

Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields

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Abstract In order to forage and to provision offspring effectively, seabirds negotiate a complex of behavioural, energetic, environmental and social constraints. In first tests of GPS loggers with seabirds in North America, we investigated the foraging tactics of free-ranging northern gannets (*Sula bassana*) at a large and a medium-sized colony that differed in oceanography, coastal position and prey fields. Gannets at Low Arctic colony (Funk Island) 50 km off the northeast coast of Newfoundland, Canada provisioned chicks almost entirely with small forage fish (capelin *Mallotus villosus*, 89%), while at boreal colony (Bonaventure Island) 3 km from shore in the Gulf of St. Lawrence, Quebec, Canada, large pelagic fish dominated parental prey loads (Atlantic mackerel *Scomber scombrus* 50%, Atlantic herring *Clupea harengus* 33%). Mean foraging range and the total distance travelled per foraging trip were significantly greater at the larger inshore colony (Bonaventure) than at the smaller offshore colony (Funk Island; 138 and 452 km vs. 64 and 196 km, respectively). Gan-

nets from Funk Island consistently travelled inshore to forage on reproductive capelin shoals near the coast, whereas foraging flights of birds from Bonaventure were much more variable in direction and destination. Birds from the Low Arctic colony foraged in colder sea surface water than did birds from the boreal colony, and dive characteristics differed between colonies, which is concordant with the difference in prey base. Differences between the colonies reflect oceanographic and colony-size influences on prey fields that shape individual foraging tactics and in turn generate higher level colony-specific foraging “strategies”.

Introduction

Animals are faced with high energetic demands and severe life history constraints during reproduction, most especially when provisioning offspring (Stearns 1992). These demands can be particularly intense among central place foragers, such as seabirds that have to travel long distances to and from colonies to find and then deliver food to chicks (Weimerskirch 2002). Social aspects of seabird foraging behaviour around breeding colonies that help them cope with these demands can involve the exploitation of colony-specific feeding areas (Furness and Birkhead 1984; Cairns 1989; Grémillet et al. 2004) and food information (Flemming and Greene 1990; Clode 1993). In contrast, negative consequences of social aggregation can include interference competition (Hunt et al. 1986; Kacelnik et al. 1992), prey depletion (Birt et al. 1987) and prey disturbance (Lewis et al. 2001). Variations in exothermic prey distributions and densities around colonies (Montevecchi and Myers 1995; Kitaysky and

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Golubova 2000) that are driven by biophysical oceanographic processes, create the ecological rationale for both individual and social foraging decisions (Hunt 1990; Ainley et al. 1995). Colonies occupied by the same species may vary in their prey fields, mostly as a function of biogeographic zones, topographic location (offshore/inshore) and hydrographic characteristics (e.g. Hamer et al. 2001).

In first tests of Global Positioning System (GPS) loggers (Weimerskirch et al. 2002) attached to marine birds in North America, we investigated the foraging tactics of free-ranging, chick-rearing northern gannets (*Sula bassana*) at two colonies. The colonies differ in population size, oceanographic regime, coastal position and prey fields. We show that oceanographic influences and prey fields and possibly population sizes shape the foraging tactics of individuals that in turn generate higher level colony-specific foraging “strategies”.

Materials and methods

Date and location

This study was carried out between 27 July and 6 August 2003 on Funk Island (49°45' N, 53°11' W), a flat 800 × 400 m granite rock located about 50 km off the northeast coast of Newfoundland, Canada, in the Low Arctic waters of the north-west Atlantic, and between 15 and 24 August 2003 on Bonaventure Island (48°29' N, 64°09' W), a 5 km² island located 3 km off the Gaspé Peninsula in the Boreal waters of the Gulf of St. Lawrence, Quebec, Canada (Nettleship and Evans 1985). Bonaventure Island is the site of the largest gannet colony in North America (ca. 50,000 pairs), and the colony on Funk Island is the fourth largest (ca. 10,000 pairs, Chardine 2000; J.W. Chardine, personal communication).

Dietary information

Prey were collected by approaching roosting gannets that often regurgitated as they moved away and from observations of feedings and food scraps in the colony. Furthermore, some birds regurgitated food while being handled for attachment or removal of GPS devices. Dietary data are presented as the percentage of total prey loads identified.

Capture and handling of birds

To equip birds with miniaturized data-logging units, adult gannets with 4 to 6-week-old chicks were captured

and recaptured with a telescoping noose-pole. Chick age was similar at both colonies. To minimize disturbance, nests were chosen on the periphery of the colony. We cannot exclude that birds breeding in the centre of the colony differ from those at the periphery, but to reduce any potential bias, birds were selected from the third or fourth row from the outer edge. Parental behaviour and chick survival appeared unaffected at nests where we attached a GPS logger to one parent. Capturing took usually 2–3 min, and attaching devices and marking a bird lasted 5–10 min at maximum. All birds were cared for in accordance with the guidelines of the Canadian Council on Animal Care. Sex was determined by DNA analysis of blood samples taken after recapture.

Devices used

Nine birds (7 males, 2 females) were successfully equipped with GPS data loggers on Funk Island, as well as 14 birds (8 males, 6 females) on Bonaventure Island. Devices were left on the birds mostly for one, in some cases for two foraging trips. We used three types of GPS data loggers (GPSlog; earth & Ocean Technologies, Kiel, Germany) that differed in the sensors incorporated. All devices were of streamlined aramide fibre/epoxy-composite housings (100 × 48 × 24 mm) with a mass of 65 g (GPS logger only) or 70 g (including temperature/pressure sensors), comprising about 2% of adult body mass. Positional information was obtained at 3 min intervals, with an additional standard 6–22 s period for satellite uplink. In this intermittent mode, 90% of the positional fixes have an error of less than 19 m. Pressure and temperature values were stored in 1 s intervals. GPS loggers were taped to body feathers on the lower back just above the uropygeal gland with Tesa® tape. Six other birds (one male, five females) were equipped with PTD data loggers (Precision Temperature-Depth-recorder; earth & Ocean Technologies, Kiel, Germany) on Funk Island, as well as eight birds (three males, five females) on Bonaventure Island. Data were obtained for at least one foraging trip from each bird except for three birds on Funk Island and three birds on Bonaventure Island when incomplete or no data were stored. The PTD data logger consisted of a streamlined lightweight carbon fiber-composite casing (length: 75 mm, diameter: 19 mm, mass 20 g) with both pressure and temperature sensors. These loggers comprised <1% of adult body mass and were attached with Tesa® tape to a plastic leg band.

Data analysis

Differences between colonies were tested for a variety of parameters. To include individual variability, data

were also used when we recorded more than one foraging trip per individual. We applied linear mixed-effects models fitted by REML (restricted maximum likelihood).

Sea surface temperature (SST) was analysed from the periods when gannets were swimming and the temperature probes were submerged. One value per bird was taken at midnight for each night birds equipped with data loggers were at sea.

Two different dive types can be distinguished from recordings from northern gannets (Garthe et al. 2000): V-shaped dives, being usually relatively short and shallow, and with the ascent period following almost immediately the descent period; U-shaped dives, being relatively long and often deep, with time spent at depth between descent and ascent periods

Results

Colony characteristics and many foraging parameters differed substantially between the two colonies (Table 1). Mean foraging range and the mean total distance travelled were significantly greater at the boreal inshore colony (Bonaventure; Fig. 1; Table 1). Foraging trip durations from Bonaventure were about double those from Funk Island, the Low Arctic offshore colony), although this difference was not significant because trip durations were also three times more variable at Bonaventure. Mean dive durations were significantly longer at Funk Island, where profiles were dominated by U-shaped dives. Conversely, significantly more V-dives were performed by gannets from the Bonaventure colony. Average and maximum dive depths did not differ between the colonies, and no differences in either the flight or dive patterns of male and female gannets were found.

Figure 2 depicts the greater spatial variety of foraging activity at the Bonaventure Island colony compared with Funk Island from which gannets consistently traveled to forage at coastal sites on spawning and post-spawning shoals of capelin (Davoren et al. 2003). Gannets from Bonaventure Island exhibited much more diverse trip routes and foraged from nearby coastal sites to distant offshore areas. While almost all dives of birds from Funk Island were between 40 and 60 km from the colony (range 32–70 km), dive locations of individuals from Bonaventure Island were more evenly distributed spatially and exhibited a much wider range (<1 to 203 km from the colony; Fig. 3). The difference in diving distance between the two colonies was significant ($Z = 6.622$, $P < 0.001$, Kolmogorov Smirnov test). Also, Funk Island birds dove at quite concentrated areas

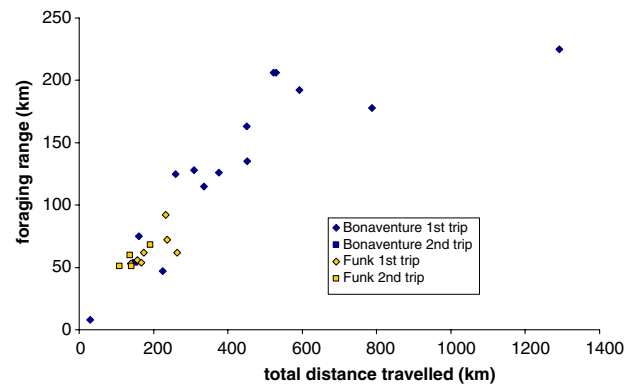


Fig. 1 Scatterplot showing total distances travelled and foraging ranges of all foraging trips of northern gannets from two colonies in eastern North America.

while foraging sites from Bonaventure birds were much more widespread. Funk Island birds dove very coastally (Fig. 4); 95% of the dives were within 12 km of land and the most distant dive was 32 km from shore. Most dives were also close to land at Bonaventure; 67% of the dives were within 20 km of land. However, 28% of the dives were ≥ 50 km from nearest land, and the furthest was 105 km from land. Gannets from the offshore colony (Funk Island) dove in closer proximity to land than did gannets from the coastal colony (Bonaventure Island; $Z = 3.526$, $P < 0.001$, Kolmogorov Smirnov test). Water depths at foraging sites of gannets from Funk Island were usually around or below 50 m, a minority of dives being located at water depths of up to 100 m. At Bonaventure, dives occurred at almost all depths up to about 500 m with no clear preference. The SST visited by gannets foraging from Funk Island were significantly colder than those used by birds from Bonaventure (Table 1).

During our study, gannets at Funk Island provisioned chicks almost entirely on capelin (*Mallotus villosus*, 89%; Fig. 5). Fish species in food loads ranking next were Atlantic salmon (*Salmo salar*; 6%), Atlantic herring (*Clupea harengus*; 3%) and Atlantic mackerel (*Scomber scombrus*; 1%). At Bonaventure Island, large pelagic fish (Atlantic mackerel, 50%; Atlantic herring, 33%) were the most important prey species, capelin (10%), sandeels (*Ammodytes* sp., 5%) and squid (*Illex loligo*, 2%) were also recorded.

Discussion

The foraging activities of individual gannets differed considerably and consistently between the two colonies. These differences include travel directions, travel

Table 1 Colony characteristics and foraging parameters of northern gannets breeding at Funk Island and Bonaventure Island in 2003

Parameter	Funk	Bonaventure	Statistics
Geographic location	Offshore	Inshore	
Ocean regime	Low Arctic	Boreal	
Population size (apparently occupied nests; Chardine 2000; J.W. Chardine, personal communication)	ca. 10,000	ca. 50,000	
Dominant prey	Small forage fishes (capelin)	Large pelagic fishes (herring, mackerel)	$X^2 = 144.8$, $df = 1$, $P = 0.001$
Mean (range) foraging range (km)	62 (51–92), $N = 7$, $n = 11$	132 (8–225), $N = 14$, $n = 15$	$t = 8.51$, $P = 0.000$
Mean (range) total distance travelled (km)	177 (108–264), $N = 7$, $n = 11$	432 (30–1,292), $N = 14$, $n = 15$	$t = 2.42$, $P = 0.025$
Mean (range) trip duration (h)	14.9 (3.8–25.0), $N = 11$, $n = 14$	28.0 (5.9–138.5), $N = 19$, $n = 20$	$t = 1.43$, $P = 0.164$
Trip duration variability (CV)	0.33	0.99	
Mean (\pm SE) dive depth (m)	4.3 ± 0.4 , $N = 10$, $n = 14$	3.9 ± 1.1 , $N = 13$, $n = 13$	$t = -0.76$, $p = 0.453$
Mean maximum (\pm SE) dive depth (m)	10.6 ± 0.4 , $N = 10$, $n = 14$	8.6 ± 1.1 , $N = 13$, $n = 13$	$t = -1.26$, $P = 0.222$
Dive depth variability (CV)	0.75, $n = 250$ dives	0.60, $n = 495$ dives	
Overall maximum dive depth (m)	19.1, $N = 10$, $n = 14$	19.1, $N = 13$, $n = 13$	
Mean (\pm SE) dive duration (s)	10.1 ± 1.0 , $N = 10$, $n = 14$	7.0 ± 1.9 , $N = 13$, $n = 13$	$t = -2.39$, $P = 0.026$
Mean maximum (\pm SE) dive duration	20.6 ± 2.5	16.0 ± 4.4	$t = -1.25$, $P = 0.224$
Dive duration variability (CV)	0.61, $n = 250$ dives	0.55, $n = 495$ dives	
Overall maximum dive duration (s)	34, $N = 10$, $n = 14$	39, $N = 13$, $n = 13$	
Mean/trip (\pm SE) of U-dives	$52 \pm 7\%$, $N = 10$, $n = 14$	$21 \pm 7\%$, $N = 13$, $n = 13$	$t = -2.94$, $P = 0.008$
Mean/trip (\pm SE) of V-dives	$48 \pm 7\%$	$79 \pm 7\%$	$t = -2.94$, $P = 0.008$
Mean (maximum, minimum, range) midnight SST ($^{\circ}$ C) measured from gannets at sea	13.2 (14.2, 12.5, 1.2), $N = 13$	16.1 (18.0, 13.9, 4.1), $N = 12$	$t = -6.977$, $P < 0.001$

All tests on distances and dive parameters between the two colonies were performed by linear mixed-effect models fitted by REML. Means and other statistical measures for distances and dive parameters are given on the basis of the foraging trips

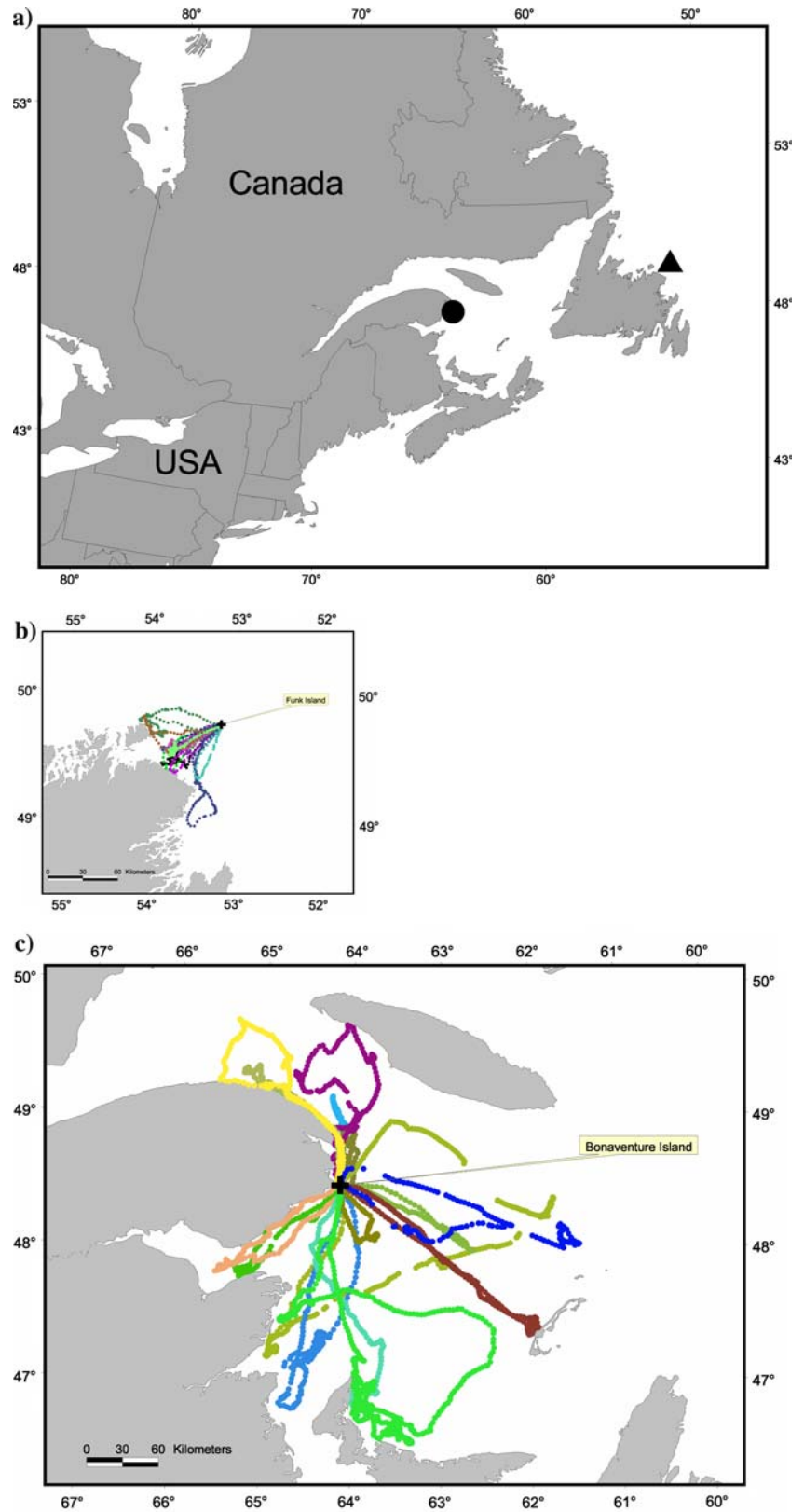
N number of individuals, n number of foraging trips, CV coefficient of variation

distances, locations of foraging sites relative to the colony and the coast, various dive parameters, and diet. The food spectrum of gannets at both colonies has been diverse (Montevecchi and Myers 1996; Nelson 2002), though a major shift in the pelagic food webs in the north-west Atlantic during the 1990s greatly narrowed prey options for gannets nesting on Funk Island (Montevecchi et al. 2006). For more than a decade, gannets have mainly provisioned their chicks with capelin, a small cold-water forage fish (Montevecchi and Myers 1997; Garthe et al. 2003). The absence of diving events near Funk Island and a diet dominated by capelin suggests poor availability of pelagic fish in offshore areas in 2003. At Bonaventure, gannet diets have shown variability, usually with large pelagic fish such as mackerel and herring as the main prey as in 2003 (Nelson 2002). These prey bases provide a good concordance with the dive patterns observed. U-shaped dives have been associated with predation on forage fish shoals, such as capelin, whereas V-dives were associated with predation on large surface-swimming pelagic fish, such as mackerel and herring (Garthe et al. 2000). Along with the variable and mostly pelagic prey, foraging trips at Bonaventure were also more variable in duration, distance and

direction. The relatively unpredictable nature of pelagic fish occurrence at Bonaventure contrasts sharply with the spatially and temporally predictable occurrence of capelin on the northeast Newfoundland coast near Funk Island (Davoren et al. 2006). Owing to these circumstances, it is not surprising that the foraging parameters of gannets such as distance to coast and water depth are clearly related to the habitat use of the prey fish. Following on this, it is quite plausible that gannets from Bonaventure fed on capelin and sandlance in shallower water to the south of the colony as both fish species are strongly related to the sea bottom (Holland et al. 2005; Davoren et al. 2006). It is of note that owing to the availability and distributions of prey fields around colonies that gannets from the offshore colony foraged predominantly inshore, whereas gannets at the inshore colony foraged predominantly offshore.

Interestingly, gannets from the large colony exhibited more diverse and longer foraging trips than the gannets from the medium-sized offshore colony, patterns that could also be influenced by colony size-related intraspecific foraging interference. In a similar approach, Hamer et al. (2001) compared the flight patterns of northern gannets from two colonies in the

Fig. 2 **a** Location of the two study colonies in north-west Atlantic Ocean. The triangle indicates Funk Island, the circle Bonaventure Island. **b–e** Foraging tracks of chick-rearing northern gannets equipped with GPS data loggers at Funk Island (**b, d**) and Bonaventure Island (**c, e**). Note that the maps are of different size to approximate the same scale. Maps **b** and **c** show all positional records of foraging trips by different individuals (*in different colours*); maps **d** and **e** delineate positions where gannets dived; a few birds from Bonaventure (e.g. the southernmost track) had GPS without pressure (dive) sensors. Distances between fixes (points) on GPS tracks reflect distance travelled, except for a few situations at Bonaventure Island when satellite fixes could not be obtained for periods up to 3 h



North Sea and the Celtic Sea. Both colonies exhibited a wide array of foraging destinations but birds from the smaller colony showed a lower degree of foraging area

fidelity, which was interpreted as to indicate a more uniform or less predictable prey field. However, no information on dive locations and dive parameters of

Fig. 2 continued

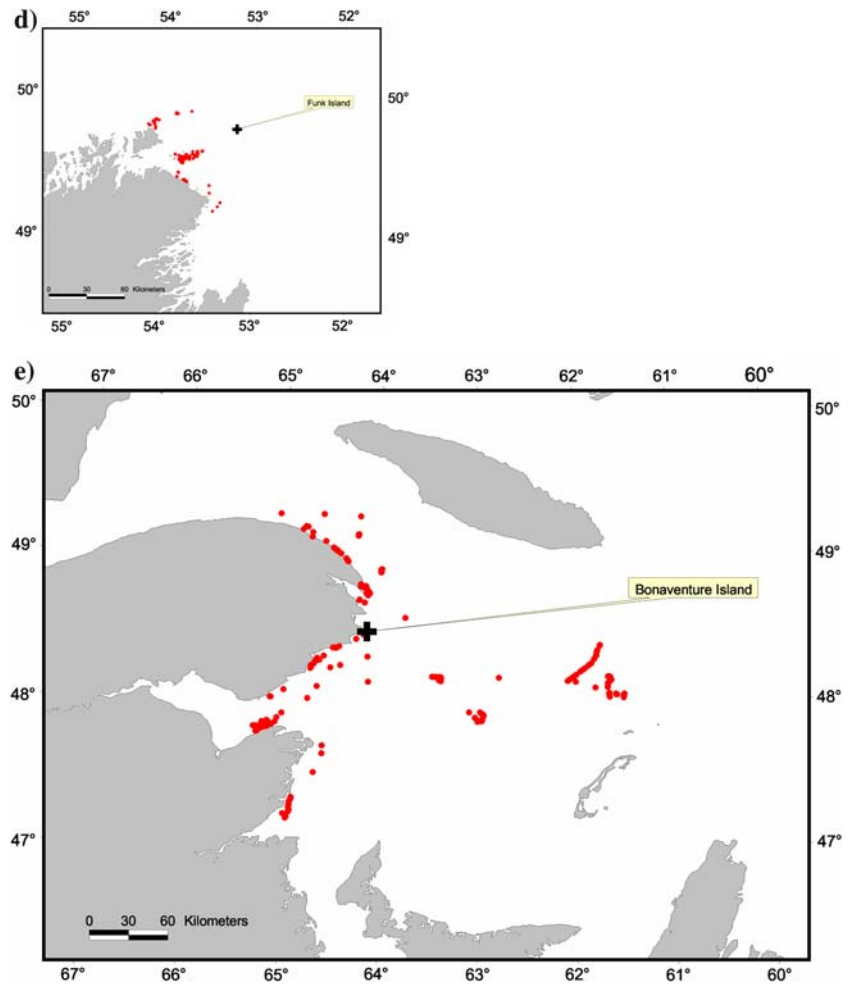
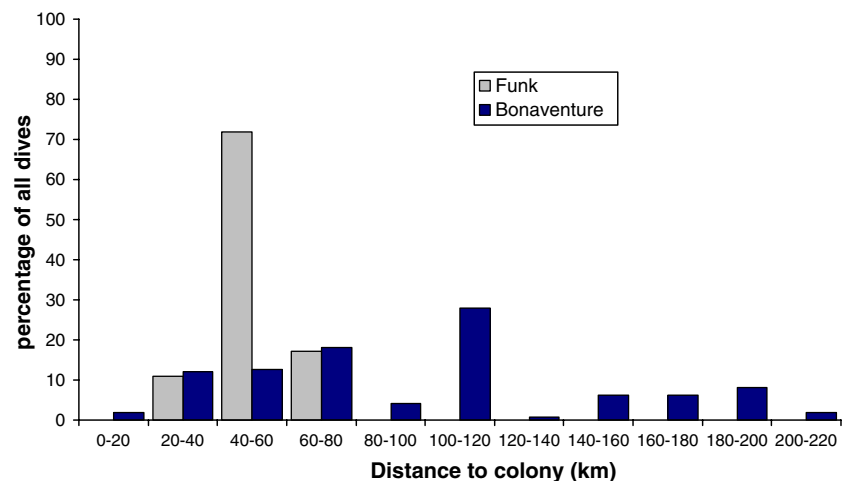


Fig. 3 Frequency distribution of the distances of all dives with positional information for northern gannets from the colonies on Funk Island and Bonaventure Island



the birds with known flight patterns were available in that study. Lewis et al. (2001) showed that colony size influences gannet foraging trip duration with birds making longer trips from larger colonies. This was explained by a decreasing likelihood to obtain sufficient prey per time unit with more birds visiting an

area. Such a phenomenon might well be working in the comparison of the two colonies investigated in our study. However, the difference in foraging trip duration were not significant (possibly due to low sample sizes); our results indicate that other aspects of foraging behaviour vary more strongly than trip length with col-

Fig. 4 Frequency distribution of the distances of all dives with positional information for northern gannets from nearest land (excluding the colony site)

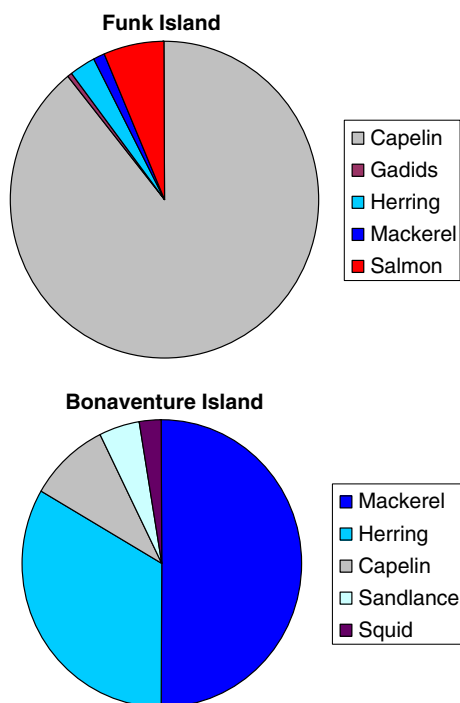
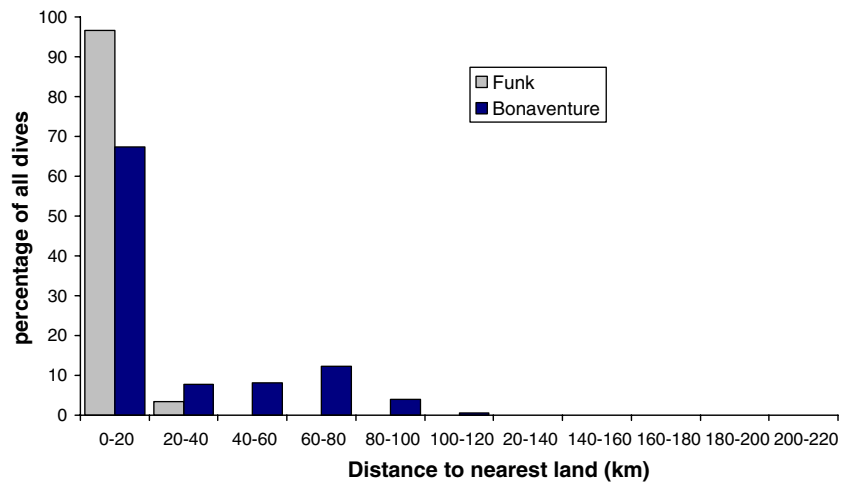


Fig. 5 Proportions of the fish species in regurgitations of northern gannets from Funk Island ($n = 348$ regurgitations) and Bonaventure Island ($n = 42$)

ony size and more especially with the ecological features within colony foraging areas (see also Ainley et al. 1995, 2003). Similarly, following Lewis et al. (2002), while sex differences might have been responsible for some variation, no sex differences in foraging behaviour were found in our study.

Cape gannets (*Sula capensis*) at two colonies about 110 km apart off the coast of South Africa, showed spatial separation in the foraging areas of birds from the different colonies (Grémillet et al. 2004). These authors speculated that wind fields and group feeding could facilitate such inter-colony foraging asymmetries, and

that memory-based foraging and site fidelity could consolidate these asymmetries into longer term traditions. Thus, the behaviour of individual predators creates higher level social expressions of colony-specific foraging strategies. We hypothesize that these colony patterns vary across temporal and spatial scales. Relatively transient occurrences could involve tracking seasonal changes in prey conditions, whereas persistent even trans-generational expressions will develop when prey conditions and their predictability around colonies are consistent over decades and longer. The latter situations would facilitate the development of long-term traditions that favour colony-specific foraging areas or hinterlands (Furness and Birkhead 1984; Cairns 1989; Grémillet et al. 2004). Different fishing practices and traditions at different colonies could be maintained by individual and social aspects of learning (Shealer 2002) and by philopatry to natal colonies (Coulson 2002). Owing to potential prey depletion, disturbance and interference competition, larger colonies might also be expected to have a more diverse array of individual foraging tactics and larger hinterlands. However, larger colonies also tend to be older than smaller ones (Nettleship and Evans 1985; Montevecchi et al. 1987) and hence more likely to have well-developed foraging traditions and hinterlands associated with them. The application of new microchip technology in data storage tags attached to free-ranging animals provide a means with which to address such behavioural and ecological questions heretofore beyond the scope of scientific inquiry (Garthe et al. 2000; Weimerskirch et al. 2002; Grémillet et al. 2004).

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