

Composition, Spatial and Temporal Variation of Common and Arctic Tern Chick Diets in the Gulf of Maine

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Abstract.—From 1990-1997, we observed food deliveries to Common (*Sterna hirundo*) and Arctic (*S. paradisaea*) tern chicks in the Gulf of Maine; deliveries were observed at four Common Tern colonies from 1991-1997 and at three Arctic Tern colonies from 1990-1997. Dietary overlap was high, 0.812. Fish comprised over 96% of the prey delivered (frequency) to Common Tern chicks. In contrast, Arctic Tern chicks were fed a diet consisting of 65% fish and 35% invertebrates. Although the two terns fed different proportions of fish, both species relied heavily on white hake (*Urophycis tenuis*), Four-bearded rockling (*Enchelyopus cimbrius*) and Atlantic herring (*Clupea harengus*). American sand lance (*Ammodytes americanus*) was an important prey for Common Terns at one island. Overall, Common Terns fed their young a greater diversity of prey than did Arctic Terns. We found significant inter-annual and inter-colony differences in the diversity and proportions of prey types. "Boom and bust" years were evident for particular prey. We suspect dietary differences in Maine were due to colony location; however, a detailed study of the relationship between prey availability and abundance and the foraging ecology of terns in Maine is needed to elucidate these relationships. We believe long-term diet data sets gathered from multiple sites are the best way to characterize waterbird diets. Received 11 October 1999, resubmitted 6 April 2000, accepted 8 April 2000.

Key words.—Arctic Tern, Common Tern, chick diet, Maine, *Sterna hirundo*, *Sterna paradisaea*.

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Many studies have compared the ecology of sympatric nesting terns (Chapdelaine *et al.* 1985; Hulsman 1987; Uttley *et al.* 1989). Although there is usually some overlap in the ecology, these studies typically show differences in phenology, growth, survival, behavior and diet. The diets of Common and Arctic terns have been studied in detail at several locations (Courtney and Blokpoel 1980; Ewins 1985). Comparative studies of the diet and foraging ecology of Common and Arctic terns in mixed colonies have noted differences in habitat use, feeding rates, prey selection and prey size (Lemmetynen 1973; Kirkham 1986; Fricks and Becker 1995). However, while these studies documented a greater use of invertebrate prey by Arctic Terns, each of these studies was conducted for only one or two seasons at a single site. Long-term diet studies are important because they indicate considerable spatial and temporal variation in diet and prey avail-

ability (Bertram and Kaiser 1993; Montevecchi and Myers 1995).

This paper compares the diet of Common and Arctic tern chicks and reports on the nature and extent of colony differences and inter-annual variation in prey type. In this paper, we describe Common and Arctic tern chick diet at Maine coastal tern colonies during 1990-1997. Although there is some diet information for Common and Arctic terns in the Gulf of Maine (Mendall 1936; Hawksley 1957; Kirkham 1986), this is the first detailed long-term study of Common and Arctic tern chick diet.

STUDY AREA

We studied prey deliveries to Common and Arctic tern chicks at five colonies in the Gulf of Maine during 1990-1997. Stratton Island (43°31'N 70°19'W), located 2 km off Prout's Neck, York Co. Maine, is an 11-ha island. In 1991, 248 pairs of Common Terns nested; by 1997, the number of nesting pairs had increased to 821. Jenny Island (43°46'N 69°54'W), located in Eastern Cas-

co Bay, one km off of West Cundy Point, Cumberland Co., is a one-ha island that supported 57 pairs of Common Terns in 1991, and 1,068 pair in 1997. Eastern Egg Rock (43°52'N 69°22'W) is located at the mouth of Muscongus Bay, nine km from New Harbor, Lincoln County. Common Terns on this four-ha island increased from 869 to 1,389 pairs during the study period while the number of Arctic Terns increased from 80 to 94 pairs. Matinicus Rock National Wildlife Refuge (43°47'N 68°51'W) is an 11-ha island located 40 km south of Rockland, Knox Co. at the head of outer Penobscot Bay; 1,252 pairs of Arctic Terns nested in 1990 and only 934 pairs nested in 1997. Seal Island National Wildlife Refuge (43°53'N 68°44' W) is a 40-ha island located 35 km from Rockland, Knox Co. In 1990, 115 pairs of Arctic Terns nested on Seal Island. In 1991, there were 369 pairs of Common Terns on Seal Island. By 1997, Seal Island was Maine's largest tern colony with an estimated 1,024 pairs of Common Terns and 773 pairs of Arctic Terns.

We categorized each island as inshore (<5 km; Stratton Island, Jenny Island), nearshore (5-10 km; Eastern Egg Rock), or offshore (>10 km; Matinicus Rock and Seal Island), using distance to the closest point of land as the measure.

METHODS

Chick Diet

Common Terns were observed from 1991-1997 at Stratton Island, Jenny Island and Eastern Egg Rock and on Seal Island in 1992, 1993 and 1996; Arctic Terns were observed from 1990-1997 at Seal Island and Matinicus Rock, and from 1990-1995 on Eastern Egg Rock. Methods were similar for all colonies and for both species. Portable observation blinds were placed in the colony between mid May and early June. Blind locations were selected to maximize the number of potential study nests. Chick provisioning observations began with hatching and continued until a chick fledged or died. Four to six nests within 5-7 m of the blind, encompassing one field of view, were marked by number prior to hatching.

Prey deliveries to chicks were observed with binoculars or unaided eye during three to four hour observation periods one or two times per day, from mid June to early August. Observations were conducted between 0530 and 2000 h daily; however, observation periods were generally concentrated during the time of greatest activity, the four hours following sunrise (Frank 1992). For each feeding, the nest number, and type and number of prey items delivered to chicks were recorded. If the prey identity was unclear, it was listed as either unknown or an unknown fish.

Many of the fish prey we observed were distinctive in size, color, and shape. White hake (*Urophycis tenuis*) and four-bearded rockling (*Enchelyopus cimbrius*) were recorded as hake. Juvenile identification of these two species is based on the number of rays in the ventral fin and the structure of the first section of the dorsal fin (Bigelow and Schroeder 1953), characteristics that are impossible to determine by remote observation. Voucher specimens collected from chicks and recovered in the colonies were identified by staff at either the Sandy Hook Marine Lab, Highlands, NJ, the Maine Dept. of Marine Resources or the National Marine Fisheries Ser-

vice, Northeast Fisheries Center. Although the similarities between juveniles of these two species prevented us from identifying them to species level in the field, nearly all samples examined in the laboratories proved to be white hake.

Staff and volunteer observers were trained in prey identification using 1) photographic slides of terns with known fish types in their bills, 2) preserved samples of known prey types and 3) a handout with drawings and descriptions of the salient field characteristics of common prey items. Observers received additional training during a three-hour practice observation period with an island supervisor. Hall (1999) found no difference in the percentage of correctly identified prey between observers.

Only nests with 15 or more identified prey deliveries were used in the final analyses. We used prey categories for intra-species comparisons of diet: herring (*Clupea harengus*), hake, sand lance (*Ammodytes americanus*), pollock (*Pollachius virens*), butterfish (*Poronotus triacanthus*), other fish and invertebrates. Infrequently delivered fish were lumped into a single category, "other fish". Marine and terrestrial invertebrates were lumped into a single category, "inverts".

Data Analysis

We calculated niche overlap and diversity indices for Common and Arctic tern chick diets. Following Diamond (1983), we used Horn's (1966) modification of Morisita's (1959) index to quantify the degree of overlap between Common and Arctic tern chick diets. This index measures the degree of utilization overlap between a pair of species. The index value ranges from zero (no resources used in common between two species) to one (complete overlap in resource use). We used the Resampling Stats in Excel program (Blank 1999) to perform Monte Carlo randomizations. One thousand overlap scores were derived from 1,000 randomly generated Common and Arctic tern chick diets for each species, on each island, during each year. Prey items not delivered to chicks of either species on a particular island during a particular year were considered to be unavailable, hence were also not available in simulated diets. Randomly-generated diets consisted of the same number of deliveries observed on an island during a specific year. P values were calculated by comparing the probability of observing, by chance, a specific mean niche overlap value that is greater than or equal to the observed mean. Diamond (1983) showed that lower level analyses (using family as the taxon) resulted in higher overlap values. We used a moderate to high level analysis (primary taxon was species).

We used Hurlbert's (1971) probability of an interspecific encounter (PIE) to compare differences in the diversity of diet between Common and Arctic tern chicks:

$$PIE = N/N - 1 \left(1 - \sum_{i=1}^S \pi_i^2 \right)$$

N = the total number of individuals in the sample; $\pi_i = N_i/N$; N_i = number of individuals of the i^{th} species in the sample and s = the number of species in the sample. PIE measures the chance that two individuals randomly cho-

sen from a sample are different species. A Hurlbert's PIE value of 0.9 indicates two randomly-selected individuals from a population have a high probability (90%) of being different. This diversity index was chosen because estimates of PIE are unbiased for small sample sizes (Gotelli and Graves 1996). We calculated PIE values for each nest using EcoSim (Gotelli and Entsminger 1997). EcoSim generates a variance and confidence interval for each PIE value, using Monte Carlo simulations. One thousand trials were conducted for each nest. A Kruskal-Wallis test was used to compare intra-species differences in PIE for islands and for years. We used a Mann-Whitney U-test to compare Hurlbert's PIE values between species and to compare Common and Arctic terns studied during the same period on Seal Island and Eastern Egg Rock.

We compared proportions of prey categories by island and year for each tern species, using two-way ANOVA (Sokal and Rohlf 1981). Significant effects were tested with a Wald statistic (StataCorp 1997).

RESULTS

Inter-species Differences in Prey

Common Tern chick diet was more diverse (Mann-Whitney U test; $z = -4.042$, $P < 0.001$) than Arctic Tern chick diet (Table 1). The mean PIE value for Common Terns was

Table 1. Composition of Common (four colonies) and Arctic (three colonies) tern chick diet in the Gulf of Maine from 1990-1997. N = number of prey items observed; % = the percent of total identified prey, (Bold type indicates prey categories used in ANOVA).

Prey Type		Common Tern		Arctic Tern	
		N	%	N	%
Atlantic herring	<i>Clupea harengus</i>	10,423	33.3	3,232	17.4
Hake	<i>Urophycis and Enchelyopus</i>	12,098	38.7	7,326	39.5
American pollock	<i>Pollachius virens</i>	1,508	4.8	144	<1.0
Butterfish	<i>Poronotus triacanthus</i>	1,168	3.7	619	3.3
Sand lance	<i>Ammodytes americanus</i>	4,240	13.6	474	2.6
Other fish		765	2.4	241	1.3
Lumpfish	<i>Cyclopterus lumpus</i>	379	1.2	38	<1.0
Bluefish	<i>Pomatomus saltatrix</i>	25	<1.0	32	<1.0
River herring	<i>Alosa</i> spp.	104	<1.0	1	<1.0
3-spined stickleback	<i>Gasterosteus aculeatus</i>	122	<1.0	153	<1.0
Mummichog	<i>Fundulus majalis</i>	11	<1.0	—	—
Silver hake	<i>Merluccius bilinearis</i>	8	<1.0	—	—
Silverside	<i>Menidia menidia</i>	17	<1.0	2	<1.0
Cunner	<i>Tautoglabrus adspersus</i>	32	<1.0	—	—
Atlantic mackerel	<i>Scomber scombrus</i>	20	<1.0	2	<1.0
Fish scrap	bait	45	<1.0	12	<1.0
Sculpin	unidentified genus	1	<1.0	2	<1.0
Eel	unidentified genus	1	<1.0	—	—
Invertebrates		1,040	3.3	6,522	35.1
Insect	unidentified order	474	1.5	85	<1.0
Moth	unidentified family	52	<1.0	16	<1.0
Ant	unidentified family	4	<1.0	70	<1.0
Earthworm		1	<1.0	2	<1.0
Amphipod	<i>Gammarus</i> spp.	432	1.4	4,749	25.6
Polycheate	<i>Nereis or Glycera</i>	8	<1.0	13	<1.0
Isopod	unidentified genus	26	<1.0	58	<1.0
Euphasiid	<i>Meganyctiphanes norvegica</i>	27	<1.0	552	3.0
Crustaceae	unidentified family	16	<1.0	977	5.3
Squid	unidentified family	—	—	1	<1.0
Unidentified item ¹		1,126	3.0	1,728	7.6
Unidentified fish		4,706	12.7	2,426	10.7
Total identified		31,242		18,559	
Horn—Morisita Overlap Index			0.812		
Hurlbert's PIE		0.5703		0.4936	

¹Proportions of unidentified items and unidentified fish from total deliveries

0.5703 ($N = 355$, $SD = 0.13$) compared to a mean of 0.4936 ($N = 245$, $SD = 0.16$) for Arctic Terns. Twenty-six prey types were delivered by Common Terns, 17 fish and 9 invertebrates; Arctic Terns delivered 13 fish and 10 invertebrate prey. Twenty-two types of prey were used by both species. The observed value of the overlap index was 0.812. The mean of the randomly generated chick diets was 0.628; the p -value of the observed overlap was 0.008. Over 96% of the prey delivered to Common Tern chicks were fish. In contrast, Arctic Tern chicks were fed 65% fish and 35% invertebrates, primarily amphipods, euphausiids and unknown crustacea. Although Common and Arctic terns fed different proportions of fish, both species relied heavily on hake. Hake comprised approximately 40% of the total prey deliveries for each species. However, hake accounted for 61% of the fish delivered to Arctic Tern chicks and 40% of the fish delivered to Common Tern chicks. Hake, herring and sand lance comprised 90% of the fish and 86% of the total prey delivered to Common Tern chicks, while hake, herring and sand lance only accounted for 60% of the total diet, but 92% of the fish delivered to Arctic Tern chicks.

Invertebrate prey use by Common and Arctic terns differed with respect to frequency and type. While invertebrates only accounted for 3% of Common Tern chick diet, terrestrial invertebrates ("insects", moths and ants) comprised 51% of invertebrate deliveries; in contrast, terrestrial invertebrates accounted for only 3% of invertebrates delivered to Arctic Tern chicks. On the other hand, marine invertebrates (amphipods, isopods, euphausiids and crustaceans) comprised 97% of invertebrate deliveries and 34% of all prey delivered to Arctic Tern chicks, but only accounted for 1.6% of all prey deliveries to Common Tern chicks.

Provisioning studies of Common and Arctic tern chicks were concurrent on Seal Island during 1992, 1993 and 1996. Common Tern ($PIE = 0.5707$, $N = 29$, $SD = 0.11$) chick diets were more diverse (Mann-Whitney U-test; $z = -2.970$, $P = 0.003$) than those of Arctic Terns ($PIE = 0.4367$, $N = 34$, $SD =$

0.17) on Seal Island. Both species delivered 11 types of prey; eight were used by both terns. The observed overlap score was 0.815 ($P < 0.001$). Both terns predominantly fed fish, they did so in different proportions: hake accounted for 64% and herring 15% of Arctic Tern chick diet, and herring comprised 47% of Common Tern chick diet and hake 38%. Arctic Terns (10%) delivered a higher percentage of invertebrates than did Common Terns (4%).

Provisioning studies were also concurrent on Eastern Egg Rock during 1991, 1992, 1994 and 1995. Arctic Terns delivered 16 types of prey (nine fish, seven invertebrates) compared to 15 prey types (nine fish and six invertebrates) used by Common Terns. Both terns used twelve prey types. The overlap in chick diet was 0.79 ($P < 0.001$). There was no difference in the diversity of prey between species ($t_{78} = 1.05$, $P = .3$). However, Arctic Terns (44%) fed a greater proportion of invertebrates to chicks. Common Terns fed a greater percentage of fish, primarily herring (20%) and hake (57%), than did Arctic Terns (herring 6%; hake 41%).

Spatial and Temporal Variation of Prey

Common Terns

Common Terns nesting on the inshore colonies (Jenny Island—24 prey types: 16 fish/eight invertebrates; Stratton Island—21 prey types: 14 fish/seven invertebrates) delivered a greater diversity of prey than did Common Terns on either the nearshore (Eastern Egg Rock—16 prey types: nine fish/seven invertebrates) or offshore (Seal Island—14 prey types: seven fish/seven invertebrates) colonies (Kruskal-Wallis ANOVA; ($\chi^2_3 = 11.995$, $P = 0.007$). Twelve of 26 identified prey were observed at all colonies, seven fish and five invertebrates. With the exception of Stratton Island, herring and hake were the most frequently delivered prey at all colonies (Appendix 1). On Eastern Egg Rock, hake comprised over 60% of chick diet, making it the most frequently delivered prey type for any island. Sand lance was the most commonly delivered prey on Stratton

Island (43%) while Atlantic herring was the dominant prey on Jenny (50%) and Seal (47%) islands.

We found significant differences in the composition ($F_{6,333} = 19.65, P < 0.001$; Fig. 1) and diversity (Kruskal-Wallis ANOVA; $\chi^2_6 = 95.551, P < 0.001$; Table 2) of Common Tern chick diet between years. Differences in the measure of diversity (PIE) between years reflect changes in diet breadth. A low diversity value indicates a reliance on few prey types, while a high diversity score suggests terns were frequently using several prey. For example, in 1993, herring comprised 56% of chick diet while only one other prey type, hake, exceeded 10%. Consequently, the PIE value (0.44) was lower than average. In contrast, in 1996, the PIE value was greater (0.66) than in all other years and the proportion of herring (17%) was below average, while the proportion of butterfish (15%) was greater than in any other year. Further, the frequency of two additional prey, sand lance and hake, exceeded 20%, indicating that Common Terns were frequently feeding chicks four types of prey.

Distinct "boom and bust" years for individual prey types are evident from changes in the annual frequency of prey delivered to chicks within a colony (Appendix 1). For example, on Jenny Island, from 1991-1997, pollock comprised 7% and butterfish 2% of the total prey deliveries, however, in 1992, pollock accounted for 39% of chick diet, more than any other prey type during that season. Similarly, in 1996, butterfish accounted for

13% of the prey deliveries; during all other years, butterfish only accounted for 1% or less of chick diet.

Arctic Terns

Prey diversity (Table 2) and composition (Appendix 2) were similar between colonies; Eastern Egg Rock (17 prey types: nine fish/eight invertebrates); Seal Island (18 prey types: 11 fish/seven invertebrates) and Matinicus Rock (18 prey types: nine fish/nine invertebrates). However, the relative proportions of fish and invertebrate prey delivered to chicks at each colony were significantly different ($\chi^2_2 = 27.78, P < 0.001$); Eastern Egg Rock (51% fish, 49% inverts); Matinicus Rock (59% fish, 41% inverts) and Seal Island NWR (85% fish, 15% inverts). Hake was the predominate fish prey on all islands, Egg Rock 72%; Seal Island 48.1% and Matinicus Rock 67.5%, while herring was the second most frequently delivered fish prey (Egg Rock 10.8%; Seal Island 45%; Matinicus Rock 18.5%). Pollock (Egg Rock—7.2%), sand lance (Seal Island—3.2%) and butterfish (Matinicus Rock—7.5%) were the next most frequently delivered fish prey on individual islands. Invertebrates, comprised 41% of chick diet on Eastern Egg Rock and 49% on Matinicus Rock; the proportion of invertebrates increased from 1% (1991) to 42% (1997) of chick diet on Seal Island. Increases in invertebrate use on Seal Island were correlated ($r_s = 0.82, n = 7, P < 0.01$) with an increase in the number of nesting pairs of Arctic Terns.

Overall, significant inter-annual differences in the composition ($F_{5,184} = 8.96, P < 0.001$; Fig. 2) and diversity (Kruskal-Wallis ANOVA; $\chi^2_3 = 45.22, P < 0.001$; Table 2) of chick diet were detected. During an average breeding season, herring, hake and invertebrate prey accounted for 92% of chick diet. However, in some years, an otherwise infrequently delivered prey could account for a significant portion of chick diet. For example, on Egg Rock in 1992, pollock comprised 42% of the diet, more than in any other year. Similarly, in 1996, like Common Terns, the frequency of butterfish increased at all colo-

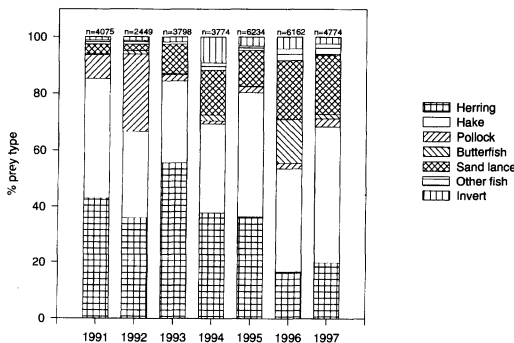


Figure 1. Variation in Common Tern chick diet between years 1991-1997.

Table 2. Mean values of diversity (PIE) and observed diet overlap scores (Horn-Morisita Index) at four Common Tern and three Arctic Tern colonies in Maine from 1990-1997. Column totals are weighted mean \pm SD; numbers of nests are in parentheses.

Year	Common Tern PIE	Arctic Tern PIE	Horn-Morisita Score
1990	—	0.68 \pm 0.06 (12)	—
1991	0.53 \pm 0.13 (37)	0.50 \pm 0.12 (42)	0.903
1992	0.58 \pm 0.12 (35)	0.44 \pm 0.15 (30)	0.743
1993	0.44 \pm 0.14 (36)	0.41 \pm 0.16 (43)	0.551
1994	0.48 \pm 0.14 (41)	0.49 \pm 0.17 (34)	0.62
1995	0.59 \pm 0.12 (58)	0.60 \pm 0.11 (29)	0.809
1996	0.66 \pm 0.09 (78)	0.54 \pm 0.15 (25)	0.777
1997	0.53 \pm 0.13 (70)	0.46 \pm 0.16 (30)	0.655
Average	0.57 \pm 0.13 (355)	0.49 \pm 0.16 (245)	0.812

nies (Fig. 2); overall, butterfish comprised 16% of prey deliveries (greater than any other year), compared to an annual average of 3%. Diversity scores fluctuated between 0.41 and 0.68. Diversity was lowest in 1993 when two prey types, hake and invertebrates, accounted for 82% of chick diet and was highest in 1990 when five prey types (hake, herring, butterfish, sand lance and invertebrates) each accounted for 8% or more of the diet.

DISCUSSION

Our observations of Common and Arctic terns in the Gulf of Maine indicate that Arctic Terns fed their young a greater percentage of invertebrates, that both species delivered primarily herring and "hake", and that Arctic Terns used fewer prey types than Common Terns. In addition, we observed considerable variation in the frequency of

prey types delivered to chicks between colonies, years and within a colony between years for both species.

The results of this study are consistent with previous studies where Arctic Terns were reported to consistently deliver a greater frequency of invertebrates than Common Terns. Explanations for the preponderance of invertebrate prey include prey switching during scarce food years (Boecker 1967); reducing the risk of kleptoparasitism (Hopkins and Wiley 1972); partitioning of foraging habitat (Lemmetynen 1976); and differential habitat use in relation to tidal cycles (Frick and Becker 1995). On Seal Island, increased invertebrate feedings were correlated with an increase in tern population size. However, on Matinicus Rock where colony size declined during the study, several individual Arctic Terns consistently supplemented their chicks' diet with a high proportion of invertebrates from year to year; while most individuals fed predominately fish (National Audubon Society [NAS]—unpublished data). We suspect that differences in invertebrate use between species reflect the feeding strategy of individual Arctic Terns (possibly in response to fluctuating tides—see Frick and Becker 1995) which increase feeding rates to cover chick energy requirements and compensate for the decreased average size of invertebrate prey (Frick and Becker 1995).

While Arctic Terns delivered more invertebrates, the dietary overlap between Common and Arctic tern chick diets was high (0.81). We calculated overlap values for Lemmetynen 's (1973) and Frick and Beck-

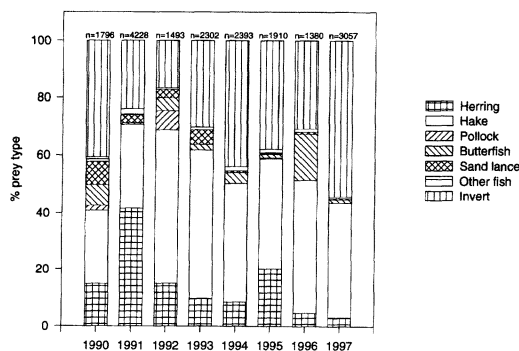


Figure 2. Variation in Arctic Tern chick diet between years 1990-1997.

er's (1995) chick diet data; the overlap value for Lemmetyinen's data was 0.947 and for Frick and Becker's data, the value was 0.56. Kirkham (1986) calculated an overlap value of 0.722 for terns in Nova Scotia. Dependence on a single prey type will result in a high overlap value, while use of several different prey will result in lower overlap values. *Gasterosteus aculeatus* accounted for 58-68% of prey deliveries in Lemmetyinen's (1973) study. In contrast, in Frick and Becker's (1995) study of Common and Arctic terns, four prey each comprised 10-42% of Common Tern chick diet while each of five prey accounted for 13-28% of Arctic Tern chick diet. In Maine, terns primarily delivered only two fish: hake and herring. These prey accounted for 58-72% of all deliveries during the study period. Differences in dietary overlap between studies are likely due to differences in the homogeneity of foraging habitat (Becker *et al.* 1997), foraging strategies and the degree of foraging habitat segregation (Boecker 1967; Lemmetyinen 1976), and/or prey movement and the variation in diversity between environments (Lemmetyinen 1973; Diamond 1983).

Diamond (1983) reported that inshore seabirds take a greater diversity of prey than offshore or pelagic seabirds and that diversity is likely the result of differences in the number of prey species between environments. Like Kirkham (1986) and Lemmetyinen (1973), we found that Common Terns fed a greater diversity of prey than Arctic Terns. Given Diamond's observations, this makes sense, if Lemmetyinen (1973) and Utley *et al.*'s (1989) conclusions are true, that Common Terns are primarily inshore feeders that prefer eutrophic bays, while Arctic Terns forage over open water or along stony shores with greater water transparency.

Kirkham (1986) reported that, when the two terns breed sympatrically, each species showed a lower degree of specialization. He attributed this increase in diversity to an abundance of local prey populations rather than factors relating to competition. This raises an interesting question concerning sympatric nesting terns and the degree of foraging habitat segregation with respect to

prey diversity and abundance. One would predict less segregation in habitats of high diversity and abundance. Lemmetyinen (1976) observed foraging habitat segregation in an area he characterized as having low productivity and diversity, while Kirkham (1986) characterized SW Nova Scotia as having patches of "superabundant" food with a diverse prey base where terns often feed in large mixed flocks. We suspect that there is little segregation of foraging habitat in Maine beyond the relationship between colony location and immediate foraging environment, except when the principal prey species are unavailable and possibly during extreme tidal cycles (Frick and Becker 1995).

Overall, changes in prey composition and diversity were noted throughout the study period (Appendix 1, 2). We believe that long-term diet data sets recorded at multiple colonies characterize diets more completely than studies conducted at single sites for only one or two seasons.

In summary, we attribute differences in prey diversity to colony location, but acknowledge that food shortages, tidal cycles and differences in the ability of each species to exploit marine resources may have contributed to differences in diet diversity during our study. We believe that long-term diet studies present a more accurate assessment of an individual species' diet and of the interactions between sympatric species and can provide information that is valuable to fisheries managers. We think that a detailed study of the foraging ecology, and relationship of prey availability and abundance to breeding performance and foraging effort of Common and Arctic terns in Maine will help to elucidate these relationships and further our insight into the system as a whole.

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Appendix 1. The frequency (%) of each of seven prey categories delivered to Common Tern chicks, on a) Stratton Island, b) Jenny Island, c) Eastern Egg Rock and d) Seal Island from 1991-1997.

Year	Herring	Hake	Pollock	Butterfish	Sand lance	Other Fish	Invert
Stratton Island							
1991	22	22	1	0	55	0	0
1993	5	21	0	0	74	0	0
1994	5	36	1	0	49	4	5
1995	27	39	2	0	29	1	2
1996	8	30	2	13	43	1	3
1997	5	39	3	2	47	3	1
Mean	12.2	34.6	1.9	4.6	42.7	1.8	2.2
Jenny Island							
1991	53	35	11	0	0	1	0
1992	32	25	39	0	2	2	0
1993	67	27	3	0	0	1	2
1994	70	23	1	1	1	2	2
1995	49	44	3	0	0	2	2
1996	30	38	2	13	2	9	6
1997	39	43	3	1	3	4	7
Mean	49.7	34.2	7.2	2.2	1.1	3.3	2.3
Eastern Egg Rock							
1991	30	57	5	1	1	3	3
1992	21	54	18	3	1	0	3
1994	2	50	1	9	0	1	37
1995	19	65	1	1	0	1	13
1996	13	55	2	27	0	1	2
1997	19	75	1	2	0	1	2
Mean	18.6	60.3	3.6	7.1	0.5	1.7	8.2
Seal Island							
1992	52	32	6	3	5	0	2
1993	49	41	0	1	4	1	4
1996	5	57	0	23	2	1	12
Mean	46.7	38.0	2.8	3.6	4.6	0.6	3.7

Appendix 2. The frequency (%) of each of seven prey categories delivered to Arctic Tern chicks, on a) Eastern Egg Rock, b) Matinicus Rock and c) Seal Island from 1990-1997.

Year	Herring	Hake	Pollock	Butterfish	Sand lance	Other Fish	Invert
Eastern Egg Rock							
1990	10	18	9	3	6	2	52
1991	3	50	1	1	4	6	35
1992	23	30	42	0	5	0	0
1993	2	30	0	0	6	0	63
1994	2	41	0	2	1	1	53
1995	9	38	1	0	0	0	52
Mean	5.5	36.8	3.7	1.0	2.9	1.3	48.8
Matinicus Rock							
1990	16	28	0	8	9	1	38
1991	25	29	0	1	2	2	41
1992	5	59	0	5	1	0	30
1993	14	53	0	4	6	2	21
1994	4	41	0	4	0	2	49
1995	20	48	0	0	1	2	29
1996	6	46	0	18	0	0	29
1997	2	40	0	1	0	0	57
Mean	10.9	39.8	0	4.4	2.5	1.3	41.1
Seal Island							
1991	72	22	0	0	4	1	1
1992	28	57	0	6	7	0	2
1993	13	79	0	0	4	0	4
1994	37	47	0	7	0	3	6
1995	27	37	0	2	0	2	32
1996	2	49	0	11	0	4	34
1997	10	43	0	4	0	1	42
Mean	38.1	40.7	0.3	2.7	2.5	1.2	14.5

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