Patterns in tern trophic diversity in a region experiencing rapid climate change

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Open Research Statement

All data used in this study are currently available as private-for-peer review in a Zenodo repository under a CC-BY license via this link. This repository will be moved from “Restricted” to “Public” once the manuscript is accepted for publication.

Chick provisioning data were provided by the United States Fish and Wildlife Maine Coastal Island National Wildlife Refuge and the National Audubon Society Seabird Institute. Chick growth and survival data for Petit Manan Island were provided by the United States Fish and Wildlife Maine Coastal Island National Wildlife Refuge. Upon publication, stable isotope data will also be uploaded to the discipline-specific repository *IsoBank*. Sea surface temperature data from the JPL MUR MEaSUREs Project (DOI: 10.5067/GHGMR-4FJ04) were downloaded from NOAA’s ERRDAP server and are publicly available; data subset for this study have been included in the Zenodo repository for convenience.

Keywords

behavioral plasticity, chick provisioning, climate change, intraspecific variation, stable isotopes, terns, trophic diversity

Abstract

Foraging plasticity provides a mechanism for long-lived species to adapt to rapidly changing environments and, when individuals vary in their plasticity, can drive changes in trophic diversity. We use chick provisioning data and stable isotope values of blood cells and plasma to test for drivers of trophic diversity in the diet of common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*) breeding in the rapidly changing Gulf of Maine. We hypothesized that individual adult terns would differ in their response to reduced food availability, driving higher diversity in tern chick diet in lower-resource contexts, and that individual-level responses would influence fitness. We used the Shannon-Wiener Diversity Index as our measure of trophic diversity for provisioning data and the size of the two-dimensional isotope ellipse as our measure of trophic diversity for stable isotope data. We compared these measures of trophic diversity to proxies for food availability, including the occurrence of preferred prey in tern chick diets and the average sea surface temperature in terns' foraging range. Additionally, we compared shifts in isotope values across time for individually paired blood cell and plasma samples and, on one island and year, for individually paired plasma samples taken approximately 10 days apart.

Trophic diversity measured using provisioning and stable isotope data were correlated across contexts. Although both measures of trophic diversity were highly variable, neither was correlated with measures of food availability. Arctic tern chicks had less-enriched δ^{13}C values, lower δ^{15}N values, and were fed smaller prey than common tern chicks, but did not differ in their trophic diversity. Isotope measures of trophic diversity were greater for plasma samples, which tended to show higher δ^{15}N values and more-enriched δ^{13}C values, than for blood cell samples. For the paired plasma samples collected on one island, chicks shifted to higher δ^{15}N values and less-enriched δ^{13}C values later in the season. Chicks that shifted to relatively high δ^{15}N values also showed greater magnitude shifts to less-enriched δ^{13}C values and, in Arctic terns, fledged at a smaller mass. Our study suggests trade-offs in individual-level foraging and diet plasticity in terns, with possible implications for fitness.

Introduction

Behavioral plasticity produces intraspecific variation that can act as a precursor to evolution (Caspi et al. 2022). In novel environments, such as those occurring under rapid climate change, behavioral plasticity may also allow species to adapt and persist over short timescales (Snell-Rood 2013). Foraging represents one of the most essential suites of behaviors across animal populations. These behaviors must be highly tuned to environmental context to be effective, and should exhibit high plasticity, but this plasticity may be limited by the time and energy needed to learn new foraging behaviors (Mery and Burns 2010; Snell-Rood 2013). Foraging plasticity can occur through changes in how an animal forages (e.g., the rate of food caching in American pika *Ochotona princeps*: Hall and Chalfoun 2019) or through changes in what they are foraging for (e.g., a higher reliance on capelin in humpback whales *Megaptera novaeangliae*: Gulka et al. 2017). In addition to individual variation in average behavior, individuals may also vary in their degree of behavioral plasticity (Dingemanse and Dochtermann 2013), leading to increases or decreases in population-level trophic diversity when environmental conditions change.

Seabirds are ideal systems for studying foraging plasticity because their demographic rates and behavior respond rapidly, and often drastically, to changes in food availability (Cairns 1988; Piatt et al. 2007; Weimerskirch 2018; Bourgeois et al. 2022). Seabirds forage on highly mobile prey in heterogenous marine environments and, to survive and raise chicks, must learn to use static and ephemeral cues to identify profitable foraging habitat (Gilmour et al. 2018). As a result of their sensitivity to ocean change and of the relative ease of studying them during the breeding season, seabirds have often been called "marine sentinels" or "ecosystem indicators" (Boyd and Murray 2001; Boersma 2008; Sydeman et al. 2015; Scopel et al. 2018). Behavioral plasticity is particularly consequential for these and other long-lived species, whose evolutionary rates are unlikely to keep pace with the current rate of environmental change (Hoffmann and Sgrò 2011; Quintero and Wiens 2013).

Previous studies have found plasticity in seabird foraging behavior and diet at multiple biological, spatial, and temporal scales. Foraging behavior can vary across populations of the same species due to differences in local environmental context (e.g., in crested terns, *Sterna bergii*: McLeay et al. 2009; in Cory's shearwater *Calonectris borealis*: Paiva et al. 2010; in Macaronesian shearwater *Puffinus baroli:* Paiva et al. 2016*;* in western gulls *Larus occidentalis*: Shaffer et al. 2017). For example, the depth and duration of dives and length of foraging trips taken by Cory's shearwater vary across productivity gradients (Paiva et al. 2010). Within a population, intraspecific variation in diet and foraging specialization may occur and persist across years as a means of reducing intraspecific competition (e.g., in thick-billed murre *Uria lomvia*: Woo et al. 2008). Changes in food availability across (e.g., in alcids: Jenkins and Davoren 2021) or within (e.g., in thick-billed murres *Uria lomvia*: Kokubun et al. 2018; in Cape Verde Shearwater *Calonectris edwardsii*: Ramos et al. 2018) breeding seasons can cause all individuals to shift their diet and/or foraging behavior, resulting in population-level changes in these parameters. In some systems, however, intraspecific variation in seabird diet (e.g., in two species of shearwater and two species of gull: Gulka et al. 2017; in Magellanic penguins *Spheniscus magellanicus*: Ciancio et al. 2021) or foraging behavior (e.g., in great black-backed gulls *Larus marinus*; Maynard et al. 2021) increases when the availability of preferred prey is low, indicating divergent individual strategies for coping with resource decline.

If individual-level plasticity in diet and foraging behavior influences fitness (e.g., in Cory's shearwater: Zango et al. 2019), rapidly changing environmental conditions may drive individual variation in contributions to population growth. In some populations, for example, plasticity may be high across individuals but low within individuals across contexts (Woo et al. 2008; Zango et al. 2019). This low individual-level plasticity may result from the high cost of learning new foraging behaviors or may indicate that the fitness benefits of different foraging strategies vary over time (Woo et al. 2008). In other populations, all individuals may show high plasticity in behavior, but this plasticity may be insufficient to keep pace with environmental change (e.g., in thick-billed murres *Uria lomvia*: Whelan et al. 2022).

Here, we rely on stable isotope data and chick provisioning data collected across three years (2017, 2018, 2021) and five tern colonies (Table 1) to examine how the trophic diversity of terns (common tern *Sterna hirundo* and Arctic tern *Sterna paradisaea*) varies across time, space, and species in the Gulf of Maine. In this region, common and Arctic terns feed on a variety of fish, particularly hake (*Urophycis spp.*), sandlance (*Ammodytes americanus* or *A. dubius*), and herring (*Clupea spp.* or *Alosa spp.*), and on marine and terrestrial invertebrates (Yakola et al. 2021). Terns may be particularly sensitive to rapid environmental change because, in addition to being central-place foragers, they are constrained to feeding in the top 60 cm of the water column (Cabot and Nisbet 2013), limiting their foraging flexibility to horizontal space (e.g., as in kittiwakes *Rissa tridactyla*: Barrett and Krasnov 1996).

In the Gulf of Maine, the foraging habitat of breeding terns is changing rapidly at multiple temporal and spatial scales, due both to global increases in sea surface temperature (SST) and to local, climate-driven changes in ocean circulation patterns (Scopel et al. 2019; Staudinger et al. 2019). Long-term warming in this region surpasses nearly anywhere else in the ocean and is punctuated by short periods of extreme events, called "marine heatwaves" (Pershing et al. 2021). As a result, SSTs in the Gulf of Maine are quickly exceeding the thermal tolerance limits of terns' optimal diet items, including herring and hake (Collette and Klein-MacPhee 2002; Shackell et al. 2014), driving these fishes deeper and farther offshore. Terns have two options to continue feeding chicks when preferred prey decline: they can change their foraging behavior (e.g., change foraging location) to maintain a diet of preferred prey or they can switch to less optimal prey (e.g., fish to invertebrates) (Figure 1). Chick provisioning studies in this region suggest that warmer waters lead to declines in the abundance of preferred prey in tern diets (Yakola 2019). Dietary shifts have only been studied at the aggregate level of colony and species, however, and it is possible that individuals differ in their response to decreased food availability, leading to changes in trophic diversity.

We examined trophic diversity metrics based on stable isotope data and chick provisioning watch data in relation to each other and to environmental context, specifically sea surface temperature derived from satellite data. We hypothesized that individual terns would differ in their response to reduced food availability, driving higher trophic diversity among diet items fed to tern chicks in lower-resource contexts (Predictions 1-4). Additionally, we hypothesized that adult terns' individual-level responses to reduced food availability would influence the fitness of their chicks (Predictions 5-6).

For stable isotope data, trophic diversity is generally quantified using measures of the two-dimensional isotope niche, where $\delta^{13}C$ provides a proxy for foraging habitat and $\delta^{15}N$ provides a proxy for the trophic level of diet (Hobson et al. 1994; Bourgeois et al. 2022; Bratton et al. 2022; Cherel and Carrouee 2022; Muller et al. 2022). Blood samples, when separated into plasma and blood cell components, can provide information on diet integrated over two timescales: 2-3 days (plasma) and 2-3 weeks (blood cells) (Hobson and Clark 1993; Hobson et al. 1994; Vander Zanden et al. 2015). Chick provisioning studies, during which researchers record the prey brought back to nests and fed to chicks by bill-carrying seabirds, provide complementary information and allow for calculation of traditional diversity metrics.

Though they provide different information on diet and foraging behavior, we predicted that measures of trophic diversity calculated using stable isotope and provisioning data would covary (P1). Additionally, we used chick provisioning and sea surface temperature data to develop proxies for food availability, and to test whether food availability related to trophic diversity in terns. We predicted greater trophic diversity among tern chicks to be associated with lower food availability (P2) and an increase in trophic diversity throughout the breeding season due to increasing sea surface temperatures and chick demands (P3). Previous research suggests that Arctic terns have more variable diets and forage over larger areas than common terns (Rock et al. 2007; Hall et al. 2000; Yakola et al. 2021), so we expected Arctic tern chick diet to reflect greater trophic diversity than that observed in common tern chick diet within and across contexts (P4).

To test for associations between plasticity and fitness, we focused on one island in one year. On Petit Manan Island in 2021, we collected paired isotope samples for a subset of chicks, allowing us to track within-season shifts in diet. We predicted individual variation in the magnitude of dietary shifts over this two-week period and trade-offs between shifts in foraging habitat and the trophic level of prey (P5). Lastly, we expected that the degree and direction of individual plasticity would influence the fledging size and survival of tern chicks (P6).

<u>Materials and Methods</u>

Study System

Maine hosts approximately 4,500 offshore islands. Ten seabird breeding islands are monitored each breeding season by biologists associated with the Maine Coastal Islands National Wildlife Refuge (MCINWR) of the United States Fish and Wildlife Service and the National Audubon Society Seabird Institute. The current study focuses on data collected during 2017, 2018, and 2021 across five islands with common and/or Arctic tern breeding colonies: Petit Manan Island, Ship Island, Seal Island, Metinic Island, and Matinicus Rock (Table 1). These islands vary in the diversity and density of breeding seabirds and in environmental characteristics, including latitude, distance offshore, and surrounding bathymetry. Additionally, the three years and five islands studied showed marked differences in SST and reproductive success (Table 1; Figure 2; Appendix S1: Table S1). While 2017 was a relatively successful year for terns breeding in the Gulf of Maine, terns experienced poor food availability and record-low reproductive success in 2021. In 2018, SSTs and tern diet shifted mid-breeding season, resulting in moderately low reproductive success (Table 1; Figure 2).

Data Collection

Stable Isotopes

We did not collect stable isotope data from tern chicks on all islands in all years and the timing of sampling and sample size varied by year and island. During all sampling events, we collected 140-210ul of blood from the brachial vein of tern chicks (minimum mass of 40g to minimize impact) using a 27-gauge needle and heparinized capillary tubes (Owen et al. 2011). On Petit Manan Island in 2021, we collected a second blood sample for all chicks that were still alive 7-16 days after the initial sample was collected. Sample collection was approved by Gettysburg IACUC Permit # 2021S2 and US Geological Service permit #22055. Within 12 hours of collection, we separated samples into blood cells and plasma using a microhematocrit centrifuge. All samples were then frozen at -20C until processing.

We homogenized dried blood cell and blood plasma samples using a mortar and pestle then weighed 1µg aliquots to the nearest thousandth of a milligram and packaged them in tin capsules for analysis. We analyzed samples using a GV Instruments IsoPrime isotope ratio mass spectrometer coupled with an Eurovector elemental analyzer. Values are reported as isotope ratios ($^{13}C/^{12}C$ for carbon, $^{15}N/^{14}N$ for nitrogen) in parts-per-thousand, calibrated to the international standards Vienna Pee Dee belemnite for carbon ($\delta^{13}C$) and atmospheric air for nitrogen ($\delta^{15}N$). We ran duplicate samples to ensure sample homogenization and ran internal laboratory standards (glycine and peptone) to test machine accuracy. These laboratory standards have been carefully calibrated using traditional methods (Dumas combustion, dual inlet IRMS) to IAEA standards N1 and N2 for nitrogen, and NBS 20, 21, and 22 for carbon.

The expected values for glycine fell within one standard deviation of those measured for $\delta^{15}N$ (expected: 10.73‰, observed 10.70±0.08‰) and $\delta^{13}C$ (expected: -34.00‰, observed -33.97±0.06‰). Similarly, the expected values for peptone fell within one standard deviation of those measured for $\delta^{15}N$ (expected: 7.40‰, observed 7.37±0.10‰) and $\delta^{13}C$ (expected: -14.73‰, observed -14.81±0.05‰). To ensure we had properly homogenized samples, we ran 43 duplicates for blood cell samples and 15 duplicates for plasma samples. Intra-sample variation, measured as absolute percent difference, was 2.89±2.62% for

$\delta^{15}N$ and 0.86±1.01% for $\delta^{13}C$ in plasma and 1.65±1.70% for $\delta^{15}N$ and 0.73±1.00% for $\delta^{13}C$ in blood cells. For all analyses that follow, we used mean isotope values for samples with duplicates.

While blood cell samples had C:N ratios of ≤3.5 (mean of 3.19±0.37), indicating low lipid content, plasma samples often had high C:N ratios (mean of 4.81±0.56). For tissue samples with high lipid content, variation in lipids may bias $\delta^{13}C$ values (Post et al. 2007). We therefore calculated normalized $\delta^{13}C$ values and used the resulting values in all analyses that follow. To calculate these values, we used the equation developed by Post et al. (2007) for aquatic species, where $\delta^{13}C_{\text{untreated}}$ is the original $\delta^{13}C$ value of the sample, C:N is the carbon to nitrogen ratio of the sample, and $\delta^{13}C_{\text{normalized}}$ is the final $\delta^{13}C$ of the sample used in data analysis (Equation 1).

$$\delta^{13}C_{\text{normalized}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 \cdot C{:}N \qquad \text{Equation 1}$$

Chick Provisioning and Growth Rates

To collect information on common and Arctic tern chick diet directly, we monitored a subset of nests throughout each breeding season during regular provisioning stints. Using a standardized protocol, National Audubon Society staff collected these data on Matinicus Rock and Seal Island and US Fish and Wildlife Service staff collected these data on Metinic Island, Ship Island, and Petit Manan Island. During each stint, staff sat in a bird blind and recorded information on prey size and prey species, the time of the feeding, and the provider and recipient of the prey item. These stints generally lasted three hours and occurred four times a week, most often in the early morning when feeding rates are highest. We used provisioning data metrics, including average feeding rate, average prey size, and average percent herring and hake among provisioned items as indicators of food availability. Additionally, we calculated diversity metrics using provisioning data to compare with those calculated using stable isotope values. These metrics are described in more detail below (Data Analysis).

At each colony, we also monitored a subset of nests (approximately 10% of the breeding population of each species on each island) to track chick growth rates and survival. Nests were enclosed in 1 m high fencing to prevent chicks from moving far from their nests. Nests were visited each day until all chicks hatched, allowing for estimation of hatch date. After all chicks hatched, nests were visited every other day to record chick status (e.g., alive, dead, unknown), mass (g), and wing chord (mm). Chicks were banded with a nine-digit USGS Bird Banding Laboratory band within two days of hatching, which allowed us to track individuals throughout the season. A chick was considered to have fledged if it was last observed alive when it was at least 15 days old. The majority of the stable isotope samples used in this study were collected from nests monitored for productivity and chick growth rates. We used data from these nest checks to examine the fitness consequences of diet plasticity using data on chick linear growth rates (LGR: average daily change in mass between age 3-13 days) and survival.

Sea Surface Temperature

Higher SSTs in the Gulf of Maine are associated with a lower availability of terns' preferred prey (Yakola 2019). Therefore, we used SST as a proxy for food availability in this system. Although there are current efforts to track the movement of Arctic and common terns in the region, we are still in the process of collecting sufficient data to define the core foraging ranges of these species. Tern foraging distance is likely to vary across space and time due to environmental conditions. Though is often reported to be approximately 10-30 km for the species in this study and for related species (Becker et al. 1993; Pratte et al. 2021), recent research suggests that Arctic terns may forage much farther from the colony, making trips of averaging 36 km and up to 219 km at one colony in Iceland (Morten et al. 2022).

We collated SST data and conducted all statistical analyses in R Version 4.3.0. Due to a lack of site-specific estimates, we used a conservative estimate of 20 km and created a foraging range buffer for each island using the gbuffer function of the rgeos package (Version 0.6-4). We used these boundaries and the dates of isotope sample collection (see below) to access SST data relevant to each island using the rxtractogon function of the rerddapXtracto package (Version 1.1.4). SST are from the Multi-scale Ultra-high Resolution (MUR) Satellite, provided by the Jet Propulsion Lab under support by the NASA MEaSUREs program, which provides information on SST at a 1-km spatial scale and 1-day temporal scale.

Data Analysis

Data Preparation

For our stable isotope analysis, we calculated the size of standard isotope ellipses (Jackson et al. 2011) using the package SIBER (Version 2.1.7) with the default settings to include 40% of the data in each group. We separated groups based on island, year, species, and isotope type. A larger SEA_c suggests greater trophic diversity due to variation in $\delta^{15}N$ values and/or $\delta^{13}C$ values among samples. We report the corrected version of the standard ellipse area (SEA_c), which is suitable for comparison across groups with variable sample sizes, provided that each sample has an $n \geq 3$ (Jackson et al. 2011). We excluded any groups that had an $n<3$ from this analysis. In cases where chicks were sampled twice (i.e., on Petit Manan in 2021), we used data from the first sampling date for that chick in all cross-context comparisons.

To account for uncertainty and estimate credible intervals, we used the SIBER package to fit Bayesian multivariate normal distributions to each group in the dataset (SEA_B). For these Bayesian estimates, which use the Gibbs Sampling technique in rjags (Version 4-14), we ran 20,000 iterations with a burn-in of 1,000 and uninformative priors. We used posterior draws from this analysis to estimate the probability that the isotopic niche of one group was greater than that of another group. Additionally, we estimated isotopic niche overlap using the posterior draws for SEA_B. We ran 10 draws for each groupwise comparison and, for each draw, defined niche overlap as the ratio of the overlapping area to the maximum area of overlap. The maximum area of overlap was calculated as the summed area of the two ellipses divided by two (i.e., 100% overlap would occur if the isotopic niches were identical). For all additional analyses, we used the median value resulting from these 10 draws.

We subset chick provisioning data and SST data for the time period relevant to blood cell samples (2-3 weeks) and SST data for the period relevant to plasma samples (2-3 days). For each group (a combination of species, colony, and year), we first calculated the median sampling date. In some cases, all sampling occurred within a day, while in others it occurred over a one-week period; in most cases the sampling periods for Arctic terns and common terns were the same. For each group, we subset SST data and calculated SST_{mean} for the two-week period preceding the median sampling date for comparison with blood cell isotopes and for the two-day period preceding the median sampling data for comparison with plasma isotopes (Appendix S1: Table S1). For example, in 2017 on Matinicus Rock, all isotope samples for both species were collected on July 7th, so we subset SST data from 23-06-2017 to 07-07-2017 for blood cell samples and from 07-05-2017 to 07-07-2017 for plasma samples. On Petit Manan in 2021, samples were collected over a one-week period, with a median sampling date of July 6th, so we subset SST data from 22-06-2021 to 06-07-2021 for blood cell samples and from 04-07-2021 to 06-07-2021 for plasma samples (Appendix S1: Table S1).

Because blood cells represent a longer-term integration of diet than plasma, shifts in isotope signatures between blood cells and plasma can provide insight into changes in trophic diversity throughout the breeding season and from long (2-3 weeks) to short (2-3 days) timescales. Blood samples were often collected from chicks in July (Julian Dates 170 to 200), as chicks often hatch in late June and are not large enough for blood sampling until early July. In this region, July is also the month during which SSTs increase rapidly and food availability begins to decline (Figure 2). For example, on Matinicus Rock in 2018, stable isotope samples were collected on July 5th (Julian Date 186). In the two weeks preceding sample collection, the SST_{mean} surrounding this island was 13.38±1.53°C, while in the two days preceding sample collection the SST_{mean} was 15.70±0.53°C (Appendix S1: Table S1).

We only subset provisioning data for comparison with blood cell isotope values, as provisioning watches often did not occur within the two-day period relevant to plasma samples. We used provisioning data as a proxy for food availability by calculating average feeding rate (prey·hr^{-1}·nest^{-1}; FR_{mean}), average prey size (culmen lengths; PS_{mean}), and average percent herring and hake among provisioned items (%; HR_{mean}) for each species throughout the two-week period prior to isotope data collection. Additionally, to provide a provisioning data measure of trophic diversity, we calculated the Shannon-Wiener Diversity Index (H') (Equation 2).

$$H' = -\sum_{j}^{S} p_j \ln p_j \qquad \text{Equation 2}$$

Where p_j is the proportion of prey species or prey group j in the diet of a tern species at each colony for a given two-week period. The Shannon-Wiener diversity index is commonly used in diet composition studies and ranges from 0 to $H'_{\max}$, where $H'_{\max}$ = ln(S). An H' value of 0 indicates no diet diversity and greater values of H' indicate greater diet diversity. We excluded prey items that were not identified to the species (e.g., butterfish) or group (e.g., amphipod) level for this analysis.

Hypothesis Testing

For each prediction, we tested a suite of relevant generalized linear models, and selected the best-supported models based on Akaike's Information Criterion (AIC). Where models were within 2 AIC, we report results of the simpler model. Due to low sample sizes (e.g., only one sampling occasion for Ship Island), we could not include "island" or "year" as random effects in our models, but exploratory analyses suggested that including these variables did not improve model performance. We assessed model fit using residual diagnostic plots; models with gaussian errors and an identity link performed similarly to other generalized linear model alternatives. We report effect sizes as estimate[CI_{95}]. Where models including predictors are supported, we include a p-value and a pseudo-R^2 value, calculated as 1 – (residual deviance/null deviance). When comparing group means, we used a Wilcoxon signed-rank test due to low sample sizes and non-normality. We report mean values as mean±SD. To compare the variance between paired isotope samples, we use a Pitman-Morgan test in the package PairedData (Version 1.1.1).

P1: Cross-method Comparison. We tested whether stable isotope and provisioning data provided consistent information on trophic diversity by comparing a null model for SEA_c to models including H', species, and their additive and multiplicative interactions. Additionally, we tested whether variation in $\delta^{13}C$ or $\delta^{15}N$ significantly predicted variation in SEA_c across contexts. Lastly, we tested for correlations among provisioning parameters (FR_{mean}, HR_{mean}, PS_{mean}) across contexts and for correlations between these parameters, $\delta^{13}C_{mean}$, and $\delta^{15}N_{mean}$.

P2: Trophic Diversity and Food Availability. We used SST_{mean} and HR_{mean} as indicators of food availability across islands and years. We tested whether these indicators of food availability were related to measures of trophic diversity in tern chicks (H' and SEA_c) using generalized linear models for the two-week period relevant to each blood cell sampling occasion. For plasma samples, we tested for relationships between SEA_c and SST_{mean} for the two days leading up to isotope sample collection but could not test for relationships with H' due to the restricted time range represented by these samples.

P3: Trophic Diversity Throughout the Breeding Season. To better understand shifts in diet throughout the breeding season, we calculated the change in isotope values from blood cell to plasma samples for each individual. We compared trophic diversity between the period represented by blood cell and plasma data using two approaches: 1) changes in the variance of $\delta^{13}C$ and $\delta^{15}N$ between blood cell and plasma samples, 2) changes in isotope niche size between blood cell and plasma samples. Additionally, we calculated isotope niche overlap among blood cell and plasma samples for each island and year using the methods described above. These analyses were restricted to chicks for which we had data on both blood cell and plasma isotope values, so sample sizes were identical for all comparisons. This restriction resulted in samples for 146 of the 196 chicks included in the study; in some cases, either the blood cell or plasma samples for a given individual did not provide sufficient material for stable isotope analysis.

P4: Interspecific Comparison. For each island by year combination with samples for both species (n = 6 for plasma, n = 7 for blood cells), we compared the mean blood cell and plasma isotope values for common tern and Arctic tern chicks using Wilcoxon-signed rank tests and quantified overlap in their Bayesian isotope ellipses. We used posterior draws of SEA_B to calculate the probability that the isotope ellipse of common tern chicks was greater than that of Arctic tern chicks. We compared variance in $\delta^{13}C$ and $\delta^{15}N$ of these two species across all samples but not for each sampling occasion, due to large differences in sample sizes for some island by year combinations.

P5: Within-Season Isotope Shifts. We examined population and individual-level plasticity using paired plasma samples collected from chicks approximately ten days apart on Petit Manan Island in 2021. The first sampling period occurred in early July and the second sampling period occurred in mid-July. We were able to collect paired samples for five common tern chicks and 14 Arctic tern chicks. Chicks ranged from 12 to 18 days old during the first sampling occasion (Julian Dates 182 to 186; SST_{mean} = 12.22±0.40°C) and from 22 to 27 days old during the second sampling occasion (Julian Dates 193 to 204, all but two between 193 and 198; SST_{mean} = 12.97±0.49°C).

Because residual error and individual slope estimates are confounded in the case of linear effects models with only two measurements per individual, we could not use this approach to statistically test for variation in individual slopes. Instead, we describe individual-level plasticity through descriptive comparison of the slope of change in $\delta^{15}N$ and $\delta^{13}C$ values for each individual chick, calculated as the change in isotope value divided by the number of days between sampling occasions. We tested for species-driven differences in slopes. Additionally, we calculated SEA_c and compared SEA_B for samples collected during the first sampling occasion to those collected during the second sampling occasion.

P6: Isotope Shifts and Fitness. For each individual with paired plasma samples, we tested whether diet ($\delta^{15}N$) and foraging ($\delta^{13}C$) plasticity correlated with two measures of fitness: chick survival and asymptotic chick size. Asymptotic chick size was calculated as the average chick mass (g) and average chick wind chord length (mm) for measurements taken between age 16 and 27 days. We did not compare plasticity to chick growth rate because plasma samples were collected after the linear growth period (2 to 13 days). Several of the chicks sampled in this study were not part of our regular productivity plots, and we did not record their final status, which is instead marked as "unknown". Importantly, the need to sample chicks twice biased our samples towards chicks that survived until the second sampling occasion, which was a relatively low number of chicks given poor reproductive success on Petit Manan in 2021. We tested whether the slope of change in $\delta^{15}N$ and in $\delta^{13}C$ were correlated with each other and with these two measures of chick fitness.

Results

We collected 100 blood cell samples and 90 plasma samples from Arctic tern chicks (n = 86 chicks, 14 sampled twice) and 115 blood cell samples and 102 plasma samples from common tern chicks (n = 110 chicks, 5 sampled twice) across the five study islands and three study years. When broken down into year and island combinations, there were nine sampling occasions for each species with sample sizes ranging from five chicks to 29 chicks for blood samples and from one chick to 29 chicks for plasma samples.

Across all islands, years, and species, $\delta^{15}N$ ranged from 10.40 to 14.59‰ in blood cell samples (mean of 12.61±0.76‰) and from 10.91 to 15.64‰ in plasma samples (mean of 13.73±0.95‰). For $\delta^{13}C$, values ranged from -22.26 to -16.52‰ in blood cell samples (mean of -19.40±0.77‰) and -22.38 to -14.75‰ in plasma samples (mean of -18.43±1.20‰) (Figure 3). The relationship between $\delta^{15}N$ and $\delta^{13}C$ varied by isotope type and species; models containing the interaction between $\delta^{13}C$ and species explained 42% of the variance in $\delta^{15}N$ for plasma samples and 35% of the variance in $\delta^{15}N$ for blood cell samples (Figure

3). For common tern chicks, $\delta^{15}N$ was positively correlated with $\delta^{13}C$ in both blood cell ($p = 0.04$, b = 0.26[0.01,0.50]) and plasma ($p < 0.0001$, b = 0.53[0.34,0.73]) samples. In Arctic tern chicks, $\delta^{15}N$ was positively correlated with $\delta^{13}C$ in blood cell samples ($p = 0.03$, b = 0.19[0.02,0.36]) but negatively correlated in plasma samples ($p < 0.0001$, b = -0.25[-0.37, -0.13]) (Figure 3).

During the two weeks prior to isotope data collection, the total time spent in provisioning watches ranged from 878 minutes (Arctic terns on Petit Manan Island in 2017) to 3,320 minutes (common terns on Petit Manan Island in 2017) (Appendix S1: Table S2). FR_{mean} ranged from 0.95 $prey \cdot hr^{-1} \cdot nest^{-1}$ (common terns on Petit Manan Island in 2021) to 3.57 $prey \cdot hr^{-1} \cdot nest^{-1}$ (Arctic terns on Matinicus Rock in 2017) with a mean of 1.68 $prey \cdot hr^{-1} \cdot nest^{-1}$ across islands, species, and years (Appendix S1: Table S2). PS_{mean} ranged from 0.56 culmen lengths (Arctic terns on Matinicus Rock in 2018) to 1.89 culmen lengths (common terns on Metinic Island in 2017), with a mean of 1.25 culmen lengths. HR_{mean} ranged from 20.89% (Arctic terns on Matinicus Rock in 2018) to 84.11% (Arctic terns on Petit Manan Island in 2018), with a mean of 57.79% (Appendix S1: Table S2).

Trophic diversity varied greatly across islands, years, and species. SEA_c ranged from $0.05‰^2$ (blood cells for common tern chicks on Seal Island in 2017) to $2.61‰^2$ (plasma cells for Arctic tern chicks on Petit Manan Island in 2021) with a mean of $0.60‰^2$ (Figure 4; Appendix S1: Table S3). H' ranged from 0.79 (common terns on Ship Island in 2021) to 2.08 (common terns on Seal Island in 2018), with a mean of 1.44. When calculated at the year and colony level, SST_{mean} for the period relevant to blood cell isotope samples ranged from 10.44±0.61°C (Petit Manan Island in 2017) to 15.06±0.92°C (Metinic Island in 2017) and for plasma isotope samples ranged from 11.45±0.50°C (Petit Manan Island in 2017) to 16.37±0.78°C (Metinic Island in 2017) (Appendix S1: Table S1).

P1: Cross-Method Comparison. Provisioning metrics were strongly intercorrelated, and the best-supported models for relationships among these parameters did not include species-specific intercepts or slopes (Table 2; Figure 5). An increase of one prey item per hour per nest was associated with a 18.6% decrease in HR_{mean} ($r^2 = 0.47$, $p = 0.002$, $b = -18.6[-29.19, -8.06)$]. Furthermore, a one culmen length increase in PS_{mean} was associated with a 38.14% increase in HR_{mean} ($r^2 = 0.32$, $p = 0.01$, $b = 38.14[8.88, 67.41]$). Because of the strong collinearity among provisioning metrics, we focused on comparing HR_{mean} across contexts and species to $\delta^{15}N_{mean}$, $\delta^{13}C_{mean}$, and measures of trophic diversity. Both $\delta^{15}N_{mean}$ ($r^2 = 0.28$, $p = 0.02$, $b = 19.81[2.97,36.65]$) and $\delta^{13}C_{mean}$ ($r^2 = 0.32$, $p = 0.01$, $b = 17.72[4.11, 31.32]$) were positively correlated with HR_{mean} and showed stronger support than a null model for this provisioning metric (Table 2).

H' and blood cell SEA_c were significantly correlated, and this relationship did not vary by species (Table 3); H' increased by approximately 0.63 for every 1‰^{2} increase in SEA_c ($r^2 = 0.24$, $p = 0.04$, $b = 0.63[0.04,1.22]$). Variation in $\delta^{13}C$ was not significantly correlated with variation in $\delta^{15}N$ across contexts ($b = 0.14[-0.08,0.45]$). While greater variation in $\delta^{15}N$ (AIC = 9.48) was correlated with larger SEA_c [$r^2 = 0.40$, $p = 0.005$, $b = 1.89[0.65,3.13]$], variation in $\delta^{13}C$ was a stronger driver (AIC = -10.13) and explained approximately 75% of the variation in SEA_c [$r^2 = 0.75$, $p < 0.001$, $b = 1.31[0.84,1.57]$).

P2: Trophic Diversity and Food Availability. There was no evidence for an impact of SST_{mean} on trophic diversity as measured using the SEA_c of blood cell samples; models including SST_{mean} and additive and multiplicative interactions with species were less supported than the null model (Table 4). Similarly, there was no support for a relationship between SST_{mean} and the SEA_c of plasma samples. As with blood cell samples, models that included SST_{mean} and additive and multiplicative interactions with species were less supported than the null model (Table 4). We found no relationship between our other measure of food availability, HR_{mean}, and SEA_c (Table 4). Additionally, we found no evidence for a relationship between provisioning study trophic diversity, H', and food availability as measured using SST_{mean} or HR_{mean} (Table 3).

P3: Trophic Diversity Throughout the Breeding Season. When comparing paired samples for each chick, plasma samples had δ^{15}N values that were on average 1.10±0.70‰ greater (range: -3.30‰ to 4.48‰) and δ^{13}C values that were on average 1.04±1.11‰ greater (range: -0.92‰ to 3.41‰) than blood cell samples (Figure 6). When averaged at the level of island, year, and species, the difference in δ^{15}N between plasma and blood cell samples was always positive (range of 0.51‰ for Arctic terns on Petit Manan Island in 2021 to 2.16‰ for Arctic terns on Seal Island in 2018). The average difference in δ^{13}C was positive for all combinations except for Arctic terns on Matinicus Rock in 2018 (-0.53±1.06‰), where approximately half of chicks shifted to less-enriched δ^{13}C values and half shifted to more-enriched δ^{13}C values. The best-supported model for shifts in δ^{15}N included shifts in δ^{13}C, a multiplicative interaction with species, and an additive interaction with island ($r^2 = 0.27$, $p < 0.0001$; Table 5; Figure 6). Across Arctic tern chicks, the magnitude of the shift in δ^{15}N value between blood cells and plasma was negatively correlated with the magnitude of the shift in δ^{13}C value ($p = 0.03$, $b = -0.24[-0.36,-0.11]$). In common terns, shifts in δ^{15}N values were positively correlated with shifts in δ^{13}C values ($p = 0.01$, $b = 0.26[0.08,0.44]$).

The overlap in SEA_B representing blood cell and plasma samples for the same individuals ranged from 4.1% (Arctic tern chicks on Matinicus Rock in 2018) to 38.5% (Arctic tern chicks on Petit Manan Island in 2018) with an average overlap of 29.6% for Arctic terns and 17.04% for common terns (Appendix S1: Table S4). The probability that the SEA_B for plasma samples was greater than that of blood cell samples ranged from 0.27 (common tern chicks on Ship Island in 2021) to 1.00 (Arctic tern and common tern chicks on Petit Manan Island in 2021), with an average probability of 0.81 across contexts for Arctic terns and 0.70 across contexts for common terns (Appendix S1: Table S4).

Across all paired samples, plasma samples had a larger δ^{15}N range (4.7‰) and standard deviation (0.97‰) than did blood cell samples (range = 3.3‰; sd = 0.82‰). Similarly, plasma samples had a larger δ^{13}C range (7.63‰) and standard deviation (1.22‰) than did blood cell samples (range = 5.74‰; sd = 0.79‰). Plasma sample variability was significantly greater for both δ^{15}N ($F = 1.40$, $p = 0.02$) and δ^{13}C (F

= 2.39, $p < 0.0001$) across all samples. When broken down by sampling occasion (n = 12 occasions with individuals with paired samples), the $\delta^{15}N$ and $\delta^{13}C$ values of plasma samples were more variable than blood cell samples in most cases, but this difference was rarely significant (Appendix 1: Table S5).

P4: Interspecific Comparison. Arctic tern chicks had significantly lower plasma $\delta^{15}N$ values ($n_1 = 76$, $n_2 = 97$, W = 1297.5, $p < 0.001$) and significantly lower blood cell $\delta^{15}N$ values ($n_1 = 86$, $n_2 = 110$, W = 2196.5, $p < 0.001$) than common tern chicks. Additionally, Arctic tern chicks had significantly less-enriched plasma $\delta^{13}C$ values ($n_1 = 86$, $n_2 = 110$, W = 2700, p = 0.003) and significantly less-enriched blood cell $\delta^{13}C$ values ($n_1 = 76$, $n_2 = 97$, W = 2312, $p < 0.001$) than common tern chicks (Figure 4). When compared at the island and year level, however, Arctic and common tern chicks were rarely significantly different in both $\delta^{15}N$ and $\delta^{13}C$ space, with the exception of Seal Island in 2017 and 2018 (Appendix 1: Table S6).

Arctic tern chicks had a lower and more variable average HR_{mean} (56.03±22.80%) than common tern chicks (59.55±18.96%) across contexts and a higher and more variable FR_{mean} (1.85±0.88 prey·hr^{-1}·nest^{-1}) than common tern chicks (1.51±0.60 prey·hr^{-1}·nest^{-1}). Neither of these differences were significant across contexts (HR_{mean}: W = 39, p = 0.93; FR_{mean}: W = 52, p = 0.34). Prey size was, however, significantly lower for Arctic tern chicks (1.09±0.29 culmen lengths) than for common tern chicks (1.41±0.23 culmen lengths) (W = 11, p = 0.008).

Given the same island, year, and isotope type, the mean SEA_B overlap between Arctic tern and common tern chicks was 16.67% (range of 0-52.93%). The overlap between these two species was slightly higher in plasma samples (mean = 20.03%, range of 0-52.93%) than in blood cell samples (mean = 14.15%, range of 0-45.84%). The overlap was greatest for plasma samples on Metinic in 2018 (52.93%), the only case with interspecific overlap of greater than 50%.

There was little consistency in the difference in $\mathrm{SEA_B}$ size for common tern and Arctic tern chicks across contexts. The average probability that Arctic tern chicks had a larger isotopic niche was 0.53 for blood cell samples (range of 0.00 to 0.98% for Petit Manan in 2017 and 2021 respectively) and 0.46 for plasma samples (range of 0.001 to 0.96% for Metinic in 2018 and Seal in 2018 respectively) (Table S7). Provisioning data resulted in similar average H' values for Arctic tern (1.44±0.42) and common tern chick diets (1.43±0.42) ($W = 40$, $p = 1.00$), though there was a greater occurrence of unknown prey items that needed to be excluded for Arctic terns (19% of prey items) than for common terns (14% of prey items). Additionally, across all samples, the variance in Arctic tern chick $\delta^{15}N$ values was not significantly greater than that of common terns in blood cell samples ($F = 0.33$, $p = 1.00$) or plasma samples ($F = 0.64$, $p = 0.98$). Arctic tern chicks did show greater variance in $\delta^{13}C$ values in plasma samples than common tern chicks ($F = 2.21$, $p < 0.005$), but not in blood cell samples ($F = 1.34$, $p = 0.14$).

P5: Within-Season Isotope Shifts. Individual terns showed substantial variation in $\delta^{15}N$ and $\delta^{13}C$ slopes between the first and second sampling occasion, but the overall shift was to higher $\delta^{15}N$ values and less-enriched $\delta^{13}C$ values (Figure 7). Across both species, 14 individuals showed negative $\delta^{13}C$ slopes and five showed positive slopes. For $\delta^{15}N$, two individuals showed a negative slope, one showed a slope within 0.01 of zero, and 16 showed positive slopes (Figure 7). $\mathrm{SEA_c}$ was nearly three times greater during the first sampling period (1.40‰^{2}) than during the second sampling period (0.44‰^{2}) for Arctic terns and nearly four times greater during the first sampling period (2.11‰^{2}) than during the second sampling period (0.54‰^{2}) for common terns (Figure 8).

Slopes for $\delta^{15}N$ and $\delta^{13}C$ were strongly correlated across individuals and the slope of this relationship did not vary by species (Figure 8). A shift to less-enriched $\delta^{13}C$ diets was associated with a shift to higher $\delta^{15}N$ diets ($r^2 = 0.66$, $p<0.001$, $b = -0.57[-0.78, -0.36]$). The average $\delta^{13}C$ slope of Arctic tern chicks (-0.12±0.12‰ day^{-1}) was more negative than that of common tern chicks (-0.05±0.12‰ day^{-1}), but this difference was not significant ($W = 24$, $p = 0.34$). Similarly, though the average $\delta^{15}N$ slope of Arctic tern chicks (0.12±0.07 ‰ day^{-1}) was double that of common tern chicks (0.06±0.11 ‰ day^{-1}), this difference was not significant (W = 52, p = 0.13).

P6: Isotope Shifts and Fitness. All common tern chicks with paired plasma samples were alive and of fledging size and age during their final nest check. Among Arctic tern chicks, seven were alive, four had died, and three had a final status of unknown. Chicks that died in the days after sampling had more negative δ^{13}C slopes (-0.138±0.159 ‰ day^{-1}) and more positive δ^{15}N slopes (mean of 0.16±0.07‰ day^{-1}) than did chicks that fledged (mean of -0.08±0.12 ‰ day^{-1} for δ^{13}C and mean of -0.09±0.07‰ day^{-1} for δ^{15}N), but these differences were not significant (δ^{13}C: W = 17, p=0.648; δ^{15}N: W = 7, p = 0.23). There was no significant relationship between asymptotic wing chord length, which ranged from 100.5 to 144.3 mm for common terns and 106.2 to 141.1 mm for Arctic terns, and isotope slopes (Table 6). Asymptotic mass was positively correlated with δ^{13}C slope and negatively correlated with δ^{15}N slope in Arctic tern chicks (range: 62.2 to 92.0 g), but not in common tern chicks (range: 102.17 to 117.5 g) (Figure 8; Table 6).

Discussion

Arctic and common terns foraging in the Gulf of Maine face rapidly changing prey landscapes. Both species have demonstrated an ability to alter their foraging behavior and diet in response to local prey availability across time and space (Hall et al. 2000; Scopel et al. 2018; Yakola 2019). For example, warmer waters in the Gulf of Maine are associated with lower proportions of hake (a preferred prey item) in the diet of common terns and Arctic terns, and with an increase in the occurrence of less-common prey (Yakola 2019). Here, using multiple approaches, we show marked variation in the trophic diversity of Arctic and common terns breeding across five islands and three years in the Gulf of Maine. Trophic diversity metrics, calculated using isotope data, varied by an order of 50 for isotope data (SEA_c) and by an order of three for provisioning data (H’), and both species exhibited a wide range of isotope values and feeding parameters. Additionally, using paired isotope samples, we show that individuals within these populations differ in their within-season responses to changing environmental conditions, with potential implications for individual-level fitness.

Trophic Diversity Across Methods

Using multiple approaches simultaneously to study trophic ecology provides a more nuanced understanding of diet and foraging behavior and helps to mitigate the shortcomings of any one approach (Sydeman et al. 1997; Woo et al. 2008; Nielsen et al. 2018; Muller et al. 2022; Hoenig et al. 2022). For terns, a burst in the delivery of small prey items (invertebrates, small larval fish) may increase provisioning trophic diversity, as these metrics are based on counts of different prey items. However, the same burst of small prey may have little influence on trophic diversity measured using stable isotope data, as isotope values are based on the amount of material assimilated from prey. Isotope data will underestimate trophic diversity when prey items have similar isotope values, such as reported for fish species in the Gulf of Maine (Legett et al. 2023). Provisioning data may underestimate trophic diversity when there is a large portion of unidentified prey that cannot be included in diversity calculations, and this may be more common when preferred prey availability is low and terns forage on less common and/or smaller prey items (i.e., invertebrates or larval fish).

Though isotope and provisioning data provide inherently different information on trophic ecology (Nielsen et al. 2018), we found that mean isotope values were correlated with key diet parameters across contexts for common and Arctic terns breeding in the Gulf of Maine. Specifically, a higher percent of herring and hake in tern chick diet was associated with higher δ^{15}N values, likely due to fewer invertebrates in the diet of these chicks, and to more enriched δ^{13}C values. Additionally, we found support for our prediction of a correlation between isotope (SEA_c) and dietary (H’) measures of trophic diversity (P1), though isotope measures of trophic diversity showed a much larger range across contexts. In some cases, such as for seabird species that regurgitate to feed their chicks, collecting provisioning data alongside stable isotope data may not be possible; our findings suggest that stable isotopes can provide insight into key diet parameters when other methods cannot be used.

The correlation between tern chick $\delta^{13}C$ values and diet composition may be driven by relationships between island location and prey availability. Ship Island and Petit Manan Island are both relatively inshore, and tern chicks on these islands had a high percent of herring and hake in their diet (≥67% for all sampling occasions), while terns breeding on islands more than 20 miles offshore, such as Matinicus Rock and Seal Island, generally fed chicks a lower percent of herring and hake (≤40% for most sampling occasions). Previous work has noted a higher proportion of invertebrates in the diet of terns on Matinicus Rock and Seal Island as compared to other Gulf of Maine Islands, though not all of the islands in our study were included in this work (Yakola et al. 2021).

Patterns in $\delta^{13}C$ were, however, less related to island location, with values from one offshore island (Seal Island) spanning the full range of average values across contexts (-20.9‰ for Arctic terns in 2018 to -18.53‰ for common terns in 2017). Importantly, while variation in $\delta^{13}C$ values in seabirds is strongly tied to spatial variation in $\delta^{13}C$ baselines (in European shag *Phalacrocorax aristotelis*: Moreno et al. 2011), these values are not always correlated with foraging distance (e.g., in yellow-eyed penguins *Megadyptes antipodes*: Muller et al. 2022). Arctic terns and common terns may also forage on terrestrial invertebrates (e.g., ants, dragonflies; Yakola et al. 2021), further complicating interpretation of $\delta^{13}C$ values.

Trophic Diversity Across Contexts

We did not find support for our prediction (P2) that terns would show greater trophic diversity under conditions of lower food availability. Within a given context (i.e., on a particular island, in a particular year), we have observed drastic changes in feeding rate and prey composition associated with increases in SST (Sund 2023; Welch pers. comm.). However, the current study aggregated data at the colony and island level, and there are likely to be many other variables that influence trophic diversity across these contexts. For example, the within-season phenology of Arctic and common tern diet in the Gulf of Maine varies by island (e.g., herring decreases in the diet of terns throughout the season on some islands and increases in others) and with pre-breeding season environmental conditions (e.g., the date of the spring thermal transition) (Yakola et al. 2021). Additionally, the islands studied vary in their breeding seabird density and community composition, so interspecific competition and the ability to alter foraging behavior and diet may vary across contexts (e.g., Patterson et al. 2022).

Our findings contrast with previous research suggesting that the trophic diversity of seabirds (e.g., Cape Verde Shearwater *Calonectris edwardsii* adults: Ramos et al. 2018; three alcid species: Jenkins and Davoren 2021) and other marine predators (e.g., in humpback whales: Gulka et al. 2017; Atlantic cod *Gadus morhua*: Berard and Davoren 2020) increases with decreasing food availability. In Magellanic penguins, for example, isotope niche decreased with forage fish biomass and the occurrence of forage fish in the diet across 12 breeding colonies and seven years (Cianco et al. 2021). In some seabird systems, however, a reduction in trophic diversity has been linked to low food availability (e.g., in the little penguin *Eudyptula minor*: Kowalczyk et al. 2013), stressing the importance of local context in driving these relationships.

Much of the previous work showing increases in trophic diversity of seabirds during periods of reduced food availability has focused on adult seabirds. In some seabird species, adults feed their chicks higher quality prey than they consume themselves (e.g., in common guillemot *Uria aalge*: Wilson et al. 2005; in crested terns *Sterna bergii*: McLeay et al. 2009; in southern rockhopper penguins *Eudyptes chrysocome*: Rosciano et al. 2019). Because poor-quality food items can reduce chick growth rate and survival in common terns (e.g., Szostek and Becker 2012; Reichert et al 2014) and Arctic terns (e.g., Suddaby and Ratcliffe 1997; Morten et al. 2022), adults may attempt to buffer chicks from changes in food availability, leading to less pronounced shifts in trophic diversity in chicks than in adults.

Trophic Diversity Across Tissue Types

The change in isotope values between blood cells and plasma varied across individuals, but were nearly always positive for both δ^{13}C and δ^{15}N. There are no published values for trophic discrimination factors in the blood cell components of terns, but controlled feeding studies on alcids suggest a lower trophic discrimination factor in plasma than in blood cells, which would suggest a shift to less-enriched δ^{13}C and lower δ^{15}N values, all else being equal (Jenkins et al. 2020). Rather, the shifts we found are in line with previous findings that terns alter their behavior, foraging for higher-trophic items closer to the colony, as their chicks grow. In Royal (*Thalasseus maximus maximus*) and Cayenne (*T. sandvicensis eurygnathus*) terns (Marinao et al. 2019) and in Sandwich terns *Sterna sandvicensis* (Stienen et al. 2000) adults meet growing chicks' needs by feeding them larger prey. In common terns, chick energy requirements are thought to peak at around 15 days (Klaassen 1994). The size of provisioned prey increases as chicks age (Wiggins and Morris 1987), and provisioning rates increase and then decrease as chicks age (Rossell et al. 2000). Similarly, Arctic and common terns breeding in northeast England alter feeding rate, prey size, and foraging areas with chick age (Robertson et al. 2014). Specifically, to maintain higher feeding rates, Arctic terns and common terns shifted their core foraging areas closer to the colony and reduced the size of their foraging area as the breeding season progressed (Robertson et al. 2014).

We found some support for our prediction (P3) that trophic diversity would be greater among plasma samples than blood cell samples, as they represent diet integrated over a shorter time period representing a later part of the chick rearing period. Intraspecific diversity in diet and foraging behavior is often higher at shorter timescales (Woo et al. 2008). Across all paired samples, plasma had more-enriched and more variable δ^{13}C values, higher and more variable δ^{15}N values, and larger isotope ellipses. However, the variability of plasma isotope values was not significantly higher than that of blood cell isotope values at the level of sampling occasion, which may have been due to a low number of paired samples at the island, year, and species level.

In previous seabird studies, measures of trophic diversity calculating using plasma samples are greater than those calculated using blood cell samples (in two species of shearwater: Carvalho and Davoren 2020; in three species of alcid: Jenkins and Davoren 2021). These differences may not be completely driven by true changes in trophic diversity across time, however. Controlled feeding studies of adult Atlantic puffins (*Fratercula arctica*) and common murres (*Uria aalge*) found that plasma samples had a larger isotopic niche than did blood cell samples, even though individuals were fed similar diets for 80 days before sample collection (Jenkins et al. 2020). Though collecting samples of different tissue types provide a promising means of examining within-individual shifts in diet over time (e.g., Klaasen et al. 2010), this type of work must be interpreted with caution and would benefit from more controlled feeding studies that compare variation in isotope values across tissue types.

Trophic Diversity Across Species

Across all samples, we found lower δ^{15}N values and less-enriched δ^{13}C values in Arctic tern chicks than in common tern chicks. For any given island and year, the two species were rarely different along both isotope axes, but overlap in two-dimensional isotope space was low (average of 17%). Lower δ^{15}N values in Arctic tern chicks are consistent with findings of previous research (Yakola et al. 2021) and with observations that we have made on the islands in this study (Welch pers. comm), both of which suggest that Arctic terns in the Gulf of Maine have a diet with a higher abundance of invertebrates than that of common terns. Though we did not find a large difference in the average percent herring and hake in the diet of common tern and Arctic tern chicks across contexts in this study, we did find that Arctic terns fed smaller prey than common terns on average.

The less-enriched δ^{13}C values of Arctic terns as compared to common terns are likely due to differences in the foraging habitat of these two species. Arctic terns breeding in Nova Scotia forage on the ocean side of their colonies, in deeper water than common terns, which forage in shallow waters between the colony and the mainland (Rock et al. 2007). Though the foraging areas of these two species were shown to overlap in other systems (e.g., in Northeast England: Robertson et al. 2014), preliminary tagging data for the Gulf of Maine suggests patterns similar to those seen in Nova Scotia (Gownaris, unpublished data). Additionally, these results are consistent with findings on the adult pre-breeding diet of common terns and Arctic terns in the Gulf of Maine, as egg membrane samples for Arctic terns showed consistently lower δ^{15}N values and less-enriched δ^{13}C values than did common terns (Bratton et al. 2022).

Contrary to our prediction (P4), however, we did not find a significant difference in the SEA_c size or H' values of these two species. Additionally, though the isotope values of Arctic tern chicks differed from that of common tern chicks, the variability in these values did not differ among the two species. Earlier studies on tern breeding colonies in the Gulf of Maine, including one island in this study (Matinicus Rock) showed that the diet of common terns was more diverse than that of Arctic terns (Hall et al. 2000). More recent studies (Yakola et al. 2021) did not find a difference between the H' values of provisioned prey of these two species. Our H' values were lower than those found by Yakola et al. (2021), which considered diet over longer time periods and a larger number of islands, only some of which overlapped with this study, for Arctic terns (our study: 1.45, their study: 1.74) and common terns (our study: 1.27, their study: 1.57). Other recent studies have shown a larger isotope niche for Arctic terns than for common terns in the Gulf of Maine, but these studies focused on pre-breeding adults (Bratton et al. 2022), which are likely to exhibit different foraging behaviors than they do while provisioning chicks.

Individual-Level Shifts in Diet

As predicted (P5), we found that individuals varied in their diet plasticity over a two-week period on Petit Manan in 2021. The data from the majority of tern chicks showed a shift to higher δ^{15}N values and less-enriched δ^{13}C values during this period, in contrast to a shift to more-enriched δ^{13}C values from blood cells to plasma. The magnitude of these shifts was surprisingly large given that seabirds often show relatively consistent diet over short time scales (Woo et al. 2008). One common tern chick, for example, showed a $\Delta\delta^{15}N$ of 2.2‰ over a nine-day period, suggesting a change of nearly one trophic level in diet using the often-assumed trophic discrimination factor of 3.4‰ (but see Stephens et al. 2023 for a discussion of variation in trophic discrimination factors).

Though the isotope values of most tern chicks shifted in the same direction, the slopes of these shifts were highly variable across individuals. Shifts in $\delta^{15}N$ and $\delta^{13}C$ between paired plasma samples showed a strong negative correlation on Petit Manan Island, with individuals that shifted to higher $\delta^{15}N$ values showing $\delta^{13}C$ values indicative of farther-offshore foraging. In comparison, shifts between paired blood cell and plasma isotope values were negatively correlated for Arctic terns, but were positively correlated for common terns. Shifts between paired blood cell and plasma samples are, however, more complex to interpret than those between paired plasma samples. The paired plasma samples represent isotope values for chicks of similar age, on just one island, and of the same tissue type. Interestingly, variation in isotope slopes among individuals resulted in lower trophic diversity, as measured using the isotope ellipse, during the second sampling period as compared to the first sampling period. Individuals became particularly constrained in $\delta^{13}C$-space during the second sampling period, potentially suggesting a movement of prey to more-offshore habitats (Figure 8).

The correlation between shifts in $\delta^{15}N$ and $\delta^{13}C$ values for terns on Petit Manan in 2021 suggests the presence of alternative mechanisms for coping with changing food availability (Figure 1). We found similar trade-offs in foraging behavior and diet among provisioning metrics, which showed that a decrease of herring and hake in the diet of terns corresponded with an increase in feeding rate. These trade-offs may have implications for chick fitness. In partial support of our prediction (P6), the magnitude of shifts in isotope values did not impact chick survival but did impact the asymptotic mass of Arctic tern chicks. This relationship was not significant for common tern chicks, for which the sample size for paired plasma samples was low.

Surprisingly, steeper slopes to more positive $\delta^{15}N$ values were associated with a lower fledging mass in Arctic tern chicks. Because $\delta^{15}N$ slopes were strongly correlated with $\delta^{13}C$ slopes, this may indicate that traveling farther to capture high trophic-level prey is a less beneficial strategy for Arctic tern parents on Petit Manan Island than is maintaining a high feeding rate of less-preferred prey. For black terns (*Chlidonias niger*), feeding rates show a negative correlation with the occurrence of large fish in the diet of chicks, and insect deliveries to chicks increased as chicks aged and helped to buffer chick growth and survival against variability in prey (Gilbert et al. 2005). Though contrary to what might be expected, incorporating near-colony, low-trophic level prey may be a beneficial strategy that helps terns to maintain chick fledging mass. Chicks that fledge at a larger size are more likely to survive and recruit to the colony in common terns (Ludwigs and Becker 2006) and other seabird species (Forester's terns *Sterna forsteri*: Ackerman et al. 2008; tufted puffin *Fratercula cirrhata*: Morrison et al. 2009). Importantly, all of the chicks that we sampled for this part of the study were past their linear growth phase; our findings may have differed if we had sampled young chicks with higher energetic needs.

Changes in $\delta^{15}N$ and $\delta^{13}C$ signatures, and relationships to asymptotic chick mass, could be confounded by starvation. This possibility is particularly acute for $\delta^{13}C$, as starvation could lead chicks to break down and incorporate $\delta^{13}C$-depleted lipid stores (e.g., in tufted puffins *Fratercula cirrhata*: Williams et al. 2007). Starvation was the major cause of mortality in chicks in 2021, and many of the chicks sampled were of low mass for their age (range: 62 g to 118 g with a mean of 86 g across all chicks). Chick mass increased (between 5 and 17 grams) between the two sampling occasions for chicks sampled twice, with the exception of two chicks that each lost two grams; all of these measurements took place during the asymptotic phase of mass growth. Importantly, we did not find higher or more variable C:N ratios for plasma samples collected during the second sampling period (mean of 4.90±0.42) than for those collected during the first sampling period (mean of 5.16±0.39), suggesting that reductions in $\delta^{13}C$ were not due to incorporation of lipids in underfed chicks.

Conclusions

We found high variation in the trophic diversity of Arctic tern and common tern chicks across five islands and three years characterized by different environmental conditions. Though trophic diversity was not correlated with indicators of food availability, we did find evidence that individuals differed in the magnitude of the shift between paired blood cell and plasma samples and between paired plasma samples, indicating intraspecific variation in trophic plasticity. Additionally, correlations among provisioning parameters and among shifts in isotope values indicated trade-offs, where smaller, lower-trophic level diet items were associated with foraging habitats closer to the breeding colony and with higher feeding rates. Contrary to what would often be expected, a greater-magnitude shift to higher trophic levels was associated with a smaller fledging size in Arctic terns on Petit Manan Island in 2021.

Studies have historically examined shifts in diet using isotopes in different tissue types, which may be more difficult to interpret due to differences in trophic discrimination factors (Quillfeldt et al. 2008) and lipid content (Jenkins et al. 2020). Our study is the first to collect paired samples of the same type and indicative of diet over short time periods for the same individuals, allowing us to examine shifts in diet without these potentially confounding variables. Though the conclusions we could reach using paired plasma samples was limited due to a low sample size, we found evidence that individual-level foraging plasticity may be influencing tern fitness through impacts on chick fledging size.

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Author Contributions

N.Gownaris led Conceptualization, Methodology, Formal Analysis, and Writing and contributed to Investigation. **L. Welch** contributed to Conceptualization, Methodology, Investigation, and Writing. **J. Tengeres** contributed to Investigation, Formal Analysis, and Writing.

Conflict of Interest Statement

The authors have no conflict of interest to declare.

References

Ackerman, Joshua T., Collin A. Eagles-Smith, John Y. Takekawa, and S. A. Iverson. 2008. "Survival of Post-fledging Forster's Terns in Relation to Mercury Exposure in San Francisco Bay." *Ecotoxicology* 17 (8): 789–801. https://doi.org/10.1007/s10646-008-0237-6.

Barrett, Robert T., and Yuri V. Krasnov. 1996. "Recent Responses to Changes in Stocks of Prey Species by Seabirds Breeding in the Southern Barents Sea." *ICES Journal of Marine Science* 53 (4): 713–22. https://doi.org/10.1006/jmsc.1996.0090.

Becker, Peter H., Dietrich Frank, and Stefan R. Sudmann. 1993. "Temporal and Spatial Pattern of Common Tern (*Sterna hirundo*) Foraging in the Wadden Sea." *Oecologia* 93 (3): 389–93. https://doi.org/10.1007/BF00317883.

Berard, Marissa T., and Gail K. Davoren. 2020. "Capelin (*Mallotus villosus*) Availability Influences the Inshore Summer Diet of Atlantic Cod (*Gadus morhua*) in Coastal Newfoundland." *Environmental Biology of Fishes* 103 (6): 771–82. https://doi.org/10.1007/s10641-020-00982-9.

Boersma, P. Dee. 2008. "Penguins as Marine Sentinels." *BioScience* 58 (7): 597–607. https://doi.org/10.1641/B580707.

Bourgeois, Karen, Jemma R. Welch, Sylvain Dromzée, Graeme A. Taylor, and James C. Russell. 2022. "Flexible Foraging Strategies in a Highly Pelagic Seabird Revealed by Seasonal Isotopic Niche Variation." *Marine Biology* 169 (2): 28. https://doi.org/10.1007/s00227-021-04011-w.

Boyd, I. L., and A. W. A. Murray. 2001. "Monitoring a Marine Ecosystem Using Responses of Upper Trophic Level Predators." *Journal of Animal Ecology* 70 (5): 747–60. https://doi.org/10.1046/j.0021-8790.2001.00534.x.

Bratton, Rachel M., Henry D. Legett, Paula Shannon, Keenan C. Yakola, Alexander R. Gerson, and Michelle D. Staudinger. 2022. "Pre-breeding Foraging Ecology of Three Tern Species Nesting in the

Gulf of Maine.” *Avian Conservation and Ecology* 17 (1): art19. https://doi.org/10.5751/ACE-02112-170119.

Cabot, David, and Ian Nisbet. 2013. *Terns*. 1st ed. Collins New Naturalist Library, United Kingdom. 461 pp.

Cairns, D.K. 1988. “Seabirds as Indicators of Marine Food Supplies.” *Biological Oceanography* 5 (4): 261–71. https://doi.org/10.1080/01965581.1987.10749517.

Carvalho, Paloma C., and Gail K. Davoren. 2020. “Niche Dynamics of Sympatric Non-breeding Shearwaters under Varying Prey Availability.” *Ibis* 162 (3): 701–12. https://doi.org/10.1111/ibi.12783.

Caspi, Tal, Jacob R. Johnson, Max R. Lambert, Christopher J. Schell, and Andrew Sih. 2022. “Behavioral Plasticity Can Facilitate Evolution in Urban Environments.” *Trends in Ecology & Evolution* 37 (12): 1092–1103. https://doi.org/10.1016/j.tree.2022.08.002.

Cherel, Y, and A Carrouée. 2022. “Assessing Marine Ecosystem Complexity: Isotopic Integration of the Trophic Structure of Seabird Communities from the Southern Ocean.” *Marine Ecology Progress Series* 694 (August): 193–208. https://doi.org/10.3354/meps14087.

Ciancio, Javier E., Pablo Yorio, Claudio Buratti, Gustavo Álvarez Colombo, and Esteban Frere. 2021. “Isotopic Niche Plasticity in a Marine Top Predator as Indicator of a Large Marine Ecosystem Food Web Status.” *Ecological Indicators* 126 (July): 107687. https://doi.org/10.1016/j.ecolind.2021.107687.

Collette, B.B., Klein-MacPhee, G. 2002. *Bigelow and Schroeder’s Fishes of the Gulf of Maine*. 3rd ed. Smithsonian Institution Press, Washington, DC. 748 pp.

Dingemanse, Niels J., and Ned A. Dochtermann. 2013. “Quantifying Individual Variation in Behaviour: Mixed-Effect Modelling Approaches.” *Journal of Animal Ecology* 82 (1): 39–54. https://doi.org/10.1111/1365-2656.12013.

Gilbert, Andrew T., and Frederick A. Servello. 2005. “Insectivory versus Piscivory in Black Terns: Implications for Food Provisioning and Growth of Chicks.” *Waterbirds* 28 (4): 436–44. https://doi.org/10.1675/1524-4695(2005)28[436:IVPIBT]2.0.CO;2.

Gilmour, Morgan E., José A. Castillo-Guerrero, Abram B. Fleishman, Salvador Hernández-Vázquez, Hillary S. Young, and Scott A. Shaffer. 2018. “Plasticity of Foraging Behaviors in Response to Diverse Environmental Conditions.” *Ecosphere* 9 (7): e02301. https://doi.org/10.1002/ecs2.2301.

Gulka, Julia, Paloma C. Carvalho, Edward Jenkins, Kelsey Johnson, Laurie Maynard, and Gail K. Davoren. 2017. “Dietary Niche Shifts of Multiple Marine Predators under Varying Prey Availability on the Northeast Newfoundland Coast.” *Frontiers in Marine Science* 4 (October): 324. https://doi.org/10.3389/fmars.2017.00324.

Hall, C., Stephen Kress, and Curtice Griffin. 2000. “Composition, Spatial and Temporal Variation of Common and Arctic Tern Chick Diets in the Gulf of Maine.” *Waterbirds: The International Journal of Waterbird Biology* 23 (January): 430. https://doi.org/10.2307/1522180.

Hall, L. Embere, and Anna D. Chalfoun. 2019. “Behavioural Plasticity Modulates Temperature-Related Constraints on Foraging Time for a Montane Mammal.” *Journal of Animal Ecology* 88 (3): 363–75. https://doi.org/10.1111/1365-2656.12925.

Hobson, Keith A., and R. G. Clark. 1993. “Turnover of ^{13}C in Cellular and Plasma Fractions of Blood: Implications for Nondestructive Sampling in Avian Dietary Studies.” *The Auk* 110 (3): 638–41. https://doi.org/10.2307/4088430.

Hobson, Keith A., John F. Piatt, and Jay Pitocchelli. 1994. “Using Stable Isotopes to Determine Seabird Trophic Relationships.” *Journal of Animal Ecology* 63 (4): 786–98. https://doi.org/10.2307/5256.

Hoenig, Brandon D, Allison M Snider, Anna M Forsman, Keith A Hobson, Steven C Latta, Eliot T Miller, Michael J Polito, et al. 2022. “Current Methods and Future Directions in Avian Diet Analysis.” *Ornithology* 139 (1): ukab077. https://doi.org/10.1093/ornithology/ukab077.

Hoffmann, Ary A., and Carla M. Sgrò. 2011. “Climate Change and Evolutionary Adaptation.” *Nature* 470 (7335): 479–85. https://doi.org/10.1038/nature09670.

Jackson, Andrew L., Richard Inger, Andrew C. Parnell, and Stuart Bearhop. 2011. “Comparing Isotopic Niche Widths among and within Communities: SIBER – Stable Isotope Bayesian Ellipses in R.” *Journal of Animal Ecology* 80 (3): 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Jenkins, Edward, Julia Gulka, David J. Yurkowski, Nathalie R. Le François, Emiko Wong, and Gail K. Davoren. 2020. “Isotopic Discrimination (δ^{15}N, δ^{13}C) in Captive and Wild Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica*).” *Physiological and Biochemical Zoology* 93 (4): 296–309. https://doi.org/10.1086/709460.

Jenkins, Edward J., and Gail K. Davoren. 2021. “Seabird Species- and Assemblage-level Isotopic Niche Shifts Associated with Changing Prey Availability during Breeding in Coastal Newfoundland.” *Ibis* 163 (1): 183–96. https://doi.org/10.1111/ibi.12873.

Klaassen, Marcel. 1994. “Growth and Energetics of Tern Chicks from Temperate and Polar Environments.” *The Auk* 111 (3): 525–44.

Klaassen, Marcel, Theunis Piersma, Harry Korthals, Anne Dekinga, and Maurine W. Dietz. 2010. “Single-Point Isotope Measurements in Blood Cells and Plasma to Estimate the Time since Diet Switches.” *Functional Ecology* 24 (4): 796–804. https://doi.org/10.1111/j.1365-2435.2010.01689.x.

Kokubun, N, A Takahashi, R Paredes, Rc Young, Nn Sato, T Yamamoto, Dm Kikuchi, et al. 2018. "Inter-Annual Climate Variability Affects Foraging Behavior and Nutritional State of Thick-Billed Murres Breeding in the Southeastern Bering Sea." *Marine Ecology Progress Series* 593 (April): 195–208. https://doi.org/10.3354/meps12365.

Kowalczyk, Nicole D., Andre Chiaradia, Tiana J. Preston, and Richard D. Reina. 2014. "Linking Dietary Shifts and Reproductive Failure in Seabirds: A Stable Isotope Approach." *Functional Ecology* 28 (3): 755–65. https://doi.org/10.1111/1365-2435.12216.

Legett, Hd, Jr Lucas, Ec Craig, and Md Staudinger. 2023. "Variation in Isotopic Niche Partitioning between Adult Roseate and Common Terns in the Northwest Atlantic." *Endangered Species Research* 50 (April): 235–47. https://doi.org/10.3354/esr01233.

Ludwigs, Jan-Dieter, and Peter Becker. 2006. "Individual Quality and Recruitment in the Common Tern, *Sterna hirundo*." *Acta Zoologica Sinica* 52 (January): 96–100.

Marinao, Cristian, Nicolás Suárez, Alejandro Gatto, and Pablo Yorio. 2019. "Forage Fish to Growing Chicks: Shared Food Resources between Two Closely Related Tern Species." *Marine Biology* 166 (9): 121. https://doi.org/10.1007/s00227-019-3570-9.

Maynard, Laurie D., Julia Gulka, Edward Jenkins, and Gail K. Davoren. 2021. "Different Individual-Level Responses of Great Black-Backed Gulls (*Larus marinus*) to Shifting Local Prey Availability." *PLOS ONE* 16 (10): e0252561. https://doi.org/10.1371/journal.pone.0252561.

McLeay, Lachlan James, B. Page, S. D. Goldsworthy, T. M. Ward, and D. C. Paton. 2009. "Size Matters: Variation in the Diet of Chick and Adult Crested Terns." *Marine Biology* 156 (9): 1765–80. https://doi.org/10.1007/s00227-009-1211-4.

Mery, Frederic, and James G. Burns. 2010. "Behavioural Plasticity: An Interaction between Evolution and Experience." *Evolutionary Ecology* 24 (3): 571–83. https://doi.org/10.1007/s10682-009-9336-y.

Moreno, Rocío, Lluis Jover, Alberto Velando, Ignacio Munilla, and Carola Sanpera. 2011. “Influence of Trophic Ecology and Spatial Variation on the Isotopic Fingerprints of Seabirds.” *Marine Ecology Progress Series* 442 (December): 229–39. https://doi.org/10.3354/meps09420.

Morrison, Kyle W., J. Mark Hipfner, Carina Gjerdrum, and David J. Green. 2009. “Wing Length and Mass at Fledging Predict Local Juvenile Survival and Age at First Return in Tufted Puffins.” *The Condor* 111 (3): 433–41. https://doi.org/10.1525/cond.2009.080099.

Morten, Joanne M., Julian M. Burgos, Lee Collins, Sara M. Maxwell, Eliza-Jane Morin, Nicole Parr, William Thurston, Freydís Vigfúsdóttir, Matthew J. Witt, and Lucy A. Hawkes. 2022. “Foraging Behaviours of Breeding Arctic Terns *Sterna paradisaea* and the Impact of Local Weather and Fisheries.” *Frontiers in Marine Science* 8. https://www.frontiersin.org/articles/10.3389/fmars.2021.760670.

Muller, Chris G., B. Louise Chilvers, Rebecca K. French, and Phil F. Battley. 2022. “Diet Plasticity and Links to Changing Foraging Behaviour in the Conservation of Subantarctic Yellow-eyed Penguins *Megadyptes antipodes*).” *Aquatic Conservation: Marine and Freshwater Ecosystems* 32 (5): 753–65. https://doi.org/10.1002/aqc.3797.

Nielsen, Jens M., Elizabeth L. Clare, Brian Hayden, Michael T. Brett, and Pavel Kratina. 2018. “Diet Tracing in Ecology: Method Comparison and Selection.” *Methods in Ecology and Evolution* 9 (2): 278–91. https://doi.org/10.1111/2041-210X.12869.

Owen, Jennifer C. 2011. “Collecting, Processing, and Storing Avian Blood: A Review.” Journal of Field Ornithology 82 (4): 339–54. https://doi.org/10.1111/j.1557-9263.2011.00338.x.

Paiva, Vh, P Geraldes, I Ramírez, A Meirinho, S Garthe, and Ja Ramos. 2010. “Foraging Plasticity in a Pelagic Seabird Species along a Marine Productivity Gradient.” *Marine Ecology Progress Series* 398 (January): 259–74. https://doi.org/10.3354/meps08319.

Paiva, Vitor H., Ana I. Fagundes, Vera Romão, Cátia Gouveia, and Jaime A. Ramos. 2016. “Population-Scale Foraging Segregation in an Apex Predator of the North Atlantic.” *PLOS ONE* 11 (3): e0151340. https://doi.org/10.1371/journal.pone.0151340.

Patterson, Allison, H. Grant Gilchrist, Sigurd Benjaminsen, Mark Bolton, Anne Sophie Bonnet-Lebrun, Gail K. Davoren, Sébastien Descamps, et al. 2022. “Foraging Range Scales with Colony Size in High-Latitude Seabirds.” *Current Biology* 32 (17): 3800-3807.e3. https://doi.org/10.1016/j.cub.2022.06.084.

Pershing, Andrew J., Michael A. Alexander, Damian C. Brady, David Brickman, Enrique N. Curchitser, Antony W. Diamond, Loren McClenachan, et al. 2021. “Climate Impacts on the Gulf of Maine Ecosystem: A Review of Observed and Expected Changes in 2050 from Rising Temperatures.” *Elementa: Science of the Anthropocene* 9 (1): 00076. https://doi.org/10.1525/elementa.2020.00076.

Piatt, John F., Ann M. A. Harding, Michael Shultz, Suzann G. Speckman, Thomas I. Van Pelt, Gary S. Drew, and Arthur B. Kettle. 2007. “Seabirds as Indicators of Marine Food Supplies: Cairns Revisited.” *Marine Ecology Progress Series* 352: 221–34.

Post, David M., Craig A. Layman, D. Albrey Arrington, Gaku Takimoto, John Quattrochi, and Carman G. Montaña. 2007. “Getting to the Fat of the Matter: Models, Methods and Assumptions for Dealing with Lipids in Stable Isotope Analyses.” *Oecologia* 152 (1): 179–89.

Pratte, I, Ra Ronconi, Sr Craik, and J McKnight. 2021. “Spatial Ecology of Endangered Roseate Terns and Foraging Habitat Suitability around a Colony in the Western North Atlantic.” *Endangered Species Research* 44 (March): 339–50. https://doi.org/10.3354/esr01108.

Quillfeldt, Petra, Leandro Bugoni, Rona A. R. McGill, Juan F. Masello, and Robert W. Furness. 2008. “Differences in Stable Isotopes in Blood and Feathers of Seabirds Are Consistent across Species, Age and Latitude: Implications for Food Web Studies.” *Marine Biology* 155 (6): 593–98. https://doi.org/10.1007/s00227-008-1048-2.

Quintero, Ignacio, and John J. Wiens. 2013. “Rates of Projected Climate Change Dramatically Exceed Past Rates of Climatic Niche Evolution among Vertebrate Species.” *Ecology Letters* 16 (8): 1095–1103. https://doi.org/10.1111/ele.12144.

Ramos, Jaime A., Isabel Rodrigues, Tommy Melo, Pedro Geraldes, and Vitor H. Paiva. 2018. “Variation in Ocean Conditions Affects Chick Growth, Trophic Ecology, and Foraging Range in Cape Verde Shearwater.” *The Condor* 120 (2): 283–90. https://doi.org/10.1650/CONDOR-17-220.1.

Riechert, Juliane, Peter H. Becker, and Olivier Chastel. 2014. “Predicting Reproductive Success from Hormone Concentrations in the Common Tern (*Sterna hirundo*) While Considering Food Abundance.” *Oecologia* 176 (3): 715–27. https://doi.org/10.1007/s00442-014-3040-5.

Robertson, G. S., M. Bolton, W. J. Grecian, L. J. Wilson, W. Davies, and P. Monaghan. 2014. “Resource Partitioning in Three Congeneric Sympatrically Breeding Seabirds: Foraging Areas and Prey Utilization.” *The Auk* 131 (3): 434–46. https://doi.org/10.1642/AUK-13-243.1.

Rock, Jennifer C., Marty L. Leonard, and Andrew W. Boyne. 2007. “Do Co-nesting Arctic and Common Terns Partition Foraging Habitat and Chick Diets?” *Waterbirds: The International Journal of Waterbird Biology* 30 (4): 579–87.

Rosciano, Natalia G., Michael J. Polito, and Andrea Raya Rey. 2019. “What’s for Dinner Mom? Selective Provisioning in Southern Rockhopper Penguins (*Eudyptes chrysocome*).” *Polar Biology* 42 (8): 1529–35. https://doi.org/10.1007/s00300-019-02538-9.

Rossell, Jr., C Reed, Christine D Hamilton, Louise M Weber, and Stephen W Kress. 2000. “Chick Provisioning by Common Terns in the Southern Gulf of Maine, U.S.A.” *Canadian Journal of Zoology* 78 (1): 158–60. https://doi.org/10.1139/z99-184.

Scopel, L, A Diamond, S Kress, and P Shannon. 2019. “Varied Breeding Responses of Seabirds to a Regime Shift in Prey Base in the Gulf of Maine.” *Marine Ecology Progress Series* 626 (September): 177–96. https://doi.org/10.3354/meps13048.

Scopel, Lauren C., Antony W. Diamond, Stephen W. Kress, Adrian R. Hards, and Paula Shannon. 2018. “Seabird Diets as Bioindicators of Atlantic Herring Recruitment and Stock Size: A New Tool for Ecosystem-Based Fisheries Management.” *Canadian Journal of Fisheries and Aquatic Sciences* 75 (8): 1215–29. https://doi.org/10.1139/cjfas-2017-0140.

Shackell, Nancy L., Daniel Ricard, and Christine Stortini. 2014. “Thermal Habitat Index of Many Northwest Atlantic Temperate Species Stays Neutral under Warming Projected for 2030 but Changes Radically by 2060.” *PLOS ONE* 9 (3): e90662. https://doi.org/10.1371/journal.pone.0090662.

Shaffer, Scott A., Sue Cockerham, Pete Warzybok, Russell W. Bradley, Jaime Jahncke, Corey A. Clatterbuck, Magali Lucia, et al. 2017. “Population-Level Plasticity in Foraging Behavior of Western Gulls (*Larus occidentalis*).” *Movement Ecology* 5 (1): 27. https://doi.org/10.1186/s40462-017-0118-9.

Snell-Rood, Emilie C. 2013. “An Overview of the Evolutionary Causes and Consequences of Behavioural Plasticity.” *Animal Behaviour* 85 (5): 1004–11. https://doi.org/10.1016/j.anbehav.2012.12.031.

Staudinger, Michelle D., Katherine E. Mills, Karen Stamieszkin, Nicholas R. Record, Christine A. Hudak, Andrew Allyn, Antony Diamond, et al. 2019. “It’s about Time: A Synthesis of Changing Phenology in the Gulf of Maine Ecosystem.” *Fisheries Oceanography* 28 (5): 532–66. https://doi.org/10.1111/fog.12429.

Stephens, Ryan B., Oliver N. Shipley, and Remington J. Moll. 2023. “Meta-Analysis and Critical Review of Trophic Discrimination Factors ($\Delta^{13}C$ and $\Delta^{15}N$): Importance of Tissue, Trophic Level and Diet Source.” *Functional Ecology* 37 (9): 2535–48. https://doi.org/10.1111/1365-2435.14403.

Stienen, Eric, Beers, Allix Brenninkmeijer, J.M.P.M. Habraken, M.H.J.E. Raaijmakers, and Tienen. 2000. “Reflections of a Specialist: Patterns in Food Provisioning and Foraging Conditions in Sandwich Terns *Sterna sandvicensis*.” *Ardea -Wageningen-* 88 (January): 33–49.

Suddaby, D., and N. Ratcliffe. 1997. “The Effects of Fluctuating Food Availability on Breeding Arctic Terns (*Sterna paradisaea*).” *The Auk* 114 (3): 524–30. https://doi.org/10.2307/4089260.

Sund, Kaiulani. 2023. "Individual-Level Responses to Rapid Climate Change in Common Terns (*Sterna hirundo*) and Arctic Terns (*Sterna paradisaea*)". Undergraduate Honor’s Thesis. The Cupola at Gettysburg College: 1091. https://cupola.gettysburg.edu/student_scholarship/1091

Sydeman, William J., Keith A. Hobson, Peter Pyle, and Elizabeth B. McLaren. 1997. “Trophic Relationships among Seabirds in Central California: Combined Stable Isotope and Conventional Dietary Approach.” *The Condor* 99 (2): 327–36. https://doi.org/10.2307/1369938.

Sydeman, William J., Elvira Poloczanska, Thomas E. Reed, and Sarah Ann Thompson. 2015. “Climate Change and Marine Vertebrates.” *Science* 350 (6262): 772–77. https://doi.org/10.1126/science.aac9874.

Szostek, K. Lesley, and Peter H. Becker. 2012. “Terns in Trouble: Demographic Consequences of Low Breeding Success and Recruitment on a Common Tern Population in the German Wadden Sea.” *Journal of Ornithology* 153 (2): 313–26. https://doi.org/10.1007/s10336-011-0745-7.

Vander Zanden, M. Jake, Murray K. Clayton, Eric K. Moody, Christopher T. Solomon, and Brian C. Weidel. 2015. “Stable Isotope Turnover and Half-Life in Animal Tissues: A Literature Synthesis.” *PLoS ONE* 10 (1): e0116182. https://doi.org/10.1371/journal.pone.0116182.

Weimerskirch, Henri. 2018. “Linking Demographic Processes and Foraging Ecology in Wandering Albatross—Conservation Implications.” *Journal of Animal Ecology* 87 (4): 945–55. https://doi.org/10.1111/1365-2656.12817.

Whelan, Shannon, Scott A. Hatch, Anthony J. Gaston, H. Grant Gilchrist, and Kyle H. Elliott. 2022. "Opposite, but Insufficient, Phenological Responses to Climate in Two Circumpolar Seabirds: Relative Roles of Phenotypic Plasticity and Selection." *Functional Ecology* 36 (7): 1782–95. https://doi.org/10.1111/1365-2435.14064.

Wiggins, David A., and Ralph D. Morris. 1987. "Parental Care of the Common Tern *Sterna hirundo.*" *Ibis* 129 (s2): 533–40. https://doi.org/10.1111/j.1474-919X.1987.tb08241.x.

Williams, Cory T., C. Loren Buck, Justine Sears, and Alexander S. Kitaysky. 2007. "Effects of Nutritional Restriction on Nitrogen and Carbon Stable Isotopes in Growing Seabirds." *Oecologia* 153 (1): 11–18. https://doi.org/10.1007/s00442-007-0717-z.

Wilson, L.J., Francis Daunt, and S. Wanless. 2005. "Self-Feeding and Chick Provisioning Diet Differ in the Common Guillemot *Uria aalge*." *Ardea* 92 (January): 197–207.

Woo, Kerry J., Kyle Hamish Elliott, Melissa Davidson, Anthony J. Gaston, and Gail K. Davoren. 2008. "Individual Specialization in Diet by a Generalist Marine Predator Reflects Specialization in Foraging Behaviour." *Journal of Animal Ecology* 77 (6): 1082–91. https://doi.org/10.1111/j.1365-2656.2008.01429.x.

Yakola, Keenan. 2019. An Examination of Tern Diet in a Changing Gulf of Maine. MsC Thesis, University of Massachusetts, Amherst. https://doi.org/10.7275/15222158

Yakola, Keenan, Adrian Jordaan, Stephen Kress, Paula Shannon, and Michelle D. Staudinger. 2021. "Interspecific and Local Variation in Tern Chick Diets Across Nesting Colonies in the Gulf of Maine." *Waterbirds* 44 (4). https://doi.org/10.1675/063.044.0402.

Zango, Laura, José Manuel Reyes-González, Teresa Militão, Zuzana Zajková, Eduardo Álvarez-Alonso, Raül Ramos, and Jacob González-Solís. 2019. "Year-Round Individual Specialization in the Feeding

Ecology of a Long-Lived Seabird.” *Scientific Reports* 9 (August): 11812. https://doi.org/10.1038/s41598-019-48214-0.

Tables

Table 1: Locations of the five islands studied showing annual productivity data (chicks fledged per nest) and linear growth rates of chicks (in parentheses; g·day^{-1}) for common terns (COTE) and Arctic terns (ARTE). Combinations in grey were not included in this study; only productivity data are shown for these combinations.

	Lat	**Long**	**2017 (COTE)**	**2018 (COTE)**	**2021 (COTE)**	**2017 (ARTE)**	**2018 (ARTE)**	**2021 (ARTE)**
Petit Manan	44.367	-67.865	1.48 (6.94)	0.83 (7.51)	0.43 (5.09)	0.78 (6.69)	0.69 (6.49)	0.16 (4.06)
Ship	44.235	-68.440	0.39	0*	0.94 (7.51)	NA	NA	NA
Seal	43.888	-68.740	1.15 (5.90)	0.48 (3.65)	0.32	1.13 (5.40)	0.76 (3.65)	0.22
Metinic	43.883	-69.125	1.48 (6.07)	0.83 (5.61)	0.43	1.58 (6.38)	0.96 (4.30)	0.64
Matinicus Rock	43.783	-68.855	1.57 (6.40)	0.54	0.28	0.89 (5.79)	0.55 (3.82)	0.25

*In 2018 the entire common tern colony on Ship Island abandoned and no chicks survived

Table 2: Comparison of generalized linear models linking the percent herring and hake in the diet of terns (HR_{mean}) to prey size (PS_{mean}), feeding rate (FR_{mean}), and average isotope values for each sampling occasion.

Model	**logLik**	**AIC**	**AIC - AIC_{null}**
~1	-79.33	162.66	0.00
Relationships between HR_{mean} and PS_{mean}			
~PS_{mean}	-75.82	157.63	-5.02
~PS_{mean} + Species	-74.86	157.73	-4.93
~PS_{mean} * Species	-74.71	159.43	-3.23
Relationships between HR_{mean} and FR_{mean}			
~FR_{mean}	-73.68	153.37	-9.29
~FR_{mean} + Species	-73.60	155.20	-7.46
~FR_{mean} * Species	-73.60	157.19	-5.46
Relationships between HR_{mean} and $\delta^{13}C_{mean}$			
~$\delta^{13}C_{mean}$	-75.82	157.64	-5.01
~$\delta^{13}C_{mean}$ + Species	-75.27	158.53	-4.12
~$\delta^{13}C_{mean}$ * Species	-74.74	159.48	-3.18
Relationships between HR_{mean} and $\delta^{15}N_{mean}$			
~$\delta^{15}N_{mean}$	-76.37	158.75	-3.91
~$\delta^{15}N_{mean}$ * Species	-76.18	160.37	-2.29
~$\delta^{15}N_{mean}$ + Species	-75.35	160.70	-1.96

Table 3: Comparison of Akaike information criterion (AIC) for generalized linear models linking the Shannon-Wiener Diversity Index of prey provisioned by terns (H’) to their stable isotope ellipse (SEA_c) and to two measured of food availability, mean sea surface temperature (SST_{mean}) and mean percent herring and hake (HR_{mean}).

Model	**logLik**	**AIC**	**AIC - AIC_{null}**
Relationships H' and Blood Cell SEA_c			
~SEA_c	-6.56	19.12	-3.01
~SEA_c + Species	-6.47	20.94	-1.20
~1	-9.07	22.13	0.00
~SEA_c * Species	-6.34	22.69	0.56
Relationships Between H' and SST_{mean}			
~1	-9.07	22.13	0.00
~SST_{mean}	-9.04	24.08	1.95
~SST_{mean} + Species	-9.04	26.08	3.95
~SST_{mean} * Species	-9.03	28.06	5.93
Relationships Between H' and HR_{mean}			
~1	-9.07	22.13	0.00
~HR_{mean}	-8.44	22.88	0.75
~HR_{mean} + Species	-8.44	24.87	2.74
~HR_{mean} * Species	-8.36	26.72	4.59

Table 4: Comparison of Akaike information criterion (AIC) for generalized linear models linking the size of the stable isotope ellipse (SEA_c) for terns to measures of food availability, including mean sea surface temperature (SST_{mean}) and mean percent herring and hake (HR_{mean}).

Model	**logLik**	**AIC**	**AIC - AIC_{null}**
Relationships Between Blood Cell SEA_c and SST_{mean}			
~1	-4.57	13.14	0.00
~SST_{mean}	-4.54	15.08	1.94
~SST_{mean} + Species	-4.29	16.58	3.45
~SST_{mean} * Species	-3.96	17.93	4.79
Relationships Between Plasma SEA_c and SST_{mean}			
~1	-16.48	36.96	0.00
~SST_{mean}	-16.48	38.96	2.00
~SST_{mean} + Species	-16.46	40.93	3.97
~SST_{mean} * Species	-16.44	42.89	5.93
Relationships Between Blood Cell SEA_c and HR_{mean}			
~1	-4.57	13.14	0.00
~HR_{mean}	-4.24	14.48	1.34
~HR_{mean} + Species	-3.91	15.82	2.69
~HR_{mean} * Species	-3.56	17.12	3.99

Table 5: Comparison of Akaike information criterion (AIC) for generalized linear models linking the magnitude of the shift in $\delta^{13}C$ values from blood cell isotope samples to plasma isotope samples for terns to the magnitude of the shift in $\Delta\delta^{15}N$ values across islands and species.

Model	**logLik**	**AIC**	**AIC - AIC$_{null}$**
~$\Delta\delta^{15}N$ + Island * Species	-139.38	296.75	-33.55
~$\Delta\delta^{15}N$ * Island + Species	-136.94	297.88	-32.42
~$\Delta\delta^{15}N$ * Island * Species	-130.19	298.39	-31.91
~$\Delta\delta^{15}N$ * Island	-141.39	304.78	-25.53
~$\Delta\delta^{15}N$ + Island	-147.60	309.20	-21.10
~$\Delta\delta^{15}N$ * Species	-154.69	319.38	-10.92
~$\Delta\delta^{15}N$ + Species	-158.64	325.28	-5.03
~$\Delta\delta^{15}N$	-160.24	326.47	-3.83
~1	-163.15	330.30	0.00

Table 6: Estimates from generalized linear models comparing the slope of the change in isotope values between paired plasma samples of Arctic tern (ARTE) and common tern (COTE) chicks to their asymptotic mass (Mass ASM; g) and wind chord length (Wing ASM; mm).

Species	**Isotope**	**Feature**	**Estimate [CI_{95}]**	**p value**
ARTE	$\delta^{13}C$	Mass ASM	50.84 [17.82, 83.86]	0.01
ARTE	$\delta^{13}C$	Wing ASM	-3.98 [-61.95, 53.98]	0.89
ARTE	$\delta^{15}N$	Mass ASM	-89.56 [-147.78, -31.33]	0.01
ARTE	$\delta^{15}N$	Wing ASM	-5.68 [-107.88, 96.51]	0.91
COTE	$\delta^{13}C$	Mass ASM	15.49 [-41.26, 72.24]	0.62
COTE	$\delta^{13}C$	Wing ASM	-44.79 [-202.48, 112.91]	0.61
COTE	$\delta^{15}N$	Mass ASM	-7.97 [-73.72, 57.79]	0.82
COTE	$\delta^{15}N$	Wing ASM	0.38 [-184.8, 185.57]	1.00

Figure Captions

Figure 1: When increasing sea surface temperatures (SST) drive declines in food availability, terns breeding in the Gulf of Maine can prey switch (Panel A) or alter their foraging behavior, including trip distance (Panel B), to continue feeding chicks optimal diet items. Individuals may vary in their response. In this illustrative example, the tern symbolized by green data points feeds chicks a higher proportion of invertebrates (Panel A) at higher SSTs but does not need to travel as far to capture these lower-value prey (Panel B). In contrast, the tern symbolized by yellow data points increases foraging distance (Panel B) to continue provisioning their chicks with fish (Panel A) at higher SSTs. Because the trophic level of diet and foraging habitat of an individual influence their isotope signatures, an increase in the space between the green and yellow lines in Panels A and B should drive an increase in the size of the isotope niche in this population through changes in variation in $\delta^{15}N$ and/or $\delta^{13}C$ (Panel c). Photographs taken by N. Gownaris.

Figure 2: Spatially averaged sea surface temperatures (top panel) across three breeding seasons for a 20 km buffer surrounding the five study islands studied (bottom panel). Sea surface temperature values are also shown spatially for July 15th, 2021 (bottom panel) to provide a visual of these buffers. Sea surface temperature data are taken from the Multi-scale Ultra-high Resolution (MUR) Satellite, provided by JPL under support by the NASA MEaSUREs program, which provide information on SST at a 1-km spatial scale and 1-day temporal scale. Island and year combinations in grey were not included in this study. Blood samples were separated into blood cells and plasma for combinations with a solid border or dashed border. At Petit Manan Island in 2021 (dashed border), paired plasma samples were also collected for fourteen Arctic tern and five common tern chicks.

Figure 3: Relationships between the $\delta^{13}C$ values and $\delta^{15}N$ values of paired blood cell and plasma isotope samples for Arctic tern (ARTE) and common tern (COTE) chicks sampled across five islands and three

years in the Gulf of Maine. The relationship between δ^{15}N and δ^{13}C values varied by isotope type and species. For common tern chicks, δ^{15}N values were positively correlated with δ^{13}C values in both blood cell (b = 0.26[0.01,0.50]) and plasma (b = 0.53[0.34,0.73]) samples. In Arctic tern chicks, δ^{15}N values were positively correlated with δ^{13}C values in blood cell samples (b = 0.19[0.02,0.36]) but negatively correlated in plasma samples (b = -0.25[-0.37,-0.13).

Figure 4: Stable isotope ellipses for common tern (COTE) and Arctic tern (ARTE) chicks across the 10 island-by-year combinations in this study. Samples were collected during the month of July and sample sizes varied from one to 29 depending on isotope type, island, and year, with a total of 100 blood cell samples and 90 plasma samples from Arctic tern chicks (n = 86 chicks, 14 sampled twice) and 115 blood cell samples and 102 plasma samples from common tern chicks (n = 110 chicks, 5 sampled twice). Ellipses were only calculated for sampling occasions that resulted in at least three samples, which was true for all but Metinic Island plasma samples in 2017. The corrected stable isotope ellipse, which accounts for sample size, varied in size from 0.05‰^{2} to 2.61‰^{2} with a mean of 0.60‰^{2}.

Figure 5: Relationships between the percent herring and hake in the diet (HR_{mean}) of common and Arctic tern chicks in the Gulf of Maine and A) mean prey size (PS_{mean}), B) mean feeding rate (FR_{mean}), C) mean δ^{13}C value, and D) mean δ^{15}N value. Each point represents an island, year, and species combination. We subset provisioning data for the two weeks preceding stable isotope sample collection, as blood cell samples represent diet over a two-to-three-week period. Percent herring and hake in the diet is a key indicator of food availability in this system, and was positively correlated with mean prey size (38.14[8.88, 67.41]), δ^{13}C (17.72[4.11, 31.32]), and δ^{15}N (19.81[2.97,36.65]), but negatively correlated with mean feeding rate -18.6[-29.19, -8.06)]).

Figure 6: Shifts in δ^{13}C and δ^{15}N values of Arctic tern (ARTE) and common tern (COTE) chicks breeding in across five island and three years in the Gulf of Maine. These data represent paired samples

for individuals for which we were able to analyze both blood cell and plasma components. This restriction resulted in samples for 146 of the 196 chicks included in the study. The magnitude and direction of the shift varied across individuals but plasma samples had $\delta^{15}N$ values that were on average 1.10±0.70‰ greater (range: -3.30‰ to 4.48‰) and $\delta^{13}C$ values that were on average 1.04±1.11‰ greater (range: -0.92‰ to 3.41‰) than blood cell samples. The best-supported model for shifts in $\delta^{15}N$ included shifts in $\delta^{13}C$, a multiplicative interaction with species, and an additive interaction with island ($r^2 = 0.27$, $p < 0.0001$).

Figure 7: Shifts in the isotope signtures of paired plasma samples for Arctic tern chicks (ARTE; n = 14) and common tern chicks (COTE; n = 5), where each line represents one chick. The first sampling period occurred in early July when chicks were between 12 and 18 days old and the second sampling period occurred in mid-July, approximately 10 days later. Chicks greater than 15 days with a final status of "alive" were considered fledged if they were not seen on subsequent nest checks. Several of the chicks sampled in this study were not part of our regular productivity plots, and we did not record their final status, which is instead marked as "unknown". Slopes, calculated as the change in isotope value divided by the number of days between samples, varied across individuals. The mean $\delta^{13}C$ slope of Arctic tern chicks was -0.11±0.12 ‰ day^{-1} and of common tern chicks was -0.05±0.11 ‰ day^{-1}. For $\delta^{15}N$, the mean slope of Arctic tern chicks was 0.12±0.07 ‰ day^{-1} and of common tern chicks was 0.06±0.10 ‰ day^{-1}.

Figure 8: Shifts in the isotope values (A) and in the stable isotope ellipses (B) of paired plasma samples for Arctic tern (ARTE; n = 14) and common tern (COTE; n = 5) chicks on Petit Manan Island in 2021 and relationship between fledging mass and these shifts for $\delta^{13}C$ (C) and $\delta^{15}N$ (D). The first sampling period (Sample 1) occurred in early July when chicks were between 12 and 18 days old and the second sampling period (Sample 2) occurred in mid-July, approximately 10 days later. Slopes for $\delta^{15}N$ and $\delta^{13}C$ were strongly correlated across individuals (b = -0.57[-0.78, -0.36]) and the slope of this relationship did not vary by species (A). Trophic diversity, as measured using the size of the stable isotope ellipse, was lower

for samples taken during the second sampling occasion than for those taken during the first sampling occasion (B). Asymptotic mass was positively correlated with C) $\delta^{13}C$ slope and negatively correlated with D) $\delta^{15}N$ slope in Arctic terns (range: 62.2 to 92.0 g), but not in common terns (range: 102.17 to 117.5 g).

Figure 1

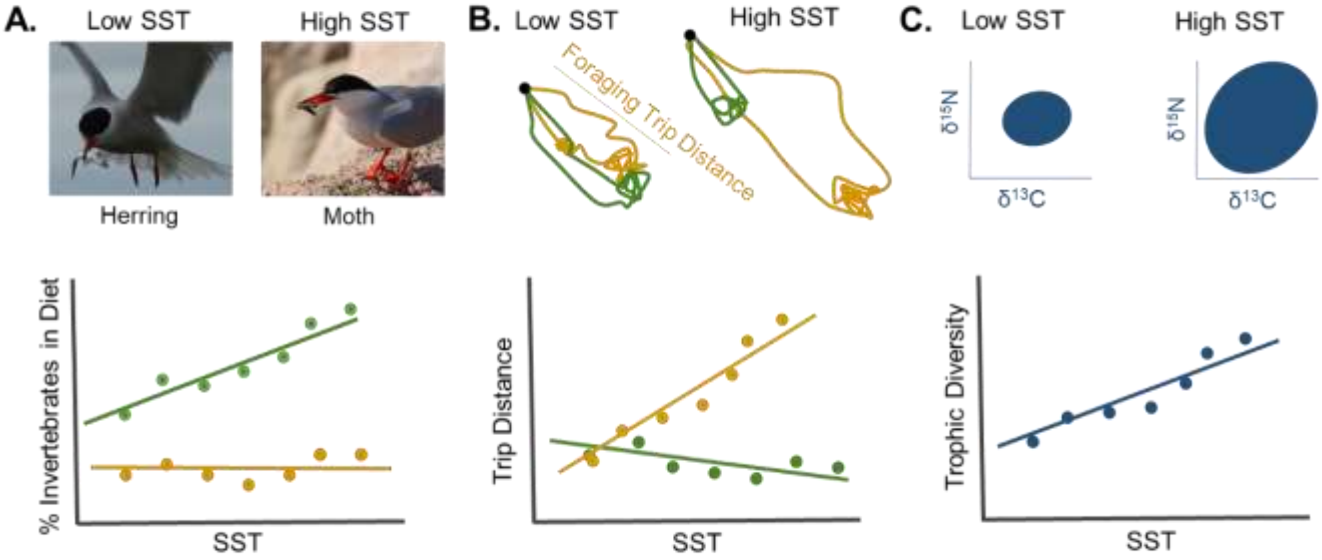

A.
Low SST
High SST
Herring
Moth
% Invertebrates in Diet
SST
B.
Low SST
High SST
Foraging Trip Distance
Trip Distance
SST
C.
Low SST
High SST
δ15N
δ13C
δ15N
δ13C
Trophic Diversity
SST

Figure 2

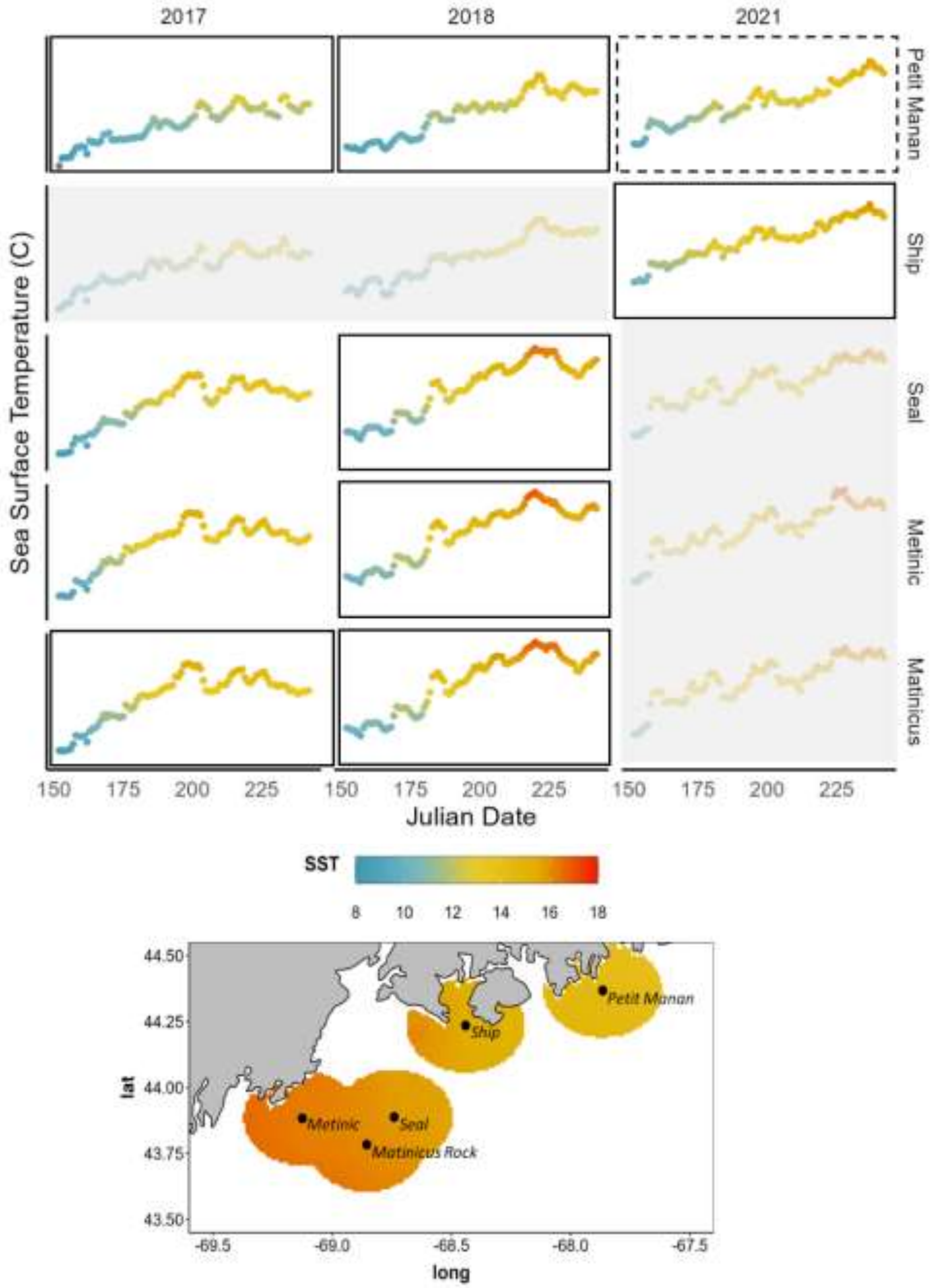

2017
2018
2021
Petit Manan
Ship
Seal
Metinic
Matinicus
Sea Surface Temperature (C)
150
175
200
225
Julian Date
SST
8
10
12
14
16
18
44.50
44.25
44.00
43.75
43.50
lat
-69.5
-69.0
-68.5
-68.0
-67.5
long
Petit Manan
Ship
Metinic
Seal
Matinicus Rock

Figure 3

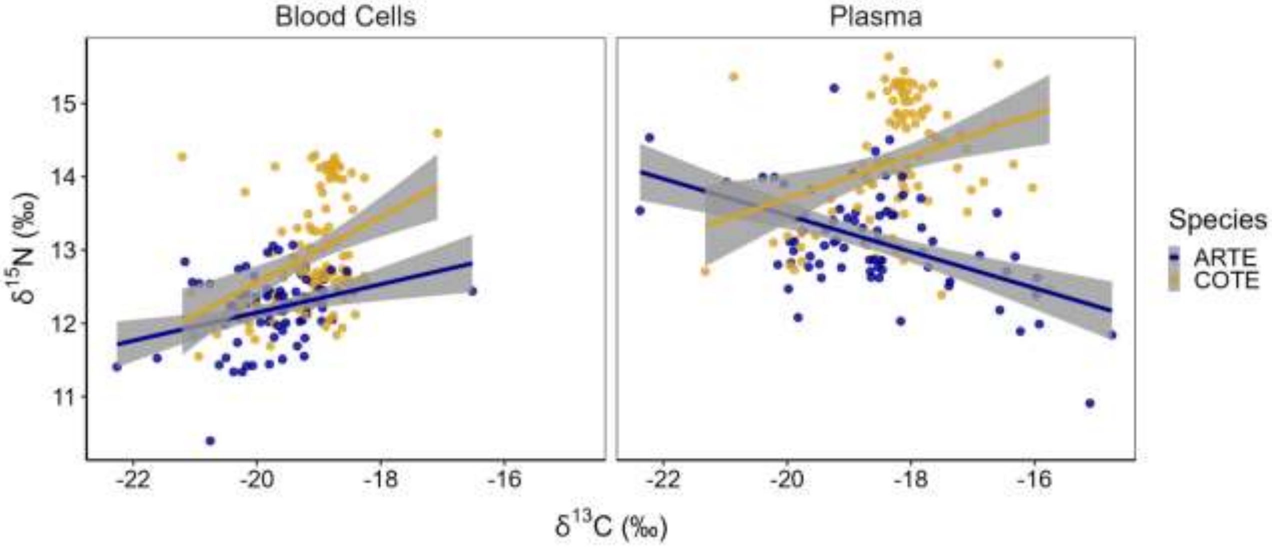

Blood Cells
Plasma
15
14
13
12
11
-22
-20
-18
-16
δ^{15}N (‰)
δ^{13}C (‰)
Species
ARTE
COTE

Figure 4

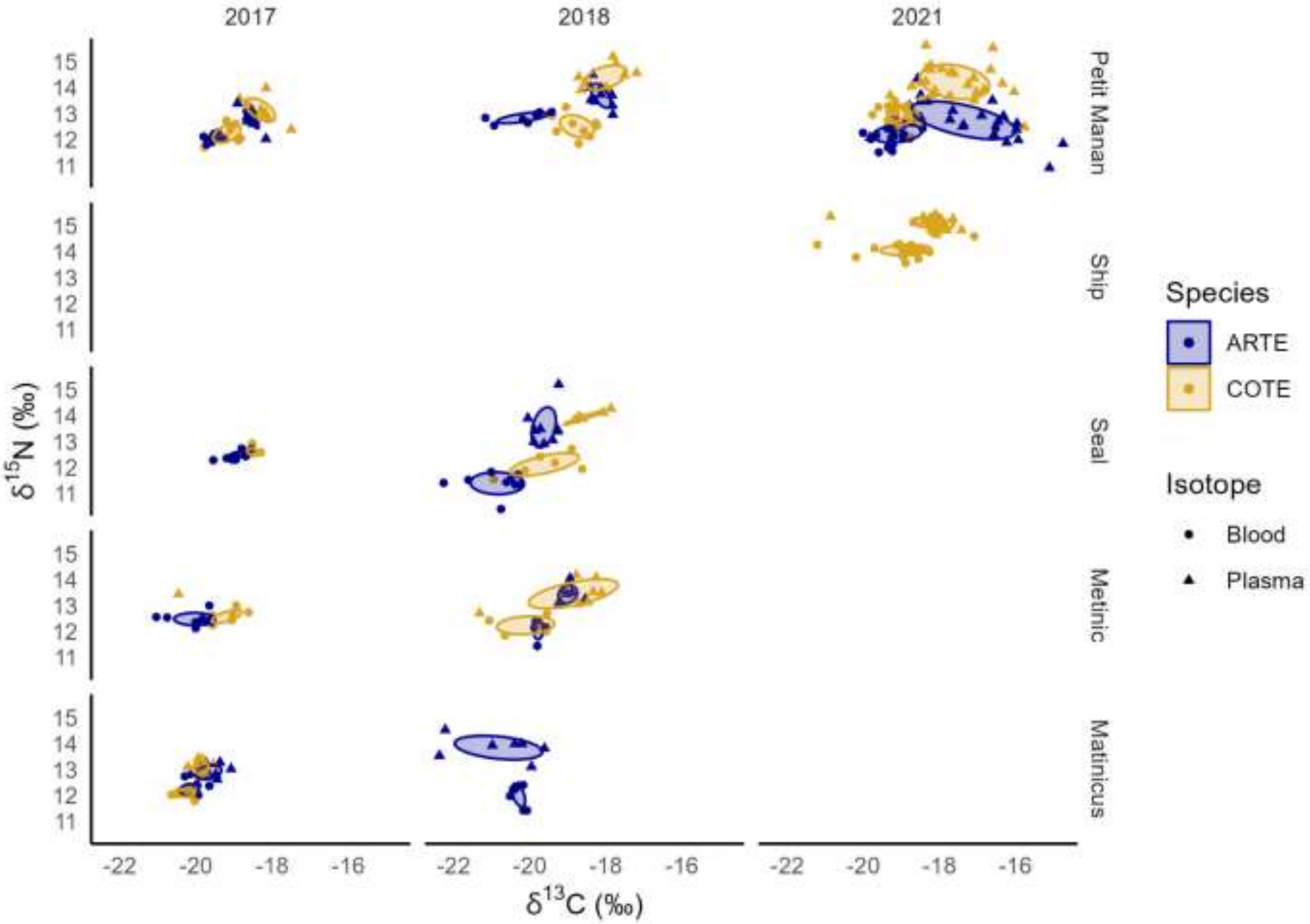

2017
2018
2021
Petit Manan
Ship
Seal
Metinic
Matinicus
δ15N (‰)
15
14
13
12
11
δ13C (‰)
-22
-20
-18
-16
Species
ARTE
COTE
Isotope
Blood
Plasma

Figure 5

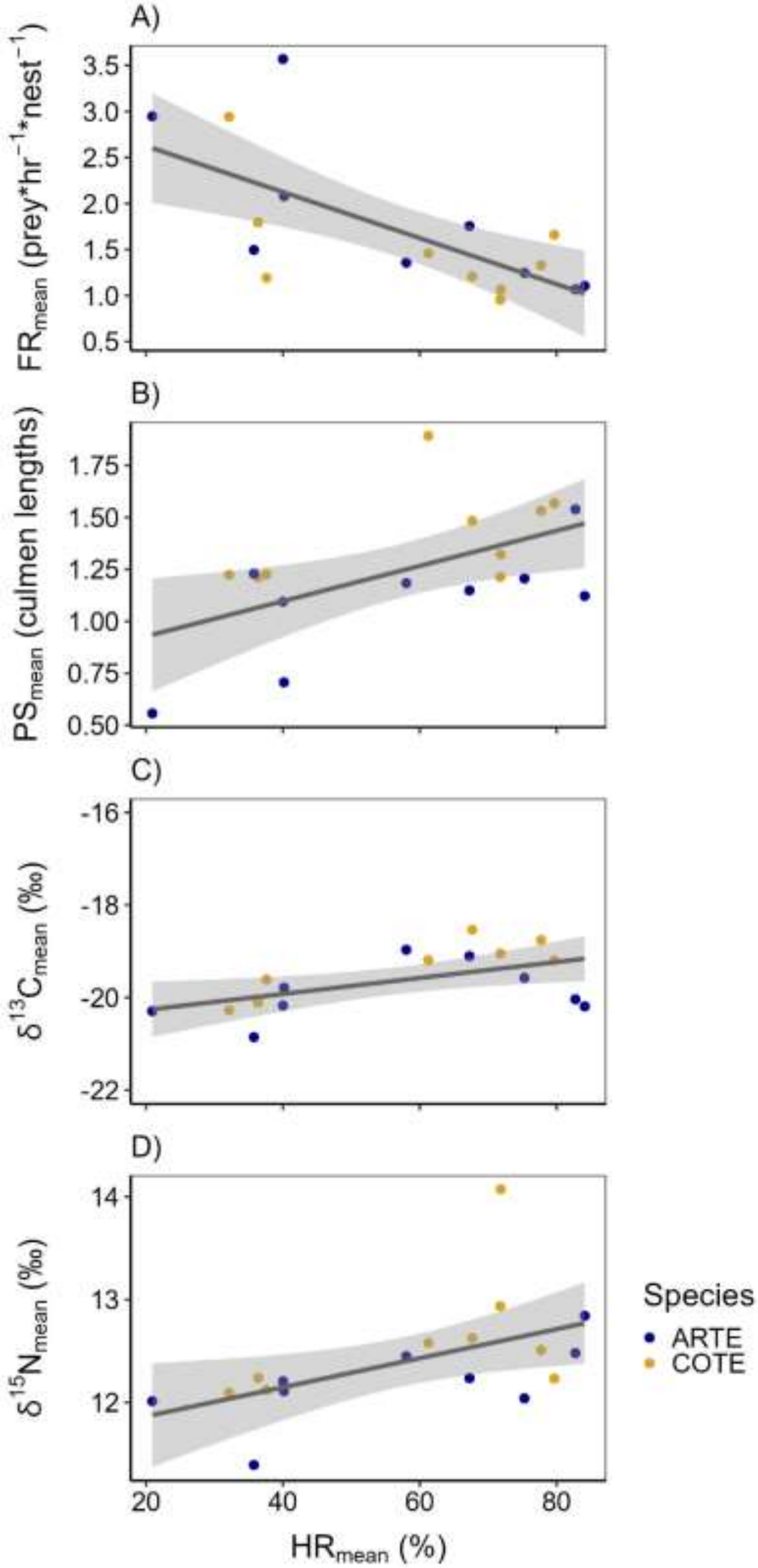
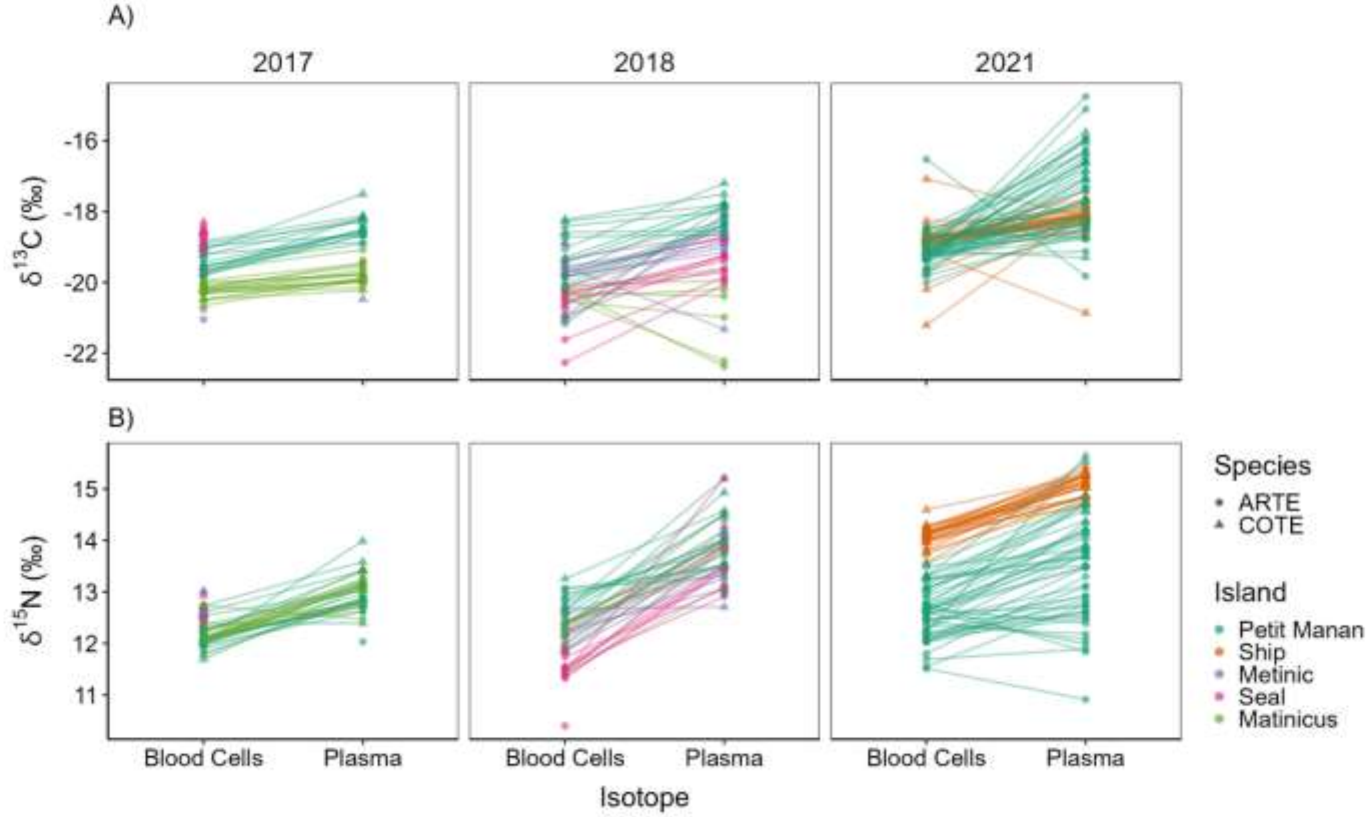

A)
FR$_{mean}$ (prey*hr^{-1}*nest^{-1})
3.5
3.0
2.5
2.0
1.5
1.0
0.5
B)
PS$_{mean}$ (culmen lengths)
1.75
1.50
1.25
1.00
0.75
0.50
C)
δ^{13}C$_{mean}$ (‰)
-16
-18
-20
-22
D)
δ^{15}N$_{mean}$ (‰)
14
13
12
20
40
60
80
HR$_{mean}$ (%)
Species
● ARTE
● COTE

Figure 6



A)
2017
2018
2021
δ 13C (‰)
-16
-18
-20
-22
B)
δ 15N (‰)
15
14
13
12
11
Blood Cells
Plasma
Isotope
Species
ARTE
COTE
Island
Petit Manan
Ship
Metinic
Seal
Matinicus

Figure 7

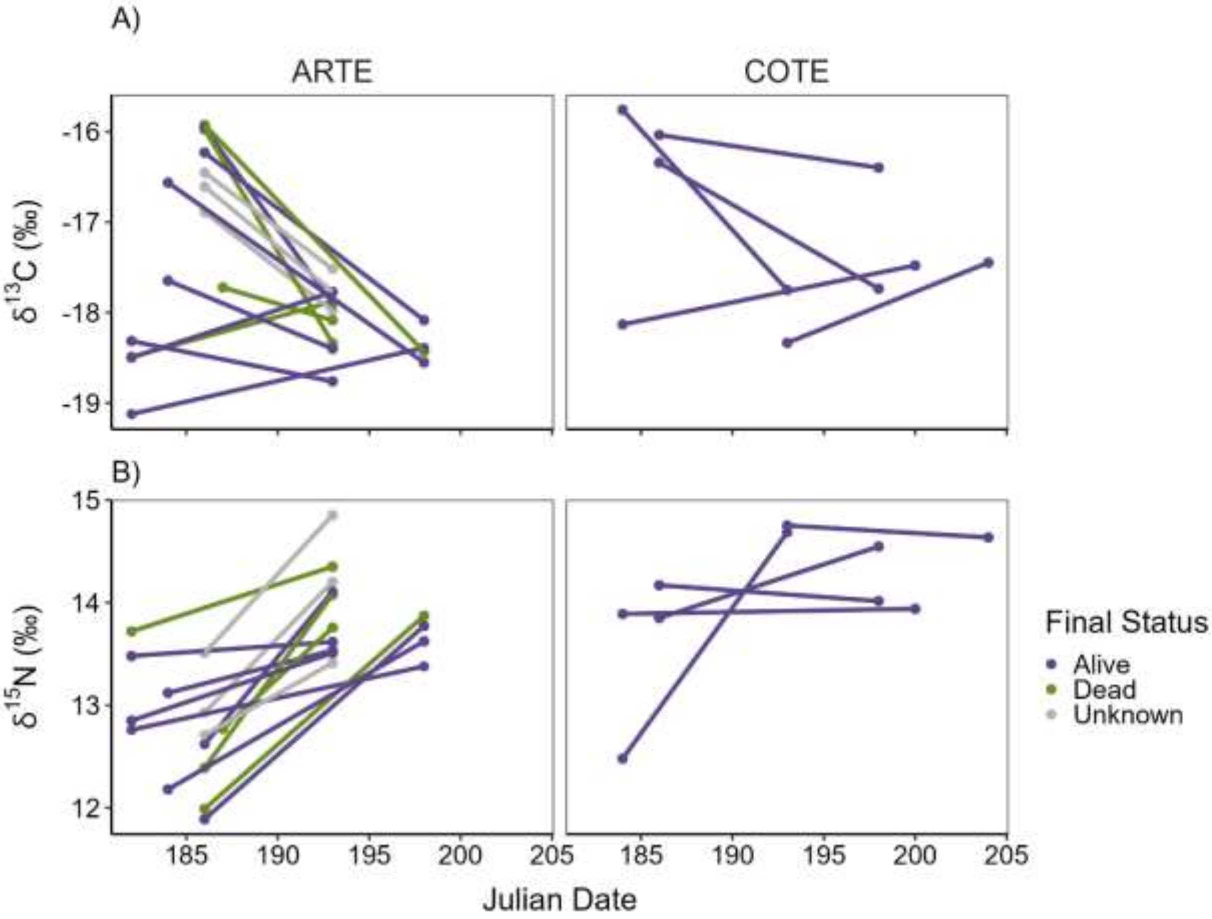
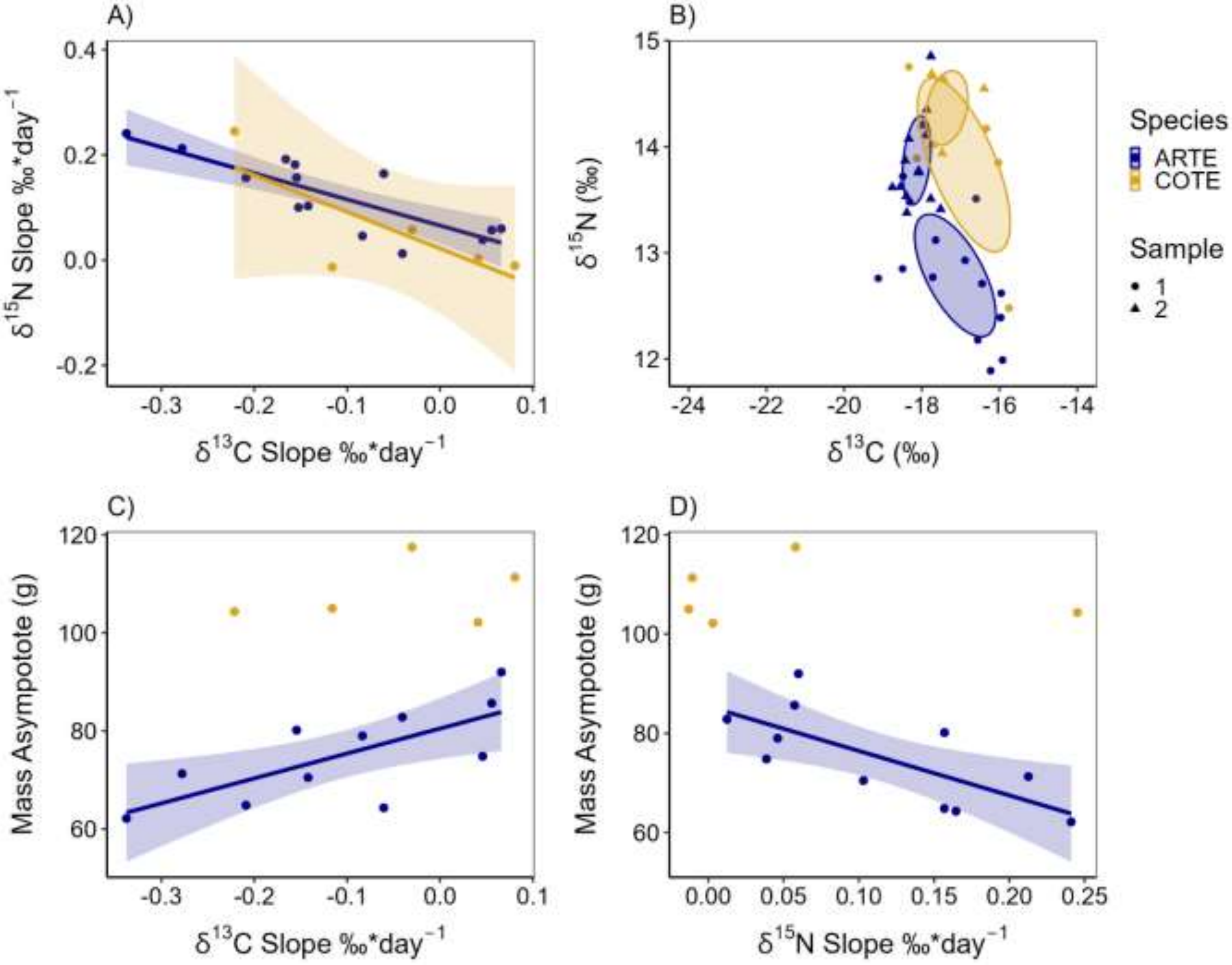

A)
ARTE
COTE
δ13C (‰)
-16
-17
-18
-19
B)
15
14
13
12
δ15N (‰)
185
190
195
200
205
Julian Date
Final Status
Alive
Dead
Unknown

Figure 8



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Appendix 1: Table Supplements

Table S1: Mean sea surface temperature (SST_{mean}) during the period represented by stable isotope data (blood cells or plasma) for each sampling occasion across five islands in the Gulf of Maine.

Island	Species	Year	Sampling Date	SST_{mean} Plasma	Start Date Plasma	SST_{mean} Blood Cells	Start Date Blood Cells
Matinicus	ARTE	2017	7/7/2017	13.98 ± 0.62	7/5/2017	13.28 ± 0.88	6/23/2017
Matinicus	ARTE	2018	7/5/2018	15.70 ± 0.53	7/3/2018	13.38 ± 1.53	6/21/2018
Matinicus	COTE	2017	7/7/2017	13.98 ± 0.62	7/5/2017	13.28 ± 0.88	6/23/2017
Metinic	ARTE	2017	7/17/2017	16.37 ± 0.78	7/15/2017	15.06 ± 0.92	7/3/2017
Metinic	ARTE	2018	7/2/2018	14.51 ± 0.96	6/30/2018	12.90 ± 0.99	6/18/2018
Metinic	COTE	2017	7/17/2017	16.37 ± 0.78	7/15/2017	15.06 ± 0.92	7/3/2017
Metinic	COTE	2018	7/2/2018	15.07 ± 0.65	6/30/2018	12.90 ± 0.99	6/18/2018
Petit Manan	ARTE	2017	7/5/2017	11.46 ± 0.50	7/3/2017	10.44 ± 0.61	6/21/2017
Petit Manan	ARTE	2018	7/16/2018	12.88 ± 0.33	7/14/2018	12.44 ± 0.55	7/2/2018
Petit Manan	ARTE	2021	7/5/2021	12.07 ± 0.46	7/3/2021	12.41 ± 0.59	6/21/2021
Petit Manan	COTE	2017	7/5/2017	11.46 ± 0.50	7/3/2017	10.44 ± 0.61	6/21/2017
Petit Manan	COTE	2018	7/16/2018	12.88 ± 0.33	7/14/2018	12.44 ± 0.55	7/2/2018
Petit Manan	COTE	2021	7/6/2021	12.28 ± 0.42	7/4/2021	12.46 ± 0.56	6/23/2021
Seal	ARTE	2017	7/20/2017	15.74 ± 0.61	7/18/2017	14.65 ± 1.01	7/6/2017
Seal	ARTE	2018	7/13/2018	14.35 ± 0.44	7/11/2018	14.09 ± 0.85	6/29/2018
Seal	COTE	2017	7/20/2017	15.74 ± 0.61	7/18/2017	14.65 ± 1.01	7/6/2017
Seal	COTE	2018	7/13/2018	14.35 ± 0.44	7/11/2018	14.09 ± 0.85	6/29/2018
Ship	COTE	2021	7/28/2021	14.62 ± 0.30	7/26/2021	14.99 ± 0.49	7/14/2021

Table S2: Average provisioning metrics, including Shannon-Weiner Diversity Index (H'), prey size (culmen length; PS_{mean}), feeding rate ($prey \cdot hr^{-1} \cdot nest^{-1}$; FR_{mean}), and percent herring and hake (%; HR_{mean}), of prey fed to tern chicks in the two weeks prior to isotope sampling. Total time (minutes) is the time spent in provisioning watches over this two-week period.

Island	**Year**	**Species**	**H'**	**PS_{mean}**	**FR_{mean}**	**HR_{mean}**	**Total Time**
Matinicus	2017	ARTE	1.22	1.09	3.57	40.00	2880
Matinicus	2017	COTE	0.90	1.22	2.94	32.12	2880
Matinicus	2018	ARTE	0.90	0.56	2.95	20.89	2700
Metinic	2017	ARTE	0.88	1.54	1.07	82.76	1440
Metinic	2017	COTE	1.53	1.89	1.46	61.25	1440
Metinic	2018	ARTE	1.99	0.71	2.08	40.15	1491
Metinic	2018	COTE	1.91	1.21	1.79	36.36	1271
Petit Manan	2017	ARTE	1.39	1.21	1.25	75.31	878
Petit Manan	2017	COTE	1.32	1.57	1.66	79.67	3320
Petit Manan	2018	ARTE	1.18	1.12	1.11	84.11	1632
Petit Manan	2018	COTE	1.23	1.53	1.33	77.72	2095
Petit Manan	2021	ARTE	1.74	1.15	1.76	67.26	2801
Petit Manan	2021	COTE	1.62	1.21	0.95	71.78	3000
Seal	2017	ARTE	1.68	1.18	1.36	58.03	2521
Seal	2017	COTE	1.51	1.48	1.21	67.67	2520
Seal	2018	ARTE	1.95	1.23	1.50	35.75	2584
Seal	2018	COTE	2.08	1.23	1.19	37.59	2730
Ship	2021	COTE	0.80	1.32	1.06	71.83	2010

Table S3: Sample sizes (n), average isotope values ($\delta^{13}C_{mean}$ and $\delta^{13}C_{mean}$), and the total area (TA), standard ellipse area (SEA), and corrected standard ellipse area (SEA_C) for each isotope group.

Island	**Year**	**Species**	**Isotope**	**n**	**$\delta^{13}C_{mean}$**	**$\delta^{15}N_{mean}$**	**$\delta^{13}C_{sd}$**	**$\delta^{15}N_{sd}$**	**TA**	**SEA**	**SEA_C**
Matinicus	2017	ARTE	Blood	9	-20.17	12.21	0.25	0.23	0.36	0.18	0.20
Matinicus	2017	ARTE	Plasma	10	-19.67	12.90	0.33	0.27	0.53	0.26	0.30
Matinicus	2017	COTE	Blood	9	-20.27	12.10	0.22	0.16	0.19	0.11	0.13
Matinicus	2017	COTE	Plasma	10	-19.87	13.10	0.18	0.25	0.26	0.14	0.16
Matinicus	2018	ARTE	Blood	7	-20.29	12.01	0.16	0.43	0.25	0.19	0.23
Matinicus	2018	ARTE	Plasma	7	-20.82	13.85	1.09	0.44	2.30	1.41	1.69
Metinic	2017	ARTE	Blood	9	-20.04	12.48	0.52	0.23	0.67	0.38	0.43
Metinic	2017	COTE	Blood	8	-19.19	12.58	0.38	0.25	0.39	0.22	0.26
Metinic	2017	COTE	Plasma	1	-20.47	13.44	NA	NA	NA	NA	NA
Metinic	2018	ARTE	Blood	5	-19.79	12.11	0.12	0.39	0.15	0.15	0.20
Metinic	2018	ARTE	Plasma	7	-19.00	13.44	0.24	0.32	0.33	0.24	0.29
Metinic	2018	COTE	Blood	5	-20.11	12.24	0.70	0.33	0.85	0.71	0.95
Metinic	2018	COTE	Plasma	7	-18.85	13.45	1.11	0.54	2.00	1.51	1.81
Petit Manan	2017	ARTE	Blood	8	-19.57	12.04	0.16	0.16	0.13	0.07	0.09
Petit Manan	2017	ARTE	Plasma	10	-18.55	12.80	0.19	0.35	0.23	0.10	0.12
Petit Manan	2017	COTE	Blood	9	-19.20	12.23	0.35	0.35	0.55	0.34	0.38
Petit Manan	2017	COTE	Plasma	10	-18.31	13.14	0.37	0.44	0.98	0.43	0.48
Petit Manan	2018	ARTE	Blood	7	-20.19	12.84	0.64	0.20	0.47	0.30	0.37
Petit Manan	2018	ARTE	Plasma	9	-18.13	13.70	0.25	0.45	0.49	0.28	0.32
Petit Manan	2018	COTE	Blood	9	-18.76	12.51	0.43	0.42	0.99	0.54	0.61
Petit Manan	2018	COTE	Plasma	9	-18.00	14.40	0.53	0.46	1.21	0.69	0.79
Petit Manan	2021	ARTE	Blood	25	-19.11	12.24	0.63	0.35	2.25	0.66	0.69
Petit Manan	2021	ARTE	Plasma	25	-17.38	12.74	1.35	0.72	9.17	2.50	2.61
Petit Manan	2021	COTE	Blood	25	-19.05	12.94	0.32	0.37	1.24	0.37	0.38
Petit Manan	2021	COTE	Plasma	25	-17.60	14.22	0.90	0.66	6.81	1.82	1.90
Seal	2017	ARTE	Blood	9	-18.97	12.45	0.29	0.17	0.21	0.11	0.12
Seal	2017	COTE	Blood	10	-18.54	12.63	0.12	0.12	0.09	0.05	0.05
Seal	2018	ARTE	Blood	9	-20.85	11.39	0.68	0.41	1.58	0.87	1.00
Seal	2018	ARTE	Plasma	8	-19.63	13.55	0.31	0.74	1.16	0.68	0.79
Seal	2018	COTE	Blood	6	-19.61	12.12	0.85	0.42	1.14	0.87	1.08
Seal	2018	COTE	Plasma	6	-18.56	13.93	0.52	0.26	0.14	0.10	0.13
Ship	2021	COTE	Blood	29	-18.89	14.07	0.66	0.20	2.06	0.41	0.43
Ship	2021	COTE	Plasma	29	-18.18	15.10	0.57	0.21	1.41	0.35	0.36

Table S4: The percent overlap in the stable isotope Bayesian ellipse (SEA_B) of plasma and blood cell samples from each sampling occasion and the probability that plasma samples had a larger SEA_B than blood cell samples for that sampling occasion.

Island	**Year**	**Species**	**% SEA_B Overlap**	**Probability of Larger SEA_B**
Matinicus	2017	ARTE	33.70	0.76
Matinicus	2017	COTE	14.67	0.70
Matinicus	2018	ARTE	4.09	1.00
Metinic	2018	COTE	4.86	0.94
Petit Manan	2017	ARTE	29.19	0.76
Petit Manan	2017	COTE	5.54	0.71
Petit Manan	2018	ARTE	38.50	0.43
Petit Manan	2018	COTE	26.96	0.58
Petit Manan	2021	ARTE	37.20	1.00
Petit Manan	2021	COTE	25.04	1.00
Seal	2018	ARTE	35.18	0.91
Ship	2021	COTE	25.19	0.27

Table S5: Output of Pitman-Morgan Test comparing variance between blood cell and plasma samples for each sampling occasion.

Island	**Species**	**Year**	**F Value Variance $\delta^{15}N$**	**p-value Variance $\delta^{15}N$**	**F Value Variance $\delta^{13}C$**	**p-value Variance $\delta^{13}C$**
Matinicus	ARTE	2017	1.13	0.43	1.79	0.21
Matinicus	COTE	2017	2.22	0.14	0.73	0.67
Matinicus	ARTE	2018	1.06	0.47	44.52	<0.01
Metinic	COTE	2018	2.87	0.17	3.42	0.13
Petit Manan	ARTE	2017	2.51	0.14	1.13	0.44
Petit Manan	COTE	2017	1.72	0.23	1.25	0.38
Petit Manan	ARTE	2018	4.16	0.05	0.15	0.98
Petit Manan	COTE	2018	1.20	0.41	1.13	0.44
Petit Manan	ARTE	2021	4.28	<0.01	4.60	<0.01
Petit Manan	COTE	2021	3.18	<0.01	8.18	<0.01
Seal	ARTE	2018	29.52	<0.01	0.16	0.98
Ship	COTE	2021	1.06	0.44	0.74	0.78

Table S6: Outputs of Wilcoxon signed-rank tests comparing isotope signatures of common terns and Arctic terns across five islands in the Gulf of Maine.

Year	**Island**	**Isotope**	**n ARTE**	**n COTE**	**W (δ^{13}C)**	**p (δ^{13}C)**	**W (δ^{15}N)**	**p (δ^{15}N)**
2017	Matinicus	Blood	9	9	44	0.80	50	0.44
2017	Matinicus	Plasma	10	10	69	0.17	31	0.17
2017	Metinic	Blood	9	8	3	<0.01	27	0.39
2018	Metinic	Blood	5	5	11	0.84	10	0.69
2018	Metinic	Plasma	7	7	9	0.05	24	1.00
2017	PMI	Blood	8	9	14	0.04	24	0.28
2017	PMI	Plasma	10	10	29	0.12	23	0.04
2018	PMI	Blood	7	9	0	<0.01	50	0.05
2018	PMI	Plasma	9	9	33	0.55	10	0.01
2021	PMI	Blood	25	25	229	0.11	48	<0.01
2021	PMI	Plasma	25	25	329	0.76	36	<0.01
2017	Seal	Blood	9	10	5	<0.01	17	0.02
2018	Seal	Blood	9	6	6	0.01	2	<0.01
2018	Seal	Plasma	8	6	2	<0.01	9	0.06

Table S7: The percent overlap in the stable isotope Bayesian ellipse (SEA$_B$) of Arctic tern and common tern samples and the probability that Arctic terns had a larger SEA$_B$ than did common terns.

Isotope	**Island**	**Year**	**% SEA$_B$ Overlap**	**Probability of Larger SEA$_B$**
Blood	Matinicus	2017	17.99	0.848
Plasma	Matinicus	2017	14.01	0.912
Blood	Metinic	2017	17.37	0.824
Blood	Metinic	2018	0.00	0.011
Plasma	Metinic	2018	52.93	0.001
Blood	PMI	2017	0.00	0.001
Plasma	PMI	2017	0.00	0.005
Blood	PMI	2018	0.00	0.181
Plasma	PMI	2018	5.56	0.036
Blood	PMI	2021	45.84	0.981
Plasma	PMI	2021	29.90	0.876
Blood	Seal	2017	26.94	0.978
Blood	Seal	2018	5.02	0.428
Plasma	Seal	2018	17.79	0.955