# Influence of prey behaviour and other predators on the foraging activities of a marine avian predator in a Low Arctic ecosystem

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ABSTRACT: Air-breathing marine predators can expend considerable time and energy searching for patchily distributed prey and, thus, likely employ varying foraging strategies to minimize these costs. We studied the diurnal foraging patterns of the northern gannet *Sula bassana* along with the distributional patterns of its main prey, capelin *Mallotus villosus*, off the NE Newfoundland coast from 1999 to 2005. We explored whether gannets minimize searching costs for near-surface (<30 m) capelin by (1) aggregating in shallow waters (<30 m) where capelin are accessible throughout the day, (2) aggregating in deeper waters where they concentrate foraging effort at dawn and dusk, when diel vertical migrations make capelin accessible, or (3) associating with other marine predators that increase the accessibility of capelin. We integrated continuous recordings of gannet foraging activities with vessel-based survey data on the density and distributional patterns of capelin, gannets and whales. Capelin typically comprised >70% of gannet diets. Gannets aggregated in shallow areas (<30 m) where spatially and temporally persistent shoals of capelin were accessible through daylight, but were also found in deeper water where capelin were inaccessible. Gannet diving activity was only recorded during daylight, and although activity peaked at the start and end of daylight, most dives occurred when capelin had migrated to inaccessible depths. Gannets were more tightly associated with whales than with near-surface capelin shoals, suggesting that they may successfully track capelin by cueing to the foraging activities of whales. A mixed strategy of memory-based and local enhancement foraging tactics appear to play important roles in minimizing the effort required to access prey.

KEY WORDS: Diet · Diel vertical migration · Whale-seabird associations · Memory-based foraging · Local enhancement · Capelin

## INTRODUCTION

In marine systems, predators can expend considerable time and energy searching for patchily distributed prey over vast areas of ocean. Air-breathing predators must expend more energy searching underwater, as they must regularly commute between the surface and prey at depth, possibly losing contact with prey in the process. To minimize energetic costs of searching, air-breathing marine predators may employ a variety of foraging strategies. There is growing evidence that marine predators may use a memory-based strategy to return to areas in the open ocean, where accessible, dense prey are temporally and spatially persistent (Norse et. al. 2005). Similarly, predators may concentrate foraging effort at certain

times of day when prey are more accessible, such as at dawn and dusk when diel vertical migrating prey may be concentrated near the surface (Hays 2003). There is also growing evidence that predators cue to the foraging activities of other predators that may make prey more accessible near the ocean surface, as evidenced by numerous descriptions of multi-species feeding assemblages of birds, mammals and fish (Hoffman et al. 1981, Camphuysen & Webb 1999), as well as experimental evidence of bird attraction to other predators (Porter and Sealy 1982) and fishing boats (Garthe & Hüppop 1994).

Using one or many strategies to minimize search costs for prey may be especially important for marine predators that are restricted to feeding in surface waters. The northern gannet *Sula bassana* is the largest pelagic seabird in the north Atlantic (adult body mass = ca. 3 kg; Nelson 1978) and populations are generally increasing, likely due to reductions in human-induced mortality (Montevecchi & Myers 1997). Their foraging mode is characterized by plunge diving, whereby they plunge dive and then swim back passively to the sea surface, and by pursuit-plunging, whereby they plunge dive and then pursuit-dive there-after, using bent wing flapping to propel themselves underwater (Garthe et al. 2000). They can also detect prey from the surface and dive without plunging (Ropert-Coudert et al. 2004). Gannets regularly dive up to 10 m deep (Garthe et al. 1999, 2003), with a max-imum recorded depth of 34 m (Brierley & Fernandes 2001). Diving profiles and maximum depths have been explained by prey species captured during the dive (Adams & Walter 1993, Garthe et al. 2000). Gannets are visual foragers, and foraging activity has only been recorded during daylight (Garthe et al. 1999, 2000). Similarly, travel speeds associated with flight have generally not been recorded during dark periods (Garthe et al. 1999, 2000, Hamer et al. 2000, 2001, Lewis et al. 2002, cf. Garthe et al. 2003) except during migration (D. A. Fifield & W. A. Montevecchi unpubl. data). Breeding gannets are opportunistic foragers on most pelagic prey species that are abundant within for-aging ranges, with the consumption of certain species highly correlated with abundance indices and fisheries catches (Montevecchi & Myers 1995). Therefore, diets during breeding indicate shifts in species composition of pelagic food webs (Montevecchi & Myers 1996, Montevecchi 2007).

In the northwest Atlantic, the dietary composition of gannets shifted from warm-water, migratory pelagic fish (e.g. Atlantic mackerel *Scomber scombrus*, Atlantic saury *Scomberesox saurus*, and short-finned squid *Illex illecebrosus*) in the 1970s and 1980s to cold-water pelagic fish (primarily capelin *Mallotus villosus*, Atlantic herring *Clupea harengus* and Atlantic salmon

*Salmo salar*), associated with a centurially-significant cold water event in 1991 (Montevecchi & Myers 1997). Capelin have remained the primary prey of gannets at the Funk Island Seabird Ecological Reserve through the 1990s and during the early 2000s (Montevecchi et al. 2005, 2009). During daylight within foraging ranges of this colony, capelin are associated with the seabed (Davoren et al. 2006), and thus, their vertical distribu-tion is primarily determined by water depth. Pre-dictable aggregations of capelin are persistent among years at shallow water (<30 m) demersal spawning sites and deep-water (100 to 150 m) staging areas between the coast and Funk Island (Davoren et al. 2006). In deep water (>50 m), capelin migrate toward the ocean surface at dusk and back toward the seabed at dawn (Mowbray 2002, Davoren et al. 2006). We explored how gannets access capelin throughout day-light by investigating whether birds: (1) concentrate in shallow areas (< 30 m), where capelin are accessible throughout the day, or use deeper areas and either (2) concentrate foraging effort during dawn and dusk transition periods, when capelin are accessible near the surface, and/or (3) associate with other marine predators that make prey accessible at the surface throughout the day. To examine which strategies may play important roles in gannet foraging behaviour, we combine continuous records of the gannets' foraging activities, with fine temporal scale quantitative data on the vertical distribution of capelin as well as the distri-butional patterns of gannets in comparison to capelin and to other predator species.

## MATERIALS AND METHODS

**Study design.** The study design combined bird-borne device recordings on the foraging activities of gannets with meso-scale, vessel-based survey data on the horizontal distributional patterns of gannets, other predators and capelin, as well as fine-scale survey data on the vertical movement patterns of capelin. Breeding northern gannets were studied from late July to mid-August (July 24 to August 12), 1999 to 2005 at their colony on Funk Island (49°45′N, 53°11′W) off the NE coast of Newfoundland in eastern Canada (Fig. 1). Funk Island, a low-lying, flat granite rock ca. 400 × 800 m, is the site of the fourth largest and most oceanic colony of gannets in the western Atlantic. In all years, regurgitations of gannets were collected to determine dietary composition (Table 1). Archival data loggers were attached to gannets in alternating years (1999, 2001, 2003, 2005) to determine at-sea foraging behav-iour (Table 1). A meso-scale survey was conducted in 2000–2003 to determine the distribution and density of gannets and other predators along with their main

prey species, capelin, aboard the 23 m Fisheries and Oceans RV 'Shamook' in mid-late July (Table 1). The survey (~800 km) was run within avian foraging ranges and prime capelin spawning and staging areas to the south and west of Funk Island (Davoren et al. 2006; Fig. 1). Nine east-west transects spaced 9 km apart on a north–south axis were run 12 h d$^{-1}$, primarily during daylight (08:00 to 20:00 h Newfoundland Daylight Savings Time = UTC minus 2.5 h). Surveys were periodically interrupted to identify the species composition of
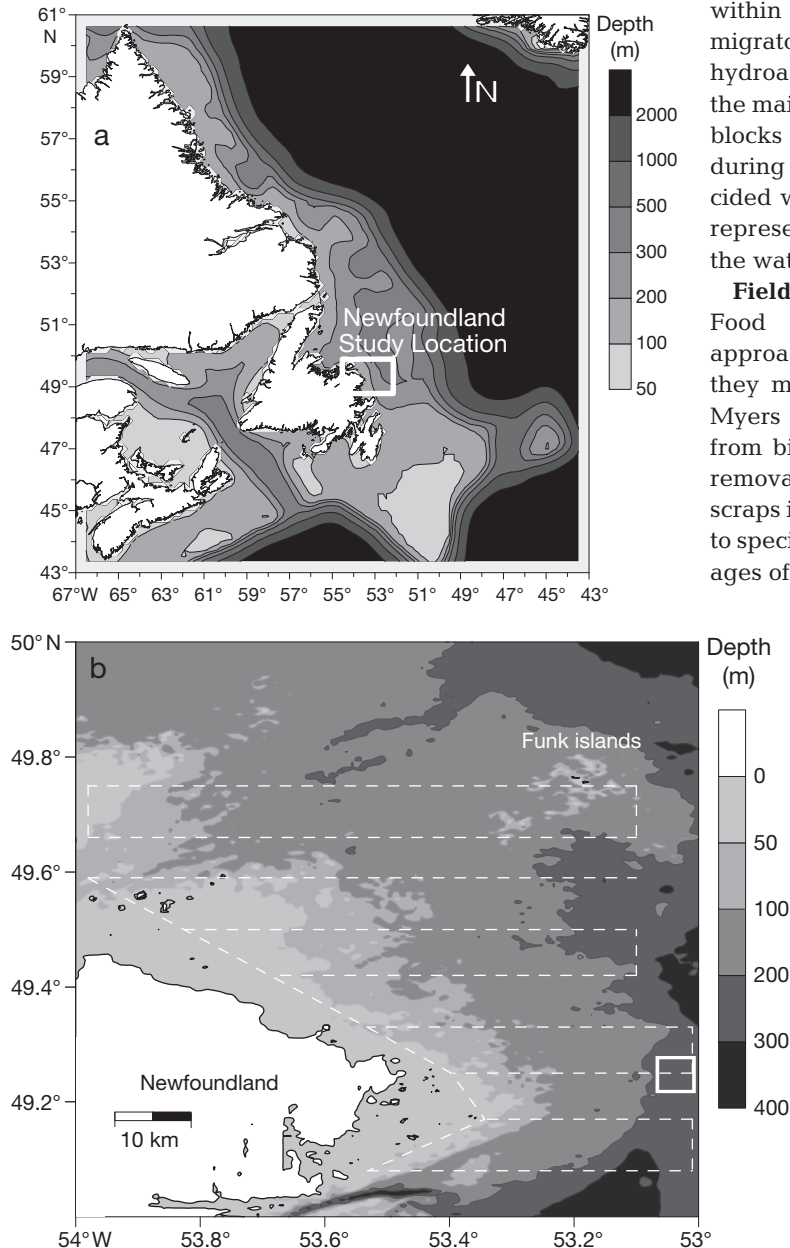


Fig. 1. Location of (a) the Newfoundland study in eastern Canada (white square) and (b) the meso-scale survey (white dashed line); fine-scale study site (white square); and Funk Island Seabird Ecological Reserve. Scale indicates the depth contours (m) in the study area

acoustic signals using a modified shrimp trawl (Davoren et al. 2006). Capelin were the numerically dominant fish species sampled (96.5%; Davoren et al. 2006).

As part of another project (Davoren et al. 2007), the diel vertical movement patterns of capelin were studied during a 4 d fine-scale study (10 to 14 August, 2005; Table 1) aboard a 60 m Fisheries and Oceans Canada RV 'Wilfred Templeman.' The fine-scale site was centered on the area (49°15′N, 53°02′W) where a large concentration of post-spawning capelin was found within avian foraging ranges (Fig. 1). To quantify the migratory patterns of capelin, we repeatedly collected hydroacoustic data along a radial survey (~30 km) over the main concentration of capelin such that all 1 h time blocks over the 24 h cycle were sampled at least once during the 4 d study. Dates of the fine-scale study coincided with the deployment of devices on gannets and represent the timing of diel vertical migrations through the water column at dawn and dusk (Table 1).

**Field work on northern gannets.** *Diet sampling:* Food samples were obtained from gannets by approaching roosting birds that often regurgitated as they moved away from researchers (Montevecchi & Myers 1995; Table 1). Samples were also obtained from birds captured for data logger attachments and removals and from discarded regurgitations and scraps in the colony. Regurgitated prey were identified to species, and prey landings are presented as percentages of total regurgitations during each year.

*Bird capture and data logger attachment:* Adult gannets with 4 to 6 wk old chicks in their nests were captured and later recaptured with a telescoping noose pole from a small portable blind to minimize disturbance to neighbouring birds. Birds were equipped with loggers, marked on the head and neck with colored markers for identification from a distance and banded with USFWS bands issued by the Canadian Wildlife Service usually within 5 to 10 min. Over all years, 5 types of data loggers were attached to derive dive depth and duration from a pressure sensor over a range of 24 to 76 h (Table 1). Lotek LTD 100s were attached by Tesa® tape to 2 plastic bands placed on one leg of each bird. The other devices were attached with Tesa® tape to either feathers on the lower back about 5 cm above the uropygial gland or the 4 central tail feathers. Breeding success was high at the sites where we worked. After each gannet carrying a logger was recaptured, devices were removed quickly, and data were downloaded onto a laptop computer.

Table 1. *Sula bassana*. Dates of vessel-based surveys and colony-based diet sampling and device deployments from 1999–2005. For detailed device descriptions refer to Garthe et al. (2000, 2003, 2007a) and Montevecchi et al. (2009). n: number of northern gannets. –: years when no data were collected

| Year | Vessel-based surveys | Diet | Device deployment | Type | % body mass | Recording interval ($s^{-1}$) | Resolution (m) | n |
|------|---------|------|------|------|------|------|------|------|
| 1999 | – | Jul 26–Aug 6 | Jul 27–Aug 5 | Lotek LTD 100[a] | 0.5 | 2 | 0.04 | 7 |
|      |   |   |   | DAR[b] | 0.9 | 4 | 0.30 | 4 |
| 2000 | Jul 18–22 | Aug 6–12 | – |   |   |   |   |   |
| 2001 | Jul 15–22 | Jul 31–Aug 6 | Jul 30–Aug 6 | Lotek LTD 100 | 0.5 | 2 | 0.04 | 3 |
|      |   |   |   | DAR compass[b] | 1.1 | 4 | 0.30 | 7 |
|      |   |   |   | PTD[c] | 0.7 | 1 | 0.025 | 4 |
| 2002 | Jul 13–18 | Aug 8-12 | – |   |   |   |   |   |
| 2003 | Jul 12–18 | Jul 26–Aug 6 | Jul 27–Aug 4 | PTD | 0.7 | 1 | 0.025 | 2 |
|      |   |   |   | GPS TDs[c] | 2.3 | 1 | 0.025 | 8 |
| 2004 | – | Jul 24–Aug 1 | – |   |   |   |   |   |
| 2005 | Aug 10–14[d] | Aug 3–11 | Aug 2–11 | GPS TDs[c] | 2.3 | 1 | 0.025 | 19 |

[a]Lotek Marine Technologies, St. John's, Newfoundland, Canada. [b]Dall'Antonia Recorders, Istituto di Elaborazione dell'Informazione, Italian Research Council (C.N.R.), Pisa, Italy. [c]Earth & Ocean Technologies, Kiel, Germany. [d]Fine-scale survey

We held the university, provincial and federal permits required to capture, equip and mark birds which were treated in accordance with the principles and guidelines of the Canadian Council on Animal Care.

**Data analysis for logging devices on gannets.** Vertical immersions were considered dives when they were deeper than 1.0 m (in 1999 and 2001) and 0.3 m (in 2003 and 2005) owing to differences in the resolution of devices used among years and to eliminate shallower measurements attributed to bathing and preening movements. There were no indications of foraging at the sea surface.

Foraging behaviour was investigated by quantifying the mean percent frequency of dives and mean dive depth per hour over all individuals throughout the 24 h cycle in a given year. To investigate diurnal diving activity, we first examined the diving activities of each individual separately. We calculated the number of dives that each individual made during each 1 h time block (e.g. 05:00 = 04:30 to 05:29 h) over all foraging trips, if more than one foraging trip was recorded. To standardize for differing number of dives performed by different individuals, we calculated the percent frequency of dives per 1 h time block for each individual in each year over the 1 h time blocks when diving activity was observed, which consistently ranged from 05:00 to 21:00 h each year. Differences in the mean percent dive frequency with time of day and year were examined using a 2-factor ANOVA. Due to non-normal distribution, percent dive frequency data were log transformed prior to analysis. For graphic purposes, we calculated the mean percent dive frequency per 1 h time block over all individuals in each year. In addition, a chi-squared analysis was conducted to determine if the total number of dives per hour performed by all individuals differed among

dawn (1 h: 04:30 to 05:29), daylight (15 h: 05:30 to 20:29), and dusk (1 h: 20:30 to 21:29) periods.

To investigate diurnal patterns in dive depth, we calculated the mean dive depth of each individual per 1 h time block, combining all foraging trips for each individual. Differences in dive depth with time of day and year were examined over the time blocks when diving activity was observed (05:00 to 21:00 h) using a 2-factor ANOVA. Due to non-normal distribution, these data were log transformed prior to analysis. When diving did not occur within a 1 h time block, this was treated as missing data as opposed to 0. For graphic purposes, we calculated the mean dive depth per 1 h time block over all individuals in each year. Statistical significance was set at $\alpha = 0.05$ and all averages are reported as ± 1SE.

**Field work on at-sea distributional patterns of gannets and capelin.** *Distribution of capelin:* During the meso-scale survey, signals of fish species were recorded continuously using 3 hydroacoustic systems. The quality of each hydroacoustic system and data processing techniques varied, although they were equally capable of determining the presence or absence of capelin shoals, and distributional patterns. Vessel speed (11 to 14 km $h^{-1}$) was held constant throughout all surveys. Short descriptions of the methods are provided here but refer to Davoren et al. (2006) for details and Table 1 for survey dates.

For the 2000 meso-scale survey, a Simrad EQ100 system was operated through a hull-mounted 38 kHz single beam transducer that operated at 1 ping $s^{-1}$ over a depth range of 8 to 250 m with a bandwidth of 0.4 to 0.6 ms. The transducer was at a depth of 3 m and a beam pattern would not form within a range of 5 m; therefore, acoustic signals were not reliable until 8 m. Echograms were continuously printed and latitude and

longitude were recorded on them every 10 min. The relative abundance of fish was quantified by estimating the percent cover of the prey image in each 250 m (~1 min) horizontal by 10 m vertical bin on the echogram (Piatt 1990). An index of percent cover of prey in each bin was estimated from 0 (no prey) to 9 (near-saturation). These index values were squared before analysis 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 the surveys in 2001, 2002 and 2003, a BioSonics DTX 6000 hydroacoustic system calibrated with a tungsten carbide standard target was used. This system operated through a 38 kHz dual beam transducer in a towed body. The transducer was at a depth of 2 m and a beam pattern would not form within a range of 5 m, therefore, acoustic signals were not reliable until 7 m. The transducer had a 2-way beam angle of 22.671 dB and the echo sounder was operated at 1 ping $s^{-1}$ over a depth range of 7 to 500 m, a bandwidth of 5.1 kHz and a pulse duration of 0.4 ms. Raw high-resolution acoustic data were recorded continuously. A $S_v$ threshold of −63 dB was applied to the raw data prior to integration and acoustic signals near the bottom that could not be distinguished as biological or due to the ocean floor (dead-zone, side-lobing; Lawson & Rose 1999) were edited out. The $S_v$ in each file was integrated to determine the average aerial backscattering coefficient ($S_a$) for capelin within the water column (MacLennan et al. 2002).

During the fine-scale survey in 2005, the same radial survey was repeated throughout the 24 h cycle to collect acoustic data on the diel vertical migration (DVM) of capelin. A Simrad EK 500 hydroacoustic system calibrated with a tungsten carbide standard target was used. This system operated through a hull-mounted 38 kHz split-beam transducer, which had a 2-way beam angle of -20.6 dB and the echo sounder was operated at 1 ping $s^{-1}$ over a depth range of 10 to 300 m, a bandwidth of 3.8 kHz and a pulse duration of 1.0 ms. The transducer was at a depth of 4 m and a beam pattern would not form within a range of 5 m; therefore, acoustic signals were not reliable until 9 m. Raw high-resolution acoustic data were recorded continuously and data processing was similar to that described in the previous paragraph with the exception of applying a threshold of −80 dB to the raw data prior to integration.

*Distribution of marine birds and mammals:* During all acoustic transects, marine birds and mammals 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 the standard strip method of Tasker et al. (1984). Counts with behavioural descriptions (on water, flying,

feeding) were entered on a laptop computer with counting software (D. Senciall, Birds & Beasty Counter, 1998, Fisheries and Oceans Canada, version 1.0) connected to the navigational system of the vessel. A latitude and longitude position was appended to each sighting and location information was used to merge bird and acoustic prey data sets into the smallest spatial bins possible (2000: 250 m; 2001 to 2005: 100 m).

**Data analysis for at-sea distributional patterns of birds, marine mammals and capelin.** To examine whether gannets concentrated in shallow bathymetric areas (<30 m) where capelin would be accessible throughout the day, we calculated the weighted frequency of occurrence of gannets (flying and on the water) in 10 m bathymetric bins during the meso-scale survey in each year by dividing the percent frequency of gannets in each bin by the percent frequency at which each bin was surveyed.

To examine whether gannets used marine mammals to access capelin near the surface, we compared the tracking scales of gannets to capelin with gannets to humpback whales *Megaptera novaeangliae* and minke whales *Balaenoptera acutorostrata* during meso-scale surveys, using ANOVA. Bivariate statistics based on the neighbour *K* statistic (Ripley 1981) were used to quantify whether there were significantly more gannets (on the water and flying) associated with acoustic fish signals or whales than would be expected if gannets were distributed randomly within a transect following a quantitative method outlined in detail in numerous publications (O'Driscoll 1998, Davoren 2000, Davoren et al. 2002, 2003). A transect was defined as a period of continuous survey, which consisted of the 12 h operational d (~140 km) and the spatial scales analyzed ranged from the smallest spatial resolution (2000: 250 m; 2001 to 2003: 100 m) and increased at increments corresponding to half the length of each transect line (~70 km). The average number of 'extra' gannets at each prey aggregation, 'extra' gannets at each whale aggregation, or 'extra' whales at each prey aggregation, at each spatial scale was calculated. The scale of maximum association, or 'tracking scale,' of gannets to acoustic fish signals, gannets to whales, or whales to acoustic fish signals was defined as the scale at which the average number of 'extra' gannets or whales was higher than the succeeding 3 values.

## RESULTS

### Gannet diets

The regurgitations of gannets were composed of >70 % capelin in most years (Fig. 2), with one major exception being 2005 when 87 % of the diet consisted
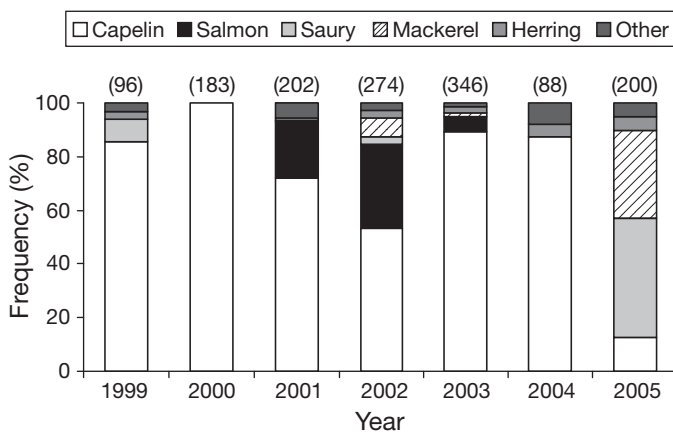
Fig. 2. *Sula bassana.* Frequency (%) of prey types in the regurgitations of northern gannets during 1999 to 2005 at Funk Island. Numbers in brackets = total no. of regurgitations examined $yr^{-1}$. Other: gadoid, squid and mixed-species regurgitations; 1999: capelin-saury; 2001: capelin-salmon, salmon-saury, salmon-herring; 2002: salmon-mackerel, salmon-saury, salmon-squid, salmon-herring, saury- mackerel; 2003: capelin-herring, gadid-salmon; 2004: capelin-herring; 2005: capelin-herring, capelin-saury, herring-saury, herring-mackerel

of large pelagic fish, mainly mackerel and saury. Food samples obtained upon recaptures for logger retrievals were similar. Regurgitations from loggered birds were comprised of capelin in 1999 (n = 5, 100 % capelin) and 2003 (n = 5, 100 % capelin), and other prey were present in 2001 (n = 5, 60 % capelin, 40 % salmon) and 2005 (n = 4, 50 % capelin, 25 % saury, 25 % mackerel).

## Diel vertical migration (DVM) of capelin

During the fine-scale survey in 2005, the radial survey was repeated 18 times, resulting in 543 km of acoustic data on the DVM of capelin. Over the diel light cycle, capelin showed a typical vertical migratory pattern. During daylight hours, distinct capelin shoals were typically concentrated in deep water (>180 m), with fish ascending toward the surface at dusk (Fig. 3). The ascent took place over approximately 30 min, lasting between 20:40 and 21:10 h local time. During dark hours, capelin remained as a layer of scattered fish (i.e. no distinct shoals) in the top 30 m, with fish forming distinct shoals and descending to deep water at dawn (Fig. 3). Again, the descent took place over approximately 30 min, lasting between 05:10 and 05:40 h local time (Fig. 3). Therefore, during dark periods (21:10 to 05:10 h), the highest percentage of $S_a$ due to capelin was observed in the upper water column (<30 m), whereas during daylight periods (05:30 to 20:40 h local time) when gannets are primarily feeding, the highest percentage of capelin was found in deeper water

(>180 m). This typical DVM pattern of capelin is consistent with other years in this (Davoren et al. 2006) and other regions (Mowbray 2002) of Newfoundland.

## Diurnal dive behaviour of gannets

Gannets did not dive during dark periods (~21:30 to 04:29 h local time; Fig. 4) and the first recorded dive at dawn was similar among years (range: 05:00 to 05:19 h), as was the last recorded dive at dusk (range: 21:05 to 21:23 h). The mean percent dive frequency per hour was generally higher during morning (05:30 to 10:30 h) and evening periods (17:30 to 21:30 h), although these patterns were non-significant and there were no differences among years ($F_{65,274}$ = 1.126, p = 0.257; Fig. 4). When all individuals and all years were combined, there were no significant differences in the number of dives per hour among dawn (04:30 to 05:29 h), daylight (05:30 to 20:29 h), and dusk (20:30 to 21:29 h) periods ($\chi^2$ = 10.525, df = 6, p > 0.05). Similarly, diurnal differences in dive depth were not significant, but the mean dive depth was significantly shallower in 2005, when gannets were feeding primarily on large pelagic fish (ANOVA, $F_{66,319}$ = 2.023, p < 0.0001; Fig. 5).

## At-sea distributional patterns of capelin, gannets and whales

Although the frequency of gannets was high in areas of shallow water (<30 m) in most years, high frequencies were found in deeper water (Fig. 6) where capelin would have been inaccessible during daylight. Gannets had significantly tighter spatial associations with whales (1.6 ± 0.3 km) over all survey years when compared to capelin in 10 to 50 m of water (27.8 ± 7.7 km; $F_{1,23}$ = 4.411, n = 25, r = 0.401, p = 0.047). Whales and capelin showed tight associations (1.2 ± 0.3 km) over all survey years when whales were present in the study area (Table 2). When whales were not encountered during the meso-scale survey in 2002, there were fewer gannets in the study area and gannets had tighter associations with capelin in the top 50 m, relative to other years (Table 2).

## DISCUSSION

Gannets tended to concentrate in shallow areas (<30 m), where capelin were accessible at all depths; however, birds also were found in deeper areas. Although diurnal patterns in dive activity were observed for gannets along with diel vertical migratory behaviour of capelin, gannets did not appear to con-
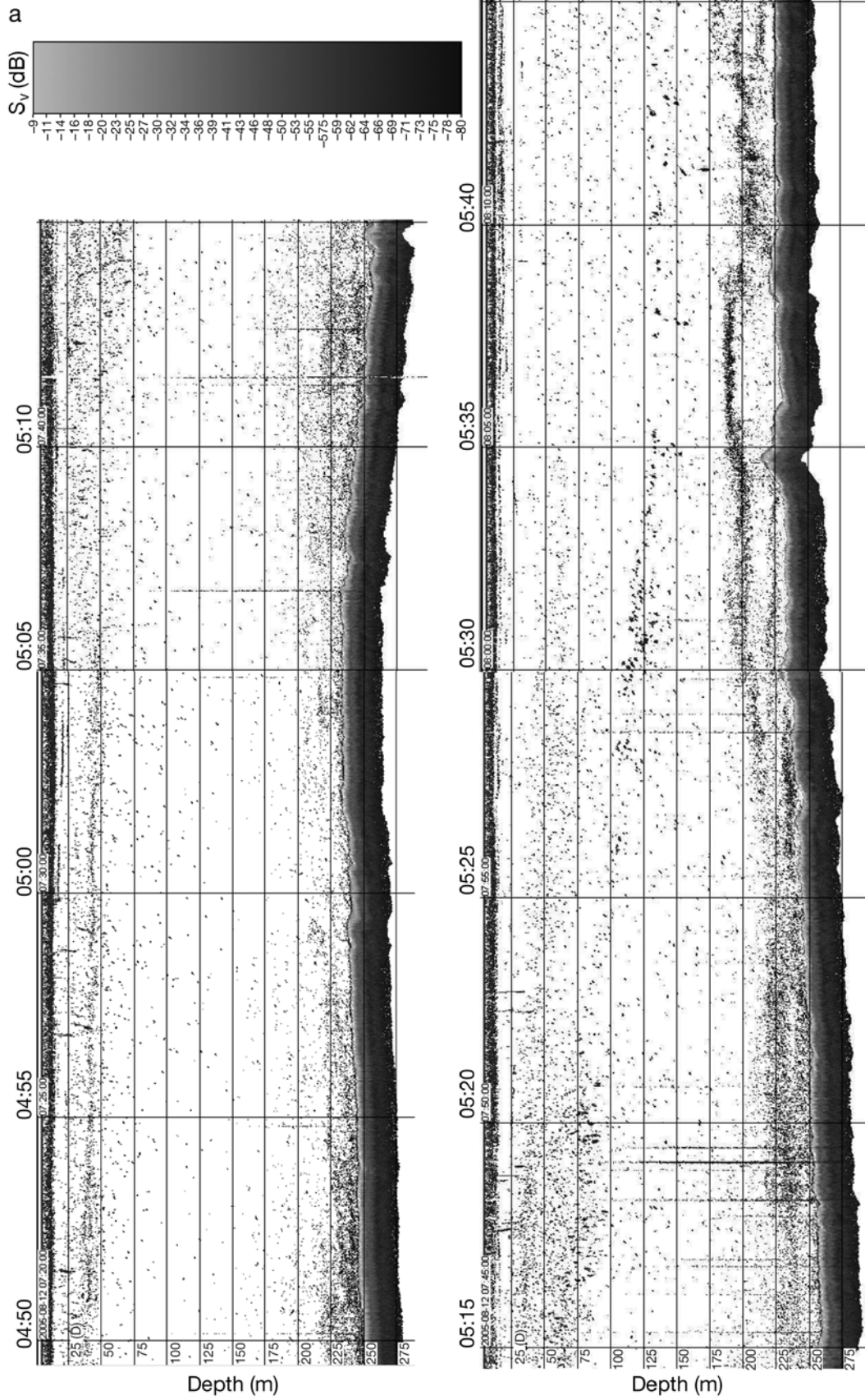
Fig. 3. (this and following page). *Mallotus villosus. Echograms* showing the fine-scale timing of capelin vertical migration toward (a) the ocean floor at dawn (05:10 to 05:30 h local time) and (b) the ocean surface at dusk (20:40 to 21:10 h local time) at the fine-scale survey site. Colour scale indicates the volume backscattering coefficient ($S_v$) from acoustic targets, with −9 dB (light gray) representing a stronger signal (more fish) and −80 dB (dark gray) representing a weak signal (less fish)
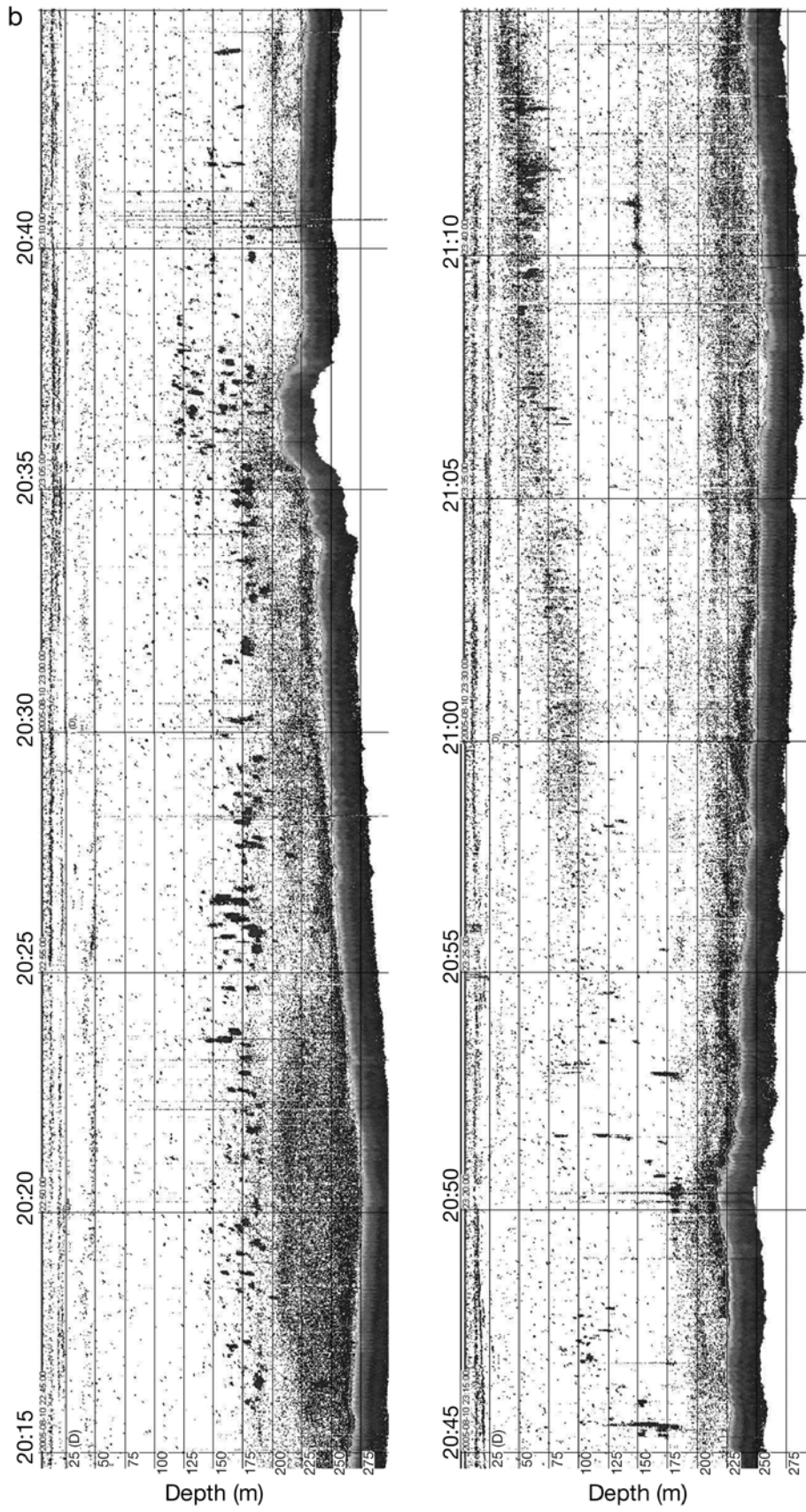
Fig. 3 (continued)
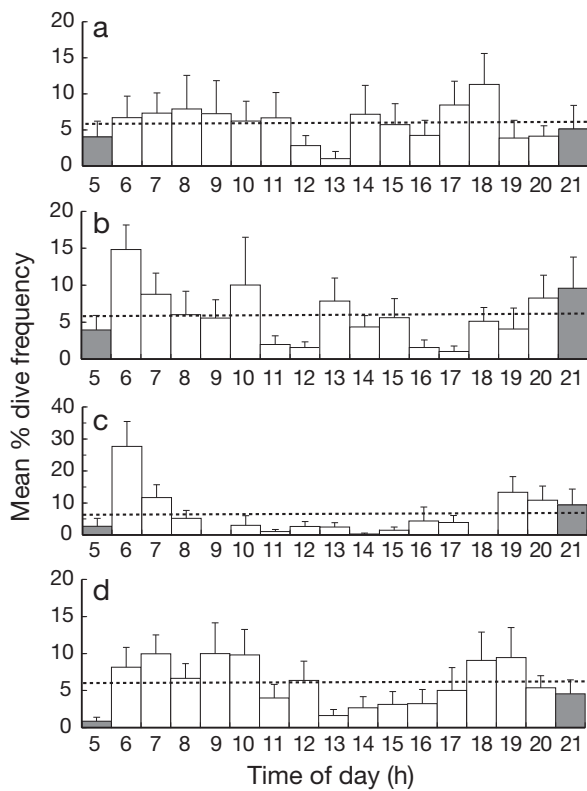
Fig. 4. *Sula bassana.* Mean dive frequency (%, ±SE) of all dives made by parental gannets on all foraging trips during each hour (e.g. 05:00 = 04:30 to 05:29 h) at Funk Island in (a) 1999, (b) 2001, (c) 2003, and (d) 2005. Dashed line: mean % frequency dives h$^{-1}$ yr$^{-1}$; grey bars: transition periods at dawn (05:10 to 05:40 h local time) and dusk (20:40 to 21:10 h local time). Note the different *y*-axis in (c)

Fig. 5. *Sula bassana.* Mean maximum depth (±SE) of all dives made by parental gannets on all foraging trips during each hour (e.g. 05:00 = 04:30–05:29 h) at Funk Island in (a) 1999 and (b) 2001, (c) 2003, and (d) 2005. Dashed line represents the mean dive depth in each year. Grey as in Fig. 4

centrate diving effort during dawn and dusk periods, shown by the low mean percent dive frequency during these periods. In addition, there was low temporal overlap (<30 min) in diving activity at dawn and dusk when capelin would have been accessible at the surface. This suggests that gannet diving behaviour is not influenced by the migratory patterns of capelin to a great extent. In contrast, gannets were tightly associated with whales relative to near surface (10 to 50 m) capelin during daylight, which is consistent with results from a previous study (Garthe et al. 2007a). Combined with the tight association of whales and capelin, these results suggest that gannets may successfully track capelin by cueing to the foraging activities of whales.

Foraging in shallow waters (<30 m) in our study area likely reflects the concentration of foraging effort in areas where capelin are accessible throughout the day. Owing to the persistent aggregations of capelin among years at shallow water (<30 m) demersal spawning sites in our study area (Davoren et al. 2006), this may also reflect a memory-based foraging strategy. In sup-
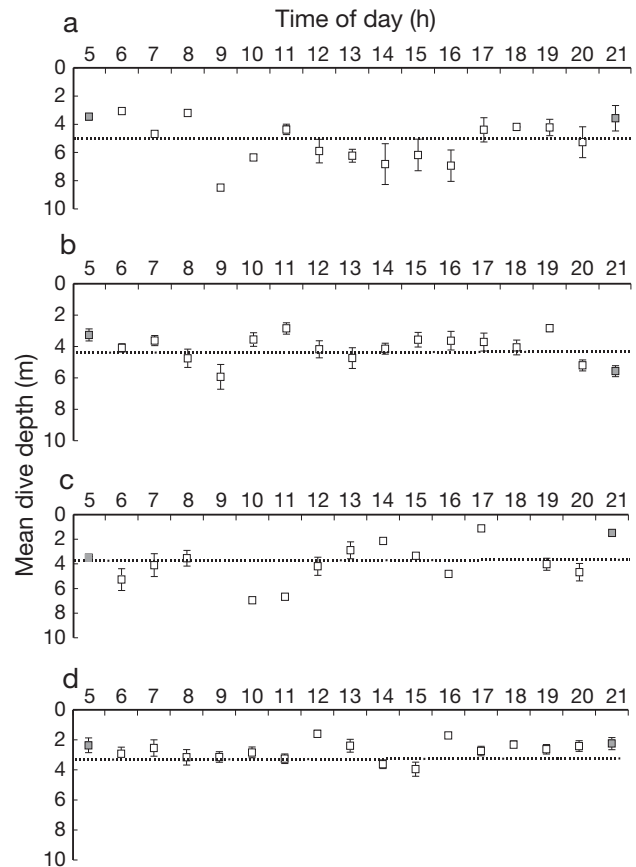
port, Garthe et al. (2007a) showed that dive locations of gannets often overlapped with these spawning aggregations of capelin (Davoren 2007). Gannets showed strong foraging area fidelity on a coarse scale for these areas on successive foraging trips, though exact dive locations within areas varied (Garthe et al. 2007a). Similar foraging patterns on successive foraging trips by parental gannets have been observed in our study area (Montevecchi et al. 2009) and in other regions (Hamer et al. 2001). This likely reflects the use of memory on a coarse-scale and network foraging or local enhancement on a finer spatial scale to locate capelin shoals that are accessible during daylight (Wittenberger & Hunt 1985).

Multispecies feeding assemblages of marine predators have been described throughout the world's oceans (Evans 1982, Hunt et al. 1988, Harrison et al. 1991, Camphuysen & Webb 1999, Silverman & Veit 2001) as have the roles of different species in initiating and suppressing (producing and scrounging) these assemblages (Hoffman et al. 1981, Chilton & Sealy 1987). Foraging whales are thought to be important
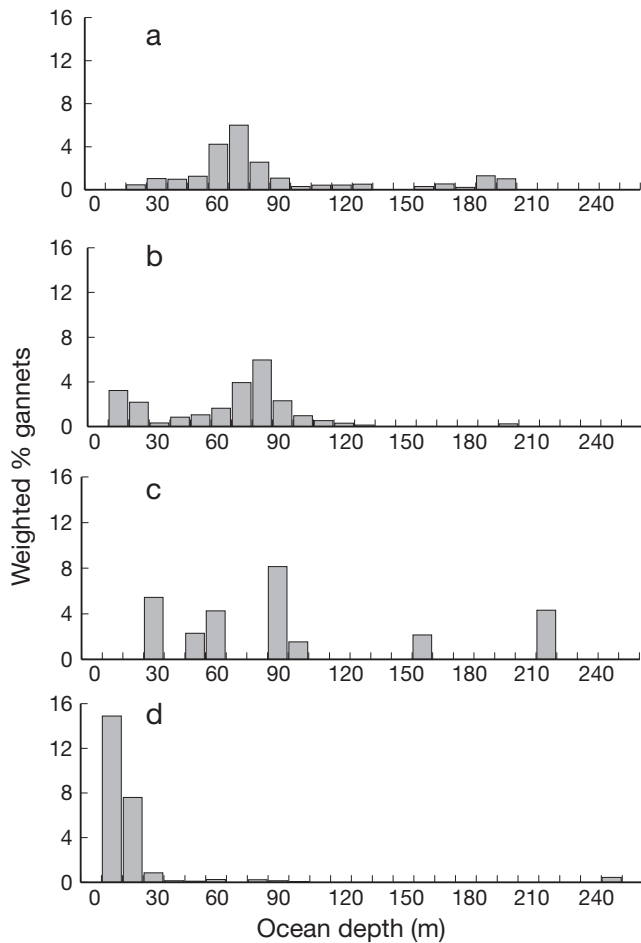
Fig. 6. *Sula bassana.* Weighted frequency of occurrence (%) of northern gannets (flying and on the water) in each 10 m bathymetric bin during each meso-scale survey in mid-late July (a) 2000, (b) 2001, (c) 2002, and (d) 2003

initiators of feeding assemblages of seabirds (Obst & Hunt 1990) and gannet–cetacean associations, in particular, are well known (Evans 1982, Camphuysen et al. 1995, Camphuysen & Webb 1999). Cetaceans may function to both minimize the time and energy spent searching for prey as well as bring otherwise inaccessible prey near the ocean surface (Camphuysen et al. 1995, Camphuysen & Webb 1999). For instance, humpback whales are known to herd schools of forage fish using 'bubble nets' near the ocean surface (Evans 1982, Sharpe & Dill 1997). Although not directly observed in our study, this is one way whales may increase the accessibility of capelin to gannets. Tracking large predators in general may be a foraging pattern used by gannets. For example, at wintering areas along the SE USA coast, gannets exhibit strong associations with bluefin tuna *Thunnus thynnus*, apparently as a means of facilitating prey capture (A. M. Boustany pers. comm.).

To our knowledge, despite numerous seabird-whale associations described in the literature, this is the first demonstration that gannets may preferentially track whales rather than prey. Overall, the tighter spatial association of gannets and whales relative to near-

Table 2. *Sula bassana*, *Megaptera novaeangliae*, *Balaenoptera acutorostrata* and *Mallotus villosus*. Number of northern gannets and whales, proxies of capelin abundance in the top 50 m, and tracking scales of gannets to capelin, gannets to whales, and whales to capelin during the meso-scale surveys in 2000, 2001, 2002 and 2003. Numbers in brackets indicate the number of transects (~140 km) for which tracking scales were calculated (i.e. transects where both gannets and capelin, gannets and whales, or whales and capelin were observed). –: years when no data were collected

|  | 2000 | 2001 | 2002 | 2003 |
|---|---|---|---|---|
| Survey length (km) | 610 | 431 | 373 | 517 |
| No. of gannets | 685 | 962 | 220 | 1191 |
| % flying | 65 | 70 | 94 | 30 |
| % plunge diving | 1 | 1 | 0 | 1 |
| % sitting on the water | 34 | 29 | 6 | 69 |
| Mean ± SE no. of gannets per km | 0.13 ± 0.03 | 0.10 ± 0.01 | 0.03 ± 0.01 | 0.23 ± 0.12 |
| No. of whales | 31 | 25 | 0 | 7 |
| No. of capelin shoals <50 m | 79 | 206 | 38 | 49 |
| Total horizontal distance of capelin shoals <50 m (km) | 5.7 | 12.0 | 13.0 | 4.5 |
| Mean ± SE width of shoals <50 m (m) | 71.8 ± 13.9 | 58.3 ± 3.8 | 341.4 ± 98.5 | 90.8 ± 16.8 |
| Tracking scale: gannets–capelin (<50 m) |  |  |  |  |
| Mean ± SE (km) | 33.4 ± 22.4 (5) | 33.9 ± 12.9 (6) | 13.3 ± 3.2 (4) | 25.5 ± 16.6 (3) |
| Range (km) | 7.8–122.8 | 4.9–84.3 | 5.3 – 16.9 | 4.3 – 58.2 |
| Tracking scale: gannets–whales |  |  |  |  |
| Mean ± SE (km) | 1.7 ± 0.5 (4) | 1.4 ± 0.8 (2) | – (0) | 1.6 (1) |
| Range (km) | 0.8–2.8 | 0.6–2.1 | – | 1.6 |
| Tracking scale: whales–capelin (total) |  |  |  |  |
| Mean ± SE (km) | 1.4 ± 0.6 (5) | 1.0 ± 0.2 (3) | – (0) | 1.1 ± 0.4 (2) |
| Range (km) | 0.5–3.8 | 0.6–1.3 | – | (0.7–1.4) |

surface capelin shoals, combined with the tight spatial association of whales and capelin, suggest that gannets may successfully track capelin by cueing to the foraging activities of whales.

Breeding gannets can also offset energy expenditure during foraging in a number of other ways. First, gannets can switch prey species and sizes captured (Montevecchi & Myers 1997, Hamer et al. 2000). Gannets tend to prefer large pelagic fish, as their dietary composition reflects the presence or absence of these fish within foraging ranges (Montevecchi & Myers 1995, Montevecchi 2007). Capelin comprise the bulk of the diet when large pelagic fish are absent (Montevecchi et al. 2005). Second, gannets appear to alter dive shape (U- versus V-shaped dives; Garthe et al. 2000), dive depth (this study) and foraging ranges (Garthe et al. 2007b) when capturing different prey types. For instance, the shallower mean dive depth in 2005 corresponds with the higher percentage of large pelagic fish (80%) in their diets. This also corresponds to concentrating foraging activity primarily in shallow water areas. By switching from flapping flight (high energetic costs) to gliding flight (lower energetic costs; Birt-Friesen et al. 1989) gannets can increase foraging ranges without much more energy expenditure relative to other more heavily wing-loaded species (e.g. murres; Monaghan et al. 1994). Along with recent reductions in human-induced mortality, this behavioural flexibility supports the increasing trends in gannet populations (Montevecchi & Myers 1997, Montevecchi et al. 2009).

Although gannets appeared to concentrate foraging effort in early morning and late evening, these trends were not significant and peaks occurred after capelin had migrated to inaccessible depths. Although endothermic, air-breathing predators are known to dive to shallower depths during dark periods when foraging for prey that undergo regular DVM (Croxall et al. 1985, Kooyman et al. 1992, Williams et al. 1992, Pütz et al. 1998, Georges et al. 2000), these dives appear to result in low ingestion rates (Wilson et al. 1993). This is supported by the lack of foraging activity by gannets under low light conditions, including dark, dawn and dusk transition periods (<1 µEinsteins m$^{-2}$ s$^{-1}$), beginning only after light levels had increased (~8 µEinsteins m$^{-2}$ s$^{-1}$; G.K.D. unpubl. data), as has been found in other studies (Wanless et al. 1999). In addition, the dispersion of near-surface capelin at dawn and dusk may also reduce capture rates. Although we did not measure ingestion rates, the similar number of dives per hour throughout dawn, dusk and daylight periods suggests that foraging success may be comparable throughout the period that gannets dive. The lower percent dive frequency at dawn and dusk compared to other daylight periods along with the low temporal overlap (<30 min) of diving activity with near-surface capelin at dusk and dawn, suggest that the diel vertical migratory patterns of capelin have little influence on gannet foraging activities. Alternately, capelin migratory patterns likely have a stronger influence on foraging strategies of other avian predators in the study area, specifically the common murre *Uria aalge*, that relies primarily on capelin as prey (Davoren & Montevecchi 2003) and forages throughout the diel cycle (Hedd et al. 2009).

Diurnal trends in diving activity may instead result from physiological processes related to digestion or provisioning behaviour. Gannets spend extended rest periods on the sea surface during foraging trips (Garthe et al. 2003, Lewis et al. 2004, Ropert-Coudert et al. 2004), which are thought to allow the digestion of ingested prey. Owing to time needed to digest prey, parents may concentrate foraging efforts during the evening, so that periods of digestion overlap with the imposed non-foraging dark period (Garthe et. al. 2003, Ropert-Coudert et al. 2004). In support, parents that depart the colony later in the day, typically stay at sea overnight and concentrate foraging activity just before dark (Garthe et al. 2003). The concentration of foraging effort in the morning could be to obtain food for the chick before returning to the colony (Garthe et al. 2003).

## CONCLUSION

The diel vertical migration of prey is an obvious explanation for observed diurnal foraging patterns of marine predators. Few studies, however, have tested this by directly comparing the fine-scale timing of vertical movement patterns of prey and predator foraging activities (Croxall et al. 1985). By doing this, we found that despite diurnal trends in the foraging activities of an opportunistic marine avian predator, these do not appear to reflect the accessibility of near-surface forage prey at dawn and dusk. Instead, predators appeared to use memory of temporally and spatially predictable aggregations of accessible prey and local enhancement associated with conspecific and marine mammals. By employing this mixed strategy, predators apparently combine advantages of increased light during daylight and decreased energy required to locate near-surface capelin aggregations, thus allowing high foraging efficiency.

There is growing evidence for consistent habitat use by marine predators, reflected by regular concentration in 'hot spots', as well as memory-based foraging tactics, where bird-borne position loggers reflect animals returning to the same fine and coarse-scale regions within and among years. A mixed strategy of

memory-based foraging tactics combined with local enhancement likely minimizes energetically costly search activities for prey in a dynamic patchy environment. This is especially notable during periods of high energetic demands, such as breeding or moulting.

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