

Flight destinations and foraging behaviour of northern gannets (*Sula bassana*) preying on a small forage fish in a low-Arctic ecosystem

Stefan Garthe^{a,*}, William A. Montevecchi^b, Gail K. Davoren^c

^aResearch and Technology Centre (FTZ), University of Kiel, Hafentörn 1, D-25761 Büsum, Germany

^bDepartments of Psychology and Biology and Ocean Science Centre, Memorial University of Newfoundland, St. John's, NL, Canada A1B 3X9

^cDepartment of Zoology, Duff Roblin Building, University of Manitoba, Winnipeg, MB, Canada R3T 2N2

Accepted 19 November 2006

Available online 22 February 2007

Abstract

We applied data loggers (temperature-depth and GPS-temperature-depth) on individual birds in combination with dietary sampling and a vessel survey of prey availability to assess the foraging behaviour of northern gannets (*Sula bassana*, Linnaeus 1758) in a low-Arctic ecosystem in the NW Atlantic. We demonstrate that the gannets foraged almost exclusively on inshore and coastal aggregations of capelin. There was a strong correspondence between the distributions of capelin and foraging gannets, and gannets exhibited persistence in successive foraging trips to the same foraging areas. The diving activity of gannets was highest during the early morning and evening, when capelin are known to be primarily available in the upper water column. Most of the gannets dive depths were less than 5 m. Flight speeds recorded by GPS were 9% higher than those estimated by previous methods and were shown to benefit from tail wind. This study shows how a combination of ship-based surveys and individually tagged birds can help understanding predator–prey intersection in a three-dimensional space in the marine environment.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Seabird; Data logger; Predator–prey interaction; Foraging behaviour; Diet; Prey availability

1. Introduction

Seabird foraging behaviour traditionally has been studied from colonies where diets were collected from regurgitations and/or pellets, or from observing birds carrying food in the bill (Furness and Monaghan, 1987). In parallel, vessel surveys of

avian distributions also have been developed (Tasker et al., 1987). More recently, surveys have been directed at measuring a variety of habitat parameters synoptically with the bird observations (Haney, 1991; Schneider, 1991). These types of studies were often paralleled with studies that quantified food availability at sea (Veit et al., 1993; Hunt et al., 1998). In addition, seabird behaviour has been recorded in detail from ship-based surveys to enable a better understanding of the different uses of the oceanic areas by birds and

*Corresponding author. Tel.: +49 4834 604 116;
fax: +49 4834 604 199.

E-mail address: garthe@ftz-west.uni-kiel.de (S. Garthe).

also of processes governing the observed distributional patterns (Veit and Prince, 1997; Camphuysen and Garthe, 2004; Schwemmer and Garthe, 2005).

A new and different approach has been developed over the past 40 years that uses telemetry and data-logging units to investigate the behaviour of animals (see Ropert-Coudert and Wilson, 2005, for a recent overview). It is now possible to track birds for the entire year (Croxall et al., 2005), study the intricacies of their diving behaviour (Wilson, 1995), examine digestive processes (Peters, 1997), and investigate energy consumption using heart rate as a proxy (Weimerskirch et al., 2000) to name only a few. However, the combination of the three different approaches, assessing prey fields from boats, studying the overall distribution of the target seabird species from boats, and investigating the individual foraging behaviour of the same predator, is still quite rare.

In this paper, we investigate how the density and distribution of a small cold-water forage fish, the capelin (*Mallotus villosus*), influences the foraging strategies of one of its main avian predators, the northern gannet (*Sula bassana*). To do this, we attached data loggers to chick-rearing gannets from Funk Island to monitor the birds foraging activity and simultaneously investigated the prey field from boats in the same area, the Northeast Newfoundland Shelf in eastern Canada. Capelin has been the staple prey of breeding northern gannets and other seabirds since 1990 (Montevecchi and Myers, 1997; Montevecchi et al., 2005). The fish spawn during the first half of the chick-rearing period of northern gannets, resulting in persistent and dense aggregations along the coast (Davoren et al., 2003, 2006).

2. Methods

2.1. Study design

The study was conducted during July and August 2003 in the NW Atlantic seaward of the northeast coast of Newfoundland, eastern Canada (Fig. 1). Northern gannets were studied from July 27 to August 6 at their colony on Funk Island (49°45'N, 53°11'W), a flat granite rock of ca. 400 × 800 m. The distribution and density of their main prey species, capelin, was investigated during a survey aboard the 23-m Canadian Coast Guard Ship (CCGS) Shamook from July 12 to 18. The survey (~800 km) was run within avian foraging ranges and prime capelin spawning and staging areas to the south and west of

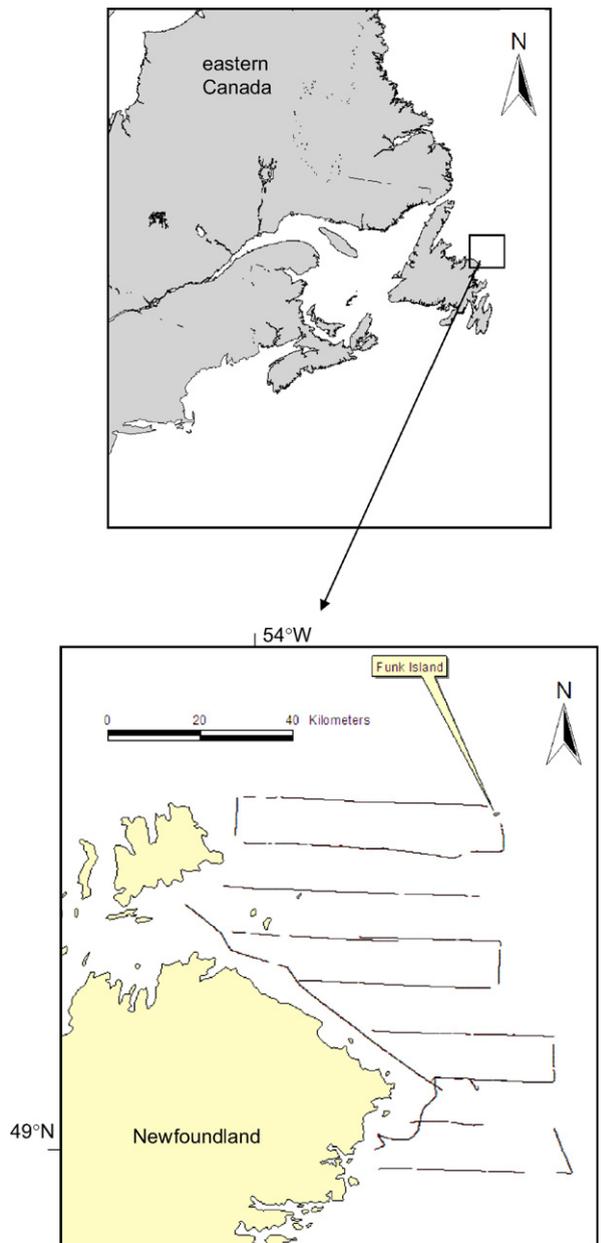


Fig. 1. Location of the study area in eastern Canada. Lines indicate the ship track of the hydroacoustic survey.

Funk Island (Davoren et al., 2003, 2006; Fig. 1). Nine east–west transects spaced 9 km apart on north–south axis were run over the 12 h d⁻¹ that the ship operated, primarily during daylight (0800–2000 Newfoundland Daylight Savings Time = UTC minus 2.5 h). Surveys were periodically interrupted to identify the species composition of acoustic signals using a modified shrimp trawl (see Davoren

et al., 2006). The numerically dominant fish species sampled was capelin (96.5%; Davoren et al., 2006). After trawling, temperature profiles of the water column were measured using a Sea Bird SBE-25 deployed at 1 m s^{-1} , allowing data capture every 20–50 cm from the ocean floor to the surface.

2.2. Field work on northern gannets

Adult northern gannets nesting on the periphery of the colony and guarding 4–5 week old chicks were captured with a telescoping noose-pole from within a blind to reduce disturbance to neighbouring birds. All birds were marked on the head and neck with different-coloured magic markers for identification from a distance and banded with U.S. Fish and Wildlife Service bands issued by the Canadian Wildlife Service. Capture lasted usually 2–3 min, and handling the bird before release took 5–10 min. Two types of data loggers were attached to the birds: one for activity and diving (vertical information) and the other for the same parameters as well as for position (horizontal information).

PTD loggers: The PTD loggers (precision temperature-depth recorders) are 12-bit multichannel data loggers with 2 MB memory, time, and sensors for pressure and external temperature (earth & OCEAN Technologies, Kiel, Germany). Temperature measurements were taken by an external, fast-responding, temperature sensor with a time constant $T_{0.9} < 2\text{ s}$. The sensor design allowed sampling of the water column with a minimum time lag in the temperature signal. The casing (outer diameter 19 mm, total length 80 mm, mass ca. 23 g) was a streamlined lightweight carbon fibre-composite. Sampling interval for temperature and pressure was 1 s. [Temperature resolution 5 mK, absolute measurement uncertainty $\pm 0.03\text{ K}$; pressure resolution 2.5 mbar (corrected to ca. 2.5 cm water column), absolute uncertainty $\pm 0.02\text{ bar}$, reduced to about 10 mbar after surface baseline correction (corrected to ca. 10 cm water column)]. Seven northern gannets were equipped with PTD loggers of which six were recaptured. Only three devices stored complete data sets.

GPS loggers: The GPS TD loggers ($100 \times 28 \times 24\text{ mm}$, 70 g) are 12-bit multi-channel data loggers with 2 MB memory (earth & OCEAN Technologies, Kiel, Germany). The casing was a streamlined aramide fibre/epoxy-composite housing with O-ring-sealed cap. The battery used was a standard 3-V Lithium cell, type CR 123A. Data obtained are latitude, longitude, speed, dilution of precision

(DOP) and time as well as external temperature and pressure. GPS position intervals were set to 3 min, resulting in positions every 3.25–3.33 min because of a 15–20 s delay to communicate with satellites and receive a position. Sensor data (temperature and pressure) were measured every second. The spatial accuracy in the intermittent mode used was that 90% of the fixes were accurate within 19 m (according to the specifications of the manufacturer). The temperature sensor was an external platinum resistance thermometer sensor with stainless steel sheath and a rapid response time, $T_{0.9} < 2\text{ s}$, at the end of a flexible 20-cm sensor stalk. [Resolution and uncertainty: as for the PreciTD (see above)]. Eleven northern gannets were equipped with GPS loggers, all of which were recaptured. However, two devices were lost (on only these birds PTDs also were attached) and two devices gave incomplete results due to internal battery detachment.

Finally, diet samplings were occasionally performed. Prey were collected by approaching roosting gannets that often regurgitated spontaneously as they moved away or from observations of feedings and food scraps in the gannet colony. Furthermore, some instrumented birds regurgitated food during the handling after recapture.

Following recapture, which mostly took 2–3 min, data loggers were removed, blood samples were taken (which together lasted another 10–15 min), and data were downloaded into a computer. Dives were analysed using MultiTrace-Dive (Jensen Software Systems, Laboe, Germany). Vertical immersions were considered dives when they were deeper than 0.3 m. There were no indications of foraging at the sea surface, based on two pieces of information. Firstly, no observations of surface-feeding northern gannets exist from boat surveys in the study area from 2000 to 2005 (Davoren, unpublished data). Secondly, in 1999, a year with a similar diet, five northern gannets were equipped successfully with stomach temperature loggers in addition to dive recorders. These stomach temperature loggers did not show any food ingestion independent of dives. Flight ground speed measurements were taken directly from the GPS data files, obtained for each positional determination. Speeds lower than 2 km h^{-1} (data not shown) can be attributed to swimming periods when the birds were subject to drift (see also Grémillet et al., 2004). Speeds up to 20 or 30 km h^{-1} are likely recorded while the birds are foraging. Flight speeds were averaged for each

inbound and outbound flight for each foraging trip (thus re-sampling some birds) in a sector located at distances between 2 and 20 km from the breeding colony on Funk Island. This sector was chosen as it was located between the colony area and the nearest foraging area. For each inbound and outbound flight of each foraging trip, 3–9 measurements were available. Hourly measurements of wind direction and wind speed were downloaded from the Internet ([http://www.climate.weatheroffice.ec.gc.ca/climate/Data/hourlydata_e.html](http://www.climate.weatheroffice.ec.gc.ca/climate>Data/hourlydata_e.html), Environment Canada) for the nearest weather station on Pools Island, located 78 km to the SSW of Funk Island, within the gannets' foraging range. For each inbound and outbound flight of each foraging trip, the respective tail wind component (TWC) was calculated by combining northern gannet flight speeds and flight direction with the wind field as taken from Pools Island. The formula for the TWC was: $TWC = \cos x * v$; with x being the difference between the opposite flight direction of the bird (i.e., the tail wind direction for the flying bird) and the wind direction (in $^{\circ}$), and v being the wind speed in m s^{-1} (Fransson, 1998).

Hydrographic analysis: Because of the rapid response of the temperature sensor in both PTD and GPS TD loggers, *in situ* measurements of the gannets at sea could be used to characterise the thermal structure of the uppermost water column. For each dive reaching at least 8 m, all values were taken that the birds collected from the deepest point of the dive back to the surface. The first phase of the dive (up to 2 or 3 s), when the bird is plunging from the air into the water, was ignored, as the temperature sensor appeared to be too slow to measure temperature accurately at that stage.

2.3. Fieldwork on capelin

During the survey, signals of prey species were recorded continuously using a BioSonics DT-X 6000 hydroacoustic system calibrated with a tungsten carbide standard target. This system operated through a 38 kHz split-beam transducer in a towed body with a frequency of 1 ping per s, a bandwidth of 5.1 kHz, and a pulse duration of 0.4 ms. The transducer was at a depth of 5 m, and acoustic signals were not reliable until 10 m. Vessel speed was maintained between 11 and 14 km h^{-1} . Raw high-resolution acoustic data (volume backscattering coefficients, s_v) were recorded continuously. A s_v threshold of -63 dB was applied to the raw data

prior to integration, allowing detection of single capelin (100 mm) at the range of depths commonly encountered ($<150 \text{ m}$), while most other “noise” would be filtered out.

During the analysis, we edited acoustic signals near the bottom that could not be distinguished as biological or due to the ocean floor (dead-zone, side-lobing; Lawson and Rose, 1999). The volume backscattering coefficient (s_v) in each file was integrated to determine the average aerial backscattering coefficient (s_a) for capelin within schools (MacLennan et al., 2002). Capelin density (fish m^{-2}) was calculated by dividing s_a by the average backscattering cross-section (σ_{bs}), which is related to target strength (TS). Target strength was estimated using the length-scaled relationship for capelin (Rose, 1998), given the mean length of capelin sampled during trawling (see Davoren et al., 2006).

To visualise the horizontal distribution of capelin over the study area, a spatial interpolation procedure was applied using the hydroacoustic data (see Section 2.1). Data of capelin were aggregated over the upper 50 m of the water column and interpolated applying ordinary kriging methods in Surfer 8 (Anon, 2002). Abundances of capelin ($n = \text{fish m}^{-2}$) over bin sizes of 100 m were log-transformed ($\log_{10}(n + 1)$) before analysis. For interpolation, an experimental variogram with a spherical model was selected. Spatial resolution for interpolation was performed on a $1 \times 1 \text{ km}$ grid (Anon, 2002) and retransformed to Lat-Long coordinates for visualisation purposes.

3. Results

3.1. Flight destinations

Complete tracks were obtained for 11 foraging trips from 7 northern gannets. All trips were oriented towards the coast, within an angle of $180\text{--}300^{\circ}$ in relation to the colony on Funk Island (Fig. 2). Dives were not spread through the whole foraging area but occurred relatively close to the coast, at distances of 32–70 km (mean $\pm \text{SD} = 51 \pm 8 \text{ km}$). Most dives were concentrated in an area southwest of Funk Island, with only a few other dives sites (Fig. 2).

Birds equipped with data loggers for two consecutive trips dove at nearly the same sites during the first and second trips. In three cases, the birds returned more or less straight to the previous dive

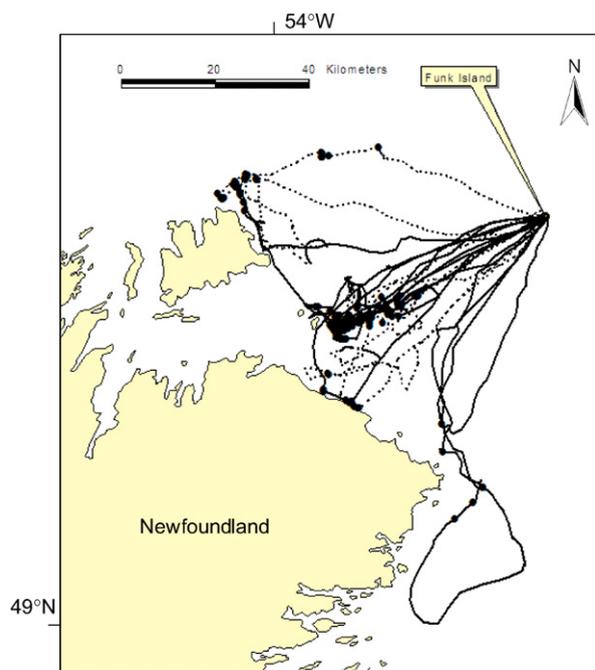


Fig. 2. Location of flight tracks (lines) and dives (filled dots) of 7 northern gannets on 11 foraging trips off the northeast Newfoundland coast in 2003. These birds were equipped with GPS TD loggers. Flight tracks of birds returning from the foraging trip with capelin in the stomach are shown by dotted lines, the definite diet of the other birds (tracks shown in solid lines) is unknown.

site (see Fig. 3A for one example), while in the last case, the bird visited a different place first before returning to the previous site (Fig. 3B).

3.2. Diet

Capelin comprised by far the most common prey taken by northern gannets (Table 1). Only 4 other species of prey fishes were found, with Atlantic salmon ranking second highest. In addition to dietary collections at the roost and elsewhere in the colony, 5 out of the 10 birds with attached devices regurgitated upon recapture. All 5 regurgitations consisted of capelin.

3.3. Movement speeds

Movement speeds of northern gannets recorded throughout their time at sea reveal essentially two peaks of different speeds. Speeds above 30 or 40 km h⁻¹ indicate direct flight between different points (e.g., in or out from the colony). Speeds >10 km h⁻¹ showed a bell-shape distribution with the grand mean (\pm standard error) flight speed over

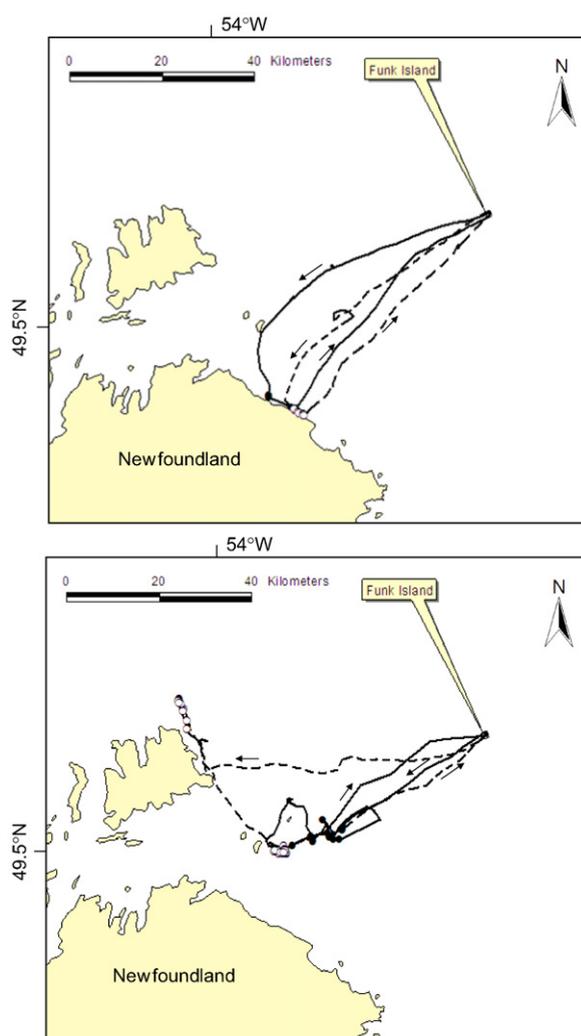


Fig. 3. Location of two consecutive foraging trips of two northern gannets. The solid line shows the first trip, the broken line the second trip. Closed dots represent dives on the first trip, open dots those on the second trip. Arrows indicate outbound and inbound flights of the respective trips. Bird F56 (a) regurgitated capelin during recapture, thus having preyed on capelin at least during the second foraging trip. (A) bird F56, (B) bird F65.

ground for straight inbound and outbound flight to and from the colony being 58.4 ± 1.9 km h⁻¹ (range 42.9–84.0 km h⁻¹; 11 trips from 7 birds equipped with GPS TD loggers, one inbound and one outbound measurement for each trip). Flight speed increased significantly with increasing TWC values (Fig. 4).

3.4. Diving behaviour

Diving activity showed strong peaks in the morning and in the evening, with much reduced

diving over the day (Fig. 5). Dives were mostly relatively shallow, with about 50% of them reaching up to 3.8 m and 10% of the dives reaching as far deep as 9.3 m. Mean dive depth was 4.7 m, and on the deepest dive a northern gannet reached 19.1 m. Dives lasted between 2 and 34 s, with a mean of 10.3 s and a median of 8 s.

3.5. Prey availability

During daylight, capelin occurred mainly in depths of around 100–200 m (Fig. 6). Signals of capelin, however, also were found in the upper 30 m, which are available to foraging northern gannets. Capelin were aggregated at some sites close to the coast while low densities were found some 10–30 km

Table 1
Diet of northern gannets on Funk Island in 2003, given as percentages by feeds

Fish species (scientific name)	By feed (%)	By mass (%)
Capelin (<i>Mallotus villosus</i>)	89.1	85.1
Atlantic salmon (<i>Salmo salar</i>)	6.3	6.8
Atlantic herring (<i>Clupea harengus</i>)	2.9	4.9
Atlantic mackerel (<i>Scomber scombrus</i>)	1.1	2.6
Cod (<i>Gadus morhua</i>)	0.3	0.3
Gadid indet	0.3	0.3

$n = 348$ regurgitations.

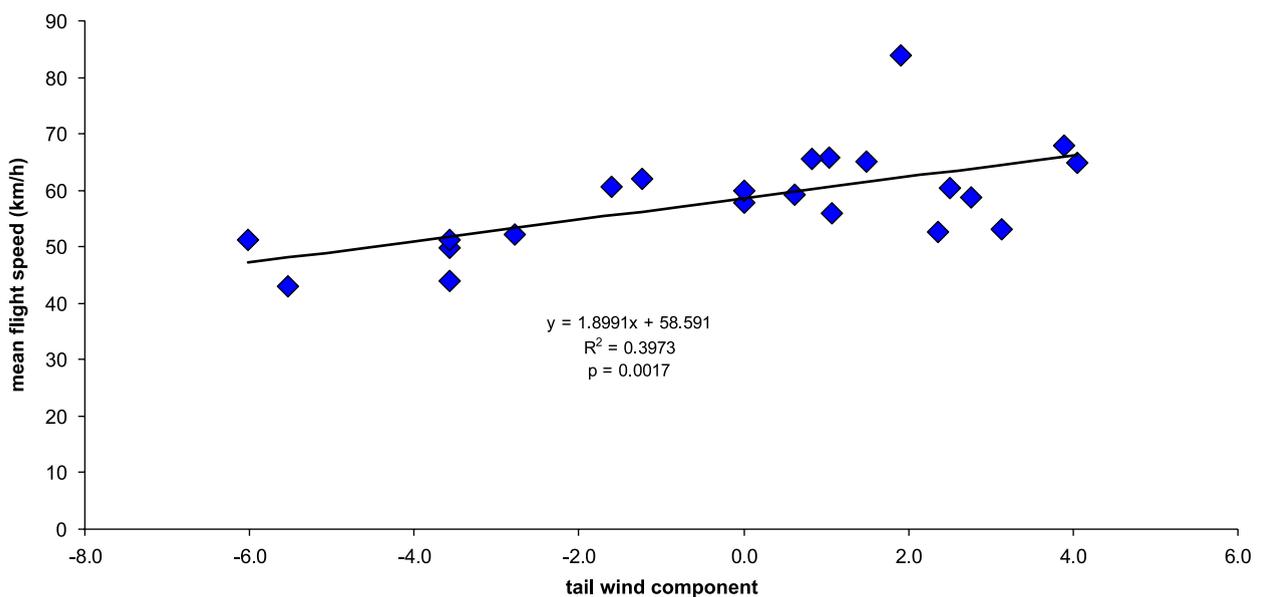


Fig. 4. Mean flight speed as a function of the tail wind component. For details see Section 3.3.

offshore (Fig. 7). Further out at sea, capelin were rarely detected.

Northern gannet dive sites overlapped with one major concentration of capelin in the upper water column but occurred usually in low to medium capelin density areas (Fig. 7).

3.6. Water temperature

The upper 5 m was of about 12–13 °C; below 5 m the water temperature fell slightly but continuously.

4. Discussion

Device effects: As in previous studies on gannets with similar devices (Garthe et al., 2000, 2003; Grémillet et al., 2004), we did not find any detectable effect of our work on the birds' behaviour on land. The birds usually returned to their nest and chick within a few minutes following release. However, we cannot rule out that catching, handling and deploying devices on birds affected them. To avoid cumulative effects, we restricted the deployment to 1–2 foraging trips, i.e. 2–3 days maximum.

Capelin was the major prey of northern gannets on Funk Island in 2003, as has been the case throughout the 1990s (Montevecchi and Myers, 1997; Montevecchi et al., 2005). From the dive positions it is obvious that foraging did not take

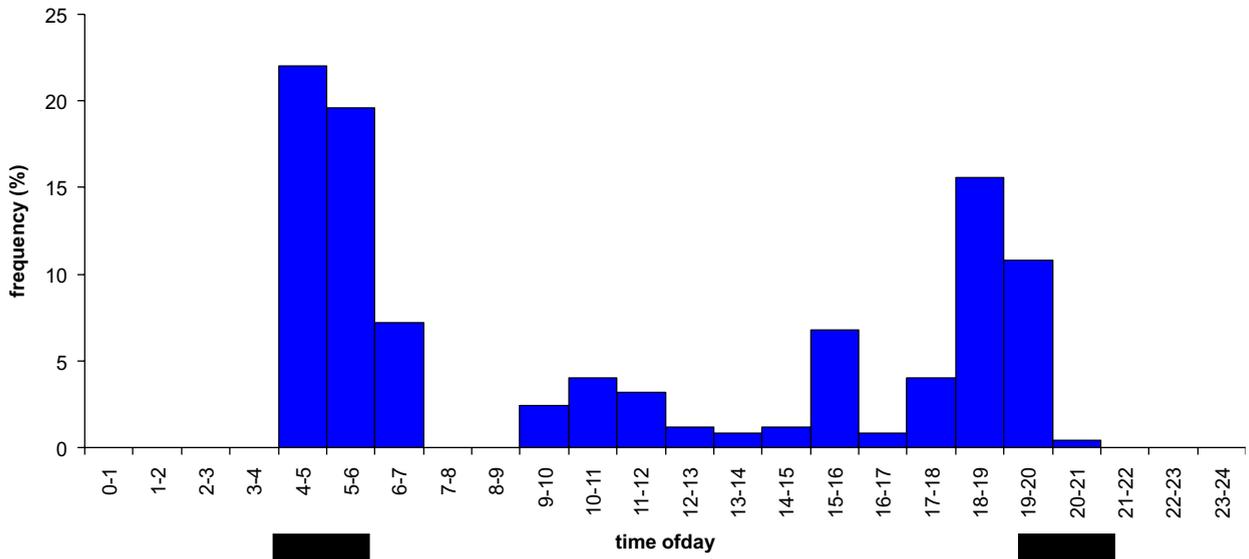


Fig. 5. Frequency distribution of diving activity of northern gannets over the 24-h cycle. Time shown is Newfoundland Daylight Savings Time (= UTC minus 2.5 h). Data originate from 10 birds on 14 foraging trips equipped with GPS TD and PTD loggers. $n = 250$ dives. Black bars under the time axis indicate twilight periods.

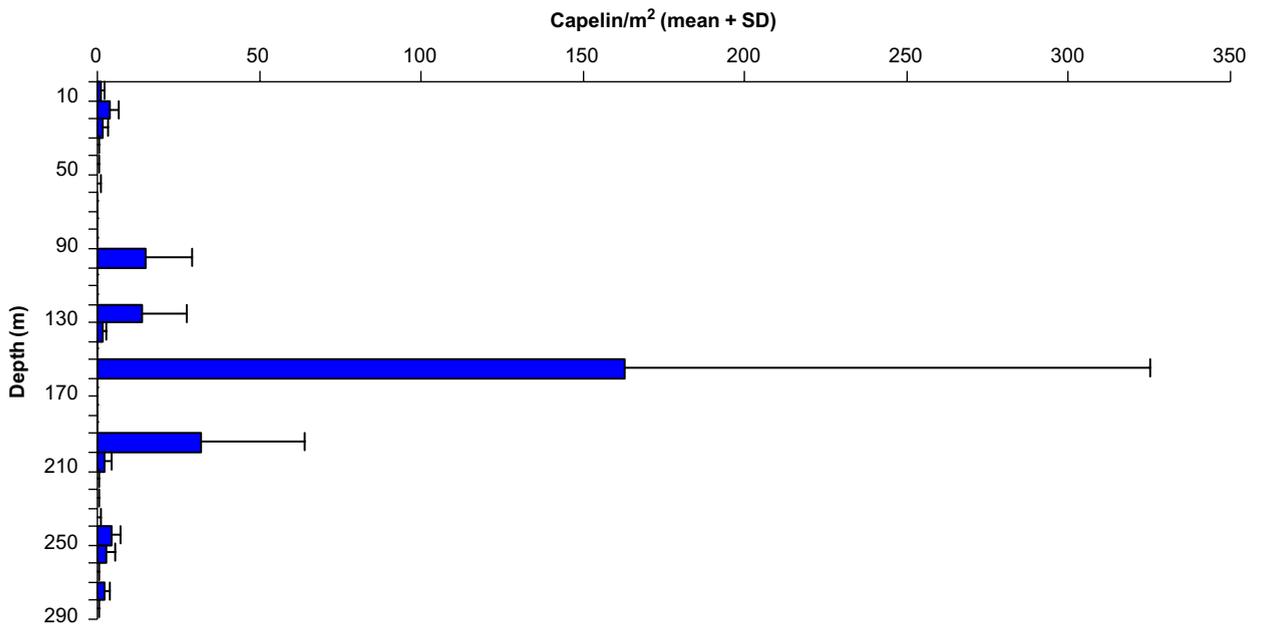


Fig. 6. Vertical distribution of capelin between 10 and 300 m. Data originate from the meso-scale hydroacoustic survey during daylight on the northeast coast of Newfoundland (see Fig. 1).

place close to Funk Island but occurred near the coast or adjacent islands (Fig. 2). Some of these areas are known demersal spawning sites of capelin, as indicated by the hydroacoustic survey in 2003 (Fig. 7) and from similar surveys in the three previous years (Davoren et al., 2006). It was

surprising that the overlap between key capelin spawning sites during the hydroacoustic survey and gannet foraging sites (Fig. 7) was not stronger. Here, it needs to be highlighted that the acoustic survey took place 2 weeks earlier than the study of northern gannets on Funk Island so that there was

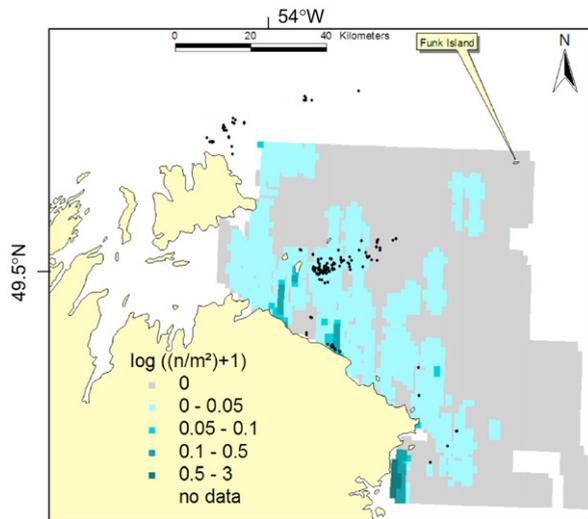


Fig. 7. Horizontal distribution of capelin (10–50 m) over the study area. The locations of the gannet dives are overlaid (filled dots).

no direct temporal overlap in the different parts of the investigation. Capelin do not remain at demersal spawning sites after spawning is complete (GKD, unpublished data). Therefore, if the majority of capelin had spawned in the study area prior to the gannet study, we would not expect a high spatial overlap between spawning areas and gannet dive locations. The high percentage of dives in the western part of the study area fits well the generally observed pattern that capelin spawning progresses gradually along the coast towards north-west (Davoren et al., 2006, unpublished data), likely indicating capelin hot spots during that period.

Dive patterns showed a distinct diel rhythm, with very intense diving in the morning and less pronounced, but still intense diving in the evening. Northern gannets are constrained when targeting prey, as they cannot dive much deeper than 20 m (Garthe et al., 2000). They forage in the warmer surface layer where capelin is least available during daylight (Petrie et al., 1988; Davoren et al., 2006). Capelin, however, are abundantly available at these water depths during dark and twilight transition periods. Northern gannets appear to respond to this by feeding extensively on this prey when they are available in surface waters (Fig. 5). These diel patterns are much more distinct than 4 years earlier in a study at the same colony (Garthe et al., 2003). In 1999, capelin made up the majority of the diet, but the overall percentage was lower compared to 2003. The concentration of the feeding effort during

the early and late hours of the day seems to be related to feeding on capelin. Capelin aggregate deep in the water during daylight and vertical migration takes place in the twilight zones, bringing capelin closer to the surface at night (Mowbray, 2002; Davoren et al., 2006). Nevertheless, it becomes obvious that some capelin remain in the upper water layers during the day on which gannets are capable to feed. However, depending on the maturation and spawning stage of this fish species, vertical migration does not always occur, possibly being responsible for a more equal distribution of diving effort over daylight in 1999 (Garthe et al., 2003). Alternatively, the foraging strategies of the birds may explain this behaviour. Intensified feeding before dark could be due to the adult consuming food for itself when staying at sea overnight, and feeding in the early morning hours for the chick after the evening meal has been digested (Garthe et al., 2003; Ropert-Coudert et al., 2004). Further data from feeding on other prey fish may be helpful in better understanding these patterns.

All foraging trips were remarkably similar in distance, direction and duration, particularly so if compared to other colonies such as Bonaventure Island (Gulf of St. Lawrence, Canada; Garthe et al., 2007), Bass Rock (North Sea, UK; Hamer et al., 2000; Lewis et al., 2002), Saltee Island (Celtic Sea, Ireland; Hamer et al., 2001) and Hermaness (North Sea, UK; Garthe et al., 1999). These foraging trip characteristics are likely driven by the distribution of available prey. At Funk Island, the dietary diversity was very limited and the accessible capelin were available inshore, whereas at the other colonies the available prey spectrum was much more diverse and dispersed.

From an energetics point of view, feeding on capelin by northern gannets seems less profitable as the energy density is much lower than that of other prey such as Atlantic mackerel and Atlantic saury (e.g., Montevicchi et al., 1984). However, these migratory warm-water prey have not been available in the low-Arctic NW Atlantic ecosystem during the 1990s and the persistence of capelin spawning sites, their high density and the relative proximity to the colony appears to be sufficiently attractive to northern gannets to select capelin as their staple diet, as suggested for other seabirds breeding at Funk Island (see Davoren et al., 2003). When looking at the four birds for which two consecutive foraging trips were recorded, persistence to feeding sites seemed to take place. In all cases, during parts

of their trips the birds visited the exact or nearby sites to forage. Memory effects could play a role in these circumstances (see also Montevecchi et al., unpublished data).

The flight speed measurements over ground (mean = 58.4 km h^{-1}) proved to be ca. 9% higher than those assessed by Pennycuik (1997, 53.6 km h^{-1}). Another presumably more valid comparison can only be carried out if TWC is set to zero in our measurements to match between flight speed over ground (as obtained from the GPS loggers) and observed flight speed in the air volume; flight speed would then be 58.6 km h^{-1} (see equation in Fig. 4). The difference between our measurements and Pennycuik (1997) could be due to different methodologies. In any case, it seems that northern gannets benefit from using the wind field in north-east Newfoundland. Data from the study period from the nearby weather station Pools Island showed that winds came from south-west predominantly in the morning but changed on some days to easterly directions. This would give the birds some options for flights, with the 'ideal' foraging trip exploiting tailwind for both the outbound and inbound flight. Similarly, using specific wind fields to facilitate performing longer and wider-ranging foraging trips has been shown for cape gannets in South Africa (Grémillet et al., 2004). As there was not much variation in the flight directions of the birds in this study, birds could not necessarily benefit from wind as much as compared to situations where foraging into all directions would be a matter of choice. Again, more variable flight destinations could help determine whether birds planned to use the wind field or simply experienced it.

The application of data loggers on the key seabird species in combination with diet-sampling at the colony, and the synoptic assessment of prey distribution, both horizontal and vertical, within avian foraging ranges from a research vessel have proved to be a very useful approach to assess seabird foraging strategies to a much larger extent than was previously possible. In addition, it gives us the unique opportunity to study predator–prey interactions, and also habitat selection. The major focus of gannets on capelin as their 'default prey' (see Montevecchi et al., 2005) is astonishing, but dietary information from other years (Montevecchi and Myers, 1997; Montevecchi et al., unpublished data) and the results presented in this paper indicate that gannets select different flight destinations and

exhibit different foraging behaviour when the prey fields differ from that experienced in 2003. Dynamic oceanographic processes as well as climatic changes may consequently influence seabirds' foraging options.

Acknowledgements

This study was a cooperative German-Canadian project supported by grants and scholarships from the Natural Sciences and Engineering Research Council of Canada (NSERC). Further support came from the Research and Technology Centre in Büsum and Memorial University of Newfoundland. The Newfoundland and Labrador Parks Division permitted us to work in the Funk Island Ecological Seabird Reserve. April Hedd assisted during fieldwork. Chantelle Burke helped with data analysis. Captain Larry Easton and family safely commuted us to and from Funk Island. Gerrit Peters from earth & Ocean Technologies (Kiel, Germany) provided technical support. The crew of CCGS Shamook supported our activities during the meso-scale survey and Fisheries and Oceans Canada provided vessel support. Special thanks to A.D. Murphy for directing, operating and managing all technical equipment and electronic data aboard the CCGS Shamook. G. Peters commented on the first draft of this manuscript.

References

- Anon, 2002. Surfer 8. Contouring and 3D Surface Mapping for Scientists and Engineers. Golden Software, Colorado.
- Camphuysen, C.J., Garthe, S., 2004. Recording foraging seabirds at sea. Standardised recording and coding of foraging behaviour and multi-species foraging associations. *Atlantic Seabirds* 6, 1–32.
- Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V., Briggs, D.R., 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* 307, 249–250.
- Davoren, G.K., Montevecchi, W.A., Anderson, J.T., 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Marine Ecology Progress Series* 256, 229–242.
- Davoren, G.K., Anderson, J.T., Montevecchi, W.A., 2006. Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland: demersal spawning and diel vertical movement patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 63 (2), 268–284.
- Fransson, T., 1998. Patterns of migratory fuelling in whitethroats *Sylvia communis* in relation to departure. *Journal of Avian Biology* 29, 569–573.
- Furness, R.W., Monaghan, P., 1987. *Seabird Ecology*. Blackie, Glasgow.

- Garthe, S., Grémillet, D., Furness, R.W., 1999. At-sea-activity and foraging efficiency in chick-rearing northern gannets (*Sula bassana*): a case study in Shetland. *Marine Ecology Progress Series* 185, 93–99.
- Garthe, S., Benvenuti, S., Montevecchi, W.A., 2000. Pursuit-plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society: Biological Sciences* 267, 1717–1722.
- Garthe, S., Benvenuti, S., Montevecchi, W.A., 2003. Temporal patterns of foraging activities of northern gannets *Morus bassanus* in the north-west Atlantic. *Canadian Journal of Zoology* 81, 453–461.
- Garthe, S., Montevecchi, W.A., Chapdelaine, G., Rail, J.-F., Hedd, A., 2007. Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains. *Marine Biology*, in press.
- Grémillet, D., Dell’Omo, G., Ryan, P.G., Peters, G., Ropert-Coudert, Y., Weeks, S.J., 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape Gannets from neighbouring colonies. *Marine Ecology Progress Series* 268, 265–279.
- Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., Wood, A.G., 2000. Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series* 200, 257–264.
- Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S., Wood, A.G., 2001. Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series* 224, 283–290.
- Haney, J.C., 1991. Influence of pycnocline topography and water column structure on marine distributions of alcids (Aves: Alcidae) in Anadyr Strait, Northern Bering Sea, Alaska. *Marine Biology* 110, 419–435.
- Hunt Jr., G.L., Russell, R.W., Coyle, K.O., Weingartner, T., 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* 167, 241–259.
- Lawson, G.L., Rose, G.A., 1999. The importance of detectability to acoustic surveys of semi-demersal fish. *ICES Journal of Marine Science* 56, 370–380.
- Lewis, S., Benvenuti, S., Dall’Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., Hamer, K.C., 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London: Biological Sciences* 269, 1687–1693.
- MacLennan, D.N., Fernandes, P.G., Dalen, J., 2002. A consistent approach to definitions and symbols in fisheries acoustics. *ICES Journal of Marine Science* 59, 365–369.
- Montevecchi, W.A., Myers, R.A., 1997. Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. *ICES Journal of Marine Science* 54, 608–614.
- Montevecchi, W.A., Ricklefs, R.E., Kirkham, I.R., Gabaldon, D., 1984. Growth energetics of nestling northern gannets (*Sula bassanus*). *Auk* 101, 334–341.
- Montevecchi, W.A., Garthe, S., Davoren, G.K., 2005. Biophysical influences on seabird trophic assessments. In: Boyd, I.L., Wanless, S., Camphuysen, C.J. (Eds.), *Top Predators in Marine Ecosystems. Their Role in Monitoring and Management*. Cambridge University Press, Cambridge, pp. 118–130.
- Mowbray, F.K., 2002. Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. *ICES Journal of Marine Science* 59, 942–949.
- Pennycuik, C.J., 1997. Actual and ‘optimum’ flight speeds: field data reassessed. *Journal of Experimental Biology* 200, 2355–2361.
- Peters, G., 1997. A new device for monitoring gastric pH in free-ranging animals. *American Journal of Physiology* 273, G748–G753.
- Petrie, B., Akenhead, S., Lazier, J., Loder, J., 1988. The cold intermediate layer on the Labrador and northeast Newfoundland shelves, 1978–1986. *NW Atlantic Fisheries Organization Science Council Studies* 12, 57–69.
- Ropert-Coudert, Y., Wilson, R.P., 2005. Trends and perspectives in animal-attached remote-sensing. *Frontiers in Ecology and Environment* 3, 437–444.
- Ropert-Coudert, Y., Grémillet, D., Kato, A., Ryan, P.G., Naito, Y., Le Maho, Y., 2004. A fine-scale time budget of cape gannets provides insights into the foraging strategies of coastal seabirds. *Animal Behaviour* 67, 985–992.
- Rose, G.A., 1998. Acoustic target strength of capelin in Newfoundland waters. *ICES Journal of Marine Science* 55, 918–923.
- Schneider, D.C., 1991. The role of fluid dynamics in the ecology of marine birds. *Oceanography and Marine Biology Annual Review* 29, 487–521.
- Schwemmer, P., Garthe, S., 2005. At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. *Marine Ecology Progress Series* 285, 245–258.
- Tasker, M.L., Webb, A., Hall, A.J., Pienkowski, M.W., Langslow, D.R., 1987. Seabirds in the North Sea. Final report of phase 2 of the Nature Conservancy Council Seabirds at Sea Project November 1983–October 1986. Nature Conservancy Council, Peterborough.
- Veit, R.R., Prince, P.A., 1997. Individual and population level dispersal of black-browed Albatrosses *Diomedea melanophris* and grey-headed Albatrosses *D. chrysostoma* in response to Antarctic krill. *Ardea* 85, 129–134.
- Veit, R.R., Silverman, E.D., Everson, I., 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *Journal of Animal Ecology* 62, 551–564.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A., Costa, D.P., 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London: Biological Sciences* 267, 1869–1874.
- Wilson, R.P., 1995. The foraging ecology of penguins. In: Williams, T.D. (Ed.), *Penguins*. Oxford University Press, Oxford, pp. 81–106.