THE INFLUENCE OF FISH BEHAVIOUR ON SEARCH STRATEGIES OF COMMON MURRES *URIA AALGE* IN THE NORTHWEST ATLANTIC

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SUMMARY

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Although distribution patterns of seabirds at sea have been described for decades, it remains difficult to identify the mechanisms underlying these patterns. For instance, researchers focusing on prey dispersion as the primary determinant of seabird distribution have found high variability in the spatial overlap of bird and prey aggregations, partially due to the scale-dependent nature of such associations. We conducted a study to identify how the behaviour of capelin *Mallotus villosus*, the primary prey species of all vertebrate predators in the Northwest Atlantic, influences the search tactics of Common Murres *Uria aalge* while acting as central-place foragers during chick-rearing. The study was conducted from 1998-2002 on and around Funk Island, the largest colony of murres in eastern Canada (~ 400 000 breeding pairs), situated on the northeast coast of Newfoundland. We made direct measurements of (1) the distribution, abundance and spatial and temporal persistence of capelin aggregations within the foraging range from the colony (~ 100 km) in combination with (2) bio-physical habitat characteristics associated with capelin aggregations, and (3) individual- and population-level arrival and departure behaviour of murres from the colony. During July of 2000, capelin were found to be persistently abundant within specific 2.25 km blocks of transect ("hotspots"). Further study revealed that capelin persisted in hotspots due to bio-physical characteristics suitable for demersal spawning and for staging areas and foraging areas prior to and after spawning. Directions of return and departure flights of murres measured from the colony did not match during the same observation period (~ 1h), indicating that murres departing the colony did not use information on prey distribution provided by the flight paths of flocks returning to the colony (Information Center Hypothesis). Specific commuting routes (regular flight paths) of murres toward and away from capelin hotspots, however, were obvious at sea, and feeding murres consistently marked the location of these hotspots. This provided excellent conditions for murres to locate capelin from memory and by cueing to activities of conspecifics (local enhancement). Hotspots were persistent across years in this region, presumably allowing marine predators to learn the locations of hotspots, resulting in the use of traditional feeding grounds through generations. Hotspots of predators and prey promote energy transfer among trophic levels, a key ecosystem process. Human predators also concentrate fishing activities within these areas and, thus, there is a need to identify hotspots for protection. Persistent hotspots would be particularly amenable to the design of marine protected areas defined by the habitats of marine predators and their prey.

Keywords: foraging, prey dispersion, capelin, *Mallotus villosus*, Common Murre, *Uria aalge*, information centre

INTRODUCTION

In marine ecosystems, focal forage fish species lie at the core of complex food webs, providing essential linkages for energy transfer between zooplankton and upper trophic predators, such as marine birds (Lavigne 1996). Schooling forage fish often form high-density aggregations (Rose & Leggett 1990). Physical characteristics, such as hydrographic regimes, in combination with biological factors, such as food and predator density, influence the distribution and persistence of these aggregations in space and time (Schneider 1991). High densities of forage fish species elicit an aggregative response in marine bird predators (e.g., Cairns & Schneider 1990) and, thus, influence the distributional patterns and foraging strategies of upper trophic consumers in marine systems (e.g., Davoren 2000, Davoren *et al*. 2002). Habitat selection by the dominant forage fish is therefore essential to comprehend the mechanisms underlying distributional patterns of top vertebrate predators and ultimately trophic interactions in marine systems.

Seabirds provisioning offspring on a colony (Central Place Foragers) are physically separated from their foraging grounds (Orians & Pearson 1979). The travel-time between the colony and prey aggregations and the foraging time within these aggregations both limit the rate of food delivery to offspring (Orians & Pearson 1979). To breed successfully, central place foragers must be proficient at locating food. The Central-Place Foraging model (Orians & Pearson 1979) predicts that colonial animals minimize the duration of round trips and, thus, seabirds likely employ tactics that minimize the time spent searching and capturing prey. An example of this is seabirds using past experience (e.g., Irons 1998). Individuals also can reduce the time spent searching by using information provided by other conspecifics (Wittenberger & Hunt 1985). The Information Center Hypothesis (ICH) postulates that information about the location of prey aggregations beyond the visual range of the colony is exchanged among individuals at the colony (Ward & Zahavi 1973). For instance, naïve birds may follow "successful" ones to prey aggregations (Ward & Zahavi 1973) or track the routes of successful birds returning to the central place from foraging grounds (Gaston & Nettleship 1981; Burger 1997). Information also can be exchanged by cueing to the foraging activities of others within sight, a process known as local enhancement (Wittenberger & Hunt 1985). The degree to which these different strategies are used by seabirds depends on the persistence of prey aggregations in time and space.

The Common Murre *Uria aalge* is a pursuit-diving marine bird that dives to depths up to 200 m (Piatt & Nettleship 1985). Their wing design compromises aerial (high surface area) and underwater flight (low surface area; Thompson *et al*. 1998) and results in high wing-loading (i.e. body mass to wing area ratio: 2.06 g cm^{-2}; Guillemette 1994). Therefore, energy expenditure is elevated during flight compared to most other seabirds. Murres are highly colonial and lay a single egg clutch. The chick is reared at the colony by both parents for 3 weeks. One parent remains at the colony with the chick while the other is on a foraging trip. After most foraging trips, the parent delivers a single fish to its chick. Prior to departure on a foraging trip, murres commonly land on the water in close proximity to the colony (splashdown area, Burger 1997). Murres also regularly return to the colony in large flocks (Gaston & Nettleship 1981, Burger 1997), which presumably indicates the direction of travel from foraging grounds. It has been suggested that these flocks provide the potential for murres in the splashdown area to use an ICH-type mechanism to determine the location of foraging areas beyond visual range of the colony (Gaston & Nettleship 1981, Burger 1997).

In Newfoundland, murres feed their chicks and themselves primarily female capelin *Mallotus villosus* (Müller, 1776) during the breeding season (Davoren & Montevecchi 2003). Capelin, a small, short-lived, pelagic fish, is the main prey of marine birds, mammals and piscivorous fish (Carscadden *et al*. 2002). Capelin migrate into coastal waters from the shelf edge during spring to spawn (Templeman 1948). At this time, capelin schools can be patchily distributed and ephemeral at small spatial scales (1-1000 m) but can also be predictably located within larger regions (1-100 km) in different seasons (e.g. Methven & Piatt 1991). Different stocks have varying spawning habitat preferences, with capelin stocks in Newfoundland primarily considered to spawn on or immediately adjacent to beaches (Templemen 1948), whereas stocks elsewhere in the world primarily spawn off-beach or demersally (Vilhjalmsson 1994). Spawning site characteristics vary, including sediment size range (0.1 - 25 mm), water depth (0 - 100 m) and water temperature (0 - 12ºC; Vilhjalmsson 1994).

We conducted a study to identify how the behaviour, particularly habitat utilization, of forage fish shapes the search tactics of central-place foraging seabirds. Due to the energetically costly nature of search activities for murres, we hypothesize that they will minimize search efforts. During July 2000, we directly measured the distribution and spatial and temporal persistence of capelin within the foraging range of murres from Funk Island, the largest colony of murres in eastern Canada, situated on the northeast coast of Newfoundland. During July-August 2001-2002, we described the bio-physical habitat characteristics that were associated with high-abundance aggregations of capelin. During July-August 1998-2000, we quantified individual- and population-level arrival and departure behaviour of provisioning murres from Funk Island within and among days. We combined this information to infer the relative use of information exchange and past experience, in locating capelin from the colony.

METHODS

Study area

This study was conducted during 1998 - 2002 on and around Funk Island (49°45’N, 53°11’W) on the east coast of Newfoundland (Fig. 1). Funk Island lies 60 km from the coast and supports a common murre population of 340 000 - 400 000 breeding pairs (Birkhead & Nettleship 1980). Throughout this study, murres delivered primarily capelin to their chicks (94% by number, Davoren & Montevecchi 2003), which is consistent with long-term dietary trends throughout Newfoundland (e.g., Burger & Piatt 1990).

Survey design

During July 2000, an 800 km survey was conducted to the southwest of Funk Island aboard the 23 m Canadian Coast Guard Vessel *Shamook*. The location of the survey track was based on observations of flight directions of murres in 1997, observations of high-abundance capelin-murre aggregations enroute to Funk Island from 1977 - 1997 (WAM unpubl. data) and the location of traditional cod and capelin fishing areas (L. Easton, pers. comm.). The survey consisted of nine east-west (across shelf) hydroacoustic transects at a 5 Nm (9 km) north - south spacing. Two east-west transects were conducted during each 12 h day. Seabirds were counted continuously during acoustic transects. The survey was periodically interrupted to sample acoustic signals using a modified shrimp trawl. This survey was conducted once over 5 days, followed by a 2 week period when shorter (2.25 km) transects were repeated

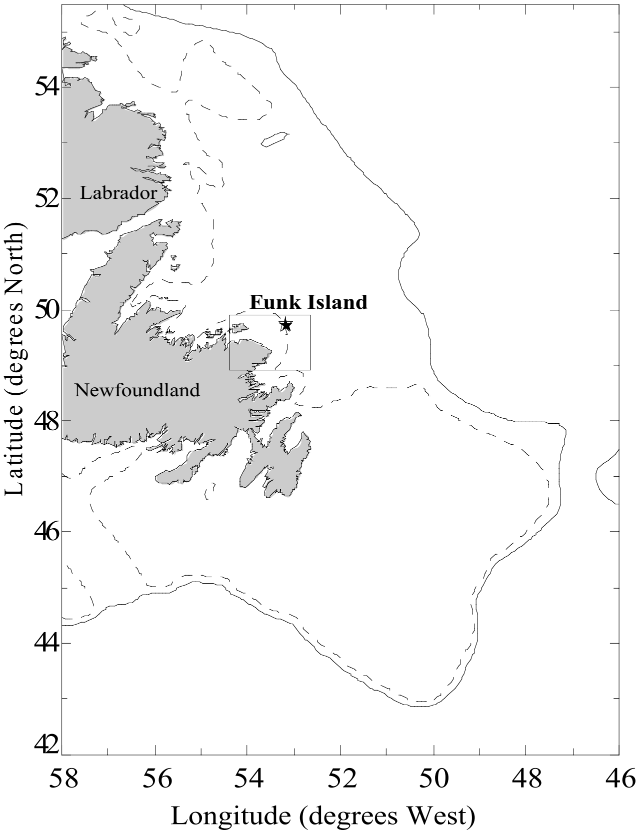

Fig. 1. The map of the study area showing eastern North America’s largest colony of Common Murres, the Funk Island Seabird Ecological Reserve. Depth contours are 200 m (– – –) and 500 m (———) and the study area is indicated (rectangle).

along the initial survey track in areas of high capelin abundance. During these shorter transects, acoustic estimates were conducted simultaneously with seabird counts, as in the initial survey.

Acoustic estimates

The relative abundance and distribution of capelin was quantified using a Simrad EQ100 echosounding system, operated through a hull-mounted single-beam transducer with a frequency of 38 kHz. This frequency is appropriate for observations of fish targets and the distinct shape of capelin schools allows them to be separated from other fish species (e.g., American sandlance *Ammodytes americanus*, Atlantic herring *Clupea harengus*) within the study area (O'Driscoll *et al*. 2000). The transducer had a 10-degree beam angle and the echosounder was operated at 1 ping per s, a range of 150 m at one-tenth power, and a bandwidth of 0.3 ms. The transducer was at a depth of 3 m and beam pattern did not form within a range of 5 m; therefore, acoustic signals were not reliable until 8 m. The sample depth of the acoustic system (8 - 250 m) and boat speed (14-16 km h^{-1}) were held constant throughout the July 2000 survey, as were all other echosounder settings. Echograms were continuously printed during transects and latitude and longitude were recorded every 10 min. Following Piatt (1990), the relative abundance of capelin was quantified by estimating the percent cover of the prey backscatter trace in each 1 min (250 m) by 10 m vertical bin on the echogram. Percent cover of prey was estimated on a scale of 0 - 9 in each bin (acoustic abundance score) and this figure was squared before analysis to attain a better estimate of relative abundance (Piatt 1990).

The species composition of acoustic signals was ground-truthed by deploying a modified shrimp trawl. Schools with the greatest uncertainty of acoustic signal were targeted and fishing primarily occurred in areas where many schools were observed. The trawl was used to fish both at the seabed and in mid-water using a standard fishing duration (15 min). The trawl had a 3.5 m headrope and a 12 m footrope, resulting in an opening of 2 m by 8 - 9 m during both bottom and mid-water tows. The mesh size of the body of the trawl was 80 mm and that of the codend was 40 mm. The total mass of the catch and the number of species were recorded immediately after each tow. Ten percent of the catch was sampled and the mass each species contributed to the total catch was calculated. A sample of up to 200 capelin was collected and frozen. In the laboratory, the sex, maturity index (1=immature, 2=maturing, 3=ripe, 4=partially spent, 5=spent) and total length (snout to tip of tail) of each fish were determined. A length stratified sample of two fish per sex per 0.5 cm length category was selected from each sample and the total mass, gonad mass, age and stomach fullness (0%, 25%, 50%, 75%, 100%) of each fish were recorded.

Seabird counts

Seabird densities were estimated during acoustic surveys using standardized strip transect methods (Method I b, Tasker *et al*. 1984) during daylight hours. One observer made continuous counts from the bridge (~3 m above sea level) using binoculars out to 300 m in a 90° arc from the tip of the bow to the port side of the ship. Counting was discontinued if visibility was < 300 m (e.g., fog, high wind). Counts and behaviour (sitting on the water, feeding, flying and flight direction) of birds were entered directly into a laptop computer. The laptop was interfaced with the navigational system of the vessel and counting software (D. Senciall, Birds & Beasty Counter, 1998, Fisheries and Oceans Canada, version 1.0) was used to append a position (latitude and longitude) to each entry. In subsequent analyses, we use murres that were flying, sitting and feeding.

Definition of hotspots

The survey was divided into a continuous series of 250 m horizontal bins, the minimum distance recognizable on the echogram. The squared acoustic abundance scores (scale: 0-81) were summed over the water column for each 250 m bin and then the mean squared abundance scores per 2.25 km block were calculated by averaging these 250 m depth integrated scores. The 2.25 km block is based on the estimate that birds on the water could visually cue to the activities of others within a distance of 4.5 km (Haney *et al*. 1992). These blocks with above average squared acoustic abundance scores were considered to be high-abundance capelin blocks. These high-abundance blocks were revisited on at least 2 occasions over a two-week period after the initial 5-day survey in July 2000, during which a 2.25 km long acoustic transect was conducted simultaneously with seabird counts along the initial survey route. The persistent presence of acoustic prey and murres within high-abundance capelin blocks was quantified by dividing the number of times each 2.25 km block contained capelin and murres by the number of times this block was visited (initial survey and revisit transects). These blocks were revisited over a two week period and, thus, this is the temporal scale of persistence. The mean squared acoustic abundance score ± S.E. was also calculated in each 2.25 km high-abundance block over all visits (maximum: n=4). The 2.25 km blocks where capelin was persistently present were defined as "hotspots".

Bio-physical habitat characteristics of hotspots

During July of 2000, we characterized the bio-physical factors within three persistent hotspots to describe habitat characters associated with persistence. Temperature profiles of the water column were measured using a SeaBird SBE-25. Devices were deployed at 1 m s^{-1}, allowing data capture every 20 - 50 cm from the ocean floor to the surface. Zooplankton biomass was measured by towing a 0.232 mm *Nitex* mesh bongo net, with a 0.29 m^2 mouth opening, at an average speed of 0.88 ± 0.15 m s^{-1} S.E. vertically upwards from the seabed to the ocean's surface. Nets were washed thoroughly into a 1 L sample jar and preserved in a 5% formalin-seawater solution. Half of the sample was oven-dried at 75ºC for 48 h and then weighed to the nearest 0.001 g. Zooplankton biomass per area of water sampled (g m^{-2}) was calculated, based on the volume of water filtered and the depth range sampled.

During July 2001, we returned to each of the three hotspots to characterize the particle size range of the seabed using a 0.3 m^2 Van Veen Benthic Grab System. A 250 ml sample was preserved in a 10% buffered formalin-seawater solution. Samples were later soaked in a 2% KOH solution for 24 h to detach biological material (e.g., fish eggs) adhered to sediment particles. Biological matter was preserved in a 5% formalin-seawater solution and remaining sediments were oven-dried at 75ºC for 48 h. Sediments were poured over a series of 12 graded sieves (0.15 - 31.5 mm), according to the Udden-Wentworth scale of sediment size classification (Wentworth 1922). Size fractions were weighed to the nearest 0.001 g. During August 2002, we again returned to these three hotspots with a Remote Operated Vehicle (ROV) equipped with an underwater video camera (VideoRay Pro) with the main goal to observe and describe capelin schooling behaviour within these persistent areas.

Colony-based departure/arrival behaviour of murres

Population-level return behaviour of murres to Funk Island was observed from 1998 - 2000. Observations were conducted from the highest point on land and each 45° sector was scanned for 1 min using compass-equipped binoculars (7 x 50) with the horizon in the mid-line of view. The number of birds returning during 1 min in each sector was recorded. Three 360° rotations were conducted and defined as a 360° scan, lasting a total of 24 min. Before and after each 360° scan, weather variables (visibility, precipitation, wind speed (km h^{-1}), using a hand-held anemometer, and direction) were recorded. Murres departing Funk Island initially landed on the water in vicinity of the colony (splashdown area), as at other colonies (Burger 1997). Individual-level departure behaviour of murres was observed immediately after each 360° scan in 1999 and 2000. The same site was always used for return and departure observations to minimize biases in the subjective determination of flight directions and to maximize the accuracy of flight directions. We chose 10 individuals leaving different regions of the splashdown area and recorded the final bearing of departure (departure scan). Zigzag flight was observed within the first min but flight direction generally stabilized before the bird was lost from view. The 360° and departure scans together were defined as a sample period, lasting approximately 1 h.

Sample periods were conducted 4 times per day, weather permitting. The 16 h of daylight (0530-2130) was broken into four 4 h intervals (0530-0930, 0930-1330, 1330-1730, 1730-2130 h) and a sample period was conducted in each interval. Sample periods that were separated by ~4 h were considered to be consecutive samples during later analysis. Weather data were used to eliminate sample periods when visibility was compromised. The total numbers of birds returning to the colony during each 360° scan and departing the colony in each departure scan was calculated for each 45° sector. The mean and modal angles of return and departure were calculated following Batschelet (1981). A Rayleigh Test was conducted on each 360° scan and each departure scan to determine if birds returned to or departed the colony in random directions within one sample period (Batschelet 1981). Circular correlations were computed for the mean return and departure angles during consecutive sample periods (separated by 4 h) to determine if successive return directions and departure directions, respectively, were similar (Zar 1996). The mean angle of departure was also compared with the mean angle of return in the same sample period using circular correlations. The results of these analyses are reported as the upper and lower circular correlation coefficients and are deemed not significant at $\alpha=0.05$ if these coefficients span zero (Zar 1996).

RESULTS

Distribution patterns of capelin and murres

During the survey in 2000, the majority of the fish collected with the trawl on 17 occasions were capelin (96% by mass; Davoren 2001) and, thus, we assume that most acoustic signals came from capelin. Capelin schools were present in 41% of the 2.25 km blocks (n=353). Five percent of these blocks had above average acoustic abundance scores (0.8 ± 0.1) (Fig. 2a). Blocks with above average capelin abundance were concentrated within three areas (Fig. 2b), each having distinct water depth characteristics. In areas 1 and 3, blocks were in deep water trenches (> 100 m), whereas blocks were in shallow slope water (< 50 m) in Area 2. In areas 1 and 3, capelin were 100% persistent in each 2.25 km block, or were always present and, thus, were defined as "hotspots" (Area 1: 1, 2; Area 3: 14; Table 1, Fig. 2b). Capelin abundance in these three hotspots remained above average among visits (Table 1). In Area 2, 11 high-abundance capelin blocks were present (3 - 13), four of which had 100% persistence of capelin (3, 7, 11, 13), but seven of which had less consistent presence of capelin (Fig. 2b; Table 1). Capelin abundance in these 2.25 km blocks in Area 2 varied among visits and was not consistently above average (Table 1).

Sitting and flying murres were always present, within all three areas where capelin hotspots were documented, but bird abundances varied widely among visits (Table 1; Fig. 3). Consistent flight paths, or commuting routes (Schneider *et al.* 1990), between these three areas and Funk Island were observed at sea along a northeast-southwest line (Fig. 3a). There also appeared to be movement of birds among these areas, evidenced by northwest-southeast flight trajectories (Fig. 3b). Overall, both sitting and flying murres constantly marked the location of hotspots at sea. For a more detailed examination of the distributional patterns and spatial overlap of murres and capelin during this study see Davoren *et al.* (2003).

Bio-physical habitat characteristics

Capelin schools within areas 1 and 3 were associated with the seabed and occupied distinct deep-water depressions or trenches (100 - 180 m). Three capelin schools were sampled via the bottom-

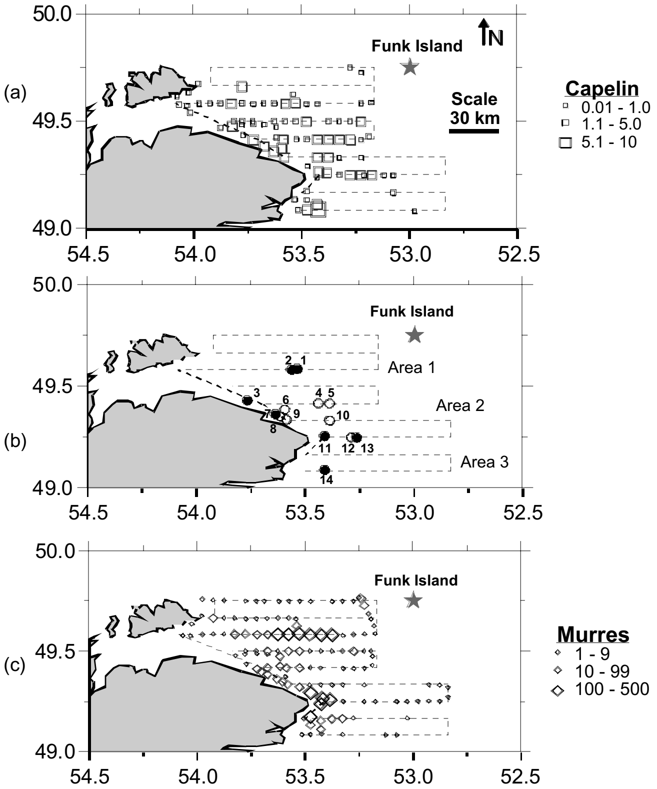

Fig. 2. The distribution of (a) capelin in 2.25 km blocks around Funk Island, (b) high-abundance 2.25 km blocks of capelin, indicating whether capelin were 100% persistent (solid circles) or whether capelin were < 100% persistent (open circles) in space and time, and (c) sitting Common Murres around Funk Island in 2.25 km blocks during the July 2000 survey. Note that hotspots 1, 7, and 14 were those that were revisited for bio-physical habitat characterization.

TABLE 1

The persistence and mean relative abundance of capelin (*Mallotus villosus*) and common murres (*Uria aalge*) ± SD per 2.25 km transect block with above average capelin abundance scores, that were visited around Funk Island in 2000 along with zooplankton densities and temperature profiles of the water column in three hotspots.

	Capelin		**Murre**		**Zooplankton**	**Temperature**					
2.25 km Block No.	No. Visits	Mean Abundance/ 2.25 km	No. Visits	Mean Abundance/ 2.25 km	Density (g m^{-2})	0 m	10 m	25 m	50 m	75 m	100 m
Area 1											
1	3*	1.21 ± 0.31	3	17.59 ± 13.00	4.6 ± 0.5 (2)**	13.2 ± 0.1 (5)	10.2 ± 0.4 (5)	3.0 ± 0.3 (5)	0.3 ± 0.1 (5)	-0.6 ± 0.1 (4)	-0.9 ± 0.1(3)
2	4*	1.05 ± 0.22	4	3.03 ± 2.39							
Area 2											
3	3*	0.80 ± 0.63	3	1.00 ± 0.88							
4	4	1.02 ± 0.79	4	2.07 ± 1.34							
5	4	0.51 ± 0.50	3	0.29 ± 0.26							
6	4	0.26 ± 0.25									
7	3*	1.02 ± 0.90	3	0.98 ± 0.91	1.4 ± 0.6 (2)	13.9± 0.1 (4)	10.6 ± 1.5 (4)	3.1 ± 0.6 (4)	0.4 ± 0.1 (3)	-	-
8	3	0.85 ± 0.78	3	2.78 ± 2.47							
9	4	0.56 ± 0.47	4	2.96 ± 2.91							
10	3	0.37 ± 0.32	4	2.71 ± 1.74							
11	4*	0.25 ± 0.24	3	2.85 ± 2.52							
12	3	0.65 ± 0.59	3	1.01 ± 0.87							
13	3*	0.86 ± 0.76									
Area 3											
14	3*	5.90 ± 2.58	4	1.00 ± 0.78	5.4 (1)	11.4 (1)	6.8 (1)	1.1 (1)	0.1 (1)	-0.4 (1)	-0.8 (1)

* Indicates the individual 2.25 km blocks where capelin were persistently present, calculated as the number of visits (initial survey and other visits) with capelin present divided by the total number of visits, and which were defined as "hotspots".

** Number in parentheses is the sample size.

trawl in Area 1. Schools were composed of near equal ratios of male and female capelin (49-64% females) and males were primarily maturing (maturing: 36-52%; spent: 0-2%; immature: 0%) as were females (maturing: 40-51%; spent: 9-15%; immature: 0%). The majority (~ 90%) of these fish also had < 50% of their stomachs full. In contrast, schools in Area 3 (n=2) were composed of female capelin (89-99%) and males were primarily immature (maturing: 0-2%; spent: 0-2%; immature: 0-10%) whereas females were primarily spent (maturing: 2-5%; spent: 76-97%; immature: 0-8%). The majority (~ 90%) these fish had > 50% of their stomachs full. In contrast, capelin schools within Area 2 were found over shallow slope water (< 50 m) and were off the seabed. These schools (n=5) were composed primarily of female capelin (92-100%), having both spent and mature females (maturing: 7-65%; spent: 30-100%; immature: 0%) with some males (maturing: 0-8%; spent: 0%; immature: 0-2%). Approximately 50% of these fish had their full stomachs.

Zooplankton biomass was similar in areas 1 and 3, but was lower in Area 2 (Table 1). The temperature profiles of the water column at hotspots in the three areas were highly stratified, with similar thermocline depths (25-50 m). There was no evidence of frontal structure or areas where the water column was well-mixed (Davoren 2001). In Area 2, water temperature remained > 0°C at all depths, indicating that capelin schools were exposed to warmer water relative to Areas 1 and 3, where capelin schools were associated with the seabed and occupied < 0°C water temperature (Table 1). Sediment samples in Area 1 (n=3) primarily consisted of silt and fine sand (68%), with smaller percentages (~ 10%) each made up of coarse sand, pebble and cobble. Samples in Area 3 (n=2) primarily consisted of silt and fine sand (99%), with no pebble or cobble and a small percentage of coarse sand (1%). Sediment samples in Area 2 (n=3) had a variety of different types, one with primarily pebble (76%), one with mostly silt and fine sand (96%), and one with half fine sand and silt and half cobble. In August 2002, high densities of fertilized capelin eggs were found adhered to sediments at two sites within one hotspot in Area 2 (hotspot # 11), using the ROV. The spawning sites were located at similar water depths (range: 27-34 m) over flat ground consisting of either coarse sand (<1 mm) or pebble (2-4 mm). The water temperature at the seabed (range: 2.9 - 9.2°C) was similar at both sites.

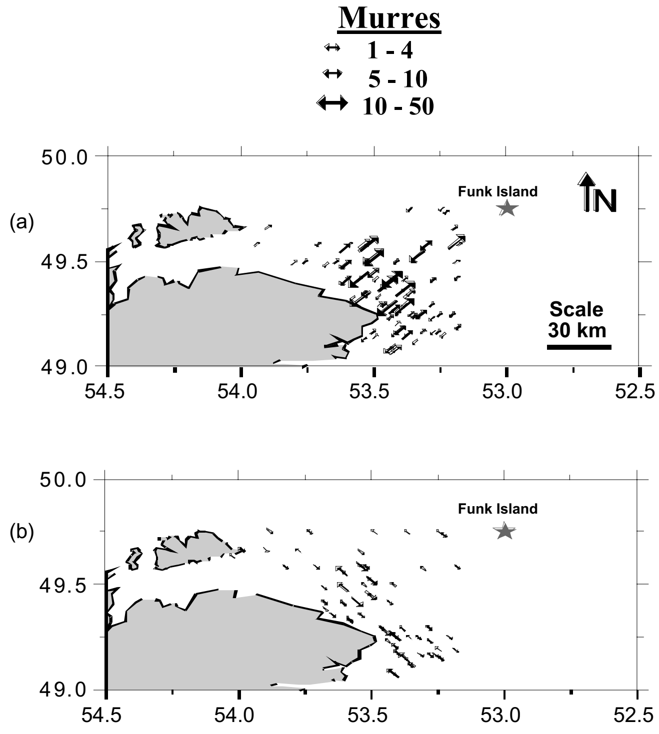

Fig. 3. The distributions and abundances of Common Murres flying in (a) northeast and southwest, and (b) northwest and southeast in 2.25 km bins around Funk Island during the July 2000 survey.

Arrival and departure behaviour of murres

Eighty-eight 360° scans were conducted during 29 d (1998: 11 d, 1999: 10 d; 2000: 8 d) on Funk Island (range: 1 - 6/d). The total number of individuals observed during a scan ranged from 228 - 6060. The modal direction of return, from the south-southwest (180° - 270°), was consistent among years of this study (1998 - 2000) and, thus, years were pooled. Birds generally returned to the colony from all eight sectors during each 360° scan; however, return directions were always nonrandom. Return directions were positively correlated with those in sample periods that were 4 h apart throughout a day (lower CI = 0.5860, upper CI = 0.5978, n= 57, $P < 0.05$; Fig. 4a), indicating similar return directions within days.

Thirty-six departure scans were conducted at Funk Island. The number of individuals observed ranged from 8-13, for a total of 293 individuals. The modal direction of departure was toward the west-southwest (225° - 270°) and was consistent among years (1999-2000) and, thus, years were pooled. Departure directions of murres were significantly nonrandom in 53% of the departure scans. Departure directions were negatively correlated with those in sample periods 4 h apart throughout a day (lower CI= -0.0872, upper CI = -0.0540, n=20, $P < 0.05$; Fig. 4b), also indicating variable departure directions of individuals within days. The majority of birds departed the colony alone (81%, n=239) and the remaining 19% left in flocks of 2 - 13 individuals (mean: 4.4 ± 0.3; median: 4; mode: 2). Return directions were negatively correlated with departure directions during the same sample period (lower CI = -0.1120, upper CI = -0.0937, n=35, $P < 0.05$; Fig. 4c), indicating dissimilar return and departure directions on a temporal scale of 1 h. Unlike other studies, coordinated feeding flocks (Hoffman *et al.* 1981) were never observed in the study area. It is also important to note that flight directions were variable and inconsistently related to wind direction and speed (see Davoren *et al.* 2003).

DISCUSSION

Capelin were persistent over a scale of two weeks within the foraging ranges of murres from Funk Island. Capelin hotspots were persistent likely due to the use of suitable habitat for spawning (Area 2), as well as deep-water depressions or trenches (> 100 m) as staging areas prior to spawning (Area 1) and as recovery areas after spawning (Area 3). Because the location of capelin was persistent, murres could have used previous experience to relocate them. This would explain why murres did not appear to use information on the direction of foraging grounds from the flight trajectories of flocks returning to the colony. Flying (commuting routes) and sitting murres consistently marked capelin hotspots, also providing opportunities for birds to locate capelin by cueing on the foraging activities of conspecifics (local enhancement; Wittenberger & Hunt 1985). Overall, the persistence of capelin hotspots due to specific habitat requirements appeared to influence the distribution patterns and foraging strategies of murres.

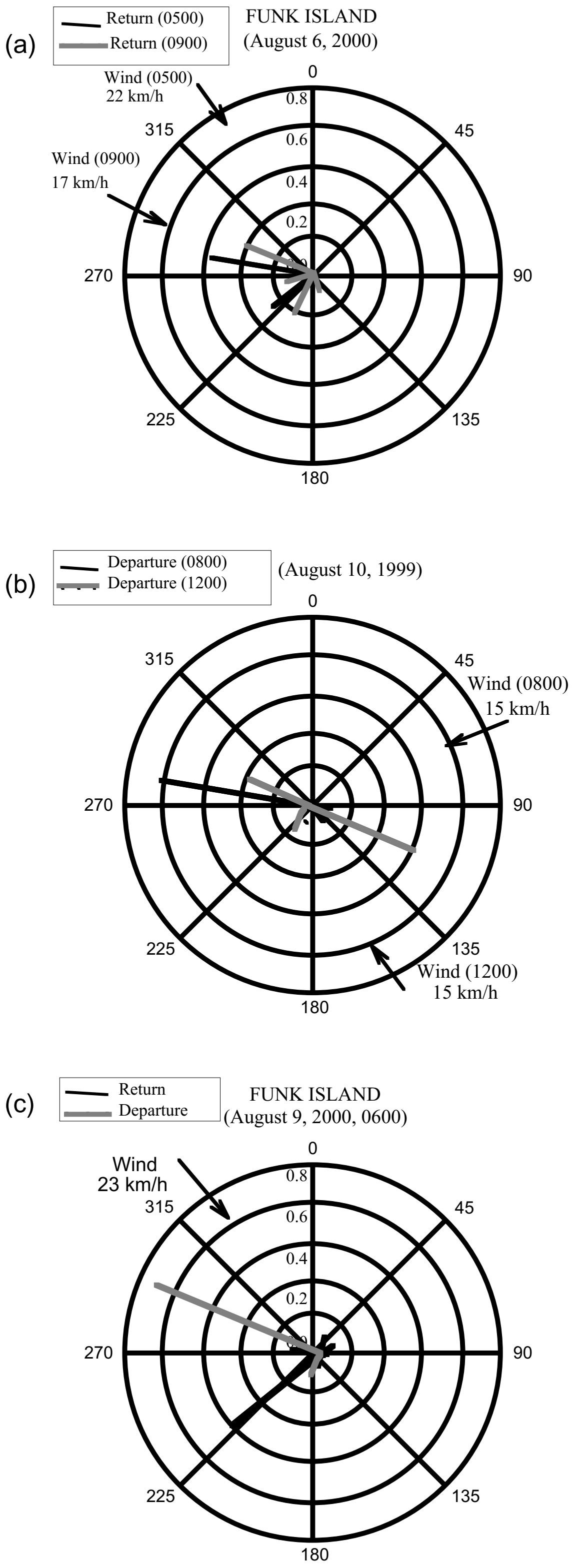

Fig. 4. Circular plots of the proportions of Common Murres returning to and departing from Funk Island in 45º sectors on three representative days, illustrating: (a) returning flight directions in successive sample periods, (b) departure flight directions from the splashdown area in successive sample periods, and (c) return and departure flight directions from the splashdown area in the same sample period. Dotted and solid lines are offset within each 45º sector for clarity.

Why were capelin hotspots persistent?

The presence of maturing capelin in Area 1 and spent capelin in Areas 3 suggests that these are staging areas prior to and after spawning, respectively. Schools in Area 1 comprised primarily maturing capelin with < 50% of their stomachs full, suggesting that feeding was not a priority for these fish. Previous studies have shown that prior to spawning, feeding rates decrease (Vesin *et al.* 1981). In contrast, the majority of spent capelin had > 50% of their stomachs full. Spent capelin begin actively feeding after spawning, increasing their fat content by 20% before the onset of winter (Vesin *et al.* 1981). The occupation of deep water, where zooplankton biomass is higher (GKD unpubl. data) and water temperatures are colder, may allow feeding and maintenance of low metabolic demands, thereby promoting recovery from spawning or gondal development. Occupying deep water also may allow predator avoidance. For fish in both areas 1 and 3, occupying depths of > 100 m is likely ineffective to escape the majority of the diving predators in the study area, but may reduce the risk of predation due to lower illumination at these depths, as well as the time available for prey location and capture by air-breathing predators. In addition, Atlantic cod generally occupy temperatures between - 0.5 to 8.5ºC (Rose & Leggett 1990) and capelin schools in area 1 and 3 were generally found in < - 0.8°C. Although few cod were observed in the study area (GKD unpubl. data), this species was the dominant capelin predator prior to the stock collapse in the early 1990s (Walters & Maguire 1996). Therefore, these habitat features may reflect previously important thermal refuges for avoiding predation by cod (Rose & Leggett 1990). Finally, the two sites found within one capelin hotspot in Area 2 were previously undescribed demersal spawning sites. The presence of suitable physical habitat characteristics for spawning, primarily particle size composition of the seabed and temperature, resulted in the persistent aggregation of capelin among years of this study.

How did capelin hotspots influence search strategies of murres?

Reducing the time spent searching for prey is important during breeding when time constraints and energetic demands are high (Cairns *et al.* 1990). We found no support for the use of directional information provided by large flocks of murres returning to colonies to locate foraging habitats beyond visual range of the colony. Using this Information Center mechanism at the colony represents a poor search tactic because the return trajectories reflect general directions of the last foraging site and are influenced by varying wind conditions (i.e., speed, direction; Burger 1997). We hypothesize that this tactic provides the least accurate information on foraging ground locations. Alternately, search effort could be minimized to a greater degree if the location of persistent food aggregations could be retained in memory. Constant streams of birds flying to and from hotspots along specific routes and high densities of murres consistently sitting within capelin hotspots resulted in capelin being marked at sea. Therefore, we hypothesize that a combination of memory and local enhancement is important in locating capelin within the study area, the importance of each likely depending on the resolution of spatial maps and perceptual constraints of murres and other marine predators in general.

One contradictory observation in this study was the inconsistent departure and return directions at the colony but the persistent movement corridors of murres at sea as well as the persistent attendance of capelin hotspots by murres. One explanation is that murres may visit a number of areas on a foraging trip (e.g.,Wanless *et al.* 1990). Evidence for this may be the highly variable abundance of murres at hotspots in this study and others (e.g., Cairns & Schneider 1990) as well as the apparent movement of murres among hotspots (Fig. 3b). Additionally, murres may depart the colony in a general direction (~270°) using memory, but alter their trajectories (226°) as they encounter returning flocks at sea (information exchange). Anecdotal observations of individual murres changing their flight direction in response to a returning flock at sea were observed. This also suggests that local enhancement may be a behavioural mechanism through which movement corridors are formed.

Conclusions

Capelin, the dominant forage fish species in the Northwest Atlantic, formed persistent hotspots, resulting from the use of specific areas as demersal spawning sites and as staging or foraging areas before and after spawning. High densities of capelin elicited an aggregative response in murres, thereby influencing their distribution patterns and foraging strategies. Owing to the reliance of top vertebrate predators on capelin in this ecosystem, persistence of capelin hotspots likely shapes distributional patterns and search strategies of most vertebrate predators. For instance, through their foraging experience in a region, predators could learn the locations of a suite of hotspots. Regular sampling of these sites would allow daily and monthly choice of foraging sites based on recent experience (Schneider, pers. comm.) and could lead to the development and long-term use of traditional feeding grounds through generations (hinterland; Cairns 1989). Major ecosystem-level perturbations could dramatically affect the predictability of key hotspots. A clear example of this is the influence that the collapse of the eastern Canadian ground-fishery has had on the biology and behaviour of capelin (Carscadden & Nakashima 1997). Therefore, these hotspots should be considered key management areas where fishers and researchers work together to minimize the negative interactions among humans and marine organisms (Hooker *et al*. 1999, Hyrenbach *et al*. 2000).

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