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Individual-Level Responses to Rapid Climate Change in Common Terns (Sterna hirundo) and Arctic Terns (Sterna paradisaea)

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Abstract

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Keywords

seabirds, intraspecific variation, Gulf of Maine, sea surface temperature, climate change

Disciplines

Environmental Indicators and Impact Assessment | Environmental Monitoring | Evolution

Comments

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Individual-Level Responses to Rapid Climate Change in Common Terns (*Sterna hirundo*) and
Arctic Terns (*Sterna paradisaea*)

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Abstract

This study examines fine-scale environmental changes and intraspecific variation in the diet and foraging behavior of two seabirds in the Gulf of Maine, one of the fastest-warming regions of the ocean. This variation on the individual level, or behavioral plasticity, may help long-lived species to persist in rapidly changing environments. As the water warms, seabirds' preferred prey (hake and herring) follow cooler waters deeper and farther offshore. It is unlikely that all individuals respond to changing food availability in the same way. For common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*) breeding on Petit Manan Island, I hypothesized that: H1: Preferred prey decline in the diet as sea surface temperature (SST) increases; H2: Individuals vary in their response to increasing SST; H3: Individual-level diet influences fitness. In June and July of 2022, we conducted daily chick provisioning watches and recorded prey size and species. While SST did not influence average feeding rate, increased SST drove declines in the average prey size and the proportion of hake and herring in the diet at the colony level (H1 supported). Slopes were similar across nests, suggesting no individual variation in diet plasticity with increasing SST (H2 not supported). At the nest level, a higher average proportion of herring and hake was associated with higher chick mortality and a declining growth rate. A higher average feeding rate was associated with an increase in growth rate while prey size did not impact chick growth rate (H3 not supported). Our findings suggest that individuals that try to maintain a diet of preferred prey may have lower fitness in a changing climate. However, individuals that decrease their foraging distance and prey switch to maintain a sufficient feeding rate are successful in raising chicks that reach fledging age.

Introduction

Climate change has resulted in steadily increasing sea surface temperatures in many regions, in addition to temporary sea surface temperature extremes ("marine heatwaves"), both of which pose a threat to marine habitats and the organisms that populate them (Ottersen et al., 2023). To survive in this changing world, animals must be able to rapidly adapt. When the abiotic factors of their environment change, some species may adapt by shifting the distributions in time or space to reduce mismatch with their prey (Evans & Moustakas, 2018). In addition to these two larger-scale adjustments, organisms can show behavioral plasticity, or the ability to adjust behavior based on environmental conditions, in their foraging and diet. Behavioral plasticity is an important mechanism for adapting to climate change, especially for long-lived species whose evolutionary rate is not able to keep pace with climate change (Karkarey et al., 2017).

Seabirds are long-lived species that return to land to breed, allowing for long-term studies to be conducted at recurring colonies. As an important group of marine megafauna who connect marine systems to terrestrial systems during the breeding season, seabirds must adjust to changes in both environments. They exist as a top predator in many marine ecosystems, so their population dynamics reflect changes in lower trophic levels (Parsons et al., 2008). Seabirds are therefore excellent indicators of changes in marine ecosystems because they are easily monitored (Robertson, 2014) and display observable, rapid changes in breeding, population, and diet in response to altered food availability (Yakola, 2019).

When preferred seabird prey are available, all individuals are likely to focus their diet on these prey. When food availability declines, however, individuals may differ in their response;

this is known as intraspecific variation, or variation among individuals of the same species. On the Newfoundland coast, for example, scientists have observed shifts in intraspecific variation in seabird diet due to changes in food availability. Capelin (*Mallotus villosus*), a forage fish that acts as a key prey item for multiple marine megafauna in this system, increases in availability during the summer months (Gulka et al., 2017). When these prey are available (mid-July to mid-August), variation in diet among individuals is low, leading to a small dietary niche. However, diet is much more variable early in the season, prior to the arrival of capelin, suggesting that individuals differ in how they cope with low food availability (Gulka et al., 2017). Individual preferences during breeding will not only influence the success of the individual, but will impact the success of populations faced with increasing environmental change.

This study examines plasticity in the diet in two species of terns, a surface-feeding seabird, in the Gulf of Maine. The Gulf of Maine is one of the fastest warming regions of the global ocean, and coastal temperatures there have been continually increasing over the past 40 years (Nye, 2010). The Gulf of Maine waters entered a period of rapid warming in 2005, accentuated by heatwaves in 2012, 2016, and 2018 (Pershing et al., 2021). The hottest year in the Gulf of Maine was 2021, and 97% of the year 2022 constituted a marine heatwave (Mills et al., 2023). Spring is arriving earlier, causing a shorter winter, while fall arrives later, extending the summer (Nye, 2010; Pershing et al., 2021). Previous research has shown that changes in the spring thermal transition in this region are leading to temporal mismatches between breeding seabirds and their prey (Yakola 2019).

In addition to temporal shifts, this increase in temperatures leads to spatial shifts of many fish species. The Gulf of Maine has traditionally been categorized as a subarctic ecosystem,

receiving cold water from Northeast; however, the region has recently been receiving an influx of warmer waters (Pershing et al., 2021). This change from subarctic to temperate waters affects the species of fish that are present. Subarctic species have declined while more mid-Atlantic species have moved into the Gulf of Maine (Pershing et al., 2021). With this altered availability of fish species, seabird diets will change, with implications for breeding success (Scopel et al., 2019). The preferred water temperature range of the prey of Gulf of Maine seabirds is generally 5-15°C, but summer water temperatures now often exceed these limits (Nye, 2010). When sea surface temperatures rise, fish chase cooler waters by moving farther offshore and deeper in the water column. To remain in their ideal temperature range, stocks have also shifted their ranges north (Nye, 2010).

Many seabird species live and breed in the Gulf of Maine, two of which are common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*). Terns are small, migratory, surface-feeding species (Robertson, 2014) that generally only carry one prey item in their bill at a time (Yakola, 2019). Like all seabirds, terns are central-place foragers and must return to their breeding colonies to feed their chicks. In other systems, common terns forage 20-30 km from their colony while Arctic terns forage closer, only traveling about 3-10 km from the colony (Eglington and Perrow, 2014). These limited ranges place a constraint on foraging terns when preferred provisioning fish like hake, herring, and sand lance (Yakola, 2019) move away from their coastal breeding colonies. Importantly, because terns are also constrained to foraging at the surface of the water, they cannot adjust their behavior by diving deeper like some other seabird species.

Tern chick diets in the Gulf of Maine are largely composed of fish, with diets consisting of about 57% hake and herring for common tern chicks and 62% hake and herring for Arctic tern

chicks (USFWS, 2022). Besides their preferred fish, common and Arctic terns will also eat crustaceans and insects (Eglington and Perrow, 2014). Previous research has found that euphausiids (krill) were a poor food item for seabirds and negatively affected the condition of the chicks (Scopel et al., 2019). Warming sea surface temperatures are associated with a lower percentage of preferred prey like hake in tern chick diets and a higher percentage of suboptimal prey like invertebrates and butterfish, a deep-bodied fish (Yakola, 2019).

To be able to successfully raise chicks, adult terns must adjust to the quantity and movement of hake, herring, and other preferred prey. On the Gulf of Maine Islands, an increase in species richness in common tern and Arctic tern diets (Yakola, 2019) has revealed that some individuals expand their dietary niches when preferred food items are low in abundance. Yakola (2019) also found diet diversity to be highest in Arctic terns when compared to common, least, and roseate terns; this diet diversity was driven by the Arctic terns also provisioning the largest proportions of invertebrates. Interestingly, the Arctic tern was found to have the lowest $\delta^{13}C$ and $\delta^{15}N$ signatures in comparison to common and roseate terns across seven islands in the Gulf of Maine; these signatures indicate more offshore foraging and lower trophic level foraging, respectively, as compared to the other two tern species (Bratton et al., 2022).

Although seabird responses in the Gulf of Maine have been tracked at the population level, there has not been much research into how individuals differ in their response. As prey availability changes, some individuals may maintain the same foraging areas and trips but bring back different prey (Maynard et al., 2021). Other individuals may forage farther to continue bringing back more energy-rich food items (Robertson, 2014). This flexibility, or lack thereof, can influence the survival of seabird chicks, but we have little understanding of which types of

plasticity are adaptive and which are maladaptive. Understanding individual-level behavior will help us to predict how species will respond to rapid climate change.

Objectives

My overall goal is to examine and quantify patterns in intraspecific variation in diet and foraging behavior in the face of rapid environmental change and to test whether this variation is linked to fitness. Linking individual variation with fine-scale environmental data will provide insight into intraspecific changes that can be hidden in colony or species-level provisioning data. Here, I pose three hypotheses to examine the relationships between diet, sea surface temperature, and reproductive success at the colony and individual level:

Hypothesis 1: With rising sea surface temperatures, preferred food items of seabirds are moving farther away from the coast and into deeper water. I predict that, as sea surface temperatures increase throughout the season and during marine heatwaves: the proportion of preferred food items (herring and hake) in tern diets will decrease (H1.1), the proportion of invertebrates in the diet will increase (H1.2), the average prey size will decrease (H1.3), and the average feeding rate will increase (H1.4).

Hypothesis 2: When sea surface temperatures increase, there will be differences in the way individuals adjust their diet and behavior to adapt to these changes. I predict that intraspecific variation in diet, as measured by diet diversity (Shannon-Wiener Index; H2.1) will increase when sea surface temperature increases. Additionally, I predict that individuals will vary in their diet flexibility, or in how much they change their diet in response to environmental change (i.e., that the slopes of the relationships predicted in Hypothesis 1 will differ across individuals; H2.2).

Hypothesis 3: How an individual changes their diet will influence the growth rate and survival of their chicks. I predict that individuals that feed their chicks a diet high in preferred food items (herring and hake) will have chicks with a higher survival rate (H3.1) and growth rate (H3.2). Similarly, I predict survival and growth rates to be positively correlated with average prey size (H3.3-H3.4) and feeding rate (H3.5-H3.6).

Methods

The fieldwork for this study took place in June and July of 2022 and consisted of daily diet watches as well as chick growth measurements. Statistical analysis was performed through the end of the year to examine diet variability and chick success in the context of environmental data.

Study Area

Here, I focus on one breeding colony of sympatrically breeding common and Arctic terns in the Gulf of Maine: Petit Manan Island (PMI; Figure 1). Common and Arctic terns build nests in coastal areas and nest on the surface of the ground. In 2022, there were 1,201 breeding pairs of terns on PMI with 752 common tern pairs and 449 Arctic tern pairs (USFWS, 2022). Terns lay eggs in May, raise chicks throughout June and July, and fledge these chicks in July, with the exact dates depending on season.

Since 2005, chick diet data has been monitored on PMI, which allows scientists to track fluctuations in provisioned prey items including hake, herring, and invertebrates. In 2021, chick survival reached historic lows, potentially due to high sea surface temperatures occurring around PMI. At times, these temperatures exceeded 15°C, the high end of the range or above the thermal

tolerance of the tern's preferred prey items. In 2022, sea surface temperatures were higher than the historical average for the entire season (Figures 2-4). There were also several marine heatwave events, marked by rapid and temporary increases in sea surface temperature (Figures 2-4). Anecdotal evidence suggests that some of these events led to mass die-offs, likely due to starvation (e.g., the heatwave on July 19th-20th resulted in widespread mortality of fledged terns).

Field Data Collection

I carried out the fieldwork for this study along with a fellow Gettysburg College student and three other island staff. Handling of birds was approved through IACUC (#2021S2). We arrived on PMI on June 6th, after the terns had nested and laid eggs. Productivity plots were already set up on the island for regular monitoring of common and Arctic tern nests. Initially, there were five plots chosen for provisioning watches, with two of these plots also being productivity plots. Due to irregular provisioning of three of the plots, only two plots were selected for daily provisioning watches and regular productivity monitoring. One plot contained four common tern nests and the other plot contained six Arctic tern nests.

We started provisioning watches when the first chick hatched within the plot. Plots were observed daily for three hour stints from 6-9am from June 23 to July 26. After setting up for a stint, we waited ten minutes to allow birds to settle before recording data. We recorded the stint length and, for each feeding, the nest number and the chick that received the prey item. Prey items were identified to the species level, and the length of the prey item was estimated as a ratio to the culmen length of the parent.

To track chick growth, we took measurements of chicks every other day from hatching to fledging. These data were used to calculate a linear growth rate for mass and for wing chord, based on the linear phase of chick growth (4-14 days old). Wing chord was measured in centimeters using an Avinet wing ruler and mass was measured in grams by using Pesola spring scales that varied in size (50 g, 100 g, and 300 g) depending on chick mass. Fate was based on whether the chick was found dead or was seen at fledging size before disappearing, in which case it was marked as fledged.

Because tern parents are difficult to identify, I was unable to look at individual-level data for chick provisioning. Therefore, I defined individuality at the nest-level, determined by nest plot location and nest number. Parameters used for analysis included prey item, prey size, feeding rate, and fledgling success (Table 1). Prey items were grouped as fish, invertebrate, and unknown. For species-level analyses, herring and hake were grouped into one category ("H or R"). It can be difficult to differentiate hake and herring in the field due to factors such as high vegetation and quickness of prey consumption, so "H or R" is a prey item option on provisioning sheets. Additionally, these are both considered optimal prey for terns. Average feeding rate, average prey size, and percent of hake and herring in diet were calculated at the colony and individual levels, while diet diversity was only calculated at the colony level (see below).

Statistical Analysis

I used RStudio for all statistical analyses (Table 2). Tern productivity data and diet data were loaded into R, as well as daily sea surface temperature (SST) data from the Multi-scale Ultra-high Resolution (MUR) satellite. The spatial resolution for these data is 0.01° and the temporal resolution is daily (NASA, 2015). These SST data were averaged daily across a 20 km

buffer around the island to coincide with the general foraging ranges of the terns, as there is no

information on the core foraging locations for this colony. Preliminary analyses also included

SST anomaly data for the same region. These analyses suggested that SST was a better predictor

than SST anomaly, so SST anomaly was not used in the full suite of models.

Hypothesis 1: Colony-Level Shifts in Diet

For colony-level analysis, I used fixed effects linear models to test for the best-supported

predictors of the following independent variables: percent of hake and herring in the diet (H1.1),

proportion of invertebrates (H1.2), prey size (H1.3), and feeding rate (H1.4). I calculated these

parameters in two ways. Using the first approach, I summed information at the level of day, then

calculated the parameter. For example, using approach one, the proportion of herring and hake

for a given date would be calculated by summing all "H", "R", or "H or R" fed at all nests on a

given date and dividing by the total number of prey items (fish or invertebrate) fed at all nests on

that date. For approach two, I first calculated metrics at the nest level (e.g., the number of herring

or hake provisioned at a nest, divided by the total number of items provisioned at that nest), then

averaged these values across nests for each date. These two approaches yielded very similar

results (r^2 values of >0.90), so I decided to use the first approach for all colony-level analyses.

I ran a suite of models for each of these parameters that included a null model and models

with dependence on species, SST mean, additive effects of these variables, and multiplicative

effects of these variables. I used AIC to choose the best supported model and noted slope, 95%

confidence intervals for each predictor, and model p-value. Models within 2 AIC of each other

were considered equally supported and, in these cases, the simpler model is the model that I

report.

Hypothesis 2: Individual-Level Shifts in Diet

I used the Shannon-Wiener Diversity Index ($H = -\sum_{i=1}^{s} p_i * lnp_i$) to quantify intraspecific

diet diversity, where *s* is number of prey item species and p_i is the proportion of individuals of

species *i* (H2.1). For this diversity measurement, I only looked at feedings where the prey item

was fish and I grouped herring and hake as one species for the reasons described above.

For individual-level response analysis, I used mixed effects linear models for the percent

of hake and herring in the diet, prey size, and feeding rate. For this analysis, I calculated all

parameters at the nest level. I compared the same suite of fixed effects as above (species, SST,

and their interaction), but also added random effects terms to test for individual-level differences

in intercept (average individual differences) and slope (differences in individual-level responses)

(H2.2). I compared models with and without random effects terms to determine whether

individuals differed significantly in their diet and dietary responses, based on AIC.

Hypothesis 3: Links Between Diet and Fitness

I used the linear growth rate (LGR) of chick mass and chick fate (dead or fledged) as

measures of reproductive success. I ran fixed effects models with LGR as a dependent variable

and feeding parameters as independent variables (hake and herring in the diet (H3.2), prey size

(H3.4), and feeding rate (H3.6)) to test for the effects of diet on fitness. These models were also

run with species, chick, and fate as additive and multiplicative factors. Additionally, I used a

t-test to examine whether feeding parameters (hake and herring in the diet (H3.1), prey size

(H3.3), and feeding rate (H3.5)) varied between chicks that died and those that fledged.

Results

There were 1,066 feeding observations total for all nests. The most common prey items were 249 hake, 281 herring, and 168 hake or herring. There were 254 unknown items (unknown, unknown fish, unknown invertebrate). Feeding rates ranged from 0.625 to 4.924 prey items per hour, with a mean of 1.87 ± 0.183 across dates.

Hypothesis 1: Colony-Level Shifts in Diet

The percent of hake and herring in tern diets significantly decreased as SST increased. The best supported model for percent of herring and hake in the diet at the colony level included additive effects of SST and species (H1.1, AIC = -39.24). The next-best model, which had similar support, was the multiplicative for SST and species (ΔAIC = -0.22). Here, I report results using the less complex of these models, the additive model. For every 1°C increase in sea surface temperature, there was a 15% decrease in herring and hake in the diet of terns (b= -0.150, CI_{95} [-0.253, -0.046] , p = 0.006) (Figure 5). Though slopes with SST were similar, common terns provisioned fewer herring and hake on average (0.475 ± 0.183 proportion) than did Arctic terns (0.557 ± 0.118 proportion).

There were 19 stints that contained invertebrate feedings (50 invertebrates total, 36 unknown), but no further analyses were conducted with these data due to low sample sizes (H1.2). I did, however, find that prey size decreased as SST increased. The best supported model for prey size at the colony level was also an additive effects model with SST and species (H1.3, AIC = -45.72). The second-best supported model included only SST (ΔAIC = -1.59). Here, I report the best-supported model. At the colony level, the average prey size decreases by 0.11

culmen lengths with every 1° increase in sea surface temperature (b = -0.11, CI$_{95}$ [-0.206, -0.0145], p = 0.025). The rate of decrease for prey size was similar for both species, but common terns fed slightly larger prey (1.053 ± 0.128) than Arctic terns (0.979 ± 0.147) (b = 0.076, p = 0.07) (Figure 5).

Feeding rate at the colony level was also impacted by SST. The best supported model for average feeding rate included an additive interaction between SST and species (H1.4, AIC = 128.71). I report the second-best supported model (ΔAIC = 0.117) because it contained fewer variables and had a very close AIC to the best-supported model. At the colony level, species was the only significant driver of feeding rate (b = 0.643, CI$_{95}$ [0.234, 1.052], p = 0.003). Common terns fed more items per hour (2.167 ± 0.85) than Arctic terns (1.525 ± 0.610) (b = 0.548, p = 0.013).

Hypothesis 2: Individual-Level Shifts in Diet

The best supported model for intraspecific variation using Shannon-Wiener (SW) diversity index used multiplicative effects of SST and species (H2.1, AIC = 150.33). The range of SW values observed across the season was 0.00 to 1.33, with a mean of 0.413. With every 1°C increase in sea surface temperatures, the SW diversity index decreased by about 0.25 (b = -0.253, p = 0.004) (Figure 6). There was a significant decrease in diet diversity for Arctic terns with increasing SST but this relationship was not significant for common terns.

At the individual level, species was the only significant driver of hake and herring in the diet (H2.2, b = -0.104, CI$_{95}$ [-0.176, -0.033], p = 0.004) (Figure 7). Models that included individual-level slopes and intercepts performed worse than those that did not. Therefore, though individuals did vary in the average herring and hake in their diet, and visually in the slopes of

these parameters, these differences were not significant. The best supported model for prey size at the individual level included the effect of SST (AIC = -10.625). Using this model, prey size declined at the same rate as using the colony-level model, with a 0.11 decrease in culmen length with each 1° C increase in SST (H2.2, b = -0.117, CI_{95} [-0.2, -0.034], p = 0.006) (Figure 7).

Hypothesis 3: Links Between Diet and Fitness

The best supported model for the impact of herring and hake in diet on the LGR of chicks included a multiplicative effect between proportion herring and hake, species, and chick hatch order (H3.2, AIC = 62.41). Here I report the second-best model and equally supported model (ΔAIC =1.50) which contained only the effect of the proportion of herring and hake. With every 1% increase of the amount of hake and herring in the diet, the linear growth rate of chicks decreased by 0.08 grams/day (b = -0.083, CI_{95} [-0.154, -0.012], p = 0.025) (Figure 8). Additionally, chicks that died had a higher percentage of hake and herring in the diet (82.58 ± 6.82) than chicks that fledged (64.00 ± 9.17) on average (H3.1, t = 4.62, p < 0.001) (Figure 9).

The best-supported model for average prey size and mass LGR was the null model (H3.6, AIC = 67.85), suggesting that average prey size did not impact mass LGR (Figure 8). However, chicks that died were fed prey that were significantly larger (1.11 ± 0.078) than chicks that fledged (0.99 ± 0.086), on average (H3.5, t = 2.82, p = 0.02) (Figure 10).

The best supported model for feeding rate and growth rate had no additional predictors (H3.4, AIC = 57.055). The linear growth rate of chicks was positively correlated with feeding rate; every additional item fed per hour led to chicks growing 5.87 grams more per day (b = 5.87, CI_{95} [2.830, 8.913], p < 0.001) (Figure 11). Chicks that died were fed at a lower rate (0.669 ±

0.138) than chicks that fledged (0.95 ± 0.216) on average (H3.3, t = -3.172, p = 0.007) (Figure 12).

Due to the unexpected relationships between herring and hake in the diet and chick growth rate and survival, I added several post-hoc tests. I tested the relationship between herring and hake in the diet and feeding rate in June and July separately, given differences in food availability during these two months. I found that feeding rate is negatively correlated with hake and herring in the diet during both months (Figure 13). But in July only, feeding rate and linear growth rate are positively correlated (Figure 14). Feeding rate seems to be driving growth rate and, because feeding rate and the proportion of herring and hake are negatively correlated, growth rate and the proportion of herring and hake are negatively correlated.

Discussion

I found that, with rising sea surface temperatures, common and Arctic terns are needing to adapt to the location shifts of their prey items, impacting their foraging behavior and in turn their ability to successfully raise chicks. Seabird populations are quickly declining from climate change effects, both from direct weather changes, and indirect changes of availability of prey (Ottersen et al., 2023; Paleczny et al., 2015). Changes in sea surface temperature have reduced prey availability in the Atlantic as species shift north and move deeper within the water column (Robertson, 2014). Previous research has shown changes in spatial distribution of larval fish, moving northward along the Northeast shelf (Walsh et al., 2015) and poleward shifts of marine fish biomass (Nye et al., 2009). These shifts of fish stocks have been seen in changes of diet composition across seasons in the Gulf of Maine, with a general decrease of hake and herring for common terns and Arctic terns since 2018 (USFWS, 2022). Here, I expanded on this work to

show that the within-season diet of terns is influenced by sea surface temperature. Though there were visually apparent differences in individual-level responses, these differences were not statistically significant. Additionally, diet sometimes had unexpected relationships on chick growth and survival parameters, highlighting the nuanced relationship between diet flexibility and fitness.

Dietary Changes at the Colony Level

As in previous studies, hake, herring, and sand lance were found to be the dominant prey items of common and Arctic terns (Yakola, 2019). In both species, however, feedings consisted of fewer hake and herring as the season progressed. Arctic terns did feed slightly more preferred food items than did common terns which brought back a greater diversity of fish species, as also seen in other studies (Yakola, 2019). I found a low proportion of invertebrates and butterfish in the diet of these two species. I did find that common terns fed larger prey on average than did Arctic terns, in agreement with previous research in the North Sea, where Arctic terns provisioned more juvenile fish than common terns (Robertson, 2014).

My results suggest that 2022 was an overall "good food" year for terns in the Gulf of Maine. The proportion of the diet made up of herring and hake was slightly higher in 2022 than in 2021 and the proportion of the diet made up of invertebrates was considerably lower (USFWS, 2022). The linear growth rates of chicks were higher for common terns in 2022 than in 2021, but lower for Arctic terns. Most importantly, fledgling rates in 2022 were more than double those in 2021 for both common and Arctic terns (USFWS, 2022).

Though food availability was generally high in 2022, it was still negatively impacted by increases in SST. As waters warmed throughout the season and during marine heatwave events,

terns fed chicks less herring and hake and smaller prey items. This reduction in prey size was met with an increase in feeding rate, suggesting that tern parents were attempting to adapt to reductions in preferred prey (large herring and hake) by feeding their chicks smaller, less optimal prey (larval fish, invertebrates) more frequently. The impacts of SST on diet were drastic, with each 1℃ leading to a 15% reduction in herring and hake in the diet and a 10% reduction in prey size. The magnitude of these changes have serious implications for the ability of terns to adapt to climate change, given that marine heatwaves led to jumps of up to 3℃ in a two-week period and 1℃ in a one-day period in 2022.

One study on Machias Seal Island, a breeding colony between the Bay of Fundy and the Gulf of Maine, found a negative correlation between abundance of herring in common tern diets, and the abundance of larval herring each previous year, suggesting that tern diet composition responds rapidly to changes in food availability (Diamond and Devlin, 2003). We may be seeing similar events in the waters around PMI, but the risk of foraging farther from the colony and returning without food may not be worth it for the adults, so they switch to feeding non-preferred food items. They may also be participating in 'size-selective' foraging (McLeay et al., 2010), where they forage in different areas to capture different sized prey items for chicks versus self-feeding. However, as chicks become large enough to eat large prey, adults may still be feeding smaller prey items which can have detrimental impacts on chick fledging success.

Individual-Level Responses

If individual terns vary in their plasticity, increases in SST in the Gulf of Maine should drive increases in intraspecific variation in diet. I found that diet diversity decreased with increasing SST, which was not what was predicted. Previous studies have shown both a

shrinkage and expansion of variation in diet in other seabirds in response to changing prey availability. A study in Newfoundland examined the isotopic niches of seabirds before and after Capelin, a common forage fish prey item, arrived in the area. They found that the niche of auks narrowed and trophic diversity decreased as preferred prey items became available, while Leach's storm petrel showed an increase in trophic position of prey items consumed and a broader niche (Jenkins and Davoren, 2021). A weakness of my study is that many of the unknown species of fish or invertebrate are fed during periods of low SST, when prey size declines and prey become more difficult to identify. This issue, coupled with the fact that invertebrates and unknown fishes were not included in the diet diversity calculation, may have influenced my diet diversity results.

I did not find significant differences at the individual level in dietary responses to changes in SST. However, Soldatini et al (2023) found differences between individuals of a diving seabird species, the black-vented shearwater. Individuals responded to variable environmental conditions by adjusting their foraging strategies and diving behavior (Soldatini et al., 2023). Because terns are surface feeders, diving is not a foraging strategy that they can adjust in response to environmental changes. There are two possible explanations for why we are not seeing individual variation. First, there is a substantial amount of noise in data collected at the individual level. During provisioning, nests may have only received one feeding. When looking at parameters like hake and herring in the diet, if the one item was a hake or herring, the diet was considered 100% of that prey item. As a result, these data contain a lot of 0s and 1s that skew the data and make it difficult to parse individual-level trends. Second, there might not be individual variation because the terns may be too constrained by their foraging behavior. As central place foragers, terns must return to the nest after every foraging trip and there may be strong selection

for low plasticity and for retaining the same proportion of hake and herring in the diet, even if that means longer foraging trips and a lower feeding rate.

Implications for Fitness

I found that changes in diet are affecting the fledging success of terns, and in ways that might be unexpected. Chicks that were fed more hake and herring had a lower survival rate and growth rate. Chicks are dependent on their parents for food until fledging, so the success of the adult terns' foraging trips has a direct influence on chick survival. In contrast to my findings, one study found that seabird parents that coordinated short and long foraging times were able to bring food back for the chick regularly, and that this variation in trip length had no effect on chick growth (Wojczulanis-Jakubas et al., 2018). On PMI, tern parents may not be coordinating foraging trips as other seabirds do, and are therefore feeding their chicks more sporadically, decreasing the fledging rate.

As expected, chicks that had a lower average feeding rate had a lower survival rate and lower growth rate. A study examining foraging trips of little auks found that chicks with parents that foraged closer to the colony and were able to maintain a higher feeding rate had a faster growth rate and fledged earlier than those with parents that foraged farther (Jakubas et al., 2013). Tern parents who may be taking shorter foraging trips are bringing back more food items, increasing the chicks' growth rate, suggesting that this might be a better strategy than maintaining optimal prey via greater foraging effort.

When examining chick growth and fate, I found feeding rate negatively correlated with hake and herring in both June and July and that feeding rate positively correlated with linear growth rate in July. Therefore, my unexpected findings about the relationship between the

proportion of preferred prey and chick growth rate and survival is likely driven by the negative relationship between preferred prey and feeding rate. Similarly, in Shetland, when sandeels decreased in abundance, seabirds increased their foraging effort, negatively impacting breeding success (Suddaby and Ratcliffe, 1997).

Terns are facing a trade-off between continuing to feed preferred prey items and maintaining feeding rate. While optimal prey are important for chick survival, feeding rate seemed to be prioritized this year by the terns on PMI. A study in the North Sea examined provisioning rates of guillemots and found that adults were able to maintain a similar feeding rate when the abundance of preferred food items changed, but this did not compensate for the possible reduction in energetic content of the new preferred prey (Smout et al., 2013). Following adult terns with GPS tags would allow us to explore this trade-off in more detail and would allow us to determine whether all tagged individuals follow preferred prey items as they move offshore when sea surface temperatures increase.

Conclusions and Future Analyses

Rising sea surface temperatures are associated with changes in common and Arctic tern diets. Colony-wide decreases in prey size and the proportion of preferred prey items were correlated with rising sea surface temperatures. Nest-level variation was not significant, but when looking at growth rate and survival of chicks, a higher feeding rate was positively correlated with growth rate while a higher proportion of hake and herring in the diet was negatively correlated with growth rate. These unexpected results in chick success can be explored further by examining the energetic values of different fish brought back. This would provide further information on the importance of the nutrient values of prey in relation to other

diet parameters like feeding rate and prey size. Future studies conducted in the Gulf of Maine can link these fine-scale provisioning data to isotope data and tagging data that will provide insight into chick diet beyond provisioning watches. Further connecting these data to adult foraging behavior will provide a more holistic view of the roles that seabirds fill in marine ecosystems and their ability to adapt to a changing environment.

Acknowledgements

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Appendix

Table 1. Parameters used for analyzing provisioning data.

Parameter	Description
Prey Item	Defined by fish species or other group (e.g. invertebrate)
Prey Size	Measured by comparing length of prey item to that of the culmen length of adult bird
Feeding Rate	Number of prey items delivered per hour
Fledgling Success	Chick considered fledged if they are not seen after day 20

Table 2. Packages used in analysis of provisioning data, productivity data, and SST data.

Package	Version
tidyverse	1.3.2
lubridate	1.8.0
broom	1.0.1
lme4	1.1-30
rstatix	0.7.0
patchwork	1.1.2
ggplot2	3.3.6
rerrdap	1.0.2
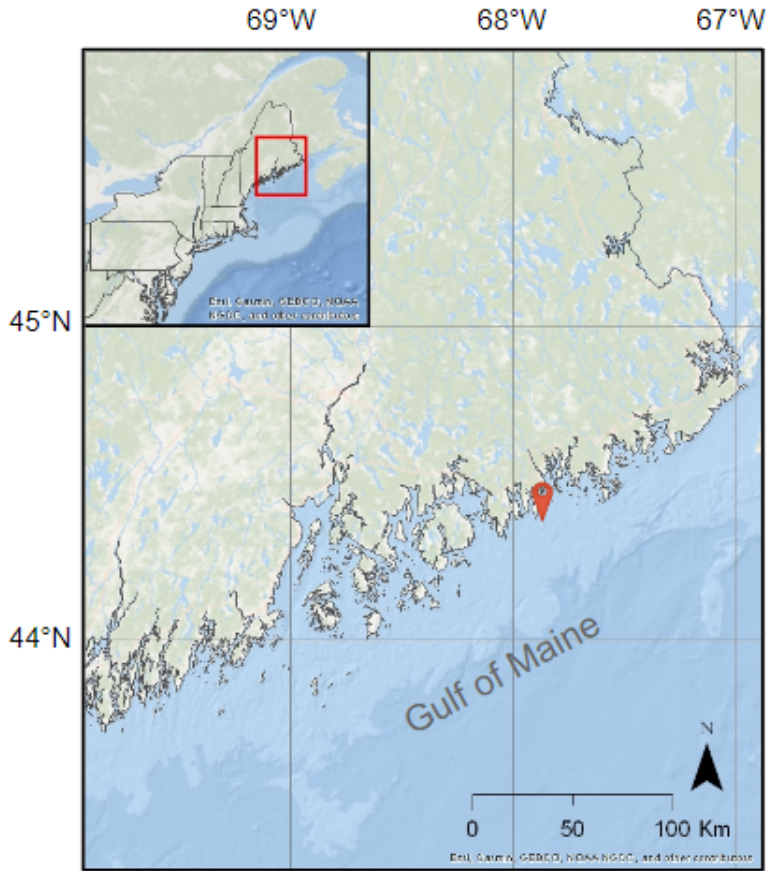
Figure 1: Map of coastal mainland of Maine: red indicator designates location of Petit Manan Island (PMI). PMI is part of the Maine Coastal Islands National Wildlife Refuge (MCINWR) and is owned and managed by the US Fish and Wildlife Service.
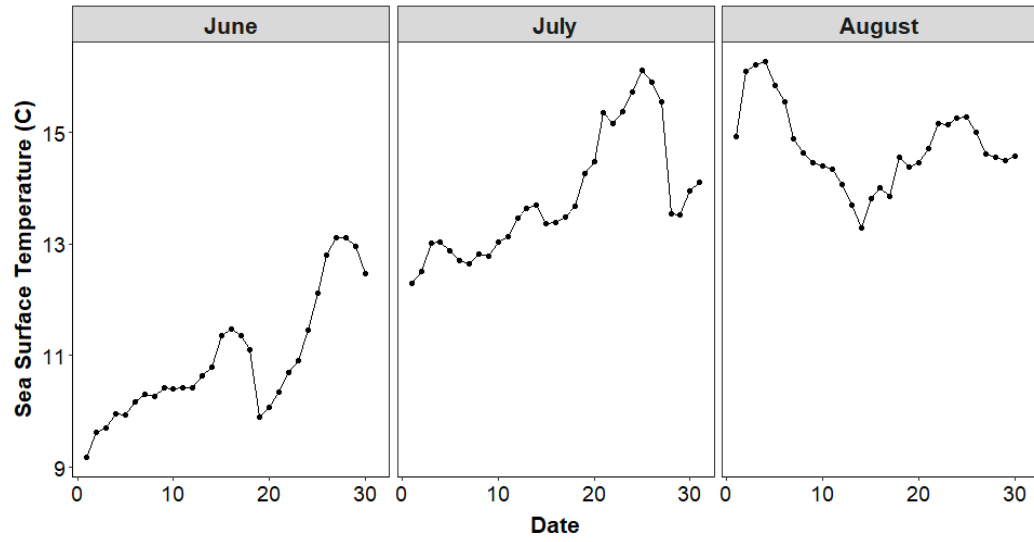
Figure 2: Daily sea surface temperatures (SST) averaged for a 20 km buffer around Petit Manan Island for June, July, and August 2022. SST data from MUR satellite with a daily temporal resolution and spatial resolution of 0.01° (NASA, 2015).
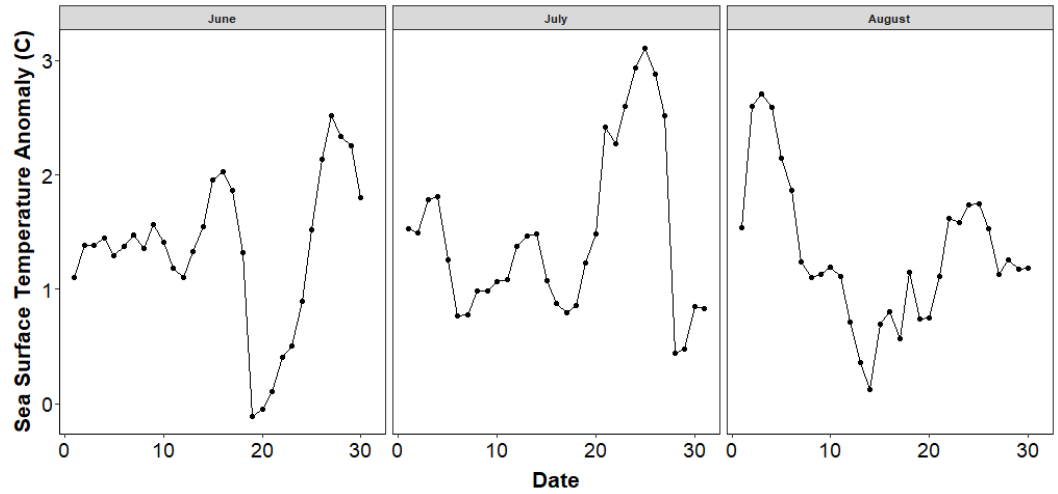
Figure 3: Graph depicting the sea surface temperature (SST) anomaly in °C during June and July of 2022. SST data from MUR satellite with a daily temporal resolution and spatial resolution of 0.01°. The anomaly data is a comparison of 2022 SST data to data from the years of 2003-2014 (NASA, 2015).
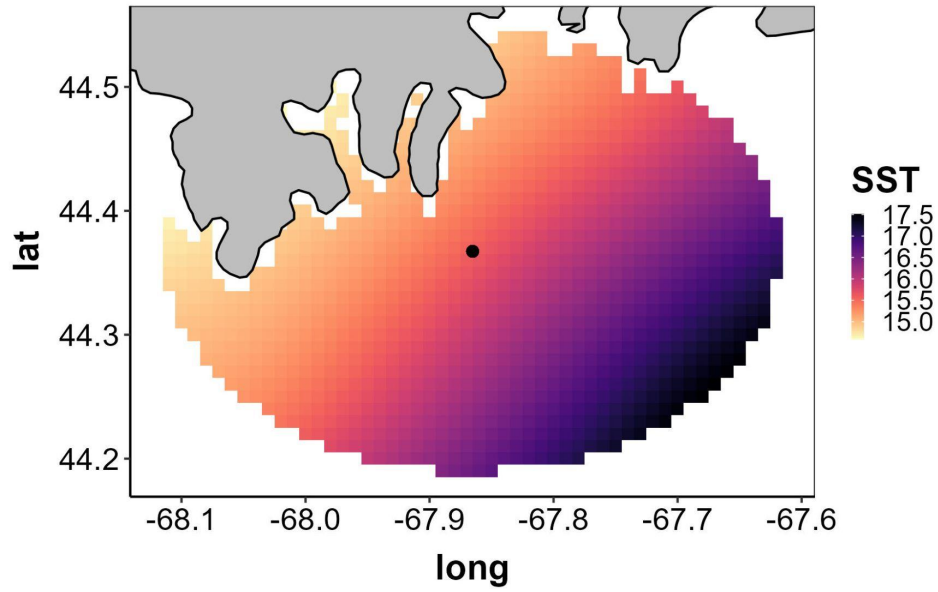
Figure 4: Sea surface temperature for the 20km buffer around Petit Manan Island for one of the

warmest days in the summer of 2022, July 25. SST data were taken from the MUR satellite,

which has a daily temporal resolution and spatial resolution of 0.01° (NASA, 2015).
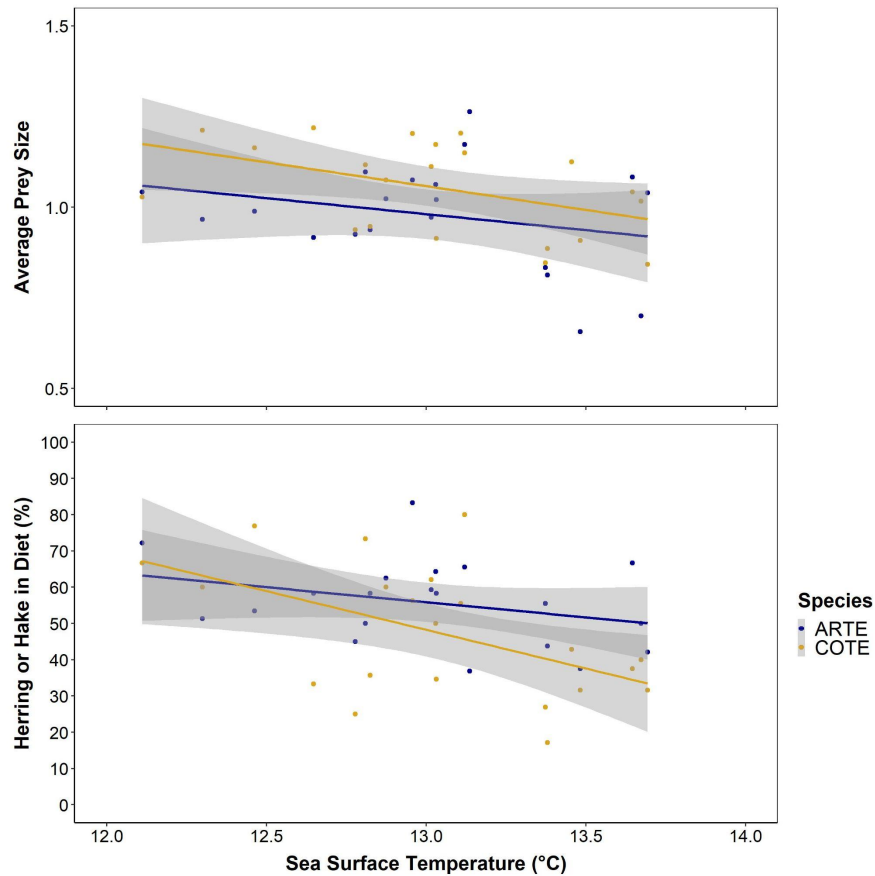
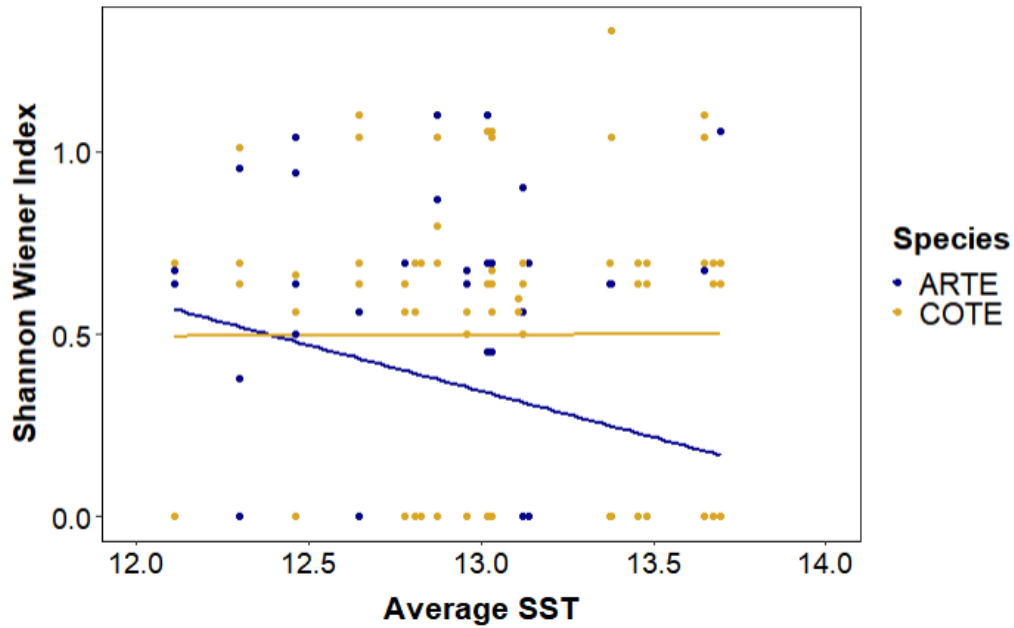Figure 5: Colony-level relationships between sea surface temperature (SST) and herring or hake in the diet and prey size for common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*) breeding on Petit Manan Island, Maine. Prey size and species were determined during three-hour provisioning stints from June 23 through July 26, 2022 and each point represents one stint (n = 41 stints). The best-supported model included an additive interaction between species and SST. For both species, herring and hake in the diet decreased by 15% and prey size decreased by 0.11 culmen lengths for each 1°C increase in SST. SST data were taken from the MUR satellite, which has a daily temporal resolution and spatial resolution of 0.01° (NASA, 2015).

Figure 6: Relationship between sea surface temperature (SST) and the Shannon Wiener Index, a diet diversity metric. These data show the colony-level correlations for common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*). The best-supported model included a multiplicative interaction between species and SST. With increasing SST, the diet diversity of Arctic terns decreased significantly, but there was no significant relationship between SST and diet diversity for common terns.
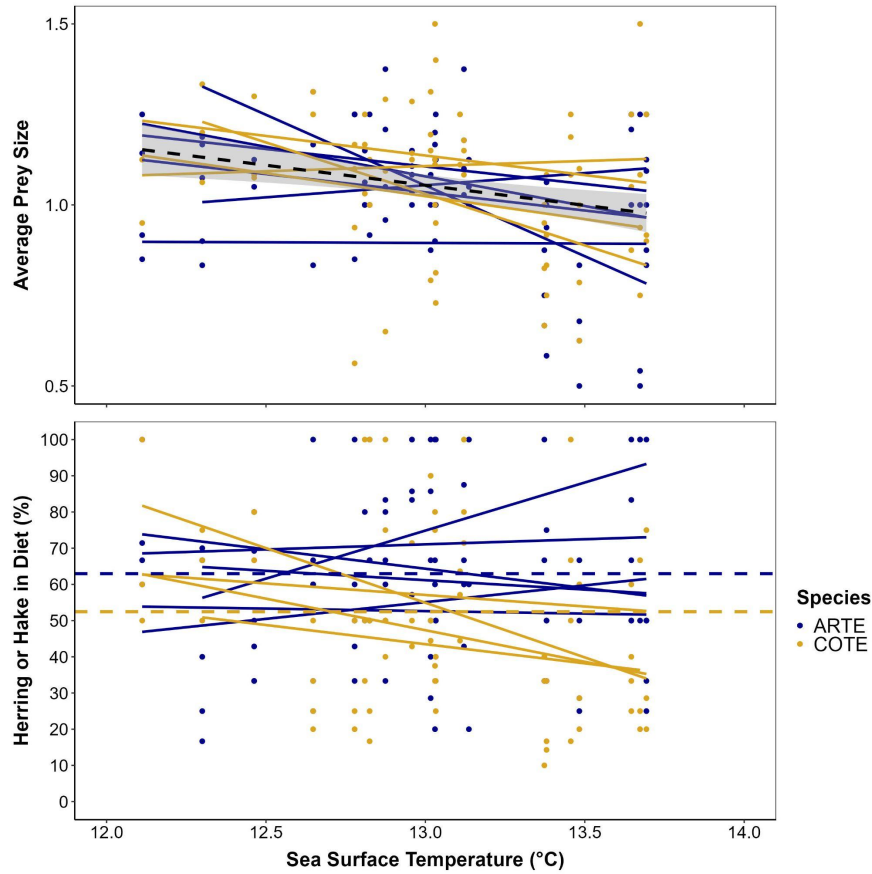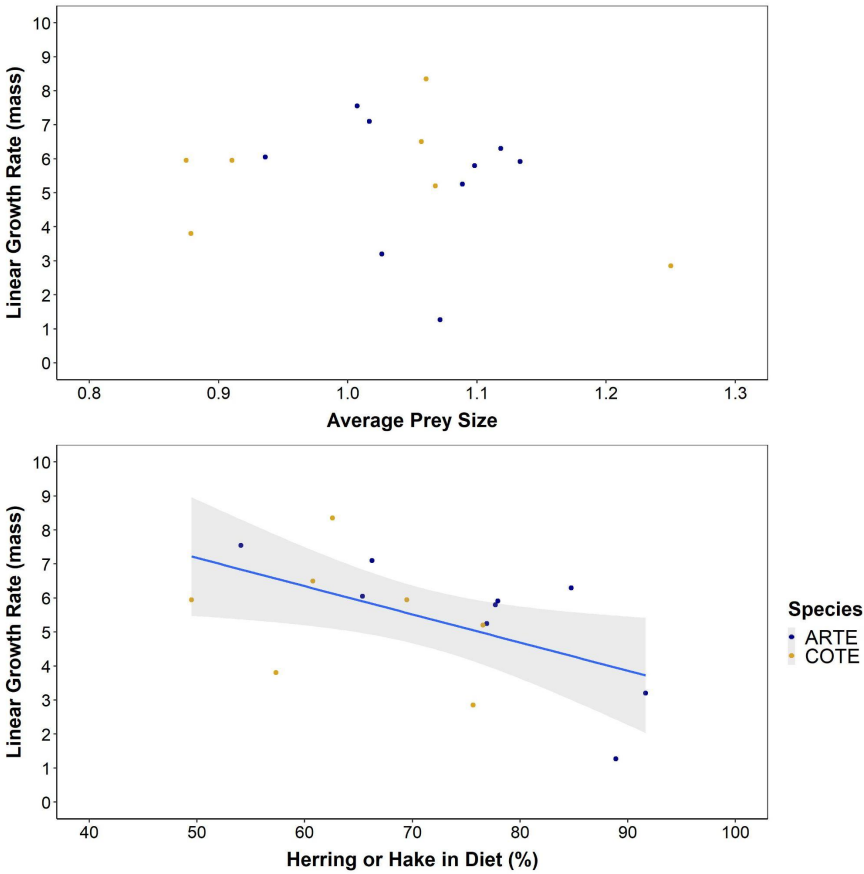
Figure 7: Nest-level relationships between sea surface temperature (SST) and herring or hake in the diet (n = 203 observations) and SST and prey size (n = 163 observations) for common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*). Each point represents one nest during one provisioning stint, conducted from June 23-July 26 on Petit Manan Island, Maine. The mixed-effects model found no evidence for nest-level differences in intercept or slope; SST was the only significant predictor for prey size and species was the only significant predictor for herring or hake in the diet. SST data were taken from the MUR satellite, which has a daily temporal resolution and spatial resolution of 0.01° (NASA, 2015).

Figure 8: Nest-level relationships between average prey size and linear growth rate (mass) (LGR) (top panel) and herring or hake in the diet and LGR (bottom panel) for common terns (*Sterna hirundo*) (n = 7 chicks) and Arctic terns (*Sterna paradisaea*) (n = 9 chicks) on Petit Manan Island, Maine. LGR is calculated using mass measurements of chicks taken between ages 4 and 14. Average prey size was not a significant driver of chick linear growth rate, but an increase in the proportion of herring and hake in the diet led to a decrease in growth rate. Provisioning data are from field work conducted in June and July of 2022.
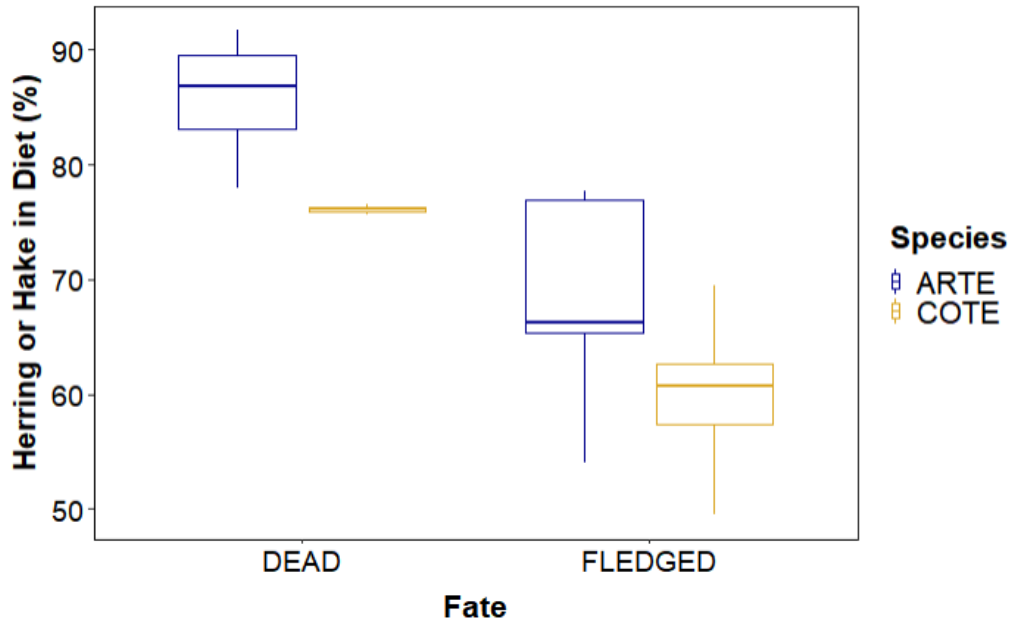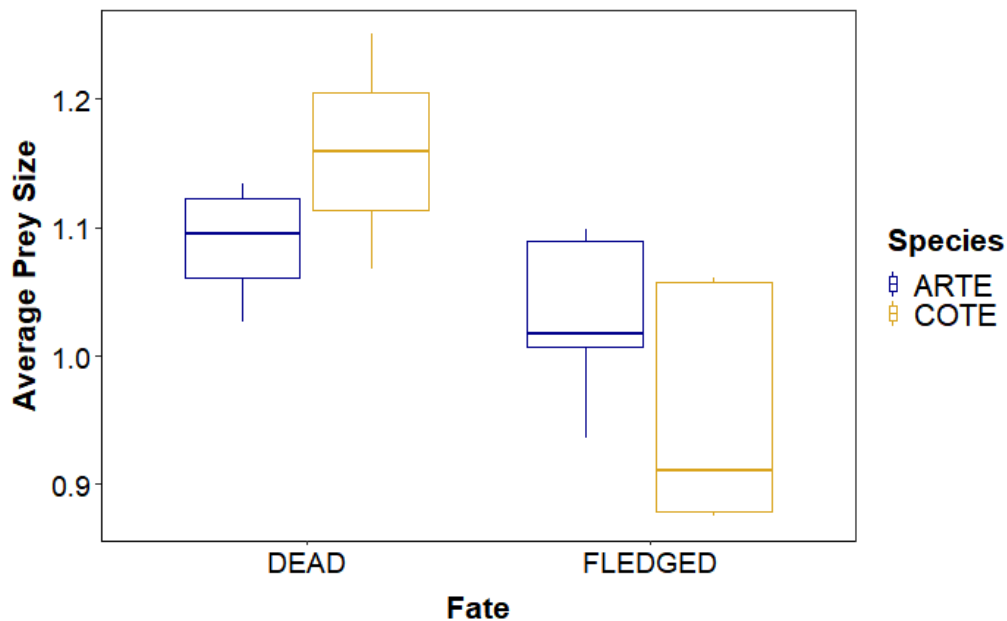
Figure 9: Relationship between the fate of the common tern chicks (*Sterna hirundo*) (n = 4 nests) and Arctic terns chicks (*Sterna paradisaea*) (n = 6 nests) on Petit Manan Island, Maine and herring or hake in the diet. Chicks were considered fledged if a threshold wing chord and mass was reached and the chick was not found during nest checks. On average, chicks that died had a higher percentage of herring or hake in the diet than chicks that fledged. Of both dead and fledged chicks, Arctic terns chicks had higher percentages of herring or hake in the diet. Data were collected from June through July of 2022.

Figure 10: Relationship between the fate of common tern chicks (*Sterna hirundo*) (n = 4 nests) and Arctic terns chicks (*Sterna paradisaea*) (n = 6 nests) and average prey size. Prey size is determined by comparing the length of the prey item to the culmen length of the adult tern. Chicks were considered fledged if a threshold wing chord and mass was reached and the chick was not found during nest checks. On average, chicks that died were fed prey that were significantly larger than chicks that fledged. Data collected during provisioning watches and productivity checks on Petit Manan Island in June-July 2022.
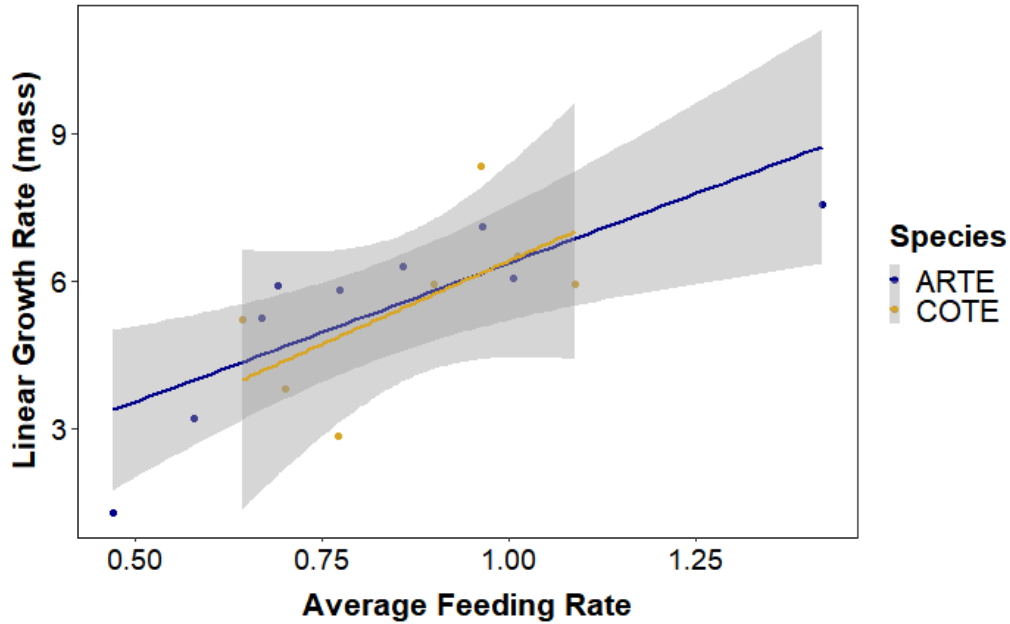
Figure 11: Colony-level relationships between average feeding rate and linear growth rate (mass) (LGR) for common terns (*Sterna hirundo*) (n = 7 chicks) and Arctic terns (*Sterna paradisaea*) (n = 9 chicks). LGR is calculated using mass measurements of chicks taken between ages 4 and 14. The best-supported model included a positive linear relationship between linear growth rate and feeding rate. Arctic terns had a larger range of values for feeding rate. Data collected during provisioning watches and productivity checks on Petit Manan Island in June-July 2022.
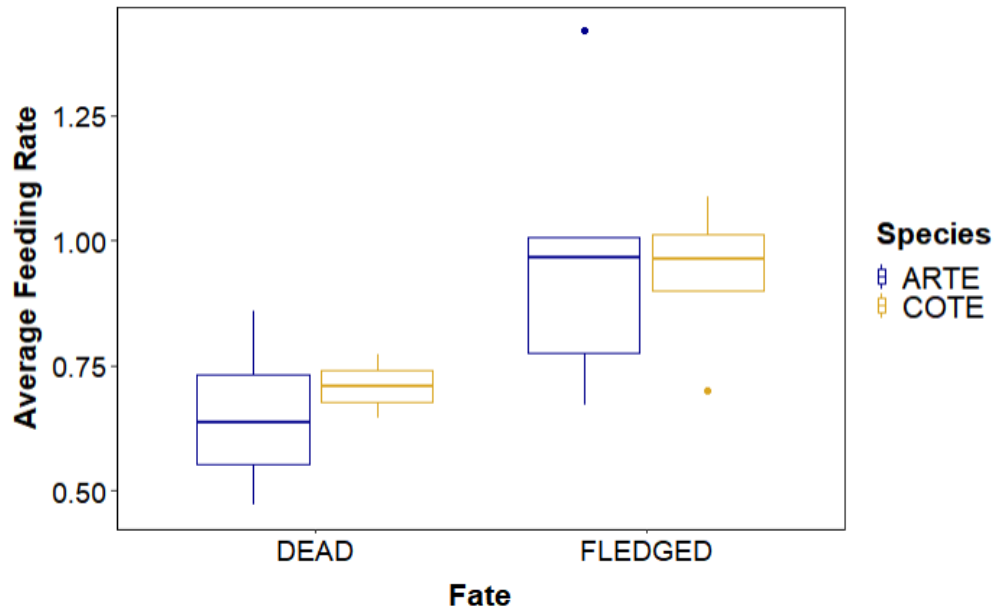
Figure 12: Relationship between the fate of common tern chicks (*Sterna hirundo*) (n = 4 nests) and Arctic terns chicks (*Sterna paradisaea*) (n = 6 nests) and average feeding rate. Chicks were considered fledged if a threshold wing chord and mass was reached and the chick was not found during nest checks. On average, chicks that died were fed at a lower rate than chicks that fledged for both species. Data collected during provisioning watches and productivity checks on Petit Manan Island in June-July 2022.
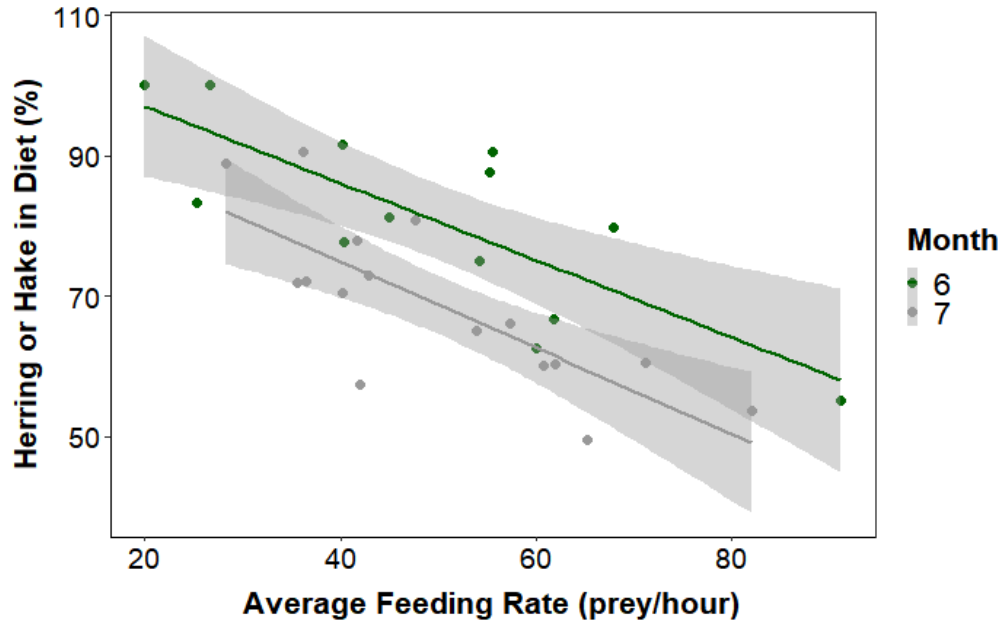
Figure 13: Nest-level relationships between average feeding rate and percent of herring or hake in the diet for common terns (*Sterna hirundo*) (n = 4 nests) and Arctic terns (*Sterna paradisaea*) (n = 6 nests) on Petit Manan Island, Maine. An increase in feeding rate was correlated to a decrease in herring or hake in the diet in both the months of June and July. Provisioning data are from field work conducted in June and July of 2022.
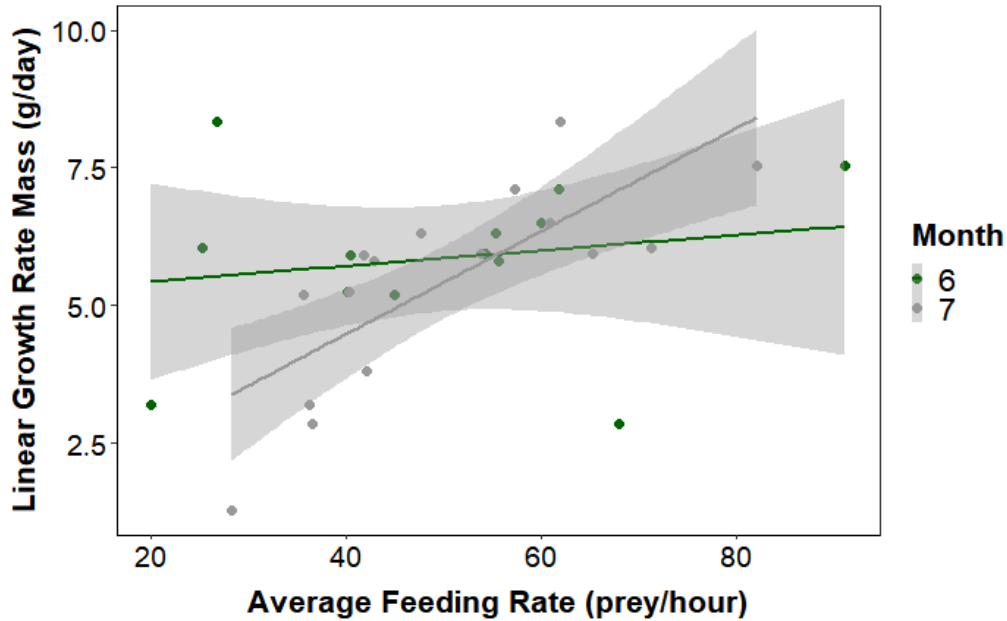
Figure 14: Nest-level relationships between average feeding rate and linear growth rate mass of tern chicks for common terns (*Sterna hirundo*) (n = 4 nests) and Arctic terns (*Sterna paradisaea*) (n = 6 nests) on Petit Manan Island, Maine. LGR is calculated using mass measurements of chicks taken between ages 4 and 14. Feeding rate was positively correlated to linear growth rate in July, but not in June. Provisioning data are from field work conducted in June and July of 2022.