Pre-breeding foraging ecology of three tern species nesting in the Gulf of Maine

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INTRODUCTION

Climate change is rapidly shifting the timing, duration, and intensity of seasonal warming and cooling cycles (Thomas et al. 2017, Dupigny-Giroux et al. 2018), which have important implications for recurring life history events, e.g., reproduction, and trophic interactions, of many species (Poloczanska et al. 2013, Staudinger et al. 2019). Marine organisms generally exhibit faster shifts in phenology and range than terrestrial species because of dispersal abilities and a lack of physical barriers to impede movements (Burrows et al. 2011, Lenoir et al. 2020). Colonial nesting seabirds are particularly at risk to seasonal shifts because of high site fidelity during the breeding season, which makes them sensitive to even slight changes in local foraging conditions (Gagne et al. 2018). A variety of seabird species, including several species of terns (Sterna sp.), migrate long distances from their wintering grounds in the Southern Hemisphere to the Gulf of Maine to take advantage of the region’s highly productive waters to breed and raise their young. Post-migration, adult seabirds depend on the spatio-temporal match of reliable food resources to replenish energy reserves before breeding. However, the conditions during this critical window of time are becoming increasingly uncertain given the magnitude and pace at which climate change is impacting the Gulf of Maine region. We investigated the pre-breeding foraging ecology of Arctic Terns (Sterna paradisaea), Common Terns (S. hirundo), and the federally endangered Roseate Tern (S. dougallii) by analyzing stable carbon (δ13C) and nitrogen (δ15N) isotopes in eggshell tissues collected from seven islands in the Gulf of Maine from 2016 to 2018. Results show at the interspecific level, adult foraging patterns are consistent with expectations based on chick diets. At interisland and interannual scales, variation in isotopic values and niche breadths suggest foraging habits are highly localized. Although uncertainty remains, interannual trends also suggest warmer ocean conditions are either affecting tern foraging behaviors and/or prey resource availability during the late spring and early summer. Overall, results provide new information on adult tern foraging ecology in an important breeding area experiencing rapid environmental change.

Écologie de l'alimentation avant la reproduction de trois espèces de sternes nichant dans le golfe du Maine

RÉSUMÉ. Diverses espèces d'oiseaux marins migrent chaque année des aires d'hivernage dans l'hémisphère Sud vers le golfe du Maine, USA pour s'y reproduire et élever leurs osillons. Après la migration, les oiseaux marins adultes dépendent de la présence spatio-temporelle de ressources alimentaires fiables pour reconstituer leurs réserves énergétiques avant la nidification. Cependant, les conditions durant cette fenêtre critique deviennent de plus en plus incertaines étant donné l'ampleur et le rythme auxquels les changements climatiques affectent la région du golfe du Maine. Nous avons étudié l'écologie de l'alimentation avant la reproduction des Sternes arctique (Sterna paradisaea), pierregarin (S. hirundo) et de Dougall (S. dougallii) - cette dernière étant une espèce menacée au niveau fédéral -, en analysant les isotopes stables du carbone (δ13C) et de l'azote (δ15N) dans les tissus de coquilles d'oeufs collectées sur sept îles du golfe du Maine de 2016 à 2018. À l'échelle interspécifique, les tendances de la recherche de nourriture par les adultes sont conformes aux attentes basées sur le régime alimentaire des poussins. Aux échelles inter-îles et interannuelles, la variation des valeurs isotopiques et de l'étendue des niches indiquent que les habitudes de recherche de nourriture sont très localisées. Bien que des incertitudes demeurent, les tendances interannuelles portent également à croire que les conditions océaniques plus chaudes affectent les comportements de recherche de nourriture des sternes ou la disponibilité des ressources en proies à la fin du printemps et au début de l'été. Dans l'ensemble, nos résultats fournissent de nouvelles informations sur l'écologie de l'alimentation des sternes adultes dans une région de reproduction importante qui connaît des changements environnementaux rapides.

Key Words: eggshells; foraging ecology; Gulf of Maine; stable isotopes; Sterna sp.; Terns; trophic niche breadth
reserves before breeding (Diamond and Devlin 2003). This pre-breeding window of time, or “honey-moon” foraging phase, is critical to breeding success, particularly to income breeders that use locally derived nutrients to support egg production (Nisbet 1977, Bond and Diamond 2010). Reduced food quality and availability prior to breeding can leave adults physically unable to lay eggs or forage to support chicks, thus affecting breeding success (Egevang et al. 2010, Scopel and Diamond 2018). However, foraging conditions during this critical window of time are becoming increasingly uncertain for seabirds in the Gulf of Maine region given the magnitude and pace at which ocean temperatures are warming and prey phenology is shifting under climate change (Saba et al. 2016, Thomas et al. 2017, Staudinger et al. 2019). The Gulf of Maine is one of fastest warming bodies of water in the world, with rates three times faster than the global mean, and projections showing the region will be significantly warmer over the coming decades (Pershing et al. 2021).

Long-term studies of seabirds in the Gulf of Maine have primarily focused on chick diets in the weeks after hatching and leading up to fledging (Hall et al. 2000, Yakola 2019). Chick diets are routinely monitored during the summer season through surveys that visually identify provisioned prey items delivered to nests. However, adult seabirds do not necessarily consume the same prey as their chicks. Adults may select different sizes and species of prey than those provided to their young, and prey availability may differ between the pre-breeding and chick rearing periods. Furthermore, a female’s pre-breeding diet comprises both the female’s own foraging effort and courtship feedings from their mate partners (Nisbet 1973, 1977, González-Solís et al. 2001). Larger prey items delivered by males to females as nuptial gifts during the pre-breeding period may reflect higher trophic level prey than would be typically provided to a chick (Nisbet 1977). Overall, the specifics of adult seabird diets remain largely unknown (Hall et al. 2000, Cabot and Nisbet 2013, Staudinger et al. 2020). This gap in knowledge is primarily due to the logistical challenges of observing adult feeding behaviors at sea. Migrating adult terns arrive on nesting islands before conditions are suitable for researchers to observe them, and adults hunt for prey at sites that are often too far offshore to monitor regularly. Thus, indirect methods of dietary assessment are required to investigate the pre-breeding foraging ecology of adult terns and other seabird species.

Stable isotope analysis has been widely used to examine the foraging patterns of a variety of marine organisms that are difficult to observe during some or all of their life history (Polito et al. 2011, Logan et al. 2015, Shiffman et al. 2019). Stable nitrogen (δ15N) ratios are indicative of trophic level, with top level consumers showing higher enrichment relative to those feeding lower in the food web. Stable carbon (δ13C) ratios differentiate between relative sources of primary productivity, with more depleted values reflecting pelagic or offshore habitats, and enriched values that of nearshore or demersal foraging habitats (Fry 2006, Oczkowski et al. 2016). Isotope values present in some seabird eggshell tissues reflect local resources consumed by female birds approximately three to five days prior to laying (Hobson 1995, Polito et al. 2011). Previous studies have provided insights into the pre-breeding foraging conditions at nesting colonies for several species of terns, gulls, grebes, and tropicbirds in Southern California, North Carolina, and Southwestern Australia (Schaffner and Swart 1991, Hobson et al. 1997, McGinnis and Emslie 2001, Strickland et al. 2008, Dunlop 2011), as well as penguins living in Antarctic waters (Polito et al. 2011). Surprisingly, few studies to date have evaluated the pre-breeding diets of seabirds in the Gulf of Maine (but see Nisbet 2002, Bond and Diamond 2010), despite the importance of the region as a seasonal nesting and foraging ground.

To better understand the pre-breeding foraging ecology of seabirds in this rapidly changing ecosystem, we evaluated stable carbon and nitrogen isotopes in eggshell tissues from Arctic Terns (Sterna paradisaea), Common Terns (S. hirundo), and the federally endangered Roseate Tern (S. dougallii), collected from nests on seven islands in the Gulf of Maine from 2016 to 2018. Common and Arctic terns are characterized as income breeders (Bond and Diamond 2010), thus isotopic values in eggshell tissues should be reflective of locally derived nutrients post-migration and just prior to laying. Differences in isotope ratios were assessed at three scales: (1) interspecific, (2) interisland within each species, and (3) interannually within each species on each island. Assessing isotope values at these scales allowed for the examination of regional dietary patterns among the three species (interspecific differences) and local dietary patterns associated with individual islands (interisland differences) during specific years (interannual differences). Interspecifically, terns in the Gulf of Maine are known to differ in the prey items provisioned to chicks (Hall et al. 2000, Yakola 2019). Among terns nesting on different islands, geographic differences can affect local prey availability and the isotopic signatures of those prey. Interannually, changing environmental conditions can affect the timing and distribution of available prey, and interannual differences have previously been observed in chick diets for terns and other seabirds (Scopel et al. 2019, Yakola 2019). Thus, we expect differences in tern eggshell isotope values at all three scales of analysis (interspecies, interisland, interannual). Furthermore, the time period when our study was conducted represents a period of anomalous warming due to climate change, with two out of the three years being the warmest on record (Dupigny-Giroux et al. 2018). Consequently, information collected during this time can provide important insights into the ecological responses by terns to foraging conditions in the coming decades. We discuss our findings in the context of long-term chick provisioning studies and highlight the potential impacts of climate change on the Gulf of Maine seabird community.

MATERIALS AND METHODS
Sample collection and stable isotope analysis
Nesting terns arrive in the Gulf of Maine in mid to late April and begin to lay eggs in May following a courtship period of approximately two to three weeks (Nisbet 1977, Bond and Diamond 2010). The incubation period for Common, Arctic, and Roseate Terns is estimated to be between 20 and 26 days (Kaufman 2001). Tern colonies located along the coast of Maine are managed and closely monitored during the breeding season by the National Audubon Society Seabird Institute (NASI) and the United States Fish and Wildlife Service (USFWS). Hatched eggshell samples were salvaged from tern colonies on seven nesting islands (Fig. 1) from mid-June to late July (USFWS Permit #MB691785-0; Table 1). These islands included Eastern Egg...
Table 1. Sample sizes for Arctic Terns (*Sterna paradisaea*), Common Terns (*S. hirundo*), and Roseate Terns (*S. dougallii*) at each island, and year. NWR, National Wildlife Refuge.

| Island                        | Abbr.  | Tern species | Number of samples |
|-------------------------------|--------|--------------|-------------------|
|                               |        |              | 2016  | 2017 | 2018 |        |
| Eastern Egg Rock              | EER    | Arctic       | -      | 10   | 7    |        |
|                               |        | Common       | -      | 10   | 10   |        |
|                               |        | Roseate      | 5      | 10   | 10   |        |
| Jenny Island                  | JI     | Common       | 11     | 10   | 10   |        |
|                               |        | Roseate      | -      | 4    | -    |        |
| Matinicus Rock NWR            | MR     | Arctic       | 6      | 7    | 9    |        |
| Outer Green Island            | OGI    | Common       | 12     | 10   | 10   |        |
| Pond Island National Wildlife | PINWR  | Arctic       | -      | -    | 6    |        |
| Seal Island National Wildlife | SINWR  | Arctic       | 10     | 3    | 10   |        |
| Stratton Island               | STI    | Common       | 13     | 7    | 10   |        |
|                               |        | Roseate      | -      | 10   | 10   |        |

Samples were prepared for stable isotope analysis following established protocols (Polito et al. 2009, 2011). Briefly, the membrane sac was separated from the shell of the egg and soaked in deionized water for 48 hours. Membrane tissues were rinsed to remove any remaining yolk, dirt, and other substances that could affect isotopic signatures. Cleaned samples were dried in an oven at 60°C for 48 hours, and 1.0 µg aliquots were weighed into Costech tin capsules. Samples were flash-combusted in a Costech 4010 Elemental Analyzer coupled to a Thermo Delta V Advantage continuous flow mass spectrometer at the University of New Mexico Center for Stable Isotopes. Raw values returned by this analysis were then normalized on a two-point scale using reference materials. Stable isotope abundances are expressed in δ notation in per mille units (‰), as ratios of 13C/12C or 15N/14N. Sample standard values were based on Vienna PeeDee Belemnite (VPDB) for 13C and atmospheric N2 for 15N. Three internal, laboratory standards were run at the beginning, at intervals between samples and at the end of analytical sessions. Analytical precision calculated from the standards is ± 0.1 ‰ (1 standard deviation) for both δ15N and δ13C. Analyses were normalized to the laboratory standards, which were calibrated against IAEA N1, IAEA N2, and USGS 43 for δ15N and NBS 21, NBS 22 and USGS 24 for δ13C. The 3 internal laboratory standards are: UNM-CSI Protein std#1, casein purchased from Sigma Aldrich with δ15N and δ13C values of 6.43 and -26.52; UNM-CSI Protein std#2, soy protein purchased from Sigma Aldrich with δ15N and δ13C values of 0.98 and -25.78; UNM-CSI protein Std#4, house made tuna protein with δ15N and δ13C values of 13.32 and -16.17. Samples with C:N ratios ≥ 3.5 were assumed to have some level of lipid or shell contamination and excluded from subsequent analysis (Ehrich et al. 2011).

**Statistical analyses**

All statistical analyses were conducted in R v. 3.5.2 (R Core Team 2018). Interspecific, interisland, and interannual δ13C and δ15N values were analyzed independently using mixed and non-mixed generalized linear models in the *glmmTMB* package (Brooks et al. 2017) with gamma error structures and log link functions. Models were fit following procedures described in Bolker et al. (2009) and evaluated using diagnostic tools, including residual plots (Zuur and Ieno 2016), in the *DHARMa* package (Hartig
Table 2. Interspecific comparisons. Mean isotope value (± standard errors), C:N ratios, and isotopic niche breadth values for Arctic Terns (*Sterna paradisaea*), Common Terns (*S. hirundo*), and Roseate Terns (*S. dougallii*) across all islands and years.

| Species       | n  | δ¹³C | δ¹⁵N | C:N | Isotopic niche breadth (SEA<sub>c</sub>) |
|---------------|----|------|------|-----|----------------------------------------|
| Arctic        | 68 | -18.4 ± 0.1 | 11.2 ± 0.1 | 3.2 ± 0.0 | 2.9                                    |
| Common        | 153| -17.8 ± 0.1 | 12.2 ± 0.1 | 3.2 ± 0.0 | 2.0                                    |
| Roseate       | 40 | -17.7 ± 0.1 | 12.0 ± 0.1 | 3.2 ± 0.0 | 1.0                                    |

2018). Post hoc Tukey contrast tests (pair-wise comparisons) and least-squares means estimates were calculated using the *enmeans* R package (Searle et al. 1980, Lenth et al. 2019). For the comparison of isotope values among Arctic, Common, and Roseate Terns, a mixed model was used with species included as a fixed factor, year as a random factor, and island as a random factor nested within year. For the interisland comparisons for each species, island was included as a fixed factor with no random factor (three non-mixed models). Given the limited sample sizes for some species-year combinations (Table 1), islands were only compared within the year with the highest sample size (2018 for Arctic Terns, 2018 for Common Terns, and 2017 for Roseate Terns). For the interannual comparisons within each species on each island, year was included as a fixed factor with no random factor (10 non-mixed models).

Dietary niche breadth and overlap were analyzed at the interspecies, interisland, and interannual levels using Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011). This analysis estimates ellipses for the distribution of δ¹³C and δ¹⁵N values calculated from a covariance matrix of the values using Bayesian inference. The area encompassed by an ellipse (sample size corrected standard ellipse area, SEA<sub>c</sub>) can be used to infer relative dietary niche breadth. In addition, the degree of overlap of two ellipses can be used as a measure of dietary niche overlap.

**RESULTS**

**Interspecific variation**

Across all islands and years, Arctic Terns had significantly lower (< 0.001) δ¹³C and δ¹⁵N isotope values (δ¹³C: -18.4 ± 0.1, δ¹⁵N: 11.2 ± 0.1) compared to both Common (δ¹³C: -17.8 ± 0.1, δ¹⁵N: 12.2 ± 0.1) and Roseate (δ¹³C: -17.7 ± 0.1, δ¹⁵N: 12.0 ± 0.1) Terns, while Common and Roseate Terns exhibited similar isotopic values (p > 0.05; Table 2, Fig. 2a). The dietary niche breadth of Arctic Terns (SEA<sub>c</sub> = 2.9) was greater than Common Terns (SEA<sub>c</sub> = 2.0) and three-fold higher than Roseate (SEA<sub>c</sub> = 1.0) Terns (Fig. 2bc). The isotopic niche of Roseate Terns was completely overlapped by Common Terns (see Appendix 1 for all interspecific pair-wise comparisons and isotopic niche overlap results).

**Interisland variation**

In 2018, δ¹⁵N values for Arctic Terns were significantly higher on EER (12.3 ± 0.7) compared to SINWR (10.8 ± 0.1; t(27) = 3.17, p = 0.019). No other significant differences were found among islands for Arctic Terns (Table 3, Fig. 3a). Dietary niche breadth was highest for Arctic Terns nesting on EER (SEA<sub>c</sub> = 6.8), lowest on SINWR (SEA<sub>c</sub> = 0.1), and intermediate for MR (SEA<sub>c</sub> = 1.0), and PINWR (SEA<sub>c</sub> = 1.7; Fig. 3d).
Table 3. Interisland comparisons. Mean isotope values (± standard errors), C:N ratios, and isotopic niche breadth values on each island for Arctic Terns (*Sterna paradisaea*) and Common Terns (*S. hirundo*) in 2018, and Roseate Terns (*S. dougallii*) in 2017. See Table 1 for island name abbreviations.

| Species | Island | n  | δ¹³C | δ¹⁵N | C:N | Isotopic niche breadth (SEA_c) |
|---------|--------|----|------|------|-----|-------------------------------|
| Arctic  | EER    | 7  | -19.6 ± 0.5 | 12.3 ± 0.7 | 3.2 ± 0.1 | 6.8 |
|         | MR     | 9  | -19.0 ± 0.2 | 11.6 ± 0.4 | 3.1 ± 0.0 | 1.0 |
|         | PINWR  | 6  | -18.7 ± 0.3 | 11.2 ± 0.3 | 3.0 ± 0.1 | 1.7 |
|         | SINWR  | 10 | -19.0 ± 0.0 | 10.8 ± 0.1 | 3.0 ± 0.0 | 0.1 |
| Common  | EER    | 10 | -18.0 ± 0.2 | 12.2 ± 0.1 | 3.1 ± 0.0 | 0.6 |
|         | JI     | 10 | -18.2 ± 0.2 | 13.0 ± 0.3 | 3.0 ± 0.1 | 1.5 |
|         | OGI    | 10 | -18.4 ± 0.3 | 12.6 ± 0.1 | 3.1 ± 0.0 | 1.0 |
|         | PINWR  | 10 | -17.7 ± 0.3 | 12.4 ± 0.1 | 3.0 ± 0.1 | 1.1 |
|         | SINWR  | 10 | -18.7 ± 0.1 | 11.3 ± 0.2 | 3.0 ± 0.0 | 0.3 |
|         | STI    | 10 | -19.0 ± 0.2 | 12.7 ± 0.3 | 3.1 ± 0.0 | 0.9 |
| Roseate | EER    | 10 | -17.4 ± 0.2 | 11.8 ± 0.3 | 3.2 ± 0.0 | 0.5 |
|         | JI     | 4  | -17.9 ± 0.1 | 11.9 ± 0.1 | 3.2 ± 0.0 | 0.2 |
|         | STI    | 10 | -18.4 ± 0.0 | 11.6 ± 0.1 | 3.2 ± 0.0 | 0.1 |

In 2018, δ¹³C values for Common Terns were significantly higher on PINWR (-17.7 ± 0.3) compared to SINWR (-18.7 ± 0.1; \( t(53) = 3.51, p = 0.012 \)) and STI (-19.0 ± 0.2; \( t(53) = 4.53, p = 0.001 \); Fig. 3b), while δ¹⁵N values were significantly lower on SINWR (-11.3 ± 0.2) compared to EER (12.2 ± 0.1; \( t(53) = -4.58, p < 0.001 \)), JI (13.0 ± 0.3; \( t(53) = -6.05, p < 0.001 \)), OGI (12.6 ± 0.1; \( t(53) = -4.61, p < 0.001 \)), PINWR (-12.4 ± 0.1; \( t(53) = -3.96, p = 0.003 \)), and STI (12.7 ± 0.3; \( t(53) = -5.05, p < 0.001 \); Table 3). Dietary niche breadth was smallest on SINWR (SEA_c = 0.3), while values for all other islands were comparable (SEA_c = 0.8-1.1; Fig. 3e,h). In 2017, δ¹³C values for Roseate Terns were significantly lower on STI (-18.4 ± 0.1) compared to EER (-17.4 ± 0.2; \( t(20) = -6.88, p < 0.001 \)) and JI (-17.9 ± 0.1; \( t(20) = -2.69, p = 0.036 \); Fig. 3c), while values for δ¹⁵N isotopes were similar (11.6–11.9) across all islands (Table 3). Dietary niche breadth was highest for Roseate Terns nesting on EER (SEA_c = 0.5), intermediate on JI (SEA_c = 0.2), and lowest on STI (SEA_c = 0.1; Fig. 3f,i; see Appendix 2 for all interisland pair-wise comparisons and isotopic niche overlap results).

**Interannual variation within species on each island**

Arctic Terns had significantly lower δ¹³C values in 2018 (-19.6 ± 0.5) compared to 2017 (-18.0 ± 0.1) on EER (\( t(14) = -4.14, p = 0.001 \); Table 4, Fig. 4a). On MR, Arctic Tern δ¹³C values were depleted during 2018 (-19.0 ± 0.2; \( t(18) = -3.66, p = 0.005 \)) and 2016 (-18.8 ± 0.3; \( t(18) = -2.89, p = 0.025 \)) compared to 2017 (-18.0 ± 0.1; Fig. 5a). Dietary niche breadth was also notably lower for Arctic Terns in 2017 (SEA_c = 0.4–0.5) compared to 2016 and 2018 (SEA_c = 1.0–6.8) on both islands (EER: Fig. 4d,g; MR: Fig. 5b, c). On SINWR, δ¹³C values for Arctic Terns exhibited a trend of more depleted values during recent years (Fig. 6a). The dietary niche breadth of Arctic Terns on SINWR was highest in 2017 (SEA_c = 0.5) compared to 2016 (SEA_c = 0.2) and 2018 (SEA_c = 0.1; Fig. 6c,e). As a consequence of the narrow dietary niche breadth in 2018, there was no overlap with niches in the preceding two years. Significant interannual differences were not detected among δ¹⁵N values on any of the islands (EER, MR, SINWR) where Arctic Terns nested.
Table 4. Interannual comparisons. Mean isotope values (± standard errors), C:N ratios, and isotopic niche breadth values on each island, for each tern species, for each year. Arctic Terns (*Sterna paradisaea*), Common Terns (*S. hirundo*), Roseate Terns (*S. dougallii*). See Table 1 for island name abbreviations.

| Island | Species | Year | n | Mean δ¹³C | Mean δ¹⁵N | C:N | Isotopic niche breadth (SEA<sup>c</sup>) |
|--------|---------|------|---|------------|------------|-----|----------------------------------------|
| EER    | Arctic  | 2017 | 10 | -18.0 ± 0.1 | 11.2 ± 0.2 | 3.2 ± 0.0 | 0.5                                    |
|        |         | 2018 | 7  | -19.6 ± 0.5 | 12.3 ± 0.7 | 3.2 ± 0.1 | 6.8                                    |
| Common |         | 2017 | 10 | -17.5 ± 0.1 | 11.9 ± 0.1 | 3.2 ± 0.0 | 0.4                                    |
|        |         | 2018 | 10 | -18.5 ± 0.2 | 12.6 ± 0.2 | 3.1 ± 0.0 | 0.6                                    |
| Roseate|         | 2016 | 5  | -17.7 ± 0.1 | 12.4 ± 0.2 | 3.2 ± 0.0 | 0.1                                    |
|        |         | 2017 | 10 | -17.4 ± 0.2 | 11.8 ± 0.3 | 3.2 ± 0.0 | 0.5                                    |
|        |         | 2018 | 10 | -17.1 ± 0.2 | 12.6 ± 0.1 | 3.0 ± 0.0 | 0.7                                    |
| JI     | Common  | 2016 | 11 | -16.9 ± 0.1 | 11.8 ± 0.3 | 3.2 ± 0.0 | 1.6                                    |
|        |         | 2017 | 10 | -17.5 ± 0.1 | 12.2 ± 0.1 | 3.2 ± 0.0 | 0.2                                    |
|        |         | 2018 | 10 | -18.2 ± 0.2 | 13.0 ± 0.3 | 3.0 ± 0.1 | 1.5                                    |
| MR     | Arctic  | 2016 | 6  | -18.8 ± 0.3 | 11.6 ± 0.3 | 3.5 ± 0.1 | 1.0                                    |
|        |         | 2017 | 7  | -18.0 ± 0.1 | 10.8 ± 0.1 | 3.3 ± 0.0 | 0.4                                    |
|        |         | 2018 | 9  | -19.0 ± 0.2 | 11.6 ± 0.4 | 3.1 ± 0.0 | 1.0                                    |
| OGI    | Common  | 2016 | 12 | -17.1 ± 0.2 | 12.7 ± 0.2 | 3.2 ± 0.0 | 1.2                                    |
|        |         | 2017 | 10 | -17.5 ± 0.1 | 12.3 ± 0.1 | 3.3 ± 0.0 | 0.3                                    |
|        |         | 2018 | 10 | -18.4 ± 0.2 | 12.6 ± 0.1 | 3.1 ± 0.0 | 1.0                                    |
| PINWR  | Common  | 2016 | 10 | -17.7 ± 0.3 | 12.4 ± 0.1 | 3.0 ± 0.1 | 1.1                                    |
|        |         | 2017 | 3  | -17.8 ± 0.3 | 10.7 ± 0.5 | 3.0 ± 0.0 | 0.7                                    |
|        |         | 2018 | 10 | -19.0 ± 0.0 | 10.8 ± 0.1 | 3.0 ± 0.0 | 0.1                                    |
| SINWR  | Arctic  | 2016 | 13 | -17.5 ± 0.1 | 11.8 ± 0.2 | 3.3 ± 0.1 | 1.3                                    |
|        |         | 2017 | 7  | -17.8 ± 0.2 | 11.5 ± 0.3 | 3.3 ± 0.1 | 1.6                                    |
|        |         | 2018 | 10 | -18.7 ± 0.1 | 11.3 ± 0.2 | 3.0 ± 0.0 | 0.3                                    |
| STI    | Common  | 2017 | 10 | -18.0 ± 0.1 | 12.0 ± 0.2 | 3.3 ± 0.0 | 0.8                                    |
|        |         | 2018 | 10 | -19.0 ± 0.3 | 12.7 ± 0.3 | 3.1 ± 0.0 | 0.9                                    |

Fig. 4. Among year diets for Arctic (*Sterna paradisaea*; left), Common (*S. hirundo*; center), and Roseate (*S. dougallii*; right) terns on Eastern Egg Rock (EER). Biplots of δ¹³C and δ¹⁵N means and standard error (A, B, C). Bayesian ellipses of isotopic niches (D, E, F). Bayesian model estimates for isotopic niche sizes (G, H, I). The corrected SIBER ellipses area (SEA<sub>c</sub>), based on maximum likelihood estimates, is indicated by an “x.”

Fig. 5. Among year diets for Arctic Terns (*Sterna paradisaea*) on Matinicus Rock (MR). Biplots of δ¹³C and δ¹⁵N means and standard error (A). Bayesian ellipses of isotopic niches (B). Bayesian model estimates for isotopic niche sizes (C). The corrected SIBER ellipses area (SEA<sub>c</sub>), based on maximum likelihood estimates, is indicated by an “x.”
Common Terns had significantly lower ($p < 0.05$) $\delta^{13}$C values in 2018 compared to 2016 and 2017 on EER (Fig. 4b, no data for 2016), JI (Fig. 7a), OGI (Fig. 7b), SINWR (Fig. 6b), and STI (Fig. 8b). The one exception to this trend was found on PINWR, where $\delta^{13}$C values were equivalent among years (Fig. 8a). $\delta^{15}$N values were significantly higher ($p < 0.05$) on EER, JI, PINWR, and STI in 2018 compared to 2016 or 2017. The dietary niche breadths of Common Terns were lower in 2017 compared to 2016 and 2018 on EER (Fig. 4e,h, no data for 2016), JI (Fig. 7c,e), OGI (Fig. 7d,f), PINWR (Fig. 8c,e), and STI (Fig. 8d,f). Common Terns on SINWR had the broadest dietary niche in 2017 (SEA$_c = 1.6$) compared to 2016 (SEA$_c = 1.3$) and 2018 (SEA$_c = 0.3$; Fig. 6d,f).

Only one island, EER, had enough samples to make an interannual comparison for Roseate Terns. $\delta^{15}$N values were significantly higher in 2018 (12.6 ± 0.1) compared to 2017 (11.8 ± 0.3; $t(21) = 3.11$, $p = 0.014$), but no other differences were detected in $\delta^{15}$N or $\delta^{13}$C among years (Fig. 4c). The dietary niche breadth of Roseate Terns on EER increased substantially across the 3-year period of this study, from SEA$_c = 0.1$ in 2016 to 0.7 in 2018 (Fig. 4f,i; see Appendices 3–9 for all interannual pair-wise comparisons and isotopic niche overlap results).
**Fig. 8.** Among year diets for Common Terns (*Sterna hirundo*) on Pond Island National Wildlife Reserve (PINWR, left) and Stratton Island (STI, right). Biplots of $\delta^{13}$C and $\delta^{15}$N means and standard error (A, B). Bayesian ellipses of isotopic niches (C, D). Bayesian model estimates for isotopic niche sizes (E, F). The corrected SIBER ellipses area (SEA), based on maximum likelihood estimates, is indicated by an “x.”

**DISCUSSION**

The results from stable isotopes measured in eggshell membrane tissues presented in this study provide a multi-scale examination of the pre-breeding foraging ecology of adult terns nesting in the Gulf of Maine. Our modeling framework was structured to account for inconsistencies in sampling effort, thus allowing us to examine regional and local patterns in eggshell stable isotopes in the three tern species. Interspecific patterns in adult tern isotopic niche breadth and overlap was generally consistent with prior studies on tern chick diets (e.g. Hall et al. 2000, Yakola 2019). Similar isotopic values for Common and Roseate Terns suggest that these species foraged at equivalent trophic levels, but that Roseate Terns had the smallest isotopic niche breadth of the three tern species. This result is consistent with prior studies indicating that Roseate Terns consume a more specialized diet (Rock et al. 2007a, Goyert 2015). Among the three tern species, differences in isotopic values suggest that Arctic Terns foraged on prey from lower trophic levels and exhibited the broadest isotopic niche, indicating a more diverse diet likely focused on a range of invertebrates and small fishes as has been reported for chick diets at similar locations (Hall et al. 2000, Yakola 2019). Both $\delta^{15}$N and $\delta^{13}$C values showed coherence at the intraspecific scale when assessed across most islands; however, a few notable differences were found for certain species-island combinations that suggest local influences on foraging habits that warrant further examination in future studies. Isotopic values for terns nesting on Seal Island NWR, one of the most offshore islands examined in this study, suggest that terns on this island foraged at the lowest trophic levels and had the smallest isotopic niche breadths compared to other islands. In addition, $\delta^{15}$N values and isotopic niche breadths of Arctic and Common Terns were generally higher during 2017 on Seal Island NWR when values at other locations showed the opposite pattern. Thus, the habitat and prey conditions surrounding Seal Island NWR during the pre-breeding period may be unique compared to other colonies. Interannual patterns in isotope values were difficult to interpret in part because of small effect sizes but showed a general trend of decreasing $\delta^{13}$C values and increasing $\delta^{15}$N values on most islands. It remains unclear whether results reflect interannual shifts in isotopic baselines, or represent true changes in foraging ecology. Isotopic baselines in marine systems are complex, and interpretation of our data is limited to the three-year period of collections as well as a lack of distributed measurements of stable isotopes across the region during this time (Magozzi et al. 2017). Further research is needed to understand the biological, e.g., behavior or physiology, and environmental effects, on isotopic variability from regional oceanographic processes, e.g., North Atlantic Oscillation, and local drivers including precipitation, salinity, and upwelling (Sherwood and Rose 2005, Jennings and van der Molen 2015, Oczkowski et al. 2016). Nonetheless, our results provide new insights into the foraging ecology of adult terns, which are income breeders reliant on local foraging conditions post-migration for successful egg production in the region (Bond and Diamond 2010).

**Interspecific variation**

Broadly comparing isotope values of eggshell membrane tissues among the three tern species suggests that Arctic Terns differ in their adult pre-breeding diets compared to Common and Roseate Terns. Depleted $\delta^{13}$C and $\delta^{15}$N values suggest Arctic Terns foraged further offshore and consumed a greater diversity of prey resources that spanned lower trophic levels. These interspecies differences are consistent with a previous radio-telemetry study that found Arctic Terns travel further from the mainland to forage (Rock et al. 2007b), and long-term provisioning studies showing Arctic Terns feed a greater proportion of invertebrate prey to their chicks (Hall et al. 2000, Yakola 2019). Because of their reliance on lower trophic levels, Arctic Terns may serve as good indicators of local and interannual changes in primary and secondary
production of the coastal habitats surrounding nesting colonies during the spring and summer in the Gulf of Maine (Diamond and Devlin 2003, Piatt et al. 2007).

Comparing isotope values between adult Common and Roseate Terns suggests that these species foraged across similar habitats and consumed prey from comparable trophic levels. Differences in isotopic niche breadths, however, indicate that Common Terns have a more diverse pre-breeding diet. Previous studies on tern chick diets in the Gulf of Maine support these results, finding that adult Common and Roseate Terns typically deliver similar chick diets in the Gulf of Maine (Hall et al., 2000, Yakola 2019). The vast majority of provisioned prey items include hakes (Urophycis sp., Merluccius sp., and Enchelyopus sp.), sand lance (Ammodytes americanus and A. dubius), and herring (Clupea spp. and Alosa spp.; Hall et al. 2000, Yakola 2019). Common Terns exhibit more generalist feeding strategies in terms of the combination of fish species and the proportion of invertebrate prey they provision to chicks across islands and years (Nisbet 1977, Yakola 2019). Roseate Terns, in comparison, are more specialized on prey fish, particularly sand lance (Ammodytes spp.), which can comprise 40–100% of the chick diet in some populations (Staudinger et al. 2020, and references therein). The relatively narrow foraging habits of adult Roseate Terns may increase their vulnerability to interannual variation in environmental and foraging conditions. Such foraging habits may have severe consequences at locations such as Jenny and Stratton Islands, where isotopic niche breadths were among the narrowest of all island-species combinations examined in this study. It should be noted however, that results from Jenny Island should be considered preliminary because of the small number of samples.

**Interisland variation**

Intraspecific isotopic patterns in both δ13C and δ15N were relatively consistent across most locations for Arctic and Common Terns with a few notable exceptions. Arctic Terns and Common Terns on Seal Island NWR, for example, exhibited depleted δ15N values compared to other islands in this region. Baseline surveys of stable isotope trends in the Gulf of Maine, however, have shown more depleted δ13C and δ15N values in offshore ocean waters compared to coastal waters because of decreased terrestrial influences (Oczkowski et al. 2016). However, while Seal Island NWR is one of the furthest offshore of the seven islands sampled (32.2 km from shore), it is uncertain that this spatial distance reflects a baseline effect of δ15N values. For comparison, Arctic Terns on the other offshore island evaluated in this study, Matinicus Rock (33.1 km from shore), exhibited a very different isotopic trend indicating that individuals foraged across a range of δ13C values. Thus, foraging conditions on Seal Island NWR appear to be limited to a narrow range of pelagic and low trophic level species as indicated by the smallest isotopic niche breadths observed among all islands for Arctic and Common Terns. Indeed, long-term chick provisioning data have shown that Common Terns on Seal Island NWR provisioned higher amounts of invertebrates (nearly 30% of the diet by frequency of occurrence), compared to 4–15% of the diets on the six other Maine coastal islands (Yakola 2019). Such differences in diet, specifically a greater reliance on invertebrate prey, may negatively impact breeding success in terns (Scopel and Diamond 2018). Future studies linking diet to productivity metrics such as clutch size and adult condition, e.g., body weight, are needed to further assess how foraging on low trophic level prey impacts reproductive potential for each species.

Isotope values for Roseate Terns indicate that they foraged at a consistent trophic level but in isotopically variable habitats among islands. Enriched δ15N values from Eastern Egg Rock suggest comparatively inshore foraging locations, while the depleted δ13C values on Stratton Island suggest offshore foraging. Such differences between islands are likely due in part to environmental factors influencing baseline isotope values. Distance from the mainland, water temperatures, dissolved CO2 concentration, microbial cycling, and phytoplankton community structure can all contribute to variation in δ13C values (Oczkowski et al. 2016, Magozzi et al. 2017, Shipley and Matich 2020). The observed differences in δ13C values may also be a consequence of the Roseate Terns’ highly specialized diet. Two species of sand lance occur in the Gulf of Maine (Staudinger et al. 2020), a nearshore shallow-water species (A. americanus) and an offshore deep-water species (A. dubius). The availability of either sand lance species likely varies for each island and fluctuates among years based on their highly dynamic “boom and bust” population cycling (Staudinger et al. 2020). Stratton Island is an inshore island located 2.6 km from shore in Saco Bay where A. americanus is usually abundant (Novak et al. 2017). However, the relatively depleted δ13C values found in Roseate Tern eggs on Stratton Island suggest they are foraging in relatively offshore environments. In this case, adult Roseate Terns could potentially be foraging on A. dubius or larval and post-larval individuals of either sand lance species before they settle into demersal habitats (Staudinger et al. 2020). Additional studies that are able to capture prey size information and employ genetic tools, e.g., environmental DNA metabarcoding, would be useful to understand the species, sizes, and relative amounts of sand lance Roseate Terns rely on at each of the three breeding colonies in the Gulf of Maine.

Lastly, it is unclear why the pattern of broader isotopic niche breadths found in Arctic and Roseate Terns on Eastern Egg Rock did not also hold true for Common Terns. Individual variation in behavior, the presence of less experienced or poor-quality parents, small sample sizes, or a combination of these factors are possible explanations (Nisbet 1977, González-Solís et al. 2001, Nisbet et al. 2020). An alternative explanation is that interspecific competition on Eastern Egg Rock is high. This site hosts a large Common Tern colony of 800–1000 pairs, which outnumber Roseate (78–104 pairs) and Arctic Terns (76–86 pairs; GOMSWG 2019). These interspecific interactions may force Roseate and Arctic Terns to travel further distances, and search for prey across a broader range of habitats or different times of day, i.e., tidal cycles, while Common Terns utilize and dominate local and preferred areas (Nisbet 1977). Tagging data that track the movements of foraging adults and additional sampling of a broader portion of the population on Eastern Egg Rock and other islands would help elucidate these trends.

**Interannual variation**

Across all species and islands, our results indicate a general trend of more depleted δ13C but more enriched δ15N values in tern eggshell tissues from 2016 to 2018. These trends may result from baseline δ13C and δ15N values, which vary interannually and are positively correlated with primary productivity (Oczkowski et al. 2016, Shipley and Matich 2020). The observed differences in δ13C values may also be a consequence of the Roseate Terns’ highly specialized diet. Two species of sand lance occur in the Gulf of Maine (Staudinger et al. 2020), a nearshore shallow-water species (A. americanus) and an offshore deep-water species (A. dubius). The availability of either sand lance species likely varies for each island and fluctuates among years based on their highly dynamic “boom and bust” population cycling (Staudinger et al. 2020). Stratton Island is an inshore island located 2.6 km from shore in Saco Bay where A. americanus is usually abundant (Novak et al. 2017). However, the relatively depleted δ13C values found in Roseate Tern eggs on Stratton Island suggest they are foraging in relatively offshore environments. In this case, adult Roseate Terns could potentially be foraging on A. dubius or larval and post-larval individuals of either sand lance species before they settle into demersal habitats (Staudinger et al. 2020). Additional studies that are able to capture prey size information and employ genetic tools, e.g., environmental DNA metabarcoding, would be useful to understand the species, sizes, and relative amounts of sand lance Roseate Terns rely on at each of the three breeding colonies in the Gulf of Maine.

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patterns (Jaatinen et al. 2016, Oczkowski et al. 2016, Magozzi et al. 2020). Seal Island NWR was again a notable exception to an anomalous warming event in the Pacific Ocean (Osborne et al. 2016, Carpenter-Kling et al. 2019). Average annual winter-spring chlorophyll concentrations in the Gulf of Maine were found to increase slightly from 2016 to 2018 (NOAA Fisheries 2019). However, the fact that δ13C and δ15N values in eggshells showed an opposite trend suggests that a regional isotopic baseline shift due to interannual changes in primary productivity may not fully explain this pattern. Previous studies on interannual variation in eggshell isotope values have found that they can be influenced by a number of factors including interannual changes in diet and foraging habitat, as well as species-specific behaviors and physiology (Boecklen et al. 2011, Shipley and Matich 2020). Shifts in diet have recently been documented in tern chicks in the Gulf of Maine, where the proportions of different types of provisioned prey fluctuated substantially from year-to-year and suggest terns are opportunistically responding to local availability (Yakola 2019).

Isotopic niche breadth values also generally indicated an interannual trend across the three-year period evaluated in this study. For most islands, Arctic and Common Terns had narrower dietary niches in 2017 compared to the year prior and after. It is notable that 2016 and 2018 were some of the warmest years ever recorded in the Gulf of Maine and spring onset occurred earlier during 2016 and 2018 (day-of-year 140–145) compared to 2017 (day-of-year 153; NOAA Fisheries 2019). This shift in seasonal warming can affect the timing and duration of spring phytoplankton blooms, with implications for higher trophic levels during subsequent seasons (Friedland et al. 2015, Thomas et al. 2017, Staudinger et al. 2019). For example, earlier onset of the growing season and warmer temperatures can stimulate faster growth rates in some prey and increase the availability of larger prey compared to cooler years (Staudinger et al. 2019).

Alternatively, the observed trend of relatively depleted δ13C values and enriched δ15N values in eggshell tissues may be interpreted as a behavioral shift to forage in more offshore/pelagic habitats and on a more diverse range of higher trophic level prey during warmer years. A similar pattern of spatially dispersed foraging was observed in Black-legged Kittiwake (Rissa tridactyla) during an anomalous warming event in the Pacific Ocean (Osborne et al. 2020). Seal Island NWR was again a notable exception to interannual isotopic trends with both Arctic and Common Terns exhibiting broader dietary niches in 2017 compared to 2016 and 2018. This reversal suggests that terns on Seal Island NWR may face distinct foraging conditions compared to other islands. However, given the small sample size of Arctic Tern eggs on Seal Island NWR, we found similarities and differences in isotopic values and niche breadths among species, islands, and years. Considered within the limitations of stable isotope ecology (Boecklen et al. 2011, Shipley and Matich 2020) and the limited sample sizes we were able to obtain for certain species-island-year combinations, these findings provide new insights into adult tern diets and avenues for future research to better understand regional and local influences on their foraging habits. With warming conditions likely impacting foraging behaviors and prey availability during the breeding season, the risk of trophic mismatch threatens migratory seabird populations in the region (Staudinger et al. 2019). Additional multi-modal monitoring studies are needed to develop predictive indicators of good and poor pre-breeding foraging conditions with direct links to breeding success, and to identify the specific foraging habitats and prey species during this important window of time.

CONCLUSIONS

The pre-breeding foraging conditions in the time post-migration and just prior to nesting is believed to be critical to the breeding success of migratory seabirds (Bond and Diamond 2010). However, the diets of adults during this window of time have remained largely unknown because of the challenges of directly observing feeding behaviors at sea. Using stable carbon and nitrogen isotopes as ecological tracers in eggshell membrane tissues, we found similarities and differences in isotopic values and niche breadths among species, islands, and years. Considered within the limitations of stable isotope ecology (Boecklen et al. 2011, Shipley and Matich 2020) and the limited sample sizes we were able to obtain for certain species-island-year combinations, these findings provide new insights into adult tern diets and avenues for future research to better understand regional and local influences on their foraging habits. With warming conditions likely impacting foraging behaviors and prey availability during the breeding season, the risk of trophic mismatch threatens migratory seabird populations in the region (Staudinger et al. 2019). Additional multi-modal monitoring studies are needed to develop predictive indicators of good and poor pre-breeding foraging conditions with direct links to breeding success, and to identify the specific foraging habitats and prey species during this important window of time.

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**Appendix 1.** Interspecific comparisons (Tables correspond to Fig. 2)

Table A1.1 Pair-wise comparisons for δ\(^{13}\)C (a) and δ\(^{15}\)N (b) ratios for each species across all islands and years calculated using the emmeans R package (df = 254).

|                   | Least squares means | Standard error | t-ratio | p-value   |
|-------------------|---------------------|----------------|---------|-----------|
| (a) δ\(^{13}\)C   |                     |                |         |           |
| Arctic - Common   | -0.028              | 0.006          | -4.663  | < 0.001   |
| Arctic - Roseate  | -0.045              | 0.008          | -5.447  | < 0.001   |
| Common - Roseate  | -0.017              | 0.007          | -2.263  | 0.063     |
| (b) δ\(^{15}\)N   |                     |                |         |           |
| Arctic - Common   | -0.072              | 0.010          | -7.147  | < 0.001   |
| Arctic - Roseate  | -0.054              | 0.014          | -3.938  | < 0.001   |
| Common - Roseate  | 0.018               | 0.012          | 1.499   | 0.293     |

Table A1.2 Percentage overlap of isotopic niche between species across all islands and years (% of columns overlapped by rows).

| Species    | Arctic | Common | Roseate |
|------------|--------|--------|---------|
| Arctic     |        | 76.13  | 81.10   |
| Common     | 51.51  |        | 100     |
| Roseate    | 26.69  | 48.64  |         |
Appendix 2. Interisland comparisons (Tables correspond to Fig. 3)

Table A2.1 Pair-wise comparisons for Arctic tern $\delta^{13}C$ (a) and $\delta^{15}N$ (b) ratios for each island in 2018, calculated using the emmeans R package (df = 27).

| Island Comparison | Least squares means | Standard error | t-ratio | p-value |
|-------------------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}C$ |                     |                |         |         |
| EER - MRNWR       | -0.031              | 0.019          | -1.591  | 0.400   |
| EER - PINWR       | -0.048              | 0.021          | -2.233  | 0.140   |
| EER - SINWR       | -0.029              | 0.019          | -1.562  | 0.416   |
| MRNWR - PINWR     | -0.017              | 0.020          | -0.836  | 0.837   |
| MRNWR - SINWR     | 0.001               | 0.018          | 0.070   | 0.999   |
| PINWR - SINWR     | 0.018               | 0.020          | 0.915   | 0.797   |
| (b) $\delta^{15}N$|                     |                |         |         |
| EER - MRNWR       | 0.061               | 0.042          | 1.461   | 0.474   |
| EER - PINWR       | 0.097               | 0.046          | 2.095   | 0.180   |
| EER - SINWR       | 0.130               | 0.041          | 3.165   | 0.019   |
| MRNWR - PINWR     | 0.036               | 0.044          | 0.814   | 0.847   |
| MRNWR - SINWR     | 0.069               | 0.038          | 1.792   | 0.299   |
| PINWR - SINWR     | 0.033               | 0.043          | 0.764   | 0.870   |

Table A2.2 Percentage overlap of isotopic niche for Arctic terns between islands in 2018 (% of columns overlapped by rows).

| Island | EER | MRNWR | PINWR | SINWR |
|--------|-----|-------|-------|-------|
| EER    | 100 | 76.14 | 100   |
| MRNWR  | 15.06 | 32.58 | 92.97 |
| PINWR  | 18.93 | 53.80 | 100   |
| SINWR  | 1.01 | 6.21  | 4.05  |
Table A2.3 Pair-wise comparisons for Common tern $\delta^{13}C$ (a) and $\delta^{15}N$ (b) ratios for each island in 2018, calculated using the emmeans R package (df = 53).

|               | Least squares means | Standard error | t-ratio | p-value |
|---------------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}C$ |                     |                |         |         |
| EER - JI      | -0.016              | 0.016          | -1.019  | 0.910   |
| EER - OGI     | -0.005              | 0.016          | -0.350  | 0.999   |
| EER - PINWR   | -0.043              | 0.016          | -2.742  | 0.084   |
| EER - SINWR   | 0.012               | 0.016          | 0.763   | 0.973   |
| EER - STI     | 0.028               | 0.016          | 1.788   | 0.482   |
| JI - OGI      | 0.010               | 0.016          | 0.670   | 0.985   |
| JI - PINWR    | -0.027              | 0.016          | -1.723  | 0.523   |
| JI - SINWR    | 0.028               | 0.016          | 1.782   | 0.486   |
| JI - STI      | 0.044               | 0.016          | 2.807   | 0.072   |
| OGI - PINWR   | -0.037              | 0.016          | -2.393  | 0.177   |
| OGI - SINWR   | 0.017               | 0.016          | 1.112   | 0.874   |
| OGI - STI     | 0.033               | 0.016          | 2.138   | 0.284   |
| PINWR - SINWR | 0.054               | 0.016          | 3.505   | 0.012   |
| PINWR - STI   | 0.070               | 0.016          | 4.531   | 0.001   |
| SINWR - STI   | 0.016               | 0.016          | 1.026   | 0.907   |

|               | Least squares means | Standard error | t-ratio | p-value |
|---------------|---------------------|----------------|---------|---------|
| (b) $\delta^{15}N$ |                     |                |         |         |
| EER - JI      | -0.035              | 0.023          | -1.478  | 0.680   |
| EER - OGI     | -0.001              | 0.023          | -0.034  | 1.000   |
| EER - PINWR   | 0.014               | 0.023          | 0.620   | 0.989   |
| EER - SINWR   | 0.107               | 0.023          | 4.576   | < 0.001 |
| EER - STI     | -0.011              | 0.023          | -0.476  | 0.997   |
| JI - OGI      | 0.034               | 0.023          | 1.444   | 0.701   |
| JI - PINWR    | 0.049               | 0.023          | 2.098   | 0.304   |
| JI - SINWR    | 0.141               | 0.023          | 6.054   | < 0.001 |
| JI - STI      | 0.023               | 0.023          | 1.002   | 0.915   |
| OGI - PINWR   | 0.015               | 0.023          | 0.654   | 0.986   |
| OGI - SINWR   | 0.108               | 0.023          | 4.610   | < 0.001 |
| OGI - STI     | -0.010              | 0.023          | -0.442  | 0.998   |
| PINWR - SINWR | 0.092               | 0.023          | 3.956   | 0.003   |
| PINWR - STI   | -0.026              | 0.023          | -1.095  | 0.881   |
| SINWR - STI   | -0.118              | 0.023          | -5.052  | < 0.001 |
Table A2.4 Percentage overlap of isotopic niche for Common terns between islands in 2018 (% of columns overlapped by rows).

| Island | EER  | JI    | OGI   | PINWR | SINWR | STI  |
|--------|------|-------|-------|-------|-------|------|
| EER    | 37.89| 52.43 | 37.06 | 34.71 | 36.69 |      |
| JI     | 92.39| 70.56 | 52.39 | 83.03 | 63.53 | 64.43 |
| OGI    | 86.38| 47.68 | 68.41 | 41.17 | 50.88 |      |
| PINWR  | 63.81| 36.99 | 71.49 |       | 40.32 | 32.49 |
| SINWR  | 15.64| 15.34 | 11.26 | 10.55 |       | 0.00 |
| STI    | 51.33| 36.45 | 43.20 | 26.40 |       | 0.00 |

Table A2.5 Pair-wise comparisons for Roseate tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios for each island in 2017, calculated using the emmeans R package (df = 20).

|                  | Least squares means | Standard error | t-ratio | p-value |
|------------------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}$C |                     |                |         |         |
| EER - JI         | 0.028               | 0.011          | 2.516   | 0.052   |
| EER - STI        | 0.059               | 0.009          | 6.883   | < 0.001 |
| JI - STI         | 0.030               | 0.011          | 2.687   | 0.036   |
| (b) $\delta^{15}$N |                    |                |         |         |
| EER - JI         | -0.004              | 0.024          | -0.174  | 0.984   |
| EER - STI        | 0.019               | 0.018          | 1.024   | 0.571   |
| JI - STI         | 0.023               | 0.024          | 0.948   | 0.617   |

Table A2.6 Percentage overlap of isotopic niche for Roseate terns between islands in 2017 (% of columns overlapped by rows).

| Island | EER | JI   | STI |
|--------|-----|------|-----|
| EER    |     | 40.93| 0.00|
| JI     | 11.82|     | 49.37|
| STI    | 0.00 | 15.61|     |
Appendix 3. Interannual comparisons for EER (Tables correspond to Fig. 4)

Table A3.1 Pair-wise comparisons for Arctic tern δ\textsuperscript{13}C (a) and δ\textsuperscript{15}N (b) ratios on EER for each year, calculated using the emmeans R package (df = 14).

|       | Least squares means | Standard error | t-ratio | p-value |
|-------|---------------------|----------------|---------|---------|
| (a) δ\textsuperscript{13}C |                     |                |         |         |
| 2017 - 2018 | 0.086              | 0.021          | 4.139   | 0.001   |
| (b) δ\textsuperscript{15}N |                     |                |         |         |
| 2017 - 2018 | -0.090             | 0.047          | -1.917  | 0.076   |

Table A3.2 Percentage overlap of isotopic niche for Arctic terns on EER between years (% of columns overlapped by rows).

| Year | 2017 | 2018 |
|------|------|------|
| 2017 |      | 5.68 |
| 2018 | 74.43|      |

Table A3.3 Pair-wise comparisons for Common tern δ\textsuperscript{13}C (a) and δ\textsuperscript{15}N (b) ratios on EER for each year, calculated using the emmeans R package (df = 17).

|       | Least squares means | Standard error | t-ratio | p-value |
|-------|---------------------|----------------|---------|---------|
| (a) δ\textsuperscript{13}C |                     |                |         |         |
| 2017 - 2018 | 0.053              | 0.010          | 5.143   | < 0.001 |
| (b) δ\textsuperscript{15}N |                     |                |         |         |
| 2017 - 2018 | -0.057             | 0.017          | -3.340  | 0.004   |
Table A3.4 Percentage overlap of isotopic niche for Common terns on EER between year (% of columns overlapped by rows).

| Year | 2017 | 2018 |
|------|------|------|
| 2017 |     | 0.00 |
| 2018 | 0.00 |      |

Table A3.5 Tukey comparisons for Roseate tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios on EER for each year, calculated using the emmeans R package (df = 21).

|        | Least squares means | Standard error | t-ratio | p-value |
|--------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}$C |                     |                |         |         |
| 2016 - 2017 | -0.018              | 0.016          | -1.135  | 0.504   |
| 2016 - 2018 | -0.031              | 0.016          | -1.991  | 0.139   |
| 2017 - 2018 | -0.013              | 0.013          | -1.048  | 0.556   |
| (b) $\delta^{15}$N |                     |                |         |         |
| 2016 - 2017 | 0.050               | 0.025          | 2.019   | 0.132   |
| 2016 - 2018 | -0.013              | 0.025          | -0.522  | 0.862   |
| 2017 - 2018 | -0.062              | 0.020          | -3.112  | 0.014   |

Table A3.6 Percentage overlap of isotopic niche for Roseate terns on EER between year (% of columns overlapped by rows).

| Year | 2016   | 2017   | 2018   |
|------|--------|--------|--------|
| 2016 | 2.98   | 9.33   |        |
| 2017 | 15.76  | 32.16  |        |
| 2018 | 69.19  | 45.07  |        |
### Appendix 4. Interannual comparisons for JI (Tables correspond to Fig. 7A,C,E)

Table A4.1 Pair-wise comparisons for Common tern $\delta^{13}C$ (a) and $\delta^{15}N$ (b) ratios on JI for each year, calculated using the emmeans R package (df = 27).

| Year  | Year  | Least squares means | Standard error | t-ratio | p-value |
|-------|-------|---------------------|----------------|---------|---------|
| 2016  | 2017  | 0.033               | 0.010          | 3.316   | 0.007   |
| 2016  | 2018  | 0.073               | 0.010          | 7.351   | < 0.001 |
| 2017  | 2018  | 0.040               | 0.010          | 3.942   | 0.002   |

| Year  | Year  | Least squares means | Standard error | t-ratio | p-value |
|-------|-------|---------------------|----------------|---------|---------|
| 2016  | 2017  | -0.029              | 0.029          | -1.022  | 0.570   |
| 2016  | 2018  | -0.094              | 0.029          | -3.260  | 0.008   |
| 2017  | 2018  | -0.064              | 0.029          | -2.187  | 0.092   |

Table A4.2 Percentage overlap of isotopic niche for Common terns on JI between year (% of columns overlapped by rows).

| Year  | 2016 | 2017 | 2018 |
|-------|------|------|------|
| 2016  | 100  | 22.05| 21.61|
| 2017  | 11.47| 8.20 | 8.20 |
| 2018  | 21.61| 70.08| 70.08|
Appendix 5. Interannual comparisons for MR (Tables correspond to Fig. 5)

Table A5.1 Pair-wise comparisons for Arctic tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios on MR for each year, calculated using the emmeans R package (df = 18).

|            | Least squares means | Standard error | t-ratio | p-value |
|------------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}$C |                     |                |         |         |
| 2016 - 2017 | -0.048              | 0.017          | -2.890  | 0.025   |
| 2016 - 2018 | 0.007               | 0.016          | 0.452   | 0.894   |
| 2017 - 2018 | 0.055               | 0.015          | 3.663   | 0.005   |
| (b) $\delta^{15}$N |                     |                |         |         |
| 2016 - 2017 | 0.074               | 0.037          | 2.005   | 0.140   |
| 2016 - 2018 | 0.004               | 0.035          | 0.110   | 0.993   |
| 2017 - 2018 | -0.070              | 0.034          | -2.098  | 0.118   |

Table A5.2 Percentage overlap of isotopic niche for Arctic terns on MR between year (% of columns overlapped by rows).

| Year | 2016  | 2017  | 2018  |
|------|-------|-------|-------|
| 2016 |       | 95.58 | 26.95 |
| 2017 | 34.48 |       | 2.35  |
| 2018 | 28.23 | 6.81  |       |
Appendix 6. Interannual comparisons for OGI (Tables correspond to Fig. 7B,D,F)

Table A6.1 Pair-wise comparisons for Common tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios on OGI for each year, calculated using the emmeans R package (df = 28).

|         | Least squares means | Standard error | t-ratio | p-value |
|---------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}$C |                     |                |         |         |
| 2016 - 2017 | 0.024              | 0.013          | 1.911   | 0.154   |
| 2016 - 2018 | 0.073              | 0.013          | 5.785   | < 0.001 |
| 2017 - 2018 | 0.049              | 0.013          | 3.709   | 0.003   |
| (b) $\delta^{15}$N |                     |                |         |         |
| 2016 - 2017 | 0.034              | 0.017          | 2.003   | 0.130   |
| 2016 - 2018 | 0.012              | 0.017          | 0.727   | 0.750   |
| 2017 - 2018 | -0.022             | 0.018          | -1.221  | 0.451   |

Table A6.2 Percentage overlap of isotopic niche for Common terns on OGI between year (% of columns overlapped by rows).

| Year | 2016  | 2017  | 2018 |
|------|-------|-------|------|
| 2016 | 21.01 | 100   | 49.24|
| 2017 | 21.01 | 20.22 |      |
| 2018 | 41.35 | 80.83 |      |
Appendix 7. Interannual comparisons for PINWR (Tables correspond to Fig. 8A,C,E)

Table A7.1 Pair-wise comparisons for Common tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios on PINWR for each year, calculated using the emmeans R package (df = 17).

|        | Least squares means | Standard error | t-ratio | p-value |
|--------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}$C |                     |                |         |         |
| 2017 - 2018 | 0.020              | 0.017          | 1.160   | 0.262   |
| (b) $\delta^{15}$N |                   |                |         |         |
| 2017 - 2018 | -0.040             | 0.013          | -3.124  | 0.006   |

Table A7.2 Percentage overlap of isotopic niche for Common terns on PINWR between year (% of columns overlapped by rows).

| Year | 2017  | 2018  |
|------|-------|-------|
| 2017 |       | 31.32 |
| 2018 | 69.81 |       |
Appendix 8. Interannual comparisons for SINWR (Tables correspond to Fig. 6)

Table A8.1 Pair-wise comparisons for Arctic tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios on SINWR for each year, calculated using the emmeans R package (df = 19).

|          | Least squares means | Standard error | t-ratio | p-value |
|----------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}$C |                      |                |         |         |
| 2016 - 2017 | 0.040               | 0.007          | 5.792   | < 0.001 |
| 2016 - 2018 | 0.103               | 0.005          | 21.842  | < 0.001 |
| 2017 - 2018 | 0.063               | 0.007          | 9.046   | < 0.001 |
| (b) $\delta^{15}$N |                    |                |         |         |
| 2016 - 2017 | -0.028              | 0.023          | -1.263  | 0.432   |
| 2016 - 2018 | -0.037              | 0.015          | -2.407  | 0.065   |
| 2017 - 2018 | -0.008              | 0.023          | -0.372  | 0.927   |

Table A8.2 Percentage overlap of isotopic niche for Arctic terns on SINWR between year (% of columns overlapped by rows).

| Year | 2016 | 2017      | 2018 |
|------|------|-----------|------|
| 2016 |      | 8.28      | 0.00 |
| 2017 | 31.63|           | 0.00 |
| 2018 | 0.00 |           |      |

Table A8.3 Pair-wise comparisons for Common tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios on SINWR for each year, calculated using the emmeans R package (df = 26).

|          | Least squares means | Standard error | t-ratio | p-value |
|----------|---------------------|----------------|---------|---------|
| (a) $\delta^{13}$C |                      |                |         |         |
| 2016 - 2017 | 0.019               | 0.014          | 1.400   | 0.356   |
| 2016 - 2018 | 0.072               | 0.013          | 5.758   | < 0.001 |
| 2017 - 2018 | 0.052               | 0.015          | 3.583   | 0.004   |
| (b) $\delta^{15}$N |                    |                |         |         |
| Year     | 2016    | 2017    | 2018    |
|----------|---------|---------|---------|
| 2016     | 73.24   | 74.66   |         |
| 2017     | 86.37   |         | 81.19   |
| 2018     | 16.20   | 14.94   |         |

Table A8.4 Percentage overlap of isotopic niche for Common terns on SINWR between year (% of columns overlapped by rows).
Appendix 9. Interannual comparisons for STI (Tables correspond to Fig. 8B,D,F)

Table A9.1 Pair-wise comparisons for Common tern $\delta^{13}$C (a) and $\delta^{15}$N (b) ratios on STI for each year, calculated using the emmeans R package (df = 17).

|               | Least squares means | Standard error | t-ratio | p-value |
|---------------|---------------------|----------------|---------|---------|
| **(a) $\delta^{13}$C** |                     |                |         |         |
| 2017 - 2018   | 0.056               | 0.015          | 3.845   | 0.001   |
| **(b) $\delta^{15}$N** |                     |                |         |         |
| 2017 - 2018   | -0.060              | 0.025          | -2.447  | 0.026   |

Table A9.2 Percentage overlap of isotopic niche for Common terns on STI between year (% of columns overlapped by rows).

| Year | 2017 | 2018 |
|------|------|------|
| 2017 |      |      |
| 2018 | 14.63| 12.68|