PREDATOR-PREY INTERACTIONS OF COMMON MURRES (Uria aagle) AND FISH IN THE NORTHWEST ATLANTIC: FORAGING STRATEGIES ON MULTIPLE SCALES

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by

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ABSTRACT

The Northwest Atlantic ecosystem is currently undergoing changes in species interactions and ocean climate. Capelin (*Mallotus villosus*), the dominant forage fish in the ecosystem, is the main prey item of marine birds, mammals and piscivorous fish. In the 1990s, spawning capelin were small, spawned later, shifted their distribution southerly to non-traditional areas compared to historical accounts, and abundance estimates have varied widely. During these changes and divergent biomass estimates, this research was initiated. The focus of this thesis is the multi-scale behavioural interactions of marine predators and prey: a marine diving bird, the common murre (*Uria aalge*), and its main prey species, capelin. This study integrates both colony-based and vessel-based techniques. I showed that some aggregations of capelin are stable in space and time on a number of scales: fine- (1-100 m, minute-hour), coarse- (1-100 km, day-week) meso-scale (100-1000 km, annual), allowing murres to use memory to locate prey at sea during different periods during their annual cycle. Social foraging techniques appeared to be important on fine- and coarse-scales (local enhancement, network foraging) while no evidence was found for social foraging techniques over larger spatial scales (Information Center Hypothesis). Spatial scales at which murres tracked capelin were highly variable, as found in other studies examining predator-prey interactions of mobile organisms. The tracking scales of murres to capelin were smallest during the breeding (0.8 – 5.1 km) and pre-breeding periods (3.1 - 8 km), compared to post-breeding (6.0 – 50.0 km). This variability in spatial associations between predators and their prey was likely due to different energetic requirements, locomotory constraints and search strategies used among these periods. Inter-colony comparisons of provisioning behaviour by murres revealed low feeding rates of chicks at the largest murre colony in eastern Canada relative to a smaller colony, which resulted in the lowest average mass and condition of fledgling murres (191 6 ± 4 0 g) reported in the literature. Density-dependence, both while foraging at sea and rearing chicks at the colony, and prey distribution around the largest colony resulted in additional provisioning constraints relative to a smaller colony and divergent life history strategies at the two colonies. Poorer chick condition, and presumably lower recruitment, may have resulted in a lack of population growth at the larger colony, which contains 85 % of the common murres in the Northwest Atlantic. Clearly, common murres interact with their prey over multiple temporal and spatial scales and these behavioural interactions are manifested in demographic parameters.

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CHAPTER I – Introduction

In the last two decades it has been recognized that there is an increasing need to shift from single-species to ecosystem-level management, through the inclusion of multiple species under one conservation regime (Ludwig et al. 1993, Pauly et al. 1998, Pitcher 2001). Although it is unclear how to proceed on a rigorous scientific basis, researchers are beginning to appreciate the importance of identifying patterns and understanding the underlying processes that influence these patterns within ecosystems at widely varying spatial scales (Schneider 1994).

Ecosystems are heterogeneous, with different processes interacting to create hierarchical patterns that change in time and space (Haury et al. 1978, Wu and Loucks 1995). The spatial scale at which researchers study an ecosystem determines the types of processes and patterns described (Dayton and Tegner 1984), with smaller-scale patterns generally being masked at larger scales (Wu and Loucks 1995). Ecosystems are characterized by small-scale patterns that are transient in space and time and, thus, appear chaotic in nature (Haury et al. 1978, Wu and Loucks 1995). In contrast, large-scale patterns are relatively stable (Haury et al. 1978, Hunt and Schneider 1987, Wu and Loucks 1995). Consequently, to accurately describe and understand the linkages between trophic levels within an ecosystem, it is important to examine multiple spatial and temporal scales. This type of research will aid us in understanding and more adequately conserving ecosystem-level processes under future management regimes.

Foraging strategies of predators are driven by the physiological requirements of individuals and are shaped by locomotory efficiency, perceptual constraints, learning capacity and memory (Piatt 1990, Horne and Schneider 1994), along with the distribution and behaviour of their prey and interactions with competitors (Allachin 1992, Barta and Szep 1992, 1995). The relative importance of each of these variables is species-specific and will determine the form of various responses of predators to prey density (Piatt 1990). Predator responses to prey density can be both behavioural, such as movements in response to prey density (aggregative response, Hassell 1966) and numerical, through changes in birth and death rates of predators (Solomon 1949). Rates at which predators consume prey (functional response), track prey (aggregative response), and reproduce (numerical response) are all non-linear functions of prey density and distribution (Solomon 1949, Hassell 1966, Holling 1966, Murdoch and Oaten 1975) and are dependent on spatial scale (Schneider and Piatt 1986). These diverse predator responses to prey can lead to complex patterns of spatial distribution that are difficult to interpret. For instance, the scale at which mobile predators track their prey (aggregative response) has been found to be highly variable (Schneider and Piatt 1986). Examination of the factors that influence foraging strategies of individual predators will increase our understanding of the causes of this variability in tracking scale and will provide an opportunity to disentangle complex spatial patterns into a more interpretable context.

Animals employ different behavioural strategies to minimize energy expenditure and augment energy intake while foraging depending on the spatial scale at which they are searching for prey (Pyke 1984, Russell et al. 1992). The use of public information to locate food patches outside of visual range (e.g. Information Center Hypothesis, Ward and Zahavi 1973) or within visual range (e.g. local enhancement, network foraging, Wittenberger and Hunt 1985) may be important in minimizing the energy spent searching for prey. These social techniques, however, may not increase energy intake due to interference with other competitors at the food patch (Sutherland 1983). Therefore, the foraging decision of an individual also will depend on the choices of its competitors and will likely reflect the balance between cooperative and competitive interactions (Miliniski and Parker 1991). Criteria used to select food patches will depend on the characteristics of prey within these patches (e.g. prey density) as well as the presence of competitors. Patterns of distribution of predators and their prey will reflect the importance of each criterion in meeting a predator's physiological requirements for survival.

In this thesis, I examine patterns and their underlying mechanisms at a number of spatial and temporal scales within the marine ecosystem of the Northwest Atlantic. Specifically, I focus on behavioural predator-prey interactions of a marine diving bird, the common murre (*Uria aalge*), and its main prey species, capelin (*Mallotus villosus*). I examine how the strategies used to search for prey and select prey patches influence population-level distribution and variability in the spatial association patterns of predators and their prey (tracking scales). Ultimately, I examine how these foraging/provisioning strategies translate into population dynamics of predators.

1.1 SPECIES BACKGROUND

The common murre (*Uria aalge*) was chosen for this study because it has been the focus of many studies on time and energy budgets (Cairns et al. 1987, 1990), responses to prey fluctuations (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994), as well as many other aspects of breeding (see Birkhead 1985) behaviour (e.g. Burger 1997) and physiology (e.g. Croll et al. 1992, Croll and McLauren 1993). The common murre is a marine diving bird of the family Alcidae (alcid) that breeds in large colonies at higher densities than any other avian species (Birkhead 1977, 1978). It lays a single-egg clutch and pairs rear one chick at the colony (Gaston and Jones 1998). During the breeding season, these birds act as central-place foragers (Orians and Pearson 1979) in that they carry food from foraging sites to offspring at a breeding site. Central place foragers are generally limited by the time and energy expended during a round trip from the breeding site (Orians and Pearson 1979) and, thus, the time spent searching and foraging within a food patch are crucial factors constraining breeding performance and foraging efficiency (Clode 1993). This is especially true for murres because their wing design is a compromise between underwater flight (low surface area) and aerial flight (high surface area; Pennycuick 1987). This results in a high wing-loading, or a high body mass to wing area ratio (2.06 g/cm^2), which places them close to the flightless threshold (2.5 g/cm^2; Guillemette 1994). Consequently, energy expended during flight is high relative to other avian species (Pennycuick 1987). Consequences of this wing design are restrictions on the amount of food ingested during a foraging bout to retain the ability to fly (Sibly 1981, Verlinden and Wiley 1989, Guillemette 1998) and low energy reserves stored in the body

(3 – 4 days of reserves in the winter, 1.5 – 2.5 days during chick-rearing; Gaston and Jones 1998). Therefore, murres must eat a large percent of their body mass in fresh food per day (40 %, Gabrielsen 1994) in order to meet energetic requirements for survival. In addition, murres only deliver a single fish to their chicks at the colony after each foraging trip (single-prey loaders) and, thus, much energy is expended to deliver relatively little energy to chicks. Therefore, murres are an excellent focal species for the study of predator-prey interactions, due to their high energetic requirements.

Murres are a long-lived species. How individuals deal with high energy requirements depends on life history strategies (Stearns 1992) and leads to various outcomes of parent-offspring conflicts (e.g. timing of fledging, Ydenberg 1989). Ultimately, individual variation in life history decisions results in varying body condition and survival probabilities of adults and young (Hatch 1983, Harris et al. 1992). Life history theory postulates that parents should maximize potential lifetime fitness by balancing present and future costs and benefits of reproduction (Stearns 1992). Provisioning effort, therefore, reflects the life history strategy of a species (Weimerskirch et al. 1997). Parents of long-lived species that invest heavily in individual offspring (K-selected) are likely to favour their own survival over that of their offspring in any given year to prolong their lifespan and chances of future reproduction (Stearns 1992). In contrast, parents of short-lived species that invest little in individual offspring (r-selected) are more likely to decide the opposite (Stearns 1992). Murres have a post-hatching development strategy that is intermediate between precocial and semi-precocial (Ydenberg 1989). Chicks are reared at the colony for approximately three weeks and depart at up to 25 % of adult body mass (Harris and Birkhead 1985). They are unable to fly or feed themselves upon colony departure and are accompanied by the male parent at sea for 2 - 3 months (Swennen 1977, Bradstreet and Brown 1985).

Common murres feed on small pelagic schooling fish (Gaston and Jones 1998) and are the primary avian consumers of capelin (*Mallotus villosus*) in the Northwest Atlantic (Cairns et al. 1990). Capelin is a small, short-lived (3 - 5 yr), pelagic schooling fish with a circumpolar distribution in Arctic and sub-Arctic regions (Vilhjalmsson 1994). In the Northwest Atlantic, capelin is a dominant forage fish species and supports the upper trophic food web with marine birds, mammals and piscivorous fish (e.g. Atlantic cod (*Gadus morhua*) depending on this species as prey in coastal waters, especially during the summer (Carscadden 1982). In Newfoundland, capelin spawn during the summer primarily on or near gravel beaches and only at one confirmed offshore spawning site on the Southeast Shoal of the Grand Banks (Carscadden 1982, Carscadden et al. 1989). The existence of both modes of reproduction in one geographic area is uncommon and in most other regions capelin either are beach-spawners (e.g. British Columbia, Carscadden et al. 1989) or offshore-spawners (e.g. Barents Sea, Vilhjalmsson 1994). Different spawning stocks have widely varying spawning habitat preferences (Vilhjalmsson 1994). Females release all of their roe in one copulation event, whereas males release their milt over a number of events (Templeman 1948). Copulation events generally involve contact with sediment, leading to injury (Fidgeirsson 1976) and resulting in a disproportionate number of females surviving spawning compared to males and, consequently, divergent life history strategies (Shackell et al. 1994).

1.2. NORTHWEST ATLANTIC ECOSYSTEM

The ocean climate off Newfoundland and Labrador has been cooling since the late 1960s, reaching a historical minimum in 1991 that has since reversed during the mid-1990s (Colbourne et al. 1997). Trophic interactions within the Northwest Atlantic ecosystem are currently undergoing changes due to the elimination of a top predator, Atlantic cod (Walters and Maguire 1996). The most remarkable and probably most important changes include the altered distribution, biology and behaviour of capelin *Mallotus villosus* (Carscadden and Nakashima 1997, Carscadden et al. 2001). During the 1990s, the major post-spawning concentrations of capelin shifted farther south into nontraditional areas (Carscadden and Nakashima 1997) but have recently returned to historical distributions (Lilly and Simpson 2000). The vertical distribution of capelin in the water column also has become variable (Shackell et al. 1994, O'Driscoll et al. 2000). This is primarily revealed in the lack of consistent vertical migration behaviour, whereas prior to the 1990s capelin used to regularly move up into surface waters at dusk and move deeper in the water column at dawn. In addition, peak spawning has been one month later during the 1990s, which was accompanied by smaller spawning fish, due to smaller age 3 fish and a higher proportion of age 2 fish spawning (Carscadden and Nakashima 1997). Coincident with these changes in the early 1990s, acoustic estimates of capelin biomass offshore have decreased significantly while estimates from research on spawning beaches have remained consistent (Carscadden et al. 2001). Seabirds appear to have responded to these changes in capelin biology and behaviour in complex ways (e.g. Regehr and Montevecchi 1997, Bryant et al. 1999, Stenhouse and Montevecchi 1999, Massaro et al. 2000, Carscadden et al. submitted).

Due to these changes and divergent biomass estimates, it has become increasingly important to investigate the behaviour of capelin and its predators to predict how predators will respond to these changes, both behaviourally and through altered demographic parameters (Veit et al. 1993). Specifically, I need to understand how the behaviour of capelin and physical characteristics of capelin schools influence the multi-scale search strategies of predators along with the selection of foraging habitat by predators. It is also important to describe variability in the scale at which predators track capelin and identify the factors causing this variability. This will allow us to predict how the foraging strategies of predators may change in relation to capelin density and abundance. Finally, I need to understand how changes in capelin behaviour, biology and distribution affect demographic parameters of predator populations. The integration of this information is the primary aim of this thesis, with the ultimate goal of improving ecosystem-level understanding and approaches to marine conservation.

1.3 CHAPTER OUTLINES

In Chapter 2, I examine the search behaviour of murres to determine how they locate prey at sea on multiple spatial scales while rearing chicks at breeding colonies. Understanding how seabirds locate prey at sea is key to understanding how they will respond to changes in prey conditions (Veit 1999). I test the relative importance of information exchange at the colony (ICH, Ward and Zahavi 1973) and memory-based foraging in locating foraging habitats and food patches from the colony during chick-rearing. I do this by quantifying the arrival and departure behaviour of murres from the breeding colony in conjunction with direct measures of the distribution, density and spatial and temporal stability of capelin aggregations within the foraging range of these animals (100 km; Cairns et al. 1987, 1990). Many studies have tested the ICH in birds but evidence of information exchange at the colony on foraging sites out of visual range of the colony is unconvincing (Bayer 1982, Mock et al. 1988) and can generally be attributed to local enhancement (Andersson et al. 1981, Evans 1983, Flemming 1990, Poysa 1992, Smith 1995, Marzluff et al. 1996, Buckley 1996, 1997). In contrast, many studies have shown that birds consistently forage at specific locations (e.g. Benvenuti et al. 1998, Irons 1998) and there is some physiological evidence that seabirds are capable to constructing and using complex spatial maps (e.g. Abbott et al. 1999). Although there is a large literature on physical features (e.g. bathymetric, hydrography) that lead to spatially predictable patchiness of seabird prey (see Schneider 1991), few studies have determined whether prey patches are in fact stable enough for birds to use memory. This is the main goal of the chapter.

In Chapter 3, I examine the physical structure of capelin schools and the scale-dependent spatial distribution of murres at sea in relation to capelin (tracking scale) during chick-rearing. I use information gleaned form the literature to qualitatively model the energetics of murres foraging in an area close to the breeding colony with persistent capelin schools and in an area distant from the colony with unstable capelin schools. I use the theoretical framework of the Ideal Free Distribution (IFD, Fretwell and Lucas 1970) and foraging theory (patch selection, Pyke 1984) as a base for my model. Linking population-level distribution patterns and predator-prey spatial associations with physiological requirements of predators provides a valuable framework to examine factors that influence patch selection decisions of individuals (Horne and Schneider 1994). I examine the consequences of interference among competitors at prey patches through modeling. Interference competition has not been studied explicitly before in alcids. I also describe some previously unknown behaviour of pre- and post-spawning capelin and confirm some behaviour of capelin previously described (Templeman 1948, Jaangard 1974, Vilhjalmsson 1994). Such behavioural studies are key in determining reasons for divergent biomass estimates of capelin and for increasing our understanding of how the changing behaviour of capelin will affect both the foraging/provisioning strategies and demographic parameters of predators. The integration of these sources of information is important for formulating mechanistic hypotheses about predator-prey interactions.

In Chapter 4, I examine whether the locomotory capability of common murres is an important influence on the scale at which these mobile predators track their prey (tracking scale) under the framework of behavioural predator-prey theory (e.g. aggregative response, Sih 1984). To do this, I describe and compare the scale-dependent patterns of distribution of murres in relation to their prey under two mobility regimes: (1) during the pre-breeding period when murres can fly and (2) during the post-breeding or moulting period, when murres are flightless and are accompanied at sea by flightless chicks. I also document the relative contribution of prey types in murre diet during the moulting period for the first time using stable isotopic analysis. I consider the perceptual constraints caused by reduced mobility (e.g. reduced knowledge of local prey patch qualities and locations), the energetic benefits of reduced mobility and how these factors interact to influence the tracking scales of predators to their prey. I also test the predictability of murre and prey distributions among years and identify key marine areas used during both periods.

In Chapter 5, I examine how capelin distribution and behaviour affects provisioning behaviour, life history strategies and the condition of chicks upon fledging and consider the implications for population dynamics (numerical response). Specifically, I examine the provisioning constraints on murres breeding at the largest and most offshore breeding colony in the Northwest Atlantic. To do this, I compare provisioning constraints of common murres at this large colony with those of conspecifics in the second largest colony in the Northwest Atlantic. I compare (1) prey types and frequency of delivery (amount of prey), (2) maximum foraging ranges, (3) parental time budgets, (4) the at-sea behaviour of adult murres near each colony and (5) the mass and condition (mass / wing length) of fledglings. I interpret inter-colony similarities and differences in provisioning constraints in terms of life history strategies and consequences for population dynamics.

Finally, I provide insight into the underlying behavioural mechanisms that drive both fine- and meso-scale patterns of distribution and spatial associations between predators and prey in the Northwest Atlantic ecosystem. I also describe how these patterns and processes influence population dynamics of predators. This is timely due to recent changes in species interactions in this system, which result in the need for a better understanding of the linkages among trophic levels.

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1.5 CO-AUTHORSHIP STATEMENT

In the chapters of this thesis, my co-supervisors (Dr. Montevecchi and Dr. Anderson) helped me formulate research questions and develop an integrated research program. Following this, I was solely responsible for determining appropriate and, where necessary, designing field-based data collection methods. I was also exclusively responsible for collecting the data or supervising data collection, determining appropriate statistical analysis techniques, analyzing the data and writing the manuscripts. The exception to this was chapter 4, where the capelin acoustic data were provided in raw form by Dr. Richard O'Driscoll (August-September 1998, 1999) and Fran Mowbray (May 1999, 2000). Upon finalizing these completed manuscripts, comments were obtained from my co-supervisors and from other members of my supervisory committee (Dr. D. Schneider and Dr. B. de Young), prior to submission to the School of Graduate Studies.

CHAPTER II - Food-finding mechanisms of breeding common murres and the stability of prey patches

2.1 INTRODUCTION

Before a resource is exploited, animals must know where it is located (Clark and Mangel 1984). Animals searching for food patches over a heterogeneous landscape must search on multiple scales (Russell et al. 1992, Fauchald et al. 2000). Therefore, the strategy used to locate prey by a predator will depend on the spatial scale over which and the temporal rate at which its foraging environment changes (Pyke 1984).

Animals provisioning young from a central place are physically separated from their foraging environment and, thus, must first search for a foraging habitat, or area where food patches are likely to be found, and then search for food patches within this habitat (Veit 1999). Travel-time between the breeding site and food patches and foraging time within patches both limit the amount of food that young can be provisioned (Orians and Pearson 1979). Central-place foragers may cope with these constraints by combining different strategies. For instance, pelagic seabirds (Procellariiformes) alternate or mix long foraging trips, where energetically efficient search strategies are used and food is primarily allocated to the parent, with short foraging trips, where less efficient search strategies are used and food is primarily allocated to the chick (Weimerskirch et al. 1993, 1994, 1997). Employing this mixed strategy doubles the frequency chicks are fed and allows parents to maintain their own body condition (Chaurand and Weimerskirch 1994, Weimerskirch et al 1997) The search tactic employed controls the round-trip time from foraging sites to the central-place and, thus, is a crucial factor constraining breeding performance (Clode 1993). Consequently, animals may employ tactics that minimize the time spent searching for prey

Information provided by other individuals may increase foraging efficiency by allowing a more rapid location and exploitation of food patches (Ryer and Olla 1991, 1992) For colonially breeding seabirds, information may be exchanged at the colony about the location of distant food patches out of visual range (4.5 km; Haney et al 1992) of the colony (Information Center Hypothesis, Ward and Zahavi 1973) or local food patches within visual range of the colony (local enhancement, network foraging, Wittenberger and Hunt 1985) There is little support for the Information Center Hypothesis in birds (e.g. Bayer 1982, Mock et al. 1988) Most information exchange at colonies can be instead attributed to local enhancement, or birds cueing to the foraging activities of other conspecifics within visual range of the colony (Andersson et al 1981, Evans 1983, Flemming 1990, Poysa 1992, Smith 1995, Marzluff et al 1996, Buckley 1996, 1997) In addition, there is a growing literature showing the consistent use of certain areas by seabirds at spatial scales from gyres down to small tidal rips (Cairns and Schneider 1990, Hunt and Harrison 1990, Schneider 1991). Telemetry studies have also shown that individual seabirds return to the same foraging sites (Benvenuti et al. 1998, Hedd 1998, Irons 1998). Therefore, foragers may learn from their past experience and rely on memory, rather than information exchange, to reduce the amount of energy expended searching for food patches (Miliniski 1994, Mackney and Hughes 1995). These different search tactics are not mutually exclusive and the extent of their use may differ depending on the spatial scale animals are searching, the behaviour of their prey, and the characteristics of their foraging environment.

The abundance, distribution and mobility of prey and the number of competitors in the vicinity of a colony are the most important factors that interact to influence search tactics (Allachin 1992, Barta and Szep 1992, 1995). If food patches are dense, ephemeral and patchily distributed, the benefits of increased foraging efficiency from information exchange outweigh costs of competition because a limited number of competitors locate food patches before they escape (Danchin and Wagner 1997). As the duration of patch persistence increases, more individuals locate the patches and competition increases (Richner and Heeb 1995, Buckley 1997). At this point, competitors may distribute themselves among patches by combining past experience, or memory, in the patches and current information on the number of competitors and prey density (Ideal Free Distribution, Fretwell and Lucas 1970; Smith 1995). As the number of individuals increase in a foraging habitat, information on the position of distant and local food patches increases. This information results in increased foraging efficiencies if the search area is large or if prey is superabundant. Otherwise, decreased foraging efficiencies may result due to the higher number of competitors. Overall, the search tactic employed by central-place foragers will reflect the balance between cooperative and competitive interactions among colony members at food patches.

The common murre (*Uria aalge*) is a marine diving bird that lays a single-egg clutch in dense colonies on islands (Birkhead 1977). At large breeding colonies of murres, massive flocks of high-flying birds returning to the colony are obvious and it has been suggested that naive murres at the colony, or on the water near the colony, may examine these return flight paths to gain information on the location of distant foraging habitats (Gaston and Nettleship 1981, Burger 1997). During the breeding season in Newfoundland, murres feed their chicks and themselves primarily female capelin *Mallotus villosus* (Piatt 1987; chapter 5). Parents deliver a single fish to their chicks after each foraging trip. Capelin is a small, schooling pelagic fish that spawns in large aggregations on coastal beaches during the summer in Newfoundland (Templeman 1948). Capelin schools are generally considered to be patchily distributed and ephemeral on a fine-scale (1 - 1000 m) but may be predictably located on a coarse-scale (1 - 100 km) within larger areas in different seasons (Schneider 1989, Piatt 1990; Rose and Leggett 1990, Methven and Piatt 1991). The stability of capelin aggregations on multiple scales in space and time, however, has not been directly measured.

The goal of this study is to examine behavioural strategies used by common murres to locate prey at sea on multiple spatial and temporal scales (Cairns and Schneider 1990). To do this, I quantify the arrival and departure behaviour of murres from the breeding colony in conjunction with direct measures of the distribution, abundance and spatial and temporal stability of capelin aggregations within the foraging range of these animals (100 km, Gaston and Nettleship 1981, Cairns et al. 1987, 1990, Benvenuti et al. 1998). Specifically, I examine the relative importance of information exchange at the colony and past experience, or memory, in locating foraging habitats on a coarse-scale and food patches within foraging habitats on a fine-scale from the colony. I do not evaluate the use of memory directly but rather use the temporal and spatial stability of capelin aggregations to indicate whether seabirds could use memory to locate prey at sea. I predict that if capelin aggregations are unstable in space and time, murres will use a higher degree of information exchange at the colony to locate prey. Alternately, if capelin aggregations are stable or predictable, I predict that murres will use a higher degree of memory. I also compare the distribution and behaviour of capelin around two breeding colonies along with the search tactics employed by murres at these colonies, which vary in population size, distance from the coast and species composition.

2.2 METHODS

2.2.1. Study Area

This study was conducted in 1998-2000 on and around Great Island, Witless Bay (47°11'N, 52°49'W) and Funk Island (49°45'N, 53°11'W) on the east coast of Newfoundland (Fig. 2.1). In Witless Bay, approximately 100,000 breeding pairs (b.p.) of murres are divided up between three island colonies within 10 km of each other (Great Island: 3,000 b.p.; Gull Island: 1,000 b.p.; Green Island: 96,000 b.p.) and, thus, are considered to act as one population (chapter 5). These islands are approximately 2 km from shore. Funk Island is approximately 60 km from shore and holds 340,000 - 400,000

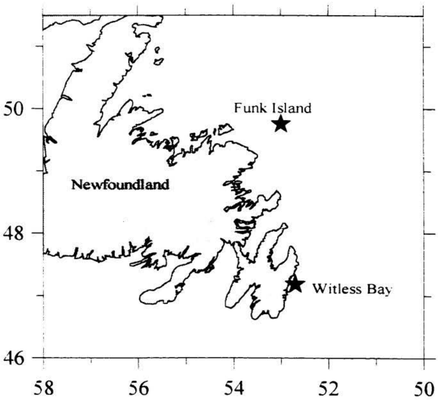


Figure 2.1. Map of the study area showing the Witless Bay and Funk Island seabird breeding colonies on the east coast of Newfoundland in the Northwest Atlantic

breeding pairs of murres (Canadian Wildlife Service unpubl. data). Other species breeding at these colonies also feed on capelin (Cairns et al. 1989); however, these species generally do not feed together (chapter 5). Therefore, Funk Island has 3 - 4 times the number of competitors and is farther from the coast than Great Island. It is important to note that Atlantic Puffins also return to colonies in large, high-flying flocks similar to common murres, and the sizes of the murre and puffin populations at each colony differs. At Great Island, 2 % of the birds returning were common murres, whereas at Funk Island, 99 % were common murres (Cairns et al. 1989).

2.2.2. Survey Methods

Broad-scale vessel-based surveys were initially conducted around Great Island and Funk Island with the objective to determine the location of areas where capelin and murres were highly abundant in July when murre chicks were being reared (Fig. 2.1). Survey routes were established through preliminary observations of returning flight directions of murres towards each colony in 1997, information from previous studies (e.g. Cairns et al. 1990, Schneider et al. 1990) and conservations with local fishers. One survey was conducted around Funk Island (800 km) in 2000 aboard a 23 m Canadian Coast Guard Vessel (*Shamook*) and one more limited survey was conducted around Great Island (35 km) in 1998 aboard an 8 m commercial fishing vessel (*Moly Baun*).

A Simrad EQ100 echo-sounding system was used, operating through a hull-mounted single-beam transducer with a frequency of 38 kHz. The transducer had a 10-degree beam angle and the echo sounder was operated at 1 ping per second, 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 would 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$\cdot$h^{-1}) were held constant throughout both surveys. Echograms were continuously printed during both surveys and Greenwich Mean Time (GMT) was marked on echograms every 10 min. A navigational software package (Bioplot) continuously recorded the ship's position (latitude and longitude) and GMT every minute. The date and GMT were used to merge position data with acoustic estimates into 1 min (250 m) bins.

A modified shrimp trawl was deployed from the *Shamook* (fishing set) around Funk Island to identify the species composition of acoustic signals. The trawl was primarily deployed in areas where many prey schools were observed. The trawl was used to fish both at the seabed and in mid-water and a standard fishing duration was used (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 the mesh size of the codend was 40 mm. The total mass of the catch and the number of species was recorded immediately after each tow. Ten percent of the catch was subsampled and the mass each species contributed to the total catch was calculated. Trawling was not possible from the *Moly Baun* and, thus, the species composition of acoustic signals around Great Island was not determined. Fish in the bills of birds, however, were identified as were fish observed from the vessel that were near the ocean's surface.

During acoustic transects, seabirds were counted simultaneously using standard strip transects (Method Ib, Tasker et al. 1984). One observer made continuous counts of seabirds from the bridge out to 300 m in a 90^{0} arc between an imagined line extending from the tip of the bow to an imagined line perpendicular from the port side of the vessel. Counts were entered directly into a laptop computer along with behavioural descriptions (on the water, feeding, flying and flight direction, flying with fish). The laptop was connected to the navigational system of the vessel and counting software designed by Fisheries Canada (D. Senciall) was used to append a position (latitude and longitude) and GMT to each bird entry. The date and GMT were used to merge bird data with acoustic estimates into 1 min (250 m) bins.

2.2.3. *Data Analysis of Survey Data and Revisit Transects*

The relative abundance of prey was quantified by estimating the percent cover of the prey image in each 1 min (250 m) by 10 m vertical bin on the echogram, following Piatt (1990). Percent cover of prey was estimated on a scale of 0 – 9 in each bin (acoustic abundance score) and this was squared prior to analysis to attain a better estimate of relative abundance (Piatt 1990). This technique was used to determine the presence of prey and the size of the school, via the acoustic abundance score, because electronic data capture technologies were not available.

Haney et al (1992) estimated that birds on the water could visually cue to the foraging activities of other birds within a distance of 4 5 km. I assumed that a murre would be able to locate food patches via local enhancement within a 4.5 km area based on this estimate and due to the high densities of birds found around both colonies. I divided the surveyed area into a continuous series of 2.25 km by 300 m blocks I refer to these 2.25 km blocks as "foraging habitats", within which prey schools could be found. The squared acoustic abundance score (scale 0-81) was summed over the water column for each 250 m by 300 m block and then the mean abundance score per 2.25 km block was calculated by averaging these depth integrated scores over each survey Foraging habitats having above average acoustic abundance scores were defined as "hot spots" (Cairns and Schneider 1990)

Hot spots were revisited on 3 - 4 occasions during the same year of the initial broad-scale survey around each colony Revisits were conducted over a two-week period and the time between revisits varied from 3 – 14 days. Upon revisit, a 2.25 km acoustic survey was conducted simultaneously with bird counts (see above) along the initial survey route. A fishing set was conducted within hot spots to determine whether species composition of prey schools changed over the two week period

I estimated the "stability", or stable presence, of acoustic prey and murres within hot spots by dividing the number of times each 2.25 km block contained prey and murres upon revisit by the number of times the hot spot was revisited. I also quantified the mean squared acoustic abundance score ± SE in each 2.25 km hot spot over the initial survey and subsequent revisits.

2.2.4. *Return and Departure Behaviour of Murres*

Return behaviour was observed in 1998, 1999 and 2000 at Great and Funk Islands. Scans were conducted from the highest point on each island to obtain a complete 360° aspect. Each 45° sector was scanned for 1 min using the same compass-equipped binoculars (7 x 50) with the horizon in the mid-line of view. The number of birds returning in each sector was noted on a tape recorder. It was difficult at times to distinguish between flocks of murres and puffins but these species were differentiated where possible. Three 360° rotations were conducted and this was defined as a 360° scan. Before and after each 360° scan, weather variables were recorded: visibility, precipitation, wind speed ($km \cdot h^{-1}$) and direction. A hand-held anemometer was used to measure wind speed.

Within visual range (1 - 2 km) of the splashdown area at Great Island, ephemeral prey patches were often exploited by mixed species feeding flocks, including common murres, Atlantic puffins *Fratercula arctica*, black-legged kittiwakes *Rissa tridactyla* and humpback whales *Megaptera novaeangliae*. These feeding flocks were consistent with type I flocks described by Hoffman et al. (1981). Feeding flocks persisted from minutes to hours and were located in different areas throughout and among days. Prey types at these flocks were not determined and murres were never observed with fish in their bills at these flocks. Similar feeding flocks were never observed from Funk Island. The number of feeding flocks observed in each 45° sector was also recorded during 360° scans.

Departure behaviour of individual murres was observed from the same observation site immediately after each 360° scan. At Great Island, 10 individuals were chosen haphazardly and each was followed as it departed a nesting ledge. Individuals were observed leaving departure ledges on Funk Island rather than breeding sites because murres nest on flat ground in the center of the island. I recorded whether each individual landed in the splashdown area (splashdown departure) or flew directly out to sea (direct departure), following Burger (1997). The final bearing of directly departing murres was recorded. Next, I chose 10 individuals leaving the splashdown area and recorded the final bearing of departure. These 20 departures were defined as a departure scan. The 360° and departure scans together were defined as a sample period.

As in Burger (1997), departure behaviour of murres was also observed from a blind on Great Island. In a subcolony situated approximately 20 m from the blind, approximately 50 murres were marked with yellow dye (picric acid) for individual recognition. This subcolony was observed during 4 h shifts, when arrivals and departures of murres were recorded to the nearest min (see chapter 5). The type of departure (splashdown or direct) of each individual was recorded and final bearings were recorded of individuals directly departing the nesting ledge.

2.2.5. Data Analysis of Return and Departure Behaviour of Murres

The total number of birds returning to the colony during each 360^0 scan and the total number of birds departing the colony in each departure scan in each 45^0 sector was calculated. Birds directly departing nesting ledges and birds departing the splashdown area were analyzed separately. The mean and modal angle of return and departure were calculated following Batschelet (1981). A Rayleigh Test was conducted on each 360^0 scan and each departure scan to determine if return and departure directions were random (Batschelet 1981). Circular correlations were conducted on the mean angle of returns and the mean angle of departures in consecutive sample periods to determine if successive return and departure directions were similar (Zar 1996). The mean angle of departure and the mean angle of return in the same sample period were also compared using circular correlations. Statistical significance was set at $\alpha=0.05$ and all means are reported as ± 1 SE.

Wind direction for each sample period was assigned to the appropriate 45^0 sector. All sample periods were divided into two wind speed categories: $<$ and ≥ 25 km·h^{-1}. These categories were chosen because wind speed does not appear to affect the flight of seabirds until in excess of 25 – 30 km/h (Spear and Ainley 1997). Circular correlations were conducted on wind and return mean angles within sample periods for each wind speed category. This determined whether wind direction influenced return directions and whether low and high wind speeds influenced return directions differentially.

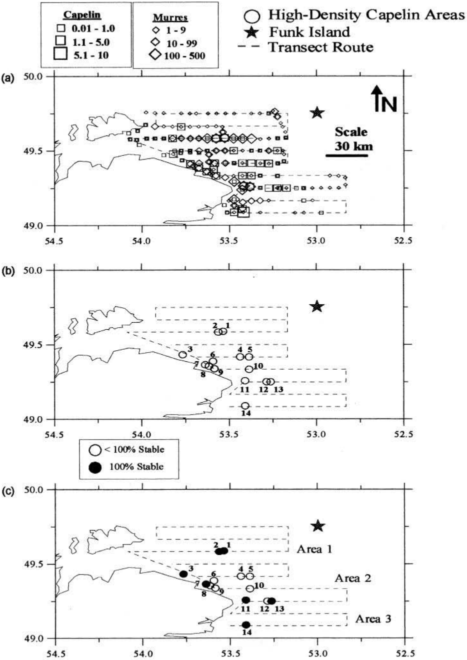
The departure behaviour of marked murres observed from the blind at Great Island was also used to determine if the time spent at the colony before a departure differed between birds that departed into the splashdown area or directly departed nesting ledges using t-tests (Burger 1997). Circular correlations were conducted on the angle of consecutive direct departures conducted by each marked murre at Great Island to determine the temporal persistence of individual departure directions.

2.3 RESULTS

2.3.1 Abundance and Distribution of Capelin and Murres

During the survey around Funk Island in 2000, a total of 353 2.25 km blocks were surveyed, 205 of which contained murres (58 %), 146 contained prey (41 %) and 205 contained prey and murres (58 %). Seventeen fishing sets were conducted, during which 96 % of catches by mass were capelin (see chapter 3 for details).

The mean squared acoustic abundance score (0 - 81) for all nonzero 2.25 km foraging habitats during the initial broad-scale survey around Funk Island was 0.8 ± 0.1 and the mean murre abundance for all nonzero blocks was 2.9 ± 0.5. Nineteen foraging habitats contained prey densities above average (5 %) and due to time limitations 14 of these hot spots were revisited (Fig. 2.2). Capelin were stable, or consistently present, in above


Capelin
□ 0.01 - 1.0
□ 1.1 - 5.0
□ 5.1 - 10
Murres
◇ 1 - 9
◇ 10 - 99
◇ 100 - 500
○ High-Density Capelin Areas
★ Funk Island
-- Transect Route
(a)
N
Scale
30 km
50.0
49.5
49.0
54.5
54.0
53.5
53.0
52.5
(b)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
○ < 100% Stable
● 100% Stable
(c)
Area 1
Area 2
Area 3

average densities in three hot spots, or two general areas (Area 1, 3, Fig. 2.2). Murres were stable, or consistently present, in these hot spots but densities varied highly among revisits (Table 2.1a). Another area (Area 2) had capelin that were stable but abundance scores varied upon revisits (Fig. 2.2, Table 2.1a). Murres were always present in this area but abundance again was highly variable (Table 2.1a). There were other hot spots where capelin was not consistently located and these areas always had variable acoustic abundance scores (Fig. 2.2, Table 2.1a).

Through trawling, I found that capelin schools encountered in Area 2 were always ephemeral in space on the temporal scale of minutes. When a school was encountered, the exact position was recorded and in the minutes it took to prepare the net for trawling, the school always disappeared. Therefore, although the presence of capelin was consistent within the 2.25 km hot spots on the temporal scale of two weeks, schools within Area 2 were not persistent on the spatial scale of meters and on a temporal scale of minutes. This ephemerality may be caused by ship avoidance behaviour because these schools were generally within 50 m of the ocean surface (chapter 3). In contrast, schools in Areas 1 and 3 were located in the exact same position at 110 m of water on different days and, thus, were spatially stable on the scale of meters and temporally persistent on the scale of one week (see chapter 3 for details).

During the more limited survey conducted around Great Island in 1998, 16 2.25 km blocks were surveyed. 11 contained prey and murres (69 %). All prey items observed in

Table 2.1a The stability and mean abundance of capelin and common murres ± SD per 2.25 km hot spot which were revisited around Funk Island

	CAPELIN			MURRE		
Area / Identification No.	No. revisits	Stability* (%)	Mean Capelin Abundance / 2.25 km	No revisits	Stability* (%)	Mean Murre Abundance / 2.25 km
Area 1						
1	3	100	1.21 ± 0.31	3	100	17.59 ± 13.00
2	4	100	1.05 ± 0.22	4	100	3.03 ± 2.39
Area 2						
3	3	100	0.80 ± 0.63	3	100	1.00 ± 0.88
4	4	75	1.02 ± 0.79	4	75	2.07 ± 1.34
5	4	50	0.51 ± 0.50	3	67	0.29 ± 0.26
6	4	25	0.26 ± 0.25			
7	3	100	1.02 ± 0.90	3	67	0.98 ± 0.91
8	3	67	0.85 ± 0.78	3	67	2.78 ± 2.47
9	4	75	0.56 ± 0.47	4	50	2.96 ± 2.91
10	3	67	0.37 ± 0.32	4	50	2.71 ± 1.74
11	4	100	0.25 ± 0.24	3	67	2.85 ± 2.52
12	3	67	0.65 ± 0.59	3	67	1.01 ± 0.87
13	3	100	0.86 ± 0.76			
Area 3						
14	3	100	5.90 ± 2.58	4	100	1.00 ± 0.78

* number of revisits with murres and capelin present divided by the total number of revisits

the bills of birds (n=49) and near the ocean's surface (n=10) around Great Island were capelin. The mean squared acoustic abundance score ± SE for all nonzero 2.25 km foraging habitats was 1.1 ± 0.3 and the mean murre abundance for all 2.25 km foraging habitats was 18.0 ± 9.7. Five 2.25 km foraging habitats contained mean acoustic squared abundance scores above the average (45 %) and these hot spots were revisited (Fig. 2.3). Capelin was always present, or stable, in three hot spots, two of which had abundances that were consistently above average for both capelin and murres (Table 2.1b). The other two hot spots had lower densities of murres and capelin that were variable (Table 2.1b).

2.3.2. Returns

A total of 201 360^0 scans were conducted (Funk Island: n=89; Great Island: n=112), where the number of individuals observed during a scan ranged from 15 - 1854 individuals at Great Island and 228 - 6060 individuals at Funk Island. Birds generally returned to both colonies from all eight sectors; however, return directions were always nonrandom (Table 2.2). The modal direction of return towards Great Island was from 180^0 - 225^0 and towards Funk Island was from 180^0 - 270^0 in all years of the study. Return directions were positively correlated with those in subsequent sample periods (Table 2.3, Fig. 2.4a), indicating that return directions remained consistent throughout and among days.

Figure 2.3 Distributions and abundances of common murres and capelin around Great Island, Witless Bay in 2.25 km bins (a), location of 2.25 km hot spots of capelin (b), and the stability of capelin within each 2.25 km hot spots on subsequent revisits (c)

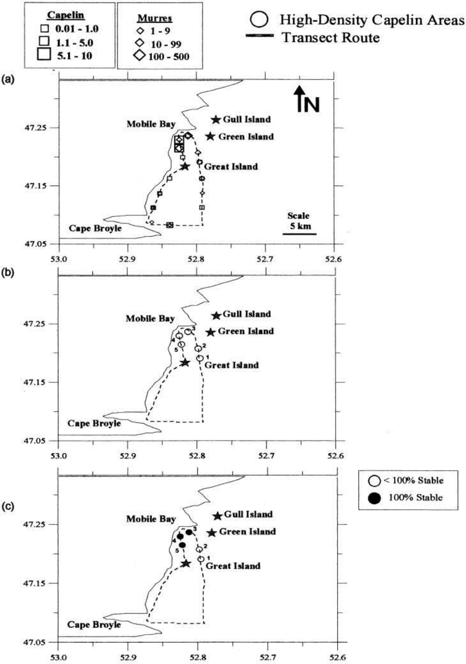

Capelin
☐ 0.01 - 1.0
☐ 1.1 - 5.0
☐ 5.1 - 10
Murres
◇ 1 - 9
◇ 10 - 99
◇ 100 - 500
○ High-Density Capelin Areas
Transect Route
(a)
N
Mobile Bay
Gull Island
Green Island
Great Island
Cape Broyle
Scale
5 km
47.25
47.15
47.05
53.0
52.9
52.8
52.7
52.6
(b)
Mobile Bay
Gull Island
Green Island
Great Island
Cape Broyle
1
2
3
4
5
47.25
47.15
47.05
53.0
52.9
52.8
52.7
52.6
(c)
○ < 100% Stable
● 100% Stable
Mobile Bay
Gull Island
Green Island
Great Island
Cape Broyle
1
2
3
4
5
47.25
47.15
47.05
53.0
52.9
52.8
52.7
52.6

Table 2.1b The stability and mean abundance of capelin and common murres ± SD per 2.25 km hot spot which were revisited around Great Island

	CAPELIN			**MURRE**		
Area / Identification No.	No revisits	Stability* (%)	Mean Capelin Abundance / 2.25 km	No revisits	Stability* (%)	Mean Murre Abundance / 2.25 km
1	3	100	0.65 ± 0.58	3	100	7.19 ± 4.77
2	3	67	0.89 ± 0.78	3	100	6.89 ± 7.58
3	3	100	2.00 ± 0.08	3	100	34.15 ± 32.48
4	3	100	2.50 ± 1.00	3	100	51.0 ± 44.00
5	3	100	1.02 ± 0.82	3	100	10.59 ± 13.14

* number of revisits with murres and capelin present divided by the total number of revisits

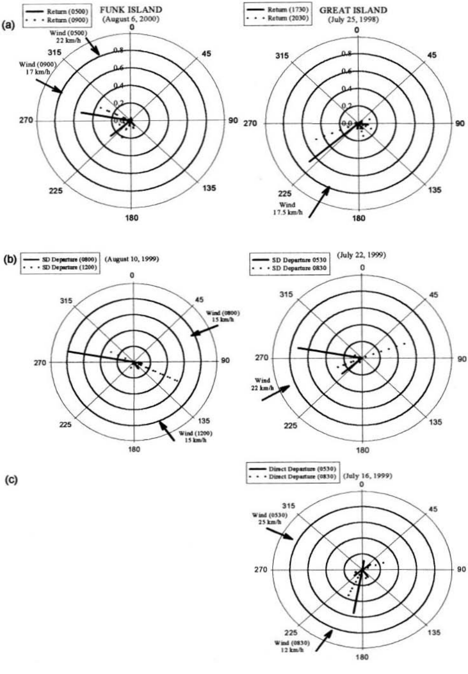
Table 2.2 Number of return and departure scans where individuals were found to return and depart the colony in a significantly nonrandom and random manner using Rayleigh Tests at Funk Island and Great Island (all years combined).

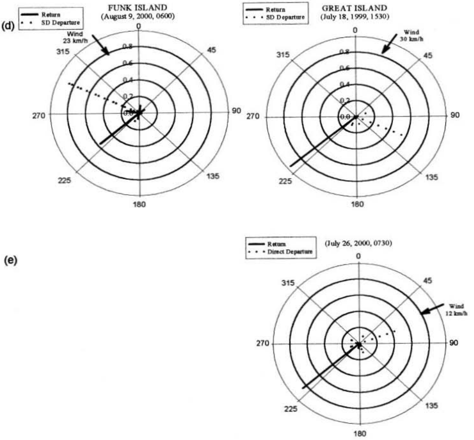
Category	Funk Island	Great Island
Return Flight		
Nonrandom	89	112
Random	0	0
Total	89	112
% Nonrandom	100 %	100 %
Departure Flight From Splashdown Area		
Nonrandom	20	42
Random	18	27
Total	38	69
% Nonrandom	53 %	61 %
Direct Departure		
Nonrandom	-	19
Random	-	42
Total	-	61
% Nonrandom	-	31 %

Table 2.3 Lower and upper circular correlation coefficients for the mean angle of departure and return directions at Funk Island and Great Island (all years combined). All are significantly correlated ($\alpha=0.05$). Numbers in parentheses are the number of sample periods on which correlations are based.

Foraging Flights	Funk Island	Great Island
Return Flight vs Departure Flight from Splashdown Area	-0.1120 / -0.0937 (35)	-0.1462 / -0.1403 (60)
Return Flight vs Direct Departure Flight		-0.2223 / -0.2104 (46)
Successive Return Flights	0.5860 / 0.5978 (57)	0.3993 / 0.4046 (73)
Successive Departure Flight from Splashdown Area	-0.0872 / -0.0540 (20)	-0.3782 / -0.3635 (42)
Successive Direct Departure Flights		0.3150 / 0.3340 (31)
Successive Direct Departure Flights by Individual Murres		0.5151 / 0.5959 (15)

Figure 2.4. Circular plots of the proportions of common murres returning and departing from colonies in 45° sectors on representative days, illustrating returning flight directions in successive sample periods (a), departure flight directions from the splashdown area in successive sample periods (b), departure flight directions from the nesting ledge in successive sample periods (c), return and departure flight directions from the splashdown area in the same sample period (d), and return and departure flight directions from the nesting ledge in the same sample periods (e). Wind direction and speed are indicated outside of plots. Dotted and solid lines are offset within each 45° sector for clarity.

(a)
Return (0500)
Return (0900)
FUNK ISLAND
(August 6, 2000)
Wind (0500)
22 km/h
Wind (0900)
17 km/h
0
45
90
135
180
225
270
315
0.8
0.6
0.4
0.2
0.0
Return (1730)
Return (2030)
GREAT ISLAND
(July 25, 1998)
Wind
17.5 km/h
(b)
SD Departure (0800)
SD Departure (1200)
(August 10, 1999)
Wind (0800)
15 km/h
Wind (1200)
15 km/h
SD Departure 0530
SD Departure 0830
(July 22, 1999)
Wind
22 km/h
(c)
Direct Departure (0530)
Direct Departure (0830)
(July 16, 1999)
Wind (0530)
25 km/h
Wind (0830)
12 km/h


(d)
Return
SD Departure
FUNK ISLAND
(August 9, 2000, 0600)
Wind
23 km/h
0
45
90
135
180
225
270
315
0.8
0.6
0.4
0.2
0.0
Return
SD Departure
GREAT ISLAND
(July 18, 1999, 1530)
Wind
30 km/h
0
45
90
135
180
225
270
315
0.8
0.6
0.4
0.2
0.0
(e)
Return
Direct Departure
(July 26, 2000, 0730)
Wind
12 km/h
0
45
90
135
180
225
270
315

2.3.3. Departures

A total of 107 departure scans were conducted (Great Island, n=69, Funk Island, n=38), during which the number of individuals observed during a scan ranged from 13 - 23 individuals. Overall, 1493 individuals were observed departing the colonies (Great Island, n=1254, Funk Island n=239). There was a significantly higher percentage of birds directly departing ledges at Great Island (30 %) compared to Funk Island (7 %, χ^2_1=53.896, n=1493, P<0.001). Therefore, I consider a single departure strategy at Funk Island (splashdown departure) and two at Great Island (splashdown departure, direct departure).

Murres generally departed both the nesting ledge and the splashdown area in all eight sectors. The modal direction of departure from Great Island was from 135° - 225° and from Funk Island was from 180° - 270°. At Funk Island, 81 % (n=239) of the birds departing the splashdown left the vicinity of the colony alone, while others left in flocks of 2 - 13 individuals. At Great Island, 89 % (n=487) of the birds departing the splashdown area left the vicinity of the colony alone, while others left in flocks of 2 - 15 individuals. Similarly, 94 % (n=290) of birds departing the nesting ledge at Great Island left the vicinity of the colony alone. At both colonies, however, over half of the sampling periods had nonrandom departure directions from the splashdown area (Table 2.2). The frequency of nonrandom departure directions from the splashdown area did not differ between Great and Funk Island (χ^2_1=0.683, n=107, P=0.043; Table 2.2). At Great Island, there were significantly more sample periods with nonrandom departure directions from the splashdown area compared to direct departures from the colony ($\chi^2_1=11.44$, n=130, $P<0.001$, Table 2.2).

At both colonies, departure directions from the splashdown area were negatively correlated with departure directions in subsequent sample periods within days (Table 2.3, Fig. 2.4b), indicating that departure directions were not consistently in the same direction throughout days. In contrast, directions of direct departure from Great Island were positively correlated with directions in subsequent sample periods within days (Table 2.3, Fig. 2.4c). In addition, successive direct departure directions of marked individuals were positively correlated within days (Table 2.3).

2.3.4. Wind

The modal wind direction at Funk Island was from 135°-270° and at Great Island was from 180°-270°. At Funk Island, returning birds generally flew with the wind (positive correlation) at wind speeds of < 25 $km \cdot h^{-1}$ but flew against the wind (negative correlation) at wind speeds ≥ 25 $km \cdot h^{-1}$ (Table 2.4). In contrast, murres departing from the splashdown area flew with the wind (negative correlation) upon departure at wind speeds < 25 $km \cdot h^{-1}$ and departure directions at wind speeds ≥ 25 $km \cdot h^{-1}$ were variable (not correlated). At Great Island, returning murres and murres departing from the splashdown area generally flew with the wind (Table 2.4), whereas murres directly departing nesting ledges generally flew into the wind (Table 2.4). Overall, directions of

Table 2.4 Lower and upper circular correlation coefficients for the mean angle of wind direction versus the mean angle of return flight directions, departure directions from splashdown areas and flight direct departures for murres from Funk Island and Great Island (all years combined). All are significantly correlated unless otherwise indicated (non-significant, NS). Numbers of 360° scans and departure scans are given in parentheses

Foraging Flights	Funk Island			Great Island		
	All	< 25 $km \cdot h^{-1}$	≥ 25 $km \cdot h^{-1}$	All	< 25 $km \cdot h^{-1}$	≥ 25 $km \cdot h^{-1}$
Wind versus						
Return Flight	0.0100 / 0.0135 (76)	0.0012 / 0.0175 (48)	-0.5615 / -0.5442 (28)	0.0298 / 0.0324 (104)	NS (56)	0.0076 / 0.0180 (48)
Departure Flights from Splashdown Area	0.2518 / 0.2584 (33)	-0.3339 / -0.3193 (21)	NS (12)	-0.1462 / -0.1403 (60)	NS (38)	-0.9134 / -0.4961 (22)
Direct Departure Flights				0.1026 / 0.1110 (45)	0.7452 / 0.7642 (28)	0.3286 / 0.6865 (17)

flight were variably related to wind direction and speed and I suggest that significant correlations observed are artifacts of flight directions to and from foraging habitats and prevailing wind directions

2.3.5. *Returns and Departures*

Return directions were negatively correlated with departure directions at both colonies during the same sample period (Table 2.3, Figs. 2.4d, e). Commuting routes of murres, or consistent flight paths towards and away from colonies (Schneider et al. 1990), however, were observed farther away from each colony at sea. Commuting routes of murres around Funk Island were along a northeast-southwest line, which are consistent with the locations of stable hot spots of capelin and murres (Fig. 2.5a, b). There also appeared to be movement among these stable hot spots (Fig. 2.5c). Commuting routes of murres around Great Island were along a north-south line (Fig. 2.6a, b), which are consistent with the routes and foraging areas previously described by Schneider et al. (1990). Flight directions at sea also indicated that Mobile Bay was an important foraging area (Fig. 2.6c).

2.3.6. *Splashdown and Direct Departure (Great Island)*

Prior to departing nesting ledges, murres spent significantly more time at the colony before a splashdown departure (181.6 ± 12.2 min) compared to a direct departure (49.9 ±

Figure 2.5 Distribution and abundance of common murres flying in all directions (a), northeast and southwest (b), and northwest and southeast (c) in 2.25 km bins around Funk Island

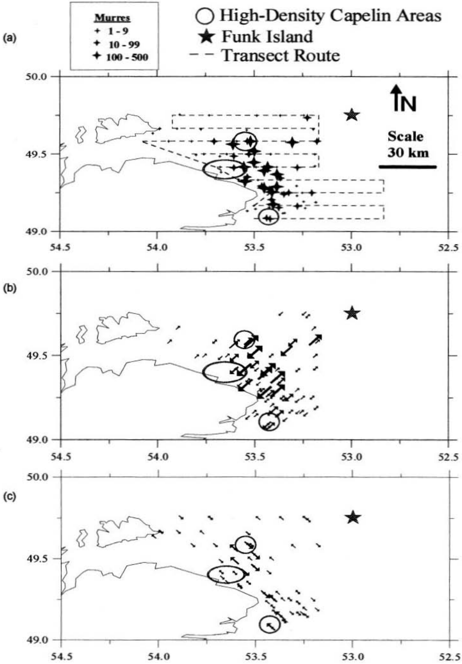
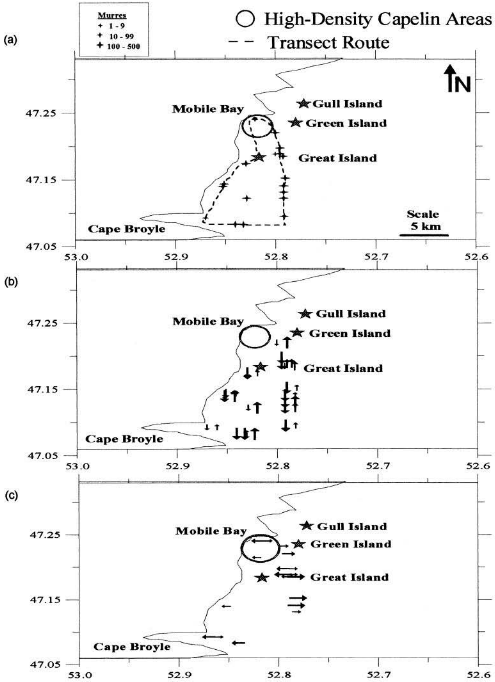

(a)
Murres
1 - 9
10 - 99
100 - 500
High-Density Capelin Areas
Funk Island
Transect Route
N
Scale
30 km
50.0
49.5
49.0
54.5
54.0
53.5
53.0
52.5
(b)
(c)

Figure 2.6. Distribution and abundance of common murres flying in all directions (a), north and south (b), and east and west (c) in 2.25 km bins around Great Island.


(a)
Murres
1 - 9
10 - 99
100 - 500
High-Density Capelin Areas
Transect Route
N
Mobile Bay
Gull Island
Green Island
Great Island
Cape Broyle
Scale
5 km
47.25
47.15
47.05
53.0
52.9
52.8
52.7
52.6
(b)
Mobile Bay
Gull Island
Green Island
Great Island
Cape Broyle
47.25
47.15
47.05
53.0
52.9
52.8
52.7
52.6
(c)
Mobile Bay
Gull Island
Green Island
Great Island
Cape Broyle
47.25
47.15
47.05
53.0
52.9
52.8
52.7
52.6

]

10.5 min, t-test $t_{176}=6.723$, $P<0.0001$). A significantly higher percentage of murres landed at feeding flocks from the splashdown area (10 ± 3 %) than from nesting ledges (4 ± 2 %, $t_{36}=2.005$, $P=0.042$) when feeding flocks were visible from the colony.

2.4 DISCUSSION

Return and departure flight directions of murres were not consistent during a sample period at either colony, showing that birds departing each colony did not cue to the flight paths of returning flocks. Hot spots of capelin, however, were stable on spatial scales of meters, 2.25 and 4.5 km (adjacent 2.25 km blocks) in certain areas and on a temporal scale of 2 weeks within the foraging ranges of murres from both colonies. The stability of murres at hot spots where capelin was stable suggests that murres used memory to locate prey at sea. The consistent flight paths, or commuting routes, towards and away from stable hot spots of capelin may also provide outbound birds with information about foraging habitats outside of visual range of colonies. I propose, however, that this information is unimportant when stable aggregations are present over the temporal scales observed in this study and that these flyways result from flight to and from stable hot spots. These flyways, however, may become more important on fine spatial scales within hot spots to locate capelin schools.

Although there was no evidence of information exchange on food patches outside of visual range at either colony, murres in the splashdown area at Great Island did depart into mixed-species feeding flocks within visual range. This use of local enhancement may explain why murres spent more time in the splashdown area at Great Island, where they could cue on the foraging activities of other seabirds within visual range ('information halo', Burger 1997), compared to Funk Island, where feeding flocks were not observed from the colony (chapter 5).

2.4.1. Search Tactics

I found no support for the Information Center Hypothesis (Ward and Zahavi 1973), or Information Halo (Burger 1997), as a mechanism for information exchange at breeding colonies. Using information about distant foraging habitats provided by returning flocks at the colony is probably the least accurate search tactic because return trajectories only reflect general directions from foraging sites, and return trajectories are altered under varying wind speeds and directions (Spear and Ainley 1997, Bryant and Furness 1995, Burger 1997, this study). For instance, murres in the present study generally returned to both colonies with a tail wind, which might increase flight efficiency of the more costly return trip when parents are carrying a fish for their chick. In addition, return trajectories of birds only indicate the location of the last food patch when possibly a number are visited on a foraging trip (Wanless et al. 1990, Benoit et al. 1993, Benvenuti et al. 1998, this study). In contrast, the exact location of a persistent food patch could be retained in memory or found by cueing to the foraging activities of other conspecifics and, in some circumstances, searching at the scale of a foraging range (100 km) could be essentially eliminated.

The spatial and temporal stability of capelin hot spots and the persistence of murres in high abundance at these hot spots suggest that murres used memory to locate food patches at sea. The successive direct departures of individual murres in similar directions also clearly implies the use of memory. Reducing the time and energy spent searching for prey is important during breeding when energetic demands are high (Cairns et al. 1990). There is much evidence for consistent habitat use by seabirds (Cairns and Schneider 1990, Hunt and Harrison 1990, Schneider 1991), which suggests that they are capable of constructing and using spatial maps of foraging habitats in a manner similar to birds that cache food (Shettleworth 1990, Smulders 1997). These food-storing birds generally have large hippocampal volumes, a region of the brain essential for spatial learning, relative to nonfood-storing birds (Squire 1992). Some seabirds have hippocampal volumes similar to food-storing birds (e.g. Leach's Storm-Petrel, Abbott et al. 1999), suggesting that they are capable of complex spatial tasks. Murres tend to visit a number of locations during a foraging trip (trapline foraging pattern, Wanless et al. 1990, Benvenuti et al. 1998), which may reflect important exploratory behaviour for developing a spatial map of prey distribution and abundance around the colony (Warburton 1990, Mackney and Hughes 1995).

Even though the majority of murres departed both colonies alone (81 – 94 %), other behaviour of murres may have promoted the spatial concentration of murres within foraging habitats and, thus, information transfer on capelin school locations on a fine-scale. For instance, there was a high percentage of nonrandom departures from splashdown areas, constant streams of birds flying to and from hot spots along specific commuter routes and high densities of murres consistently sitting on the water near capelin schools within hot spots. This combined behaviour of murres and capelin resulted in food patches being consistently marked at sea by high abundances of both flying and sitting murres. Therefore, even if foraging habitats are initially located based on memory, local enhancement may be important in locating food patches within habitats, especially where prey schools are ephemeral on a finer scale (e.g. Area 2, Funk Island; Cairns and Schneider 1990). The exception to this was murres directly departing nesting ledges at Great Island, where after a brief return to the colony individuals left nesting ledges in different directions. This behaviour could reflect an urgency to return to an ephemeral food patch before it moved or before competitors accumulated there.

Despite the benefits of simply cueing to the foraging activities of conspecifics, this search tactic may not always be preferentially used to locate prey. In the case of mixed-species feeding flocks, the exact location of a food patch is provided but competition among flock members can be high (Hoffman et al. 1981, Shealer and Burger 1993, Mills 1998). Seabirds have been observed by-passing feeding flocks on their way to more distant foraging habitats (e.g. Hunt and Harrison 1990, Irons 1998), as was observed for murres directly departing Great Island in this study. Increased travel times to patches to forage in less crowded conditions may offset increased foraging durations at a patch due to increased interference and reduced prey capture rates while foraging in a group (Obst et al. 1995, Gremillet 1997). Even though murres departing the splashdown area at Great

Island landed at feeding flocks to a greater extent than those directly departing nesting ledges, a low percentage of these individuals actually landed at feeding flocks (10 %). Birds that hold fish in their bills for delivery to their chicks tend to be the focus of kleptoparasitic attacks by gulls at feeding flocks (Hoffman et al. 1981) and, thus, parents may avoid collecting prey in flocks when provisioning young (e.g. Davoren and Burger 1999).

An alternate hypothesis for by-passing feeding flocks could be that these birds rely on memory to return to a fixed foraging location (perseveration, Pinel 1997). This behaviour would be reinforced under continuing high prey abundance but would be extinguished after a number of visits to the area when prey abundance had decreased (win-stay, lose-shift, Kamil 1983). Only after this behaviour had been extinguished would birds switch search tactics. Reinforcement schedules, or high feeding success, after a number of visits to a food patch can have an enormous impact on patch selection of foragers (Kamil 1983). If a patch has highly variable and irregular prey presence and abundance, foragers will learn quickly to visit the patch frequently. In addition, as foragers gain experience in a particular foraging habitat, they will likely remain there (Rissing 1981, Werner et al. 1981).

Overall, the use of memory by murres is consistent with the commuting behaviour observed in this study and others (Schneider et al. 1990) and the consistent use of certain foraging areas while other areas remain unused (e.g. Hunt and Harrison 1990). The abundance of murres at persistent capelin hot spots, however, were highly variable in this study and others (e.g. Cairns and Schneider 1990), suggesting that murres may visit a number of foraging habitats (e.g. Wanless et al. 1990, Benvenuti et al. 1998) and/or use a combination of searching strategies (Cairns and Schneider 1990), and, thus, are behaviourally flexible when searching.

2.4.2. *Summary*

Understanding how seabirds locate prey at sea is key to understanding how they will respond to changes in prey conditions (Veit 1999). Evidence of information exchange at the colony about foraging sites out of visual range of the colony remains elusive (Bayer 1982, Mock et al. 1988). The information provided by returning flocks of birds, however, was consistent with the direction of the main hot spots and, thus, may act as "insurance" when food conditions change because individuals have the option of cueing on the flight paths of "successful" individuals, or those individuals carrying fish, both at the colony and at sea (Ward and Zahavi 1973, Greene 1987, Summers and Feare 1995, Zahavi 1995, Burger 1997). In addition, even though feeding flocks were not used to a great extent, they may also be important in reducing the variation in food intake, thereby minimizing the risk of starvation under poor foraging conditions (Clark and Mangel 1984, 1986, Eckman and Hake 1988). The absence of such social foraging techniques is generally associated with increased time and energy spent foraging (e.g. Davoren 2000). Consequently, the lack of feeding flocks within visual range of Funk Island along with the longer distances to stable foraging sites could have reduced the foraging efficiency of murres breeding at Funk Island. This could explain the reduced resting time in the splashdown area, provisioning rates and fledgling condition at Funk Island compared to Great Island (chapter 5).

Animals likely use different techniques to locate prey depending on the spatial and temporal scale on which they are searching (Russell et al. 1992, Noda et al. 1994, Prevot-Julliard and Lebreton 1999, Fauchald et al. 2000). In this study, the persistence of murres at stable hot spots of capelin was consistent with the use of memory to locate foraging habitats on the scale of foraging ranges from the colony (coarse scale, 1-100 km). The commuting behaviour of murres and stable behaviour of capelin both appeared to promote the spatial concentration of birds within foraging habitats. This is consistent with the use of local enhancement or network foraging to locate prey schools within foraging habitats on a fine-scale (1 - 1000 m). The temporal scale at which prey aggregations are stable may also shape search strategies throughout the lifetime of an individual. Fluid motion combined with strong bathymetric relief, or specific habitat requirements of prey, often result in aggregations of seabird prey that are spatially stable among years (see Schneider 1991). Throughout a lifetime in a specific region (e.g. area surrounding a breeding colony), seabirds could learn the locations of a suite of foraging sites. Regular sampling of these sites would allow daily choice of foraging sites based on recent experience (Schneider pers. comm.) and could lead to the use of traditional foraging areas from year to year (hinterland; Cairns 1989).

Overall, the flexible use of memory and social learning rather than fixed decision rules in locating prey patches will be essential under changing prey conditions. Animals likely use a variety of mechanisms to locate prey and how they are combined into various strategies will depend on the behavioural and energetic constraints of predators and prey as well as the spatial scale on which predators search for prey.

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CHAPTER III - Spatial associations of common murres and capelin: integrating predator patch selection and prey behaviour

3.1 INTRODUCTION

Foraging theory states that animals should select food patches on the basis of their 'profitability' and the optimal strategy of patch selection will be influenced by the distribution, frequency and magnitude of changes in patch quality and location and the consistency in quality and location over time (Pyke 1984). Ideal Free Distribution theory (IFD, Fretwell and Lucas 1970) is a major theoretical framework that links behavioural foraging theory, in the context of habitat selection within patchy environments, with ecological predator-prey theory (Huntingford 1993, Miliniski 1994). In IFD models, animals are assumed to be "free" to exploit any available patch without restriction and to distribute themselves "ideally" among these patches to obtain the highest benefits (Fretwell and Lucas 1970, Sutherland 1983, Parker and Sutherland 1986). All individuals are assumed to have similar average gains among patches and are assumed to have complete knowledge of all prey patch locations and qualities (Fretwell and Lucas 1970). An individual's decision is considered to depend on the choices of its competitors as well as the distribution and density of its prey (Miliniski and Parker 1991). Competitors can reduce intake rates of prey in a patch by reducing encounter rates with prey (exploitative or scramble competition) or by altering the behaviour of a competitor independent of prey availability through aggressive interactions or avoidance behaviour (interference or contest competition; Milinski and Parker 1991, Stillman et al. 1996, Cresswell 1997, Hughes 1997) The underlying premise of this model and its modifications is that predator populations are subject to density-dependent control due to small scale interactions within patches (Fretwell and Lucas 1970, Tregenza 1995) and although individual benefits may increase as competitor density increases up to some maximum, they will decrease thereafter (Allee Principle, Allee 1931).

The 'profitability' or quality of a prey patch is likely assessed using a number of criteria. A common deviation from IFD models reported in the literature is the under use of high-quality patches and overuse of lower-quality patches ('undermatching', Kennedy and Gray 1993). This is generally thought to result from a lack of integration of other factors that might influence patch selection decisions of individuals (Kennedy and Gray 1993). Modifications of the IFD to account for deviations from the original model generally include factors that fall into two categories: (1) patch and habitat characteristics, other than prey and competitor density, and (2) physiological and perceptual constraints of the predator (see Tregenza 1995 for review). Patch characteristics include composition of prey types in the patch, behaviour of prey in a patch (e.g. stability of a patch in space and time) and the rate of change of prey abundance within a patch (Harper 1982, Croy and Hughes 1991). Habitat features may also be important, such as proximity to nest sites or other high-density prey patches, among others (Cairns and Schneider 1990, Mehlum et al. 1996, Maniscalco et al. 1998). The physiological requirements along with perceptual and learning constraints of predators may also alter patch selection (Piatt 1990, Horne and Schneider 1994). For instance, the energetic state of predators may preclude them from continuously sampling their environment, resulting in a lack of knowledge of prey patch locations and qualities (Shettleworth et al. 1988). A similar deficiency may arise from a reduction in sampling due to predators outweighing past foraging experiences over present assessments of patch qualities (Abrahams 1989, Miliniski 1994). Determining which patch characteristics are preferred over others and understanding the physiological mechanisms underlying this selection are important when attempting to understand distribution patterns and ultimately how individuals meet their energetic requirements for survival (Ostrand et al. 1998).

The common murre breeds in colonies on islands. They lay a single egg and rear one chick at the colony for approximately 3 weeks. One parent remains at the colony with the chick while the other leaves on a foraging trip and parents deliver a single fish to their chick after each foraging trip. Murres are marine birds that dive underwater up to 200 m to collect small forage fish (Gaston and Jones 1998). In Newfoundland, murres primarily feed their chicks female capelin (chapter 5). The wing design of murres is a compromise between underwater flight (low surface area) and aerial flight (high surface area, Thompson et al. 1998). This results in a high wing-loading, or body mass to wing area ratio (2.06 g/cm^2, Guillemette 1994), which places them close to the flightless threshold (2.5 g/cm^2, Guillemette 1994). Murres are visual predators and primarily forage during daylight (Swennen and Duiven 1991), although they may concentrate foraging efforts during low light conditions (dawn, dusk) when prey migrates to more accessible depths (Croll et al. 1992). Therefore, the amount of food delivered to chicks each day, and their subsequent probability of survival, depends on the size and quality of fish and the frequency of fish deliveries during daylight.

Capelin is a small, short-lived (3 - 5 yrs), pelagic schooling fish with a circumpolar distribution in Arctic and sub-Arctic regions (Jangaard 1974, Vilhjalmsson 1994). In Newfoundland, capelin is a dominant forage fish and supports the upper trophic food web with marine birds, mammals and piscivorous fish (e.g. Atlantic cod) depending on this species as prey in coastal waters during the summer (Bundy 2001). In Newfoundland during the summer, capelin spawn primarily on gravel beaches with only one confirmed off-beach spawning site (Carscadden 1982). The existence of both modes of reproduction in one geographic area is uncommon and in most other regions capelin either are beach-spawners (e.g. British Columbia, Carscadden et al. 1989) or offshore-spawners (e.g. Barents Sea, Vilhjalmsson 1994). Different spawning stocks have widely varying spawning habitat preferences (Vilhjalmsson 1994). For instance, capelin spawn at a wide range of temperatures (0 – 12°C, Vilhjalmsson 1994) but appear to prefer temperatures above 2°C in Newfoundland waters and 12 – 14°C on beaches (Carscadden et al. 1989). Similarly, particle size of substrates varies considerably (0.1 - 15.0 mm, Vilhjalmsson 1994).

In a previous study, I examined the search tactics used by common murres to locate food patches at sea from breeding colonies during chick-rearing (chapter 2). As a preliminary step, I quantified the distribution, abundance and spatial and temporal stability of capelin and murres within a series of 2.25 km areas around the Funk Island breeding colony. I identified a number of 2.25 km areas that had above average abundances of capelin ("hot spots"). Some hot spots had a consistently high abundance of capelin and capelin was also consistently present in these areas on a temporal scale of two weeks (Area 1, chapter 2). In contrast, some hot spots had a fluctuating abundance of capelin and capelin was not always present in these hot spots (Area 2, chapter 2). The first objective of this study is to describe in detail the characteristics of both stable (Area 1) and unstable (Area 2) hot spots of capelin and their physical surroundings. Second, I examine the scale at which murres track capelin within both stable and unstable hot spots. Finally, I generate steady state and dynamic patch selection models to compare energetic costs and benefits of murres foraging within stable and unstable hot spots. Linking population-level distribution patterns and predator-prey spatial associations with physiological requirements of predators provides a valuable framework with which to examine factors that influence foraging decisions by individuals (Horne and Schneider 1994, Wanless et al. 1997). Investigating behavioural mechanisms that underlie distribution patterns (e.g. behavioural cascades, Russell et al. 1992) is useful in formulating mechanistic hypotheses about predator-prey interactions and ultimately ecosystem-level processes.

3.2. METHODS

3.2.1. Study Area

This study was conducted in July 2000 in an area southwest of the Funk Island Ecological Seabird Reserve (49°00'N-49°45'N, 53°30'W-54°00'W) off the east coast of Newfoundland (Fig. 3.1). Funk Island lies approximately 60 km from the coast and houses a breeding population of 340,000 – 400,000 pairs of common murres during the summer (Canadian Wildlife Service unpubl. data). Funk Island is the largest breeding colony of common murres in eastern Canada and represents 80 % of the population in the Northwest Atlantic (Cairns et al. 1989). South Cabot Island is another small breeding colony of common murres (2,600 breeding pairs) located within the study area (Fig. 3.1, Cairns et al. 1989).

3.2.2. Survey Design

A broad-scale survey was conducted over 5 days (July 18 - 22, 2000) to determine the location of areas where capelin and murres were highly abundant around the Funk Island breeding colony on a meso-scale (Fig. 3.1). The survey was carried out aboard a 23 m Fisheries Canada research vessel *Shamook*, which operated 12 h per day. Nine east-west (across shelf) hydroacoustic transects were conducted at a 5 Nm (9 km) north – south spacing. Marine birds and mammals were counted continuously during acoustic transects. A navigational software package (Bioplot) continuously recorded the ship's position (latitude and longitude) and Greenwich Mean Time (GMT) every minute. The date and

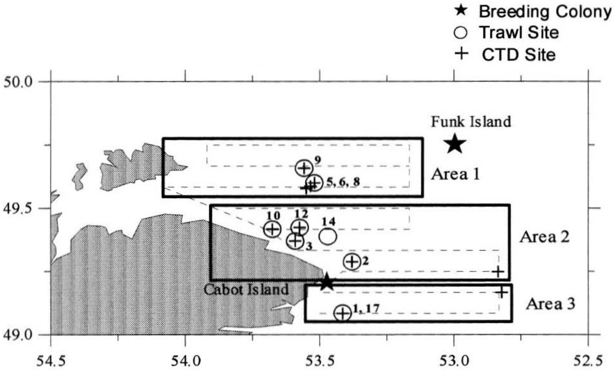


Figure 3.1. A map of the study area, showing the survey track (dashed line), seabird breeding colonies (stars), trawling sites (circles) with identifying set numbers, temperature/salinity sites (crosses) and the three different foraging sub-areas (bold rectangles) defined in chapter 2.

GMT were used to merge bird/mammals counts with acoustic estimates and the cruise track data sets into 1 min (250 m) bins.

3.2.3. Acoustic Estimates

The distribution and relative abundance of prey in the water column were estimated using a Simrad EQ100 echo-sounding system, which operated through a hull-mounted single-beam transducer with a frequency of 38 kHz. The transducer had a 10-degree beam angle and the echo sounder was operated at 1 ping per second, 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 would 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) were held constant throughout the survey. Echograms were continuously printed during transects and GMT was marked on the echograms every 10 min.

The relative abundance of prey was quantified by estimating the percent cover of the prey image in each 1 min (250 m) by 10 m vertical bin on the echogram, following Piatt (1990). Percent cover of prey was estimated on a scale of 0 – 9 in each bin (acoustic abundance score) and this was squared prior to analysis to attain a better estimate of abundance (Piatt 1990). This technique was used to determine the presence of prey and the size of the school, via the acoustic abundance score, because electronic data capture technologies were not available.

I quantified four characteristics of each prey school encountered during the broad scale survey: vertical distance the school covered in the water column (height, m), maximum depth of the school (m), distance of the bottom of the school off the seabed (m) and distance of the top of the school from the surface of the ocean (m, Maniscalco et al. 1998, Ostrand et al. 1998, LeFeuvre et al. 2000). A correlation analysis was performed to determine if these variables were independent ($r < 0.5$, Ostrand et al. 1998). I also quantified location of each school with reference to: (1) the distance from the shore (km, potential spawning areas), (2) distance from Funk Island (km; predator aggregations), and (3) ocean depth in which the school was located (m). Another correlation analysis was performed to determine if these variables were independent ($r < 0.5$, Ostrand et al. 1998). Statistical significance was set at $\alpha=0.05$ and all averages are reported as ± 1 SE.

3.2.4. Physical and Biological Sampling

A modified shrimp trawl was deployed from the *Shamook* (fishing set) around Funk Island to identify the species composition of acoustic signals. At least one fishing set was conducted on each day of the broad-scale survey. Schools with the greatest uncertainty of acoustic signal were targeted and fishing primarily occurred in areas where many prey schools were observed (Ostrand et al. 1997). The trawl was used to fish both at the seabed and in mid-water and a standard fishing duration was used (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 the mesh size of the codend was 40 mm. A number of parameters were recorded during the tow, maximum depth of trawl (m) and trawl dimensions (m) using SCANMAR monitoring devices, speed of vessel (km/h), and distance traveled (km).

The total mass of the catch and the number of species was recorded immediately after each tow. Ten percent of the catch was subsampled and the mass each species contributed to the total catch was calculated. A subsample 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 was determined. Two fish per sex per 0.5 cm length category in each subsample were selected and the total mass, gonad mass, age and stomach fullness (0 %, 25 %, 50 %, 75 % and 100 %) of each fish were recorded.

Temperature and salinity profiles of the water column were measured using an Applied Micro-Systems STD-12 or a SeaBird SBE-25 after each fishing set. Devices were deployed at 1 m/s, which allowed data to be collected at 20 – 50 cm intervals from the surface to the ocean floor and to the surface again. I characterized the thermal stratification of the water column in two ways. First, I used the temperature profiles collected during the survey at fishing stations. Second, I used historical oceanographic data obtained from Fisheries and Oceans Canada (courtesy of E. Colbourne) to characterize the temperature and salinity profiles of the water column in the surveyed area during July throughout the 1990s. These datasets were combined to determine if conditions during the survey were similar to historic data. I defined the thermocline as the range of vertical depths during which the rate of change of temperature was highest. Finally, I placed each prey school into one of two categories: above and within the thermocline or below the thermocline.

3.2.5. Seabird Counts

Seabirds were counted simultaneously during acoustic transects using standard strip transects (Method I b, Tasker et al. 1984). Continuous counts of marine birds and mammals were conducted from the bridge by one observer out to 300 m in a 90^0 arc between an imagined line extending from the tip of the bow to an imagined line perpendicular from the port side of the ship. Counts were entered directly into a laptop computer along with behavioural descriptions (on water, feeding, flying, flight direction, flying with fish). The laptop was connected to the navigational system of the ship and counting software designed by Fisheries Canada (D. Senciall) was used to append the GMT, latitude and longitude to each bird/mammal entry.

3.2.6. Collection of Stomach Contents of Murres

Dead common murres found floating near stationary fishing gear (i.e. gill nets set on the bottom) were collected during the survey. In the laboratory, the cause of death was determined along with the breeding status of each bird through presence or absence of a brood patch. The total mass of stomach contents and the number of intact fish were recorded. Intact fish were identified to species and other characteristics of the fish (total length, sex, maturity) were recorded where possible. Digested material was placed in a glass tray and hard parts (e.g. otoliths) were removed from the digested material for later species identification.

3.2.7. Statistical Analyses

The survey area was divided into the three sub-areas (Fig. 3.1) based on the spatial clustering of 2.25 km hot spots of capelin (chapter 2). Univariate statistics based on the neighbour K statistic (Ripley 1981) were used to assess whether the distribution of murres sitting on the water and acoustic prey separately in each area was significantly different from random at a number of spatial scales (see O'Driscoll 1998). For each transect, the test statistic E[N(t)], or the average number of neighbours of each murre or squared acoustic abundance score in each 250 m bin, was calculated at different spatial scales (t) using the following equation:

$$E = \sum_{\substack{i=1 \\ i\neq j}}^{N} \sum_{j=1}^{N} I_t\,(u_{ij})$$

where N is the total number of individuals observed in an area, u_{ij} is the distance from individual i to individual j and $I_t(u_{ij})$ is an indicator function, which is equal to 1 if $u_{ij}<t$ but equal to 0 otherwise (O'Driscoll 1998). The spatial scales analyzed (t) ranged from 250 m and increased at 250 m increments up to half the length of the transect in each area (Area 1: 38 km; Area 2: 71 km, 25 km; Area 3: 56 km). After half the length of the transect, the bias in E[N(t)] will be great because some individuals may lie less than that distance from the ends of the transect (O'Driscoll 1998). I calculated the average number

of murres and average acoustic abundance score expected from a random distribution using Monte Carlo procedures (O'Driscoll 1998). I generated 999 realizations of the data, where each murre or acoustic abundance score was randomly reallocated to a bin along the transect. I calculated the percent of the 999 E[N(t)] that was greater than, equal to or less than the E[N(t)] of the observed data. If the E[N(t)] of the observed data was greater than 95 % of the 999 E[N(t)], then birds were determined to be significantly clustered. This was repeated at all spatial scales (t).

The average E[N(t)] if random was calculated from the 999 realizations at each spatial scale. I subtracted the observed average E[N(t)] from the expected E[N(t)] if randomly distributed to determine the average number of "extra" neighbours (L(t)) at each spatial scale. I conducted a similar calculation for acoustic abundance scores but instead of the number of neighbours, I averaged the acoustic abundance score of neighbouring spatial blocks with a nonzero acoustic abundance score. The scale of aggregation of murres and acoustic prey was defined by the spatial scale at which the average number of "extra" neighbours (or neighbouring acoustic abundance scores) was higher than the succeeding three values to avoid identifying small jumps in groups as peaks (O'Driscoll et al. 2000). The first peak was used because it provides a description of the characteristic scale of clustering of birds or prey independent of the variation in abundance within the survey area (O'Driscoll 1998). The number of individuals per aggregation (crowding) was determined by the average number of "extra" neighbours (L(t)) at the scale of aggregation. Therefore, the units of crowding are given as the number of murres and the squared acoustic abundance score. The distance between aggregations of murres and aggregations of acoustic prey is a function of the distance between high counts in the distribution (O'Driscoll 1998). Therefore, the distance between aggregations of murres and aggregations of acoustic prey were defined by the spatial scale at which the average number of "extra" neighbours reached its maximum for a given transect.

Bivariate K analysis was used to assess whether there were significantly more murres associated with a given aggregation of prey than would be expected if murres were distributed randomly (O'Driscoll 1998). For each transect, the observed and expected random distribution of murre neighbours at each spatial scale to each prey aggregation in 250 m block increments was calculated, using 999 Monte Carlo simulations as above. The average number of "extra" murres at each prey aggregation (L(t)) at each spatial scale (t) was again calculated by subtracting expected neighbours if random from the observed average number of neighbours. The scale of maximum association between murres and prey ("tracking scale") was defined by the scale at which the average number of "extra" murres was first higher than the succeeding three values. The number of "extra" murres associated with any given prey aggregation (crowding) was determined by the average number of "extra" murres at the scale of maximum association.

3.2.8. Patch Selection Model

I examine habitat selection of murres flying out from Funk Island on a foraging trip to aggregations of prey that had similar mean abundances but where the abundance and presence of prey was stable in one area (Area 1) and the abundance and presence of prey was variable in another area (Area 2). I do not include Area 3 in my considerations because murres do not appear to fly farther than 60 - 70 km from Funk Island (chapter 5) and, thus, murres foraging in Area 3 were likely breeding at South Cabot Island (Fig 3.1). I itemized parameters involved in flying and diving activities by combining knowledge gained from the literature and from characteristics of the foraging habitats found in this study to develop a patch selection model of foraging murres (Appendix 1). In this model the maximization criterion is the net energy of adults and chicks per foraging trip and per day, the constraint is competitor density and the decision variable is which area to select for foraging. I compare the relative energetic gain from various patch selection decisions on a hypothetical foraging trip and over a number of foraging trips in one area during a hypothetical 16 h day using a steady state model.

Due to the high variability in murre abundances in my study area (chapter 2), my main goal was to examine the effects of competitor density on patch selection decisions in each area. I predict that increased competitor density will influence prey capture rates while foraging. I made some assumptions regarding the relationship between competitor density and capture success (intake rate) per dive for murres because very little is known about intake rates of waterbirds in the field and because they generally swallow prey underwater (Swennen and Duiven 1991, but see Gotmark et al. 1986). The majority of work has focused on shorebirds feeding on benthic prey (e.g. Stillman et al. 1996) or song birds (e.g. Cresswell 1997, 1998). Observations of foraging murres reported in the literature suggest that murres take no more than one fish per dive (Sanford and Harris 1967, Swennen and Duiven 1991). I set the spatial scale of murre-murre interaction while diving to be 300 m^2 because murres were observed to move horizontally at this scale during underwater pursuit of prey. Next, I determined the frequency distribution of 300 m^2 blocks that contained various densities of murres throughout my survey. The strength of interference (m) among individuals is usually quantified as the slope of the line in a log-log plot of competitor density versus intake rate (Begon et al. 1996). Without this information, I instead determined the slope of the line from the log competitor density versus log frequency plot. I calculated the intake rate of an individual murre in an area using the following equation from Stillman et al. (1996):

$$I = IFIR\,[(D + 1) / (Do + 1)]^{-m}$$

where IFIR is the intake rate without interference, which I assumed was 1 fish per dive; Do was the threshold density of murres per 300 m^2, and D was the density of murres per 300 m^2, which I varied to obtain intake rates (I) at different competitor densities in both areas. I then calculated the net energy of a murre as the amount of energy consumed in an area minus the amount of energy spent flying to and diving in an area.

Energy expended flying was calculated by combining the time spent flying to an area, based on an average flight speed of 60 km/h, and the energy expended during flight, expressed as multiples of the basal metabolic rate (10 x BMR or 10 x 163 kJ/h; Appendix 1). I assumed that an additional 30 min was spent flying in Area 2 because murres must presumably search to locate ephemeral schools of capelin in this area.

The energy consumed in an area was calculated in a number of steps. First, the amount of energy obtained per fish in each area was calculated by multiplying the mean mass of fish collected in trawl samples from that area by the energy densities reported in the literature for the type of fish found in that area (Appendix 1). I assumed that murres always fill their stomachs to maximum capacity (200 g) during a foraging trip. Second, I calculated the number of fish required to fill the stomach by dividing the mass of a full stomach by the mean mass of fish collected in trawl samples from each area. Finally, I multiplied the energy consumed per fish by the number of fish required to fill the stomach.

The energy expended diving in an area also was calculated in a number of steps. First, the time spent diving was calculated by multiplying the number of fish required to fill the stomach by the time spent underwater, which incorporated both the time spent traveling to prey schools and capturing prey. I assumed that the time spent capturing prey underwater was fixed at 20 s for both areas (maximum dive duration reported: 224 s; Croll et al. 1992). The energy spent diving was calculated by multiplying the total time spent underwater in each area by the energy expended while diving, expressed as multiples of BMR (10 x BMR or 10 x 163 kJ/h, Appendix 1). Finally, this was divided by the intake rate in an area, which varied over a range of competitor densities.

Such steady state decisions of adults throughout a day may be unrealistic because parents likely make different decisions on each foraging trip based on their current energetic states and those of their chicks (Caraco 1981, Weimerskirch 1998). With this in mind, I examined patch selection decisions over a day through a dynamic programming model (Mangel and Clark 1988). I used a discrete time model where the objective was to relate the energy reserves at the start of a foraging trip "t" to that at start of the next foraging trip "t+1" up to the end of the day "T". Each murre was assumed to conduct two foraging trips per day. The energy state of a murre was assessed at the start of each of the two foraging trips and the energy state of a murre "x" was assumed to change between t and t+1. I calculated a lifetime fitness function, F(x,t,T), or the probability that a murre survives until the end of the day. I assumed a bird was dead if $F(x,t,T)=0$ and alive if $F(x,t,T)>0$. F(x,t,T) was calculated using the following equation from Mangel and Clark (1988)

$$F(x,t,T) = F(xi',t,T) \qquad \text{where } xi' = (x - \alpha_i + Y_i)$$

I assumed that patch parameters were constant over time but that these parameters varied among patches. The increment of energy gain (Y_i) was held constant in both areas (Area 1: 920 kJ, Area 2: 780 kJ) because I assumed that birds would always fill their stomachs on a foraging trip (Appendix 1). The value of x, or the energy reserves of a murre at the start of each foraging trip (t) was varied from 0 to 600 kJ. The energetic costs of choosing an area (α_i), or the combined costs of flying and diving activities in each area (Appendix 1), was held constant in Area 2 (1 competitor/300m^2: 480 kJ) but varied in Area 1 according to the costs of flying and diving with increased interference from conspecifics (1 competitor/300m^2: 340 kJ; 5 competitors/300m^2: 550 kJ; 10 competitors/300m^2: 820 kJ; 15 competitors/300m^2: 1100 kJ; Appendix 1).

3.3 RESULTS

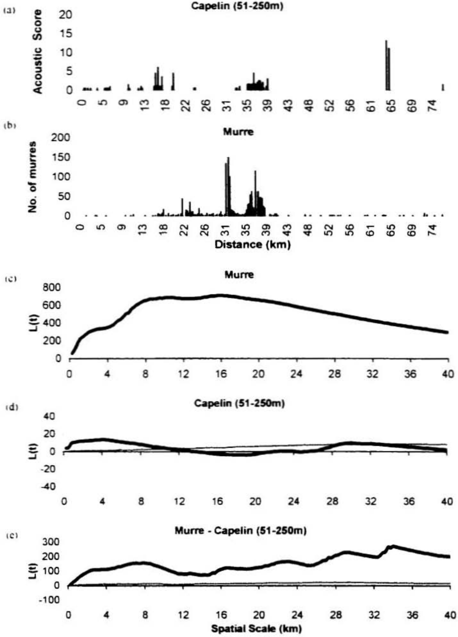
3.3.1. Foraging Habitat Characteristics

Acoustic prey were significantly clustered ($L(t) > 0$) at most spatial scales, except at larger spatial scales (10 – 40 km) where their distribution generally became uniform ($L(t) < 0$). Crowding of acoustic prey was low at small spatial scales and increased up to the scale of aggregation, after which it declined. Exceptions were observed in Area 1, where acoustic prey were uniformly distributed at intermediate spatial scales, and on July 20 in Area 2, where prey were significantly clustered at all spatial scales (Fig. 3.2). The scale of aggregation of acoustic prey varied from 1 – 9 km (Table 3.1). The scale of aggregation of acoustic prey was generally smaller in Area 2 and there were larger distances between aggregations, compared to Area 1 and 3 (Table 3.1).

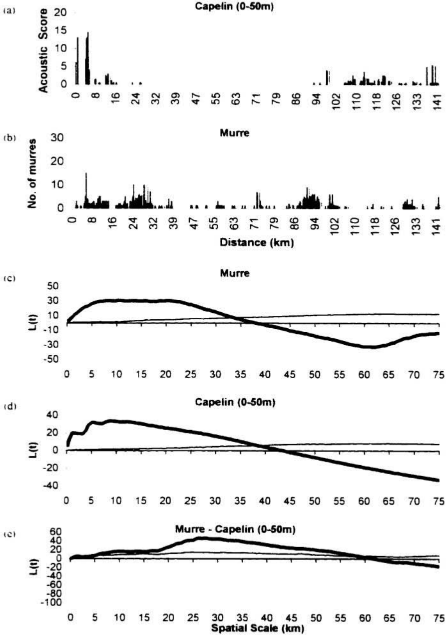
I conducted 17 fishing sets and fish were collected in 11 sets at 8 different sites (Fig. 3.1). Acoustic signals were similar throughout the study area and all catches were primarily composed of capelin (96 % by mass). Therefore, I conclude that the majority of prey schools observed acoustically were capelin. Approximately 76,000 capelin (1833 kg) were collected during the survey, of which 1809 were subsampled (female: n=1475, male: n=334). Other species were observed incidentally in catches: shrimp *Pandalus* species (n=466), American plaice *Hippoglossoides platessoides* (n=66), daubed shanny *Lumpenus maculatus* (n=50), Atlantic hookear sculpin *Artediellus atlanticus* (n=12), Vahl's eelpout *Lycodes vahlii* (n=9), alligatorfish *Aspidophoroides monopterygius* (n=7), mailed sculpin *Triglops murrayi* (n=7), longhorn sculpin *Myoxcephalus*

Figure 3.2. The distribution of capelin (a) and murres (b) along transects and the univariate plots of the number of 'extra' neighbours against the spatial scale of analysis for murres (c) and capelin at specific depths (d) along with the bivariate plots of the number of 'extra' murre neighbours to capelin schools against the spatial scale of analysis (e) in the three main foraging areas of common murres. Area 1 (July 21), Area 2 (July 19, 20) and Area 3 (July 18). In univariate (c, d) and bivariate (e) plots the bold line represents the number of 'extra' neighbours and the thin line represents the upper 95 % confidence limit.

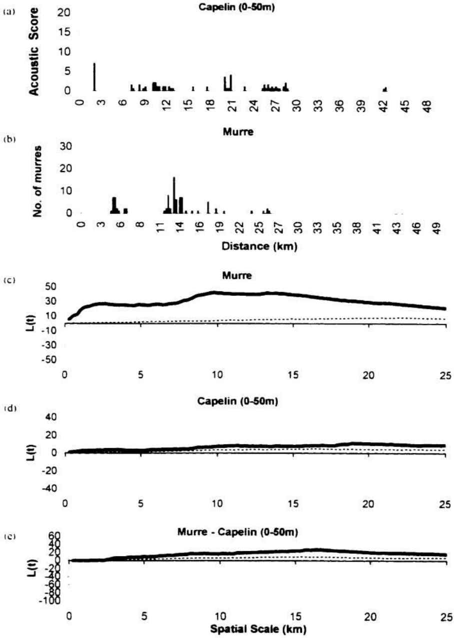
Area 1


(a)
Capelin (51-250m)
Acoustic Score
20
15
10
5
0
0 5 9 13 18 22 26 31 35 39 43 48 52 56 61 65 69 74
(b)
Murre
No. of murres
200
150
100
50
0
0 5 9 13 18 22 26 31 35 39 43 48 52 56 61 65 69 74
Distance (km)
(c)
Murre
L(t)
800
600
400
200
0
0 4 8 12 16 20 24 28 32 36 40
(d)
Capelin (51-250m)
L(t)
40
20
0
-20
-40
0 4 8 12 16 20 24 28 32 36 40
(e)
Murre - Capelin (51-250m)
L(t)
300
200
100
0
-100
0 4 8 12 16 20 24 28 32 36 40
Spatial Scale (km)

Area 2 (July 19)



Area 2 (July 20)



Area 3

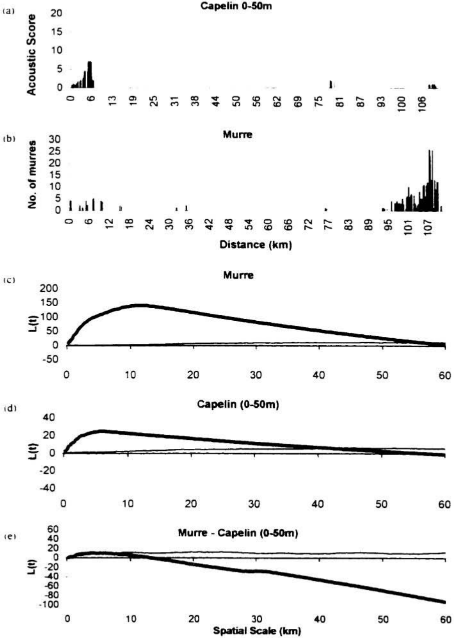

(a)
Capelin 0-50m
Acoustic Score
20
15
10
5
0
0
6
13
19
25
31
38
44
50
56
62
69
75
81
87
93
100
106
(b)
Murre
No. of murres
30
25
20
15
10
5
0
0
6
12
18
24
30
36
42
48
54
60
66
72
77
83
89
95
101
107
Distance (km)
(c)
Murre
L(t)
200
150
100
50
0
-50
0
10
20
30
40
50
60
(d)
Capelin (0-50m)
L(t)
40
20
0
-20
-40
0
10
20
30
40
50
60
(e)
Murre - Capelin (0-50m)
L(t)
60
40
20
0
-20
-40
-60
-80
-100
0
10
20
30
40
50
60
Spatial Scale (km)

Table 3.1 The spatial scale of aggregation of murres and capelin (univariate), the extent of crowding (see text for explanation) within these aggregations (univariate), the distances between major aggregations and crowding within these aggregations shown in parentheses (univariate) and the scale of maximum association between murres and capelin (bivariate) on July 18 (Area 3), July 19 and 20 (Area 2) and July 21 (Area 1)

	Area 1		**Area 2**		**Area 3**	
Category	Aggregation Scale (km)	Crowding	Aggregation Scale (km)	Crowding	Aggregation Scale (km)	Crowding
Univariate						
Murre	9.5 (15.7)	682.4 (712.0)	6.2[1] (10.3) 2.7[2] (9.7)	29.0 (30.8) 27.1 (42.2)	10.8 (11.9)	141.2 (141.6)
Capelin 0-250 m	3.5 (4.1)	12.5 (12.7)	1.4 (8.9) 3.0 (18.9)	4.4 (33.6) 3.6 (11.3)	5.4 (7.3)	123.6 (125.2)
Capelin 0-50 m	4.9 (32.1)	3.2 (5.9)	1.1 (5.1) 2.2 (18.9)	10.5 (16.8) 2.9 (8.4)	3.0 (3.0)	109.8 (109.8)
Capelin 51-250 m	4.1 (4.1)	13.6 (13.6)	8.7 (44.8) 2.4 (2.4)	34.2 (54.4) 0.9 (0.9)	6.0 (6.0)	25.0 (25.0)
Bivariate						
Murre & Capelin 0-250 m	8.1	215.3	1.4 5.1	5.5 8.9	NS[1]	
Murre & Capelin 0-50 m	8.1	491.7	0.8 5.1	0.7 9.7	2.4	9.3
Murre & Capelin 51-250 m	3.0	110.9	60.2 45.9	20.3 4.8	NS	

It took two days to survey Area 2 [1] July 19, [2] July 20

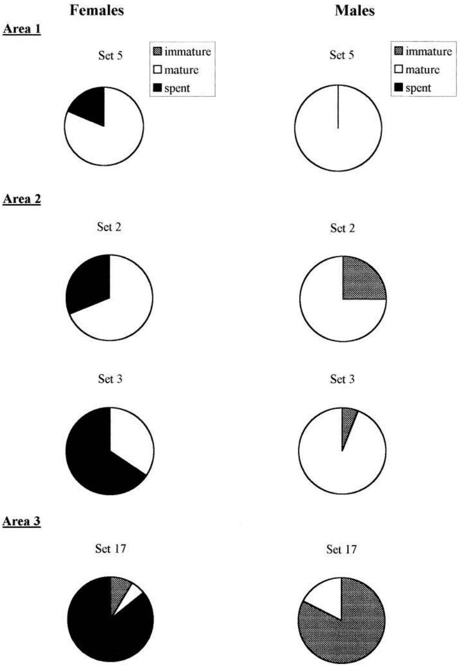
[1] NS represents non-significant clustering of murres with capelin patches or murres randomly distributed in relation to capelin

octodecemspinosus (n=6), Atlantic cod *Gadus morhua* (n=3), Greenland cod *Gadus ogac* (n=1), American sand lance *Ammodytes americanus* (n=1) and Greenland seasnail *Liparis tunicatus* (n=1).

The maturity stages of capelin differed among areas. Area 1 contained an approximately equal ratio of males and females and 98 % of these fish were maturing (maturity index=2, Fig. 3.3). The highest densities of capelin were caught in this area with the bottom trawl and capelin were larger on average, although in one fishing set (# 9) I caught mainly female capelin, 78 % of which were spent (Table 3.2). Area 2 was characterized by spent female capelin (maturity index=5), although in one fishing set (# 2) I caught a high proportion of mature females (Fig. 3.3). Area 3 was characterized by a high proportion of spent female capelin and immature male and female capelin (Fig. 3.3). Overall, in Areas 2 and 3, where there were predominantly spent females, there were few males, however, in Area 1, where the majority of capelin were mature, approximately 50% of the catch was males (Fig. 3.3). Very few spent male capelin were subsampled in catches (0.3 %, n=6) compared to spent female capelin (56.5 %, n=1022). A higher percent of mature capelin had stomachs that were less than 50 % full (79 %) compared to immature (38 %) or spent fish (52 %, χ^2 test: $\chi^2_4=47.85$, $P<0.001$; Fig. 3.4).

A total of 204 schools were observed on echograms throughout the survey. The four school characteristics were independent ($r<0.5$) for the most part. The maximum depth of the school and the distance from the surface of the ocean increased ($r=0.987$) because

Figure 3.3. The proportion of immature, mature and spent female and male capelin collected during trawling in the three main foraging areas of common murres. Area 1 (July 21), Area 2 (July 19, 20) and Area 3 (July 28).



Females
Males
Area 1
Set 5
▨ immature
☐ mature
■ spent
Set 5
▨ immature
☐ mature
■ spent
Area 2
Set 2
Set 2
Set 3
Set 3
Area 3
Set 17
Set 17

Table 3.2 The mean ± SE lengths and masses of capelin caught in the trawl along with the location of the trawl, maximum tow depth and density of capelin caught in the trawl from July 18 – 28, 2000. Sample size (n) is given in parentheses.

			Female		Male				
Date	Area / Set No	Percent Females	Length (mm)	Mass (g)	Length (mm)	Mass (g)	Trawl Location	Tow Depth (m)	Capelin Density (kg/km)
	Area 1								
July 21	5	49	163.4 ± 1.1 (97)	21.2 ± 1.5 (20)	175.2 ± 0.7 (103)	30.7 ± 1.3 (16)	Bottom	125	625.0
July 22	6	64	158.6 ± 1.1 (128)	20.7 ± 1.4 (21)	172.9 ± 0.9 (72)	28.4 ± 1.9 (14)	Bottom	125	313.4
July 23	8	58	161.4 ± 1.0 (116)	20.0 ± 1.2 (20)	172.3 ± 1.1 (84)	29.0 ± 1.6 (18)	Bottom	125	943.1
July 24	9	92	159.7 ± 0.8 (183)	15.1 ± 0.8 (22)	162.4 ± 2.6 (17)	23.5 ± 2.4 (11)	Bottom	150	43.5
	Area 2								
July 19	2	94	150.8 ± 1.4 (64)	18.1 ± 1.2 (19)	167.0 ± 3.2 (4)	26.1 ± 3.5 (4)	Midwater	90	1.4
July 20	3	92	158.3 ± 0.9 (183)	14.6 ± 0.9 (22)	138.0 ± 2.5 (17)	25.9 ± 1.5 (13)	Midwater	70	3.8
July 25	10	95	144.7 ± 1.2 (78)	14.3 ± 1.2 (21)	163.3 ± 3.8 (4)	26.0 ± 1.4 (4)	Bottom	40	2.6
July 25	12	100	149.5 ± 2.0 (37)	13.3 ± 0.9 (19)	- (0)	-	Midwater	70	0.25
July 25	14	97	157.0 ± 0.9 (193)	14.7 ± 0.9 (24)	164.6 ± 4.0 (7)	240.0 ± 2.4 (7)	Bottom	115	316.7
	Area 3								
July 18	1	99	166.1 ± 0.6 (201)	16.3 ± 0.9 (19)	169.7 ± 7.3 (3)	20.5 ± 3.1 (3)	Bottom	170	535.5
July 28	17	89	143.7 ± 1.4 (177)	9.9 ± 1.0 (35)	152.4 ± 2.9 (23)	16.2 ± 1.6 (17)	Bottom	170	20.0

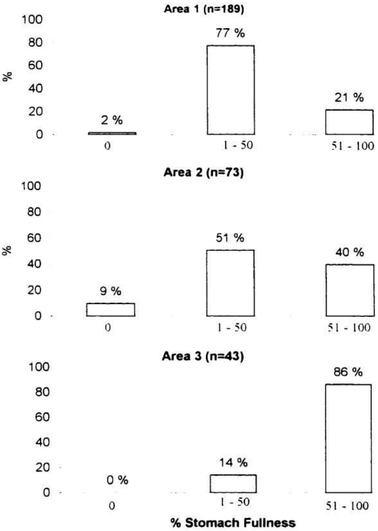


Figure 3 4. The percent of capelin with empty (0 %), less than 50 % and greater than 50 % of their stomach full of food in the three main foraging areas of common murres: Area 1 (maturing males and females), Area 2 (spent females) and Area 3 (spent females).

most schools were found near the ocean floor Two school types were obvious from echograms those that were on the substrate and those that were in the water column. I defined these school types based on the following characteristics (Table 3.3): deep schools (> 50 m) on the substrate (type A) and shallow schools (< 50 m) in the water column (type B) The height of the schools were similar among school types (Table 3.3). It is important to note that type A schools were always spatially stable on the temporal scale of two weeks. I could return to the same position to trawl on different days and consistently catch high amounts of capelin (Table 3.2). In contrast, type B schools were never encountered in the exact same position, although they were generally found in a similar area (2.25 km, chapter 2) but had variable catch densities (Table 3.2).

The three location characteristics of capelin schools were not independent of one another. Bottom depth increased with distance from shore (r=0.647) and, as a consequence, varied inversely with distance from Funk Island (r=-0.656). Type B schools that were found in the water column were primarily found closer to shore, or farther from Funk Island, in water less than 50 m deep, while type A schools that were on the substrate were closer to Funk Island in water greater than 50 m deep (Table 3.3) Both school types were found in each of the three foraging areas, however, type B schools composed the majority of schools found in Area 2 (73 %) and half in Area 3 (52 %), whereas the majority of schools found in Area 1 were type A (76 %).

Table 3.3 The mean ± SE capelin school characteristics and the characteristics of their physical surroundings. The degrees of freedom for these t-tests are 202.

	On Substrate	In Water Column	t	P
<u>School Characteristics</u>				
Vertical Extent (m)	9.1 ± 0.8	10.7 ± 0.9	1.227	0.221
Distance from Seabed (m)	0 ± 0	7.0 ± 1.0	1.972	<0.0001
Distance from Surface (m)	92.3 ± 4.8	45.4 ± 4.5	6.799	<0.0001
Maximum Depth of School (m)	101.4 ± 4.8	56.0 ± 4.7	6.449	<0.0001
<u>Physical Characteristics</u>				
Bottom Depth (m)	97.2 ± 4.7	59.3 ± 4.9	5.370	<0.0001
Distance from Shore (km)	26.3 ± 1.8	16.0 ± 1.3	4.055	<0.0001
Distance from Funk Island (km)	99.0 ± 2.5	119.5 ± 1.8	6.029	<0.0001
N	123	81		

Using the historical data, I found that the water layer above the thermocline (0 - 10 m) had an average temperature of 8.5 ± 0.07 °C (n=1811), the thermocline layer (11 - 50 m): 1.6 ± 0.05 °C (n=3077), and the layer below the thermocline (51 - 250 m): -1.3 ± 0.01 °C (n=1960; Fig. 3.5). This was consistent with the temperature and salinity profiles conducted throughout the study area (Fig. 3.1) and remained consistent in Areas 1, 2, 3 over a two-week period. The majority of type B schools (62 %) were found within and above the thermocline or in above zero temperature water (< 50 m), while the majority of type A schools (76 %) on the substrate were found mainly below the thermocline or in subzero temperature water (> 50 m). This distribution in the water column was significantly different (χ^2 test: χ_4^2=41.55, P<0.001).

3.3.2. Bird Characteristics

I counted a total of 14,652 birds and 119 marine mammals in 800 km of transect, giving a sighting frequency of 17 birds per km and 0.1 mammals per km. The majority of the birds sighted were murres (85 %, n=12387), followed by Atlantic puffins *Fratercula arctica* (5 %, n=760), northern gannets *Morus bassanus* (5 %, n=690), leach's storm-petrels *Oceanodroma leucorhoa* (2 %, n=246), herring gulls *Larus argentatus* (1 %, n=166) and sooty shearwaters *Puffinus griseus* (1 %, n=127). The other 1 % consisted of incidental sightings of greater shearwaters *Puffinus gravis*, great black-backed gulls *Larus marinus*, black-legged kittiwakes *Rissa tridactyla* and northern fulmars *Fulmarus glacialis*. The majority of mammals sighted were harp seals *Phoca groenlandica* (58 %, n=69),

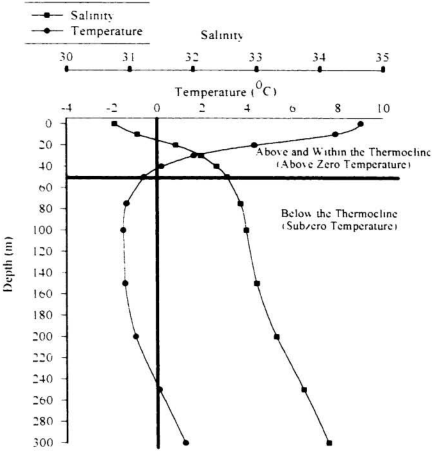


Figure 3.5 The temperature and salinity in the study area from historic data in July during the 1990s with the areas above and below the thermocline indicated

followed by humpback whales *Megaptera novaeangliae* (18 %, n=22), minke whales *Balaenoptera acutorostrata* (13 %, n= 16), and fin whales *Balaenoptera physalus* (11 %, n=10).

Murres were significantly clustered ($L(t) > 0$) at all spatial scales, except at spatial scales higher than 35 km in Area 2 on July 19 at which point murres became uniformly distributed ($L(t) \sim 0$; Fig. 3.2). The average number of murres (crowding) was low at small spatial scales, increased up to the scale of aggregation and then declined (Fig. 3.2). A characteristic scale of aggregation for murres was found at approximately 10 km, with the exception of Area 2, where the scales of aggregation were much lower (Table 3.1).

I collected 15 dead murres at sea on July 28 in Area 2. The cause of death of all individuals was drowning. Of these individuals, 8 were males (7 breeders) and 7 were females (6 breeders). All intact fish (n=75), otoliths (n=85) and other hard parts (vertebrae, n=2) were identified as capelin by an experienced fisheries biologist (P. Eustace pers. com.). Of the intact capelin, 53 % were gravid females, 3 % were spent females, 7 % were males of unknown maturity and 37 % were unidentifiable to sex. Fifteen of these fish were fresh enough to measure total length (male capelin: 147 mm, n=1, gravid capelin: 128 ± 3 mm, n=14). Stomachs that contained fish (4 empty stomachs) had an average of 6.2 ± 0.8 intact fish (n=11, range: 3 – 11 fish). I was able to determine total weight of only eight of the nonempty stomachs due to the deteriorated state of three carcasses. Stomachs contained an average of 86.4 ± 27.8 g (n=8, range: 2.4 - 200.4 g) of fish and undigested material.

3.3.3. Murre-Capelin Interaction

Murres always had higher scales of aggregation than the types of capelin aggregations (type A, B) they were tracking (Table 3.1). The scale of aggregation of murres increased with increasing aggregation scales of capelin that murres were tracking. Crowding of murres within aggregations was highest in Area 1, intermediate in Area 3 and low in Area 2. Crowding of fish within capelin aggregations that murres were tracking was highest in Area 3 and intermediate in Areas 1 and 2. The crowding of murres at capelin aggregations was highest in Area 1, intermediate in Area 2 and Area 3.

In all areas, murres were significantly clustered with capelin at most spatial scales (Fig. 3.2). In Areas 2 and 3, the maximum scale of association between murres and capelin at 51 - 250 m and 0 - 250 m were only significant at large spatial scales (Table 3.1). Alternately, the maximum scale of association between murres and capelin at 0 - 50 m in these areas were significant at much smaller scales (Table 3.1). Therefore, in Areas 2 and 3 murres appeared to track capelin in 0 - 50 m but were uninterested or unaware of prey below 50 m. In Area 1, the maximum scale of association between murres and capelin schools in 0 - 50 m or 0 - 250 m was at large scales; however, the maximum scale of association between murres and capelin schools in 51 - 250 m was at smaller scales (Table 3.1). This suggests that murres in Area 1 preferentially tracked capelin schools below 50 m (Table 3.1). In general, murres preferentially tracking capelin in 0 – 50 m, which were mainly type B schools (Areas 2 and 3), showed a smaller scale of association with capelin in comparison to murres tracking capelin in 50 – 250 m, which were mainly type A schools. In addition, there appeared to be a tendency for patches with low acoustic abundance scores to be used by murres if they were close to patches with high scores, while isolated patches with high scores were often ignored (Fig. 3.2).

3.3.4. Patch Selection Model

Based on the capelin characteristics summarized for Area 1 and 2 (Table 3.4), I defined Area 2 as a low quality foraging habitat and Area 1 as a high quality habitat. Area 2 has unstable presence of capelin with variable abundance, primarily ephemeral schools, low-energy capelin (spent females) and is more distance from the breeding colony, while Area 1 has stable presence of capelin with low variability in abundance, primarily stable schools, high-energy capelin (maturing males and females) and is closer to the breeding colony. The consistently high variability in murre abundance in both areas suggested that intraspecific competition may be important in the selection of foraging habitats by murres. Therefore, I developed a patch selection model based on the premise that intraspecific competition would reduce prey capture rates of murres on a fine-scale (300 m) within a foraging area. My specific question was why would a murre every fly past Area 1, the high quality habitat, to forage in Area 2, the lower quality habitat.

Table 3.4 A comparison of the foraging habitat characteristics in Areas 1, 2 and 3 distance from Funk Island and from shore and the composition of capelin and capelin school types Information taken from chapter 2 including the stability of capelin and murre presence per 2.25 km "hot spot" (2.25 km areas with above average abundance scores of capelin) and the range of mean ± SE abundance scores of capelin and the range of mean ± SE abundance of murres per 2.25 km hot spot in foraging Areas 1, 2 and 3

Characteristics	Area 1	Area 2	Area 3
Distance from Funk (km)	45	60	90
Distance from Shore (km)	30	10	15
Capelin Composition	Maturing males & females	Spent females	Spent females & immatures
School Type Composition[1]	A (Stable)	B (Ephemeral)	A & B (Stable & Ephemeral)
Stability of Capelin Presence / 2.25 km [2]	100 %	25 100 %	100 %
Stability of Murre Presence / 2.25 km [2]	100 %	50 100 %	100 %
Capelin Abundance Score / 2.25 km [2] (Scale from 0 9)	1.1 ± 0.3 1.2 ± 0.2	0.3 ± 0.2 - 1.0 ± 0.9	5.9 ± 2.6
Abundance of Murres / 2.25 km [2]	3.0 ± 2.4 17.6 ± 13.0	0.3 ± 0.3 3.0 ± 2.9	1.0 ± 0.8
No of 2.25 km hot spots	2	11	1

[1] A associated with substrate & stable, B in the water column & ephemeral

[2] Information obtained from Table 2a in chapter 2 Average abundance for all 2.25 km foraging areas during the broad-scale survey of murres was 2.9 ± 0.5 birds and of capelin was 0.8 ± 0.1 (acoustic abundance score)

The majority of the 300 m^2 blocks throughout the survey contained 1 murre (62 %, Fig. 3.6a) and, thus, I assumed that murres would forage without interference at a density of 1 individual per 300 m^2 (Do = 1). This seems reasonable due to the tendency for there to be a low average number of murres (crowding) per 300 m^2 (Area 1: 29, Area 2: 3 - 6, Area 3: 9 extra neighbours, Fig. 3.2) and a tendency towards a more uniform distribution at small spatial scales in all areas (Fig. 3.2). In addition, coordinated feeding flocks, as described by Hoffman et al. (1981), were never observed in the survey area but rather murres tended to aggregate loosely in foraging habitats. Type A capelin schools were spatially and temporally stable and, thus, benefits of cooperative foraging (e.g. herding of prey, Angell and Balcomb 1982) were presumably relatively low in the study area compared to other areas where prey are highly mobile and can escape between successive dives (e.g. Hoffman et al. 1981, Ydenberg and Forbes 1988, Ydenberg & Clark 1989).

When competitor density was held constant at 1 murre per 300 m^2 in both areas on a foraging trip, a number of differences among the areas became apparent (see Appendix 1). Dive efficiency in Area 2 was double that in Area 1, owing to the shallower depths at which capelin schools were found in Area 2. The number of fish required to fill the stomach of a murre in Area 2, however, was nearly double that of Area 1, due to the lower mean mass of spent versus maturing capelin. Therefore, the time and energy spent foraging were similar in both areas (Appendix 1), resulting in higher net energy gains in Area 1 relative to Area 2 due to the divergent flying durations to either area. In the dynamic model, when competitor densities were equal at 1 murre per 300 m^2 (Scenario

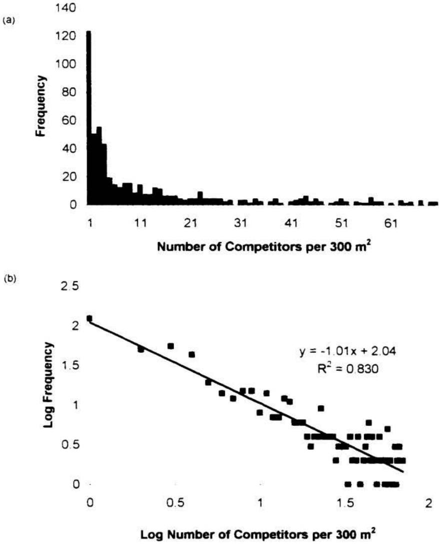


Figure 3.6 The frequency of 300 m by 300 m blocks along the entire survey route that contained increasing numbers of common murres (a) and the corresponding log-log plot (b).

A), a murre with low initial energetic reserves should choose Area 1 during its first foraging trip of the day; however, selection among the two foraging areas did not appear to be important at higher energetic states and on the second foraging trip (Table 3.5). This is in contrast to the steady state model, which would predict that at similar competitor densities in both areas, a murre should always choose Area 1.

I calculated the net energy gained or lost by adults at varying competitor density per 300 m^2 in Area 1 while holding competitor density in Area 2 constant at different levels using the steady state model (Fig. 3.7). The net energy gained by an adult per foraging trip and per day was higher in Area 1 than in Area 2 at initial densities in Area 1 (< 5 individuals per 300 m^2), but thereafter it became better to forage in Area 2 because the higher dive costs in Area 1 outweighed the higher flying costs in Area 2 (Fig. 3.7a, b). At moderate densities in both areas (> 12 individuals per 300 m^2), the net energy gained by an adult per foraging trip and per day became negative in both areas (Fig. 3.7a, b). In contrast, the net energy of the chick never became negative because the chick at the colony did not have to expend energy collecting prey (Fig. 3.7c). The chick did better during a day if the parent foraged in Area 1 at initial densities (< 3 individuals per 300 m^2), but generally did worse at higher densities in both areas (~ 15 individuals per 300 m^2) if the parent stayed in Area 1 due to lower provisioning rates over the day (Fig. 3.7c).

Using the dynamic model, I varied competitor densities in Area 1 while keeping competitor densities in Area 2 constant at 1 individual per 300 m^2. As competitor

Table 3.5 Lifetime fitness functions, F(x,t,T), of an individual murre and its patch selection decisions (Area 1 or 2) on its first and second foraging trip during a 16 h day. Initial energy reserves (x) were varied when leaving Funk Island on a foraging trip, and competitor densities were fixed at 1 murre per 300 m^2 in Area 2 (D_2) but varied in Area 1 (D_1).

Competitor Density Scenario	Trip Decision	Energy Reserves (kJ)						
		0	100	200	300	400	500	600
Area 2	First	0.98	0.98	0.98	0.99	0.99	1.00	1.00
	Second	0.99	0.99	0.99	0.99	0.99	0.99	1.00
Scenario A	First	0.99	0.99	0.99	0.99	1.00	1.00	1.00
(D_1=D_2=1)	Decision	1	1	1	1 or 2	1	1 or 2	1 or 2
	Second	0.99	0.99	0.99	0.99	1.00	1.00	1.00
	Decision	1 or 2	1 or 2	1 or 2	1 or 2	1	1	1 or 2
Scenario B	First	0.99	0.99	0.99	0.99	1.00	1.00	1.00
(D_1=5, D_2=1)	Decision	2	2	2	1 or 2	2	1 or 2	1 or 2
	Second	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	Decision	1 or 2	1 or 2	1 or 2	1 or 2	1 or 2	1 or 2	2
Scenario C	First	0.98	0.98	0.98	0.98	0.98	0.98	0.98
(D_1=10, D_2=1)	Decision	2	2	2	2	2	2	2
	Second	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	Decision	1 or 2	1 or 2	1 or 2	1 or 2	1 or 2	1 or 2	2
Scenario D	First	0.00	0.00	0.00	0.00	0.00	0.98	0.98
(D_1=15, D_2=1)	Decision	2	2	2	2	2	2	2
	Second	0.00	0.00	0.00	0.99	0.99	0.99	0.99
	Decision	2	2	2	1 or 2	1 or 2	1 or 2	2

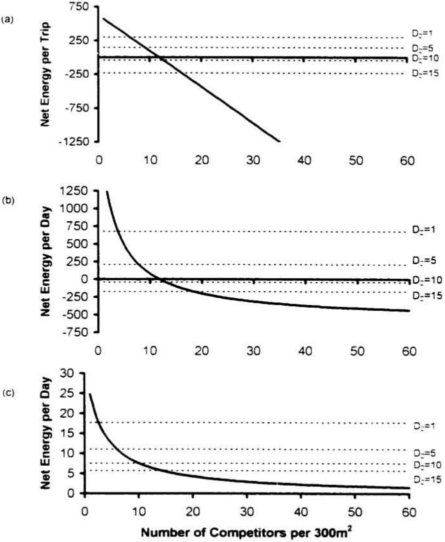


Figure 3 7 The output from the steady state foraging model, with competitor densities in Area 2 held at 1, 5, 10 and 15 competitors per 300 m^2 while densities in Area 1 were varied, showing the net energy gained by the adult per foraging trip (a), by the adult per 16 h day (b) and by the chick per 16 h day (c).

densities initially increased in Area 1 (D_1=5 competitors per 300 m^2, Scenario B), Area 2 should be selected when birds had lower energetic reserves (Table 3.5). As competitor densities increased further in Area 1 (D_1=10, Scenario C), it was only profitable to choose Area 2 at lower energetic states on the first trip and eventually the murre would die if it chose Area 1 at most energetic states (D_1=15, Scenario D, Table 3.5). Overall, on the first foraging trip and at lower energy reserves, it was always most important to replenish reserves, after which the decision became equivocal.

3.4 DISCUSSION

3.4.1. Capelin Behaviour

Type B schools were composed primarily of spent females, most of which had stomachs more than 50 % full, were located primarily close to shore, and were ephemeral in space and time. The disproportionate number of spent females to males in these schools was probably due to the higher proportion of female capelin that survive spawning (Shackell et al. 1994). Females release all of their roe in one copulation event, whereas males release their milt over a number of events (Fidgeirsson 1976). Copulation usually involves contact with the sediment, resulting in higher incidence of injury and mortality for males compared to females (Fidgeirsson 1976). The composition and behaviour of these capelin schools suggest that they were comprised of fish moving away from beaches after spawning, which had begun to actively feed to recover from spawning and prepare for over-wintering. Feeding and movement away from spawning beaches may result in the ephemeral nature of these schools on the fine-scale of meters, shown by trawling The high predictability of finding abundant capelin aggregations close to shore on the coarse-scale of kilometers (chapter 2) may reflect the distribution of key spawning beaches The high variability in abundance within Area 2 may reflect the movement of different schools towards and away from spawning beaches

In contrast, type A schools were stable in space and time and were composed of a nearly equal ratio of maturing male and female fish These fish generally had stomachs that were less than 50 % full, suggesting that these fish were feeding but that this was not a priority Therefore, the stability of these schools may result from fish not actively pursuing prey It is also possible that these aggregations were stable because fish were spawning in this area (Area 1) Saetre and Gjosaeter (1975) described two types of schools of mature capelin at spawning grounds in Norway The first type was composed of regularly oriented fish in low densities with highly variable school sizes and swim speeds These schools appeared to be searching wide areas for suitable spawning beds The second was composed of irregularly oriented fish in high densities in a continuous layer on the seabed that were stationary These schools were thought to represent fish that had found a suitable place to spawn and were in the last stage before spawning The latter school type described by Saetre and Gjosaeter (1975) might be at a similar stage of spawning as the type A schools observed in this study and, thus, Area 1 may be a previously undocumented off-beach spawning area in Newfoundland

Other evidence suggests, however, that type A schools do not represent off-beach spawning aggregations. First, 98 % of the fish in type A schools had a maturity index of 2, which indicates that fish were maturing but not completely ripe and ready to spawn. Second, sexes generally segregate into different schools just prior to spawning (Jangaard 1974, Saetre and Gjosaeter 1975, Vilhjalmsson 1994), whereas type A schools had a nearly equal ratio of males to females. Third, capelin generally have empty stomachs in Newfoundland during spawning (83 %, Vesin et al. 1981) but only 2 % of fish in Area 1 had empty stomachs. Finally, the physical characteristics in which type A schools were found did not appear to be ideal for off-beach spawning of capelin in Newfoundland (Carscadden et al. 1989). For instance, type A schools were found in subzero temperature water, whereas capelin generally prefer to spawn off-beach in temperatures above 2^0C in Newfoundland (Carscadden et al. 1989). Even though different spawning stocks of capelin have widely varying habitat preferences (Carscadden et al. 1989, Vilhjalmsson 1994), Area 1 is more likely an important area for the final stages of gonadal development just prior to spawning.

The rate of gonadal development, however, is reduced in colder temperature water (Vilhjalmsson 1994). Type A schools in Area 1 consistently underwent vertical migrations to above or within the thermocline at dusk and back down to the seabed, or below the thermocline, at dawn (GKD unpubl. data) and, thus, might accelerate development rates or may migrate to feed by entering warm water at night (Neverman and Wurtbaugh 1994). In addition, type A schools were often found in depressions where fish would not have to swim against currents to maintain position and, thus, reduce energy expenditure. Their occupation of deeper, colder water during daylight also could reflect a predator avoidance strategy. All seabird species observed in the study area are incapable of diving to these depths, except murres (maximum: 210 m, Croll et al. 1992; common: 20 - 50 m, Piatt and Nettleship 1985, Burger 1991). Although the numerically dominant predator in Area 1 was common murres, marine mammals may consume a similar or greater amount of capelin due to their much larger body sizes (Schmidt-Nielson 1997). Therefore, occupying depths of 110 m is likely ineffective to avoid predation but may reduce the risk of predation, due to lower accessibility from the ocean surface and low illumination at this depth. Vertical migration upward to more vulnerable depths at night supports this contention, although I do not exclude other reasons for this migratory behaviour (e.g. foraging). In addition, Atlantic cod generally occupy temperatures between – 0.5 to 8.5 °C (Rose and Leggett 1990) and capelin schools in Area 1 were generally found in water colder than this (< -1.0 °C). Although few cod were observed in the study area, this species was the dominant predator of capelin prior to stock collapse in the early 1990s (Walters and Maguire 1996). Therefore, these habitat features may reflect previously important thermal refuges for avoiding predation by cod (Rose and Leggett 1990).

3.4.2. Capelin-Murre Interaction

Murres were significantly clustered with capelin aggregations at a wide range of spatial scales in all areas (0.3 – 61 km), suggesting that prey distribution had a strong influence on bird distribution (Logerwell et al. 1998). The scale of aggregation of murres was higher than those of capelin, as has been found in other seabird studies (e.g. Piatt 1990), and associations between murres and capelin were at similar spatial scales or were smaller than the aggregation scale of capelin. This suggests that murres attempted to maximize encounter rates with their prey, thereby maximizing their net energetic benefit (Horne and Schneider 1994). In contrast, researchers in Newfoundland found that Atlantic cod and capelin had no characteristic scale of association and demonstrated that the energetic costs of tracking capelin at small spatial scales would be higher than the benefits (Horne and Schneider 1994). This reflects the divergent energetic demands of endothermic predators, who have high metabolic rates to maintain their body temperature, relative to ecothermic predators (Lustick 1984, Nagy 1987).

Murres tracked capelin at smaller spatial scales in Area 2 than in Area 1. This might reflect different foraging strategies in areas with stable versus ephemeral capelin schools. Murres foraging in Area 2 at ephemeral capelin schools may need to maintain close contact with schools among dive bouts on a foraging trip to avoid expending energy searching for prey if schools escape between dive bouts. The smaller tracking scales of murres to capelin in Area 2 also may reflect an urgency to exploit ephemeral schools quickly before they relocate away from predators among dives in a dive bout (Ydenberg and Forbes 1988). The presumably shorter dive durations due to the closer proximity of capelin to the ocean's surface would allow shorter recovery periods at the surface between dives (Ydenberg and Clark 1989), allowing murres to maintain close contact with schools of capelin among dives.

In addition, if murres forage based on past experience and do not regularly sample their foraging environment, they would likely have knowledge of stable schools of capelin but not of schools moving through Area 1. Therefore, I would expect tight associations with stable schools in Area 1 but not necessarily all schools in the area, resulting in larger tracking scales of predators to prey. In addition, murres in Area 2 must presumably sample to some extent to locate capelin schools because they could not be predictably located. Sampling, either physically or visually (e.g. cueing to the foraging activities of conspecifics, local enhancement, Wittenberger and Hunt 1985), would allow more current information on the locations and qualities of prey schools, resulting in smaller spatial scales of association between predators and prey relative to using memory.

There was a tendency for murres to aggregate at capelin aggregations with low abundance scores if they were close to high abundance aggregations, while isolated capelin aggregations with high abundance scores were ignored (Fig. 3.2). This suggests that strategies, such as local enhancement and area-restricted search, are important for locating prey at sea (Veit et al. 1993). The use of local enhancement to reduce search costs in Area 2 may have been important due to the smaller aggregation scales of capelin and the larger distances between aggregations compared to the other areas. This observation also illustrates how this behavioural mechanism can lead to deviations from the Ideal Free Distribution.

3.4.3. Murre Foraging Behaviour

I observed unexpected fine-scale behaviour of capelin aggregations, owing to the stability and ephemerality of two types of capelin schools, during my two-week survey. Murres revisit prey aggregations much more often (daily) than I could during my survey (3 - 4 visits over 2 weeks, chapter 2) and, therefore, I suggest that they have knowledge of the capelin characteristics within foraging habitats that I identified. For instance, murres could remember that type A schools of high energy density capelin (Montevecchi and Piatt 1984) were available at 110 m at specific sites in consistently above average abundance closer to the colony (Area 1, chapter 2). Murres could also remember that type B schools of lower energy density capelin (Montevecchi and Piatt 1984) were available closer to the surface but farther from the colony and the exact locations and abundances of these schools were highly variable (chapter 2).

During the initial survey, the number of murres in the higher quality foraging habitat (Area 1) was an order of magnitude higher than that found in the lower quality habitat (Area 2). Therefore, murres appeared to distribute themselves, at least qualitatively, according to the Ideal Free Distribution. Abundances of murres over a two-week period following the initial survey, however, were highly variable in both foraging areas (Table 3.4; chapter 2). This suggests that murres may deviate from the Ideal Free Distribution.

due to either a lack of knowledge of all the characteristics within these foraging habitats or due to varying criteria used to select among these areas over larger temporal scales. I suggest that murres would have incomplete information on competitor densities within each area due to the high variability in murre abundance. Interference during prey capture on a small scale (300 m^2), or other factors causing lower energy intake rates and increased dive costs (e.g. lower quality prey), may cause murres to occupy foraging habitats with seemingly less suitable prey conditions in my study area. This implies that the Ideal Free Distribution works at small temporal and spatial scales but may become unrealistic at larger scales due to the complex integration of many prey and competitor characteristics of habitats that change in importance under varying conditions (e.g. energetic states).

It is also possible that murres do not make sequential patch selection decisions, as assumed in my model. Individuals may integrate past experience with current knowledge differently, therefore, causing some birds to make sequential decisions during foraging habitat selection and others to simply continue returning to the same habitats despite changes in prey and competitor densities (perseveration; Pinel 1997). For instance, if an individual did not sample its foraging environment and only had knowledge of Area 2, it might continue returning to this area despite changing characteristics (e.g. prey and competitor density). Alternately, individuals may always visit and sample both areas during a foraging trip (e.g. trap-lining strategy). Without knowledge of individual-based foraging behaviour (e.g. Benvenuti et al. 1998, Irons 1998), I cannot determine whether birds made sequential patch selection decisions. Even though my model may not be quantitatively accurate, depending on the appropriateness of my assumptions, the model served as an important heuristic tool and allowed us to compare the behavioural mechanisms underlying patterns of spatial distribution.

3.4.4. Summary

The integration of many behavioural theories is required to fully understand foraging habitat selection. For instance, Central Place Foraging theory would predict that murres should always choose the closest foraging habitat to the breeding colony. Therefore, this model alone could not explain why birds would fly past Area 1 to go to Area 2. Incorporating interference among individuals within foraging habitats into the Ideal Free Distribution theory (Sutherland 1983) provided another explanation why murres would fly to a more distant foraging habitat with lower quality prey conditions. Incorporating energetic state-dependent considerations also provided an explanation for variability in selection of foraging habitats of the same individual within a day. Other theories that incorporate the variance as well as the mean competitor and prey densities (Risk Sensitive Foraging Theory; Caraco et al. 1980) also may be important. Overall, even though murres did not appear to adhere to an Ideal Free Distribution, this was an important theoretical framework allowing the integration of prey characteristics, predator energetic states and competitor densities to explain the seemingly variability in patch selection decisions of predators and to explore why murres would ever forage at a seemingly lower quality habitat.

Categorizing important foraging areas, or "hot spots" (Cairns and Schneider 1990), is key in identifying significant marine areas to be protected from human activities (Wanless et al. 1997). In addition, understanding how foraging decisions of individuals lead to spatial patterns at the population level will allow us to make predictions about how foraging decisions of predators will change with fluctuating abundance and distribution of their prey (Veit et al. 1993). This will allow the use of spatial patterns and foraging behaviour of predators to reveal information about changes in distribution and abundance of prey (e.g. Boyd 1996). The integration of all such sources of information is the first step to generating ecosystem approaches to marine conservation.

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CHAPTER IV - Spatial associations of predators and prey: constraints imposed by flightlessness of common murres

4.1 INTRODUCTION

A key theme in ecology is the quantification of predator responses to prey (Sih 1984). Predator-prey theory is concerned with the effects of prey density on demographics and behaviour of predators (Solomon 1949). Responses of predators to prey density can be categorized as (1) numerical, through survival and reproduction, (2) behavioural, through individual-level consumption rates (functional response) and (3) distributional, through movement patterns (aggregative response, Hassell 1966, Holling 1966). The spatial overlap of high predator density areas with high prey density areas depends on the spatial and temporal scales at which predators track their prey (Schneider and Piatt 1986). Tracking scales of mobile predators and prey are highly variable and characteristic scales of association are rarely identified (Schneider and Piatt 1986). The study of tracking scales of predators and prey simultaneously integrates individual-level foraging behaviour and population-level foraging habitat selection (Fretwell and Lucas 1970).

Seabirds are highly mobile predators. They can disperse and aggregate at greater speeds than their mobile prey and, thus, respond quickly to spatial variations in their prey (Russell et al. 1992). Many factors likely influence how seabirds perceive the heterogeneity in prey density within their environment (Grunbaum 1998) and, subsequently contribute to the range of tracking scales observed for seabirds (see

Schneider 1991, Haney and Solow 1992, Russell et al. 1992 for reviews). The physiological requirements for survival, or time to starvation (Horne and Schneider 1994), is likely the most important determinant of the tracking scale of seabirds, due to their high metabolic rates and low energy reserves compared to other marine animals. Physical characteristics of the foraging environment of seabirds, such as hydrographic regimes, combined with prey behaviour influence the spatial scale and density of prey patchiness (Mehlum et al. 1996, Ostrand et al. 1998) and the stability of prey patches in space and time (Cairns and Schneider 1990, Hunt and Harrison 1990, Coyle et al. 1992, Decker and Hunt 1996, Irons 1998), which in turn affect tracking scales (Davoren 2000, chapter 3). In addition, hydrographic regimes may produce intermittent contact between marine predators and their prey (Rose and Leggett 1990). Physiological requirements of seabirds and the bio-physical characteristics of their foraging environment likely change during the annual cycle of seabirds, resulting in multi-scale dynamic foraging strategies and, thus, variable tracking scales within seabird species (Russell et al. 1992).

Common murres (*Uria aalge*) are pursuit-diving seabirds that feed primarily on small pelagic schooling fish (Gaston and Jones 1998). They commonly dive to 20 - 50 m and can attain maximum dive depths of 180 - 210 m (Piatt and Nettleship 1985, Croll et al. 1992). Owing to adaptive compromises that permit both flying and pursuit-diving, murres and other auks have high energy requirements (Gaston and Jones 1998). Due to their large body size (~ 950 g), murres have higher requirements than other auks and can fast for only 1.5 – 2.5 days while rearing chicks (Gabrielsen 1994). Chicks leave the colony with the male parent after being reared at the colony for approximately three weeks (Gaston and Nettleship 1981). Upon colony departure, chicks have not completely developed their flight feathers and are unable to fly. The male parent feeds the chick at sea for 45 – 60 days or until it reaches adult body mass (Varoujean et al. 1979). During this period, adult murres moult, where they simultaneously shed their primary (flight) feathers (Thompson et al. 1998) and cannot fly for approximately 30 – 45 days (Birkhead and Taylor 1977). Consequently, post-breeding dispersal is accomplished by swimming. Secondary feathers are not lost until the primary feathers are half grown, which maintains the surface area of the wing for efficient pursuit-diving (Birkhead and Taylor 1977).

It is important to determine the relative contribution of different prey types to predators' diets to appropriately examine the scale at which predators track prey because certain prey available may be preferentially consumed. Seabird dietary analysis has generally been limited to the breeding season when seabirds are accessible at colonies and parental food-loads can be assessed (Bradstreet and Brown 1985). Dietary analysis during nonbreeding periods has generally been restricted to shooting birds at sea. Stable-isotopic analysis, or determinations of species-specific trophic positions based on stepwise enrichments of ^{15}N at each trophic level, of bird tissue can provide important trophic information during the nonbreeding season without destructive sampling techniques (Hobson 1993). For instance, feathers are primarily composed of keratin and, thus, can reliably indicate the protein intake during the period of feather growth (Mizutani et al.

1992, Cherel et al. 2000). I use primary feathers, or flight feathers, to examine the diets of seabirds during the post-breeding moult.

In this paper, I examine whether the locomotory capabilities of common murres is an important influence on the scale at which they track prey. To do this, I examine the scale-dependent patterns of distribution of murres in relation to their prey under two mobility regimes: (1) during the pre-breeding when murres can fly and (2) during the post-breeding or moulting period when murres are flightless and are accompanied by flightless chicks. I also document the relative contribution of different trophic level prey in murre diet during the moulting period for the first time through stable isotopic analysis of feathers. Diets of murres during the pre-breeding period were previously documented in my study area (Piatt 1987). I make two predictions about murre-prey spatial associations based on behavioural predator-prey theory (Sih 1984). First, I predict that at the scale of underwater searching for prey (fine-scale: 1 – 1000 m; Haurey et al. 1978) and the daily foraging ambit (coarse-scale: 1 km – 100 km; Haury et al. 1978), pre-breeding murres that can fly will track prey at smaller spatial scales than flightless murres. This is based on the reduced ability of flightless murres to move rapidly over large areas in response to changing prey density, compared to murres that can fly. Owing to reduced prey-response capabilities, flightless murres may require large areas containing closely spaced patches of high prey density to increase their probability of encountering prey. Consequently, I predict that at the scale of pre- and post-breeding migration (meso-scale: > 100 km; Haury et al. 1978), aggregations of flightless murres will be restricted to areas with closely spaced patches of high prey density compared to aggregations of murres in the pre-breeding season when they can fly. Foraging theory predicts that the decision to specialize or generalize on specific prey types depends on the search time involved for the preferred prey types and, thus, on their relative abundance (Emlen 1966, Perrins and Birkhead 1983). Due to the presumably reduced rates of search of post-breeding murres, I make a third prediction that flightless murres will have a more general diet than during pre-breeding. These predictions are discussed in the context of foraging constraints imposed by differential mobility and physiological requirements during the pre- and post-breeding periods.

4.2 METHODS

4.2.1. Study Area

The focal part of this study was on the eastern Newfoundland Shelf, covering three of the Northwest Atlantic Fisheries Organization (NAFO) Divisions (2J, 3K, 3L, Fig. 4.1). Within this area there are six common murre breeding colonies: Cape St. Mary's (10,000 breeding pairs, b.p.), Witless Bay Islands (100,000 b.p.), Baccalieu Island (4,000 b.p.), South Cabot Island (2,600 b.p.), Funk Island (340,000 – 400,000 b.p.) and the Gannet Islands (50,000 b.p., Cairns et al. 1989, Canadian Wildlife Service unpubl. data; Fig. 4.1).

Oceanography on the eastern Newfoundland shelf is primarily governed by the Labrador Current, which results in a mean southward transport of water along the Labrador coast and the east coast of Newfoundland (Petrie and Anderson 1983, Colbourne et al. 1997).

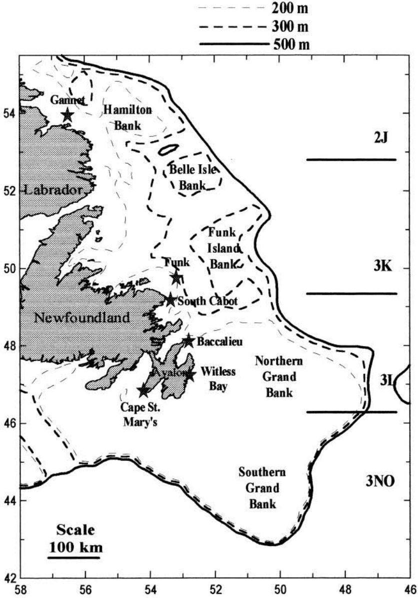


Figure 4.1. The map of the study area showing the 6 main breeding colonies of common murres (stars) and the 200m, 300 m and 500 m depth contours.

Wind direction, however, appears to be of greater importance than the mean flow of currents in determining movements of floating objects, such as flightless murres sitting on the ocean's surface (Flint and Fowler 1998). The prevailing wind direction in Newfoundland is southwest in the summer and fall, and, thus, most floating objects are likely to drift in an easterly - northeasterly direction.

Capelin (*Mallotus villosus*), the dominant forage fish in the Northwest Atlantic, is a major prey for piscivorous fish, birds and mammals (Carscadden 1982, Carscadden et al. submitted). Prior to spawning, capelin occur mainly in offshore feeding areas near the shelf edge and undergo extensive migrations to spawn primarily on inshore beaches (Carscadden et al. 1989). They generally begin migrating inshore about March or April and they are first observed inshore near southeastern Newfoundland (Carscadden et al. 1997). From southeastern Newfoundland, capelin migrate north along the east coast to spawn on beaches (Nakashima 1992). After spawning, survivors move away from beaches and join immature fish, forming large schools (Carscadden 1982). Fish feed heavily after spawning until November and large schools are found in offshore waters from northeast Newfoundland to southern Labrador (Carscadden 1982).

4.2.2. Survey Design

I quantified the distribution and density of marine birds and mammals in Divisions 2J3KL (Fig. 4.1) from 1998 - 2000 as part of two Department of Fisheries and Oceans Canada (DFO) research programmes: (1) on the distribution and abundance of pelagic juvenile fish (August-September; Anderson and Dalley 1996) and (2) on the distribution and abundance of capelin (May). Both surveys were conducted aboard the 60 m Canadian Coast Guard research vessel *Teleost*. Acoustic transects were conducted continuously throughout both surveys, whereas bird and mammal counts were limited to daylight (conditions permitting, see below).

In August-September 1999, a survey grid at 54-km (30 Nm) station spacing was used (systematic stratified sampling design), where the first station was selected randomly from one 54 x 54 km stratum (Snedecor and Cochrane 1967). Fifteen primarily east-west (cross-shelf), one north-south (along shelf) and six inshore-irregular acoustic transects were conducted from 23 August – 14 September 1999 (Fig. 4.2a). Pelagic juvenile fish were sampled systematically at stations from 20 – 60 m water depth using a midwater pelagic trawl, International Young Gadoids Pelagic Trawl (IYGPT, see Anderson et al. 2002 for trawl description). In May, five east-west approximately linear transects, one northeast-southwest and three irregular-inshore acoustic transects were conducted from 13 – 28 May 1999 generally at 54 km (30 Nm) north-south spacing (Fig. 4.2b). In this survey, biological samples were not sampled systematically at predetermined stations, but instead schools were targeted to identify acoustic signals. The IGYPT trawl was used to sample midwater signals, while the Campelen Trawl was used to target signals near the ocean floor (see O'Driscoll et al. 2002 for trawl description). The total mass of the catch and the number of all species was recorded immediately after each tow. Ten percent of

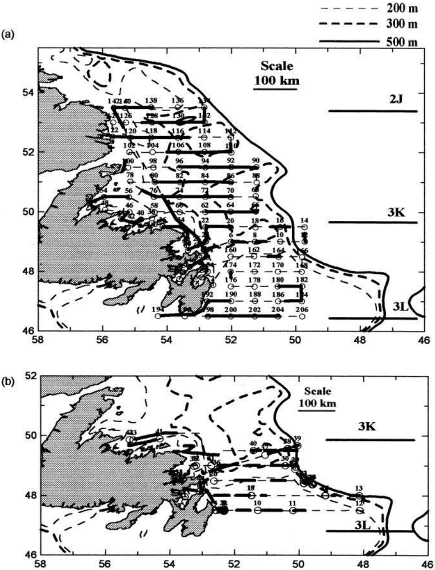


Figure 4.2. The cruise track for the August-September 1999 survey (a) and the May 1999 survey (b) showing the location of acoustic transects (dashed lines), the continuous segments of transect where bird/mammal counts were conducted simultaneously with acoustic recordings of prey (sold lines) and the locations of fishing sets where biological samples were collected (circles).

the catch was subsampled and the mass each species contributed to the total catch was estimated.

I conducted similar surveys in August-September 1998 (*Teleost*: August 25 – September 8, *Templeman*: August 25 – September 10) and May 2000 (May 10 – 27) but due to different acoustic recording methods and varying survey design among years, I used these surveys to examine relative abundance and distribution patterns of birds and prey between years on a meso-scale using expanding symbol plots constructed in SURFER (version 7.0, Golden Software). This also added a temporal (interannual) component to my description of distribution patterns. I focus my detailed analysis of fine-scale distribution patterns and spatial associations of birds and prey during the surveys conducted in 1999.

4.2.3. Acoustic Estimates

The distribution and abundance of plankton and nekton in the water column were estimated based on acoustic backscattering strength using a Simrad EK500 echo-sounding system calibrated with a tungsten carbide standard target. This echo-sounder operated through a hull-mounted 38 kHz split-beam transducer. The transducer was at a depth of 6 m and acoustic signals were not reliable until 15 m deep. Vessel speed during acoustic transects was maintained between 8 – 10 knots. High-resolution data (volume backscattering strengths, S_v) were recorded using CH1 acquisition software and were stored on CDs for later processing using CH2 echo-integration software (Simard et al. 1998).

Prior to integration, an integration threshold of − 80 dB was applied. This threshold was chosen because even a single small capelin (< 100 mm) would exceed this threshold at the range of depths commonly encountered in this study (< 300 m), while most other biological and nonbiological "noise" would be filtered out (R. O'Driscoll pers. comm.). In addition, I examined acoustic files and edited acoustic signals near the bottom where I was unsure whether the signal was biological or due to the ocean floor (dead-zone, side-lobing, Lawson and Rose 1999). Capelin schools were visually identified in acoustic files prior to integration by experienced capelin acoustic biologists (August-September 1999: R. O'Driscoll, May 1999: F. Mowbray). Visual discriminations were ground-truthed using biological samples when possible (see Appendix 2). I integrated the volume backscattering (S_v) in each file to determine the average backscatter area (S_a) for all plankton and nekton signals (total prey) and the backscatter area due to capelin. The output from CH2 is the average backscatter area (S_a, m^2/m^2), which was converted to average area of scattering (S_A) by multiplying by 4π. I was then able to subtract 'capelin' from 'total' to determine the average area of scattering due to 'non-capelin'. All acoustic terminology follow the recommendations made by the ICES – FAST working group (MacLennan and Fernandes 1999). Biological samples were used again to determine the composition of 'non-capelin' targets in different areas. Average area of scattering, however, was not converted into density due to the high proportion of unknown acoustic signals and unknown target strengths of all plankton and nekton in my study area. I used area scattering for consistency between the two surveys, which differed both in biological sampling gear and design.

I acknowledge that comparisons of area scattering that are not scaled by an appropriate target strength can result in biased interpretations due to the varying scattering characteristics of different organisms (e.g. fish versus zooplankton). Without adequate species composition data and without scaling the area scattering values, noncapelin biomass should be interpreted with caution because the same area scattering values could indicate very different biomass levels if species composition changed throughout the surveyed areas. In addition, I do not preclude that some of the acoustic targets were outside of the size ranges consumed by murres.

The capelin and total area scattering (S_A) were integrated at two different spatial scales: (1) 100 m horizontal bins over whole water column (15-500 m) and (2) 2000 m horizontal bins over the whole water column. Murres typically feed at depths between 10 - 210 m (Croll et al. 1992) but plankton and nekton are known to undergo extensive vertical migrations into surface waters at dusk and back to the ocean bottom at dawn (Shackell et al. 1994). Therefore, analyses are conducted for the whole water column because prey in any area may become accessible due to vertical migration at dawn and dusk. Data are presented as the average S_A per distance category (100 m or 2000 m) and all S_A values (10^{-6}) were multiplied by 1,000,000 for easier viewing.

4.2.4. Seabird Counts

Densities of seabirds were estimated during standardized strip transects (Method I b, Tasker et al. 1984) conducted simultaneously with acoustic estimates. Continuous counts of marine birds and mammals were made by one trained and dedicated observer using binoculars out to 300 m in a 90^0 arc ahead and on the port side of the ship from the bridge at an elevation of 20 m above sea level. The 300 m transect width was maintained throughout the survey using methods outlined in Heinemann et al. (1981). Bird and mammal counts were stopped if visibility was reduced due to extreme weather conditions (< 300 m visibility due to fog or > 35 knots of wind). Individuals spaced within 10 m of each other were considered a group. Counts were entered directly into a laptop computer along with behavioural descriptions (on water, feeding, flying and flight direction, flying with fish). The laptop was connected to the navigational system of the ship and counting software designed by DFO (D. Senciall) was used to append the Greenwich Mean Time (GMT), latitude and longitude to each bird/mammal entry. These time and position references were later used to merge bird and mammal counts with acoustic data. Bird data are presented as the total number of birds per distance category (100 m or 2000 m).

Although many species of marine birds and mammals were observed during surveys (Appendix 3), I focus on common murres. During all surveys, both common murres and thick-billed murres (*Uria lomvia*) occurred within the survey area, however, the vast majority of murres breeding in the area are common murres (99 %, Cairns et al. 1989) and, thus, all were considered to be common murres unless reliably identified otherwise.

It is also important to note that 75 % of both murre species in the study area breed at Funk Island (Cairns et al. 1989). Murre chicks observed during the August – September surveys were distinguished from adults by their smaller size, high-pitched calls and white colouration on the head (Hope Jones and Rees 1985).

4.2.5. Analysis of Scale-Dependent Distribution Patterns

Distribution patterns and spatial associations of predators and prey are scale-dependent (Schneider and Piatt 1986). I produced new data sets by aggregating the murre and S_A data at three spatial scales both along continuous individual transects within the survey (bin size= 0.1 km) and along noncontinuous transects over the whole survey (bin size = 2 km, 10 km, 100 km). To aggregate the data at different bin sizes, I used the position (latitude, longitude) of each murre and S_A at 0.1 km to average the number of murres and S_A into each desired bin size using a Matlab© routine (R. O'Driscoll pers. comm.). Distribution patterns of murres and S_A and spatial associations of murres and S_A were examined and compared using these different data sets by the following univariate and bivariate techniques, respectively. Due to my interest in predator-prey interactions (e.g. aggregative response), I only used murres that were either observed to be feeding (i.e. diving) or assumed to be feeding (i.e. sitting on the water).

I performed both one- and two-dimensional analyses. For the one-dimensional analysis, I used the 0.1 km binned data along continuous segments of acoustic transects, or between fishing sets, where birds and prey were simultaneously recorded ("continuous segments"). The length of continuous transects was not significantly different between surveys in 1999 (range: 0.1 – 20 km; t-test: $\alpha=0.05$, $t_{53}=1.733$, $P=0.089$), allowing comparison of scale-dependent distribution patterns and associations between birds and prey at fine- and coarse-scales between August-September and May 1999 surveys. For the two-dimensional analysis I used the 2 km, 10 km and 100 km binned data for the whole water column and for the whole survey ("noncontinuous analysis": 2 – 2000 km, 10 – 2000 km, 100 – 2000 km), allowing a meso-scale comparison of scale-dependent distribution and association patterns of birds and prey between the August-September and May 1999 surveys.

I tested the hypothesis that murres and S_A were randomly distributed along continuous segments within a survey. Univariate neighbour K statistics were used to assess whether murres, capelin, total prey and non-capelin separately within each continuous segment were distributed significantly different from random at a number of spatial scales (see O'Driscoll 1998, O'Driscoll et al. 2000a). For each transect, the test statistic E[N(t)], or the average number of neighbours of each murre or average S_A in each 100 m bin, was calculated at different spatial scales (t) using the following equation:

$$E = \sum_{\substack{i=1 \\ i \neq j}}^{N} \sum_{j=1}^{N} I_t\,(u_{ij})$$

where N is the total number of individuals observed in an area, u_{ij} is the distance from individual i to individual j and $I_t(u_{ij})$ is an indicator function, which is equal to 1 if $u_{ij}<t$ but equal to 0 otherwise (O'Driscoll 1998). The spatial scales analyzed (t) for continuous

segments ranged from 100 m and increased at 100 m increments up to half the length of the continuous segment. The spatial scales for noncontinuous analyses ranged from 2 km, 10 km and 100 km and increased at 2 km, 10 km and 100 km respectively for each of the three analysis scales, up to 2000 km or half the length of the survey area. After half the length of the transect or survey area, the bias in $E[N(t)]$ will be great because some individuals may lie less than that distance from the ends of the transect (O'Driscoll 1998). I calculated the average number of murres and average S_A expected from a random distribution using Monte Carlo procedures (O'Driscoll 1998). I generated 999 realizations of the data, where each murre or S_A value was randomly reallocated to a bin along the transect. I calculated the percent of the 999 $E[N(t)]$ that was greater than, equal to or less than the $E[N(t)]$ of the observed data. If the $E[N(t)]$ of the observed data was greater than 95 % of the 999 $E[N(t)]$, then birds or S_A values were determined to be significantly clustered. This was repeated at all spatial scales (t).

The average $E[N(t)]$ if random was calculated from the 999 realizations at each spatial scale. I subtracted the observed average $E[N(t)]$ from the expected $E[N(t)]$ if randomly distributed to determine the average number of "extra" neighbours ($L(t)$) at each spatial scale. I conducted a similar calculation for S_A values but instead of the number of neighbours, I averaged the S_A values of neighbouring spatial blocks with a nonzero value. The scale of aggregation of murres and acoustic prey was defined by the spatial scale at which the average number of "extra" neighbours (or neighbouring S_A values) was higher than the succeeding three values to avoid identifying small jumps in groups as peaks

(O'Driscoll et al. 2000a). The first peak was used because it provides a description of the characteristic scale of clustering of birds or prey independent of the variation in abundance within the survey area (O'Driscoll 1998). The number of individuals per aggregation (crowding) was determined by the average number of "extra" neighbours (L(t)) at the scale of aggregation. Therefore, the units of crowding are given as the number of murres and the S_A values. The distance between aggregations of murres and aggregations of acoustic prey is a function of the distance between high counts in the distribution (O'Driscoll 1998). Therefore, the distance between aggregations of murres and aggregations of acoustic prey were defined by the spatial scale at which the average number of "extra" neighbours reached its maximum for a given transect. A similar analysis was conducted for noncontinuous segments over entire surveys, although during the Monte Carlo simulations, murres were restricted to segments where counts were conducted

I tested the hypothesis that murres were distributed randomly in relation to S_A due to total prey, non-capelin and capelin along continuous segments within a survey. Bivariate K analysis was used to determine whether there were significantly more murres associated with a given prey aggregation than would be expected if murres were distributed randomly (O'Driscoll 1998). For each continuous segment, the observed and expected random distribution of murre neighbours at each spatial scale to each prey aggregation in 100 m block increments was calculated, using 999 Monte Carlo simulations as above. The average number of "extra" murres at each prey aggregation (L(t)) at each spatial scale (t) was again calculated by subtracting expected neighbours if random from the observed average number of neighbours. The scale of maximum association between murres and prey ("tracking scale") was defined by the scale at which the average number of "extra" murres was first higher than the succeeding three values. The number of "extra" murres associated with any given prey aggregation (crowding) was determined by the average number of "extra" murres at the scale of maximum association. A similar analysis was conducted for noncontinuous segments over whole surveys and again the analysis was restricted to where bird counts were conducted. Statistical significance was set at $\alpha=0.05$ and all means are reported as ± 1 SE

4.2.6. Dietary Analysis

All primaries on the left wing were collected from dead common murres found at the Funk Island colony in August 2000 (n=9) and found drowned near fishing gear in July 2000 (n=16) near Funk Island. These feathers would have been grown during the August - September 1999 moult. Capelin samples were collected during July 2000 during a different survey (see chapter 3). Thirty spent female capelin were subsampled from a bottom trawl catch (see chapter 3). Spent female capelin were used because these fish had survived spawning and would be the fish available to murres during post-breeding dispersal.

Fish samples were frozen immediately after capture and were thawed later in the laboratory and the total fish length was measured (snout to tip of tail). The spent female capelin sampled had a mean ± SE length of 149 ± 9 mm (135 – 165 mm, n=30). A piece of muscle was removed from each fish and placed into a glass scintillation vial. Samples were freeze-dried for 48 h. The samples were broken apart in the scintillation vials and each vial was filled with a 2 : 1 chloroform : methanol solution to extract lipids. The vials were left in a fume hood for 24 h, after which the solution was drained from samples and air dried for 48 h. Each sample was then ground into a fine powder using a mortar and pestle. A 0.9 – 1.0 mg subsample from each specimen was weighed into a 6 x 4 mm tin capsule.

Feathers were also placed in glass scintillation vials along with a 2 : 1 chloroform : methanol solution to clean feathers and left for 30 min. The solution was then drained from vials and feathers were air dried for 24 h. Sections of all feathers from one specimen were removed from the base to include a section of rachis with barbs. These subsamples were then cut into small pieces to obtain a homogenous feather sample, due to variability observed previously among primary feathers on an individual bird (see Thompson and Furness 1995). A 0.9 – 1.0 mg subsample of homogenized primary feathers was weighed into a tin capsule for each individual bird. All instruments were cleaned between samples with acetone to avoid cross contamination.

Specimens were mailed to David Harris at the University of California, Davis (Stable Isotope Facility). Samples for $^{15}N/^{14}N$ analysis were converted to ammonia by Kjeldahl reaction and then to N_2 gas using LiBrOH. Samples for $^{13}C/^{12}C$ analysis were placed into pyrex tubes with 1 g of wire form CuO and silver foil, sealed under vacuum, and combusted at 550^{0}C for 6 h to produce CO_2. The N_2 and CO_2 were analyzed using a mass spectrometer. Standards for ^{15}N and ^{13}C were atmospheric N_2 (AIR) and the Pee Dee Belemnite, respectively. Delta notation was used to express isotope ratios (see Hobson 1993). The abundance of stable isotopes in prey may change when incorporated into tissues of the predator (Hobson et al. 1994) and, thus, stable isotopic fractionation values are required to relate isotopic concentrations in feathers to those in a predator's diet (Tieszen et al. 1983). Mizutani et al. (1992) derived a nitrogen fractionation factor of 4.4 for feathers of fish-eating birds. Using the following equation, taken from Hobson (1993), I determined the trophic position of common murres in the Northwest Atlantic.

$$TI_{murre} = 2 + (D_t - \Delta_{dt} - 5.4) / 3.8$$

where D_t is the murre's feather $\delta^{15}N$ value, Δ_{dt} is the isotopic fractionation factor between diet and feather, 5.4 is the $\delta^{15}N$ of phytoplankton, or the first trophic level, in the study area, and 3.8 is the nitrogen enrichment factor between trophic levels in the study area (Hobson 1993). I could not calculate the trophic level of capelin because the isotopic fractionation factor appropriate for capelin was not found in the literature.

The relative contribution of each prey type to the diet of a murre was estimated following equation 4 in Hobson (1993):

$$P_a = (D_t - D_b) / (D_b - D_a)$$

Where P_a is the proportion of the diet derived from prey type 'a', D_t is isotopic value of the feather tissue and D_a and D_b is the predator tissue ^{15}N isotopic values corresponding to exclusive diets of prey type 'a' and 'b', respectively ($D_a = \delta^{15}N_a + \Delta_{dt}$). This model is simple and based on the assumption that murres only have dietary options of prey types 'a' and 'b'. I measured isotope ratios of carbon and nitrogen in capelin, however, I used published isotope ratios for euphausiids in the study area ($\delta^{15}N$ of euphausiids = 7.9; Hobson and Montevecchi 1991) and compared a diet of capelin versus euphausiids (Hobson 1993, Lawson and Hobson 2000).

Diets were not collected for murres during the pre-breeding season (May) because murre diets have been described previously during this period in Newfoundland as dominated by capelin with some sand lance (Piatt 1987). Similarly, stomach content analysis of murres drowned near Funk Island during July 2000 showed that capelin were the only prey species taken by adult murres in this area (chapter 3).

4.3 RESULTS

A total of 47 continuous segments of transect with a mean length of 24.7 ± 2.2 km (range: 4.4 – 83.2 km) were conducted in May 1999 when birds and prey were both recorded. Seventeen segments (36 %) contained > 2 murres and had a mean length of 29.8 ± 5.0 km (range: 21.0 – 83.2 km). Thirteen of these segments (27 %) contained capelin. A total of 66 continuous segments of transect with a mean length of 34.9 ± 2.4 km (range: 5.7 – 109 km) were conducted during August - September 1999 when birds and prey were both recorded. Forty-four (67 %) contained > 2 murres and had a mean length of 38.6 ± 2.6 km (range: 19.0 – 69.7 km). Twenty-two of these segments (33 %)

contained capelin. Analyses were restricted to segments with > 2 murres (August-September: n=44; May: n=17).

4.3.1. Murre Diet

Murres occupied a range of trophic positions (2.9 – 3.7) during the moulting period and $\delta^{15}N$ values were consistent with a variable diet (Table 4.1). The percent of crustaceans in the diet was generally low but varied widely among individuals, as shown by the high standard deviations of $\delta^{15}N$ compared to $\delta^{13}C$ (Table 4.1). This indicates that diets are highly diverse during moult. Murres collected at sea that had drowned near fishing gear (n=15) were fresh enough to determine sex and breeding condition: 8 males (7 breeders) and 7 females (6 breeders; see chapter 3 for details). Male murres occupied a higher trophic position than females, shown by their higher $\delta^{15}N$ values and lower proportion of crustaceans in their diets (Table 4.1); however, this difference was not statistically significant (t-test: t_{13}=2.07, P=0.059).

4.3.2. Murre Distribution

An average of 67 % of the murres observed during each survey (Appendix 3) were identified to species and the majority of these (98 %) were identified as common murres. In May, murres were mainly found near breeding colonies, although a large number of murres were found east near the shelf edge in May (Figs. 4.3, 4.4). Murres at the shelf edge were still undergoing their pre-breeding moult (white under the bill) and, thus, may

Table 4.1 Stable nitrogen and carbon isotope concentrations (± SD) in primary feathers of common murres and muscle tissue of capelin, the derived trophic levels of common murres and the estimated mean proportion of crustaceans in the diets of common murres ± SE collected in the Northwest Atlantic Fisheries Organization Division 3K, near the Funk Island seabird breeding colony. The number of samples is given by n and ranges are given in parentheses.

Organism	n	$\delta^{15}N$ ‰	$\delta^{13}C$ ‰	Trophic Level	% of crustaceans
Common Murre	25	14.8 ± 0.7 (13.4 - 16.1)	-17.9 ± 0.3 (-18.5 to -17.3)	3.3 ± 0.2 (2.9 – 3.7)	23 ± 20 (63 – 0.2)
Male	8	15.0 ± 0.5 (14.6 – 16.1)	-17.9 ± 0.2 (-18.1 to -17.6)	3.4 ± 0.1 (3.3 – 3.7)	16 ± 15 (61 – 0.2)
Female	7	14.3 ± 0.7 (13.4 – 15.3)	-18.0 ± 0.4 (-17.3 to -18.5)	3.2 ± 0.2 (2.9 – 3.4)	27 ± 20 (54 – 0.7)
Capelin	30	10.2 ± 1.9 (5.4 - 12.5)	-19.9 ± 0.6 (-18.8 to -21.1)		

Figure 4.3 The distribution of common murres flying (a) and sitting on the water (b) and the distribution of acoustic backscatter area (S_A) due to total prey (c) and due to capelin (d) binned into 5 km^2 blocks during the May 1999 survey in the Northwest Atlantic Fisheries Organization Divisions 3KL

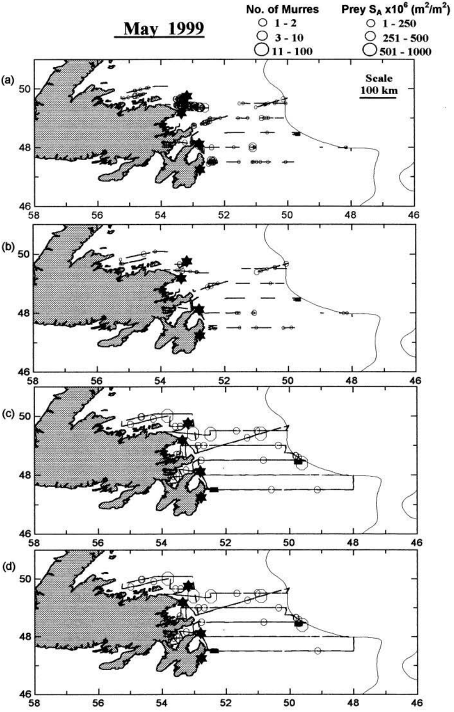
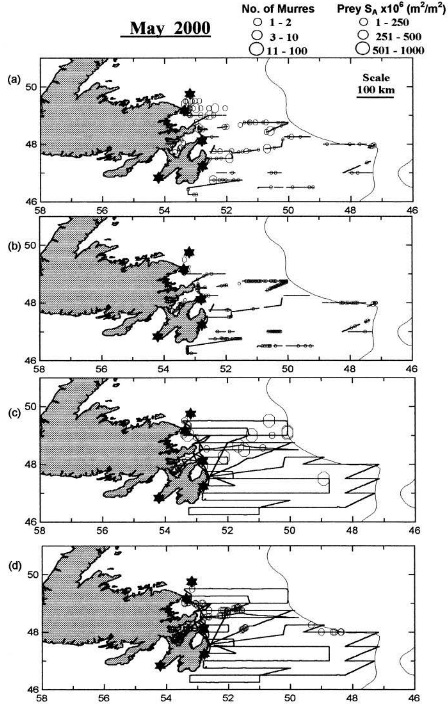

May 1999
No. of Murres
1 - 2
3 - 10
11 - 100
Prey S_A x10^6 (m^2/m^2)
1 - 250
251 - 500
501 - 1000
Scale
100 km
(a)
(b)
(c)
(d)
50
48
46
58
56
54
52
50
48
46

Figure 4.4 The distribution of common murres flying (a) and sitting on the water (b) and the distribution of acoustic backscatter area (S_A) due to total prey (c) and due to capelin (d) binned into 5 km^2 blocks during the May 2000 survey in the Northwest Atlantic Fisheries Organization Divisions 3KL


May 2000
No. of Murres
1 - 2
3 - 10
11 - 100
Prey S_A x10^6 (m^2/m^2)
1 - 250
251 - 500
501 - 1000
Scale
100 km
(a)
(b)
(c)
(d)
50
48
46
58
56
54
52
50
48
46

have been nonbreeding birds or thick-billed murres preparing for departure to breeding areas in the Arctic. During August-September, murres were primarily dispersed throughout the study area, with some aggregations around breeding colonies (Figs. 4.5, 4.6). In both years, large aggregations of murres were found in the northern part of the study area (southern Div. 2J, northern Div. 3K) and very few murres were found farther south (southern Div. 3L, Divs. 3NO). These distribution patterns were similar among years.

On 4-7 September 1999 (southern Div. 2J, northern Div. 3K) I counted 71 % (n=1189) of all murre adults during the survey. I refer to this area as the "northern area", whereas the rest of the survey area is referred to as the "southern area". The northern area had significantly higher densities of murres (3.1 ± 1.6 birds/km^2, n=15 continuous segments) compared to the southern area (0.2 ± 0.1 birds/km^2, n=29; t-test: t_{42}=2.49, P=0.017, Fig. 4.6). In contrast, only 12 % (n=7) of murre chicks were observed in the northern area. Chicks observed in the northern area were much larger and harder to distinguish from adults than those farther south and, thus, I do not preclude that there were more young of the year in this area that were mistaken as adults. Chick-adult associations were different in the northern area compared to farther south. In the northern area, chicks were generally accompanied by many adults (1 chick – 1 adult: 14 %, 1 chick – more than 1 adult: 86 %) and it was not obvious which adult was the accompanying parent. In contrast, the majority of chick-adult associations observed farther south were solitarily pairs (1 chick – 1 adult: 58 %, 1 chick – more than 1 adult: 42 %). In the southern area, when chicks were

Figure 4.5. The distribution of flying common murres (circles) and murre chicks sitting on the water (squares, a), adult murres sitting on the water (b) and the distribution of acoustic backscatter area (S_A) due to capelin (c) binned into 5 km^2 blocks during the August-September survey of 1998 in the Northwest Atlantic Fisheries Organization Divisions 2J3KLNO

August-September 1998

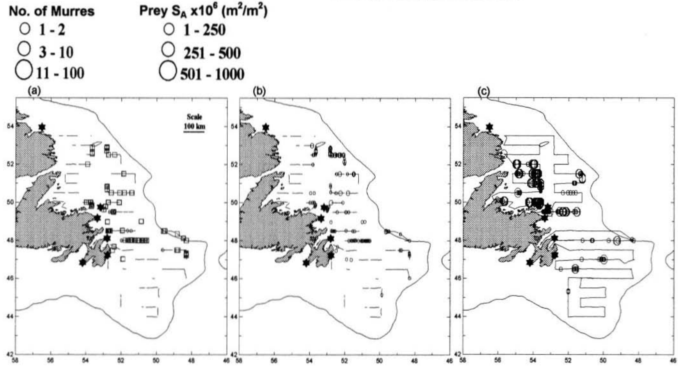
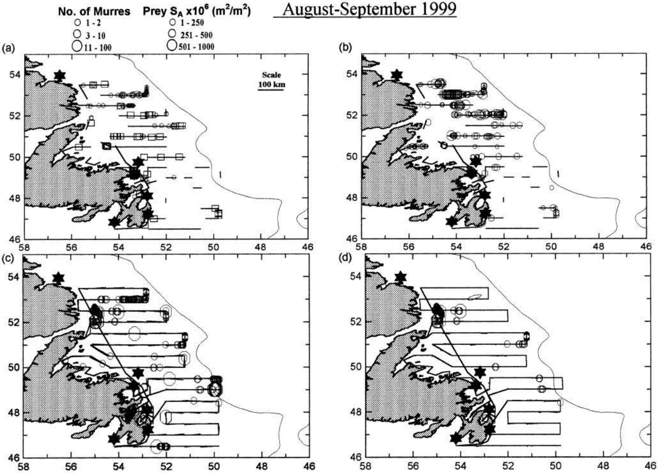


Figure 4 6 The distribution of flying common murres (circles) and murre chicks sitting on the water (squares. a). adult murres sitting on the water (b) and the distribution of acoustic backscatter area (S_A) due to total prey (c) and due to capelin (d) binned into 5 km^2 blocks during the August-September survey of 1999 in the Northwest Atlantic Fisheries Organization Divisions 2J3KLNO



August-September 1999

observed with more than one adult, it was obvious which one was the accompanying parent due to their close proximity (within 1 m of each other). In addition, 91 % of the total murres observed flying (n=181) during the survey were observed in this northern area, while only 9 % were observed farther south near breeding colonies (Fig. 4.6).

4.3.3. Prey Distribution

In May, the highest S_A values due to total prey were mainly found along the shelf edge, Bonavista Corridor and within major bays (Figs. 4.3, 4.4). Most of the total prey observed in May was comprised of capelin. Very few acoustic signals were recorded on the shelf elsewhere. In August-September, the highest signal of capelin was found near the northern coast of Newfoundland and southern coast of Labrador (southwestern Div. 2J, northwestern Div. 3K), Funk Island Bank and along the shelf edge in Div. 3L (Fig. 4.6). Very little signal of capelin was found in the southern part of Div. 3K or farther south in Div. 3L and 3NO (Fig. 4.6). These trends were consistent among years (Figs. 4.5, 4.6). Capelin dominated the acoustic scattering area in May compared to the August-September in 1999. The relative dominance of the nekton by capelin in May compared to August-September has been documented in other studies (e.g. Lilly and Simpson 2000).

Within the August-September survey in 1999, the northern area had significantly higher mean S_A per continuous segment due to total prey (north: 6021 ± 2189 x^{10-6} m^2/m^2, south: 5.9 ± 0.1 x^{10-6} m^2/m^2, t-test: $t_{42}=3.87$, P=0.0004), non-capelin (north: 5382 ± 2217 x^{10-6}

m^2/m^2, south: $5.3 \pm 0.1 \times^{10-6}$ m^2/m^2, $t_{42}=3.41$, $P=0.001$), and capelin, although the latter was not statistically significant (north: $639 \pm 480 \times^{10-6}$ m^2/m^2, south: $0.6 \pm 0.02 \times^{10-6}$ m^2/m^2, $t_{42}=1.87$, $P=0.068$; Fig. 4.6). In the northern area, biological samples in the top 20 – 60 m were dominated by euphausiids, copepods and amphipods (Appendix 2b: fishing sets 102 – 142). There were acoustic signals of capelin deeper in the water column, but capelin in this area did not migrate vertically into the diving range of murres (O'Driscoll et al. 2000b).

4.3.4. Murre-Prey Interaction in Continuous Segments of Transects (Fine-Scale)

At the scale of continuous segments of acoustic transects (one-dimensional, fine- and coarse-scale analysis), the scale of aggregation of murres was significantly higher in May (3.7 ± 1.5 km) compared to August (0.4 ± 0.1 km) but there appeared to be fewer individuals within these larger aggregations (crowding) in May compared to August, although this was not statistically significant (Table 4.2). Overall, a higher number of murres were clustered into smaller aggregations in August compared to May. The distance between murre aggregations, however, was similar in August (6.3 ± 1.2 km) and in May (4.0 ± 1.4 km; Table 4.2). In May, murres had larger scales of aggregation than capelin, total prey and non-capelin, whereas the opposite was true in the August-September survey (Table 4.2).

Table 4.2 The mean ± SE of the aggregation scales of common murres and acoustic area scattering ($S_A \times 10^{-6}$) from prey (capelin, total prey, non-capelin), the number of murres and S_A ($\times 10^{-6}$) of prey within aggregations (crowding), the maximum scale of association between murres and prey, and the number of murres associated with prey aggregations (crowding) for continuous segments of transect (0.1 – 20 km, 0.1 km binned data) during pre-breeding (May) and post-breeding (August-September) periods in 1999. The number of continuous segments with significant clustering of murres and prey and murres at prey are indicated in parentheses and the percent of the total number of transects is presented ("% SIG"). Results of t-tests testing differences between May and August-September are given.

	May (M)		August-September (A-S)					
	Spatial scale (km)	Crowding	Spatial scale (km)	Crowding	% SIG (M/A-S)	df	P (scale)	P (crowd)
Aggregation Scale								
Murres	3.7 ± 1.5 (16)	0.9 ± 0.1	0.4 ± 0.1 (37)	3.9 ± 1.5	94/100	51	0.002	0.183
Capelin	2.8 ± 1.3 (13)	1136.2 ± 504.6	3.1 ± 0.5 (22)	284.9 ± 117.5	100/100	33	0.818	0.052
Total prey	2.0 ± 0.5 (17)	1245.9 ± 384.4	5.4 ± 1.0 (37)	364.4 ± 134.4	100/100	53	0.041	0.009
Non-capelin	2.0 ± 0.6 (17)	712.0 ± 278.3	6.0 ± 1.2 (37)	260.4 ± 126.5	100/100	51	0.035	0.094
Distance between Aggregations								
Murres	4.0 ± 1.4 (16)	1.5 ± 0.3	6.3 ± 1.2 (36)	8.7 ± 2.6	94/97	50	0.280	0.070
Capelin	6.8 ± 2.2 (13)	1394.5 ± 536.2	7.6 ± 1.6 (21)	306.4 ± 119.3	100/95	32	0.764	0.020
Total Prey	7.0 ± 1.7 (17)	1530.3 ± 147.6	8.7 ± 1.3 (35)	433.6 ± 400.5	100/95	50	0.469	0.003
Non-capelin	6.7 ± 2.5 (17)	776.3 ± 278.7	8.6 ± 1.3 (34)	325.3 ± 141.6	100/92	49	0.459	0.114
Maximum Scale of Association								
Murre - Capelin	4.1 ± 1.2 (6)	1.8 ± 0.5	9.2 ± 2.8 (4)	0.3 ± 0.2	30/27	8	0.047	0.026
Murre - Total prey	3.9 ± 1.7 (17)	1.1 ± 0.4	6.6 ± 1.8 (5)	2.9 ± 1.9	30/46	20	0.063	0.611
Murre - Non-capelin	3.1 ± 1.5 (5)	0.6 ± 0.3	6.0 ± 1.1 (8)	1.2 ± 0.4	30/22	11	0.138	0.263

The scales of aggregation of total prey (2.0 ± 0.5 km) and non-capelin (2.0 ± 0.6 km) were significantly smaller in May than in August-September (total prey: 5.4 ± 1.0 km; non-capelin: 6.0 ± 1.2 km) and there was also higher crowding of total prey and capelin in May compared to August-September (Table 4.2). Overall, there was a tendency towards higher crowding of prey in smaller aggregations in May compared to August-September (Table 4.2). The distance between aggregations of capelin, total prey and non-capelin did not differ during these two surveys (Table 4.2).

There were similar maximum scales of association ("tracking scales") between murres and prey within continuous segments in May and August-September; however, there was a trend towards smaller tracking scales in May (3.1 – 4.1 km) compared to August-September (6.0 – 9.2 km) and this was significant for murre-capelin associations (Table 4.2). There was higher crowding of murres at capelin aggregations in May compared to August-September (Table 4.2). Most transects (92 – 100 %) had a scale of aggregation at which murres, total prey, capelin and non-capelin were significantly clustered. In contrast, only approximately one third of all transects had significant tracking scales of murres to prey (Table 4.2).

I compared the distribution patterns of murres and prey in the northern area versus the southern area in the August-September survey in 1999 (Table 4.3). There was higher crowding of murres and capelin at the scales of aggregation in the northern area compared to farther south, although the spatial scale of aggregation did not differ among

Table 4.3. The mean ± SE of the aggregation scales of common murres and acoustic area scattering ($S_A \times 10^{-6}$) from prey (capelin, total prey, non-capelin), the number of murres and S_A ($\times 10^{-6}$) of prey within aggregations (crowding), the maximum scale of association between murres and prey, and the number of murres associated with prey aggregations (crowding) for continuous segments of transect (0.1 – 20 km, 0.1 km binned data) in the northern area (Northwest Atlantic Fisheries Organization Divisions 2J and northern 3K) and the southern area (southern part of NAFO Division 3K and Divisions 3LNO) in August-September, 1999. The number of continuous segments with significant clustering of murres and prey and murres at prey are indicated in parentheses and the percent of the total number of transects is presented ("% SIG"). Results of t-tests testing differences between May and August-September are given

	Southern Area (S)		Northern Area (N)					
	Spatial scale (km)	Crowding	Spatial scale (km)	Crowding	% SIG (S / N)	df	P (scale)	P (crowd)
Aggregation Scale								
Murres	0.3 ± 0.1 (23)	1.3 ± 0.2	0.6 ± 0.3 (14)	8.1 ± 3.6	100/100	35	0.294	0.021
Capelin	3.0 ± 0.7 (17)	155.4 ± 62.7	4.0 ± 0.9 (4)	835.4 ± 519.1	100/100	19	0.467	0.019
Total prey	6.0 ± 1.7 (21)	247.5 ± 88.8	4.0 ± 1.2 (14)	527.9 ± 298.8	91/100	34	0.386	0.310
Non-capelin	7.4 ± 1.9 (21)	193.0 ± 79.8	4.0 ± 1.2 (14)	354.9 ± 9.1	91/100	34	0.174	0.536
Distance between Aggregations								
Murres	5.5 ± 1.7 (22)	2.1 ± 0.3	7.5 ± 1.9 (14)	19.0 ± 15.7	96/100	34	0.438	0.001
Capelin	8.4 ± 1.9 (17)	177.2 ± 68.2	4.4 ± 0.8 (4)	855.4 ± 518.5	100/100	19	0.325	0.021
Total Prey	10.2 ± 1.8 (22)	319.0 ± 1.8	6.2 ± 1.8 (13)	627.6 ± 347.0	96/93	33	0.047	0.319
Non-capelin	10.3 ± 1.8 (21)	261.6 ± 1.8	5.9 ± 1.5 (13)	428.3 ± 329.0	91/93	32	0.099	0.575
Maximum Scale of Association								
Murre – Capelin	6.9 ± 4.0 (4)	1.7 ± 0.6	1.7 (1)	2.5	17/25	3	0.606	0.553
Murre - Total prey	6.1 ± 1.8 (10)	0.7 ± 0.2	6.7 ± 2.9 (7)	6.0 ± 4.4	43/50	15	0.856	0.161
Murre - Non-capelin	4.2 ± 1.4 (6)	0.9 ± 0.4	11.6 ± 7.0 (2)	2.0 ± 0.1	35/14	6	0.128	0.221

areas (Table 4 3) Generally, in the northern area, there were shorter distances between aggregations of capelin, total prey and non-capelin (4.4 – 6.2 km) compared to farther south (8.4 – 10.2 km), although these trends were only significant for total prey (Table 4 3) Only four of the 14 continuous segments (29 %) where murres were counted in the northern area contained acoustic capelin signals. The tracking scale of murres and prey, however, did not differ among the areas (Table 4 3).

4.3.5. Murre-Prey Interaction Over Surveys (Meso-scale)

At the scale of an entire survey (two-dimensional, meso-scale analysis), murres, total prey, capelin and non-capelin were not significantly clustered, nor were significant spatial associations observed between murres and prey, at any spatial scale up to 2000 km using the 10 km and 100 km binned data sets. Therefore, these datasets are not discussed further. Significant distribution patterns and association patterns were found using the 2 km binned data set and these were consistent with trends resulting from analyses at fine- and coarse-scales using the continuous segments (Table 4 4). Murres had the same scale of aggregation in May and August-September (2 km), although crowding of murres within aggregations was higher in August-September (26 1 birds) compared to May (0.1 birds). In contrast, crowding of prey in aggregations was much higher in May (2063 – 2973 S_A) compared to August-September (562 – 866 S_A). In May, aggregations of capelin (4 km) and non-capelin (24 km) were smaller compared to August-September (capelin: 76 km; non-capelin: 84 km), although the scale of aggregation of total prey was similar among seasons (May: 48 km; August-September: 42 km). Overall, more prey was

Table 4.4. The scale of aggregation of common murres and acoustic scattering area (S_A x10^{-6}) from prey (capelin, total prey and non-capelin), the number of murres and the S_A x10^{-6} of prey within aggregations (crowding), the maximum scale of association between murres and prey and the number of murres associated with prey aggregations (crowding) for the whole survey (2 – 2000 km, 2 km binned data) during pre-breeding (May) and post-breeding (August-September) periods in 1999. The distance between aggregations of prey and crowding are given in parentheses.

	May		August-September	
	Scale (km)	Crowding	Scale (km)	Crowding
Scale of Aggregation				
Murres	2	0.1	2	26.1
Total prey	48	2062.5	42	726.9
	(1308)	(3732.1)	(326)	(1329.3)
Capelin	4	2118.1	76	562.1
	(1708)	(9349.5)	(1950)	(1313.5)
Non-capelin	24	2973.1	84	866.0
	(32)	(3047.6)	(326)	(1470.3)
Maximum Scale of Association				
Total prey	Ns[1]	-	50	3.9
Capelin	8	1.2	Ns	-
Non-capelin	4	2.9	50	4.6

[1] Ns= Not Significant

found in each aggregation in May compared to August-September. The distance between capelin aggregations was similar in both surveys (May: 1708 km; August-September: 1950 km), however, the distance between total prey aggregations was higher in May (1308 km) than in August-September (326 km), while non-capelin aggregations were more closely spaced in May (32 km) compared to August-September (326 km). In August-September, murres were significantly clustered with total prey and non-capelin at the scale of 50 km, while in May, murres were significantly clustered with non-capelin (4 km) and capelin (8 km) at smaller scales (Table 4.4).

4.4 DISCUSSION

4.4.1. Murre Diets

The diets of flightless birds were highly variable during the moulting or post-breeding period, supporting my third prediction. Flightless murres occupied a trophic position similar to those reported in other studies of common murres using stable isotope analysis on a variety of tissues (egg albumen, liver, muscle and bone collagen, Hobson and Montevecchi 1991, Hobson et al. 1994, Jarman et al. 1996, Sydeman et al. 1997, Thompson et al. 1999). In contrast, during the pre-breeding season in Newfoundland murres are piscivorous, primarily feeding on capelin (Piatt 1987). Common murres are generally considered to be piscivorous (Bradstreet and Brown 1985) but may take a higher proportion of crustaceans during certain times of the year (Ainley et al. 1996, Rowe et al. 2000). Crustaceans, such as euphausiids, generally have a lower caloric content than fish (Spear 1993). The elevated proportion of crustaceans in diets of flightless murres may simply reflect the high abundance of crustaceans in the northern area where murres were moulting or generally the lower proportion that capelin contributed to the total nekton biomass in August-September compared to May. Adult murres may be less selective for prey types during the post-breeding period compared to pre-breeding due to their lower dispersal capabilities and higher search durations or due to the lower energetic requirements of their flightless state. Adult murres, however, do not feed their chicks crustaceans at sea (Scott 1990), probably because adults feed chicks one prey item at a time and, thus, maximize energy transfer by supplying larger prey items (Ainley et al. 1996). This might explain why male common murres, which usually accompany and feed chicks at sea, generally occupied a higher trophic position than females during this study. Differences in diets among pre- and post-breeding murres may explain the smaller tracking scales of murres to capelin during pre-breeding compared to post-breeding.

4.4.2. Fine- and Coarse-Scale Associations of Murres and Prey

At the scale of a daily foraging ambit (coarse-scale: 1 km – 100 km), pre-breeding murres that can fly tracked prey at smaller spatial scales (4 – 8 km) than flightless murres (50 km). Similarly, at the scale of prey capture (fine-scale 1 – 1000 m), murres during the pre-breeding season that could fly tracked prey at smaller spatial scales (3 - 4 km) than flightless murres (6 - 9 km). This supports my first prediction.

Smaller tracking scales of prey by murres that can fly compared to flightless murres can be explained in a number of ways. First, prey aggregations were smaller and contained more prey during the pre-breeding period compared to post-breeding and, thus, murres may have simply been responding to the distribution and density of prey aggregations. Second, larger tracking scales of flightless murres may result from the reduced ability of these birds to move in response to changing prey density. Restricted mobility and higher costs of switching among aggregations may lead to unpredictable patterns of spatial association between murres and prey, with low quality aggregations used more than high quality aggregations (Abrahams 1989, Tregenza 1995). In addition, reduced dispersal capabilities may lead to perceptual constraints in flightless murres through a reduction in the ability to physically and visually (local enhancement) sample their foraging environment to locate prey, resulting in a much more restricted knowledge of local concentrations of prey compared to birds that can fly. Flightless murres formed smaller aggregations that contained more individuals than during pre-breeding when murres can fly. This might reflect the tendency of flightless murres to be more closely spaced, allowing individuals independently sampling for prey to maintain visual contact and cue to the foraging activities of each other (network foraging, Wittenberger and Hunt 1985).

It is also possible that flying and egg formation for females during the pre-breeding period are more energetically demanding activities than swimming and moulting during post-breeding (Murphy and King 1992, Croll and McLauren 1993). Therefore, murres would require more energy to maintain higher activity levels during pre-breeding compared to post-breeding, which would also explain their smaller-scale associations with prey. In support, peak mortality does not appear to occur during moult, suggesting that this period does not represent an energetic bottleneck for chicks and adults (Birkhead 1974, but see Holdgate 1971). Very little is known, however, about the energetic demands of birds during moulting periods and, thus, I do not conclude that the energetics of moulting is negligible. In fact, moulting has been assumed to contribute significantly to annual energy expenditure of seabirds (Diamond et al. 1993), although this has yet to be confirmed experimentally (Adams et al. 2000). Higher metabolic rates of waterbirds during moult compared to the winter are likely due to both the energy expended in growing new feathers and higher thermogenesis due to increased surface area exposed to the environment and, thus, increased heat loss (Payne 1972). Murres are not thermally neutral in temperatures less than 15°C but generally occupy ocean temperatures colder than this (Croll and McLaren 1993). Thermal conductance in water is two times higher than in air for swimming birds (de Vries and van Eerden 1995) and, thus, heat loss is high due to reduced insulation and increased blood flow to areas of feather growth during moulting (Payne 1972).

4.4.3. Meso-scale Associations of Murres and Prey

At the scale of the pre- and post-breeding migration (meso-scale: > 100 km), murres appeared to be aggregated in areas of high prey density. During pre-breeding, murres were concentrated around breeding colonies and their distribution coincided with the distribution of high prey density areas on a meso-scale within inshore bays. During post-breeding, flightless murres and chicks were aggregated on a meso-scale in an area of high prey density just off the southern Labrador coast ("northern area"). In this northern area, there were significantly higher densities of prey and shorter distances between prey aggregations compared to the rest of the study area. This supports my second prediction, that aggregations of flightless murres will be restricted to areas where prey aggregations have high densities and are closely spaced. There were no differences, however, in the distance between prey aggregations where murres were located in the pre-breeding and post-breeding periods.

The northern area off southern Labrador appears to be an important staging and nursery area for flightless murres and their chicks, respectively. Tuck (1961) concluded through recoveries of banded birds that murres from breeding colonies farther south moved north into this area during their post-breeding dispersal. Northward movement against the mean flow of the Labrador Current is probably not energetically expensive because prevailing southwest winds during the fall likely aid in the transport surface waters containing birds towards the northeast (D. Schneider pers. comm.). My data support the northward movement from breeding colonies farther south, the most important of which is Funk Island. First, chicks observed in this northern nursery area were larger and more difficult to distinguish from adults than those farther south. This indicates that chicks in the northern part of the study area had been at sea for approximately 1 – 2 months in order to approach adult body mass (Varoujean et al. 1979). Common murres at the Gannet

Islands, farther north of the nursery area, do not finish rearing their chicks until late August (Bryant et al. 1999). Therefore, although chicks from the Gannet Islands could have reached this area by the time of my surveys (early September), chicks would have only recently left the colony and would be easily distinguished from adults. More evidence that suggests these birds had been away from the colony at least a month was the large number of murres observed flying, which may have already completed moulting (4 – 6 weeks, Birkhead and Taylor 1977). It is also possible, however, that these flying murres were females that had recently entered the area and had not begun moulting. Female murres usually occupy nest sites at the colony for 14 days after the male parent and chick leave the colony (Wanless and Harris 1986) and are known to fly to nursery staging areas and then begin the flightless moulting period (Hatch et al. 2000). I do not preclude that some flying birds were females that had recently arrived, however, the high numbers of flying adults and older chicks together indicate that at least some of the flying birds observed might have finished moulting.

Overall, the distribution of murres during pre- and post-breeding periods were similar to pre- and post-spawning migrations of capelin. Migration routes of spawning capelin are considered to be a predictable and highly abundant food source for murres and may have historically influenced the timing of breeding and colony locations (Montevecchi and Tuck 1987). The predictable nature of these routes is also supported by the little interannual variation in the distribution of murres in both the spring and fall during my surveys and other surveys conducted from 1969 – 1983 in this area (Brown 1986).

Migration routes of capelin have been relatively consistent since surveys began in the 1970s (e.g. Lilly and Simpson 2000); however, during the 1990s, capelin distribution, biology and behaviour have undergone remarkable changes (Carscadden and Nakashima 1997). Post-spawning migrations shifted farther south into nontraditional areas (1991-1997), peak spawning and migration to inshore areas has been one month later and there has been smaller fish spawning, due to smaller age 3 fish and higher proportion of age 2 fish spawning (Carscadden and Nakashima 1997, Carscadden et al. 2001). These changes coincided with variability in the vertical migration behaviour of capelin among years (Shackell et al. 1994), seasons (O'Driscoll and Rose 1999) and regions within a season (O'Driscoll et al. 2000b) in my study area. For instance, the main concentration of capelin in southern Labrador during the post-breed survey in 1999 did not show typical migratory behaviour but rather remained at depth (> 200 m) throughout the day (O'Driscoll et al. 2000b). This alteration of capelin behaviour made these high-density aggregations of capelin inaccessible to post-breeding murres.

Even though there was little spatial overlap between flightless murres and capelin in the area off southern Labrador and even though the diets of moulting birds contained higher proportions of crustaceans, I do not preclude that capelin may have historically played a more significant role in the post-breeding dispersal patterns of murres. Alterations in both the behaviour and predictability of migration routes of capelin may have significant consequences on demographic parameters of murres (Montevecchi and Myers 1992, Rowe et al. 2000). This is supported by the declining chick mass of murres at Funk Island during the 1990s (Davoren et al. 2001), which may have led to the stable population trend at Funk Island (chapter 5).

4.4.4. Summary

Overall, trends observed at fine- and coarse-scales were consistent with those observed at larger scales. As found in other studies (e.g. Schneider and Piatt 1986), the scales at which seabirds tracked their prey were highly variable (range: 0.2 – 50 km) and only around 30 % of the transects showed significant clustering of murres at prey patches. I found that differential dispersal capabilities of flightless murres compared to those that can fly was a factor causing alterations in tracking scales on the scale of prey capture and the daily foraging ambit. On a meso-scale (> 100 km), association patterns became complex and murres were not significantly clustered with prey. The obscuring of individual-level behavioural interactions between predators and prey by patterns and processes at larger, population-level scales has been demonstrated previously (e.g. Fauchald et al. 2000). The variability in individual-level behavioural interactions, however, was integrated at the population level to show that murres were qualitatively aggregated in areas of high prey density. These results have important implications for the scale of study during different periods of the annual cycle of a predator, where various constraints and dietary considerations may interact to produce variation in behavioural responses to prey distribution and densities (Ives et al. 1993).

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CHAPTER V - Consequences of foraging trip duration on parental provisioning behaviour and chick condition of common murres

5.1 INTRODUCTION

Birds that bring back food to offspring at a breeding site are central-place foragers (Orians and Pearson 1979). Provisioning effort, chick growth and subsequent chick survival is limited by the parents' ability to transport food between the feeding and breeding sites. The primary factor limiting a parent's ability to provision chicks is the time and energy expended during a round trip from the breeding site (Orians and Pearson 1979). Many factors alter travel times either directly or indirectly. Direct factors include the abundance, types and distribution of prey relative to the breeding site (Pyke 1984). Indirect factors include density-dependent competitive interactions with conspecifics on foraging grounds in the vicinity of the colony (Drent and Daan 1980) and other environmental conditions (e.g. tidal cycle, Slater 1980; sea state, Birkhead 1976). Density-dependent factors are primarily important when there are large numbers of breeders in an area, evidenced by negative relationships of reproductive performance (Wittenberger and Hunt 1985, Hunt et al. 1986, Brown et al. 1990) and per capita growth rates with increasing colony size (Lewis et al. 2001). The behavioural mechanisms causing these trends have only been studied recently (e.g. Kitaysky et al. 2000) and they are the focus of this study.

Life history theory states that parents should maximize potential lifetime fitness by balancing present and future costs and benefits of reproduction (Stearns 1992). Therefore, the provisioning efforts of parents should increase until the probability of survival is reduced, at which point, effort should stabilize (Drent and Daan 1980). Such trade-offs could produce a pattern of increased provisioning effort through modification of time budgets, until chick growth and survival decline (Cairns 1987). This is especially true for parents of long-lived species that invest heavily in individual offspring (K-selected) and are likely to favour their own survival over that of their offspring in any given year to prolong their lifespan and chances of future reproduction. In contrast, parents of short-lived species invest little in individual offspring (r-selected) and are likely to decide the opposite (Stearns 1992). Owing to these trade-offs, provisioning effort depends on the physiological state of the parent (e.g. body mass or condition, Chaurand & Weimerskirch 1994, Weimerskirch et al. 1997, Weimerskirch 1998) but may be influenced by other factors (e.g. predation risk, Harfenist 1995, Harfenist and Ydenberg 1995, Ydenberg et al. 1995). Overall, K-selected parents likely provision chicks at levels below their physiological capabilities to reduce the costs of reproduction on adult survival and to increase future reproductive chances (Drent and Daan 1980).

The common murre (*Uria aalge*) is a long-lived, colonial seabird that lays a single-egg clutch. This species breeds in large colonies both on cliff-ledges and on flat terrain and breeds at higher densities than most other avian species (Birkhead 1977, 1978). Colonies on flat terrain have the highest densities of breeders (> 10 birds/m^2) and are considered to be the highest quality habitats because they offer maximum protection from nest-predators (Birkhead 1977). Breeding common murres compete vigorously to occupy and maintain these sites (Birkhead 1985). Murres have a post-hatching development strategy that is intermediate between precocial and semi-precocial (Ydenberg 1989). Chicks are reared at the colony for approximately three weeks and depart at up to 25 % of adult body mass (Harris and Birkhead 1985). They are unable to fly or feed themselves upon colony departure and are accompanied by the male parent at sea for 2 - 3 months (Swennen 1977).

Murres deliver a single fish to their chicks after each foraging trip, which in Newfoundland is primarily capelin (*Mallotus villosus*) (Cairns et al. 1987, Burger and Piatt 1990). Capelin is a small pelagic fish that spawns on coastal beaches and in shallow water during the summer in Newfoundland (Templeman 1948). Large aggregations of capelin form inshore near beaches prior to spawning and provide dense concentrations of prey for breeding seabirds (Montevecchi 2000), large piscivorous fishes and marine mammals (Carscadden et al. 2001). Capelin is an important fish species in the Northwest Atlantic owing to its biomass dominance as a forage fish (Carscadden et al. 2001).

To gain a better perspective on provisioning constraints and life history strategies of a pursuit-diving seabird in a cold ocean regime, I compare the provisioning behaviour of common murres breeding at two colonies: (1) Funk Island, the site of the largest and most offshore colony in eastern Canada and (2) Witless Bay Ecological Reserve, the second largest colony located near-shore. Specifically, I compare: (1) prey types and frequency of delivery (amount of prey), (2) prey distribution and maximum foraging ranges, (3) parental time budgets, (4) the at-sea behaviour of adult murres near each colony and (5) the mass and condition (mass / wing length) of fledglings. I interpret inter-colony similarities and differences in terms of provisioning constraints that translate into life history strategies and subsequently influence demographic parameters of populations.

5.2. METHODS

5.2.1. Study Area

This study was conducted during 1997 - 2000 on Great Island (47°11'N, 52°49'W), Witless Bay and on Funk Island (49°45'N, 53°11'W) on the east coast of Newfoundland (Fig. 5.1). Funk Island lies approximately 60 km from the coast, whereas Great Island is approximately 2 km from the coast, and the colonies are 280 km apart. The population of common murres on Funk Island has been relatively stable in the vicinity of 340,000 - 400,000 breeding pairs (b.p.) since the 1980s (Birkhead and Nettleship 1980, Canadian Wildlife Service unpubl. data). In contrast, the population of murres in Witless Bay has increased over the last decade and is now estimated at more than 100,000 breeding pairs (Canadian Wildlife Service unpubl. data). The population of murres in Witless Bay occurs on three islands: Great Island (3,000 b.p.), Gull Island (1,000 b.p.) and Green Island (96,000 b.p.). These three colonies are within 10 km of each other and observations of returning flocks to Great Island suggest that murres at all three colonies

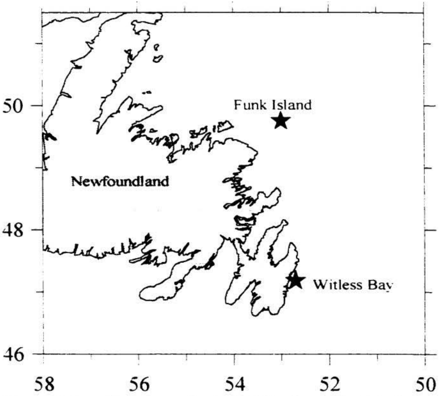

Figure 5.1 Map of the study area showing the Witless Bay and Funk Island seabird breeding colonies on the east coast of Newfoundland.

use similar feeding sites (chapter 2) Therefore, for the purposes of this paper, murres at the three colonies in Witless Bay are considered a single population.

A diversity of seabird species breed in Witless Bay and at Funk Island, most of which have high proportions of capelin in their diets (Montevecchi and Myers 1997, Regehr and Montevecchi 1997). These species include Atlantic puffins (*Fratercula arctica*), northern gannets (*Morus bassanus*) and black-legged kittiwakes (*Rissa tridactyla*). The proportion of these species breeding at Funk Island and Witless Bay vary considerably, however, the total population of capelin-feeders is similar at the two breeding aggregations (Cairns et al. 1989). Hunt et al. (1986) found that the total number of breeding pairs of species with considerable dietary overlap in an area (effective population size) is not important for considerations of competitive interactions if these species feed at different sites. Piatt (1990) showed that murres competitively exclude puffins from high-density prey aggregations in Witless Bay. Gannets and murres may feed in the same areas but gannets primarily collect male capelin and murres primarily collect female capelin (Davoren et al. 2001). Murres and kittiwakes may feed together opportunistically at mixed species feeding flocks, however, murres collect capelin in the water column, while kittiwakes feed at the ocean's surface. Therefore, the effective population size is not considered further in this paper, leaving Funk Island with a murre population 3 - 4 times larger than that at Witless Bay.

5.2.2. Colony Observations

At both colonies, 20-25 nest sites were observed in July and August of 1998 and 1999. Observations on Great Island were conducted from a blind approximately 20 m above a cliff-side colony of common murres. Yellow dye (picric acid) was used to mark breeders for individual recognition. On Funk Island, nesting pairs in a flat-ground subcolony were observed using a spotting scope from a distance of ~ 75 m. Individuals were not marked but ~ 75 % of the pairs used included bridled and non-bridled mates, making within-pair individual recognition possible. Essentially the same subcolonies were observed in both years, but different nest sites were selected in each year to increase the number of different individuals observed.

Breeding sites were observed over 4 h shifts (0530 – 0930, 0930 – 1330, 1330 – 1730, 1730 – 2130 h) during 1 - 4 shifts per day. Instantaneous visual scans (Martin and Bateson 1986) of nests were made every 15 min to record which individuals were present. Arrivals and departures of birds were recorded to the nearest minute between scans. The times that chicks were fed and the species delivered to each chick were recorded. Whole fish observed during chick feeds were allocated to one of three broad size classes: small (100 mm), medium (130 mm) and large (160 mm). Adult bill length (46 mm; Harris and Wanless 1985) was used as a size reference (Uttley et al. 1994). Fish delivered to chicks were also collected on Funk Island in 1997 - 1999 using a dipnet attached to a long pole to capture returning adults (Montevecchi and Myers 1997). The species, sex, maturity (gravid, spent, immature), total length and mass of each fish were recorded.

5.2.3. Data Analysis of Colony Observations

Arrival and departure times of each individual were used to calculate the time spent away from the colony (foraging trip duration) and percent of time mates spent paired at the colony (mate paired duration). Mean foraging trip duration was calculated for each individual over all observational periods. These were compared among colonies and years using a two-way ANOVA. Interaction terms that were non-significant (α=0.05) are not reported and all means are reported as ± 1 SE.

The mean feeding rate per h for each chick and the mean percent of mate paired duration were calculated over each 4 h period and over dawn to dusk observations (0530-2130, 4 shifts). A 4 h period was selected at each colony to compare chick-feeding rates and mate paired durations between colonies and years when the number of shifts per day were unequal. There were no interannual differences in feeding rates or mate paired duration (GKD unpubl. data) and, thus, this 4 h period was selected by pooling data for both years on each colony and comparing each 4 h period with dawn to dusk observations (Table 5.1). The 0930-1330 period was chosen because both the mate paired durations and chick-feeding rates during this 4 h shift were not significantly different from those recorded during the 16 h dawn to dusk observations on both colonies (Table 5.1). This was similar to the 1330-1730 period but the 0930-1330 period was chosen because there

Table 5.1 The mean ± SE mate paired durations (%) and chick feeding rates per h at Great Island and Funk Island colonies in 1998 and 1999 combined. N = the number of pairs observed. T-tests compared means during 4 h observation periods with those of the entire 16 h day

	% Mate paired duration					Chick feeding rate				
	Comparison with full day					Comparison with full day				
Colony / Observation Period	*n*	Mean ± SE	*t**	df	*P*	*n*	Mean ± SE	*t**	df	*P*
Great Island (inshore)										
0530-930	47	14.6 ± 1.2	1.55	71	0.126	53	0.22 ± 0.02	0.10	76	0.922
0930-1330	44	11.6 ± 1.2	0.11	68	0.915	52	0.22 ± 0.01	0.13	75	0.894
1330-1730	45	14.4 ± 1.6	0.84	69	0.402	50	0.18 ± 0.02	1.50	73	0.139
1730-2130	26	18.9 ± 2.0	2.59	50	0.013	28	0.24 ± 0.03	0.70	51	0.487
0530- 2130	26	14.1 ± 2.2	-	-	-	25	0.22 ± 0.02	-	-	-
Funk Island (offshore)										
0530-930	33	12.4 ± 2.7	0.38	76	0.707	53	0.22 ± 0.02	2.19	104	0.030
0930-1330	28	11.5 ± 1.7	0.15	71	0.883	52	0.16 ± 0.02	0.31	103	0.758
1330-1730	33	12.4 ± 2.3	0.34	76	0.735	52	0.19 ± 0.02	0.93	103	0.354
1730-2130	27	15.0 ± 2.3	1.05	70	0.296	52	0.12 ± 0.02	1.98	103	0.049
0530- 2130	45	12.7 ± 1.1	-	-	-	53	0.16 ± 0.01	-	-	-

* Two-tailed paired t-test

was less variation around the means and analyses revealed the same results using either 4 h shift. The mean mate paired durations and mean chick feeding rates per h per chick in the 0930-1330 shift were compared among colonies and years using two-way ANOVAs. The percent composition of chick diets, by number of fish delivered to chicks, was calculated at each colony. The visually estimated lengths of fish were compared between colonies and years using a two-way ANOVA.

5.2.4. At-Sea Observations

Outside of the 4 h observation periods in 1998, individuals were selected haphazardly and followed as they departed the colony (focal animal technique, Martin and Bateson 1986). At both colonies the majority of departing birds (> 70 %) landed within 1 km of the colony (chapter 2), called 'splashdown areas' (Burger 1997). The behaviour of each individual was observed and recorded for up to 5 min, or less if the individual left the area. Instantaneous scans were also conducted to compare whether the percentage of murres resting in splashdown areas differed between colonies, as it was very difficult to track focal birds for longer than 5 min due to confusion with conspecifics. Instantaneous visual scans were conducted using a 15 - 40 x spotting scope from a fixed land point. The number of murres head dipping, resting, and preening/bathing in the splashdown area were counted during three consecutive 5-min intervals.

Ship-based observations of adults at sea were conducted during chick-rearing to document the locations of the main foraging areas of murres around both colonies.

Arrival and departure directions of murres at each colony were quantified during another study (chapter 2) and were used as a basis to establish survey routes around each colony. Surveys were conducted from a variety of vessels. 8 m commercial fishing vessel *Moly Baun* (Great Island. 1998), 23 m Fisheries and Oceans Canada vessel *Shamook* (Funk Island. 2000) and a 60 m Fisheries and Oceans Canada vessel *Teleost* (Great Island 2000). Densities of seabirds at sea were estimated using standard strip transect methods (Method I, Tasker et al. 1984), where continuous counts of seabirds were conducted out to 300 m in a 90^0 arc ahead and on the port side of the ship. Counts were entered directly into a laptop computer along with behavioural descriptions (on water, feeding, flying and flight direction, flying with fish). The laptop was connected to the navigational system of the ship, and counting software designed by Fisheries and Oceans Canada (D. Senciall) was used to append the Greenwich Mean Time (GMT), latitude and longitude to each bird entry.

5.2.5. Data Analysis of At-Sea Observations

For the focal animal scans, the time spent resting in splashdown areas by each individual within a 5 min period was compared among colonies using a t-test. In addition, a χ^2 test was performed to determine whether the number of birds that left the splashdown area before 5 min and the number that stayed at least 5 min differed between colonies. For the instantaneous scans, the number of murres resting in splashdown areas during each successive 5-min scan was summed to obtain 15-min totals. The total number of murres resting did not differ throughout the day (GKD unpubl. data), so scans from all times of day were pooled. A χ^2 test was performed to determine if the number of birds resting versus non-resting (preening, bathing and head dipping) in the splashdown area differed between colonies.

Maximum foraging distances of murres from both colonies were estimated as in Cairns et al. (1987, 1990). Calculations were based on the assumptions that birds flew directly to and from foraging sites along a straight line, spent 10 % of their foraging trip flying (Cairns et al. 1990) and flew at the average speed of 60 km/h (Pennycuick 1987). Calculated potential foraging ranges were qualitatively compared with distribution of murres at sea.

5.2.6. Fledgling Measurements

The masses and wing chord lengths of chicks were recorded immediately prior to colony departure on Great Island (July 13, 15, 19, 23) and Funk Island (August 6, 10, 12) in 2000. Capelin spawning becomes progressively later with increasing latitude (Nakashima 1992), which causes delayed breeding of murres at colonies farther north relative to those farther south. This explains why my measurement periods of fledglings did not overlap temporally at the two colonies. Flattened wing chord was measured to the nearest 1 mm using a wing rule. Fledgling mass was measured to the nearest 1 g using a 500 g Pesola spring balance. Condition indices (body mass divided by wing length) were calculated for each fledgling and were compared between colonies using a t-test, while wing length and body mass were compared among colonies using a two-way ANOVA.

5.3 RESULTS

5.3.1. Amount of Prey Delivered

I identified 73 % of the 915 observed fish deliveries to chicks. Almost all were capelin at both colonies in both years (Table 5.2). Seventy-one percent of the fish that were identified were allocated to a size class. There was no significant difference in fish length among years (ANOVA, $F_{1, 469}=0.33$, $P=0.567$) or colonies (Great Island: 132 ± 2 mm, Funk Island: 135 ± 2 mm, $F_{1, 469}=0.06$, $P=0.806$). Visual observations of prey types and sizes were confirmed at Funk Island by capturing adults returning to the colony with fish. There was a high percentage of female capelin (1998: 86 %, 1999: 98 %) and fish lengths were similar to those observed (1998: 139.4 ± 1.4 mm, $n=101$, 1999: 144.7 ± 1.6 mm, $n=62$). Chick-feeding rates, however, were significantly higher at Great Island than at Funk Island (ANOVA, $F_{1, 100}=8.76$, $P=0.004$, Table 5.3). There were no significant differences in chick-feeding rates among years ($F_{1, 100}=3.53$, $P=0.063$, Table 5.3).

5.3.2. Maximum Foraging Distances

Most murres appeared to forage within 100 km of each colony (Fig. 5.2). At Funk Island, foraging distances peaked at 40 - 70 km from the colony in both years (Fig. 5.2). These estimated maximum distances corresponded to the three high-density areas of murres on the water observed during a boat survey on July 18 - 22, 2000: 45 km, 60 km and 90 km (Fig. 5.3, chapters 2 and 3). Murres with fish in their bills ($n=98$) were only observed in

Table 5.2 The percent by number of known fish species delivered to common murre chicks that were visually identified at Great Island and Funk Island in 1998 and 1999. The number of prey items, or sample size, is given in parentheses

	1998		1999	
Prey Species	Great	Funk	Great	Funk
Capelin	94 % (225)	100 % (34)	99 % (94)	85 % (257)
Male	3 % (6)	0 (0)	0 (0)	0 (0)
Female / Immature	91 % (219)	100 % (34)	99 % (94)	85 % (257)
Sandlance	6 % (15)	0 (0)	1 % (1)	15 % (46)

Table 5.3 Comparisons of parent resting times, chick-feeding rates and chick measurements of common murres from this study and similar studies involving intercolony or interannual comparisons. All data are reported as mean ± SE or range and only values for dawn to dusk watches are used unless otherwise indicated. Other fledging masses are 202 g (Johnson 1944), 250 g (Pearson 1968), 215 g (Birkhead 1976, 1977), 253 g (Belopol'skii 1957), 274 g (Cody 1973) and 208 g (Johnson and West 1975).

Colony/Year	% Mate paired duration in daylight	Chick feeding rate (fish/hr)	Chick measurements	Author (s)
Great I, Newfoundland (1998-2000)	11.9 ± 1.4 (1998) 11.4 ± 1.9 (1999)	0.22 ± 0.02 (1998) 0.22 ± 0.02 (1999)	Fledgling mass 245.4 ± 4.1 g^{1} (2000) Fledgling condition 3.9 ± 0.1 g/mm^{1}	This study
Funk I, Newfoundland (1998-2000)	14.6 ± 4.0 (1998) 10.6 ± 2.0 (1999)	0.10 ± 0.02 (1998) 0.17 ± 0.04 (1999)	Fledgling mass 191.6 ± 4.0 g^{1} (2000) Fledgling condition 2.9 ± 0.1 g/mm^{1}	
Gull I, Newfoundland				Burger & Piatt 1990
(poor food year 1984)	19.4 ± 9.7 (1984)	0.29 ± 0.02 (1984)^{2}	Fledging success 100 %	
(good food yr 1983, 85)	33.5 ± 10.8 (1983)^{2} 28.4 ± 13.0 (1985)^{2}	0.24 ± 0.02 (1983)^{2} 0.26 ± 0.03 (1985)^{2}	Fledging success 82 % Fledging success 92 %	
Skomer I, Wales (1985 - 87)	-	0.20 ± 0.01	Fledging mass 211.6 ± 2.1 g	Hatchwell 1991
(1973 - 75)	-	0.17 ± 0.01	Fledging mass 214.9 g	Birkhead 1976, 77
Sumburgh Head,				Uttley et al. 1994
Shetland (good food year 1991)	40 (range 6 - 78)	0.31 ± 0.01	-	
(poor food year 1990)	2.4 (range 0 - 18)	0.15 ± 0.01	-	

Table 5.3 continued

Colony/Year	% Mate paired duration in daylight	Chick feeding rate (fish/hr)	Chick measurements	Author (s)
Chisik I, Alaska	3 - 5 (late & early)	0.29 ± 0.03	Condition Index: 3.7 ± 0.2 g/mm	Zador & Piatt 1999
Gull I, Alaska	7.8 (late) 28 - 32 (early)	0.37 ± 0.05	Condition Index: 4.2 ± 0.2 g/mm	
Gannet Is, Labrador (1981-83)	-	0.18 - 0.28 [2,3]	Fledging success: 95-97 % [3] Fledging mass: 238 ± 2.2 g	Birkhead & Nettleship 1982, 85, 87
(1996-97)	-	0.21 - 0.28 [2,3]	Fledging success: 96-97 % [3] Fledging mass: 233 ± 9.4 g	Bryant et al 1999
Stora Karlso, Baltic Sea	-			Hedgren &
(Control)		0.11 ± 0.02	Fledging mass: 255 - 260 g	Linnman 1999
(Experimentally Delayed)		0.14 ± 0.03	Fledging mass: 220 g	

[1] Significant differences in chick measurements between years or colonies

[2] Calculated from 4 hr observation periods

[3] Values estimated from figures

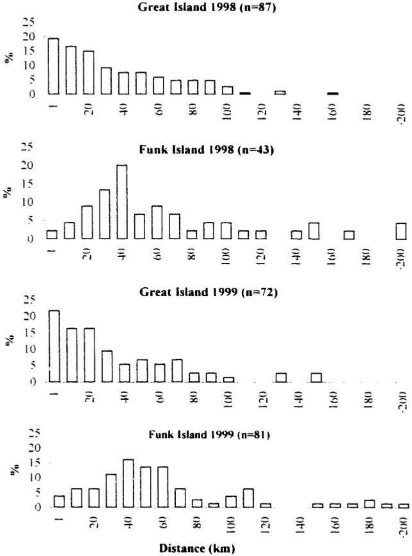

Fig 5.2 The percent frequency of maximum potential distances of foraging trips preceding deliveries of fish to chicks by common murres at Great Island and Funk Island during 1998 and 1999. The number of foraging trips observed at each colony in each year is represented by n.

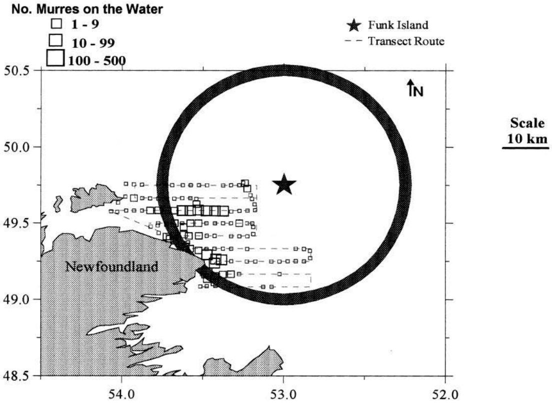

Fig. 5.3. Map of the survey area around Funk Island on July 18-22, 2000. Bird counts are binned into continuous 4.5 km blocks and the 100 km foraging range from the colony is indicated.

these three areas, which were associated with high-density capelin aggregations (chapters 2 and 3).

The majority of murres foraged closer to Great Island, with a decline in the number of birds flying farther than 30 km (Fig. 5.2). Three 40 km boat surveys around Great Island on July 20, 24 and 26, 1998 revealed high densities of murres on the water ~ 5 km north of the colony in Mobile Bay (Fig. 5.4). Eighty-two percent of murres with fish in their bills (n=49) were also observed in Mobile Bay. High-density capelin aggregations occurred in Mobile Bay where systematic observations showed it to be an important foraging area for murres (chapter 2).

Due to the restricted nature of the transects in Witless Bay, I conducted 3 additional transects on May 27, 30 and June 2, 2000, when murres were incubating. I did not observe any murres in a previously identified 'hot spot' (70 km southeast of Great Island, Schneider et al. 1990, Fig. 5.4). In fact, relatively few birds were observed on the water during any of these transects farther offshore. I do not preclude that murres foraged between my inshore and offshore transects; however, most murres appeared to be concentrated along the coast (see also Schneider et al. 1990 and Cairns et al. 1987, 1990).

5.3.3. Parental Time Budgets

There was no significant difference in mate paired durations during 0930 – 1330 shifts among colonies ($F_{1,67}$=0.004, P=0.953) or among years ($F_{1,67}$=0.99, P=0.322; Table 5.3).

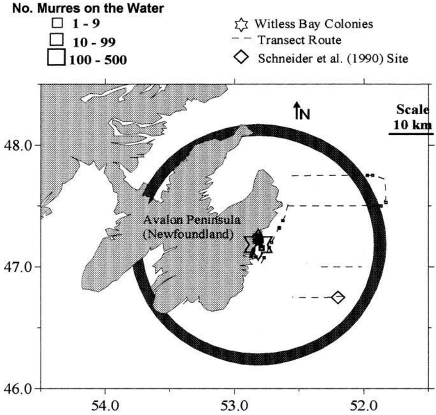

Fig. 5.4. Map of the survey area around Great Island on July 24, 1998; May 26 and 29, 2000; and June 2, 2000. Bird counts are binned into continuous 4.5 km blocks and the 100 km foraging range is indicated.

Mean foraging trip durations per individual were significantly longer at Funk Island (1998: 244.9 ± 42.5 min, 1999: 214.6 ± 21.8 min) than at the Great Island (1998: 163.3 ± 1.5 min, 1999: 147.6 ± 12.1 min, $F_{1,179}=11.10$, $P=0.001$) but there were no interannual differences ($F_{1,179}=1.19$, $P=0.276$). During colony observations, chick loss due to predation was not observed among study pairs but was observed in surrounding areas. Herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*) were always present on the periphery of all study sites and also preyed and scavenged on unattended and abandoned eggs.

5.3.4. Splashdown Behaviour

Upon landing in splashdown areas adjacent to each colony, murres departing from breeding sites began immediately to preen, bathe and head dip. Significantly more birds left the splashdown area before the first 5 min at Funk Island (50 %, n=20) compared to the Great Island (11 %, n=38, $\chi^2_1=9.10$, $P<0.001$). Of the murres that departed within the first 5 min, those at Great Island rested significantly longer after preening/bathing but before departing (74.5 ± 5.9 s) than those at Funk Island (2.8 ± 0.5 s; t-test: $t_{12}=21.24$, $P<0.0001$), suggesting that murres spent less time resting in the vicinity of Funk Island. Instantaneous visual scans corroborated this result: a significantly lower percentage of murres were resting in the splashdown area at Funk Island (36 ± 3 %, number of scans = 38) compared to Great Island (47 ± 2 %, n=37; $\chi^2_1=104.15$, $P<0.001$).

5.3.5. Fledgling Condition

Fledging murres had a significantly higher condition index at Great Island (n=35) compared to Funk Island (n=43, *t*-test: $t_{76}=2.31$, $P<0.0001$, Table 5.3). These differences were due primarily to significantly higher body masses at Great Island compared to Funk Island ($F_{1,76}=86.98$, $P<0.0001$, Table 5.3), whereas wing lengths were similar at Great (63.1 ± 1.3 mm) and Funk Islands (66.3 ± 1.1 mm; $F_{1,76}=3.84$, $P=0.058$; Fig. 5.5).

5.4. DISCUSSION

Prey items delivered to chicks were similar at both colonies but feeding rates of chicks were lower at Funk Island compared to Great Island. The lower feeding rate of chicks at Funk Island can be explained by longer foraging trip durations or potentially farther foraging distances compared to Great Island. Murres may visit a number of locations on a foraging trip (Wanless et al. 1990, Benvenuti et al. 1998), resulting in the duration of a foraging trip being a poor indicator of foraging ranges. Foraging trip durations, however, are positively correlated with distances flown from the colony to foraging areas in other seabirds (Lewis et al. 2001). In support, my estimated maximum foraging distances from both colonies corresponded well with observed distributions at sea. Parents did not compensate for the longer foraging trip durations at Funk Island by decreasing the time spent paired at the colony. The shorter resting periods in the splashdown area combined with longer foraging trips at Funk Island suggest that murres were working harder to provision chicks compared to Great Island. Overall, this resulted in chicks having a

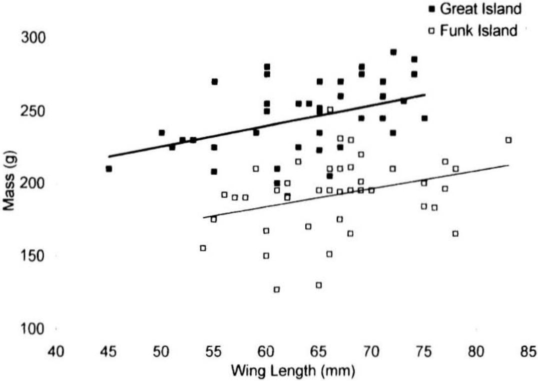

Fig. 5.5 Relationship between body masses and wing lengths of common murre fledglings at Great and Funk Islands in 2000. Funk Island fledglings $r = 0.335$, $n = 43$, $P < 0.02$, $y = 1.2x + 108.8$. Great Island fledglings $r = 0.432$, $n = 35$, $P < 0.005$, $y = 1.4x + 154.4$

significantly lower body mass and condition prior to colony departure at Funk Island compared to Great Island.

5.4.1. Foraging Trip Durations and Maximum Foraging Distances

Longer foraging trip durations at the larger, offshore colony (Funk Island) relative to the smaller, inshore colony (Great Island) were partly responsible for lower chick-feeding rates and poorer fledgling condition. The duration of a foraging trip may reflect both the consumption rates of prey at sea and the distance to foraging areas. The 3 - 4 times higher concentration of murre competitors on foraging grounds around Funk Island compared to Great Island may reduce an individual's foraging efficiency in at least two ways. Competitors may interfere with the foraging activities of others (Hoffman et al. 1981, Shealer and Burger 1993), resulting in reduced intake rates of prey (e.g. Stillman et al. 1996, Creswell 1997, 1998) or individuals may avoid areas with high competitor density (e.g. Davoren and Burger 1999). Competitors also may directly depress prey abundance within foraging ranges by depleting prey bases near colonies (Birt et al. 1987), causing individuals to fly to more distant foraging areas. Positive correlations between colony size and foraging range (Gaston and Nettleship 1981, Wittenberger and Hunt 1985) and colony size and foraging trip duration (Lewis et al. 2001) have been documented. Foraging ranges are also heavily dependent on prey distribution (Kitaysky et al. 2000). In support, the distribution of murres around both colonies corresponded to that of capelin, their main prey species (chapters 2 and 3). Capelin spawn primarily on or near beaches during the summer in Newfoundland and, thus, their distribution is primarily driven by the proximity to suitable beaches (Carscadden 1982, chapter 3). This near-shore distribution of capelin resulted in foraging areas being closer to the smaller, inshore colony (< 5 km) compared to the larger, offshore colony (40 - 60 km; chapter 2). Overall, a combination of longer distances to capelin aggregations and higher avian densities within foraging areas may have contributed to increased foraging trip durations from Funk Island compared to Great Island.

5.4.2. Provisioning Behaviour and Life History Strategies

Even though parents made longer foraging trips, they did not reduce the time spent paired with mates at Funk Island relative to Great Island. This paired time at nest sites is usually referred to as off-duty, resting or 'buffer' time, due to the parents' ability to adjust this when more time and energy is required for self-feeding and chick-provisioning ('time-buffering hypothesis', Burger and Piatt 1990). The percentage of time murres spent paired with mates at both colonies was well within ranges reported in the literature for this species (Table 5.2). So why didn't parents at Funk Island reduce this paired time to increase food delivery rates to chicks?

Murres at Funk Island breed in flat-ground colonies at much higher densities than the cliff-nesters at Great Island (Montevecchi and Tuck 1987). Aggressive interactions are more frequent in high-density areas owing to higher encounter rates among individuals and also because they are the highest quality sites due to the reduced risk of predation (Birkhead 1977). Aggressive interactions at breeding sites peak in chick-rearing, possibly due to high numbers of prospecting birds at the colony (Birkhead 1985). Parents that are brooding chicks avoid aggressive interactions by making high proportions of appeasement displays (Birkhead 1985). This may prevent the chick from being injured or lost during hostile interactions among adults. When both parents are at the breeding site, the non-brooding parent initiates and engages in most of the aggressive interactions towards other individuals entering its breeding site (Birkhead 1978). Therefore, if the maintenance of a breeding site depends on how vigorously it is defended, the time a non-brooding parent is in attendance will be important. Overall, the paired time at Funk Island may reflect a minimum amount of time required to maintain breeding sites when breeding at high densities and may not be as flexible as in other colonies where murres nest at lower densities.

The maintenance of breeding sites and pair bonds are important because they influence future reproductive output. For instance, if a breeding site is lost, there is a high probability that individuals will not breed during the next year (Harris et al. 1996). Furthermore, if pairs divorce, individuals must find new mates and breeding sites (Harris et al. 1996). Therefore, maintaining breeding sites and pair bonds by sustaining the time spent paired at the colony with mates reflect provisioning constraints imposed by higher breeding densities, which result in a life history strategy that outweighs the potential for future reproductive output over current efforts.

Alternately, the maintenance of this 'buffer time' at Funk Island may reflect provisioning constraints imposed by longer foraging trips. Murres reduce 'buffer time' when increased energy must be expended to maintain self-feeding and chick-provisioning (Burger and Piatt 1990, Bryant et al. 1999, Finney et al. 1999). When a threshold level of energy expenditure is reached during provisioning, parental murres appear to maximize their own fitness while compromising that of their chicks (Cairns 1987, Uttley et al. 1994). This threshold may be species-specific and may not vary among environments (Obst et al. 1995). The decision of a parent to favour its own survival over that of its chick is not surprising for long-lived species because it maximizes future reproductive potential (Trivers 1974, Charnov 1982). Murres at Funk Island seemed to work harder to provision chicks compared to Great Island. In addition, the provisioning rates at Funk Island were sufficiently low to result in lower chick condition compared to Great Island. This all suggests that murres at Funk Island may be working at or near a threshold level of provisioning behaviour, at which they decide not to reduce the buffer time but rather to favour their fitness over that of their chick. In comparison, murres at Great Island may have been working below this threshold and, thus, maintained chick condition.

5.4.3. Fledgling Condition and Survival

Poor condition and low body mass of fledglings may reduce the chances of survival during the first winter at sea. No significant relationship, however, has been found between fledging mass and the probability of being resighted at the colony in future years (Hedgren 1981, Harris et al. 1992). Growth rates are higher at sea (Birkhead 1977, Varoujean et al. 1979), however, attaining an adequate wing length is important for safe transition from nesting ledges to the sea (Gilcrest and Gaston 1997). These together suggest that there is a trade-off between wing growth at the colony and mass gain at sea. Higher provisioning constraints at Funk compared to Great Island may lead to a shift in this trade-off, with slow-growth chicks at Funk Island fledging younger and at lower masses than chicks at Great Island (Hipfner and Gaston 1999). Moving chicks to the food source, rather than bringing food to chicks, may be the only way for fledglings from Funk Island to attain an adequate body mass before independence from adults at sea (Bayer et al. 1991) and the onset of winter (Harris et al. 1992). In support, the duration of chick development at the breeding site is shorter at large colonies than at small ones (Gaston and Nettleship 1981, Hunt et al. 1986). Other researchers have predicted that slower-growing murre chicks will fledge at an older age and lighter mass (Ydenberg 1989), however, growth and mortality rates at the colony and at sea may vary among and within species under different conditions (Gaston 1998, Ydenberg 1998).

Despite the relevance of growth at the colony versus at sea to the subsequent survival of fledglings, the mass and condition of fledglings at Funk Island were the lowest reported in the literature for common murres (Table 5.2). The poor condition of fledglings corresponds to the stable population trend at Funk Island, while the higher condition of fledglings at Great Island corresponds to the growing population in Witless Bay. Body mass reflects energy reserves, or fasting endurance (Hatch 1983), and a higher surface area to volume ratio is important for thermoregulation once fledglings are at sea (Lustick

1984). Together this evidence suggests that the low body mass of fledglings at Funk Island has led to lower recruitment into the breeding population.

5.4.4. Population Dynamics

If fledgling survival is lower at Funk Island due to higher foraging and provisioning constraints, then why do murres continue to breed there? Breeding murres may remain at Funk Island for many reasons. First, the costs of moving to another colony (e.g. breeding site establishment) may reduce future reproductive output below that experienced at larger colonies (Brown et al. 1990). This is supported by the high breeding site fidelity reported at other colonies (91 %, Harris et al. 1996). Second, larger colonies may permit greater public information exchange, owing to higher numbers of individuals accumulating and perpetuating social information about foraging sites (Ward and Zahavi 1973, Gaston and Nettleship 1981, Buckley 1997, Parrish and Edelstein-Keshet 1999). Higher rates of information availability may reduce variation in breeding success among years (Wooller et al. 1992), which may be more important to birds than maximizing average breeding success (Brown et al. 1990, Caraco et al. 1995). Third, Funk Island is distant from shore, which may reduce human or other mammalian and avian predation and disturbance (Montevecchi and Tuck 1987). In general, restricted mobility of individuals among colonies will tend to result in large colonies, where lifetime reproductive success is not maximized (Sibly 1983, Brown et al. 1990).

It is also possible that many first-time breeders do not recruit to Funk Island. Immature murres ('prospectors') are known to visit both nearby (< 350 km) and distant colonies (>350 km) before becoming sexually mature (Halley and Harris 1993). These visits may allow assessment of habitat qualities (e.g. food abundance, nest density) at different colonies, possibly by appraising conspecific cues (Forbes and Kaiser 1994, Danchin and Wagner 1997). This is supported by the high number of prospecting murres present at colonies during chick-rearing (Halley and Harris 1993), when fitness enhancing cues on nesting habitat quality (e.g. chick condition) would be most reliable (Wooller et al. 1992). Murre populations show low genetic variation, possibly indicating that colonies are not discrete populations (Moum et al. 1991, Birt-Friesen et al. 1992, Wooller et al. 1992). Dispersal of first-time breeders from Funk Island to Witless Bay, which are 280 km apart, may also help explain the stable versus the increasing population trends at these colonies, respectively.

5.4.5. Summary

Conservation and management of populations require detailed knowledge of the underlying behavioural mechanisms leading to changes in demographic parameters (Forbes and Kaiser 1994). Density-dependence, both while foraging at sea and rearing chicks at the colony, and prey distribution at the largest murre colony in eastern Canada resulted in augmented provisioning constraints relative to a smaller colony. Additional provisioning constraints at the larger colony subsequently led to parents at the larger colony outweighing future over present reproductive output, while those at the smaller colony were able to focus on current reproductive efforts. This resulted in reduced condition of fledglings, possibly resulting in a combination of lower survival and increased recruitment to other colonies, evidenced by the stable population trend at the larger colony versus an increasing trend at the smaller colony. Funk Island is the breeding site of approximately 85 % of the common murres in the Northwest Atlantic (Cairns et al. 1989). Therefore, lowered potential for population growth at this colony will impact the entire Northwest Atlantic population of common murres. Integrating the interactions of provisioning behaviour, life history strategies, and prey distribution with colony size will help refine population models and increase understanding of population dynamics at a range of breeding aggregations.

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CHAPTER VI - DISCUSSION

In this thesis, I examined how the behaviour of capelin and the physical characteristics of their schools influence the multi-scale search strategies and selection of foraging habitat by murres. I also described the variability in the scale at which murres track capelin in different periods of their annual cycle and identified some factors causing this variability. Finally, I examined how changes in capelin behaviour, biology and distribution affect demographic parameters of murre populations. The following sections are an integrated account of the results and conclusions from all four chapters.

6.1 BEHAVIOURAL RESPONSE OF MURRES TO CAPELIN

During the breeding and the pre-breeding periods, murres were clustered around breeding colonies, compared to the post-breeding period. This is not surprising because murres are central-place foragers during breeding and pre-breeding periods and, thus, are constrained by the time and energy expended during round trips from the colony (Orians and Pearson 1979). During the pre-breeding season, murres visit the colony daily (Wanless and Harris 1986) but are not feeding chicks and, thus, are less constrained than during breeding due to the lower frequency with which they need to return to the colony. This might explain the more dispersed distribution patterns around breeding colonies during pre-breeding compared to when breeding. During post-breeding murres and fledglings became even more dispersed over the shelf away from colonies, as found in other regions (Gaston

1982, Hope Jones and Rees 1985), however, many individuals were found aggregated in a high prey density area father north of the main breeding colony (Funk Island).

The numbers of murres at prey aggregations were much higher during breeding than pre- and post-breeding periods. The concentration of birds with similar food habits around breeding colonies can lead to increased competition for food resources. Most studies on seabird competitive interactions have focused on interactions among birds within feeding flocks (e.g. Shealer and Burger 1993, Balance et al. 1997, Mills 1998) or on prey depletion around colonies (e.g. Birt et al. 1987). Small-scale interference and avoidance behaviour of seabirds interacting outside of feeding flocks, however, has received little attention. Unlike other studies, coordinated feeding flocks (Hoffman et al. 1981) were rarely observed in my study area (chapter 2). Even though murres were consistently found in high densities at stable aggregations of capelin, the majority of individuals (62 %) were not found within a 300 m^2 area of another murre. This suggests that even though murres are highly concentrated around breeding colonies on a meso-scale and maintain visual contact with one another (network foraging, Wittenberger and Hunt 1985), they have a tendency towards a uniform distribution at finer spatial scales (chapter 3). Further investigation of the mechanisms (e.g. avoidance or aggressive behaviour) influencing more uniform distributions at small scales is needed. This will contribute significantly to our understanding of the mechanisms influencing competition among colony members and how this results in population regulation by subsequently affecting time budgets, provisioning efforts, breeding success and, ultimately, adult survival (Cairns 1987, Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994).

During the breeding season, the scale of aggregation of murres was much larger (7.3 ± 1.8 km, n= 4) than during pre-breeding (3.7 ± 1.5 km, n=16) and post-breeding (0.4 ± 0.1 km, n=37). Capelin, however, had similar scales of aggregation during pre-breeding (2.8 ± 1.3 km, n=13), breeding (3.3 ±0.8 km, n=4) and post-breeding seasons (3.1 ± 0.5, n=22). Therefore, during breeding and pre-breeding, aggregations of murres were larger than capelin aggregations, whereas the opposite was true during post-breeding. This indicates that murres maximized encounter rates with prey during breeding and pre-breeding periods but not as much during post-breeding. In support, the scales at which murres tracked their prey were small and less variable during the breeding (0.8 – 5.1 km) and pre-breeding periods (0.5 – 23.4 km), compared to post-breeding (0.2 – 50.0 km).

Overall, the reduced dispersal capabilities of flightless murres during post-breeding may have hindered their ability to maximize encounter rates with prey relative to other parts of the year. Divergent locomotory constraints during these different periods likely result in a variety of spatial scales at which birds perceive their foraging environment (Kotliar and Wiens 1990). Murres with higher dispersal capabilities likely have knowledge of prey patch locations and qualities over larger spatial scales than when flightless. Locomotory constraints and knowledge of prey patch locations on smaller spatial scales might result in murres using different search strategies and criteria to select foraging habitats. For instance, flightless murres formed high-density aggregations, where individuals were closely spaced, compared to murres that can fly, possibly reflecting a tendency to use social foraging techniques (local enhancement, network foraging, Wittenberger and Hunt 1985) to locate prey patches (chapter 2). In addition, flightless murres appeared to prefer foraging habitats with low inter-patch distances (chapter 4). Another explanation for the variable scales at which murres track their prey is deviating energetic requirements during these periods. Chick-rearing is thought to be the most active and, thus, energetically expensive period of the year for most birds (Drent and Daan 1980), followed by pre-breeding and finally by post-breeding (moult, Murphy and King 1992). Therefore, larger tracking scales of flightless murres to capelin may suggest that during post-breeding, the energetic costs of tracking prey at small scales is greater than the benefits. Very little, however, is known about the energetic costs of moult in seabirds or waterfowl (Adams et al. 2000). A critical area for future research is to determine whether the post-breeding period acts as a bottleneck to survival for both moulting adults and growing chicks at sea (Birkhead 1974, Holdgate 1971, Bayer et al. 1991).

Search is more efficient if prey aggregations are predictably located in space and time or individuals can cue to the foraging activities of others. It is for these reasons and the high metabolic demands of seabirds that seabirds at sea are generally patchily distributed with a high proportion of birds encountered in a few large, dense prey aggregations ('hot spots', Schneider 1991). My results support the contention that predictable aggregations of prey are important on short temporal and small spatial scales (e.g. foraging trip;

chapter 2) and on long temporal and large spatial scales (e.g. post-breeding dispersal, chapter 4). In addition, local enhancement also appears to be important in increasing search efficiency at fine scales within areas where prey might be predictably located on a large scale but aggregations are ephemeral at smaller scales (chapter 2).

Using memory and social foraging techniques may lead to deviations from optimal distributions (e.g. Ideal Free Distribution, IFD, Fretwell and Lucas 1970). For instance, using memory of fixed foraging locations could lead to perseveration (Pinel 1997), where birds continue returning to food patches despite their depleted condition. This behaviour would likely be extinguished after a number of visits to an area with low prey density; however, before this behaviour was extinguished, I might observe high bird densities in areas of low prey density. In addition, if some prey patches are predictable in time and space, predators likely reduce the amount they sample for other prey patches. This may cause larger scale associations between predators and prey, compared to when prey patches are ephemeral and predators need to continuously track the movement of their prey (chapter 2). In addition, visually cueing to the foraging activities of other conspecifics (local enhancement, Wittenberger and Hunt 1985), as opposed to physical sampling, appears to lead to the use of low prey density patches that are near high prey density patches, while isolated patches of high density are ignored (Mehlum et al. 1996, chapter 3). Therefore, reduced physical sampling of the foraging environment through the use of memory or local enhancement may lead to 'undermatching' at the population level, or the under use of high-quality patches and overuse of lower-quality patches

(Kennedy and Gray 1993). This phenomenon is the most widespread deviation from the IFD reported in the literature (Kennedy and Gray 1993).

I showed in this thesis that murres at breeding colonies do not cue to the flight trajectories of conspecifics returning to the colony to locate foraging areas outside of visual range of the colony (chapter 2). Burger (1997) showed that birds landed on the water in the vicinity of colonies ('splashdown area') after long-periods at the nest site and hypothesized that individuals could readily observe and track the returning flight paths of "successful" individuals, or those carrying a fish ('Information Halo', Burger 1997). I propose instead that this area is important for cueing to feeding flocks within visual range of breeding colonies and for cleaning feathers after being at the nest site for extended periods. With the continued lack of support for the Information Center Hypothesis (Bayer 1982, Mock et al. 1988), I propose that future studies on colonial birds should focus on multi-scale search tactics using both vessel-based (e.g. Veit 1999) and device-based techniques (e.g. Weimerskirch 1998). Individuals will likely use a variety of mechanisms to locate prey at different spatial scales ('behavioural cascades', Russell et al. 1992) and understanding how these are combined into various strategies is essential in determining how seabirds will respond to varying prey conditions (Veit et al. 1993). This will generate knowledge of how behavioural responses of predators to prey result in fluctuations of predator populations.

6.2 NUMERICAL RESPONSES OF MURRES TO CAPELIN

Low feeding rates of chicks and, thus, the poor condition of fledglings at the species' largest colony in eastern Canada (Funk Island) appeared to result from long foraging trip durations and maintaining the time mates spend paired at nest sites. Burger and Piatt (1990) hypothesized that the time mates spend paired at the colony is flexible and that parents can adjust this time to increase foraging effort under poor prey conditions up to some limit ('time-buffer hypothesis'). I propose that the time mates spend paired at high density breeding sites, such as large, flat-ground colonies of murres (Birkhead 1977, 1978), constrains the degree of flexibility due to the time required to defend and maintain breeding sites. This suggests that adults at high and low density breeding sites might use different provisioning strategies under varying prey conditions and, thus, responses to altered prey conditions will be complex and not necessarily consistent among colonies (Obst et al. 1995).

Chick mass upon departure from Funk Island was the lowest reported in the literature to date (chapter 5). Cairns (1987) hypothesized that reduced prey conditions will sequentially alter time-budgets, reduce breeding success and finally reduce adult survival. I documented altered time-budgets (e.g. adults working harder than at other colonies) and presumably lower breeding success (e.g. lower condition of fledglings), which appear to have led to a stabilized population trend at this colony. Whether reduced adult survival or other factors (e.g. emigration) have contributed to this trend remains to be determined. Whether the stabilized population trend is a result of an 'over-sized' population (competition) or the changing biology and behaviour of capelin in the 1990s or a combination of these factors is another important avenue of future research. Murres have responded to delayed spawning dates of capelin by breeding two weeks later (Montevecchi and Myers 1992). In addition, the condition of murre chicks has declined significantly throughout the 1990s simultaneously with the decline in the mean length of spawning capelin (Davoren et al. 2001). It is also possible that the southerly shift in the distribution of capelin during the fall from 1991 - 1997 may have led to reduced adult survival during moulting. The predictable nature of capelin aggregations during the moulting period is likely important due to the low dispersal capabilities of murres and, thus, the reduced rate at which they can search for prey. Murres breeding at Funk Island represent 85 % of the Northwest Atlantic population and, thus, higher adult morality and lower potential for growth at this colony would impact the entire population. I stress the imminent need for long-term monitoring/research programs at this breeding colony (Gaston et al. 1983, 1994). I also emphasize the need to understand the bio-physical mechanisms driving recent changes in the behaviour, biology and distribution of capelin, along with the determination of accurate biomass estimates.

6.3 FUTURE RESEARCH

Although I have highlighted many gaps in current scientific knowledge above, there are a number of more general areas that I would like to outline for future research. First, I follow other authors in emphasizing the importance of scale in behaviour-based and pattern-based studies examining predator-prey interactions (Schneider 1994, Wu and

Loucks 1995). Second, I emphasize the importance of studying individual-based foraging decisions to understand population-level patterns. Specifically, device-based studies of foraging behaviour are important to directly elucidate foraging decisions of individual seabirds (e.g. Weimerskirch 1998). A foraging study on seabirds, however, can only be comprehensive through the integration of colony-based (e.g. diets), device-based (e.g. foraging strategies) and vessel-based (e.g. distribution and behaviour of birds and prey) techniques. In addition, research must cover a range of species, from small marine invertebrates (e.g. copepods, euphausiids) to avian and mammalian predators, to gain a better impression of ecosystem-level patterns and processes and bio-physical linkages between marine trophic levels.

Although I emphasize the importance of device-based studies, researchers should embark on these studies only after much consideration. Failures of research techniques often go unreported in the literature but the dissemination of this knowledge is critical so that future researchers do not make similar mistakes. I attempted to use radio-telemetry to directly examine whether murres returned to specific foraging sites while rearing their chicks, as evidence of memory use (e.g. Irons 1998). I was unsuccessful because all murres outfitted with devices (Great Island, Witless Bay n=7, Funk Island n=3) did not continue to breed and, thus, either traveled outside the limits of my detection range or died. Devices were 16 g with a 25 cm antenna and, thus, were within the acceptable 5 % of the adult body mass (950 g). Attachment methods were standard: external attachment to feathers on the back using 5 min epoxy (e.g. Wanless et al. 1990, Croll et al. 1992, Ollason et al. 1999). So why did this device-based study fail? My impression was that handling of murres was not a problem. Murres at the study sites had continued to breed normally after being captured for blood sampling and colour marking. This suggested that the acceptable 5 % of body mass may be too high for murres, due to their high wing-loading. This was the conclusion of another study using 35 g devices on murres (Meyers et al. 1998). One problem with this was that Cairns et al. (1987, 1990) attached smaller devices with a combined mass similar to my devices at the same study colony and this did not appear to affect breeding or foraging behaviour. The length of the antenna was unlikely a problem because similar-sized antennae have been successfully used (Wanless et al. 1990, cf. Bannash et al. 1994). Overall, there appears to be highly variable individual responses to the attachment of devices within species at different colonies (S. Benvenuti and S. Garthe pers. comm.). These considerations are important for device-based research in the future and I generally conclude that every effort should be made to minimize disturbance during research activities.

Finally, I emphasize the importance of determining actual fish density through the use of sophisticated hydroacoustic techniques. I was unable to do this during my research because I either was unable to capture sophisticated hydroacoustic data electronically (chapters 2 and 3) or was unable to accurately sample the species composition of acoustic signals (chapter 4). Without electronic data capture, researchers are reduced to merely examining the presence or absence of marine organisms. In order to scale electronically captured data to estimate fish abundance, the mean target strength of the various species causing the scattering must be determined (Rose 1992). Variations in target strength within and among species are considered to be among the largest sources of error in estimates of fish abundance (Rose and Porter 1996). Therefore, both the species composition of schools must be determined along with the target strength for the length range of each species (Rose 1992). I follow other researchers in emphasizing the importance of using electronically captured hydroacoustic data combined with regular sampling to obtain accurate target strength information for different species throughout a survey (Rose 1998). Overall, the key factors that cause uncertainty in fish abundance estimates from hydroacoustic measures should be addressed prior to the survey in the study design (Rose et al. 2000).

6.4. IMPLICATIONS FOR CONSERVATION

An important by-product of this study was the description of the distribution of murres and capelin during three periods of the year on the eastern Newfoundland Shelf. This information is critical to provide baseline data on seabird and fish populations at sea during the 1990s (Veit et al. 1996) for comparison with earlier surveys (e.g. Brown 1986, Lilly and Simpson 2000) and surveys in the future. This information is also essential to identify key habitats where birds congregate during different times of the year. A number of important foraging areas were identified in this study. During breeding, murres from Funk Island were predominantly found southwest of this colony in three areas: along the Straight Shore on the northeast coast, Wadham Islands and Cape Freels North. In July 2000, I found hundreds of drowned common murres floating near fishing gear (i.e. gill nets) around Cape Freels North, most of which were breeding adults (see chapters 2, 3). This illustrates the sensitivity of key inshore foraging areas to human fishing activities. Another area that appears to be critical is the southeastern coast of Labrador during the fall, due to the high concentration of flightless adults and chicks. An encounter of birds having limited dispersal capabilities with fishing gear or oil from a spill would be catastrophic, killing a large proportion of the breeding adults. The rise in hydrocarbon development on the Grand Banks in recent decades has led to an increasing oiling rate of seabirds at sea (3 % per year, Wiese and Ryan 1999), primarily due to increasing shipping activity and, thus, increased chronic illegal dumping of oily bilge water. These realized and potential bird-human interactions illustrate the imminent need for these marine areas to be designated as Important Bird Areas (Canadian Nature Federation) and/or Ecological Reserves (Provincial Ministry of Parks and Tourism) to reduce negative impacts of human activities on birds during these critical periods of their annual cycle.

With changing species interactions in the marine environment worldwide due to over-fishing and ocean climate change (Safina 1995, Pauly et al. 1998), it is becoming increasingly important to enhance my understanding of processes acting within marine ecosystems. It is important for humans to change their perception of marine systems from unlimited supplies of renewable resources to nonrenewable resources due to the technological efficiency and rate of human exploitation. Such a perceptual shift is critical because humans have a better chance of managing their own attitudes than 'managing' complex ecosystems. I also need to shift our view of an 'ecosystem' from a stable system to instead focus on the dynamic properties of systems (e.g. regime shifts, Wu and Loucks 1995, Steele 1996). Changing human perceptions of the current state of marine environments may be aided by examining the status of marine environments over longer temporal scales (Pitcher 2001).

With limited funding, I need to develop well-designed and scientifically rigorous monitoring programs, where hypotheses are stated and then tested over long time scales. This type of research will allow us to gain insight into the mechanisms driving ecosystem change, allowing ecosystems to be rebuilt to baselines of the past (Pitcher 2001). I need to shift our focus off conserving single species to conserving ecosystem-level processes. Before this paradigm shift can be realized, however, researchers must design appropriate studies and begin identifying key multi-scale processes and patterns, beginning at the behavioural level.

6.5 LITERATURE CITED

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Appendix 1. Variables and parameters of the basic patch selection model for a murre in each foraging area.

Calculations		Area 1	Area 2
FLIGHT COSTS			
Flight distance (km) *	CONSTANT	45	60
Round trip distance (km)	CONSTANT	90	120
Flight speed (km/h) [1]	CONSTANT	60	60
Basal metabolic rate (kJ/h) [2]	CONSTANT	16.3	16.3
Flight and dive cost (10 x BMR, kJ/h)	CONSTANT	163	163
Additional search time (h)	PARAMETER	0	0.5
Total Flight Time (h)	CALCULATION	1.5	2.5
Total Flight Costs (kJ)	CALCULATION	245	408
DIVE COSTS			
Travel time to capelin school (s) *	CONSTANT	110	45
Round trip (s)	CONSTANT	220	90
Bottom time (s) (or prey capture time)	PARAMETER	20	20
Total dive time (s)	CALCULAT!ON	240	110
Surface time (s) [3]	CALCULATION	316	139
Total dive cycle (s)	CALCULATION	556	249
Dive efficiency [4]	CALCULATION	0.04	0.08
Caloric content of fish (kJ/g) [5]	CONSTANT	4.6	3.9
Mass of fish (g) *	CONSTANT	23.6	14.4
Maximum stomach content mass (g) *	PARAMETER	200	200
Number of fish required per trip	CALCULATION	8.5	13.9
Number of fish: self-feeding and provisioning	CALCULATION	9.5	14.9
Number of dives	CALCULATION	9.5	14.9
Total Energy Gained (kJ)	CALCULATION	920	780
Total Underwater Time (h)	CALCULATION	0.6	0.5
Total Foraging Time (h)	CALCULATION	1.5	1.0
Total Dive Costs (kJ)	CALCULATION	103	74.2
COMPETITOR DENSITY CALCULATIONS			
Competitor Density per 300 m^2 (D) *,[6]	PARAMETER	1	1
Intake Rate without interference (IFIR=1)	CONSTANT	1	1
Density Threshold (Do)	CONSTANT	1	1
M	CONSTANT	-1.0	-1.0
Intake Rate (I) [7]	CALCULATION	1.0	1.0

Appendix 1 continued

Calculations		Area 1	Area 2
ENERGY TIME TERMS (units kJ and h)			
Net Energy of Adult per Trip	VARIABLE	573	298
Energy Gain of Chick per trip	VARIABLE	109	56
Number of foraging trips per parent per day	CALCULATION	2.7	2.3
Net Energy of Adult per Day	VARIABLE	1546	676
Total Foraging Trip Time	CALCULATION	3.0	3.5
Number of chick-feeds per day	CALCULATION	5.4	4.5
Energy Gain of chick per Day	VARIABLE	25	18

*- This study

[1]- Pennycuick 1987

[2]- Basal Metabolic Rate (BMR) -390 kJ / day - Bryant and Furness (1995)

[3]- Surface Time=(Total Dive Time)$^{1.05}$ - Croll et al. (1992)

[4]- Dive Efficiency=(Bottom Time)/(Total Dive Time) – Ydenberg and Clark (1989)

[5]- Montevecchi and Piatt (1984)

[6]- Calculated from Piatt (1987) maximum number of fish is 12 per stomach and average mass was 20.4 g (total stomach mass = 244.8 g)

[7]- I=(IFIR) x [(D − 1)/(Do − 1)]$^{-m}$ - Stillman et al. (1996)

Appendix 2a. The percent composition by mass of each fishing set in the May 1999 survey along with the total mass of the catch.

Set	Date	Time	Percentage					Catch Mass (kg)
			Capelin	Atlantic Cod	Arctic Cod	Shrimp	Other Species[1]	
1	12-May	2324	27	0	0	0	73	3.2
2	13-May	317	91	0	0	0	9	8.7
3	13-May	1030	7	0	9	40	44	6.4
4	13-May	2025	6	0	1	0	93	37.5
5	13-May	2335	39	1	3	7	51	35.3
6	14-May	241	96	0	4	0	0	0.2
7	15-May	1422	59	0	1	0	41	1.7
8	14-May	1558	84	0	2	1	14	3.0
9	14-May	1750	65	0	2	0	33	45.2
10	15-May	900	0	0	0	0	100	0.2
11	15-May	1513	0	0	0	0	100	481.4
12	16-May	256	30	0	1	2	67	27.6
13	16-May	855	0	8	0	24	68	104.9
14	16-May	1447	32	0	3	34	31	31.6
15	17-May	1735	0	0	0	0	100	0.7
16	16-May	1855	26	0	0	0	74	2.2
17	17-May	805	4	0	0	0	96	1.4
18	18-May	1015	80	0	17	0	3	114.9
20	17-May	2015	9	7	1	58	25	77.3
21	18-May	57	35	0	0	62	3	362.2
22	18-May	1522	61	0	0	25	14	16.3
23	18-May	1930	29	0	0	0	71	5.7
24	19-May	450	76	0	0	0	24	2.7
25	19-May	615	15	0	0	75	9	216.9
26	19-May	755	62	0	4	13	22	25.3
27	19-May	1746	93	0	0	0	6	22.5
28	20-May	1950	2	14	0	18	66	24.7
29	20-May	323	0	27	0	0	73	121.6
30	20-May	534	5	1	0	88	6	177.3
31	20-May	806	41	0	0	44	14	1.4
32	20-May	1952	100	0	0	0	0	27.7
33	20-May	2304	28	0	13	0	59	0.7
34	21-May	1559	21	1	2	0	76	3.1
35	21-May	1834	76	0	4	0	20	9.4
36	22-May	102	82	0	0	0	18	1.0
37	22-May	1109	0	1	0	77	22	369.5
38	23-May	731	0	2	0	78	20	22.9

Appendix 2a. continued

			Percentage					
Set #	Date	Time	Capelin	Atlantic Cod	Arctic Cod	Shrimp	Other Species[1]	Catch Mass (kg)
39	23-May	1636	0	0	0	0	100	15.7
40	23-May	2017	0	1	0	75	24	152.3
41	24-May	1921	19	4	9	85	16	19.5
42	26-May	300	48	0	2	13	37	1.1
43	26-May	1129	5	4	13	53	25	58.9
44	26-May	1251	100	0	0	0	0	41.8
45	27-May	1305	90	0	0	2	7	425.5

Appendix 2b The percent composition by weight of each fishing set in the August-September 1999 survey along with the total weight of the catch.

			Percentage						
Set #	Date	Time	Plankton[2]	Capelin	Atlantic Cod	Arctic Cod	Shrimp	Other Species[1]	Catch Mass (kg)
2	23-Aug	2132	69	0	6	6	0	19	0.2
4	24-Aug	854	44	0	11	11	0	33	0.1
6	24-Aug	1611	95	1	0	0	0	5	4.8
8	24-Aug	2119	95	1	0	1	0	4	1.7
10	25-Aug	457	89	0	0	0	0	11	5.9
12	25-Aug	1022	0	4	0	0	0	96	0.3
14	25-Aug	1543	0	5	0	0	0	95	0.2
16	25-Aug	2041	65	1	0	0	0	34	0.7
18	26-Aug	212	88	0	0	0	7	5	3.8
20	26-Aug	753	22	0	0	0	0	77	4.1
22	26-Aug	1253	92	0	0	0	0	8	5.7
24	26-Aug	1751	97	0	0	0	0	1	2.2
26	26-Aug	2130	31	3	41	8	0	18	0.4
28	27-Aug	240	33	2	1	4	55	6	2.0
30	27-Aug	725	30	4	0	3	62	2	7.5
32	27-Aug	1256	69	2	2	7	0	20	0.5
34	27-Aug	1813	28	6	6	11	0	50	0.2
36	28-Aug	2231	0	24	10	3	0	62	0.3
38	28-Aug	503	91	0	0	2	0	6	3.6
40	28-Aug	911	81	1	1	2	0	15	2.2
42	28-Aug	1335	90	0	0	4	0	6	3.46
44	28-Aug	1736	52	41	1	3	0	3	3.9
46	28-Aug	2141	94	0	0	2	0	4	5.6
48	29-Aug	329	3	6	0	0	0	91	21.9
50	29-Aug	919	92	0	1	1	0	6	3.1
52	29-Aug	1241	96	0	0	1	0	2	9.7
54	29-Aug	1653	86	1	1	1	0	13	1.9
56	29-Aug	2155	87	3	0	1	0	9	1.4
58	30-Aug	324	92	2	0	2	0	4	4.5
60	30-Aug	815	3	96	0	0	0	1	21.2
62	30-Aug	1259	96	0	0	0	0	3	2.3
64	30-Aug	1741	64	0	0	0	0	36	0.5
66	30-Aug	2231	0	0	0	0	0	100	0.4
68	31-Aug	314	18	0	0	0	75	7	7.5
70	31-Aug	747	35	60	0	0	0	4	3.7
72	31-Aug	1302	75	22	0	0	0	3	3.8
74	31-Aug	1727	98	0	0	0	0	2	4.8

Appendix 2b. continued

Set #	Date	Time	Percentage Plankton[2]	Capelin	Atlantic Cod	Arctic Cod	Shrimp	Other Species[1]	Catch Mass (kg)
76	31-Aug	2140	89	0	0	1	0	10	5.6
78	1-Sep	333	79	1	0	0	1	19	7.6
80	1-Sep	851	95	0	0	0	0	4	3.3
82	1-Sep	1306	99	0	0	0	0	1	11.5
84	1-Sep	1720	94	0	0	1	0	5	0.9
86	1-Sep	2240	1	98	0	0	0	1	10.7
88	2-Sep	312	77	15	0	0	8	1	55.4
90	2-Sep	814	92	0	0	0	0	8	1.0
92	2-Sep	1220	96	0	0	0	0	3	2.3
94	2-Sep	1657	66	0	0	32	0	2	3.2
96	2-Sep	2214	98	0	0	0	0	2	6.2
98	3-Sep	243	52	4	0	0	23	22	13.6
100	3-Sep	704	0	0	0	0	0	100	88.7
102	4-Sep	120	40	0	0	0	0	60	19.6
104	4-Sep	712	95	2	0	0	0	3	7.7
106	4-Sep	1144	97	0	0	0	0	3	3.7
108	4-Sep	1614	96	0	0	0	0	4	2.5
110	4-Sep	2041	96	0	0	0	0	4	2.2
112	5-Sep	118	76	0	0	1	13	10	1.6
114	5-Sep	631	83	0	0	0	9	7	2.1
116	5-Sep	1101	99	0	0	0	0	1	4.9
118	5-Sep	1557	65	0	0	0	0	35	8.2
120	5-Sep	1933	95	0	0	0	0	5	5.0
122	6-Sep	2255	0	94	0	2	0	3	9.8
124	6-Sep	306	25	4	0	0	0	71	6.3
126	6-Sep	700	59	0	0	0	0	41	4.9
128	6-Sep	1109	99	0	0	0	0	1	7.2
130	6-Sep	1516	13	0	0	7	0	80	0.2
132	6-Sep	1924	0	8	0	0	0	92	0.1
134	7-Sep	20	66	0	0	0	0	34	6.4
136	7-Sep	529	88	0	0	0	1	11	9.6
138	7-Sep	941	96	0	0	0	0	4	1.9
140	7-Sep	1455	98	0	0	0	0	1	5.9
142	7-Sep	1745	72	0	0	0	0	28	5.1
144	8-Sep	2100	0	11	11	11	0	66	0.1
146	9-Sep	122	77	0	0	0	21	2	20.1
148	9-Sep	634	88	0	0	0	10	1	47.6

Appendix 2b continued

					Percentage				
Set #	Date	Time	Plankton[2]	Capelin	Atlantic Cod	Arctic Cod	Shrimp	Other Species[1]	Catch Mass (kg)
150	9-Sep	1413	40	7	7	7	0	40	0.2
152	9-Sep	1822	55	2	2	2	0	38	0.4
154	9-Sep	2213	77	1	1	3	0	17	0.7
156	10-Sep	235	0	99	1	0	0	0	156.7
158	10-Sep	614	6	11	0	6	51	26	4.2
160	11-Sep	736	36	62	0	0	1	1	23.3
162	11-Sep	1251	0	0	50	0	0	50	0.1
164	11-Sep	1826	86	2	2	2	0	8	0.5
166	12-Sep	2311	99	0	0	0	0	0	12.6
168	12-Sep	330	84	10	0	0	1	4	6.4
170	12-Sep	927	0	65	0	0	0	35	2.7
172	12-Sep	1342	13	38	0	0	0	50	0.1
174	12-Sep	1818	85	4	0	4	0	8	0.3
176	12-Sep	2239	39	43	4	4	0	11	0.3
178	13-Sep	402	0	8	0	0	0	92	38.8
180	13-Sep	925	0	0	0	0	0	100	10.6
182	13-Sep	1457	0	0	0	0	0	99	5.7
184	13-Sep	1938	2	0	0	0	0	98	0.6
186	14-Sep	2355	80	6	0	0	0	13	4.4
188	14-Sep	423	4	12	0	0	0	83	3.4
190	14-Sep	858	0	2	2	1	0	95	1.3
192	14-Sep	1357	0	12	12	12	0	62	0.1
194	15-Sep	2335	21	33	4	4	8	29	0.2
196	15-Sep	358	52	0	1	0	3	43	2.2
198	15-Sep	901	4	41	4	0	0	52	0.3
200	15-Sep	1318	10	10	5	0	0	75	0.2
202	15-Sep	1809	15	0	0	0	0	85	0.4
204	16-Sep	2318	1	0	0	0	0	99	3.2
206	16-Sep	359	4	0	2	0	0	94	0.5

[1] Other species include lumpfish (*Cyclopterus lumpus*, American sand lance *Ammodytes americanus*, lanterfish species (Myctophidae), sculpin species (Cottidae), alligatorfish *Aspidophoroides* species, daubed shanny *Lumpenus maculatus*, seasnail species *Liparis* species, redfish *Sebastes* species, striped wolfish *Anarhichas lupus*, American plaice *Hippoglossoides platessoides*, Atlantic saury *Scomberesox saurus*, Greenland halibut *Reinhardtius hippoglossoides*, Arctic shanny *Stichaeus punctatus*, flounder species (Pleuronectidae), fourbeard rockling *Enchelyopus cimbrius*, hake species *Urophycis* species, Atlantic herring *Clupea harengus harengus*, haddock *Melanogrammus*

aeglefinus, grenadier species (Macrouridae) and threespine stickleback *Gasterosteus aculeatus*.

[2] Plankton includes amphipods, copepods and euphausiids.

Appendix 3 The number of marine birds and mammals observed during ship surveys in the Northwest Atlantic Fisheries Organization Divisions 2J3KL (August-September) and 3KL (May) in 1998, 1999 and 2000.

Species		**August**		**May**	
		1998	**1999**	**1999**	**2000**
Birds					
Murre species	*Uria* species	506	1691	2686	5526
Murre species chicks	*Uria* species	121	60		
Atlantic Puffin	*Fratercula arctica*	2113	825	791	1886
Dovekie	*Alle alle*	2		42	33
Black Guillemot	*Cepphus grylle*		3	19	13
Leach's Storm-Petrel	*Oceanodroma leucorhoa*	3829	1238	747	3021
Sooty Shearwater	*Puffinus carneipes*	766	166	5	8
Greater Shearwater	*Puffinus gravis*	965	665		24
Manx Shearwater	*Puffinus puffinus*	6	68	2	2
Northern Fulmar	*Fulmarus glacialis*	259	329	115	172
Northern Gannet	*Morus bassanus*	156	244	89	61
Black-legged kittiwake	*Rissa tridactyla*	393	545	460	476
Herring Gull	*Larus argentatus*	18	31	218	40
Great Black-backed Gull	*Larus marinus*	54	27	9	10
Gull Species	*Larus* species		38		
Pomarine Jaeger	*Stercorarius pomarinus*	73	16		1
Parasitic Jaeger	*Stercorarius parasiticus*	6	5		5
Long-tailed Jaeger	*Stercorarius longicaudus*	2	4	1	1
Skua Species	*Catharacta* species		2		
Great Skua	*Catharacta skua*	5	8		1
South Polar Skua	*Catharacta maccormicki*	18			
Phalarope spp.	*Phalaropus* species	104	73	12	22
Total		9396	6038	5196	11241
Marine Mammals					
Humpback Whale	*Megaptera novaeangliae*	28	68	4	3
Minke Whale	*Balaenoptera acutorostrata*	8	5		2
Fin Whale	*Balaenoptera physalus*	25	14		19
Dolphin spp	*Lagenorhynchus* species	180	529	6	
Sei Whale	*Balaenoptera borealis*		4		
Pothead Whale	*Globicephala melaena*	20		11	
Killer Whale	*Orcinus orca*	3	3		
Harp Seal	*Phoca groenlandica*			2326	990
Harbour Seal	*Phoca vitulina concolor*			5	7
Total		264	623	2352	1021