BEHAVIOURAL ECOLOGY OF COMMON MURRE AND ATLANTIC PUFFIN PREDATION ON CAPELIN: IMPLICATIONS FOR POPULATION BIOLOGY

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Behavioural Ecology of Common Murre and Atlantic Puffin Predation on Capelin: Implications for Population Biology

©John Forrest Piatt, B.Sc. (Hons.)

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ABSTRACT

Relationships between capelin (*Mallotus villosus*), common murres (*Uria aalge*), and Atlantic puffins (*Fratercula arctica*) were studied at Witless Bay, Newfoundland, during the summers of 1982 to 1984. Capelin occurred inshore from May to August, but abundance peaked during periods of maximal tidal oscillations and increasing water temperatures in late June and early July. From 1982 to 1984, capelin abundance declined by an order of magnitude, but school densities remained similar. Capelin size varied by 30-40% seasonally, and up to 20% annually, partly due to temporal variations in age-class composition of schools. Capelin dominated by weight in diets (4842 items identified) of murres (adult:82.7% and chick:90.8%) and puffins (78.8% and 93.2%), but juvenile cod (*Gadus morhua*) and sandlance (*Ammodytes dubius*) were also important prey. Numbers of capelin in bird stomachs declined from 1982 to 1984, and were seasonally correlated with local capelin density; suggesting sigmoidal (Type III) functional responses. Numerical proportions of capelin in diets (from gizzard contents or chick meals) were not correlated with seasonal or annual variations in local capelin density. Variations in size of prey eaten by birds generally reflected natural variations in prey size. Bird diet overlap was extremely high, and diet diversities were low (puffin > murre). Numbers and flock sizes of birds were best correlated with capelin abundance and density, respectively. Murres were best correlated with higher density capelin schools in deeper offshore waters, and formed larger, more aggregated flocks than puffins. Both murres and puffins exhibited sigmoidal (Type III) aggregative responses to capelin density, with murres having a significantly higher prey density threshold. Density thresholds varied with overall capelin density. Murres had a larger maximum foraging range than puffins, and ranges varied annually with capelin abundance. Murre and puffin feeding ecology and behaviour may be best explained within the context of optimal foraging and predation theory. Ecological differences between murres and puffins may be largely due to their differing body sizes (murre > puffin). Implications for population biology of the Atlantic Alcidae are discussed.

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Chapter 1

INTRODUCTION

The Prey: Capelin

Capelin (*Mallotus villosus*) are one of the most important components of the food web in Newfoundland marine waters. Although other similarly sized forage species including sandlance (*Ammodytes spp.*) and juvenile cod (*Gadus morhua*) are widely distributed and common, none appear to be as singularly important, abundant, or seasonally predictable as capelin (Jangaard 1974, Carscadden 1984).

At certain times of year, capelin are the predominant prey of cod, salmon (*Salmo salar*), and many other abundant fish species (Carscadden 1984). They are also important prey for several baleen whale and seal species (Mitchell 1973, 1975, Sargeant 1973). Virtually all the dominant seabirds in Newfoundland consume capelin during summer (Brown and Nettleship 1984). Black-legged kittiwakes (*Rissa tridactyla*), herring gulls (*Larus argentatus*), greater and sooty shearwaters (*Puffinus gravis* and *P. griseus*), and northern gannets (*Sula bassanus*) consume and feed their chicks (except shearwaters) varying proportions of capelin (Maunder 1971, Pierotti 1979, Montevecchi and Porter 1980, Brown et al. 1981, Brown and Nettleship 1984). During their breeding seasons, common murres (*Uria aalge*) and Atlantic puffins (*Fratercula arctica*) are particularly dependent on capelin (Nettleship 1972, Mahoney 1979, Brown and Nettleship 1984).

Due to their importance as a forage and commercial fish species, much research has been conducted on capelin in Newfoundland and elsewhere in the North Atlantic. However, most studies have dealt with aspects of capelin biology relevant to commercial fisheries (e.g., stock sizes, recruitment, mortality).

Newfoundland capelin stocks declined in the late 1970's (Carscadden 1981), and concern has been expressed about the effects of that decline on seabird, cod, and salmon populations (Reddin and Carscadden 1981, Akenhead et al. 1982, Brown and Nettleship 1984). However, predator-prey dynamics of capelin and their dominant predators have not been well-defined (Carscadden 1983).

Recently, more attention has focused on the role of capelin as a forage species (Carscadden 1983, 1984, Brown and Nettleship 1984, Furness and Barrett 1985), and on nutritional (Hendersen et al. 1984, Montevecchi and Piatt 1984) and behavioural (Whitehead 1981, Akenhead et al. 1982) aspects of capelin important to marine predators. Simple estimates of capelin consumption by some predators have been calculated (Winters and Carscadden 1978, Brown and Nettleship 1984). More sophisticated and perhaps more accurate estimates of capelin predation require more precise data on the feeding ecology of capelin predators in relation to temporal variability in size, quality, and availability of capelin (e.g., Eliassen and Grotnes 1985), and on oceanographic factors which influence the size, distribution, and density of capelin schools. These data are also essential for interpreting the behaviour of capelin predators (Whitehead 1981).

Thus, in this study of the feeding ecology and behaviour of common murres and Atlantic puffins, emphasis was placed on quantifying some aspects of capelin ecology important to predators including:

1. Physical characteristics (e.g., length, weight, sex, age, and maturity) of capelin throughout their inshore spawning period.
2. Chronology of capelin arrival at, spawning period in, and post-spawning departure from, the Witless Bay study area.
3. Relative abundance, density, size, and distribution of capelin aggregations around the Witless Bay seabird colonies.
4. Influence of meterological and oceanographic conditions on the abundance and distribution of capelin.

Data were obtained from fishery collections of capelin, repeated hydroacoustic surveys around seabird colonies, and measurements of oceanographic conditions at sites in and near Witless Bay.

The Predators: Common Murres and Atlantic Puffins

Common murre and Atlantic puffin diets have been reasonably well-studied in several areas of the North Atlantic. However, most studies have been on the composition of meals fed to chicks rather than on adult diets, and these may differ significantly (Belopol'skii 1957, Cairns 1984). Adult puffin diets are poorly known for any region (Bradstreet and Brown 1985). There have been few concurrent studies of murre and puffin chick diets from a single study site (e.g., Harris and Wanless 1985), and none of adult diets. These data are essential for interspecific comparisons of diet diversity, estimating dietary overlap and assessing the degree of interspecific competition for food (Schoener 1982, Diamond 1984).

Seabird diets can change markedly within and between years, and there has been much speculation about how diet composition may vary in relation to potential prey abundance (e.g., Vermeer 1980, Brown and Nettleship 1984, Springer et al. 1984). The functional relationship between local abundance of prey and occurrence in diets, however, has never been quantitatively demonstrated for any seabird species. Furthermore, few studies have shown whether temporal variability in characteristics of prey in diets (e.g., age-class composition, or size) is due to active selection on the part of seabirds or to natural, background variability of prey (Croxall et al. 1985). Data on diet variability (quantity and composition) in relation to potential prey abundance are required to demonstrate functional responses (Holling 1959), and may be useful in assessing intraspecific and interspecific competition (Schoener 1982, Steenhof and Kochert 1985).

The distribution of seabirds at sea has received considerable attention, beginning with opportunistic surveys of oceanic bird fauna (e.g., Wynne-Edwards 1935, Tuck 1961) and progressing to the systematic cataloging of temporal and spatial patterns of seabird abundance in different oceanographic regions (e.g., Brown et al. 1975). General relationships between diversity, abundance, and distribution of seabirds and oceanography have been well described (Ashmole 1971, Brown 1980, 1985, Ainley and Boekelheide 1983). Fine-scale relationships between seabirds and their prey, however, are poorly known. Although some studies have clearly shown that seabirds aggregate in productive areas (e.g., Brown 1980, Obst 1985), none have demonstrated significant spatial correlations between predators and prey (Schneider and Piatt 1986). The aggregative response of predators to prey is a fundamental ecological characteristic of animals (Hassell and May 1974, Taylor 1984) that has not been described for any seabird species. Measurements of predator group size and dispersion in relation to prey density and dispersion are required to determine the form of aggregative responses (Hassell and May 1974).

Similarly, selection of feeding habitat by seabirds has been observed on a gross scale (e.g., Brown 1980, 1985, Schneider and Hunt 1984), but has rarely been quantified over small spatial scales (e.g., Cairns 1984). Competition within habitats is apparently common between avian species which share food resources and is most often manifested as assymetric interference competition for feeding sites (Maurer 1984). Differential feeding habitat use over small spatial scales, due either to selection or interspecific interference competition, or both, has rarely been demonstrated for coexisting marine birds (e.g., Cairns 1984, Goudie 1984).

In this study, I measured temporal and spatial variations in the diet, distribution, and foraging behaviour of murres and puffins at Witless Bay by quantifying:

1. Diets of adult murres and puffins through the breeding season in each year of study. Most data on murre and puffin chick meals were obtained by Drs. A.E. Burger and D.N. Nettleship (unpubl. data).

2. Seasonal and annual variability in feeding aggregations of murres and puffins on the ocean surface (flock size and composition, distribution and habitat use).

Data on flock sizes, distribution, etc., were collected in synchrony with hydroacoustic capelin surveys allowing for analyses of spatial relationships between murres, puffins, and capelin; the aggregative response of birds to capelin schools; and temporal and spatial overlap between species in use of feeding habitat. Using diet and survey data, it was possible to examine the functional response of birds to capelin and effects of variability in capelin characteristics and abundance on bird diet composition. Diet data were also used to contrast adult and chick diets, compare murre and puffin diet diversity, estimate diet overlap between species, and consider potential competitive interactions; all with regard to seasonal and annual variability in capelin abundance.

Predator-Prey Interactions: Competition and Coexistence

Common murres and Atlantic puffins are related members of the Alcidae and coexist over most of their ranges in the North Atlantic (Nettleship and Evans 1985). They often breed at the same colonies and exhibit high overlap in use of food resources (Pearson 1968, Bradstreet and Brown 1985), moderate temporal overlap in colony attendance (Birkhead and Harris 1985), and possibly low overlap in use of feeding habitat (Cody 1973). Although there might be some degree of competition between the species, the traditional view of this situation would be that overlap in use of one or more critical resources (food, time, space) has been reduced enough to permit coexistence (Hutchinson 1959, MacArthur and Levins 1967, Cody 1973, 1974).

In recent years, however, attempts to explain competitive coexistence have taken an exciting new direction. Whereas previous theory suggested that coexistence was wholly a function of species overlap in 'resource utilization curves' (MacArthur and Levins 1967), newer models suggest that if species have significantly different, non-linear responses to resource density, they can coexist indefinitely on resources that fluctuate due to depletion or stochastic events (Stewart and Levin 1973, Koch 1974, Armstrong and McGehee 1976, 1980, Kaplan and Yorke 1977, Levins 1979, Butler 1980, reviewed by Abrams 1983). Under this hypothesis, coexistence is possible *regardless* of the degree of overlap in resource use between competitors (Abrams 1983).

Food is arguably the most important factor regulating seabird populations (Lack 1954, 1966, 1967, Ashmole 1963, Birkhead and Furness 1985). Thus, it is also likely to be the most important resource shared by seabirds. Relationships between the rate at which food can be exploited and food density (functional and aggregative responses) have been thoroughly examined (e.g., Holling 1959, Ivlev 1961, Hassel and May 1974) and are characteristically non-linear (hyperbolic or sigmoidal) for most animals (Holling 1965, Murdoch and Oaten 1975). The relationship between food density and population growth (numerical response) is also typically non-linear (Holling 1959, Readshaw 1973, Eveleigh and Chant 1981b). Therefore, according to the above hypothesis, food overlap between seabird competitors could be high, but if they exhibited sufficiently different functional and numerical responses to prey density, they could coexist indefinitely on a shared food supply.

Functional and aggregative responses to prey density are manifestations of optimal foraging behaviour (Cook and Cockrell 1978). The benefit/cost ratio for feeding on a given prey increases hyperbolically (Type II) or sigmoidally (Type III) with prey density depending on the degree of aggregation of the prey and foraging behaviour of the predator (Holling 1965, 1966, Murdoch and Oaten 1975, Hassell et al. 1977, Cook and Cockrell 1978). For related, different-sized predators feeding in a similar style on the same prey, the biggest differences between them are i) how much food they require daily for existence, and ii) costs of foraging (Pyke et al. 1977, Werner and Mittelbach 1981), and both are functions of body size (Peters 1983). Thus, body size must be fundamental factor influencing functional and aggregative responses to prey density and coexistence between predators.

Thesis Presentation

After presenting data collected on capelin, murre and puffin diets, and foraging behaviour, I will discuss these results with regard to other studies, and interpret them in light of competition, predation, and optimal foraging theory. I will attempt to demonstrate through results and discussion that murres and puffins exhibit differing functional and aggregative responses to capelin density largely because of their differing body sizes, and that interspecific differences in diet, residence period, and habitat use in Witless Bay, are also functions of body size - prey density requirements. Finally, I will review foraging ecology and behaviour of other Atlantic alcids to see if patterns observed for murres and puffins extend allometrically to the rest of the Atlantic Alcidae.

Despite the fact that functional and numerical responses are intimately related (Holling 1959), they "have been treated largely as separate components of the predation process: few or no ... studies have been done to ... understand the dynamics of an interactive system" (Eveleigh and Chant 1981a). In my final discussion, I will draw upon published literature to see if population biology in the Atlantic Alcidae might be explained by aspects of their foraging behaviour, and in particular, by body size - prey density relationships.

Chapter 2

METHODS AND STUDY AREA

2.1. STUDY AREA

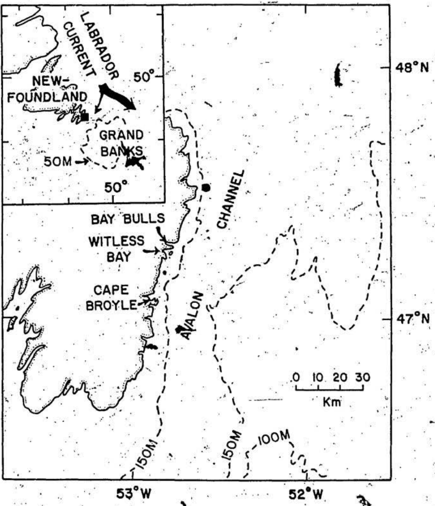
The study was carried out around the Witless Bay Seabird Sanctuary (47°15' N, 52°46' W) located on the eastern edge of the Avalon Penninsula of Newfoundland (Figure 2-1). The sanctuary comprises three islands with a total population of about 1.1 million breeding seabirds, including several species of procellarids, gulls, and alcids (Brown et al. 1975).

Boat surveys were conducted around Gull and Green Islands in Witless Bay which have a combined total of about 75,000 breeding pairs of murres (>99% *Uria aalge*) and 74,000 breeding pairs of Atlantic puffins. Great Island is located 10 km southwest of Gull Island and has approximately 2,800 pairs of murres and 148,000 pairs of puffins breeding on it. Coastal surveys extended as far south as Cape Broyle (25 km) and offshore surveys were run 30 km offshore from Green Island into the Labrador Current. Capelin collections were made at Lance Cove, near Cape Broyle (Figure 2-1).

Marine waters in the study area are classified as Low Arctic (Dunbar 1968, Nettleship and Evans 1985) and are dominated by the nearshore branch of the cold Labrador Current that flows south through the Avalon Channel adjacent to the Avalon Penninsula (Figure 2-1). Primary and secondary production are relatively high in the Avalon Channel and nearshore where upwelling and frontal processes mix oxygen and nutrient rich Labrador Current water (Hollibaugh and Booth 1981).

A narrow ledge runs the length of the coast with the 50 m contour generally less than 1 km from shore in the study area. East of Gull and Green islands, the

Figure 2-1: Study area located in southeastern Newfoundland, Canada. Black circle north of Bay Bulls indicates location of hydrographic station 27.


LABRADOR CURRENT
NEW-FOUNDLAND
50°
GRAND BANKS
50M
50°
BAY BULLS
WITLESS BAY
CAPE BROYLE
CHANNEL
AVALON
48°N
47°N
0 10 20 30
Km
150M
150M
100M
53°W
52°W

ocean floor drops rapidly to >150 m at 3-4 km offshore (Figure 2-1). These depths persist for more than 40 km before rising up to the shallow Grand Bank, the resulting trough forming the Avalon Channel. Nearshore ocean floor topography is typically irregular with numerous shoals, ledges, and boulders.

The ocean climate in May-September is characterized (Banfield 1981) by cold ocean temperatures (0-15° C at surface), moderate air temperatures (average about 14° C), moderate rainfall (about 100 mm per month), frequent fog (20-40% of days), and predominantly southwesterly winds (average 15-30 km/hr). Arctic pack-ice may persist until May, and icebergs until July-August (frequently grounding on inshore shoals). Tidal range is small (<2 m) and wave conditions typically moderate owing to a combination of exposed coastline, bathymetric features, and sustained moderate winds. Nearshore currents are largely influenced by tides, seldom exceed 2 km/hr, and may run north or south depending on the tide cycle (Farmer 1981).

2.2. SEABIRD AND CAPELIN SURVEYS

General Methods

Boat surveys were conducted around the seabird colonies on Gull and Green Islands to record the abundance and local distribution of schooling fish (primarily capelin), Atlantic puffins and common murres. Surveys were conducted from May/June to August, 1982-1984 (see Appendix A). In 1982, surveys were conducted in a 7 m open boat with a side-mounted Skipper 609 acoustic sounder. In 1983-84, surveys were conducted in a 12 m longliner, the MV 'Elsie G', equipped with a Kelvin-Hughes acoustic sounder (Mark 2, Model 5, 48 kc/s), radar, and autopilot for accurate positioning under most conditions. Before starting each survey, date, time, type of survey, sea state, cloud cover, approximate wind speed and direction, visibility, and observers were noted on tape recorder. Two observers were usually present on each survey and observation duties were exchanged at 30 min intervals. Most surveys were begun between 0600-0700 hr Newfoundland Daylight Time.

Each survey was initiated by marking the acoustic sounder echogram and by starting a stopwatch for synchronous recording (hr:min:sec) of all bird and fish observations on the survey. At each change of direction on the survey route, the echogram was marked and the time recorded. The sounder and stopwatch were both stopped at hydrographic stations and re-started when the survey resumed. The echogram was marked and time recorded at the end of each survey. All puffins and murres observed in a 50 m radius semi-circle in front of and on either side of the boat were recorded with details on exact time, species (puffin, murre), activity (swimming on the water, flying and flight direction) and number of individuals (flock size). Except in 1982, all bird observations were made from inside the boat. Using these general survey methods, four different types of surveys were conducted, each of which is described below.

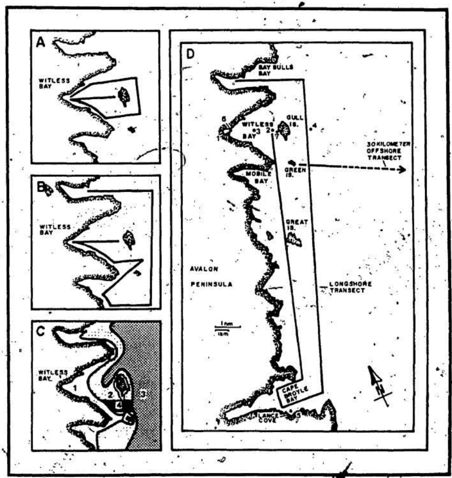
Standard Surveys

Standardized boat surveys were conducted regularly along a fixed transect route around Gull and Green Islands, Witless Bay. The transect was designed to cover a variety of potential habitats including pelagic offshore to depths of 120 m, neritic inshore to less than 10 m, over ledges, around headlands, and islands. Surveys were long enough (30 km) to gather adequate spatial information, but short enough to ensure repeated daily sampling. In 1982, the standard survey made a full circuit of Witless Bay and Gull Island (Figure 2-2). With the larger boat in 1983-84,the standard survey route was expanded. Surveys began in Bay Bulls Harbour, passed outside of Gull and Green Islands, and made circuits of both Mobile and Witless Bays (Figure 2-2). In 1982, surveys took about 2.5 hr. In 1983-1984, surveys usually required between 3.5-4 hr to complete. The capelin-bird observations required about 120 min with about 30 min required for hydrographic sampling; the remainder of time being in transit.

24-Hour Surveys

On two occasions, standard surveys were repeatedly conducted over a 24-hr period to examine diel behaviour of birds and fish. A total of 8 surveys were conducted in 1983, 4 on 26-27 June and 4 on 5 July. No hydrographic sampling

Figure 2-2: Location maps showing: A) standard survey route in 1982; B) standard-survey route in 1983-1984; C) habitats in Witless Bay: 1) "inshore" inside 30 m bathymetric contour line, 2) "bay" between 30 and 70 m contour, 3) "offshore" greater than 70 m, 4) "ledge" area between Gull and Green Islands where underwater ledges from both islands converge and depths range from 30-70 m; and D) longshore and offshore survey routes; and * hydrographic CTD and thermograph stations 1-7.


A
WITLESS BAY
B
WITLESS BAY
C
WITLESS BAY
1
2
3
4
5
D
BAY BULLS BAY
6
1
WITLESS BAY
3
2
7
GULL IS.
4
30 KILOMETER OFFSHORE TRANSECT
GREEN IS.
MOBILE BAY
GREAT IS.
AVALON
PENINSULA
LONGSHORE TRANSECT
1nm
1km
CAPE BROYLE BAY
LANCE COVE
5
N

was done, and surveys conducted at night were done at reduced speed. The last survey on 5 July ended early because of extreme darkness (overcast, no moonlight). Bird observations were not recorded under poor light conditions. The route followed on 24-hr surveys was the same as the standard survey route for 1983-1984.

Offshore Surveys

Offshore surveys conducted in 1984 originated on the east side of Green Island and ran in a straight line east-southeast for about 30 km (2 hr) offshore (Figure 2-2). Capelin and bird observations were not recorded on the return portion of the trip as this time was reserved for bird collections. Each trip lasted about 4.5-5.0 hr. No hydrographic sampling was done on these surveys.

Coastal Surveys

Coastal (longshore) surveys to Cape Broyle, about 25 km south of Witless Bay, were conducted in 1982 and 1984. These surveys originated behind the north end of Gull Island and ran parallel to the coastline at a distance of about 1 km east of Gull, Green and Great Islands, south to Cape Broyle Bay, and went into the bay as far as Lance Cove. The return portion of the survey followed the coastline west of the islands (Figure 2-2). Bird and sometimes capelin observations were recorded for the entire trip which lasted about 4.5-5.0 hr, with about 3 hr of actual survey time. Hydrographic sampling was not conducted on coastal surveys.

2.3. HYDROGRAPHY AND METEOROLOGY

Hydrographic data were collected using an Applied Microsystems conductivity-temperature-depth probe (CTD) from the 'Elsie G' at hydrographic stations 1-2 in 1983 and at stations 1-4 in 1984 (Figure 2-2). Additional temperature data were collected using three continuous recording Ryan thermographs at shallow water (5-10 m) stations 5-7 in 1984 (Figure 2-2). Thermographs were placed on the bottom, or within 1 m of the bottom, by SCUBA divers. Complete information on depths, locations, and sampling periods of CTD and thermograph recorders is given in Appendix B. The CTD recorded salinity, temperature and depth at the surface and at each 10 m interval to the bottom. Stations 1 and 2 were sampled on nearly every survey in 1983 and 1984. The less protected hydrographic stations, 3 and 4, were sampled on approximately every second survey. Hydrographic data for stations 1-4 were usually collected between 0615-1000 hr.

To calibrate the CTD and monitor its performance, surface temperature (read from a hand held mercury thermometer) and salinity (determined by an Autosal Salinometer, Guildline Instruments) were recorded at station 2, usually on alternating surveys. In addition, bottom temperatures and salinity samples were taken by a Nansen bottle and reversing thermometer.

Additional hydrographic data were obtained from the Department of Fisheries and Oceans, St. John's, (S. Akenhead), for May-August, 1982-1984, from ocean climate station 27 which is located about 4 km east of Cape Spear, and about 35 km northeast of Witless Bay (Figure 2-2) in 173 m of water (Akenhead 1983). We used hydrographic data from station 27 for depths between 0-125 m since temperature and salinity were nearly constant below 125 m and since none of the Witless Bay hydrographic stations (1-7) exceeded 125 m.

Tidal information was extracted from Canadian Tide and Current Tables published annually by the Government of Canada, Fisheries and Oceans Scientific Information and Publications Branch, Ottawa. Predicted tides for the reference port of St. John's were used for analyses.

Meteorological data (wind speed and direction) from the airport station at St. John's were obtained from the Atmospheric Environment Service, St. John's, (J. Bursey) for the months May-September, 1982-1984.

2.4. CAPELIN COLLECTIONS

Capelin were collected by a commercial fisherman (A. Dalton) using a capelin trap located at Lance Cove, in Cape Broyle Bay (Figure 2-1), in June and July, 1982-1984. The trap was set perpendicular to, and about 10 m from the shoreline in water 7 m deep. The trap fished from the surface to the bottom and was designed and operated as described by Jangaard (1974). Stretched mesh size of the net was 19.5 mm.

Samples of approximately 200 capelin were collected, usually on alternating days, between 0400-1000 hr. Capelin were selected from top, middle, and bottom layers of fish in the boat to ensure selection was not biased by heavier fish sinking to the bottom. Samples were frozen and later thawed for examination. Each sample was sorted to determine the sex composition and proportion of females that were ovid and spent. A subsample of at least 15 males, 15 ovid and 15 spent females were then selected for measurements of total length (TL, mm) and weight (g). The age composition of capelin from Lance Cove were provided by B. Nakashima (Fisheries and Oceans, St. John's). Water temperature data were collected by a thermograph moored in 7 m of water beside the capelin trap in 1984 (station 5).

Additional capelin collections were made in Witless Bay in July, 1984 using a surface set gill-net with three panels of varying mesh size (19.5, 25.4, and 38.1 mm stretched). Collections ended when the net was destroyed by a whale.

2.5. SEABIRD AND CHICK MEAL COLLECTIONS

The bycatch of common murres and puffins in fishing nets is a common phenomenon in the study area (Piatt et al. 1984, Piatt and Nettleship 1987), and large samples were obtained at fishing wharves during June and July of each year. A total of 1494 net-drowned murres and 459 puffins were collected for autopsies and stomach examinations. To supplement these collections, an additional 31 murres and 53 puffins were collected by shooting around the colony in late May to early June (murres) and in August (puffins) in different years. All stomach and gizzard contents were identified, if possible, immediately after collection. Unidentified fish and otoliths were saved for later identification. Intact capelin from stomachs were measured and, if undigested, weighed.

A total of 95 common murre chick meals were collected on Gull Island by Dr. A.E. Burger (Department of Biology, Memorial University of Newfoundland, St. John's) in 1982-84. Chicks of varying ages were collared with wire pipe cleaners so they could not swallow food delivered to them (Gaston and Nettleship 1981). After leaving chicks for 2-4 hr, food items found in chick mouths or on ledges near chicks were identified, weighed and measured. Unidentified specimens were preserved for later examination. In addition, visual observations were made of 754 meals delivered to chicks by adults in 1982-84. Since there was no significant difference in meal compositions as determined by observation or collection (A.E. Burger, pers. comm.), these data were combined to calculate composition of chick diets.

A total of 514 puffin chick meals were obtained in 1982-84 by waiting for incoming adults to deliver food to chicks in their burrows and then taking these food items (Nettleship 1972). Food items were identified, weighed, measured, and returned to chicks. In 1982, all chick meals (n=325) were collected on Great Island (D.N. Nettleship unpubl. data). In 1983, meals (n=63) were collected on Gull Island, except for one sample (n=36) collected in late August on Great Island. In 1984 all chick meals (n=90) were collected on Gull Island.

2.6. NET-BYCATCH SURVEYS

Surveys of murre and puffin by-catch in fishing gear were conducted in the study area from 1981-1984 (see Piatt et al. 1984 for details). A total of 14 fishermen from communities at varying distances (up to 50 km) from Green Island kept track of daily catches of birds in salmon and cod gill-nets, with details on: net type, depths set, number and species caught, date and amount of fish caught. Records were kept from mid-June to August in each year. Bird catches in Witless Bay were monitored daily over this period by quantifying numbers of birds brought to the community wharf by different fishing crews. Additional by-catch data from other areas (Cape St. Mary's, Baccalieu Island, Cape Freels, Fogo Island) were used for analysis of the frequency distributions of numbers of murres and puffins caught in nets.

2.7. DATA ANALYSES

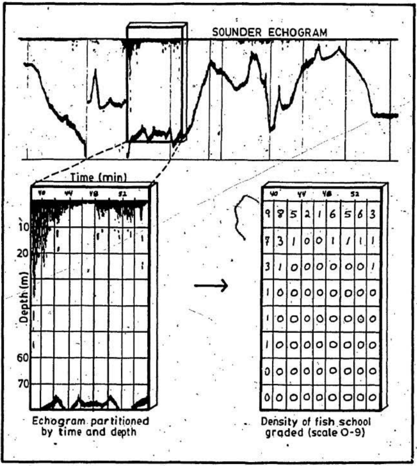
Routine data handling and basic statistical analyses (e.g, ANOVA, multiple means comparisons, regressions, correlations, χ^2 tests, tests of significance, etc.,) were conducted using SAS and SPSS statistical packages on a Digital Vax computer. Spectral analysis and lagged correlation analysis were conducted using BMDP on VAX. G-tests were conducted using a Hewlett-Packard hand calculator with statistical programs.

2.7.1. Estimating Relative Abundance and Relative Density of Fish Schools

The method used to quantify capelin school registrations on the echograms is illustrated in Figure 2-3 (based on an actual data record). Each of the echograms was partitioned by time (1 min intervals of transect time in 1982/84, and 2 min intervals in 1983) and depth (10 m intervals). Each survey leg was time-partitioned separately based on the start and end times of the leg. After partitioning, the quantity of fish appearing in each block was graded visually on a scale of 0 to 9. Even very small registrations were given a grade of at least 1 since they might represent significant schools that had been grazed by the echosounder beam (Forbes and Nakken 1972). At the other extreme, blocks that were completely filled with heavy registrations were given a grade of 9. This method of visually grading echo recordings has been used previously to assess relative year-class strengths of O-group fishes in the Barents Sea and with trained observers can provide reasonably nonbiased relative estimates of fish abundance (Forbes and Nakken 1972).

Because echo signal strength attenuates with depth, abundance of deep fish schools may have been underestimated. Time varied gain (TVG) adjustments were made to compensate for this effect (Forbes and Nakken 1972). Most capelin schools were located within 30 m of the surface, however, so signal attenuation likely had little effect on overall capelin abundance estimates. The spread of acoustic signals with depth tends to overestimate deep school dimensions, but this

Figure 2-3: Illustration of how acoustic echograms were graded for estimation of fish abundance (note abundance scale is **relative**, see text for details).



Echogram partitioned by time and depth

40			44		48		52	
9	8	5	2	1	6	5	6	3
7	3	1	0	0	1	1	1	1
3	1	0	0	0	0	0	0	1
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

Density of fish school graded (scale 0-9) was adjusted for (Forbes and Nakken 1972) in calculations of capelin school volumes (Appendix E1).

Because fish abundance is proportional to the squared value of the intensity of registration on the echogram (Forbes and Nakken 1972), total abundance per survey was calculated as the sum of all squared grades on the echogram trace (Figure 2-4). Estimates of mean abundance per survey or per min were obtained by dividing the total survey abundance grade by the number of graded blocks (including zeros) in the survey or min, respectively. Several more parameters are required to calculate absolute fish abundance from acoustic surveys. Because these were not determined, **the measure of fish abundance is relative and not absolute.**

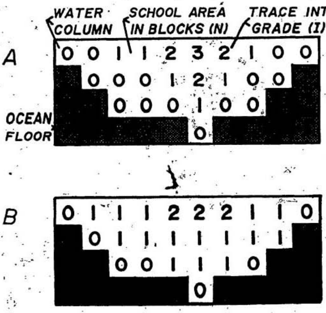
Density of fish schools was determined (Figure 2-4) by dividing the calculated abundance by the number of blocks containing some fish (i.e., with grades > 0). This was calculated per survey or per min by dividing the abundance score by the number of >0 blocks per survey, or per min, respectively. Again, **because abundance is a relative measure, the calculated school densities are also relative. To simplify presentation and discussion, the term 'relative' is not used in the following text but it should be noted that, unless specifically stated otherwise, all references to capelin abundance or density imply relative and not absolute measures.** As shown in Figure 2-4, abundance and density are not equivalent (although they are correlated).

2.7.2. Measuring Wind Effects on Water Temperature

Wind and water temperature data were analysed to determine if winds oriented in a cross-shore (onshore-offshore) or longshore direction were related to fluctuations in water temperature (Csandy 1982). The effects of both cross-shore winds (approximately east-west direction) and longshore winds (approximately north-south direction) were examined by testing correlations between wind vectors and water temperature. Cross-shore and longshore wind vectors were derived from the wind stress equation given by Roll (1965) and Csandy (1982):

Figure 2-4: Illustration of how fish abundance and density were determined from graded echograms (note abundance/density scales are relative, see text for details).

ILLUSTRATION OF ABUNDANCE vs. DENSITY OF FISH SCHOOLS



A: ABUNDANCE = $\Sigma I^2 = 27$

DENSITY = $\dfrac{\Sigma I^2}{N} = 2.7$

B: ABUNDANCE = 27

DENSITY = 1.4

cross-shore wind vector=$[s^2][\sin(d \pm a)]$

longshore wind vector=$[s^2][\cos(d \pm a)]$

where s=mean daily wind speed, d=prevailing wind direction and a=340 if wd ≤ 20 or a=-20 if wd > 20. The value of 'a' is a simple correction factor to put true wind direction in terms of its orientation to the east coast of the Avalon Penninsula (about 20° off north-south axis). The above equations do not yield absolute measures of wind stress as calculated by Roll (1965) but are proportional to them.

2.7.3. Measuring Spatial Variability

Dependence of bird and fish spatial variability (aggregation) on measurement distance (frame size) was determined by computing variance-to-mean ratios (I') over increasing frame sizes of each survey (Schneider and Duffy 1985, Schneider and Piatt 1986). A plot of I' versus frame size reveals which frame size yields the strongest evidence of aggregation (Pielou 1977). As frame size increases, so will I' until a frame size is reached with dimensions close to that of the dimensions of the patch of birds or fish (Pielou 1977, Schneider and Duffy 1985). **Computations were based on frame size intervals measured in minutes of transect, which equates to distance traveled (about 250 m per min of transect, or 4 min/km).**

2.7.4. Estimating Spatial Correlation and Thresholds

The measured strength of bird association with fish schools can also be scale-dependent (Schneider and Piatt 1986). Therefore, relationships between bird and fish aggregations were studied at varying frame sizes. After preliminary examination it was apparent the relationship was non-linear and often took the form of a sigmoidal or step function. Literature review indicated that sigmoidal aggregative responses were to be expected of higher vertebrates (e.g., Holling 1965, Hassell and May 1974). Thus, simple linear correlation was not a realistic way of analyzing bird density as a function of fish density or the strength of association. Non-linear regression models were an obvious alternative, but i) sigmoidal models require good prior estimates of one parameter (asymptote or inflection point), ii) like most field data gathered for this purpose (Goss-Custard 1970, Hassell et al. 1977) data obtained in this study were too variable to warrant making estimations for each case (ca. 70 surveys x2 species x6 frames=840 cases), and iii) I was interested in locating and contrasting thresholds in murre and puffin response curves, not in estimating goodness of fit.

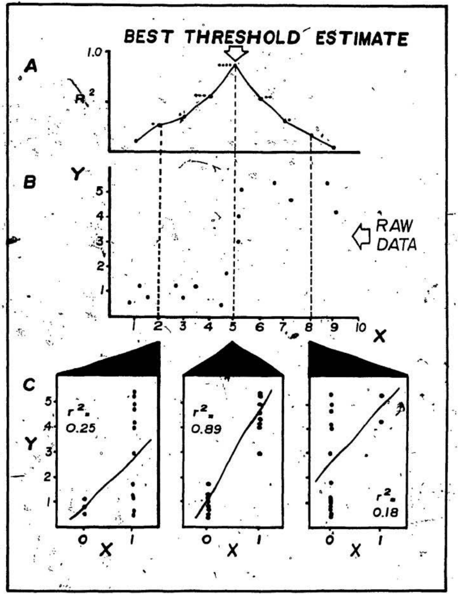
Thus, a simple box model was used for determining where thresholds occurred in murre and puffin response curves and the strength of bird-capelin correlations (given a box model). The model used was:

$$B=k_1F \quad if \; F > F_T$$
$$B=k_2F \quad if \; F < F_T$$

where B=bird density, F=relative fish density, F_t=test threshold fish density, and k_1 and k_2 are the mean densities of birds above and below the test threshold F_T. An iterative procedure was used to estimate the location of T, the threshold (inflection point), and least squares regression was used to estimate k_1 and k_2.

An example of the method used is shown in Figure 2-5 using a near ideal case with simulated data. For any set of raw data where the relationship between variables Y (e.g., bird density) and X (e.g., fish density) appears to be sigmoidal (Figure 2-5 B), the relationship can be reduced to a simple box model by dummy coding (0,1) of the independent variable (X) after selecting a test threshold value X_T (Figure 2-5 C). Simple linear regression of Y on X then yields an estimate (r^2) of the dependence of Y on X. This analysis is performed iteratively for values of X (0,1,2,...X_i), which generates an r^2 value for each test threshold value of X (Figure 2-5 A). In the example shown in Figure 2-5, when the test threshold was set at X_T=2, the resulting r^2 value of Y on X was 0.25; at X_T=5, r^2=0.89; at X_T=8, r^2=0.18. If the form of the relationship is sigmoidal, r^2 increases up to the real threshold and decreases thereafter. The highest, most significant r^2 value is obtained when the test threshold equals the real threshold, and this is therefore

Figure 2-5: Illustration of how thresholds were located in sigmoidal response curves (see text for details).


BEST THRESHOLD ESTIMATE
A
1.0
R^2
B
Y
5
4
3
2
1
RAW DATA
1
2
3
4
5
6
7
8
9
10
X
C
Y
5
4
3
2
1
r^2 =
0.25
r^2 =
0.89
r^2 =
0.18
0
1
X
0
1
X
0
1
X

the best threshold estimate. The value of r^2 at the real threshold yields the best estimate of the dependence of Y on X.

When data are grouped over increasing frame sizes, the number of data points available for threshold location analysis decreases (e.g., grouping a 120 min survey into 12 min blocks gives only 10 data points for analysis). For this reason, data were grouped only up to a maximum frame size of 16 min (about 4 km). Because of the low number of data points at large frame sizes, it is possible to encounter a situation in threshold analysis where r^2 does not reach a maximum (significant) value and then decline, but rather increases continuously up to the last data point, with the last few consecutive regressions being significant. In this case, the real threshold *may* occur before the last data point, but because there is only one point at the extreme end of the X co-ordinate, the threshold cannot be located using this test. In my analysis, if the last two or more test thresholds yielded the highest significant regressions, a threshold was assumed to occur before the terminal data point.

Monte Carlo methods were used to test the reliability of the above method for estimating correlations and locating thresholds. Two surveys were chosen at random and an International Mathematics and Statistics Library subroutine (GGPER) was used to generate random permutations to reassign each 1 min bird count to a new location along the transect. One hundred runs were conducted for each survey and after each run, the iterative threshold location test was conducted for appropriate values of the independent variable (relative fish density). For each test threshold value, the proportion of significant to non-significant regressions was calculated to determine the probability that a significant regression could be obtained from randomized data. This was compared to the probability level associated with the regression of the original data to determine if the significance levels obtained with the F-statistic were valid. In total, 2400 comparisons were made between randomized and original data. Results indicated that F-statistics were generally conservative, and therefore the F-test was used to estimate probabilities of significance.

To determine if a threshold effect could be generated from randomized data, the proportion of randomized surveys yielding a threshold, or a threshold with a significant regression, was calculated. Four hundred runs were examined for thresholds. Because of the possibility that real thresholds could occur at extreme values of the X co-ordinate, and thus not be located by the threshold test (see above), the randomized surveys were also examined to determine the proportion with r^2 values increasing up to a significant level at extreme test threshold values of the X co-ordinate, and the proportion with 2 or more consecutive significant r^2 values.

2.7.5. Temporal Variability

The apparent strength and form of association between birds (e.g., abundance, diets) and capelin may also depend on the temporal scale at which it was examined. Variability may be small over short time frames (e.g., 1 day) if there is some correlation between variable values on consecutive days. If there is an underlying cause for auto-correlation (e.g., tides), then variability may be best observed when the data are grouped over time scales (frame sizes) appropriate to the underlying causal factor (e.g., 1 week for half a tide cycle). This is one way in which spectral analysis and time series analysis handle data. Unfortunately, both these analyses have certain data requirements that were not met with the data obtained from Witless Bay (e.g., not enough data points, inconsistent time intervals) and could not be applied here. However, the simple approach of grouping data over increasing time frames, and then examining variability or associations, was employed to help resolve biological patterns at Witless Bay. In cases where data being compared were not always collected on the same day (e.g., diet collections vs. boat surveys), grouping the data into larger time frames also served to increase data sets used for analyses of association.

2.7.6. Estimating Temporal and Spatial Overlap

Temporal and spatial overlap of murres and puffins in Witless Bay were estimated using Pianka's (1975) modified equation for calculating α overlap from field data:

$$\alpha = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of the ith resource used by the jth and the kth species, respectively.

2.7.7. Diet Analysis

To calculate diet composition by weight from numbers of prey items, the masses of prey items that could not be weighed were extrapolated from measured lengths. In the case of otoliths from bird gizzards, total fish lengths were extrapolated from otolith lengths, and weights were extrapolated from these fish lengths. Adult male and female (ovid or spent) capelin weights were extrapolated from lengths for each year using regression equations derived from annual capelin trap collections. Sandlance (*Ammodytes dubius*) and immature capelin length-weight regressions were based on combined measurements of fish collected from chicks over all 3 yr. Juvenile cod (*Gadus morhua*) length-weight, and otolith length-fish length regressions were based on cod collected at Bellevue Beach, Newfoundland, in 1983-1984 (D. Methven, unpubl. data). Sandlance otolith length-fish length regressions were based on fish collected from the Grand Bank in July, 1968 (data courtesy of J.S. Scott, Department of Fisheries and Oceans, New Brunswick). All regression equations used for analyses are found in Appendix C.

Analyses of capelin size distributions from different predators (adult/chick murre/puffin, and trap) were made using ANOVA after the size distributions of the individual sex/age classes were found to be normally distributed. Student-

Neuman-Keuls (SNK) multiple range tests were used to test the significance of differences in mean length and weight of capelin taken by different predators. To determine the contribution of collection date to size variations, the effect of year and sampling period (2 wk intervals (6) from 1 June to 31 August) were examined by calculating partial sums of squares and associated F-values in an analysis of size variance as a function of predator, year, period, and the corresponding interactions. Sandlance and cod size frequency distributions were skewed and therefore comparisons were made using Wilcoxon 2-way tests.

To compare adult murre and puffin feeding success on the data on frequency of capelin in stomachs were reduced to a dichotomous comparison of either no capelin (0) or capelin present (1) and the proportion of murre stomachs with capelin was compared to the proportion of puffin stomachs with capelin using a χ^2 test. For each within-year comparison, only birds collected on the same days were used in the analyses. Phi (ϕ) coefficients were also calculated to compare foraging success. The ϕ coefficient is a measure of association between proportions and yields values between 0-1. Like χ^2 values from which it is derived ($\phi=(\chi^2/N)^{1/2}$; where N is the number of cases), high values of ϕ indicate low similarity (Brown 1983).

To calculate diet overlap, I followed Diamond (1984) and used Horn's (1966) modified version of Morisita's (1959) overlap index, C, which is given by:

$$C=\frac{2\sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i^2+\sum_{i=1}^{s} y_i^2}$$

where s is the number of common prey categories in the two species being compared, and x is the proportion of prey in category i taken by one predator while y is the proportion of prey in category i taken by the other.

To test for significant differences in the proportion of different fish, or of different capelin age/sex classes in the diets of adult and chick birds, and capelin from traps, G-tests of prey frequency distributions were performed for each of the following comparisons: Adult murre vs. adult puffin, adult murre vs. murre chick, adult puffin vs. puffin chick. Only data collected over equivalent time periods were used in each comparison, hence data sets for each comparison were different. If sufficient concurrent data were available in different years, then interaction terms involving year were also calculated; otherwise concurrent data from all three years were grouped for comparisons.

Diet diversity was calculated using the Shannon-Weiner information function (Diamond 1984):

$$H = - \sum_{i=1}^{s} p_i \, log \, p_i$$

where H is the diversity index, and p_i is the proportion of of the total prey spectrum belonging to the *ith* category, and s is the total number of prey categories in the diet sample.

Chapter 3

OCEANOGRAPHY AND CAPELIN ECOLOGY

3.1. OCEANOGRAPHY

3.1.1. Annual Variation in Water Temperatures

Average seasonal 0-50 m water temperatures at Station 27 (offshore, Figure 2-1) and Gull Island (inshore) were warmest in 1982, and became progressively colder in 1983 and 1984 (Figure 3-1). At Station 27, warmer water (>0°C) extended deeper and comparable isotherms generally formed earlier in 1982 than in 1983 or 1984 (Figure 3-2). A similar trend was observednearshore at Gull Island between 1983 and 1984.

This general cooling trend of summer water temperatures in the Avalon Channel was likely due to the increased occurrence in spring of pack ice and icebergs in eastern Newfoundland waters in 1983 and 1984. Pack ice was especially prolonged nearshore in 1984, and extensive ice-sheets were observed on the first standard survey in May. Large icebergs were commonly observed being carried south by the Labrador Current in the Avalon Channel. Small icebergs frequently grounded inshore, remaining in the study area until July in 1983 and 1984.

Figure 3-1: Mean 0-50 m water temperatures at Station 27 and Gull Island in 1982 (2), 1983 (3) and 1984 (4).

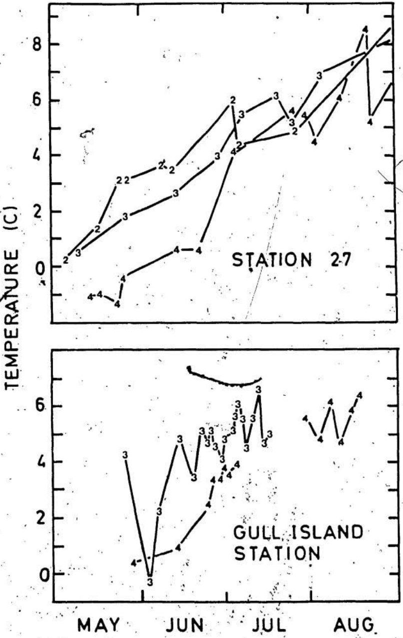
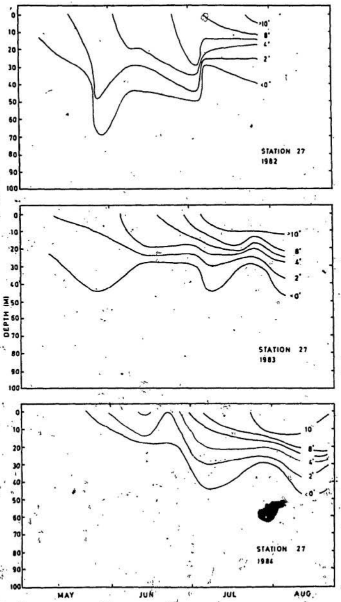

TEMPERATURE (C)
8
6
4
2
0
STATION 27
6
4
2
0
GULL ISLAND STATION
MAY
JUN
JUL
AUG

Figure 3-2: Water temperature isotherms at Station 27, May to August, 1982-1984.


>10°
8°
4°
2°
<0°
STATION 27
1982
STATION 27
1983
10°
STATION 27
1984
DEPTH (M)
0
10
20
30
40
50
60
70
80
90
100
MAY
JUN
JUL
AUG

3.1.2. Seasonal Variations in Water Temperatures: Influence of Winds

Prevailing winds blow from the southwest during summer at Witless Bay. Moderate to strong southwesterly winds resulted in large cross-shore and longshore wind vectors. Northerly and easterly winds occurred infrequently and were of shorter duration and lower magnitude. The magnitude of longshore wind vectors was significantly correlated with water temperatures over 1-3 day lags at two of the three stations (Gull Island and Witless Bay wharf; Figure 3-3), whereas cross-shore wind vectors were correlated over 1-4 day lags with only the Witless Bay wharf station. Winds were not significantly correlated with water temperatures on the same day at any of the three stations. Further significant wind-temperature correlations appeared over longer periods of 20-24 days at some stations (Figure 3-3).

These data strongly suggest that over short time periods, nearshore water temperature fluctuations occur in response to wind events. Fluctuations in water temperature lag wind events by 1-4 days because it takes time for water mass exchange to occur in response to wind stress (Frank and Leggett 1981, Csandy 1982).

Water temperatures at Cape Broyle Bay, Witless Bay wharf, and Gull Island were significantly correlated with each other over periods of a few days (Figure 3-4), with highest correlations occurring on the same day. This indicates that changes in water temperature occurred synchronously over the whole region.

3.2. BIOLOGICAL CHARACTERISTICS OF CAPELIN

3.2.1. Temporal Variation in Capelin Sex Ratios

The sex composition of capelin from trap collections varied annually (Table 3-1). The overall proportion of female capelin decreased each year from 1:2.73 (male:female) in 1982, 1:1.59 in 1983, to 1:1.02 in 1984 for a 3-yr average of 1:1.56 (Table 3-1). Most female capelin were ovid, the proportion of which increased each year from a low of 1:1.76 (spent:ovid) in 1982, 1:2.29 in 1983, to 1:2.75 in 1984 for a 3-yr average of 1:2.25 (Table 3-1).

Figure 3-3: Lagged correlations between longshore wind vectors and nearshore water temperatures at Witless Bay, Cape Broyle Bay, and Gull Island in 1984. Significant correlations are represented by solid dots.

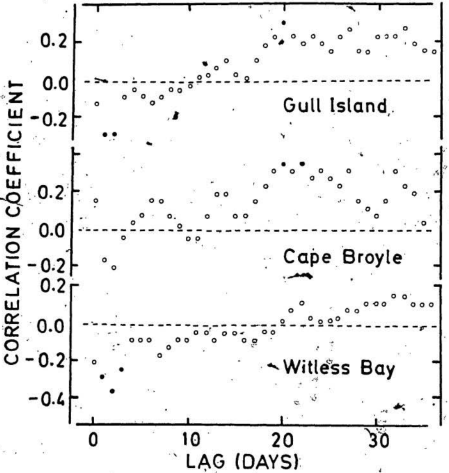

CORRELATION COEFFICIENT
0.2
0.0
-0.2
Gull Island
0.2
0.0
-0.2
Cape Broyle
0.2
0.0
-0.2
-0.4
Witless Bay
0
10
20
30
LAG (DAYS)

Figure 3-4: Lagged correlations between nearshore water temperatures at Witless Bay, Cape Broyle Bay, and Gull Island in 1984. Significant correlations are represented by solid dots.

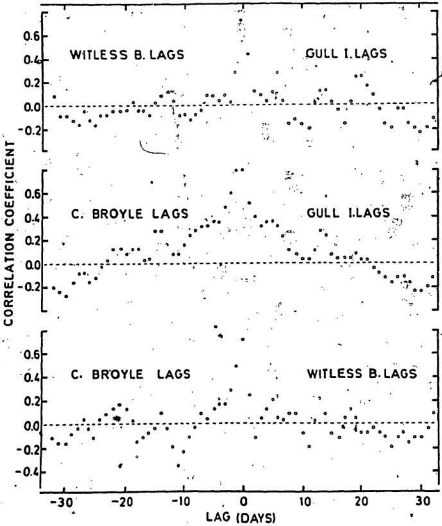

WITLESS B. LAGS
GULL I. LAGS
C. BROYLE LAGS
GULL I. LAGS
C. BROYLE LAGS
WITLESS B. LAGS
CORRELATION COEFFICIENT
0.6
0.4
0.2
0.0
-0.2
-0.4
-30
-20
-10
0
10
20
30
LAG (DAYS)

Table 3-1. Numbers, collection dates, and overall sex ratios of capelin collected at Lance Cove, Cape Broyle Bay, 1982-1984. Numbers in parentheses = % total capelin. Abbreviations: M, male; F, female; Sp, spent; Ov, ovid.

Date	No. of Samples	No. of Males	No. of Females			Total Capelin	Ratio	
			Spent	Ovid	Total		M:F	Sp:Ov
23Jun to 8 Jul 1982	14	520 (26.8)	514 (26.4)	908 (46.8)	1422 (73.2)	1942	1:2.73	1:1.76
22Jun to 22Jul 1983	21	2295 (38.5)	1113 (18.7)	2553 (42.8)	3666 (61.5)	5961	1:1.59	1:2.29
28Jun to 28Jul 1984	17	1486 (47.6)	440 (14.1)	1199 (38.3)	1639 (52.4)	3125	1:1.02	1:2.75
1982-1984	52	4301 (39.0)	2067 (18.7)	4660 (42.2)	6727 (60.9)	11028	1:1.56	1:2.25

There were pronounced seasonal variations in sex ratios of capelin from trap collections (Figure 3-5). Dominance by one sex for a few days was often reversed suddenly, or over a few days, to dominance by the other sex. Despite variation between and within years, two trends were apparent: The proportion of male capelin tended to increase in late July (except in 1982 owing to incomplete sampling) and, except for the initial and final few days of trap collections in 1983 and 1984, ovid females were usually more abundant than spent females (Figure 3-5).

A total of 180 capelin were collected with gill-nets set near the surface in Witless Bay in early July, 1984. No other fish species were taken in gill-nets. Most capelin were females (F/M=1.64), and most of these were ovid (ovid/spent females=27.0).

3.2.2. Age Class Composition of Spawning Capelin

There was a marked change in year-class composition of capelin collected at Lance Cove between 1982 and 1984 (Figure 3-6). In 1982, the vast majority of male and female capelin were 3 yr-olds. In 1983, 3 yr-olds still dominated, but both 4 and 2 yr-olds were well represented. By 1984, female collections were comprised mostly of 3 and 4 yr-olds, while 2 yr-olds declined, and 5 yr-olds increased substantially in number. Males in 1984 were comprised mostly of 4 and 3 yr-olds, and like females, 5 yr-olds were more common than in 1983. Six yr-old capelin were rare, appearing only in female collections in 1982 and 1984.

Collections in 1983 and 1984 indicated that older capelin arrived first at the spawning grounds (Figure 3-6). Proportions of older fish (4 and 5 yr-olds) were highest during the first two weeks of collections, whereas proportions of younger fish (2 and 3 yr-olds) were higher during the last two weeks of spawning (data on this period in 1984 only).

Figure 3-5: Seasonal variation in sex composition of capelin from trap collections at Lance Cove, Cape Broyle Bay, 1982-1984.

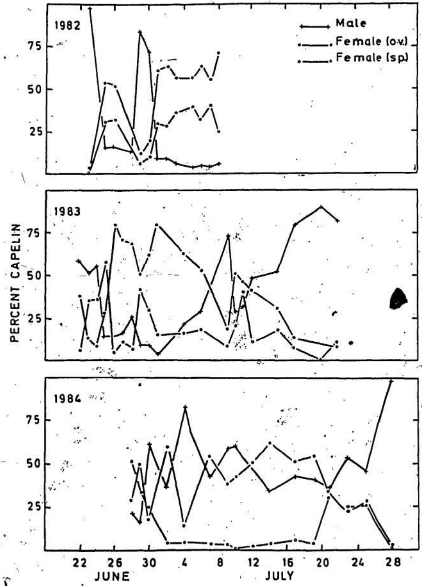
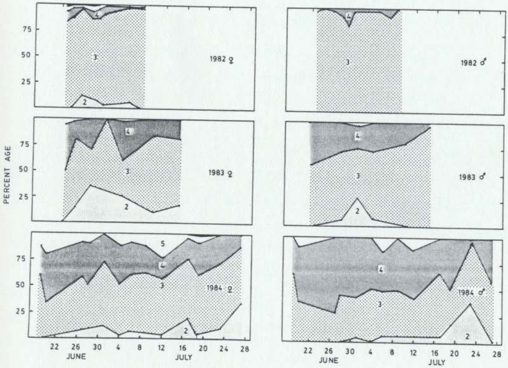

1982
Male
Female (o.v.)
Female (sp)
75
50
25
1983
PERCENT CAPELIN
75
50
25
1984
75
50
25
22
26
30
4
8
12
16
20
24
28
JUNE
JULY

Figure 3-6: Age class composition of capelin from trap collections at Lance Cove, Cape Broyle Bay, 1982-1984. Age-classes 1-6 yr indicated from bottom to top, respectively, of each figure.


PERCENT AGE
75
50
25
1982 ♀
1982 ♂
1983 ♀
1983 ♂
1984 ♀
1984 ♂
2
3
4
5
22
26
30
4
8
12
16
20
24
28
JUNE
JULY

3.2.3. Capelin Size Distributions and Temporal Variability in Size

Average Size of Capelin

The greatest source of variation in mean size of capelin from trap collections was due to differences in sex and maturity (Tables 3-2 and 3-3). Averaged over 3 yr, males were 22 mm longer, and 14 g heavier than females, and this marked difference in size was significant in all years (Table 3-2). Although differences were sometimes marginal on a daily basis (see below), spent female capelin were, on average, significantly longer than ovid females (except in 1984), and weighed significantly less than ovid females in all years (Table 3-2).

Temporal Variability in Size of Capelin

Mean lengths and weights of capelin were also a function of the year and period of summer that trap collections were made (Table 3-3). After sex, collection period accounted for most size variance in capelin because mean sizes generally decreased over each season (Figures 3-7 and 3-8). Interactions between capelin class, year, and period were relatively unimportant.

When sexes were analyzed separately, it appeared that most of the variance in male size was due to inter-year variability, whereas most of the variance in ovid and spent female size was due to seasonal variability (Table 3-4).

The greatest decrease in mean weights of capelin occurred during the first two weeks of trap collections (Figure 3-7). Seasonal decrease in weight of females between first and last collections was considerable, being 31.4% in 1982 (note shorter sampling period), 45.5% in 1983, and 46.8% in 1984. The mean weight of male capelin decreased 24.3% between first and last collections in 1982, 32.4% in 1983 and 20.4% in 1984.

Decreases in mean lengths of capelin (Figure 3-8) were much less marked than decreases in weight. The last collections of male capelin in 1983 and 1984 were only 8.2% and 3.4% shorter, respectively, than the first males collected about one month earlier. The seasonal decrease in length was more pronounced for females. There was an 8.2% decrease in length between the first and last collections for female capelin in 1982, 11.0% in 1983 and 15.4% in 1984.

Table 3-2. Mean lengths and weights of capelin from collections at Lance Cove, Cape Broyle Bay, 1982-1984.

Year		Total Length (mm)				Weight (g)			
		Male	Female			Male	Female		
			Total	Ovid	Spent		Total	Ovid	Spent
1982	mean	179.4 >	150.5	148.9 <	154.4	38.4 >	19.1	20.7 >	17.4
	s.e.	0.9	0.7	1.1	1.0	0.6	0.3	0.5	0.3
	range	147- 202	116- 204	116- 204	121- 190	20.5- 57.1	7.6- 52.7	10.7- 52.7	7.6- 31.8
	n	132	351	180	171	132	351	180	171
1983	mean	169.3 >	149.8	148.8 <	150.9	30.1 >	16.8	18.9 >	14.6
	s.e.	0.5	0.4	0.6	0.6	0.3	0.2	0.2	0.2
	range	138- 199	118- 191	120- 191	118- 188	14.7- 52.1	6.6- 43.0	8.9- 43.0	6.6- 26.9
	n	561	1042	543	499	561	1041	542	499
1984	mean	177.8 >	152.8	153.8 =	151.2	34.4 >	18.2	20.7 >	14.3
	s.e.	0.6	0.7	0.9	1.2	0.4	0.3	0.4	0.4
	range	146- 200	119- 190	120- 190	119- 190	17.3- 50.1	5.6- 43.2	9.5- 43.2	5.6- 26.9
	n	255	401	242	159	239	372	225	147
1982- 1984	mean	173.1 >	150.7	149.7 <	151.7	32.4 >	17.6	19.7 >	15.2
	se	0.4	0.3	0.5	0.5	0.2	0.1	0.2	0.2
	range	138- 202	116- 204	116- 204	118- 190	14.7- 57.1	5.6- 52.7	8.8- 52.7	5.6- 31.8
	n	948	1794	965	829	932	1764	947	817

SNK multiple means comparison, <>: significantly larger or smaller, =: no significant difference. Weight ANOVA 1982: F=505.2, p<0.0001; 1983: F=957.1, p<0.0001; 1984: F=598.5, p>0.0001. Length ANOVA 1982: F=239.2, p<0.0001, 1983: F=386.2, p<0.0001, 1984: F=299.6, p<0.0001.

Table 3-3. Contribution of capelin class (male, ovid and spent female), year, and collection period (7-day intervals) to variance in length and weight of capelin after all other effects removed (ANOVA, partial sums of squares analysis, n=2742 for length, 2696 for weight. Whole model ANOVA for length: df= 37, F=63.8, p<0.0001; for weight; df=37, F=140.0, p<0.0001).

Source of variance	df	Length		Weight	
		F	prob.	F	prob.
Capelin class (CC)	2	343.42	<0.0001	849.05	<0.0001
Year	2	12.47	<0.0001	22.63	<0.0001
Period	4	37.08	<0.0001	57.39	<0.0001
CC * Year	4	6.69	<0.0001	10.65	<0.0001
CC * Period	8	4.07	<0.0001	1.25	NS
CC * Year * Period	17	1.83	<0.05	2.80	<0.0001

Figure 3-7: Seasonal variation in mean wet weight of capelin from trap collections at Lance Cove, Cape Broyle Bay, 1982-1984.

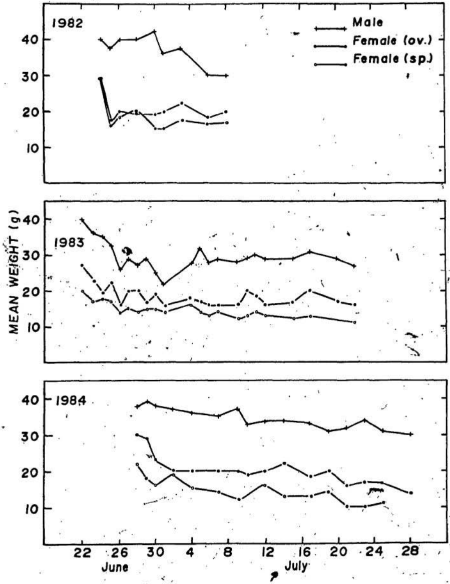

1982
Male
Female (ov.)
Female (sp.)
1983
1984
MEAN WEIGHT (g)
10
20
30
40
22
26
30
4
8
12
16
20
24
28
June
July

Figure 3-8: Seasonal variation in mean total length of capelin from trap collections at Lance Cove, Cape Broyle Bay, 1982-1984.

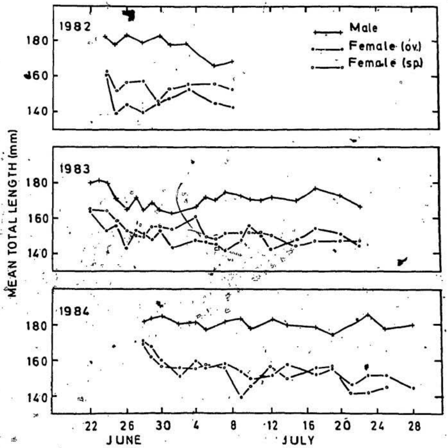

1982
Male
Female (ov.)
Female (sp)
180
160
140
MEAN TOTAL LENGTH (mm)
1983
180
160
140
1984
180
160
140
22
26
30
4
8
12
16
20
24
28
JUNE
JULY

Table 3-4. Contribution of year, and collection period (7-day intervals) to variance in length and weight of male, ovid and spent female capelin after other effects removed (ANOVA, partial sums of squares analysis).

Capelin	Source of variance	df	Length F	Length prob.	Weight F	Weight prob.
Male	Year	2	36.5	<0.0001	27.3	<0.0001
	Period	4	6.7	<0.0001	12.5	<0.0001
	Year * Period	6	1.8	NS	2.7	<0.05
Ovid female	Year	2	3.1	<0.05	0.8	NS
	Period	4	18.1	<0.0001	23.5	<0.0001
	Year * Period	6	2.1	NS	2.8	<0.01
Spent female	Year	2	1.0	NS	17.6	<0.0001
	Period	4	20.1	<0.0001	41.8	<0.0001
	Year * Period	5	1.6	NS	3.0	<0.05

To test the significance of between-year differences in mean size of male, ovid and spent female capelin, only data from the first two periods of collection (14 days) in each year were used for comparison to reduce bias from the incomplete 1982 collection (Table 3-5). In general, capelin were significantly larger in 1984 than in 1983; with 1982 males being larger than 1984 males, whereas 1982 females were smaller or similar to 1984 females. Males showed the greatest inter-year differences in size, decreasing by 7.5 g (about 20%) between 1982 and 1983.

3.2.4. Relations Between Water Temperature, Tide, and Capelin Characteristics

Water temperatures ranged from 1.8 to 6.1°C, and averaged 4.2 ± 1.2°C, during the period (28 June to 28 July) capelin were caught in traps at Lance Cove in 1984. Water temperature on the first day of capelin catches was 2.5°C. There was a significant positive correlation ($n=17$, $r=0.59$, $p<0.001$) between the proportion of male capelin present each day and water temperatures at the trap site The proportion of male capelin in trap collections increased to >50% when water temperatures were greater than about 4.5°C. There were no significant correlations between water temperatures and the proportion of females that were ovid or spent. It is not known whether males or females were responding to water temperatures because changes in sex proportions could have been effected by the movements of either sex.

There were no significant correlations between sex proportions and daily tidal amplitude. There was some indication, however, that fluctuations in mean weight of capelin were related to tidal rythyms. Mean weights of ovid and spent female capelin were positively correlated with tidal oscillations in 1984 (ovid: $n=15$, $r=0.37$, $p<0.05$; spent: $n=15$, $r=0.42$, $p<0.01$).

Table 3-5. Between-year comparison of mean lengths and weights of male, ovid and spent female capelin using only data collected over equivalent time periods (first 14 days after intial collection in each year). Means with common underlining not significantly different ($p>0.05$) using SNK multiple range test (n's range from 71 to 292).

Capelin	Mean Length			Mean Weight		
	1984	1982	1983	1984	1982	1983
Male	179.6	180.6	169.9	36.6	38.7	31.2
	------	------				
Female:						
Ovid	157.4	151.6	150.8	22.7	20.9	20.2
		------	------		------	------
Spent	157.9	154.6	154.5	17.3	17.5	16.0
	------	------	------	------	------	

3.3. TEMPORAL VARIABILITY IN CAPELIN ABUNDANCE AND DENSITY AT WITLESS BAY

3.3.1. Annual Variability

There was an order of magnitude decline in relative capelin abundance between 1982 and 1984 (Table 3-6). Differences between years are easily seen by examining the frequency of echogram block intensity grades in each year (Figure 3-9). There was a marked increase in the number of empty blocks between years, particularly between 1982 and 1983 (note log scale). There was also a pronounced shift to the left in the frequency distributions of echogram block grades greater than zero. The shifts in frequency distributions between 1982-1983 and 1983-1984 were both highly significant (Table 3-7).

The relative density of capelin schools recorded each year did not change as markedly as school abundance (Table 3-6 and Figure 3-9). There was a gradual increase in the frequency of low density grade 1 blocks from 1982 to 1984, but between 1982 and 1983 there was actually an upward shift in the frequency of very high density schools (grades 7-9). The shift to lower densities between 1983 and 1984 was more pronounced, although still not as dramatic as the downward shift in abundance (Figure 3-9). The differences in school density frequency distributions between years were statistically significant (Table 3-7).

3.3.2. Seasonal Variability

Echogram registrations of pelagic schooling fish believed to be capelin were recorded on all surveys in the Witless Bay region from May/June to August, in 1982-1984 (Figure 3-10). Periods of high relative abundance occurred each year between the last week of June and the third week of July (Figure 3-10). There were two peaks of abundance in 1983 (ca. 23 June and 13 July) and only one peak in 1984 (ca. 1 July). Relative school density followed a very similar seasonal pattern to relative abundance (for economy and owing to their similarity, density patterns are not shown). Capelin abundance and density were strongly correlated ($r=0.74$, $p<0.001$; all years combined).

Table 3-6. Survey effort, and mean capelin abundance and density at Witless Bay in 1982-1984. Abundance and density calculated from standard surveys only, using relative scale (see Methods).

	1982	1983	1984
Effort:			
Number of surveys	6	37	35
Total survey time (min)	634	4066	3881
Total survey distance (km)	95	1017	970
Total no. of 1 min x 10 m blocks graded	2,853	17,362	19,161
Abundance and Density:			
Mean abundance (s.e.)	2.3 (0.10)	0.83 (0.05)	0.11 (0.02)
Mean densi[illegible]s.e.)	3.9 (0.16)	4.1 (0.21)	2.4 (0.19)

Figure 3-9: Frequency distributions of echogram block intensity grades for capelin abundance and density in Witless Bay, 1982-1984 (note capelin abundance/density scales are **relative**, see Methods).

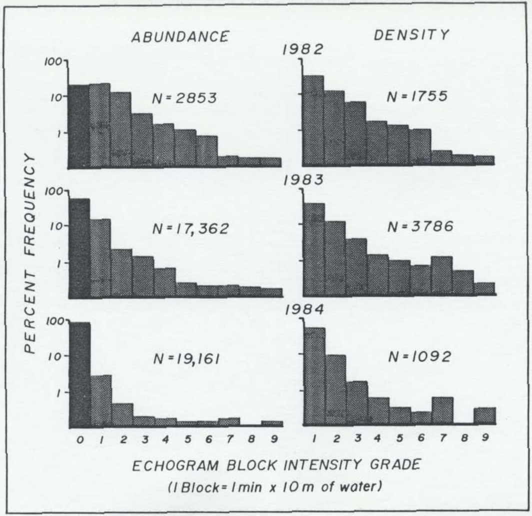
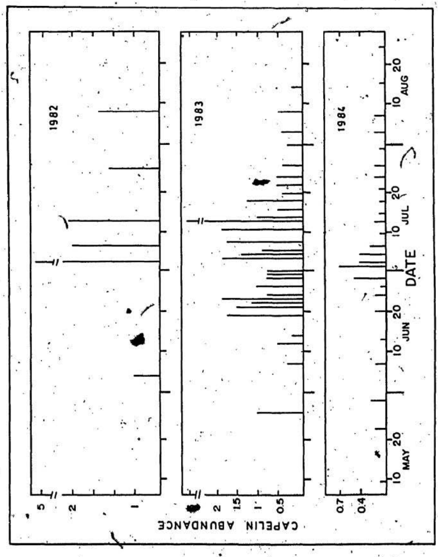

ABUNDANCE
DENSITY
1982
100
10
1
N = 2853
N = 1755
1983
100
10
1
N = 17,362
N = 3786
1984
100
10
1
N = 19,161
N = 1092
PERCENT FREQUENCY
0 1 2 3 4 5 6 7 8 9
1 2 3 4 5 6 7 8 9
ECHOGRAM BLOCK INTENSITY GRADE
(1 Block = 1 min x 10 m of water)

Table 3-7. Kolmogorov-Smirnov tests of between-year differences in relative capelin abundance and density at Witless Bay, 1982-1984.

Years	Abundance			Density		
	no. cases	Z	prob.	no. cases	Z	prob.
1982 * 1983	20,215	18.4	<0.0001	5,541	2.3	<0.0001
1983 * 1984	36,523	12.5	<0.0001	4,878	3.4	<0.0001
1982 * 1984	22,014	27.8	<0.0001	2,847	5.4	<0.0001

Figure 3-10: Seasonal trends in capelin abundance at Witless Bay, 1982-1984.

Note that abundance scale is **relative**, see Methods.


1982
1983
1984
CAPELIN ABUNDANCE
5
2
1
2
1.5
1
0.5
0.7
0.4
10 MAY 20
10 JUN 20
10 JUL 20
10 AUG 20
DATE

Periods of high capelin abundance in Witless Bay coincided each year with the duration of capelin catches in nearshore traps set at Lance Cove, Cape Broyle Bay. Capelin were first sighted nearshore at Lance Cove on 16 June in 1982, on 21 June in 1983 and on 27 June in 1984. Based upon these initial sightings and on the duration of trap collections (Table 3-1), capelin were relatively abundant at Lance Cove for at least 23 days in 1982 (16 June-8 July), 32 days in 1983 (21 June-22 July) and 32 days in 1984 (27 June-28 July). The 1982 period represents a minimum because traps were removed from the water when the commercial capelin fishery ended on 8 July. In 1983 and 1984, however, one trap was left in the water for sampling purposes for at least a week after the last catches of capelin were made on the indicated dates. Thus, the average period of capelin residence inshore was about 4.5 weeks.

3.3.3. Diel Variability

Results of surveys conducted over 24-hr periods on 26-27 June and 5 July, 1983 (Table 3-8), indicate that capelin schools remain in the upper water column throughout daylight (ca. 0500-2130 hr during study period). On both surveys (Table 3-8) conducted near and after night-fall (2030-2330 hrs.), capelin abundance was considerably lower than on previous surveys conducted late in the day (1430-1800 hr). This may indicate that capelin schools disperse overnight. On one survey, started about an hour before sunrise (26 June), capelin abundance was relatively low; increasing slightly on the next survey conducted in late morning. Conversely, after the other early morning survey (5 July), capelin abundance declined by late morning; remaining similar through the day (1025-1740 hr).

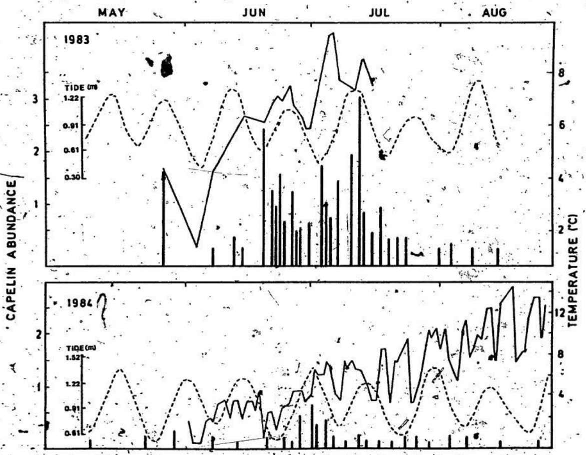
3.3.4. Relations Between Water Temperature, Tide, and Capelin Abundance

There appeared to be a weak relationship between water temperatures, tidal oscillations, and fluctuations in capelin abundance. Peaks in capelin abundance occurred after water temperatures increased to over 4-6°C in mid-June, 1983, and

Table 3-8. Diel variability in mean capelin abundance at Witless Bay during two series of consecutive standard surveys conducted over 24-hr periods in 1983. Capelin were not detected below 60 m. (Note capelin abundance scale is relative, see Methods).

Depth (m)	Survey date (1983) and start time							
	26 Jun 1430	26 Jun 2134	27 Jun 0400	27 Jun 0940	5 Jul 0525	5 Jul 1025	5 Jul 1553	5 Jul 2032
0- 9	5.2	3.0	1.8	2.1	2.1	1.2	1.5	0.4
10-19	1.1	0.4	0.5	0.4	1.1	0.5	0.3	0.3
20-29	0.3	<0.1	0.1	<0.1	0.3	<0.1	<0.1	<0.1
30-39	<0.1	0.0	<0.1	0.0	<0.1	0.0	0.0	<0.1
40-49	<0.1	0.0	0.0	0.0	<0.1	0.0	<0.1	0.0
50-59	<0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Figure 8-11: Relationship between capelin abundance, tides and water temperature at Witless Bay, 1983-1984. Note that capelin abundance scale is **relative**, see Methods.


MAY
JUN
JUL
AUG
1983
TIDE (m)
1.22
0.91
0.61
0.30
3
2
1
8
6
4
2
1984
TIDE (m)
1.52
1.22
0.91
0.61
2
1
12
8
4
CAPELIN ABUNDANCE
TEMPERATURE (°C)

late June, 1984 (Figure 3-11). Each period of peak capelin abundance in 1983 and 1984 was associated with a neap or spring tide and was preceded by an increase in water temperatures (Figure 3-11). The trough between the two peak periods of abundance in 1983 was associated with decreasing water temperatures and decreasing tidal oscillations.

Abundance was significantly correlated with tidal range in 1984 ($n=25$, $r_s=0.27$, $p<0.05$). When only data from periods of peak abundance (ca. mid-June to mid-July) were included in the analysis correlations were stronger for 1983 ($n=19$, $r_s=0.38$, $p=0.06$) and 1984 ($n=12$, $r_s=0.63$, $p<0.05$).

There were no significant simple correlations between abundance and water temperatures over the same time period, but spectral analysis revealed significant correlations over 3-5 day time frames in both 1983 and 1984. As the data were too limited to apply time-series analysis, the relationship between daily fluctuations in capelin abundance and water temperature remains unclear. However, it seems reasonable to suggest that there is some minimum preferred temperature (ca. 4-6°C) above which capelin may occur in high abundance (see below also).

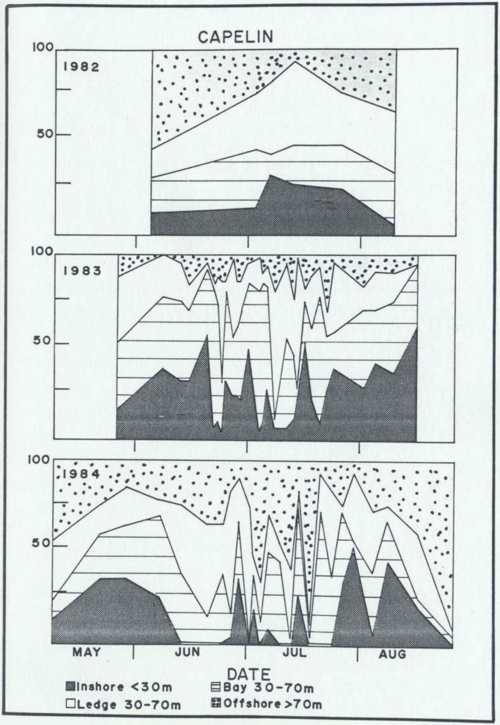
3.4. SPATIAL DISTRIBUTION OF CAPELIN

3.4.1. Distribution of Capelin in Witless Bay

Habitats in the study area were defined on the basis of bird diving abilities and bottom topography (see Methods and Figure 2-2) as being: inshore (<30 m), bay (30-70 m), ledge (30-70 m), and offshore (>70 m). These categories are also convenient for describing the distribution of capelin schools in the study area (Figure 3-12).

Most capelin were recorded in bay and ledge habitats in 1982 (55%), 1983 (64%) and 1984 (50%). Given the small total area of ledge habitat (Figure 2-2), the proportions occurring there (Figure 3-12) indicate that the ledge was an important area of concentration for capelin.

Figure 3-12: Seasonal distribution of capelin in different habitats at Witless Bay, 1982-1984 (adjusted for survey effort in each habitat).


CAPELIN
100
50
1982
1983
1984
MAY
JUN
JUL
AUG
DATE
Inshore <30m
Bay 30-70m
Ledge 30-70m
Offshore >70m

Although the proportion of capelin found in mid-depth habitats changed little between years, there was a notable shift in abundance from inshore to offshore habitats between 1982 and 1984 (Figure 3-12). This shift was associated with decreasing water temperatures between these years (see below). In 1983, more capelin were concentrated inshore (24%) than offshore (11%), whereas in 1984, more capelin were found offshore (35%) than inshore (14%).

3.4.2. Longshore and Offshore Distribution of Capelin

Offshore and longshore surveys for capelin were conducted in May-August of 1984. Most capelin were recorded within about 5 km of the coast, although small concentrations occurred at least 15-20 km offshore (Figure 3-13A). Much higher concentrations were found near shore on the outside (Figure 3-13B) and inside (Figure 3-13C) legs of the longshore survey route (Figure 2-2). Peaks of capelin abundance on the longshore surveys generally occurred around the seabird colony islands, prominent headlands, and in Cape Broyle, Mobile, and Witless Bays.

Few capelin were found on the offshore survey in late May, but significant concentrations were encountered near the surface (<10 m) along most of the offshore survey route on 6 June (Table 3-9 and Figure 3-13). Some capelin were still found offshore in mid-July, but most schools occurred within 5 km of the coast. By mid-August few capelin were recorded offshore. Longshore surveys indicated that capelin were present nearshore from 14 June to 18 July, being most abundant on the 8 July survey.

3.4.3. Vertical Distribution of Capelin in the Water Column

Most capelin were recorded in the upper 20 m of the water column on standard, longshore, offshore, and 24-hr surveys in 1983 and 1984 (Tables 3-8, 3-9 and 3-10), but in 1982 significant concentrations were found to depths of 50 m (Table 3-10.) Ninety-five percent of total capelin biomass on standard surveys was estimated to occur above 60 m in 1982, 30 m in 1983 and 20 m in 1984.

Figure 3-13: Relative abundance of capelin on combined A) offshore (n=4) and, B) and C) longshore (n=3) surveys, 1984. B and C are outside and inside legs, respectively, of longshore survey (see Fig. 2-2).

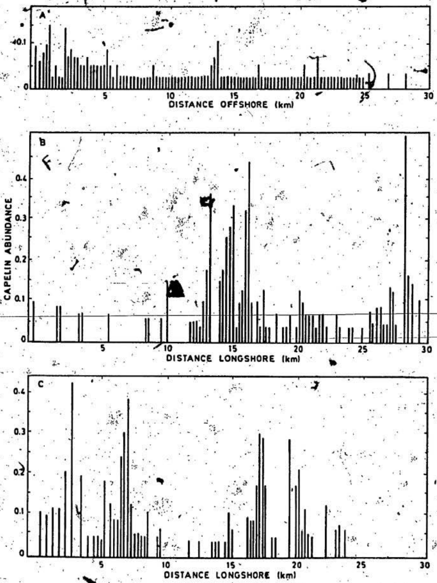

A
0.1
0
5
10
15
20
25
30
DISTANCE OFFSHORE (km)
B
CAPELIN ABUNDANCE
0.4
0.3
0.2
0.1
0
5
10
15
20
25
30
DISTANCE LONGSHORE (km)
C
0.4
0.3
0.2
0.1
0
5
10
15
20
25
30
DISTANCE LONGSHORE (km)

Table 3-9. Mean capelin abundance at different depths on offshore and longshore surveys in 1984. Capelin were not detected below 70 m. (Note capelin abundance scale is relative, see Methods).

Depth (m)	Survey date (1984), start time and number						
	Offshore surveys				Longshore surveys		
	30 May 0834 05	6 Jun 0835 06	16 Jul 0753 23	14 Aug 0735 33	14 Jun 0700 09	8 Jul 1010 19	18 Jul 0745 25
0- 9	<0.1	1.0	0.2	<0.1	0.2	0.5	0.4
10-19	0.0	0.0	<0.1	<0.1	0.1	0.2	0.3
20-29	0.0	0.0	<0.1	<0.1	<0.1	0.2	<0.1
30-39	0.0	0.0	<0.1	<0.1	0.0	<0.1	0.0
40-49	0.0	0.0	0.0	<0.1	0.0	<0.2	0.0
50-59	0.0	0.0	0.0	<0.1	0.0	0.0	0.0
60-69	0.0	0.0	0.0	<0.1	0.0	<0.1	0.0

Table 3-10. Total* capelin abundance and mean capelin density at different depths on standard surveys at Witless Bay, 1982-84.

Depth (m)	Capelin abundance						Mean school density		
	1982		1983		1984		1982	1983	1984
	Total	%**	Total	%	Total	%			
0- 10	2102	31.1	5508	71.4	2119	82.5	4.7	5.2	2.5
10- 20	1273	49.9	1763	94.3	332	95.4	3.9	3.0	2.0
20- 30	1325	69.5	361	99.0	86	98.7	4.1	2.0	1.5
30- 40	867	82.3	69	99.9	30	99.9	3.3	1.4	2.0
40- 50	557	90.5	6	99.9	2	99.9	3.3	1.0	1.0
50- 60	377	96.1	1	99.9	1	100.0	3.3	1.0	1.0
60- 70	165	98.5	0	99.9	0	100.0	2.8	0.0	0.0
70- 80	84	99.7	0	99.9	0	100.0	2.4	0.0	0.0
80- 90	11	99.9	0	99.9	0	100.0	1.0	0.0	0.0
90-100	6	100.0	2	100.0	0	100.0	2.0	1.0	0.0
100-110	0	100.0	0	100.0	0	100.0	0.0	0.0	0.0
110-120	0	100.0	0	100.0	0	100.0	0.0	0.0	0.0

* Total sum of all echograms intensity grades (note that abundance and density scales are relative, see Methods).

** Cumulative percent.

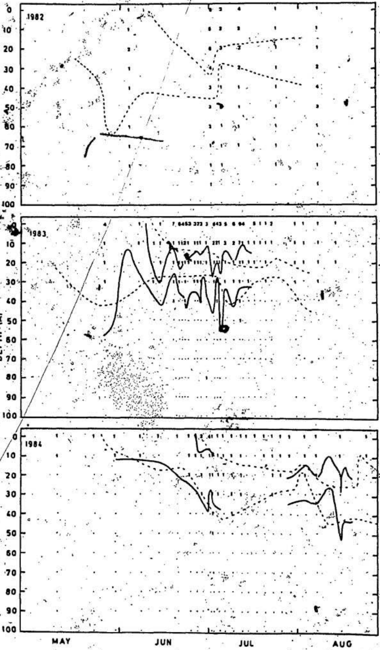
Although the maximum depth at which capelin were recorded varied each year, they were never observed below 100 m on any survey. The maximum depth recorded for capelin in 1982 was 90-100 m, 80-90 m in 1983, and 50-60 m in 1984. On a few surveys, capelin were observed to be concentrated on or very near the bottom in some areas, presumably as they were engaged in spawning activities (Bakke and Bjorke 1973). Usually, these schools were encountered in shallow, nearshore areas where bottom depths were less than 30 m, but some bottom concentrations were found at 50-60 m in 1982.

3.4.4. Relationship Between Water Temperatures and the Spatial Distribution of Capelin

In 1982, the warmest of the 3 years studied (Figure 3-1), capelin were recorded as deep as 90-100 m, although most concentrations were found above 40 m (Figure 3-14). In 1983, the next warmest year (Figure 3-1), capelin were most abundant between 0-20 m and seldom occurred below 40 m (Figure 3-14). In 1984, the coldest of the three years (Figure 3-1), capelin were most abundant between 0-10 m and were seldom recorded below 30 m (Figure 3-14).

Thus, in general, highest concentrations of capelin occurred between the surface and the 5°C isotherm. The maximum depth of the 5°C isotherm was ca. 20-30 m in 1982-1983 and 10-15 m in 1984. The average maximum depth of capelin was usually near the 1°C isotherm, which occurred at ca. 40-50 m in 1982 and 30-40 m in 1983 and 1984. These data strongly suggest that for the time period examined, capelin have marked temperature preferences which determine their distribution in the water column.

Figure 3-14: Relative abundance of capelin (scale 1-9) at 10 m depth intervals in relation to water temperatures at Witless Bay, 1982-1984. Solid lines are depth of 5°C and 1°C isotherms at Gull Island. Dashed lines are 5°C and 1°C isotherms at Station 27 off Cape Spear. Dots indicate no capelin detected.


1982
1983
1984
DEPTH (M)
0
10
20
30
40
50
60
70
80
90
100
MAY
JUN
JUL
AUG

3.5. SUMMARY OF OCEANOGRAPHY AND CAPELIN ECOLOGY

1. The size of capelin available to predators varies seasonally and annually with variations in sex and age-class composition of schools, spawning chronology, and growth and maturation rates.

2. Seasonal variations in inshore capelin abundance are related to water temperatures and tidal rythyms. The bulk of mature capelin biomass appears inshore in one or two pulses between late June and late July. Tides may provide a proximate cue for inshore migration and water temperature may provide the ultimate cue for spawning.

3. The vertical and geographic distribution of capelin is influenced by water temperatures. During the spawning period most capelin school above the 5°C isotherm throughout the day, and virtually all capelin remain above the 1°C isotherm.

4. During their spawning period, adult capelin concentrate near islands and headlands, and within ca. 5-10 km of shore, presumably as they await appropriate conditions for spawning on beaches or shallow inshore areas.

5. Whereas capelin abundance may vary widely between and within years, the average density of schools is much less variable.

6. Over the long term, nearshore water temperatures are influenced by the Labrador Current, pack ice, and icebergs, whereas daily variations in nearshore water temperatures are tightly coupled with wind events. These physical phenomena have a direct influence on temporal and spatial patterns of abundance.

Chapter 4

FEEDING ECOLOGY OF COMMON MURRES AND ATLANTIC PUFFINS

Stomach and gizzard contents of adult birds, and prey fed to chicks, are considered separately because each provides different information on the feeding ecology of murres and puffins at Witless Bay. Owing to rapid digestion, only recently (<2 hr) consumed prey are found in stomachs (Uspenski 1956, Bradstreet 1980). In contrast, gizzards may retain identifiable prey remains for 1-12 hr, though prey lacking otoliths, bony skeletons, or chitinous exoskeletons may be under-represented (Uspenski 1956, Bradstreet 1980). Prey delivered to chicks are usually intact and do not suffer from a decomposition bias, but chick meal composition may differ significantly from that of adults (Belopol'skii 1957, Harris and Hislop 1978).

4.1. STOMACH CONTENTS OF ADULT MURRES AND PUFFINS

4.1.1. Type and Condition of Prey in Stomachs

Most of the food items found in adult murre and puffin stomachs in 1982-1984 were capelin or unidentified fish remains (Table 4-1). A very small proportion of identified fish were juvenile cod (*Gadus morhua*) and sandlance (*Ammodytes* spp.). A few unidentified crustaceans and squid tentacles were also found in some years (see Appendix F for yearly data).

Capelin found in bird stomachs were often in very good condition. Most of the birds collected for stomach analyses were drowned very early each morning in

Table 4-1. Number and percent of total different prey items found in common murre and Atlantic puffin stomachs at Witless Bay, 1982-1984.

Prey items	Murre			Puffin		
	no.	total % no.	mean* % no.	no.	total % no.	mean* % no.
Total no. of stomachs examined	1358			496		
Total no. of items	1350	100.0	100.0	278	100.0	100.0
Ovid female capelin	545	40.4	42.4	126	45.3	38.7
Spent female capelin	64	4.7	5.9	14	5.0	9.3
Mature male capelin	210	15.6	12.8	3	1.1	2.0
Immature capelin	83	6.1	4.3	10	3.6	2.2
Unidentified capelin	322	23.9	24.5	58	20.9	15.6
Cod (spp.)	2	0.1	0.2	0	0.0	0.0
Sandlance (spp.)	1	<0.1	<0.1	0	0.0	0.0
Unidentified fish	120	8.9	9.8	55	19.8	26.2
Crustaceans	1	<0.1	<0.1	12	4.3	6.0
Squid	2	0.1	0.2	0	0.0	0.0
Identifiable capelin	900	100.0	100.0	153	100.0	100.0
Mature female (total)	609	67.7	74.5	140	91.5	91.6
Ovid female	545	60.6	66.0	126	82.4	74.0
Spent female	64	7.1	8.6	14	9.2	19.4
Mature male	210	23.3	18.9	3	2.0	3.6
Immature	81	9.0	6.6	10	6.5	4.0

* mean % no. is the unweighted average of all 3 yr (to compensate for unequal sample sizes between yr).

bottom-set cod gill-nets, probably while foraging near the bottom for capelin (Piatt and Nettleship 1985). This may explain why stomach contents were so often fresh: Feeding birds were entangled, drowned, and cooled rapidly in the cold water (-1° to 5°C) found at depths of net-entanglement (most >20 m), resulting in preservation of stomach contents until nets were emptied and birds were examined later in the day.

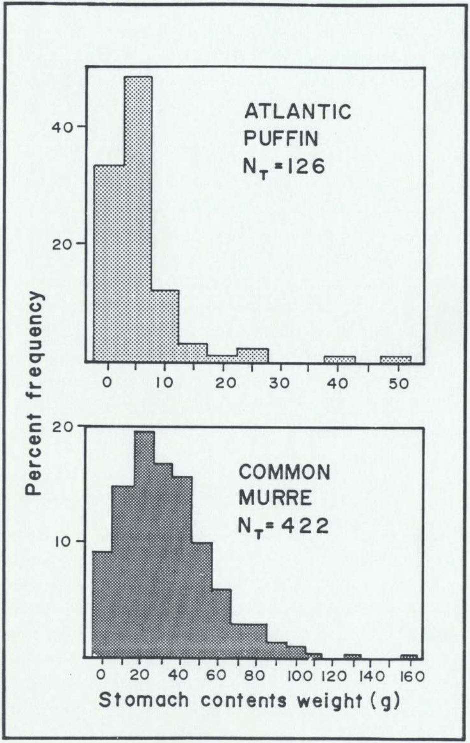
All birds were collected within the boundary of the standard survey route (Figure 2-2), and therefore stomach contents suggest that capelin were the only abundant prey species in the immediate area of the bird colonies. Other prey remains were commonly found in gizzards (below), but most of these could have been i) captured away from the study area, or ii) captured locally, but later in the previous day (i.e., varying diurnal availability). Otherwise, intact non-capelin specimens should have been found more frequently in stomachs.

4.1.2. Adult Meal Sizes

Because stomachs were often full, it was possible to determine the full range of murre and puffin meal sizes (Figure 4-1). These data were collected over the same time period in 1982 when large samples of stomachs containing food were available (see below). Murre stomach contents ranged in weight from 0 to 162 g, with a median weight of 30 g. Puffin stomach contents ranged in weight from 0 to 51 g, with a median weight of 5 g. Ignoring empty stomachs, however, the median number of capelin found in murre and puffin stomachs in 1982 was two and one, respectively, and their average weights were 21.0 and 16.4 g, respectively, so normal meals should have been at least 42 and 16 g, respectively. The disparity between observed and estimated weights must have been due to digestion and was greater in puffins (16:5) than murres (40:30), indicating that digestion rates were faster in puffins. This was predictable because murres are about twice the size of puffins, and therefore should have lower specific metabolic and digestion rates (Peters 1984).

Based on calculated meal sizes, puffins and murres consumed about 3.6 and 4.2%, respectively, of their body mass in a normal meal, although birds were

Figure 4-1: Frequency distribution of stomach content weights of common murres and Atlantic puffins at Witless Bay in 1982.


ATLANTIC
PUFFIN
N_T = 126
40
20
0
10
20
30
40
50
COMMON
MURRE
N_T = 422
20
10
0
20
40
60
80
100
120
140
160
Percent frequency
Stomach contents weight (g)

capable of consuming far more on occasion. Based on estimates of total daily requirements at Witless Bay (100 and 200 g/day for puffins and murres, respectively; Brown and Nettleship 1984), puffins and murres should have fed at least six and five times a day, respectively, during the period examined in 1982. However, either species could have obtained their daily quota in 2-3 meals if they ate maximal rations at each meal.

4.1.3. Feeding Success in Different Years

There was a significant decline in the frequency of capelin found in both murre and puffin stomachs from 1982 to 1983 and from 1983 to 1984 (Table 4-2, Figure 4-2), corresponding to the decrease in capelin abundance between these years (Figure 3-6). For both species, the frequency of empty stomachs increased markedly each year (note log scale). In murres, the frequency of stomachs containing five or more capelin hovered around 1%, increasing slightly between 1982 and 1983, and decreasing again in 1984. Murre stomachs containing one or two capelin decreased steadily in frequency between 1982 and 1984. In puffins, the frequency of stomachs containing two or more capelin declined markedly from 1982 to 1984. There was no significant change in the frequency of capelin found in murre stomachs between 1981-1982, but the 1981 sample was comparatively small.

4.1.4. Comparison of Murre and Puffin Feeding Success

To take body size differences into account and compare feeding success between species, the frequency of capelin in stomachs was reduced to a dichotomous comparison of capelin either absent or present and the proportion of murre stomachs with capelin was compared to the proportion of puffin stomachs with capelin using only data from same-day collections of both species. In 1982, there was a small, but significant difference between species in the proportion of stomachs containing capelin (Table 4-3). In 1983 and 1984, however, an increasingly greater proportion of murres had capelin in their stomachs than puffins.

Table 4-2. Comparison of the numbers of capelin (mean, median and maximum) found in common murre and Atlantic puffin stomachs collected at Witless Bay, 1981-1984.

Year	Murre					Puffin				
	KS*	n	mean	med	max	KS*	n	mean	med	max
1981		84	1.6	1	12		0	-	-	-
	NS									
1982		655	1.1	1	10		229	0.76	1	5
	****					****				
1983		353	1.0	0	8		116	0.31	0	3
	****					****				
1984		350	0.39	0	9		151	0.14	0	1
TOTAL		1442	0.97	0	12		496	0.47	0	5

* Statistical comparison of frequency distributions between years made using Kolmogorov-Smirnov (KS) tests (see appendix K1 for details). Significant differences between years indicated: NS not significant; **** $p<0.0001$.

Figure 4-2: Frequency distributions of the numbers of capelin found in common murre and Atlantic puffin stomachs in 1982-1984. Note that frequency scale is logarithmic.

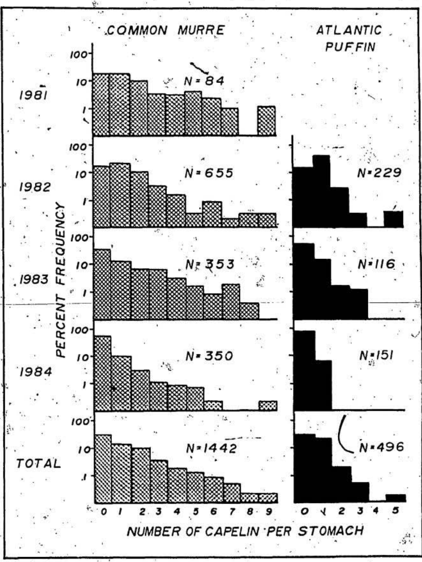

COMMON MURRE
ATLANTIC PUFFIN
1981
1982
1983
1984
TOTAL
PERCENT FREQUENCY
100
10
1
N=84
N=655
N=229
N=353
N=116
N=350
N=151
N=1442
N=496
0 1 2 3 4 5 6 7 8 9
0 1 2 3 4 5
NUMBER OF CAPELIN PER STOMACH

Table 4-3. Between-species χ^2 tests of the proportion of bird stomachs containing some capelin (using only birds collected on the same days in each year). The ϕ coefficient is a measure of association based on χ^2, with higher values indicating greater dissimilarity (see Methods).

Year	n	χ^2	prob.	ϕ
1982	349	4.8	0.029	0.12
1983	228	8.8	0.003	0.20
1984	207	41.2	<0.0001	0.45
TOTAL	784	23.0	<0.0001	0.17

Although differential digestion rates probably account for some of the difference between species in stomach contents (see above), this bias should have been consistent between years. Phi (ϕ) coefficients (Table 4-3) indicate, however, that the difference between species in feeding success increased between 1982 and 1983, and particularly between 1983 and 1984 (note that increasing ϕ values indicate decreasing similarity in proportions, Brown 1983 and see Methods).

4.1.5. Seasonal Variations in Feeding Success: The Functional Response to Prey Density

The frequency of capelin in bird stomachs varied through the summers of 1982-1984 (Figure 4-3), with peaks corresponding to peaks in density of capelin at Witless Bay. The functional relationship between capelin in stomachs and local capelin school density was examined for its form and strength of association using combined data from all 3 years of study. Examined over different time frame intervals (see Methods), the highest and most significant correlations for both murres ($r_s=0.69$, $p<0.001$) and puffins ($r_s=0.74$, $p<0.01$) were found when the data were grouped into 5-day blocks. The form of the relationship between food intake and prey density appeared to be sigmoidal for both species (Figure 4-4). Both plotsexhibited inflection points as indicated by the threshold location test (inset, Figure 4-4, see Methods). This suggests that both murres and puffins exhibited Type III functional responses to prey density (Holling 1959). The puffin response should be interpreted with caution, however, because it could become hyperbolic (Type II), or the inflection point might shift considerably along the prey density axis, with the addition of only a few more data points.

Figure 4-3: Seasonal trends in mean numbers of capelin found in bird stomachs, 1982-1984.

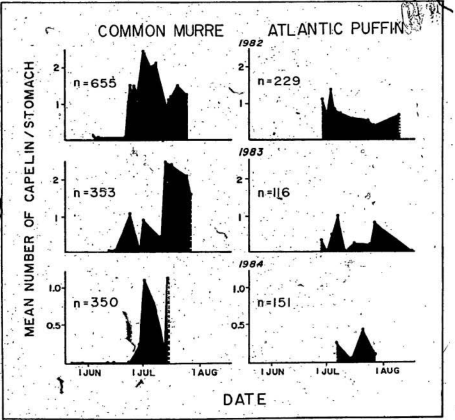
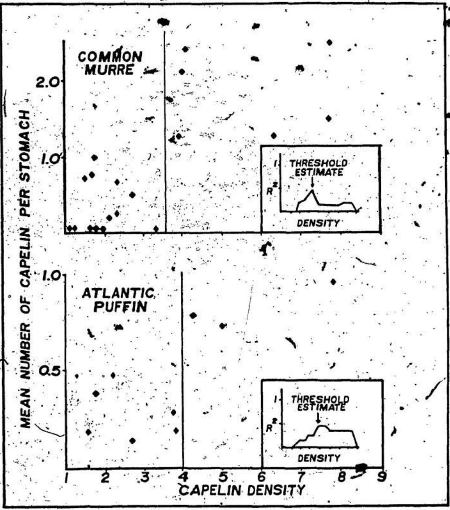

COMMON MURRE
ATLANTIC PUFFIN
1982
1983
1984
MEAN NUMBER OF CAPELIN / STOMACH
n = 655
n = 353
n = 350
n = 229
n = 116
n = 151
2
1
1.0
0.5
1 JUN
1 JUL
1 AUG
DATE

Figure 4-4: Mean number of capelin found in bird stomachs versus capelin density (note capelin density scale is **relative**, see Methods). Data from 1982-84 combined. Thresholds (solid vertical lines) determined from Threshold location test (inset).


COMMON MURRE
2.0
1.0
THRESHOLD ESTIMATE
R²
DENSITY
ATLANTIC PUFFIN
1.0
0.5
THRESHOLD ESTIMATE
R²
DENSITY
MEAN NUMBER OF CAPELIN PER STOMACH
1
2
3
4
5
6
7
8
9
CAPELIN DENSITY

4.2. OVERALL DIET COMPOSITION OF ADULTS AND CHICKS

4.2.1. Numerical Proportions of Different Prey in Adult Diets

Adult diets (Table 4-4 and Figure 4-5) were dominated by three fish species: capelin, cod (predominantly *Gadus morhua* and $<1\%$ *Boreogadus saida*), and sandlance (presumably *Ammodytes dubius*; Reay 1970). The only other prey items found were squid beaks (*Illex illecebrosus*) and unidentified crustacean remains (see Appendix G for yearly data).

Adult murres consumed predominantly capelin in all years (Figure 4-5). The numerical proportion of capelin in murre diets increased each year from 49% in 1982 to 69% in 1984. The unweighted average proportion was 60% (Table 4-4). Cod and sandlance accounted for the remainder, averaging about 16% and 24%, respectively, of the total diet (Table 4-4). Cod were markedly less frequent in 1984, while the proportion of sandlance decreased substantially between 1982 and 1983, being nearly the same between 1983 and 1984.

Consistent with the increase in proportion of capelin otoliths found in murre gizzards between 1982 and 1983, there was a significant upward shift in the frequency distribution of capelin otoliths per gizzard between 1982-1983 (although this could have been partially due to the small number of gizzard samples in 1982). No significant shift in frequencies was observed between 1983-1984 (Table 4-5), despite an increase in the proportion of capelin in the diet. Frequency distributions of sandlance and cod otoliths per gizzard shifted significantly downward and upward, respectively, between 1982 and 1983, but there were no differences in frequency distributions between 1983 and 1984, although the median and maximum numbers of cod otoliths per gizzard were considerably lower in 1984 (Table 4-5).

The numerical proportion of capelin in adult puffin diets ranged from 28% in 1982 to 58% in 1984 (Figure 4-5). The unweighted average capelin proportion was 41% (Table 4-4). Cod were most numerous in 1982 (58%) and 1983 (56%); whereas sandlance (37%) replaced cod (3%) as the most common alternative to

Table 4-4. Number and percent of total different prey items found in common murre and Atlantic puffin gizzards at Witless Bay, 1982-1984.

Prey items	Murre			Puffin		
	no.	total % no.	mean* % no.	no.	total % no.	mean* % no.
Total no. of gizzards examined	889			299		
Total no. items	1869			706		
Total no. identified food items	1525	100.0	100.0	596	100.0	100.0
Capelin otoliths	971	63.7	60.0	274	46.0	41.1
Cod (spp.) otoliths	224	14.7	15.5	180	30.2	39.1
Sandlance (spp.) otoliths	326	21.4	24.3	127	21.3	16.1
Unidentified otoliths **	344	-	-	110	-	-
Squid beaks	0	0.0	0.0	15	2.5	3.9
Crustaceans	4	0.3	0.2	0	0.0	0.0
Pebbles **	217	-	-	132	-	-

* mean % no. is the unweighted average of all 3 yr (to compensate for unequal sample sizes between yr).

** not included for calculation of percent total items.

Figure 4-5: Numerical proportions of different prey in diets of adult and chick common murres and Atlantic puffins at Witless Bay, 1982-1984. "Other" category comprises squid for puffins, and unidentified crustaceans for murres.

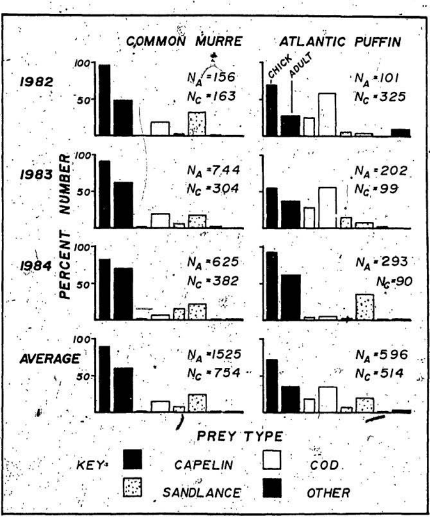

COMMON MURRE
ATLANTIC PUFFIN
CHICK
ADULT
1982
$N_A = 156$
$N_C = 163$
$N_A = 101$
$N_C = 325$
1983
$N_A = 744$
$N_C = 304$
$N_A = 202$
$N_C = 99$
1984
$N_A = 625$
$N_C = 382$
$N_A = 293$
$N_C = 90$
AVERAGE
$N_A = 1525$
$N_C = 754$
$N_A = 596$
$N_C = 514$
PERCENT NUMBER
100
50
PREY TYPE
KEY:
CAPELIN
COD
SANDLANCE
OTHER

Table 4-5. Comparison of the numbers of capelin, cod, and sandlance otoliths found in common murre and Atlantic puffin gizzards at Witless Bay, 1982-1984.

Otolith	Year	Murre					Puffin				
		KS*	n**	mean	med	max	KS*	n	mean	med	max
Capelin	1982		76	2.7	1	22		28	1.3	1	5
		****					****				
	1983		461	2.8	2	24		76	2.0	2	5
		NS					NS				
	1984		434	2.7	2	25		170	1.9	2	6
	TOTAL		971	2.7	2	25		181	1.8	1	6
Cod	1982		30	1.6	2	3		59	3.4	3	8
		****					*				
	1983		147	2.6	2	29		111	3.9	3	12
		NS					NS				
	1984		47	2.2	1	13		10	1.4	1	2
	TOTAL		224	2.3	1	29		180	3.4	2	12
Sandlance	1982		50	3.6	2	18		4	1.3	1	2
		**					NS				
	1983		136	3.0	2	15		15	2.5	2	5
		NS					**				
	1984		140	2.6	2	13		108	3.1	3	11
	TOTAL		326	2.8	2	18		127	2.9	2	11

* Statistical comparisons of frequency distributions between years made using Kolmogorov-Smirnov tests (see appendix K2 for details). Significant differences between years indicated: NS not significant; * $p<0.05$; ** $p<0.01$; *** $p<0.001$; **** $p<0.0001$.

** Total number of otoliths found in gizzards.

capelin in 1984. Proportions of 'other' prey (largely squid) were small in 1982, and negligible in 1983 and 1984.

As with murres, the frequency distribution of capelin otoliths per puffin gizzard shifted upward between 1982 and 1983, but there was no significant difference in frequency distributions between 1983 and 1984 (Table 4-5). Also like murres, the frequency distribution of cod otoliths per puffin gizzard shifted upward from 1982 to 1983, but did not change significantly between 1983 and 1984, although the median and maximum numbers of cod otoliths per gizzard declined substantially in 1984. Corresponding to the increased proportion of sandlance in the puffin's diet, there was a significant upward shift in the frequency distribution of sandlance otoliths per gizzard between 1983 and 1984.

4.2.2. Comparison of Adult Murre and Puffin Diets

To compare adult diets within and between years, only data from murres and puffins collected over the same time periods in 1983 and 1984 were analyzed using a G-test of frequencies (see Appendix K5). Analysis revealed a highly significant interaction between predator and prey species ($G_{1,735}$=90.6, $p<0.0001$), which indicates there were marked differences between the diets of murres and puffins. Most differences were due to greater consumption by puffins of cod in 1983, and sandlance in 1984 (Figure 4-5). The interaction between bird and prey frequencies was not independent of year ($G_{1,735}$=12.5, $p<0.0001$). There was also a highly significant interaction between prey proportions and year ($G_{1,735}$=116.1, $p<0.0001$), indicating that there were marked between-year differences in prey proportions independent of selection by the two predators. This was reflected in the disappearance of cod from the diets of both bird species in 1984, and the corresponding increase in proportions of capelin and sandlance (Figure 4-5).

4.2.3. Comparison of Adult and Chick Diets

The primary difference between adult and chick diets was that adults took more cod and sandlance, whereas chicks were always fed a higher proportion of capelin (Figure 4-5 and Table 4-6). For murre chicks, capelin were by far the most important prey fed to chicks in all years, with only sandlance occurring in any abundance as an alternative prey. Puffin chicks were maintained on a predominantly capelin diet also, but in 1982 and 1983, juvenile cod constituted a significant proportion of the diet (Figure 4-5).

To test the significance of differences between adult and chick diets, only data collected over equivalent time periods were analyzed using a G-test of frequencies (see Appendices K6 and K8). Temporally overlapping adult-chick collections were made in 1983 and 1984 for murres, but only in 1983 for puffins. For murres, there was a highly significant difference between adult and chick diets ($G_{1,1270}=151.7$, $p<0.0001$), which was independent of year ($G_{1,1270}=3.0$, $p>0.05$). Prey proportions also changed significantly between years ($G_{1,1270}=53.4$, $p<0.0001$), independent of adult-chick selection. For puffins, there was also a highly significant difference between adult and chick diets ($G_{1,204}=16.5$, $p<0.001$).

4.2.4. Proportions of Different Sex/Age Classes of Capelin in Adult Diets

There is considerable variation in size and wet weight energy content of different sex/age classes of capelin (Montevecchi and Piatt 1984, this study). It is therefore of interest to consider diet composition with respect to capelin alone.

In general, adult murres and puffins fed mostly on ovid female capelin (Table 4-1) in all years (Figure 4-6). Murres always consumed a slightly higher proportion of ovid females, and a much higher proportion of males, than did puffins. Neither species consumed many immature capelin. Both species consumed markedly different proportions of adult male and female capelin than found in trap collections. As the ratio of males to females increased in trap

Table 4-6. Number and percent of total different prey items delivered to common murre and Atlantic puffin chicks at Gull and Great Islands, 1982-1984.

Prey items	Murre			Puffin		
	no.*	Total % no.	Mean % no.	no.	Total % no.	Mean % no.
Total no. of chick meal items	754 (95)	100.0	100.0	534	100.0	100.0
Capelin	665 (81)	88.2	89.6	363	68.0	72.3
Cod (spp.)	0 (2)	0.2	0.2	111	20.8	18.7
Sandlance (spp.)***	76 (11)	10.1	8.5	57	10.7	7.9
Total other	13 (1)	1.7	1.7	3	0.6	1.0
Other:						
Stichaeidae****	13 (1)	1.7	1.7			
Cottidae				1	0.2	0.3
Pleuronectidae				1	0.2	0.3
Aspidophoroides monopterygius				1	0.2	0.3
Identifiable capelin	507 (80)	100.0	100.0	363	100.0	100.0
Total mature female	389 (66)	76.7	76.1	208	57.3	66.8
Condition known	286 (65)			156		
Ovid female	198 (48)	54.3**	56.3**	35	12.7**	9.9**
Spent female	88 (17)	23.2**	22.7**	121	44.6**	56.9**
Mature male	30 (2)	5.9	6.2	19	5.2	8.4
Immature	88 (12)	17.4	18.8	136	37.5	24.8

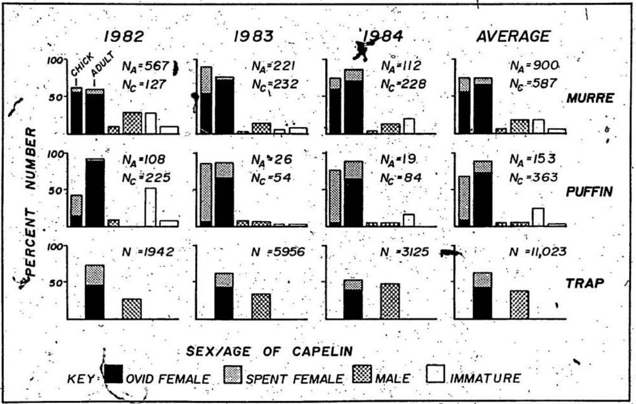
* Numbers based on visual observations of chick meal deliveries and (in parentheses) on collections from collared chicks. There were no significant differences between proportions observed by the two methods and results were combined to obtain the total percentages.

** Percentages extrapolated from the proportions of females where the spawning condition was known to the total number of mature females observed.

*** All of 10 specimens identified were *Ammodytes dubius*.

**** 1 specimen identified as Radiated Shanny, *Ulvaria subbifurcata*.

Figure 4-6: Numerical proportions of different capelin age/sex classes in diets of adult and chick common murres and Atlantic puffins at Witless Bay, 1982-1984.


1982
1983
1984
AVERAGE
PERCENT NUMBER
100
50
CHICK
ADULT
N_A=567
N_C=127
N_A=221
N_C=232
N_A=112
N_C=228
N_A=900
N_C=587
MURRE
N_A=108
N_C=225
N_A=26
N_C=54
N_A=19
N_C=84
N_A=153
N_C=363
PUFFIN
N =1942
N =5956
N =3125
N =11,023
TRAP
SEX/AGE OF CAPELIN
KEY: ■ OVID FEMALE ▨ SPENT FEMALE ▩ MALE □ IMMATURE

collections from 1982 to 1984, the male-female ratio decreased in adult murre diets (Figure 4-6).

To test the significance of these differences in capelin composition, only data collected over equivalent time periods were used in a G-test of frequencies (see Appendices K10 and K11). The number of identifiable capelin in puffin stomachs was small in 1983 and 1984, so the data were combined over 3 yr for comparison with murre diet. Analysis indicated there was a highly significant between-species difference in the composition of capelin in diets ($G_{3,520}=43.9$, $p<0.0001$). Trap collections were relatively brief in 1982, so comparison of adult bird diets (excluding immature capelin) with trap collections included only data from 1983 and 1984. Analysis indicated highly significant between-source differences in proportions of different capelin sex-classes taken ($G_{4,9523}=169.4$, $p<0.0001$).

4.2.5. Comparison of Capelin Age/Sex Classes in Diets of Adults and Chicks

The biggest difference between capelin in the diets of adult and chick murres was in the higher proportion of male capelin taken by adults, and the higher proportion of immature capelin fed to chicks (Figure 4-6). A G-test of frequencies using only data collected over equivalent time periods in 1982, 1983, and 1984 (see Appendix K7) indicated that these differences were highly significant ($G_{3,1139}=112.1$, $p<0.0001$), and only slightly dependent on year of collection ($G_{6,1136}=10.3$, $p<0.05$). There was also a highly significant interaction between capelin sex/age class proportions and year ($G_{6,1136}=117.9$, $p<0.0001$), which was independent of adult-chick selection. This inter-annual variation in the proportions of different classes of capelin is also indicated from trap collections.

For puffins, adult diets differed from chicks mostly in the higher proportions of immature and spent female capelin fed to chicks (Figure 4-6). The difference in spent female proportions was largely an artifact of sampling, however, because most adults were collected in July, whereas chick meals were collected mostly in August when female capelin in spawning condition are relatively rare (Templeman 1948). Comparing only data from temporally overlapping collections (all years combined, see Appendix K8), a G-test of frequencies indicated no significant difference in the proportions of different capelin classes consumed by adults or chicks ($G_{3,168}$=7.7, $p>0.05$).

4.2.6. Proportions by Weight of Different Prey in Murre and Puffin Diets

When expressed as the wet weight proportion of total prey, instead of the numerical proportion (see Methods), capelin overwhelmingly dominated the diets of adult and chick murres and puffins (Figure 4-7, Table 4-7). Only sandlance maintained its relative importance as a prey item in the diets of adult puffins and of both murre and puffin chicks (Figure 4-7). Most of the cod consumed by murres and puffins, and sandlance consumed by adult murres, were so small that their relative contributions to diet diminished greatly when expressed on a weight basis.

On a weight basis, chicks were fed almost-exclusively capelin, whereas adult diets were more diverse in all years (Table 4-7 and Figure 4-7). For adult puffins, sandlance were the most important alternative prey to capelin (Figure 4-7). For adult murres, cod and sandlance were about equally important alternative prey.

4.2.7. Proportions by Weight of Different Capelin Age/Sex Classes in Diets

Because of the disparity in weights of adult male and female capelin, and immature capelin, the relative contribution of these sex/age classes to diet also changed considerably when considered on a wet weight basis (Table 4-8 and Figure 4-8). For both murre and puffin chicks, the relative contribution of immature capelin diminished greatly, whereas the relative contribution of adult male capelin increased slightly. For adult birds, the most important difference was in the increased contribution of adult male capelin to diets. This was particularly notable for murres where the weight proportion of male capelin varied from a low of 23% in 1984 to a high of 47% in 1982. On average, 32% of capelin biomass consumed by murres were adult males.

Table 4-7. Percent wet weight composition of adult and chick common murre and Atlantic puffin diets at Witless Bay, 1982-1984.

Fish	Murre		Puffin	
	Adult	Chick	Adult	Chick
Capelin	82.7	90.8	78.7	93.2
Cod	7.6	0.2	2.4	1.3
Sandlance	9.7	8.0	14.2	6.3
Other	< 0.1	1.0	4.7	< 0.1

Figure 4-7: Percent wet weight composition of adult and chick common murre and Atlantic puffin diets at Witless Bay, 1982-1984.

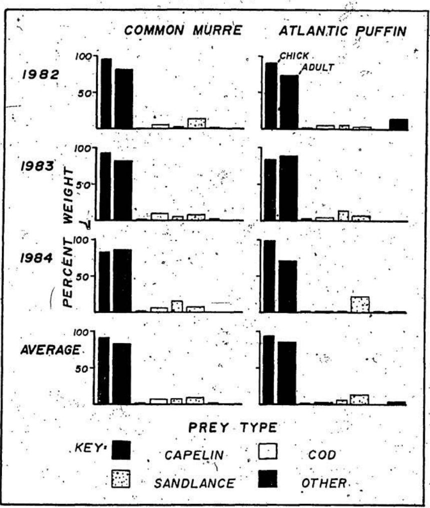
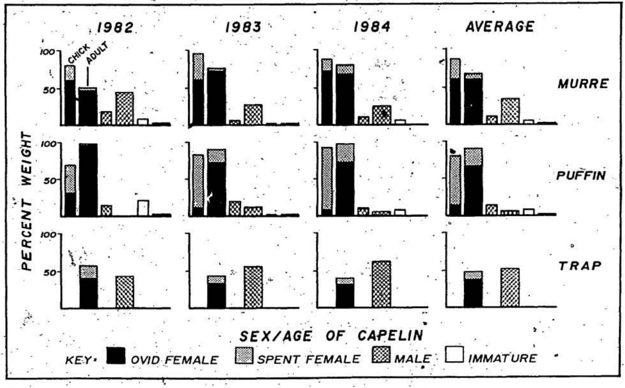

COMMON MURRE
ATLANTIC PUFFIN
1982
1983
1984
AVERAGE
CHICK
ADULT
PERCENT WEIGHT
100
50
PREY TYPE
KEY:
CAPELIN
COD
SANDLANCE
OTHER

Table 4-8. Percent wet weight composition of adult and chick common murre and Atlantic puffin capelin diets at Witless Bay, 1982-1984.

Capelin	Murre		Puffin	
	Adult	Chick	Adult	Chick
Adult female				
Total	67.1	84.9	93.9	79.0
Ovid	61.3	62.0	80.3	12.2
Spent	5.8	22.9	13.6	66.8
Adult male	31.8	10.1	5.2	13.3
Immature	1.1	4.9	0.8	7.7

Figure 4-8: Wet weight proportions of different capelin age/sex classes in diets of adult and chick common murres and Atlantic puffins at Witless Bay, 1982-1984.


1982
1983
1984
AVERAGE
CHICK
ADULT
MURRE
PUFFIN
TRAP
PERCENT WEIGHT
100
50
SEX/AGE OF CAPELIN
KEY: ■ OVID FEMALE ▨ SPENT FEMALE ▩ MALE □ IMMATURE

4.3. SEASONAL VARIATION IN DIETS AND RELATION TO CAPELIN DENSITY AT WITLESS BAY

4.3.1. Seasonal Variation in Adult and Chick Diets

There was a great deal of seasonal variability in diets of adult murres and puffins (Figure 4-9). Although this variability was sometimes reflected in chick diets (e.g., compare adult murres and murre chicks before 1 July, 1984, or adult puffins and puffin chicks after 1 August, 1983), chick diets were generally less variable than those of adults (Figure 4-10). This suggests that when capelin were relatively scarce, adults consumed a greater variety of prey themselves while maintaining chicks on a capelin diet whenever possible.

4.3.2. Seasonal Variation in Diet Composition in Relation to Local Capelin School Density

As for capelin in stomachs, the strength of correlation between capelin density in Witless Bay and the proportion of capelin in overall diets was examined over increasing time frame intervals using combined data from all years (see Methods). No significant correlations were found at any time frame interval for either murres or puffins. This lack of correlation is not surprising, however, because even when capelin were not locally abundant, birds could have flown out of the study area to obtain capelin elsewhere. Thus, the seasonal patterns of capelin proportions in total diets as determined from gizzards (Figure 4-9) differed from the patterns of capelin frequencies in bird stomachs (Figure 4-3), except during periods of high relative capelin density in Witless Bay.

Figure 4-9 Seasonal variation in diets of adult common murres and Atlantic puffins at Witless Bay, 1982-1984.

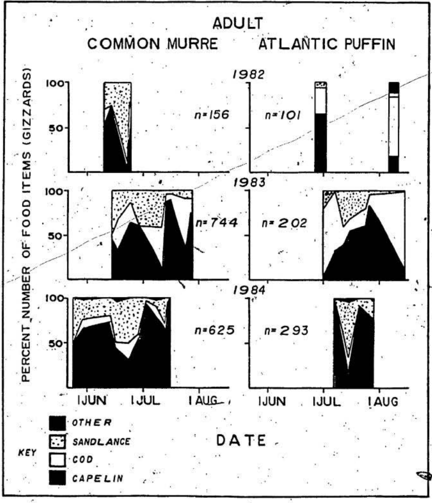
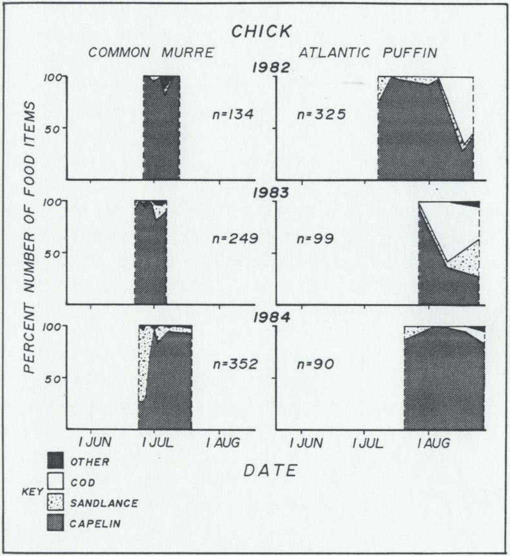

ADULT
COMMON MURRE
ATLANTIC PUFFIN
PERCENT NUMBER OF FOOD ITEMS (GIZZARDS)
1982
100
50
n=156
n=101
1983
100
50
n=744
n=202
1984
100
50
n=625
n=293
1 JUN
1 JUL
1 AUG
1 JUN
1 JUL
1 AUG
DATE
KEY
OTHER
SANDLANCE
COD
CAPELIN

Figure 4-10: Seasonal variation in diets of common murre and Atlantic puffin chicks at Witless Bay, 1982-1984.


CHICK
COMMON MURRE
ATLANTIC PUFFIN
1982
n=134
n=325
1983
n=249
n=99
1984
n=352
n=90
100
50
PERCENT NUMBER OF FOOD ITEMS
1 JUN
1 JUL
1 AUG
DATE
KEY
OTHER
COD
SANDLANCE
CAPELIN

4.4. SIZE DISTRIBUTIONS OF PREY CONSUMED BY MURRES AND PUFFINS

4.4.1. Prey Length Distributions

The mean lengths of capelin (all sex/age classes combined) taken by different "predators" (adult and chick murres and puffins, and traps) varied considerably (Table 4-9). However, such a comparison is simplistic because overall mean lengths depend on the proportions of different capelin sex/age classes in the diet of each predator. Analyzed (ANOVA) by sex/age classes, there were significant between-predator differences in length distributions of male ($F_{3,1025}=10.7$, $p<0.0001$), ovid female ($F_{4,1203}=27.1$, $p<0.0001$), and spent female capelin ($F_{4,1020}=10.1$, $p<0.0001$), but not of immature capelin ($F_{2,144}=1.5$, $p>0.05$). However, most of the variance was due to differences between trap-caught and bird-caught capelin, and a multiple means comparison (Student-Neuman-Keuls (SNK) test) revealed no significant differences in mean lengths of ovid or spent females, males, or immature capelin consumed by adult or chick murres or puffins (Table 4-9).

A comparison of intact otoliths from murre and puffin gizzards revealed no significant between-species differences in capelin otolith lengths in either 1983 or 1984 (Table 4-10). There were also no significant between-species differences in lengths of sandlance otoliths from adult birds (Table 4-10), or in lengths of sandlance fed to chicks (Wilcoxon test, $z=1.7$, $df=45$, $p>0.05$). Cod otoliths removed from murre gizzards, however, were significantly bigger than cod otoliths from puffins in both years. No comparisons were made between lengths of cod and sandlance from chicks versus adults because these fish lengths were estimated in different ways (measured length vs. extrapolation from otoliths, see Methods).

Table 4-9. Number, mean length (and standard error) of fish collected from common murre (Mu) and Atlantic puffin (Pu) adults (Ad) and chicks (Ch), and capelin trap, 1982-1984.

Fish		Trap	Mu Ad	Mu Ch	Pu Ad	Pu Ch
Capelin: Total	n	2742	225	64	36	339
	mean	159	144	138	137	126
	mean*	159	145	137	135	132
	s.e.	0.3	1.9	2.0	2.5	1.6
Ovid female	n	965	111	38	28	67
	mean	150	143	139	137	138
	s.e.	0.5	1.4	2.1	3.0	1.6
Spent female	n	829	23	24	7	141
	mean	152	139	139	134	147
	s.e.	0.5	2.6	2.4	3.3	1.3
Male	n	948	59	-	1	21
	mean	173	175	-	155	159
	s.e.	0.4	1.2	-	-	2.8
Immature	n	-	32	4	-	110
	mean	-	92	93	-	87
	s.e.	-	2.1	4.4	-	1.7
Sandlance	n	-	*** 80	9	*** 83	37
	mean	-	136	170	142	123
	s.e.	-	1.8	8.3	1.6	10.8
Cod	n	-	***105	-	***138	91
	mean	-	90	-	36	43
	s.e.	-	3.8	-	0.7	1.0

* Mean size weighted by percent of total number in diet.

** Means with common underlining were not significantly ($p > 0.05$) different according to SNK multiple range test on capelin and Wilcoxon two-way tests on sandlance and cod.

*** Extrapolated from otoliths.

Table 4-10. Between-species comparison (Wilcoxon test) of capelin, sandlance, and cod otolith lengths from common murre and Atlantic puffin gizzards collected at Witless Bay, 1983-1984.

Otolith	Year	N		Mean length		Z	Prob.
		Murre	Puffin	Murre	Puffin		
Capelin	1983	41	11	2.27	2.36	0.6	NS 0.53
	1984	44	20	2.76	2.66	-0.3	NS 0.77
	TOTAL	85	31	2.53	2.55	0.9	NS 0.38
Sandlance	1983	35	2	2.31	2.35	0.6	NS 0.52
	1984	38	81	2.30	2.39	-1.6	NS 0.12
	TOTAL	73	83	2.30	2.39	-1.1	NS 0.32
Cod	1983	16	25	3.63	1.64	4.7	<0.0001
	1984	70	113	4.38	1.44	11.0	<0.0001
	TOTAL	86	138	3.98	1.48	12.5	<0.0001

4.4.2. Prey Weight Distributions

The between-species patterns observed for prey lengths did not change much when weights rather than lengths were considered (Table 4-11 and Figure 4-11). Adult birds took heavier male and ovid female capelin than they fed to chicks. Murres took heavier ovid female capelin than did puffins. No significant between-predator differences were detected in weights of spent female or immature capelin. Sandlance fed to murre chicks were significantly heavier than those fed to puffin chicks (Wilcoxon test, $z=2.3$, $df=45$, $p<0.05$). The weights of cod consumed by adult murres provided the greatest contrast in diet with puffins, with murres taking juvenile cod greater than 50 g in weight, whereas puffins only consumed cod weighing less than 10 g (Figure 4-11).

4.4.3. Variation in Capelin Size with Time of Sampling

Some of the apparent differences in size of capelin consumed by different predators could have been due to differences in sampling times and natural temporal variation in size of capelin (see Figures 3-7 and 3-8). The effect of sampling period was examined by calculating the partial variance in capelin lengths and weights due to predator, year, period of collection (2-wk intervals), and the interactions between these variables, after the effects of other sources of variance were removed (Tables 4-12 and 4-13).

After the effects of year and sampling period were removed, there were still significant between-predator differences in both lengths and weights of male and ovid female capelin, but not of spent female or immature capelin. Male capelin lengths did not vary significantly with year or collection period, but weights did vary significantly with period. Lengths and weights of ovid and spent female capelin, and immature capelin, varied significantly with year and collection period. Many 2- and 3-way interactions between predator, year, and period were also significant indicating that these variables were not independent of each other. In general, most of the variance in male and ovid female capelin size was due to predator selection; in spent female size was due to year and collection period; and in immature size was due to yearly variations.

Table 4-11. Number, mean wet weight (and standard error) of fish collected from common murre (Mu) and Atlantic puffin (Pu) adults (Ad) and chicks (Ch), and capelin trap, 1982-1984.

Fish		Trap	Mu Ad	Mu Ch	Pu Ad	Pu Ch
Capelin: Total	n	2696	225	64	36	339
	mean	22.7	20.4	12.3	15.7	9.0
	mean*	23.4	20.6	12.2	14.6	9.6
	s.e.	0.2	0.8	0.5	0.9	0.3
Ovid female	n	947	111	36	28	67
	mean	19.7	19.1	13.5	16.8	11.8
	**	-------	-------			
				-----		-----
	s.e.	0.2	0.6	0.7	1.0	0.4
Spent female	n	817	23	24	7	141
	mean	15.2	13.8	12.0	10.3	10.9
		-------	-------	-------	-------	-------
	s.e.	0.2	0.7	0.6	0.8	0.3
Male	n	932	59	-	1	21
	mean	32.4	34.6	-	22.6	20.0
		-------	-------	-------	-------	
	s.e.	0.2	1.2	-	-	1.2
Immature	n	-	32	4	-	110
	mean	-	3.3	3.2	-	3.0
			-------	-------	-------	-------
	s.e.	-	0.2	0.4	-	0.2
Sandlance	n	-	*** 80	9	*** 83	37
	mean	-	6.8	12.5	7.3	7.2
			-----		-----	
	s.e.	-	0.2	1.8	0.2	1.1
Cod	n	-	***105	-	***138	91
	mean	-	12.4	-	0.61	0.62
	s.e.	-	1.4	-	0.04	0.05

* Mean size weighted by percent of total number in diet.

** Means with common underlining were not significantly different (p> 0.05) according to SNK multiple range test on capelin and Wilcoxon two-way tests on sandlance and cod.

*** Extrapolated from otoliths.

Figure 4-11: Wet weight frequency distributions of prey collected from adult and chick common murres and Atlantic puffins at Witless Bay, 1982-1984.

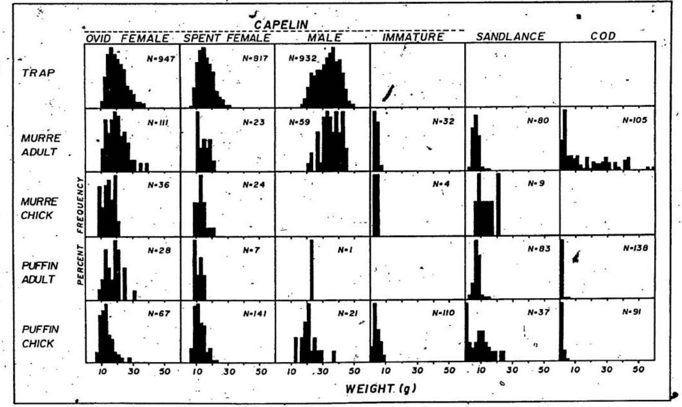

CAPELIN
OVID FEMALE
SPENT FEMALE
MALE
IMMATURE
SANDLANCE
COD
TRAP
MURRE ADULT
MURRE CHICK
PUFFIN ADULT
PUFFIN CHICK
PERCENT FREQUENCY
N=947
N=817
N=932
N=111
N=23
N=59
N=32
N=80
N=105
N=36
N=24
N=4
N=9
N=28
N=7
N=1
N=83
N=138
N=67
N=141
N=21
N=110
N=37
N=91
10
30
50
WEIGHT (g)

Table 4-12. Contribution of predator class (adult/chick, murre/puffin, and capelin trap), year, and period (2 weeks) to variance in length of all capelin collected in 1982-1984 (unbalanced ANOVA partial sums of squares analysis).

Capelin class	Source of variance	df	F	prob.
Adult male	Predator (Pr)	3	4.59	<0.01
	Year	2	1.38	NS
	Period	4	0.85	NS
	Pr * Year	4	1.15	NS
	Pr * Period	2	1.24	NS
	Pr * Year * Period	5	2.52	<0.05
Adult female (ovid)	Predator (Pr)	4	8.65	<0.0001
	Year	2	3.98	<0.05
	Period	5	4.34	<0.001
	Pr * Year	7	2.99	<0.01
	Pr * Period	6	1.38	NS
	Pr * Year * Period	8	3.82	<0.001
Adult female (spent)	Predator (Pr)	4	2.26	NS
	Year	2	4.22	<0.05
	Period	4	4.02	<0.01
	Pr * Year	5	3.58	<0.01
	Pr * Period	4	1.50	NS
	Pr * Year * Period	8	3.23	<0.01
Immature	Predator (Pr)	2	0.21	NS
	Year	2	12.70	<0.0001
	Period	5	3.42	<0.01
	Pr * Year	1	1.11	NS
	Pr * Period	1	2.11	NS
	Pr * Year * Period	5	7.46	<0.0001

Table 4-13. Contribution of predator class (adult/chick, murre/puffin, and capelin trap), year, and period (2 weeks) to variance in weight of all capelin collected in 1982-1984 (unbalanced ANOVA partial sums of squares analysis).

Capelin class	Source of variance	df	F	prob.
Adult male	Predator (Pr)	3	9.10	<0.0001
	Year	2	1.94	NS
	Period	4	2.51	<0.05
	Pr * Year	4	1.53	NS
	Pr * Period	2	1.42	NS
	Pr * Year * Period	5	3.60	<0.01
Adult female (ovid)	Predator (Pr)	4	15.73	<0.0001
	Year	2	0.04	NS
	Period	5	4.13	<0.001
	Pr * Year	7	1.66	NS
	Pr * Period	6	0.99	NS
	Pr * Year * Period	8	3.96	<0.0001
Adult female (spent)	Predator (Pr)	4	0.88	NS
	Year	2	5.94	<0.01
	Period	4	4.02	<0.01
	Pr * Year	5	2.41	<0.05
	Pr * Period	4	1.07	NS
	Pr * Year * Period	8	2.88	<0.01
Immature	Predator (Pr)	2	0.99	NS
	Year	2	12.23	<0.0001
	Period	5	3.78	<0.01
	Pr * Year	1	13.31	<0.001
	Pr * Period	1	0.00	NS
	Pr * Year * Period	5	11.27	<0.0001

4.5. OVERLAP AND DIVERSITY OF MURRE AND PUFFIN DIETS

4.5.1. Diet Overlap

Based on numbers of prey items, overlap in total and just capelin diets of adults increased from 1982-1984 (Table 4-14), averaging 0.88 and 0.96, respectively, over all years. Overlap between total and capelin portions of chick diets was always higher than between adults, with average values of 0.95 and 0.99, respectively, over all years.

Calculated on a wet weight basis, overlap in total or capelin diets between adults or chicks was extremely high and similar in all years, having an overall value of 0.99 for all comparisons.

4.5.2. Diet Diversity

There were no clear trends in diet diversity between years (Table 4-15). The diversity of adult murre diets decreased from 1982 to 1984, whereas the diversity of murre chick diets increased over the same period. On a numerical basis, adult puffin diet diversity was relatively similar in different years, whereas chick diet diversity varied considerably. On a weight basis, both adult and chick puffins exhibited considerable variability in diet diversity.

Within species, it was clear that chick diets were always less diverse than adult diets, except in the case of puffins in 1983. Between species, murres and puffins alternated in terms of which species had the more diverse diet within any given year. This was observed for both adults and chicks. When all three years were considered in total, however, puffin diet diversity was considerably higher than murre diet diversity. The reason puffins had a higher total diversity score than in any individual year is because sandlance almost totally replaced cod in 1984 as the most common alternate prey to capelin (Figure 4-5). Adult murre diversity scores were quite consistent from year-to-year, and the total diversity score was similar to scores from individual years, reflecting a generally stable pattern of prey selection over all years (Figure 4-5).

Table 4-14. Calculated overlap (C) between common murre and Atlantic puffin diets at Witless Bay, 1982-1984.

C based on	Year	All prey		Capelin	
		Adults	Chicks	Adults	Chicks
Number	1982	0.65	0.95	0.92	0.90
	1983	0.78	0.82	0.98	0.99
	1984	0.96	0.98	0.9[illegible]	0.99
	TOTAL	0.88	0.95	0.96	0.99
Weight	1982	0.99	0.99	0.82	0.98
	1983	0.99	0.99	0.97	0.98
	1984	0.97	0.97	0.95	0.99
	TOTAL	0.99	0.99	0.99	0.99

Table 4-15. Diversity indices (H′) calculated from diets of adult and chick common murres and Atlantic puffins at Witless Bay, 1982-1984.

H′ based on	Year	Common Murre		Atlantic Puffin	
		Adult	Chick	Adult	Chick
Number	1982	0.45	0.09	0.39	0.34
	1983	0.40	0.16	0.39	0.46
	1984	0.35	0.22	0.38	0.14
	TOTAL	0.41	0.17	0.50	0.35
Weight	1982	0.26	0.07	0.35	0.14
	1983	0.26	0.14	0.20	0.23
	1984	0.23	0.22	0.28	0.02
	TOTAL	0.25	0.15	0.30	0.13

4.6. SUMMARY OF MURRE AND PUFFIN FEEDING ECOLOGY

1. Capelin dominated diets of adult and chick common murres and Atlantic puffins. Sandlance and cod were also important prey.

2. Although murre and puffin diet composition differed significantly, there was a high degree of overlap in all years.

3. Diet diversity was low at Witless Bay, and puffins had more diverse diets than murres.

4. Adult diets were more diverse than chick diets.

5. Proportions of different sex/age classes eaten by birds differed from background proportions available in their habitat. This may have resulted from differential prey availability in the water column, or active selection of most profitable prey, or both.

6. On average, murres ate larger prey than puffins, but this was mostly because murres ate a higher proportion of large sex/age classes of fish rather than because they selected large-sized fish of a given class.

7. Murre and puffin stomach contents reflected seasonal and annual capelin abundance trends, and provided evidence for competition and Type III functional responses to capelin density.

8. Murre and puffin gizzard contents reflected seasonal variations in local capelin abundance only when birds and capelin co-occurred at Witless Bay, and chick meals never did.

9. Annual variations in diet composition did not reflect an order of magnitude change in capelin abundance between years, nor provide evidence for competition.

10. Murres and puffins ate more of the most energy-rich capelin sex classes when capelin abundance was highest.

11. Most temporal variability in biological characteristics of prey eaten by birds was a result of natural, background variability in prey characteristics.

Chapter 5

FORAGING BEHAVIOUR OF MURRES AND PUFFINS

5.1. TEMPORAL RELATIONSHIPS BETWEEN BIRDS AND CAPELIN

5.1.1. Seasonal Patterns in Abundance

In all years, common murres and Atlantic puffins occurred in very low abundance on the water around their breeding colonies in May and early June (Figures 5-1, and 5-2). During this same period the colonies were very active because most breeders are usually in attendance at the islands by late May (Nettleship 1972, Mahoney 1979). Flights of birds to and from the islands were heavy on all early surveys, and presumably birds were foraging at distances greater than about 10 km from the islands (i.e., outside the standard survey route).

The first survey in 1984 on 9 May was remarkable for the large numbers of murres found between Green and Great Islands in one great raft on the water estimated at more than 100,000 birds. On this survey, pack ice extended offshore for about 150 km from the eastern edge of the survey route. The high concentration of murres might therefore have resulted from a lack of offshore foraging area, or it may have been a pre-breeding aggregation of birds which gathered on the water *en masse* before going to their ledges (Tuck 1961). This unusual survey was removed from analyses of bird/capelin relationships.

The abundance of murres and puffins in the survey area increased sharply in late June of each year (Figures 5-1 and 5-2) corresponding to an increase in

Figure 5-1: Seasonal abundance of common murres swimming on the water during standard surveys around the Witless Bay islands, 1982-1984. Dots indicate survey conducted, but no birds observed.

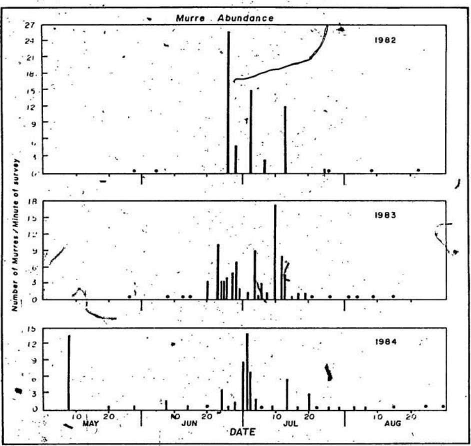
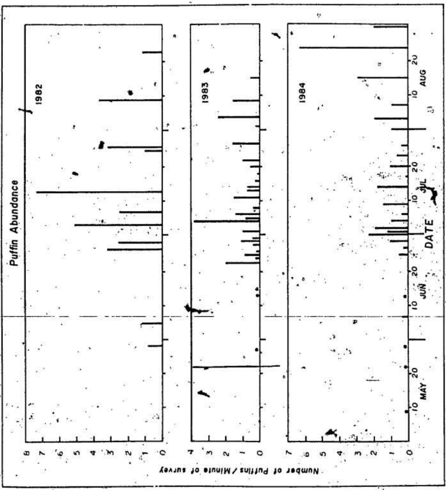

Murre Abundance
1982
1983
1984
Number of Murres / Minute of survey
27
24
21
18
15
12
9
6
3
0
18
15
12
9
6
3
0
15
12
9
6
3
0
10
20
MAY
10
20
JUN
10
20
JUL
10
20
AUG
DATE

Figure 5-2: Seasonal abundance of Atlantic puffins swimming on the water during standard surveys around the Witless Bay islands, 1982-1984. Dots indicate survey conducted, but no birds observed.


Puffin Abundance
1982
1983
1984
Number of Puffins / Minute of survey
8
7
6
5
4
3
2
1
0
4
3
2
1
0
7
6
5
4
3
2
1
0
10
MAY
20
10
JUN
20
10
JUL
20
10
AUG
20
DATE

abundance of capelin around the islands (Figure 3-10). After this time, murres and puffins exhibited quite different seasonal patterns of abundance. Murre abundance fluctuated in much the same way capelin did, showing one peak in 1982 and 1984, and two peaks in 1983. Murres, like capelin, were very scarce after mid- to late July in each year. Murre chicks and adults usually go to sea and leave the area by late July (Tuck 1961, Mahoney 1979), accounting for the lack of murres in August.

Although puffins were also very abundant in late June and July, their pattern of abundance did not correspond as well as the murres' to capelin abundance patterns. Puffins were as, or more, abundant around the islands in August as they were in July, even though capelin were relatively scarce in August of each year.

The ratio of murres to puffins varied through each season, but during peak months of abundance (June-July), murres usually outnumbered puffins by more than 2 or 3 to 1 (Figures 5-1 and 5-2). Because transect width was narrow and most birds were easily identified to species with the naked eye, the between-species difference in abundance was probably not biased much by differential visibility (murres > puffins) except, perhaps, under rough sea conditions when puffins may have been under-counted.

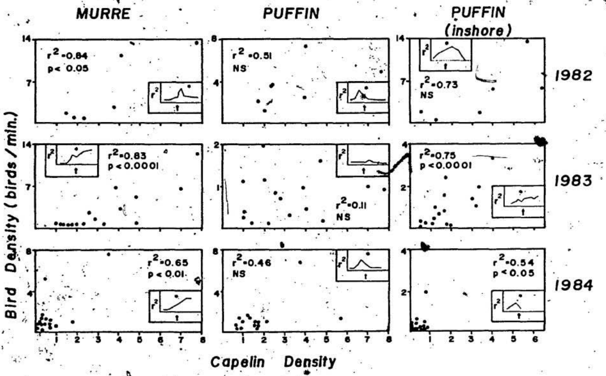
Using Pianka's (1975) α index of resource overlap (see Methods), temporal overlap of murres and puffins in the study area was moderate and varied little between years; being 0.41, 0.32, and 0.44, in 1982, 1983, and 1984, respectively.

5.1.2. Temporal Correlation of Birds with Capelin

The temporal correlation between bird and capelin abundance on different days was significant ($p<0.01$-0.0001) over all time frames examined (1-10 days, see Methods). Both murres and puffins were most strongly correlated with capelin when the data were grouped over 5-day frame sizes. Murres were more strongly correlated with capelin than puffins at all frame sizes examined.

Using data from all standard surveys (except 9 May, 1984, see above) grouped over 5-day frames, murre density was significantly correlated with

Figure 5-3: Temporal correlation between birds and capelin density on individual standard surveys at Witless Bay, 1982-1984 (note capelin density scale is **relative**, see Methods). Data grouped over 5-day time frames. Atlantic puffin-capelin correlations using all survey data (middle), and data from inshore portions of surveys only (right). Insets show results of threshold location test (see Methods, and note that capelin density scale expanded for inshore puffins in 1984), with significance of maximum r indicated (* $p<0.05$).


MURRE
PUFFIN
PUFFIN (inshore)
1982
1983
1984
$r^2 = 0.84$ $p < 0.05$
$r^2 = 0.51$ NS
$r^2 = 0.73$ NS
$r^2 = 0.83$ $p < 0.0001$
$r^2 = 0.11$ NS
$r^2 = 0.75$ $p < 0.0001$
$r^2 = 0.65$ $p < 0.01$
$r^2 = 0.46$ NS
$r^2 = 0.54$ $p < 0.05$
r^2
14
7
8
4
2
1
1 2 3 4 5 6 7 8
1 2 3 4 5 6
Bird Density (birds / min.)
Capelin Density

capelin density in all three years (Figure 5-3). Correlations were higher in 1982 and 1983 than in 1984, the year of lowest capelin abundance. There was a threshold in the temporal aggregative response of murres to capelin in 1982 at a relative capelin density of about 4.0 (see inset, Figure 5-3). If the high terminal data point in the 1983 response curve were excluded, a threshold would occur at a relative capelin density of about 3.5. There was no apparent threshold in 1984, but there were few days of high capelin density with which to establish the form of the relationship.

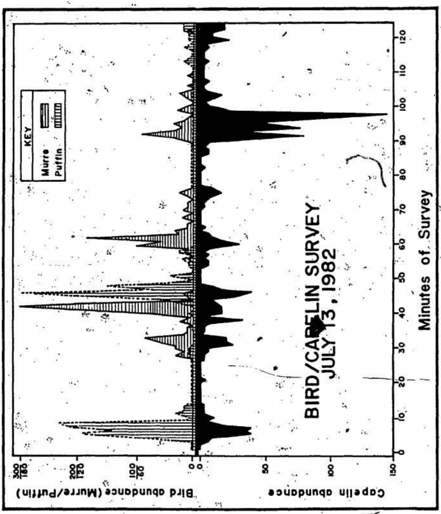
No significant correlation was found in any year between puffin and capelin density, although density thresholds were observed in each year (at a relative capelin density of 2.5 in both 1982 and 1984, see insets in Figure 5-3). Spatial analysis (below) suggested that puffins were restricted more to inshore habitat, and when only data from inshore portions of surveys were used, puffins were highly correlated with capelin in all three years (Figure 5-3). Thresholds were observed at relative capelin densities of 3.5 in 1982, and 0.9 in 1984 (see insets, Figure 5-3). Although analysis suggested a threshold for inshore puffins in 1984, the low number of high density points precludes any meaningful interpretation. No threshold was detected in 1983, though most puffins were found when relative capelin density exceeded 2.0 (Figure 5-3).

5.2. SPATIAL RELATIONSHIPS BETWEEN BIRDS AND CAPELIN

5.2.1. Fine-scale Association of Birds with Capelin

Some of the 1982 hydroacoustic echograms were selected for quality of capelin traces and a few capelin aggregations in shallow and deep water were carefully measured to estimate school volumes (see Appendix E). In conjunction with bird observations, these data reveal fine-scale associations between birds and capelin (Figure 5-4).Several features of this and other 1982 surveys were frequently observed in 1983 and 1984 also:

Figure 5-4: Standard survey showing common murre, Atlantic puffin, and capelin abundance along the survey route. Note differing scales for murre and puffin abundance, and that capelin abundance scale is **relative**, see Methods).


BIRD/CAPELIN SURVEY
JULY 13, 1982
KEY
Murre
Puffin
Bird abundance (Murre/Puffin)
300/180
200/120
100/60
0
0
50
100
150
Capelin abundance
0
10
20
30
40
50
60
70
80
90
100
110
120
Minutes of Survey

1. The pattern of total bird distribution was generally similar to the pattern of capelin distribution.

2. Murres and puffins were spatially segregated with variable, low overlap between species in different habitats.

3. Aggregations of birds and capelin occurred over spatial scales of approximately 2-4 km (8-16 min of survey).

4. Correlations between capelin and bird aggregations were not perfect on either large or small spatial scales. Note the relatively low abundance of murres over the large capelin aggregation between 90-100 min.

When some of the capelin schools and aggregations recorded on the above survey were measured in detail using methods described by Forbes and Nakken (1972), the fine-scale association between birds and capelin was revealed (Table 5-1). Between minutes 3-10, 24 capelin schools were found with an estimated mean volume of 399 m^3, and an estimated total volume of 9,575 m^3. The minimum and maximum school depths were 0.3 and 16.7 m, respectively. The total number of capelin in the aggregation was estimated at 150,000 individuals (assuming mean fish density of 15.7 ± 15% ; Zaferman 1973), yielding a total biomass of 3.8 mt (assuming mean capelin weight of 25.3 g). Details of capelin school dimensions in this and other aggregations in 1982 are given in Appendix E. Only puffins were found feeding on this aggregation, and in general, the number of puffins at the surface was proportional to the volume of capelin schools below the surface although the correlation was not exact on a minute-by-minute basis.

Between minutes 37-49, 58 capelin schools were found with an estimated mean volume of 680 m^3, and a total volume of 39,452 m^3. The minimum and maximum school depths recorded were 0.3 and 42.4 m, respectively. The total number of capelin in the aggregation was estimated at 619,000 individuals, yielding a total biomass of 15.7 mt. Both murres and puffins were found feeding on this aggregation, although there was a marked division between the areas occupied by the two species. Murres were found mostly over large schools with biomass concentrated between 10-30 m; whereas puffins were over shallower

Table 5-1. Fine-scale common murre and Atlantic puffin association with selected capelin aggregations, July 13, 1982.

Minute	No. of schools	Estimated* school volume (m^3)	Mean depth (m)**	No. of puffins	No. of murres
3	2	572	13.3	0	0
4	4	599	2.5	30	0
5	3	2213	4.7	100	0
6	4	2229	3.7	75	0
7	4	2055	4.2	110	0
8	2	781	2.3	125	0
9	4	475	4.7	6	0
10	1	651	3.1	3	0
37	7	350	30.1	0	3
38	8	3698	24.7	0	25
39	4	222	25.2	1	4
40	12	1686	24.2	5	70
41	5	2840	18.6	0	190
42	4	9026	11.9	0	300
43	5	723	19.3	9	201
44	2	68	8.9	25	1
45	3	7594	13.5	85	5
46	3	12,365	11.4	160	15
47	2	620	2.8	41	2
48	2	254	2.6	78	2
49	1	16	3.5	26	0

* Total volume of all schools in aggregation (see appendix E for details).

** Mean depth weighted by volume.

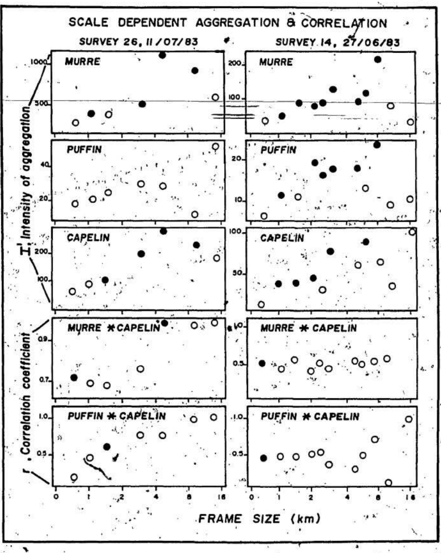
schools concentrated between 2-15 m. Again, murre and puffin abundance was generally highest over capelin schools with large volumes, but the relationship was not exact on a minute-by-minute basis.

5.2.2. Scale-Dependent Aggregation and Correlation

Bird and capelin aggregation intensities (I') were estimated using variance-to-mean ratios. Aggregation intensity and bird-capelin correlations were examined to determine the effect of measurement scale on I' and r^2 (see Methods, Schneider and Duffy 1985, Schneider and Piatt 1986). For most surveys, murre (86%, n=63 surveys), puffin (76%, n=70), and capelin (88%, n=73) aggregation intensity increased with frame size (e.g., Figure 5-5), yielding significantly higher values of I' at spatial scales of 0.5-12.0 km (2-48 min of survey). In most cases (e.g., Figure 5-5), I' increased quickly over small time frame intervals, reached a plateau or peak after 2-4 km (8-16 min), and in many cases (62%, n=206), decreased again at large time frame intervals (8-16 km). Maximal I' values, which indicate the scale of aggregations (Pielou 1977, Schneider and Piatt 1986) generally occurred between 2-4 km (8-16 min) for puffins, and between 2-6 km (8-24 min) for murres and capelin.

On most surveys, murres (68%, n=63 surveys) and puffins (54%, n=70) were significantly correlated with capelin at some, mostly minimum, frame size. Correlations became significantly higher with increasing frame size in only 35% and 27% of all murre and puffin surveys, respectively (e.g., survey 26, Figure 5-5). On many surveys, the strength of correlation did not increase significantly with frame size, in spite of an increase in I' with frame size (e.g., survey 14, Figure 5-5). In only 2% and 7% of murre and puffin surveys, respectively, did r^2 decrease significantly with increasing frame size.

Figure 5-5: Scale dependent aggregation and correlation of common murres, Atlantic puffins, and capelin. Closed circles for measure of aggregation intensity indicate significantly higher I' values than observed at minimum frame size (tested by Monte Carlo analysis). Closed circles for r at minimum frame size indicates significant correlation; at other frame sizes closed circles indicate that r was significantly higher than that calculated at minimum frame size (tested by Monte Carlo analysis).


SCALE DEPENDENT AGGREGATION & CORRELATION
SURVEY 26, 11/07/83
SURVEY 14, 27/06/83
I', Intensity of aggregation
r, Correlation coefficient
MURRE
PUFFIN
CAPELIN
MURRE * CAPELIN
PUFFIN * CAPELIN
1000
500
40
20
200
100
0.9
0.7
1.0
0.5
200
100
20
10
100
50
1.0
0.5
1.0
0.5
0
1
2
4
8
16
FRAME SIZE (km)

5.3. THE AGGREGATIVE RESPONSE OF BIRDS TO CAPELIN.

5.3.1. Scale-dependent Aggregative Response

Because fine-scale correlation between birds and capelin was never perfect, plots of bird versus capelin density at minimum frame sizes gave the impression that large numbers of birds occurred in areas with relatively low capelin densities (see 2 or 4 min frame sizes, Figure 5-6). However, when data were grouped over spatial scales*appropriate* to the scale of bird/capelin aggregations (see above) spatial variance was maximized (Pielou 1977, Schneider and Piatt 1986) and in many cases the form of the aggregative response of birds to capelin became sigmoidal, with apparent thresholds to prey density (8 or 16 min frame sizes, Figure 5-6). Because i) aggregation intensity (I') tended to plateau or peak after grouping into frame sizes greater than about 8 min (2 km, see above), ii) the number of points available for modeling an aggregative response decreases with increasing frame size (Figure 5-6), and iii) most seabird surveys use 10 min observation periods (e.g., Brown et al. 1975), an intermediate frame size of 10 min (2.5 km) was used to compare thresholds between species and surveys. At a 10 min frame size many plots exhibited thresholds in the aggregative response of birds to capelin (Figures 5-6 and 5-7, Table 5-2).This indicates that murres and puffins exhibit Type III aggregative responses to prey density (Hassell and May 1974).

5.3.2. Estimating Prey Density Thresholds

Using the threshold location test (see Methods), many plots exhibited simple thresholds, i.e., a maximum correlation (r^2) between bird and capelin density occurred somewhere in the middle of the plot, but not all of these correlations were statistically significant (Table 5-2). Some plots had very few (or one) high density data points, making threshold location difficult or impossible. In some cases, maximum significant r^2 values were obtained when a terminal high density data point was regressed against all the other points.

Figure 5-6: Effect of increasing frame size on the form of the relationship (aggregative response) between bird and capelin densities (note capelin density scale is **relative**, see Methods).

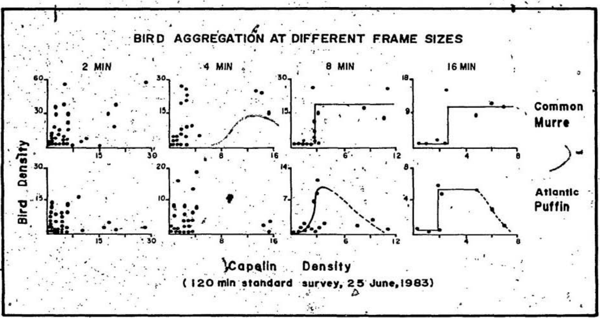

BIRD AGGREGATION AT DIFFERENT FRAME SIZES
2 MIN
4 MIN
8 MIN
16 MIN
60
30
15
30
30
15
8
16
30
15
6
12
18
9
4
8
Common Murre
Bird Density
30
15
15
30
20
10
8
16
14
7
6
12
8
4
4
8
Atlantic Puffin
Capelin Density
(120 min standard survey, 25 June,1983)

Figure 5-7: Aggregative response of common murres and Atlantic puffins to capelin density on four surveys at Witless Bay, 1983. For each date and bird species, the aggregative response is shown in the lower panel, with the estimated threshold indicated by a solid line. Upper panels show the results of threshold location tests, with r^2 values increasing to a maximum at the estimated threshold, and decreasing thereafter. Solid circles indicate significant ($p<0.05$) regressions associated with test thresholds (see Methods).

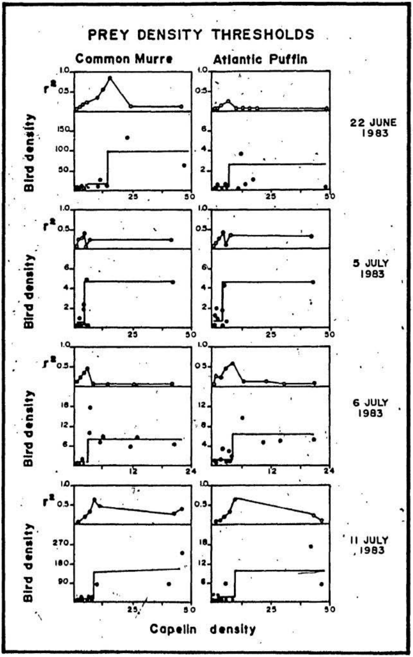

PREY DENSITY THRESHOLDS
Common Murre
Atlantic Puffin
r^2
1.0
0.5
Bird density
150
100
50
6
4
2
25
50
22 JUNE 1983
5 JULY 1983
16
12
6
8
24
6 JULY 1983
270
180
90
18
11 JULY 1983
Capelin density

Table 5-2. Frequency of thresholds and significant regressions in all bird-capelin plots, 1982-1984 (at 10 min frame size).

Analysis	1982				1983				1984			
	murre		puffin		murre		puffin		murre		puffin	
	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)
Total no. of surveys	3		5		32		35		26		25	
No. with simple threshold	2	(66)	3	(60)	17	(53)	23	(66)	7	(27)	8	(32)
No. with threshold and significant r^2	0	(0)	0	(0)	10	(31)	8	(23)	5	(19)	2	(8)
No. with ≥ 2 consecutive significant r^2	1	(33)	1	(20)	19	(59)	10	(38)	8	(31)	6	(24)

To estimate the probability of finding a i) simple threshold, ii) a threshold with a significant r^2 value associated with it, or iii) any significant regression (i.e., a significant r^2 value whether it occurred in the middle or at the end of a plot), Monte Carlo tests were conducted to see how frequently these events occurred using randomized survey data plots (Table 5-3). Monte Carlo results indicated that:

1) there was a high probability of finding a simple threshold within a plot by chance alone. The proportion of real survey plots with simple thresholds (Table 5-2) was about the same as the proportion of randomized plots with simple thresholds (Table 5-3). Therefore, simple thresholds were not reliable for indicating the presence of thresholds in bird-capelin density plots.

2) there was a low probability ($p<0.06$-0.09) of finding a threshold with a significant r^2 value associated with it (Table 5-3). Many more of the actual survey plots in 1983 and 1984 had thresholds with significant r^2's than would be expected by chance, though none were found in 1982 (Table 5-2). Although not as definitive as desired (i.e., $p<0.05$), this criteria was reasonably reliable for indicating thresholds.

3) the probability of finding at least one significant maximum r^2 value anywhere in a plot quite high at 13-17% (Table 5-3). However, the probability that at least two significant regressions would occur consecutively in a plot of randomized data was quite low, and usually less than or equal to 5% (Table 5-3). A much greater proportion of actual survey plots exhibited two or more consecutive significant regressions than would be expected by chance (Table 5-2). Consecutive significant regressions are a useful criteria for locating thresholds because i) consecutive regression coefficients (r^2's) *should* be high and significant in the vicinity of a definitive threshold (see Figure 2-5), and ii) they may indicate if a threshold occurs at terminal points in survey plots, whereas (1) and (2) above can not (see Methods).

In summary, thresholds in bird versus capelin density plots were estimated to occur where i) a maximum r^2 was encountered in the middle of a plot ii) a significant maximum r^2 was encountered in the middle of a plot, or iii) two

Table 5-3. Monte Carlo tests: probability of finding thresholds and significant regressions when conducting threshold location tests on randomized survey plots of bird versus capelin density.

Probability of obtaining *:	Murre		Puffin	
	A	B	A	B
Simple threshold	0.56	0.58	0.56	0.62
Threshold with significant r^2	0.08	0.07	0.09	0.06
$\geq$1 significant r^2	0.15	0.16	0.13	0.17
$\geq$2 consecutive significant r^2's	0.02	0.03	0.07	0.05

* Based on 100 runs on two different surveys (A,B) for each species (conducted at 10 min frame size).

consecutive significant r^2 values were encountered anywhere in a plot. For each survey, the best criterion possible was used to estimate the location of thresholds for comparison of murre and puffin responses (below). Estimated thresholds, r^2 values, and significance levels for all murre and puffin plots are given in Appendix L.

Although the proportion of bird-capelin plots with reliable thresholds might seem low, particularly in 1984, there is no reason to expect that more should have been detected. Data required to demonstrate aggregative responses to prey density are difficult to obtain from field studies and notably variable (Goss-Custard 1970). Also, the aggregative response was clearly scale-dependent but for simplicity, thresholds were estimated at one frame size only (10 min). Finally, resolving thresholds in aggregative response curves requires an adequate number of data points below *and* above the threshold (Hassell and May 1974). Not all surveys offered many high density points for analysis, particularly in 1984 when capelin were abundant on only a few surveys. Furthermore, the density of puffins sometimes appeared to be suppressed at high capelin densities (e.g., Figure 5-6) and this made it more difficult to estimate where thresholds occurred.

5.3.3. Comparison of Murre and Puffin Prey Density Thresholds

For interspecific comparisons of prey density thresholds, surveys were partitioned into three data sets according to the criteria above: i) all survey data, ii) only surveys exhibiting thresholds with significant r^2's, and iii) only surveys exhibiting two or more consecutive significant regressions (which includes 73% and 60% of murre and puffin plots, respectively, meeting criteria (ii) above, as well as plots where significant maximal r^2 values occurred at terminal data points).

On individual surveys, estimated murre (prey density) thresholds were usually higher than puffin thresholds (Appendix L). Using grouped data, mean murre thresholds were higher than mean puffin thresholds in all years, although the difference was significant only in 1983, or when the data were combined over years (Table 5-4). Murre and puffin thresholds both decreased from 1982 to 1984

Table 5-4. Capelin density threshold (Thr) estimates for common murres and Atlantic puffins, 1982-1984 (at 10 min frame-size).

Case	Year	Murre			Puffin			t*	prob.
		n	Thr	(s.e.)	n	Thr	(s.e.)		
All data	1982	3	9.7	(6.2)	5	3.6	(1.0)	1.2	NS
	1983	32	6.9	(1.6)	35	3.4	(0.3)	2.1	<0.05
	1984	26	1.1	(0.3)	25	1.0	(0.3)	0.7	NS
	Total	61	4.6	(0.9)	65	2.6	(0.3)	2.3	<0.05
If Mt and Pt significant**	Total	4	4.1	(3.6)	4	3.4	(2.2)	0.9	NS
If Mr and Pr significant***	Total	9	9.5	(2.6)	9	3.7	(0.5)	2.4	<0.05

* Value of t computed for paired comparisons under the hypothesis that the mean murre threshold minus the mean puffin threshold = 0.

** If both murre and puffin plots had thresholds with significant r^2 values.

*** If both murre and puffin plots had ≥ 2 consecutive significant regressions.

corresponding to the decline in capelin abundance between these years (Table 3-6). Using only data where both murres *and* puffins exhibited thresholds with significant r^2,s on the same surveys (only 4 surveys in 3 years), the mean murre threshold was higher than the mean puffin threshold although the difference was not statistically significant (Table 5-4). Using only survey data where both murre *and* puffin plots exhibited two or more consecutive significant regressions, murres had a significantly higher threshold than puffins (Table 5-4). Thus, it appears that the threshold capelin density at which murres aggregate is higher than the threshold density at which puffins aggregate.

Because it was not known what effect measurement scale would have on estimation and comparison of thresholds, they were estimated at varying frame sizes for all 1983 surveys. At every frame size, the estimated mean murre threshold was greater than the mean puffin threshold (Table 5-5), although the difference was not significant at frame sizes of 12 and 16 min. Lower significance at large frame sizes probably occurred because grouping the data into increasing blocks lowered mean bird and capelin density values and simultaneously reduced the number of data points available for analysis, thereby reducing the sensitivity of the test for significance.

5.3.4. Threshold Variability in Relation to Overall Capelin Density

Significant positive correlations were found between estimated murre and puffin prey density thresholds and overall capelin density at Witless Bay in each year (except for puffins in 1982), and when data from all years were combined (Table 5-6, Figure 5-8). Strong correlations were found between prey density thresholds and overall capelin density regardless of which selected data set was used (Table 5-6). These results suggest that aggregation thresholds changed daily depending on the overall density of capelin around the colonies.

Using all survey data, the absolute *difference* between estimated murre and puffin thresholds was also significantly correlated with capelin density in 1983, and for all years combined (Figure 5-8 and Table 5-6). Interspecific threshold differences were strongly correlated with capelin density in all selected data sets,

Table 5-5. Effect of frame size on estimates of mean bird capelin density thresholds (Thr) using all survey data in 1983 for murres (n=32) and puffins (n=35).

Frame size	Murre			Puffin		t*	prob.
	Thr	s.e.		Thr	s.e.		
2	7.4	(1.6)	>	3.2	(0.4)	2.5	<0.02
4	7.6	(1.5)	>	3.1	(0.3)	2.7	<0.02
8	7.9	(1.7)	>	2.6	(0.4)	3.4	<0.002
10	6.9	(1.6)	>	3.4	(0.3)	2.1	<0.05
12	6.5	(1.4)	>	3.6	(0.4)	2.0	NS (0.06)
16	4.9	(0.9)	>	3.0	(0.4)	2.0	NS (0.05)

* Value of t computed for paired comparisons under the hypothesis that the mean murre threshold minus the mean puffin threshold =0.

Figure 5-8: Plots of estimated common murre and Atlantic puffin prey density thresholds, and the difference between thresholds, versus capelin density (note capelin density scale is **relative**, see Methods). Spearman rank correlations calculated using data from all surveys combined (open and closed circles) or using only plots exhibiting thresholds with significant regressions associated with them (closed circles). Difference plot using all data. RANK CORRELATIONS: common murre- open and closed circles:$r_s=0.82$, $p<0.0001$; closed circles only:$r_s=0.58$, $p<0.05$; Atlantic puffin - open and closed circles:$r_s=0.73$, $p<0.0001$; closed circles only:$r_s=0.89$, $p<0.001$; murre-puffin difference:$r_s=0.33$, $p<0.05$;

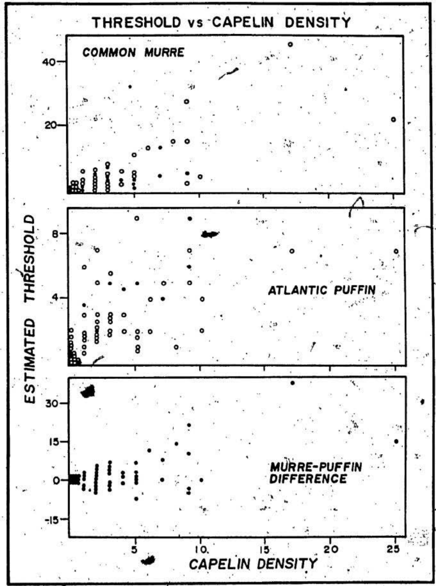

THRESHOLD vs CAPELIN DENSITY
COMMON MURRE
40
20
8
4
ATLANTIC PUFFIN
ESTIMATED THRESHOLD
30
15
0
-15
MURRE-PUFFIN DIFFERENCE
5
10
15
20
25
CAPELIN DENSITY

Table 5-6. Spearman rank correlations between common murre (M) and Atlantic puffin (P) thresholds (Thr), the difference between thresholds (Diff) and overall capelin density (CD), 1982-1984 (at 10 min frame size).

Case	Year	MThr * CD			PThr * CD			Diff * CD		
		n	r	prob.	n	r	prob.	n	r	prob.
All data	1982	3	0.99	<0.0001	5	0.76	NS	3	0.50	NS
	1983	32	0.66	<0.0001	35	0.51	<0.01	32	0.38	<0.05
	1984	26	0.67	<0.001	25	0.76	<0.0001	20	-0.09	NS
	Total	61	0.82	<0.0001	65	0.73	<0.0001	55	0.33	<0.05
If Mt and Pt significant*	Total	4	0.99	<0.01	4	0.80	NS	4	0.80	NS
If Mt or Pt significant**	Total	15	0.58	<0.05	10	0.89	<0.001	-	-	-
If Mr and Pr significant***	Total	9	0.75	<0.01	9	0.69	<0.05	9	0.59	<0.05

* If both murre and puffin plots had thresholds with significant r^2 values.

** Calculated using all plots in which murre or puffin plots exhibited thresholds with significant r^2 values. Difference (Diff) cannot be calculated because data for each species taken from different surveys.

*** If both murre and puffin plots had ≥ 2 consecutive significant regressions.

although the correlation was significant for the consecutive significant regression data set only (Table 5-6). These results suggest that as overall capelin density increased, murre thresholds increased more rapidly than puffin thresholds, and so the difference between thresholds widened. Conversely, as overall capelin density fell, murre and puffin prey density thresholds converged.

5.4. FORAGING HABITAT SELECTION AND SPATIAL OVERLAP OF MURRES AND PUFFINS

Defining habitats

It appear that puffins dive regularly to depths of 30 m and less commonly to 60 m, whereas common murres regularly forage to depths of 70 m and less frequently to 180 m (Piatt and Nettleship 1985). Therefore, these approximate depths were used to define habitats around the islands as: 'inshore' <30 m, 'bay' 30-70 m, and 'offshore' >70 m. In addition, one area between Gull and Green Islands where ledges from both islands extended underwater towards each other seemed to be an area where capelin and birds concentrated. Water depths in the ledge area ranged from 30-70 m like 'bay' habitat, but because of its unusual topography and importance, the 'ledge' was considered as a separate habitat in the following discussions (see Methods, and Figure 2-2).

5.4.1. Foraging Habitat Use

Most murres were found in deeper waters in bay, ledge, and offshore habitats (Figure 5-9). During the period that capelin were particularly abundant in each year (late June to late July), the pattern of habitat use was quite variable with daily shifting of murres between habitats (Figure 5-9). There was a general shift of murres from inshore and bay habitats to ledge and offshore habitats from 1982 to 1984 corresponding to a similar shift in capelin between these years (Figure 3-12).

In contrast to murres, most puffins occupied inshore and bay habitats in all years (Figure 5-10). Like murres, puffins shifted between habitats on a daily basis,

Figure 5-9: Distribution of common murres on the water in different habitats at Witless Bay, 1982-1984 (adjusted for survey effort in each habitat). Closed circles indicate survey conducted but fewer than 10 birds observed.

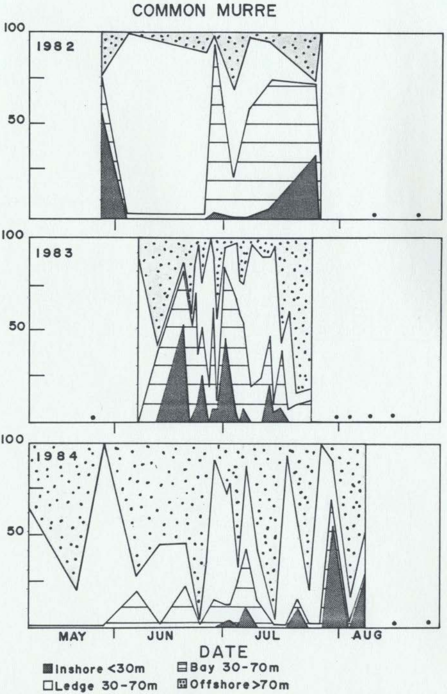
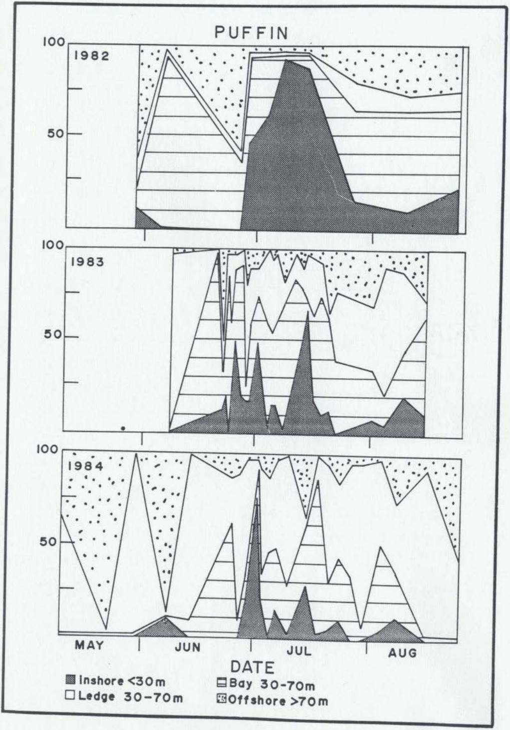

COMMON MURRE
100
1982
50
100
1983
50
100
1984
50
MAY
JUN
JUL
AUG
DATE
■ Inshore <30m
▤ Bay 30-70m
☐ Ledge 30-70m
▨ Offshore >70m

Figure 5-10: Distribution of Atlantic puffins on the water in different habitats at Witless Bay, 1982-1984 (adjusted for survey effort in each habitat). Closed circles indicate survey conducted but fewer than 10 birds observed.


PUFFIN
100
1982
50
100
1983
50
100
1984
50
MAY
JUN
JUL
AUG
DATE
Inshore <30m
Bay 30-70m
Ledge 30-70m
Offshore >70m

again reflecting the movement of capelin around the study area. There was also a general shift of puffins from inshore and bay habitats to ledge and offshore habitats between 1982 and 1984, although the proportion of puffins occupying offshore habitat increased only slightly (Figure 5-10).

5.4.2. Correlation Between Birds and Capelin in Different Habitats

Combining all survey data collected in 1982, murres were significantly correlated with capelin in all habitats, but the strength and significance of correlations increased from inshore to offshore habitats (Figure 5-11 and Table 5-7). Only 4% of all murres were found inshore (Table 5-7). In 1982, puffins were significantly correlated with capelin only in the inshore habitat, with 56% and 36% of all puffins being found in inshore and bay habitats, respectively (Figure 5-11 and Table 5-7). The correlation between murres and puffins in 1982, which is a measure of spatial overlap *within* habitats, was significant only in the inshore habitat. Although large numbers of murres and puffins co-occupied bay habitat (Table 5-7), spatial correlation between birds within that habitat was extremely low and non-significant.

Similar trends were observed in 1983 and 1984 (Figure 5-11 and Table 5-7). Murres were best correlated with capelin in ledge and bay habitats, while puffins were best correlated with capelin in inshore and bay habitats. Within-habitat spatial correlation between murres and puffins was highest inshore in 1983, and extremely low and non-significant in all habitats in 1984.

The net effect of this differential distribution of birds between habitats was the equitable exploitation of capelin biomass in all habitats. Figure 5-12 illustrates the overall distribution (corrected for effort) of capelin, murres and puffins in different habitats from Bay Bulls to Mobile Bay in 1983 using combined data from all surveys. Murres were most densely concentrated in mid- to deep-waters of Mobile and Witless Bays, whereas puffins were more widely distributed over all habitats, and in particular, occupied shallow-water inshore areas neglected by murres. Similar trends were observed in 1982 and 1984.

Figure 5-11: Correlations between birds and capelin density in different habitats at Witless Bay, 1982-1984 (using all standard survey data at minimum frame size). Significant ($p < 0.05$) correlations indicated by closed symbols.

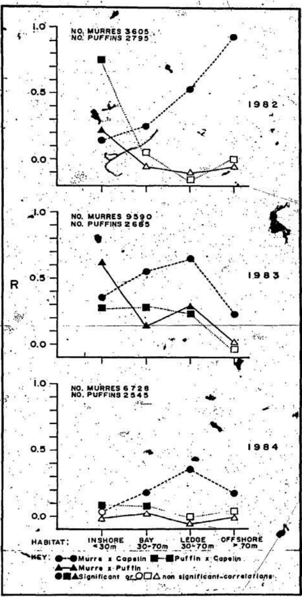
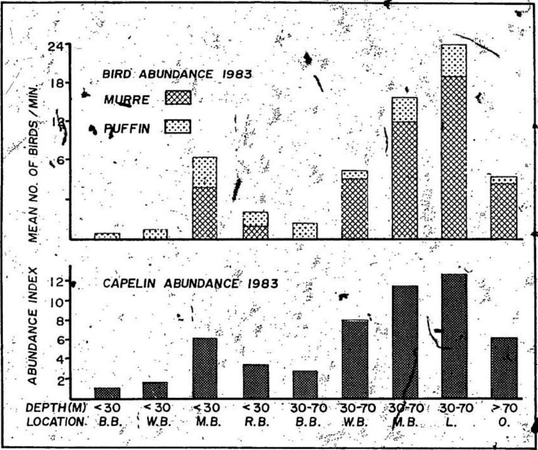

NO. MURRES 3605
NO. PUFFINS 2795
1982
NO. MURRES 9590
NO. PUFFINS 2665
1983
NO. MURRES 6728
NO. PUFFINS 2545
1984
R
1.0
0.5
0.0
HABITAT:
INSHORE <30m
BAY 30-70m
LEDGE 30-70m
OFFSHORE >70m
KEY: ●-● Murre x Capelin ■-■ Puffin x Capelin
▲-▲ Murre x Puffin
●■▲ Significant or ○□△ non significant correlations

Table 5-7. Correlations between common murres (M), Atlantic puffins (P) and capelin (C) in different habitats in Witless Bay, 1982-1984, using data for all surveys combined at minimum frame sizes. Probability levels: NS not significant, * p< 0.05, ** p< 0.01, *** p< 0.001, **** p< 0.0001.

Habitat		1982			1983			1984		
		M*C	P*C	M*P	M*C	P*C	M*P	M*C	P*C	M*P
Inshore	r	0.17	0.75	0.21	0.34	0.32	0.51	0.02	0.09	0.03
<30m	prob.	**	****	***	****	****	****	NS	*	NS
	no.birds	144	1570		478	500		22	130	
Bay	r	0.26	0.05	-0.03	0.56	0.30	0.14	0.19	0.09	0.02
30-70	prob.	**	NS	NS	****	****	**	****	**	NS
	no.birds	2045	998		2182	807		208	369	
Ledge	r	0.62	-0.19	-0.17	0.63	0.21	0.27	0.36	-0.02	-0.02
30-70m	prob.	****	NS	NS	****	**	****	****	NS	NS
	no.birds	665	48		3660	827		1812	1037	
Offshore	r	0.92	0.01	-0.06	0.21	-0.02	-0.01	0.17	0.01	0.00
>70m	prob.	****	NS	NS	****	NS	NS	****	NS	NS
	no.birds	751	179		3270	551		4686	1009	

Figure 5-12: Distribution of birds and capelin in different habitats in 1983 (adjusted for survey effort in each habitat). Locations were B.B. = Bay Bulls; W.B. = Witless Bay; M.B. = Mobile Bay; R.B. = Ragged Beach (in Witless Bay); L. = Ledge (in Witless Bay); and O. = Offshore.


BIRD ABUNDANCE 1983
MURRE ▩
PUFFIN ▒
MEAN NO. OF BIRDS / MIN.
24
18
12
6
CAPELIN ABUNDANCE 1983
ABUNDANCE INDEX
12
10
8
6
4
2
DEPTH(M) <30 <30 <30 <30 30-70 30-70 30-70 30-70 >70
LOCATION. B.B. W.B. M.B. R.B. B.B. W.B. M.B. L. O.

5.4.3. Spatial Overlap between Murres and Puffins

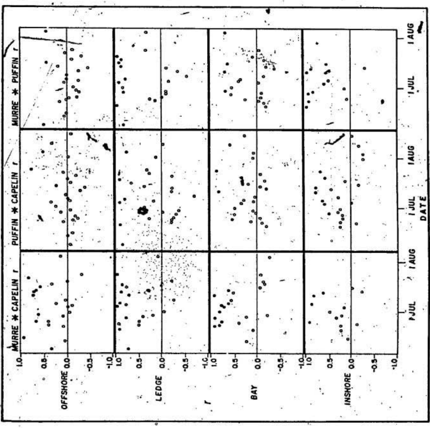
Spatial overlap between murres and puffins, as measured by correlation analysis, was quite low in all years and dependent on the habitat in which it was measured (above). To standardize comparisons of spatial overlap with estimates of temporal and food overlap, spatial overlap was calculated using Pianka's (1975) index of α overlap (see Methods).

Spatial α overlap between murres and puffins was very low in all years and on all surveys. Overlap values ranged from 0.00 to 0.21. Average overlap was significantly lower in 1984 (mean $\alpha=0.075\pm0.01$), the year of lowest capelin abundance, than in 1983 (mean $\alpha=0.14\pm0.01$; t-test adjusted for heterogeneity of variances: $t=4.59$, $p<0.001$), but not in 1982 (mean $\alpha=0.14\pm0.03$; $t=2.06$, $p>0.05$). There was no significant correlation between spatial overlap and capelin abundance within any year, or over all years. Thus, spatial segregation of murres and puffins was maintained under a variety of conditions.

5.4.4. Correlation between Birds and Capelin in Different Habitats on Individual Surveys

When simple correlations between murres and capelin in different habitats were considered for individual surveys in 1983, highly significant correlations were frequently observed between murres and capelin in all habitats, but were particularly common in offshore, ledge, and bay habitats (Figure 5-13). Murres were significantly correlated with capelin inshore on only four surveys. Puffins were significantly correlated with capelin most frequently in ledge and inshore habitats and were significantly correlated with capelin offshore only after most murres had departed from the study area in late July (Figure 5-13). The number of negative correlations between puffins and capelin increased from inshore (7 of 23 surveys) to offshore (14 of 26 surveys) habitats. Spatial correlation between murres and puffins was highest and most frequently significant in ledge and inshore habitats, and the highest number of negative correlations occurred in offshore habitat (11 of 23).

Figure 5-13: Correlations between birds and capelin in different habitats on individual surveys at Witless Bay, 1983 (calculated using minimum frame sizes). Closed circles indicate significant ($p < 0.05$) correlations.


MURRE * CAPELIN r
PUFFIN * CAPELIN r
MURRE * PUFFIN r
OFFSHORE
LEDGE
BAY
INSHORE
1.0
0.5
0.0
-0.5
-1.0
1 JUL
1 AUG
DATE

The trends observed in 1983 were also observed in 1982 and 1984 (Table 5-8). In 1982, puffins were significantly correlated with capelin inshore more frequently than murres, and vice-versa for bay, ledge, and offshore habitats. Significant spatial correlation between murres and puffins occurred most frequently in inshore and ledge habitats. In 1984, murres were significantly correlated with capelin more frequently than puffins in all habitats. Again, significant spatial correlation between murres and puffins occurred most frequently in inshore and ledge habitats.

5.4.5. Behavioural Interactions between Murres and Puffins

Between 1-7 July, 1985, some observations were made on murres and puffins in mixed flocks at Witless Bay to determine if there were any behavioural interactions which might contribute to the spatial segregation of these species in the study area. Observations were made on mixed flocks of birds from the east side of Gull Island (Figure 2-2). Bird densities in these mixed flocks were often quite high (e.g., 1-10 birds/m^2), and murres and puffins encountered each other regularly as they milled about on the water's surface.

Several behaviour patterns were repeated regularly. When murres and puffins encountered each other head-on, one almost invariably made an abrubt left/right turn to avoid contact with the other (deference). When both turned simultaneously, the interaction was considered neutral. A similar behaviour was observed when one species swam up directly behind the other. Sometimes, the effort involved in getting out of the way was so vigorous that the defering bird rose off the water with wing-flapping and scrambled off to one side (induced scrambling). On rare occasions, an approaching bird would vigorously attack another bird, usually by jabbing at the head with its bill, and sometimes biting the neck.

The frequency of these behaviours were noted over about 12 hours of observation on four different days. Because encounters required that birds be in close contact, most interactions were observed over short time periods when bird densities on the water were high. Of 189 documented encounters between murres

Table 5-8. Correlations by habitat between common murres, Atlantic puffins, and capelin on individual surveys, 1982-1984.

Year	Habitat	Positive correlations between:						
		Murre-Capelin			Puffin-Capelin		Murre-Puffin	
		n*	%sig**		n	%sig	n	%sig
1982								
	Inshore	3	67	<	5	80	3	33
	Bay	4	25	>	6	17	4	0
	Ledge	5	20	>	6	0	5	20
	Offshore	3	33	>	6	17	3	0
1983								
	Inshore	14	29	<	23	30	12	67
	Bay	22	45	>	26	12	21	19
	Ledge	21	48	>	25	24	21	38
	Offshore	23	39	>	26	8	23	13
1984								
	Inshore	5	40	>	9	22	6	17
	Bay	13	46	>	18	22	13	8
	Ledge	19	21	>	17	18	18	17
	Offshore	19	47	>	21	10	18	11

* n = number of surveys with birds in habitat.

** %sig = percent of all surveys yielding significant correlations between variables.

Table 5-9. Frequency of behavioural interactions between common murres and Atlantic puffins while swimming on the water.

Behaviour	Dominant Species		Neutral encounter
	Murre	Puffin	
Deference when meeting head-on	80	6	7
Deference when approached from behind	58	1	19
Induced scrambling	14	1	-
Attack with contact	2	1	-
Total (%)	154 (81)	9 (5)	26 (14)

and puffins (Table 5-9), 81% resulted in puffins deferring to murres, only 5% resulted in murres deferring to puffins, and 14% of encounters were considered neutral. Though not quantified, deference behaviour of puffins appeared to be most vigorous when murres were encountered in groups.

5.5. FLOCKING BEHAVIOUR OF MURRES AND PUFFINS

5.5.1. Surface Flocking Behaviour

Individual flock sizes were recorded on all surveys. Flocks of greater than 15 birds were usually estimated to the nearest multiple of five (20, 25, 30, etc.) when flocks were numerous. Murres generally formed larger flocks than puffins (Figure 5-14), and the mean or median size of murre flocks was about twice that of puffin flocks (Table 5-10). The between-species difference in flock size frequency distributions was highly significant in all years examined (Table 5-11).

There was a significant shift in flock size frequency distributions between years (Tables 5-10 and 5-11). Murre flock sizes shifted upward slighty between 1982 and 1983, while puffin flock sizes shifted slightly downward. Between 1983 and 1984, murre flock sizes shifted slightly downward, while puffin flock sizes shifted slightly upward.

Whereas the total abundance of birds on surveys declined substantially between years (Figures 5-1 and 5-2, Table 5-10), corresponding to an order of magnitude decline in the abundance of capelin (Table 3-8), the analyses of flock size characteristics suggest that, despite being statistically significant, there was relatively little variation in murre and puffin flock sizes between years. This parallels the findings on capelin school densities which suggest that compared to fluctuations in capelin abundance, variation in average density of schools was relatively small.

Figure 5-14: Common murre and Atlantic puffin flock size frequency distributions at Witless Bay, 1982-1984. (n=number of flocks observed; note logarithmic scale).

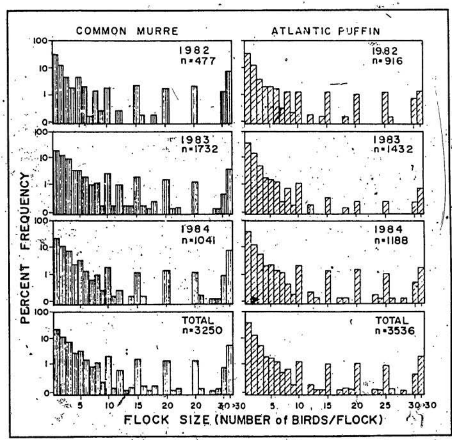

COMMON MURRE
ATLANTIC PUFFIN
PERCENT FREQUENCY
100
10
1
0
1982
n=477
1983
n=1732
1984
n=1041
TOTAL
n=3250
1982
n=916
1983
n=1432
1984
n=1188
TOTAL
n=3536
5
10
15
20
30
>30
25
FLOCK SIZE (NUMBER of BIRDS/FLOCK)

Table 5-10. Common murre and Atlantic puffin flock characteristics at Witless Bay, 1982-1984.

Species	Year	No. of flocks	No. of birds	Flock characteristics*			
				mean	(s.e.)	med	Q3
Murre	1982	477	7318	15.3	(4.3)	2	8
	1983	1732	12558	7.3	(0.5)	2	5
	1984	1041	8110	7.8	(1.1)	2	5
	Total	3250	27986	8.6	(0.8)	2	5
Puffin	1982	916	4070	4.4	(0.3)	1	3
	1983	1432	3772	2.6	(0.2)	1	2
	1984	1193	4699	3.9	(0.2)	1	3
	Total	3541	12541	3.5	(0.1)	1	2

* Characteristics: med= median, Q3= third quartile

Table 5-11. Kolmogorov-Smirnov tests of common murre and Atlantic puffin flock size frequency distributions.

	Year(s)	No. of cases	Z	Signif-icance
Between-year:				
Common Murre	82-83	2209	1.52	$p<0.02$
	83-84	2708	1.75	$p<0.004$
Atlantic Puffin	82-83	2348	2.31	$p<0.0001$
	83-84	2625	2.42	$p<0.0001$
Between-species:				
Murre * Puffin	1982	1393	3.95	$p<0.0001$
	1983	3164	7.57	$p<0.0001$
	1984	2247	2.87	$p<0.0001$
	Total	6804	8.23	$p<0.0001$

5.5.2. Seasonal Trends in Flock Sizes and Relation to Capelin

Seasonal trends in size of bird flocks (Figure 5-15) were similar to trends in bird and capelin abundance (Figures 5-1, 5-2 and 3-10). In general, bird flock size was strongly correlated with bird abundance (Table 5-12). This parallels the finding that capelin abundance and density were well correlated.

Murre flock size was better correlated with capelin density than capelin abundance in 1983, 1984, and overall, but was better correlated with abundance in 1982. Puffin flock size was better correlated with capelin density in 1982 and 1983, but was negatively correlated with capelin density and abundance in 1984.

In general then, bird flock sizes were only weakly related to capelin trends and more strongly related to overall bird abundance. This suggests that intraspecific behavioural interactions are at least as, or more, important in flock formation than capelin density.

5.5.3. Underwater 'Flocking' Behaviour

From 1980-1984, 319 and 1299 incidents involving gill-net catches of 1326 puffins and 22,013 murres, respectively, were recorded around several different seabird colonies in eastern Newfoundland. Frequency distributions of the number of birds caught per incident revealed that murres were caught in greater numbers underwater than puffins (Figure 5-16). This difference was observed in all years, and on average, catches of murres underwater were about 2-4 times greater than puffin catches (Table 5-13). If catches were indicative of underwater 'flock' sizes; then like surface flocks, underwater 'flock' sizes of murres were consistently larger than puffins.

While the total abundance (catch/net-day of effort) of birds underwater varied by an order of magnitude between different years (1980-1984), the density of birds underwater (catch/incident) changed relatively little between years. This parallels the observation (above) that abundance of surface flocks varied greatly between years, while average flock sizes were relatively similar.

Figure 5-15: Seasonal trends in mean common murre and Atlantic puffin flock sizes at Witless Bay, 1982-1984.

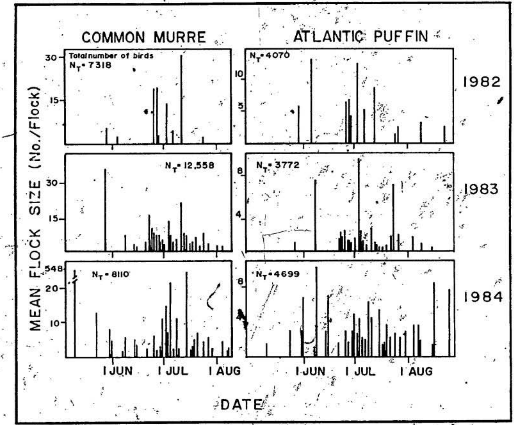

COMMON MURRE
ATLANTIC PUFFIN
1982
1983
1984
Total number of birds
N_T = 7318
N_T = 4070
N_T = 12,558
N_T = 3772
N_T = 8110
N_T = 4699
MEAN FLOCK SIZE (No./Flock)
30
15
30
15
548
20
10
10
5
8
4
8
1 JUN
1 JUL
1 AUG
1 JUN
1 JUL
1 AUG
DATE

Table 5-12. Spearman rank correlations between mean flock sizes (F) of common murres (M) and Atlantic puffins (P), bird abundance (A), and capelin abundance (CA) and density (CD), 1982-1984. Probabilities: NS not significant, * p<0.05, ** p<0.01, *** p<0.001, **** p<0.0001.

Year		MF*MA	PF*PA	MF*CA	MF*CD	PF*CA	PF*CD
1982	n	9	11	5	5	6	6
	r	0.85	0.43	0.90	0.60	0.14	0.37
	prob	**	NS	*	NS	NS	NS
1983	n	27	28	27	27	28	28
	r	0.66	0.66	0.63	0.76	0.36	0.38
	prob	*	****	***	****	*	*
1984	n	20	20	20	20	20	20
	r	0.74	0.39	0.21	0.29	-0.06	-0.10
	prob	***	*	NS	NS	NS	NS
Total	n	56	59	52	52	54	54
	r	0.70	0.58	0.31	0.46	0.08	0.14
	prob	****	****	*	***	NS	NS

Figure 5-16: Frequency distributions of the number of common murres and Atlantic puffins caught in fishing nets per catch incident (n=number of catch incidents).

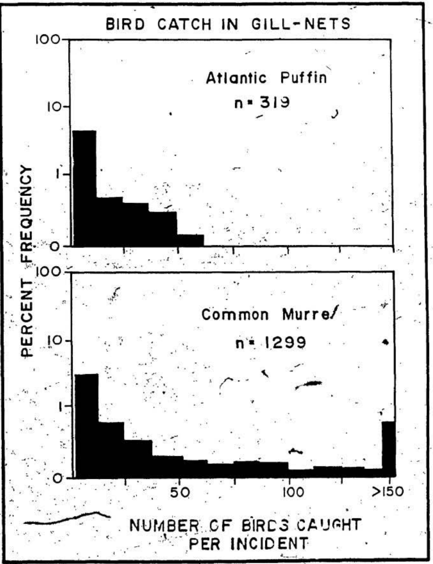

BIRD CATCH IN GILL-NETS
Atlantic Puffin
n = 319
Common Murre
n = 1299
PERCENT FREQUENCY
100
10
1
0
50
100
>150
NUMBER OF BIRDS CAUGHT PER INCIDENT

Table 5-13. Mean catch of common murres and Atlantic puffins in fishing gear in different years. Net-days is total fishing effort (no. nets x no. days used), incidents include only occasions when birds were taken in nets.

Year	Net-days	No. of incidents	No. of birds caught	Catch/incident		Catch/net-day*	
				mean	(s.e.)	mean	(s.e.)
Murre							
1980	337	36	288	8.0	(1.1)	2.22	(0.66)
1981	9749	273	3367	12.3	(1.9)	0.81	(0.25)
1982	16252	357	8066	22.6	(4.0)	1.74	(0.53)
1983	13999	415	6486	15.6	(2.1)	0.71	(0.16)
1984	9256	203	3326	16.4	(3.4)	0.61	(0.14)
Total	49700	1299	22013	16.9	(1.5)	1.06	(0.17)
Puffin							
1980	337	9	61	6.8	(1.7)	1.10	(0.52)
1981	9749	96	412	4.3	(0.6)	0.19	(0.03)
1982	16252	61	356	5.8	(1.1)	0.06	(0.02)
1983	13999	94	250	2.7	(0.3)	0.07	(0.01)
1984	9256	57	201	3.5	(0.9)	0.07	(0.01)
Total	49700	319	1326	4.2	(0.4)	0.11	(0.01)

* Catch/net-day is mean of catch/net-day values calculated for each day and fisherman (which is not the same as simply dividing total birds caught by total net-days observed).

5.6. MURRE AND PUFFIN FORAGING RANGES

5.6.1. Foraging Ranges Indicated by Boat Surveys

In both 1982 and 1984, four extended surveys were conducted parallel to the shoreline (Figure 2-2) on similar dates each summer (see Appendix A) to determine foraging ranges of murres and puffins from Witless Bay. These longshore surveys consisted of an outside leg, which ran south from Gull Island to Cape Broyle (30 km) on the outside (east) of the bird colonies; and an inside leg which ran inside (west) of the bird islands from Cape Broyle to Gull Island (30 km) within a few km of shore (Figure 2-2). Since foraging ranges and areas of bird concentration are of interest here (rather than seasonal trends), the surveys were combined to get mean bird abundances along each survey leg (Figures 5-17 and 5-18).

In both 1982 and 1984, murres were found mostly on the outside leg of longshore transects, reflecting the preference of murres for deeper waters. In 1982, most murres were found in one large aggregation between 5-10 km from Gull Island which corresponds to an area of deep water between Green Island and Great Island. In 1984, when capelin were less abundant, murre aggregations were smaller and dispersed along the transect between 0-20 km from Gull Island. In both 1982 and 1984, murres were found on the inside leg in an area about 5-15 km from Gull Island, corresponding to deeper water areas of Mobile Bay and nearby Great Island.

In contrast to murres, puffins were found in smaller, more dispersed aggregations, and greater numbers were found on the inside leg of surveys in both 1982 and 1984. Puffins were usually found all along the survey route, even at maximum transect distances of 30 km, but many of these may have come from the large population on Great Island. On the outside leg, peaks in abundance occurred around Gull Island (0-5 km), southeast of Great Island (15-20 km), and in Cape Broyle Bay (25-30 km). On the inside leg, peaks tended to occur around headlands along the shoreline, reflecting the concentrations of capelin around these areas (Figure 3-13).

Figure 5-17: Distribution of common murres on the water during offshore (n=4) and longshore (n=4) surveys in 1982 and 1984.

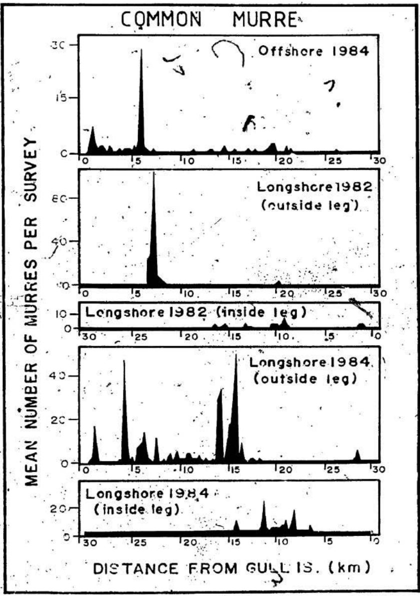
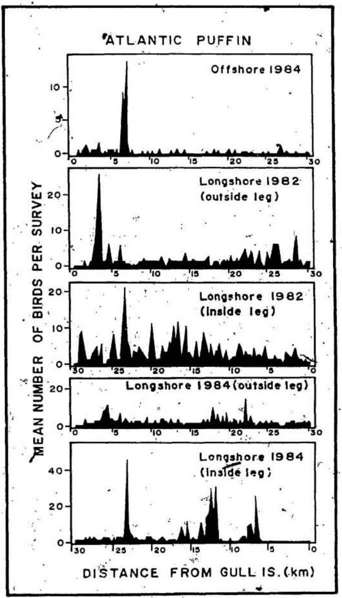

COMMON MURRE
Offshore 1984
Longshore 1982 (outside leg)
Longshore 1982 (inside leg)
Longshore 1984 (outside leg)
Longshore 1984 (inside leg)
MEAN NUMBER OF MURRES PER SURVEY
DISTANCE FROM GULL IS. (km)
30
15
0
80
40
0
10
0
40
20
0
20
0
0
5
10
15
20
25
30
30
25
20
15
10
5
0

Figure 5-18: Distribution of Atlantic puffins on the water during offshore (n=4) and longshore (n=4) surveys in 1982 and 1984.


ATLANTIC PUFFIN
Offshore 1984
Longshore 1982 (outside leg)
Longshore 1982 (inside leg)
Longshore 1984 (outside leg)
Longshore 1984 (inside leg)
MEAN NUMBER OF BIRDS PER SURVEY
0
5
10
20
40
0
5
10
15
20
25
30
DISTANCE FROM GULL IS. (km)

In 1984, four extended surveys (30 km) were conducted perpendicular to the coastline (Figure 2-2) to examine the distribution of birds offshore. Most murres and puffins were encountered within 10 km of Green Island (Figures 5-17 and 5-18), reflecting the general nearshore distribution of capelin during summer (Figure 3-13).

5.6.2. Foraging Ranges Indicated by Net-catch Surveys

When the catch per effort of murres and puffins in fishing nets set south of the Witless Bay colonies in 1981-1984 was plotted against distance from Green Island, several trends became apparent (Figure 5-19):

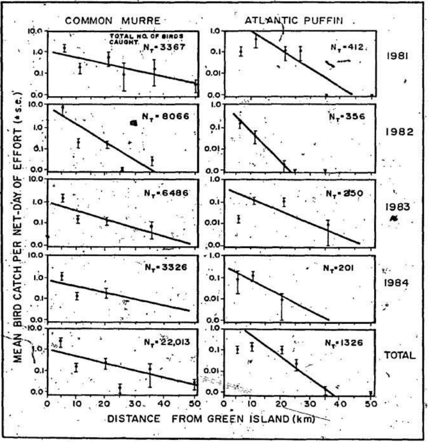
1) The (log) catch of murres decreased steadily with distance from their major breeding colony at Green Island. Puffin catches were usually greater at 10 km south of Green Island, corresponding to the large puffin population found on nearby Great Island. From there on, puffin catches also declined with distance.

2) Murres were caught at greater distances than puffins in each year indicating they have a larger maximum foraging range. Murres were regularly caught at 30-40 km from Green Island, although the vast majority were taken within 20 km. Puffins were regularly caught at 20-30 km from Green Island (10-20 from Great Island), although most were caught within 20 km of Green Island (10 km of Great Island).

3) Catch at distance of both murres and puffins varied between years, apparently in response to annual variations in capelin abundance. In 1982, the year of greatest capelin abundance, most murres and puffins were caught within 10 km of Green and Great Islands. As capelin abundance declined in 1983 and 1984, foraging ranges apparently increased to 20-50 km. Although there are no data for capelin abundance at Witless Bay in 1981, it was a year of low capelin abundance in eastern Newfoundland (Miller 1985) and puffins had difficultly provisioning chicks (Brown and Nettleship 1984). Accordingly, birds were foraging up to 30-50 km of Green Island in 1981.

These data provide information on foraging ranges only during the time that capelin were abundant nearshore. Before and after capelin were abundant in the study area, birds must have been foraging offshore at greater distances.

Figure 5-19: Catch per effort of common murres and Atlantic puffins with distance from Green Island, 1981-1984.


COMMON MURRE
ATLANTIC PUFFIN
TOTAL NO. OF BIRDS CAUGHT
N_T=3367
N_T=412
1981
N_T=8066
N_T=356
1982
N_T=6486
N_T=250
1983
N_T=3326
N_T=201
1984
N_T=22,013
N_T=1326
TOTAL
10.0
1.0
0.1
0.0
0.01
MEAN BIRD CATCH PER NET-DAY OF EFFORT (± s.e.)
0
10
20
30
40
50
DISTANCE FROM GREEN ISLAND (km)

5.7. SUMMARY OF MURRE AND PUFFIN FORAGING BEHAVIOUR

1. There was a strong temporal correlation between bird and capelin abundance at Witless Bay.

2. Murres foraged locally only during periods of peak local capelin abundance whereas puffins were also locally abundant for ca. one month after the peak capelin period.

3. Birds and capelin were aggregated over spatial scales of 2-6 km. Aggregation intensity, bird-capelin correlations, and aggregative responses were scale-dependent.

4. Murres and puffins exhibited sigmoidal Type III aggregative responses to capelin density.

5. Murres exhibited higher capelin density thresholds for aggregation than puffins.

6. Murre and puffin density thresholds for aggregation varied daily in relation to overall capelin density at Witless Bay.

7. Spatial overlap between murres and puffins was very low through each season in all years. There was evidence for assymetric interference competition between murres and puffins for feeding sites around their colonies (murre>puffin).

8. The pattern of combined total abundance and distribution of murres and puffins closely matched the pattern of total capelin abundance and distribution in all habitats.

9. Murres formed larger, more aggregated feeding flocks than puffins. Average flock sizes and capelin school densities varied little compared to variations in flock and school abundance.

10. Murres exhibited larger maximum foraging ranges than puffins, and ranges for both species varied with overall capelin abundance between years.

Chapter 6

DISCUSSION

6.1. CAPELIN BIOLOGY, BEHAVIOUR, AND DISTRIBUTION

6.1.1. Biological Characteristics of Capelin

Observations in this study of marked daily variations in the sex ratio of capelin at spawning sites, and the predominance of male capelin toward the end of the spawning period, have previously been noted inshore (Templeman 1948, Atkinson and Carscadden 1979) and offshore on the Southeast Shoal (Winters and Campbell 1974, Carscadden 1978). These variations probably occur because males remain near spawning sites throughout the spawning period, and large numbers of moribund males remain inshore after spawning, whereas females periodically move in and out of spawning sites *en masse*. (Templeman 1948).

Overall, female capelin were more numerous than males and the ratio averaged about 1.6:1, respectively, over all years. Similarly, males dominated in catches of Southeast Shoal capelin from 1967-1969 (51-71%), whereas females dominated from 1970-1973 (51-62%, Winters and Campbell 1974). However, differential sex ratios may result from sex-selective fishing techniques because capelin segregate by sex at spawning grounds offshore, with females being more pelagic and males more demersal (Baake and Bjorke 1973, Winters and Campbell 1974, Saetre and Gjosaeter 1975), and inshore, where males remain near beaches while females reside nearshore in discrete schools (Templeman 1948). Capelin collections in all years of this study, however, were made with the same trap set in the same location. Thus, besides natural variation in relative abundance of different sexes, there is no obvious explanation for the annual differences in overall sex ratios observed in this study.

There were marked changes in year-class composition of capelin schools from 1982 to 1984, owing to recruitment of a strong 1979 year-class to the spawning population in 1982 (Miller et al. 1982), and dominance of this cohort in subsequent years. Thus in 1982, the majority of capelin were 3 yr-olds; in 1983, 4 yr-olds were well represented; and by 1984, 4 and some 5 yr-old capelin dominated catches. Marked inter-year variability in year-class composition is not unusual for short-lived species like capelin (Carscadden 1978, Bakanev and Ermolchev 1982).

On average, male capelin 22 mm longer and 14 g heavier than females. This marked sexual size dimorphism is a well-known characteristic of capelin (Templeman 1948, Jangaard 1974). The observed seasonal trends of decreasing mean length (up to 15%) and mean weight (up to 47%) of capelin, most of which occurred during the first two weeks of spawning, have also been noted in other studies (Templeman 1948, Winters and Campbell 1974, Nakashima 1983). Several factors contribute to this seasonal decline in size. Mean lengths decrease because older fish tend to spawn first (Templeman 1948, this study), and because among fish of the same year-class, fast-growing fish spawn before slow-growing, later maturing individuals (Winters and Campbell 1974). Mean weights-at-length decrease because of egg and milt deposition, and reduced feeding activity during spawning (Winters and Campbell 1974).

There were also significant between-year differences in sizes of capelin (up to 20% in weight). Inter-year size variability occurs because of differences in age-class composition of schools between years, but also because of annual variations in growth rates (Winters and Campbell 1974, Carscadden et al. 1981). Thus, although capelin in 1984 comprised a high proportion of 4-5 yr-olds, mean sizes were similar to those in 1982 when 3 yr-olds dominated.

6.1.2. Seasonal Abundance and Distribution of Capelin

Registrations on acoustic sounder echograms indicated capelin were present at Witless Bay during all months of study (May-August). Seasonal peaks in abundance occurred between late June and late July in each year. Templeman (1948) and Whitehead (1981) also reported capelin were most abundant inshore on the east coast during this period. Templeman (1948) noted capelin may reside inshore as late as September in some years and locations.

It is not known whether all echogram traces were of capelin schools, but evidence suggests capelin were the most abundant schooling fish recorded inshore. Echogram traces assumed to be capelin were typical of small, pelagic schooling fish and were easily distinguished from plankton or larger fish like mature cod (Forbes and Nakken 1972, Whitehead 1981). Echogram traces were similar to those reported by Atkinson and Carscadden (1979) and Whitehead (1981) for capelin schools observed nearshore in Trinity and Conception Bays, Newfoundland. Only capelin were caught in the sampling gill-net at Witless Bay and in the trap at Cape Broyle. Capelin occurred in stomachs of locally caught cod from mid-May to late August in some years, with peak numbers in cod coinciding with estimated capelin abundance peaks (D. Methven and J. Piatt, unpubl. data). Sandlance, juvenile cod, and squid were rarely found in cod stomachs. Similarly, stomachs of locally collected murres and puffins contained almost exclusively capelin. Capelin were observed being captured by seabirds at sea, swimming around fishing wharves, spawning on beaches from Witless Bay to Cape Broyle in June and July, and swimming in dispersed schools (particularly moribund males) in late July.

On the other hand, juvenile cod reside nearshore in eastern Newfoundland (Lear et al. 1980, D. Methven unpubl. data) and schools were observed near the wharf in Bay Bulls in 1983 and 1984. Furthermore, bird gizzards contained otoliths of juvenile cod and sandlance and adult birds delivered these prey to chicks. This indicates these species were available within foraging range of the colonies (ca. <60 km). Finally, mature herring and mackerel were occasionally caught in locally set traps in August. Thus, it is likely that some echogram traces were of fish other than capelin, but these were probably insignificant compared to the number of capelin traces.

Capelin abundance at Witless Bay was weakly correlated with the magnitude of tidal oscillations. Similarly, peak periods of capelin spawning at Bryant's Cove, Conception Bay, occurred during periods of maximal tidal oscillations in 1978 and 1979 (Frank and Leggett 1981). Templeman (1948) also found that capelin at Holyrood, Conception Bay, and Grand Beach, Fortune Bay, usually spawned during periods of maximal tidal oscillations, although he attributed this to an indirect effect of tidal exchange on nearshore water temperatures. Both Templeman (1948) and Frank and Leggett (1981) observed that beach spawning almost always occurred on an ebbing tide. Periods of maximal tidal oscillations may be preferred for spawning so that eggs can be deposited as far up on the beach as possible. Egg densities are highest and hatching times are shortest in the high tide zone (Frank and Leggett 1981).

Water temperature appeared to be an important environmental factor affecting capelin at Witless Bay. Capelin did not appear in abundance until the upper water column (< 30m) was warmer than ca. 5°C, and most capelin schools occurred above the 5°C isotherm throughout summer. Virtually all capelin were observed above the 1°C isotherm (<50 m). Capelin were concentrated near the surface on all surveys, regardless of date or time of day. This contrasts with capelin behaviour outside spawning periods, when diel vertical migrations (down in daylight, up in dark) are normal (Bakanev and Ermolchev 1982; Miller and Carscadden 1979). These observations corroborate studies in the Gulf of St. Lawrence where most spawning capelin concentrations were found above the 0°C isotherm, i.e., at depths above ca. 50 m (Bailey et al. 1977). Similarly, Atkinson and Carscadden (1979) found no relationship between time of day and depth of capelin spawning schools in Trinity and Conception Bays. They suggested that capelin school depths and densities were related to water temperatures. Although some loosely-scattered schools were found as deep as 110 m, greater and denser concentrations usually occurred above 50 m.

Water temperatures were progressively colder from 1982 to 1984 and thermoclines developed later and were shallower each successive year. Vertical capelin school distribution followed this same pattern, with considerable capelin biomass occurring to depths of 60 m in 1982, but most biomass occurring above 30 and 20 m in 1983 and 1984, respectively. Similarly, capelin schools around Baccalieu Island, Newfoundland, were abundant at depths to 50 m in 1977, but virtually all capelin biomass was found above 30 m in 1978 and 1979 (Whitehead 1981).

Major physical factors influencing water temperatures were pack ice, icebergs, and winds. Waters adjacent to the east coast of Newfoundland are dominated by an inshore branch of the Labrador Current that flows south through the Avalon Channel. In the springs of 1983 and particularly 1984, heavy pack ice extended offshore from the northeast and east coasts of Newfoundland until about May of each year. In 1984, heavy pack ice was present only one mile east of Gull Island on the first survey on 9 May. Icebergs were observed drifting south up to late July in each year. In 1983 and 1984, many small icebergs grounded and remained for weeks in Bay Bulls, Witless and Mobile Bays. The continuous presence of pack ice and icebergs nearshore can have a direct effect on sea-surface water temperatures (Farmer 1981), and undoubtedly contributed to the cold water temperatures observed at Witless Bay in 1983 and 1984.

On a smaller time scale, winds markedly influenced nearshore water temperatures at Witless Bay. The strength and direction of winds were significantly correlated with nearshore water temperatures. There was a 1-3 day lag between wind events and changes in water temperature, however, because it takes time for water mass exchange to occur in response to wind stress (Csandy 1982). Temperature fluctuations were better correlated with longshore than cross-shore winds, probably because Ekman flow of surface water occurs perpendicular and to the right of wind flow (Csandy 1982). These results support Templeman's (1966) hypothesis and corroborate Frank and Leggett's (1981, 1982) observations that wind events influence nearshore water temperatures. The strong, synchronous correlation in water temperatures Witless Bay and Cape Broyle also supports the suggestion of Leggett et al. (1984) that wind events may regulate nearshore water temperatures and therefore biological events over large geographic areas.

Based on offshore, longshore, and standard surveys, it appeared that capelin concentrated around islands and near coastal headlands. It may be that topographically induced upwelling currents or turbulent eddies created favourable habitat for feeding (although feeding activity is much reduced in spawning capelin; Jangaard 1974), or they created hydrodynamic traps (Borovkov and Kovalyov 1977). Whatever the cause, it was clear that some areas (e.g., the 'Ledge' and an area down-current from Green Island) were consistently occupied by capelin and associated predators. Offshore surveys were limited, but indicated that during the main period of inshore capelin abundance, few significant capelin aggregations occurred farther than ca. 5-10 km from the coast.

Standard surveys indicated an order of magnitude decline in capelin abundance at Witless Bay between 1982 and 1984. The decrease in abundance between 1982 and 1983 was consistent with Department of Fisheries and Oceans (DFO, St. John's, NF) hydroacoustic survey-based estimates of offshore capelin abundance in those years (Miller 1985). However, DFO surveys indicated that offshore capelin abundance increased between 1983 and 1984 whereas Witless Bay surveys indicated a large decline inshore. Observations of predator abundance and behaviour corroborate the 1984 Witless Bay capelin abundance estimates. The total abundance of murres in the study area decreased substantially between 1983 and 1984. The seasonal pattern of murre abundance, which was closely resembled capelin abundance patterns in 1982 and 1983, was also very similar to the capelin abundance pattern in 1984, showing only one major peak around 1 July. Similarly, abundance of humpback whales and catch-per-effort of cod in gill-nets declined substantially in the study area between 1983 and 1984, and both these predators also exhibited seasonal peaks in abundance around 1 July (J. Piatt and D. Methven, unpubl. data).

The discrepency between Witless Bay capelin abundance estimates and those of DFO in 1984 may be related to cold water temperatures experienced nearshore in that year. Migration of capelin from overwintering sites to spawning grounds is known to be strongly influenced by water temperatures (Devold et al. 1972, Carscadden 1978, Luka 1979). Growth and maturation rates of capelin also vary with water temperature, being slower in cold water (Winters and Campbell 1974). Thus, it is possible that many capelin did not spawn at Witless Bay in 1984 owing to cold water temperatures, moving instead to other inshore areas where water temperatures were warmer or remaining offshore until the following year. Another explanation for the discrepency is that most offshore capelin examined by DFO in 1984 were 1 and 2 yr-old fish, none or few of which, respectively, achieve sexual maturity and therefore would not be expected to occur at inshore spawning grounds (Templeman 1948, Miller 1985).

Although capelin abundance varied by an order of magnitude between 1982 and 1984, there was relatively little variation in average density of capelin schools. Indeed, school densities increased slightly between 1982 and 1983 despite a large decline in abundance, possibly because the shallower 5° isotherm caused a denser packing of schools in the upper-water layer. These observations emphasize the distinction between abundance and density, and point to the role of behaviour in maintaining school size and structure (Pitcher and Partridge 1979, Pitcher 1980).

6.2. MURRE AND PUFFIN DIET COMPOSITION

The diets of adult and chick **common murres** (Kaftanovskii 1938, Uspenski 1956, Belopol'skii 1957, Madsen 1957, Tuck 1961, Swartz 1964, Pearson 1968, Scott 1973, Ogi and Tsujita 1973, 1977, Wiens and Scott 1975, Birkhead 1976, Hedgren 1976, Baltz and Morejohn 1977, Mahoney 1979, Krasnow and Sanger 1982, Baird et al. 1983, Bradstreet 1983, Matthews 1983, Sanger 1983, Blake 1984, Schneider and Hunt 1984, Springer et al. 1984, Harris and Wanless 1985, Birkhead and Nettleship 1987c) and **Atlantic puffins** (Belopol'skii 1957, Myrberget 1962, Pearson 1968, Nettleship 1972, Corkhill 1973, Ashcroft 1976, Harris 1970, 1978, 1984, Harris and Hislop 1978, Hudson 1979, Lid 1981, Birkhead and Nettleship 1982, Bradstreet 1983, Brown and Nettleship 1984, Anker-Nilssen 1984, Hislop and Harris 1985, Barrett et al. 1986) have been extensively studied in the Atlantic and Pacific (murres only).

It is not the objective of this discussion to review all these studies, especially since two reviews of reports available up to 1983 have recently been published (Harris 1984, Bradstreet and Brown 1985). Rather, I will focus on the main findings of this study, supplement Harris' and Bradstreet and Brown's reviews where appropriate, and discuss some aspects of murre and puffin diets which have not previously been considered in detail.

6.2.1. Overall Murre and Puffin Diet Composition

Diets of murres and puffins at Witless Bay were typical of these species, being comprised mostly of pelagic schooling fish (Bradstreet and Brown 1985). Capelin dominated adult (82.7% and 78.8% of murre and puffin, respectively) and chick (90.8% and 93.2%, respectively) diets by weight. Sandlance and juvenile Atlantic cod comprised most of the remainder. Out of 3574 adult and 1268 chick prey items identified, only eight different fish species (or genera) were observed, with squid and a few unidentified crustaceans contributing to overall diversity. These observations are consistent with previous reports of capelin-dominated common murre (Tuck 1961, Mahoney 1979, Birkhead and Nettleship 1987c) and puffin (Nettleship 1972, Brown and Nettleship 1984) diets in Newfoundland and southern Labrador.

Murres and puffins have more varied diets in other regions. In Britain, sprat (*Sprattus sprattus*) and sandlance dominate murre and puffin diets, but several cod and rockling species are also eaten and over 35 species fish species have been recorded in diets (Harris and Hislóp 1978, Harris and Wanless 1985, 1986). Off Oregon, pacific sandlance (*A. hexapterus*), juvenile rockfish (*Sebastes* spp.) and tomcod (*Microgadus proximus*) are taken most frequently by common murres (Matthews 1983). Diet diversity is very high (>35 fish and invertebrate species) and on average, no prey composes more >25% of the diet (by number). Similarly in the Gulf of Alaska, capelin (30% by volume) comprises most of the fish (81%) diet of common murres, and ca. ten crustacean species make up most (18%) of the remainder (Sanger 1983).

In contrast, diet diversity is low in some regions. The diet of common murres at St. Paul Island in the Bering Sea is composed mostly of walleye pollock (*Theragra chalcogramma*) and capelin (>90% by number or volume, Schneider and Hunt 1984). Cod (56%; *B. saida* and *Eleginus gracilis*) and sandlance (27%) dominate common murre diet (by volume) in northwest Alaska (Springer et al. 1984). In northern Norway, puffins consume capelin and sandlance almost exclusively (by weight), but diversity increases and composition changes markedly at southern colonies (Anker-Nilssen 1984, Barrett et al. 1986).

Thus it appears that murre and puffin diet composition largely reflects potential prey diversity in different oceanographic regions. The above regions exhibiting low diet diversity (including Newfoundland) are part of high/low arctic ecosystems and are strongly influenced by ice-cover and waters of arctic origin, whereas the other regions are boreal in nature. This probably accounts for differences in biological diversity more than any other factor (Dunbar 1968, Ashmole 1971, Springer et al. 1984). Similar relationships between diet diversity, oceanography, and geography have been observed for other seabirds in polar, temperate, and tropical regions (Belopol'skii 1957, Ogi and Tsujita 1973, 1977, Ogi 1980, Croxall and Prince 1980, Harrison et al. 1983, Diamond 1984, Brown 1985, Gaston 1985a, Croxall et al. 1985).

Selection of Different Sex/Age Classes of Capelin

Selection of specific sex- or age-classes of capelin was a notable feature of capelin predation by murres and puffins at Witless Bay. Mature female capelin were eaten by birds in higher proportions relative to their proportions in trap collections, and more ovid than spent females were eaten. In contrast, cod (n=1001 examined) at Witless Bay ate a higher proportion of male capelin, averaging 88% (by weight) in 1982-1984 (D. Methven and J. Piatt, unpubl. data). Passive selection by different predators may result from i) differential availability of male and female capelin in the water column (see page 203), ii) differential ability of predators to swallow larger male capelin (cod>murre>puffin; Swennen and Duiven 1977), and iii) differential foraging behaviour of predators. Murres dive deeper than puffins (Piatt and Nettleship 1985) and cod feed demersally

(Templeman 1966). These factors do not explain selection of ovid over spent female capelin. However, ovid females have a higher wet weight energy density than spent females (Montevecchi and Piatt 1984), and hence should be actively selected if both are available at the same foraging cost (Pyke et al. 1977, Montevecchi and Piatt 1984). Similarly, males might be actively selected because of their larger size and hence, higher total energy content (Montevecchi and Piatt 1984).

Sex-selective penguin and seal predation on krill (*Euphausia superba*) has been observed in the Antarctic (Croxall and Pilcher 1984, Croxall et al. 1985). Croxall et al. (1985) drew several conclusions which aptly summarize the Witless Bay situation (for krill, also read capelin): i) krill schools exhibit seasonal and regional variations in sex ratios; ii) different predators may take krill in ratios similar to, or markedly different from, background ratios; iii) energy densities of female krill can increase substantially during maturation yielding an energy bonus to predators; and iv) predation on krill during their breeding season, and particularly on one sex, may have a greater impact on krill population dynamics than would be deduced simply from comparison of food requirements and stock size,

6.2.2. Comparison of Murre and Puffin Diets

Diet Diversity

Considered over all years by number or weight of prey consumed, puffins ($H = 0.50$ or 0.30, respectively) had a more diverse diet than murres ($H = 0.41$ or 0.25) at Witless Bay. Adult murres usually feed on only one or two fish species at any one time and place (Belopol'skii 1957, Matthews 1983, Bradstreet and Brown 1985), whereas adult puffins consume more non-fish prey like amphipods, euphausiids, and polychaetes (Belopol'skii 1957, Bradstreet 1983, Harris 1984, Bradstreet and Brown 1985). In other studies where adults of both species were sampled at the same time and place, puffins had more diverse diets than murres (Belopol'skii 1957, Bradstreet 1983).

Chick diet diversity at Witless Bay was low and variable between years (H =0.09-0.46 by number). Puffin chick diets were more diverse than murre chick diets in two of three years, and over all years combined (H=0.35 and 0.17, respectively). Many studies indicate that puffins normally feed chicks a wider spectrum of food types than murres (Nettleship 1972, Corkhill 1973, Birkhead 1976, Harris and Hislop 1978, Mahoney 1979, Anker-Nilssen 1984, Brown and Nettleship 1984, Harris 1984, Harris and Wanless 1985). Where both species were studied at the same time and place, puffin chick diets were more diverse than murre chick diets in two of three years, and over all years combined (H=0.38 and 0.23, respectively; calculated from Harris and Wanless 1986).

Because i) murres and puffins have simlar foraging styles (pursuit divers), ii) they have equivalent constraints in their shared environment (e.g., wind and sea conditions), and iii) small prey are more common than large prey (Peters 1983), then murres *should* be more stenophagic than puffins because fewer prey types will be worth foraging on by murres because of their larger size and higher total food demands (Pyke et al. 1977, Werner and Mittelbach 1981).

Diet Overlap

Overlap between adult murre and puffin diets at Witless Bay was high in all years whether calculated on a numerical (C= 0.65-0.96, overall C=0.88) or weight basis (C=0.97-0.99, overall C=0.99). In two other studies where adult murre and puffin diets could be qualitatively compared, they also overlapped extensively (Belopol'skii 1957, Bradstreet 1983).

Chick diet overlap was higher than adult diet overlap in all years (overall C=0.95 and 0.99 by number and weight, respectively). Harris and Wanless (1986) reported much lower diet overlap between murre and puffin chicks at the Isle of May (C=0.13-0.21 by weight) but these were calculated using different length classes of sandlance as prey categories (see Diamond 1984). Calculated with the same prey categories used in this study, overlap over all years combined was 0.90.

Diet overlap of murres and puffins with other predators at Witless Bay is probably high. Kittiwakes and herring gulls (*Larus argentatus*) are abundant at Witless Bay and capelin may comprise 30-40% of their summer diets (Maunder

1971, Pierotti 1979, Brown and Nettleship 1984). Atlantic cod are the dominant fish predators of capelin at Witless Bay, and capelin were the most common prey eaten by cod in 1981-1984, comprising 76% (by weight) of their diets in summer, 1984 (D. Methven and J. Piatt unpubl. data). Humpback and minke (*Balaenoptera acutorostrata*) whale abundance at Witless Bay was strongly correlated with capelin abundance in 1982-1984 (J. Piatt, unpubl. data), and both species probably fed extensively on capelin (Mitchell 1973, 1975, Whitehead 1981).

High diet overlap between seabird species with similar foraging styles has been observed at colonies in high/low arctic (Belopol'skii 1957, Ainley and Sanger 1979, Krasnow and Sanger 1982, Sanger 1983), boreal (Pearson 1968, Crawford and Shelton 1978, Furness and Barrett 1985), and tropical waters (Ashmole and Ashmole 1967, Harrison et al. 1983, Diamond 1984). High diet overlap between seabirds and marine mammals has been documented in the Antarctic (Croxall et al. 1985).

Prey Size Selection

On average, murres at Witless Bay ate larger prey than puffins, but they did this by selecting larger sex/age classes of fish rather than by selecting larger individuals of a given sex/age class. Puffins ate higher proportions of larval and juvenile capelin, cod, and sandlance. Murres ate few larval fish, larger juvenile cod, and a higher proportion of male capelin.

It has been widely reported that prey size is correlated with predator body size (Peters 1984). This is also generally true for seabirds (Ashmole and Ashmole 1967, Pearson 1968, Harrison et al. 1983, Diamond 1984). Other studies have demonstrated that murres select larger prey than puffins (Pearson 1968, Harris and Wanless 1986). 'Size-selection' appears to be largely a consequence of body size because: i) murres *can* swallow larger fish than puffins (Swennen and Duiven 1977), and ii) murres have higher maintenence and foraging costs due to their larger size (Werner and Mittelbach 1981, Peters 1984). Thus, small fish that might satisfy puffin requirements may not be worth pursuit and capture by murres because foraging costs outweigh benefits (Royoma 1970, Krebs et al. 1977, Mittelbach 1981, Werner and Mittlelbach 1981).

Morphological constraints may also influence size selection of fish for chick meals. Murres can usually carry only one prey and thus would profit most by bringing only large prey back to chicks. Multiple-prey loading puffins, on the other hand, may carry one large prey or many small ones at similar cost depending on available prey densities and costs of foraging (Orians and Pearson 1977, Montevecchi and Piatt 1984).

6.2.3. Comparison of Adult and Chick Diets

There have been few comparisons of adult and chick seabird diets. Belopol'skii (1957) found razorbill and puffin chicks were fed exclusively fish, whereas adult diets comprised 97% and 87% fish, respectively, with crustaceans, polychaetes and other invertebrates comprisisng the remainder. Of the fish portion of diets, sandlance were more frequent in chick meals than in adult diets. Similarly, Gaston and Nettleship (1981) found that thick-billed murres fed chicks almost exclusively fish (mostly *B. saida*), while adults consumed a large number of crustaceans as well. Cairns (1984) also observed marked differences between diets of adult and chick black guillemots. Chicks were fed fish (99.8%), of which most (91.7%) were blennies, whereas adults consumed a wider variety of fish (including ca. 30-35% *B. saida* and 30% blennies, by % occurrence) and crustaceans (ca. 55% by occurrence).

At Witless Bay, murre and puffin chicks were fed higher proportions of capelin, and lower proportions of cod, sandlance and other prey, than were eaten by adults. During the peak period of capelin abundance (mid-June to late July), chicks were fed mostly ovid female capelin despite marked seasonal variations in capelin abundance and sex ratios, and in adult diets. It is likely that capelin (particularly ovid females) were preferentially fed to chicks because of their size and high nutritive value (Montevecchi and Piatt 1984). As central place foragers, murres and puffins would profit most by consuming lower quality prey at sea and bringing larger, more nutritious prey back to chicks (Orians and Pearson 1977, Gaston and Nettleship 1981, Harris 1984).

6.3. TEMPORAL DIET VARIATION IN RELATION TO CAPELIN ABUNDANCE

6.3.1. Stomach Contents

As overall capelin abundance at Witless Bay declined between 1982 and 1984, the frequency of capelin in murre and puffin stomachs decreased accordingly. This parallels observations of Gaston and Noble (1984) and Springer et al. (1984) on inter-year variability in stomach contents of thick-billed murres, and supports their suggestion that this variability resulted from annual fluctuations in local prey abundance.

If capelin were always so abundant that competition never occurred (Lack 1966), then birds should have fared equally well in all years at capturing capelin, but they did not. This may indicate that intraspecific competition for capelin occurred at Witless Bay. Alternatively, foraging may have been more difficult when capelin were scarce irrespective of bird density.

Proportions of murre stomachs containing capelin were always greater than proportions of puffin stomachs with capelin (differing digestion rates?), and this difference was greatest when capelin were least abundant. This suggests there may have been interspecific competition for capelin, with murres being the superior competitor (which is likely from morphological considerations, Stettenheim 1959, Bédard 1969). Alternatively, murres may be better adapted than puffins for foraging at low prey densities, although morphological and ecological considerations suggest otherwise (Bédard 1969, this study).

Functional Response to Capelin Density

Numbers of capelin in bird stomachs varied with capelin density at Witless Bay. The form of the relationship appeared to be sigmoidal for murres and puffins, suggesting Type III functional responses to prey density (Holling 1959). The functional response is essentially a manifestation of optimal foraging behaviour (Cook and Cockrell 1978, and see page 223) and has been well described for various insects (Utida 1958, Hassell and May 1974, Hassell et al.

1977, Eveleigh and Chant 1981a), crustaceans (Hassell et al. 1976), fish (Ivlev 1961, Heller and Milinski 1979), birds (Goss-Custard 1970, 1977c; Smith and Dawkins 1971, Wood and Hand 1985), and mammals (Holling 1959). Type III functional responses are most common among higher vertebrates (Holling 1965), and are probably more widespread than the literature would indicate (Hassell et al. 1977).

6.3.2. Diet Composition

Although seabird diet composition is often reported to reflect local prey abundance (e.g., Belopol'skii 1957, Vermeer 1980, Krasnow and Sanger 1982, Brown and Nettleship 1984, Harris 1984, Springer et al. 1984, Vermeer and Westrheim 1984), murre and puffin diet composition did not reflect annual variations in overall capelin abundance at Witless Bay. Several possible factors, alone or together, may explain these results:

1) Although capelin abundance at Witless Bay varied by an order of magnitude between years, the total amount of capelin within colony foraging range may have always been adequate to meet food demands. Birds may have compensated for low local capelin abundance by feeding farther from colonies (for which there is good evidence, see page 230), thereby maintaining similar diets in all years. In other words, there may be some *critical* level of sustained prey abundance within the whole foraging zone, above which birds can maintain preferred diets, and below which birds must increasingly rely on alternate prey (if available), or experience a food shortage. It is probable that capelin abundance fell below critical levels for puffins at Witless Bay in 1981 (Brown and Nettleship 1984).

2) Alternate prey may have been so locally rare that birds *had* to forage largely on capelin in all years (Brown and Nettleship 1984). Circumstantial evidence (bird and cod stomach contents, fish collections, etc., see page 205) supports this hypothesis. Sandlance are scarce in the deep Avalon Channel and nearshore. They prefer sandy substrate on the shallow Grand Bank, about 80 km east of Witless Bay (Reay 1970, Winters 1983). Juvenile cod reside inshore in

most bays of eastern Newfoundland (Lear et al. 1980, D. Methven unpubl. data), but nothing is known of their abundance or availability.

3) The proportion of capelin in diets probably does not depend on the absolute abundance of capelin, but on capelin abundance *relative* to other prey species. Many studies have demonstrated that prey selection by predators is a function of the relative densities of complementary prey (e.g., Ivlev 1961, Goss-Custard 1977b,c, Rapport 1980).

Bird diet composition ~~also~~ did not reflect the composition of capelin in trap collections. The proportion of male capelin in bird (particularly adult murre) diets decreased while the proportion of males in trap collections increased between 1982 and 1984. Similarly, birds ate more spent female capelin while spent:ovid proportions in traps decreased between years. Possible explanations include:

1) Male capelin may have shifted inshore between 1982 and 1984, thereby being less available to birds near/offshore, and relatively more abundant in beach trap collections. Similarly, proportions of spent to ovid females in traps may not have reflected availability to birds.

2) Considerable evidence indicates that as density of the most profitable prey falls, less profitable prey are included more frequently in predator diets (Ivlev 1961, Krebs et al. 1977, Pyke et al. 1977). If they could be caught and swallowed as easily as females, male capelin would be more profitable because of their larger size (Montevecchi and Piatt 1984). Similarly, ovid females should be more profitable than spent females because of their higher wet weight energy density (Montevecchi and Piatt 1984). Thus, optimal foraging theory would have correctly predicted that birds would consume less males, and less ovid than spent females, as overall capelin abundance declined between 1982 and 1984. Similarly, proportions (by weight) of male capelin eaten by cod also decreased from 92% to 81% to 53% in 1982, 1983, and 1984, respectively (D. Methven and J. Piatt, unpubl. data).

Despite problems of interpretation, some studies have clearly shown that seabird diet composition can change markedly in response to long-term variations in prey abundance (Harris 1984, Furness 1984, Burger and Cooper 1984, Hislop and Harris 1985, Montevecchi et al. 1986). This is especially evident from extreme cases where forage fish stocks declined substantially owing to overfishing and/or poor recruitment. In these instances, marked changes in seabird diet composition were usually accompanied by lower chick feeding rates, smaller meal sizes, and reduced breeding success (Tschantz 1978, Vermeer et al. 1979, Lid 1981, Brown and Nettleship 1984, Burger and Cooper 1984).

Variability in Prey Characteristics

Temporal variations in biological characteristics of capelin eaten by birds at Witless Bay were due in large part to natural, background variations, which in turn, were influenced by environmental conditions. Other recent studies have also demonstrated that temporal variations in sex and age-class composition of prey schools, and environmental conditions, markedly influence characteristics of prey eaten by seabirds (e.g., Harris 1984, Springer et al. 1984, Vermeer and Westrheim 1984). "Very comprehensive data are thus necessary to conclude that differences between seasons, sites, sexes and species reflect any more than differences in what predators encounter, because of the timing of foraging or the location of foraging areas." (Croxall et al. 1985).

Diversity and Overlap

Competition theory predicts that diets of competitors should diversify and diverge during "lean" (Schoener 1982) or "crunch" (Wiens 1977) periods. In contrast, bird diet diversities decreased as capelin abundance declined at Witless Bay between 1982 and 1984, and murre and puffin diet overlap increased.

Either interspecific competition did not occur at Witless Bay, or conditions were never "lean" enough, or at least one assumption underlying the hypothesis - that alternate prey were available in suitable densities - may not be valid. Invoking competition theory to explain diet trends in the absence of data on all important prey is probably inappropriate (Steenhof and Kochert 1985). In this study, diet composition "can be explained adequately in the context of simple foraging theory without implicating interspecific competition as a mediating factor" (Steenhof and Kochert 1985).

6.4. FORAGING BEHAVIOUR

6.4.1. Temporal Relationship between Birds and Capelin

Murre and puffin abundance at Witless Bay was significantly correlated with local capelin abundance in each season of study. Murre numbers were always better correlated than puffin numbers with capelin abundance. However, murres and puffins have different breeding schedules and this affected the strength of temporal correlations with capelin.

Both murres and puffins at Witless Bay normally hatch chicks in late June (Nettleship 1972, Mahoney 1979) as capelin appear inshore (Templeman 1948, this study). Murre chicks go to sea about 19-25 days after hatching and because breeding is well synchronized, most murres leave the colony within 4-5 weeks after mid-hatching (Mahoney 1979, Harris and Birkhead 1985, Piatt and McLagan 1987). In contrast, puffins take about a month longer to fledge chicks in Newfoundland and fledging is less synchronized (45-60 days, Nettleship 1972). Thus, the chick-rearing period of peak food demand by murres (Wiens and Scott 1975, Furness 1978) at Witless Bay corresponds well with periods of peak capelin abundance around the colonies (ca. 4 weeks, see page 60), whereas puffin food demands extend well beyond this period. Similar interspecific differences in breeding chronology and use of temporally variable food resources have been observed in many marine (Belopol'skii 1957, Birkhead and Harris 1985, Croxall 1985) and terrestrial (e.g., MacArthur 1958, Terbough and Diamond 1970, Folse 1982, Feinsinger et al. 1985) bird communities.

The conventional view is that timing of reproduction evolves to coincide with peak food availability for provisioning chicks (Lack 1954, 1967, Birkhead 1977b, Croxall 1984, Birkhead and Harris 1985). The emphasis on chicks is somewhat misleading, however, because only about 5% of total food biomass taken by murres and puffins during breeding is fed to chicks (Brown and Nettleship 1984). The bulk of energy required for reproduction goes towards fueling adult foraging activities (Gaston 1985b). Thus, adult foraging and food requirements may impose the greatest constraints on evolution of breeding schedules, and may best account for interspecific differences in breeding strategies.

Data collected in this study suggest that murres have higher prey density thresholds for foraging than puffins (see page 222). On a daily basis, murres require nearly twice as much food as puffins. Thus, the murres' breeding strategy may have evolved because adults could not provision *themselves* after departure of a local high density food supply. If adult rather than chick constraints have been the key factor shaping evolution, it is less paradoxical that murres evolved to be the most proficient (living) alcid at underwater foraging (Stettenheim 1959, Piatt and Nettleship 1985), but never evolved better methods of provisioning chicks, e.g., multiple prey deliveries. There would be little adaptive value in being able to carry several prey to chicks under low prey density conditions if adults could not sustain themselves at the same time.

On the other hand, puffins have lower prey density thresholds for foraging, both adults can forage simultaneously, and they are multiple prey loaders. Thus, adult puffins can continue to forage successfully for themselves and feed chicks for some time after a peak in prey abundance around their colonies. Interestingly, puffin chick growth is subject to negative-feedback metabolic control independent of food supply (Nettleship 1972, Hudson 1983) which effectively extends the chick-rearing period and reduces *daily* chick and adult energy requirements. Thus, puffin energy demand is spread over a longer period, resulting in a higher net total cost of production, but lower daily expenditures.

6.4.2. Spatial Relationship between Birds and Capelin

Scale-dependent aggregation and correlation

Studies of seabird distribution in relation to oceanographic features (e.g., fronts, ice-edges, etc.) have repeatedly demonstrated that seabirds aggregate in areas of high productivity (Bradstreet 1980, Brown 1980, Schneider 1982, Briggs et al. 1984, Cairns 1984, Bradstreet and Brown 1985, Haney 1986). However, spatial relationships between seabirds and their prey are poorly known (Schneider and Piatt 1986). In marine systems, biological and physical processes combine to impart spatial structure to plankton and fish communities (Platt 1972, Steele 1974), and seabird aggregations reflect the scale at which these processes occur (Schneider 1982, Schneider and Duffy 1985).

At Witless Bay, aggregation intensity of birds and capelin on most surveys increased significantly with measurement scale, peaking at scales ranging from 0.25 to 12.0 km. Most patch chord lengths ranged between 2-6 km. Seabird patch chord lengths of 12-44 km have been reported elsewhere (Schneider 1982, Briggs et al. 1984, Woodby 1984), but owing to methods of data collection, patches smaller than 12 km could not be resolved (Schneider and Piatt 1986).

Because seabirds aggregate over a range of spatial scales, presumably reflecting the scale of prey aggregations (Schneider and Duffy 1985), any analysis of seabird distribution in relation to their prey should examine the effect of scale on spatial correlations (Schneider and Piatt 1986). In this study, birds were significantly correlated with capelin on more than half of all surveys before effects of scale were examined. Spatial correlations increased to higher, significant levels with increased frame size on about one-third of all surveys, and on more than half of all surveys exhibiting significant correlations before scale analysis. No other studies (e.g., Woodby 1984, Obst 1985, Safina and Burger 1985) have found significant spatial correlations between seabirds and their prey, though they might have if scale effects had been considered (Schneider and Piatt 1986).

Aggregative response to prey density

Animals searching for food spend more time where food is plentiful, and this behaviour forms the basis of the aggregative response (Hassell and May 1974). It has been suggested that most vertebrates should exhibit sigmoidal (Type III) aggregative responses to prey density (Holling 1966, Murdoch and Oaten 1974, Hassell et al. 1977). In the only study of a vertebrate population foraging under natural conditions, Goss-Custard (1970, 1977c) showed that the aggregative response of redshank (*Tringa totanus*) to prey density *was* sigmoidal.

In this study, the aggregative response of birds to capelin was examined over different sized areas (frame sizes) because aggregation was clearly scale-dependent (see above). Like aggregation intensity and spatial correlations, aggregative responses were scale-dependent and the form of the response was best revealed at measurement scales of 2-6 km. Both murres and puffins often exhibited sigmoidal (Type III) aggregative responses to capelin density. Moreover, murres had a higher capelin density threshold for aggregation than puffins, and this was reflected in their flocking behaviour (murres formed denser flocks than puffins, see page 228). Finally, the threshold capelin density above which murres and puffins aggregated was not fixed, but changed daily in relation to overall capelin density. These features of murre and puffin foraging behaviour may be explained within the context of optimal foraging theory by considering effects of i) body size, and ii) experience, on foraging behaviour.

The effect of body size on foraging behaviour

Holling (1965) showed that simple foraging behaviour could be modeled by the equation:

$$N/T = aD / (1+ahD)$$

where N=total number of prey captured, T=total time spent hunting, a=instantaneous rate of discovery, D=density of prey, and h=handling time of prey. Plotted against prey density, the rate of food intake (N/T) may be a hyperbolic (Type II) or sigmoidal (Type III) function depending on the degree of prey aggregation (Cook and Cockrell 1978), hunger state of the predator (Holling 1965, 1966), presence of alternate prey (Holling 1965, Murdoch and Oaten 1975), or learning ability of the predator (Holling 1966). *It is likely that vertebrates may exhibit either form of the response depending on the conditions and prey with which it is measured* (Holling 1965, 1966, Murdoch and Oaten 1975).

The principal feature of Holling's 'disc' equation, and many subsequent models of foraging behaviour (e.g., Royoma 1971, Werner and Hall 1974, Murdoch and Oaten 1975, Hassell et al. 1977, Cook and Cockrell 1978, Werner and Mittelbach 1981) is that:

$$N/T \alpha D/(1+D)$$

i.e., the potential rate of food intake (N/T) is a non-linear function of prey density. This simple, physical relationship between prey dispersion and capture rate appears to be an invariable law (Ivlev 1961). *Above all else, predators are* *constrained in their foraging by how often they encounter prey* (Lotka 1925, Ivlev 1961). Coexisting predators are faced with equivalent constraints arising from the dispersion of shared prey. **Thus, the most important distinction between coexisting predators with similar foraging styles and shared prey is N_{tot}, the total amount of food required for daily existence. N_{tot} is a sum product of food required for 24-hr maintenence and costs of foraging, and both are functions of body size** (Calder 1983, Peters 1983, Werner and Mittelbach 1981).

Murres and puffins at Witless Bay feed in a similar manner on the same prey and under the same environmental conditions. Thus, interspecific differences in foraging efficiency should be small relative to N_{tot} (Werner 1974, Kooyman et al. 1982, Nagy et al. 1984a). To maximize N_{tot}/T (the basic premise of optimal foraging theory), murres and puffins can only adjust D or T, because N_{tot} is a relatively constant function of body size and T, time spent foraging. Murres require about twice as much food as puffins (Brown and Nettleship 1984). Thus, murres can only obtain their daily ration in the same time (T) as puffins if they forage at about $2[D/(1+D)]$ the prey density at which puffins forage. In fact, murres may actually spend *less* time foraging than puffins (Pearson 1968) even though murres forage at greater distances (see page 230). If so, then they *must* forage on higher densities of the same prey.

Under low prey density conditions, a small interspecific difference in choice of prey patch densities would yield a large difference in rate of food intake. As prey density increases, the rate at which prey can be captured levels off. Thus, under high prey density conditions, a larger difference in prey patch densities would be required for murres to obtain their daily ration in the same time as puffins. In this study, the *difference* between murre and puffin thresholds *did* increase significantly with increasing capelin density at Witless Bay.

As prey density (D) varies, murres and puffins may adjust time spent foraging (T) to obtain daily rations. Time available for foraging is limited, however, and there must be some lower prey density limit (critical density) below which neither species can obtain their daily rations. Because murres require twice the daily ration of puffins, they should have a higher *critical* prey density threshold than puffins, and this should influence breeding strategies (see page 220).

During the chick-rearing period, murres and puffins may 'normally' spend only 10-40% of their day foraging (Pearson 1968, Cairns et al. 1987). This suggests they have considerable flexibility in dealing with prey fluctuations. Indeed, much evidence indicates that murres and puffins rarely have difficulty foraging or rearing chicks (Bradstreet and Brown 1985, Harris and Birkhead 1985). This suggests that critical prey density thresholds are rarely encountered under natural conditions over a time scale of years or perhaps even decades.

An alternative explanation for differing prey density thresholds may be that puffins were excluded by murres from high density prey patches. There is evidence that interference competition occurred at Witless Bay (see page 227). However, this would not explain why i) the interspecific threshold difference increased with increasing capelin density, ii) puffins continued to forage on low density prey aggregations in the absence of murres (see page 227), or iii) murres formed denser feeding flocks than puffins (see page 228).

Therefore, I believe the interspecific difference in prey density thresholds may result from species-specific responses to food density and dispersion. Similarly, Davidson (1977a) concluded from her careful study of coexisting ant species that different foraging behaviours "appear to represent evolutionary responses to resource dispersion and are not simply maintained by high density specialists aggressively excluding other species from richer resource patches".

In summary, murres and puffins differ in their responses to prey density. The fact that they exhibited Type III aggregative responses is not surprising (Holling 1965, 1966), nor is the fact that they responded at different prey densities (Holling 1959, Eveleigh and Chant 1981a). In a recent experimental study, J. B. Dunning (pers. comm.) also found that three coexisting bird species (towhees *Pipilo fuscus, P. aberti, and P. erythrophthalmus*) exhibited differing thresholds to food density. I believe that interspecific differences in prey density thresholds promotes coexistence, and I explore this in more detail below (see page 232).

The effect of experience on foraging behaviour

Most models of foraging behaviour assume that foragers change behaviour at threshold levels of foraging success (e.g., MacArthur and Pianka 1966, Murdoch and Oaten 1974, Charnov 1976, Hassell et al. 1977, Krebs 1978, Oaten 1977, Green 1980, Iwasa et al. 1981). In typical experimental studies (e.g., Krebs et al. 1974, Smith and Sweatman 1974, Werner and Hall 1974, Zach and Falls 1976a, Lima 1983), animals are presented with two or three foraging situations (diet items or habitat patches), and allowed to choose between them. These type of experiments provide valuable insight into foraging behaviour, but thresholds are never actually measured. In this study of a natural system, thresholds observed to change from survey to survey in relation to overall capelin density. Such behaviour is predicted by many models.

Charnov (1976) developed a Marginal Value Theorem (MVT) which predicted that a predator should leave a patch when the foraging success rate in that patch drops below the average capture rate in a habitat. This average capture rate is the threshold 'marginal value' which the organism must obtain to continue foraging in the original patch. Thus, as the distribution and density of prey patches vary, so should the threshold 'marginal value'.

More recent foraging models include experience and memory in the foraging decision-making equation. The role of previous experience in foraging has generally been neglected by ecologists (Kamil 1983, Pyke 1984, Kagel et al. 1986), and this has undoubtedly contributed to some apparent failures of optimal foraging predictions (e.g., Smith and Sweatman 1974, Zach and Falls 1976a, 1976b, 1976c, Lima 1983).

Foraging by Expectation (FBE) models also assume that behaviour changes at threshold levels of foraging success. The threshold is based on the success rate experienced during recent foraging. An animal should switch patches when its current success rate drops below what it has come to 'expect' (Ollason 1980, Iwasa et al. 1981, Lima 1983). Similarly, Green (1980) developed the concept of a "Bayesian bird" which assesses patch quality from both *a priori* expectations and from recent capture rates to decide whether to switch patches. Iwasa et al. (1981)

also concluded that foragers employing Bayesian statistical decision theory would, as a minimum, only need to keep track of the number of prey taken in a patch and the total time spent foraging to estimate the availability of unexploited prey in a random search situation.

All these models include the concept of assessment based on experience, and all would predict the behaviour of murres and puffins observed in this study. The application of Bayesian probability theory to models of foraging behaviour appears promising, and has been successful in modeling other forms of animal behaviour (e.g., mating decisions, Hunte et al. 1985).

6.4.3. Habitat use and spatial overlap

Much evidence indicates that murres and puffins selected different feeding areas around their colonies, and that murres excluded puffins from feeding in some sites, but puffins did not exclude murres:

1. Measured by an index of α overlap or by correlation analysis, fine-scale spatial overlap of murres and puffins was very low through each season in all years.

2. As total capelin abundance declined between 1982 and 1984, species overlap in use of habitats increased.

3. Murres and puffins aggregated over the same capelin schools inshore (high spatial overlap), but were spatially segregated in other habitats.

4. Capelin schools were generally larger and denser in deep-water bay and offshore habitats. Murres were spatially correlated with capelin in all (especially deep-water) habitats, whereas puffins were consistently correlated with capelin only in shallow inshore habitat.

5. Puffins were significantly correlated with capelin in offshore habitat only after murres departed from the study area in late July.

6. Puffin abundance in the study area increased to highest levels in August, i.e., after murres departed in late July.

7. Puffins usually deferred to murres when individuals met while swimming on the sea surface.

These observations are consistent with a hypothesis that murres and puffins were competing for feeding areas around their colonies, and that murres excluded puffins from some sites. Interference competition is common between bird species exploiting abundant shared food resources (Carpenter 1978, Edington and Edington 1983, Maurer 1984), and it is reasonable that murres should dominate because of their larger body size (Morse 1974, Schoener 1983). Assymetric interference competition is the most common form of competition observed in field studies (Connell 1983, Schoener 1983, Maurer 1984).

Alternatively, puffins may have preferentially fed in shallower inshore waters because of their more limited diving ability (Piatt and Nettleship 1985), and their ability to exploit lower density prey aggregations.

Whether interference competition occurred or whether puffins and murres selected different feeding sites on the basis of prey densities, or both, the end result was that capelin biomass was equitably exploited in all habitats. The pattern of *combined* total abundance and distribution of murres and puffins was remarkably similar to the pattern of total capelin abundance and distribution in each habitat.

6.4.4. Flocking behaviour

Where the two species reside in similar abundances, common murres occur in higher densities at sea than Atlantic puffins (Brown et al. 1975, Blake et al. 1984). In the northeast Pacific, murres have a greater tendency to flock than all other alcids and most other seabirds (Porter and Sealy 1981).

At Witless Bay, three important characteristics of bird flocks were observed: i) murres formed significantly larger feeding flocks than puffins, ii) murre flocks were more aggregated than puffin flocks, and iii) whereas capelin and bird abundance varied by an order of magnitude between years, capelin school densities and bird flock sizes remained relatively constant.

Spatial distribution (group size and dispersion) is one of the least variable ecological characteristics of a species. Unlike rates of reproduction, growth, and mortality, which may vary more between generations within a species than between species, spatial distribution may vary little within species under a wide variety of conditions (Taylor 1984). Although modified by biological and physical environments, spatial distribution is maintained by *behaviour* in most animals, and much of this behaviour is conserved genetically (Taylor 1984).

Coexisting predators often range from those that are *behaviourally constrained* to 'forage widely' in groups for dense prey concentrations to those that 'sit and wait' in isolation for dispersed prey (Davidson 1977a, Huey and Pianka 1981, Nagy et al. 1984b). The conservative nature of foraging style is evident because animals rigidly maintain their foraging style even in situations where it would be clearly advantageous (over the short term) to switch styles (Davidson 1977a, Nagy et al. 1984b). Murres and puffins would both fall into the 'forage widely' category of predators as they both forage in dense, widely-searching groups on schooling pelagic fish. However, murres and puffins occupy different positions in this continuum of behaviours as murres forage in denser flocks on denser fish schools.

I believe that the marked difference in flocking behaviour between murres and puffins results from behavioural adaptation to prey dispersion. For many animals, it can be shown both empirically and mathematically that high density aggregations are rarer than low density aggregations (Hassell and May 1974, Murdoch and Oaten 1975). This is certainly true for capelin (Zaferman 1973, this study). Predators choosing (or constrained) to forage on high density prey patches *must* therefore aggregate more than predators foraging on low density patches. To cope with this *physical* constraint, animals forced (e.g., by increasing food demands through increasing body size) to forage on high density prey should evolve behavioural traits conducive to group living, i.e., become more social. Natural selection must operate to balance prey density requirements (body size) and social behaviour. Accordingly, murres not only flock in higher densities, they also breed in higher densities (no./m^2) than puffins at their colonies (Harris 1984, Birkhead 1985).

The idea that sociality is a function of food dispersion is not new (Lack 1954, Wynne-Edwards 1962, Crook 1965). I am merely refining the argument by suggesting that *for coexisting predators with similar foraging styles and prey types*, one might be able to predict sociality entirely on the basis of body size/prey density constraints. Indeed, for a diverse group of animal families there is a strong positive correlation between group size and body size (protozoa, Taylor 1978; ants, Davidson 1977b; seaducks, Goudie 1984; terns, Erwin 1978; bee-eaters, Fry 1972, 1984; kangaroos, Kaufmann 1974; deer, Clutton-Brock et al. 1980; antelope, Jarman 1974; carnivores, Kruuk 1975, Bekoff et al. 1984; primates, Clutton-Brock and Harvey 1977, Ripley 1984). This does not imply that other factors (e.g., predator defense, increased food searching efficiency, etc., Birkhead 1985) do not contribute to the evolution of sociality. But like Davidson (1977b), I suggest that these may represent beneficial consequences of sociality rather than explanations for its existence.

Territoriality complicates interpretation of the relationship between body size and group size. However, it may be that in territorial animals, body size is correlated with local density (as opposed to 'group' size). For example, MacArthur (1958) found that of five sympatric warbler species with high food overlap and fixed territories, the largest species (bay-breasted *Dendroica castanea* and cape may warblers *D. tigrina*) had higher food density requirements and occurred in higher densities (no./km^2) than the smaller warbler species (e.g., blackburnian *D. fusca*, and myrtle warblers *D. coronata*). The rank order of maximal densities matched the rank order of body sizes.

6.4.5. Foraging ranges

Most murres and puffins foraged within 20 (range:0-60) and 10 (range:0-40) km, respectively, of their breeding colonies during periods of chick-rearing and peak capelin abundance at Witless Bay in 1981-1984. From time budget studies at Great Island in 1985, Cairns et al. (1987) estimated median murre foraging ranges of ca. 38 and 5 km for incubating and chick-rearing birds, respectively. These estimated foraging ranges for the Witless Bay colonies are similar to ranges reported from other colonies (Bradstreet and Brown 1985). For example, Bradstreet (1983) found most murres and puffins foraged within 20 and 10 (range:0-50) km, respectively, of the Gannet Islands, Labrador. At Skomer Island, Wales, most murres and puffins foraged within 10 and 5 km, respectively, of the colony (Corkhill 1973, Birkhead 1976).

Like group size, interspecific differences in foraging range *may* be explained by differences in prey density requirements and body size. A large predator seeking high density prey patches *must*, on average, range farther because high density patches are rarer than low density patches (see above). Furthermore, a large predator can go farther on fuel reserves because of lower specific metabolic rates, and need not feed as often as small predators eating similar prey (Calder 1983, Peters 1983). Like group size, foraging range is strongly correlated with body size in many animal families (ants, Davidson 1977; raptors, Newton 1984; terns, Erwin 1978; bee-eaters, Fry 1972, 1984; antelope, Jarman 1974; carnivores, Kruuk 1975; primates, Clutton-Brock and Harvey 1977), and within larger taxonomic groups (lizards, Turner et al. 1969; birds, Schoener 1968; mammals, Harestad and Bunnell 1979, Lindstedt et al 1986; for review see Peters 1983).

Murre and puffin foraging ranges changed markedly between years, being shortest in years of high capelin abundance and longest in years of low capelin abundance. Similarly, estimated murre and puffin prey density thresholds were highest in years of high capelin abundance and lowest in years of low capelin abundance. This is consistent with a hypothesis that intraspecific competition for food or feeding sites occurred around the Witless Bay colonies (Ashmole 1963). Capelin school abundance varied, but distribution remained similar between years. Thus, it is unlikely that range variation resulted simply from shifts in capelin distribution.

Ashmole (1963) and Lack (1966) suggested that if intraspecific competition for food does occurred at seabird colonies, it would be manifested in depressed chick growth, fledging, and feeding rates. Based on this type of evidence, it appears that intraspecific competition for food *does* occur at large seabird colonies (Gaston et al. 1983, Furness and Birkhead 1984, Birkhead and Furness 1985, Hunt et al. 1986).

Despite an order of magnitude variation in capelin abundance at Witless Bay between years, however, there was no evidence of marked variations in murre and puffin breeding success (A.E. Burger and D.N. Nettleship, pers. comm.). However, Burger (pers. comm.) found that murres spent progressively more time obtaining food from 1982 to 1984, which corroborates my observations on foraging ranges. Thus, for murres at least, breeding success may not be a good barometer of competition or food stress except under extreme conditions. Increased search effort would increase stress associated with reproduction (Siegel 1978, Drent and Daan 1980), thereby reducing fitness, but might otherwise not visibly affect breeding performance.

6.5. SYNTHESIS

The purpose of the following discussion is to address the question of how common murres and Atlantic puffins, two sympatric members of the Alcidae, coexist temporally and spatially on a shared food resource. I will focus on relationships between body size, foraging ecology, and population biology and consider whether these relationships extend allometrically to all members of the Atlantic Alcidae.

6.5.1. The Differential Use of Resources by Murres and Puffins

It is widely accepted that animal coexistence is promoted by differential use of resources, and that there is a limit to how similar coexisting species can be and still coexist (MacArthur and Levins 1967, Abrams 1983). Ecologists almost invariably find that coexisting species exhibit limited overlap in one or more resource dimensions (Pianka 1978). This was certainly true for murres and puffins at Witless Bay. Of the three critical resources shared by these birds, there was high overlap in use of food resources, moderate temporal overlap and low spatial overlap. To summarize:

1) Food overlap was high, but reduced because murres took some larger fish than puffins. Interspecific differences in size selection may be a double consequence of body size: murres *can* eat bigger fish than puffins, and because murres have a higher metabolic demand, they *should* eat bigger fish. Murres were more stenophagic than puffins, and diets were less variable. This may also be a consequence of body size because fewer prey will satisfy energetic demands of a large predator.

2) Temporal overlap in use of food and space was moderate, and was a function of murre and puffin breeding schedules. I speculated that because they have high critical prey density thresholds owing to their large size, murres have evolved to rear chicks only during peak periods of prey density. With lower critical prey density thresholds because of their smaller size, puffins can rear chicks over a longer period.

3) Spatial overlap was consistently low. I speculated that spatial distribution of murres and puffins at Witless Bay was a function of body size because murres, being larger, had to feed on higher density prey aggregations than puffins. As a consequence of this, murres fed at higher specific densities (larger group size, more aggregated), and foraged farther for food. Spatial overlap was probably also limited by assymetric interference competition.

Thus, overlap in all resourse dimensions, as well as interspecific differences in breeding strategy, group size and foraging range, *could* all be functions of body size. If so, then the patterns of resource use observed for murres and puffins should extend allometrically to other members of the Atlantic Alcidae. This will be considered in the following discussions. Information on characteristics of common murres (ca. 975 g), Atlantic puffins (ca. 475 g) and other Atlantic alcids were obtained from numerous sources, most of which have recently been reviewed in *The Atlantic Alcidae* by Nettleship and Birkhead (1985).

6.5.2. Body Size and Resource Use in the Atlantic Alcidae

Black guillemots (*Cepphus grylle*) are the smallest (ca. 400 g) of the fish-eating Atlantic alcids. The black guillemot "prey spectrum is wider than that of the other Atlantic alcids", they "tend to forage closer to their breeding sites than do the other alcids" (e.g., <5 km), and they tend to feed more on dispersed, territorial, benthic fish, and less on dense pelagic schooling fish than other alcids (Cairns 1984, Bradstreet and Brown 1985). Black guillemots are the least gregarious of the alcids, and forage individually or in small groups, especially in southern parts of their range where they overlap extensively with other alcids (Cairns 1984, Harris and Birkhead 1985). Black guillemots have a slightly shorter chick-rearing period than puffins (which they are similar to in weight), but have the longest period of more or less constant residence at breeding sites of all the alcids (Harris and Birkhead 1985). Thus, in every respect, black guillemots exhibit characteristics consistent with their small body size.

Razorbills (*Alca torda*) are intermediate in size (ca. 700 g) between puffins and common murres. Their ecology is poorly known, however, and this limits interpretation. Like murres and puffins with which they coexist, razorbills feed largely on dense schools of pelagic schooling fish, and diets are more varied than in common murres, and possibly less varied than in puffins (Bradstreet and Brown 1985). Foraging ranges are poorly documented, but best estimates range from 10-15 km (Bradstreet and Brown 1985), ie., intermediate between common murres and puffins. Nothing is known about foraging group size, but if it parallels breeding density (which is true for murres and puffins), then razorbills are less gregarious than common murres but more gregarious than puffins (Tuck 1961, Nettleship 1972, Birkhead 1985). The razorbill's incubation and chick-rearing period is similar to the common murre's, being much shorter than the puffin's (Harris and Birkhead 1985). Finally, razorbills have morphologically intermediate adaptations allowing them to carry more prey to chicks than murres, but less than puffins (Bradstreet and Brown 1985).

Thick-billed murres (*Uria lomvia*) have been well studied and provide an interesting comparison with common murres. Of all Atlantic alcids, thick-billed and common murres are most closely related, and most similar in form and body size (commons (ca. 950 g) being slightly larger than thick-bills (ca. 900 g) where they co-occur, e.g., Birkhead and Nettleship 1987a). Although thick-billed and common murres overlap in their distribution, the vast majority are segregated into arctic and boreal zones, respectively, which suggests they are too similar to coexist. Adult thick-billed murres feed on pelagic schooling fish, but usually have more diverse diets than common murres as they consume more invertebrates and benthic fishes (Bradstreet and Brown 1985). Where chick meal composition of both species has been examined in one location, however, common murre chicks had slightly more diverse diets than thick-billed murre chicks (Kaftanovskii 1938, Furness and Barret 1985, Birkhead and Nettleship 1987c). But in all these studies, common murre chick meal collections outnumbered thick-billed murre chick meals by an order of magnitude and therefore it is likely that the full range of thick-billed murre prey items was not observed. Furthermore, adults, and particularly thick-billed adults, consume a greater variety of prey than they feed their chicks (Gaston and Nettleship 1981, this study). Thick-billed murres may forage more than 100 km from colonies in the high arctic, but this does not contradict my thesis because (Bradstreet and Brown 1985): i) the largest foraging ranges reported are from observations early in the breeding season and ranges contract (e.g., from 80 to 30 km in one case) during the chick-rearing period, ii) there are several reports of thick-billed murres foraging within 20 km of their colonies and large ranges may be exceptional and/or associated only with large colonies, and iii) where the two species have been studied at one location, estimated foraging ranges were similar (10-11 km, North Norway, Furness and Barrett 1985) or common murres foraged considerably farther than thick-billed murres (medians: 47 vs 41 km, and 56 vs. 39 km, in 1982 and 1983, respectively, at the Gannet Islands, Labrador. Calculated from Birkhead and Nettleship 1987c). There are no comparable data on foraging group size of thick-billed murres, but they do feed in dense aggregations like common murres (Gaston and Nettleship 1981). If foraging densities parallel breeding densities, then thick-bills are slightly less gregarious than common murres (Birkhead 1977a, Harris and Birkhead 1985,Birkhead and Nettleship 1987b). Incubation and chick-rearing periods of thick-billed and common murres are very similar (Harris and Birkhead 1985), and where each species occurs allopatrically, common murres have slightly shorter chick-rearing periods. Where the two species were studied at one location, thick-billed murres had a longer (Belopol'skii 1957) or shorter (Birkhead and Nettleship 1987b) chick-rearing period than common murres. Thus in most respects, thick-billed murres differ slightly from common murres in ways consistent with their slightly smaller body size.

On first inspection, the last member of the Atlantic Alcidae appears totally inconsistent with my thesis. Dovekies (*Alle alle*) are the smallest (ca. 160 g) of the alcids, yet are as stenophagic as common murres, forage at great distances (up to 100 km), form dense feeding aggregations, and are highly gregarious at colonies (Bradstreet and Brown 1985). Their breeding period is similar to those of murres and razorbills, but shorter than those of black guillemots and puffins (Harris and Birkhead 1985). In fact, this apparent exception provides support for my thesis which has been that the ecology and behaviour of related, coexisting predators *with shared food resources* may be largely explained by differences in body size. The emphasis on food type is important, as the dovekie, which is almost entirely planktivorous, illustrates.

The predictions I have made about body size - foraging relationships are built on a cost/benefit analysis of foraging. For different animals feeding on the same prey, the most important prey variable is density and the most important predator variable is size. When different prey types are compared, however, prey size and energy content, as well as predator foraging costs become important variables in the cost/benefit analysis. With their high total metabolic demands, and morphological adaptions for a piscivorous life-style (Bédard 1969) it appears unlikely that any of the piscivorous alcids could subsist solely on North Atlantic zooplankton. In contrast, dovekies are well-adapted for subsistence on zooplankton (Bédard 1969). What we know of their behavioural ecology suggests that Dovekies assume the same ecological role on zooplankton that common murres do on schooling fish.

The above species discussions are simplistic because of the enormous variability in ecological relationships in different geographic regions. For example, black guillemots tend to be more social at colonies where they breed alone than at large, mixed alcid colonies (Harris and Birkhead 1985). Total abundance of birds may influence diets and foraging behaviour because in large, mixed colonies both intra- and interspecific competition probably reduces the number of prey options birds have, and may strongly influence foraging ranges and spatial overlap in foraging habitats. Furthermore, results of this study suggest that feeding flock size is strongly correlated with overall bird abundance and thus, may vary considerably for birds in the centre rather than the periphery of their areas of abundance (e.g., razorbills in Iceland vs. Newfoundland, respectively).

Although I do believe that available data supports my suggestion of an allometric relationship between body size and foraging ecology in the piscivorous alcids, the above discussions and conclusions should be viewed as a framework for developing testable hypotheses rather than as my 'conclusive' evidence that such relationships exist.

6.5.3. Implications for Population Ecology

Theoretical considerations

Until recently, predation and competition were modelled separately using similar equations. Following the leads of Lotka (1925) and Volterra (1926), predation was modelled using equations in which predator population density was set as a linear function of prey population density (Rosenzweig and MacArthur

1963, Hutchinson 1978, Pianka 1978). However, Soloman (1949) and Holling (1959) pointed out that predation has two components: functional and numerical responses to prey density. Thus, population dynamics (numerical response) are related to feeding behaviour (functional response). Furthermore, both responses are *non-linear* functions of prey density for most animals (Holling 1959, 1965, Readshaw 1973).

Competition has been modelled using modified predator-prey equations (Pianka 1978) where: changes in population density of competitor A are equated to growth of population A (density times growth rate 'r') minus an intraspecific competition term (a function of carrying capacity 'K' of A) and an interspecific competition term (a function of the population density of competitor B times α, an index of similarity between competitors A and B). This type of competition equation, and accompanying predictions, has played a prominent role in modern ecology (Hutchinson 1978). Because it has generally been assumed that growth rate and carrying capacity terms are constants, most research has focused on α, the competition coefficient (Pianka 1978). The usual assumption is that α is wholly a function of species overlap in their 'resource utilization curves' (MacArthur and Levins 1967). Gause's 'exclusion principle' arises from the notion that no two species can coexist if they occupy exactly the same niche (e.g., Gause 1934), and the 'principle of limiting similarity' is a corollary of Gause's principle which suggests there is a limit to how large α can be for species to coexist (MacArthur and Levins 1967).

There are serious flaws in the competition equations. They do not account for systems where predation or stochastic environmental perturbations are dominant forces influencing population densities (Simberloff 1982). Indeed, the equations do not even contain a predation component. More importantly, the assumption that growth rate and carrying capacity terms are constant is clearly not true (Pianka 1978): both vary with environmental conditions, and both are functions of predator and prey population densities. (Utida 1957, Huffaker 1958, Holling 1959, Eveleigh and Chant 1981b, 1982a,e,f).

If competition and predation equations are combined, however, and *competitors exhibit different* **non-linear** *responses to resource (prey) density,* then, infinite coexistence of two or more competitors limited by one resource is possible if resource fluctuations occur because of stochastic events or depletion by competitors. (Utida 1958, Stewart and Levin 1973, Koch 1974, Armstrong and McGehee 1976, 1980, Kaplan and Yorke 1977, Levins 1979, Butler 1980, for a review see Abrams 1983).

The workings of these coexistence models can be summarized for a simple system with low initial densities of one prey and two competing predators with 'low' and 'high' level responses to prey density:

1) As prey density increases, it eventually passes a threshold level required for maximal growth of the 'low density' predator population (r_{max}^{low}). As the 'low density' predator population grows, it increasingly affects the prey population through predation and itself through intraspecific competition.

2) As prey density increases further, it eventually passes a threshold level required for maximal growth of the 'high density' predator population (r_{max}^{high}). For stability $r_{max}^{high} >> r_{max}^{low}$. With growth, the 'high density' predator population increasingly affects the prey population through predation, the 'low density' predator population through interspecific competition, and itself through intraspecific competition.

3) Eventually, predators may outstrip prey production and the prey population crashes, followed by crashes in the 'high density' and then 'low density' predator populations because of strong intra- and interspecific competition for a now rare resource. If this occurs, or if prey and then predator populations crash due to stochastic events, the cycle repeats itself at ('1').

In this scenario, the competitive advantage first goes to the 'low density' predator, then to 'high density' predator, and with a crash in prey, it reverts back to the 'low density' predator. In theory, the infinite coexistence of two or more competitors on one prey is possible *regardless* of the degree of α overlap between competitors. This is an apparent contradiction of Gause's exclusion principle and the principle of limiting similarity in its usual form (Utida 1958, Koch 1974, Armstrong and McGehee 1978, Abrams 1983). Instead, it appears there is a limit to how similar resource density thresholds can be for competitive coexistence to occur (Abrams 1983). For simplicity, I will refer to this as the RDT (resource density threshold) model for coexistence.

Experimental evidence

There have been no specific tests of the RDT model for coexistence. However, a few experimental studies provide strong evidence to support it. Utida (1958) studied the fecundity and long-term population dynamics of two related wasps preying entirely on one food source. Holling (1959) studied functional and numerical responses of larval sawflies by three small rodents. Eveleigh and Chant (1981a,b,c, 1982a,b,c,d,e,f,g) conducted a detailed study of predation by two related mites on a single prey; examining functional and numerical responses, fecundity, mortality, and feeding behaviour at varying predator and prey densities

In summary, all investigators found each study animal exhibited a suite of traits for optimal performance over a specific range of prey densities. Optimal densities differed between the animals being compared. Functional and numerical responses were non-linear in all cases. Maximal fecundity and mortality rates were higher in 'high density' predators than in 'low density' predators, and non-linear functions of prey density in both types of predator.

Population biology of the Atlantic Alcidae

I have speculated that prey density requirements are largely a function of body size for Atlantic alcids. If population dynamics are related to prey density, as suggested by RDT models and experimental evidence, then alcid population dynamics should also be related to body size. Four points are germane to this argument:

1) Because high density prey offer the greatest rate of energy extraction from the environment, any predator feeding on high prey density should be able to marshal more energy for reproduction than any coexisting predator feeding on low density prey. Field measurements of foraging energetics support this contention (Nagy et al. 1984b).

2) Large animals have lower specific metabolic rates than small animals (Peters 1983) and therefore a higher proportion of energy and mass assimilated from food can be channeled into reproduction.

3) Predators feeding in dense aggregations engender a high risk of starvation and mortality from competition and/or stochastic events. If mortality is density-dependent, which it appears to be for higher vertebrates at least (Fowler 1981), then aggregated predators should have a higher mortality rate than dispersed predators sharing resources in the same environment.

4) Higher reproduction and mortality rates result in faster and larger population fluctuations.

Thus, I would predict that like the 'high density' predators of Utida (1958), Holling (1959) and Eveleigh and Chant (1981b, 1982e,f,g), common murres should exhibit: i) higher breeding success and recruitment, ii) higher natural mortality, and iii) faster and larger population fluctuations, than any other Atlantic alcids, and that these life-history parameters should be scaled to body size in the remaining piscivorous alcids. Breeding success, recruitment, absolute and relative mortality, and population fluctuations of Atlantic alcids have been documented for natural populations in a large number of short and long-term studies (Hudson 1985, Harris and Birkhead 1985).

As in my assessment of foraging behaviour, the following discussion of alcid population parameters must be considered in light of the enormous variability in alcid ecology in different geographic regions. Indeed, alcids are poor subjects for testing hypotheses about population dynamics because of their long life-spans, variety of ecosystems they occupy, and the variety of mortality factors influencing populations in different regions. Furthermore, it is difficult to examine or statisically test allometric trends within families because of the low number of family members available for establishing trends. Nonetheless, the following discussion provides a framework for future considerations. Dovekies have been excluded from this analysis because so little is known about their population biology. For convenience, species names have been abbreviated: common murre CM, thick-billed murre TM, razorbill RZ, Atlantic puffin AP, and black guillemot BG.

Absolute mortality rates for the best-studied alcids conform to predictions with CM > RZ > AP (Hudson 1985). Very few thick-billed murre and black guillemot mortality rates are available so little can be concluded about these species. These differences in absolute mortality are also reflected in estimates of relative alcid mortality. The magnitude of common murre mortality from oil pollution, gill-nets, and starvation is usually greater than razorbill mortality, which in turn, usually exceeds puffin mortality (Piatt and Nettleship 1987, Piatt et al. 1984, 1985, Evans and Nettleship 1985). Large 'wrecks' involving tens or even hundreds of thousands of common murres are not unusual (Tuck 1961, Bailey and Davenport 1972), but rarer for razorbills, more so for puffins (Harris 1984) and unknown for black guillemots.

Comparing breeding success, at least three species conform to predictions: CM > RZ > AP (Harris and Birkhead 1985). Thick-billed murre breeding success is lower than predicted but this may be biased by reports of exceptionally low breeding success in the arctic owing to weather or ice conditions rather than biological constraints (Birkhead and Nettleship 1981). In terms of breeding success, black guillemots provide an exception to predictions. They are unique among Atlantic alcids because they normally have a two-egg clutch. Breeding success varies widely between regions (0.28-1.60 chicks/pair). In some regions, they exhibit the lowest breeding success among alcids, whereas in other regions they exhibit the highest success rate (Harris and Birkhead 1985). Predation is greater on black guillemots than other alcids (Harris and Birkhead 1985) and despite their high breeding success, recruitment is very low (see below). Thus, increased clutch size and fledging success may be an evolutionary response to breeding and post-fledging predation pressure (Harris and Birkhead 1985) that over-rides other constraints.

The predicted pattern for recruitment is observed in that the three largest alcids (CM, TM, RZ) usually exhibit higher recruitment rates than puffins and black guillemots, and for these small alcids: AP > BG (Hudson 1985). However, recruitment in the large alcids does not conform to predictions because available studies suggest that TM > RZ > CM. Razorbill estimates can be disregarded for now, however, because only two widely disparate values (16.2%, 48.0%) are available, the higher of which is based on a very low number (9) of band returns. However, the reversal of thick-billed and common murre recruitment rates deserves discussion. In all cases it is important to consider that band return rates may better reflect the rate at which birds return to natal colonies than actual recruitment rates (Hudson 1985, Birkhead pers. comm.).

One could argue that averaging recruitment estimates from different banding studies with widely varying numbers of band returns (e.g., from 32 to 319 in common murres, Hudson 1985) gives undue emphasis to less reliable estimates. If recruitment values compiled by Hudson (1985) were averaged by weighting for total band returns, then mean common and thick-billed murre recruitment rates would be 34.6% and 33.9%, respectively, which fits the rank order predicted. Similar weighting of mean puffin and black guillemot recruitment estimates would yield values of 29.8% and 26.4%, respectively; thus still fitting predictions. The low recruitment rate estimated for black guillemots is interesting because it cannot be reconciled with estimates of very high adult mortality rates (Hudson 1985). If both were correct, black guillemots would be extinct. Recruitment rate estimates are based on a large number (1136) of band recoveries from several different regions (Petersen 1981, Hudson 1985). Thus, it seems likely that adult black guillemot mortality estimates compiled by Hudson (1985) are inaccurate or unrepresentative of normal adult mortality rates in this species.

My final prediction was that population fluctuations should be more extreme in large alcids because high breeding success and recruitment under optimal conditions should result in rapid population growth, whereas high mortality from starvation or stochastic events (including man-made sources of mortality) should lead to rapid population declines. With lower recruitment and mortality rates smaller alcids should not respond to optimal conditions as quickly, but should not suffer from heavy mortality during 'lean' periods either, and so population fluctuations should be less extreme. I view this prediction as a valuable test of my thesis because it incorporates predictions about breeding success, recruitment and mortality, but provides an independent assessment of these parameters.

Hudson (1985) compiled data on alcid population changes which "were chosen to represent the best estimates available taken over a time span of several years, from wherever possible, large colonies in different areas of the Atlantic". Based on absolute changes in numbers (total=1.24 million birds) and time spans covered (total=661 yr), Hudson calculated rates of change (% per annum) for each species at several colonies. I further reduced these to average values using absolute values of negative changes since we are interested in the magnitude and not the direction of population fluctuations.

These data strongly support my thesis as the magnitude of population fluctuations were mostly in the order predicted from body size with CM (9.1% p.a.) > TM (6.8%) > [RZ (4.6%) < AP (6.0%)] > BG (3.4%). Only razorbills and puffins did not fall in the order predicted with respect to each other. However, it is still improbable ($p<0.025$) that the rank order of alcid population variability would so closely match ($r_s=0.90$, df=3, t=3.58) the order predicted from body size considerations.

'r' and 'K' selection

I am suggesting that for piscivorous Atlantic alcids, large body size is associated with: i) patchy, less predictable food supplies; ii) higher prey (resource) density thresholds; iii) greater aggregation intensity (larger group sizes); iv) greater (interfernce) competitive ability; v) higher mortality rates (shorter life-span); vi) higher maximal reproduction rates (r_{max}); vii) higher mass-specific productivity; and viii) faster and larger population fluctuations. Conversely, small body size is associated with opposing characteristics.

In other words, I am suggesting that large alcids exhibit r-selected traits, whereas small alcids exhibit K-selected traits. This is contrary to what would be predicted from the theory of r-K selection as proposed by MacArthur and Wilson (1967) and Pianka (1970). They argued that selection for fitness in unpredictable environments should favour *small* body size, rapid reproduction rates, high productivity, etc., whereas selection for predictable environments should favour *large* body size, stable population dynamics, low reproduction rates, high competitive ability, etc. Only the suggestion that larger animals should have higher competitive ability is consistent with my conclusions about the Atlantic Alcidae.

Attempts to relate body size to population parameters within large taxonomic groups have been instructive (e.g., body size accounts for 68-75% of the covariation in life-history traits of mammals, Stearns 1983), but have revealed little about selective pressures on naturally coexisting animals (Taylor 1978). It has become increasingly clear that within taxa which, as a group, have been labeled as r- and K-type animals, there exist a full range of species exhibiting r- or K-type traits (Stubbs 1977, Taylor 1978). I know of at least three other studies which offer evidence that *within groups of coexisting animals*, larger species exhibit r-selected traits whereas smaller species exhibit K-selected traits.

1) Not only did all of MacArthur's *Dendroica* warblers exhibit high/low density foraging characteristics expected from their body sizes (see page 228), but the largest species (cape may and bay-breasted warblers) had the largest clutch sizes, most dramatic population fluctuations, and were clearly adapted for existence on a highly unpredictable, but periodically dense, food supply (MacArthur 1958). Smaller species (e.g., myrtle and black-throated green warblers) exhibited opposing traits.

2) Taylor (1978), specifically tested the theory of r-K selection on a group of eleven coexisting bactivorous ciliates. Contrary to expectations, he found that, species designated as r-strategists by their fast population growth rates were large and aggregated, whereas species designated as K-strategists with slow growth rates were small and dispersed. Furthermore, Legner (in Taylor 1978) found large r-strategists dominated when food supplies were enriched, whereas small K-strategists only flourished in non-enriched environments.

3) Sternberger and Gilbert (1985) examined population growth in eight coexisting species of planktonic rotifers.Their study provides strong support for my thesis as they quantified relationships between rotifer body size, food density thresholds, and maximal reproduction rates. To quote: "The food concentrations for which population growth rate was zero (the threshold food level) varied by a factor of 17 among species. The log of threshold food concentration was positively

and significantly related to the log of body mass. Similarly, a strong positive log-log relationship was found between rotifer body mass and the food concentration supporting one-half the maximum population growth rate ($r_{max}/2$); this food concentration varied by a factor of 35 between species. There was a positive relationship between rotifer body mass and maximum population growth rate. **Because the smallest species have the lowest threshold food levels and the food levels necessary for them to attain $r_{max}/2$ are lowest, they appear well adapted to living in food-poor environments. Large species appear to be restricted to food-rich environments but may thrive there because of their high reproductive potential."** (my emphasis).

These conclusions may appear to contradict standard r-K theory, but I believe they only represent a different interpretation of the allometric relationship between body size and reproductive capacity. It has been shown (Peters 1983) that for a variety of taxa, r_{max} is scaled with body mass to the power of about -0.25 ($\propto W^{-0.25}$). Shrews unquestionably produce a greater number of offspring each year than elephants. But considered on a weight specific basis, large animals are much more productive *for their size* than small animals ($r_{max} \propto W^{0.75}$, Blueweiss, et al. 1978, Peters 1983). In comparing shrews to elephants, which differ in size by several orders of magnitude and use different resources over vastly different time scales, such an interpretation is ecologically meaningless. But for coexisting animals with body sizes that vary within an order of magnitude, this means that large species can produce more from an equivalent quantity of the same food than small species. If large species also exploit higher density prey aggregations it seems counter-intuitive to suggest they should have a lower reproductive capacity than small, 'low density' species

I believe there is a need to re-examine r-K theory as it applies to feeding guilds of coexisting animals. It has been widely observed in allometric studies that correlations between life history parameters and body size within large taxonomic groups are weakened by within-family variability (Peters 1983). Perhaps selection operates in opposing directions within and between families or habitats.

6.5.4. Another Way to Promote Differing Prey Density Thresholds and Coexistence

Up to this point, I have emphasized the relationship between predator body size and prey density thresholds and considered the implications of this relationship for animal coexistence. It is prey density thresholds, however, and not body size that appears to be the key to promoting coexistence because *differing in body size is not the only way to maintain different prey density thresholds.* The significance of body size is that it determines metabolic demands and hence food density thresholds (Stemberger and Gilbert 1985). *Two equal-sized predators can have different total metabolic demands and hence different food density thresholds if they adopt radically different foraging strategies.*

For example, Nagy et al. (1984b) and Huey et al. (1984) found that the 'sit and wait' predatory lizard *Eremias lineoocellata* (3.3 g) is physiologically and behaviourally constrained to forage at low prey densities. It spends 43% of its day foraging with a total daily metabolic demand of **544 KJ/day**, of which 292 KJ (54%) is expended on foraging. The near-equal mass (3.8 g) 'widely foraging' lizard *E. lugubris* feeds mostly on high density prey aggregations, spends only 11% of its day foraging, and has a higher total metabolic demand **(800 KJ/day)**, of which most (589 KJ, or 74%) results from its expensive foraging mode.

Thus, despite the fact these equal-sized, sympatric lizards have nearly identical standard and specific metabolic rates (Nagy et al. 1984b), they have markedly different total metabolic demands, and hence, different food density thresholds because of their different foraging behaviours. In this case, the lizards fed on different prey types with different aggregative properties instead of different densities of the same prey as in the case of murres and puffins. But in either case, differential prey density thresholds are maintained.

In other communities, it appears that both 'widely foraging' and 'sit and wait' type predators with equal body masses coexist as well as predators with differing body masses and similar foraging styles (Schoener 1971, Davidson 1977a,b, Huey and Pianka 1981, Nagy et al. 1984b). Davidson's (1977 a,b) study of foraging behaviour in coexisting ant communities is particularly illuminating:

"Analysis of the species composition of 10 local ant communities (Davidson 1977a) revealed that species with similar worker body sizes could coexist if they employed different foraging strategies, while species that were alike in both body size and foraging behaviour never coexisted, but acted as ecological replacements for one another. In addition, both foraging strategies were represented in all two-species communities." (Davidsón 1977b).

In the Atlantic alcid community, there do not appear to be any 'sit and wait' equivalents. It may be that for piscivorous alcids, prey are too patchily distributed and/or ephemeral to support the kind of 'sit and wait' type predators found in terrestrial communities. This may have been fortuitous, however, because it simplified my interpretation of relationships between body size, foraging ecology, and population dynamics in the Atlantic Alcidae.

6.5.5. Concluding Remarks

The body size distribution of coexisting species has long been of interest to ecologists. Hutchinson (1959) proposed that divergence in body size between competitors would proceed until differences in size exceeded some minimum required for coexistence. He tentatively proposed 1.3 as the critical size difference. This proposal contributed to a shift away from the Gause-Volterra concept of competitive exclusion towards questions of limiting similarity (MacArthur and Levins 1967). This led to a large number of studies that sought to explain coexistence and community structure as being mediated by competition, and permitted by differences in niche overlap.

I propose that for the piscivorous Atlantic alcids, coexistence is permitted because each species is adapted for existence on different prey densities, largely because of differences in body size. Between-species overlap in use of resources (food, time, space) may be largely a function of body size - prey density requirements and if so, interspecific competition may be unimportant in mediating coexistence (Abrams 1983). Atlantic alcids exhibit a suite of body sizes, foraging behaviours, and life-history traits which are characteristic of the prey densities to which they are adapted. As a group, they use a full spectrum of available prey densities. This maximizes efficiency of energy/biomass flow between trophic levels, and provides a mechanism for regulation of prey populations (Holling 1959).

Predator-prey equations which set competing predator population growth rates as non-linear functions of prey density (RDT models, Abrams 1983) provide a plausible model for coexistence of the Atlantic Alcidae. Interspecific differences in prey density thresholds, which may result largely from body size differences in Atlantic alcids, but which may also be maintained by differences in foraging behaviour in other feeding guilds, could provide the basis for a new synthesis of population ecology: One that integrates predation, competition, and optimal foraging theories, and suggests new interpretations of life-history and social phenomena. Differential resource thresholds among coexisting species may also provide the best explanation for the observed diversity, stability and structure of ecosystems (Steele 1974, Davidson 1977b, Tilman 1977, 1985, Stemberger and Gilbert 1985).

Literature Cited

Aarssen, L.W. 1983. Ecological combining ability and competitive combining ability in plants: Towards a general evolutionary theory of coexistence in systems of competition. Am. Nat. 122:707-731.

Abrams, P. 1983. The theory of limiting similarity. Ann. Rev. Ecol. Syst. 14:359-376.

Ainley, D.G. and R.J. Boekelheide. 1983. An ecological comparison of oceanic seabird communities of the south Pacific Ocean. Stud. Avian Biol. 8:2-23.

Ainley, D.G. and G.A. Sanger. 1979. Trophic relations of seabirds in the northeastern Pacific Ocean and Bering Sea. Pages 95-122 *in*: *Conservation of marine birds in northern North America*. Bartonek, J.C. and D.N. Nettleship (eds.). U.S. Dept. Inter. Wildl. Res. Rept. 11. 319 pp.

Akenhead, S.A., J.E. Carscadden, H. Lear, G.R. Lilly and R. Wells. 1982. Cod-capelin interactions off northeast Newfoundland and Labrador. Pages 141-148 *in*: *Multispecies approaches to fisheries management advice*. Mercer, M.C. (ed.). Can. Spec. Publ. Fish. Aquat. Sci. 59. 169 pp.

Akenhead, S.A. 1983. Mean temperatures and salinities from an ocean climate station by Newfoundland. NAFO SCR Doc. 83/V1/30, Serial No. N682, 28pp.

Anker-Nilssen, T. 1984. Lunde. Pages 40-56 *in*: *Sjofuglprosjektet 1979-1984*. Røv, N. (ed.). Direktoratet For Vilt Og Ferskvannsfisk Viltforskningen. Viltrapport 35. Trondheim, Norway. 109 pp.

Armstrong, R.A., and R. McGehee. 1976. Coexistence of species competing for shared resources. Theor. Popul. Biol. 9:317-328.

Armstrong, R.A., and R. McGehee. 1980. Competitive exclusion. Am. Nat. 115:151-170.

Ashcroft, R.E. 1976. Breeding biology and survival of puffins. Unpublished D.Phil. thesis. University of Oxford. Oxford. 246 pp.

Ashcroft, R.E. 1979. Survival rates and breeding biology of puffins on Skomer Island, Wales. Ornis Scand. 10:100-110.

Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458-473.

Ashmole, N.P. 1971. Sea bird ecology and the marine environment. Pages 223-286 in: Avian Biology Vol 1. Farner, D.S. and J.R. King (eds.) Academic Press. New York and London.

Ashmole, M.P. and M.J. Ashmole. 1967. Comparitive feeding ecology of seabirds of a tropical oceanic island. Peabody Mus. Nat. Hist. Yale Univ. Bull. No. 24. pp. 1-131.

Atkinson, D.B. and J.E. Carscadden. 1979. Biological characteristics of inshore capelin, Mallotus villosus (Müller), June-July 1977. Fish. Mar. Serv. Tech. Rep. 881, 18 pp.

Bailey, E.P. and G.H. Davenport. 1972. Die-off of common murres on the Alaska peninsula and Unimak Island. Condor 74:213-219.

Bailey, R.F.J., K.W. Able and W.C. Leggett. 1977. Seasonal and vertical distribution and growth of juvenile and adult capelin (Mallotus villosus) in the St. Lawrence estuary and western Gulf of St. Lawrence. J. Fish. Res. Board Can. 34:2030-2040.

Baird, P.A., S.A. Hatch, R.D. Jones, D.R. Nysewander and M.R. Petersen. 1983. The breeding biology and feeding ecology of marine birds in the Gulf of Alaska. Final report to the Outer Continental Shelf Environmental Assessment Program (OCSEAP). 350 pp.

Bakanev, V.S. and V.A. Ermolchev. 1982. Hydroacoustic assessment of capelin abundance in NAFO Divisions 3LNO in May-June 1981. NAFO SCR Doc. 82/VI/61, Ser. No. N554, 10 pp.

Bakke, S. and H. Bjorke. 1973. Diving observations on Barents Sea capelin at the spawning grounds off northern Norway. Fisk. Dir. Skv. Ser. Hav Unders. 16:140-147.

Baltz, D.M. and G.V. Morejohn. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. Auk 94:526-543.

Banfield, C.C. 1981. The climatic environment of Newfoundland. Pages 83-153 in: The Natural Environment of Newfoundland Past and Present. Macpherson, A.G. and J.C. Macpherson (eds.). Memorial University of Newfoundland, St. John's, Nfld. 265 pp.

Barrett, R.T., T. Anker-Nilssen, F. Rikardsen, K. Valde, N. Røv and W. Vader. 1986. The food, growth and fledging success of Norwegian puffin chicks Fratercula arctica in 1980-1983. Ornis Scand. in press.

Bédard, J. 1969. Adaptive radiation in Alcidae. Ibis 111:189-198.

Bekoff, M., T.J. Daniels and J.L. Gittleman. 1984. Life history patterns and the comparative social ecology of carnivores. Ann. Rev. Ecol. Syst. 15:191-232.

Belopol'skii, L.O. 1957. Ecology of sea colony birds of the Barents Sea. (English translation 1961: Israel program for scientific translations). 346 pp.

Birkhead, T.R. 1976. Breeding biology and survival of guillemots Uria aalge. Unpublished D.Phil. thesis, University of Oxford. Oxford. 204 pp.

Birkhead, T.R. 1977a. The effect of habitat and density on breeding success in the common guillemot Uria aalge. J. Anim. Ecol. 46:751-764.

Birkhead, T.R. 1977b. The adaptive significance of the nestling period of guillemots Uria aalge. Ibis 119:544-549.

Birkhead, T.R. 1985. Coloniality and social behaviour in the Atlantic Alcidae. Pages 355-382 in: The Atlantic Alcidae, Nettleship, D.N. and T.R. Birkhead. (eds.). Academic Press. Orlando. 574 pp.

Birkhead, T.R. and R.W. Furness. 1985. Regulation of seabird populations. Brit. Ecol. Soc. Symp. 21:145-167

Birkhead, T.R. and M.P. Harris. 1985. Ecological adaptations for breeding in Atlantic Alcidae. Pages 205-231 in: The Atlantic Alcidae, Nettleship, D.N. and T.R. Birkhead. (eds.). Academic Press. Orlando. 574 pp.

Birkhead, T.R. and D.N. Nettleship. 1981. Reproductive biology of thick-billed murres Uria lomvia: an inter-colony comparison. Auk 98:258-269.

Birkhead, T.R. and D.N. Nettleship. 1987a. Ecological relationships between common murres Uria aalge and thick-billed murres U. lomvia at the Gannet Islands, Labrador: I. Morphometrics and timing of breeding. Can. J. Zool. 65: in press.

Birkhead, T.R. and D.N. Nettleship. 1987b. Ecological relationships between common murres Uria aalge and thick-billed murres U. lomvia at the Gannet Islands, Labrador: II. Breeding success and site characteristics. Can. J. Zool. 65: in press.

Birkhead, T.R. and D.N. Nettleship. 1987c. Ecological relationships between common murres Uria aalge and thick-billed murres U. lomvia at the Gannet Islands, Labrador: III. Feeding ecology of the young. Can. J. Zool. 65: in press.

Blake, B.F. 1984. Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. J. Exp. Mar. Ecol. 76:89-103.

Blake, B.F., M.L. Tasker, P.H. Jones and T.J. Dixon. 1984. Distribution of seabirds in the North Sea. Final report of the Nature Conservancy Council's Seabirds at Sea Team, Nov. 1979- Nov. 1982. Nature Conservancy Council, Edinburgh. 443 pp.

Blueweiss L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. Oecologia 37:257-272.

Borovkov, V.A. and S.M. Kovalyov. 1977. Some data on the hydrological conditions in the Great Newfoundland Bank area during capelin spawning. Tr. Polyaru. Nauchno. Issled. Proektm. Inst. Morsk. Rybn. Khoz. Okeanogr. 37:61-68, 1976. (English transl. for Dept. of Fish. and Environ., St. John's, Nfld., 1977, Transl. Ser. No. 4067).

Bradstreet, M.S.W. 1980. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. Can. J. Zool. 58:2120-2140.

Bradstreet, M.S.W. 1983. The feeding ecology of alcids near the Gannet Islands, Labrador. Unpublished report by LGL Ltd., Toronto, for Petro-Canada Exploration, Calgary. 117 pp.

Bradstreet, M.S.W. and R.G.B. Brown. 1985. Feeding ecology of the Atlantic Alcidae. Pages 264-318 in: The Atlantic Alcidae, Nettleship, D.N. and T.R. Birkhead. (eds.). Academic Press. Orlando. 574 pp.

Briggs, K.T., K.F. Dettman, D.B. Lewis and W.B. Tyler. 1984. Phalarope feeding in relation to autumn upwelling off California. Pages 51-62 in: Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Brown, M.B. 1983. Two-way and multiway frequency tables, measures of association and the log-linear model. Pages 143-206 in: BMDP statistical software. Dixon, W.J. (ed.). Univ. Calif. Press, Berkeley. 734 pp.

Brown, R.G.B. 1980. Seabirds as marine animals. Pages 1-39 in: Behaviour of Marine Animals Vol. 4. Burger, J., B.L. Olla and H.E. Winn (eds.). Plenum Press. New York. 515 pp.

Brown, R.G.B. 1985. The Atlantic Alcidae at sea. Pages 383-426 in: The Atlantic Alcidae, Nettleship, D.N. and T.R. Birkhead (eds.). Academic Press. Orlando. 574 pp.

Brown, R.G.B. and D.N. Nettleship. 1984. Capelin and seabirds in the northwest Atlantic. Pages 184-194 in: Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Brown, R.G.B., S.P. Barker, D.E. Gaskin, and M.R. Sandeman. 1981. The foods of great and sooty shearwaters Puffinus gravis and P. griseus in eastern Canadian waters. Ibis 123: 19-30.

Brown, R.G.B., Nettleship, D.N., Germain, P., Tull, C.E., and Davis, T. 1975. Atlas of Eastern Canadian Seabirds, Canadian Wildlife Service, Ottawa, 220 pp.

Burger, A.E. and J. Cooper. 1984. The effects of fisheries on seabirds in South Africa and Namibia. Pages 150-160 in: Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Butler, G.J. 1980. Coexistence in predator-prey systems. Pages 199-207 in: Modeling and Differential Equations in Biology. T.A. Burton (ed.). Marcel Dekker. New York.

Cairns, D.K. 1984. The foraging ecology of the black guillemot (Cepphus grylle). Unpublished Ph.D. thesis, Carleton University. Ottawa. 206 pp.

Cairns, D.K., K.A. Bredin, and W.A. Montevecchi. 1987. Activity budgets and foraging ranges of breeding common murres. Auk 104: in press.

Calder, W.A. 1983. Ecological scaling: Mammals and birds. Ann. Rev. Ecol. Syst. 14:213-230.

Carpenter, F.L. 1978. A spectrum of nectar-eater communities. Am. Zool. 18:809-819.

Carscadden, J.E. 1978. The capelin, Mallotus villosus, population spawning on the southeast shoal of the Grand Bank, 1976. ICNAF Sel. Papers 3: 61-71.

Carscadden, J.E. 1983. Capelin as a forage species: A review of selected studies. NAFO SCR Doc. 83/IX/72, Ser. No. N738.

Carscadden, J.E. 1984. Capelin (Mallotus villosus) in the northwest Atlantic, Pages 170-183 in: Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Carscadden, J.E., G.H. Winters, and D.S. Miller. 1981. Assessment of the Division 3L capelin stock, 1967-1980, using SCAM. NAFO Scr. Doc. No. 3, Serial No. N267.

Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. Theor. Pop. Biol. 9:129-136.

Clutton-Brock, T.H., and P.H. Harvey. 1977. Primate ecology and social organization. J. Zool. Lond. 183:1-39.

Clutton-Brock, T.H., S.D. Albon and P.H. Harvey. 1980. Antlers, body size and breeding group size in the Cervidae. Nature (London) 285:565-567.

Cody, M.L. 1973. Coexistence, coevolution, and convergent evolution in seabird communities. Ecol. 54: 31-44.

Cody, M.L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey. 318 pp.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. Am. Nat. 122:661-696.

Cook, R.M. and B.J. Cockrell. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. J. Anim. Ecol. 47:529-547.

Corkhill, P. 1973. Food and feeding ecology of puffins. Bird Study 20:207-220.

Crawford, R.J.M. and P.A. Shelton. 1978. Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. Biol. Conserv. 14:85-109.

Crook, J.H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. Lond. 14:181-218.

Croxall, J.P. 1984. Seabirds. Pages 533-618 in: Antarctic Ecology Vol. 2. Academic Press. London.

Croxall, J.P. and P.A. Prince. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biol. J. Linnaean. Soc. 14:103-131.

Croxall, J.P. and M. Pilcher. 1984. Length-frequency distribution and sex ratio of krill eaten by Antarctic fur seals *Arctocephalus gazella* at South Georgia. Bull. J. Linn. Soc. 14:103-131.

Croxall, J.P., P.A. Prince and C. Ricketts. 1985. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. Pages 516-533 *in*: *Antarctic Nutrient Cycles and Food Webs*. Siegfried, W.R., P.R. Condy and R.M. Laws (eds.). Springer-Verlag. Berlin.

Csandy, G.T. 1982. *Circulation in the Coastal Ocean*. D. Reidel Publ. Boston. 279 pp.

Davidson, D.W. 1977a. Species diversity and community organization in desert seed-eating ants. Ecol. 58:711-724.

Davidson, D.W. 1977b. Foraging ecology and community organization in desert seed-eating ants. Ecol. 58:725-737.

Devold, F., N. Devold and T. Westergaard. 1972. Loddeundersokelser ost av Labrador og Newfoundland i juli-august 1971 (Capelin investigations east of Labrador and Newfoundland in July-August 1971). Fisk. Gang 58(3):49-55. (Transl. from Norwegian by Fish. Res. Board Can. Transl. Ser. No. 2124, 1973).

Diamond, A.W. 1984. Feeding overlap in some tropical and temperate seabird communities. Stud. Avian Biol. 8:24-46.

Drent, R.H., and S. Daan. 1980. The prudent parent: Energetic adjustments in avian breeding. Ardea 68:225-252.

Dunbar, M.J. 1968. *Ecological Developments in Polar Regions: A Study in Evolution*. Prentice-Hall. Englewood Cliffs, New Jersey. 119 pp.

Edington, J.M. and M.A. Edington. 1983. Habitat partitioning and antagonistic behaviour amongst the birds of a West African scrub and plantation plot. Ibis 125:74-89.

Eliassen, J.E. and P. Grotnes. 1985. Feeding habits of cod (*Gadus morhua*) in Balsfjorden, northern Norway in relation to the distribution and availability of potential food species. ICES Demersal fish committee report C.M. 1985/G:58, 15 pp.

Erwin, M. 1978. Coloniality in terns: The role of social feeding. Condor 80:211-215.

Evans, P.G.H. and D.N. Nettleship. 1985. Conservation of the Atlantic Alcidae. Pages 427-488 in: The Atlantic Alcidae, Nettleship, D.N. and T.R. Birkhead (eds.). Academic Press. Orlando. 574 pp.

Eveleigh, E.S. and D.A. Chant. 1981a. Experimental studies on acarine predator-prey interactions: effects of predator age and feeding history on prey consumption and the functional response (Acarina: Phytoseiidae). Can. J. Zool. 59:1387-1406.

Eveleigh, E.S. and D.A. Chant. 1981b. Experimental studies on acarine predator-prey interactions: the numerical response of immature and adult predators (Acarina: Phytoseiidae). Can. J. Zool. 59:1407-1418.

Eveleigh, E.S. and D.A. Chant. 1981c. The feeding and searching behaviour of two species of phytoseiid mites, Phytoseiulus persimilis Athias-Henriot and Amblyseius degenerans (Berlese), at different prey densities (Acarina: Phytoseiidae). Can. J. Zool. 59:1419-1430.

Eveleigh, E.S. and D.A. Chant. 1982a. Experimental studies on acarine predator-prey interactions: the effects of predator density on prey consumption, predator searching efficiency, and the functional response to prey density (Acarina: Phytoseiidae). Can. J. Zool. 60:611-629.

Eveleigh, E.S. and D.A. Chant. 1982b. Experimental studies on acarine predator-prey interactions: the effects of predator density on immature survival, adult fecundity and immigration rates, and the numerical response to prey density (Acarina: Phytoseiidae). Can. J. Zool. 60:630-638.

Eveleigh, E.S. and D.A. Chant. 1982c. Experimental studies on acarine predator-prey interactions: the response of predators to prey distribution in an homogeneous area (Acarina: Phytoseiidae). Can. J. Zool. 60:639-647.

Eveleigh, E.S. and D.A. Chant. 1982d. The searching behaviour of two species of phytoseiid mites, Phytoseiulus persimilis Athias-Henriot and Amblyseius degenerans (Berlese), in relation to the density and distribution of prey in an homogeneous area (Acarina: Phytoseiidae). Can. J. Zool. 60:648-658.

Eveleigh, E.S. and D.A. Chant. 1982e. Experimental studies on acarine predator-prey interactions: the distribution of search effort and the functional and numerical responses of predators in a patchy environment (Acarina: Phytoseiidae). Can. J. Zool. 60:2979-2991.

Eveleigh, E.S. and D.A. Chant. 1982f. Experimental studies on acarine predator-prey interactions: effects of temporal changes in the environment on searching behaviour, predation rates, and fecundity (Acarina: Phytoseiidae). Can. J. Zool. 60:2992-3000.

Eveleigh, E.S. and D.A. Chant. 1982g. Experimental studies on acarine predator-prey interactions: distribution of search effort and predation rates of a predator population in a patchy environment (Acarina: Phytoseiidae). Can. J. Zool. 60:3001-3009.

Farmer, G.H. 1981. The cold ocean environment of Newfoundland. Pages 56-82 in: The Natural Environment of Newfoundland Past and Present. Macpherson, A.G. and J.C. Macpherson (eds.). Memorial University of Newfoundland. St. John's. 265 pp.

Feinsinger, P., L.E. Swarm and J.A. Wolfe. 1985. Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. Ecol. Monogr. 55:1-28.

Folse, L.J. 1982. An analysis of avifauna-resource relationships on the Serengeti plains. Ecol. Monogr. 52:111-127.

Forbes, S.T. and O. Nakken. 1972. Manual of methods for fisheries resource survey and appraisal, Part 2. The use of acoustic instruments for fish detection and abundance estimation. FAO Manuals in Fisheries Science No. 5, 138 pp.

Fowler, C.W. 1981. Density dependence as related to life history strategy. Ecol. 62:602-610.

Frank, K.T. and W.C. Leggett. 1981. Wind regulation of emergence times and early larval survival in capelin (Mallotus villosus). Can. J. Fish. Aquat. Sci. 38:215-223.

Frank, K.T. and W.C. Leggett. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (Mallotus villosus). Can. J. Fish. Aquat. Sci. 39: 991-1003.

Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47:39-53.

Furness, R.W. 1984. Seabird - fisheries relationships in the northeast Atlantic and North Sea. Pages 162-169 in: Marine Birds: Their Feeding Ecology and

Commercial Fisheries Relationships. Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Furness, R.W. and R.T. Barrett. 1985. The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scand. 16:305-313.

Furness, R.W. and T.R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 331: 655-656.

Fry, C.H. 1972. The social organization of bee-eaters (Meropidae) and co-operative breeding in hot-climate birds. Ibis 114:1-14.

Fry, C.H. 1984. *The Bee-eaters*. T and A D Poyser. Calton. 304 pp.

Gaston, A.J. 1985a. The diet of thick-billed murre chicks in the eastern Canadian Arctic. Auk 102:727-734.

Gaston, A.J. 1985b. Energy invested in reproduction by thick-billed murres *Uria lomvia*. Auk 102:447-458.

Gaston, A.J. and D.N. Nettleship. 1981. *The Thick-billed Murres of Prince Leopold Island*. Can. Wildl. Ser. Monograph No. 6. Ottawa. 350 pp.

Gaston, A.J. and D.G. Noble. 1985. The diet of thick-billed murres (*Uria lomvia*) in west Hudson Strait and northeast Hudson Bay. Can. J. Zool. 63:1148-1160.

Gaston, A.J., J.G. Chapdelaine and D.G. Noble. 1983. The growth of thick-billed murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. Can. J. Zool. 61:2465-2475.

Gause, G.F. 1934. *The Struggle for Existence*. Hafner, New York, (reprinted by William and Wilkins, Baltimore, Md.). 163 pp.

Goss-Custard, J.D. 1970. The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. J. Anim. Ecol. 39:91-113.

Goss-Custard, J.D. 1977a. The energetics of prey selection by redshank *Tringa totanus* (L.), in relation to prey density. J. Anim. Ecol. 46:1-19.

Goss-Custard, J.D. 1977b. Predator responses and prey mortality in redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). J. Anim. Ecol. 46:21-35.

Goss-Custard, J.D. 1977c. Responses of redshank, (Tringa totanus), to the absolute and relative densities of two prey species. J. Anim. Ecol. 46:867-874.

Goudie, R.I. 1984. Comparative ecology of common eiders, black scoters, oldsquaws, and harlequin ducks wintering in southeastern Newfoundland. Unpublished M.Sc. thesis, University of Western Ontario, London. 137 pp.

Green, R.F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. Theor. Pop. Biol. 18:244-256.

Haney, J.C. 1986. Seabird segregation at Gulf Stream frontal eddies. Mar. Ecol. Prog. Ser. 28:279-285.

Harestad, A.S. and F.L. Bunnell. 1979. Home range and body weight - a reevaluation. Ecol. 60:389-402.

Harris, M.P. 1978. Supplementary feeding of young puffins Fratercula arctica. J. Anim. Ecol. 47:15-23.

Harris, M.P. 1970. Differences in the diet of British auks. Ibis 112:540-541.

Harris, M.P. 1984. The Puffin. T. and A.D. Poyser, Calton. 224 pp.

Harris, M.P. and T.R. Birkhead. 1985. Breeding ecology of the Atlantic Alcidae. Pages 155-204 in: The Atlantic Alcidae. Nettleship, D.N. and T.R. Birkhead (eds.). Academic Press. Orlando. 574 pp.

Harris, M.P. and J.R.G. Hislop. 1978. The food of young puffins. J. Zool. (Lond.) 185:213-236.

Harris, M.P. and S. Wanless. 1985. Fish fed to young guillemots Uria aalge and used in display on the Isle of May, Scotland. J. Zool. (Lond.) 207:441-458.

Harris, M.P. and S. Wanless. 1986. The food of young razorbills on the Isle of May and a comparison with that of young guillemots and puffins. Ornis Scand. 17:41-46.

Harrison, C.S., T.S. Hida and M.P. Seki. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. No. 85. 71 pp.

Hassell, M.P., and R.M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol. 43:567-594.

Hassell, M.P., J.H. Lawton, and J.R. Beddington. 1976. The components of arthropod predation: I. The prey death-rate. J. Anim. Ecol. 45:135-164.

Hassell, M.P., J.H. Lawton, and J.R. Beddington. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. J. Anim. Ecol. 46:249-262.

Hedgren, S. 1976. Om sillgrisslans Uria aalge foda vid Stora Karlso. Var Fagelvarld 35:287-290.

Heller, R. and M. Milinski. 1979. Optimal foraging of sticklebacks on swarming prey. Anim. Behav. 27:1127-1141.

Henderson, R.J., J.R. Sargent, and C.C.E. Hopkins. 1984. Changes in the content and fatty acid composition of lipid in an isolated population of the capelin Mallotus villosus during sexual maturation and spawning. Mar. Biol. 78:255-263.

Hislop, J.R.G. and M.P. Harris. 1985. Recent changes in the food of young Puffins Fratercula arctica on the Isle of May in relation to fish stocks. Ibis 127:234-239.

Hollibaugh, J.T. and J.A. Booth. 1981. Observations on the dynamics and distribution of phytoplankton and primary production on the Grand Banks. Oceanography Study, Report for Mobil Oil Canada, Ltd. 68 pp.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91:293-320.

Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Ent. Soc. Can. 45:1-60.

Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Mem. Ent. Soc. Can. 48:1-86.

Horn, H.S. 1966. Measurement of overlap in comparative ecological studies. Am. Nat. 100:419-424.

Hudson, P.J. 1979. The parent-chick fledging relationship of the puffin, Fratercula arctica. J. Anim. Ecol. 48:889-898.

Hudson, P.J. 1983. The variation and synchronization of daily weight increments of puffin chicks Fratercula arctica. Ibis 125:557-561.

Hudson, P.J. 1985. Population parameters for the Atlantic Alcidae. Pages 233-261 in: The Atlantic Alcidae, Nettleship, D.N. and T.R. Birkhead (eds.). Academic Press.. Orlando. 574 pp.

Huey, R.B. and E.R. Pianka. 1981. Ecological consequences of foraging mode. Ecol. 62:991-999.

Huey, R.B., A.F. Bennett, H. John-Alder, and K.A. Nagy. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. Anim. Behav. 32:41-50.

Huffaker, C.B. 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.

Hunt, G.L., Z.A. Eppley and D.C. Schneider. 1986. Reproductive performance of seabirds: the importance of population and colony size. Auk 103: 306-317.

Hunte, W., R.A. Myers and R.W. Doyle. 1985. Bayesian mating decisions in an amphipod, Gammarus lawrencianus Bousfield. Anim. Behav. 33:366-372.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93:145-159.

Hutchinson, G.E. 1978. An Introduction to Population Ecology. Yale University Press. London. 260 pp.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven. 302 pp.

Iwasa, Y., M. Higashi and N. Yamamura. 1981. Prey distribution as a factor determining the choice of optimal foraging stategy. Am. Nat. 117:710-723.

Jangaard, P.M. 1974. The capelin (Mallotus villosus): biology, distribution, exploitation, utilization, and composition. Bull. Fish. Res. Board Can. 186: 70 pp.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. Behav. 48:215-267.

Johnson, L.K. and S.P. Hubbell. 1975. Contrasting foraging strategies and coexistence of two bee species on a single resource. Ecol. 56:1398-1406.

Kaftanovskii, Y.M. 1938. Colony nesting of the murre and factors causing the death of eggs and nestlings. Zool Zhur. 17:695-705.

Kagel, J.H., L. Green and T. Caraco. 1986. When foragers discount the future: constraint or adaption? Anim. Behav. 34:271-283.

Kamil, A.C. 1983. Optimal foraging theory and the psychology of learning. Amer. Zool. 23:291-302.

Kaplan, J.L. and J.A. Yorke. 1977. Competitive exclusion and nonequilibrium coexistence. Am. Nat. 111:1032-1036.

Kaufmann, J.H. 1974. The ecology and evolution of social organization in the kangaroo family (Macropodidae). Amer. Zool. 14:51-62.

Koch, A.L. 1974. Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. J. Theor. Biol. 44:387-395

Kooyman, G.L., R.W. Davis, J.P. Croxall, and D.P. Costa. 1982. Diving depths and energy requirements of king penguins. Science 217:726-727.

Krasnow, L.D. and G.A. Sanger. 1982. Feeding ecology of marine birds in the nearshore waters of Kodiak Island. Final report to the Outer Continental Shelf Environmental Assessment Program. 113 pp.

Krebs, J.R., T. Ericksen, M.I. Webber, and E.L. Charnov. 1977. Optimal prey selection in the great tit (Parus major). Anim. Behav. 25:30-38.

Krebs, J.R. 1978. Optimal foraging : Decision rules for predators. Pages 26-63 in: Behavioural Ecology. Krebs, J.R. and N.B. Davies (eds.). Sinauer Associates. Sunderland.

Kruuk, H. 1975. Functional aspects of social hunting by carnivores. Pages 119-141 in: Function and Evolution in Behaviour. Baerends, G., C. Beer and A. Manning (eds.) Clarendon Press. Oxford. 393 pp.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press. Oxford. 343 pp.

Lack, D. 1966. Population Studies of Birds. Oxford University Press. London. 341 pp.

Lack, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Proc. 14th Intern. Ornithol. Cong. 14:3-42.

Lear, W.H., A.M. Fleming, and R. Wells. 1980. Results of small cod surveys in eastern Newfoundland during 1959-64. NAFO SCR Doc. 80/IX/144. Ser. No. N218. 12 pp.

Leggett, W.C., K.T. Frank and J.E. Carscadden. 1984. Meteorlogical and hydrographic regulation of year-class strength in capelin (Mallotus villosus). Can. J. Fish. Aqua. Sci. 41: 1193-1201.

Levins, R. 1979. Coexistence in a variable environment. Am. Nat. 114:765-783.

Lid, G. 1981. Reproduction of the puffin on Røst in the Lofoten Islands in 1964-1980. Fauna Norv. Ser. C, Cinclus. 4:30-39.

Lima, S.L. 1983. Downy woodpecker foraging behaviour: foraging by expectation and energy intake rate. Oecologia 58:232-237.

Lindstedt, S.L., B.J. Miller, and S.W. Buskirk. 1986. Home range, time, and body size in mammals. Ecol. 67:413-418.

Lotka, A.J. 1925. Elements of Physical Biology. Williams and Wilkins Co., Baltimore. 460 pp.

Luka, G.I. 1979. The use of hydrometeorological factors in rapid exploratory fishing for Barents Sea capelin. Canadian Transl. of Fish. and Aq. Sci., No. 4581, Dept. of Fish. and Oceans, 12 pp.

MacArthur, R. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecol. 39:599-619.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101:377-385.

MacArthur, R. and E.R. Pianka. 1966. On the optimal use of a patchy environment. Am. Nat. 100:603-609.

MacArthur, R. and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press. Princeton, New Jersey. 203 pp.

Madsen, E.J. 1957. On the food habits of some fish-eating birds in Denmark. Danish Rev. Game Biol. 3:19-83.

Mahoney, S. 1979. Breeding biology and behaviour of the common murre (Uria aalge aalge (Pont.)) on Gull Island, Newfoundland. Unpublished M.Sc. thesis, Memorial University of Newfoundland, St. John's. 155 pp.

Matthews, D.R. 1983. Feeding ecology of the common murre, Uria aalge, off the Oregon coast. Unpublished M.Sc. thesis, University of Oregon, Charleston. 108 pp.

Maunder, J.E. 1971. The breeding biology of the black-legged kittiwake (Rissa tridactyla L.) in Newfoundland. Unpublished B.Sc. (Hons.) thesis. Memorial University of Newfoundland, St. John's. 59 pp.

Maurer, B.A. 1984. Interference and exploitation in bird communities. Wilson Bull. 96:380-395.

Miller, D.S. 1985. Capelin (Mallotus villosus) hydroacoustic surveys in NAFO divisions 3L and 3LNO in 1984. NAFO Scr. Doc. 85/73. 7 pp.

Miller, D.S. and J.E. Carscadden. 1979. An acoustic estimate of capelin biomass in ICNAF divisions 2J and 3K, October 1978. ICNAF Res. Doc. 79/II/34, Ser. No. 5360, 8 pp.

Miller, D.S., B.S. Nakashima and J.E. Carscadden. 1982. Capelin acoustic surveys in NAFO divisions 2J+3K, 3LNO, and 3L, 1981-1982. NAFO Scr. Doc. 82/VI/54. 12 pp.

Mitchell, E. 1973. Draft report on humpback whales taken under special scientific permit by eastern Canadian land stations, 1969-1971. Rep. Int. Whal. Comm. 23: 138-154.

Mitchell, E. 1975. Trophic relationships and competition for food in northwest Atlantic whales. Proc. Can. Soc. Zool. Ann. Meeting 1974: 123-133.

Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. 1981. Ecol. 62:1370-1386.

Montevecchi, W.A. and J.F. Piatt. 1984. Composition and energy contents of mature inshore spawning capelin (Mallotus villosus): Implications for seabird predators. Comp. Biochem. Biophys. 78A: 15-20.

Montevecchi, W.A. and J.M. Porter. 1980. Parental investments by seabirds at the breeding area with emphasis on northern gannets (Morus bassanus). Pages 323-365 in: Behaviour of Marine Animals. Vol. 4. Burger, J., B.L. Olla, and H.E. Winn (eds.). Plenum Publ. Corp. New York. 515 pp.

Montevecchi, W.A., V.L. Birt and D.K. Cairns. 1986. Dietary changes of seabirds associated with local fisheries failures. Unpubl. ms.

Morse, D.H. 1974. Niche breadth as a function of social dominance. Am. Nat. 108:818-830.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ. Ser. E. Biol. 3:65-80.

Murdoch, W.W. and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. 9:1-125.

Myrberget, S. 1962. Undersokelser over forplantnings biologien til lunde (Fratercula arctica (L.)). Egg, ruging og under. Meddelelser fra Statens Viltundersokelser 2(11):1-51.

Nakashima, B.S. 1983. Differences in mean lengths and percentages of females in capelin schools. NAFO SCR Doc. 83/VI/46, Serial No. N704, 5pp.

Nagy, K.A., W.R. Siegfried, and R.P. Wilson. 1984a. Energy utilization by free-ranging jackass penguins, Spheniscus demersus. Ecol. 65:1648-1655.

Nagy, K.A., R.B. Huey, and A.F. Bennett. 1984b. Field energetics and foraging mode of Kalahari lacertid lizards. Ecol. 65:588-596.

Nettleship, D.N. 1972. Breeding success of the common puffin (Fratercula arctica L.) on different habitats at Great Island, Newfoundland. Ecol. Monogr. 42:239-268.

Nettleship, D.N. and T.R. Birkhead (eds.). 1984. The Atlantic Alcidae. Academic Press. Orlando. 574 pp.

Nettleship, D.N. and P.G.H. Evans. 1985. Distribution and status of the Atlantic Alcidae. Pages 53-154 in: The Atlantic Alcidae, Nettleship, D.N. and T.R. Birkhead (eds.). Academic Press. Orlando. 574 pp.

Newton, I. 1979. Population ecology of raptors. T and A D Poyser, Berkhamsted. 399 pp.

Oaten, A. 1977. Optimal foraging in patches: a case for stochasticity. Theor. Pop. Biol. 12:263-285.

Obst, B.S. 1985. Densities of antarctic seabirds at sea and the presence of the krill Euphausia superba. Auk 102:540-549.

Ogi, H. 1980. The pelagic feeding ecology of thick-billed murres in the North Pacific, March-June. Bull. Faculty Fish., Hokkaido University 31:50-72.

Ogi, H. and Tsujita, T. 1973. Preliminary examination of stomach contents of murres (Uria spp.) from the eastern Bering Sea and Bristol Bay, June-August 1970 and 1971. Jap. J. Ecol. 23:201-209.

Ogi, H. and Tsujita, T. 1977. Food and feeding habits of common murre and thick-billed murre in the Okhotsk Sea in summer, 1972 and 1973. Res. Inst. North Pac. Fish. Spec. Vol. pp. 459-517.

Ollason, J.G. 1980. Learning to forage - optimally? Theor. Pop. Biol. 18:44-56.

Orians, G.H. and N.E. Pearson. 1977. On the theory of central place foraging. Pages 155-177 in: Analysis of ecological systems. Horn, D.J., G.R. Stairs, and R.D. Mitchell (eds.). Ohio State University Press. Columbus.

Pearson, T.H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

Peters, R.H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge. 329 pp.

Petersen, A. 1981. Breeding biology and feeding ecology of black guillemots. Unpublished D.Phil. thesis. Oxford University, Oxford. 378 pp.

Pianka, E.R. 1970. On r- and K-selection. Am. Nat. 104:592-597.

Pianka, E.R. 1978. Evolutionary Ecology. Harper and Row, New York. 397 pp.

Piatt, J.F. and R.L. McLagan. 1987. Common murre Uria aalge attendance patterns at Cape St. Mary's, Newfoundland. Can. J. Zool. in press.

Piatt, J.F. and D.N. Nettleship. 1985. Diving depths of four alcids. Auk 102: 293-297.

Piatt, J.F. and D.N. Nettleship. 1987. Incidental catch of marine birds and mammals in fishing nets off Newfoundland, Canada. Mar. Poll. Bull. in press.

Piatt, J.F., R.D. Elliot and A. MacCharles. 1985. Marine birds and oil pollution in Newfoundland, 1951-1984. Nfld. Inst. Cold Ocean Sci. Ms. Rep. No. 105.

Piatt, J.F., Nettleship, D.N., and Threlfall, W. 1984. Net-mortality of common murres and Atlantic puffins in Newfoundland, 1951-1981. Pp. 196-206 in: Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Pielou, E.C. 1977. Mathematical Ecology. John Wiley. New York. 385 pp.

Pierotti, R.J. 1979. The reproductive behaviour and ecology of the Herring Gull in Newfoundland. Unpublished Ph.D. thesis. Dalhousie University, Halifax. 134 pp.

Pitcher, T.J. 1980. Some ecological consequences of fish school volumes. Freshwater Biol. 10: 539-544.

Pitcher, T.J. and B.L. Partridge. 1979. Fish school density and volume. Mar. Biol. 54: 383-394.

Platt, T. 1972. Local phytoplankton abundance and turbulence. Deep Sea Research 19:183-187.

Porter, J.M. and S.G. Sealy. 1981. Dynamics of seabird multispecies feeding flocks: chronology of flocking in Barkley Sound, British Columbia, in 1979. Col. Waterbirds 4:104-113.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15:523-575.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quar. Rev. Biol. 52:137-154.

Rapport, D.J. 1980. Optimal foraging for complementary resources. Am. Nat. 116:324-346.

Readshaw, J.L. 1973. The numerical response of predators to prey density. J. Appl. Ecol. 10:342-351.

Reay, P.J. 1970. Synopsis of biological data on North Atlantic sandeels of the genus Ammodytes. FAO Fisheries Synopsis No. 82. 42 pp.

Reddin, D.G. and J.E. Carscadden. 1981. Salmon - capelin interactions. CAFSAC Res. Doc. 81/2. 33 pp.

Ripley, S. 1984. Environmental grain, Niche diversification and feeding behaviour in primates. Pages 33-72 in:Food Acquisition and Processing in Primates. Chivers, D.J., B.A. Wood and A. Bilsborough (eds.) Plenum Press. London.

Roll, H.U. 1965. Physics of the Marine Atmosphere. Academic Press. New York. 426 pp.

Rosenzweig, M.L. 1981. A theory of habitat selection. Ecol. 62:327-335.

Rosenzweig, M.L., and R.H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. Am. Nat. 97:209-223.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.). J. Anim. Ecol. 39:619-668.

Saetre, R. and J. Gjosaeter. 1975. Ecological investigations on the spawning grounds of the Barents Sea capelin. Fisk. Div. Skr. Ser. Hav Unders. 16:203-227.

Safina, C. and J. Burger. 1985. Common tern foraging: seasonal trends in prey fish densities and competition with bluefish. Ecol. 66:1457-1463.

Sanger, G.A. 1983. Diets and food web relationships of seabirds in the Gulf of Alaska and adjacent marine regions. Final report to the Outer Continental Shelf Environmental Assessment Program (OCSEAP). 130 pp.

Sargeant, D.E. 1973. Feeding, growth, and productivity of Northwest Atlantic seals. J. Fish. Res. Board Can. 30: 17-29.

Schneider, D.C. 1982. Fronts and seabird aggregations in the southeastern Bering Sea. Mar. Ecol. Prog. Ser. 10:101-103.

Schneider, D.C. and G.L. Hunt. 1984. A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska. Pages 86-95 *in*: *Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships.* Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Schneider, D.C. and D.C. Duffy, 1985. Scale-dependent variability in seabird abundance. Mar. Ecol. Prog. Ser. 25:211-218.

Schneider, D.C. and J.F. Piatt. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Mar. Ecol. Prog. Ser. 32:237-246.

Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecol. 49:123-141.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

Schoener, T.W. 1982. The controversy over interspecific competition. Am. Sci. 70:586-595.

Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. 122:240-285.

Scott, J.M. 1973. Resource allocation in four syntopic species of marine diving birds. Unpublished Ph.D. thesis. Oregon State University, Corvallis. 97 pp.

Simberloff, D. 1982. The status of competition theory in ecology. Ann. Zool. Fennici 19:241-253.

Smith, J.N.M. and R. Dawkins. 1971. The hunting behaviour of individual great tits in relation to spatial variations in their food density. Anim. Behav. 19:695-706.

Smith, J.N.M. and H.P.A. Sweatman. 1974. Food-searching behavior of titmice in patchy environments. Ecol. 55:1216-1232.

Soloman, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-32.

Springer, A.M., D.G. Roseneau, E.C. Murphy, and M.I. Springer. 1984. Environmental controls of marine food webs: food habits of seabirds in the eastern Chukchi Sea. Can. J. Fish. Aquat. Sci. 41:1202-1215.

Stearns, S.C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos 41:173-187.

Steele, J.H. 1974. The Structure of Marine Ecosystems. Harvard Univ. Press. Cambridge, Mass. 128 pp.

Steenhof, K. and M.N. Kochert. 1985. Dietary shifts of sympatric buteos during a prey decline. Oecologia 66:6-16.

Stemberger, R.S., and J.J. Gilbert. 1985. Body size, food concentration, and population growth in planktonic rotifers. Ecol. 66:1151-1159.

Stettenheim, P. 1959. Adaptations for underwater swimming in the common murre (Uria aalge), Unpublished Ph.D. thesis, University of Michigan, Ann Arbor. 295 pp.

Stewart, F.M., and B.R. Levin. 1973. Partitioning of resources and the outcome of interspecific competition: A model and some general considerations. Am. Nat. 107:171-198.

Stubbs, M. 1977. Density dependence in the life cycles of animals and its importance in K- and r-strategies. J. Anim. Ecol. 46:677-688.

Swartz, L.G. 1964. Investigation of sea-cliff birds, Cape Thompson, Alaska. Project Chariot- Final Report. University of Alaska. 128 pp.

Swennen, C. and P. Duiven. 1977. Size of food objects of three fish-eating seabird species: Uria aalge, Alca torda and Fratercula arctica (Aves, Alcidae). Netherlands J. Sea Res. 11:92-98.

Taylor, L.R. 1984. Assessing and interpreting the spatial distributions of insect populations. Ann. Rev. Entomol. 29:321-357.

Taylor, W.D. 1978. Maximum growth rate, size, and commonness in a community of bactivorous ciliates. Oecologia (Berl.). 36:263-272.

Templeman, W. 1948. The life history of the capelin (Mallotus villosus O.F. Müller) in Newfoundland waters. Nfld. Gov. Lab. Bull. 17. 151 pp.

Templeman, W. 1966. Marine resources of Newfoundland. Fish. Res. Bd. Can. Bull. No. 154. 170 pp.

Terbough, J. and J.M. Diamond. 1970. Niche overlap in feeding assemblages of New Guinea birds. Wilson Bull. 82:29-52.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecol. 58:338-348.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125:827-852.

Tschanz, B. 1978. Untersuchungen zur Entwicklung des Trottellummenbestandes auf Vedøy (Røst, Lofoten). J. Orn. 119:133-145.

Tuck, L.M. 1961. The Murres, Canadian Wildlife Service Monograph Series No. 1, Ottawa, 260 pp.

Turner, F.B., R.I. Jennrich and J.D. Weintraub. 1969. Home range and body size of lizards. Ecol. 50:1076-1081.

Uspenski, S.M. 1956. The bird bazaars of Novaya Zemyla. Can. Wildl. Serv. Translations of Russian Game Reports. Vol. 4. Ottawa. 159 pp. (Translated from Russian 1958).

Utida, S. 1958. Population fluctuation, an experimental and theoretical approach. Cold Spring Harbour Symp. on Quant. Biol. 22:139-151.

Vermeer, K. 1980. The importance of timing and type of prey to reproductive success of rhinoceros auklets *Cerorhinca monocerata*. Ibis 122:343-350.

Vermeer, K., L. Cullen and M. Porter. 1979. A provisional explanation of the reproductive failure of tufted puffins *Lunda cirrhata* on Triangle Island, British Columbia. Ibis 121:348-354.

Vermeer, K. and S.J. Westrheim. 1984. Fish changes in diets of nestling rhinoceros auklets and their implications. Pages 51-62 *in*: *Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships*. Nettleship, D.N., G.A. Sanger and P.F. Springer (eds.). Can. Wildl. Serv. Spec. Publ., Ottawa. 220 pp.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature. 188:558-560.

Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Board Can. 31:1531-1536.

Werner, E.E. and D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecol. 55:1042-1052.

Werner, E.E., and G.G. Mittelbach. 1981. Optimal foraging: Field tests of diet choice and habitat switching. Amer. Zool. 21:813-829.

Whitehead, H.P. 1981. The behaviour and ecology of the humpback whale in the northwest Atlantic. Unpublished Ph.D. thesis, Cambridge University. Cambridge. 149 pp.

Wiens, J.A. 1977. On competition and variable environments. Am. Sci. 65:590-597.

Wiens, J.A. and J.M. Scott. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77:439-452.

Winters, G.H. 1983. Analysis of the biological and demographic parameters of northern sandlance, *Ammodytes dubius*, from the Newfoundland Grand Bank. Can. J. Fish. Aquat. Sci. 40:409-419.

Winters, G.H. and J.S. Campbell. 1974. Some biological aspects and population parameters of Grand Bank capelin. ICNAF Res. Doc. 74/76, Ser. No. 3309, 23 pp.

Winters, G.H. and J.E. Carscadden. 1978. Review of capelin ecology and estimation of surplus yield from predator dynamics. ICNAF Res. Bull. 13:21-30.

Wood, C.C. and C.M. Hand. 1985. Food-searching behaviour of the common merganser (Mergus merganser) I: Functional responses to prey and predator density. Can. J. Zool. 63:1260-1270.

Woodby, D.A. 1984. The April distribution of murres and prey patches in the southeastern Bering Sea. Limnol. Oceanogr. 29:181-188.

Wynne-Edwards, V.C. 1935. On the habits and distributions of birds on the North Atlantic. Proc. Boston Soc. Nat. Hist. 40:233-346.

Wynne-Edwards, V.C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd. Edinburgh. 653 pp.

Zach, R. and J.B. Falls. 1976a. Ovenbird (Aves: Parulidae) hunting behaviour in a patchy environment: an experimental study. Can. J. Zool. 54:1863-1879.

Zach, R. and J.B. Falls. 1976b. Foraging behaviour, learning, and exploration by captive ovenbirds (Aves: Parulidae). Can. J. Zool. 54:1880-1893.

Zach, R. and J.B. Falls. 1976c. Do ovenbirds (Aves: Parulidae) hunt by expectation? Can. J. Zool. 54:1894-1903.

Zafermann, M.L. 1973. Observations on capelin in the area of Hope Island. Mat. Rybokh. Issledov. Severn. Bass., 19:93-100, 1972. (English translation for Fish. Res. Board Can., St. John's, Nfld.)

Appendices

Appendix A1. Details of Witless Bay boat surveys, 1982.*

Survey No.	Date	Survey type	Duration	Start time	Sea state (0-9)	Observations	
						Fish	Birds
1	29May	L	174	0830	0	-	X
2	05Jun	S	109	0915	1	X	X
3	26Jun	S	156	1024	2	-	X
4	28Jun	L	223	0849	2	-	X
5	03Jul	S	105	0835	2	X	X
6	07Jul	S	99	0725	2	X	X
7	13Jul	S	171	0955	1	X	X
8	25Jul	L	286	0700	1	-	X
9	26Jul	S	84	0825	1	X	X
10	09Aug	S	93	0837	1	X	X
11	23Aug	L	199	1125	2	-	X

* "X" indicates sampling was done, "-" indicates no sampling. Abbreviations: L, longshore; O, offshore; S, standard; 24, 24 hr.

+ indicates surveys where all fish and bird observations could not be used.

Appendix A2. Summary of Witless Bay boat surveys, 1983.*

Survey No.	Date	Survey type	Duration	Start time	Sea state (0-9)	Observations		Hydro stations	
						Fish	Birds	1	2
1	27May	S	140	0928	3	X•	X	X	X
3	8Jun	S	135	0620	2	X	X	X	X
4	13Jun	S	126	0834	1-2	X	X	X	X
5	15Jun	S	116	0810	1-2	X	X	X	X
6	20Jun	S	120	0713	1-2	X•	X	X	X
7	22Jun	S	112	0625	2	X	X	X	X
8	~~23Jun~~	S	112	0619	-	X	X	X	X
9	24Jun	S	128	0630	1	X-	X	X	X
10	25Jun	S	124	0630	1	X	X	X	X
11	26Jun	24	114	1430	1	X	X	X	X
12	26Jun	24	122	2134	1	X	X•	-	-
13	27Jun	24	126	0400	1	X•	X•	-	-
14	27Jun	24/S	124	0940	2	X	X	X	X
15	28Jun	S	140	0635	1	X•	X	X	X
16	29Jun	S	114	0635	1	X	X	X	X
17	30Jun	L	278	0702	3-4	X•	X	X	X
18	1Jul	S	114	0633	1	X	X	X	X
19	4Jul	S	122	0626	1	X	X	X	X
20	5Jul	24	100	0528	1	X	X	X	X
21	5Jul	24/S	114	1025	2	X	X	-	-
22	5Jul	24	106	1553	3	X	X	-	-
23	5Jul	24	86	2032	1	X	X•	-	-
24	6Jul	S	110	0615	1	X	X	X	X
25	8Jul	S	80	0620	4	X•	X	X	X
26	11Jul	S	1[illegible]	1533	3	X	X	X	X
27	13Jul	S	130	0602	3	X	X	X	X
28	14Jul	S	106	0425	3	X	X	X	X
30	16Jul	S	118	0726	2	X	X	X	X
31	18Jul	S	112	0828	3	X	X	X	X
32	20Jul	S	130	0631	1	X	X	X	X
33	22Jul	S	114	0627	2	X	X	X	X
34	24Jul	L	246	1139	3	X•	X	X	X
35	27Jul	S	110	0640	3	X	X	X	X
36	1Aug	S	112	0615	1	X	X	X	X
37	4Aug	S	124	0628	2	X•	X	X	X
38	9Aug	S	116	0618	1	X	X	X	X
39	15Aug	S	108	0721	1	X	X	X	X

* See footnote Appendix A1 for explanation of symbols/abbreviations.

Appendix A3. Summary of Witless Bay boat surgeys, 1984.*

Survey No.	Date	Survey type	Duration	Start time	Sea state	Observations Fish	Observations Birds	Hydro stations 1 2 3 4
1	9May	S	144	0649	0	X	X	- - - -
2	22May	S	127	0745	2	X	X	- - - -
4	29May	S	125	1445	3	X	X	- X - -
5	30May	O	133	0834	1	X	X	- - - -
6	6Jun	O	102	0835	3-4	X	X	- - - -
7	7Jun	S	120	0740	2	X	X	- - - -
8	13Jun	S	108	0725	2	X	X	X X X X
9	14Jun	L	228	0700	1	X	X	- - - -
10	20Jun	S	131	0648	3-4	X+	X	X X X -
11	24Jun	S	116	0800	2	X	X	- X - -
12	26Jun	S	116	0648	1	X	X	- X X X
13	28Jun	S	101	0725	3	X	X	- X - -
14	30Jun	S	105	0630	1	X+	X	X X X X
15	1Jul	S	117	0822	0	X	X	- X X X
16	2Jul	S	118	0730	2	X	X	- X - -
17	4Jul	S	117	0650	2	X+	X+	- - - -
18	6Jul	S	108	0720	4	X	X	- - - -
19	8Jul	L	221	1010	2	X	X	- - - -
20	9Jul	S	118	0650	2	X	X	- - - -
21	12Jul	S	127	0700	2	X	X+	- - - -
22	14Jul	S	128	0705	1-2	X	X	- - - -
23	16Jul	O	123	0753	2	X	X	- - - -
24	17Jul	S	129	07[illegible]	2-3	X	X	- - - -
25	18Jul	L	215	0745	3-4	X+	X	- - - -
26	20Jul	S	115	0720	1	X	X	- - - -
27	23Jul	S	113	0700	2	X	X	- - - -
28	26Jul	S	119	0700	1-2	X	X	- - - -
29	30Jul	S	123	0700	1-2	X	X	X X - -
30	3Aug	S	121	0700	1	X	X	- X X X
31	6Aug	L	213	0710	2-3	-	X	- - - -
32	7Aug	S	107	0650	-	X	X	- X - -
33	14Aug	O	120	0735	1-2	X	X	- X X -
34	15Aug	S	108	0830	1	X	X	- X X X
35	24Aug	S	101	0704	2	X	X	- - - -
36	30Aug	S	115	0705	1	X+	X	- - - -

* See footnote Appendix A1 for explanation of symbols/abbreviations.

Appendix B. Details of hydrographic data collection, 1982-1984. "X" indicates sampling was done for temperature (T) and salinity (S). "n" is number of days each station was sampled. - indicates no sampling.

Station number	Location	Year	Depth sampled	Gear	T	S	n
1	Witless Bay	1983	0- 5 m	CTD	X	X	33
	(off wharf)	1984	0- 5 m	CTD	X	X	4
2	Gull Island	1983	0-60 m	CTD	X	X	33
		1984	0-60 m	CTD	X	X	14
3	Witless Bay	1983	-	-	-	-	-
	(middle of bay)	1984	0-40 m	CTD	X	X	8
4	Offshore	1983	-	-	-	-	-
	(1.5-2.0 km off Gull Island)	1984	0-110 m	CTD	X	X	6
5	Lance Cove	1983	-	-	-	-	-
	(Cape Broyle Bay)	1984	5 m	RYAN	X	-	55
6	Witless Bay	1983	-	-	-	-	-
	(at wharf)	1984	5 m	RYAN	X	-	71
7	Gull Island	1983	-	-	-	-	-
		1984	10 m	RYAN	X	-	116
27	Station 27	1982	0-125 m		X	X	9
		1983	0-125 m		X	X	8
		1984	0-125 m		X	X	18

Appendix C. Regression equations used for calculating fish lengths and weights (WT = weight in g, TL = total fish length in mm, OTL = fish otolith total length in mm).

Fish	No.	r^2	Regression equation
Capelin *			
(*Mallotus villosus*)			
Adult capelin 1982:			
Male	141	0.81	$WT = TL^{2.97} \times 0.00000759$
Ovid female	189	0.87	$WT = TL^{2.81} \times 0.0000166$
Spent female	180	0.83	$WT = TL^{2.64} \times 0.0000288$
Adult capelin 1983:			
Male	620	0.79	$WT = TL^{2.98} \times 0.00000676$
Ovid female	617	0.86	$WT = TL^{3.02} \times 0.00000525$
Spent female	483	0.87	$WT = TL^{2.84} \times 0.00000891$
Adult capelin 1983:			
Male	258	0.71	$WT = TL^{2.81} \times 0.0000158$
Ovid female	230	0.87	$WT = TL^{2.90} \times 0.00000891$
Spent female	180	0.77	$WT = TL^{3.19} \times 0.00000168$
Immature capelin **	121	0.82	$WT = TL^{2.72} \times 0.0000138$
Sandlance **	45	0.93	$WT = TL^{2.11} \times 0.000209$
(*Ammodytes dubius*)	265	0.78	$TL = 60.9 \times OTL - 3.86$
Cod ***	424	0.99	$WT = TL^{3.17} \times 0.00000479$
(*Gadus morhua*)	24	0.99	$TL = 21.2 \times OTL + 5.17$

* Capelin data from Cape Broyle, Nfld., beach trap collections 1982-1984 (Methven and Piatt, unpubl. data).

** Immature capelin and sandlance fish length-weight data from Witless Bay, Nfld., common murre and Atlantic puffin chick meal collections, 1982-1984 (J. Piatt, A.E. Burger, and D. Nettleship, unpubl. data). Sandlance otolith-fish length data from the Grand Bank, July, 1968 (J.S. Scott, unpubl. data).

*** Juvenile cod fish length-weight and otolith-fish length data from Bellevue, Nfld., beach seine collections, 1982-1983, (D.A. Methven, unpubl. data).

Appendix D1. Composition by number of capelin collected from a beach trap at Cape Broyle, Newfoundland, 1982-1984

Year	Total no.	Male		Female					
				Total		Ovid		Spent	
		no.	%	no.	%	no.	% *	no.	% *
1982	1942	520	(26.8)	1422	(73.2)	908	(63.9)	514	(36.1)
1983	5956	2295	(38.5)	3661	(61.5)	2548	(69.5)	1113	(30.5)
1984	3125	1486	(47.6)	1639	(52.4)	1199	(73.2)	440	(26.8)
Total	11,023	4301	(39.0)	6722	(61.0)	4655	(69.3)	2067	(30.7)
**			(37.6)		(62.4)		(68.9)		(31.1)

* Percent of total females.
** Unweighted mean percentages.

Appendix D2. Composition by weight of capelin collected from a beach trap at Cape Broyle, Newfoundland, 1982-1984

Year	Total no.	Male		Female					
				Total		Ovid		Spent	
		no.	%	no.	%	no.	% *	no.	% *
1982	1942	520	(41.8)	1422	(58.2)	908	(67.7)	514	(32.3)
1983	5956	2295	(57.0)	3661	(43.0)	2548	(74.7)	1113	(25.3)
1984	3125	1486	(62.4)	1639	(37.6)	1199	(79.8)	440	(20.2)
Total	11,023	4301	(53.1)	6722	(46.9)	4655	(74.6)	2067	(25.4)
**			(51.6)		(48.4)		(74.2)		(25.8)

* Percent of total females.
** Unweighted mean percentages.

Appendix E1. Characteristics of capelin schools found in a large aggregation at Witless Bay, 3 July 1982.

School no.	Height (m)	Width * (m)	Volume ** (m^3)	Depth (m)
1	2.1	13.4	46	1.0
2	13.9	4.9	743	10.4
3	2.8	7.3	45	1.4
4	1.0	8.8	7	0.3
5	9.0	5.7	362	4.5
6	10.4	12.7	1078	5.2
7	9.0	3.4	216	4.5
8	3.5	7.3	70	1.2
9	8.3	0.5	27	4.2
10	16.3	40.5	8447	8.3
1[illegible]	4.2	5.7	79	2.1
12	1.7	28.9	65	0.7
13	2.1	17.3	60	1.0
14	10.4	0.3	26	10.4
mean	6.8	11.2	805	7.7 ***

* Width corrected for sounder beam width at depth (Forbes and Nakken 1972).

** Volume = 3.14 h^2 w/4 (Forbes and Nakken 1972).

*** Mean depth weighted by volume.

Appendix E2. Characteristics of some capelin schools and aggregations in Witless Bay, 1982.

School (S) and aggregation (Ag) characteristics	Aggregation no.			
	1	2	3	4
	(July 3)		(July 13)	
No. schools in Ag	14	49	24	58
Ag surface length (m)	432	494	485	789
S min. depth (m)	1.0	1.4	0.3	0.3
S max depth (m)	16.3	77.8	16.7	42.4
S mean depth (m)	7.7	28.7	4.4	10.7
S mean height (m)	6.8	11.2	4.5	6.4
S mean width (m)	11.2	7.4	16.4	9.8
S mean volume (m^3)	805	992	399	680
Ag total volume (m^3)	11,272	48,631	9,575	39,452
No. fish in Ag ($x10^3$)*	177	764	150	619
Ag biomass (mt)**	4.5	19.3	3.8	15.7

* Assuming fish density = 15.7 fish/m^3 (± 15%, Zaferman 1973)
** Assuming mean weight of capelin = 25.3 g.

Appendix E3. Fine-scale murre and puffin association with capelin schools, 3 July 1982.

Minute	No. of schools	Total school volume (m^3)	Mean depth (m)*	No. of puffins	No. of murres
43	1	46	1.0	0	0
44	1	743	10.4	3	1
45	1	45	1.4	7	0
46	2	369	0.3	11	0
47	3	1365	4.9	35	0
48	1	27	4.2	19	0
49	1	8447	8.3	75	2
50	2	144	1.4	32	0
51	1	60	1.0	3	0
52	1	25	10.4	0	0
74	3	111	11.9	1	1
75	10	3905	14.0	38	0
76	5	3537	18.9	15	0
77	5	16,472	27.4	2	50
78	7	5208	22.0	0	5
79	5	9295	32.0	0	21
80	11	9043	32.6	0	6
81	3	1060	12.4	0	1

* Mean depth weighted by volume.

Appendix F1. Frequency of occurrence of different prey items in common murre and Atlantic puffin stomachs at Witless Bay, 1982-1984.

Prey items	Murre		Puffin	
	n*	% freq.	n*	% freq.
Total no. of stomachs examined	1358		496	
Ovid female capelin	290	21.4	112	22.6
Spent female capelin	45	3.3	14	2.8
Mature male capelin	171	12.6	4	0.8
Immature capelin	32	2.4	10	2.0
Unidentified capelin	197	14.5	57	11.5
Cod (spp.)	2	0.1	0	0.0
Sandlance (spp.)	1	<0.1	0	0.0
Unidentified fish	120	8.8	53	10.7
Fish vertebrate	451	33.2	137	27.6
Crustaceans	1	<0.1	11	2.2
Squid	2	0.1	0	0.0

* n = number of stomachs containing item

Appendix F2. Number and percent of total different prey items found in common murre and Atlantic puffin stomachs at Witless Bay, 1981.

Prey items	Murre		Puffin	
	no.	% no.	no.	% no.
Total no. of stomachs examined	84			
Total no. of items	139	100.0	-	-
Ovid female capelin	35	25.2	-	-
Spent female capelin	0	0.0	-	-
Mature male capelin	41	29.5	-	-
Immature capelin	22	15.8	-	-
Unidentified capelin	37	26.6	-	-
Cod (spp.)	0	0.0	-	-
Sandlance (spp.)	0	0.0	-	-
Unidentified fish	2	1.4	-	-
Crustaceans	0	0.0	-	-
Squid	2	1.4	-	-
Identifiable capelin	98	100.0	-	-
Mature female (total)	35	35.7	-	-
Ovid female	35	35.7	-	-
Spent female	0	0.0	-	-
Mature male	41	41.8	-	-
Immature	22	22.4	-	-

Appendix F3. Number and percent total of different prey items found in common murre and Atlantic puffin stomachs at Witless Bay, 1982.

Prey items	Murre		Puffin	
	no.	% no.	no.	% no.
Total no. of stomachs examined	655		229	
Total no. of items	749	100.0	176	100.0
Ovid female capelin	304	40.6	97	55.1
Spent female capelin	39	5.2	2	1.1
Mature male capelin	163	21.8	0	0.0
Immature capelin	63	8.4	9	5.1
Unidentified capelin	132	17.6	46	26.1
Cod (spp.)	0	0.0	0	0.0
Sandlance (spp.)	0	0.0	0	0.0
Unidentified fish	46	6.1	21	11.9
Crustaceans	0	0.0	1	0.6
Squid	2	0.3	0	0.0
Identifiable capelin	567	100.0	108	100.0
Mature female (total)	343	60.5	99	91.7
Ovid female	304	53.6	97	89.8
Spent female	39	6.9	2	1.9
Mature male	163	28.7	0	0.0
Immature	61	10.8	9	8.3

Appendix F4. Number and percent of total different prey items found in common murre and Atlantic puffin stomachs at Witless Bay, 1983.

Prey items	Murre		Puffin	
	no.	% no.	no.	% no.
Total no. of stomachs examined	353		116	
Total no. of items	441	100.0	69	100.0
Ovid female capelin	161	36.5	17	24.6
Spent female capelin	8	1.8	6	8.7
Mature male capelin	32	7.3	2	2.9
Immature capelin	20	4.5	1	1.4
Unidentified capelin	158	35.8	10	14.5
Cod (spp.)	2	0.5	0	0.0
Sandlance (spp.)	1	0.2	0	0.0
Unidentified fish	58	13.2	23	33.3
Crustaceans	1	0.2	10	14.5
Squid	0	0.0	0	0.0
Identifiable capelin	221	100.0	26	100.0
Mature female (total)	169	76.5	23	88.5
Ovid female	161	72.9	17	65.4
Spent female	8	3.6	6	23.1
Mature male	32	14.5	2	7.7
Immature	20	9.0	1	3.8

Appendix F5. Number and percent of total different prey items found in common murre and Atlantic puffin stomachs at Witless Bay, 1984.

Prey items	Murre		Puffin	
	no.	% no.	no.	% no.
Total no. of stomachs examined	350		151	
Total no. of items	160	100.0	33	100.0
Ovid female capelin	80	50.0	12	36.4
Spent female capelin	17	10.6	6	18.2
Mature male capelin	15	9.4	1	3.0
Immature capelin	0	0.0	0	0.0
Unidentified capelin	32	20.0	2	6.1
Cod (spp.)	0	0.0	0	0.0
Sandlance (spp.)	0	0.0	0	0.0
Unidentified fish	16	10.0	11	33.3
Crustaceans	0	0.0	1	3.0
Squid	0	0.0	0	0.0
Identifiable capelin	112	100.0	19	100.0
Mature female (total)	97	86.6	18	94.7
Ovid female	80	71.4	12	63.2
Spent female	17	15.2	6	31.6
Mature male	15	13.4	1	5.3
Immature	0	0.0	0	0.0

Appendix G1. Frequency of occurrence of different prey items in common murre and Atlantic puffin gizzards at Witless Bay, 1982-1984.

Prey items	Murre		Puffin	
	n*	% freq.	n*	% freq.
Total no. of gizzards examined	889		299	—
Capelin otoliths	335	24.7	127	42.5
Cod (spp.) otoliths	97	6.7	52	17.4
Sandlance (spp.) otoliths	115	8.0	46	3.0
Unidentified otoliths	68	4.7	17	5.7
Otolith fragments	78	5.4	25	8.4
Fish vertebrate	451	31.4	172	57.5
Squid beaks	0	0.0	7	2.3
Crustaceans	4	0.3	0	0.0
Pebbles	135	9.4	83	27.8

* n = number of gizzards containing item.

Appendix G2. Number and percent of total different prey items found in common murre and Atlantic puffin gizzards at Witless Bay, 1982.

Prey items	Murre		Puffin	
	no.	% no.	no.	% no.
Total no. of gizzards examined	186		32	
Total no. items	190		104	
Total no. identified food items	156	100.0	101	100.0
Capelin otoliths	76	48.7	28	27.8
Cod (spp.) otoliths	30	19.2	59	58.4
Sandlance (spp.) otoliths	50	32.1	4	4.0
Unidentified otoliths *	6	-	2	-
Squid beaks	0	0.0	10	9.9
Crustaceans	0	0.0	0	0.0
Pebbles *	28	-	12	-

* not included for calculation of percent total items.

Appendix G3. Number and percent total of different prey items found in common murre and Atlantic puffin gizzards at Witless Bay, 1983.

Prey items	Murre		Puffin	
	no.	% no.	no.	% no.
Total no. of gizzards examined	353		116	
Total no. items	942		265	
Total no. identified food items	744	100.0	202	100.0
Capelin otoliths	461	62.0	76	37.6
Cod (spp.) otoliths	147	19.8	111	55.0
Sandlance (spp.) otoliths	136	18.3	15	7.4
Unidentified otoliths *	112	-	18	-
Squid beaks	0	0.0	0	0.0
Crustaceans	0	0.0	0	0.0
Pebbles *	86	-	45	-

* not included for calculation of percent total items.

Appendix G4. Number and percent total of different prey items found in common murre and Atlantic puffin gizzards at Witless Bay, 1984.

Prey items	Murre		Puffin	
	no.	% no.	no.	% no.
Total no. of gizzards examined	350		151	
Total no. items	960		471	
Total no. identified food items	625	100.0	293	100.0
Capelin otoliths	434	69.4	170	58.0
Cod (spp.) otoliths	47	7.5	10	3.4
Sandlance (spp.) otoliths	140	22.4	108	36.9
Unidentified otoliths *	232	-	92	-
Squid beaks	0	0.0	5	1.7
Crustaceans	4	0.6	0	0.0
Pebbles *	103	-	86	-

* not included for calculation of percent total items.

Appendix H1. Number and percent of total different prey items delivered to common murre and Atlantic puffin chicks at Gull and Great Islands, Newfoundland, 1982.

Prey items	Murre		Puffin	
	no.*	% no.	no.	% no.
Total no. of chick meal items	134 (29)	100.0	325	100.0
Capelin	129 (27)	95.7	225	69.2
Cod (spp.)	0 (0)	0.0	80	24.6
Sandlance (spp.)	2 (2)	2.5	20	6.2
Total other	3 (0)	1.8	0	0.0
Other:				
Stichaeidae	3 (0)	1.8		
Identifiable capelin	100 (27)	100.0	225	100.0
Total mature female	58 (20)	61.4	97	43.1
Condition known	0 (20)		45	
Ovid female	- (15)	55.6**	17	16.3**
Spent female	- (5)	18.6**	28	26.8**
Mature male	13 (0)	10.2	9	4.0
Immature	29 (7)	28.3	119	52.9

* Numbers based on visual observations of chick meal deliveries and (in parentheses) on collections from collared chicks. There were no significant differences between proportions observed by the two methods and results were combined to obtain the total percentages.

** Percentages extrapolated from the proportions of females where the spawning condition was known to the number of mature females observed.

Appendix H2. Number and percent of total different prey items delivered to common murre and Atlantic puffin chicks at Gull, and Great Islands, Newfoundland, 1983.

Prey items	Murre		Puffin	
	no.*	% no.	no.	% no.
Total no. of chick meal items	268 (36)	100.0	99	100.0
Capelin	245 (30)	90.5	54	54.5
Cod (spp.)	0 (1)	0.3	28	28.3
Sandlance (spp.)	17 (4)	6.9	15	15.2
Total other	6 (1)	2.3	2	2.0
Other:				
Stichaeidae***	6 (1)	2.3		
Cottidae			1	1.0
Pleuronectidae			1	1.0
Identifiable capelin	202 (30)	100.0	54	100.0
Total mature female	180 (29)	90.1	47	87.0
Condition known	146 (28)		47	
Ovid female	87 (17)	53.8**	4	7.4**
Spent female	59 (10)	36.3**	43	79.6**
Mature male	7 (0)	3.0	5	9.3
Immature	15 (2)	6.9	2	3.7

* Numbers based on visual observations of chick meal deliveries and (in parentheses) on collections from collared chicks. There were no significant differences between proportions observed by the two methods and results were combined to obtain the total percentages.

** Percentages extrapolated from the proportions of females where the spawning condition was known to the number of mature females observed.

*** One specimen identified as Radiated Shanny, *Ulvaria subbifurcata*.

Appendix H3. Number and percent of total different prey items delivered to common murre and Atlantic puffin chicks at Gull and Great Islands, Newfoundland, 1984.

Prey items	Murre		Puffin	
	no.*	% no.	no.	% no.
Total no. of chick meal items	352 (30)	100.0	90	100.0
Capelin	291 (24)	82.5	84	93.3
Cod (spp.)	0 (1)	0.3	3	3.3
Sandlance (spp.)	57 (5)	16.2	2	2.2
Total other	4 (0)	1.0	1	1.1
Other:				
Stichaeidae	4 (0)	1.0		
Aspidophoroides monopterygius			1	1.1
Identifiable capelin	205 (23)	100.0	84	100.0
Total mature female	151 (17)	73.7	64	76.2
Condition known	140 (17)		64	
Ovid female	111 (16)	59.6**	5	6.0**
Spent female	29 (1)	13.2**	59	70.2**
Mature male	10 (2)	5.3	5	6.0
Immature	44 (4)	21.1	15	17.9

* Numbers based on visual observations of chick meal deliveries and (in parentheses) on collections from collared chicks. There were no significant differences between proportions observed by the two methods and results were combined to obtain the total percentages.

** Percentages extrapolated from the proportions of females where the spawning condition was known to the number of mature females observed.

Appendix I1. Percent weight composition of adult and chick common murre and Atlantic puffin diets at Witless Bay, Nfld., 1982.

Fish	Murre		Puffin	
	Adult	Chick	Adult	Chick
Capelin	81.0	96.8	73.9	91.6
Cod	5.8	0.0	5.6	1.9
Sandlance	13.2	2.2	4.5	6.4
Other	0.0	1.1	15.9	0.0

Appendix I2. Percent weight composition of adult and chick common murre and Atlantic puffin diets at Witless Bay, Nfld., 1983.

Fish	Murre		Puffin	
	Adult	Chick	Adult	Chick
Capelin	81.9	92.0	87.7	83.8
Cod	9.9	0.2	4.8	2.5
Sandlance	8.2	6.3	7.5	13.7
Other	0.0	1.5	0.0	< 0.1

Appendix I3. Percent weight composition of adult and chick common murre and Atlantic puffin diets at Witless Bay, Nfld., 1984.

Fish	Murre		Puffin	
	Adult	Chick	Adult	Chick
Capelin	85.1	83.0	74.5	99.3
Cod	6.5	0.2	0.2	0.1
Sandlance	8.4	16.1	23.8	0.6
Other	< 0.1	0.7	1.5	< 0.1

Appendix I4. Percent weight composition of adult and chick common murre and Atlantic puffin capelin diets at Witless Bay, Nfld., 1982.

Capelin	Murre		Puffin	
	Adult	Chick	Adult	Chick
Adult female				
Total	51.9	77.4	98.7	68.5
Ovid	47.7	60.0	97.3	28.5
Spent	4.2	17.4	1.4	40.0
Adult male	46.5	15.7	0.0	12.5
Immature	1.6	6.9	1.3	19.0

Appendix I5. Percent weight composition of adult and chick common murre and Atlantic puffin capelin diets at Witless Bay, Nfld., 1983.

Capelin	Murre		Puffin	
	Adult	Chick	Adult	Chick
Adult female				
Total	72.6	93.5	89.1	81.8
Ovid	70.8	60.9	72.5	9.6
Spent	1.8	32.6	16.6	72.2
Adult male	24.7	4.8	10.2	17.2
Immature	1.7	1.7	0.7	1.0

Appendix I6. Percent weight composition of adult and chick common murre and Atlantic puffin capelin diets at Witless Bay, Nfld., 1984.

Capelin	Murre		Puffin	
	Adult	Chick	Adult	Chick
Adult female				
Total	77.2	84.5	95.6	82.8
Ovid	66.9	70.2	72.2	6.8
Spent	10.3	14.3	23.4	76.0
Adult male	22.8	9.6	4.4	9.9
Immature	0.0	5.9	0.0	7.3

Appendix J1. Number and mean lengths (mm, and standard error) of fish collected from common murre and Atlantic Puffin adults (Ad) and chicks (Ch), and capelin traps, at the Witless Bay study area in 1982.

Fish		Trap	Murre		Puffin	
			Ad	Ch	Ad	Ch
Capelin:						
Total	n	483	188	26	27	203
	mean	158	144	135	136	113
	s.e.	0.8	2.1	3.1	3.0	2.3
Ovid female	n	180	89	15	25	60
	mean	147	143	135	136	137
	s.e.	1.1	1.7	2.8	3.3	1.7
Spent female	n	171	22	9	2	40
	mean	154	140	143	139	138
	s.e.	1.0	2.6	3.6	-	2.1
Male	n	132	50	-	-	10
	mean	179	177	-	-	156
	s.e.	0.9	1.1	-	-	5.5
Immature	n	-	27	2	-	93
	mean	-	92	96	-	82
	s.e.	-	2.1	-	-	1.7
Sandlance	n	-	7*	1	-	12
	mean	-	134	148	-	143
	s.e.	-	5.6	-	-	11.4
Cod	n	-	17*	-	-	63
	mean	-	63	-	-	42
	s.e.	-	7.3	-	-	0.6

* Extrapolated from otolith lengths.

Appendix J2. Number and mean lengths (mm, and standard error) of fish collected from common murre and Atlantic Puffin adults (Ad) and chicks (Ch), and capelin traps, at the Witless Bay study area in 1983.

Fish		Trap	Murre		Puffin	
			Ad	Ch	Ad	Ch
Capelin:						
Total	n	1603	32	27	7	54
	mean	157	140	133	135	146
	s.e.	0.4	4.3	3.2	3.6	2.1
Ovid female	n	543	19	11	2	4
	mean	149	143	139	141	155
	s.e.	0.6	2.2	4.2	4.0	8.3
Spent female	n	499	-	14	5	43
	mean	151	-	136	133	145
	s.e.	0.6	-	2.5	4.4	1.7
Male	n	561	8	-	-	5
	mean	169	163	-	-	163
	s.e.	0.5	3.7	-	-	4.2
Immature	n	-	5	2	-	2
	mean	-	94	90	-	105
	s.e.	-	7.2	-	-	14.5
Sandlance	n	-	35*	3	2*	15
	mean	-	137	176	140	149
	s.e.	-	2.6	18.5	-	15.6
Cod	n	-	16*	-	25*	2
	mean	-	82	-	40	30
	s.e.	-	6.7	-	0.9	8.5

* [illegible]trapolated from otolith lengths.

Appendix J3. Number and mean lengths (mm, and standard error) of fish collected from common murre and Atlantic Puffin adults (Ad) and chicks (Ch), and capelin traps, at the Witless Bay study area in 1984.

Fish		Trap	Murre		Puffin	
			Ad	Ch	Ad	Ch
Capelin:						
Total	n	656	5	11	2	82
	mean	163	132	147	154	147
	s.e.	0.7	9.6	3.8	1.0	2.5
Ovid female	n	242	3	10	1	3
	mean	154	123	145	153	144
	s.e.	0.9	8.8	3.6	-	2.3
Spent female	n	159	1	1	-	58
	mean	151	125	166	-	156
	s.e.	1.2	-	-	-	1.9
Male	n	255	1	-	1	6
	mean	178	165	-	155	160
	s.e.	0.6	-	-	-	1.7
Immature	n	-	-	-	-	15
	mean	-	-	-	-	110
	s.e.	-	-	-	-	3.6
Sandlance	n	-	38*	5	81*	10
	mean	-	136	171	142	59
	s.e.	-	2.8	10.9	1.7	3.0
Cod	n	-	70*	-	113*	3
	mean	-	98	-	36	41
	s.e.	-	15.5	-	0.8	5.2

* Extrapolated from otolith lengths.

Appendix J4. Number and mean weight (g. and standard error) of fish collected from common murre and Atlantic Puffin adults (Ad) and chicks (Ch), and capelin traps, at the Witless Bay study area, 1982.

Fish		Trap	Murre		Puffin	
			Ad	Ch	Ad	Ch
Capelin:						
Total	n	483	188	26	27	203
	mean	24.4	21.0	13.0	16.4	7.5
	s.e.	0.5	0.9	0.8	1.0	0.4
Ovid female	n	180	89	15	25	60
	mean	20.7	19.8	14.5	16.8	11.6
	s.e.	0.5	0.7	0.7	1.1	0.5
Spent female	n	171	22	9	2	40
	mean	17.5	13.7	12.6	11.9	9.9
	s.e.	0.3	0.7	0.9	-	0.5
Male	n	132	50	-	-	10
	mean	38.4	36.0	-	-	20.7
	s.e.	0.6	0.7	-	-	1.9
Immature	n	-	27	2	-	93
	mean	-	3.3	3.5	-	2.4
	s.e.	-	0.2	-	-	0.1
Sandlance	n	-	7*	1	-	12
	mean	-	6.6	5.0	-	8.0
	s.e.	-	0.6	-	-	1.1
Cod	n	-	17*	-	-	63
	mean	-	4.9	-	-	0.60
	s.e.	-	2.5	-	-	0.05

* Extrapolated from otolith lengths.

Appendix J5. Number and mean weight (and standard error) of fish collected from common murre and Atlantic Puffin adults (Ad) and chicks (Ch), and capelin traps, at the Witless Bay study area, 1983.

Fish		Trap	Murre		Puffin	
			Ad	Ch	Ad	Ch
Capelin:						
Total	n	1602	32	27	7	54
	mean	21.5	17.4	12.0	11.5	11.3
	s.e.	0.2	1.5	0.8	1.4	0.6
Ovid female	n	542	19	11	2	4
	mean	18.9	17.2	14.6	16.3	14.4
	s.e.	0.2	0.8	1.0	-	1.3
Spent female	n	499	-	14	5	43
	mean	14.6	-	11.2	9.6	10.1
	s.e.	0.2	-	0.7	0.9	0.5
Male	n	561	8	-	-	5
	mean	30.1	26.7	-	-	20.5
	s.e.	0.3	1.8	-	-	2.0
Immature	n	-	5	2	-	2
	mean	-	3.4	2.9	-	7.1
	s.e.	-	0.8	-	-	-
Sandlance	n	-	35*	3	2*	15
	mean	-	6.8	13.7	7.0	9.3
	s.e.	-	0.3	3.4	-	1.9
Cod	n	-	16*	-	25*	25
	mean	-	7.5	-	0.60	0.69
	s.e.	-	1.5	-	0.04	0.13

* Extrapolated from otolith lengths.

Appendix J6. Number and mean weight (g, and standard error) of fish collected from common murre and Atlantic Puffin adults (Ad) and chicks (Ch), and capelin traps, at the Witless Bay study area, 1984.

Fish		Trap	Murre		Puffin	
			Ad	Ch	Ad	Ch
Capelin:						
Total	n	611	5	11	2	82
	mean	25.5	15.9	11.4	20.9	11.2
	s.e.	0.4	2.5	1.6	1.6	0.5
Ovid female	n	225	3	10	1	3
	mean	20.7	12.9	10.8	19.3	12.7
	s.e.	0.4	1.7	1.7	-	0.6
Spent female	n	147	1	1	-	58
	mean	14.3	17.1	17.5	-	12.1
	s.e.	0.4	-	-	-	0.4
Male	n	239	1	-	1	6
	mean	34.4	26.9	-	22.6	16.5
	s.e.	0.4	-	-	-	2.1
Immature	n	-	-	-	-	15
	mean	-	-	-	-	4.5
	s.e.	-	-	-	-	0.4
Sandlance	n	-	38*	5	81*	10
	mean	-	6.8	13.2	7.4	3.0
	s.e.	-	0.3	2.2	0.2	1.8
Cod	n	-	70*	-	113*	3
	mean	-	15.6	-	0.49	0.37
	s.e.	-	1.9	-	0.05	0.17

* Extrapolated from otolith lengths.

Appendix K1. Kolmogorov-Smirnov test of between-year differences in the number of capelin found in common murre and Atlantic puffin stomachs at Witless Bay, 1981-1984.

Comparison	Murre			Puffin		
	no. cases	Z	prob.	no. cases	Z	prob.
Including empty stomachs						
1981 • 1982	739	1.0	NS 0.31	-	-	-
1982 • 1983	1009	3.5	<0.0001	345	3.9	<0.0001
1983 • 1984	703	2.6	<0.0001	267	1.2	<0.0001
Excluding empty stomachs						
1981 • 1982	472	1.2	NS 0.11	-	-	-
1982 • 1983	561	2.7	<0.0001	188	0.5	NS 0.98
1983 • 1984	217	1.7	<0.0001	46	0.4	NS 0.99

Appendix K2. Kolmogorov-Smirnov test of between-species differences in the number of capelin found in common murre and Atlantic puffin stomachs from Witless Bay, 1982-1984.

Year	No. cases	Z	Prob.
Including empty stomachs:			
1982	884	2.8	<0.0001
1983	469	2.1	<0.0001
1984	501	1.1	NS (0.16)
TOTAL	1891	3.6	<0.0001
Excluding empty stomachs			
1982	577	3.7	<0.0001
1983	17[illegible]	2.3	<0.0001
1984	90	1.4	<0.05
TOTAL	886	4.9	<0.0001

Appendix K3. Kolmogorov-Smirnov test of between-year differences in the numbers of capelin, cod, and sandlance otoliths found in Common Murre and Atlantic puffin gizzards at Witless Bay, 1982-1984.

Comparison/ Otolith type	Murre			Puffin		
	no. cases	Z	prob.	no. cases	Z	prob.
1982 • 1983						
capelin	1008	6.4	<0.0001	345	2.1	<0.0001
sandlance	1008	1.7	<0.01	345	0.3	NS 0.99
cod	1008	2.0	<0.0001	345	1.5	<0.05
1983 • 1984						
capelin	703	0.3	NS 0.99	267	0.4	NS 0.99
sandlance	703	0.4	NS 0.99	267	1.8	<0.01
cod	703	1.3	NS 0.65	267	1.3	NS 0.72

Appendix K4. Kolmogorov-Smirnov test of between-species differences in the number of capelin, sandlance, and cod otoliths found in common murre and Atlantic puffin gizzards from Witless Bay, 1982-1984.

Year	Otolith type	No. cases	Z	Prob.
1982	capelin	884	0.7	NS 0.78
	sandlance	884	0.1	NS 0.99
	cod	884	0.6	NS 0.88
1983	capelin	469	1.4	<0.05
	sandlance	469	0.7	NS 0.65
	cod	469	0.9	NS 0.36
1984	capelin	501	0.9	NS 0.41
	sandlance	501	1.3	NS 0.08
	cod	501	0.1	NS 0.99
TOTAL	capelin	1854	1.2	NS 0.07
	sandlance	1854	0.3	NS 0.99
	cod	1854	0.8	NS 0.50

Appendix K5. G-test of the frequency of capelin, cod, and sandlance in the diets of adult murres and puffins, 1983-1984 (737 prey items only from birds collected over the same time period at Witless Bay).

Source	G	df	prob.
Bird species (BS)	67.23	1	
Fish species (FS)	246.11	2	
Year	0.18	1	
BS * Year	16.60	1	
BS * FS	90.56	2	<0.0001
FS * Year	116.13	2	<0.0001
BS * FS * Year	12.54	2	<0.0001

Appendix K6. G-test of the frequency of capelin, cod, and sandlance in the diets of adult and chick murres, 1983-1984 (1272 prey items only from meals collected over the same time period at Witless Bay).

Source	G	df	prob.
Murre class (MC)	23.91	1	
Fish species (FS)	1067.43	2	
Year	13.79	1	
MC * Year	0.31	1	
MC * FS	151.69	2	<0.0001
FS * Year	53.38	2	<0.0001
MC * FS * Year	2.98	2	NS (0.11)

Appendix K7. G-test of the frequency of adult male, ovid and spent female, and immature capelin in the diet of adult and chick murres, 1982-1984 (1142 capelin only from meals collected over the same time period at Witless Bay).

Source	G	df	prob.
Murre class (MC)	0.90	1	
Capelin class (CC)	676.52	3	
Year	55.49	2	
MC * Year	214.19	2	
MC * CC	112.06	3	<0.0001
CC * Year	117.85	6	<0.0001
MC * CC * Year	10.33	6	<0.05

Appendix K8. G-test of the frequency of adult male, ovid and spent female, and immature capelin in the diet of adult and chick puffins, data from 1982-1983 combined (171 capelin from meals collected over the same time period at Witless Bay).

Source	G	df	prob.
Puffin class (PC)	78.23	1	
Capelin class (CC)	73.72	3	
PC * CC	7.74	3	>0.05

Appendix K9. G-test of the frequency of capelin, cod, and sandlance in the diet of adult and chick puffins, 1983 (206 prey items from meals collected over the same time period at Witless Bay).

Source	G	df	prob.
Puffin class (PC)	31.90	1	
Fish species (FS)	115.69	2	
PC * FS	16.54	2	<0.001

Appendix K10. G-test of the frequency of adult male, ovid and spent female capelin in the diet of adult murres and puffins, and from the capelin trap; data from 1983-1984 combined (9527 capelin from collections over the same time period at Witless Bay).

Source	G	df	prob.
Source	16874.60	2	
Capelin class (CC)	1338.00	2	
Source * CC	169.43	4	<0.0001

Appendix K11. G-test of the frequency of adult male, ovid and spent female, and immature capelin in the diet of adult murres and puffins, data from 1982-1984 combined (523 capelin from birds collected over the same time at Witless Bay).

Source	G	df	prob.
Bird species (BS)	208.90	1	
Capelin class (CC)	292.33	3	
BS * CC	43.89	3	<0.0001

Appendix L1. Estimated capelin density thresholds, correlations, and significance of correlations for common murres on all surveys at Witless Bay.

Year	Survey Number	Estimated Threshold	r^2	Significance	S*	T**
1982	05	22.00	0.38	<0.01	Y	N
1982	06	4.00	0.13	>0.05	N	N
1982	07	3.00	0.14	>0.05	N	N
1983	01	2.50	0.10	>0.05	N	N
1983	03	1.00	0.22	>0.05	N	N
1983	04	1.00	0.21	>0.05	N	N
1983	05	1.25	0.52	<0.01	N	Y
1983	06	1.75	0.47	>0.05	N	N
1983	07	13.00	0.85	<0.0001	Y	Y
1983	08	3.25	0.56	<0.005	Y	Y
1983	09	15.00	0.94	<0.0001	Y	N
1983	10	8.00	0.63	<0.001	Y	Y
1983	13	6.00	0.99	<0.0001	Y	N
1983	14	2.00	0.46	<0.01	Y	Y
1983	15	4.50	0.68	<0.0005	Y	Y
1983	16	7.00	0.83	<0.0001	Y	N
1983	17	3.00	0.16	>0.05	N	N
1983	18	7.00	0.95	<0.0001	Y	N
1983	19	27.00	0.84	<0.0001	Y	N
1983	20	4.00	0.43	<0.03	Y	Y
1983	21	3.00	0.99	<0.0001	Y	Y
1983	22	4.00	0.35	>0.05	N	N
1983	23	1.00	0.19	>0.05	N	N
1983	24	2.75	0.48	<0.01	Y	Y
1983	25	15.00	0.84	<0.001	Y	N
1983	26	9.00	0.66	<0.0012	Y	Y
1983	27	45.00	0.65	<0.0005	Y	N
1983	28	11.00	0.95	<0.0001	Y	N
1983	30	4.00	0.22	>0.05	N	N
1983	31	13.00	0.75	<0.0003	Y	N
1983	32	2.50	0.16	>0.05	N	N
1983	33	2.50	0.61	<0.003	Y	N

Appendix L1 continued. (Murre thresholds).

Year	Survey Number	Estimated Threshold	r^2	Significance	S*	T**
1983	34	1.00	0.16	>0.05	N	N
1983	35	2.00	0.18	>0.05	N	N
1983	37	2.00	0.07	>0.05	N	N
1984	01	0.25	0.17	>0.05	N	N
1984	02	0.75	0.95	>0.05	N	N
1984	05	0.30	0.06	>0.05	N	N
1984	06	0.75	0.59	<0.04	N	Y
1984	07	0.30	0.20	>0.05	N	N
1984	08	0.10	0.40	>0.05	N	N
1984	09	0.30	0.16	>0.05	N	N
1984	10	0.60	0.44	>0.05	N	N
1984	11	1.20	0.57	<0.038	Y	N
1984	12	0.40	0.36	>0.05	N	N
1984	13	4.50	0.43	<0.045	N	Y
1984	15	1.00	0.94	<0.0001	Y	Y
1984	16	1.00	0.07	>0.05	N	N
1984	17	6.00	0.99	<0.0001	Y	N
1984	18	1.00	0.39	<0.037	Y	Y
1984	19	1.00	0.83	<0.0001	Y	N
1984	20	0.25	0.21	>0.05	N	N
1984	22	0.60	0.96	<0.02	Y	N
1984	23	1.20	0.51	<0.01	Y	N
1984	24	0.10	0.10	>0.05	N	N
1984	25	6.00	0.21	>0.05	N	N
1984	26	0.50	0.39	<0.049	N	Y
1984	27	0.20	0.32	>0.05	N	N
1984	29	0.40	0.33	>0.05	N	N
1984	30	0.40	0.67	<0.047	Y	N
1984	32	0.20	0.12	>0.05	N	N

* Indicates whether (Y = yes, N = no) two or more significant consecutive correlations were observed in threshold test (see methods).

** Indicates whether (Y = yes, N = no) a threshold with significant r^2 was observed in threshold test (see methods).

Appendix L2. Estimated capelin density thresholds, correlations, and significance of correlations for Atlantic puffins on all surveys at Witless Bay.

Year	Survey Number	Estimated Threshold	r^2	Significance	S*	T**
1982	05	7.00	0.10	>0.05	N	N
1982	06	2.00	0.10	>0.05	N	N
1982	07	4.00	0.31	>0.05	N	N
1982	09	1.00	0.49	<0.025	Y	N
1982	10	4.00	0.35	>0.05	N	N
1983	01	2.00	0.08	>0.05	N	N
1983	02	3.50	0.44	<0.01	N	Y
1983	04	1.50	0.07	>0.05	N	N
1983	05	2.00	0.04	>0.05	N	N
1983	06	7.00	0.18	>0.05	N	N
1983	07	5.00	0.21	>0.05	N	N
1983	08	1.50	0.29	>0.05	N	N
1983	09	15.00	0.51	<0.007	Y	N
1983	10	2.00	0.10	>0.05	N	N
1983	13	3.00	0.39	<0.045	Y	N
1983	14	9.00	0.14	>0.05	N	N
1983	15	2.50	0.44	<0.01	Y	N
1983	16	3.00	0.24	>0.05	N	N
1983	17	2.00	0.17	>0.05	N	N
1983	18	2.00	0.11	>0.05	N	N
1983	19	6.00	0.33	<0.04	Y	Y
1983	20	4.00	0.43	<0.03	Y	Y
1983	21	5.50	0.40	<0.03	N	N
1983	22	5.00	0.71	<0.001	Y	Y
1983	23	3.00	0.87	<0.0002	N	N
1983	24	4.50	0.64	<0.002	Y	Y
1983	25	1.00	0.06	>0.05	N	N
1983	26	5.00	0.59	<0.003	N	Y
1983	27	27.00	0.14	>0.05	N	N
1983	28	5.00	0.38	<0.04	Y	Y
1983	30	3.00	0.15	>0.05	N	N
1983	31	2.00	0.73	<0.0004	Y	N
1983	32	1.00	0.22	>0.05	N	N

Appendix L2 continued. (Puffin thresholds).

Year	Survey Number	Estimated Threshold	r^2	Significance	S*	T**
1983	33	1.75	0.67	<0.001	Y	Y
1983	34	2.00	0.35	>0.05	N	N
1983	35	7.00	0.16	>0.05	N	N
1983	36	0.50	0.08	>0.05	N	N
1983	37	5.00	0.33	<0.04	N	N
1983	38	1.50	0.54	<0.006	N	N
1983	39	1.50	0.05	>0.05	N	N
1984	04	1.50	0.91	>0.05	N	N
1984	05	0.10	0.08	>0.05	N	N
1984	07	0.10	0.20	>0.05	N	N
1984	09	0.60	0.48	<0.02	Y	N
1984	10	0.20	0.89	>0.05	N	N
1984	11	0.20	0.23	>0.05	N	N
1984	12	1.00	0.76	<0.002	Y	N
1984	13	2.50	0.25	>0.05	N	N
1984	15	1.00	0.12	>0.05	N	N
1984	16	1.50	0.27	>0.05	N	N
1984	17	2.00	0.22	>0.05	N	N
1984	18	1.50	0.19	>0.05	N	N
1984	19	3.00	0.05	>0.05	N	N
1984	22	0.40	0.34	>0.05	N	N
1984	23	1.20	0.53	>0.05	N	N
1984	25	6.00	0.94	<0.0001	Y	N
1984	26	0.20	0.40	<0.046	N	Y
1984	27	0.60	0.34	>0.05	N	N
1984	28	0.20	0.99	<0.0004	Y	N
1984	29	0.40	0.57	<0.007	Y	N
1984	30	0.80	0.26	>0.05	N	N
1984	32	0.20	0.13	>0.05	N	N
1984	33	0.30	0.90	<0.0001	Y	Y
1984	34	0.20	0.25	>0.05	N	N
1984	35	1.00	0.65	<0.03	N	N

* Indicates whether (Y = yes, N = no) two or more significant consecutive correlations were observed in threshold test (see methods).

** Indicates whether (Y = yes, N = no) a threshold with significant r^2 was observed in threshold test (see methods).