Interspecific and Local Variation in Tern Chick Diets Across Nesting Colonies in the Gulf of Maine

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Abstract.—The Gulf of Maine, USA is home to four colonial co-nesting tern species: Least Tern (*Sternula antillarum*), Common Tern (*Sterna hirundo*), Arctic Tern (*Sterna paradisaea*), and the federally endangered Roseate Tern (*Sterna dougallii*). Over three decades of visual observations of chick provisioning were compiled for a comparative dietary study in the region, including the first detailed descriptions of Least and Roseate Tern chick diets. Three prey groups comprised the majority of chick diets among tern species between 1986–2017: hake (*Urophycis* spp. *or Enchelyopus cimbrius*) 28–37% frequency of occurrence (FO), sand lance (*Ammodytes americanus or A. dubius*) 8–22% FO, and herring (*Clupea* spp. *or Alosa* spp.) 3–30% FO. Dietary contributions varied across species and islands. At two inshore colonies, Common Tern diets contained higher amounts of sand lance (30–42% FO), while offshore islands contained lesser amounts (5–9% FO). Overall dietary diversity (H′) was similar between Common (H′ = 1.57) and Arctic Terns (H′ = 1.74) and notably lower in Roseate (H′ = 1.24) and Least Terns (H′ = 1.37), whose diets were primarily piscivorous. The degree of dietary plasticity and general feeding ecology provided by baseline dietary information can inform holistic assessments of risk to ongoing and future disturbances from fishing and climate change. *Received 12 June 2020, accepted 11 Nov 2021.*

Key words. —Arctic Tern, climate change, Common Tern, Gulf of Maine, hake, herring, Least Tern, long-term diet, Roseate Tern, sand lance.

Loss of biodiversity is threatening global ecosystems (Díaz *et al.* 2006) as current extinction exceeds the historical background rate by 10–1000 fold (Barnosky *et al.* 2011). Species losses have been associated with climate change, hunting, overharvest of prey, invasive species, and habitat degradation (Lotze and Milewski 2004). Seabirds have been particularly impacted due to the historical harvest of eggs and hunting for the millinery trade and human consumption (Lotze and Milewski 2004). In response to century-long declines and extirpations, successful restoration activities have been implemented throughout the world (Jones and Kress 2012). Yet, over the past several decades, the acceleration of climate change impacts has become a primary concern, especially to long distant migrants and habitat or foraging specialists, which are particularly vulnerable to these disturbances (Hof *et al.*

2017). Basic natural history data, including a knowledge of ecological niche breadth, are important factors in determining a species' resilience to further disturbances and environmental change (Hof *et al.* 2017; Foden *et al.* 2013).

Many seabirds form large multi-species nesting colonies and are centralized, place-based foragers during the breeding season (Orians and Pearson 1979; Cabot and Nisbet 2013). These assemblages provide a unique opportunity to study trophic interactions, shifting phenology, and potential resource mismatches across local, regional, and even global scales (Nisbet 1989; Diamond and Devlin 2003; Sydeman *et al.* 2017; Moore and Kuletz 2018). Seabirds are also good model organisms to investigate how sympatric species partition their environment under different environmental conditions and population densities (Ashmole and Ashmole

1967; Pearson 1968; Diamond 1983; Surman and Wooller 2003). Further, geographic variation in diets (e.g., dietary diversity) serves as an indicator of foraging plasticity and adaptive capacity at the species-level (Beever *et al.* 2016; Evans & Moustakas 2018).

Terns are a widely distributed group of seabirds, with forty-five species in the sub-family *Sterninae* occurring from pole to pole (Bridge *et al.* 2005). Terns are social feeders, often forming large flocks (Cabot and Nisbet 2013; Goyert 2015). Medium and small terns in the genus *Sterna* and *Sternula* forage at the water's surface by plunge diving or dipping their bill and can only access prey in the top 60 cm of the water column (Cabot and Nisbet 2013). They may also "hawk" terrestrial invertebrates out of the air or pluck marine invertebrates off the water's surface. Terns often forage within only a 10 km radius of their nesting site, but in some cases may travel as far as 30 km and perhaps further (Cabot and Nisbet 2013; Unpublished Data Maine Coastal Islands National Wildlife Refuge). Because terns generally capture a single prey item in a foraging bout, this limits the distance an individual can travel when provisioning young to make the journey energetically worthwhile and reduces the time chicks are unattended and exposed to weather and predation (Emlen 1966; Cabot and Nisbet 2013).

Four co-nesting tern species, the Least Tern (*Sternula antillarum*), Common Tern (*Sterna hirundo*), Arctic Tern (*Sterna paradisaea*), and Roseate Tern (*Sterna dougallii*) migrate to breed and raise their young in the Gulf of Maine, USA (hereafter, GoM) during late spring and summer. The GoM is a temperate semi-enclosed system characterized by high productivity that has served as a historically important seasonal foraging and breeding area for a diversity of migratory fishes, marine mammals, and colonial nesting seabirds. However, the region is rapidly warming, driven by oceanographic and climatic processes (Mills *et al.* 2013; Pershing *et al.* 2015; Thomas *et al.* 2017), which have already resulted in shifts in forage fish distribution and phenology (Nye *et al.* 2009; Walsh *et al.* 2015; Staudinger *et al.* 2019; Per-

shing *et al.* 2021). A recent regional climate change vulnerability assessment suggested that seabirds are highly sensitive to changes in prey availability, particularly during the breeding season when they are tightly linked to nesting colonies (Whitman *et al.* 2013); however, uncertainty remains on how adaptable terns are to these fluctuating prey conditions, particularly for species where basic dietary information remains undescribed. The GoM is currently the northern extent of Least Tern's breeding range (Thompson *et al.* 2020) and the most southerly limit of the holarctic breeding range of Arctic Terns (Hatch *et al.* 2020). With the near disappearance of breeding Arctic Terns south of the GoM (Mostello *et al.* 2016), the GoM assemblage of breeding terns is unique, and offers the opportunity for a multispecies comparative study. While individual and paired comparisons have been conducted at a few locations (e.g., Burroughs 1966; Hall *et al.* 2000; Rock *et al.* 2007a,b), no studies to date have simultaneously evaluated chick diets across all four of these co-occurring tern species in the region.

To better understand dietary flexibility and foraging niche overlap among the four co-nesting species of terns in the GoM, we quantified and compared chick diet composition across seven nesting islands over a 32-year period. On a regional scale, we hypothesized that if terns were adaptive to changing prey conditions, diets would vary based on local prey availability; however, if foraging behavior was highly specialized (i.e. low adaptive capacity), then diets would show stability (low variance) across sites. Based on previous studies conducted in the northwest Atlantic, at the species level we expected Common Terns to have diverse diets relative to other tern species (Hall *et al.* 2000; Rock *et al.* 2007b), Roseate Terns to specialize on sand lances (*Ammodytes* spp.) (Safina *et al.* 1990a; Goyert 2015; Staudinger *et al.* 2020), and Arctic Tern diets to contain higher amounts of marine invertebrates and hake (*Urophycis and Enchelyopus* spp.) (Hall *et al.* 2000). Lastly, we predicted Least Tern diets would be comprised of more estuarine fishes compared to other terns in the region,

primarily due to their affinity towards nesting at coastal beaches and inshore islands.

Methods

Diet Data Collection

Tern chick provisioning data were collected by the National Audubon Society Seabird Institute on Stratton Island, Outer Green Island, Jenny Island, Pond Island National Wildlife Refuge (hereafter, NWR), Eastern Egg Rock, Matinicus Rock, and Seal Island NWR (Fig. 1, Table 1). All seven islands are closely monitored and managed during the nesting season for chick provisioning, productivity and growth. Survey years varied among species and study islands (Table 1), spanning 1986–2017. Approximately 16 nests per tern species on each island were selected annually for chick provisioning studies based on their proximity to bird blinds. Typically, the 16 nests were split between two bird blinds in separate areas of each colony. Data were collected at varying hours throughout the day, though most observations occurred during the morning hours, which is typically the most active foraging period. Observations began when chicks hatched and continued until fledging, about three to four weeks later. A unique number and color code was assigned to each nest that distinguishes it from surrounding nests. During the chick-rearing period, nests were observed for four, three-hour stints per week. Following a feeding, observers record the time and prey species delivered to each nest and chick. These protocols were standardized across decades, and staff were trained annually on methods and prey identification.

Diet data were standardized as percent frequency of occurrence (% FO), the number of observations of each prey group or species divided by the total number of observations for each year. The tern species in this study typically deliver a single prey item during each feeding, thus each prey delivery was treated as an independent observation. On the few occasions when multiple prey items were delivered during a feeding delivery (< 1% of all deliveries), each item was counted as separate prey observation in % FO. Prey species and groups were adapted from Hall *et al.* (2000). Intraspecific geographic variation in chick diet was calculated by group mean % FO values for all tern species-island combinations.
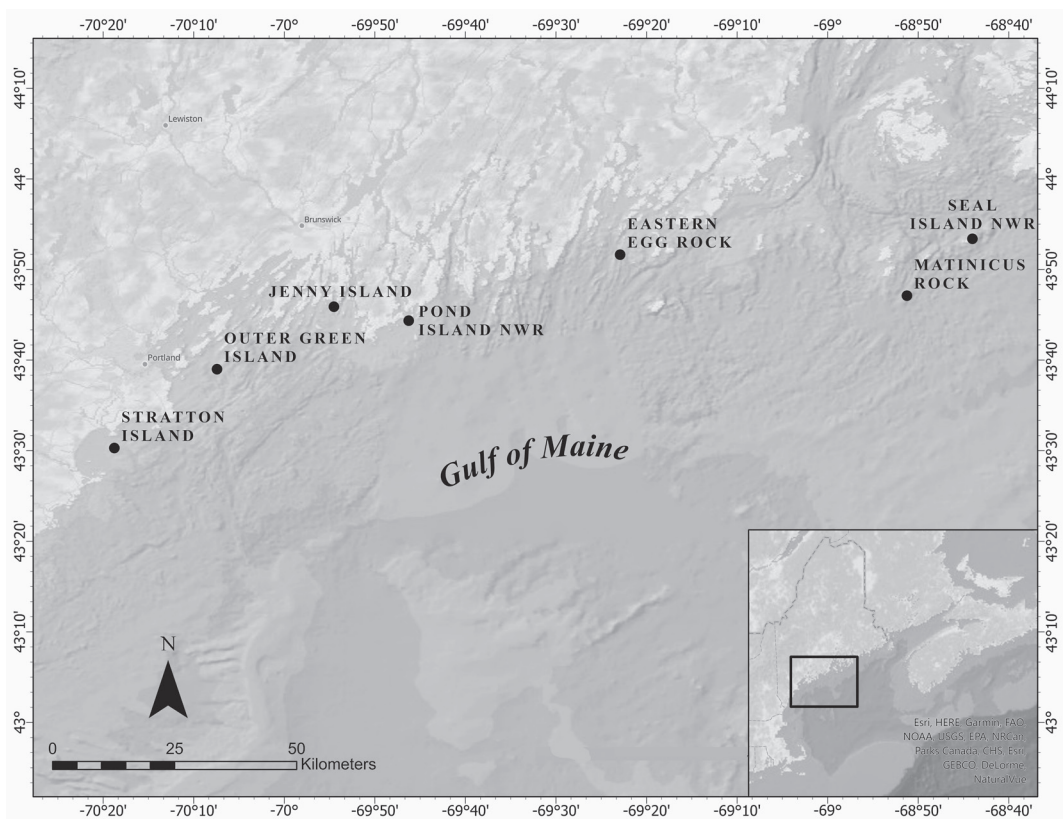

Figure 1. Study area map with inset of the Gulf of Maine coastline in the northeastern portion of the United States. Stratton Island, Outer Green Island, Jenny Island, and Eastern Egg Rock are managed by the National Audubon Society Seabird Institute. Pond Island National Wildlife Refuge (NWR), Matinicus Rock, and Seal Island NWR are managed in collaboration with and owned by the USFWS Maine Coastal Islands NWR.

Table 1. Summary of data collection efforts across islands and species, island coordinates, proximity to shore (inshore < 5 km, nearshore 5–10 km, and offshore > 10 km from shore) in the Gulf of Maine, 1986–2017.

Island	Coordinates	Proximity	Species	Time Series	No. Years of Data
Seal Island NWR	43°53'33"N 68°43'58"W	Offshore	Arctic Tern	1990–2017	28
			Common Tern	1992–1993, 1996, 2003–2017	18
Matinicus Rock	43°47'01"N 68°51'19"W	Offshore	Arctic Tern	1986–2017	32
			Common Tern	2003–2017	15
Eastern Egg Rock	43°51'40"N 69°22'56"W	Nearshore	Arctic Tern	1990–1991, 1993–1995, 2002–2017	20
			Common Tern	1988–1992, 1994–2017	29
			Roseate Tern	1990–1995, 1999–2017	25
Pond Island NWR	43°44'22"N 69°46'15"W	Inshore	Common Tern	1999–2010, 2012–2017	18
Jenny Island	43°45'54"N 69°54'30"W	Inshore	Common Tern	1991–2017	27
			Roseate Tern	2007, 2012, 2016–2017	4
Outer Green Island	43°38'59"N 70°07'26"W	Nearshore	Common Tern	2003–2017	15
			Roseate Tern	2005, 2007	2
Stratton Island	43°30'15"N 70°18'43"W	Inshore	Common Tern	1988–1992, 1994–2017	29
			Least Tern	2006–2014, 2016–2017	11
			Roseate Tern	1990, 1993, 1995, 1999 – 2002, 2004, 2006–2017	20

Dietary Diversity

Dietary niche width was evaluated for each tern species-island combination by calculating the Shannon Diversity Index (H′) using the 'diversity' function (Oksanen *et al.* 2018) in R (R Core Team 2021):

$$H' = \Sigma[pi \log(pi)]\Sigma[pi \log(pi)]$$

Where p_i is the count of the prey in the diet belonging to the ith prey taxon (Shannon and Weaver 1949). Differences among each tern species-island combination were evaluated with a one-way analysis of variance (ANOVA) with a Tukey's Test of Honest Significance using R.

Regional Community Analysis

To evaluate variation across the GoM tern community, we used a hierarchal cluster analysis (CA; McGarigal *et al.* 2000a; Vihtakari *et al.* 2018), grouping tern-species-island combinations, independent of year, into clusters based on similarities in the mean % FO of each major prey species or group. A Bray-Curtis dissimilarity matrix (vegdist in Oksanen *et al.* 2018) with Ward's clustering criterion (Ward 1963) was employed using the 'hclust' function in R. To visualize clusters within the multidimensional data matrix of prey groups, data were plotted using non-metric multidimensional scaling (nMDS), in R's 'metaMDS' package (Oksanen *et al.* 2018).

Interspecific Analysis

To detect patterns of mean % FO across prey groups, we used a Principal Component Analysis (PCA, McGarigal *et al.* 2000b), 'prcomp' in R. We retained the mean % FO for each year to maximize the observed variation in diet at the species and island levels; however, interannual variation was not assessed and was beyond the scope of the present study. Two outliers (Common Terns on Jenny Island in 1992 and Roseate Terns on Eastern Egg Rock in 1992) were dropped from the PCA, as they were found to be over-influencing results due to the unusually high percentages of pollock observed in the diets of those tern species, island, year combinations. The first and second principal components were plotted using 'ggbiplot' (Vu 2011). We visualized dietary niches with color-coded ellipses for each tern species representing one standard deviation from the mean using 'ellipse.prob' (Vu 2011). To test for dietary variation among tern species, we used pairwise permutational multivariate analysis of variance (PerMANOVA), 'pairwise.perm.manova' (Hervé 2018), using 10,000 permutations (Anderson 2001).

Across Island Intraspecific Analysis

PerMANOVAs using 10,000 permutations tested if diet varied within tern species respective to individual nesting islands. Intraspecific differences in diets were compared across all seven islands for Common Terns, across three islands for Arctic Terns (Eastern Egg Rock, Matinicus Rock, and Seal), and across four islands (Stratton, Outer Green, Jenny, and Eastern Egg Rock) for Roseate Terns. Least Tern diet was not tested with this method because they only nested on Stratton Island.

RESULTS

Overall Dietary Composition and Diversity

Common Tern. We recorded 160,004 prey observations between 1988–2017 (Table 2; see online Appendix 1 for full dietary details) across seven islands. Common Terns had a relatively large dietary diversity (H′ = 1.57), and the greatest prey species richness overall, including 30 fish species (88% FO) and 16 invertebrate taxa (8% FO; Table 2, Fig. 2). Hake (*Uriphycsis* spp. or *Enchelyopus cimnrius*, 26% FO), herring (*Clupea* spp. or *Alosa* spp., 24% FO), and sand lance (*Ammodytes americanus* or *A. dubius*, 14% FO) collectively comprised 64% FO of total Common Tern chick diet (Table 2, online Appendix 1). Other fishes observed in Common Tern chick diet included butterfish (*Peprilus triacanthus*), Atlantic pollock (*Pollachius virens*), lumpfish (*Cyclopterus lumpus)*, three-spined stickleback (*Gasterosteus aculeatus)*, Atlantic silverside (*Menidia menidia*), rosefish (*Helicolenus dactylopterus)*, cunner (*Tautogolabrus adspersus)*, and rock gunnel (*Pholis gunnellus)* (< 2% FO for each species, Table 2). Tomcod (*Microgadus tomcod*), red hake (*Urophycis chuss*), American eel (*Anguilla rostrataI*), smelt (*Osmerus mordax*), and moonfish (*Vomer setapinnis*) were rare and unique to the diet of Common Terns. Common Terns also provided their chicks small amounts of invertebrates including euphausiids (3% FO) and amphipods (1% FO). Additionally, Common Terns provisioned marine isopods, as well as small quantities of terrestrial insects including ants, moths and beetles (< 2% FO, Table 2).

Arctic Tern. Arctic Tern diet included 88,315 prey observations of 25 fishes (63% FO) and 15 invertebrates between 1986–2017 (30% FO, Table 2, online Appendix 1). Dietary diversity (H′ = 1.64) was similar to Common Terns (Fig. 2, p = 0.611), but significantly greater than both Least (p = 0.016) and Roseate Terns p = < 0.001*)*. Hake was the

Table 2. Regional diet composition for each tern species across all years (1986–2017) and islands (7) in the Gulf of Maine. *n* = the number of observations of each prey item. %FO = the frequency of occurrence of each prey group, or species, divided by the total observations for each year. A full table including all "Other Fish" and "Other Invertebrate" is available in supplemental online Appendix 1.

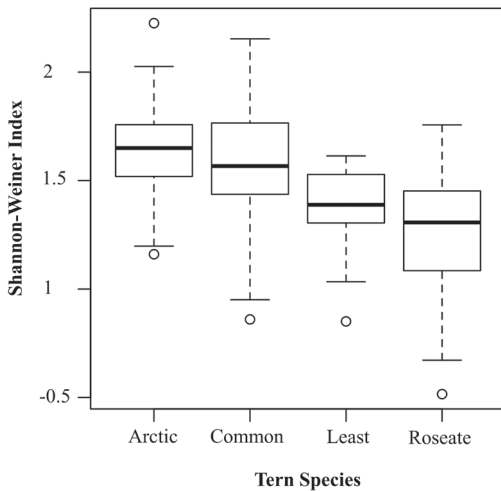| Major Fishes		Common Tern		Arctic Tern		Roseate Tern		Least Tern	
		n	%FO	n	%FO	n	%FO	n	%FO
Hake	*Urophycis* spp. *& Enchelyopus cimbrius*	41,934	26	33,530	38	5,388	26	2,984	41
Herring	*Clupea & Alosa* spp.	39,028	24	7,228	8	2,508	12	858	12
Sand lance	*Ammodytes* spp.	22,291	14	2,670	3	7,593	37	1,821	25
Pollock	*Pollachius virens*	3,739	2	262	<1	512	2	19	<1
Butterfish	*Peprilus triacanthus*	5,825	4	2,342	3	126	1	1	<1
Other Fish		5,077	3	1,496	2	114	1	655	9
Unknown Fish	*Not Identified to Species*	22,329	14	7,821	9	3,653	18	881	12
Total Fish Observations		**140,223**	**88**	**55,349**	**63**	**19,894**	**96**	**7,219**	**98**
Major Invertebrates									
Amphipod	*Amphipoda* spp.	2,385	1	15,585	18	17	<1	25	<1
Euphausiid	*Euphausia* spp.	5,122	3	7,146	8	3	<1	0	0
Other Invertebrate		3,809	2	2,514	3	10	<1	11	<1
Unknown Invertebrate	*Not Identified to Species*	1,616	1	1,653	2	15	<1	19	<1
Total Invertebrate Observations		**12,932**	**8**	**26,898**	**30**	**45**	**<1**	**55**	**1**
Unknown	*Not Identified to Fish or Invertebrate*	6,849	4	6,068	7	700	3	64	1
Total Prey Observations		**160,004**		**88,315**		**20,639**		**7,338**	

Figure 2. Boxplot of the Shannon-Weiner Diversity Index by tern species; Arctic Tern, Common Tern, Roseate Tern, and Least Tern. The box represents the interquartile range, the bold line in the center of the box represents the median, and the whiskers represent 1.5 times the interquartile range.

most commonly observed prey group (38% FO) and other fishes including herring, sand lance, pollock and butterfish each contributed < 9% FO to chick diet (Table 2). Small amounts of three-spined stickleback, lumpfish, snipefish (*Macroramphosus scolopax*), and goosefish (*Lophius americanus*) represented occasionally observed prey items (< 2% FO). Compared to the other three tern species in this study, Arctic Terns provisioned the largest quantities of invertebrates (30% FO) overall. Marine amphipods (18% FO) and euphausiids (8% FO) were most common, while polycheates, squid, terrestrial insects (ants, and moths) were observed in small quantities (< 2 % FO, Table 2).

Roseate Tern. Roseate Tern chick diet included 19 fishes and 7 invertebrates in 20,639 prey observations between 1990–2017 (Table 2, online Appendix 1). Roseate Tern diet was almost exclusively piscivorous (96% FO) and invertebrates were rarely provisioned (< 1% FO, Table 2). Sand lance, hake and herring were most frequently provisioned and comprised 75% FO of total chick diet. This strong reliance on only three prey species led to the lowest dietary diversity of all tern species examined in this

study (H′ = 1.24, Fig. 2); significantly less than both Common ($p = < 0.001$) and Arctic terns ($p = < 0.001$). Other fish species were rarely observed, but included bluefish (*Pomatomus saltatrix*), Atlantic saury (*Scomberesox sarus*) and filefish (*Monacanthus hispidus*), all ≤ 1% FO (Table 2).

Least Tern. Least Tern chick diet consisted of eight fishes (98% FO) and five invertebrates (1% FO) recorded in 7,338 prey observations on Stratton Island between 2006–2017 (Table 2, online Appendix 1). Dietary diversity was relatively low (H′ = 1.37, Fig. 2), but only significantly different from Arctic terns ($p = 0.016$). The majority (78% FO) of Least Tern diet was comprised of three species groups: hake (41%), sand lance (25%), and herring (12%). Killifish (*Fundulus* spp., 8% FO) was the most common prey species in the "other fish" category. Overall, invertebrates were rarely observed in Least Tern diet (< 1% FO; Table 2).

Regional Community Analysis

Three distinctive groups, or clusters, were identified across all island-tern species combinations (Table 3). The first cluster contained Common Terns from Eastern Egg Rock, Outer Green, Jenny and Seal Island, and Roseate Terns from Eastern Egg Rock. This cluster was defined by a high mean per-

Table 3. Percent prey means derived from a hierarchal cluster analysis. Clusters are defined by differences in these means and tern species-island combinations are placed in each cluster based on their respective diets.

Fishes	Cluster 1	Cluster 2	Cluster 3
Sand lance	3.7	4.7	36.0
Hake	33.0	36.8	25.3
Herring	25.0	6.7	14.6
Butterfish	3.5	4.4	0.7
Pollock	3.2	1.0	0.6
Other Fish	3.0	2.4	2.3
Unknown Fish	14.5	9.8	15.6
Invertebrates			
Euphausiid	6.1	7.9	0.2
Amphipod	1.3	14.6	0.4
Other Invertebrate	1.7	2.5	0.1
Unknown Invertebrate	0.5	2.6	0.6
Unknown	4.3	6.5	2.7

centage of hake (33%) and herring (25%), and low percentages of sand lance (3.7%) and amphipods (1.3%; Fig. 3). The second cluster consisted of Arctic Terns from Matinicus Rock, Eastern Egg Rock, and Seal Island, and Common Terns from Matinicus Rock. This cluster was characterized by relatively high percentages of hake (36.8%), amphipods (14.6%), and euphausiids (7.9%; Table 3). The three island-species combinations that included Arctic Terns were in cluster two, with large amounts of invertebrates.
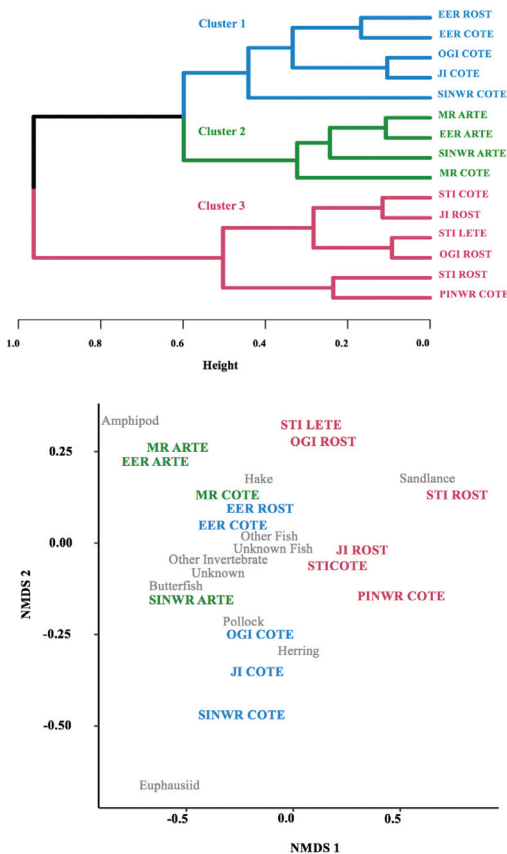

Figure 3. Hierarchical cluster analysis (CA; top) and nonmetric multidimensional scaling plot (NMDS; bottom) using the frequency of occurrence (%FO) of major prey species and groups in diet combinations of tern species, island, and year (*n* = 291). CA was used to define groups, shown as cluster 1, 2 and 3 and the colors of each cluster correspond with the NMDS; bottom plot. Common Tern (COTE), Arctic Tern (ARTE), Roseate Tern (ROST), and Least Tern (LETE). Stratton Island (STI). Outer Green Island (OGI), Jenny Island (JI), Pond Island NWR (PINWR), Eastern Egg Rock (EER), Matinicus Rock (MR), Seal Island NWR (SINWR).

Cluster three was defined by higher amounts of sand lance (36%) compared to clusters one and two (Table 3), and notably different dietary means (Fig. 3).

Interspecific Analysis

The sum of the first two principal components explained 31.89% of variation in diet data across all possible combinations of species-island-year combinations (online Appendix 1). The first principal component (PC1) explained 18.31% of the variance and with high loadings for sand lance and herring, and low loadings for hake and invertebrates. The second principal component (PC2) explained 13.50% of the variance, with high loadings on sand lance and low loadings for hake and pollock (Fig. 4, online Appendix 1).

Arctic Tern chick diet was associated with lower loadings on PC1 and less variation across PC2 (Fig. 4), suggesting invertebrates and hake, rather than sand lance or herring, are dominant prey items. Roseate and Least Tern diets were similar, with most variation across PC2 driven by high loadings on sand lance, low-loadings on hake and pollock, and nearly all data points positively correlated on PC1 (Fig. 4). Common Tern chick diet varied widely across both PC1 and PC2 suggesting they forage on a wider variety of prey items compared to the other three tern species.

Significant differences were detected between all combinations of Common, Arctic, and Roseate Tern chick diets. Least Tern diet was significantly different than Arctic and Common Terns but not statistically different than Roseate Terns ($p = 0.803$), most likely due to less invertebrate prey for Least and Roseate Terns compared to others.

Intraspecific Analysis

Common Tern. Significant intraspecific differences in chick diet were identified for Common Terns among most combinations of islands. Exceptions included Outer Green Island and Eastern Egg Rock ($p = 0.059$), Jenny and Outer Green Island ($p = 1.0$), as
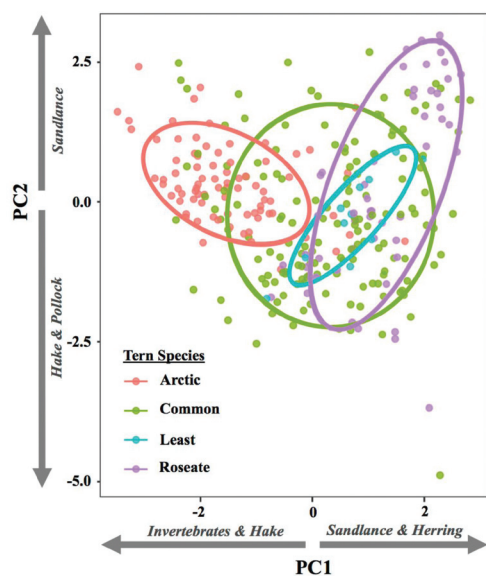
Figure 4. Principal Components Analysis bi-plot of the first (x-axis) and second (y-axis) components of the model. Annotations of prey group or species along each axis are derived from the loadings on each principal component listed in supplemental online Appendix 1. Each probability ellipse represents tern chick diet around one standard deviation from the mean. Each point and ellipse is color coded by tern species found in the figure legend.

well as Seal Island and Matinicus Rock ($p = 0.063$). Eastern Egg Rock, Jenny, Seal, and Outer Green Islands grouped together likely due to a shared lack of sand lance and high amounts of hake and herring (Table 4). The greatest amounts of invertebrates were provisioned on Matinicus Rock and Seal Island compared to all other islands with hake the most common fish (Table 4). Although Pond and Stratton Islands grouped together, diets were significantly different ($p = 0.019$). Sand lance was a shared feature for Stratton and Pond Islands, although hake was more important on Stratton Island and herring more important on Pond Island (Table 4).

Arctic Tern. Arctic Terns in this study foraged on similar amounts of fishes and invertebrates across all three islands (Table 5). However, intraspecific differences in diet were detected between Seal Island and Matinicus Rock in addition to Seal Island and Eastern Egg Rock ($p = < 0.001$), but not between Matinicus Rock and Eastern Egg Rock ($p = 0.559$). The Arctic Tern diet on Seal Island included much higher amounts of euphausiids compared to Matinicus Rock and Eastern Egg Rock (Table 5) as well as more herring compared to Matinicus Rock and Eastern Egg Rock. Additionally, similar amounts of hake and amphipods were found on Matinicus Rock and Eastern Egg Rock (Table 5). Despite some of these differences, all three Arctic Tern-island combinations were grouped together in cluster two (Fig. 3).

Roseate Tern. Roseate Tern diets differed between Jenny Island and Eastern Egg Rock ($p = 0.004$) as well as Stratton Island and Eastern Egg Rock ($p = 0.001$), but not between Eastern Egg Rock and Outer Green Island, Jenny Island and Outer Green Island, Jenny Island and Stratton Island, or Outer Green Island and Stratton Island ($p > 0.05$). Roseate Terns from Stratton Island, Jenny Island and Outer Green Island grouped together; however, Roseate Terns from Eastern Egg Rock were placed in a different cluster (Fig. 3). Eastern Egg Rock diet was dominated by hake and relatively small amounts of sand lance (Table 6), whereas diets on Stratton Island, Jenny Island and Outer Green Island contained higher frequencies of sand lance (Table 6). Herring was provisioned to chicks in higher amounts on Outer Green Island, Jenny Island, and Eastern Egg Rock compared to Stratton Island (Table 6).

DISCUSSION

This study provides new insights into tern chick diets, spanning across three decades and seven islands at mixed tern colonies in the GoM. Dietary analyses of Least Terns are the first in the region, and one of the few across the broader northwest Atlantic (Burroughs 1966). Comprehensive analysis of Roseate Tern chick diets at northern latitudes has also been scarce (but see Rock *et al.* 2007a for a report from Nova Scotia, Canada); consequently, this work fills a knowledge gap in Roseate Tern foraging ecology in the GoM and provides a comparative dataset for better known areas to the

Table 4. Summary of Common Tern chick diet by island. Values represent the mean percent frequency of occurrence (%FO) ± 1 SD rounded to nearest decimal.

Fishes	Stratton Island %FO ±SD	Outer Green Island %FO ±SD	Jenny Island %FO ±SD	Pond Island NWR %FO ±SD	Eastern Egg Rock %FO ±SD	Matinicus Rock %FO ±SD	Seal Island NWR %FO ±SD
Hake	24.1 ± 13.3	31.8 ± 12.5	28.8 ± 15.3	10.4 ± 10.9	42.1 ± 11.1	34.3 ± 15.6	21.0 ± 12.4
Sand lance	29.7 ± 17.2	3.8 ± 10.7	3.3 ± 3.9	42.3 ± 15	1.7 ± 2.3	9.2 ± 15.8	4.7 ± 10.3
Herring	16.4 ± 13.7	31.5 ± 16.1	36.8 ± 14	20.7 ± 14.7	18.3 ± 13	6.2 ± 9.5	20.2 ± 18.5
Butterfish	2.1 ± 3.5	4.2 ± 5.3	2.7 ± 4.5	<1 ± 1.5	5.9 ± 8.6	10.0 ± 10.9	5.9 ± 10.5
Pollock	1.0 ± 2.1	1.8 ± 2.6	4.3 ± 6.9	<1 ± <1	2.6 ± 2.6	3.2 ± 3.1	1.5 ± 1.6
Unknown Fish	15.6 ± 8.8	14.7 ± 5.5	13.8 ± 7.7	13.8 ± 7.7	14.9 ± 6.8	13.2 ± 6.7	11.1 ± 6.7
Other Fish	1.2 ± 1.3	4.4 ± 4.7	4.4 ± 3.5	1.6 ± 2.3	3.1 ± 2.4	4.4 ± 2.6	2.2 ± 1.9
Total Fishes	**90.4**	**92.1**	**92.9**	**90.6**	**88.6**	**77.5**	**66.8**
Invertebrates							
Amphipod	1.7 ± 4.6	2.2 ± 2.7	<1 ± 1.5	<1 ± <1	2.7 ± 5.5	3.1 ± 3.2	1.2 ± 1.4
Euphausiid	<1.0 ± <1.0	<1.0 ± <1.0	<1.0 ± 1.2	1.0 ± 2.8	<1.0 ± <1.0	7.5 ± 12.4	23.1 ± 26.7
Other Invertebrate	1.5 ± 1.6	1.7 ± 2.4	2.2 ± 2.7	2.9 ± 4.3	3 ± 3.8	2 ± 2.5	1.3 ± 1.0
Unknown Invertebrate	2.1 ± 7.7	<1.0 ± <1.0	<1.0 ± <1.0	1.2 ± 2.2	1.0 ± 1.6	2.3 ± 2.7	1.1 ± 1.4
Total Invertebrates	**5.6**	**4.9**	**3.8**	**5.4**	**6.8**	**14.8**	**26.7**
Unknown	**4 ± 3.0**	**3 ± 2.1**	**3.3 ± 3.2**	**4 ± 3.8**	**4.7 ± 4.5**	**4.7 ± 3.7**	**6.5 ± 4.0**
Dietary Diversity	**1.56 ± 0.22**	**1.60 ± 0.26**	**1.52 ± 0.27**	**1.45 ± 0.34**	**1.56 ± 0.16**	**1.72 ± 0.24**	**1.58 ± 0.28**

Table 5. Summary of Arctic Tern chick diet by island. Values represent the mean percent frequency of occurrence (%FO) +/- 1 SD rounded to the nearest decimal.

Fishes	Eastern Egg Rock %FO ± SD	Matinicus Rock %FO ± SD	Seal Island NWR %FO ± SD
Hake	40.1 ± 8.3	39.9 ± 14.2	30.8 ± 12.3
Sand lance	1.3 ± 1.6	3.7 ± 8.1	3.7 ± 9
Herring	4.8 ± 4.3	7.2 ± 10.7	12.1 ± 13.6
Butterfish	2.5 ± 3.3	4.6 ± 5.9	3.2 ± 5
Pollock	<1.0 ± <1.0	<1.0 ± <1.0	<1.0 ± <1.0
Unknown Fish	11.2 ± 7.6	9 ± 5.3	11.2 ± 5.9
Other Fish	1.9 ± 2.1	1.9 ± 1.4	1.6 ± 2.8
Total Fishes	**62.5**	**66.4**	**63.0**
Invertebrates			
Amphipod	16.5 ± 14.7	16.3 ± 10	11.4 ± 13.5
Euphausiid	3.4 ± 6.8	5.0 ± 7.9	14.9 ± 18.2
Other Invertebrate	3.3 ± 5.0	2.8 ± 6.3	1.6 ± 2.8
Unknown Invertebrate	6.5 ± 8.9	3.0 ± 5.7	2.0 ± 2.7
Total Invertebrates	**29.6**	**27.1**	**29.8**
Unknown	**7.8 ± 5.2**	**6.5 ± 4.7**	**7.2 ± 3.5**
Dietary Diversity	**1.63 ± 0.16**	**1.63 ± 0.21**	**1.66 ± 0.22**

south in New York and Massachusetts, USA (Safina *et al.* 1990a; Goyert 2015). In addition, this study greatly extends prior knowledge of Arctic and Common Tern chick diets in the region, adding twenty years of data and two new islands to previous analy-

ses conducted by Hall *et al.* (2000). Our findings largely support prior expectations for species-specific patterns in provisioning habits. On a regional scale, we found three forage fish groups–hake, herring, and sand lance–dominate tern chick diets. However,

Table 6. Summary of Roseate Tern chick diet by island. Values represent the mean percent frequency of occurrence (%FO) +/- 1 SD rounded to the nearest decimal.

Fishes	Stratton Island %FO ± SD	Outer Green Island %FO ± SD	Jenny Island %FO ± SD	Eastern Egg Rock %FO ± SD
Hake	10.9 ± 11.5	45.4 ± 3	21.1 ± 23.1	45.4 ± 15.4
Sandlance	59.1 ± 18.4	21.8 ± 10.3	34.8 ± 23.6	6.1 ± 6.0
Herring	8.6 ± 7.8	20.2 ± 18.5	19.5 ± 5.3	16.7 ± 12.8
Butterfish	<1.0 ± <1.0	1.0 ± 1.5	<1.0 ± <1.0	1.5 ± 2.8
Pollock	<1.0 ± <1.0	0 ± 0	<1.0 ± <1.0	5.3 ± 7.1
Unknown Fish	17.2 ± 9.5	14.1 ± 5.3	21.2 ± 16.4	20.5 ± 11.5
Other Fish	<1.0 ± <1.0	<1.0 ± <1.0	<1.0 ± <1.0	<1.0 ± 1.2
Total Fishes	**96.7**	**99.2**	**98.4**	**96.4**
Invertebrates				
Amphipod	<1.0 ± <1.0	<1 ± <1	0 ± 0	<1.0 ± <1.0
Euphausiid	<1.0 ± <1.0	0 ± 0	<1 ± <1	<1.0 ± <1.0
Other Invertebrate	<1.0 ± <1.0	<1 ± <1	0 ± 0	<1.0 ± <1.0
Unknown Invertebrate	<1.0 ± <1.0	0 ± 0	0 ± 0	<1.0 ± <1.0
Total Invertebrates	**<1.0**	**<1.0**	**<1.0**	**<1.0**
Unknown	**3.1 ± 2**	**<1.0 ± <1.0**	**1.6 ± 1.7**	**3.3 ± 3.3**
Dietary Diversity	**1.08 ± 0.30**	**1.32 ± 0.01**	**1.28 ± 0.07**	**1.34 ± 0.25**

we also found evidence of foraging plasticity. This was evidenced through variation in the relative amounts of the three primary prey groups and the overall diversity of other prey items consumed across locations. Although terns in the GoM specialize on hake, herring, and sand lance, they can switch prey and supplement their diets with alternative species. However, future studies are still needed to elucidate if tern foraging behaviors are truly opportunistic and responsive to changes in availability (i.e., random feeding), or if selection (active or passive) is occurring through species-specific behavioral or physical constraints (Greene 1986). This could be advanced by pairing spatial assessments of prey abundance and distribution with concurrent tracking studies of terns (Powers *et al.* 2017). In addition, the ecological consequences of regional variation in foraging behavior on chick fitness and survival remains unclear. Models that combine our results on the frequency of occurrence of provisioned prey with information on prey size and nutritional value will be useful to determine the relationship between prey profitability and tern productivity (Massias & Becker 1990, Evans & Moustakas 2018).

Tern Chick Diets in the Northwest Atlantic

The additional data collected during the past 20 years nearly doubled the total number of fish species observed in Common (*n* = 17–30 prey species) and Arctic Tern (from *n* = 24–41 species) chick diets in comparison to the prior 10 year period evaluated by Hall *et al.* (2000). The increased number of total observations and two additional nesting islands for Common Terns (Outer Green Island and Pond Island NWR) undoubtedly contribute to the increases in dietary diversity found in our study. Decreases in the overall contributions of herring in Common (from 24%–33% FO) and Arctic (from 8%–17%) Tern chick diets were also notable changes since the 1990s (Hall *et al.* 2000) and may reflect recent declines in the regional Atlantic Herring population (Scopel *et al.* 2018; NEFSC 2018).

Prey species richness and diversity were higher for Common Tern chicks in the GoM compared to southern colonies in New York and Massachusetts where sand lance (17–41%), herring (11–27%), and bay anchovy (5–20%, *Anchoa mitchilli*) are the primary prey consumed (Safina *et al.* 1990a; Goyert 2015). Another key difference with tern diets at the southern extent of their breeding range, is the relative importance of hake and invertebrates in the GoM. Notably, 30% of the Arctic Tern diet was composed of invertebrates. Hall *et al.* (2000) suggested that increased competition from co-nesting Common Terns reduced the ability of Arctic Terns to obtain preferred fish prey, while Hopkins & Wiley (1972) hypothesized Arctic Terns may consume invertebrates to avoid kleptoparasitism, as pirating Common Terns and Laughing Gulls (*Leucophaeus atricilla*) often target large and highly nutritious prey items. At Country Island, Nova Scotia, CA, Arctic Tern chick diet was comprised of hake (45.6%), sand lance (22%) and herring (6.2%) while invertebrates only comprised around 3.5% of diet between 1995 and 2005 (Rock *et al.* 2007b). Consuming invertebrates with relatively low nutritional value comes with an energetic cost that requires an increase in provisioning rates to compensate for a loss in either biomass or calories (Kirkham 1986; Diamond and Devlin 2003). Still, this foraging behavior may provide benefits to Common and Arctic Tern in the GoM when invertebrate prey are readily available and fish prey are not, or through the cessation of kleptoparasitic attacks from other birds. Understanding the benefits and consequences to this behavior are important for future consideration, especially if populations of more energetically valuable forage fish species, such as hake, herring and sand lance, are impacted by fisheries or climate change.

In the northwest Atlantic, Roseate Terns are considered sand lance specialists; this is especially true at nesting colonies located south of the GoM where the majority of the northwest Atlantic population breeds and most research has been conducted to date (Richards and Schew 1989; Safina *et*

al. 1990a; Goyert 2015; Staudinger *et al.* 2020). Sand lance was also a major component of chick diet on Country Island, Nova Scotia, CA, northeast of the GoM (Rock *et al.* 2007a). While sand lance was an important prey item in the present study, overall, it was provisioned in lower amounts than have been reported elsewhere (Staudinger *et al.* 2020). Roseate Terns provisioned chicks with more hake and herring on Eastern Egg Rock, Outer Green Island and Jenny Island, while sand lance was delivered in relatively lower frequencies. Only on Stratton Island was sand lance the most commonly provisioned prey item. Continued data collection on Jenny and Outer Green Islands, where Roseate Terns only recently have begun to nest, as well as any other newly colonized islands in the GoM, will help gain additional insights into how their foraging behavior may vary across the cool and warm habitats in the northwest Atlantic.

One of the most anomalous foraging behaviors recorded over the time series for Roseate Terns was observed during 1992 on Eastern Egg Rock where they consumed unusually high amounts of pollock (28% FO). This was also reflected in Common Tern diets on Jenny Island (35% FO). We hypothesize that this event shows preliminary evidence for foraging plasticity and prey switching towards a non-traditional prey species. What is interesting about this result is that regional stock assessment data for pollock do not indicate high recruitment or spawning stock biomass during this time-period (early 1990s). Because fine scale data on juvenile pollock distribution does not exist in this area, it is unclear whether this foraging behavior was driven by relative shortages in primary prey species or high local abundances of this alternative species (NEFSC 2017).

Least Tern diets were characterized at a single nesting colony in the GoM, Stratton Island, where like other terns, they were found to rely on the three primary forage fish–hake, herring, and sand lance; however, their diet contained unique contributions from other species such as killifish (*Fundulus* spp.). Obtaining killifish requires Least Terns

to feed in inshore habitats such as saltmarshes and shallow, tidally influenced waters, and salt ponds that occur predominantly on the mainland but also on leeward coastlines of GoM islands (Jordaan 2010). Least Terns typically nest on mainland coastal beaches in the northwest Atlantic (Thompson *et al.* 2020); therefore, additional studies would be useful to characterize their foraging ecology in these distinct habitats.

Influence of Island Location and Geomorphology

The seven islands examined in this study have varying habitat characteristics including bathymetry, bottom substrate, and distance from mainland, which likely play important roles in determining local prey assemblages (Ainley *et al.* 1981; Cairns and Schneider 1990; Safina *et al.* 1990b; Ladd *et al.* 2005; Watanuki *et al.* 2008; Jordaan 2010). Foraging opportunities also vary across daily, seasonal, and annual scales (Suryan *et al.* 2000) depending on local tidal cycles, weather and climate patterns. Previous studies have suggested that seabirds nesting on inshore islands should have access to greater prey diversity compared to conspecifics nesting further offshore due to the varied structure of coastal habitats compared with open ocean environments (Diamond 1983; Hall *et al.* 2000).

Subtleties are related to prey availability and diversity across the gradient of inshore to offshore nesting sites. For example, both Arctic and Common Terns nesting on offshore islands (Seal Island NWR and Matinicus Rock), consumed notably more invertebrates, which were observed in low frequency at inshore islands. This could be explained by the prevalence of open ocean habitat found surrounding the offshore islands and decreased access to shallower shelf and mainland habitats. Furthermore, sand lance was most common in tern diets on two inshore islands (Pond Island NWR and Stratton), while relatively lower frequencies were provisioned on nearshore and offshore islands (Eastern Egg Rock, Matinicus Rock, Outer Green and Seal Island NWR).

American sand lance (*Ammodytes americanus*) are found in shallow waters with sandy substrates (Robards *et al.* 1999; Collette and Klein-MacPhee 2002), a habitat type present surrounding Stratton Island, but less so around Pond and Jenny Islands, which consisted of more silty and fine grain sand (Northeast Ocean Data 2019). Pond and Stratton Islands are in proximity to coastal river estuaries and marsh systems of the Kennebec and Saco Rivers. Outwash from these systems likely provides good habitat for juvenile and adult American sand lance (Novak *et al.* 2017) compared to more offshore islands. Population surveys of prey availability and associated habitats surrounding tern nesting islands could inform management decisions of where to select any potential new restoration sites in the region.

Vulnerability of Terns to Dietary Shifts

Specialization on a particular habitat or prey species is an ecological trait often associated with higher vulnerability to climate change and other stressors (Clavel *et al.* 2011; Foden *et al.* 2013). The GoM is warming rapidly (Mills *et al.* 2013; Pershing *et al.* 2015; Thomas *et al.* 2017), and many fish species have already shown or are expected to shift their distributions and phenology in response to increasing ocean temperatures (Nye *et al.* 2009; Walsh *et al.* 2015; Morley *et al.* 2018; Staudinger *et al.* 2019). Commercial fishing pressure can also have significant impacts on the availability of forage fish during the seabird nesting season (Kress *et al.* 2016; Scopel *et al.* 2018). Changes to the abundance, distribution or phenology of hake, herring and sand lance in the GoM could negatively impact tern populations if they are unable to switch to alternative prey of equal nutritional value.

Due to a string of low recruitment years, Atlantic herring has shown population declines in recent decades, as documented by fisheries assessments and regional studies of seabird diets (Diamond and Devlin 2003; Kress *et al.* 2016; Scopel *et al.* 2018; NEFSC2018). White hake (*Urophycis tenuis*) are considered a cold-water adapted species whose population has been shifting poleward since 1968 (Nye *et al.* 2009) and whose thermal habitat is expected to shift up to 568 km over the current century (Morley *et al.* 2018). Although no current fishery exists for sand lance in the GoM, their distribution is constrained to areas with sandy bottom substrates, which are necessary to bury themselves in order to evade predators (Staudinger *et al.* 2020; Collette and Klein-MacPhee 2002). This habitat association contributes to a patchy distribution throughout their range, and may explain higher frequencies of sand lance occurring at only a few islands in the GoM.

The data assembled here provides baseline information to inform further analyses of the impacts of dietary shifts on tern productivity and fitness across decadal and landscape scales. Such studies are necessary next steps in assessing risk and vulnerability for terns in the GoM to future impacts from cumulative impacts from climate change, fishing and other stressors. Impact studies have already been conducted for a variety of alcid species nesting in the GoM region (Kress *et al.* 2016; Scopel *et al.* 2019). Rapid warming since 2005 and concurrent declines in herring in the chick diets of Razorbills (*Alca torda*) and Common Murres (*Uria aalge*) were associated with increases of lower energy density prey items, as well as declines in chick condition and overall breeding success (Scopel *et al.* 2019). Experimental studies have also shown seabird chicks that were fed higher energy density prey items, compared to those fed an equal biomass of prey with lower energy densities, experienced significantly higher growth rates (Romano *et al.* 2006). Therefore, future studies in the GoM would benefit from analyses of the impacts of dietary shifts, the energetic value of alternative prey, and the foraging behavior of adults.

Fish Identification Challenges and Data Limitations

Visual assessments of provisioning events show that most fish delivered to chicks during the summer are young of the

year (YoY) or juvenile size/age classes (Scopel *et al.* 2018). Some fishes are distinctive enough to be identified to species through visual observations, while other require closer inspection. The most common hake species in tern diets is likely white hake (Kress *et al.* 2016); however, juveniles are notoriously difficult to identify and may be confused with other similar species such as four-bearded rockling (*Enchelyopus cimbrius*) or offshore hake (*Merluccius albidus*). Atlantic Herring (*Clupea harengus*) likely comprise much of the "herring" category in this study, as they are the numerically dominant *Clupeidae* in the GoM (Dias *et al.* 2019); however two species of river herring, alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), may also occur in chick diets. Two species of sand lance occur in the GoM and are indistinguishable based on visual observations alone. However, some inferences can be made based on the habitat preference of species relative to the geographic location of potential foraging grounds (Nizinski *et al.* 1990; Staudinger *et al.* 2020). For example, northern sand lance (*Ammodytes dubius*) generally occur in more offshore habitats (20-100m water depth) compared to American sand lance (*A. americanus*), which prefers more inshore, coastal waters < 2m in depth. Species-level identification in tern diets is important because differences in population status, fishery pressure, and climate vulnerability may affect species availability differently under changing ecological and environmental conditions. Molecular techniques using eDNA and metabarcoding of seabird feces could help resolve some prey identification issues. In addition, the data presented in this study focused on frequency of occurrence, which does not include information on prey size and life stage, which are directly linked to the energetic value of prey items and influence prey species distributions.

CONCLUSIONS

Interspecific and geographic variation in tern diets observed across the GoM suggests some level of foraging plasticity and ecological resilience to changing prey community composition. However, future studies are still needed to elucidate if terns are actively seeking out and selecting specific prey species or if they are responding opportunistically to local availability. This can be accompanied through studies that track the abundance and distribution of prey species at local scales across the region and develop novel methods to observe *in situ* tern foraging behaviors. Finally, analyses that directly link interannual trends in chick diets to productivity metrics and evaluate the interactive effects of climate change and fishing pressure on prey populations are critical to understand cumulative impacts on tern populations in the region.

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