Flexible foraging tactics by a large opportunistic seabird
preying on forage and large pelagic fishes

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ABSTRACT: Generalist and opportunistic marine predators use flexible foraging behaviour to
exploit prey bases that change in diversity and spatial and temporal distributions. Behavioural
flexibility is constrained by individual cognitive and physical capabilities, age, reproductive
condition, central place foraging, etc. To assess flexibility in the foraging tactics of a marine bird,
we investigated the diets and foraging behaviour of the largest seabird predator in the North
Atlantic Ocean. Northern gannets Sula bassana exploit a broad spectrum of pelagic prey that range
in mass by more than two orders of magnitude. We investigated their foraging activity at their
largest offshore colony in the western Atlantic during 1998-2002, when they preyed primarily on
shoals of spawning and post-spawning capelin Mallotus villosus, a small forage fish (~15 grams),
and also on a much larger pelagic fish, post-smolt Atlantic salmon Salmo salar (~200 grams). Inter-
annual dietary variation is associated with gannet and prey fish distributions. Landings of capelin at
the colony by gannets were correlated with returns of larger foraging flocks from inshore, whereas
landings of Atlantic salmon were associated with smaller flocks returning from offshore. Maximum
foraging trip distances ranged from 20 – 200 km and averaged 57 ± 12 (SE) km, consistent with
distances to inshore capelin aggregations. When capelin abundance was low (2002), more gannets
foraged offshore, preyed on large pelagic fishes (mostly Atlantic salmon), and exhibited greatest
dietary diversity. Though the outbound portions of foraging trips were more sinuous than inbound
routes, individual gannets exhibited general fidelity to foraging sites. These large avian predators
used flexible foraging tactics to adjust to changing prey conditions and to generate longer-term
strategies to take advantage of diverse trophic interactions over a range of ocean ecosystems.
INTRODUCTION

Predators behave opportunistically to take advantage of changing prey and environmental conditions. Many apex marine predators exhibit flexible foraging behaviour to exploit shifting prey diversity and their changing spatial and temporal distributions (Croxall 1987, Bowen et al. 2006, Watanuki et al. 2008). This behavioural flexibility is mediated by the decision-making of individual predators each being constrained by its own cognitive and physical capabilities. Individuals bring both transient and steady-state behavior to navigate their daily lives in dynamic marine environments (Ollason et al. 2006). Breeding seabirds are further constrained by working to meet the increasing energy demands of offspring while foraging from a fixed colony-site (Orians & Pearson 1979).

Among large seabird predators, gannets employ flexible tactics to capture a variety of ephemeral pelagic prey that can vary in mass from tens to many hundreds of grams (Montevecchi & Berruti 1991, Bunce 2000, Hamer et al. 2001). They also scavenge discards and offal from fishing vessels (Burger & Cooper 1984, Garthe et al.1996). The largest gannet and the largest North Atlantic seabird, the northern gannet (Sula bassana) delivers loads of from one to tens of prey (numbers inversely related to prey mass that range from < 10 to > 500 grams) to rapidly growing, lipid-loading chicks during a 13-week nestling period (Montevecchi et al. 1984). Chicks are fed primarily large oily pelagic fish (e.g. mackerel Scomber scombrus, herring Clupea harengus) and at times small forage fishes (e.g. capelin Mallotus villosus, sandeels Ammodytes spp.; Nelson 1982, Montevecchi & Myers 1995, Garthe et al. 2007b).
Associated with a centennially anomalous cold water perturbation in the northwest Atlantic during 1991 (Drinkwater 1996), gannets switched from preying on large migratory, warm-water species (mackerel, Atlantic saury *Scomberesox saurus*, short-finned squid *Illex illecebrosus*; their dominant prey during the late 1970s and 1980s) to cold-water fishes, primarily capelin, for longer than a decade (Montevecchi 2007). Throughout this period, gannets have successfully provisioned offspring, and their populations in the Northwest Atlantic have grown substantially (Chardine 2000).

In this paper, we integrate different levels of dietary and behavioural analyses to highlight the foraging tactics of gannets, when preying on small forage fishes (capelin) and large pelagic fishes (Atlantic salmon *Salmo salar*) during 1998-2002. Inter-annual variation in diets is compared with concurrent avian and capelin distributions and densities obtained from vessel surveys during 1998-2002. Off the northeast Newfoundland coast, capelin shoals exploited by avian and mammalian predators often persist in fixed locations (Davoren et al. 2003b), and we assessed the gannets’ fidelity to foraging areas (e.g. Hamer et al. 2001, Watanuki et al. 2003) by comparing the directions and distances of successive trips by the same individuals equipped with compass loggers. The returning directions and sizes of foraging flocks were related to landings of capelin and of large pelagic fish, mostly Atlantic salmon, and foraging trip patterning was explored by comparing the fractal dimensions of outbound and inbound routes. Because seabirds often use different foraging strategies when provisioning themselves versus when gathering food for offspring (Weimerskirch et al. 1994, Davoren & Burger 1999), we compared the distances from the colony of terminal diving bouts on a foraging trip (chick provisioning dives) with the distances of previous diving bouts (presumably those for self-provisioning). We use this information to assess the flexible foraging tactics used by the largest seabird predator in the North Atlantic.

METHODS
Study site and period. Research was carried out on Funk Island (49° 45’ N, 53° 11’ W), a small
(800 x 400 m) flat granite rock in the northwest Atlantic (Montevecchi & Tuck 1987), about 50 km
off the northeast coast of Newfoundland (Fig. 1), Canada. The island has an estimated population of
9,800 pairs of northern gannets (Chardine 2000) and is the fourth largest and most oceanic of the six
gannet colonies in North America. Researchers were on the island from 4 - 17 August 1998, 26 July

Diet sampling. Food samples were obtained by approaching roosting gannets that often
regurgitated as they moved away from researchers (Montevecchi & Myers 1995). Samples were
also obtained from birds captured for data logger attachments and removals and from discarded
regurgitations and scraps in the colony. While there are likely differences between samples
collected in roosts and in the colony, samples from these sources are comparable (WAM unpub
data), and we opted to minimize disturbance to breeders by collecting regurgitations at roosts well
outside the colony. Regurgitated prey were identified to species, fresh fish samples were measured
for total length, and very fresh fish were weighed with spring scales. Prey landings are presented as
percentages of total regurgitations during each year.

360° scans for flocks returning to colony. From the island’s highest point near the northeast
end, using compass-directional binoculars, the numbers of gannets in incoming flocks were
recorded within each 45° sector during 360° scans at various times of day. Binoculars were held
with the horizon at mid-diameter as the observer slowly scanned the sector for 1-min. Three full
rotations (24 min) comprised a scan session. Wind speed and direction were recorded with a hand-
held anemometer and the directional binoculars at the outset of scans and if conditions changed also
at the end. Two or three observers counted each year, usually working in pairs with one person
counting and the other recording; counts were recorded on a portable tape recorder when a single
observer counted. Because observers worked in multiple years most often in pairs of the same
observers, and because data were analyzed in 90° quadrants, influences of individual differences
were minimized. Frequencies of returning foragers within 90° quadrants were compared on daily
and annual bases with chi square tests, and numbers were plotted as percentages of total counts.

Comparisons of the percentages of gannets returning from inshore (135° to 315°) and offshore (315° to 135°) directions were correlated with the numbers of regurgitations of the four most common prey (capelin, Atlantic salmon, Atlantic saury, herring) landed in the colony on the same day. The average sizes of flocks returning from inshore and offshore were compared with one-way analysis of variance.

**Vessel surveys and spatial distribution calculations.** A meso-scale (1 – 800 km) survey aboard the 23 m Canadian Coast Guard research vessel *Shamook* was run over 5 days within avian foraging ranges and prime capelin spawning and staging areas to the south and west of the Funk Island during July and August 2000 – 2002 (Fig. 1). Nine east-west cross-shelf transects 9 km apart on north-south axis were run during the 12 h d⁻¹ that the *Shamook* operated. Surveys were periodically interrupted to identify the species composition of acoustic signals using a modified shrimp trawl. The majority of fish sampled by mass were capelin in each year (2000: 96%; 2001: 71%; 2002: 55%).

During transects, vessel speed (11 - 16 km/h) was held constant and signals of prey species were recorded continuously using two hydroacoustic systems. For the 2000 survey, a Simrad EQ100 system was operated through a hull-mounted single 38 kHz beam transducer that operated at 1 ping per sec over a range of 250 m with a bandwidth of 0.4 – 0.6 ms. The transducer was at a depth of 3 m and acoustic signals were reliable at 8 m and deeper. The sample depth of the acoustic system (8 - 250 m) and vessel speed (14 - 16 km/h) were held constant throughout all surveys. Echograms were continuously printed and the relative abundance of fish was quantified by estimating the percent cover of the prey image in each 250 m by 10 m vertical bin (Piatt 1990). An index of percent cover of prey in each bin was estimated from 0 (no prey) to 9 (near-saturation). Values were squared before analysis (0 - 81) to account for the non-linear change in sounder intensity relative to fish school density (Piatt 1990), giving a relative measure of acoustic prey abundance.
During 2001 and 2002, a BioSonics DT 6000 hydroacoustic operated through a 38 kHz split-beam transducer in a towed body. The transducer had a 2-way beam angle of 22.671 dB and the echo sounder was operated at 1 ping per sec, a bandwidth of 5.1 kHz and a pulse duration of 0.4 ms. The transducer was at a depth of 5 m and the upper resolution of the acoustic signals (8-10 m) was well within the diving range of northern gannets to 20 m (Garthe et al. 2001). Vessel speed was maintained between 11 - 14 km/h. Raw high-resolution acoustic data (volume backscattering coefficients, $s_v$) were recorded continuously and used to derive a capelin biomass estimates ($g m^{-2}$; see Davoren et al. 2006). Variability in the quality of hydroacoustic systems used and data processing techniques precluded comparing capelin abundance among years but allowed inter-annual comparisons of distributional patterns.

During acoustic transects, seabirds were counted continuously by a single observer in a 90° arc out to 300 m from the bow to the port side of the ship using standard strip methods (Tasker et al. 1984). Counts with behavioural descriptions (on water, flying, feeding) were entered on a laptop computer with counting software (D. Senciall, Birds & Beastly Counter, 1998, Fisheries and Oceans Canada, version 1.0) connected to the vessel’s navigational system. A latitude-longitude position was appended to each sighting.

**Capture of birds.** Adult gannets with 4– 6 week old chicks in their nests were captured with a telescoping noose pole from a small portable blind to minimize disturbance to neighbouring birds. We avoided capturing pairs with younger poikilothermic chicks as this was more disturbing to parents, and because parents with older chick had greater energetic demands. Pairs on the colony periphery were used to avoid disruption to the interior colony; to reduce possible sampling bias in potential differences between peripheral and interior nesting pairs, we captured birds in the third or fourth rows from the colony edge. Breeding success was high at the sites where we worked (WAM, SG per obs). Birds were captured, marked on the head and neck with colored markers for identification from a distance, equipped and banded with USFWS bands issued by the Canadian Wildlife Service usually within 5 – 10 min. We held the necessary university, provincial and federal
permits, and birds were treated in accordance with the guidelines of the Canadian Council on Animal Care.

**Data loggers.** Four types of data loggers were used on 24 breeding adults for a total of 49 foraging trips. Durations of attachments varied from 27 to 75 h. Lotek LTD_100 tags were attached to seven gannets that made 9 foraging trip in 1999. Dall’Antonia (DA) activity-depth recorders were deployed on seven gannets that completed 16 foraging trips in 2001, DA compass loggers were attached to seven gannets that completed 14 foraging trips in 2002, and Earth & Oceans compass Tlog devices (length = 65 mm, diameter = 16 mm, 14.5 g, 2 MB memory) with horizontal direction recorders were also used to track 10 successive foraging flight paths of three gannets in 2003 (2) and 2004(1). The data recording intervals set on each bird-borne device (below) allowed continuous recording for up to 3 - 4 days, and the weight of each device weighed < ~1% of a gannet’s body mass. With the exception of the Lotek LTDs (see below), all loggers were attached with Tesa® tape to feathers on the lower back about 5 cm above the uropygeal gland or atop four central tail feathers. When an equipped gannet was recaptured, devices were removed quickly, and data were downloaded onto a laptop computer.

**LTD loggers:** LTD_100 tags (Lotek Marine Technologies, St. John's, Newfoundland, Canada; 57 mm length, 18 mm diameter, 16 g, 1 MB memory) were attached with Tesa ® tape to two plastic bands on one leg. Activity was inferred from records every 30 s of thermal fluctuations (following Wilson et al. 1995, Garthe et al. 1999); dive depth data are reported elsewhere (Garthe et al. 2000, 2003). When temperature indicated sea surface temperature (SST) and remained constant, the bird was considered to be swimming or resting on the water with the logger submerged. When temperature varied slightly within the range of recorded air temperature (some degrees higher than SST), the bird was considered to be flying. When the temperature varied in higher ranges (as the logger was warmed by the bird’s and chick’s body heat and often solar and terrestrial radiation) and with other diurnal thermal rhythms, the bird was considered to be in the colony (i.e. at the nest most of
These occurrences were validated by observations using a spotting scope from outside the colony to check when marked birds carrying loggers were present at nest-sites (Garthe et al. 2003).

**DA activity-depth loggers:** Dall’Antonia devices (80 mm length, 22 - 31 mm width, 13 - 18.5 mm height, 28 g, 128 kB memory) recorded activity (from a motion sensor) every 6 s and depth (from a pressure sensor) every 4 s (Dall'Antonia et al. 1993, Benvenuti et al. 1998). In previous research (e.g. Garthe et al. 2000, 2007), we have demonstrated that U-shaped dives for capelin and V-shaped dives for large pelagic fishes like post-smolt Atlantic salmon are typically in excess of 4 s, and we are confident that we recorded the foraging dives by the gannets in our study. The activity sensor (a 5 mm diameter modified microphone membrane) was activated by flight signals produced by accelerations and/or body vibrations, caused by wing beats. During diving, signals are produced by wing and/or foot propulsions. Flight activity was identified on graphs as regular high-level deflections, easily distinguishable from the low-frequency signals produced when the bird is on the sea surface and from weak irregular or absent signals when the bird is at the nest. Devices were attached either to feathers on the lower back about 5 cm above the uropygial gland or the four central tail feathers with Tesa® tape.

**Compass loggers:** DA compass loggers (length = 93 mm, width = 22 - 33 mm, height = 15 - 20 mm, 33 g, 128 kB memory) with direction recorders, flight and pressure sensors and one with a flight recorder but no pressure sensor were used to track flight directions and activities (Benvenuti et al. 1998, 2001). Intervals between successive recordings were 6 – 8 s for both the compass and flight sensor and 4 s for the pressure sensor. Used in conjunction with satellite tags, these loggers indicated similar general foraging areas (Falk et al. 2001). Earth & Oceans compass Tlog devices (length = 65 mm, diameter = 16 mm, 14.5 g, 2 MB memory) with horizontal direction recorders were also used to track foraging routes. Intervals between successive directional records were 6 s.

**Foraging routes, ranges and diving activity.** Twenty-four compass routes from 10 parental gannets were plotted; one of these birds had four consecutive foraging routes recorded, three had three, five had two, and one had one route recorded. Foraging routes and ranges were reconstructed...
by multiplying an estimated average flight speed of 14.9 m s$^{-1}$ (54 km h$^{-1}$; Pennycuick 1997) by the
summed flight time along outbound and inbound foraging routes, time on water, a corrected
magnetic declination (-28°) and wind influences (wind speeds and directions were recorded at the
colony (above) and also obtained from the Environment Canada weather station at Pool’s Island
near the mouth of Bonavista Bay and within the gannets’ foraging range). Potential sources of error
include imperfect alignment of a device with a gannet’s body axis, drift when birds are on water and
variable flight speeds in different wind conditions (Grémillet et al. 2004; Fifield & Montevecchi
unpubl data). For the seven gannets equipped in 2002, we estimated distances to all diving bouts
(groups of dives, excluding those shallower than 1 m, separated by long intervals of flying or
swimming) and from the last dives of a foraging trip to the colony. Points of maximum trip distance
were mapped for all 10 compass-equipped birds by extrapolating distances and directions from
Funk Island on a 1:250,000 map of the northeast Newfoundland coast.

Scanned images of foraging trip routes during 2002 printed on 27.9 x 43.2 cm paper were
subjected to box-counting fractal analysis using the HarFa Harmonic and Fractal Image Analyzer
(www.fch.vutbr.cz/lectures/imagessci/download/harfasp.html). Fractal dimensions of the a) entire
route, b) outbound route to the most distant point and c) to the last or terminal dive, d) inbound
route from the most distant point and e) from the last or terminal dive. Fractal dimensions of b
versus d and of c versus e were compared with t-tests for related samples and with binomial tests of
differences (Siegel 1957). We describe the number and temporal and spatial patterning of diving
bouts performed throughout trips; depth profiles of different diving patterns are reported by Garthe
et al. (2000). We also assessed the consistency of foraging route directions on successive trips by 10
individual gannets.

RESULTS
Prey landings. Capelin comprised 77% of the prey loads returned to the colony, ranging from 51 to 100% on per annum bases from 1998 – 2002 (Table 1). Atlantic salmon was the next most common prey with high annual variation ranging from 0 to 34% of landings. Atlantic saury, herring and mackerel made up relatively minor dietary components. During 1998 – 2000, capelin comprised more than 80% of prey landings, though the situation was somewhat different in 2001 and very different in 2002, when Atlantic salmon made up significant dietary components and when dietary diversity was greatest (Table 1). Gannet landings of capelin contained six to 20 fish compared to landings of salmon that contained one to three much larger fishes.

Directions and sizes of returning flocks and prey landings at colony. The flight directions of incoming gannets are shown in Fig. 2. In all years, most birds returned to the colony from inshore foraging sites southwest of the island, except during 2002 when most returned from offshore sites north of the colony ($\chi^2 = 902.7$, df = 12, $p < 0.001$).

Comparisons of the directions of returning birds and proportions of prey species landed at the colony revealed significant relationships between inshore returns and landings of capelin ($Y = 0.49X + 38.5$, n = 12, $R^2 = 0.33$, $p = 0.049$) and between offshore foraging and landings of Atlantic salmon ($Y = 1.15X + 19.1$, n = 12, $R^2 = 0.60$, $p = 0.003$; Fig. 3). No relationships for other common prey (herring, Atlantic saury) were detected ($p > 0.05$). The sizes of flocks returning from inshore were significantly larger than those returning from offshore in each year and in all years combined (Fig. 4). Flock sizes were lowest in the year (2002) when capelin was least abundant.

Distributions of gannets along vessel transects. Observers on research vessels noted consistent general travel routes of gannets to and from Funk Island from areas southwest of the colony. Capelin abundance was substantially lower in 2002, showing a 7-fold decrease from 2001 (Fig. 5; Table 2). The number of gannets per km along the survey route was also significantly lower during 2002, being less than a third of those recorded in 2000 and 2001 (Table 2). Interestingly, 2002 was the only year when more foragers returned from offshore areas north of the island (Fig. 2) and the year when most Atlantic salmon were landed at the colony (Table 1).
Foraging trips, range and area. Foraging trips consisted of alternated series of flights and stops of variable durations that include dives and sitting on the water, with one or two longer flights performed most often at the beginning and end of the trips. Most diving activity occurred during the middle segments of foraging flights ($\chi^2 = 48.26$, df = 4, $p < 0.001$; Fig. 6), indicating that there was little foraging activity in close proximity to the colony. Colony departures occurred between sunrise and sunset with no apparent diurnal concentration (see also Garthe et al. 2003). Foraging trip durations of birds with compass loggers were variable, ranging from 3.3 to 26.2 hr, with mean and median durations of $9.5 \pm 5.8$ ($\pm$ SD) and 8 hr (Table 3). Birds that departed in the morning usually returned before sunset, whereas those that left in the afternoon usually remained at sea overnight and returned the next morning.

On foraging trips, gannets with compass loggers spent about half (49%) of the daylight time away flying, with a range from 31 to 71%. Birds remained on the water and did not fly after dark. Total flight durations ranged between 1.9 and 13.7 hr, with mean ($\pm$ SD) and median durations of $3.8 \pm 3.0$ and 2.9 hr. Time spent flying increased with trip duration ($r = 0.90$, $n = 14$, $p < 0.001$), indicating more travelling and potentially more searching on longer foraging trips. The more birds dived the longer they rested on water after diving ($r = 0.82$, $n = 18$, $p < 0.001$ for first dive bouts, and for all dive bouts $r = 0.53$, $n = 75$, $p < 0.001$).

Based on a flying speed of 54 km h$^{-1}$ (Pennycuick 1997), values for maximum outbound distances from the colony (foraging range) on individual trips during 2002 averaged ($\pm$ SD) $61 \pm 44$ km ($n = 14$ trips; median and mode = 50 km and ranged from 30 - 200 km (Table 4, Fig. 7). Estimated flight distances between the colony and the first feeding site ranged from 10 - 193 km.

Foraging ranges were shorter in 2003 and 2004, when capelin again predominated gannet landings (Montevecchi 2007), and averaged $41 \pm 21$ km ($n = 10$ trips; Table 4).

The mean number of activity changes from swimming to flying and vice versa was significantly greater on outbound (5.3) than on inbound flights ($t = 2.986$, $n = 24$, $p = 0.007$). The mean ($\pm$ SD) fractal dimensions of outbound flights ($1.29 \pm 0.12$) were not significantly different from those
of inbound ones (1.24 ± 0.13; t = 0.12, n = 14, p > 0.05) nor were the mean (± SD) fractal
dimensions foraging routes out to (1.26 ± 0.14) and back from terminal dive bouts (1.18 ± 0.15; t =
0.12, n = 14, p > 0.05). Yet, 11 of 14 outbound routes had higher fractal dimensions than
the corresponding inbound routes on the same trips by the same individuals (binomial test, p = 0.029),
and 10 of 12 routes to the terminal dive bout had higher fractal dimensions than their corresponding
inbound routes (binomial test, p = 0.019).

There was no significant difference in the average (± SD) number of dives during the last or
terminal diving bouts of a trip (5.1 ± 4.1, range = 1 – 16) compared to previous diving bouts on the
same trip (4.7 ± 7.2, range = 1 – 30; F = 0.61; df = 1,31, p > 0.05). Eleven of 12 terminal diving
bouts involved multiple dives compared to 10 of 19 previous diving bouts on the same trip ($\chi^2 =
5.13, df = 1, p = 0.024$). On a foraging trip, the time spent resting on the water after terminal diving
bouts (20.8 ± 23.0 min) was about half that than after previous diving bouts (36.8 ± 31.5 min)
though owing to variability this tendency was not statistically significant (t = 0.157, df = 1,12, p >
0.05).

Individual gannets returned to the colony from all directions, ranging from 30° t 355° (Table 4).
Consistent with the scan data in 2002, mean (± SD) and median return directions of foraging flocks
were 187° ± 100° and 200°. Six of seven successive trips were within 90° of one another, and the
average difference in flight direction between successive foraging trips by the same individual was
45° ± 17° (Table 4). Again in 2003 and 2004, mean and median return directions of foraging trips
were from the south at 181° ± 78° and 192°. As well, six of seven of foraging trips by three
individuals tracked during 10 foraging trips a were also within 90° of one another, averaging 46° ±
35° directional differences between successive foraging trip (Table 4). Combing data for the 10
compass-equipped gannets, the average and median directions of returning foraging flocks were
191° ± 92° and 200°, and the overall mean angular deviation between 14 successive foraging trips
by these individuals was 43° ± 40°, with a median angular difference between successive trips of
34°.
DISCUSSION

Responses of gannets to device attachments

Birds were likely influenced by device attachments. Yet as in our other studies that have employed some of the same attachments on gannets in this same colony, there was little evidence to indicate deleterious effects (Garthe et al. 2000, 2003, 2007a). Following attachments, birds returned quickly to nest-sites, and parental behaviour, feeding and chick care and condition appeared normal. The foraging trip durations of equipped birds were not significantly different from those of their unequipped mates (Garthe et al. unpubl.). Of 24 birds equipped with loggers, only three were not recaptured (two of these were at sea when we had to depart the island due to weather), indicating that the stress related to capture, handling and attachments was surmountable. The other bird that we did not recapture had an approximately 8-day old chick that was knocked from the nest and died. This was the only chick mortality observed during the study, and the only time we equipped a bird with a chick this young.

Prey exploitation

Following a centennially-significant cold water perturbation in 1991 (Drinkwater 1996), large warm-water pelagic fishes and squid did not migrate into the region and the dietary diversity of gannets decreased markedly (Montevecchi & Myers 1995). During 1998-2002, the gannets preyed mostly on capelin, which are among the smallest prey that they exploit, often carrying 20 or more in a single load. Most capelin were spent females and males, with very few gravid females. Male capelin are larger than females, but gravid females have the highest energy density (Montevecchi & Piatt 1984) and are the preferred prey of common murres (Uria aalge; Davoren & Montevecchi
Rather, the gannets’ landings likely reflect capelin availability (determined by temperature-dependent spawning times) within the constraints of their maximum 20 m dive depths and 200 km foraging ranges.

When capelin stocks decreased, gannets landed substantial numbers of Atlantic salmon and other large pelagic fishes. Salmon were a minor prey the gannets’ diets during the 1980s and 1970s but increased significantly after an anomalous cold-water perturbation in 1991 (Montevecchi et al. 2002, Montevecchi & Cairns 2003, Montevecchi 2007). Due to shifting pelagic food webs during the 1990s, the gannets’ prey options were fewer and their diet breadth narrowed.

**Foraging tactics and foraging sites**

Large seabird colonies occur in proximity to robust predictable prey fields, giving individuals opportunities to learn about productive foraging sites and to use memory-based foraging strategies (Hamer et al. 2001, Davoren et al. 2003b). Gannets from the large offshore Funk Island colony foraged consistently inshore when persistent shoals of capelin provided the bulk of their prey. Common murres from Funk Island and other large predators also forage consistently on these persistent inshore shoals of capelin, i.e. hotspots (Davoren et al. 2003a). During 2002, when these shoals were reduced in abundance and dispersed, more gannets foraged opportunistically offshore from the colony and exploited post-smolt Atlantic salmon.

Individual gannets showed consistency in successive foraging trips, returning to areas where they were recently successful (Benvenuti et al. 1998, Irons 1998, Hamer et al. 2001, Watanuki et al. 2003). Fidelity to feeding areas on successive foraging trips is indicative of memory-based foraging tactics. In the long-term such tactics could facilitate the development of behavioural “traditions” or hinterlands as has been demonstrated in other studies of seabird foraging ecology (Furness & Birkhead 1984, Cairns 1989, Grémillet et al. 2004; Garthe et al. 2007a).
Generally, the gannets used a mixed foraging strategy that involved a general fidelity to inshore areas and some wider offshore foraging when capelin were less available and when post-smolt Atlantic salmon moved through the area. Flocks returning from inshore sites were significantly larger than those from offshore, suggesting that it might also have been easier for gannets to exploit information (local enhancement) from conspecifics foraging inshore on concentrated shoals of capelin (Wittenberger & Hunt 1985, Fleming & Greene 1990). Larger inshore flocks are likely related to the high numbers of gannets foraging there, giving greater opportunity to return to the colony in linear aggregations thereby gaining aerodynamic and energetic benefits. Like other opportunistic generalists (Watanuki et al. 2004), the gannets integrated a mixed array of flexible and repetitive tactics to engage changes in prey availability driven by dynamic oceanographic conditions.

Foraging trip patterning

Gannets flew for about half of their daylight time at sea and stayed on the water at night (see also Hamer et al. 2001, Garthe et al. 2003). The longer birds were at sea, the more they flew and the farther they traveled. Gannets tended to make relatively long initial and final flights from and to the colony in the order of 50 to 60 km. Outbound flights were interrupted more by time on the water than were return flights. Following more intense diving bouts, gannets spent more time on the water, likely for digestion, resting and self-maintenance (Diamond et al. 1986); very long pauses likely follow self-feeding bouts and shorter ones followed by direct returns to the colony are indicative of chick-provisioning activity (see also Ropert-Coudert et al. 2004).

Prey depletion (Birt et al. 1987) and conspecific interference hypotheses (Hunt et al. 1986, Lewis et al. 2001) predict longer foraging ranges at large colonies. Maximum foraging distances of birds carrying compass loggers ranged between 10s and 100s of km with ranges that extended up to 262 km (Garthe et al. 2007a.). These ranges are similar to those of gannets nesting in Shetland
(Garthe et al. 1999) but shorter than those at larger colonies in the North Sea (Hamer et al. 2000, Lewis et al. 2001) and Gulf of St. Lawrence (Garthe et al. 2007a). Substantial inter-annual changes in foraging ranges from a single colony are also associated with major shifts in prey bases (Garthe & Montevecchi 2007).

Coping with changing prey conditions

Gannets use flexible tactics to cope effectively with changes in prey availability and diversity over seasonal, annual and decadal scales. In the northwest Atlantic, the prey landings of gannets shifted from a predominance of large migratory warm-water pelagic fishes and squid during the 1970s and 1980s, to what appears to be a “default” diet of primarily small forage fish (capelin) through to 2004 (Montevecchi 2007). Yet this major alteration in feeding ecology and diet has had no negative influence on the gannets’ breeding populations that have grown considerably during these decades (Chardine 2000, pers. comm.).

Under lower availability of capelin (biomass, number of shoals) in 2002, gannets responded by foraging farther offshore. This is evidenced by foraging locations and lower densities and total numbers of gannets observed during the inshore vessel survey. Gannets caught more large pelagic fishes, increasing dietary diversity during 2002. The single gannet equipped with a compass logger that foraged offshore in 2002 exhibited the greatest effort of any bird in our study, i.e. highest percentage of time flying (63 %) and most dives during a foraging trip (66 % higher than the next highest effort). The gannets’ ability to alter their foraging strategies (e.g. foraging location, prey-type) under varying conditions (see also Watanuki et al. 2004) is essential for their success in a dynamic pelagic environment.

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Table 1. *Sula bassana.* Percentages of regurgitations of each prey species in regurgitations (numbers in parentheses) by gannets on Funk Island, 1998 - 2002

<table>
<thead>
<tr>
<th>Prey/Year</th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>1998-02</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capelin</td>
<td>84 (384)</td>
<td>87 (86)</td>
<td>100 (183)</td>
<td>72 (153)</td>
<td>51 (145)</td>
<td>77 (951)</td>
</tr>
<tr>
<td>Atl Salmon</td>
<td>1 (5)</td>
<td>0</td>
<td>0</td>
<td>25 (54)</td>
<td>34 (95)</td>
<td>12 (154)</td>
</tr>
<tr>
<td>Atl Saury</td>
<td>12 (56)</td>
<td>10 (10)</td>
<td>0</td>
<td>1 (3)</td>
<td>3 (9)</td>
<td>6 (78)</td>
</tr>
<tr>
<td>Herring</td>
<td>3 (15)</td>
<td>3 (3)</td>
<td>0</td>
<td>2 (4)</td>
<td>3 (8)</td>
<td>2 (30)</td>
</tr>
<tr>
<td>Mackerel</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>9 (25)</td>
<td>2 (25)</td>
</tr>
<tr>
<td>Totals</td>
<td>100 (460)</td>
<td>100 (99)</td>
<td>100 (183)</td>
<td>100 (214)</td>
<td>100 (282)</td>
<td>99 (1,238)</td>
</tr>
</tbody>
</table>
Table 2. *Sula bassana* and *Mallotus villosus*. Number, aggregation scales and tracking scales of northern gannets to capelin and the number, density, biomass estimates, and aggregation scales of capelin within the survey area in 2000, 2001, 2002. A different hydroacoustic technique was used in 2000 (see Methods), so capelin biomass could not be quantified and compared with 2001 and 2002.

* = significant difference

<table>
<thead>
<tr>
<th></th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. gannets *1</td>
<td>685</td>
<td>962</td>
<td>220</td>
</tr>
<tr>
<td>% Flying</td>
<td>65</td>
<td>70</td>
<td>94</td>
</tr>
<tr>
<td>% Plunge diving</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>% Sitting on the water</td>
<td>34</td>
<td>29</td>
<td>6</td>
</tr>
<tr>
<td>Mean ± SE number of gannets per km *2</td>
<td>0.13 ± 0.03</td>
<td>0.10 ± 0.01</td>
<td>0.03 ± 0.01</td>
</tr>
<tr>
<td>No. capelin shoals</td>
<td>204</td>
<td>358</td>
<td>79</td>
</tr>
<tr>
<td>Mean capelin length (mm)</td>
<td>159.5</td>
<td>151.2</td>
<td>151.4</td>
</tr>
<tr>
<td>Mean capelin mass (g)</td>
<td>18.7</td>
<td>17.7</td>
<td>19.7</td>
</tr>
<tr>
<td>Mean capelin density (fish/m^2)</td>
<td>-</td>
<td>53.2</td>
<td>7.3</td>
</tr>
<tr>
<td>Total areas of the survey (x 10^6 m^2)</td>
<td>5,487</td>
<td>5,487</td>
<td>5,487</td>
</tr>
<tr>
<td>Estimated number of capelin (x 10^6)</td>
<td>-</td>
<td>291,942</td>
<td>39,821</td>
</tr>
<tr>
<td>Estimated biomass of capelin (t)</td>
<td>-</td>
<td>5,171</td>
<td>785</td>
</tr>
<tr>
<td>Survey Length (km)</td>
<td>610</td>
<td>431</td>
<td>373</td>
</tr>
</tbody>
</table>

*1 (χ^2 test: df = 4, χ^2 = 68.74, p < 0.0001); *2 (F = 5.963, df = 1020, p = 0.003)
Table 3. *Sula bassana*. Durations (hr) of compass logger attachments, foraging trips (and numbers of trips), and flight activity during each trip of 7 northern gannets rearing 4 to 6 week old nestlings on Funk Island during 2001.

<table>
<thead>
<tr>
<th>Gannet</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. trips</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Duration</th>
<th>Equipment attachment</th>
<th>29.3</th>
<th>51.1</th>
<th>44.0</th>
<th>44.0</th>
<th>49.9</th>
<th>40.2</th>
<th>51.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trip 1</td>
<td></td>
<td>5.8</td>
<td>14.4</td>
<td>9.1</td>
<td>3.3</td>
<td>12.1</td>
<td>5.4</td>
<td>5.7</td>
</tr>
<tr>
<td>Trip 2</td>
<td></td>
<td>6.7</td>
<td>4.7</td>
<td>4.9</td>
<td>14.5</td>
<td>26.2</td>
<td>11.9</td>
<td></td>
</tr>
<tr>
<td>Trip 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Flight activity</th>
<th>Trip 1</th>
<th>2.7</th>
<th>4.6</th>
<th>2.9</th>
<th>1.8</th>
<th>2.7</th>
<th>2.8</th>
<th>3.6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trip 2</td>
<td>2.7</td>
<td>2.9</td>
<td>1.9</td>
<td>5.1</td>
<td>13.7</td>
<td>3.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trip 3</td>
<td></td>
<td>2.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


Table 4. *Sula bassana*. Foraging trip directions and maximum distances (ranges) during first, second, third and fourth foraging trips by gannets equipped with compass loggers.

<table>
<thead>
<tr>
<th>Gannet</th>
<th>Direction (°)</th>
<th>Maximum Distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1st</td>
<td>2nd</td>
</tr>
<tr>
<td>2001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>200</td>
<td>190</td>
</tr>
<tr>
<td>2</td>
<td>355</td>
<td>345</td>
</tr>
<tr>
<td>3</td>
<td>205</td>
<td>190</td>
</tr>
<tr>
<td>4</td>
<td>130</td>
<td>80</td>
</tr>
<tr>
<td>5</td>
<td>205</td>
<td>340</td>
</tr>
<tr>
<td>6</td>
<td>200</td>
<td>250</td>
</tr>
<tr>
<td>7</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>278</td>
<td>278</td>
</tr>
<tr>
<td>9</td>
<td>173</td>
<td>222</td>
</tr>
<tr>
<td>2004</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>51</td>
<td>152</td>
</tr>
</tbody>
</table>
FIGURE CAPTIONS

Fig. 1. Chart of study area showing Funk Island and vessel survey routes off the northeast coast of Newfoundland.

Fig. 2. *Sula bassana*. Polar plots of directions (in 90° sectors) of flocks of foraging gannets returning to the colony on Funk Island, 1998–2002 and all years combined.

Fig. 3. *Sula bassana*. Percentages of flocks A) returning from inshore and associations with the percentages of capelin loads landed at the colony (Y = 0.49X + 38.5, R² = 0.33) and B) returning from offshore foraging sites and associations with salmon loads landed at colony on Funk Island (Y = 1.15 + 19.1, , R² = 0.60).

Fig. 4. *Sula bassana*. Average sizes of flocks returning from inshore (white bars) and offshore (black bars) foraging areas, 1998–2002.

Fig. 5. *Sula bassana* and *Mallotus villosus*. Abundances of gannets and capelin on vessel transects within the gannets’ foraging range from Funk Island, 2000-2002. Dashed lines represent the survey track in each year.

Fig. 6. *Sula bassana*. Percentages of dives during each 20% flight segment of foraging trips.

Fig. 7. *Sula bassana*. Maximum distances from the colony during foraging trips by parental gannets (dots) and first dives, median and maximum foraging range estimates (circles) for northern gannets nesting on Funk Island off the northeast Newfoundland coast.
Fig. 1. Chart of study area showing Funk Island and the vessel survey route (dashed line) off the northeastern coast of Newfoundland
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Fig. 3. *Sula bassana* Percentages of flocks A) returning from inshore and associations with the percentages of capelin loads landed at the colony ($Y = 0.49X + 38.5, R^2 = 0.33$) and B) returning from offshore foraging sites and associations with salmon loads landed at colony on Funk Island ($Y = 1.15X + 19.1, , R^2 = 0.60$)
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Fig. 5. *Sula bassana* and *Mallotus villosus*. Abundances of gannets and capelin on vessel transects within the gannets foraging range from Funk Island, 2000-2002. Dashed lines represent the survey track in each year.
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