Vol. 50: 235–247, 2023
https://doi.org/10.3354/esr01233

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published April 6

Variation in isotopic niche partitioning between adult roseate and common terns in the Northwest Atlantic

Henry D. Legett[1,5,*], Jeffrey R. Lucas[1], Elizabeth C. Craig[2], Michelle D. Staudinger[3,4]

[1]Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907, USA
[2]Shoals Marine Laboratory (Joint Program of University of New Hampshire and Cornell University), Durham, New Hampshire 03824, USA
[3]US Geological Survey, Department of the Interior, Northeast Climate Adaptation Science Center, Amherst, Massachusetts 01003, USA
[4]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, Massachusetts 01003, USA
[5]*Present address:* Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USA

ABSTRACT: Co-occurring species with similar resource requirements often partition ecological niches at different spatial and temporal scales. In the Northwest Atlantic (NWA), federally endangered roseate terns *Sterna dougallii* nest almost exclusively in coastal island colonies alongside common terns *S. hirundo*. Roseate terns are prey specialists compared to common terns, which are opportunistic generalists; however, the 2 species forage on similar resources during the breeding season. The degree to which these species overlap in their adult foraging ecologies is not well understood. We compared the isotopic niches of nesting adult roseate and common terns by analyzing stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in eggshell membrane tissues collected in 2018 and 2019 from 10 colonies that span their NWA breeding range. Our aim was to characterize interspecific patterns in $\delta^{13}C$ and $\delta^{15}N$ values, isotopic niche breadth, and isotope niche overlap. We additionally examined interannual and subregional differences between 'cold-water' colonies in the Gulf of Maine and 'warm-water' colonies in Southern New England and Long Island Sound. At the range-wide scale, there was a high degree of overlap in the overall isotopic niches of the 2 species; however, more variable patterns were observed at the colony scale, ranging from nearly complete overlap to complete separation. The isotopic niches of roseate terns were generally narrower than those of common terns, consistent with their respective specialist/generalist tendencies. While the influence of isotopic baselines limits our interpretation of interannual and subregional differences, isotopic niche breadths and overlap suggest consistency of relative foraging ecologies across these scales.

KEY WORDS: Roseate tern · *Sterna* sp. · Stable isotopes · Foraging · Isotopic niche analysis · Dietary competition · Eggshells · Northwest Atlantic

1. INTRODUCTION

Co-occurring species with similar resource requirements often partition ecological niches to limit competitive overlap (Hardin 1960). For example, seabirds that nest in multispecies colonies can be constrained to foraging in similar areas and on similar types of prey (Jessopp et al. 2020). When prey and suitable foraging patches are limited, interspecific competition can drive the partitioning of these resources in multiple ways, such as through spatial or temporal segregation of resources or segregation of

---

[*]Corresponding author: LegettH@si.edu

Publisher: Inter-Research · www.int-res.com

resource type (Schoener 1974). Factors such as climate change can cause shifts in prey communities resulting in asymmetric impacts on seabird species within breeding colonies (Oro et al. 2009). Thus, understanding the dynamics of interspecific resource partitioning is important for identifying drivers of seabird distributions, especially as they relate to the conservation of vulnerable populations (Bolton et al. 2019).

During the spring, roseate terns *Sterna dougallii* migrate to the Northwest Atlantic (NWA) to forage and provision their young on seasonally abundant prey at island colonies located throughout the Gulf of Maine, southern New England, and Long Island Sound (Spendelow et al. 2010). This population is listed as endangered and as a regional species of greatest conservation need in the USA (USFWS 1987, USGS 2017) as well as endangered in Canada (COSEWIC 2009). Accordingly, there has been a decades-long effort to recover roseate terns in the NWA region (Nisbet & Spendelow 1999, USFWS 2010, 2020). Recovery efforts include annual monitoring and management of roseate tern breeding colonies by multiple state and federal agencies and conservation organizations.

Roseate terns in the NWA nest almost exclusively on coastal islands and almost always in association with colonies of the more abundant common tern *S. hirundo* (Cabot & Nisbet 2013). During the breeding season, terns are central-place foragers, restricting their range to within 15 km around the colony as they maintain their nests and provision their young (Jessopp et al. 2020, Pratte et al. 2021). Previous studies on the foraging strategies of roseate and common terns in this region have largely focused on the chick-provisioning period, where the prey that adults deliver to chicks is directly viewed by observers stationed at the colonies (Richards & Schew 1989, Safina 1990a, Safina et al. 1990, Goyert 2015, Yakola et al. 2022). From these studies, roseate terns have been characterized as resource specialists. Roseate terns forage across fewer areas, in deeper water, and chick diets are comprised exclusively of forage fishes, primarily sand lances (*Ammodytes americanus* and *A. dubius*), but also hakes (*Urophycis* sp., *Merluccius* sp., and *Enchelyopus* sp.), herrings (*Clupea* spp. and *Alosa* spp.), silversides (*Menidia menidia*), and anchovies (*Anchoa* sp.; Richards & Schew 1989, Safina 1990a, Safina et al. 1990, Goyert 2015, Staudinger et al. 2020, Yakola et al. 2022). In comparison, common terns are resource generalists, using relatively more opportunistic foraging tactics and provisioning their chicks with a more diverse diet that includes a broad range of fishes and both marine and terrestrial invertebrates (Kirkham 1986, Safina 1990a, Tims et al. 2004, Goyert 2015, Yakola et al. 2022). This specialist/generalist dynamic between roseate and common terns has also been observed in breeding colonies in other regions, including the Northeast Atlantic (Robertson et al. 2014). Although their intrinsic foraging strategies are distinct, direct observations (Goyert 2015, Yakola et al. 2022) and stable isotope analyses (Kimmons 2012) have indicated a high degree of similarity in the prey that the 2 tern species delivered to their chicks. In addition, both tern species have been observed foraging in mixed-species flocks on the same schools of fish (Duffy 1986, Goyert 2014). The success of roseate terns in these flocks is thought to be dependent on the composition of the flock and the prey fish community (Safina 1990a,b). Thus, the degree of dietary overlap between roseate and common terns can vary over space and time and is dependent on behavioral, social, and environmental conditions (Goyert 2014, 2015).

While the chick diet has been relatively well studied (e.g. Hall et al. 2000, Yakola et al. 2022), less is known about the diets of adult terns in the NWA region (USFWS 2010, 2020, Cabot & Nisbet 2013, Staudinger et al. 2020). The quality of adult tern diets is critical for breeding success and recruitment. The time after spring migration and just before breeding is particularly important, as adult terns must replenish energy reserves to support egg production and raise chicks (Nisbet 1977, Diamond & Devlin 2003, Bond & Diamond 2010, Egevang et al. 2010, Scopel & Diamond 2018). However, adult terns forage at sea, making it challenging to directly monitor their diets (but see Goyert 2014, Robertson et al. 2014).

Because of the logistical difficulties of making direct measurements of diet, indirect methods can be valuable tools to gain insights into the foraging ecologies of adult seabirds and other hard to sample marine organisms across different habitats and time periods (Hobson et al. 1994, Inger & Bearhop 2008, Bond & Jones 2009). Measurements of stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) in organismal tissues are common indicators of diets integrated over days to years depending on the turnover time of different tissue types (Inger & Bearhop 2008, Bond & Jones 2009). Broad geographic and interannual patterns of δ^{13}C and δ^{15}N values observed in food webs are influenced by underlying isotopic baselines, variations which are driven by environmental factors like annual chlorophyll concentrations, continental runoff, and upwelling (Oczkowski et al. 2016). For marine and coastal organisms, relatively higher δ^{13}C values in tissues reflect foraging in more nearshore or benthic habitats, while lower values reflect offshore or pelagic foraging (Graham et al. 2010). $\delta^{13}C$ values are also influenced by the extent of freshwater resource use, with relatively lower values indicating foraging in inland waters (Farquhar et al. 1989, Hobson 1990, Mizutani et al. 1990, Bearhop et al. 1999). $\delta^{15}N$ values are used to indicate trophic level, with relatively higher values indicating consumption of larger, higher trophic level prey (Fry 2006, Bond & Jones 2009). The distribution of $\delta^{13}C$ and $\delta^{15}N$ values across a population can be used to define the isotopic niche of the population, and the breadths of isotopic niches can reflect the relative diversity of foraging resources (Yeakel et al. 2016, Rader et al. 2017). The degree of overlap between isotopic niches can indicate the potential degree of dietary niche similarity or partitioning across species (Newsome et al. 2007; recent examples in seabirds include Maynard & Davoren 2020, Lee et al. 2021, and Gal et al. 2021).

In this study, we assess and compare the relative foraging ecologies of adult roseate and common terns during the post-spring migration, pre-breeding period of their lifecycles. Specifically, we analyzed eggshell membrane tissues collected in 2018 and 2019 from 10 colonies across the species' NWA breeding range to examine interspecific differences in $\delta^{13}C$ and $\delta^{15}N$ values, isotopic niche breadth, and isotopic niche overlap. We compare these differences at 2 spatial scales: range-wide and within each individual colony. The isotope ratios of eggshell membrane tissues reflect local resources consumed by female birds after they have reached the breeding colony, approximately 3 to 5 d before the egg is laid (Hobson 1995, Polito et al. 2011, Cabot & Nisbet 2013). Based on previous studies characterizing roseate terns as piscivorous specialists (e.g. Yakola et al. 2022), we predicted that roseate terns will exhibit higher $\delta^{15}N$ values and narrower isotopic niche breadths than common terns. Furthermore, if roseate and common terns are foraging in similar habitats and on similar prey species within each colony, we would predict a high degree of similarity in $\delta^{13}C$ and $\delta^{15}N$ values and isotopic niche overlap between the 2 species. Alternatively, if roseate and common terns are partitioning foraging locations and prey, then we would expect divergent isotopic niches with little overlap.

In addition to our primary aim of assessing interspecific isotopic differences between roseate and common terns, our secondary aim was to examine subregional and interannual trends in isotopic niches. In the NWA, the roseate tern population is informally divided by the United States Fish and Wildlife Service (USFWS) into 2 subregional groups: 'cold-water' colonies located north of Cape Cod in the Gulf of Maine and 'warm-water' colonies located south of Cape Cod in southern New England and Long Island Sound (Nisbet & Spendelow 1999, USFWS 2010, 2020). Notably, the adult tern diet in each subregion may also differ in composition. Fewer prey types have been observed in roseate and common tern chick diets in warm-water colonies, with sand lance being the most commonly occurring item provisioned (>90% of the roseate chick diet; Kirkham 1986, Safina et al. 1990, Tims et al. 2004, Goyert 2015), while in cold-water colonies, chick diets are more diverse (Hall et al. 2000, USFWS 2010, Yakola et al. 2022). Given these previously documented differences in tern diets between the subregions, we predicted there would be lower isotopic niche breadth and higher isotopic niche overlap in warm-water colonies compared to cold-water colonies. Furthermore, as both $\delta^{13}C$ and $\delta^{15}N$ isotopic baselines are lower in the cold-water subregion compared to the warm-water subregion (Oczkowski et al. 2016), we expected subregional differences in isotope ratios consistent with these baselines. Because eggshells were sampled over 2 years, 2018 and 2019, we also examined interannual differences in the isotopic niches of roseate and common terns. Overall, our results provide multiscale information on isotopic niche partitioning in co-occurring populations of adult roseate and common terns in the NWA.

2. MATERIALS AND METHODS

2.1. Sample collection

Hatched eggshells of roseate and common terns were collected from colonies on 10 coastal islands throughout the breeding season from June to July in 2018 and 2019 (USFWS Permit #MB84377C-0, TE83097C-0; Fig. 1). All colonies included in this study had both nesting roseate and common terns. The collection effort was conducted in partnership with the USFWS National Wildlife Refuges (USFWS NWR), the National Audubon Society Seabird Institute (NASSI), Massachusetts Department of Fish and Wildlife (MA DFW), the Shoals Marine Laboratory, the Great Gull Island Project, and the American Museum of Natural History (AMNH), who manage and monitor the tern colonies in the NWA region during the breeding season. Colonies in both subregions of the population were sampled, including 4 on cold-water islands north of Cape Cod (Eastern Egg Rock,

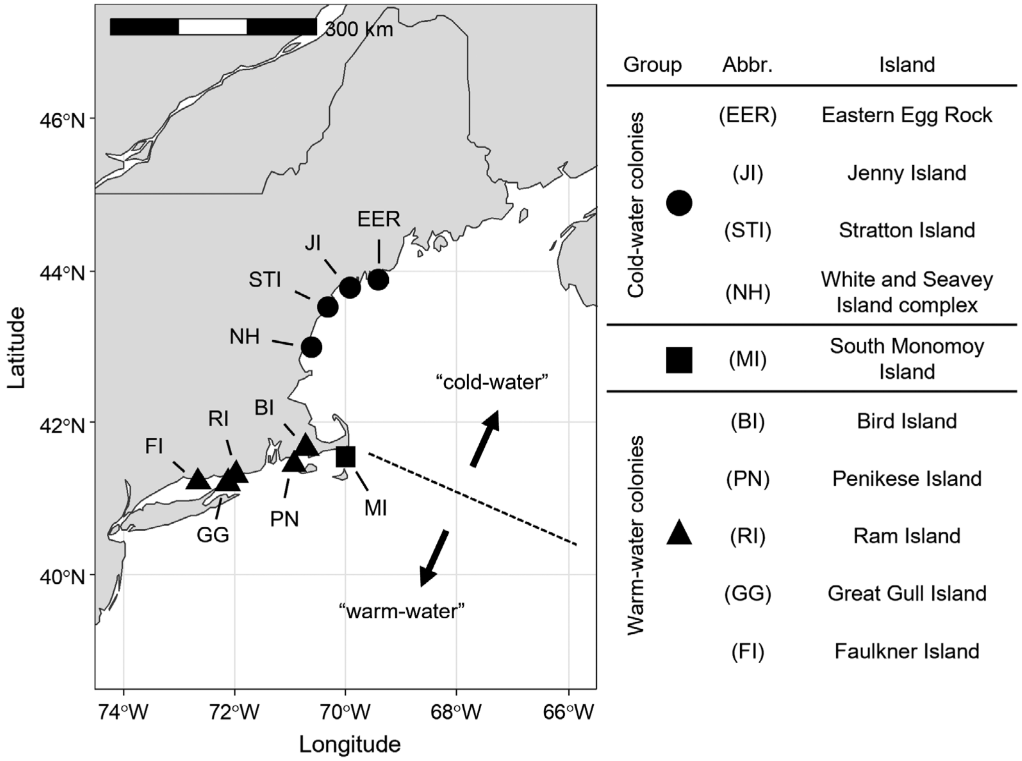

Fig. 1. Locations of the 10 seabird nesting colonies with both roseate and common terns in the Northwest Atlantic. Colonies are divided into cold-water (circles) and warm-water (triangles) subregions, with 1 boundary island (square)

Jenny Island, Stratton Island, and the White and Seavey Island complex), 5 on warm-water islands south of Cape Cod (Bird Island, Penikese Island, Ram Island, Great Gull Island, and Falkner Island), and 1 'boundary island' located between the cold-warm subregions near the southeastern extent of Cape Cod (South Monomoy Island). A target sample size of 10 eggshells was collected for each species per colony per year. However, the realized sample size was lower in some cases due to the low abundances of roseate terns on some islands and the ability to collect samples suitable for stable isotope analysis. For example, only 30 or fewer nesting pairs of roseate terns were observed on several islands in 2018 and 2019, including Jenny Island, South Monomoy Island, Penikese Island, and Falkner Island (USFWS 2020). All eggshells came from different nests and were collected only if the parent species was known. A total of 363 eggshells was collected and analyzed over the 2 yr period of this study (Tables 1 & 2).

2.2. Stable isotope analysis

Our analyses of $\delta^{13}C$ and $\delta^{15}N$ values and carbon to nitrogen (C:N) ratios in tern eggshell membranes followed established methods (Polito et al. 2009, Polito et al. 2011). Briefly, the membrane sac was separated from the outer shell, cleaned using deionized water, and then dried in an oven at 60°C. Subsamples (1.0 µg) of the tissue were weighed in tin capsules and analyzed using a Thermo Delta V isotope ratio mass spectrometer interfaced to an NC2500 elemental analyzer at the Cornell Isotope Laboratory (Ithaca, New York; https://cobsil.cornell.edu/). Delta values (δ) for stable carbon and nitrogen ratios were measured in units of per mille (‰) against references of Vienna PeeDee belemnite (VPDB) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. The accuracy and precision of this analysis was measured using an in-house standard (white-tailed deer *Odocoileus virginianus*) analyzed after every 10 eggshell membrane samples. Our samples showed a standard deviation of 0.06‰ for $\delta^{13}C$ and 0.03‰ for $\delta^{15}N$. Raw $\delta^{13}C$ and $\delta^{15}N$ values were linearly corrected using a 2-point normalization using an additional in-house plant standard (corn *Zea mays*) and animal standard (Cayuga Lake brown trout *Salmo trutta*).

2.3. Statistical analyses

All statistical analyses were conducted in R v. 4.0.3 (R Core Team 2020). We compared $\delta^{13}C$ and

Table 1. Stable isotope analyses of eggshell membranes of roseate terns and common terns on 10 islands collected in 2018 including sample sizes (n), results from permutation tests comparing $\delta^{13}C$ and $\delta^{15}N$ values (*$p < 0.05$), standard ellipse areas corrected for small sample sizes (SEAc), and the degree of overlap of isotopic niches (Overlap). Islands are ordered north to south, with the intermediate island (South Monomoy Island, MI) separating the cold- and warm-water subregional groups. Isotope ratios are means ± SE. Island abbreviations as in Fig. 1

2018				$\delta^{13}C$			$\delta^{15}N$			SEAc	Overlap
Group	Island	Species	n	Value (‰)	*Z*-score	p	Value (‰)	*Z*-score	p	(‰^{2})	(%)
Cold water	EER	Roseate	10	−17.8 ± 0.1	1.37	0.172	12.5 ± 0.1	−0.65	0.516	0.3	66.7
		Common	10	−18.0 ± 0.1			12.6 ± 0.1			0.8	23.4
	JI	Roseate	8	−17.2 ± 0.1	2.61	0.009*	12.3 ± 0.1	−1.52	0.129	0.9	0
		Common	10	−18.2 ± 0.2			12.8 ± 0.2			1.0	0
	STI	Roseate	10	−18.4 ± 0.2	3.29	0.001*	12.1 ± 0.2	−1.04	0.297	0.1	0
		Common	10	−19.1 ± 0.2			12.2 ± 0.3			0.2	0
	NH	Roseate	10	−18.5 ± 0.1	−1.69	0.091	12.4 ± 0.1	0.98	0.329	0.2	37.4
		Common	10	−18.1 ± 0.2			12.2 ± 0.1			1.1	7.7
	MI	Roseate	8	−18.4 ± 0.2	1.59	0.111	12.7 ± 0.2	0.14	0.888	0.5	24.4
		Common	9	−18.9 ± 0.2			12.6 ± 0.2			0.3	35.5
Warm water	BI	Roseate	6	−17.6 ± 0.2	−2.10	0.036*	13.9 ± 0.2	−2.54	0.011*	0.3	2.1
		Common	7	−17.2 ± 0.2			14.3 ± 0.1			0.1	5.0
	PN	Roseate	9	−16.1 ± 0.1	−1.04	0.300	13.5 ± 0.1	−1.15	0.252	0.4	36.2
		Common	10	−16.0 ± 0.2			13.7 ± 0.2			0.2	84.0
	RI	Roseate	9	−16.6 ± 0.1	−3.17	0.002*	13.8 ± 0.2	−2.53	0.012*	0.3	0
		Common	10	−15.8 ± <0.1			14.7 ± 0.1			0.2	0
	GG	Roseate	10	−17.7 ± 0.2	0.82	0.411	14.3 ± 0.4	3.02	0.003*	0.1	0.1
		Common	9	−17.8 ± 0.1			13.7 ± 0.1			0.3	<0.1
	FI	Roseate	10	−18.5 ± 0.1	1.55	0.121	15.3 ± 0.1	−1.59	0.112	0.7	56.0
		Common	10	−18.9 ± 0.1			15.8 ± 0.1			2.0	18.7

Table 2. Stable isotope analyses of eggshell membranes of roseate terns and common terns on 10 islands collected in 2019. Details as in Table 1

2019				$\delta^{13}C$			$\delta^{15}N$			SEAc	Overlap
Group	Island	Species	n	Value (‰)	*Z*-score	p	Value (‰)	*Z*-score	p	(‰^{2})	(%)
Cold water	EER	Roseate	10	−17.5 ± 0.1	−2.20	0.028*	12.0 ± 0.1	−3.04	0.002*	0.2	4.0
		Common	10	−16.9 ± 0.2			12.9 ± 0.2			1.0	0.8
	JI	Roseate	10	−18.0 ± 0.1	−1.69	0.090	11.9 ± 0.1	−2.25	0.024*	0.2	61.1
		Common	10	−17.6 ± 0.2			12.4 ± 0.2			0.7	14.2
	STI	Roseate	10	−18.2 ± 0.1	−2.48	0.013*	11.7 ± 0.1	−0.99	0.324	0.1	37.3
		Common	10	−17.9 ± 0.1			11.8 ± 0.2			0.4	6.5
	NH	Roseate	7	−17.9 ± 0.1	−0.63	0.532	12.0 ± 0.1	−0.62	0.534	0.2	98.9
		Common	10	−17.8 ± 0.1			12.1 ± 0.2			0.5	35.1
	MI	Roseate	3	−17.8 ± 0.2	1.18	0.239	13.6 ± 0.3	2.47	0.013*	0.8	0
		Common	10	−18.0 ± 0.1			12.6 ± 0.2			0.3	0
Warm water	BI	Roseate	10	−17.8 ± 0.1	−1.99	0.047*	14.5 ± 0.1	−2.88	0.004*	0.2	9.0
		Common	10	−17.2 ± 0.3			15.0 ± 0.1			0.8	1.9
	PN	Roseate	9	−17.5 ± 0.1	0.44	0.659	14.5 ± 0.1	1.55	0.120	0.2	64.3
		Common	10	−17.6 ± 0.1			14.2 ± 0.1			0.2	46.3
	RI	Roseate	10	−17.6 ± 0.1	0.12	0.902	14.6 ± 0.1	1.72	0.086	0.2	80.4
		Common	5	−17.6 ± 0.1			14.3 ± 0.2			0.5	33.2
	GG	Roseate	3	−17.1 ± 0.1	2.40	0.017*	15.4 ± 0.1	−1.44	0.151	0.1	0
		Common	10	−17.6 ± 0.1			15.6 ± 0.1			0.1	0
	FI	Roseate	10	−18.3 ± 0.1	0.74	0.458	16.2 ± 0.1	−0.59	0.557	0.1	81.6
		Common	10	−18.4 ± 0.1			16.3 ± 0.1			0.3	35.3

δ^{15}N values from eggshell membranes and isotopic niches (the relative distribution of δ^{13}C and δ^{15}N values) in 3 ways: (1) interspecific differences between roseate and common terns both at a range-wide scale and within individual colonies, (2) subregional differences between cold-water and warm-water tern colonies, and (3) interannual differences between 2018 and 2019. Isotopic niche breadth and overlap between roseate and common terns were evaluated using the R package 'SIBER' (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011), which uses maximum likelihood estimates to calculate standard ellipse areas (SEAs) for the distributions of δ^{13}C and δ^{15}N values as a measure of isotopic niche. The area encompassed by the ellipse (isotopic niche breadth) was corrected for sample size (corrected standard ellipse area, SEAc). We also calculated the percentage of overlap of roseate and common tern ellipses on each island to infer similarities or differences in isotopic niches. This created 2 measures of isotopic niche overlap per island, one for roseate terns (the percentage the roseate tern ellipse was overlapped by the common tern ellipse) and one for common terns (the percentage the common tern ellipse was overlapped by the roseate tern ellipse). Roseate and common tern δ^{13}C and δ^{15}N values (per mille, ‰), isotopic niche breadths (SEAc, ‰^{2}), and isotopic niche overlap (%) were compared at a range-wide scale using 2-tailed permutation tests in the R package 'coin' (Hothorn et al. 2008), testing the null hypothesis that these variables did not differ between the species. Permutation tests, i.e. non-parametric statistical tests of independence between 2 sets of measured variables, were chosen because of the small sample sizes being compared and to avoid making assumptions about the distribution of δ^{13}C and δ^{15}N values. To account for inter-colony differences in the permutation tests, variables (δ^{13}C and δ^{15}N values, isotopic niche breadths, and isotopic niche overlap) were blocked (i.e. grouped) within colony. Asymptotic approximations of the exact distributions were obtained using a randomized quasi-Monte Carlo method to calculate p-values (Genz & Bretz 2009). Separate comparisons between the species were also conducted for each colony. Subregional differences between cold- and warm-water colonies, and interannual differences between 2018 and 2019, were independently assessed for each species using similar permutation tests. The 'boundary island' (South Monomoy Island) was independently compared to the cold- and warm-water subregions.

3. RESULTS

3.1. Carbon-to-nitrogen ratios and extreme outliers

Eggshell membrane samples collected in 2018 had an average C:N ratio of 3.3 ± 0.0 (mean ± SE), ranging from 3.0 to 3.8. Samples collected in 2019 had an average C:N ratio of 3.1 ± 0.1, ranging from 2.9 to 3.4. These C:N ratios indicate low lipid content in our samples, which could otherwise bias stable isotope ratios (Post et al. 2007, Ehrich et al. 2011). Two samples were identified as extreme outliers. First, one roseate tern eggshell membrane (C:N = 3.5) collected from Ram Island in 2018 had a δ^{13}C value that was >11 SDs from the rest of the roseate tern samples on that island in that year (−18.7‰ vs. −16.4 ± 0.1‰, SD = 0.2‰) and a δ^{15}N value that was >8 SDs from the rest of the samples (10.8‰ vs. 14.2 ± 0.1‰, SD = 0.4‰). Second, one common tern eggshell membrane (C:N = 3.0) collected from South Monomoy Island in 2019 had a δ^{13}C value that was >15 SDs from the rest of the common tern samples on that island in that year (−13.3‰ vs. −18.0 ± 0.1‰, SD = 0.3‰). Both extreme outliers were removed from the rest of the analyses.

3.2. Interspecific differences between roseate and common terns

Stable isotope ratios were similar (differing <1‰) for roseate and common terns overall, resulting in a high degree of isotopic niche overlap at the range-wide scale (Tables 1 & 2, Fig. 2). On average across the colonies, roseate tern eggshell membranes had slightly higher δ^{13}C values than common terns in 2018 (−17.7 ± 0.1‰ vs. −17.8 ± 0.1‰; Z = 1.99, p = 0.046), but lower δ^{13}C values in 2019 (−17.8 ± 0.0‰ vs. −17.7 ± 0.1‰, Z = −2.76, p = 0.006). Roseate terns had slightly lower δ^{15}N values than common terns in both years, 2018 (13.3 ± 0.1‰ vs. 13.4 ± 0.1‰, Z = −2.12, p = 0.034) and 2019 (13.5 ± 0.2‰ vs. 13.7 ± 0.2‰, Z = −2.37, p = 0.018).

On average, roseate terns had narrower isotopic niche breadths compared to common terns in both years: 2018 (SEAc: 0.4 ± 0.1‰^{2} vs. 0.6 ± 0.2‰^{2}; Table 1, Fig. 3A) and 2019 (0.2 ± 0.1‰^{2} vs. 0.5 ± 0.1‰^{2}; Table 2, Fig. 3B). These interspecific differences in isotopic niche breadth were significant in 2019 (Z = −1.96, p = 0.050), but not in 2018 (Z = −1.42, p = 0.155). Isotopic niche overlap between roseate and common terns was variable among colonies and years, and isotopic niches were completely separated (0% overlap) in 5

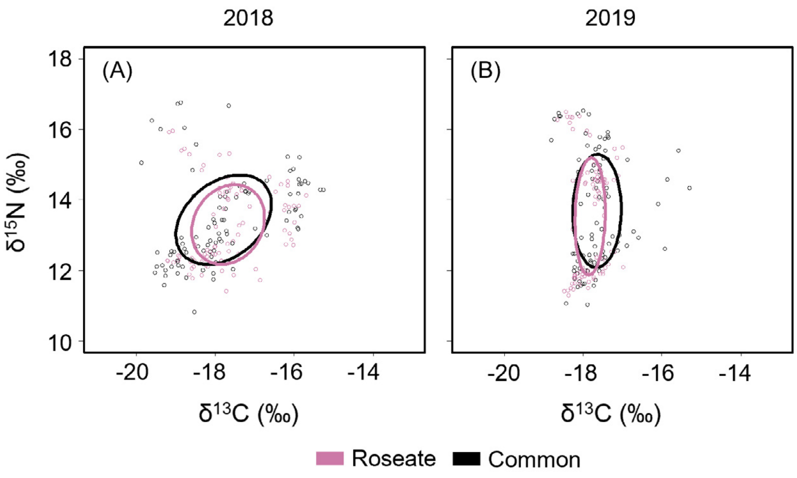

Fig. 2. Estimated standard ellipse areas corrected for small sample sizes (SEAc) showing range-wide isotopic niches of roseate and common terns pooled across all 10 islands in (A) 2018 and (B) 2019

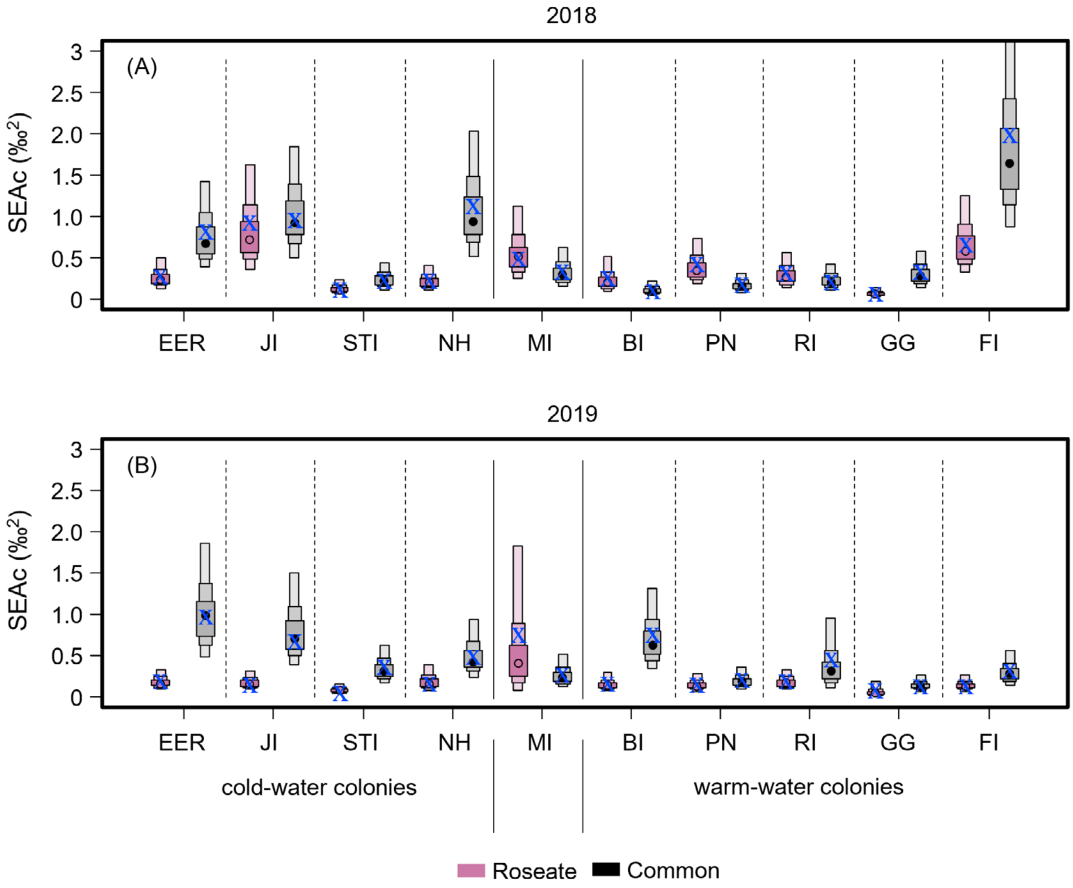

Fig. 3. Among-island isotopic niche breadths for roseate (pink, first in each island pair) and common (black/gray, second in each island pair) terns in (A) 2018 and (B) 2019. Islands are ordered north to south separated with vertical dotted lines, with the intermediate island (Monomoy Island NWR; MI) separating the cold and warm-water island groups with vertical solid lines. Points are the total isotopic niche area occupied by each species (SEA), and boxes represent 95, 75, and 50 % confidence regions based on maximum likelihood estimates. The sample-size corrected ellipse area (SEAc), based on maximum likelihood estimate, is indicated by a blue 'x'. Island abbreviations as in Fig. 1

cases: on Jenny Island, Stratton Island, and Ram Island in 2018; and on South Monomoy Island and Great Gull Island in 2019. Isotopic niches only slightly overlapped (<10%) in 4 additional cases: Bird Island and Great Gull Island in 2018; and Eastern Egg Rock and Bird Island in 2019. The highest degree of overlap occurred on the White and Seavey Island complex in 2019, where the roseate tern isotopic niche was overlapped 98.9% by the common tern isotopic niche. On average, the isotopic niches of roseate tern were overlapped to a greater extent by common tern niches (2018: 22.3 ± 8.1%, 2019: 43.7 ± 12.1%), compared to the extent that common tern niches were overlapped by roseate tern niches (2018: 17.4 ± 8.3%, 2019: 17.3 ± 5.8%; Tables 1 & 2). These interspecific differences in isotopic niche overlap were significant in 2019 ($Z = 2.41$, $p = 0.016$), but not in 2018 ($Z = 0.60$, $p = 0.549$). Figures of isotopic niches for roseate and common terns in individual colonies can be found in Figs. S1–S10 in the Supplement at www.int-res.com/articles/suppl/n050p235_supp.pdf, including figures of isotopic niches that include outliers (South Monomoy Island: Fig. S5, Ram Island: Fig. S8).

3.3. Subregional differences between cold-water and warm-water colonies

The cold- and warm-water subregions were completely separated in isotopic niche space for both tern species in both years (0% overlap, Fig. 4). Eggshell membranes from the warm-water colonies had significantly higher δ^{15}N values compared to cold-water colonies for both tern species in both 2018 (roseate terns: 14.3 ± 0.1‰ vs. 12.3 ± 0.1‰, $Z = 7.72$, $p < 0.001$; common terns: 14.5 ± 0.1‰ vs. 12.4 ± 0.1‰, $Z = 7.30$, $p < 0.001$; Table 1, Fig. 4A,C) and 2019 (roseate terns: 15.0 ± 0.1‰ vs. 11.9 ± 0.1‰, $Z = 8.27$, $p < 0.001$; common terns: 15.1 ± 0.1‰ vs. 12.3 ± 0.1‰, $Z = 8.05$, $p < 0.001$; Table 2, Fig. 4B,D). In 2018, eggshell membranes from warm-water colonies also had significantly higher δ^{13}C values compared to cold-water colonies (roseate terns: −17.2 ± 0.2‰ vs. −18.0 ± 0.1‰, $Z = 3.84$, $p < 0.001$; common terns: −17.1 ± 0.2‰ vs. −18.3 ± 0.1‰, $Z = 4.79$, $p < 0.001$; Table 1, Fig. 4A,C). Statistically significant differences were not detected ($p > 0.05$) in δ^{13}C values between subregions in 2019 for either species (Table 2, Fig. 4B,D). Isotopic niche breadths also did not differ between the cold- and warm-water subregions for either tern species in 2018 (Table 1, Fig. 3A) or 2019 (Table 2, Fig. 3B).

Terns on South Monomoy Island, the 'boundary island', generally had δ^{15}N values similar to the cold-water colonies for both species, except for roseate terns in 2019 (Fig. 4). However, only 3 eggshell samples were analyzed for roseate terns on South Monomoy Island in 2019 (Table 2). This low sample size was due to the small size of the roseate tern colony at this location, as only 12 breeding pairs were observed on South Monomoy Island in 2019 (USFWS 2020).

3.4. Interannual differences between 2018 and 2019

On average across all 10 colonies, δ^{15}N values were significantly lower in 2018 than 2019 for both roseate terns (13.3 ± 0.1‰ vs. 13.5 ± 0.2‰; $Z = -3.28$, $p = 0.001$) and common terns (13.4 ± 0.1‰ vs. 13.7 ± 0.2‰; $Z = -2.89$, $p = 0.004$). δ^{13}C values were significantly higher in 2018 compared to 2019 for roseate terns (−17.7 ± 0.1‰ vs. −17.8 ± 0.0‰; $Z = 2.62$, $p = 0.009$), but no interannual differences in δ^{13}C values were detected for common terns (−17.8 ± 0.1‰ vs. −17.7 ± 0.1‰; $Z = -1.91$, $p = 0.057$). No notable interannual differences in isotopic niche breadth or isotopic niche overlap were detected for either species ($p > 0.05$; Figs. 2 & 3).

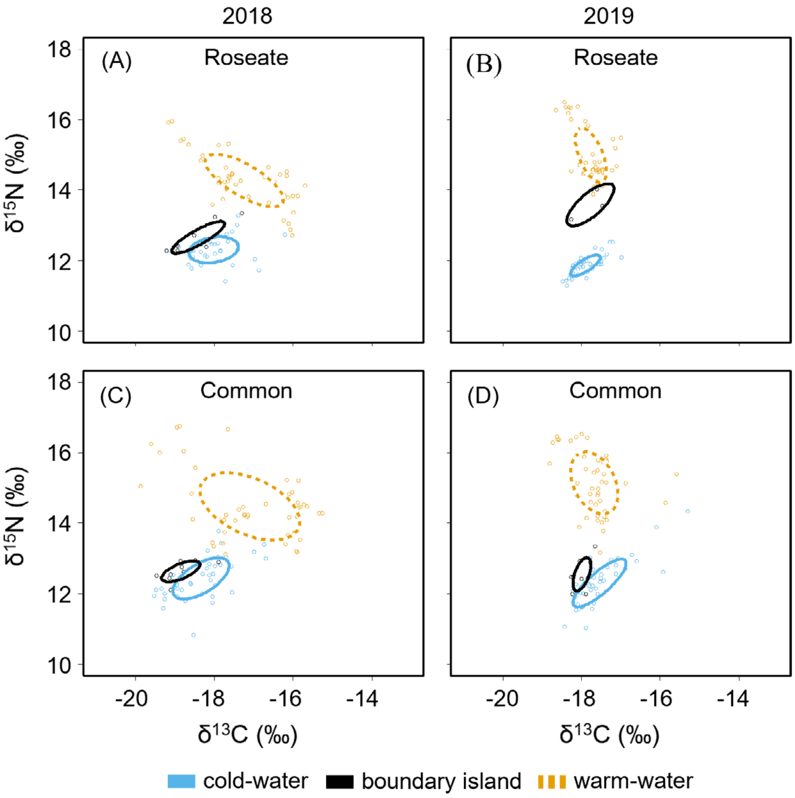

Fig. 4. Subregional estimated standard ellipses areas corrected for small sample sizes (SEAc) showing isotopic niches of (A,B) roseate terns and (C,D) common terns in (A,C) 2018 and (B,D) 2019 from cold-water islands, warm-water islands, and a boundary island (South Monomoy Island)

4. DISCUSSION

4.1. Interspecific differences between roseate and common terns

Our stable isotope analyses of eggshell membrane tissues characterize multi-scale patterns in the isotopic niches of adult roseate and common terns in the NWA during the post-migration period, just prior to breeding. At the range-wide scale, similarities in $\delta^{13}C$ and $\delta^{15}N$ values resulted in high degrees of overlap in the isotopic niches of the 2 tern species, suggesting similar overall resource use. Isotopic niche overlap was more variable at the individual colony scale, with half the colonies analyzed showing nearly complete separation in isotopic niches, and others overlapping at varying degrees up to nearly complete correspondence (98.9%).

Interspecific separation of isotopic niches was due to differences in both $\delta^{13}C$ and $\delta^{15}N$ values. $\delta^{13}C$ values varied on an interannual basis, with no discernable pattern of higher or lower for either species. Contrary to expectations for a species with a more piscivorous diet, $\delta^{15}N$ values were consistently lower on average for roseate terns compared to common terns, which consume a mixture of marine and terrestrial invertebrates (Yakola et al. 2022). Stable isotope analyses of forage fish in the western Atlantic indicate that sand lance have slightly lower $\delta^{15}N$ values on average compared to other forage fish species like hakes and herrings, although this difference was often only around 1‰ (Lesage et al. 2001, Estrada et al. 2005, Logan et al. 2011, 2015, Jenkins & Davoren 2021). Thus, interspecific differences in $\delta^{15}N$ values may reflect a higher proportion of sand lance in the diets of adult roseate terns compared to common terns, consistent with previous studies on provisioned chick diets (Safina et al. 1990, Goyert 2015, Staudinger et al. 2020, Yakola et al. 2022).

Measures of isotopic niche breadth of the 2 species support the characterization of adult roseate terns as foraging specialists compared to common terns (e.g. Safina 1990a, Goyert 2015, Yakola et al. 2022). Roseate tern isotopic niche breadths were narrower, and in colonies and years when isotopic niches of the tern species overlapped, roseate tern isotopic niches were more overlapped by common tern niches than vice versa. While isotopic niche overlap has been used in previous studies as a measure of potential foraging competition among species (e.g. Maynard & Davoren 2020, Gal et al. 2021, Lee et al. 2021), without simultaneous reference measurements of primary or secondary producers or values derived from prey consumed at each site, we are limited in our interpretation of niche overlap (i.e. overlap of isotopic niches does not necessarily indicate overlap in resource use; Hette-Tronquart 2019, Matich et al. 2021).

Limitations of stable isotope analyses restrict our ability to detect distinct differences in foraging habitats or the exact species and sizes of consumed prey (Fry 2006, Boecklen et al. 2011). The major groups of forage fish prey in the Northwest Atlantic that terns consume (e.g. sand lance, hake, herring, anchovies, and silversides) are isotopically similar, within 1 or 2‰ difference for both $\delta^{13}C$ and $\delta^{15}N$ values (Estrada et al. 2005, Logan et al. 2015). Different species of fish can exhibit similar $\delta^{13}C$ and $\delta^{15}N$ values at various life stages or body sizes depending on their life histories and ecological traits (Lesage et al. 2001, Logan et al. 2015). Thus, for colonies and years where we found a high degree of isotopic niche overlap, common and roseate terns may still be foraging on distinct prey species, life stages, or sizes of prey. Direct measures of diet are needed to link isotopic niche overlap to relative competition among roseate and common terns, such as visual observations of courtship displays and nuptial gifts to determine prey size, or genomic analysis of feces to determine prey species diversity. Regarding relative foraging location, we do not know how steeply $\delta^{13}C$ gradients change around the islands in this study. If the isotopic gradients within the foraging range are too gradual or if the waters are well-mixed, then roseate and common terns on the same island may forage in locations that are simply not isotopically distinct enough to differentiate. The incorporation of freshwater species in the diet of some individuals may further confound the interpretation of $\delta^{13}C$ in the context of onshore vs. offshore foraging (e.g. Bearhop et al. 1999). Future studies using compound-specific isotope analysis of individual amino acids in eggshell tissues might produce more precise $\delta^{13}C$ values that are distinguishable between foraging locations (Boecklen et al. 2011, Magozzi et al. 2021).

Previous studies tracking roseate terns have found that adults restrict their foraging range to within 15 km of the colony during the incubation and early chick-rearing periods of their lifecycles (Pratte et al. 2021), but foraging range during the pre-breeding period is not known. After the adult terns have reached the breeding colonies post-migration, they forage in the vicinity of colonies to replenish energy reserves, engage in courtship, and build nests, but may be less spatially constrained during this time period (Cabot & Nisbet 2013). Radio-telemetry studies of roseate and common terns (e.g. Loring et al. 2019, Pratte et al. 2021) could inform spatial partitioning or overlap of foraging locations, how foraging range changes from the pre-breeding period to chick rearing, and how partitioning changes with shifting environmental and social conditions. Finally, prey availability can also shift throughout the breeding season (Safina & Burger 1985, Safina et al. 1988). Foraging conditions on an island likely differ for terns nesting earlier in the season compared to later in the season. Stable isotope analysis of tissues collected from terns at high temporal resolution during the season could be used to assess within-season changes in isotope ratios, and isotopic niche breadths and overlap.

4.2. Subregional differences between cold-water and warm-water colonies

We found clear geographic patterns in the stable isotope ratios ($\delta^{13}C$ in 2018, $\delta^{15}N$ in 2018 and 2019) of roseate and common tern eggshell membranes, with higher values in warm-water colonies compared to cold-water colonies. These isotopic subregional differences may be partially explained by subregional differences in foraging ecology, as the cold- and warm-water subregions of the Northwest Atlantic roseate tern population are known to differ in productivity (i.e. average annual number of chicks fledged per breeding pair) and diet (Safina et al. 1990, Goyert 2015, USFWS 2020, Yakola et al. 2022). In particular, previous chick provisioning studies suggest that roseate and common terns in warm-water colonies may have more specialized diets comprised more heavily of sand lance (Kirkham 1986, Safina et al. 1990, Tims et al. 2004, Goyert 2015), while tern diets at the cold-water colonies are more diverse (Hall et al. 2000, USFWS 2010, Yakola et al. 2022). However, we found no difference in isotopic niche breadth between the subregions, suggesting that there is no detectable difference in the dietary diversity of adult terns between cold- and warm-water colonies using stable isotope analysis.

Critically, known geographic trends in isotopic baselines for these subregions (Oczkowski et al. 2016) underly our observed geographic patterns in $\delta^{13}C$ and $\delta^{15}N$ values. Both $\delta^{13}C$ and $\delta^{15}N$ isotopic baselines and isotope ratios of tern eggshell membrane tissues are lower in the cold-water subregion compared to the warm-water subregion. Thus, our results do not necessarily provide evidence of subregional differences in diet or foraging ecology of roseate and common terns in the Northwest Atlantic, as we cannot separate our observed patterns from differences in isotopic baselines. Future studies where isotopic baselines are concurrently collected with tissues from seabirds and their prey are needed to control for baseline geographic pattern in the stable isotope ratios and distinguish inter-regional and inter-island differences in $\delta^{13}C$ and $\delta^{15}N$ values.

Tern $\delta^{13}C$ and $\delta^{15}N$ values from South Monomoy Island, located at the boundary between the cold- and warm-water subregions, were more aligned with the cold-water islands than the warm-water islands. The similarity in $\delta^{15}N$ values specifically may reflect the spatial isotopic baseline patterns in the Northwest Atlantic rather than foraging ecology (Oczkowski et al. 2016). The isotopic niche breadth of roseate terns on South Monomoy Island was unique compared to the other islands. Roseate terns had consistently broader isotopic niche breadths on South Monomoy Island than on the other islands in both years of this study. In addition, while isotopic niche breadths decreased or did not differ in the other 9 colonies from 2018 to 2019, isotopic niche breadth increased on South Monomoy Island. Thus, terns on South Monomoy Island may experience foraging conditions that are distinct from the cold/warm subregions during the post-migration/pre-breeding period. However, given the low numbers of roseate tern breeding pairs on South Monomoy Island (30 in 2018 and 12 in 2019; USFWS 2020), and the low sample size of roseate tern eggshells collected in 2019 ($n = 3$), longer-term analyses of foraging ecology are needed to substantiate the presence of unique foraging conditions on this island.

4.3. Interannual differences between 2018 and 2019

Interpretation of interannual differences in $\delta^{13}C$ and $\delta^{15}N$ values are also complicated by potential temporal shifts in isotopic baselines (due to changes in annual chlorophyll concentrations, continental runoff, or upwelling; Oczkowski et al. 2016). To assess changes in tern resource use, further studies that control for baselines are needed to separate shifts in the $\delta^{13}C$ and $\delta^{15}N$ values of eggshell membranes from spatiotemporal patterns in the environment. While there were no notable range-wide changes in isotopic niche breadth or isotopic niche overlap for adult roseate and common terns, interannual differences in niche breadth and overlap at the individual colony scale suggest that dietary diversity and the degree of resource partitioning between roseate and common terns vary over time within colonies and are likely dependent on local resource availability. These results are consistent with previous stable isotope analyses of adult roseate, common, and arctic tern *Sterna paradisaea* eggshell membranes from the Gulf of Maine, which also found interannual shifts in isotopic niche breadths at the individual colony level between 2016 and 2018 (Bratton et al. 2022).

4.4. How will changes in the prey community affect the roseate–common tern relationship in the NWA?

Warming ocean conditions due to climate change are impacting, and will continue to impact, primary production and the availability of forage fish prey in the NWA (Oczkowski et al. 2016, Staudinger et al. 2019, Pershing et al. 2021). The opportunistic generalist foraging strategy used by common terns should make them more resilient to changes in the environment and the prey community compared to the more specialized roseate terns (Goyert 2015, Thurman et al. 2022). In addition, roseate terns have been shown to be less successful foragers in large, multispecies assemblages with common terns (Safina 1990a) and other non-tern seabird species (Shealer & Burger 1993). However, the relative climate resiliency of tern species has not been well studied. Recent observations in warm-water colonies suggest that roseate terns are comparatively more productive than common terns in years when prey are scarce (C. Mostello, K. Vagos, S. von Oettingen, J. Walsh pers. comm.). Roseate–common tern relationships on shared islands likely depend on the specific composition of the prey community in addition to the relative abundance of particular prey species. Prey scarcity may cause interspecific similarity in isotopic niches as species compete for fewer resources (Newsome et al. 2007, Jessopp et al. 2020). Prey abundance may also cause interspecific similarity in isotopic niches if a high-quality foraging area in the vicinity of a colony strongly attracts both tern species. Longer-term studies are needed to understand the mechanistic links between changing environmental regimes, the prey community, and competition between roseate and common terns. Overall, our results indicate that adult roseate and common terns forage in isotopically similar habitats and on isotopically similar prey, but that isotopic niche partitioning varies across spatial and temporal scales. Such spatiotemporal variation suggests the birds are responding to local prey availability at different colonies and in different years and could indicate some plasticity in foraging behaviors. Thus, the birds may not be uniformly vulnerable to changes in the environment across colonies in their NWA breeding range.

Data archive. Data for this study are publicly available on ScienceBase at doi.org/10.5066/P9LVSGAM.

Acknowledgements. We thank all island managers and technicians who coordinated and collected eggshell samples and provided insights for this project, including Don Lyons and Paula Shannon (NASSI); Kate Iaquinto, Stephanie Koch, Eileen McGourty, Susi von Oettingen, Linda Welch, and Kris Vagos (USFWS); Helen Hays (AMNH); Carolyn Mostello (MA DFW); Margaret Rubega (UCONN); and Joan Walsh (Mass Audubon), and the Isles of Shoals Tern Conservation Program (supported by the New Hampshire Fish and Game Department's Nongame and Endangered Wildlife Program, the USFWS New Hampshire State Wildlife Grants, and the Shoals Marine Laboratory). We are grateful to Lindsay Yue, Rachel Bratton, and Kate Keery for helping prepare samples for analysis and Alex Gerson for use of laboratory space. We thank Rachel Lim for providing insightful feedback on early drafts of the manuscript and Tammy Wilson for conducting an internal USGS review, and we appreciate the constructive comments of 3 anonymous reviews as part of the peer review process. Support for this project was provided by the National Science Foundation INTERN program (through Integrative Organismal Systems 1353326) for H.D.L., the Five College Coastal & Marine Sciences Program, the University of Massachusetts Amherst, the US Department of the Interior, US Geological Survey, and the Northeast Climate Adaptation Science Center. This manuscript is submitted for publication with the understanding that the US government is authorized to reproduce and distribute reprints for governmental purposes. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

LITERATURE CITED

Bearhop S, Thompson DR, Waldron S, Russell IC, Alexander G, Furness RW (1999) Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. J Appl Ecol 36:75–84

Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. Annu Rev Ecol Evol Syst 42:411–440

Bolton M, Conolly G, Carroll M, Wakefield ED, Caldow R (2019) A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment. Ibis 161: 241–259

Bond AL, Diamond AW (2010) Nutrient allocation for egg production in six Atlantic seabirds. Can J Zool 88: 1095–1102

Bond AL, Jones IL (2009) A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. Mar Ornithol 37:183–188

Bratton R, Legett HD, Shannon P, Yakola K, Gerson AR, Staudinger MD (2022) Pre-breeding foraging ecology of three tern species nesting in the Gulf of Maine. Avian Conserv Ecol 17:19

Cabot D, Nisbet I (2013) Terns. Collins, London

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2009) COSEWIC assessment and update status report on the roseate tern *Sterna dougallii* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

Diamond AW, Devlin CM (2003) Seabirds as indicators of changes in marine ecosystems: ecological monitoring on Machias Seal Island. Environ Monit Assess 88:153–181

Duffy DC (1986) Foraging at patches: interactions between common and roseate terns. Ornis Scand 17:47–52

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JR (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. Proc Natl Acad Sci USA 107:2078–2081

Ehrich D, Tarroux A, Stien J, Lecomte N, Killengreen S, Berteaux D, Yoccoz NG (2011) Stable isotope analysis: modelling lipid normalization for muscle and eggs from arctic mammals and birds. Methods Ecol Evol 2:66–76

Estrada JA, Lutcavage M, Thorrold SR (2005) Diet and trophic position of Atlantic bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen isotope analysis. Mar Biol 147:37–45

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Biol 40:503–537

Fry B (2006) Stable isotope ecology. Springer, New York, NY

Gal JK, Choi B, Kim BK, Jung JW and others (2021) Trophic niche of seabirds on the Barton Peninsula, King George Island, Antarctica. Estuar Coast Shelf Sci 258:107443

Genz A, Bretz F (2009) Computation of multivariate normal and *t* probabilities. Springer-Verlag, New York, NY

Goyert HF (2014) Relationship among prey availability, habitat, and the foraging behavior, distribution, and abundance of common terns *Sterna hirundo* and roseate terns *S. dougallii*. Mar Ecol Prog Ser 506:291–302

Goyert HF (2015) Foraging specificity and prey utilization: evaluating social and memory-based strategies in seabirds. Behaviour 152:861–895

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes: understanding movement, pattern and process on Earth through isotope mapping. Springer, Dordrecht, p 299–318

Hall CS, Kress SW, Griffin CR (2000) Composition, spatial and temporal variation of common and arctic tern chick diets in the Gulf of Maine. Waterbirds 23:430–439

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297

Hette-Tronquart N (2019) Isotopic niche is not equal to trophic niche. Ecol Lett 22:1987–1989

Hobson KA (1990) Stable isotope analysis of marbled murrelets: evidence for freshwater feeding and determination of trophic level. Condor 92:897–903

Hobson KA (1995) Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. Condor 97:752–762

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786–798

Hothorn T, Hornik K, Wiel MA, Zeileis A (2008) Implementing a class of permutation tests: the coin package. J Stat Softw 28:1–23

Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology. Ibis 150:447–461

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602

Jenkins EJ, Davoren GK (2021) Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. Ibis 163:183–196

Jessopp M, Arneill GE, Nykänen M, Bennison A, Rogan E (2020) Central place foraging drives niche partitioning in seabirds. Oikos 129:1704–1713

Kimmons JB (2012) Life history variation of common terns in the Gulf of Maine. PhD dissertation, University of Arkansas, Fayetteville, AR

Kirkham IR (1986) Comparative foraging and breeding habits of arctic and common terns. PhD thesis, Dalhousie University, Halifax

Lee WY, Park S, Kim KW, Kim JH, Gal JK, Chung H (2021) Inter-specific and intra-specific competition of two sympatrically breeding seabirds, chinstrap and gentoo penguins, at two neighboring colonies. Animals 11:482

Lesage V, Hammill MO, Kovacs KM (2001) Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. Mar Ecol Prog Ser 210:203–221

Logan JM, Rodríguez-Marín E, Goni N, Barreiro S, Arrizabalaga H, Golet W, Lutcavage M (2011) Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. Mar Biol 158:73–85

Logan JM, Golet WJ, Lutcavage ME (2015) Diet and condition of Atlantic bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine, 2004–2008. Environ Biol Fishes 98:1411–1430

Loring PH, Paton PW, McLaren JD, Bai H and others (2019) Tracking offshore occurrence of common terns, endangered roseate terns, and threatened piping plovers with VHF arrays. OCS Study BOEM 2019-017. Bureau of Ocean Energy Management, Sterling, VA

Magozzi S, Thorrold SR, Houghton L, Bendall VA and others (2021) Compound-specific stable isotope analysis of amino acids in pelagic shark vertebrae reveals baseline, trophic, and physiological effects on bulk protein isotope records. Front Mar Sci 8:673016

Matich P, Bizzarro JJ, Shipley ON (2021) Are stable isotope ratios suitable for describing niche partitioning and individual specialization? Ecol Appl 31:e02392

Maynard LD, Davoren GK (2020) Inter-colony and interspecific differences in the isotopic niche of two sympatric gull species in Newfoundland. Mar Ornithol 48:103–109

Mizutani H, Fukuda M, Kabaya Y, Wada E (1990) Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk 107:400–403

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436

Nisbet ICT (1977) Courtship-feeding and clutch size in common terns *Sterna hirundo*. In: Stonehouse B, Perrins C (eds) Evolutionary ecology. Palgrave, London, p 101–109

Nisbet ICT, Spendelow JA (1999) Contribution of research to management and recovery of the roseate tern: review of a twelve-year project. Waterbirds 22:239–252

Oczkowski A, Kreakie B, McKinney RA, Prezioso J (2016) Patterns in stable isotope values of nitrogen and carbon in particulate matter from the Northwest Atlantic Continental Shelf, from the Gulf of Maine to Cape Hatteras. Front Mar Sci 3:252

Oro D, Pérez-Rodríguez A, Martínez-Vilalta A, Bertolero A, Vidal F, Genovart M (2009) Interference competition in a threatened seabird community: a paradox for a successful conservation. Biol Conserv 142:1830−1835

Pershing AJ, Alexander MA, Brady DC, Brickman D and others (2021) Climate impacts on the Gulf of Maine ecosystem: a review of observed and expected changes in 2050 from rising temperatures. Elem Sci Anthropocene 9:00076

Polito MJ, Fisher S, Tobias CR, Emslie SD (2009) Tissue-specific isotopic discrimination factors in gentoo penguin (*Pygoscelis papua*) egg components: implications for dietary reconstruction using stable isotopes. J Exp Mar Biol Ecol 372:106−112

Polito MJ, Lynch HJ, Naveen R, Emslie SD (2011) Stable isotopes reveal regional heterogeneity in the pre-breeding distribution and diets of sympatrically breeding *Pygoscelis* spp. penguins. Mar Ecol Prog Ser 421:265−277

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179−189

Pratte I, Ronconi RA, Craik SR, McKnight J (2021) Spatial ecology of endangered roseate terns and foraging habitat suitability around a colony in the western North Atlantic. Endang Species Res 44:339−350

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rader JA, Newsome SD, Sabat P, Chesser RT, Dillon ME, Martínez del Rio C (2017) Isotopic niches support the resource breadth hypothesis. J Anim Ecol 86:405−413

Richards SW, Schew WA (1989) Species composition of food brought to roseate tern chicks on Falkner Island, Connecticut in summer 1984. Conn Warbler 9:1−5

Robertson GS, Bolton M, Grecian WJ, Wilson LJ, Davies W, Monaghan P (2014) Resource partitioning in three congeneric sympatrically breeding seabirds: foraging areas and prey utilization. Auk 131:434−446

Safina C (1990a) Foraging habitat partitioning in roseate and common terns. Auk 107:351−358

Safina C (1990b) Bluefish mediation of foraging competition between roseate and common terns. Ecology 71: 1804−1809

Safina C, Burger J (1985) Common tern foraging: seasonal trends in prey fish densities and competition with bluefish. Ecology 66:1457−1463

Safina C, Burger J, Gochfeld M, Wagner RH (1988) Evidence for prey limitation of common and roseate tern reproduction. Condor 90:852−859

Safina C, Wagner RH, Witting DA, Smith KJ (1990) Prey delivered to roseate and common tern chicks; composition and temporal variability (Entrega de alimento a polluelos de *Sterna dougallii* y *S. hirundo*: composición y variabilidad temporal). J Field Ornithol 61:331−338

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27−39

Scopel LC, Diamond AW (2018) Predation and food−weather interactions drive colony collapse in a managed metapopulation of Arctic terns (*Sterna paradisea*). Can J Zool 96:13−22

Shealer DA, Burger J (1993) Effects of interference competition on the foraging activity of tropical roseate terns. Condor 95:322−329

Spendelow JA, Mostello CS, Nisbet IC, Hall CS, Welch L (2010) Interregional breeding dispersal of adult roseate terns. Waterbirds 33:242−245

Staudinger MD, Mills KE, Stamieszkin K, Record NR and others (2019) It's about time: a synthesis of changing phenology in the Gulf of Maine ecosystem. Fish Oceanogr 28:532−566

Staudinger MD, Goyert H, Suca JJ, Coleman K and others (2020) The role of sand lances (*Ammodytes* sp.) in the Northwest Atlantic Ecosystem: a synthesis of current knowledge with implications for conservation and management. Fish Fish 21:522−556

Thurman LL, Gross JE, Mengelt C, Beever EA and others (2022) Applying assessments of adaptive capacity to inform natural-resource management in a changing climate. Conserv Biol 36:e13838

Tims J, Nisbet ICT, Friar MS, Mostello C, Hatch JJ (2004) Characteristics and performance of common terns in old and newly-established colonies. Waterbirds 27: 321−333

USFWS (US Fish and Wildlife Service) (1987) Endangered and threatened wildlife and plants: determination of endangered and threatened status for two populations of the roseate tern. Fed Regist 52:42064−42071

USFWS (2010) Caribbean roseate tern and North Atlantic roseate tern (*Sterna dougallii dougallii*) 5-year review: summary and evaluation. USFWS, Concord, NH

USFWS (2020) Roseate tern Northeastern North American population (*Sterna dougallii dougallii*) 5-year review: summary and evaluation. USFWS, Concord, NH

USGS (U.S. Geological Survey) (2017) State wildlife action plans (SWAP). https://www1.usgs.gov/csas/swap/ (accessed 12 April 2022)

Yakola K, Jordaan A, Kress SW, Shannon P, Staudinger MD (2022) Interspecific and local variation in tern chick diets across nesting colonies in the Gulf of Maine. Waterbirds 44:397−414

Yeakel JD, Bhat U, Elliott Smith EA, Newsome SD (2016) Exploring the isotopic niche: isotopic variance, physiological incorporation, and the temporal dynamics of foraging. Front Ecol Evol 4:1

Editorial responsibility: Rory Wilson,
Swansea, UK
Reviewed by: A. D. Lowther and 3 anonymous referees

Submitted: April 23, 2022
Accepted: February 23, 2023
Proofs received from author(s): March 28, 2023