</th>
<th>δ¹³C (‰) Mean ± SE</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>whole blood</td>
<td>14.35 ± 0.12</td>
<td>16</td>
<td>-18.20 ± 0.13</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>egg†</td>
<td>14.27 ± 0.16</td>
<td>12</td>
<td>-17.88 ± 0.12</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>feather</td>
<td>8.73 ± 0.10</td>
<td>36</td>
<td>-24.45 ± 0.20</td>
<td>36</td>
</tr>
<tr>
<td>2008</td>
<td>chick plasma</td>
<td>15.76 ± 0.07</td>
<td>24</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>adult plasma</td>
<td>14.99 ± 0.09</td>
<td>31</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>egg† (A &amp; B pooled)</td>
<td>15.50 ± 0.15</td>
<td>35</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>egg† (A only)</td>
<td>15.71 ± 0.24</td>
<td>18</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>feather</td>
<td>9.62 ± 0.17</td>
<td>33</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2009</td>
<td>adult plasma</td>
<td>13.58 ± 0.20</td>
<td>23</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

† all eggs were whole homogenized lipid-free eggs

Trophic positions

Nitrogen ratios of incubating males and females did not differ within any year (t-tests, all p > 0.1), so nitrogen ratios of known-sex and unknown-sex adults were pooled. There was no difference in trophic position between pre-breeding (eggs) and incubating adults in 2008, but all other comparisons were significantly different (Figure 3-1). In 2008,
pre-breeding adults, incubating adults and chicks all had significantly higher trophic positions than 2009 incubating adults, while the chicks in 2008 had significantly higher trophic positions than both pre-breeding and incubating adults. Therefore, 2008 chicks occupied the highest trophic positions, and 2008 terns occupied higher trophic positions than 2009 terns. However, these differences, though statistically significant, are small and may not have large ecological significance.

Unfortunately too few chick-rearing adults (n=2) were caught to include in analyses, however, they had similar trophic positions to the other tern groups (Figure 3-2).

Figure 3-1: Adults and chicks from 2008 foraged at higher trophic positions than incubating adults in 2009 ($H_3=59.7$, $p\leq0.001$; all $Q>4.1$, all $p<0.05$). Chicks occupied a higher trophic position than all adults (all $Q>3.6$, all $p<0.05$). Bars show medians, errors are 25th and 75th quartiles, numbers on top of bars are sample sizes, and different letters show statistically differences.
Trophic positions calculated for Arctic cod muscle and plankton tow groups are shown in Figures 3-2 and 3-3, and clearly showed differences in the trophic position occupied by the different groups in the marine food web at Nasaruvaalik Island. Invertebrates and fish were not corrected for tissue type. For tern diet items sampled in 2008 and 2009, trophic position was similar (small harpacticoid copepods: 2.0 in each year; large harpacticoid copepods: 2.7; calanoid copepods: 3.3 in each year; amphipods: 2.2-4.4; Figures 3-2 and 3-3). Notably, there was no significant difference found between the small harpacticoids in each year, which served as the base for the calculations of trophic positions for terns in each year ($U_{2,2}=2.0, p=1.0$).
Figure 3-2: Trophic positions of plankton tow groups, Arctic Cod muscle, and Arctic Terns collected in 2008 at Nasaruvaalik Island, based on $\delta^{15}$N. Bars show means ± 95% CI; those without error bars are calculated from one sample composed of many pooled individuals. Numbers on top of bars show sample size.
Collectively, the 2009 incubating adults had a wider trophic niche width (i.e., variance in $\delta^{15}$N) than incubating adults in 2007 and 2008, and than 2008 chicks, but were similar to pre-breeding females in both 2007 and 2008. Chicks in 2008 had a similar trophic niche width to incubating adults in 2007 and 2008, but had a narrower niche than the pre-breeders of those years and incubators of 2009. While the pre-breeding adults from 2007 and 2008 had similar niche widths to each other, those from 2008 had a wider niche than incubating adults of 2007 and 2008. However, 2007 pre-breeders also had similar niche widths to incubating adults in all years. Incubating terns in 2007 and 2008 had similar niche widths, but were narrower than the 2009 incubators. To summarize,
pre-breeding females in 2007 and 2008 and incubating adults in 2009 had the widest
niches, while chicks and incubating adults in 2007 and 2008 held the narrowest niches.

All niche width comparisons are shown in Figure 3-4 and statistics for each test are in
Table 3-4.

Figure 3-4: In this figure, niche width is depicted by the error bars that show
variance. The niche width of the Arctic Terns at Nasaruvaalik Island varied by age,
year, and period of the breeding season. Points show the means of each group,
numbers beside points indicate sample size, and different letters above the lines
indicate significant differences.

<table>
<thead>
<tr>
<th>Year</th>
<th>Age or Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>pre-breeding adults (eggs)</td>
</tr>
<tr>
<td>2007</td>
<td>incubating adults</td>
</tr>
<tr>
<td>2008</td>
<td>pre-breeding adults (eggs)</td>
</tr>
<tr>
<td>2008</td>
<td>chicks</td>
</tr>
<tr>
<td>2008</td>
<td>incubating adults</td>
</tr>
<tr>
<td>2009</td>
<td>incubating adults</td>
</tr>
</tbody>
</table>
Table 3-4: Results of $F$-tests comparing sets of two variances (isotopic niche width) of Nasaruvaalik Island terns grouped by year, age and period of breeding season.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>$F$-statistic</th>
<th>numerator degrees of freedom</th>
<th>denominator degrees of freedom</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>07 pre-breeders - 08 chicks</td>
<td>2.8</td>
<td>11</td>
<td>23</td>
<td>0.036  *</td>
</tr>
<tr>
<td>07 incubators - 08 pre-breeders</td>
<td>0.3</td>
<td>15</td>
<td>34</td>
<td>0.019  *</td>
</tr>
<tr>
<td>07 incubators - 09 incubators</td>
<td>0.3</td>
<td>15</td>
<td>22</td>
<td>0.011  *</td>
</tr>
<tr>
<td>08 pre-breeders - 08 incubators</td>
<td>0.3</td>
<td>30</td>
<td>34</td>
<td>&lt;0.001  *</td>
</tr>
<tr>
<td>08 pre-breeders - 08 chicks</td>
<td>0.1</td>
<td>23</td>
<td>34</td>
<td>&lt;0.001  *</td>
</tr>
<tr>
<td>08 incubators - 09 incubators</td>
<td>0.3</td>
<td>30</td>
<td>22</td>
<td>&lt;0.001  *</td>
</tr>
<tr>
<td>08 chick - 09 incubators</td>
<td>8.7</td>
<td>22</td>
<td>23</td>
<td>&lt;0.001  *</td>
</tr>
<tr>
<td>07 pre-breeders - 07 incubators</td>
<td>0.8</td>
<td>15</td>
<td>11</td>
<td>0.732</td>
</tr>
<tr>
<td>07 pre-breeders - 08 incubators</td>
<td>1.3</td>
<td>11</td>
<td>30</td>
<td>0.559</td>
</tr>
<tr>
<td>07 pre-breeders - 09 incubators</td>
<td>0.3</td>
<td>11</td>
<td>22</td>
<td>0.054</td>
</tr>
<tr>
<td>07 pre-breeders - 08 pre-breeders</td>
<td>0.4</td>
<td>11</td>
<td>34</td>
<td>0.084</td>
</tr>
<tr>
<td>07 incubators - 08 chicks</td>
<td>2.2</td>
<td>15</td>
<td>23</td>
<td>0.066</td>
</tr>
<tr>
<td>07 incubators - 08 incubators</td>
<td>1.1</td>
<td>15</td>
<td>30</td>
<td>0.833</td>
</tr>
<tr>
<td>08 pre-breeders - 09 incubators</td>
<td>1.2</td>
<td>22</td>
<td>34</td>
<td>0.674</td>
</tr>
<tr>
<td>08 incubators - 08 chicks</td>
<td>2.2</td>
<td>30</td>
<td>23</td>
<td>0.059</td>
</tr>
</tbody>
</table>
Qualitative observations of tern diet

In 2007 and 2008, pre-breeding and incubating terns were observed bringing large (5+ cm long), dark polychaete worms to the colony, both as courtship display food and as food for mates. However, in 2009 and 2010, I noticed a distinct absence of these large prey items; most prey that terns carried over the colony were small amphipods (<2 cm) or unidentifiable items. In 2010, while I observed many feeding flocks just offshore of the south colony in upwellings, I noted that such foraging activity did not translate into mate feedings until later in the season, that courtship displays occurred only rarely, and that any prey items brought into the colony were small amphipods, small, pale polychaetes, or small fish.

Nutrient allocation

In 2007, only 12 eggs of unknown laying order were available for stable isotope analyses. In 2008, 35 eggs were available, but only first-laid eggs (A-eggs; n=18) were used in analysis because there was a significant difference in δ^{15}N between A and B eggs and I was unable to account for paired eggs in SIAR. Carbon values of 2008 plasma could not be used because 2008 samples were contaminated, leaving the carbon values unusable (see Methods). Therefore, while isotopic ratios of carbon and nitrogen were used in the 2007 model, only nitrogen was used in the 2008 model.

No significant differences were found between the sexes in either isotope (carbon or nitrogen) from feather, whole blood or plasma in either year [MANOVA (2007) and t-
tests (2008), all $p>0.5$], so data from sexed and unsexed birds were pooled. SIAR analyses suggested that breeding terns derived almost all of their nutrients for egg formation in 2007 and 2008 from local, exogenous sources, a pattern consistent across both years (Table 3-5).

Table 3-5: Proportional nutrient contribution to Arctic Tern tissue at Nasaruvaalik Island from local exogenous resources and distant endogenous resources as determined using SIAR, a Bayesian mixing model. In this model, blood acted as a proxy for the local breeding diet, and feathers acted as the distant wintering diet.

<table>
<thead>
<tr>
<th></th>
<th>% Exogenous sources (blood)</th>
<th></th>
<th>% Endogenous sources (feather)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>median $\pm SE$</td>
<td></td>
<td>median $\pm SE$</td>
</tr>
<tr>
<td></td>
<td>Cr. I.$^*$</td>
<td></td>
<td>Cr. I.</td>
</tr>
<tr>
<td>2007</td>
<td>93.20 $\pm$ 0.02</td>
<td>87.91 - 99.61</td>
<td>6.80 $\pm$ 0.02</td>
</tr>
<tr>
<td>2008</td>
<td>97.13 $\pm$ 0.01</td>
<td>94.97 - 99.84</td>
<td>2.87 $\pm$ 0.01</td>
</tr>
</tbody>
</table>

$^*$Cr.I. = Credible interval, a Bayesian equivalent to confidence interval

**Discussion**

Stable isotopes have been used to examine seabird diet in many studies (e.g., Hobson et al. 1994, Bearhop et al. 2006, Bond and Diamond 2010). Here, I used stable isotopes to explore the trophic position and niche width of Arctic Terns in different portions of the breeding season and in different years at one colony. I also examined the nutrient allocation for egg formation in this species at this High Arctic colony. I have shown that there is little difference in trophic position among pre-breeding adults, incubating adults, and chicks in each year, though chicks in 2008 occupied a slightly higher trophic position than adults, and all terns in 2008 occupied a slightly higher trophic position than those in 2009. Incubating terns in 2009 and pre-breeding females in 2007 and 2008
held the widest niche widths, while chicks, along with incubating adults in 2007 and 2008, held the narrowest niche widths. Finally, I found that like Arctic Terns from other locations, these High Arctic-breeding terns used almost exclusively local exogenous resources for egg formation.

**Trophic positioning and niche width**

Though I found statistically significant differences between the chicks and adults in 2008, those differences were small and likely not ecologically significant because the magnitude of the difference in $\delta^{15}$N between chicks and adults was small ($<1\%e$). Growing animals preferentially excrete $^{14}$N at a faster rate than non-growing animals, thereby enriching their tissues with $^{15}$N and increasing the difference of $\delta^{15}$N between the chick plasma and that of their prey, or the diet-to-tissue discrimination factor, $\Delta^{15}$N (Hobson et al. 1993, Martínez del Rio et al. 2009, Sears et al. 2009). In this study, I minimized the growth-related effects by sampling blood from chicks when they were approaching fledging, and all but three of 24 sampled chicks were out of their linear growth phase, approaching their weight and wing growth asymptotes. I also used only the plasma portion of the blood in analyses to ensure the tissue in question had turned over isotopically after hatching and therefore represented the diet provisioned by adults. Furthermore, our qualitative observations support the notion that chicks were fed prey representing higher trophic positions (e.g., Arctic cod), whereas adults were observed feeding on fish only rarely. Despite these efforts and observations, I cannot exclude the possibility that the small difference seen between the chicks and the pre-breeding and
incubating adults in 2008 may be attributable to differences in metabolism or some other minor variation in the ecosystem rather than true ecological differences. Until studies of captive terns have been completed, the methods I have used are the best comparison possible, but I cannot conclude that the differences seen within 2008 are ecologically significant.

The isotopic data from terns in 2008 showed that all were occupying higher trophic positions compared to incubating adults in 2009. Comparing the incubating adults within each year directly, I noted a drop in trophic position from a median of 4.3 to 4.0, a difference of about a third of a trophic level. These differences were slightly larger than the differences observed between adults and chicks within 2008, but may be also subject to variability in the system. However, because these values are derived from the same tissue of the same species at the same period in the breeding season, because I corrected each year's isotopic data with baseline $\delta^{15}N$ data from each respective year, and because the baseline $\delta^{15}N$ values were similar between years, I believe this drop is ecologically valid. Furthermore, and perhaps more importantly, the drop in clutch sizes and hatching success from 2008 to 2009 (Chapter 2) suggests that the observed drop in trophic position is likely real.

The drop in trophic position of the terns from a median of 4.3 in the incubation period of 2008 to 4.0 in 2009 was accompanied by a shift towards a wider niche width during incubation compared to the more narrow focus in both 2007 and 2008. Elsewhere in the Arctic, Arctic Tern diet is composed of Arctic cod and various marine invertebrates (Boekelheide 1980, Węsławski et al. 1994). These shifts in trophic position and niche
width suggest that the birds moved away from a diet rich in cod and higher-level invertebrates towards a more varied diet as they took what prey was available, likely lower-quality food items. Though speculative, it is also possible that the cod and marine invertebrates usually taken by terns were in poorer condition than usual at this stage of the season, thus occupying lower trophic positions and providing less energy to consumers; other forage species are known to vary significantly in condition among years (Diamond and Devlin 2003, Wanless et al. 2005). These ideas are supported by my qualitative observations of food brought to the colony, wherein fewer and smaller prey items were brought in 2009 and 2010 compared to the larger, far more frequently observed prey items of 2007 and 2008.

Pre-breeding females in 2008 had a much wider niche width than incubating adults in 2007 and 2008, and chicks in 2008. Pre-breeding females of 2007 also had a wider niche width compared to 2008 chicks. This suggests that pre-breeding females in both years were less specialised in diet and that the chicks and incubating adults (at least in 2007 and 2008) were more specialised. These differences may be explained by optimal foraging theory (Stephens and Krebs 1986) in the context of the spring-initiated trophic pulse in the Arctic (e.g., Laidre et al. 2008). While pre-breeding females forage for themselves, they do not need to travel back to the colony to eat the prey they gather, nor must they complete foraging within a limited time to relieve their mate from incubation. Therefore, they will be more likely to travel farther and eat easily-obtained prey of all sizes and types. Incubating adults are similar to pre-breeding females in that they eat
prey in situ immediately after capture, however they are time- and colony-constrained. They will therefore likely take the most energy-rich prey that is easiest to capture in the shortest time as the pre-breeders would, but must do so in a smaller area. However, incubating terns have the advantage of foraging later in the Arctic season, when the trophic pulse initiated by the spring sea-ice melt has allowed reproduction and growth of prey, meaning larger prey and greater prey diversity are most likely easier to obtain than they were during pre-breeding. Once chicks hatch, adults will likely take the large, high-energy prey they were eating during incubation to their chicks: since adults foraging to provision chicks can only carry one large or occasionally several small prey items in their bill at once, they need to bring each item back to the colony after capture. Adults likely choose only the largest prey to take to the chicks so they may reduce energy expenditure of transit between the colony and foraging locations (Diamond 1983). The narrow niche width of chicks implies that chick-provisioning adults made similar prey selections to take back to the colony, resulting in the chicks, as a group, having a much more specialised diet than pre-breeders, akin to incubating adults. From these arguments, I further suggest that if I had been able to gather samples from chick-rearing adults as intended, we should see an increase in niche width of the adults during chick-rearing, indicating a difference in chick and adult diet during that period.

Nutrient allocation

At Nasaruvaalik Island, Arctic Terns derived over 93% of the nutrients for egg formation from sources local to the breeding colony. This is consistent with findings
Arctic Terns breeding at this High Arctic location occupied a high trophic position, as would be expected of seabirds as top predators within a food web. Notably however, this is one of the first studies to use stable isotopes to compare the diet of a species of seabird within different stages of the breeding season that includes information about the chick-rearing portion of the season. It provides detailed information about the diet of surface-feeding central-place foragers throughout their breeding season, and suggests that despite being located near several recurrent polynyas that provide reliable access to food supplies (see Chapter 2), the diet of these birds varies significantly within and between breeding seasons. In demonstrating these temporal differences, I have confirmed this non-destructive technique can track responses of terns to local food supplies through time. This is a technique that could be replicated in short visits to breeding colonies, and would be a fairly straightforward addition to many monitoring programs.
This study also provides the first verification that Arctic Terns breeding in the High Arctic of Canada are like their conspecifics elsewhere in requiring locally-derived nutrients for egg formation, as expected. This emphasizes the importance of access to high quality food to the terns on arrival at the breeding colony, and underscores the negative implications that the predicted climate change-related, predator-prey mismatch would have on High Arctic tern colonies, as well as changes to the food web that may result as development of the Arctic proceeds.

**Literature cited**


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Systat Software. 2008. SigmaPlot version 11.2.0.11.


Chapter 4: Machias Seal Island and Nasaruvaalik Island: a comparison of Arctic Tern (Sterna paradisaea) breeding ecology in the High Arctic and Boreal oceanographic zones

Abstract

Arctic Terns have been studied in detail at the southern edge of their breeding range in the Boreal oceanographic zone, but have been studied very little in the two other oceanographic zones they breed in, the Low and High Arctic. Since seabirds breeding in different oceanographic zones may differ in their breeding biology, it is unknown if knowledge gained about Arctic Terns from the Boreal oceanographic zone studies are applicable to those breeding in the High Arctic. To assess this, I compared the breeding biology of a colony in the Boreal oceanographic zone and a colony in the High Arctic oceanographic zone. I found that the High Arctic colony was generally more successful than the Boreal colony. I also found that the High Arctic colony had higher clutch sizes than the High Arctic mean, while the Boreal colony had lower clutch sizes than the Boreal mean. I concluded that local environmental factors are likely more important to the productivity of a colony than the oceanographic zone it is in. I also concluded that knowledge gathered from Boreal or other Arctic Tern colonies cannot be applied to High Arctic colonies.
Introduction

Seabird species often have different breeding tactics and success in different oceanographic zones, related to physical features of their environment (Gaston et al. 2005a, Hipfner et al. 2005, Garthe et al. 2007). An extreme example is South American Terns (*Sterna hirundinacea*), which have a completely different breeding season depending on which oceanographic current their colony lies within (Faria et al. 2010). Additionally, in several seabird families, including the tern subfamily (Sterninae), breeding success varies with latitude; both breeding success and latitude correspond to sea surface temperature (Sandvik et al. 2008), which is itself an oceanographic feature. Because Arctic Terns (*Sterna paradisaea*) breed in three oceanographic zones spanning more than 40° of latitude, they may differ in their breeding ecology in different zones across their breeding range, and are thus an excellent candidate species for study.

Arctic Terns are small seabirds with a global range. They spend the northern winter in the Southern Ocean where different breeding populations appear to mix (Egevang et al. 2010). In the spring, they migrate back to their breeding colonies, which range from 42°N along the coast of North America to 84°N on the coast of Greenland (Hatch 2002). Arctic Tern colonies have been studied extensively in the Boreal oceanographic zone, but most of their breeding population lies within the marine Low Arctic (also called marine Subarctic) and High Arctic zones (Dunbar 1953, 1972, Birdlife International 2011). While some studies have been undertaken outside the Boreal zone (Boekelheide 1980, Kirkham 1986, Węsławski et al. 1994, 2006, Egevang and Frederiksen 2011), few
have made comparisons between zones. As a result, little is known about how breeding Arctic Terns in the High Arctic of Canada differ from those in the Boreal zone.

To examine this potential difference, I compared the breeding ecology and diet of Arctic Terns nesting in the Canadian High Arctic on Nasaruvaalik Island, approximately 130 km northwest of Resolute Bay, Nunavut, Canada, to those breeding on Machias Seal Island at the entrance to the Bay of Fundy in eastern Canada. In 2004 and 2005 the Machias Seal Island tern colony experienced extremely low productivity, while in 2006, though eggs were laid, few hatched, and none survived; all subsequent nesting attempts have been unsuccessful (A.W. Diamond pers. comm.). Low food availability combined with increased predation from gulls appear to have caused this decline and abandonment (Gaston et al. 2009a, A.W. Diamond pers. comm.).

On Nasaruvaalik Island, during this study, I witnessed a similar pattern of decline and abandonment. In 2007 and 2008, the tern colony had large clutch sizes and high hatching success, but these were reduced in 2009, and even more so in 2010 when predation increased dramatically, leading to eventual abandonment. A storm occurring in late incubation (early chick-hatching) may have contributed to the abandonment in 2010, however because few chicks had hatched at the time of the storm and eggs are thermally robust (Bennett and Dawson 1979), I do not believe it was a major contributor. The latter two years (2009 and 2010) were also marked by evidence of low food supplies (Chapters 2 and 3).

In this chapter, I compared Arctic Tern breeding parameters on Nasaruvaalik Island and Machias Seal Island, including all years, and hence all variation, within each site for
overall comparisons. I also compared the sites within their "good" and "poor" years. It should be noted that there may be some bias to the overall comparisons, because there were only four years of data from Nasaruvaalik Island, and twelve from Machias Seal Island. As it turned out, this meant that half of the years at Nasaruvaalik Island were considered to be years of poor tern success. Therefore, parameters from that site in overall comparisons may be skewed more negatively than may be typical for Nasaruvaalik Island.

The objective of this study was to highlight similarities and differences between Arctic Terns breeding in oceanographic zones near the northern and southern limits of their breeding latitudes. Specifically, as outlined in Chapter 1, I predicted that the timing of breeding parameters would be later at the Arctic colony, that the adults at the Arctic colony would be larger, and that the daily feeding rates at the Arctic colony would be higher, and show less of a diel pattern than their southern counterparts. However, I examined other features of the breeding populations at each site, and made overall comparisons between High Arctic colonies, and those in other oceanographic zones. These comparisons will allow us to discern whether generalizations made from the many long-term studies of terns in Boreal zones are applicable to those nesting in the High Arctic, and perhaps even allow us to better define critical breeding habitat for Arctic Terns.
Methods

Study sites

The two study sites are Nasaruvaalik Island, Nunavut (NI; 75°49.5'N, 96°18.8'W) and Machias Seal Island, New Brunswick (MSI; 44°30'N, 67°06'W). Nasaruvaalik Island is described in detail in Chapter 2, and Machias Seal Island is described in Diamond and Devlin (2003). Other seabird species breeding on Machias Seal Island include Common Terns (*Sterna hirundo*), Razorbills (*Alca torda*), Atlantic Puffins (*Fratercula arctica*), and, in smaller numbers, Common Murres (*Uria aalge*) and Leach's Storm-petrels (*Oceanodroma leucorhoa*). Great Black-backed and Herring Gulls (*Larus marinus* and *L. argentatus* respectively) are major predators of tern eggs and chicks on the island. Though they have bred for a number of years on a small islet called Gull Rock immediately beside Machias Seal Island, they have recently begun breeding in greater numbers there and on the island itself (A. W. Diamond pers. comm.).

Most breeding data were available from Machias Seal Island from 1995-2006, and from Nasaruvaalik Island from 2008-2010. Some data, however, were available only from a subset of these or additional years (Table 4-1).
Table 4-1: Data were not available from each of the two study sites, Nasaruvaalik Island and Machias Seal island, for the same years. Below are the years in which data were collected for each parameter compared between sites.

<table>
<thead>
<tr>
<th></th>
<th>Nasaruvaalik Island</th>
<th>Machias Seal Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest initiation</td>
<td>2008-2010</td>
<td>1995-2006</td>
</tr>
<tr>
<td>Incubation period</td>
<td>2008-2010</td>
<td>1995-2006</td>
</tr>
<tr>
<td>First egg volume index</td>
<td>2008-2010</td>
<td>2000-2005</td>
</tr>
<tr>
<td>Clutch size</td>
<td>2002-2010</td>
<td>1995-2006</td>
</tr>
<tr>
<td>Chick growth rates</td>
<td>2008 &amp; 2010</td>
<td>1995-2005</td>
</tr>
<tr>
<td>(weight and wing)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chick feeding rate</td>
<td>2007-2008</td>
<td>1995-2005</td>
</tr>
<tr>
<td>Adult morphometrics</td>
<td>2007-2010</td>
<td>1999-2006</td>
</tr>
<tr>
<td>(including weight)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Breeding parameters

All Machias Seal Island methods are described in detail by Diamond (2011), and Devlin et al. (2004). For further clarification, I consider the period of linear growth in Arctic Tern chicks to be between age five and fifteen days (Bond et al. 2006). Breeding success is defined here as the number of chicks fledged per egg laid, and chicks surviving to 20 days of age were considered to have fledged (Hatch 2002).

All Nasaruvaalik Island methods were described in detail in Chapter 2, with one exception. The calculation of chick feeding rate in this chapter differs from Chapter 2 in the additional detail of time-of-day. At Nasaruvaalik Island, the sun does not set during the breeding season, so there is daylight throughout the 24-hour period; accordingly, feeding watches were conducted around the clock. On Machias Seal Island, terns do not feed chicks during nocturnal hours, but return to the island to roost (Paquet 2001). To enable comparisons to Machias Seal Island, chick feeding watches on Nasaruvaalik
Island were categorised into nocturnal and diurnal hours. Nocturnal hours were considered those hours after sunset (21:00) and before sunrise (5:30) in July and August at Machias Seal Island. Poor weather on Nasaruvaalik Island prevented many watches through the nocturnal hours, which led to a small sample size during these times.

**Statistical analyses**

For all statistical tests, alpha was set at 0.05. Normality and equality of variance were determined by visual inspection of residuals. The factors for all two-way ANOVAs used were site and year-type (good and poor). All analyses, including the data exploration portion of the analyses, were conducted in R (R Development Core Team 2011) or SigmaPlot 11 (Systat Software 2008).

**Data exploration**

Because I was interested in the overall difference between sites, I pooled the data collected for each parameter at each site among all years to incorporate all of the variation among years at each site. I then made 'overall' comparisons between sites using these pooled data. Because both sites featured a period of good years, decline through poor years, and abandonment, I also wanted to conduct comparisons between sites in their respective 'good' and 'poor' years. On Nasaruvaalik Island, it was clear that 2007 and 2008 were good years for the terns, while 2009 and 2010 were poor ones (Chapter
2). To determine which years I would consider good and poor on Machias Seal Island, I tested among years for differences in nest initiation date, incubation period, first-laid egg volume index (as calculated in Chapter 2), chick weight and wing growth rates, and chick feeding rates using Kruskal-Wallis rank-based tests with Dunn's multiple comparisons if significance was detected. For adult weight, I used a one-way ANOVA among years followed by multiple t-tests using the Holm-Sidak method of family-wise error control. For clutch size, hatching success (number of chicks hatched per egg laid), and breeding success (number of chicks fledged per egg laid), I fit generalized linear models to the data using binomial logit links, first converting hatching and breeding successes to proportional success and failure. These were followed by Tukey's multiple comparisons.

A decline from 1995 to 2005 on Machias Seal Island was visible in many of the results of the initial tests, such as clutch size and hatching success, but there was no clear delineation between good years and poor that was observable in almost every parameter as was seen on Nasaruvaalik Island. The only measurement that showed an abrupt decline prior to abandonment on Machias Seal Island was breeding success. Parameters such as nest initiation date and clutch size may influence breeding success (Cairns 1987), and may be used as proxies when breeding success cannot be measured directly, as was the case on Nasaruvaalik Island. However, the abrupt decline in breeding success was the best indicator of the change from good to poor years. Therefore, I have used breeding success as the indicator of good and poor years on Machias Seal Island.
Breeding success on Machias Seal Island declined abruptly between 2003 and 2004 and remained low in 2005 before dropping to zero in 2006 (Figure 4-1). Based on these data, I consider the years from 1995 to 2003 inclusive as good years for the Arctic Tern colony at Machias Seal Island, and 2004 to 2005 (or 2006 when data are available) as poor years.

![Breeding success chart](image)

Figure 4-1: Breeding success at Machias Seal Island dropped significantly in 2004, and has remained low (or zero) ever since. Bars show proportion of chicks fledged per egg laid, error is 95% confidence limit. Shared letters above bars denote lack of significance, and numbers above bars are the number of eggs laid in plots each year.
Nests, eggs and hatching success

All dates were measured using the ordinal system, with 1 January as day 1. Nest initiation, incubation period and egg volume comparisons were made using first-laid eggs. Overall differences between the colonies in the onset of laying as well as incubation period were compared with separate Mann-Whitney rank sum tests. To allow comparisons of good years and poor years between colonies, nest-initiation data were centred on the mean of each site to eliminate the approximate one-month difference in nest initiation between the two sites. As centred nest-initiation data did not approximate normality, they were square-root transformed after first adding the minimum centred value to each centred value to obtain positive numbers; incubation period approximated normality, so original data were used. Comparisons between colonies in good years and poor were made with two-way ANOVAs followed by Holm-Sidak-corrected multiple comparisons.

To compare synchrony of lay dates and incubation periods at each site, variances of nest initiation and incubation period were tested using Fligner-Killeen tests between sites overall, as well as between sites during good years and poor.

To compare incubation periods in relation to nest initiation date within Machias Seal Island terns, I divided incubation period into categories (in number of days: <21, 22, 23, 24, 25+), and compared it to nest initiation date (centred on the annual mean, pooled among years) using a Kruskal-Wallis test followed by Dunn's multiple comparisons. These categories differ from those used on Nasaruvaalik Island because terns on Machias Seal Island had a wider range of incubation periods. Nasaruvaalik Island
incubation periods were examined in relation to nest initiation date in the same way in good years and poor, but incubation period categories remained the same as in Chapter 2.

To compare egg sizes between sites, I calculated an egg volume index for each egg using the equation in Chapter 2:

\[
\text{Volume index} = \text{length} \times \text{breadth}^2/1000
\]

For overall comparisons, I pooled egg volume indices within each site. For a separate test to compare between sites among good years and poor, I pooled egg volume indices within good years and poor at each site; comparisons between sites and year-types were made using a two-way ANOVA followed by multiple comparison \(t\)-tests using the Holm-Sidak method of family-wise error rate control.

To assess egg volume index at Machias Seal Island for possible trends with advancing lay date, I first centred nest initiation dates on annual means to remove any trend in lay dates among years. I then performed a regression of centred lay dates against egg volume indices including all years at each site, and then again within good years and within poor.

I analysed clutch size and hatching success overall between the sites, and clutch size only was then compared in good years and in poor by fitting generalized linear models to the data using binomial logit links. These were followed by Tukey's multiple comparisons. Comparisons between good years and poor year were not made for hatching success since the good and poor years on Machias Seal Island were defined by
breeding success. Since breeding success is dependent on hatching success, the
correlation between the two is too close to make any comparisons of hatching success
between good and poor years meaningful.

Chick feeding and growth rates

To compare chick feeding rates over all times of day observed at each site, I analysed
feeding rates from all observations from each site. I also compared only diurnal feeding
rates from Nasaruvaalik to diurnal feeding rates on Machias Seal. The comparisons of
all times of day and diurnal-only were made overall and within good years by pooling
data among all years and within good years only. Each comparison was made using
Mann-Whitney rank sum tests. Poor years could not be compared between sites because
feeding rates were not observed during the poor years on Nasaruvaalik Island. However,
feeding rates in good years and poor were compared within Machias Seal Island using a
Mann-Whitney rank sum test.

I compared chick weight and wing growth rates between the sites overall and within
each year-type using two-way ANOVAs for each measurement type, followed by
multiple comparison t-tests using the Holm-Sidak method of family-wise error rate
control. In 2010 on Nasaruvaalik Island, all chicks died prior to the end of the linear
period of growth, but 2010 was the only poor year in which growth rates were
measured. Since chicks that die before leaving the colony may have slower growth rates
than those that fledge (Watanuki 1988), the comparisons between the sites in poor years
may be skewed towards higher growth rates at Machias Seal Island for that reason alone. I could not exclude chicks that died prior to leaving the colony from Nasaruvaalik in 2010, but I wished to account for differences in growth rates when chicks die prior to fledging. I therefore compared 2010 chick growth rates from Nasaruvaalik Island to 2005 chick growth rates from Machias Seal Island, where enough chicks survived to provide some growth rates, but 50% of those died prior to fledging (mean chicks/nest that survived to day 20 ± SD for 2005: 0.05 ± 0.30). Growth rates from 2004 were also included in the comparisons between sites in poor years; on Machias Seal, 0.30 ± 0.50 chicks/nests survived to day 20 in that year. Comparisons between 2010 on Nasaruvaalik and 2005 on Machias Seal were conducted using a Mann-Whitney rank sum test.

Adult body condition and morphometrics

I used body weight as a proxy of body condition of terns on Machias Seal Island, as no linear body measurements were correlated with body weight (Chapter 2, Peig and Green 2009). To make the overall comparison of adult body weight between the two sites, I first considered the matter of recaptured adults on Machias Seal Island, where several terns were recaptured in multiple years, but many of the first captures took place in good years (1995-2003). Because using only the first capture weights would bias the mean adult tern weight at the site towards good years, to avoid pseudoreplication, the mean weight of each tern that was recaptured in multiple years was calculated. Each individual tern thus had one value for weight. Terns on Nasaruvaalik Island were not
recaptured in different year-types, so first capture weight was used at that site (Chapter 2). A \( t \)-test was used for the overall comparison of tern body weight between sites.

For between-site comparisons within good years and poor years, I again first considered the recaptured terns on Machias Seal Island. To avoid pseudoreplication and be consistent with the overall comparison, I calculated the mean weight of each tern within each year-type in which it was caught [i.e. if tern 802-00001 was caught in 1998, 2002, 2004 and 2005, I calculated the mean of its 1998 and 2002 weights (good years), and another mean of its 2004 and 2005 weights (poor years)]. Any terns that were caught in both good years and poor years were then compared within Machias Seal Island using a one-way, repeated-measures ANOVA. Terns that were caught within only one year-type (good or poor) had one value each; body weight of these terns were compared within Machias Seal Island between year-types using a \( t \)-test. Since the outcome of the repeated-measures ANOVA and the \( t \)-test did not differ, I used only those terns that were caught in only one year-type to simplify further calculations. I compared body weight of incubating adult terns among years and between sites using a two-way ANOVA followed by multiple comparison \( t \)-tests using the Holm-Sidak method of family-wise error control.

To analyse structural body measurements, I first compared measurements between good and poor years within each site by conducting a MANOVA on a subset of non-covarying measurements for which there were data in both year-types (wing, head and tail fork). I then conducted a series of post-hoc \( t \)- or Mann-Whitney tests on each measurement (wing, tarsus, culmen, bill depth, head, tail streamer, R5 and tail fork),
correcting for family-wise error using the Holm-Bonferroni method. To compare body measurements between sites, I again conducted a MANOVA on non-covarying measurements that included measurements that did not differ between year-type within each site (tarsus, head and fork). I then conducted a series of post-hoc tests: I conducted \( t \)- or Mann-Whitney tests for all measurements except wing and tail streamer, which differed within Nasaruvaalik Island between good and poor years. For wing and tail streamer, I conducted two separate two-way ANOVAs followed by post-hoc \( t \)-tests. I applied the Holm-Bonferroni method of family error rate control to all \( t \)-test results.

**Trophic positioning and niche width**

At Nasaruvaalik Island, I assessed Arctic Tern diet at the breeding colony using stable isotope analyses of blood plasma and whole, lipid-free homogenized eggs, and determined the trophic positioning of adults in each period of the breeding season (Chapter 3). Isotopic ratios from yolk, albumen and whole blood at Machias Seal Island in 2005 and 2006 were available from Bond and Diamond (2010), but because local food webs probably differ in baseline isotope ratios, direct comparisons between sites were not possible (Vander Zanden and Rasmussen 1999). However, it was possible to compare the relative trophic position of adult terns in different periods of the breeding season between sites. To do this, I made some assumptions. It is unlikely that the trophic position of the base of the food web at Machias Seal Island changed \( \delta^{15}N \) values within the 2-month period that contains the pre-breeding and incubation portions of the breeding season. Though it is possible that the base changed from 2005 to 2006, as they
were both poor years it is less likely than if the years spanned good and poor. Hence, I assumed that the base did not change between years. Comparing the $\delta^{15}N$ values of each tissue-type at Machias Seal Island can provide information about the relative trophic position of adult terns in the pre-breeding and incubation periods of the breeding season.

The diet of the pre-breeding female is represented in eggs; Arctic Terns arrive at the colony at least two weeks prior to nest initiation, and eggs are formed with local, exogenous resources (Chapter 3, Bond and Diamond 2010). Specifically, yolk incorporates the diet of the pre-breeding female from approximately eight days prior to laying, while the albumen will incorporate the last few hours (Hobson 1995). To ensure the entire pre-breeding period was represented, I used yolk in my analysis. Whole blood, in which isotope ratios turn over within 2-4 weeks (Hobson and Clark 1992a), was collected towards the end of incubation, so reflects the diet of the incubating adults. To determine if pre-breeding females and incubating terns differed in their trophic positioning, $\delta^{15}N$ values (corrected for diet-tissue discrimination factors, $\Delta N$; see Chapter 3) of Machias Seal Island tern lipid-free yolk and whole blood were compared using a $t$-test.

Because different tissues were collected at Nasaruvaalik Island (blood plasma, homogenized eggs) and Machias Seal Island (whole blood, separated egg yolk and albumen), I did not make comparisons of niche width between sites. Different tissues turn over at different rates (Hobson and Clark 1992a, 1993) and would represent niche width over different periods.
Oceanographic zone comparisons

For comparisons between oceanographic zones, data from the literature were gathered from other Arctic Tern breeding colonies in all oceanographic zones (High Arctic, Low Arctic and Boreal zones). Clutch size was the only parameter available from all zones. Multiple records from any one site, regardless of year, were pooled to provide one value for each site, thereby minimizing pseudoreplication. Nasaruvaalik Island and Machias Seal Island were included in their respective zones for the initial test, and I used a one-way ANOVA to compare clutch size among zones. A second test was conducted to determine if each of the two sites in this study differed from their zone. To avoid pseudoreplication in this second test, clutch size at each study site was excluded from calculations of the respective oceanographic zone means and standard errors. For this second test, I used a one-way ANOVA to compare clutch size among zones and my two sites, where the sample size of the oceanographic zone was comprised of sites, while each year at the two study sites was considered a sample. Both ANOVAs were followed by multiple comparison $t$-tests using the Holm-Sidak method of family-wise error rate control.

In single-test graphics, differing letters above bars or above points on graphs denote significant differences, while bars or points topped with the same letters are not significantly different. In multiple-test graphics, an asterisk over a pair of bars or boxes indicates a significant difference between the pair, and absence of the asterisk indicates no difference. Numbers above bars, boxes or alongside points are sample sizes.
Results

Nests: initiation and incubation period

Breeding terns were more synchronous in their nest initiation and incubation period at Nasaruvaalik Island compared to Machias Seal Island overall, in good years and poor (Figures 4-2 and 4-3; all median $\chi^2 > 5.1$, all $p < 0.02$).

Figure 4-2: Variances of nest initiation dates of Arctic Terns were higher at Machias Seal Island than at Nasarvuaalik Island in every time period measured between sites. Boxes represent the 25th and 75th percentiles, whiskers show the 10th and 90th percentiles, and circles show outliers. Horizontal lines within boxes show medians, and numbers are sample sizes. Asterisks in each panel denote significant differences between the sites.
Terns initiated nests on Machias Seal Island significantly earlier (29 days) than on Nasaruvaalik Island (Table 4-2). Centered nest initiation dates show that in good years, terns at Machias Seal Island nested significantly earlier than their site mean (Table 4-5), while in poor years, they nested significantly later; the opposite was true at Nasaruvaalik Island (Table 4-6). This translated into a significantly earlier nest initiation at Machias Seal Island in good years compared to Nasaruvaalik Island, while in poor years, Machias Seal Island terns were significantly later than Nasaruvaalik terns in onset of
laying, both with respect to the overall average of each site (Tables 4-3 & 4-4; Figure 4-4).

Within both Nasaruvaalik and Machias Seal Islands, terns incubated for similar lengths of time in each year-type (Tables 4-5 & 4-6). Overall, and within good years and poor, Nasaruvaalik Island terns incubated for a significantly shorter period than Machias Seal Island terns: almost one full day, or 5% of the incubation period (Tables 4-2 to 4-4; Figure 4-5).

Figure 4-4: Arctic Tern nest initiation, considered in comparison to the overall mean for each site (0 on the y-axis), was significantly later on Nasaruvaalik Island than on Machias Seal Island in good years, but significantly earlier in poor years. Bars show means ± 95% CI, numbers above or below bars are sample sizes, and asterisks in a panel denotes a significant difference between sites.

Within both Nasaruvaalik and Machias Seal Islands, terns incubated for similar lengths of time in each year-type (Tables 4-5 & 4-6). Overall, and within good years and poor, Nasaruvaalik Island terns incubated for a significantly shorter period than Machias Seal Island terns: almost one full day, or 5% of the incubation period (Tables 4-2 to 4-4; Figure 4-5).
Arctic Terns that initiated nests later in the season had a shorter incubation period on Machias Seal Island overall \((H_5=54.9, p<0.001; \text{largest difference between medians}=4.2\text{ days}, Q=6.3, p<0.05)\), during good years \((H_5=64.7, p<0.001; \text{largest difference between medians}=5\text{ days}, Q=6.2, p<0.05)\) and in poor years \((H_5=48.0, p<0.001; \text{largest difference between medians}=10\text{ days}, Q=6.0, p<0.05; \text{Figure 4-6})\). This trend was also apparent at Nasaruvaalik Island overall (Chapter 2).

Figure 4-5: Breeding Arctic Terns had a shorter incubation period on Nasaruvaalik Island than on Machias Seal Island in all year types. Bars show means ± 95% CI. numbers above bars show sample sizes, and asterisks in each panel denotes a significant difference between sites.
Eggs: volume, clutch size and hatching success

Terns did not lay eggs of significantly different volumes in good years or poor within each site, nor did they lay eggs of different volumes at each site (Tables 4-2 to 4-6).

On Machias Seal, terns that initiated nests earlier in poor years had eggs of greater volume than later-laid eggs by about 2.4 index points (Figure 4-7; \( t = -2.394, \beta = -0.101, p = 0.017 \)). No relationship between nest initiation date and egg volume indices were
found overall or in good years on Machias Seal Island, and no relationship was found overall, in good years or poor years at Nasaruvaalik Island.

At both sites, terns laid larger clutches in good years than poor (Tables 4-5 and 4-6; Figure 4-8). Between sites overall, as well as during good years and poor, Nasaruvaalik Island terns laid more eggs than terns nesting at Machias Seal Island (Tables 4-2 to 4-4).

Figure 4-7: During poor years on Machias Seal Island, Arctic Tern first-laid egg volume index showed a weak trend of decreasing volume with later lay dates.
Like clutch size, hatching success (number of chicks hatched per egg laid) was significantly higher at Nasaruvaalik Island overall (Figure 4-9).
**Chick feeding and growth rates**

Comparisons of hourly chick feeding rates on Nasaruvaalik Island and Machias Seal Island showed no differences overall during diurnal watches (Table 4-2), nor in good years between sites (Table 4-3). On Nasaruvaalik Island, the differences between diurnal and nocturnal watches were not significant, but with a sample size of only seven nests, the power to detect a difference was extremely weak (Chapter 2). On Machias Seal Island, hourly chick feeding rates were not significantly different in good years compared to poor years (Table 4-5).
At both sites, weight and wing growth rates were significantly lower in poor years than in good years (Tables 4-5 and 4-6). Weight growth rates showed no difference between sites overall (Table 4-2), but in poor years, Machias Seal Island terns increased weight at a significantly faster rate than Nasaruvaalik Island chicks (Table 4-4). In good years, Nasaruvaalik Island chicks increased weight significantly faster than those of Machias Seal Island (Table 4-3; Figure 4-10). Wing growth rates showed no differences between sites overall, in good years or poor though power to detect a difference was very low (overall: $t=-1.2$, $p=0.2$, $n_{NI}=17$, $n_{MSI}=331$, power to detect a difference of 0.6g/day at $\alpha=0.05$ was 9%; good: $t=0.9$, $p=0.4$, power to detect a difference of 0.5g/day at $\alpha=0.05$ was 5%; poor: $t=0.6$, $p=0.5$, power to detect a difference of 0.6g/day at $\alpha=0.05$ was 5%). Comparing the two years in which most chicks died before fledging at each site, there were no differences between 2010 at Nasaruvaalik Island and 2005 at Machias Seal Island in either weight or wing growth rates.
Adult body condition and morphometrics

Body weight, as a proxy for condition, of Machias Seal Island terns was significantly higher overall than Nasaruvaalik Island terns. Within Nasaruvaalik Island, terns in good years were significantly heavier than terns in poor years. At Machias Seal Island, no change in weight was seen between good years and poor years either in the group of terns captured in one year-type or in the group of terns recaptured in both year-types. Comparing between sites during good years, terns on Nasaruvaalik Island had
significantly higher body weight compared to those on Machias Seal Island, while in poor years, Machias Seal Island terns were significantly heavier (Figure 4-11).

![Bar chart showing adult weight comparison between Machias Seal Island (MSI) and Nasaruvaalik Island (NI) in good and poor years.](image)

Figure 4-11: Arctic Terns at Machias Seal Island were significantly heavier than Nasaruvaalik Island terns overall and in poor years; in good years, the reverse was true. Bars show means ±95% CI, numbers above bars show sample size, and the presence of an asterisk in a panel indicates a significant difference between sites in those year-types.

The results for other adult morphometrics varied. Terns had significantly shorter wing and tail streamer lengths in poor years than in good years on Nasaruvaalik Island. There were no differences in structural measurements between good and poor years on Machias Seal Island, though there were no measurements for tarsus, culmen and bill depth in poor years from that site. Comparing between sites, terns had shorter tail streamers at Nasaruvaalik Island than at Machias Seal Island in poor years only, and wing length did not differ between sites. Terns had statistically significantly deeper bills
at Nasaruvaalik Island, though the difference was probably trivial biologically (NI_{median} – MSI_{median} = 0.10mm). All other measurements were significantly smaller at Nasaruvaalik Island than at Machias Seal Island (Table 4-7).
Table 4-2: Summary data and test statistics of each Arctic Tern breeding parameter compared between sites overall. Test statistics are denoted by letters: $U = \text{Mann-Whitney rank sum test}; z = \text{generalized linear model}; t = \text{t-test}; \chi^2 = \text{chi-squared test}$. Significant differences are marked with an asterisk at the end of each row. Medians are reported only for parameters for which non-parametric tests were used.

<table>
<thead>
<tr>
<th>Overall comparisons</th>
<th>Nasaruaalik Island</th>
<th>Machias Seal Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest initiation (date)</td>
<td>6 July ± 0.23</td>
<td>7 June ± 0.22</td>
</tr>
<tr>
<td></td>
<td>9 June; 7 Jul; 8 Jul</td>
<td>3 Jun; 12 Jun</td>
</tr>
<tr>
<td>Incubation period (# days)</td>
<td>21.5 ± 0.10</td>
<td>22.0 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>21.0; 22.0</td>
<td>21.0, 24.0</td>
</tr>
<tr>
<td>First egg volume index</td>
<td>35.04 ± 0.13</td>
<td>34.95 ± 0.09</td>
</tr>
<tr>
<td></td>
<td>35.0; 35.2</td>
<td>34.9; 35.0</td>
</tr>
<tr>
<td>Clutch size (# eggs)</td>
<td>1.8 ± 0.02</td>
<td>1.5 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>3 Jul, 8 Jul</td>
<td>3 Jun, 12 Jun</td>
</tr>
<tr>
<td>Hatching success (# chicks/egg)</td>
<td>68.36%</td>
<td>53.86%</td>
</tr>
<tr>
<td></td>
<td>414</td>
<td>2161</td>
</tr>
<tr>
<td>Clutch size (# eggs)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chick weight growth rate (g/day)</td>
<td>4.77 ± 1.50</td>
<td>5.05 ± 0.15</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>307</td>
</tr>
<tr>
<td>Chick wing growth rate (mm/day)</td>
<td>6.69 ± 0.60</td>
<td>7.34 ± 0.12</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>331</td>
</tr>
<tr>
<td>Chick feeding rate (# feeds/nest/hr)</td>
<td>2.4 ± 0.57</td>
<td>1.6 ± 0.11</td>
</tr>
<tr>
<td></td>
<td>0.8; 2.7</td>
<td>0.7; 1.9</td>
</tr>
<tr>
<td>Diurnal chick feeding rate (# feeds/nest/hr)</td>
<td>2.8 ± 0.70</td>
<td>1.6 ± 0.11</td>
</tr>
<tr>
<td></td>
<td>0.8; 2.9</td>
<td>0.7; 1.9</td>
</tr>
<tr>
<td>Nocturnal chick feeding rate (# feeds/nest/hr)</td>
<td>1.1 ± 0.25</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>1.2; 0.5, 1.4</td>
<td>-</td>
</tr>
<tr>
<td>Adult weight (g)</td>
<td>105 ± 0.42</td>
<td>108 ± 0.25</td>
</tr>
<tr>
<td></td>
<td>367</td>
<td>926</td>
</tr>
</tbody>
</table>

Test statistic: $U = 4936 <0.001 *$  
Test statistic: $U = 41567 <0.001 *$  
Test statistic: $\chi^2 = 29.1 <0.001 *$  
Test statistic: $t = -4.7 <0.001 *$
Table 4-3: Summary data and test statistics of each Arctic Tern breeding parameter compared between sites within good years. Test statistics are denoted by letters: $U =$ Mann-Whitney rank sum test; $z =$ generalized linear model; $t =$ $t$-test; $\chi^2 =$ chi-squared test. Significant differences are marked with an asterisk at the end of each row. Medians are reported only for parameters for which non-parametric tests were used.

<table>
<thead>
<tr>
<th>Good years</th>
<th>Nasaruvaalik Island</th>
<th>Machias Seal Island</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Centred nest initiation</td>
<td>Incubation period (# days)</td>
</tr>
<tr>
<td></td>
<td>mean ± SE</td>
<td>median; 25%, 75%</td>
</tr>
<tr>
<td>Nasaruvaalik Island</td>
<td>0.5 ± 0.28</td>
<td>172</td>
</tr>
<tr>
<td>Machias Seal Island</td>
<td>21.3 ± 0.11</td>
<td>90</td>
</tr>
<tr>
<td>Good years</td>
<td>34.88 ± 0.17</td>
<td>244</td>
</tr>
<tr>
<td>Good years</td>
<td>1.8 ± 0.02</td>
<td>688</td>
</tr>
<tr>
<td>Good years</td>
<td>7.24 ± 0.53</td>
<td>13</td>
</tr>
<tr>
<td>Good years</td>
<td>7.31 ± 0.63</td>
<td>13</td>
</tr>
<tr>
<td>Good years</td>
<td>2.4 ± 0.57</td>
<td>1.3; 0.8, 2.7</td>
</tr>
<tr>
<td>Adult weight (g)</td>
<td>110 ± 0.70</td>
<td>122</td>
</tr>
</tbody>
</table>
Table 4-4: Summary data and test statistics of each Arctic Tern breeding parameter compared between sites within poor years. Test statistics are denoted by letters: $U =$ Mann-Whitney rank sum test; $z =$ generalized linear model; $t =$ $t$-test; $\chi^2 =$ chi-squared test. Significant differences are marked with an asterisk at the end of each row. Medians are reported only for parameters for which non-parametric tests were used.

<table>
<thead>
<tr>
<th>Poor years</th>
<th>Nasaruvaalik Island</th>
<th>Machias Seal Island</th>
<th>test statistic</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$mean \pm SE$</td>
<td>$n$</td>
<td>$mean \pm SE$</td>
<td>$n$</td>
</tr>
<tr>
<td>Centred nest initiation</td>
<td>-1.4 $\pm$ 0.33</td>
<td>69</td>
<td>3.2 $\pm$ 0.38</td>
<td>545</td>
</tr>
<tr>
<td>Incubation period (# days)</td>
<td>21.8 $\pm$ 0.17</td>
<td>67</td>
<td>22.6 $\pm$ 0.13</td>
<td>174</td>
</tr>
<tr>
<td>First egg volume index</td>
<td>35.24 $\pm$ 0.19</td>
<td>198</td>
<td>34.78 $\pm$ 0.18</td>
<td>235</td>
</tr>
<tr>
<td>Clutch size (# eggs)</td>
<td>1.5 $\pm$ 0.04</td>
<td>205</td>
<td>1.4 $\pm$ 0.02</td>
<td>543</td>
</tr>
<tr>
<td>Chick weight growth rate (g/day)</td>
<td>-3.24 $\pm$ 4.41</td>
<td>4</td>
<td>3.43 $\pm$ 0.21</td>
<td>61</td>
</tr>
<tr>
<td>Chick wing growth rate (mm/day)</td>
<td>4.67 $\pm$ 1.05</td>
<td>4</td>
<td>5.29 $\pm$ 0.21</td>
<td>61</td>
</tr>
<tr>
<td>Chick feeding rate (# feeds/nest/hr)</td>
<td>- -</td>
<td>-</td>
<td>- -</td>
<td>- -</td>
</tr>
<tr>
<td>Adult weight (g)</td>
<td>103 $\pm$ 0.45</td>
<td>245</td>
<td>107 $\pm$ 0.69</td>
<td>143</td>
</tr>
</tbody>
</table>
Table 4-5: Summary data and test statistics of each Arctic Tern breeding parameter compared within Machias Seal Island between year-types. Test statistics are denoted by letters: \( U \) = Mann-Whitney rank sum test; \( z \) = generalized linear model; \( t \) = \( t \)-test; \( \chi^2 \) = chi-squared test. Significant differences are marked with an asterisk at the end of each row. Medians are reported only for parameters for which non-parametric tests were used.

<table>
<thead>
<tr>
<th>Machias Seal Island</th>
<th>Good years</th>
<th>Poor years</th>
<th>test statistic</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean ± SE</td>
<td>median; 25%, 75%</td>
<td>n</td>
<td>mean ± SE</td>
</tr>
<tr>
<td>Nest initiation (date)</td>
<td>7 June ± 0.25</td>
<td>5 Jun; 2 Jun, 10 Jun</td>
<td>866</td>
<td>12 June ± 0.38</td>
</tr>
<tr>
<td>Centred nest initiation</td>
<td>-2.0 ± 0.25</td>
<td>866</td>
<td>3.2 ± 0.38</td>
<td>545</td>
</tr>
<tr>
<td>Incubation period (# days)</td>
<td>22.3 ± 0.10</td>
<td>539</td>
<td>22.6 ± 0.13</td>
<td>174</td>
</tr>
<tr>
<td>First egg volume index</td>
<td>35.02 ± 0.11</td>
<td>605</td>
<td>34.78 ± 0.18</td>
<td>235</td>
</tr>
<tr>
<td>Clutch size (# eggs)</td>
<td>1.6 ± 0.02</td>
<td>873</td>
<td>1.4 ± 0.02</td>
<td>543</td>
</tr>
<tr>
<td>Chick weight growth rate (g/day)</td>
<td>5.45 ± 0.16</td>
<td>246</td>
<td>3.43 ± 0.21</td>
<td>61</td>
</tr>
<tr>
<td>Chick wing growth rate (mm/day)</td>
<td>7.80 ± 0.13</td>
<td>270</td>
<td>5.29 ± 0.21</td>
<td>61</td>
</tr>
<tr>
<td>Chick feeding rate (# feeds/nest/hr)</td>
<td>1.6 ± 0.12</td>
<td>217</td>
<td>1.7 ± 0.24</td>
<td>56</td>
</tr>
<tr>
<td>Adult weight (g)</td>
<td>108 ± 0.27</td>
<td>742</td>
<td>107 ± 0.69</td>
<td>146</td>
</tr>
</tbody>
</table>
Table 4-6: Summary data and test statistics of each Arctic Tern breeding parameter compared within Nasaruvaalik Island between year-types. Test statistics are denoted by letters: $U = \text{Mann-Whitney rank sum test}; z = \text{generalized linear model}; t = t\text{-test}; \chi^2 = \text{chi-squared test}$. Significant differences are marked with an asterisk at the end of each row. Medians are reported only for parameters for which non-parametric tests were used.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Good years</th>
<th>Poor years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest initiation (date)</td>
<td>7 July ± 0.28</td>
<td>5 July ± 0.33</td>
</tr>
<tr>
<td>Centred nest initiation</td>
<td>0.5 ± 0.28</td>
<td>172 -1.4 ± 0.33</td>
</tr>
<tr>
<td>Incubation period (# days)</td>
<td>21.3 ± 0.11</td>
<td>90 21.8 ± 0.17</td>
</tr>
<tr>
<td>First egg volume index</td>
<td>34.88 ± 0.17</td>
<td>244 35.24 ± 0.19</td>
</tr>
<tr>
<td>Clutch size (# eggs)</td>
<td>1.8 ± 0.02</td>
<td>688 1.5 ± 0.04</td>
</tr>
<tr>
<td>Hatching success (# chicks/egg)</td>
<td>94.94%</td>
<td>178 48.31%</td>
</tr>
<tr>
<td>Chick weight growth rate (g/day)</td>
<td>7.24 ± 0.53</td>
<td>13 -3.24 ± 4.41</td>
</tr>
<tr>
<td>Chick wing growth rate (mm/day)</td>
<td>7.31 ± 0.63</td>
<td>13 4.67 ± 1.05</td>
</tr>
<tr>
<td>Chick feeding rate (# feeds/nest/hr)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Adult weight (g)</td>
<td>110 ± 0.70</td>
<td>122 103 ± 0.45</td>
</tr>
</tbody>
</table>
Table 4-7: Body measurements of adult Arctic Terns at Nasaruvaalik and Machias Seal Islands. The test statistics are from post-hoc $t$- and Mann-Whitney tests conducted to compare measurements between sites, as described in Methods. Test statistics are denoted by letters: $U$ = Mann-Whitney rank sum test; $t$ = $t$-test. Significant differences are marked with an asterisk at the end of each row.

<table>
<thead>
<tr>
<th></th>
<th>Nasaruvaalik Island</th>
<th>Machias Seal Island</th>
<th>test statistic</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>median 25% 75% mean ± SE n</td>
<td>median 25% 75% mean ± SE n</td>
<td>test statistic</td>
<td>p</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>good years</td>
<td>270 ± 0.65</td>
<td>117</td>
<td>269 ± 0.28</td>
<td>649</td>
</tr>
<tr>
<td>poor years</td>
<td>266 ± 0.54</td>
<td>151</td>
<td>268 ± 0.65</td>
<td>143</td>
</tr>
<tr>
<td>Tail streamer (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>good years</td>
<td>180 ± 1.18</td>
<td>115</td>
<td>181 ± 0.71</td>
<td>459</td>
</tr>
<tr>
<td>poor years</td>
<td>173 ± 1.03</td>
<td>148</td>
<td>179 ± 1.30</td>
<td>143</td>
</tr>
<tr>
<td>Culmen (mm)</td>
<td>30.82 ± 0.11</td>
<td>265</td>
<td>32.54 ± 0.12</td>
<td>233</td>
</tr>
<tr>
<td>Head+bill (mm)</td>
<td>70.05 ± 0.15</td>
<td>261</td>
<td>71.77 ± 0.09</td>
<td>792</td>
</tr>
<tr>
<td>Bill depth (mm)</td>
<td>6.90</td>
<td>6.69 7.20</td>
<td>6.94 ± 0.02</td>
<td>261</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>15.63</td>
<td>15.16 16.28</td>
<td>15.71 ± 0.05</td>
<td>200</td>
</tr>
<tr>
<td>Fifth tail retrix (mm)</td>
<td>122</td>
<td>116 125</td>
<td>121 ± 0.64</td>
<td>176</td>
</tr>
<tr>
<td>Tail fork (mm)</td>
<td>72</td>
<td>70 75</td>
<td>72 ± 0.35</td>
<td>174</td>
</tr>
</tbody>
</table>

† despite $p<0.05$, this is not significant, because the Holm-Bonferroni family error rate correction indicates that $α = 0.05/10 = 0.005$
Relative trophic positions

For terns from Machias Seal Island, the corrected stable nitrogen isotope ratio ($\delta^{15}N$) of lipid-free yolk (trophic position of pre-breeding females) was significantly higher than that of whole blood (trophic position of incubating adults; Table 4-8). However, because I made many assumptions about the base of the food web around Machias Seal Island in 2005 and 2006, and because the difference between the pre-breeding females and incubating adults was less than 1‰, the difference is likely not ecologically significant. At Nasaruvaalik Island, the trophic position of pre-breeding females did not differ from that of incubating adults (Chapter 3).

Table 4-8: Stable nitrogen isotope ratios of pre-breeding and incubating Arctic Terns nesting on Machias Seal Island.

<table>
<thead>
<tr>
<th>Tissue</th>
<th>Breeding stage</th>
<th>Mean $\delta^{15}N$ ± SE (‰)</th>
<th>n</th>
<th>Diet-tissue $\Delta N$ (‰)</th>
<th>Source of $\Delta N$</th>
<th>$t$-statistic</th>
<th>$p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>whole blood</td>
<td>incubation</td>
<td>7.78 ± 0.06</td>
<td>23</td>
<td>3.00</td>
<td>Hobson and Clark 1992, Ogden et al. 2004</td>
<td>-7.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>lipid-free yolk</td>
<td>pre-breeding</td>
<td>8.74 ± 0.13</td>
<td>18</td>
<td>3.50</td>
<td>Hobson 1995, Polito et al. 2009</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Oceanographic zone comparisons

Arctic terns laid significantly larger clutch sizes in the Boreal oceanographic zone than in the High Arctic zone ($F_{2, 20}=4.9, p=0.02; t=3.0, p=0.023$), but there were no differences in clutch size between Boreal and Low Arctic zones, or the Low Arctic and High Arctic zones. These relationships remained the same when data from Nasaruvaalik
and Machias Seal islands were excluded (Boreal vs. High Arctic clutch size: $F_{4,37}=5.4$, $p=0.002$; $t=3.5$, $p=0.011$). Terns nesting at Nasaruvaalik Island laid significantly larger clutch sizes than the mean for the High Arctic oceanographic zone (Table 4-10, Figure 4-12; $F_{4,37}=5.4$, $p=0.002$; $t=3.0$, $p=0.037$), while the reverse was true on Machias Seal Island ($F_{4,37}=5.4$, $p=0.002$; $t=3.3$, $p=0.019$). Sources of the data used for these comparisons are in Table 4-9.

Table 4-9: Mean clutch sizes of Arctic Terns at colonies in three oceanographic zones.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Site</th>
<th>Year(s) of study</th>
<th>Mean clutch size ± SE</th>
<th>n</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal</td>
<td>Machias Seal Island, New Brunswick</td>
<td>1937, 1947, 1948, 1995-2005</td>
<td>1.55 ± 0.01*</td>
<td>1552</td>
<td>Pettingill 1939, Hawksley 1957, this study</td>
</tr>
<tr>
<td>Boreal</td>
<td>Peters Island, Nova Scotia</td>
<td>1983</td>
<td>1.64 n.r.</td>
<td>83</td>
<td>Kirkham 1986</td>
</tr>
<tr>
<td>Boreal</td>
<td>Ravenglass, England</td>
<td>1909</td>
<td>1.70 n.r.</td>
<td>209</td>
<td>Bickerton 1909</td>
</tr>
<tr>
<td>Boreal</td>
<td>Farne Islands, England</td>
<td>1966-1968</td>
<td>1.62 ± 0.04</td>
<td>146</td>
<td>Coulson et al 1976</td>
</tr>
<tr>
<td>Boreal</td>
<td>Coquet Island, England</td>
<td>1987</td>
<td>1.80 ± 0.04</td>
<td>80</td>
<td>Monaghan et al 1992</td>
</tr>
<tr>
<td>Boreal</td>
<td>Orkney, Scotland</td>
<td>1988</td>
<td>1.94 ± 0.07</td>
<td>64</td>
<td>Monaghan et al 1992</td>
</tr>
<tr>
<td>Boreal</td>
<td>Alexander Archipelago, Alaska</td>
<td>1945</td>
<td>2.00 ± 0.00</td>
<td>45</td>
<td>Williams 1947</td>
</tr>
</tbody>
</table>

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Table 4-9: continued from previous page

<table>
<thead>
<tr>
<th>Zone</th>
<th>Site</th>
<th>Year(s) of study</th>
<th>Mean clutch size ± SE</th>
<th>n</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Arctic</td>
<td>Belcher Islands, Nunavut</td>
<td>1997</td>
<td>1.64 ± 0.03</td>
<td>270</td>
<td>Gilchrist &amp; Robertson 1999</td>
</tr>
<tr>
<td>Low Arctic</td>
<td>Kitsissunnguit, Greenland</td>
<td>2002-2006</td>
<td>1.85 ± 0.00*</td>
<td>1752</td>
<td>Egevang 2010</td>
</tr>
<tr>
<td>Low Arctic</td>
<td>Frederickshaab Glacier, Greenland</td>
<td>1943</td>
<td>1.67 ± 0.03</td>
<td>279</td>
<td>Elkund 1944</td>
</tr>
<tr>
<td>Low Arctic</td>
<td>Mingan Archipelago, Gulf of St. Lawrence</td>
<td>1983</td>
<td>1.98 ± 0.03</td>
<td>163</td>
<td>Chapdelaine 1985</td>
</tr>
<tr>
<td>Low Arctic</td>
<td>Cooper Island, Alaska</td>
<td>1975-1977</td>
<td>1.73 ± 0.02</td>
<td>116</td>
<td>Boekelheide 1980</td>
</tr>
<tr>
<td>High Arctic</td>
<td>Sand Island, Greenland</td>
<td>2007-2008</td>
<td>1.55 ± 0.04†</td>
<td>169</td>
<td>Egevang 2010</td>
</tr>
<tr>
<td>High Arctic</td>
<td>East Bay, Southampton Island, Nunavut</td>
<td>1929-1930, 2010</td>
<td>1.63 ± 0.05*</td>
<td>57</td>
<td>Mallory pers. comm., Sutton 1932</td>
</tr>
<tr>
<td>High Arctic</td>
<td>Resolute Bay, Nunavut</td>
<td>1969</td>
<td>1.50 ± 0.29</td>
<td>4</td>
<td>Geale 1971</td>
</tr>
<tr>
<td>High Arctic</td>
<td>Herschel Island, Yukon</td>
<td>between 1971-1976</td>
<td>1.30 n.r.</td>
<td>11</td>
<td>Salter 1980</td>
</tr>
<tr>
<td>High Arctic</td>
<td>Bylot Island, Nunavut</td>
<td>1954</td>
<td>1.56 ± 0.12</td>
<td>18</td>
<td>Drury 1960</td>
</tr>
<tr>
<td>High Arctic</td>
<td>Truelove Lowland, Devon Island, Nunavut</td>
<td>1966-1969</td>
<td>1.55 ± 0.11</td>
<td>22</td>
<td>Hussell and Holroyd 1974</td>
</tr>
<tr>
<td>High Arctic</td>
<td>Ny Ålesund, Svalbard, Norway</td>
<td>1967-1970</td>
<td>1.77 ± 0.01*</td>
<td>198</td>
<td>Bengtson 1971, Lemmetyinen 1972</td>
</tr>
<tr>
<td>High Arctic</td>
<td>Nasaruaalik Island, Nunavut</td>
<td>2002-2010</td>
<td>1.75 ± 0.01</td>
<td>893</td>
<td>this study</td>
</tr>
</tbody>
</table>

SE reported for these sites are derived from the standard deviations of the means of means for multiple years.
SD reported was the same in the two years of this study; SE is derived from this value.
n.r. = not reported
Table 4-10: Mean clutch sizes of each of the three oceanographic zones compared. These means include Nasaruvaalik and Machias Seal Islands in their respective zones.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Zone mean clutch size ± SE</th>
<th>n (# of sites)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal</td>
<td>1.79 ± 0.06</td>
<td>9</td>
</tr>
<tr>
<td>Low Arctic</td>
<td>1.76 ± 0.05</td>
<td>6</td>
</tr>
<tr>
<td>High Arctic</td>
<td>1.57 ± 0.05</td>
<td>8</td>
</tr>
</tbody>
</table>

Figure 4-12: Mean clutch size of Arctic Terns in the High Arctic oceanographic zone was significantly smaller than that of terns in the Low Arctic oceanographic zone, but there were no differences between High Arctic and Boreal oceanographic zones or between Low Arctic and Boreal oceanographic zones. Terns at Nasaruvaalik Island had a significantly larger clutch size than the mean from other studies in its High Arctic oceanographic zone, while Machias Seal Island had significantly smaller clutch size than the mean from other studies in its Boreal oceanographic zone. Bars show means ± 95% CI.
Discussion

The differences in breeding biology at Nasaruvaalik Island and Machias Seal Island included higher clutch sizes and hatching rates, more nesting synchronicity and shorter incubation periods at Nasaruvaalik Island. No differences existed in chick growth rates overall between sites, but in good years, chicks at Nasaruvaalik Island gained weight more rapidly than those at Machias Seal Island. Compared to their respective oceanographic zones, clutch sizes at Nasaruvaalik Island were larger than the zone mean, and those at Machias Seal Island were smaller than the zone mean; see Table 4-11. I will discuss the implications of each of these comparisons, and comparisons within each site between good and poor years below.
Table 4-11: Summary of similarities and differences between Nasaruvaalik Island and Machias Seal Island

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Nasaruvaalik Island (NI)</th>
<th>Machias Seal Island (MSI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Synchrony of nest initiation</td>
<td>Initiated nests more synchronously than MSI</td>
<td></td>
</tr>
<tr>
<td>(variance)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Synchrony of incubation period</td>
<td>Incubated nests for more similar lengths of time than MSI</td>
<td></td>
</tr>
<tr>
<td>(variance)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest initiation, by date</td>
<td></td>
<td>Nested a month earlier than NI</td>
</tr>
<tr>
<td>Nest initiation, centred on site</td>
<td>Nested later compared to site mean in good years</td>
<td>Nested earlier compared to site mean in good years and later in poor years</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Incubation period</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Incubation period compared to nest</td>
<td>No correlation between nest initiation date and incubation period</td>
<td>Terns nesting later had shorter incubation periods</td>
</tr>
<tr>
<td>initiation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg volume</td>
<td>No difference between sites</td>
<td></td>
</tr>
<tr>
<td>Egg volume compared to nest</td>
<td>No correlation between egg volume and nest initiation date</td>
<td>Earlier nesters had larger eggs in poor years. No correlation between egg volume and</td>
</tr>
<tr>
<td>initiation</td>
<td></td>
<td>nest initiation in good years or overall</td>
</tr>
<tr>
<td>Clutch size</td>
<td>Higher clutch size than at MSI</td>
<td></td>
</tr>
<tr>
<td>Hatching success</td>
<td>Higher hatching success than at MSI</td>
<td></td>
</tr>
<tr>
<td>Chick feeding rates</td>
<td>No differences between sites overall (only good years were included at NI) or in good years</td>
<td></td>
</tr>
</tbody>
</table>

continued on next page
Table 4-11: continued from previous page

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Nasaruvaalik Island (NI)</th>
<th>Machias Seal Island (MSI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chick growth:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>weight</td>
<td>No differences overall between sites</td>
<td></td>
</tr>
<tr>
<td>NI chicks grew faster than MSI chicks in good years</td>
<td>MSI chicks grew faster than NI chicks in poor years</td>
<td></td>
</tr>
<tr>
<td>wing</td>
<td>No differences between sites</td>
<td></td>
</tr>
<tr>
<td>Adult body weight †</td>
<td>Heavier than MSI in good years</td>
<td>Heavier than NI overall and in poor years</td>
</tr>
<tr>
<td>Adult structural measurements †</td>
<td>Bill depth slightly larger than at MSI</td>
<td>Most measured structural elements were larger at MSI: tail streamer (in poor years only), culmen, head+bill, tarsus, fifth tail retix, tail fork</td>
</tr>
<tr>
<td>Relative trophic position</td>
<td>No difference between prebreeders and incubators at NI (cannot compare directly)</td>
<td>Prebreeders had higher trophic position than incubators at MSI (cannot compare directly)</td>
</tr>
<tr>
<td>Oceanographic zone comparisons</td>
<td>NI terns had larger clutch sizes than High Arctic mean</td>
<td>MSI terns had smaller clutch sizes than Boreal mean</td>
</tr>
</tbody>
</table>

† adult body weights and measurements differed statistically between sites, but were biologically very similar; see discussion below
In good years on Nasaruvaalik Island, breeding Arctic Terns experienced higher food availability, as demonstrated by higher adult body weights, large and plentiful courtship food, low chick mortality, and fewer predators (Chapter 2). Although the number of predators did not increase at Machias Seal Island in the poor years, the risk of predation did, and changing food availability meant that these two factors were likely the two main drivers behind the differences between good and poor years on Machias Seal Island (Gaston et al. 2009a, A.W. Diamond pers. comm.).

Despite the importance of predators and food availability as determinants of breeding success at both sites, there are differences between the sites regarding these factors. Arctic waters can provide more energy to top predators than Atlantic waters through shorter food chains and larger, more lipid-rich prey items (Lack 1968, Węsławski et al. 2006). Additionally, the bottom of the sea ice acts as a second ocean floor and hosts a wide variety of sympagic (ice-associated) prey. The constantly changing array of dislodged ice pack brings many food items within reach of the terns as currents sweeping beneath them create sympagic upwellings, a source unavailable to Machias Seal Island terns during breeding. Furthermore, terns at Nasaruvaalik Island forage throughout the 24 hour period (see Chick feeding rates, below), with 35% more daylight in which to forage than at Machias Seal Island. Finally, when the Arctic Tern colony was active, Machias Seal Island supported approximately 2000 pairs of Arctic Terns as well as about 1000 pairs of Common Terns, 6000-8000 pairs of Atlantic Puffins, 700 pairs of Razorbills and hundreds of Leach’s Storm-petrels (A.W. Diamond, pers.comm.).
In contrast, only about 500-600 pairs of terns and about 20 pairs of Sabine's Gulls 
\((Xema sabini)\) breed at Nasaruvaalik Island (K. Boadway, unpublished data). As central-
place foragers, breeding seabirds will deplete the food resources in the waters 
immediately around the colony, and as the season progresses, they must travel farther 
from the colony to obtain prey items, a phenomenon known as Ashmole's halo 
(Ashmole 1963, Gaston et al. 2007). As a seabird colony increases in number of 
individuals, the size of halo, or area around the colony that has been depleted in prey, 
will increase to the point that is predicted by Ashmole (1963) to negatively affect the 
ability of adults to raise chicks. Since the colony at Machias Seal Island included many 
more breeding seabirds than Nasaruvaalik Island, this theory states that the food 
availability near Machias Seal Island should be depleted in comparison to Nasaruvaalik 
Island (unless local productivity is higher or currents replenish food stocks at a faster 
rate at Machias Seal Island). All of these factors lead to a higher functional food 
availability at the High Arctic site.

Predators at Nasaruvaalik Island were not numerous, with fewer than six avian predators 
observed daily and fewer than four during pre-breeding in years when laying was not 
delayed (Chapter 2). This can be compared to 13.4/day in Scotland (Fuchs 1977). At 
Machias Seal Island, numbers of the two main predators of tern nests (Great Black-
backed Gull and Herring Gull) were not counted systematically until recently, but are 
estimated to be around 20 and 50 individuals per day respectively, and there were as 
many as 500 roosting on Gull Rock even when the monitoring program began in 1995 
(Diamond pers. comm.). Other less common potential tern and egg predators include 
Laughing Gulls \((Leucophaeus atricilla)\), Merlins \((Falco columbarius)\), Peregrine
Falcons (*Falco peregrinus*), Common Ravens (*Corvus corax*) and Bald Eagles (*Haliaeetus leucocephalus*). At least two of these potential predators were observed on most days at Machias Seal Island. These predator numbers suggest that predation risk is much lower at Nasaruvaalk Island than other colonies, and certainly lower than at Machias Seal Island. This is consistent with the experimental demonstration that shorebirds at higher, Arctic latitudes face lower predation risk than those at lower latitudes (McKinnon et al. 2010).

*Nests: initiation and incubation period*

*Variance*

The variation in nest initiation and incubation period at Machias Seal Island was much higher than at Nasaruvaalk Island. The low variability in nest initiation at Nasaruvaalk Island was somewhat unexpected, since the onset of laying in Arctic seabirds is often highly variable among years (Bird and Bird 1940, Evans and McNicholl 1972, Gaston et al. 2005b, Hipfner et al. 2005). These studies attribute the high degree of variation in nest initiation to variability in local environmental conditions, specifically snowmelt and sea ice break-up. Because Arctic Terns are marine surface-feeders, access to open seawater is essential to their ability to attend their colony. Further, terns and other seabirds require snow-free locations in which to lay eggs (Lack 1933, Abraham 1986, Stenhouse et al. 2001). However, in the four years of this study at Nasaruvaalk Island, snow cover was never a constraint in mid-June during the arrival of the terns at the island; this is
likely due to the site being mostly flat so that wind blows what snow falls into banks, leaving bare patches as it melts. The break-up of sea ice immediately around Nasaruvaalik Island has a minimal effect on the terns since the area contains many polynyas within reach of the colony (Chapter 2). These polynyas provide terns access to their prey source upon arrival to the colony every year. The unvarying nature of these factors, so different at Nasaruvaalik than at other colonies, meant that the terns there were able to initiate nests at roughly the same time each year.

Another driver leading the terns at Nasaruvaalik Island to initiate nests at the same time each year and to minimize the length of incubation is the short High Arctic summer, which provides a small window of suitable conditions in which to breed. This encourages some birds to begin nesting as soon as they can so they may successfully reproduce and fledge before migrating south ahead of severe Arctic weather (e.g. Klaassen et al. 2006). Arctic Terns in Low Arctic Alaska experienced low reproductive success when the sea ice broke up early, leading to a mismatch in timing of prey availability during chick-rearing (1980). Unusually early ice break-up is functionally the same as later lay dates: terns that lay late would also miss the peak prey availability associated with the trophic pulse caused by spring sea-ice melting that occurs across the Arctic (Sakshaug and Slagstad 1992, Niebauer et al. 1995). Adaptation to the short season could mean that terns in more southerly locations that may have been able to delay laying until reaching a critical threshold of body condition that would allow them to breed (Drent and Daan 1980), instead forgo breeding in a High Arctic season altogether, leaving only birds that will nest synchronously. Similarly, protracted incubation periods at Nasaruvaalik Island would be maladaptive, as they would reduce
the likelihood of meeting the peak prey abundance during the appropriate stage of chick-rearing, leading to reduced reproductive success (Chapter 2). It is likely that all of these reasons contribute to the narrow variance in nest initiation and incubation period at Nasaruvaalik Island.

Why then is the nest initiation and incubation period variance so broad at Machias Seal Island? Nest initiation at Machias Seal Island is unevenly distributed with the onset of laying trailing off into the later part of the season; it is largely these later nesters that drive the wide variance in nest initiation at this site. Increased risk of predation can increase the variation in nest initiation and incubation period, because higher numbers of predators at a colony during pre-breeding can cause birds to delay nesting and can also cause them to spend more time off their nests defending them, allowing eggs to cool and consequently to develop more slowly (Chapter 2, Boekelheide 1980, Levermann and Tottrup 2007). Lower food availability can also cause delays in nest initiation since, as income breeders, females must replenish their reserves after migration prior to egg formation (Chapter 3, Bond and Diamond 2010). Typically, the earlier females can gather nutrients required for egg formation, the earlier they will lay (Perrins 1970, Drent and Daan 1980). However, it may take lower quality females or young, inexperienced breeders longer to accumulate the resources they need to form eggs, or it could be the shorter day length at Machias Seal Island that may restrict the ability of females to acquire enough resources in a short time. Because terns at Machias Seal Island do not have the short-season pressure to lay as early as possible, these lower quality females may take more time to gather nutrients but still breed in a given season, leading to
higher variance in nest initiation and incubation period at Machias Seal Island compared to Nasaruvaalik Island.

**Timing**

The timing of nest initiation was earlier at Machias Seal Island than Nasaruvaalik Island by about a month, which is expected, since temperatures in the High Arctic are not high enough in the first week of June to melt what snow and ice is present to allow the terns to begin nesting. However, when centred on their overall site means, terns initiated nests at Nasaruvaalik Island relatively later than Machias Seal Island in good years, and earlier in poor years. In good years, it is reasonable to expect that terns would initiate nesting earlier than they do in poor years, since in good years, they may have access to more or better food, or experience lower predation pressures. Because females must acquire enough energy for egg formation prior to laying (Perrins 1970), higher food availability earlier in the season means that females can acquire the nutrients and energy required more quickly in good years. This was the pattern observed at Machias Seal Island: good years had significantly earlier nest initiation relative to poor years. However, the opposite was true at Nasaruvaalik. This was probably due to the only 'good year' of data available for nest initiation on Nasaruvaalik Island also being one of the two years in which there were higher numbers of predators present around the island during the pre-breeding period, a time in which terns make decisions about when or if they will breed in a season (Levermann and Tottrup 2007). I suspect that the response of delayed breeding by terns to high numbers of predators during pre-breeding probably
outweighed their tendency to nest earlier if environmental conditions were good. Hence, the earlier laying in poor years compared to good years that we saw on Nasaruvaalik Island is unusual, and is likely due to the small number of seasons from which data were collected.

Incubation period on Nasaruvaalik Island was almost a full day shorter than on Machias Seal Island, perhaps attributable to the lower number of predators at the site. As discussed above, lower predation risk allows the terns to continue incubating on their nests, while less competition for food at Nasaruvaalik would reduce the need for adults to forage for longer periods compared to Machias Seal Island. Both of these factors likely increased nest attendance at Nasaruvaalik Island, reducing cooling periods that extend chick development within the eggs (Boersma 1982, Hepp et al. 2006).

Terns that initiated nests later in the breeding season had shorter incubation periods, but only at Machias Seal Island, suggesting that earlier-laying terns may be able to spend more time off their nests than late layers, though not in the High Arctic. As early-laying birds generally have higher reproductive success (Drent 2006), birds that arrive at breeding colonies in better body condition or better able to gain resources required to form eggs may lay earlier (Wendeln 1997). Presumably, terns must time their nesting activities to meet peak prey availability during chick-rearing (Boekelheide 1980) and to ensure chicks fledge before inclement Arctic weather returns; earlier-layers would have greater flexibility to depart the nest site to forage or avoid predators during incubation compared with their late-laying counterparts. The trend of later nest initiation dates leading to shorter incubation periods seems to be driven by the fewer later-layers that
are more likely to remain on the nest throughout incubation. I did not know the ages of breeding terns, nor did I measure incubation period and body condition on the same individuals so I could not discern between these possible explanations, but this seems to be a fertile area for future investigation.

_Eggs: volume, clutch size and hatching success_

The lack of difference in egg volume index between good and poor years within sites and between sites in all comparisons suggests that egg volume is relatively constant in this species. However, in poor years on Machias Seal Island, there was a weak decline in egg volume associated with later lay dates. Since some birds of lower body condition and quality may lay eggs of lower volume (Østnes et al. 1997, Sorensen et al. 2009), this trend hints that terns that are unable to lay earlier in the season (because of low body condition on arrival or a lesser ability to locate prey than those that lay earlier) take longer to accumulate enough nutrients for egg formation. Indeed, in Common Terns, earlier-laying females were heavier than later-layers at one colony (Wendeln 1997). The trend of smaller eggs associated with later lay dates has also been seen in other Arctic Tern colonies and other seabirds (Lemmetyinen 1973b, Suddaby and Ratcliffe 1997, Sorensen et al. 2009).

At the Farne Islands in England, Arctic Tern clutch volume varied more than the egg volume (Coulson and Horobin 1976), similar to my observations at both sites in this study. Clutch size declined in poor years at Nasaruvaalik and Machias Seal islands, and
since egg volume did not change between year-types, clutch volume declined as well. Arctic Terns laid larger clutches at Nasaruvaalik Island than at Machias Seal Island overall, in good years and in poor. This is probably attributable to higher functional food availability at Nasaruvaalik (lower food availability leads to smaller clutch sizes; Suddaby and Ratcliffe 1997, Oro et al. 1999), and perhaps access to higher quality food through the shorter food chains in the Arctic (above).

Hatching success was higher at Nasaruvaalik Island compared to Machias Seal Island overall, which may be a consequence of the many predators present at Machias Seal Island that take more eggs prior to hatching. Additionally, when prey was less available, adult terns may have left their nests undefended longer as they replenished their reserves, exposing eggs to increased predation risk during the incubation period. I caution that the reported hatching success during poor years on Nasaruvaalik Island may be higher than the true hatching success, since researchers departed the study colony prior to the anticipated end of incubation periods for 51% of eggs laid in one of the two poor years. As such, the true difference between the sites may be less than reported.

*Chick feeding rates*

There were no differences between the two sites in hourly chick feeding rates in any comparison made, and there was no difference between good years and poor years at Machias Seal Island. The lack of difference between year-types at Machias Seal Island suggests that either prey was not scarce, or that terns were able to compensate for low
prey abundance by using time normally allocated to other tasks to increase feeding effort (Paquet 2001). Either way, the lower chick growth rates and breeding success in poor years coupled with the similar chick feeding rates between good and poor years implies that though the chicks were being fed as often in poor years as they were in good years, the new prey items were lower in quality, and contained less energy.

Machias Seal Island researchers observed that after 2001, there was a switch in chick diet from yearling Atlantic herring (Clupea harengus) to euphausiids and larval herring (Gaston et al. 2009a). Prior to 2000, seabird productivity at Machias Seal Island was linked to annually fluctuating energy density in their herring prey, but after the diet switch, this association was gone (Diamond and Devlin 2003). The decreased growth rates and breeding success despite similar feeding rates in good and poor years is an example of the 'junk food hypothesis', which predicts that equal quantity but lower quality food fed to chicks will lead to decreases in growth rates and breeding success (reviewed by Öesterblom et al. 2008).

Though there were no differences between the sites in hourly chick feeding rates, there was also no statistically detectable difference in feeding rates at Nasaruvaalik Island diurnally or nocturnally (Chapter 2). Other birds that nest in areas of 24-hour daylight also show no diel pattern in their activity levels (Karplus 1952, Barrett et al. 1997, Mehlum et al. 2001). In addition to the extended fishing opportunities afforded by constant daylight, in 24-hour daylight, some zooplankton do not undergo diel vertical migration (Błachowiak-Samotyk et al. 2006). The constant availability of prey near the surface also allows other potential prey species like Arctic cod to be active at all times of day, which in turn would bring them within reach of the terns. Indeed, in some
locations where a diel vertical migration of prey items is present in 24-hour daylight, birds will adjust their feeding times to suit availability of prey (e.g., Falk et al. 2000, Regular et al. 2010).

As was mentioned in Chapter 2, the low number of observation periods throughout the night at Nasaruvaalik Island made it difficult to detect potential differences between diurnal and nocturnal feeding. Despite this, we were able to detect that terns breeding under the midnight sun did forage throughout the 24-hour period, at roughly half of the rate at which they fed during the day. This means that terns at Nasaruvaalik Island have 8.5 hours more in which to forage compared to those at Machias Seal Island, which are roosting on the colony or otherwise not feeding chicks overnight (Paquet 2001). Since terns at Nasaruvaalik Island are feeding chicks throughout the 24-hour period, and the hourly feeding rate throughout the daylight hours between sites did not differ, the amount of food fed to the chicks at Nasaruvaalik Island must be greater. This, combined with the likely higher energy density of prey in the Arctic (discussed above; Lack 1968, Węsławski et al. 2006) means that chicks at Nasaruvaalik Island are provided with more energy per unit time than Machias Seal Island chicks.

**Chick growth rates**

Chick weight and wing growth rates were, unsurprisingly, lower in poor years than in good ones within each site, because tern chick weight gain is reduced when quality food is limited (Chapter 2). Wing growth rate is typically constant in most species of birds
and only weight increase will be affected by short-term fluctuations in food resources (Ricklefs and White 1975). However, when food availability is low enough, wing growth will decrease as well (Phillips et al. 1996, Lyons and Roby 2011).

Terns at Nasaruvaalik Island increased weight faster than those at Machias Seal Island in good years, while in poor years this was reversed. The reversal was driven by the drastic drop in the weight growth of the terns at Nasaruvaalik Island. Though both sites saw a decrease in weight growth between good and poor years, Nasaruvaalik terns on average lost weight through their linear growth phase (days five to fifteen). Ultimately, in the one poor year for which there are measurements, all chicks at Nasaruvaalik Island died before any reached the end of the linear growth phase. Because of the great variance in the weight growth rates between good and poor years on Nasaruvaalik Island, the power to detect a difference overall between the sites was extremely low. However, there was a significantly higher growth rate at Nasaruvaalik Island in good years compared to Machias Seal Island, and no difference in growth rates between sites in the single year in which most chicks died prior to fledging.

That Arctic Tern chicks at Nasaruvaalik Island grew faster than Machias Seal Island chicks in good years again suggests that Nasaruvaalik Island terns had more food available to them and can thus provide their chicks with more food or better quality prey in a shorter period of time than their Machias Seal Island counterparts. Higher quantities of food have been linked to increased growth rates in terns (discussed in Chapter 2), and by feeding their chicks throughout the 24-hour period (above), Nasaruvaalik chicks are provided with more prey items. Furthermore, the Arctic waters provide short food webs
and higher concentration of fats in larger invertebrates, which favour larger predators like seabirds more than the complex food webs of warmer waters do (Węsławski et al. 2006), as predicted by Lack (1968).

Nasaruvaelik Island terns must also cope with lower temperatures throughout the chick-rearing period. Although Arctic Tern chicks in colder climates do have a higher energy requirement if left to thermoregulate on their own, up to 2/3 of their requirements can be made up by parental brooding of the chicks (Klaassen 1994). Though Klaassen (1994) noted that terns in Spitsbergen brooded their chicks only 10% more than those in the Netherlands, he reasoned that this could be due to low food availability and the resultant need for adults to spend time foraging rather than brooding (Uttley 1992, Paquet 2001). Presumably then, if the food availability at a site was sufficiently high, one parent may stay at the nest brooding the chicks while the other forages. This is consistent with my qualitative observations at Nasaruvaalik Island while conducting time budget watches for another project: chicks were rarely left completely unattended by a parent. This contrasts with Arctic Terns at Machias Seal Island, where in two good years chicks were attended by at least one parent only 32% of the time, and time spent foraging by chick-rearing adults at Machias Seal was as high as 70% (Paquet 2001). Thus, the higher functional food availability at Nasaruvaalik Island was likely the reason for higher weight growth rates compared to Machias Seal Island.

Wing growth rates between sites did not differ, possibly a statistical consequence of the low power I had for my analyses of these data (see Results), or because wing growth is affected only by severe shortages of food. If the latter is the case, it is likely that wing
growth rates between sites varied by the same amount in good years and poor, showing no differences between sites.

*Adult body condition and morphometrics*

Nasaruvaalik Island adults were heavier in good years than in poor years, while at Machias Seal Island, there was no difference between year-types. Much like the chick growth rates, this led to Nasaruvaalik Island terns being heavier than Machias Seal Island terns in good years, and lighter in poor years. A drop in adult weight in years when food is less available or quality is poor is expected (Monaghan et al. 1989, Gaston et al. 2005b). Adults will continue their breeding attempt, possibly compensating by adjusting their behaviour (e.g. decreasing attendance to and feeding of the chicks) until they reach a lower threshold beyond which they will abandon their breeding attempt (Lack 1968, Drent and Daan 1980, Monaghan et al. 1989, 1992). The reason for the lack of change in body weight between good years and poor years at Machias Seal Island is unknown, but it suggests that female body condition was perhaps not the primary factor for reduced reproductive effort or success in poor years.

The wing and tail streamer of terns at Nasaruvaalik Island were significantly shorter in poor years compared to good years at the same site, which was unexpected. This may have resulted from more broken feather tips from increased time foraging that likely occurred in poor years. Alternatively, it could be that smaller birds have an advantage in
poor years, as it may be easier for them to find enough food to support them through the breeding season than it would be for larger birds.

Though terns on Machias Seal Island had statistically larger body sizes in some respects than those at Nasaruvaalik Island, the actual differences were biologically minute. There was a large difference in the tail fork length between sites, however I suspect it results from an unanticipated difference in measurement methods. Furthermore, the significantly lighter terns at Nasaruvaalik Island are likely so because of the aforementioned skew towards poor years at that site, which could affect overall comparisons. This parameter shows this bias more clearly than others, since Nasaruvaalik Island adult terns were clearly much lighter in poor years than in good ones. As such, it is likely that there is very little difference in size or weight of adult terns between the two sites. Though Bergmann's Rule suggests that endotherms in warmer environments should be smaller than those in colder climates (Meiri and Dayan 2003), there are many bird species that do not conform to this "rule" (Meiri et al. 2007).

**Oceanographic zone comparisons**

Arctic Terns breeding in the Boreal oceanographic zone had significantly larger clutches than those breeding in the High Arctic oceanographic zone. In a similar comparison, Kirkham (1986) found no correlation between latitude and clutch size. These results are counter to Lack's (1947) observation that clutch size within species increases with increasing latitude. Lack (1966) later observed that clutch sizes were larger where larger
broods can be fledged, and this has been confirmed in various studies (e.g. Heaney and Monaghan 1995, Monaghan et al. 1998). That the Boreal zone supported higher clutch sizes implies that terns in that zone were able to raise and fledge larger broods than terns in the High Arctic. Terns breeding in the High Arctic probably experience more stressors than those in the Boreal zone (e.g., long migration, variable sea-ice potentially blocking access to prey, snow on the colony on arrival, and higher thermoregulatory costs and therefore energetic demands due to colder temperatures), which may make it more difficult to raise larger broods. However, Arctic Terns in the High Arctic do not compete with other tern species for similar resources, as they must in the Boreal zone.

Neither Nasaruvaalik Island nor Machias Seal Island had clutch sizes typical of their respective zones: terns nesting at Nasaruvaalik Island had significantly higher clutch sizes than conspecifics nesting elsewhere in this zone, while terns nesting at Machias Seal Island laid significantly smaller clutches than other Boreal-nesting Arctic Terns. This implies that local conditions contribute more to tern breeding success than the general similarities of the larger spatial scale of the oceanographic zone. In support of this contention, there is a wealth of studies of Arctic Terns comparing colonies that are quite near to each other in geographical space, but function quite differently due to differences in local food supply or other factors. For example, Lemmetyinen (1973b) found that reproductive success of tern colonies in the Southwest Finnish archipelago differed significantly according to whether the colony was situated in the outer portion or middle of the archipelago. Ultimately, the differences were a result of the amount of suitable prey available to the adults. Similarly, Arctic Terns at Coquet Island and Orkney (Shetland Islands) fared differently depending on their local food availability.
(Monaghan et al. 1992). Hall et al. (2000) attributed prey diversity seen in the diets of Arctic and Common Terns within the Gulf of Maine to colony location. In Svalbard, different nest initiation times and clutch sizes were attributed to snow and ice melting at different times, which itself was related to local conditions (Gullestad and Norderhaug 1967). Another study from Svalbard (Bengtson 1971) related breeding success at different colonies to differential food availability and fox predation at one of the two sites, the other of which had few foxes due to local hunting.

The factors associated with higher latitude and different oceanographic zones play a role in the differences in tern reproduction between Nasaruvaalik Island and Machias Seal Island. However, my data suggest that local conditions at these colonies result in colony-specific characteristics that may differ annually from patterns observed elsewhere at Arctic Tern colonies within the same oceanographic zone.

Conclusions

At the Nasaruvaalik Island colony, I observed more synchrony among the breeding terns (associated with higher reproductive success; Birkhead 1977, Becker 1995, Hernandez-Matias et al. 2003), larger clutch sizes, and higher hatching success overall and between sites within good and poor years. In good years, I observed more rapid growth of chicks at the northern site, but this was countered by higher growth rates in poor years at Machias Seal Island. Using clutch sizes as a proxy for “good years”, data extending back to 2002 suggest that seven of the past nine breeding seasons at Nasaruvaalik Island
have been good (Chapter 2). Therefore, compared to breeding at Machias Seal Island, it is probably energetically more costly for an Arctic Tern to breed at Nasaruvaalik Island (e.g. colder temperatures and consequent higher thermoregulatory costs, greater migration distance), but these costs seem to be balanced by a more predictably abundant food supply, typically reduced predation risk, and less competition with other seabirds for prey.

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Chapter 5: General Discussion

Arctic Terns breed in a wide range of latitudes spanning three oceanographic zones: High Arctic, Low Arctic and Boreal (Salomonsen 1965, Hatch 2002). Though some comparisons of their breeding biology and foraging behaviour have been made between zones (Kirkham 1986, Klaassen 1994), mine is the first to explore differences in their breeding and diet between a well-studied colony in the Boreal, and one of many poorly-studied High Arctic colonies. Because the changing climate is affecting polar regions most clearly (Arctic Climate Impact Assessment 2005), and because seabird species vary in breeding ecology in different oceanographic zones (Mallory et al. 2008c), it is important to establish which, if any, results of research conducted in one zone may be applied to another.

Seabirds have long been recognized as useful indicators of marine ecosystem health (Cairns 1987, Montevecchi 1993, Diamond and Devlin 2003, Piatt et al. 2007b, Mallory et al. 2010). As surface feeders, rather than divers, Arctic Terns cannot pursue prey to depths as it becomes increasingly unavailable at the surface. Furthermore, they carry fresh prey in the bill to chicks, rather than regurgitate partly-digested prey, so they cannot fly long distances away from the colony in search of surface prey either. As a result, they are more likely to provide earlier indications of changes in the ocean than pursuit-divers and long-distance foragers. However, it has recently been demonstrated that the phenotypic plasticity of seabirds may reduce the utility of some species in indicating marine ecosystem change (Grémillet and Charmantier 2010). At present, our
knowledge of breeding seabirds in the High Arctic is limited to pursuit-divers and long-distance foragers (Thick-billed Murres, Dovekies, and Northern Fulmars; Gaston et al. 2005a, Harding et al. 2008, Mallory et al. 2008b, Wojczulanis-Jakubas et al. 2011). My study of surface-feeders in the High Arctic increases our ability to assess potential indicators of ecological change in this critically vulnerable region, and provides quantification of the plasticity of this species in two regions of its breeding range widely separated in latitude.

**High Arctic colony**

The Arctic Tern colony at Nasaruvalik Island was subject to years of high and low breeding success, as other Arctic Tern colonies are. These variations were related to the two main factors affecting reproductive success at other seabird colonies: predators, and food availability (Monaghan et al. 1992, Levermann and Tottrup 2007). Many aspects of their breeding ecology indicated changes in the levels of these two factors, including nest initiation date, clutch size, incubation period, hatching success, adult body condition, and chick growth rates. Their diet, as measured through stable-isotope analyses, also reflected the switch between good and poor years. I found that incubating terns in poor years gathered prey at lower trophic positions and had a wider dietary niche width than in good years, when pre-breeding females fed on a wider array of prey than incubating adults without changing trophic positions. Chicks were at the highest trophic position measured, with the narrowest niche width (i.e. the most specialised).
High Arctic and Boreal comparisons

Arctic Terns breeding at Nasaruvaalik Island were more synchronous, laid larger clutches, and hatched more chicks which grew faster than those on Machias Seal Island. Predation risk and food availability appeared to influence tern reproduction at both sites, but these affected each colony partly in accordance with predictions made about their respective oceanographic zones. Nasaruvaalik Island (High Arctic) had fewer predators than Machias Seal Island (Boreal), a trend also seen in other birds (e.g. McKinnon et al. 2010). Nasaruvaalik also had higher functional food availability, largely attributable to the 24 hours of daylight at that site, which provided more foraging time for breeding terns. Chicks grew faster at Nasaruvaalik Island as well, at least in good years, despite the colder temperatures; the scarcity of predators and abundance of food at that site allowed adults to brood chicks and absorb the extra costs of thermoregulation themselves.

While the differences between these two colonies are consistent with known oceanographic and latitudinal trends, the departure of clutch size from the average within their respective zones implies that local conditions may be more relevant to breeding terns than broad oceanographic trends. I found that terns at Nasaruvaalik Island laid larger clutches than are typical across High Arctic studies, while terns at Machias Seal Island laid smaller clutches than terns at other colonies within the Boreal oceanographic zone. Since birds will lay larger clutch sizes where larger broods can be raised (Lack 1966, Monaghan and Nager 1997), this supports the idea that there are
local differences in the ability of terns to raise young at these two sites relative to other sites in their zones. In addition to higher clutch sizes at Nasaruvaalik Island, terns have bred there for at least the past nine years continuously, with only one known year of complete failure that occurred well into the breeding season. Seven of these nine years were 'good' for breeding, as indexed by clutch size. At Greenland's High Arctic Sand Island, terns either did not attempt to breed, or the colony experienced complete breeding failure early in the season in two of four years. Predators were blamed for these failures. Sand Island may be more typical of High Arctic islands, with solid sea ice around the island until mid-July, more variation in the timing of sea ice break-up around the island, and delays in nesting related to late snow melt on the colony (Egevang et al. 2008). With the available data from these sites, Nasaruvaalik Island seems to be a relatively good colony for breeding Arctic Terns within the High Arctic oceanographic zone, while Machias Seal Island appears to be a relatively poor colony within the Boreal oceanographic zone.

Why might Nasaruvaalik Island be a particularly good site for Arctic Terns in the High Arctic? Terns at this site have multiple polynyas near the colony, so sea ice does not restrict access to prey at any time during the pre-breeding and breeding season, unlike many sites in the High Arctic (Gaston et al. 2005b), and food production appears to be predictable and relatively high. Although ambient temperatures are cold at Nasaruvaalik Island, relatively high food availability and short transit distances to food provided by the polynyas may allow adults to spend more time brooding chicks, thereby reducing the cost of chick thermoregulation (at least in good years). Many High Arctic seabird
colonies still have snow when the birds arrive (Sealy 1975, Madsen et al. 2007), but this does not occur on low-lying, windswept Nasaruvaalik Island.

Why might Machias Seal Island be a poorer site for Arctic Terns in the Boreal zone? Because this thesis focused on the High Arctic colony, I did not make a detailed comparison between Machias Seal Island and other Boreal colonies. However, there are a few factors at that site that I suggest may set it apart from the others. The colony at Machias Seal Island is composed of more than Arctic Terns. Rather, it includes (in good years) large numbers of Common Terns (~1,000 pairs), Atlantic Puffins (6-8,000 pairs), Razorbills (~700 pairs), and Common Murres (1-2,000 pairs), which greatly increases competition for resources at that site. Additionally, the high numbers of uncontrolled predators (gulls and raptors) at Machias Seal Island increases the likelihood of predation on exposed nests, and local crashes to the herring fishery likely caused a significant strain on the population.

My study has greatly increased our knowledge about Arctic Tern breeding biology across its entire latitudinal range, but especially in the High Arctic. I have presented new information about their behaviour, reproduction, diet and responses to predation and environmental conditions. I have shown that Arctic Terns in the High Arctic can be sensitive to changes in food availability at their colony (like terns breeding elsewhere), despite having access to open water available to them from arrival after migration until they depart in the fall. My study has added to the growing body of knowledge stressing the importance and value of polynyas to Arctic wildlife. As well, we now know that Arctic Terns forage throughout the 24-hour period in areas under the midnight sun, and
that, in good years, contributes to the ability of chicks to grow faster than they do in Boreal regions. Collectively, the phenotypic plasticity shown by these birds that is illustrated in my results indicate that we cannot simply use tern reproduction parameters from elsewhere and apply them to tern colonies in the Canadian Arctic; colony-specific differences should be considered in management decisions about this species.

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Appendix A

This appendix provides Arctic Tern breeding data collected at Nasaruvaalik Island, Nunavut.

Table A - 1. Clutch sizes of Arctic Terns breeding at Nasaruvaalik Island.

<table>
<thead>
<tr>
<th>Year</th>
<th>Clutch size</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>6 eggs 19 eggs</td>
</tr>
<tr>
<td>2003</td>
<td>2 eggs 23 eggs</td>
</tr>
<tr>
<td>2004</td>
<td>2 eggs 18 eggs</td>
</tr>
<tr>
<td>2005</td>
<td>3 eggs 22 eggs</td>
</tr>
<tr>
<td>2006</td>
<td>1 egg 14 eggs</td>
</tr>
<tr>
<td>2007</td>
<td>65 eggs 199 eggs</td>
</tr>
<tr>
<td>2008</td>
<td>48 eggs 266 eggs</td>
</tr>
<tr>
<td>2009</td>
<td>44 eggs 48 eggs</td>
</tr>
<tr>
<td>2010</td>
<td>55 eggs 58 eggs</td>
</tr>
</tbody>
</table>

Table A - 2: Morphometrics (means ± SE) of Arctic Tern eggs on Nasaruvaalik Island. 2007 eggs were of unknown laying order, and weights were not taken. Weights in 2008 to 2010 were taken on finding the egg, in most cases, within a day of laying.

<table>
<thead>
<tr>
<th>Year</th>
<th>Length</th>
<th>Breadth</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>40.70 ± 0.08</td>
<td>29.44 ± 0.04</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>n 443</td>
<td>n 443</td>
<td>n --</td>
</tr>
<tr>
<td>2008</td>
<td>40.41 ± 0.14</td>
<td>29.37 ± 0.05</td>
<td>18.14 ± 0.09</td>
</tr>
<tr>
<td></td>
<td>n 245</td>
<td>n 245</td>
<td>n 237</td>
</tr>
<tr>
<td>2009</td>
<td>40.45 ± 0.21</td>
<td>29.67 ± 0.06</td>
<td>17.91 ± 0.10</td>
</tr>
<tr>
<td></td>
<td>n 183</td>
<td>n 183</td>
<td>n 175</td>
</tr>
<tr>
<td>2010</td>
<td>40.44 ± 0.27</td>
<td>29.28 ± 0.10</td>
<td>18.08 ± 0.15</td>
</tr>
<tr>
<td></td>
<td>n 45</td>
<td>n 45</td>
<td>n 42</td>
</tr>
</tbody>
</table>

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Table A - 3: Arctic Tern egg volume indices of paired first and second-laid eggs calculated according to the equation: $EV = length \times breadth^2$

<table>
<thead>
<tr>
<th>Year</th>
<th>Paired A Mean ± SE</th>
<th>Median</th>
<th>25th, 75th</th>
<th>Paired B Mean ± SE</th>
<th>Median</th>
<th>25th, 75th</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>34.81 ± 0.21</td>
<td>34.92</td>
<td>33.23, 34.16</td>
<td>34.33 ± 0.19</td>
<td>34.06</td>
<td>32.57, 35.82</td>
<td>183</td>
</tr>
<tr>
<td>2009</td>
<td>35.13 ± 0.49</td>
<td>35.61</td>
<td>34.73, 34.80</td>
<td>34.92 ± 0.23</td>
<td>35.10</td>
<td>32.91, 37.14</td>
<td>45</td>
</tr>
<tr>
<td>2010</td>
<td>34.75 ± 0.30</td>
<td>35.04</td>
<td>33.58, 33.90</td>
<td>34.00 ± 0.31</td>
<td>33.99</td>
<td>35.83, 35.80</td>
<td>57</td>
</tr>
</tbody>
</table>

Table A - 4: Pooled egg and first-laid egg volume indices of Arctic Terns at Nasaruvaalik Island.

<table>
<thead>
<tr>
<th>Year</th>
<th>Combined A and B Mean ± SE</th>
<th>Median</th>
<th>25th, 75th</th>
<th>First egg Mean ± SE</th>
<th>Median</th>
<th>25th, 75th</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>35.34 ± 0.14</td>
<td>35.16</td>
<td>33.73, 37.04</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2008</td>
<td>34.67 ± 0.16</td>
<td>34.54</td>
<td>33.01, 36.29</td>
<td>34.92 ± 0.23</td>
<td>35.10</td>
<td>33.47, 36.48</td>
<td>245</td>
</tr>
<tr>
<td>2009</td>
<td>35.34 ± 0.26</td>
<td>35.69</td>
<td>33.57, 37.60</td>
<td>35.66 ± 0.31</td>
<td>35.97</td>
<td>34.21, 37.90</td>
<td>87</td>
</tr>
<tr>
<td>2010</td>
<td>34.38 ± 0.28</td>
<td>34.65</td>
<td>33.00, 36.01</td>
<td>34.61 ± 0.38</td>
<td>35.03</td>
<td>33.52, 36.18</td>
<td>111</td>
</tr>
</tbody>
</table>

Table A - 5: Chick growth rates.

<table>
<thead>
<tr>
<th>Year</th>
<th>Weight growth rate Mean ± SE</th>
<th>Median</th>
<th>25th, 75th</th>
<th>n</th>
<th>Wing growth rate Mean ± SE</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>7.24 ± 0.53</td>
<td>7.88</td>
<td>5.38, 8.51</td>
<td>13</td>
<td>7.31 ± 0.63</td>
<td>13</td>
</tr>
<tr>
<td>2010</td>
<td>-3.24 ± 4.41</td>
<td>-2.05</td>
<td>-11.86, 4.20</td>
<td>4</td>
<td>4.67 ± 1.05</td>
<td>4</td>
</tr>
</tbody>
</table>

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Table A - 6: Adult body weight was used as a proxy for body condition.

**Adult weight (g)**

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean ± SE</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>110 ± 0.80</td>
<td>96</td>
</tr>
<tr>
<td>2008</td>
<td>112 ± 1.85</td>
<td>20</td>
</tr>
<tr>
<td>2009</td>
<td>104 ± 0.95</td>
<td>49</td>
</tr>
<tr>
<td>2010</td>
<td>103 ± 0.53</td>
<td>184</td>
</tr>
</tbody>
</table>

Table A - 7: Number of avian predators observed daily at Nasaruvaalik Island.

<table>
<thead>
<tr>
<th>Year</th>
<th>Prebreeding</th>
<th>Incubation</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SE</td>
<td>n</td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>2007</td>
<td>3.5 ± 0.39</td>
<td>20 a</td>
<td>3.9 ± 0.47</td>
</tr>
<tr>
<td>2008</td>
<td>6.4 ± 0.64</td>
<td>18 b</td>
<td>4.5 ± 0.55</td>
</tr>
<tr>
<td>2009</td>
<td>3.6 ± 0.34</td>
<td>16 a</td>
<td>5.9 ± 0.60</td>
</tr>
<tr>
<td>2010</td>
<td>7.2 ± 0.56</td>
<td>20 b</td>
<td>18.5 ± 3.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>13.0 ± 1.82</td>
</tr>
</tbody>
</table>
Table A - 8: Morphometrics (means ± SE) of incubating adult Arctic Terns on Nasaruvaalik Island.

<table>
<thead>
<tr>
<th></th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Culmen (mm)</strong></td>
<td>31.15</td>
<td>31.22</td>
<td>30.86</td>
<td>30.47</td>
</tr>
<tr>
<td>± 0.16</td>
<td>± 0.34</td>
<td>± 0.25</td>
<td>± 0.14</td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>96</td>
<td>28</td>
<td>49</td>
<td>185</td>
</tr>
<tr>
<td><strong>Head + Bill (mm)</strong></td>
<td>70.49</td>
<td>70.54</td>
<td>70.04</td>
<td>69.63</td>
</tr>
<tr>
<td>± 0.23</td>
<td>± 0.45</td>
<td>± 0.36</td>
<td>± 0.19</td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>92</td>
<td>28</td>
<td>49</td>
<td>186</td>
</tr>
<tr>
<td><strong>Bill Depth (mm)</strong></td>
<td>6.94</td>
<td>7.12</td>
<td>6.98</td>
<td>6.84</td>
</tr>
<tr>
<td>± 0.03</td>
<td>± 0.07</td>
<td>± 0.05</td>
<td>± 0.03</td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>93</td>
<td>28</td>
<td>48</td>
<td>186</td>
</tr>
<tr>
<td><strong>Tarsus (mm)</strong></td>
<td>15.56</td>
<td>15.88</td>
<td>15.77</td>
<td>15.96</td>
</tr>
<tr>
<td>± 0.09</td>
<td>± 0.18</td>
<td>± 0.10</td>
<td>± 0.09</td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>100</td>
<td>28</td>
<td>49</td>
<td>82</td>
</tr>
<tr>
<td><strong>Wing (mm)</strong></td>
<td>270</td>
<td>270</td>
<td>267</td>
<td>265</td>
</tr>
<tr>
<td>± 0.70</td>
<td>± 1.41</td>
<td>± 0.92</td>
<td>± 0.50</td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>99</td>
<td>28</td>
<td>49</td>
<td>186</td>
</tr>
<tr>
<td><strong>Tail streamer</strong></td>
<td>180</td>
<td>176</td>
<td>174</td>
<td>173</td>
</tr>
<tr>
<td>± 1.31</td>
<td>± 2.35</td>
<td>± 1.56</td>
<td>± 0.92</td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>97</td>
<td>28</td>
<td>49</td>
<td>178</td>
</tr>
<tr>
<td>5th retrix (mm)</td>
<td>--</td>
<td>122</td>
<td>123</td>
<td>121</td>
</tr>
<tr>
<td>± 1.62</td>
<td>± 1.09</td>
<td>± 0.58</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>--</td>
<td>28</td>
<td>49</td>
<td>185</td>
</tr>
<tr>
<td><strong>Tail fork (mm)</strong></td>
<td>--</td>
<td>72</td>
<td>73</td>
<td>71</td>
</tr>
<tr>
<td>± 0.76</td>
<td>± 0.48</td>
<td>± 0.41</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>--</td>
<td>28</td>
<td>49</td>
<td>186</td>
</tr>
</tbody>
</table>
Table A - 9: Clutch sizes of Arctic Terns breeding at colonies across the High Arctic

<table>
<thead>
<tr>
<th>High Arctic location</th>
<th>Year(s) of study</th>
<th>Mean clutch size ± SE</th>
<th>n</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resolute Bay, NU</td>
<td>1969</td>
<td>1.5 ± 0.29</td>
<td>4</td>
<td>Geale 1971</td>
</tr>
<tr>
<td>Sand Island, Greenland</td>
<td>2007-2008</td>
<td>1.6 ± 0.04*</td>
<td>169</td>
<td>Egevang 2010</td>
</tr>
<tr>
<td>Truelove Lowland, Devon Island, NU</td>
<td>1967</td>
<td>1.6 ± 0.11</td>
<td>22</td>
<td>Montecvecchi 1993, Hussell and Holroyd 1974</td>
</tr>
<tr>
<td>Bylot Island, NU</td>
<td>1954</td>
<td>1.6 ± 0.12</td>
<td>18</td>
<td>Drury 1960</td>
</tr>
<tr>
<td>Svalbard</td>
<td>1967, 1970</td>
<td>1.8 ± 0.01*</td>
<td>152</td>
<td>Piatt et al. 2007, Bengtson 1971, Lemmytyinen 1972</td>
</tr>
<tr>
<td>Nasaruvaalik Island, NU</td>
<td>2002-2010</td>
<td>1.8 ± 0.02</td>
<td>893</td>
<td>this study</td>
</tr>
<tr>
<td>Southampton Island, NU</td>
<td>1929 – 1930, 2010</td>
<td>1.6 ± 0.05</td>
<td>57</td>
<td>Sutton 1932, Mallory pers. comm.</td>
</tr>
</tbody>
</table>

* these represent the means of means from each year these sites were studied
§ SE at these sites are derived from the mean of means.
† SE at Sand Island was the same in each year; this is what is reported for this site.

Literature cited


Egevang, C. 2010. Migration and breeding biology of Arctic terns in Greenland. PhD. thesis. Greenland Institute of Natural Resources, Department of Arctic Environment, National Environmental Research Institute, Aarhus University and Department of Biology, Center for Macroecology, Evolution and Climate, University of Copenhagen. Aarhus University, Denmark.


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M.Sc., Biology, University of New Brunswick, 2012

Refereed Publications:


Non-refereed Publications:


Conference Presentations: