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Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator

Stefan Garthe,[a,*] William A. Montevecchi,[b] and Gail K. Davoren[c]

[a] Research and Technology Centre (FTZ), University of Kiel, Büsum, Germany
[b] Departments of Psychology, Biology and Ocean Science Centre, Memorial University of Newfoundland, St. John's, Newfoundland, Canada
[c] Department of Zoology, Duff Roblin Building, University of Manitoba, Winnipeg, Manitoba, Canada

Abstract

We report on inter-annual comparisons of the foraging behavior of Global Positioning System–equipped chick-rearing northern gannets (*Morus bassanus*) in the western Atlantic during years with contrasting oceanographic and prey conditions. We hypothesized that the predators would modify their foraging tactics when small fishes (capelin [*Mallotus villosus*]) and large pelagic fishes (mackerel, saury) varied in inter-annual abundances. We predicted differences in (1) diving behavior, (2) spatial, and (3) temporal patterning of foraging behavior. Predictions 1 and 2 were supported, prediction 3 rejected. Dives were significantly deeper (4.3 ± 0.4 vs. 2.7 ± 0.3 m) and longer (10.1 ± 1.0 vs. 5.0 ± 0.2 s), and more U-shaped dives (dives where birds stayed at more or less one depth) were performed (52% ± 7% vs. 7% ± 2%) in the year with higher abundance of forage fishes. Flight patterns exhibited remarkable spatial and geographic differences: gannets flew significantly (17%) more and foraging ranges were about twice as long when they pursued large pelagic fishes (mean = 122 ± 81 km vs. 62 ± 12 km). The 95% kernel feeding range was 34 times larger when large pelagic fishes were available. Yet foraging trip durations were not different between years. Inter-annual variation in foraging tactics by the same species at the same colony in successive years was strongly related to prey availability, showing that spatial foraging parameters can be determined largely by ocean and prey conditions.

Breeding seabirds are limited by central-place foraging constraints that tie them to colony locations. Consequently, many species have evolved highly flexible foraging behavior. At colony level comparisons, intraspecific variability in seabird foraging behavior can reflect differences in colony size and location (Ashmole 1963; Furness and Birkhead 1984; Grémillet et al. 2004). As colony size increases, so too can competition for resources, prey depletion, and intraspecific interference (Hunt et al. 1986; Birt et al. 1987; Elliott et al. 2009). For example, Lewis et al. (2001) showed that the foraging trip duration of northern gannets (*Morus bassanus*) increases with increasing colony size. From this relationship, they infer density-dependent disturbance of fish by diving gannets such that relatively more birds in large colonies have to fly to more distant areas to find undisturbed fish schools than birds breeding in smaller colonies. This finding implies that foraging ranges will tend to be longer as a function of increasing colony size (Lewis et al. 2001).

There is also substantial evidence that oceanographic conditions and prey availability influence the foraging behavior of seabirds (Litzow and Piatt 2002; Lescroël and Bost 2005; Harding et al. 2007). Foraging ranges around colonies are also reflective of differences in prey fields. For example, common murres (*Uria aalge*) exhibited substantial differences in foraging range from the same colony in successive year when the availability of their primary prey, capelin (*Mallotus villosus*) showed marked differences in density and distribution (Burke and Montevecchi 2009).

In an ongoing multiyear and multicolony study of seabird foraging ecology, Garthe et al. (2007*a*) demonstrated significant inter-colony differences in foraging ranges and diving behavior by northern gannets from colonies in different oceanographic regimes with different prey fields. The seabirds used different tactics to provision offspring with different prey. Garthe et al. (2007*a*) hypothesized that the inter-colony differences were related to the different ocean conditions and prey availability around the colonies. However the two colonies compared also had about a five-fold difference in population size, and significantly longer foraging ranges were associated with the larger colony. Hence, this inference was confounded by inter-colony differences in colony size, oceanography, and prey fields.

Oceanographic conditions and their associated prey also at times change markedly on inter-annual and longer time scales (Perry et al. 2005). Hence in some circumstances it is possible to compare intraspecific foraging tactics at the same colony in successive years when ocean conditions and prey field are radically different (Burger and Piatt 1990; Harding et al. 2007). We took advantage of such circumstances in the Northwest Atlantic to compare the colony foraging tactics of northern gannets at a large offshore colony around which ocean conditions and prey availability were profoundly different in two different years. These circumstances allowed us to assess how differences in prey fields independent of colony size influence foraging behavior and ranges.

Northern gannets exhibit great flexibility both in the species and sizes of prey consumed and in foraging trip durations, ranges, and total distances traveled (Garthe et

* Corresponding author: garthe@ftz-west.uni-kiel.de

al. 2007*a*; Hamer et al. 2007; Montevecchi 2008). In a study in the North Sea, Hamer et al. (2007) showed that adults were able to exploit prey resources over very large foraging areas and also exhibited marked annual variation in trip durations, foraging ranges, and total distances traveled. The longest trip performed was in the year when the abundance of 0-group sandeels, their staple food over several years, was an order of magnitude lower in abundance than in the other 2 yr studied. Prey distribution and abundance is a plausible explanation for the inter- and intra-colony differences (Lewis et al. 2003; Garthe et al. 2007*a*). It is important in this context to consider that birds from larger colonies would need to select higher quality prey items to compensate for longer foraging trips and lower parental provisioning rates due to any colony size effect (Lewis et al. 2003).

We investigated the foraging behavior of chick-rearing northern gannets on Funk Island, eastern Canada, in 2 yr with contrasting oceanographic conditions and prey bases and markedly different prey harvests. We investigated the hypothesis that different prey fields drive predator foraging behavior. From observations on contrasting diets and prey availability, we predicted inter-annual differences in (1) diving behavior, (2) spatial patterns in foraging flights and foraging range, and (3) foraging trip duration. We evaluate these predictions on the basis of the data presented here and findings from other recent studies (Lewis et al. 2001; Garthe et al. 2007*a*; Hamer et al. 2007) to assess how differences in prey base independent of colony size can influence spatial and temporal foraging patterns.

Methods

Study area and design—The study was conducted during July and August 2003 and 2005, off the northeast Newfoundland coast, eastern Canada in the Northwest Atlantic (Fig. 1). Northern Gannets were studied from 27 July to 06 August 2003 and from 02 to 11 August 2005 in the colony on Funk Island (49°45′N, 53°11′W), a flat granite rock (~ 400 × 800 m). The distribution and density of one of their main prey species during the 1990s (Montevecchi 2008), capelin, was investigated during vessel surveys from 12 July to 18 July 2003 (23-m Fisheries and Oceans R/V *Shamook*) and from 15 August to 19 August 2005 (60-m Fisheries and Oceans Canada R/V *Wilfred Templeman*). The survey was run within avian foraging ranges and prime capelin spawning and staging areas to the south and west of Funk Island (Davoren et al. 2003, 2006). The timing of the capelin surveys and gannet studies did not overlap directly, and though the 2003 capelin survey was prespawning while the 2005 survey was postspawning, the abundance data obtained provide robust prey base indices (*see* also Results and Discussion).

Prey base—Capelin: During vessel surveys, signals of fish prey species were recorded continuously using two scientific high-resolution hydroacoustic systems that were similarly capable of detecting and recording the volume backscattering coefficient (s_v) from capelin shoals at the depth range encountered. Vessel speed (11–14 km h^{-1}) was constant throughout all surveys. Brief descriptions of the methods are provided here (for details *see* Davoren et al. 2006, 2007). During 2003, a BioSonics DTX 6000 hydroacoustic system was operated through a 38-kHz dual beam transducer. During the 2005 survey, a Simrad EK 500 hydroacoustic system was operated through a 38-kHz split-beam transducer. Raw high-resolution acoustic data (s_v) were recorded continuously during both years and a s_v threshold of −63 dB was applied to the raw data before integrating to determine the average aerial backscattering coefficient (s_a) for capelin in the water column (MacLennan et al. 2002). Although s_a due to capelin in the top 30 m is accessible to gannets, we examined s_a over the entire water column owing to divergent shoaling behavior and depth of capelin between daylight and dark periods (Davoren et al. 2010).

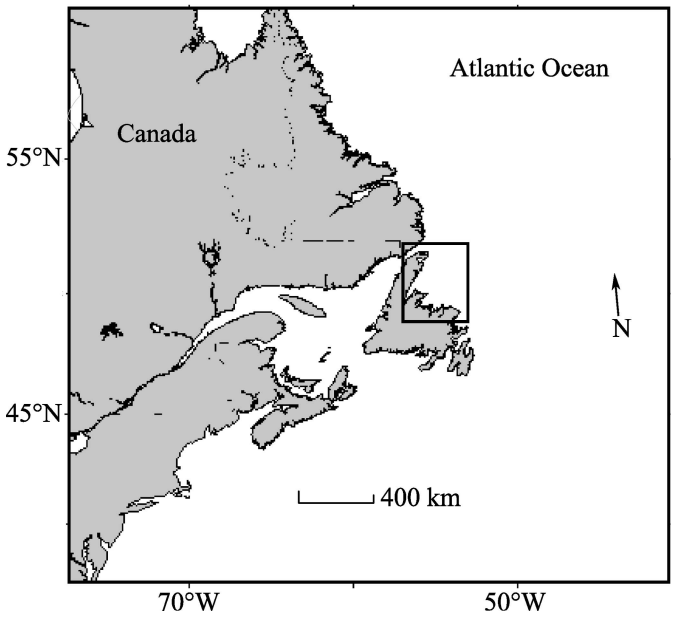

Fig. 1. Location of the Funk Island study area in the Northwest Atlantic off Newfoundland, Canada.

Atlantic mackerel: Data on Atlantic mackerel (*Scomber scombrus*) catches were obtained from the 'Preliminary Catch and Effort - Northwest Atlantic Fisheries Organization (NAFO) Division Report' from Fisheries and Ocean, Canada. Catch data were used for NAFO division 3K off the northeast Newfoundland coast, which fits well with our study area and has an excellent coherence with the foraging range of the gannets breeding on Funk Island.

Northern gannet diet—As in previous long-term studies of the feeding ecology of gannets (Montevecchi 2008), almost all prey were collected throughout the duration of research visits on the island by approaching roosts of breeding and nonbreeding gannets that often regurgitated as they moved off. A few data were obtained from observations of feedings and food scraps in the colony and from regurgitations from equipped birds when they were handled before and after recapture in the colony.

Table 1. Numbers and types of devices used and data retrieved from northern gannets foraging from Funk Island in the Northwest Atlantic.

Year	Device type	No. birds equipped	No. birds recaptured	No. birds with complete positions and dive data	No. birds with dive data only
2003	GPS TD	9	9	7	0
2003	PTD	7	6	0	3
2005	GPS TD	22	20	19	0
Totals	All devices	38	35	26	3

Data-logger applications—To equip birds with miniaturized data-logging units, adult gannets with 4–5-week-old chicks in their nests on the colony periphery were caught with a telescoping noose-pole from within a blind to reduce disturbance to neighboring birds. Recaptures took place the same way. In 2005, birds were weighed to the nearest 25 g before device deployment and after recapture. Two types of data-loggers (described below) were attached to 38 gannets to study foraging behavior, 35 were recaptured (Table 1). Equipped birds were marked on the head and neck with different-colored magic markers for identification from a distance. Devices were retrieved after 16–101 h in 2003 and after 14–88 h in 2005, with the aim to recapture birds after they had completed one or two foraging trips.

Precision temperature-depth (PTD) loggers: PTD loggers were 12 bit-multichannel data-loggers with 2-Megabyte memory, time, and sensors for pressure, internal, and external temperature (Earth & Ocean Technologies). Temperature measurements were obtained from an external, fast-responding, temperature sensor that allowed sampling of the water column with minimal time lag in thermal signals. A streamlined lightweight carbon-fiber–composite casing (outer diameter 19 mm, length 80 mm) weighed $\sim$ 23 g. Recording intervals for temperature and pressure were set at 1 s^{-1} (temperature resolution 5 mK, absolute measurement uncertainty $\pm$ 0.03 K; pressure resolution 2.5 hPa [corrected to $\sim$ 2.5-cm water column], absolute uncertainty $\pm$ 20 hPa, reduced to about 10 hPa after surface baseline correction [corrected to $\sim$ 10-cm water column]).

Global Positioning System - Temperature Depth (GPS TD) loggers: GPS TD loggers were 12-bit multichannel data-loggers with 2-Megabyte memory (Earth & Ocean Technologies); max. length $\times$ width $\times$ height = 100 $\times$ 48 $\times$ 24 mm, mass = 70 g. A streamlined aramide fiber epoxy-composite housing with O-ring-sealed cap contained a standard 3-V Lithium cell (type CR 123A). Latitude, longitude, speed, dilution of precision, time, and external temperature and pressure were recorded. The rapid-response external temperature sensor at the end of a flexible 20-cm stainless-steel sheath had resolution and uncertainty that were the same as for the PTD.

GPS position intervals were set at 3 min, resulting in positions every 3.25–3.33 min due to 15–20-s delays to uplink with the satellites. 90% of the fixes were accurate to within 19 m (according to manufacturer's specifications). Temperature and pressure data were obtained once per s.

Data-logger analysis—In 2003, spatial data were obtained from seven individuals. Three birds recorded one foraging trip, four birds recorded two trips. In 2005, spatial data were collected from 19 individuals: 15 gannets recorded one foraging trip, 4 birds recorded two trips. In terms of dive data, 2005 had the same sample size as only GPS TD loggers were used. In 2003, dive data were recorded from 10 individuals, 6 of which performed one trip only and 4 birds performed two trips.

Locations of birds at sea were examined in ArcView GIS 3.2. Foraging areas in both years were compared using kernel home-range analysis applying the Animal Movement Extension (Hooge and Eichenlaub 1997). We considered the 95%, 75%, and 50% probability polygons of dive locations to represent the overall, mean, and core foraging areas. Foraging range was calculated as the distance between the most distant location during the foraging trip and the colony. Total distance traveled is the sum of all flight paths performed by the bird, taking into account all flight segments irrespective of the final or most outbound position.

During foraging trips, activities of gannets were determined from movement speeds recorded by GPS data-loggers. Following Grémillet et al. (2004), movements $>$ 10 km h^{-1} were defined as flying periods, those $<$ 10 km h^{-1} as swimming periods. Movement speeds were ground-truthed by nocturnal swimming periods.

Kolgomorov–Smirnov two-sample tests were used to assess the frequency distributions of certain parameters. Due to small sample sizes, exact tests were applied for foraging range and foraging trip duration with a Monte Carlo calculation to determine *p*-values (SPSS 11.5).

To test for differences in key parameters of foraging and diving behavior, generalized linear mixed-effect models (GLMM) were applied (Faraway 2006). Data sets were first explored for possible sex differences; none were found for the two main dive parameters (mean dive depth; proportion of U-shaped dives) or for the two main foraging flight parameters (trip duration; range). Dives were classified as U-shaped if the birds stayed at more or less one depth, apparently not moving vertically to a considerable extent, for at least three depth measurements (Garthe et al. 2000, 2007*a*). All other dives were V-dives. All data were then tested for inter-annual differences. GLMMs accounted for multiple measurements of some individuals by including 'individual' as a random effect. Tests with quasi-Poisson error distribution were performed using the open-source software package R 2.7.1 (R Development Core Team 2008) and the LME4 library (Bates et al. 2008*b*). The quasi-

Table 2. Diets of northern gannets on Funk Island in 2003 (n = 348 regurgitations) and 2005 (n=210), given as percentages both by feeds and by biomass.

Fish species (scientific name)	2003 % feed	2003 % mass	2005 % feed	2005 % mass
Capelin (*Mallotus villosus*)	89.1	85.1	13.3	8.5
Atlantic salmon (*Salmo salar*)	6.3	6.8	—	—
Atlantic herring (*Clupea harengus*)	2.9	4.9	9.0	10.3
Atlantic mackerel (*Scomber scombrus*)	1.1	2.6	31.4	48.1
Cod (*Gadus morhua*) (discard)	0.3	0.3	—	—
Unidentified gadid (discard)	0.3	0.3	—	—
Atlantic saury (*Scomberesox saurus*)	—	—	45.7	32.8
Short-finned squid (*Illex illecebrosus*)	—	—	0.5	0.3

Poisson function was selected in the model frame to prevent overdispersion (Zuur et al. 2007).

Dives were analyzed using MultiTrace-Dive (Jensen Software Systems). Vertical immersions were considered dives when they were deeper than 0.3 m; with shallower measurements attributed to bathing and preening movements. There were no indications of foraging at the sea surface. From the variety of dive parameters investigated, only the most behaviorally relevant parameters were selected for statistical comparisons (i.e., mean dive depth, proportion of U-dives). All other parameters were excluded because of their high correlation with the parameters mentioned above.

Results

Observations: Diet and prey base—Gannet diets exhibited substantial inter-annual differences. Capelin comprised almost 90% of prey landings in 2003, but only 10% in 2005, when Atlantic mackerel and Atlantic saury (*Scombrus scomberesox*) were the major prey species (Table 2).

Total capelin detected per km of survey was less in 2005, when most were in dispersed, low-density shoals compared to 2003 (Table 3), due in part to capelin forming loose aggregations at the surface at night and also during daylight survey periods.

Table 3. Average aerial backscattering (s_a), a proxy of density, due to capelin per survey, along with percent of nonzero 100-m bins in each s_a range per survey. The s_a ranges due to capelin presented are 'very low' (1.0×10^{-9} to 1.0×10^{-7} m^2 m^{-2}), 'low' (1.1×10^{-7} to 1.0×10^{-5} m^2 m^{-2}), 'moderate' (1.1×10^{-5} to 1.0×10^{-3} m^2 m^{-2}), and 'high' (1.1×10^{-3} to 1.0×10^{-1} m^2 m^{-2}).

	2003	2005
Total s_a due to capelin	0.1275	0.0019
Total No. 100-m bins (survey length)	2429	1689
s_a due to capelin per km	0.00050	0.00001
Total No. of nonzero 100-m bins	152	1507
% nonzero bins	6.3	89.2
% of 100-m nonzero bins in each s_a range		
Very low	3.9	84.9
Low	72.4	14.9
Moderate	22.4	0.3
High	1.3	0.0

Catches by the commercial mackerel fishery in NAFO subdivision 3K were 40–50 times greater in 2005 than in 2003: inshore (55,000 kg in 2003; 2,821,000 kg in 2005), nearshore (552,000 kg in 2003; 21,381,000 kg in 2005). Body mass did not differ significantly before and after logger attachments (paired samples t-test, t = 1.04, df = 1, p = 0.34). From our hypothesis that prey bases drive the foraging tactics of marine avian predators and diets, we tested three derived predictions:

Prediction 1: Differences in diving behavior: Diving behavior varied markedly between 2003 and 2005, as shown by a variety of parameters (Table 4). Mean dive depth was significantly deeper in 2003 (χ^2 = 6.39, df = 1, p = 0.011, GLMM). Dives deeper than 10 m occurred only in 2003, when 19.1 m was the deepest dive recorded. Dives were also longer in 2003, and the proportion of U-shaped dives was significantly higher during 2003 than 2005 (χ^2 = 7.36, df = 1, p = 0.007, GLMM).

Prediction 2: Differences in spatial foraging patterns: Spatial patterns in foraging behavior differed in many ways between 2003 and 2005 (Table 5), and overall flight patterns exhibited remarkable spatial and geographic differences (Fig. 2). Foraging ranges appeared longer in 2005 (mean = 122 km) than in 2003 (mean = 62 km) but owing to high variability were not significantly different (χ^2 = 3.35, df = 1, p = 0.067, GLMM). However, the frequency distribution of individual foraging ranges differed significantly (Kolgomorov–Smirnov Z = 1.50, df = 1, p = 0.014; Fig. 3).

The geographic dispersion of diving behavior over the study area was even more obvious than the flight patterns (Fig. 4). Kernel home range analyses for feeding areas showed very large inter-annual differences being 34 times greater in 2005 compared to 2003: a 95% home range area of 532 km^2 in 2003 contrasting with 18,053 km^2 in 2005 based on an equal sample size of individuals and foraging trips (Table 5). On average, dives were not significantly further away from the colony in 2005 than in 2003 (χ^2 = 0.90, df = 1, p = 0.34, GLMM) due to much higher variability in 2005. Yet, the frequency distribution of dive distances from the colony was highly significantly different (Kolgomorov–Smirnov Z = 2.08, df = 1, $p < 0.001$; Fig. 5).

The distance between successive individual dives within foraging trips exhibited large (11.4 km in 2005 vs. 1.9 km in

Table 4. Various dive parameters for all dives performed by northern gannets foraging from Funk Island in the Northwest Atlantic during 2003 and 2005. Sample sizes: 2003: 14 foraging trips from 10 birds; 2005: 23 foraging trips from 19 birds.

	2003	2005
Mean (±SE) dive depth (m)	4.3±0.4	2.7±0.3
Mean max. (±SE) dive depth (m)	10.6±0.4	6.0±0.5
Max. dive depth (m)	19.1	9.7
Mean (±SE) dive duration (s)	10.1±1.0	5.0±0.2
Mean max. (±SE) dive duration (s)	20.6±2.5	9.9±0.9
Max. dive duration (s)	34	18
Mean per trip (±SE) of U-dives	52%±7%	7%±2%
Mean per trip (±SE) of V-dives	48%±7%	93%±2%

2003 on average; Table 5) and significant ($\chi^2 = 10.84$, df = 1, $p = 0.001$, GLMM) inter-annual variation.

Prediction 3: Differences in temporal foraging patterns: Foraging trips were not significantly longer in 2005 ($\chi^2 = 0.02$, df = 1, $p = 0.89$, GLMM), The frequency distribution of foraging trip duration was similar (Fig. 6), as were inter-annual differences (Kolgomorov–Smirnov $Z = 0.75$, df = 1, $p = 0.37$). Overall, variability in foraging trip duration was remarkable, ranging from < 4 h to almost 43 h (Table 5). Neither the number of dives per foraging trip ($\chi^2 = 0.05$, df = 1, $p = 0.82$, GLMM) nor intervals between individual dives within foraging trips ($\chi^2 = 0$, df = 1, $p = 1$, GLMM) showed any inter-annual differences (Table 5). On average, gannets flew 17% more of the time during a foraging trip in 2005 than in 2003 ($\chi^2 = 9.34$, df = 1, $p = 0.002$, GLMM; Table 5).

Summary—Predictions 1 and 2 were strongly supported. Prediction 3 was rejected with the only difference in the temporal patterns of foraging behavior being the higher proportion of flight activity during foraging trips in 2005.

Combining spatial and temporal features of foraging, there was a clear relationship between the foraging range and foraging trip duration in 2005 (Linear Model [LM], $t = 8.35$, df = 1, $p < 0.0001$) but not in 2003 (LM, $t = 0.41$, df = 1, $p = 0.69$; Fig. 7).

Discussion

Our results document that the foraging behavior and ranges used by northern gannets from the same colony are markedly different in years when prey availability in the colony vicinity differs. There were differences in almost all foraging parameters investigated, most notably in spatial patterns and least notably in temporal patterns. Although the sample size of birds was relatively low in 2003, individuals for whom two successive foraging trips were recorded behaved according to this pattern and returned almost to the same sites as on their respective previous trip (*see* also fig. 3 in Garthe et al. [2007*b*] and table 3 in Montevecchi et al. 2009). Again, this stood in contrast to the birds that were telemetered for two foraging trips in 2005, exhibiting variable target locations. Home range was > 30 times larger in 2005 when large pelagic fishes were available than in 2003 when they were not and capelin were the major prey. These sharp contrasts in foraging patterns coincided with differences in diving behavior and diet. In terms of oceanography and prey availability, warmer water conditions that facilitated the movement of large migratory warm-water fishes, such as Atlantic mackerel and Atlantic saury into the region prevailed in 2005 (Fig. 8). As a reflection of this, 2005 witnessed the first significant commercial fishery for mackerel in 16 yr. These warm-

Table 5. Various parameters for the foraging trips performed by northern gannets from Funk Island in the Northwest Atlantic in 2003 and 2005.

	2003				2005			
Parameter	Mean±SD	Range	No. ind.	No. trips	Mean±SD	Range	No. ind.	No. trips
Foraging range (km)	62±12	[51–92]	7	11	122±81	[25–269]	19	23
Total distance traveled (km)	177±49	[108–264]	7	11	353±222	[73–742]	19	23
Foraging trip duration (h)	14.9±5.0	[3.8–25.0]	10	14	17.3±9.6	[4.3–42.8]	19	23
No. of dives per foraging trip	18±11	[1–38]	10	14	20±17	[1–76]	19	23
	Mean±SE	Range	No. ind.	No. trips	Mean±SD	Range	No. ind.	No. trips
Inter-dive distance (km)*	1.9±0.4	[0.4–5.3]	6	10	11.4±2.3	[1.4–38.3]	18	22
Inter-dive interval (min)*	44±12	[4–133]	6	10	46±6	[6–103]	18	22
Percentage flying during foraging trips	27±3	[16–56]	7	11	44±3	[16–87]	19	23
	Area		No. ind.	No. trips	Area		No. ind.	No. trips
Home range estimate of foraging area (km²)†:								
95% kernel home range	532		7	11	18,053		7	11
75% kernel home range	130		7	11	9,178		7	11
50% kernel home range	67		7	11	3,764		7	11

* Calculations were done first per bird and trip and then over the respective means. Sample sizes in both years were reduced by one, because in both years one trip each consisted of just a single dive.

† The sample size in 2005 was reduced to match the sample size in 2003 (individuals were randomly selected). If calculated for the whole data set ($N = 19$, n=23), the respective kernel home-range values would be 29,094 km², 10,154 km² and 3,954 km².

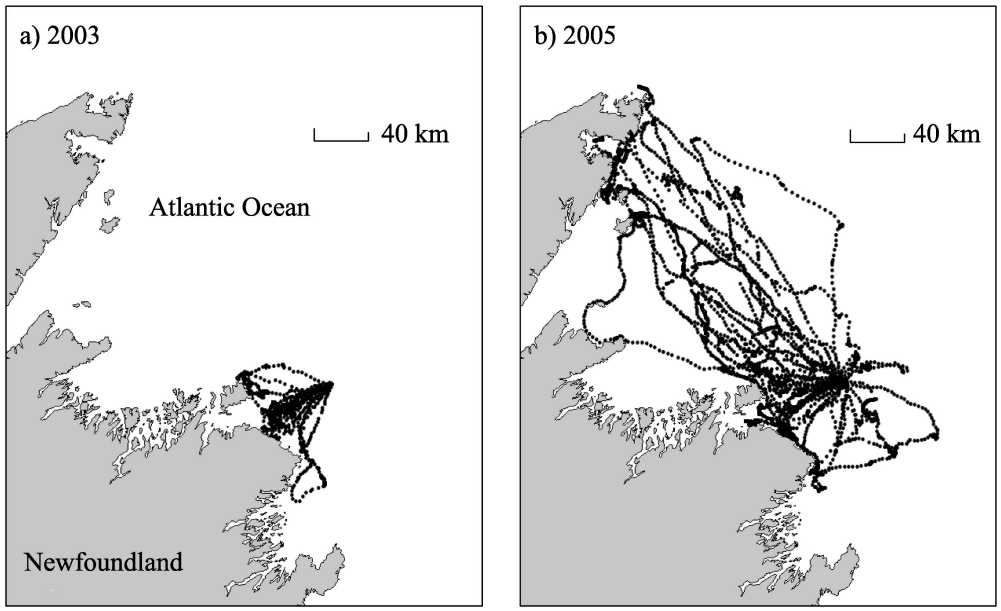

Fig. 2. Flight tracks from Funk Island of northern gannets equipped with GPS loggers in (a) 2003 and (b) 2005.

water pelagic fishes were not present during 2003, when smaller cold-water capelin were the sole prey that gannets used to provision offspring.

Compared to our previous study (Garthe et al. 2007*a*), which demonstrated longer and more variable foraging trips from a large colony (Bonaventure Island in the Gulf of St. Lawrence) than from the smaller colony on Funk Island, here we show a striking inter-annual change in foraging range at the same colony, which corresponds to a change in ocean conditions and prey availability. The spatial foraging patterns exhibited by gannets at Bonaventure in 2003 were similar to those shown here for Funk Island in 2005. In both cases, diets were clearly dominated by large pelagic fish species. So even though the colony on Bonaventure Island is about five times larger than the one on Funk Island (J. W. Chardine and J.-F. Rail pers.

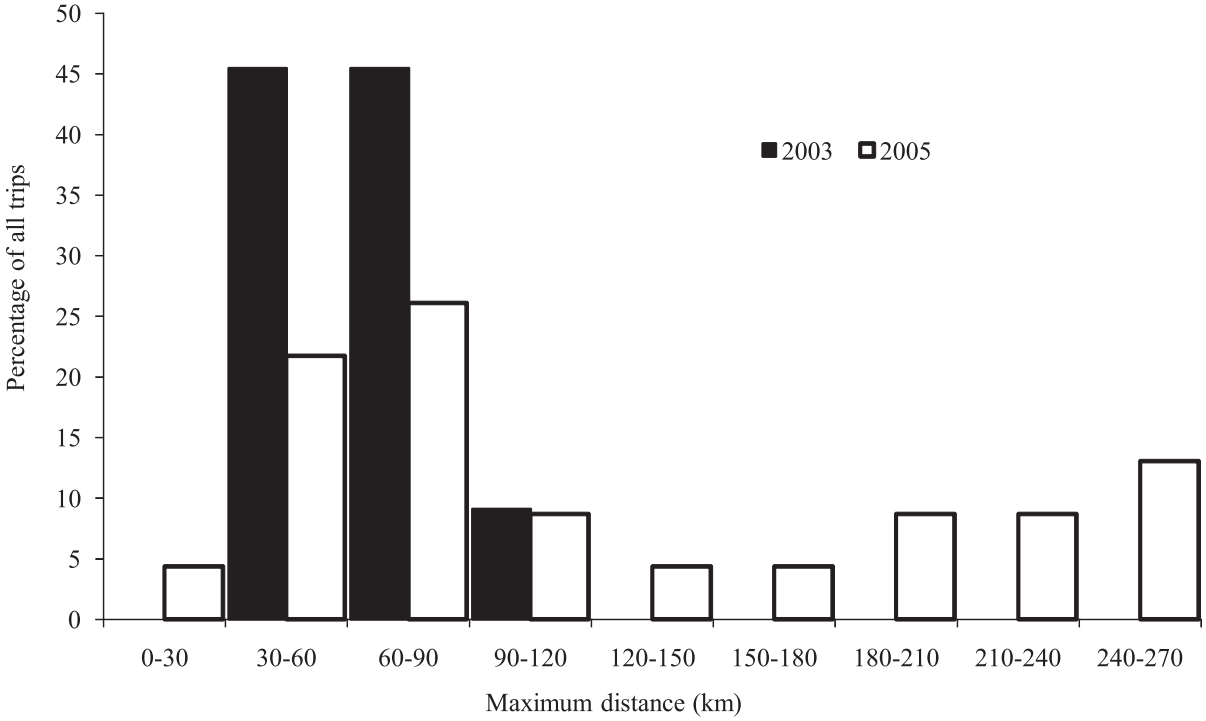

Fig. 3. Frequency distribution of foraging ranges of northern gannets from Funk Island in (a) 2003 (n = 11 trips) and (b) 2005 (n = 23 trips).

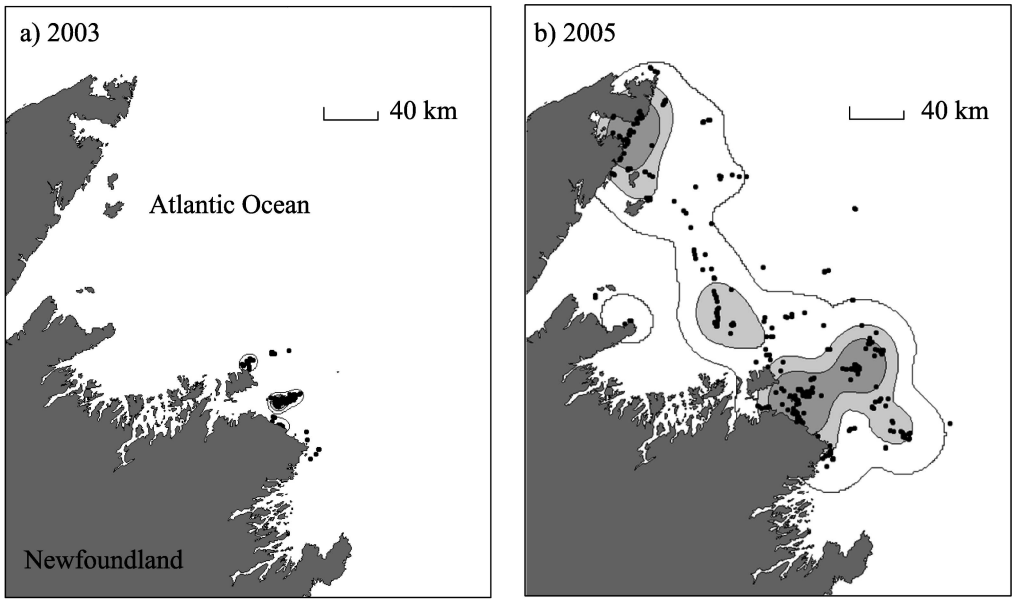

Fig. 4. Locations of the diving activities by northern gannets foraging from Funk Island in (a) 2003 and (b) 2005. The dots show the position of all dives, the kernel polygons indicate 95% (dark grey), 75% (light grey), and 50% (white) foraging home ranges.

comm.), the foraging patterns of northern gannets from Funk Island in 2005 were much more similar to those used by gannets from Bonaventure than those from the same colony on Funk Island just 2 yr previously.

The inter-annual comparison of Funk Island data provides a strong demonstration of the foraging flexibility that generalist and opportunistic avian predators use in coping with variation in their highly dynamic pelagic prey

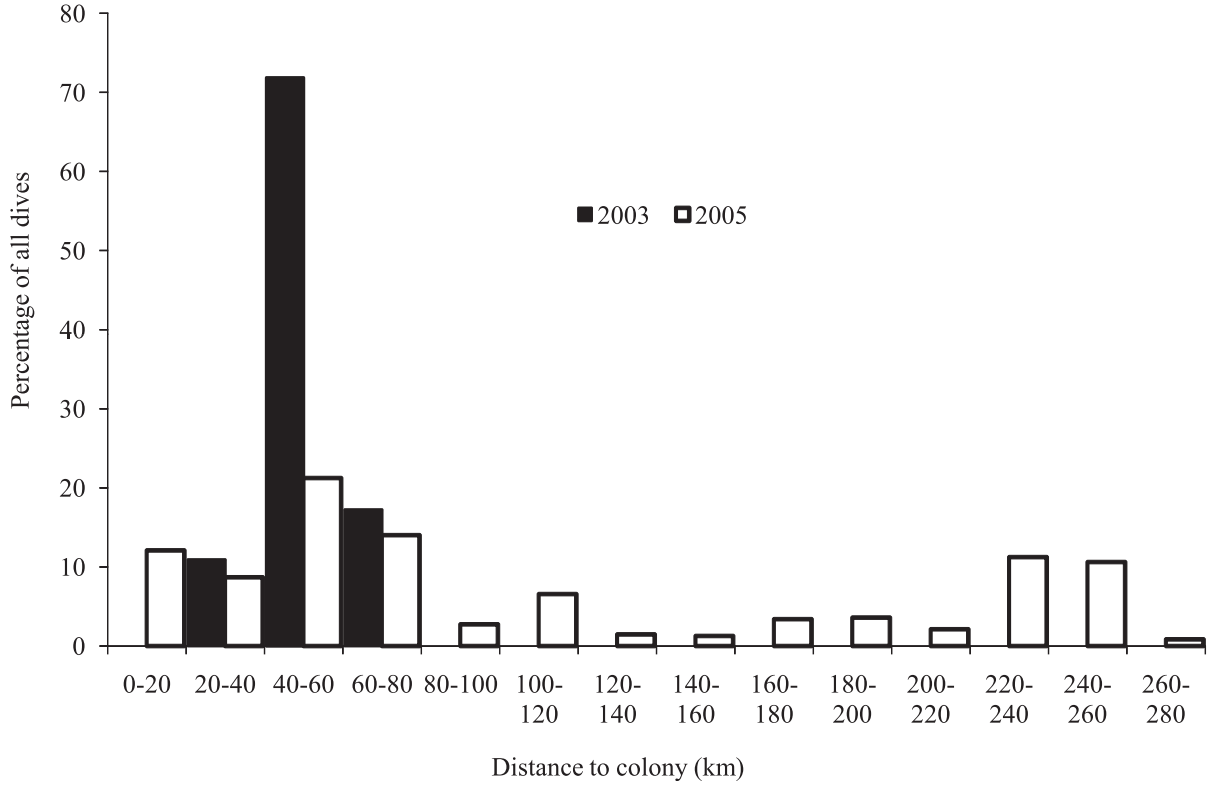

Fig. 5. Frequency distribution of the distances of dives from the gannet colony on Funk Island in (a) 2003 (n = 174 dives) and (b) 2005 (n = 471 dives).

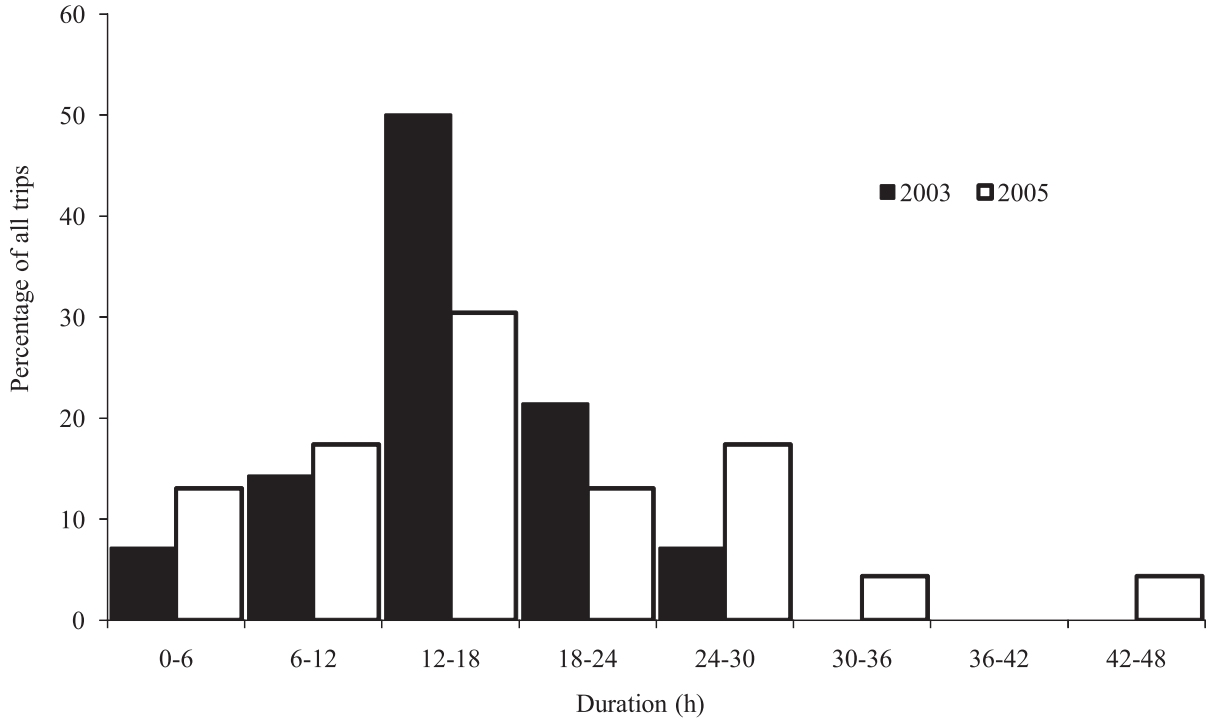

Fig. 6. Frequency distribution of foraging trip durations of northern gannets from Funk Island in (a) 2003 (n = 14 trips) and (b) 2005 (n = 23 trips).

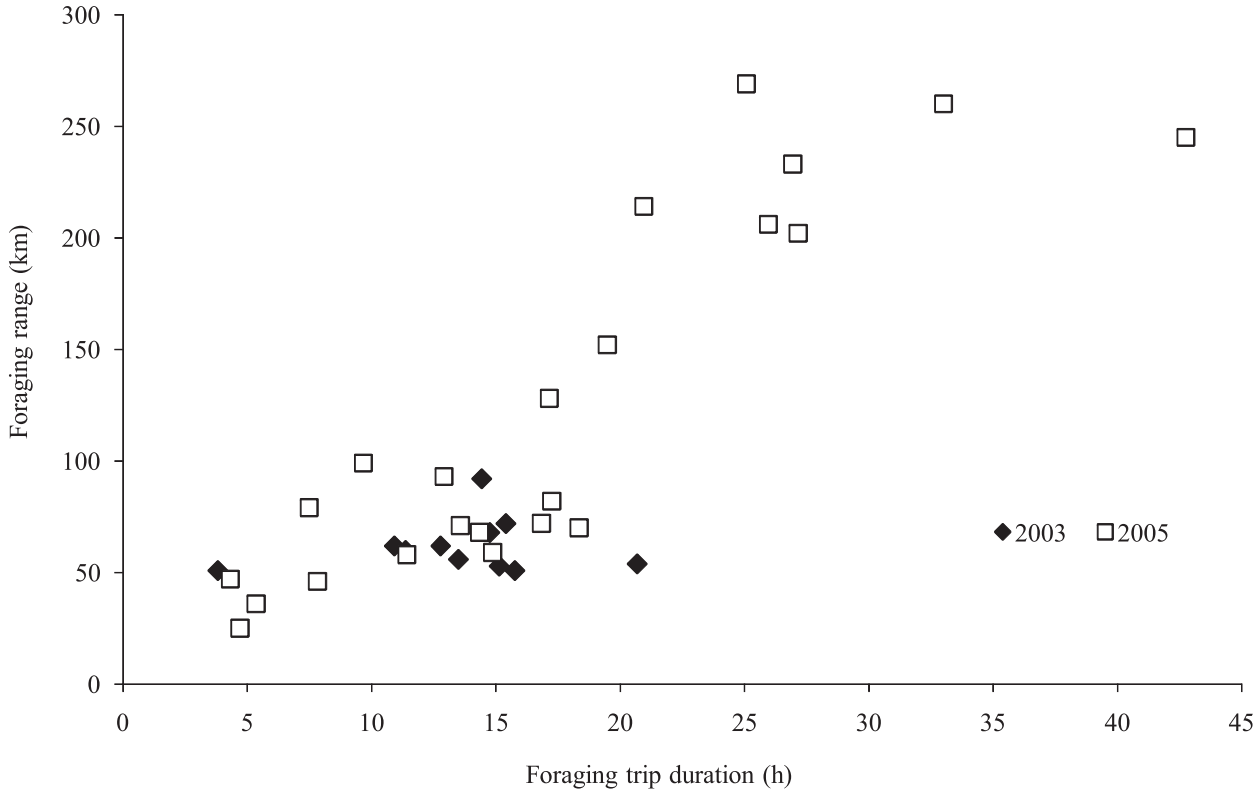

Fig. 7. Relationship between foraging range and foraging trip duration of northern gannets foraging from Funk Island in 2003 (black diamonds) and 2005 (white squares).

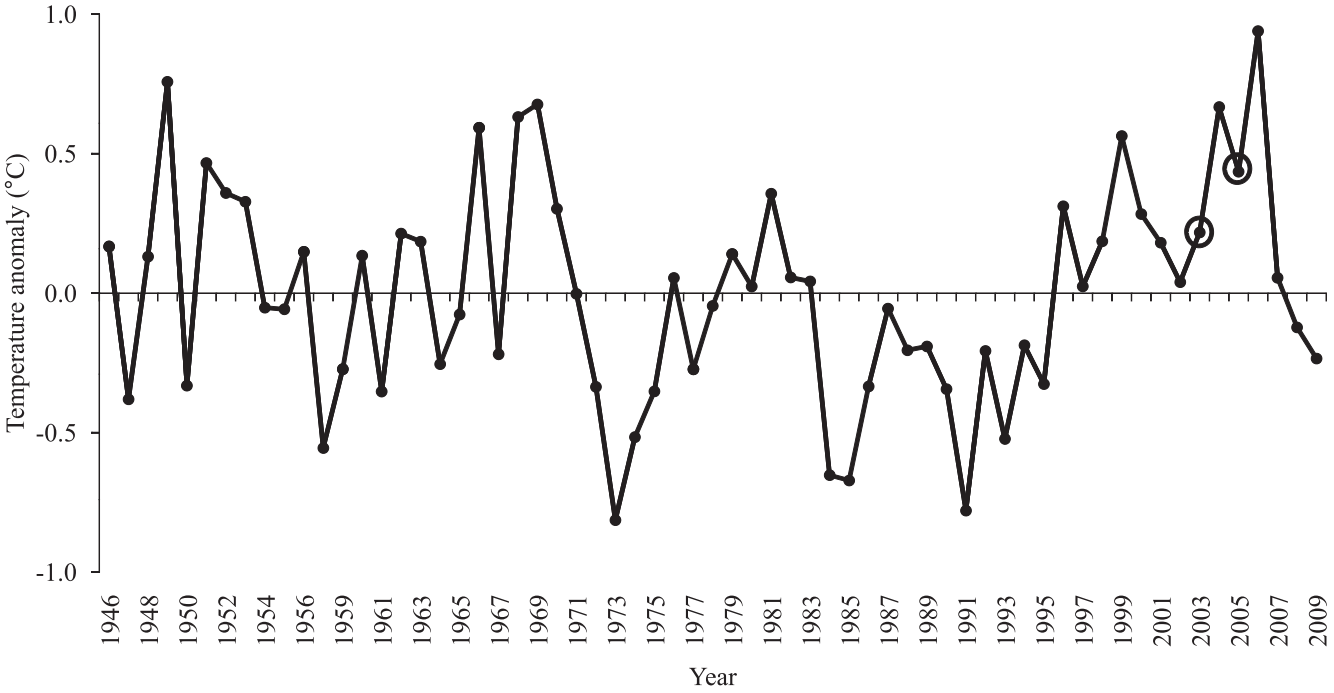

Fig. 8. Mean annual temperature anomalies for 1946–2009, using the standard January to June index from 0 m to 150 m, at Hydrographic Station 27 east of St. John's Newfoundland in the Avalon Channel of the Labrador Current. The two study years are indicated by squares.

fields. During the past 20 yr, the gannet colony has continued to grow, despite radical oceanographic perturbations and shifts in pelagic food webs (Montevecchi 2008). Foraging flexibility is a widespread seabird characteristic. For example, Harding et al. (2007) have shown that common murres are capable of buffering offspring from strong variations in food availability by adjusting their daily effort to maintain a consistent provisioning rate. Similarly, black-headed gulls (*Larus ridibundus*) switch between marine and terrestrial prey for chicks, depending on colony location and food accessibility (Schwemmer and Garthe 2008).

It is important to emphasize that inter-annual variability such as shown in this paper can override differences found in studies of foraging range among different-sized colonies. It is also notable that at the same colony, no significant relationship could be established between foraging distance and foraging trip duration in 2003, in strong contrast to 2005 when this was so. Potential relationships between colony size and foraging range can only be unraveled by combining data on the foraging behavior of the birds with data on prey availability. Inter-colony and inter-annual variability in prey availability need to be accounted for to make inferences about the associations of foraging range and colony size. As well as intraspecific competition, prey depletion, and interference as density-dependent responses to increasing colony size, factors associated with changing oceanography and prey fields clearly influence central-place foraging patterns. These latter factors are highly sensitive to climate (Montevecchi and Myers 1997) and, hence, can be expected to change in view of ocean climate models that predict increasing environmental variability and extreme weather events (Bates et al. 2008*a*). Interestingly, the temporal parameters associated with trip duration are apparently much more conservative and support colony-size effects as has been reported by Lewis et al. (2001) but warrant further investigation on the mechanisms acting here.

Studies employing bird-borne tracking, behavioral, and environmental recording devices add new dimensions to studies of foraging ecology in particular and to colony size influences in general. Research is needed to better understand environmental influences including colony size on predator foraging tactics and most importantly on the mechanisms that produce intraspecific and geographic differences. Different prey fields require seabirds to alter search patterns and feeding techniques (Harding et al. 2007). Different diving behavior by the gannets was associated with different prey types, as has been shown in other species such as rockhopper penguins (*Eudyptes chrysocome*; Tremblay and Cherel 2000) and thick-billed murres (*Uria lomvia*; Elliott et al. 2008).

In conclusion, our study revealed substantial inter-annual variation in foraging tactics by the same species at the same colony. This variability was strongly related to prey availability, indicating that foraging parameters are determined to a large extent by oceanographic and prey field conditions that are independent of colony size.

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