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**Winter Distribution and Pre-breeding Survival of the
Thick-billed Murre, *Uria lomvia*, from the Northwestern Atlantic.
Implications for Management of the Newfoundland Turr Hunt.**

by
Garry Michael Donaldson

Thesis submitted to the
School of Graduate Studies and Research
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Université d'Ottawa
en vue de l'obtention de la maîtrise ès sciences à

L'institut de biologie d'Ottawa-Carleton



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ABSTRACT

New legislation which entrenches regulations of the turr hunt in Newfoundland into the Migratory Birds Convention Act, will require good knowledge of thick-billed murre (*Uria lomvia*) population biology for proper implementation. The impact of hunting on the population is determined by factors such as total bag, season length and timing, and the age of birds killed. These in turn depend on the temporal and spatial distribution of murrelets of different ages and from different colonies. To provide information on the distributions of murrelets in winter I analyzed recovery data from birds banded at colonies in the eastern Canadian Arctic and in Greenland.

Distributions of recoveries of birds banded at colonies on Coats, Digges, and Coburg Islands, at Cape Hay and in Greenland, showed some similarities in the timing of arrival in Newfoundland of different aged birds. Birds in their first winter were recovered in greater numbers than birds from older age categories and were usually recovered earlier in the season. Some similarities were also observed among colonies from similar geographic regions with respect to timing of arrival in Newfoundland. Birds from Hudson Strait colonies were recovered later in the hunting season than birds from other areas. At the same time, significant differences were detected between colonies located relatively closely to one another. Recovery rates of first winter and second winter birds from Digges Island were significantly lower than those for birds of the same age from the adjacent colony on Coats Island suggesting different spatial distributions of the young birds from the two colonies. Differences in the overwintering areas for adults from Coburg Island and Cape Hay, again located closely together, differed significantly with Coburg adults recovered in greater numbers in Newfoundland while Cape Hay adults were recovered most often in Western Greenland.

Solid estimates of annual survival for pre-breeding birds are required to calculate survival probabilities from fledging to breeding age, thus, allowing recruitment to be approximated. The latter is a key term in the population model used to monitor population flux. Using recoveries of birds banded on Coats Island, annual survival from fledging to first year was estimated at 0.53 using the program SURVIV. Based on the principle of parsimony, models were chosen using the Akaike Information Criterion and knowledge of the basic biology of the thick-billed murre. For the recovery estimates the best models were those which incorporated year-dependent recovery probabilities. Mark-recapture methods were used to calculate annual survival for older pre-breeders using SURGE. Models were selected using similar criterion to those used for recovery models. The best models were those which incorporated year-dependent recapture probabilities to account for variation in observer effort during data collection. Survival from second to third year was estimated at 0.83, from third to fourth year was 0.74, from fourth to fifth year was 0.86. The estimate from third to fourth year was considered to be an underestimate as a result of the high mobility of third year birds at the colony. Based on these survival probabilities, survival to breeding age, using the best estimates from band recoveries and resightings was estimated at 0.27.

RÉSUMÉ

La nouvelle loi qui régit les règlements de la chasse aux marmettes à Terre-Neuve à l'intérieur de la convention sur les oiseaux migrateurs nécessite une connaissance étendue de la biologie des populations de la marmette de Brünnich (*Uria lomvia*). L'impact de la chasse sur les populations de marmettes est lié à des facteurs comme les quotas de chasse, la chronologie et la durée des périodes de chasse, et l'âge des oiseaux récoltés. Ces facteurs dépendent, par ailleurs, de la distribution spatio-temporelle des marmettes d'âges différents et provenant de colonies distinctes. Afin d'étudier la distribution hivernale des marmettes, j'ai analysé les données de récolte des oiseaux bagués dans des colonies de l'est de l'arctique canadien et au Groenland.

Les oiseaux bagués sur les îles Coats, Digges et Coburg, au Cap Hay et au Groenland et récoltés à Terre-Neuve montrent des périodes d'arrivée sur les aires d'hivernage similaires en fonction de l'âge. Les jeunes de l'année ont été récoltés en plus grand nombre et plus hâtivement que les oiseaux plus âgés. Aussi, les dates d'arrivée sur les aires d'hivernage à Terre-Neuve des marmettes provenant de colonies situées dans les mêmes régions géographiques étaient similaires. Les oiseaux provenant des colonies situées dans le détroit d'Hudson ont été récoltés plus tard que ceux provenant des autres colonies. Par ailleurs, des différences significatives ont été observées entre des colonies relativement rapprochées. La récolte des jeunes de l'année et de ceux à leur deuxième hiver bagués sur l'île Digges était inférieure à celle des oiseaux d'âge semblable provenant de la colonie adjacente de l'île Coats ce qui suppose une distribution spatiale différente des jeunes de ces colonies. Bien que les colonies de l'île Coburg et du Cap Hay soient rapprochées, les aires d'hivernage des adultes provenant de ces colonies étaient significativement différentes; les adultes de l'île Coburg étant surtout récoltés à Terre-Neuve alors que ceux provenant du Cap Hay l'ont

majoritairement été sur la côte ouest du Groenland.

Afin d'obtenir une approximation du taux de recrutement, de solides évaluations du taux de survie annuel des individus non reproducteurs sont nécessaires pour évaluer leurs chances d'atteindre l'âge adulte. Le taux de recrutement est d'ailleurs une variable importante dans la modélisation de la fluctuation des populations. D'après la récolte des oiseaux bagués à l'île Coats et selon le programme SURVIV, le taux de survie des jeunes de l'envol à la première année est estimé à 0.53. Selon le principe de la parcimonie, les modèles ont été choisis en fonction du critère de l'information de Akaike. Pour l'évaluation des récoltes, les modèles les plus fiables ont été ceux qui tenaient compte de la probabilité de récolte de l'année en cours. Les méthodes de capture-recapture ont été utilisées pour évaluer le taux de survie annuel des individus non reproducteurs les plus âgés avec le programme SURGE. Le taux de survie de la deuxième à la troisième année a été estimé à 0.83, de la troisième à la quatrième année à 0.74, et de la quatrième à la cinquième à 0.86. Les meilleurs modèles prédictifs ont été ceux qui tenaient compte de la probabilité de recapture intra-annuelle en fonction de l'effort fourni lors de la récolte des données. L'estimation du taux de survie de la troisième à la quatrième année serait sous-estimée en raison des déplacements prononcés des individus de la troisième année aux colonies. En tenant compte de ces probabilités de survie et selon les meilleures estimations de retour des bagues et de l'observation des oiseaux bagués, les chances d'atteindre l'âge de reproduction sont estimées à 0.27.

CHAPTER 1 GENERAL INTRODUCTION

The thick-billed murre, *Uria lomvia*, is a pursuit diving seabird of the order Alcidae. It is the most numerous species of seabird breeding in the Arctic and is hunted by Canadians in large numbers, second only to the mallard duck, *Anas platyrhynchos*, in some years (Lévesque *et al.* 1993, Filion *et al.* 1993). Murres are of economic importance in Canada, especially for residents of Newfoundland where murres have been enthusiastically hunted for many decades. This hunt is significant in that it occurs predominantly in winter within a single province, without the regulations listed in the Migratory Birds Convention Act which protect other migratory game species. A small number of murres are also hunted by native Canadians but with insignificant effects to local breeding populations (Gaston *et al.* 1985). The importance of the species to Newfoundlanders and Inuit, and the need to impose regulations has been recognized by the Canadian government and demonstrates the need for a good understanding of thick-billed murre population biology.

In this thesis I investigate two aspects of thick-billed murre populations that are important to the management of the Newfoundland hunt: winter distribution and survival to breeding age. Knowledge of the distribution of birds in Newfoundland during winter is important for hunt regulation, particularly for setting season lengths and bag limits in different areas of the province. I present data based on band recoveries to investigate questions of age and colony specific distributions and relate these distributions to hunt management. Survival to breeding age is a critical component of any population model as it indicates the number of individuals that can be expected to recruit into the breeding population. Projections of productivity cannot be carried out without an

estimate of recruitment. Models currently in use for murre populations in the Northwest Atlantic, include estimates of this parameter along with estimates of adult survival, reproductive productivity, and population size (Croxall and Rothery 1991, Hatchwell and Birkhead 1991, Danchin and Monnat 1992, J. Chardine pers comm.). Here I present survival probabilities for pre-breeding birds based on band recovery and capture-recapture methods.

Turr Hunt:

The annual hunt of murre, or turrs as they are referred to in Newfoundland, is the most significant source of adult mortality for thick-billed murre in the Northwestern Atlantic population. It is believed to be responsible for more than seventy five percent of expected annual adult mortality (Elliot 1991). Other sources of mortality including predation, disease, reduced prey availability, ice conditions, weather, and a variety of human induced pressures such as hunting in places other than Newfoundland, entrapment in fishing nets, and mortality caused by oiling, account for the remaining proportion of deaths (Hudson 1985, Elliot 1991). Between 500,000 and 1,000,000 turrs have been harvested each year in the hunt which, historically, supplemented the diets of Newfoundlanders when other country foods, primarily caribou and cod, were not available (Elliot 1991, Elliot *et al.* 1991). With the relocation of remote communities and the increased accessibility of market foods in most places, there has been a reduction in need for the hunt, as the availability of food is now consistent throughout the year. Although some genuine need may still exist in Canada's poorest province where funds to purchase market foods are limited, the modern hunt persists mainly for sport and tradition.

Technological advances in boats and firearms have made the modern turr hunter much more effective than in the past. Traditional hunters had to row to the birds in dories and shoot with muskets which were very limiting compared to modern motor driven boats and shotguns. Efficiency has facilitated larger kills made with less effort in comparison to the historical hunts. Larger kills have also been made possible by the lack of regulations which currently apply to game bird hunting under the Migratory Birds Convention Act of 1917. Up until the winter of 1993-94, murrees could neither be sold for profit nor could they be hunted during the breeding season from April to August. This left a rather long hunting season, from early September through the end of March, during which daily bag limits and Migratory Game Bird Permits were not required.

The combination of reduced need by Newfoundlanders and greater mortality through increased hunting efficiency has created a need for the introduction of regulations to control the hunt. A clear understanding of population dynamics, demographics, and the role the turr hunt is likely to play in these processes is needed before regulations, just for both hunter and murre, can be realistically designed.

During the 1993-94 hunting season, a more stringent management plan was implemented by the Canadian Wildlife Service. It imposed a reduced hunting season of three months based on the time period murrees are most likely to be located in particular areas, and a bag limit of 20 murrees/day. These measures, along with better control of illegal market hunting are expected to reduce the annual harvest by 50% to between 300,000 and 450,000 birds (J. Chardine pers. comm.). This management plan was based on a standard population model which includes some parameters which have been crudely estimated out of necessity. For, example, population size estimates rely on labour intensive monitoring of a large number of colonies, and are therefore difficult to determine

accurately. Another important parameter of the model, survival of young murrelets between colony departure and age at first breeding is currently being estimated until a more exact value can be determined. Other demographic factors such as the spatial and temporal distribution of murrelets around Newfoundland may play an important role in management decisions. An understanding of these parameters will better able hunt managers to anticipate the effects of season lengths in various areas around Newfoundland and Labrador.

Thick-billed Murrelets:

Thick-billed murrelets breed in summer months on cliff habitat at colonies located at high latitudes throughout the northern hemisphere. At these colonies, breeding pairs lay a single egg which hatches after roughly thirty two days. The chick is fed on the ledge for a period of about three weeks after which it departs for the sea with its male parent. The chick-adult pair then begins its migration to the wintering area, mostly by swimming as the chick will not develop flight feathers for a number of weeks. Murrelets winter not far from the southerly extent of winter pack ice. Murrelets breeding in the Canadian Arctic winter predominantly off the coast of Newfoundland as far south as the tip of the Grand Banks (Brown 1989). Chicks departing the breeding colonies will not return until their second year. Murrelets are a long lived species with low annual production and thus are vulnerable to chronic disturbances, such as the effects of contamination by xenobiotic compounds, in their environment. This is a further argument for an increased understanding of murrelet population dynamics.

Many murre populations world wide are currently declining as a result of a number of natural and man-made influences (Nettleship and Evans 1985). Populations of common murres in the Shetland Islands in Northern Scotland have declined since 1982, indicated by decreases in counts of birds at breeding colonies there (Heubeck *et al.* 1991). Birds from this population have been affected by a variety of human-based stresses. Entrapment in fishing equipment in Scandinavia and mass starvation, probably due to depletion of food resources through over fishing by humans, have been identified as the cause of the decline (Heubeck *et al.* 1991). Declines have also been recorded at common murre colonies in Norway and are thought to be the result of drowning of birds in cod and salmon nets (Strann *et al.* 1991).

In Greenland, hunting of adult thick-billed murres at the breeding colonies has caused a severe decline in numbers, to the point of extinction in some places (Salomonsen 1979, Evans and Kampp 1991, Falk and Durinck 1992). Despite these declines, Canadian populations appear to be stable, showing no sign of decrease at colonies that have been monitored in the recent past. The colony at Coats Island has in fact expanded since 1972 although it is believed to be stable at present; however, this may not likely be representative of the population as a whole (Gaston *et al.* 1993). The nature of the impact anthropogenic stresses are imposing on Canadian murre populations requires a good current understanding of population dynamics and demographics. Accurate knowledge of the status of current murre populations can be used as a base from which time series data may indicate population trends in the future.

Winter Distributions of Thick-billed Murres:

Data from the recovery of banded birds has been a traditional method to establish geographical distributions of birds including seabirds and waterfowl (eg. Mead 1974, Anderson 1975, Gaston 1980, Ewins 1988, Francis and Cooke 1992). However, other methods of following birds do exist and the determination of thick-billed murre movements during the winter need not rely solely on data from band recoveries. Seabirds spend much time far out at sea where they are unlikely to be recovered; thus, band recoveries may give an incomplete picture of seabird distribution. For murre, this means that recoveries will only give an indication of movements of the fraction of the population that uses inshore waters. For the purposes of management of the turr hunt, this is sufficient as it is these birds that are affected. It must be kept in mind that birds that remain farther out at sea will not be recovered. Surveys from fixed wing aircraft and from ships were carried out on the continental shelf in the early 1980's (Brown 1989). These surveys show large concentrations of thick-billed murre off Central Labrador in early fall (September). By early winter, murre were seen to move south as far as Notre Dame Bay and the northern Grand Banks (October-December). Late winter (January-March) distributions indicated concentrations of murre south of Notre Dame Bay especially on the Grand Banks. These surveys gave good indications about the presence of birds at particular times of the year but cannot resolve possible differences in distribution among demographic groups and colonies of origin.

Murre harvest estimates based on postal surveys carried out in five years in the 1980s gave another indication of distributions other than can be gained from band returns or observational surveys at sea. These distributions are derived from turr hunters which makes the information gained from surveying hunters directly applicable to management of the hunt. Survey returns showed that

the peak harvest occurred in November in most of those years, after which the numbers of birds shot stabilized at a somewhat lower level for December-March (Elliot *et al.* 1991). Elliot *et al.* also made age determinations based on a dockside survey of murre as they were brought to shore. First winter birds were distinguished from older birds primarily through a series of skull measurements (Gaston 1984). The breakdown of age categories at the dockside indicated that first winter birds made up a large proportion of the birds harvested until December (Elliot *et al.* 1991). Previously, it had been suggested that young birds arrive in Newfoundland in advance of older birds (Gaston 1980), which could partly explain their prevalence in the first few months of the hunt. After the end of December, the proportion of first winter birds decreased and larger numbers of older birds were collected. The surveys conducted by Elliot *et al.* gave important insight into differences in age distributions in the areas accessible to hunters but were not able to distinguish differences in distribution based on colony of origin.

Given the different distances that murre from differing colonies must travel and given the possibility that yearling birds may arrive in Newfoundland before older birds, it is possible that there may be a partitioning on the wintering grounds with respect to age and colony of origin. If this is indeed the case, knowledge of when and where birds of a particular age and colony of origin are expected to occur could be valuable for management of the population. For example, the population impact of an oil spill near a colony could be ameliorated through a ban on hunting in areas where large concentrations of breeders from that colony are known to occur in the winter.

For long lived species, such as the thick-billed murre, it is those individuals that are currently breeding that are most valuable to the population and should be the focus of management efforts. Most birds will not breed until age 4 or 5 (Gaston *et al.* 1994), and the normal annual survival of

younger birds may be lower than that of breeders. Survival to breeding age for thick-billed murres has been previously estimated at 0.19-0.53 (Birkhead and Hudson 1977); consequently, many young murres will not survive to recruitment and the reproductive potential of a younger bird is consequently lower than that of an adult.

Survival:

In an ideal situation, an analysis of survival would be set up such that the fate of all individuals could be determined. This complete registration of individuals is rarely attained except for studies in human or veterinary medicine. For wildlife biologists, populations under study are often open and individuals observed initially may elude observation in future time periods. This incomplete registration has been dealt with using two major approaches. A portion of marked individuals are either recorded at death (recovery) or repeatedly as live individuals (recapture).

Annual survival probabilities based on recoveries have been estimated from a variety of approaches. One widely used method has been the use of composite dynamic life tables to analyze data from the recovery of marked individuals at death. Results from these studies have been found to be inaccurate as a result of data not adhering to some fairly restrictive and unrealistic assumptions (Burnham and Anderson 1979). The method requires that annual mortality rates be constant over time, that recovery rates remain a constant proportion of mortality rates, and that no individuals are alive at the end of the study. The first two requirements are not usually met within most populations and the third is very restrictive for long lived species such as the thick-billed murre because individuals may live for decades after the end of the banding program. Burnham and Anderson (1979) tested the assumptions of this method using 45 different sets of waterfowl data and found that

the assumptions were not met in any. Violation of the assumptions produced overestimated first year mortality rates and an artifactual increase in adult mortality with time. They suggested that this method not be used and caution be exercised when interpreting studies based on composite life tables. These views were also expressed by Anderson *et al.* (1981). Instead, newer models which are less sensitive to violations of assumptions and will allow for inter-year variation in recovery probabilities are preferred (Brownie *et al.* 1985, White 1983). Analyses of this sort are favourable for species like seabirds where birds in younger age classes might not be seen otherwise for a number of years. For most seabirds, this is the only method to obtain crucial estimates of juvenile survival.

The other class of survival models rely on data from the repeated observation of marked individuals over time, or recaptures. The models most widely used have built on methods used originally to determine population size (Cormack 1964, Jolly 1965, Seber 1965), recently they have been used more frequently to estimate survival and as such are more flexible to violations of the underlying assumptions (Begon 1983). Because individuals are recorded on several occasions, precision of estimates derived from this method are greater than those of recovery methods where individuals can contribute to the data set only once (Lebreton *et al.* 1993). Recently, software has been developed that is able to adjust for small violations of the assumptions of standard survival models based on recoveries (White 1983, Brownie *et al.* 1985) or the resighting of live individuals (Colbert *et al.* 1987, Pollock *et al.* 1990, Lebreton *et al.* 1992).

Survival is a dynamic quality of a species or population and may be affected by a host of environmental or demographic factors. Newer methods of survival probability estimation have allowed for a number of studies which look far beyond calculation of average annual survival for a species. Severity of drought conditions in Western Africa has been correlated with changes in adult

annual survival probabilities of the White Stork (Kanyamibwa *et al.* 1990). Aebischer and Coulson (1990) suggested that mean annual survival of adult Kittiwakes was independently affected by sex, breeding experience, and position of the nest within the breeding colony. Long-term studies of survival have indicated that, for some species, annual survival rates may change over time. This has been demonstrated for Kittiwakes (Coulson and Thomas 1985, Aebischer and Coulson 1990) and Lesser Snow Geese (Francis *et al.* 1992b). In the case of Shags breeding in the Firth of Forth, long term banding of individuals allowed monitoring of survival through a population crash. For these seabirds, estimation of adult survival showed no significant change through the crash and was not implicated as the cause. Depleted food resources were thought to have caused a delay in laying dates and a decrease in juvenile survival, resulting in the observed population decline (Aebischer 1986).

Survival has also been demonstrated to vary with age. Age specific survival has been demonstrated in a variety of species; specifically, young individuals have a lower probability of surviving into the next year and adults show the greatest probability for survival. For Lesser Snow Geese, Francis *et al.* (1992a) demonstrated lower than adult survival rates for birds up to two years old. For many birds, significant mortality certainly occurs in the period immediately after fledging (Tuck 1961, Birkhead and Hudson 1977) when young inexperienced birds are vulnerable to risks imposed by predation, quality of parental care, food availability, weather, and a host of other environmental variables. Surveys of beaches in Oregon revealed a consistently higher recovery of first year common murrelets compared to older birds after fledging had occurred (Bayer *et al.* 1991). Eventually, if individuals survive long enough, birds will achieve adult survival probabilities; however, the determination of exactly when this occurs has been difficult to calculate given the problems associated with following the outcomes of marked individuals over time. For seabirds this

is difficult because mortality usually occurs at sea and therefore goes undetected, which for many seabird species is problematic. Such is not the case for thick-billed murres because many are recovered in the turr hunt.

Hudson (1985) describes studies that estimate the survival of young thick-billed murres to breeding age which may range from 0.19 to 0.53, compared to adult survival which was estimated at 0.91 (Birkhead and Hudson 1977). These estimates were based on life table estimates, the analysis for which is limited in terms of overall robustness and suffers the drawbacks noted above (Lebreton *et al.* 1993). A detailed assessment of pre breeding survival, one that can incorporate the insights into survival in the first two years of life that recovery methods can give, with the greater precision offered by mark-recapture methods, has yet to be performed for thick-billed murres.

Thick-billed murres are phylopatric and site tenacious (Noble *et al.* 1991); therefore, surviving birds can be expected to breed on a site in the colony close to where they were hatched and will be expected to return to the same breeding location year after year. Phylopatry is common among auks, 87% of Puffins on the Isle of May in Scotland, banded as chicks and subsequently observed breeding on the colony bred within 100m of where they were banded (Harris 1983). Likewise, most non-breeding thick-billed murres attend the colony close to their natal site (discussed in chapter 4). This type of behaviour is an advantage for mark-recapture studies where observation sites are limited and only a portion of the population to be observed can be seen as is the case with this study.

Coats Island:

Much of the information presented in this thesis is derived from thick-billed murres banded at the Coats Island breeding colony located in northern Hudson Bay ($62^{\circ}57'N$, $82^{\circ}00'W$)(see figure 2.1). Coats Island supports 30,000 breeding pairs of thick-billed murres located in two sub-colonies located on adjacent headlands (see Figure 4.1). Roughly equal numbers of murres breed in each of the two sub-colonies (Gaston *et al.* 1993). Research efforts have been centred on the western sub-colony as the accessibility of these birds is significantly greater than those in the east sub-colony. Recovery data do not require as great of a degree of accessibility, distributions were estimated from the recoveries of murres banded at several colonies in the western Atlantic (see Figure 2.1).

In summary, this study will focus on some of the parameters which are important to effective management of thick-billed murres in the Newfoundland turr hunt. The following concerns are addressed in subsequent chapters:

- In chapter 2, the distributions of hunted murres, based on recoveries of banded birds, are assessed. This chapter suggests when and where birds are recovered by hunters. Data from a number of colonies are examined to determine whether age and colony of origin affect winter distributions.

- In chapter 3, band recovery data is used to determine survival probabilities for thick-billed murres during their first winter with consideration of the assumptions of the survival methods employed.

- In chapter 4, survival probabilities of pre-breeding murres based on the resighting of individuals at the breeding colony are estimated while addressing the method assumptions. Estimates of survival from fledging to age of first breeding are also given.

- In chapter 5, the significance of winter distribution, and survival of pre-breeding thick-billed murres, for the management of the Newfoundland turr hunt is discussed.

CHAPTER 2.
WINTER DISTRIBUTIONS OF THICK-BILLED MURRES
FROM THE EASTERN CANADIAN ARCTIC
AND FROM GREENLAND.

INTRODUCTION:

The implementation in 1956 of legal hunting rights in Newfoundland for turr hunters through the Migratory Birds Convention Act (MBCA) was done without any provision for bag limits and within a lengthy, seven month season (see Chapter 1). Hunting is one of the largest sources of mortality for adult thick-billed murres (Elliot *et al.* 1991) and under previous regulations, management of the species was difficult given the limited options. Recent movements towards legislation which would better restrict the hunt have brought about the need for a plan from which management of the murre population could be facilitated.

In 1992 and 1993, the turr hunt was closed early in areas of Newfoundland under section 37 of the MBCA which allowed the Minister of the Environment to vary hunting quotas and seasons for conservation purposes (Chardine 1994). It was argued successfully that hunting levels had become excessive in these areas resulting in the first modifications of turr hunt regulations. Section 37 was then used in the 1993-94 hunting season to restrict the hunt on a province-wide basis (Chardine 1994).

New restrictions, expected to reduce the annual harvest by 50%, were implemented with the support of the majority of hunters. The reduction was achieved by shortening the hunt to a three-

month period in three new management zones. The timing of the hunt in each zone was chosen with the help of hunters to coincide with the times of year when murre were plentiful in each area. In addition to the shortened season length, bag limits of 20 murre/hunter/day and a possession limit of 40 murre were set (Chardine 1994).

The regulations adopted through section 37 are temporary until the Migratory Bird Convention, the international agreement with the U.S. from which the Canadian act arises, can be amended. The successful implementation of the amendment to the MBCA will require population monitoring and, if needed, alterations in hunting pressure to ameliorate adverse effects caused by the hunt or any other threat to population numbers. Thick-billed murre segregate into separate breeding populations at colonies each summer and may require unique management strategies should conservation issues develop at specific colonies. Knowledge of expected winter distributions of birds from different colonies of origin is essential for the execution of policy, so that the full impact of hunting in specific areas in Newfoundland at particular times of the year will be known. In this chapter, I address the following distribution questions based on data from recoveries of banded birds from colonies in Northeastern Canada and Greenland:

- 1) Does the temporal distribution of recoveries from a given colony vary according to age? Are there differences among colonies?
- 2) How do numbers of recoveries of murre vary among geographical areas around the island of Newfoundland and does age affect their geographical distribution? Are there differences among colonies?

METHODS:

The Canadian Wildlife Service has been banding thick-billed murres at colonies across the Eastern Canadian Arctic since 1954. To date, the largest banding effort has been at the colony on Coats Island (62°N, 82°W) in northern Hudson Bay. Banding has been carried out to a lesser extent at other colonies including: Digges Island (62°N, 77°W), Hantzsch Island (61°N, 65°W), The Minarets (Reid Bay, 67°N, 62°W), Cape Hay (73°N, 80°W), Prince Leopold Island (70°N, 90°W), and at Coburg Island (75°N, 79°W), (see Table 2.1 and Figure 2.1).

Table 2.1 Banding efforts in the eastern Canadian Arctic by the Canadian Wildlife Service.

Colony	Banding Years	Adults Banded	Chicks Banded
Cape Hay	1957	1363	1137
Coats Is.	1981, 1984-91	1231	17654
Coburg Is.	1981, 1987	0	4756
Digges Is.	1955, 1979-82	2596	13107
Hantzsch Is.	1982	72	448
The Minarets	1985	117	35

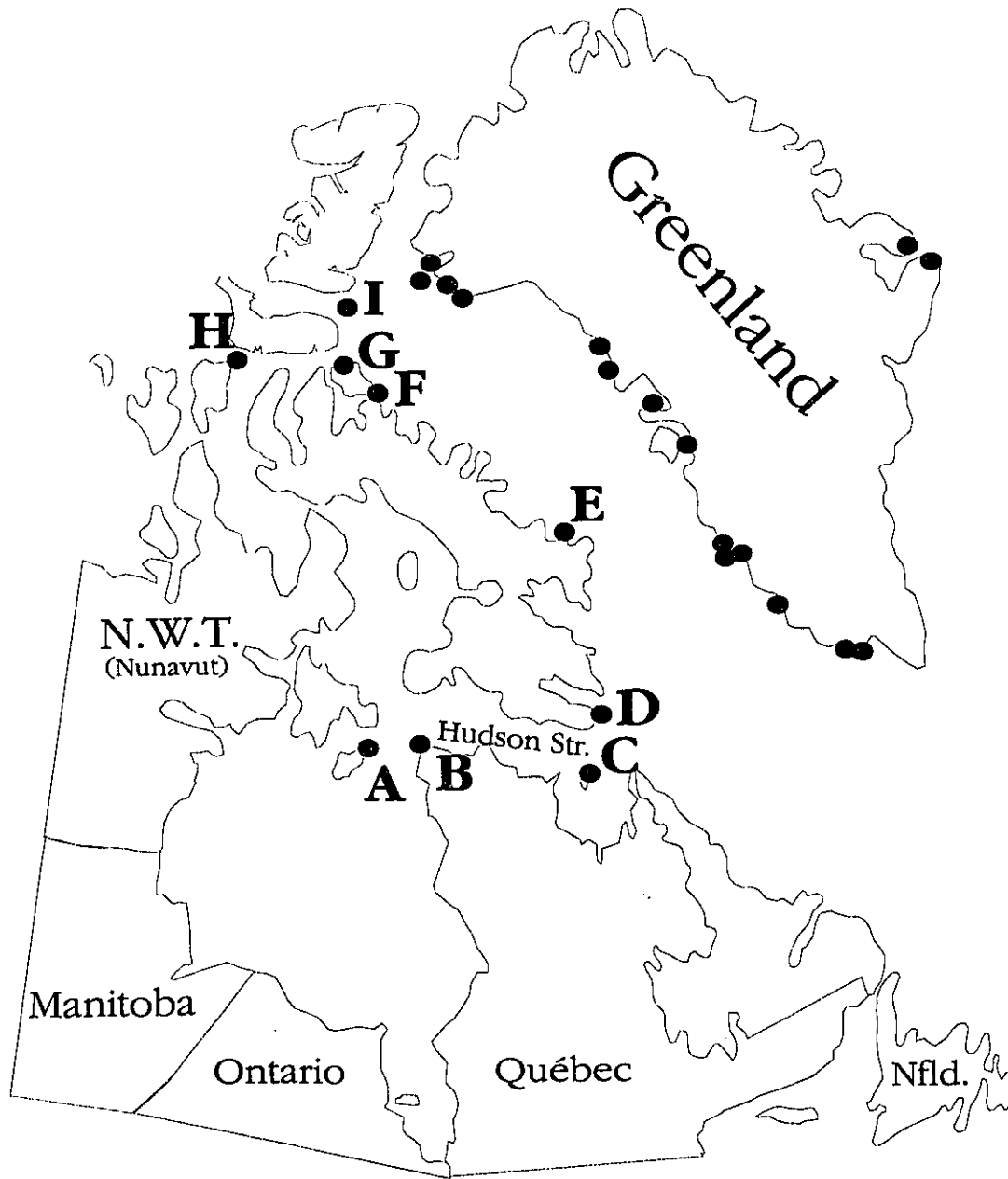


Figure 2.1 Distribution of thick-billed murre breeding colonies in the eastern Canadian Arctic and Greenland. Canadian colonies are as follows: Coats Island (A), Digges Sound (B), Akpatok Island (C), Hantzsch Island (D), Reid Bay (The Minarets)(E), Cape Graham Moore (F), Cape Hay (G), Prince Leopold Island (H), and Coburg Island (I)

Table 2.2 Numbers of adults and chicks banded in each season at the colony on Coats Island.

Year	Adults	Chicks
1981	14	1584
1984	141	1453
1985	134	1619
1986	278	2237
1987	161	2250
1988	193	2686
1989	80	2408
1990	88	1331
1991	142	2086
total	1231	17654

Recent banding operations at Coats Island began in 1981. Banding of both chicks and adult birds has been carried out annually since 1984 (Table 2.2). Other colonies have been banded at various times since the mid 1950's (Table 2.1). Murres banded prior to the mid-1970's received circular aluminum bands, standard to all those used by the joint US Fish and Wildlife Service (USFWS)/ Canadian Wildlife Service (CWS) banding programme. Aluminum was used because of its low mass. However, they were found to wear significantly if in place for a number of years and were subject to corrosion in salt water. For long lived birds like murres, there was a potential problem with band loss a number of years after banding as the aluminum wore down. After the mid-1970's, murres from all colonies listed were banded with stainless steel USFWS bands, greatly reducing the risk of band loss as stainless steel bands show little sign of wear even after many years (A.J. Gaston pers. comm.). Bands used at Coats Island in 1985 consisted of roughly half stainless steel USFWS bands and half special stainless steel Alcid bands. After 1985 all murres from Coats Island received the special stainless steel bands. They are triangular, allowing the entire band number to be stamped on two of the flat surfaces. Numbers on these bands are much easier to read

than on the standard circular bands because the likelihood of observing the entire band number is greatly increased. Each special band carried the address "CWS, Box 9158, St. John's, NF." Reports of recovered birds were directed to the St. John's office and then transferred to the Bird Banding Laboratory of the USFWS in Washington. The regular USFWS bands instruct the finder to "AVISE BIRD BAND, WRITE WASHINGTON D.C. USA."

Recoveries contained in the USFWS/CWS database up to and including the winter of 1991-1992 were used for these analyses. Only recoveries from Newfoundland and Labrador were considered because the focus of these analyses is to provide input for the management of the turr hunt. The few outside recoveries are of little value in this respect. For most colonies, very few murrens are recovered outside of the province (Table 2.3); consequently, few data were discarded because of this constraint. An exception to this was made for recoveries from Cape Hay and Coburg Island where an unusually large proportion of recoveries were made in Greenland (Table 2.3). These recoveries were dealt with in separate analyses.

Table 2.3 Recovery locations of thick-billed murrens banded at colonies in the Canadian Arctic.

Colony	No. of recoveries	% recovered		
		Newfoundland	Greenland	Other
Cape Hay	192	23.0	76.5	0.5
Coats Island	515	93.6	1.9	4.5
Coburg Island	176	80.1	15.3	4.5
Digges Island	199	79.9	7.5	13.1*
Hantzsch Island	11	81.8	9.1	9.1*
Prince Leopold Is.	6	0.0	100.0	0.0

* predominantly birds hunted by residents of communities adjacent to the colonies

Additional information was derived from the large number of murrelets banded in western Greenland. Recovery information from murrelets banded in Greenland and recovered in Newfoundland was supplied by Dr. Kaj Kampp from the Danish Zoological Museum in Copenhagen.

Assuming no reporting errors in the particular details of a recovery, the information contained can yield important data on the locations of individuals at various times. For these analyses, I have assumed no errors in reporting, and, wherever possible, the data in the USFWS database were checked against information from the Canadian Wildlife Service office in St. John's, Newfoundland. Any discrepancies (of which there were very few) were corrected in favour of the CWS information, as this was the original data source and is therefore least likely to contain transcription errors.

Selection of Data

When a recovery is reported, the finder must indicate how the bird was located from a list of categories from the North American Bird Banding manual. The accuracy of the recovery particulars for the categories, "found dead", "oiled" or "recovered by unknown means" birds is hard to evaluate if birds have been floating dead for an indeterminate amount of time. Birds falling into these categories accounted for less than two percent of recoveries and were excluded from the analyses. Because the questions that are examined have age related components, the first few recovery seasons for Coats Island have been omitted in order to better represent the older age classes. In addition, recovery enhancement programs in place by the Canadian Wildlife Service in 1984 and 1985, may have changed the recovery patterns for those years. Thus, recoveries from 1987 to 1991 only (representing five hunting seasons) are included from banding efforts at Coats Island. Other colonies in the Canadian Arctic have been banded only a few years; consequently, all data from birds

banded at Cape Hay and on Coburg Island, Digges Island, Prince Leopold Island, and Hantszch Island were used.

For the analysis of monthly distributions, only those recoveries for which the month of recovery was known were included. Recoveries were categorized by month and by age. The hunting season for murrelets off Newfoundland extends from the beginning of September to the end of March. Only 3 recoveries have been recorded in September since banding began in 1981. Consequently, analyses were restricted to the period of October-March. For most analyses, small samples in the fall and early winter required the lumping of months of recovery. Where possible, three categories were formed, October-November, December-January, and February-March. Data from some colonies were too sparse to analyze with three month categories, these colonies were analyzed with months combined into two categories: early (October-November-December) and late (January-February-March). The categories used are indicated with the analyses for each colony.

Age classes were combined in all cases to create three categories: first winter, second winter, and birds in their third winter or greater. The latter category includes any recovered birds that were banded as breeding adults on the colony. Preliminary analysis by year suggested that there was no significant difference in the pattern of recovery for ages greater than two years.

Data were analyzed using a contingency analysis. Because of cell counts that produced an unacceptable number of expected counts that were too low (Bishop *et al* 1975), a multivariate approach categorising recoveries according to age, month of recovery, and year of recovery, was not possible. Instead, a series of two dimensional contingency tables, usually collapsed between years, were used. An adjusted alpha = 0.025 was adopted in order to reduce the possibility of type I errors resulting from multiple comparisons.

For the analysis of recovery distributions by area, only recoveries for which the recovery location was documented were included. Areas were created to correspond as closely as possible to the murre management zones described by Elliot *et al.* (1991). This allows the comparison of recovery distributions with previously determined harvests in each recovery area. The zones were derived from those used for fisheries management in the province and then modified to reflect the biology of the thick-billed murre and local variations in hunting pressures (R.D. Elliot pers. comm.) For some of the areas described by Elliot, there were too few recoveries to permit analysis. Consequently, area A integrates the data from Labrador, the west coast of the Northern Peninsula, and Notre Dame Bay (Figure 2.2) all of which were treated separately by Elliot *et al.* (1991). Bonavista Bay makes up murre recovery zone B. Area C comprises Trinity and Conception Bays. Area D includes the eastern and southern coasts of the Avalon Peninsula and Placentia Bay. The remainder of the southern coast makes up area E. Only 4 of the 515 recoveries came from the west coast of the island which is not a traditional area for the turr hunt (P. Ryan pers. comm.). Recoveries from this part of Newfoundland were not considered in these analyses.

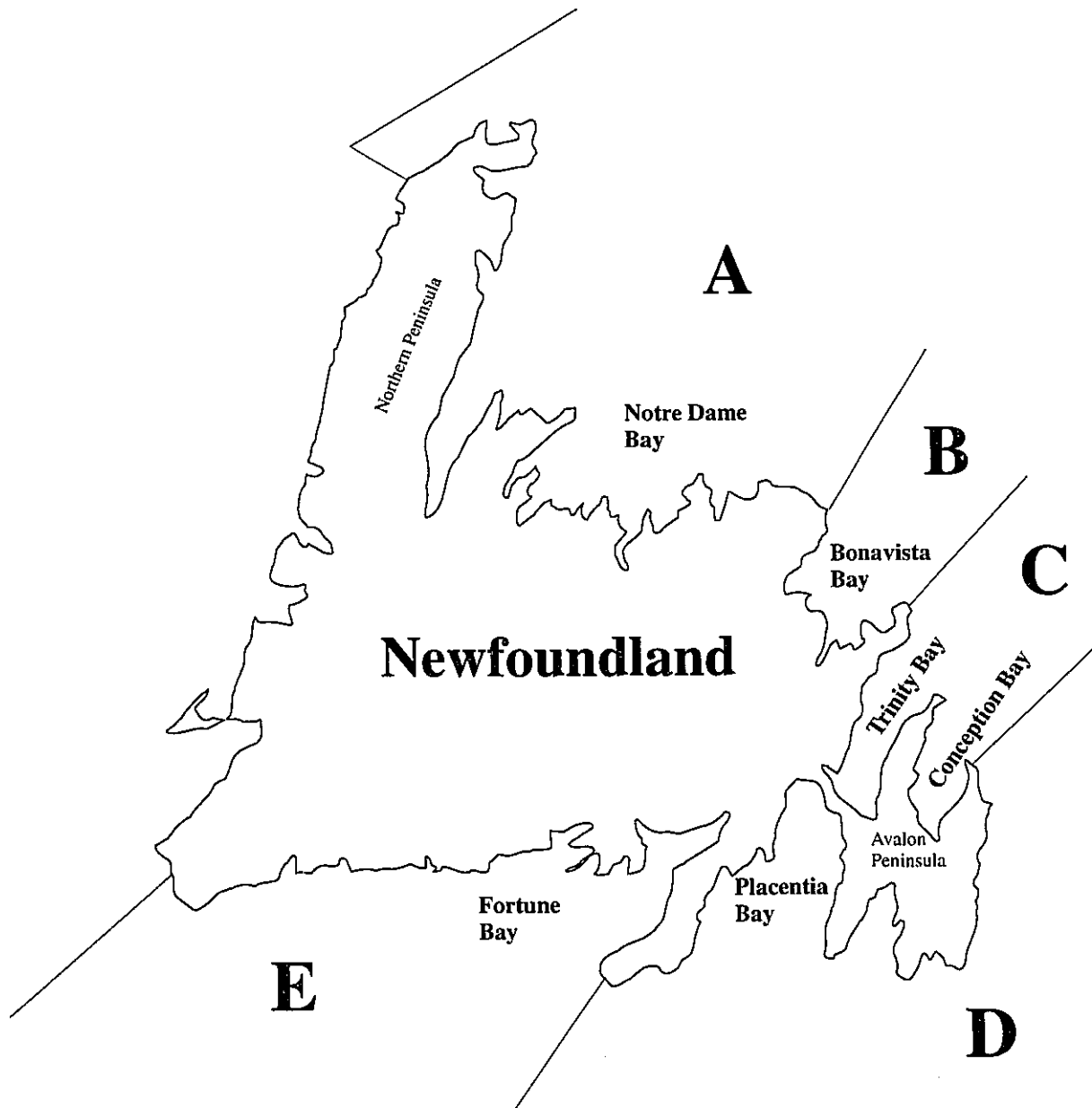


Figure 2.2 Areas used to describe spatial distributions of recoveries. "A" included recoveries in Labrador (not shown).

Inter-colony Comparisons

In almost all cases, the recovery patterns of second-year murre were intermediate between those of first and third year or greater murre and were never significantly different from either distribution on their own (see below). Consequently, inter-colony comparisons were restricted to two age categories: first years and, third year or older.

Due to the small number of first year recoveries from Digges Island and Cape Hay, data from these colonies were not included in inter-colony comparisons of first-year murre. Murre at Coburg Island were banded in 1981 and 1987, so in order to minimize the biases introduced by inter-year variation only data from those two years were included from Coats Island. As it was not possible to extract data for the Greenland sample by year, all recoveries were included. Because of the large number of first year recoveries from Coats Island, Coburg Island, and Greenland, month categories did not have to be combined for the first year temporal analysis.

Numbers of third year or older murre from Cape Hay and Digges Island were sufficient for their inclusion in the inter-colony comparison of third year or older birds with those from Coats Island, Coburg Island, and Greenland. Because older birds may be recovered over several hunting seasons, the effects of year are masked by the number of years over which data is collected, unlike first year birds which are only recovered in the hunting season following banding. Thus, for older birds, all years of data available for analysis were combined to increase sample sizes.

RESULTS:

Banding

Between 5 and 95 thick-billed murre recoveries from Coats Island have been reported annually since 1981 (Table 2.4). With the exception of the 1990 banding year, all cohorts were recovered in greatest numbers as first year birds. The proportion of birds recovered at this age varied between 2.7% (1984) and 0.7% (1990) of the number of chicks banded (Table 2.5). Taking the recoveries of birds in their fifth year or younger for the banding years 1984-1987, of 262 recoveries, 58% were in the first, 25% in the second, 8% in the third, 6% in the fourth and 2% in the fifth year. Numbers of first years recovered represented approximately double the number of older birds in all seasons except 1990-91 (Table 2.4).

Table 2.4 Recoveries in Newfoundland categorized by age at recovery for hunting seasons from 1981 to 1991. Data are based on banding done at Coats Island in 1981 and 1984-91. "A" denotes birds banded as adults.

Recovery Season	Age									Total
	1	2	3	4	5	6	7	8	A	
1981-82	10							0		10
1982-83	9							0		9
1983-84		5						0		5
1984-85	39		5					0		44
1985-86	37	20		4				6		67
1986-87	20	13	2		2			1		38
1987-88	57	18	10	4			1	5		95
1988-89	35	15	7	3	2			0	4	66
1989-90	23	10	1	1	1	1		3		42
1990-91	9	15	12	9	3	4	2	8		64
1991-92	20	9	3	3	0	0	0	1	2	38

Table 2.5 Percentage of the number of chicks banded at the colony on Coats Island and recovered in Newfoundland at ages from their first to their fifth winter.

Banding Year	% Recovered at Age				
	1	2	3	4	5
1984	2.7	1.4	0.1	0.3	0.1
1985	2.3	0.8	0.6	0.2	0.1
1986	0.9	0.8	0.3	0	0.1
1987	2.5	0.7	0	0.4	0
1988	1.3	0.4	0.5	0.1	
1989	1.0	0.6	0.1		
1990	0.7	0.7			
1991	1.0				

Temporal Distributions

Coats Island

The number of birds banded at Coats Island that were subsequently recovered in Newfoundland increased over the hunting season as shown in Figure 2.3 (appendix, Table A1). This pattern is different from that found for murrelets from all colonies by Elliot *et al.* (1991) where the peak kill of first year birds in the turr hunt occurred in November and in subsequent months made up a noticeably smaller proportion of the total kill. For birds banded on Coats Island, the peak month of recovery for first year birds was January; second year and older birds were recovered most often in February. Although all age classes appeared to behave similarly in relation to time of year, significant differences were detected among the three age categories ($\chi^2_4=13.93$, $p=0.008$), using three month categories (October-November, December-January, and February-March). Further breakdown of this analysis indicated that the significance is probably the result of differences between third year or greater murrelets and the younger two age categories (1 vs 2: $\chi^2_2=2.69$, $p=0.261$; 1 vs 3+: $\chi^2_2=10.34$, $p=0.006$; 2 vs 3+: $\chi^2_2=7.16$, $p=0.028$).

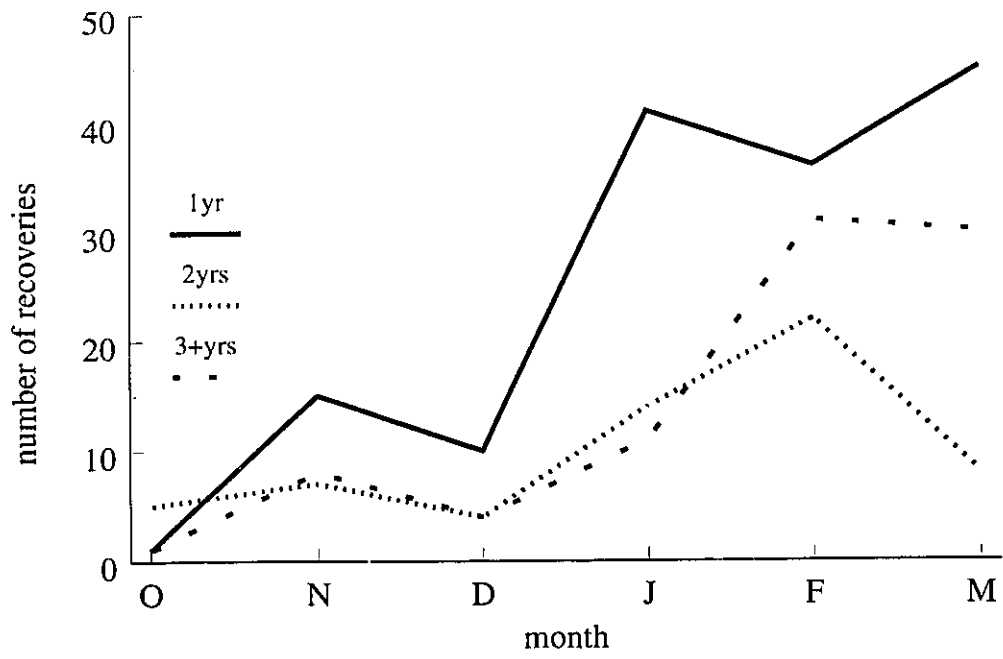


Figure 2.3 Temporal recovery distribution for Coats Island murrelets in their first, second, and third year or greater.

Digges Island

Based on the 5110 chicks banded between 1979 and 1982, birds in their first and second years were recovered fairly evenly over the hunting season but both were recovered in low numbers. Of all chicks banded on Digges Island, 0.2% were recovered in both their first and second year while 0.7% were recovered in their third winter or later (Figure 2.4, appendix Table A2).

A comparison of recoveries from banding on Coats and Digges islands was carried out using only the data derived from banding in 1981 and 1984 at Coats Island and from Digges Island in 1979-82. Compared to recoveries of similarly aged birds from Coats Island, recoveries of the younger two age classes from Digges Island were low (Table 2.6). This difference in recovery rates between the two colonies was significant for murrelets in their first year, and in their second year, but not for birds in their third or greater winter. Digges Island birds in their third year or older, like those from Coats Island, were mainly recovered after December (Figure 2.4). For Digges Island, there was no significant difference among age classes in the proportions recovered in early and late periods ($\chi^2_2=7.12$, $p=0.029$, $\alpha=0.025$).

Table 2.6 Comparison of the proportion of murrelets recovered from Coats and Digges Islands.

Age	% recovered		χ^2_1	p
	Coats	Digges		
1	1.6	0.2	53.26	<0.0001
2	1.0	0.2	23.55	<0.0001
3+	1.0	0.7	2.35	0.13

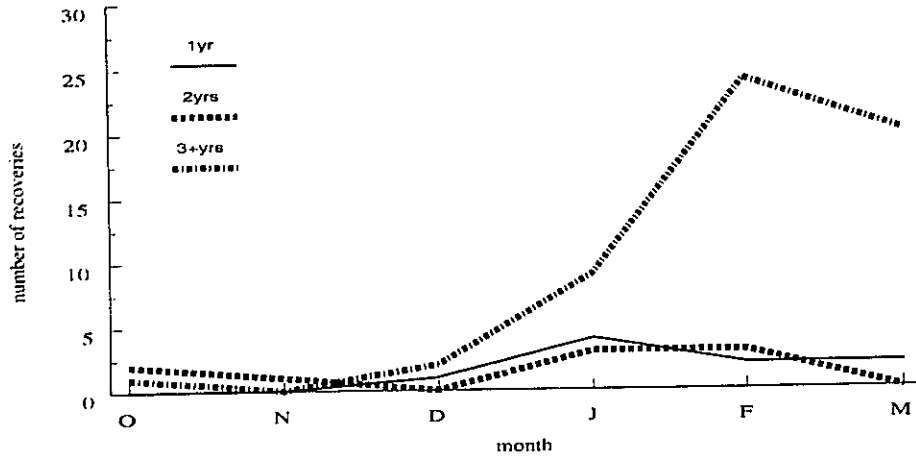


Figure 2.4 Temporal distribution of recoveries from birds banded on Digges Island in the period from 1979 to 1983. First, second and third year or greater murre are indicated.

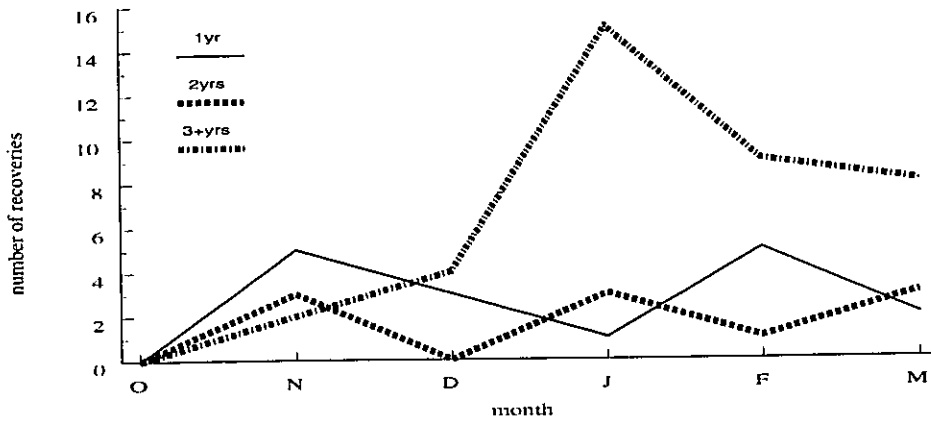


Figure 2.5 Temporal distribution of recoveries from birds banded on Digges Island in 1955. First, second and third year or greater murre are indicated.

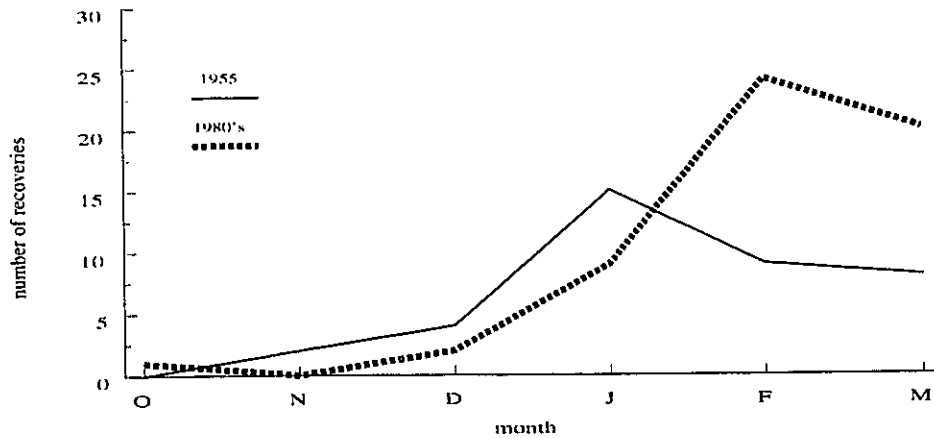


Figure 2.6 Comparison of temporal recovery distribution from banding efforts on Digges Island in 1955 and 1979-83. Only recoveries of murre in their third year or greater were used.

The murrelets banded in 1955 by Leslie Tuck at Digges Sound offer an interesting inter-decadal comparison of the distributions of birds in the 1950's as compared to those in the 1980's. As with the recoveries in the 1980's, relatively few first and second year birds were recovered from the banding effort in 1955 as compared to birds in their third winter or greater. Most murrelets in the older age category were recovered in the January-March period with the greatest number of birds being reported in January (Figure 2.5, appendix Table A3). The proportions of early and late recoveries did not differ significantly among age classes ($\chi^2_3=6.83$, $p=0.03$).

Because too few Digges murrelets were recovered in the two younger age classes to speculate on their distributions, an inter-year comparison of recoveries of Digges Island murrelets was restricted to birds in their third winter or greater. No significant difference in the timing of recoveries was detected between the decades ($\chi^2_1=2.85$, $p=0.092$) (Figure 2.6, appendix Table A4).

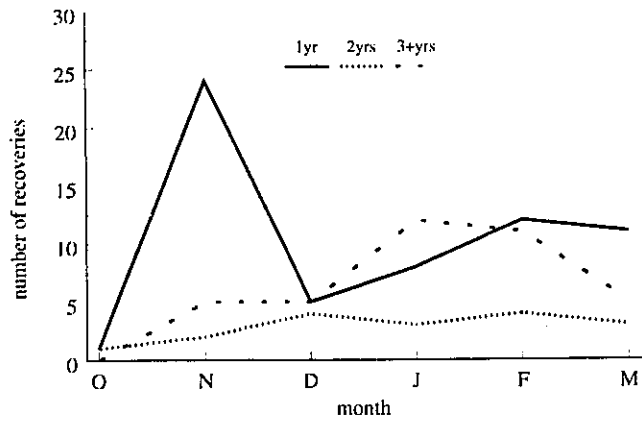


Figure 2.7 Temporal recovery distribution of first year, second year, and third year or greater murrelets banded on Coburg Island.

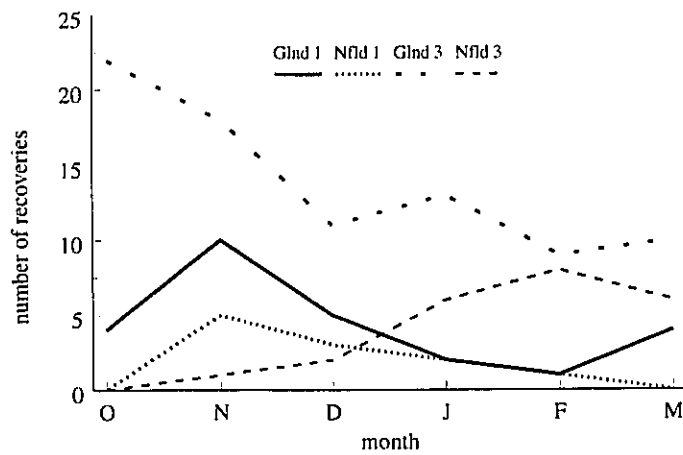


Figure 2.8 Temporal recovery distribution of murrelets banded at Cape Hay. Recoveries in Greenland (Glnl) and Newfoundland (Nfld) are indicated for birds in their first year or in their third year or greater.

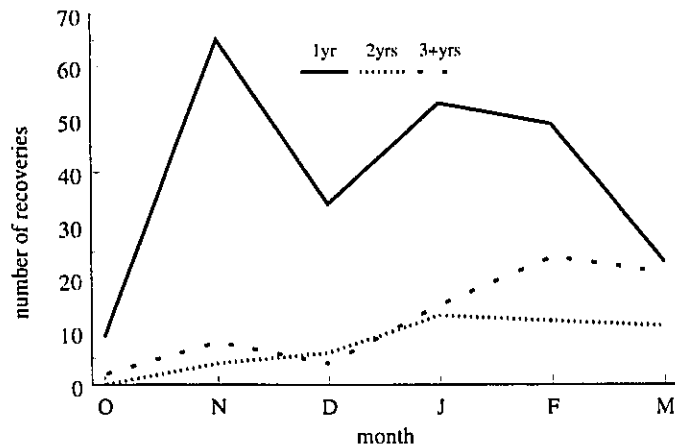


Figure 2.9 Temporal recovery distribution of birds banded in Greenland and recovered in Newfoundland. Murrelets in their first, second, and third year or greater are indicated.

Coburg Island

A total of 4756 chicks were banded on Coburg Island, in the High Arctic, in 1981 and 1987 (3073 and 1683 respectively). The peak of recoveries of first year birds banded on Coburg Island occurred in November with another, smaller peak in February-March (Figure 2.7, appendix Table A5). This differs from the results from Coats Island where the peak recovery of first winter murres occurred in January. Recoveries of second winter birds were evenly distributed over the winter, while older birds were most often recovered in January and February. Analysis of the temporal distribution of Coburg recoveries showed that the proportions of the three age classes differed significantly ($\chi^2_4=11.88$, $p=0.018$) between early and late periods. The main difference was found to lie between the distributions of birds in their first and third or greater years ($\chi^2_2=10.34$, $p=0.006$).

Cape Hay

Murres at the colony on Bylot Island at Cape Hay were banded in 1957 with a total of 2500 adults and chicks banded. First year birds were most commonly recovered in November while the older age classes were recovered more often later in the hunting season (Figure 2.8, appendix Table A6). Contingency analysis suggested a significant difference between age categories ($\chi^2_2=13.72$, $p<0.001$), using two time periods. The distribution of first year birds did not differ significantly from second winter birds but was highly significant from the distribution of third winter or older birds (1vs2: 2 tailed Fisher exact test, $p=0.049$; 1vs3+: $\chi^2_1=12.11$, $p=0.0005$). Differences between the older two age categories were not significant ($\chi^2_1=0.01$, $p=0.93$).

The majority of recoveries of murres banded at Cape Hay occurred in west Greenland (77%) indicating that Greenland might be an important wintering area for birds from that colony. Of the

153 birds recovered in Greenland, most were shot (86%), some entangled in fishing gear (3%), and the remaining were reported without recovery means listed (11%). Similar in pattern to the Cape Hay recoveries were the 6 recoveries of murrelets banded on Prince Leopold Island which were all recovered in Greenland. This tendency may be a characteristic of murrelets from Lancaster Sound. Recoveries of murrelets from the other High Arctic colony, at Coburg Island, were predominantly in Newfoundland with only 15% of recoveries in Greenland.

A comparison of the monthly distributions of murrelets banded at Cape Hay and recovered in either Greenland or Newfoundland suggests no difference in distribution between the two areas for birds in their first winter ($\chi^2_2=3.10$, $p=0.212$). In both Greenland and Newfoundland there was a peak in recoveries in November (figure 2.8) for birds in their first winter. However, the timing of recoveries differed significantly for birds in their third winter or greater ($\chi^2_2=17.50$, $p=0.0002$). In Greenland, older birds showed a gradual decline from a peak in October while a gradual increase to a peak in February was observed in Newfoundland. This suggests that older birds may be more likely to remain in the waters off Greenland well into the winter before moving to Newfoundland. A large proportion of the birds recovered in Greenland were in their third year or older (76%) lending evidence to the idea that many adult Cape Hay birds may remain there for the winter.

Greenland

Recoveries of birds banded in Greenland represent a large number of banding years, 1946-1988, and include birds banded at a number of colonies along the Greenland coast. The exact number of individuals banded during this time period is not known due to incomplete information from banders (Kampp 1988). The distribution of recoveries by month for second year and older birds was similar to the distributions noted from the Coats Island data. First year birds were recovered more frequently than the other two age classes for both Greenland and Coats Island murre. In addition, greater numbers of birds of all age categories were recovered in the January to March time period (Figure 2.9, appendix Table A7). However, the proportion of first year birds from Greenland recovered in October-December (46%) was higher than the corresponding proportion from Coats Island (19%). Significant differences in temporal distribution among age categories were detected ($\chi^2_4=15.29$, $p=0.004$), based on a three time category analysis. Within the complete contingency table, the recovery distribution of first year birds differed significantly from the two older age categories (1 vs 2, $\chi^2_2=11.58$ $p=0.003$; 1 vs 3+, $\chi^2_2=22.23$, $p<0.0001$) while differences between the two older age categories were not significant ($\chi^2_1=3.34$ $p=0.189$).

Spatial Distributions

Coats Island

Figure 2.10 (see also appendix, Table A8) indicates that large numbers of Coats Island first winter birds were recovered in areas A, B and E (80%), whereas second winter birds were more evenly spread and older birds were recovered mainly in areas B, and C (71%). A highly significant difference in the distributions of the different age categories was detected ($\chi^2_8=48.90$, $p<0.0001$). Subdivision of the age vs area table revealed a highly significant difference between first winter birds and birds in their third or greater winters ($\chi^2_4=47.39$, $p<0.0001$). Comparisons of first winter and second winter birds and second winter vs older birds were not considered to be significant ($\chi^2_4=10.72$, $p=0.03$, and $\chi^2_4=10.73$, $p<0.03$ respectively). Birds recovered in their second winter appeared to be intermediate in their geographical distribution between first year and older birds. The proportion of second years recovered in areas A (23%) and E (17%) were higher than those of older birds (8%, 12%), but lower than those of first years (27%, 29%). Conversely, the proportion recovered in area C (20%) was higher than that of first years (7%), but lower than that of older birds (38%). Most Coats Island recoveries in all areas, except area A, occurred after December 31 (Figure 2.11; appendix, Table A9) and the contingency analysis revealed independent distributions between areas and time of year ($\chi^2_4=83.14$, $p<0.0001$). Among years it is interesting to note that the area of peak recovery differs significantly from year to year ($\chi^2_{16}=84.61$, $p<0.0001$) (Figure 2.12; appendix, Table A10). With the exception of area D, which has few recoveries overall, all other areas had the most recoveries in at least one of the hunting seasons included in this analysis. Only area E had the largest number of recoveries in two different years.

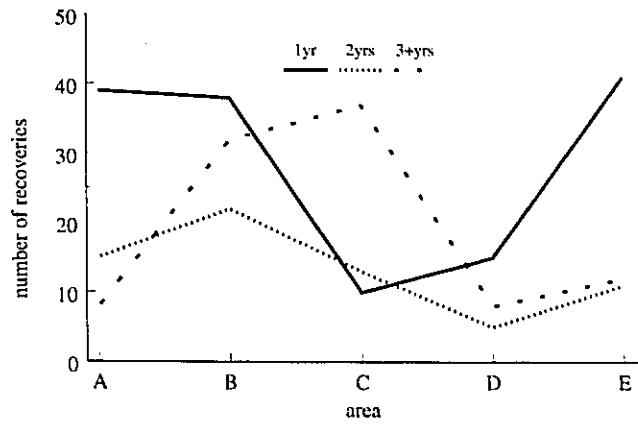


Figure 2.10 Spatial recovery distribution of Coats Island murrelets in three age categories; areas described in Figure 2.2.

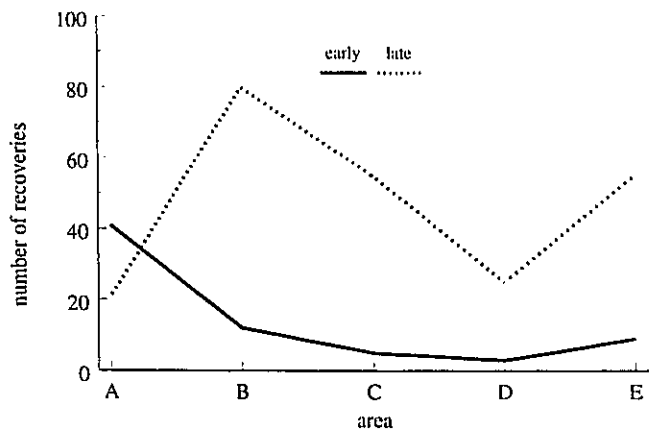


Figure 2.11 Recovery of all Coats Island birds by area (Figure 2.2), for the "early" (October-December) and "late" (January-March) part of the turr hunting season.

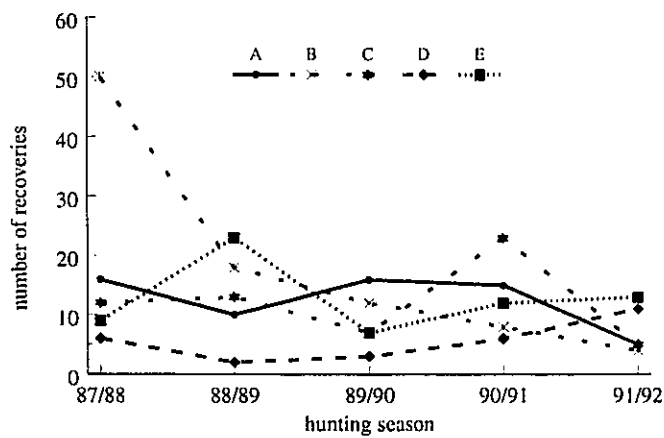


Figure 2.12 Yearly variation in number of recoveries among areas (Figure 2.2).

Digges Island

Most recoveries of older, Digges Island birds in the period from 1979-83 occurred in areas B and C (Bonavista, Trinity, and Conception Bays) (Figure 2.13, appendix Table A11). This pattern is also similar to that observed for older birds from Coats Island. The first and second winter recoveries reported were roughly evenly distributed among areas but, due to the low frequency of recovery, little can be inferred about their distributions.

The spatial pattern of Digges Island recoveries from the 1955 banding efforts were not significantly different among the age classes (Figure 2.14, appendix Table A12; $\chi^2_8=11.83$, $p=0.17$). There were differences in the location of recoveries between the 1950's and the 1980's, primarily with respect to areas A and B. In the 1950's fewer birds were recovered in area B and more in area A than was found for birds banded in the 1980's (Figure 2.15, appendix Table A13, $\chi^2_4=29.55$, $p<0.0001$).

Coburg Island

First year birds from Coburg Island were most often recovered along the Northern Peninsula and in Notre Dame Bay (area A), with relatively few recoveries in the other areas (Figure 2.16, appendix Table A14). Second year birds were evenly distributed while older birds were most often recovered along the Northern Peninsula, Notre Dame Bay, Bonavista Bay, and the South Shore (areas A, B, and E). The differences among age categories were not significant ($\chi^2_8=14.60$, $p=0.067$).

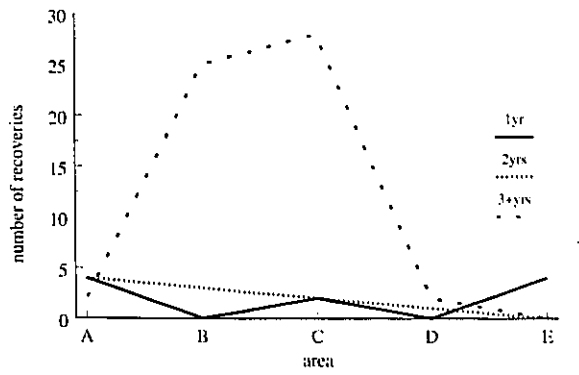


Figure 2.13 Spatial recovery distribution of murrelets banded on Digges Island (1979-83). Areas described in figure 2.2.

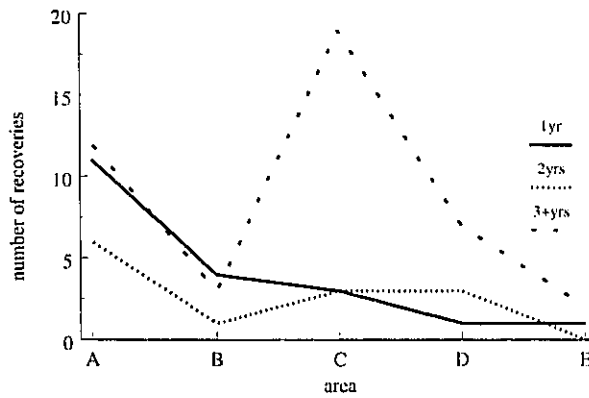


Figure 2.13 Spatial recovery distribution of murrelets banded on Digges Island (1955).

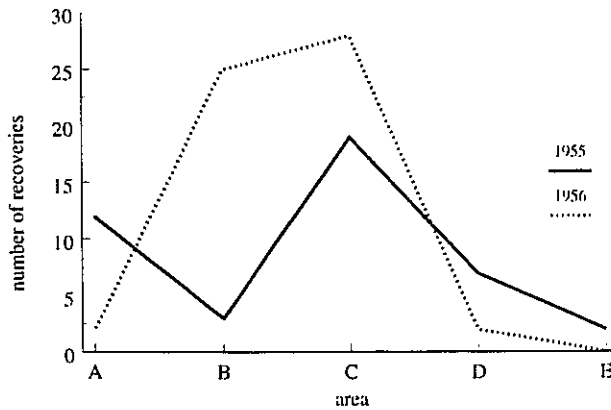


Figure 2.15 Comparison of spatial distributions of third year or older murrelets from Digges Island, banded in 1955 and in the early 1980's.

Cape Hay

Of the few birds recovered in Newfoundland from those banded at Cape Hay (Figure 2.17, appendix Table A15), most first year birds (67%) were recovered in area A. Second year birds showed a mixed distribution with most birds being recovered in areas A and E. Third year or older birds were most often recovered in area D, a pattern not seen for any other sample. In most cases, area D produced the fewest recoveries for other colonies. Low numbers of first and second year recoveries precluded statistical analysis of this data.

Greenland

The spatial distributions of recoveries of birds banded in Greenland showed a preponderance of recoveries of first winter birds in area A (Figure 2.18, appendix Table A16). Nearly one third (32%) of all birds banded in Greenland and recovered in Newfoundland were shot as first year birds in area A. Very few (3% of total recoveries) birds were recovered in area B as first winter birds. This is quite different from the distributions of Coats Island birds where the proportion of all birds recovered in their first winter in areas A and B was 13% for both areas. Significant differences were detected in the spatial distribution of recoveries among age classes ($\chi^2_8=32.46$, $p<0.0001$). Subdivision of the overall table revealed that the significant differences in these distributions were the result of differences between first winter birds and the older two age categories (1 vs 2, $\chi^2_4=14.99$, $p=0.005$; 1 vs 3+, $\chi^2_4=26.48$, $p<0.0001$). Distributions of second and third and older murre were not significantly different ($\chi^2_4=1.26$, $p=0.87$).

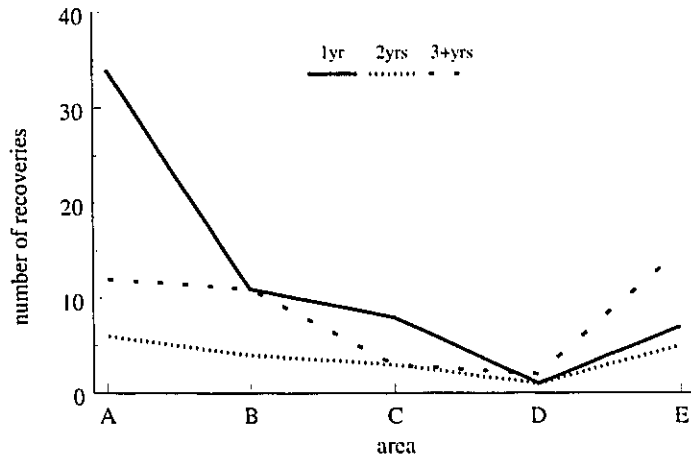


Figure 2.16 Recovery distribution by area for birds in three age categories from Coburg Island. Areas described in figure 2.2.

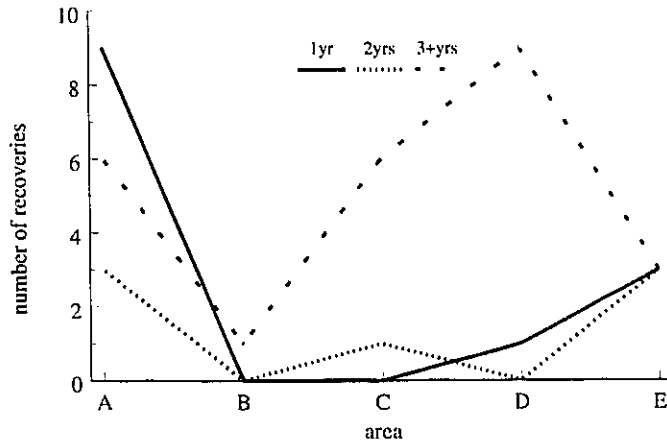


Figure 2.17 Recovery distributions by area for birds in three age categories from Cape Hay.

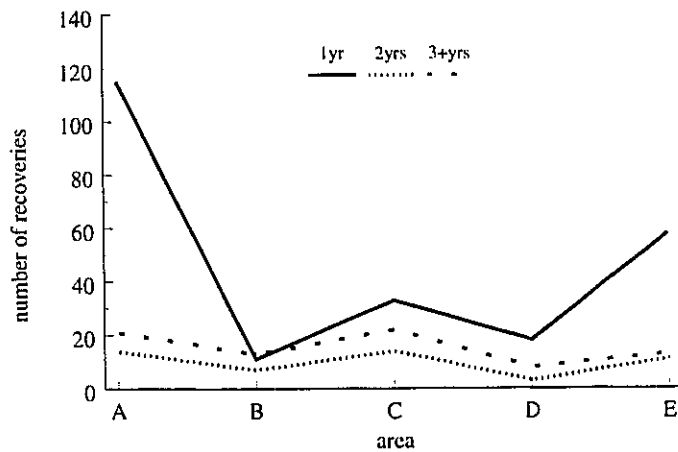


Figure 2.18 Recovery distribution by area for birds in three age categories, banded in Greenland.

Inter-colony Comparisons

First Year Murres

Figure 2.19 (see also appendix Table A17) illustrates the high proportion of first winter birds from Coats Island, Coburg Island, and from Greenland that were shot in the early months of the hunt, particularly November. For birds from Coats Island, greater proportions are harvested later on with the greatest proportions being shot in February and March for the years 1981 and 1987. Distributions by month differed significantly among Coats Island, Coburg Island, and Greenland murres ($\chi^2_{10}=34.43$, $p=0.0002$), further analysis suggested that the significance was largely due to differences between Coats Island recoveries and those from Greenland ($\chi^2_5=27.75$, $p<0.0001$). Coats Island and Coburg Island recoveries were not found to be significantly different ($\chi^2_5=10.50$, $p=0.062$).

Comparing the same three banding areas, distributions of first year birds by area again suggested highly significant differences among colonies ($\chi^2_8=81.63$, $p<0.0001$). Subdivision of the complete contingency table implied that the differences existed between all colonies (Coats and Coburg: $\chi^2_4=17.66$ $p=0.001$, Coats and Greenland: $\chi^2_4=77.19$ $p<0.0001$, and Coburg and Greenland: $\chi^2_4=18.67$ $p=0.0009$). Of note was the high proportions of birds from Coburg Island, Cape Hay and from Greenland in area A whereas Coats Island murres were most often recovered in area B (Figure 2.20, appendix Table A18).

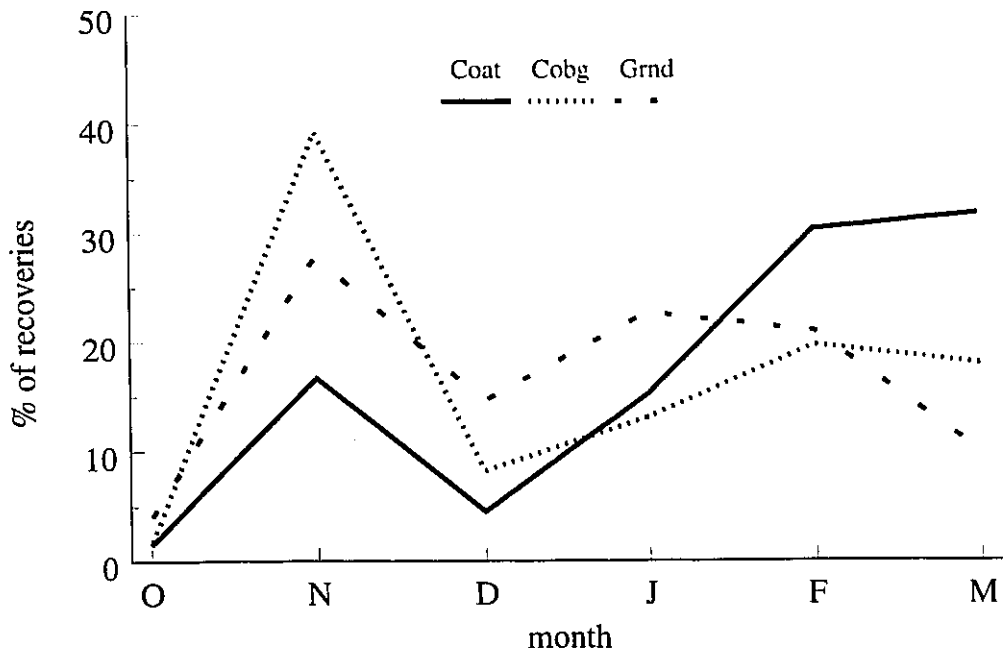


Figure 2.19 Intercolony comparison of the temporal recovery distribution for first year murrelets from Coats Island (Coat), Coburg Island (Cobg), and Greenland (Grnd).

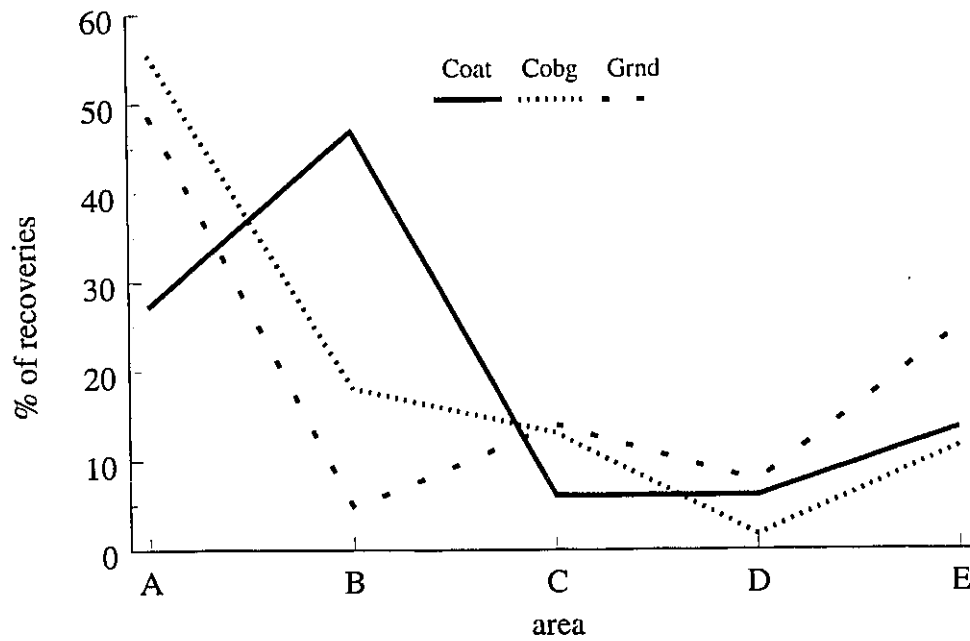


Figure 2.20 Intercolony comparison of the spatial recovery distribution for first year murrelets from Coats Island (Coat), Coburg Island (Cobg), and Greenland (Grnd).

Third Year and Older Murres

For all colonies banded, there were more recoveries of older birds after January 1 (Figure 2.21, appendix Table A19). Significant differences in temporal distributions among colonies were detected ($\chi^2_4=11.57$, $p=0.021$). Contingency table subdivision suggested that the significance detected was due to differences in distribution between Digges and Coburg ($\chi^2_1=10.84$, $p=0.001$). However, this pairing was merely the most extreme expression of the apparent tendency for the two Hudson Strait colonies (Coats and Digges Islands) to be recovered proportionately more often than the others in February and March. No other pairwise colony comparisons differed significantly.

The spatial distributions of recoveries in the third winter or later differed significantly among Cape Hay, Coats, Digges, and Coburg Islands, and Greenland ($\chi^2_{16}=92.95$, $p<0.0001$) (Figure 2.22, appendix table A20). All pairwise comparisons were also significant (Table 2.7) with the exception of the difference between Cape Hay and Greenland which was not significant.

Table 2.7 Pairwise comparisons of spatial distributions of third year or older murres in Newfoundland.

Colony Comparison	χ^2_4	p
Cape Hay vs Greenland	10.22	0.047
Coburg vs Greenland	12.15	0.016
Coats vs Digges	11.71	0.020
Coats vs Greenland	15.61	0.004
Cape Hay vs Coburg	20.46	<0.001
Cape Hay vs Coats	22.59	0.0002
Cape Hay vs Digges	39.35	<0.0001
Coburg vs Coats	27.09	<0.0001
Coburg vs Digges	46.70	<0.0001
Digges vs Greenland	34.59	<0.0001

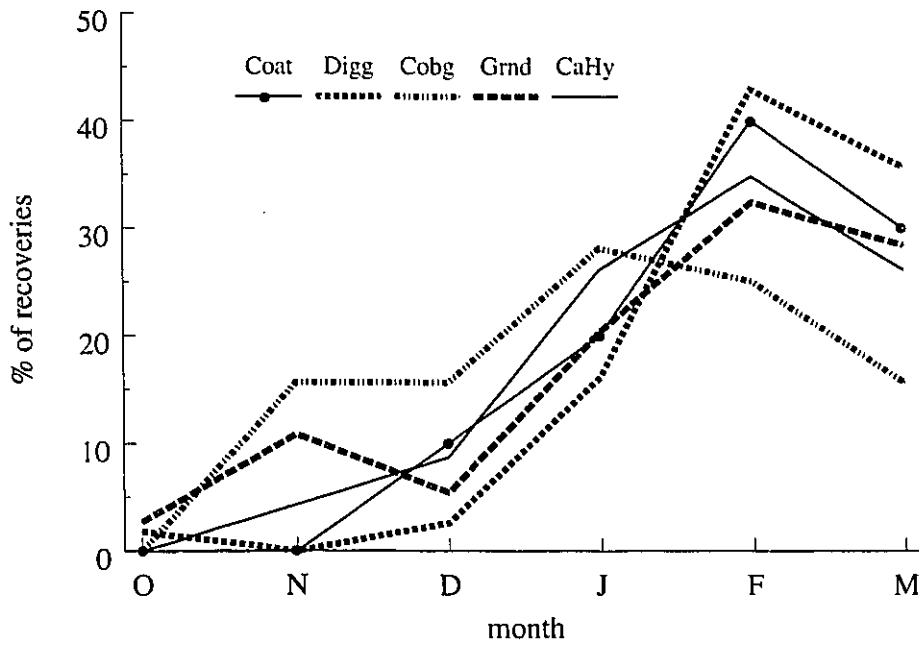


Figure 2.21 Intercolony comparison of the temporal recovery distribution for third year or greater murrelets from Coats Island (Coat), Digges Island (Digg), Cape Hay (CaHy), Coburg Island (Cobg), and Greenland (Grnd).

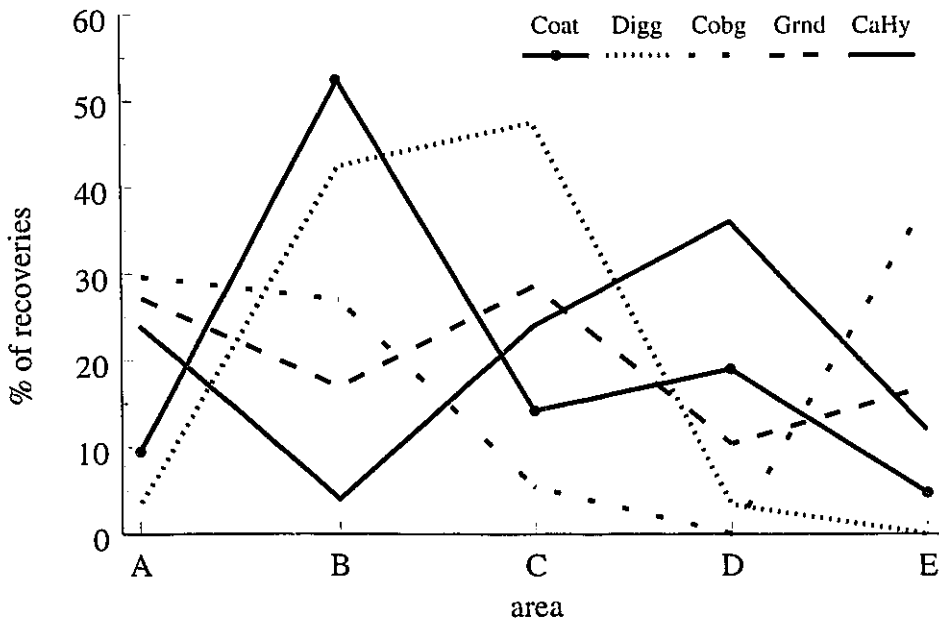


Figure 2.22 Intercolony comparison of the spatial recovery distribution for third year or greater murrelets from Coats Island (Coat), Digges Island (Digg), Cape Hay (CaHy), Coburg Island (Cobg), and Greenland (Grnd).

DISCUSSION:

Temporal Distributions

The observed distributions of recoveries by month are presumably the result of several factors. Of primary concern for the management of hunted birds are changes in recovery patterns, through changes in hunting effort and reporting rates, which may produce an artifactual shift in recovery patterns. The tremendous inter-year variation observed for successive cohorts banded at Coats Island indicate that year to year changes can be substantial and appear too large and rapid to be caused by changes in reporting rates.

Hunting pressure will vary between months and among years due to weather, ice conditions, the numbers of birds present, and economic conditions in Newfoundland. The degree to which these variables contribute to recovery patterns is hard to ascertain. Because hunters are not required to obtain migratory game permits, the numbers of active turr hunters and harvest levels can only be estimated (Elliot *et al.* 1991). Variations in these estimates from year to year cannot be realistically determined. I attempted to minimize the effects of inter-year variation by combining many seasons' data where possible.

For wildlife management concerned with the determination of the timing and length of the hunting season for species with high adult survival, low reproductive output, and delayed maturity, the number of older, breeding murre shot is of greater concern than the numbers of younger birds. For these species, adults have a greater reproductive potential than pre-breeders. Simple demographic models have shown that in highly K-selected species like seabirds, declines in population are most sensitive to changes in adult survival (Croxall and Rothery, 1991). It has been

demonstrated for a variety of species including Greater Flamingos (Johnson *et al.* 1991), Atlantic Puffins (Harris and Wanless 1991), petrels (Croxall *et al.* 1991) that adult survival is the most influential demographic parameter in affecting population size. Based on this information, the pattern of recoveries of thick-billed murres three years or older has the most significant of implications for management of the turr hunt as murres show life history characteristics of highly K-selected species (Tuck 1961, Bédard 1985).

Making the jump from the distribution of hunted birds to that of the entire population can only be done if accurate accounts of the size of the kill, the numbers of hunters involved, and the length of time spent hunting is known. This is not the case for the thick-billed murre in Newfoundland where the turr hunt has gone on largely unregulated. The long season without bag limits and lack of requirements for hunting permits makes an accurate assessment of hunting pressures difficult and thereby making it difficult to tease out the effects of hunting pressure on the observed distribution of murres.

The recovery patterns of murres in their third year or older were similar for those from Coats Island, Digges Island, Cape Hay, Coburg Island and Greenland, with the largest numbers being recovered after the end of December. Relatively few murres of that age were recovered during the peak hunting month of November, when large numbers of young birds are shot, indicating that older birds from all colonies generally arrive later than young birds, or were much less vulnerable to hunting at that time of year. This pattern was especially evident for the recoveries of older Hudson Strait birds which arrived later than birds from colonies further north. These data agree with the finding of Elliot *et al.* (1991) in their dockside assessment of the age of birds killed at various times in the hunt.

A comparison of the pattern of first year and third year or older recoveries from Cape Hay in Greenland and Newfoundland shows that more old birds than first year birds were being shot in Greenland at a time when the reverse was true in Newfoundland and suggests that age ratios observed among recovered samples may tell us something about the relative abundance of age classes in the hunted populations.

Spatial Distributions

The spatial distribution of recoveries from Coats Island showed a significant amount of inter-year variation (Figure 2.12) and differed between decades for Digges Island. Part of this variation can probably be attributed to changes in hunter effort among years due to variable weather and ice conditions (J. Chardine pers comm). Within these inter-year differences, some interesting patterns have emerged.

Older birds from Coats Island showed a general preference for Bonavista, Trinity and Conception Bays (areas B and C). The same was true for older Digges Island birds banded in the early eighties while banding in 1955 produced recoveries of older birds mainly in Trinity and Conception Bays. The latter may have been the result of poor conditions in Bonavista Bay at that time. Low numbers of recoveries of birds older than two years in area A may be the result of the timing of arrival of Hudson Strait murre, which usually arrive after December, when the hunt in this region is finished. At the same time, the lower numbers of older birds recovered from the south coast (area E), compared to first year birds suggests that the two age classes prefer different feeding conditions, or that young birds are displaced from northern areas by the arrival of older birds. An arm of deep water, more than 200 metres in depth, comes into these bays and may provide good

feeding areas to seabirds because of the occurrence of upwellings here. This bathymetry does not occur along the southern coast or in the waters off the Avalon Peninsula.

The recovery of birds from colonies outside of Hudson Strait showed a greater tendency to be located in area A (Northeastern Newfoundland, figure 2.2) where the hunt takes place mainly in November and December. This is likely a function of their early arrival and the fact that, because hunting is precluded by ice in that area later in the winter, hunters may put in an extra effort early in the season.

Birds banded in Greenland showed a relatively even distribution of older birds among the areas. Most older Greenland birds probably remain in Greenland waters throughout the winter (Kampp 1988); therefore, these populations are probably little affected by changes in the hunt in Newfoundland. The large number of Cape Hay birds recovered in Greenland suggests that a significant number of these birds may winter off Greenland. Recent declines of populations in Greenland have been attributed to hunting at the colonies there during the breeding season (Kampp 1988 and Falk and Durnick 1992). The majority of Cape Hay birds are recovered there during the winter months and are not likely to be affected as greatly. Of the birds from Cape Hay which were recovered in Newfoundland, many came from Placentia Bay (area D). Few birds of three years or greater from any other colony were recovered in this bay. This includes the large number of Coats Island murrelets for which area D was consistently the area of fewest recoveries over a number of years (Figure 2.12). Because these data represent banding done in 1957, it is possible that hunting or reporting efforts have changed; however, the distribution of recoveries of older murrelets banded on Digges Island in 1955 show low numbers recovered in area D. Hunting in Placentia Bay may therefore affect birds from Cape Hay more than those from other colonies. As the majority of birds

from Cape Hay are recovered in Greenland, they are likely impacted more than other colonies by both the hunt there and in Newfoundland. There is some suggestion that the colony at Cape Hay declined between the 1950's and 1970's (Nettleship and Evans 1985) possibly as a result of combinations of hunting pressure and deaths due to the entanglement of murres in salmon drift nets during the 1970's when the by-catch of murres approached numbers being killed in the turr hunt (Tull *et al.* 1972).

The location of recoveries of first winter murres reflects their arrival time and the timing of the hunt in different locations of the province. Hunting prior to January first occurs largely in area A, north of and including Notre Dame Bay. Murres from outside Hudson Strait make up the bulk of birds present in the early part of the season and are recovered in large numbers in area A. First year birds from Greenland, Coburg Island and Cape Hay were recovered predominantly in this area with relatively few birds recovered in any of the other areas. However, slight differences in the distributions of birds in the other areas resulted in the detection of significant differences between these colonies. Young Coats Island murres are recovered in large numbers in areas A, B and E. Presumably these birds arrive in Newfoundland during the end of the hunt in area A and then move south and west to be shot later in the winter in Bonavista Bay and along the southern coast of the province. Management of young Coats Island murres may require an overall reduction in the hunt as they are prevalent in all but areas C and D. However, the Coats Island population is stable or expanding (Gaston *et al.* 1993) and, given the new regulations put in place in 1993-94, this population appears secure.

Conspicuous by their absence are the first and second year murrelets from Digges Island. Clearly the majority of these birds are wintering in areas that are out of reach of the turr hunt such as the Labrador Sea or the Grand Banks.

Inter-colony Differences

My analyses suggest that thick-billed murrelets may move in blocks according to age and colony of origin. Clearly, first year birds from all colonies are arriving in Newfoundland in advance of older individuals. Similarities in the distributions of first years from the High Arctic (Cape Hay and Coburg Island) exist in that they appear to arrive in Newfoundland in advance of birds from Coats Island in Hudson Strait. However, it cannot be generalized that all first year birds from colonies in these two areas behave similarly as the near absence of first and second year recoveries of birds from Digges Island illustrates. The temporal distribution of older birds in the hunt was relatively similar for all colonies with the greatest number of recoveries occurring after the end of December. Second year recoveries remained intermediate to those of first years and older birds.

Also, it appears first year birds from Coats Island, Coburg Island and from Greenland are hunted heavily over much of the eastern and southern coasts of Newfoundland with the exception of the southern and eastern Avalon Peninsula. The large proportion of Coburg Island and Greenland murrelets recovered in area A is likely due to their early arrival and the timing of the hunt. As the hunt intensifies in Bonavista Bay, the first year birds from Coats Island are arriving in large numbers to be shot in area B. First year murrelets from all colonies probably move to the south coast, possibly displaced by later arriving older birds, explaining the large numbers of birds from all colonies except Coburg Island, recovered in this area. Movement of young murrelets to the south coast possibly occurs

quite rapidly and would explain the low numbers of birds of this age in areas B, C, and D. Thus, the spatial distribution of first year birds can be characterized by timing of arrival.

The observed spatial distribution of older Coats Island and Digges Island birds suggests a definite preference for Bonavista, Trinity, and Conception Bays. By remaining in these bays, Hudson Strait birds have much to benefit from. The energy expended in migration is minimised as areas B and C represent the most northerly open water which is the shortest distance from colonies in Hudson Strait. The area likely offers good feeding as the bathymetry of the bays suggests. By remaining in the bays, birds avoid rough seas in both in the shelter that the bays themselves offer, and the protection offered in the lee of floating pieces of ice (Divoky 1975). The large number of recoveries of older birds from Cape Hay off Southwest Greenland in winter may be explained for similar reasons. It may be profitable for Cape Hay breeders, in terms of energy expenditure, to stay in Greenland and feed in the shelter of its fjords and in the protection of broken ice. Birds from Northwestern Greenland winter in the waters off of Greenland and Newfoundland, as would be expected for a bird minimizing energy output (Kampp 1988). Although more Coburg Island birds are recovered off Greenland than Hudson Strait birds, the proportion is small compared to birds from Cape Hay (Table 2.3) which is curious given the close proximity of the two colonies.

The recovery distributions of murres from different colonies have revealed some similarities between colonies within similar geographic regions. This is illustrated by the later arrival of murres from Coats and Digges Islands as compared to birds banded at colonies at higher latitudes and the fact that adults from Coats and Digges Islands prefer to winter in Bonavista, Trinity, and Conception Bays. However, it is probably incorrect to suppose that the distributions of murres from neighbouring colonies should be similar. The lower recovery rates of first and second year murres

from Digges Island as compared to those from Coats Island suggest that young murrelets from Digges Island are wintering in a different area than birds of similar age from Coats Island. The recovery distributions of adult murrelets from Coburg Island suggest that they mainly winter off the coast of Greenland while adults from the nearby colony at Cape Hay move down to Newfoundland. These differences in distributions between colonies must be considered for future management of the species as it is clear that birds from different colonies are distributed differently in time and space. Chapter 5 considers the implications of these distributions for turr hunt management.

CHAPTER 3
ANNUAL SURVIVAL OF JUVENILE THICK-BILLED MURRES
BASED ON BAND RECOVERY METHODS

INTRODUCTION:

The young of several seabird species, where reproduction is delayed for several years, may not return to their breeding colonies for an extended period of time after fledging, remaining at sea for the duration. The best method available to estimate survival probabilities when birds are at sea, is through the recovery of dead, banded individuals. In order to be effective, sufficient numbers of deceased birds must be recovered and subsequently reported to the appropriate authority. It is therefore essential that animals carrying marks disperse in close proximity to human activity to allow for their recovery and eventual reporting. Heavily hunted species like the Thick-billed Murre, allow reasonable estimates of survival using recovery methods because hunters actively seek out the places where birds are over-wintering.

Management of the Canadian murre population requires accurate estimates of survival to breeding age. When reproductive input is known, survival to breeding age gives an indication of recruitment. Survival probabilities to first year are often the lowest making this estimate an important component of the determination of survival to first breeding as it will account for the greatest mortality in a single year.

In order to estimate unbiased survival probabilities, it is necessary that the data do not deviate from the assumptions of recovery models. Brownie *et al.* (1985) described the assumptions of this method. A series of assumptions are directed at operations in the field. Marked individuals must

be chosen as representative of the target population and the age and sex of individuals, if possible, must be correctly determined when marked. The marking procedure should not affect the survival probability of individuals, banded individuals cannot lose their marks and the particulars of each recovery must be recorded correctly.

Other assumptions are related to stochastic model components. It is important that the outcome of banded individuals be independent of the outcome of other banded individuals and the fate of a given banded individual, that is recovery time, is a multinomial random variable. The structure of the model assumes that all banded individuals of an identifiable class, which may include species, sex or age, in the sample have the same annual survival and recovery rates. Models allow for yearly variation in annual survival and recovery rates. Survival and recovery may also vary yearly for age, sex or area of marking.

In this chapter I address the assumptions of band recovery models with respect to the data set of recoveries in Newfoundland of Thick-billed Murres banded on Coats Island, and estimate survival to first year based on these recoveries.

METHODS:

Data for the estimation of annual survival of pre-breeders based on band recoveries came from the same US Fish and Wildlife Service/Canadian Wildlife Service database used to analyze the winter distribution of birds in Newfoundland (see chapter 2). Chapter 2 describes banding efforts and reporting methods for birds carrying standard US Fish and Wildlife Service bands and those carrying special murre bands. For these analyses, only recoveries of birds banded on Coats Island were used.

Regression analysis of the proportion of cohorts recovered in their first and second year was performed to determine if there were any indications of inter-year differences in recovery rates. If present, changes in recovery rate would have to be accounted for in the model chosen to estimate survival.

A variety of computer software packages are currently available to analyze band recovery data. Two commonly used programs are BROWNIE (Brownie *et al.* 1985) and SURVIV (White 1983). BROWNIE was considered because it allows testing of a variety of age dependant survival hypotheses (Brownie *et al.* 1985) but was not used because of its inability to handle the small adult data set that exists for Coats Island Murres. BROWNIE does not constrain parameter estimates and when data are sparse, survival probabilities greater than one can result. In addition, if critical values in the data matrix are zero then some estimators go undefined (White 1983). Data were eventually analyzed using SURVIV software (version 1.5, 1990), which is better able to handle small data sets by restricting estimated parameters into a range of values that are realistic (White 1983). SURVIV also allows the testing of age dependant survival models and gives the results of a goodness of fit test.

Model selection was carried out using a combination of prior biological knowledge and Akaike's Information Criterion (AIC). In long lived species it is common for juvenile birds to exhibit a reduced annual survival compared to that of adults. For Coats Island thick-billed murre, such a difference might be expected in light of the behavioral differences among age classes described in Chapter 2. Consequently, models incorporating age dependent survival as well as ones incorporating constant survival between age groups were considered for the Coats Island data. Within the biological framework, AIC values identify the best model selections in conjunction with a goodness-of-fit test. AIC adheres to the Principle of Parsimony, taking the quality of fit of the data (or deviance from a perfect fit) and the number of parameters into consideration (Lebreton *et al.* 1992, Lebreton *et al.* 1993). Good models are considered to be those which offer the best fit to the data set (or have low deviance) and do so with the fewest degrees of freedom (or have the fewest parameters). Scores are computed as the sum of the deviance (computed as -2 times the value of the log-likelihood) and two times the number of parameters (equation 3.1) (Lebreton *et al.* 1992). The model that best describes the data will have the lowest AIC score.

$$AIC = -2 \ln L + 2np \quad (3.1)$$

Where AIC fails to select a single model that is significantly better than others, biological justifications are used to indicate the model which was most likely to describe the data. This is a common occurrence, because often AIC values will only identify a sub-set of good models (Anderson *et al.* 1993).

Calculations of survival to first year must incorporate data from the recovery of birds banded

as adults to reduce bias. Survival rates based on band recoveries must consider reporting probabilities in their calculation. I have already demonstrated that the behaviour among age classes differs in terms of distribution during the time of when recoveries are to be reported (Chapter 2). Greater numbers of young birds are recovered which translates into a greater reporting rate for birds of this age, older birds can be expected to have a correspondingly lower reporting rate. This is likely to negatively bias survival probabilities, if life table methods are employed, due to the unrealistic assumption that reporting rates are constant among age classes (Anderson *et al.* 1985). Few data exist from the recovery of birds banded as adults on Coats Island. This could affect the resulting estimates of juvenile survival. However, reliable estimates of survival for adult birds at Coats Island have been produced (Gaston *et al.* 1994). SURVIV allows parameters to be constrained to a predetermined value so the best models from runs with SURVIV of the entire data set were re-run incorporating a constant adult survival probability of 0.89 which was calculated from the proportion of breeding birds returning to the colony.

RESULTS:

Recoveries

Between 5 and 95 Thick-billed Murre recoveries from Coats Island have been reported annually since 1981 (table 2.4, table 3.1). With the exception of the 1990 banding year, all cohorts were recovered in greatest numbers as first year birds. The proportion of birds recovered at this age varied between 2.7% (1984) and 0.7% (1990) of the number of chicks banded (table 2.5).

Table 3.1 Recoveries of birds banded as adults or chicks in the turr hunt off Newfoundland. Hunting seasons commence in September of the year indicated and end in March of the next year.

Banding Year	Number Banded	Recoveries/Season							
		84	85	86	87	88	89	90	91
ADULTS:									
1984	141	0	5	0	0	0	1	0	0
1985	134		1	1	0	0	1	1	0
1986	278			0	3	2	0	2	0
1987	161				2	1	0	0	0
1988	193					1	1	4	1
1989	80						0	1	0
1990	88							0	0
1991	142								1
CHICKS:									
1984	1453	39	20	2	4	2	1	2	1
1985	1619		37	13	10	3	1	4	0
1986	2237			20	18	7	1	3	0
1987	2250				57	15	1	9	0
1988	2686					35	10	12	3
1989	2408						23	15	3
1990	1331							9	9
1991	2086								20

Taking the recoveries of birds in their fifth year or younger for the banding years 1984-1987, of 262 recoveries, 58% were in the first, 25% in the second, 8% in the third, 6% in the fourth and 2% in the fifth year. Numbers of first years recovered represented approximately double the number of older birds in all seasons except 1990-91. Looking at inter-year variation in the proportions recovered, the proportion of both first ($r=0.75$, $f=6.48$, $P<0.05$, $y=-0.29+27.11$) and second year ($r=-0.72$, $f=5.48$, $P<0.07$, $y=-0.10+9.78$) recoveries appears to have fallen between 1984 and 1991 (table 2.4, figure 3.1), although the relationship was significant only for first year recoveries.

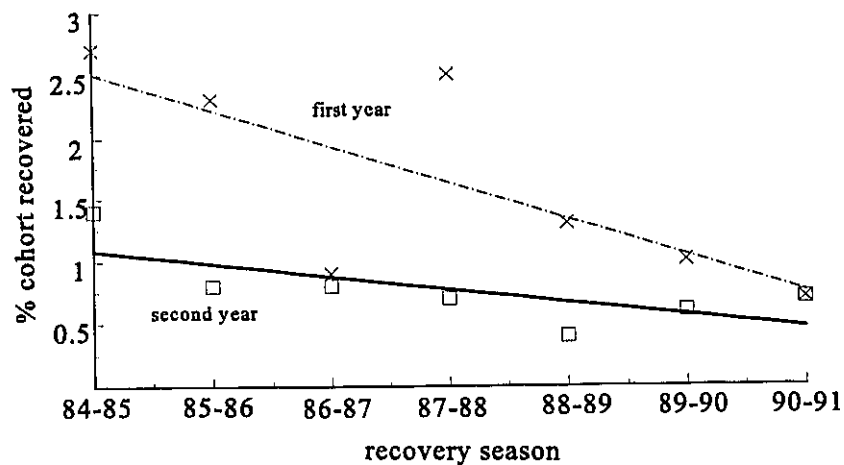


Figure 3.1 Percent of initial cohort recovered during the indicated hunting seasons for first (cross) and second year (box) murrelets between fall 1984 and spring 1991.

In 1985, roughly half of the chicks banded were given standard USFWS bands (N=791), the

other half were given special stainless steel murre bands (N=828). The former had an address directing the recoverer to report the band to the USFWS in Washington, D.C., while the latter directed recoveries to the Canadian Wildlife Service in St. John's, Newfoundland. The differences in address between the band types might introduce a bias into the reporting of recovery data if hunters had a preference for a Canadian address. In fact, a significant difference was detected between the band types. Only 27 (37.5%) of the 72 recoveries of 1985 birds were USFWS bands ($\chi^2_1=3.89$, $p=0.049$). Although significant, the value of p was very close to α . Because of this, all recoveries from the 1985 cohort were used in order to benefit from maximum sample sizes.

Survival Estimates.

A combination of constant or year dependent survival and/or recovery probabilities were considered in table 3.2. SURVIV gives the results of a goodness of fit test which is based on a χ^2 approximation, comparing the observed values from the model with those expected from a saturated model. SURVIVE also gives scores obtained from Akaike's Information Criterion (AIC). Both were considered in a biological context when determining which models were likely to best represent the data and thereby produce the best survival estimates.

Table 3.2 Models tested with the data from table 3.1 using SURVIV software. The p values are derived from the results of a goodness of fit test which compares observed values to those expected from a saturated model (H_0 = distribution of model values does not differ from that expected from the saturated model).

No.	Adult		Juvenile		AIC	p
	surviv.	recov.	surviv.	recov.		
1	year	year	year	year	279.7	0.0929
2	const	year	year	year	270.7	0.1624
3	const	year	const	year	270.0	0.0837
4	const	year	year	const	352.4	0.0000
5	const	const	year	const	355.4	0.0000
6	const	const	const	const	359.2	0.0000
7	0.89*	year	year	year	269.7	0.1644
8	0.89*	year	const	const	355.2	0.0000

* from Gaston *et al.* 1994

The goodness of fit tests and AIC values indicate that the best models were those which incorporated year dependent recovery probabilities.. Given the decline in recoveries previously mentioned (Figure 3.1), this was not surprising. Of the models listed in Table 3.2, the best model (based on AIC values) was model #3 in which survival probabilities for both adult and juvenile murre were constant while recovery rates were time-dependent. However, models incorporating constant survival did not provide a significantly better fit to these data. Given the similarity in AIC values for all models with time-dependent recovery probabilities, perhaps the best models are those which fit what might be expected from a biological perspective. Survival probabilities for any cohort vary from year to year as a result of sensitivity to environmental factors for young birds. Observations of banded birds at Coats Island have clearly shown that the survival of the 1986 cohort was lower than that of other cohorts (Noble *et al.* 1991). The latter is also evident from the recovery

probabilities of that cohort in models involving time-dependent recovery (see appendix, Table B1). Adult birds are not as affected by such events and may be expected to exhibit a more constant survival probability. The best compromise between AIC and what is logical in a biological sense is model #2 which includes time-dependent recovery for both adults and juveniles and constant survival for adults and time-dependent survival for juveniles. This model had the second best AIC score and included the only acceptable fit to the data (#2, Table 3.2); Lebreton *et al.* (1992) suggest adopting an α level of 0.15 to reduce the risk of both Type I and Type II errors. Survival probabilities calculated from this model suggest adult survival to be 0.78 (95CI: 0.59-0.98) and survival to first year to range from 0.34-0.94 with a mean of 0.58. Confidence intervals for the juvenile estimates were broad (see appendix B Table B1) and some of the estimates were not considered realistic. For example, the estimate for the survival of the 1988 cohort to first year was 0.94 which is not likely. The model did detect a low survival probability for the 1986 cohort which was expected based on the lower than average number of birds from this cohort observed at the colony (Noble *et al.* 1991).

When a reliable estimate of adult survival from Gaston *et al.* (1994) was substituted into model #2 (model #7) there was no change in estimated juvenile survival probabilities (appendix B, Table B1). Of greatest use to wildlife managers are models which give them the greatest predictive power. In this case, the ability to describe juvenile survival. It would be very difficult to predict just how a combination of environmental factors will combine to affect survival so a model that will give a single estimate which can be used in any year would be best. Model #8 estimated survival to first year to be 0.52 (95CI: 0.46-0.56) when adult and juvenile survival was held constant.

DISCUSSION:

Recovery of Banded Birds

Because significantly fewer US Fish and Wildlife Service bands than special bands were recovered in the 1985 cohort (see Chapter 2), the possibility exists that a smaller proportion of cohorts banded with these bands were reported than of the newer bands used on Coats Island which carry the Canadian return address. Only two Coats Island cohorts are affected, 1984, and 1985 and because these years had some of the highest recovery rates, this is unlikely to have changed the temporal trend described in Figure 3.1. The recovery enhancement programme in 1984 and 1985 may have caused an increase in the general reporting rate during these years which may have counteracted a decrease in reporting rates due to band type. The apparent downward trend in reporting rates with time may reflect changes in hunting pressure and/or reporting rates. Because this decline could actually be the result of a wide range of factors, such as the effects of weather or ice conditions on hunting effort, it was impossible to attribute it to a single cause. Based on the results of surveys carried out between 1981 and 1991, there appears to be no downward trend in overall hunting activities in Newfoundland over the decade (Filion *et al.* 1993), although hunting trends for particular species were not listed. If hunting pressure on thick-billed murre has remained constant, the observed decline in recoveries may be due to a decline in reporting rates. Rates in the early 1980's may have been high due to an active campaign by the Canadian Wildlife Service to solicit bands from communities. This practice was reduced after 1987 and might explain the decline in the latter part of that decade. The decline was significant for first year birds which make up over 50% of the annual harvest. Based on differences in reporting rates for different band types and an

overall decrease in the proportion of bands recovered with time, it is apparent that survival models which account for inter-year differences in reporting rates must be used for this population. Second year birds are more erratic in their behaviour, showing similarities to first year and older birds.

Model Assumptions

Given the differences in distribution of birds from different colonies (chapter 2), it is possible that annual mortality due to hunting may vary among them. This difference, if it does exist, may or may not be large enough to cause a significant difference in survival among colonies. Such variation would violate the assumption that the sample is representative of the population, as only recoveries of murrelets from Coats Island have been analyzed. Variation in survival among colonies could only be tested by a large scale banding program carried out over a number of years at a minimum of two colonies. To date this has not been carried out for murrelets. For this analysis, given the management focus, we need not assume that the Coats Island population is representative of the Northwestern Atlantic population of Thick-billed Murrelets.

It is also important that the age and/or sex of individuals be correctly determined depending on the questions posed. For this data set, where questions of age are asked, aging of birds is straightforward. All birds are banded as either a chick or a breeding adult. At banding, both age categories are easy to distinguish on the cliffs at the breeding colony; therefore, any errors must relate to data recording and are probably few. The sex of Murrelets cannot be distinguished at banding, therefore, this type of data was not included in the data sent to the US Fish and Wildlife Service. Birds can be sexed subsequently through observation of bands during copulation or observation of

banded birds departing with fledged chicks (it is the male parent which escorts the chick from the colony). Survival of birds sexed at the colony is discussed in Gaston *et al.* (1994); from the data collected to date, no significant difference in survival between the sexes has been detected but there was an indication that a lower survival probability for females might exist.

Birds that lose their bands will never be reported and therefore recovery rates will be lower and the survival probabilities that are reported would be biased towards lower than actual values. Simulation experiments have shown that the actual biases imposed by band loss are likely to be insignificant (Nelson *et al.* 1980). Effects would be greatest for long lived species, like the Thick-billed Murre, but only where band loss is high. Band loss was not thought to be a problem as the stainless steel bands placed on birds on Coats Island have shown little indication of wear (A.J. Gaston pers. comm.). In addition, no birds have been observed with plastic bands and no metal band which we would expect if some metal bands had been lost.

Recovery models also assume that survival is not affected by the banding process itself. There is no evidence to suggest that the banding process adversely affects adults or chicks. After banding, adult birds usually return to their sites within minutes. Some mortality of chicks does occur during banding. The majority is caused by the disturbance of banders descending to the ledges which causes some chicks to fledge prematurely to their deaths. Usually, this happens soon after arrival on a ledge before any bands are placed on chicks; as a result, this mortality will not bias survival estimates. A small proportion of banded chicks do jump to their deaths immediately after banding. Some of this can be accounted for if banders keep track of lost chicks. Unattended chicks, exposed either during banding or at other times by the ineptitude of brooding parents, may fall prey to Glaucous Gulls (*Larus hyperboreus*) and Iceland Gulls (*Larus glaucoides*). A few bands have

been recovered from gull nest sites and are likely from chicks fledged prematurely during banding, from chicks taken at fledging, or from chicks stolen off ledges.

Recovery data obtained from the US Fish and Wildlife Service is assumed to be accurate. The USFWS does do some checking to verify the data and for birds banded on Coats Island with special murre bands, records sent to the Canadian Wildlife Service were used to double check the accuracy of the USFWS database.

Recovery models require that the outcome for banded individuals be mutually independent and that the fate of banded individuals is a multinomial random variable. The mutual independence of outcomes for banded individuals is impossible to test and is usually assumed to be true. Brownie *et al.* (1985) state that violations of this assumption are unlikely to make the results of the analysis questionable. They also show that the fate of banded individuals is indeed a multinomial random variable.

That all individuals of a given age class have the same annual survival rate is generally not testable and must be accepted as true (Brownie *et al.* 1985).

Survival to First Year.

Survival probabilities based on the data set shown in table 3.1 did not produce reasonable estimates of adult mortality for several possible reasons. Small numbers of adults banded each year resulted in very few recoveries. Estimation of adult survival was difficult using recovery methods because of too few data. The confidence limits of 0.59-0.98 embrace the extreme range of possible values; therefore, no useful information can be extracted. The mean value was likely an underestimate, by roughly 10%, based on estimates derived from more accurate methods (Gaston *et al.* 1994, Birkhead and Hudson 1977). Assuming that adult survival was underestimated, juvenile survival would have been overestimated to allow for the reduced number of adults. The latter was demonstrated when estimates based on adult survival, constrained to a constant 0.89, were included in model #8 with survival to first year being reduced to 0.52. Increased confidence can be placed on this estimate since the fixed adult survival rate was based on careful observations at the Coats Island colony.

SURVIV models indicated that for the input data, the best fit was observed for models incorporating year to year variation (Table 3.2). Because a host of environmental factors affect both natural mortality and hunting ability, and because these factors are variable among years, it is not difficult to see why these models best described the data set. However, models incorporating inter-year variation produced some estimates that were not considered to be realistic. For example, a survival probability to first year of 0.94 for the 1988 cohort, as was calculated from both models 2 and 7, exceeds most estimates of adult survival and is therefore highly unlikely. Although it is important to note inter-year variation, the estimates produced by these models were suspect and their confidence intervals were too broad to draw conclusions which would be useful for making

management decisions. Of greater use to managers are the estimates derived from models in which survival among years was assumed to be constant. Survival estimates based on these models will have averaged out the effects of inter-year variation which can be used in management decisions which must be effective over a number of years.

Estimates of juvenile survival on their own are of little value. When placed into a broader perspective they become more useful. For example, if banding is carried out for a number of years on Coats Island to include adequate data after the implementation of regulations on the turr hunt, the effects of the hunt may be described by a comparison of juvenile survival rates before and after the hunt was regulated. The actual values may not be trustworthy due to broad confidence intervals; however, changes in survival estimates over the course of the time series may indicate temporal changes. Also, juvenile survival probabilities can be utilized right away as a component of an estimate of survival to breeding age which is included in Chapter 4.

CHAPTER 4.
ANNUAL SURVIVAL OF PRE-BREEDING THICK-BILLED MURRES
BASED ON MARK-RECAPTURE METHODS

INTRODUCTION:

Mark-recapture technique was first used by John Graunt in 1662 to estimate the population size of the city of London (Krebs 1989). This method was later used to estimate wildlife population size in the late nineteenth century using models based on the proportion of marked individuals from an initial capture event, during later recapture attempts (Krebs 1989). Recently, these models have been developed with a shift in intent towards the estimation of survival based primarily on the work of Cormack (1964), Jolly (1965), and Seber (1965). Currently used models are more powerful, allowing for testing of more complex hypotheses with variation in survival based on age or environmental variables and differences in recapture probabilities (Lebreton *et al.* 1993).

Survival probabilities derived from the Cormack-Jolly-Seber method are based on a number of assumptions. In the case of the modified Cormack-Jolly-Seber approach, these assumptions are (from Pollock *et al.* 1990):

1) Equal probability of capture of individuals in a given age class. This assumption is most important when individuals must be trapped in order to record recaptures. In some cases, animals learn to avoid traps thus decreasing recapture probabilities. For this study, equal catchability equates with equal detectability or that individuals are equally likely to be observed on the ledges at the Coats Island colony.

- 2) Permanent emigration. Individuals who are recorded in a population will be considered dead if they emigrate and are not detected in subsequent sampling efforts.
- 3) Equal survivability. In studies of age specific survival it is assumed that all individuals of a given age class have equal annual survival probabilities in any given year.
- 4) No marks are lost from marked animals.
- 5) All individuals are aged correctly.

Failure to acknowledge these assumptions has led a number of studies to derive biased estimates. Begon (1983) found that 66% of 100 papers citing Jolly (1965) between 1966 and 1980 did not test or justify any assumptions. A further 8% did no testing but did justify the assumptions, 19% tested only one assumption finding it to be valid, and in the remaining 8% all assumptions were tested and found invalid. In the latter case, all studies ignored these violations and continued to apply the method.

Heterogeneity in capture probability, violation of the first assumption, has been shown to negatively bias the results of survival or population estimates using the Cormack-Jolly-Seber method. This can occur when there is a tendency for some animals to become more likely to be trapped (trap happy) than others. In such a case, recapture probabilities are higher than they should be resulting in a slight negative bias in survival (Pollock *et al.* 1990). Such a bias was discovered in a mark-recapture study of northern fulmars (*Fulmarus glacialis*) using resightings at a breeding colony (Carothers 1979). The effects of this bias were small, less than one percent; therefore, violations of this assumption for similar studies is not likely to be significant.

Temporary emigration will result in a positive bias of survival probability. The severity of this bias has not been quantified; however Pollock *et al.* suggest that this violation of the assumption of permanent emigration is common in field studies and is potentially serious.

Birds that loose bands will be recorded as dead such that if enough bands are lost survival is likely to be underestimated (Arnason and Mills 1981, Nelson *et al.* 1980). Generally violations of this assumption will significantly bias estimates if band loss is large (Nelson *et al.* 1980).

Violations of the equal survivability assumption are thought to be small (Pollock *et al.* 1990) although the effects of violations here have not been tested. Cormack (1972) suggests that survival estimates represent an average survival probability of all individuals within a given class; therefore, variation will not affect the results these models as long as there is no effect which can be correlated to the banding process.

In this chapter, I address the assumptions of mark-recapture methods in relation to data collected on Coats Island. Annual survival probabilities for pre-breeding birds are estimated. In addition, survival estimates from Chapter 3 are used with estimates derived from this chapter to estimate survival to first breeding.

METHODS:

Banding and Band Reading:

Data for these analyses were collected at the Thick-billed Murre colony at Coats Island, (see figures 2.1 and 4.1). Mark-recapture studies rely on the identification of individuals over several time periods. On Coats Island, individuals were identified through observations of unique band number sequences stamped on stainless steel bands. Some of the older banded cohorts (1981, 1984, and half of 1985) were banded with standard US Fish and Wildlife Service circular bands while all older cohorts received special stainless steel murre bands (see methods chapter 2). These bands are triangular in shape allowing the entire number to be stamped on a single face of the band thus enabling observers to record the entire number sequence permitting identification of individual birds. In comparison, the numbers stamped on circular USFWS bands are rarely oriented so that all numbers can be recorded, making the identification of individuals difficult. On Coats Island, roughly two thousand chicks were banded each season starting in 1981 and then on an annual basis after 1984 (see table 2.2). All birds received a metal band and a colour darvic band, the latter being colour specific to the year of banding.

Birds, banded as chicks, return to the colony for the first time as two year olds (Noble *et al.* 1991). Any survival estimates based on resightings of birds returning to the colony can therefore begin estimating survival only from the second year.

Only chicks on the northern half of the west sub-colony were banded (figure 4.1). Beginning in 1988, observations were made of individuals present at the colony based on the recording of band number combinations. At each observation, the date, time, location within the colony, and observed band colours and numbers were recorded. Most observations were recorded on ledges visible from

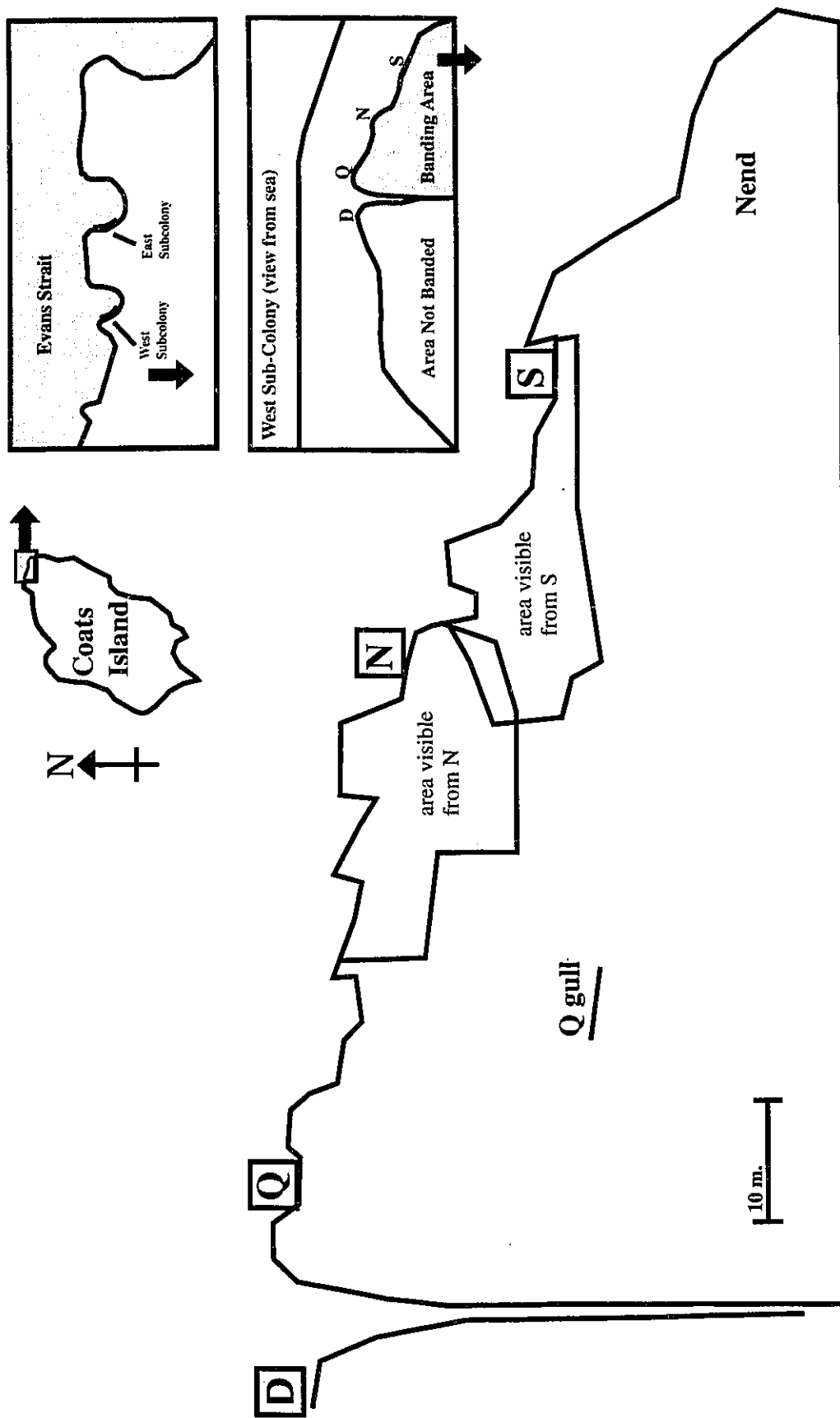


Figure 4.1 Locations of the breeding colonies on the north end of Coats Island. Blinds D, Q, N and S are indicated as well as the locations of important band reading sites (Qgull and Nend) found within the banding area.

blinds "N" and "S" and to a lesser extent from blinds "D", "Q" and at the extreme north end of the colony at "Nend" (figure 4.1). Bands were read with the aid of telescopes which allowed recording of numbers to a distance of up to 30 metres from the blinds.

Data were collected either during dedicated band reading sessions or opportunistically from the blinds during times when the focus of the observer was on other data collection. For example, a few band numbers might be recorded during observations of the breeding status of birds within the observation area. Otherwise, specific times were set aside for reading of bands only. In order to determine the effects of band reading effort on the return of band numbers, some band reading sessions in 1991 and 1992 were standardized to an hour of reading daily from the N blind and the S blind.

Overall, regular scheduling of band reading sessions was not considered necessary as there were many factors that affect the efficiency with which bands could be read. A host of environmental factors can affect an observers ability to read bands on any particular day. These centre primarily on conditions affecting the quality of light on the colony. Combinations of quality and angle of light, cloud, fog, and the condition of snow, ice, or water below the colony can increase or decrease the contrast of ambient light making bands much easier or more difficult to see. Strong sunlight, reflected off of snow or water onto the colony made for good band reading conditions. The effects of light on the ability to read bands also affected the distance over which bands could be read. Greater contrast allowed bands from a greater distance to be recorded. Precipitation in the form of snow, rain, mist, and fog severely reduces the capability of an observer to read bands by reducing visibility. The effects of precipitation carried over for hours or days after it had stopped as the layer of excrement that has built on the cliff ledges becomes pasty when wet and coats bands, concealing

their numbers.

Colony attendance in terms of numbers of birds of particular ages changes throughout a season, young birds arrive later than older birds (Noble 1990, Gaston 1991). Two year olds arrive at the colony for the first time in mid-July, although this may vary considerably from year to year, and increase in numbers into early August. Only a portion of two year olds are thought to attend the colony. Three year olds are present in very small numbers at the beginning of the breeding season in late May and increase in numbers throughout the incubation period so that most birds of this age probably attend the colony by the end of the breeding season. Most murrelets older than three years appear to be present from the beginning of the season (Noble 1990, Gaston 1991). Consequently, to record the bands of younger birds it may be wise to concentrate band reading efforts to a period when young birds are present from mid-July on. Data for the analyses in this chapter were recorded over a number of seasons differing in length; however, all seasons included the most critical period when all age classes are present. Band reading prior to the time when all birds are present is useful for recording the presence of older individuals especially before the commencement of egg laying when breeding birds may be more likely to spend time loafing at the colony. The tarsi, and therefore the bands, of loafing birds are easier to detect than the tarsi of breeding birds which are sitting on sites with their legs concealed. Therefore, resighting rates of individuals will decrease as they begin to breed. Survival models for thick-billed murrelets must take this into account.

All chicks banded on Coats Island were banded on the right leg. By scanning the colony for colour banded right legs, it was possible to address questions of age-related diurnal activity based on the relative proportions of birds of a given age seen at different times of day (time of day watches).

Time of day watches were carried out every five days over the course of the 1991 breeding season. Each watch consisted of a series of right leg counts of all visible colony area from the S blind. The number of all visible tarsi were recorded every ten minutes, including totals of all colour bands observed, for a one hour period to ensure adequate detection of banded individuals present. One hour watches were done every three hours for as long as light would allow. Watches done early in the season could be done for an entire 24 hour period but increasing length of night later in the season reduced the length of time in which watches could be carried out. Increasing night affected watches at midnight and 0300hrs relatively early in the season, these time periods were not considered for the analysis. Watches at 0600, 0900, 1200, 1500, 1800, and 2100 hours were done over a 26 day period thus including seven watches in the analysis. A Kruskal-Wallis nonparametric analysis of variance, was used to detect differences in the number of individuals of a particular age present at the different times of day over the seven days of watches. Analyses were done for each of the age groups present in 1991 (two to seven years).

Ideally, if an observer spent enough hours at an observation spot they would record most of the individuals present within the visible area. Analytical software in wide use at present has the capability to allow for differences in resighting rates among years; thus, it is not crucial for the computation of survival probabilities to record all individuals present in a season, provided that observations are made over several years. Resighting and survival probabilities are estimated and therefore have some variance associated with them. This variance decreases as the proportion of birds recorded approaches the total number of individuals present. In order to determine how many hours of observation might be required to record most bands present, a series of one hour band reading sessions were carried out in 1991 and 1992 from the main observation blinds at N and S

(figure 4.1) over the duration of the complete breeding season in both years. From the data collected during these sessions, a plot of number of observation hours and the cumulative number of new bands read per hour was produced.

Pre-breeding Survival

Data from observations of individuals attending the colony on Coats Island were analyzed using SURGE software (version 4.0). SURGE is a widely used analytical package (Colbert *et al.* 1987, Lebreton *et al.* 1992) which calculates survival estimates based on the Cormack-Jolly-Seber method. There are many programs available to do analyses of capture-recapture data. Of those available, Lebreton *et al.* (1992), list SURGE as the only program which will allow users to define models, use general parameters within the models. It also has documentation which makes use of the program easy for the non-mathematician. The software was chosen for these analyses because of its applicability to a wide range of data sets and its prevalent use in the literature.

SURGE allows for models which incorporate constant survival and recapture probabilities or those which vary with year or age (Colbert *et al.* 1987). As the aim of this chapter was to look at pre-breeding survival, models were chosen to reflect this and incorporated either constant survival rates or those which varied with age (see tables 4.4 and 4.6). Recapture rates have been modeled to reflect yearly variation which is likely here because of differences in band reading effort among years. Recapture rates are affected by age as well, because as birds reach breeding age they tend to sit on their nest sites for the much of the time they attend the colony. The probability of recording the presence of these breeders is reduced in comparison with pre-breeders which tend to be highly mobile and visible on "loafing" ledges. Age specific recapture rates were also modeled.

The model of best fit for the data was chosen using the Akaike information criterion (AIC) (Lebreton *et al.* 1992, Lebreton *et al.* 1993) which selects the best model based on the principle of parsimony choosing the model with the fewest parameters that best fits the data set (Chapter 3).

In order to reduce the possible biases introduced by band reading errors, only bands that were recorded at least twice in the initial year of observation were used. This prevents the apparent mortality of birds that were never there in the first place. Only a portion of birds arrive at the colony at two years of age (table 4.1, Noble 1990); therefore, the sample sizes of capture recapture estimates based on these birds are smaller than estimates based on birds sighted as three year olds when most are attending the colony. I have included the smaller number of initial sightings of birds at two years old because estimates of survival based on this sample give insight into the population dynamics of very young birds. Survival probabilities of birds based on sightings beginning at three years old were estimated because the larger sample sizes should provide better estimates.

Constraints dictated by limits on the distance over which bands could be read and the structure of the cliff face which provided areas of the colony not visible to an observer, made it impossible to record all banded individuals present at the colony. Consequently, survival estimates are based on those birds visible from blinds N and S (Figure 4.1) only. Young birds, observed at the colony for the first time, became the original marked sample thus precluding the need to see all banded individuals over the entire colony. This approach requires that non-breeding birds do not move significantly within the colony to ensure that the individuals seen from the blinds represent a sample of the colony as a whole.

Emigration.

Emigration, in terms of this mark-recapture study, can occur when individuals move permanently from the natal colony (inter-colony) or when they move permanently to a part of the colony away from areas visible from the observation blinds (intra-colony). Of biggest concern for survival estimates are the biases which might be introduced by temporary emigration.

Inter-colony emigration was assessed by visiting the two closest neighbouring colonies: the east sub-colony on Coats Island (figure 4.1) and at the colony on East Digges Island (figure 2.1). It is at these two colonies that emigrants would be most likely to be found. It has been shown in kittiwakes that emigrants are most likely to breed in colonies which are closer to the natal colony (Coulson and de Mévergnies 1992). Right leg counts at these colonies consisted of single sweeps of the visible portions of each colony. Observations of the east colony on Coats Island have been carried out in 1989, 1991, 1992, and 1993. East Digges Island was visited in 1992 and 1993. At both locations the total number of right tarsi seen was recorded indicating any birds with colour band combinations used on the west sub-colony on Coats Island.

Intra-colony emigration, the movement of individuals within the colony, may affect their detectability and thereby their resighting probability. This is a potential source of temporary emigration. The degree to which this occurs was examined by measuring the movements between ledges used by individuals. Every observation of a banded bird at the Coats Island colony included the location of the ledge on which the observation took place. Movements of individuals were monitored from areas D, Q., Q gull, and Nend (figure 4.1). These areas are located peripherally from the more intensely observed areas at N and S; therefore, there is a greater likelihood that movements from these sites will be detected. Where more than one movement was detected, the distance

between the two locations furthest apart was used. Some of the ledges where birds were observed were up to five metres long making precise measurements between ledges impossible. The mid point of long ledges was used as the point from which measurements were taken.

RESULTS:

Band Reading Efforts

Results presented here are derived from a database of observations from 1988 to 1993. The quantity of complete band numbers observed in each season are given in Table 4.1. These numbers represent a minimum of the individuals present as it was not possible to observe all individuals (see Figure 4.2). Sample sizes are dictated by effort, which was inconsistent between years, and the initial number of chicks banded in each year (Table 2.2).

Table 4.1. The number of complete band number combinations read for different aged birds during visits to the Coats Island colony from 1988 to 1993.

Obs. Year	Age							
	2	3	4	5	6	7	8	9
1988	97	148	46					
1989	48	103	57	16				
1990	125	241	175	95	27			
1991	90	413	229	132	71	8		
1992	75	450	407	273	150	67	16	
1993	111	142	185	172	107	76	37	7

Timed Watches

Standardized band reading sessions gave an indication of the proportion of total bands read in a season. Figure 4.2 depicts the return of band reading efforts in 1991 and 1992 respectively. The curves represent the cumulative total of complete band numbers read from two blinds, N and S, over time. Of all the years of data collection, 1992 was the most intensive in terms of total number of hours spent reading bands; therefore, there is a greater probability that the point where most available bands were read would be reached in this year. There was no indication that this was the case for observations from either blind. Data from 1991 similarly indicated that the number of hours spent reading bands was not sufficient to record all individuals present. Consequently, conclusions drawn from this data must be considered as coming from a minimum of individuals present at the colony in each year.

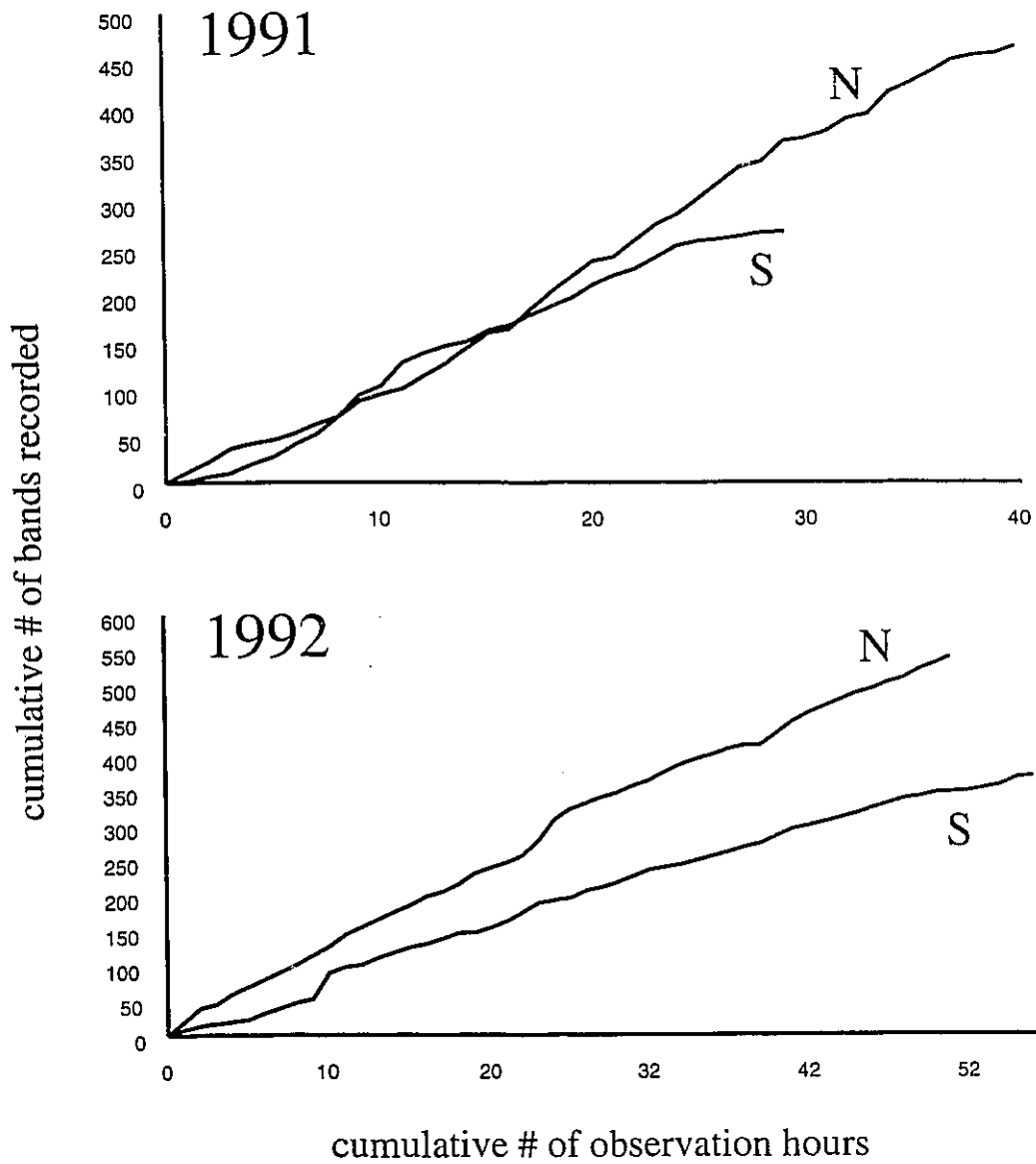


Figure 4.2 Return from band reading efforts, as indicated by the number of new bands read with accumulated time spent observing from blinds N and S in 1991 and 1992.

Attendance patterns at different times of day:

Time of day did not appear to influence the attendance of any age class based on right leg counts carried out every three hours throughout the day (Figure 4.3). A non-parametric analysis of variance failed to detect time of day attendance effects among birds in all age categories ($p > 0.3$ for birds aged two through seven). No biases are therefore expected by the lack of scheduled band reading efforts which would ensure that all time periods in the day were covered equally.

Inter-colony Emigration

In several years of visitation to the two closest colonies to the west sub-colony on Coats Island, only 4 emigrants have been detected. All were at the east sub-colony on Coats Island. A seven year old murre seen in 1992 on Coats Island was incubating an egg suggesting a permanent attachment to this colony. The band number of this bird was recorded and no sightings of it had been recorded at the west sub colony. Three, three year old birds were spotted at the east sub-colony in 1989 and 1993 (one and two birds respectively). Observations of 4893 birds with visible right legs at Digges Island in 1992 and 1993 produced no indications of Coats Island birds attending this colony. Clearly, emigration of Coats Island birds away from the island is rare but this is not to say that it does not occur. An eight year old murre, banded as a chick on Coats Island, was recovered in the Thule district of northern Greenland during the breeding season in 1993 (K. Kampp pers. comm.).

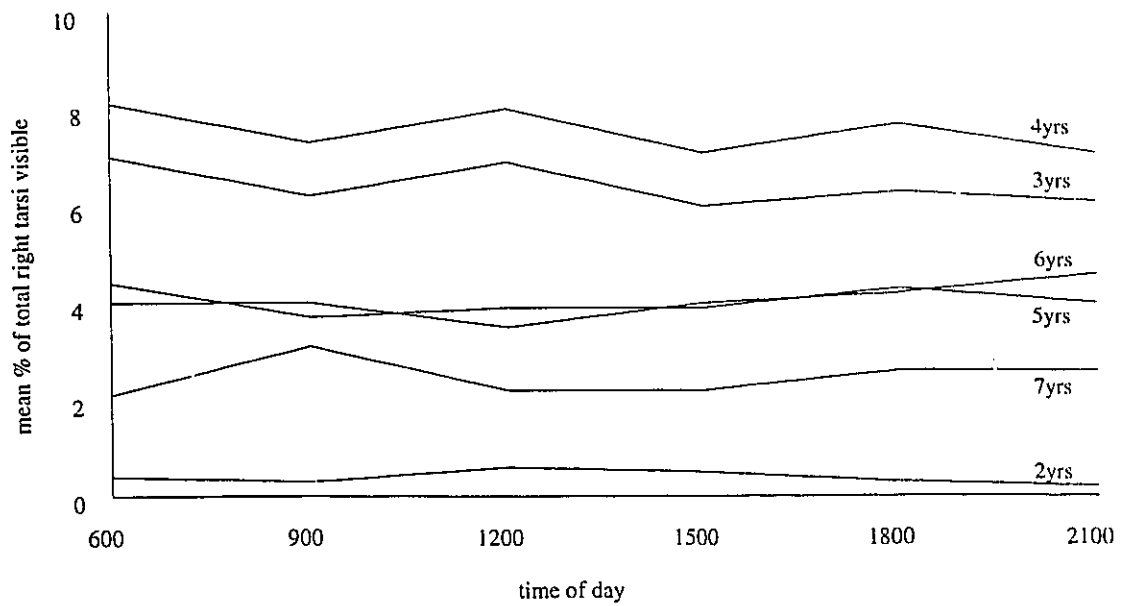


Figure 4.3 Activity of cohorts at the colony at different times of day as indicated by the percentage of visible colour banded individuals of each age class.

Intra-colony Emigration

Cases where individuals permanently move away from areas of intense band observation at N and S will be incorrectly classified as deaths. Consequently, recorded movements of individuals were used to detect differences in movement among age classes. Pre-breeding birds (all birds younger than 5) were more likely to move distances that might take them out of range of observers at N and S (Table 4.2). For analysis, small sample sizes required collapsing Table 4.2 to produce three distance categories, such that the largest distance category was >40m for the two age categories: breeders (all birds 5 and older) and pre-breeders (all birds younger than 5). Movement patterns of pre-breeders and breeders were considered to be significantly different ($\chi^2_2=8.42$, $p=0.014$) with older birds more likely to use a smaller proportion of the colony.

Table 4.2 Detected movements, as indicated by the percentage of each class moving various distances, of 176 birds observed at locations peripheral to the area of intense band observation in 1992.

age	N	% at distance			
		0-20m	21-40m	41-60m	61-80m
2	3	100	0	0	0
3	53	72	7	4	17
4	59	90	2	2	7
5	34	77	14	6	3
6	20	80	15	0	0
7	7	100	0	0	0

Annual Survival (Pre-breeders)

The data set of individuals seen initially as two year olds is the only data available to estimate survival from second to third year. Estimates of survival for subsequent years is better handled by the larger data set of birds seen as three year olds (see tables 4.3 and 4.5 for comparison).

Table 4.3 The number of two year old murrelets seen a minimum of two times at the colony and then seen again as older birds in subsequent years.

Year Banded	No. Recorded at Age					
	2	3	4	5	6	7
1986	22	10	9	7	11	6
1987	21	13	9	10	5	
1988	35	27	20	13		
1989	29	25	13			
1990	25	11				

AIC values indicate that the most parsimonious model is the one that suggests that survival is constant among age groups and that recapture rates are year specific. This model was significantly better than the most general model of constant age and survival (table 4.4). With this model survival is estimated at 0.83 (95% CI 0.77-0.88).

One other model was significantly better than the general model, it suggested that age dependant survival is different from second to third year but is constant from then on with recapture rates dependant on year. This model gives a survival probability from second to third year of 0.86 (95CI: 0.75-0.92), annual survival for all older birds is 0.81 (95CI: 0.72-0.89). A complete list of survival and resighting probabilities for all models is given in Appendix B (Table B2).

Table 4.4 Model selection for survival estimates of murrelets seen initially in their second year. The number of parameters in the model (np), Akaike information criterion (AIC), and a G statistic comparing deviance of the simplest model (constant survival and recapture probabilities) with the deviance of other models introducing effects of age or year on survival and/or recapture estimates are given. The results of the latter are an indication of improvement over the simplest model (H_0 = deviance of the models is the same).

Model		np	AIC	G (df)	p<
Surv.	Recap.				
const	const	2	472.7	-	-
const	year	6	458.7	14.0 (4)	0.025
const	age ¹	6	476.4	3.7 (4)	0.90
const	age ²	5	475.2	2.5 (3)	0.90
const	age ³	4	473.5	0.8 (2)	0.95
const	age ⁴	3	471.5	1.2 (1)	0.90
age ¹	year	10	465.7	7.0 (8)	0.90
age ²	year	9	463.7	9.0 (7)	0.90
age ³	year	8	461.7	11.0 (6)	0.10
age⁴	year	7	460.4	12.3 (5)	0.05
age ¹	age ¹	10	482.0	9.3 (8)	0.90
age ²	age ²	8	478.1	5.4 (6)	0.90
age ³	age ³	6	477.3	4.6 (4)	0.90
age ⁴	age ⁴	4	473.3	0.6 (2)	0.98

- 1 - 5 age groups; all ages separate (2 to 7 years)
- 2 - 4 age groups; 2-3, 3-4 and 4-5 years separate, all older ages combined
- 3 - 3 age groups; 2-3 and 3-4 years separate, all older ages combined
- 4 - 2 age groups; 2-3 years separate, all older ages combined

The larger sample from the many birds seen as three year olds (Table 4.5) offers a better estimate of survival of birds to their fourth and fifth year. After this age, most birds are likely breeding (Gaston *et al.* 1994) and can be expected to exhibit adult survival probabilities.

Table 4.5 The number of three year old murre seen a minimum of two times at the colony and then seen again as older birds in subsequent years.

Year Banded	No. Recorded at Age					
	3	4	5	6	7	8
1985	63	12	21	13	19	7
1986	42	30	24	21	13	
1987	76	49	48	28		
1988	178	119	72			
1989	242	94				

AIC values of models based on birds seen at least twice as three year old birds suggests that the best models are those incorporating year dependant recapture rates (Table 4.7), all of which were significantly better fits to the data than the general model with constant survival and recovery probabilities. Of the models including year dependant recovery and age dependant survival, the one estimating different annual survival probabilities for all age categories had the lowest AIC value but was not significantly better than any of the 21 models incorporating age dependant survival.

Table 4.6 Model selection for survival estimates of murrelets seen initially in their third year. The number of parameters in the model (np), Akaike information criterion (AIC), and a G statistic comparing deviance of the simplest model (constant survival and recapture probabilities) with the deviance of other models introducing effects of age or year on survival and/or recapture estimates are given. The results of the latter are an indication of improvement over the simplest model (H_0 = deviance of the models is the same).

Model		np	AIC	G (df)	p<
Surv.	Rcap.				
const	const	2	1619.8		
const	year	6	1535.3	84.5 (4)	0.005
const	age ¹	6	1617.8	2.0 (4)	0.90
const	age ²	4	1620.2	0.4 (2)	0.90
const	age ³	3	1618.6	1.2 (1)	0.90
age¹	year	10	1534.9	84.9 (8)	0.005
age²	year	8	1533.2	86.6 (6)	0.005
age³	year	7	1536.8	83.0(5)	0.005
age ¹	age ¹	10	1619.5	0.3 (8)	0.975
age ²	age ²	6	1619.5	0.3 (4)	0.990
age ³	age ³	4	1623.3	3.5 (2)	0.90

- 1 - 5 age groups; all ages separate (3 to 8 years)
- 2 - 3 age groups; 3-4 and 4-5 years separate, all older ages combined
- 3 - 2 age groups; 3-4 years separate, all older ages combined

Of greatest interest from this data are survival probabilities which fill the gap between the estimates from second to third year, previously estimated, to birds which are five years old, the age by which most are breeding. The model listed as age² year in table 4.7 produced these survival probabilities as 0.74 (95CI: 0.68-0.79) from third to fourth year and 0.86 (95CI: 0.77-0.91) from fourth to fifth year. According to this model, survival of birds older than five years was 0.80 (95CI: 0.70-0.87) which is lower than has been estimated by other methods for breeding birds (Gaston *et al.* 1994). This estimate is certainly biased by individuals which are no longer observed as they spend the majority of their time on breeding sites. A complete list of survival and resighting probabilities for all models listed in table 4.6 is given in Appendix B (Table B2).

Estimate of Survival to Breeding Age

In the overall population model, survival to breeding age is required for determining recruitment. Assuming most murres begin to breed at age 5 (Gaston *et al.* 1994), survival to this age is given by the product of annual survival probabilities for the first five years. Estimates of annual survival up to breeding are given in table 4.7.

Table 4.7 Summary of estimates of annual survival for pre-breeding murres based on mark-recapture and recovery methods.

Age	s	95%CI	Source
s_{0-1}	0.52	0.46-0.56	Chapter 3
s_{1-2}	0.76	-	equation 4.3
s_{2-3}	0.83	0.77-0.88	Chapter 4 (from Table 4.4)
s_{3-4}	0.74	0.68-0.79	Chapter 4 (from Table 4.6)
s_{4-5}	0.86	0.77-0.91	Chapter 4 (from Table 4.6)

Estimate of survival from first to second year (s_{1-2})

Survival from first year to second year, s_{1-2} , was not calculated due to constraints imposed by limits in software capability combined with murre behavioral characteristics. During this missing year, survival can be estimated given survival probabilities listed in table 4.7; the actual value is likely intermediate between s_{0-1} and s_{2-3} . Survival of banded birds during the first year (s_{0-1}) can be partitioned into survival of chicks on the cliffs before fledging (s_c), survival through fledging (s_f), and survival at sea after fledging (s_s)(equation 4.1). More precisely, s_{1-2} is likely intermediate between s_s from equation 4.1 and s_{2-3} ; therefore, s_{1-2} can be estimated if both values are known.

$$s_{0-1} = (s_c)(s_f)(s_s) \quad (4.1)$$

Survival of Coats Island murre chicks on the cliffs (s_c) and at fledging (s_f) has been previously approximated. During the chick rearing period, survival has been estimated at an average 0.87 for 1990 and 1991 (de Forest 1993). Chicks are usually banded during a seven day window during which roughly 80% of chicks will range in age from 2-19 (Gaston and Donaldson 1994). If it is assumed that chicks are banded at an intermediate age of 10 days, and chicks are brooded on the colony for 21 days (Gaston *et al.* 1994), as much as half of the mortality incurred by chicks on the ledges may involve banded birds. From this we get $s_c=0.93$. The transition from colony to sea is a source of significant mortality for chicks, primarily due to the separation of the chick and its parent as the chick falls to the sea from the breeding site. Gilchrist and Gaston (in prep) have estimated survival of chicks at fledging (s_f) based on observations at Coats Island to be 0.80.

From equation 4.1 we get:

$$ss = (s_{0-1})/(s_c)(s_f) \quad (4.2)$$

$$s_s = 0.70$$

Presumably, much of s_s occurs soon after fledging and before reaching Newfoundland waters (Gaston and Nettleship 1981) where chicks are exposed to environmental stresses without the protection of the cliff and without the size and experience of older birds (Tuck 1960). Consequently, the estimate for s_s should be considered a minimum survival probability for murrelets from first to

second year. In reality s_{1-2} would be more appropriately described as the mid-point between s_s and s_{2-3} (equation 4.3).

$$s_{1-2} = (s_s + s_{2-3})/2 \quad (4.3)$$

$$s_{1-2} = 0.76$$

Survival to breeding age (s_b) is given by the product of annual survival probabilities for the first five years of age (equation 4.4). Because the estimate for s_{1-2} had to be calculated and the predicted value of s_{3-4} was suspect, survival to breeding age was calculated using a number of alternatives which are listed in table 4.8.

$$s_b = (s_{0-1})(s_{1-2})(s_{2-3})(s_{3-4})(s_{4-5}) \quad (4.4)$$

Table 4.8 Estimates of survival to breeding (s_b) based on values listed in table 4.7. Rationale for alternative estimates is also given.

#	Changes made in values listed in table 4.7	s_b
1	s_b using values from Table 4.7 (no changes)	0.21
2	as #1 with s_{3-4} changed to 0.86 (same as s_{4-5})	0.24
3	as #1 with s_{1-2} changed to 0.83 (same as s_{2-3})	0.23
4	s_{1-2} changed to 0.83 and s_{3-4} changed to 0.86	0.26
5	s_{1-2} to s_{4-5} changed to 0.89 (s_{adult})	0.33

DISCUSSION:

Assumptions of Mark-Recapture Methods:

Ordinarily, the assumption of equal catchability refers to the ability to recapture animals without the effects of trap happy or trap shy individuals. For the data collected here, equal catchability refers to the probability of an observer to record individuals as present. This assumption is likely to be violated to some degree by aspects of behaviour at the colony. The most obvious problem arises when birds begin to breed, their bands become more difficult to detect when they are stationary on their breeding sites for prolonged periods of time. This reduces their probability of being detected, in essence they become trap-shy. A reduced number of breeders will be seen in subsequent years which would imply more deaths are occurring than is real and will result in underestimates of survival. However, Cormack-Jolly-Seber models are robust to violations of this assumption as has been shown in similar studies on seabirds (Carothers 1979).

Emigration from the natal colony, although common in other seabirds including kittiwakes and puffins, was demonstrated to be rare and therefore insignificant for the estimates presented here. The few instances of emigration of Coats Island birds probably occur during the first two years before they can be recorded as being present at the colony and there would be no effect on results presented here. Movement of three year olds away from the observation blinds constitutes local, and potentially temporary emigration. Temporary emigration may cause a significant positive bias in survival estimates although the extent to which this may affect results is unknown (Pollock *et al.* 1990). Estimates of survival for birds from three to four years could have been underestimated as a result of individuals settling permanently in areas away from observers.

The assumption that individuals within a given age class will have equal survival probabilities within a given year is difficult to test as it would involve following closely a number of individuals through the winter. To date the effects of this bias have not been tested but are thought to be small (Pollock *et al.* 1990). For this study, homogenous survival can be justified based on behavioral data. There is some evidence to suggest that thick-billed murres occur in age specific blocks in the winter (see Chapter 2). If this is the case, then survival is likely similar for all as they face similar predation pressure (including turr hunters), and environmental conditions.

Band loss was not thought to be a concern for survival estimates produced from mark-recapture methods for the same reasons mentioned in Chapter 3 for band recovery methods. Stainless steel is strong enough to wear well on long lived seabirds such as murres and biases introduced by a small number of bands lost is likely insignificant (Nelson *et al.* 1980).

Annual Survival (Pre-breeders)

Different aspects of the data set used to calculate survival in this chapter, required consideration during model selection. Band reading effort at the colony on Coats Island differed between years. SURGE can take this into account by including year specific recapture probabilities in the survival model. Models providing the best fit to the data were those which included year specific recapture. Age specific recapture probabilities would intuitively seem appropriate given the differences in detection between breeding and non-breeding birds and the possible changes in colony use by different aged birds. However, models containing age specific recapture rates were not significantly better than the simplest models where recapture was considered constant.

The survival probability of murres from their second to third year of 0.83 is likely a reasonable estimate. Breeding at three years is an uncommon event so the probability of biases introduced by breeding behaviour is slight. Three year old birds appear to use the largest amount of colony space which increases their probability of being recorded on the ledges near N and S. Therefore, birds seen at two years have a good chance of being recorded again in their third year. They also stand the greatest chance of being recorded in a subsequent year if they are not recorded in their third year.

The survival estimate of 0.74 for murres from their third to their fourth year is low compared to estimates for birds one year younger and one year older. There are no known life history traits which would explain why this age class might exhibit a reduced survival probability; the estimate is therefore likely to be biased. Enough murres moving over greater distances in their third year than in subsequent years probably resulted in emigration to areas of the colony which were not observable. These murres will have the same effect on survival calculations as birds which have died during the year. Realistically, the estimate for birds of this age is probably closer to adult survival probabilities of 0.89, certainly higher than the 0.83 estimated for murres from second to third year.

Survival estimates for murres from their fourth to their fifth year are clearly similar to those of adult birds. Breeding at four years of age is not uncommon and may be slightly negatively biasing the SURGE estimate of 0.86. Moreover, the mobility of three year olds may continue in some four year olds and hence depress apparent survival. Overall, there is no evidence that the survival of four and five year old breeders differs measurably from that of older breeders. Adult survival probabilities are within the 95% confidence interval of this estimate.

A more accurate calculation of survival for all pre-breeding murres would have to use a more complex model which will introduce terms to reflect proportions of recruitment and intra-colony emigration in addition to considerations for differences in observational effort from year to year. The resulting model, although inconsistent with the principals of parsimony, would add life history characteristics specific to thick-billed murres which appear to have affected the results of the simpler models available with SURGE.

Survival to Breeding Age

Previous estimates of survival to breeding age for thick-billed murres, based on banding done in the Northwestern Atlantic, ranged from 0.19 to 0.53 (Birkhead and Hudson 1977). The former estimate came from Western Greenland where populations had declined markedly due to hunting at the colonies and was probably not a result that would be considered representative. An additional two data sets have produced estimates that were in between those extremes: 0.35, 0.33 (Birkhead and Hudson 1977)

All of the previous estimates were higher than or at the high end of the range of estimates produced using Coats Island data. Earlier estimates were mostly derived from small data sets, recoveries of between 39 and 70 birds (Birkhead and Hudson 1977), which would not have produced as accurate results as those presented here based on a much larger data set.

Estimates of survival to first year (Chapter 3) based on the Coats Island colony may not be representative of thick-billed murres in the eastern Arctic as a whole because Coats Island is a small colony. Chicks from here are therefore heavier at fledging compared to the larger colonies where

chick growth is slowed due to limits on local food resources (Gaston *et al.* 1983). If condition at colony departure causes differences in subsequent survival, then it may be anticipated that survival at other, larger colonies is lower.

Table 4.8 provided a range of estimates of survival probabilities from banding to first year. The first estimate, #1, of 0.19 was low due to $s_{1,2}$, which had to be calculated in an ad hoc fashion after the fact, and $s_{3,4}$ which may have been underestimated, because of emigration of a proportion of three year olds away from intensely observed areas of the colony. Estimates #2 and #3 attempted to compensate for each of these underestimates separately and were again probably underestimates because they did not address the other underestimate. Based on considerations of general biology, estimate #4, 0.27, is probably close to the actual probability of survival to breeding age and is probably the best estimate based on SURVIV and SURGE estimates.

There exists a strong possibility that birds achieve adult survival prior to reaching breeding age. Estimate #5 looked at what could be expected if this were true in an extreme sense, where birds achieved adult survival after one year. The estimate in this scenario, 0.33, was not greatly different from the best estimate which used a combination of survival estimates derived from banding data. As a result, we may expect survival from colony departure to breeding age between 0.23 and 0.26, with the actual value near the upper end of this range.

CHAPTER 5.
GENERAL DISCUSSION:
MANAGEMENT OF THE NEWFOUNDLAND TURR HUNT

Turr Hunt

Changes to the Migratory Birds Convention Act are designed to ensure that regulatory protection of thick-billed murre populations is secured. Factors like environmental fluctuation, changes in habitat, and the magnitude of the turr hunt will affect the size of murre populations which will in turn affect the sustainable harvest of turrs annually. Continued monitoring of population parameters is therefore necessary for effective management. This chapter translates new biological information I have presented with respect to winter distribution (Chapter 2) and pre-breeding survival (chapters 3 and 4) into recommendations for future management of thick-billed murre populations in eastern Canada.

Strictly from an anthropocentric view, the importance of thick-billed murres goes far beyond the benefit gained each year by the people of Newfoundland in the annual turr hunt. Seabirds have long been used as bioindicators, in the 17th century by Basque mariners used sightings of the great auk to indicate the closeness of the North American continent (Montevecchi 1991), and in more recent times, seabirds have been considered as valuable indicators of the health of oceanographic conditions (Gilbertson *et al.* 1987). Because they occupy a high trophic level in arctic marine food chains and are the dominant seabird in Arctic waters, thick-billed murre populations may integrate the ramifications of marine food web alterations, expressing their effects as visible changes at breeding colonies. Murres breed in a finite number of highly visible colonies; therefore, population trends, possibly reflecting changes in the marine environment, are relatively easy to detect. Murres

are also important to Inuit populations who harvest eggs and adult birds from colonies located near their communities. As with any species which becomes associated with human populations, management of thick-billed murre has become unavoidable.

Turr hunters exert a significant pressure on murre populations. Considering a breeding population of 4×10^6 birds out of a total population of 6.8×10^6 , an estimated reproductive success of 0.72 will result in the fledging of 1.44×10^6 chicks annually (Chardine 1994). Mortality at fledging will reduce this number to approximately 1.15×10^6 (Gilchrist and Gaston in prep.). Current estimates of harvest levels vary between 400,000 and 900,000 birds. Roughly 50% of these are assumed to be first year birds; consequently, between 200,000 and 450,000 of the just over one million first year birds produced may be harvested in Newfoundland. Keeping in mind that significant mortality may occur soon after fledging (Tuck 1961, Birkhead and Nettleship 1981), the actual number of first winter birds reaching Newfoundland may be considerably less than the number of chicks surviving past fledging; consequently, the harvested proportion may be even higher. Although, older age classes are not as strongly affected as first winter birds, their importance to the population as the source of future reproduction is noteworthy. Management of murre populations should address the effects the hunt has on both breeders and pre-breeders alike.

Winter Distributions

Currently, the high annual mortality generated by the Turr hunt has not had any visible effect on Canadian murre populations; that is, no Canadian colonies have declined significantly in the past two decades (Gaston *et al.* 1993). Regulations, imposed for the first time in the 1993-94 hunting season, were aimed at halving the annual harvest. The new regulations are believed to have been

effective, with harvests for that season estimated at 432,000 (J. Chardine pers. comm.). This reduction of a significant source of mortality will have a positive influence in terms of population size in the absence of density dependant factors. Consequently, no changes in policy governing management strategy are presently required. If however, problems arise in subsequent years from, for example, the effects of oil spills or depletion of prey stocks, ameliorative action will require a review of current understanding of murre population biology. Knowledge of when and where individuals may be expected to occur, will be essential for execution of this task.

In Chapter 2, I described a number of differences in the distribution of birds of different ages and of birds from different colonies of origin. Some regional differences, based on colony of origin were detected. For example, murrelets from Hudson Strait were seen to arrive in Newfoundland later than murrelets from other colonies to the north. Regional differences were however not absolute, and significant differences were detected among birds from colonies which were located in similar geographic areas. First year birds from Digges Island were recovered in significantly lower proportions than the same aged birds from Coats Island. Clearly the young of these two colonies, located adjacent to one another in Hudson Strait, tend to winter in different areas. The young from Coats Island wintered within gunshot of Newfoundland while the young from Digges Island wintered in an as yet unknown location. These examples, along with many others in Chapter 2, paint an increasingly complex picture of behaviour with respect to distributions in winter of birds from different colonies of origin. Compounding this complexity is the unknown behaviour of murrelets from colonies where no banding has been carried out. Further complicating distribution patterns are environmental fluctuations which account for much of the inter-year variation. When added to the information presented in chapter 2, these effects produce a complex pattern of similarities and

differences among colonies. For managers of the turr hunt, trying to decide on strategies which would sustain or improve population numbers would be a highly complex task if all of this information were to be assimilated. The best approach is to simplify.

Some distribution attributes of the population were found to be broad in application. For example, young murrens arrive in Newfoundland earlier than older birds and as a consequence, the early hunt affects mostly birds in their first winter. Proactive alterations of harvest levels would best be aimed at the later hunting season when more breeders are involved.

Figure 5.1 shows the zonation currently being used to manage the turr hunt. Based on the proportion of banded individuals recovered in Labrador, activity in zone 1 is not likely to have a noticeable effect on populations. Changes in management in this zone need only apply in cases where extreme action is required and an across the board closure of the hunt needed. Zone 2 roughly corresponds to area A in chapter 2, the hunt occurs here earlier in the winter (October-December) and therefore it is expected that mostly first year birds will be affected. Alterations of season length or bag limits in zone 2 is therefore likely to affect recruitment, and to have a delayed impact on the breeding population (as birds start to breed at 4-5 years). As in zone 1, actions taken here are only necessary in extreme cases. Zone 3 includes areas B, C, D, and E, hunting activity here occurs later in the winter (January-March) and will affect some first year birds. More important though is the fact that most of the older birds recovered, which includes the important breeding population, have been shot in zone 3. Changes to the hunt, through altered bag limits and/or season length will have its greatest impact on the population as a whole when carried out in zone 3. Gradual, negative population trends may be reversed by a reduction of the hunt here, especially if the mortality of breeders is believed to be a critical factor.

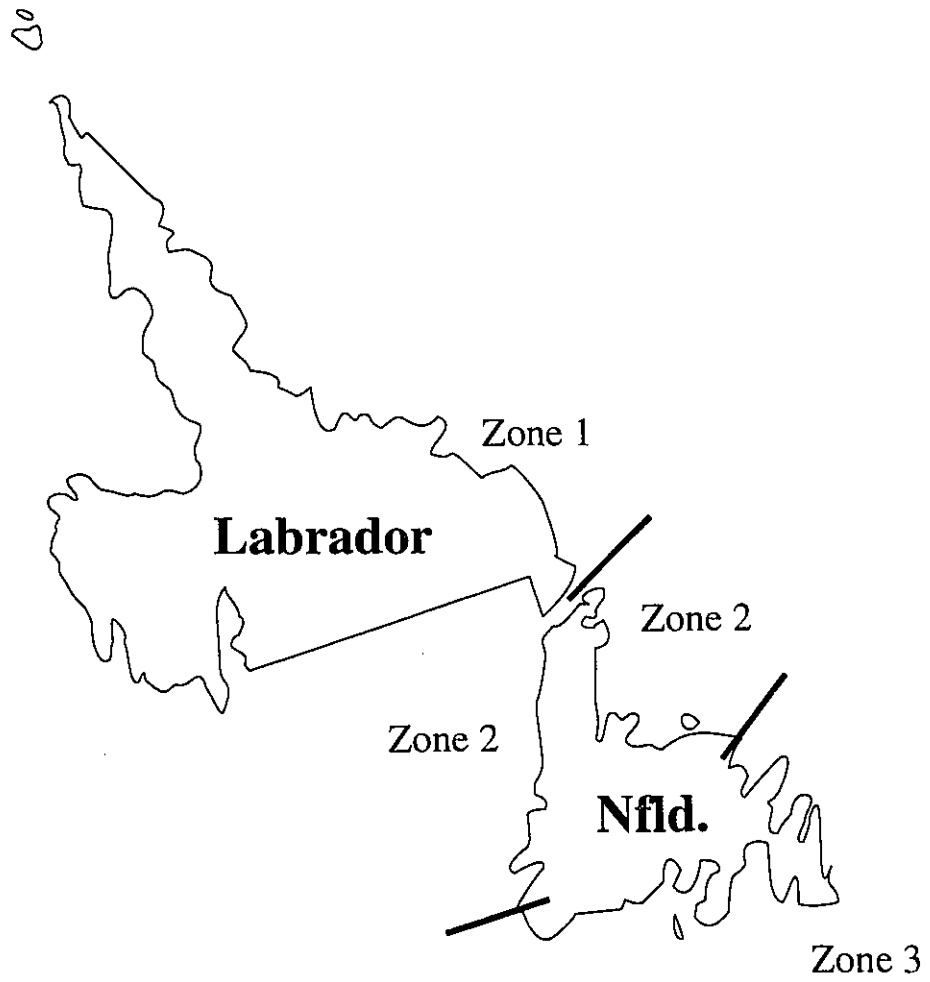


Figure 5.1 Zones used for the management of the Newfoundland Turr hunt.

Current management plans appear to be suitable for maintenance of sustainable Canadian population levels; therefore, no changes are required at present. In the future, gradual population declines may be reversed by adopting a selective hunt, mentioned previously, which takes the emphasis away from breeding birds. Stronger measures in the form of total hunting bans would be required for more severe population declines.

Indications of preferred wintering areas for birds, dependant on their colony of origin, was demonstrated in Chapter 2 and could be of use for determining the impacts of localized disturbances during the winter. For example, an oil spill during the winter in Bonavista Bay might produce significant mortality. Adults from Digges and Coats Islands have shown a preference for Bonavista, Conception and Trinity Bays making a spill here more problematic for those two breeding colonies. Subsequent monitoring could be focused on these colonies during the breeding seasons following such an incident.

To date, distribution information from some of the largest colonies at Akpatok Island, The Minarets (Reid Bay), and Prince Leopold Island is not available due to difficulties in banding chicks at these colonies. Given the inter-colony differences illustrated between other colonies, knowledge of temporal and spatial trends of first winter, second winter, and third winter or greater birds from these unknowns may prove important in the future. Banding efforts in the coming years should focus on banding large numbers of birds at colonies other than those which have already been banded, especially at large colonies such as Akpatok, Canada's largest thick-billed murre colony, where a significant proportion of the total population breeds. Only small numbers of chicks have been banded there to date. Such efforts will prove a challenge due to the difficulties imposed by unstable cliff faces at these colonies. However, alternatives do exist such as was demonstrated at Akpatok

Island in 1993 where about 500 chicks were banded on the beach as they left the colony.

Dramatic declines at colonies in Greenland have been attributed largely to hunting at the colonies during the breeding season (Kampp 1988, Falk and Durnick 1992). Restoration of colonies there may require measures beyond the changes to hunting regulations adopted by the Greenland Home Rule government in the form of a cooperative management plan between the governments of Canada and Greenland. Large numbers of first winter Greenland birds are shot early in the season in Notre Dame Bay (Area A or Zone 2) and it is here that management efforts in Canada might help enhance the number of birds returning to Greenland. By reducing the hunt in Notre Dame Bay there would be a corresponding increase in the number of Greenland birds available to be recruited into the breeding population. Although breeders are more valuable to the population, there is little that can be done in Newfoundland to benefit Greenland breeders. This is because their numbers in Newfoundland waters are small and they are relatively evenly distributed geographically. Perhaps the only practice which might improve the status of this group would be a total ban of the Newfoundland hunt along with corresponding measures in Greenland. Realistically this is unlikely to occur. However the occurrence of substantial numbers of Greenland birds in the Newfoundland harvest indicates the need for managers to take an international approach to managing this population.

Pre-breeding Survival

Survival to breeding is currently estimated at 0.40 for management of thick-billed murre populations in Eastern Canada (J. Chardine 1994). This figure represents estimated survival for the population without the effects of hunting considered. The hunt is expected to have an additive mortality of about 5% reducing estimated survival to breeding to about 0.35. The best case estimate for survival to breeding age produced in this thesis, 0.33 (Table 4.9), used survival probabilities where young birds were assumed to reach adult levels after first year. This is the closest to the estimate currently being used; however, given the behavioral differences among birds in their first winter, second winter, and third winter or greater, it may be unrealistic to assume that all birds older than one year will have similar annual survival probabilities. The estimate based on banding data which allowed for a more gradual increase in survival probabilities with age (Table 4.9, estimate #4) produced a survival to breeding probability of 0.26. The latter is likely an underestimation as the annual survival of older pre-breeders was likely underestimated at a value slightly lower than adult survival; 0.86 as opposed to 0.89. The real survival to breeding age probably falls in the range 0.26 - 0.33.

In a standard population model, the broad range in the survival to breeding age estimates could have serious implications if the actual value were to fall at one end of the range or the other. In this case, the actual value is likely towards the higher end of the range, given that no appreciable decline in numbers has been observed at Canadian breeding colonies. Based on direct observations of banded birds at the Coats Island colony, survival to age three may be as high as 0.52 (Gaston *et al.* 1994). Based on the population trends observed at most Canadian colonies and the estimate reported by Gaston *et al.*, the values derived in this thesis could be underestimates. At the very

least, it appears that survival probabilities likely fall towards the higher ends of the ranges reported.

For safety sake, in terms of maintaining population levels, wildlife managers should err on the side of underestimation of survival. Overestimation of survival to breeding translates into an overestimation of recruitment which leads to a model where more individuals are recruited into the breeding population than actually occurs. In terms of wildlife management, overestimations such as this could affect future projections of population trends, biasing predictions toward increases in total numbers of birds. The calculation of survival to breeding that uses primarily banding data (see estimate #4, Table 4.9) is suitable because it probably represents a slight underestimate of survival for older pre-breeders.

Estimates of survival to breeding for seabirds are difficult to evaluate because of the tendency of young birds to disperse from the colony at fledging and not return for several years. For species with a high emigration rate such as the Atlantic puffin, the task can be even more difficult. These difficulties are reflected in the small number of published estimates for Alcid species and by a recent estimate of survival to breeding age for the common murre which selected among previously published estimates to explain changes in observed population size (Hatchwell and Birkhead 1991). In this case, population size had increased and a high survival to breeding age, 0.41, was chosen. The latter figure was derived from an older estimate from a colony on the opposite side of the Atlantic Ocean (Birkhead and Hudson 1977), which may have been flawed because the original estimate failed to account for dispersal (Kampp 1991).

Hudson (1985) lists three estimates of survival to breeding age for Canadian thick-billed murre colonies; the mean of these was 0.40. This figure is higher than current estimates possibly due

to the fact that two of the values are derived from recovery data collected in the 1950's (Birkhead and Hudson 1977) when, perhaps, survival probabilities were higher. The third estimate was based on observations of non-breeders (Gaston and Nettleship 1981) and has since been found to be based on faulty assumptions (A.J. Gaston pers. comm.). Kampp (1991) offers an estimate of survival to age five of 0.13 for thick-billed murre from Greenland. This may have been an underestimation due to errors in recording the actual size of each banded cohort, but is consistent with steep declines in Greenland thick-billed murre populations seen over the past forty years (Evans and Kampp 1991).

The estimate of survival to breeding age produced in Chapter 4 was derived from several estimates having relatively broad confidence intervals (see Chapters 3 and 4). The reliability of the probability of survival to breeding age is thereby questionable, however the figure produced is not far off estimates produced for murre from other studies. Perhaps the best use for the survival estimates in this thesis is in a time series approach to explain effects of environmental change as has been done for European white storks (Kanyamibwa *et al.* 1990) Banding operations at Coats Island have produced reasonable estimates of survival to breeding age for thick-billed murre, prior to the implementation of regulations. Now that regulations have been implemented, banding at the Coats Island colony should be continued to determine the effects of reduced hunting mortality. Monitoring birds at colonies will give indications of changes in population size, as indicated by changes in the number of birds attending the colony. Recovery and mark-recapture estimates of survival may help explain population flux if any is detected.

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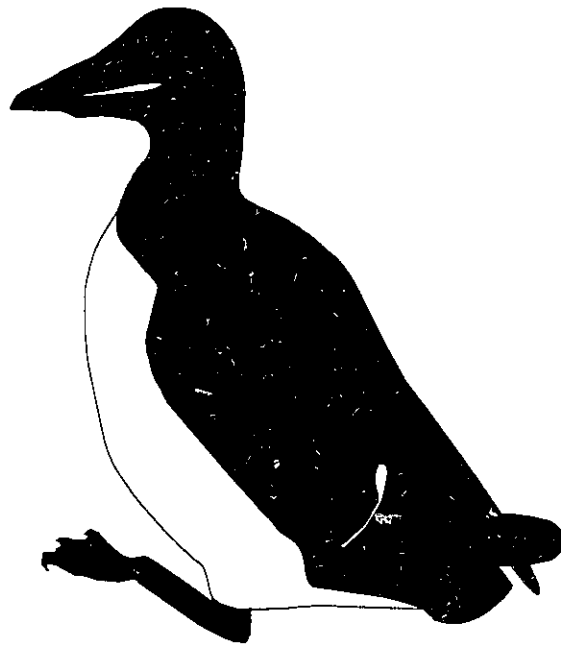
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APPENDIX A

Table A1. Distribution of different age classes in relation to date of recovery of birds banded on Coats Island. Ages classes include birds in their first winter, second winter or third winter or older.

		<u>Month</u>			<u>Total</u>
		<u>O-N</u>	<u>D-J</u>	<u>F-M</u>	
AGE	1	16	51	71	138
	2	12	18	30	60
	3+	9	15	61	85
<u>Total</u>		37	84	162	283

Table A2. Distribution of recoveries from birds banded on Digges Island in the period from 1979 to 1982. Age classes are distributed over three month categories and include birds in their first, second or third or greater winter. Month categories (time of year) refer to recoveries in either October, November, and December (early), or January, February, and March (late).

		<u>Time of Year</u>		<u>Total</u>
		<u>early</u>	<u>late</u>	
AGE	1	1	8	9
	2	3	6	9
	3+	3	53	56
<u>Total</u>		7	67	74

Table A3. Temporal distribution of recoveries of birds banded on Digges Island in 1955. Categories are as described for table A2.

Age	Time of Year		Total
	early	late	
1	8	8	16
2	3	7	10
3+	6	32	38
Total	0	7	64

Table A4. Comparison of temporal distribution of recoveries from banding efforts on Digges Island in 1955 and those in the early 80's. Only recoveries of third year or greater murrees were used for this analysis. Time of year categories are as described in table A2.

Year	Time of Year		Total
	early	late	
1955	6	32	38
1979-83	3	53	56
Total	9	85	94

Table A5. Distribution of recoveries from birds banded on Coburg Island. Age classes are distributed over three month categories. Ages classes include birds in their first, second or third or greater winter.

Age	Month			Total
	O-N	D-J	F-M	
1	25	13	23	61
2	3	7	7	17
3+	5	17	16	38
Total	33	37	46	116

Table A6. Temporal distribution of recoveries of birds banded at Cape Hay in 1957. Categories are as described for table A2.

Age	Time of Year		Total
	early	late	
1	8	3	11
2	1	6	7
3+	3	20	23
Total	12	29	41

Table A7. Temporal distribution of birds banded in Greenland and recovered in Newfoundland. Results are based on banding efforts carried out from 1946 to 1988. Only bands recovered during the legal Turr hunt from October 1 to March 31 were considered.

Age	Month			Total
	O-N	D-J	F-M	
1	74	87	72	233
2	4	19	23	46
3+	10	19	45	74
Total	88	125	140	353

Table A8. Recovery of Coats Island murres in different age categories among the recovery zones described in figure 2.2. Data are inclusive of five hunting seasons from 1 October to 31 March.

	Age	Recovery Area					Total
		A	B	C	D	E	
	1	39	38	10	15	41	143
	2	15	22	13	5	11	66
	3+	8	32	37	8	12	97
	Total	62	92	60	28	64	306

Table A9. Recovery of Coats Island murrelets of all age classes in the areas described in figure 2.2 according to time of year. "Early" recoveries are those reported between 1 October and 31 December; "late" recoveries are those reported between 1 January and 31 March.

	Recovery Area					total
	A	B	C	D	E	
early	41	12	5	3	9	70
late	21	80	55	25	55	236
Total	62	92	60	28	64	306

Table A10. Recoveries of Coats Island murrelets in the different recovery areas described in figure 2.2 over the five hunting seasons from 1987 to 1992. Time of year and age categories are combined in this table.

		Recovery Year					Total
		87/88	88/89	89/90	90/91	91/92	
Rec. Area	A	16	10	16	15	5	62
	B	50	18	12	8	4	92
	C	12	13	7	23	5	60
	D	6	2	3	6	11	28
	E	9	23	7	12	13	64
Total		93	66	45	64	38	306

Table A11. Recovery by area of birds banded on Digges Island from 1979 to 1982. Different age categories are distributed among the recovery areas described in figure 2.2.

Age	Area					Total
	A	B	C	D	E	
1	4	0	2	0	4	10
2	4	3	2	1	0	10
3+	2	25	28	2	0	57
Total	10	28	32	3	4	76

Table A12. Recovery by area of birds banded on Digges Island in 1955. Different age categories are distributed among the recovery areas described in figure 2.2.

Age	Area					Total
	A	B	C	D	E	
1	11	4	3	1	1	20
2	6	1	3	3	0	13
3+	12	3	19	7	2	43
Total	29	8	25	11	3	76

Table A13. Comparison of spatial distribution of recoveries from banding efforts on Digges Island in 1955 and those in the early 80's. Only recoveries of third year or greater were used for this analysis. Area categories are as described in figure 2.2.

Year	Area					Total
	A	B	C	D	E	
1955	12	3	19	7	2	43
1979-83	2	25	28	2	0	57
Total	14	28	47	9	2	100

Table A14. Recovery of birds from Coubrg Island. Different age categories are distributed among the recovery zones described in figure 2.2.

Age	Area					Total
	A	B	C	D	E	
1	34	11	8	1	7	61
2	6	4	3	1	5	19
3+	12	11	3	2	15	43
Total	52	26	14	4	27	123

Table A15. Spatial distribution of recoveries of birds banded at Cape Hay and recovered in Newfoundland. Results are based on banding efforts carried out in 1957.

Age	Area					Total
	A	B	C	D	E	
1	9	0	0	1	3	13
2	3	0	1	0	3	7
3+	6	1	6	9	3	25
Total	18	1	7	10	9	45

Table A16. Spatial distribution of birds banded in Greenland and recovered in Newfoundland. Results are based on banding efforts carried out from 1946 to 1988.

Age	Area					Total
	A	B	C	D	E	
1	115	11	33	18	58	235
2	14	7	14	3	11	49
3+	21	13	22	8	13	77
Total	150	31	69	29	82	361

Table A17. Temporal distribution of recoveries of first year murre: an intercolony comparison of murre banded on Coats Island, Coburg Island, and in Greenland.

Colony	Month						Total
	O	N	D	J	F	M	
Coats	1	11	3	10	20	21	66
Coburg	1	24	5	8	12	11	61
Greenland	9	65	34	53	49	23	233
Total	11	100	42	71	81	55	360

Table A18. Spatial distribution of recoveries of first year murre: an intercolony comparison of recoveries of murre banded on Coats, Digges, and Coburg Islands, Cape Hay, and in Greenland.

Colony	Area					Total
	A	B	C	D	E	
Coats	18	31	4	4	9	66
Coburg	34	11	8	1	7	61
Greenland	115	11	33	18	58	235
Total	167	53	45	23	74	362

Table A19. Temporal distribution of third year or greater recoveries: an intercolony comparison of murre banded on Coats, Digges, and Coburg Islands, Cape Hay, and in Greenland.

Colony	Time of Year		Total
	Early	Late	
Cape Hay	3	20	23
Coburg	10	22	32
Coats	2	18	20
Digges	3	53	56
<u>Greenland</u>	<u>14</u>	<u>60</u>	<u>74</u>
Total	32	173	205

Table A20.

Spatial distribution of third year or greater murre recoveries: an intercolony comparison of recoveries of murre banded on Coats, Digges, and Coburg Islands, Cape Hay, and in Greenland.

Colony	Area					Total
	A	B	C	D	E	
Cape Hay	6	1	6	9	3	25
Coburg	12	11	3	2	15	43
Coats	8	32	37	8	12	97
Digges	2	25	28	2	0	57
<u>Greenland</u>	<u>21</u>	<u>13</u>	<u>22</u>	<u>8</u>	<u>13</u>	<u>77</u>
Total	49	82	96	29	43	299

APPENDIX B

Table B1. SURVIV results from the models listed in table 3.2. In the parameter column: F=recovery probability, S=survival probability.

Model #1	Parameter	Value	95% Confidence Interval		
			Standard Error	Upper	
	F adult year 1	0.222045E-15	0.125490E-08	- .245961E-08	0.245961E-08
	F adult year 2	0.218182E-01	0.112195E-01	- .171971E-03	0.438083E-01
	F adult year 3	0.223699E-02	0.229564E-02	- .226246E-02	0.673644E-02
	F adult year 4	0.821721E-02	0.524607E-02	- .206510E-02	0.184995E-01
	F adult year 5	0.879537E-02	0.514658E-02	- .129191E-02	0.188827E-01
	F adult year 6	0.560192E-02	0.504869E-02	- .429351E-02	0.154973E-01
	F adult year 7	0.144243E-01	0.121437E-01	- .937730E-02	0.382259E-01
	F adult year 8	0.704225E-02	0.701741E-02	- .671188E-02	0.207964E-01
	F juvenile year 1	0.268410E-01	0.423993E-02	0.185308E-01	0.351513E-01
	F juvenile year 2	0.239407E-01	0.352116E-02	0.170392E-01	0.308422E-01
	F juvenile year 3	0.833317E-02	0.161721E-02	0.516343E-02	0.115029E-01
	F juvenile year 4	0.233349E-01	0.293245E-02	0.175873E-01	0.290825E-01
	F juvenile year 5	0.125905E-01	0.192320E-02	0.882106E-02	0.163600E-01
	F juvenile year 6	0.341328E-02	0.887143E-03	0.167448E-02	0.515208E-02
	F juvenile year 7	0.102941E-01	0.251073E-02	0.537311E-02	0.152152E-01
	F juvenile year 8	0.958773E-02	0.213358E-02	0.540591E-02	0.137695E-01
	S adult year 1	1.000000	0.621051	- .217260	2.21726
	S adult year 2	0.616288	0.434285	- .234912	1.46749
	S adult year 3	1.000000	0.665760	- .304889	2.30489
	S adult year 4	0.432140	0.304868	- .165401	1.02968
	S adult year 5	1.000000	0.871703	- .708539	2.70854
	S adult year 6	1.000000	1.13721	-1.22894	3.22894
	S adult year 7	0.227583	0.366305	- .490374	0.945540
	S juvenile year 1	0.524351	0.110798	0.307187	0.741516
	S juvenile year 2	0.824519	0.179331	0.473030	1.17601
	S juvenile year 3	0.372379	0.729580E-01	0.229382	0.515377
	S juvenile year 4	0.586869	0.118616	0.354383	0.819356
	S juvenile year 5	0.938880	0.244148	0.460351	1.41741
	S juvenile year 6	0.515303	0.163846	0.194165	0.836440
	S juvenile year 7	0.336840	0.131281	0.795293E-01	0.594151

Table B1 (continued). Model #2

Parameter	Value	Standard Error	95% Confidence Interval	
			Lower	Upper
F adult year 1	0.00000E+00	0.834522E-01	-.163566	0.163566
F adult year 2	0.245029E-01	0.100616E-01	0.478215E-02	0.442237E-01
F adult year 3	0.213356E-02	0.213898E-02	-.205884E-02	0.632596E-02
F adult year 4	0.946378E-02	0.444618E-02	0.749272E-03	0.181783E-01
F adult year 5	0.663557E-02	0.353562E-02	-.294244E-03	0.135654E-01
F adult year 6	0.544221E-02	0.347125E-02	-.136145E-02	0.122459E-01
F adult year 7	0.173384E-01	0.818254E-02	0.130066E-02	0.333762E-01
F adult year 8	0.365836E-02	0.287690E-02	-.198037E-02	0.929709E-02
F juvenile year 1	0.268410E-01	0.423993E-02	0.185308E-01	0.351513E-01
F juvenile year 2	0.239407E-01	0.352116E-02	0.170392E-01	0.308422E-01
F juvenile year 3	0.833317E-02	0.161722E-02	0.516343E-02	0.115029E-01
F juvenile year 4	0.233349E-01	0.293245E-02	0.175873E-01	0.290825E-01
F juvenile year 5	0.125905E-01	0.192320E-02	0.882106E-02	0.163600E-01
F juvenile year 6	0.341328E-02	0.887143E-03	0.167448E-02	0.515208E-02
F juvenile year 7	0.102941E-01	0.251073E-02	0.537311E-02	0.152152E-01
F juvenile year 8	0.958773E-02	0.213358E-02	0.540591E-02	0.137695E-01
S adult year 1-7	0.780567	0.103016	0.578656	0.982478
S juvenile year 1	0.524351	0.110798	0.307187	0.741516
S juvenile year 2	0.824519	0.179331	0.473030	1.17601
S juvenile year 3	0.372380	0.729580E-01	0.229382	0.515377
S juvenile year 4	0.586869	0.118616	0.354383	0.819356
S juvenile year 5	0.938880	0.244148	0.460351	1.41741
S juvenile year 6	0.515303	0.163846	0.194165	0.836440
S juvenile year 7	0.336840	0.131281	0.795293E-01	0.594151

Table B1 (continued). Model #3

Parameter	Value	Standard Error	95% Confidence Interval Lower	Upper
F adult year 1	0.00000E+00	0.834522E-01	-.163566	0.163566
F adult year 2	0.245029E-01	0.100616E-01	0.478215E-02	0.442237E-01
F adult year 3	0.213356E-02	0.213898E-02	-.205884E-02	0.632596E-02
F adult year 4	0.946378E-02	0.444618E-02	0.749272E-03	0.181783E-01
F adult year 5	0.663557E-02	0.353562E-02	-.294244E-03	0.135654E-01
F adult year 6	0.544221E-02	0.347125E-02	-.136145E-02	0.122459E-01
F adult year 7	0.173384E-01	0.818254E-02	0.130066E-02	0.333762E-01
F adult year 8	0.365836E-02	0.287690E-02	-.198037E-02	0.929709E-02
F juvenile year 1	0.268328E-01	0.423847E-02	0.185254E-01	0.351402E-01
F juvenile year 2	0.233387E-01	0.308594E-02	0.172903E-01	0.293872E-01
F juvenile year 3	0.961013E-02	0.164053E-02	0.639469E-02	0.128256E-01
F juvenile year 4	0.206285E-01	0.229716E-02	0.161261E-01	0.251309E-01
F juvenile year 5	0.120688E-01	0.160494E-02	0.892317E-02	0.152145E-01
F juvenile year 6	0.449205E-02	0.943331E-03	0.264312E-02	0.634098E-02
F juvenile year 7	0.116482E-01	0.181882E-02	0.808331E-02	0.152131E-01
F juvenile year 8	0.786579E-02	0.140472E-02	0.511254E-02	0.106190E-01
S adult year 1-7	0.780567	0.103016	0.578656	0.982478
S juv. year 1-7	0.569711	0.287442E-01	0.513373	0.626050

Table B1 (continued). Model #4

Parameter	Value	Standard Error	95% Confidence Interval Lower	Upper
F adult year 1	0.000000E+00	0.834522E-01	-.163566	0.163566
F adult year 2	0.245029E-01	0.100616E-01	0.478215E-02	0.442237E-01
F adult year 3	0.213356E-02	0.213898E-02	-.205884E-02	0.632596E-02
F adult year 4	0.946377E-02	0.444618E-02	0.749270E-03	0.181783E-01
F adult year 5	0.663557E-02	0.353562E-02	-.294244E-03	0.135654E-01
F adult year 6	0.544221E-02	0.347125E-02	-.136145E-02	0.122459E-01
F adult year 7	0.173384E-01	0.818254E-02	0.130066E-02	0.333762E-01
F adult year 8	0.365836E-02	0.287690E-02	-.198037E-02	0.929709E-02
F juv. years 1-8	0.135305E-01	0.831178E-03	0.119014E-01	0.151596E-01
S adult years 1-7	0.780567	0.103016	0.578656	0.982478
S juvenile year 1	0.754891	0.150970	0.458989	1.05079
S juvenile year 2	0.558331	0.105500	0.351551	0.765111
S juvenile year 3	0.619819	0.103783	0.416404	0.823234
S juvenile year 4	0.468101	0.818754E-01	0.307626	0.628577
S juvenile year 5	0.403387	0.712446E-01	0.263748	0.543027
S juvenile year 6	0.642681	0.112486	0.422208	0.863155
S juvenile year 7	0.284572	0.776415E-01	0.132395	0.436750

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Table B1 (continued). Model #5

Parameter	Value	Standard Error	95% Confidence Interval Lower	95% Confidence Interval Upper
F adult year 1-8	0.814324E-02	0.207425E-02	0.407772E-02	0.122088E-01
F juv. years 1-8	0.135305E-01	0.831178E-03	0.119014E-01	0.151596E-01
S adult years 1-7	0.791754	0.871312E-01	0.620977	0.962531
S juvenile year 1	0.754891	0.150970	0.458989	1.05079
S juvenile year 2	0.558331	0.105500	0.351551	0.765111
S juvenile year 3	0.619819	0.103783	0.416404	0.823234
S juvenile year 4	0.468101	0.818754E-01	0.307626	0.628577
S juvenile year 5	0.403387	0.712446E-01	0.263748	0.543027
S juvenile year 6	0.642681	0.112486	0.422208	0.863154
S juvenile year 7	0.284572	0.776415E-01	0.132395	0.436750

U
S

Model #6

Parameter	Value	Standard Error	95% Confidence Interval Lower	95% Confidence Interval Upper
F adult years 1-8	0.814324E-02	0.207425E-02	0.407772E-02	0.122088E-01
F juv. years 1-8	0.136326E-01	0.832896E-03	0.120001E-01	0.152651E-01
S adult year 1-7	0.791754	0.871312E-01	0.620977	0.962532
S juv. years 1-7	0.515698	0.242453E-01	0.468178	0.563219

Table B1 (continued). Model #7

Parameter	Value	Standard Error	95% Confidence Interval Lower	Upper
F adult year 1	0.000000E+00	0.830170E-01	-0.162713	0.162713
F adult year 2	0.229525E-01	0.934725E-02	0.463193E-02	0.412731E-01
F adult year 3	0.195815E-02	0.196002E-02	-0.188349E-02	0.579978E-02
F adult year 4	0.810680E-02	0.362243E-02	0.100683E-02	0.152068E-01
F adult year 5	0.541428E-02	0.270036E-02	0.121572E-03	0.107070E-01
F adult year 6	0.406576E-02	0.234360E-02	-0.527704E-03	0.865923E-02
F adult year 7	0.120811E-01	0.401066E-02	0.422020E-02	0.199420E-01
F adult year 8	0.248642E-02	0.175604E-02	-0.955430E-03	0.592826E-02
F juvenile year 1	0.268410E-01	0.423993E-02	0.185308E-01	0.351513E-01
F juvenile year 2	0.239407E-01	0.352116E-02	0.170392E-01	0.308422E-01
F juvenile year 3	0.833317E-02	0.161722E-02	0.516343E-02	0.115029E-01
F juvenile year 4	0.233349E-01	0.293245E-02	0.175873E-01	0.290825E-01
F juvenile year 5	0.125905E-01	0.192320E-02	0.882106E-02	0.163600E-01
F juvenile year 6	0.341328E-02	0.887143E-03	0.167448E-02	0.515208E-02
F juvenile year 7	0.102941E-01	0.251073E-02	0.537311E-02	0.152152E-01
F juvenile year 8	0.958773E-02	0.213358E-02	0.540591E-02	0.137695E-01
S adult year 1-7	0.890000	0.000000E+00	0.890000	0.890000
S juvenile year 1	0.524351	0.110798	0.307187	0.741516
S juvenile year 2	0.824519	0.179331	0.473030	1.17601
S juvenile year 3	0.372380	0.729580E-01	0.229382	0.515377
S juvenile year 4	0.586869	0.118616	0.354383	0.819356
S juvenile year 5	0.938880	0.244148	0.460351	1.41741
S juvenile year 6	0.515303	0.163846	0.194165	0.836440
S juvenile year 7	0.336840	0.131281	0.795293E-01	0.594151

Table B1 (continued). Model #8

Parameter	Value	Standard Error	95% Confidence Interval Lower	95% Confidence Interval Upper
F adult year 1	0.00000E+00	0.830170E-01	-.162713	0.162713
F adult year 2	0.229525E-01	0.934725E-02	0.463193E-02	0.412731E-01
F adult year 3	0.195815E-02	0.196002E-02	-.188349E-02	0.579978E-02
F adult year 4	0.810679E-02	0.362243E-02	0.100683E-02	0.152068E-01
F adult year 5	0.541428E-02	0.270036E-02	0.121572E-03	0.107070E-01
F adult year 6	0.406576E-02	0.234360E-02	-.527704E-03	0.865923E-02
F adult year 7	0.120811E-01	0.401066E-02	0.422020E-02	0.199420E-01
F adult year 8	0.248642E-02	0.175604E-02	-.955430E-03	0.592826E-02
F juv. years 1-8	0.136326E-01	0.832896E-03	0.120001E-01	0.152651E-01
S adult years 1-7	0.890000	0.000000E+00	0.890000	0.890000
S juv. years 1-8	0.515698	0.242453E-01	0.468178	0.563219

Table B.2 Survival and recapture estimates for a selection of models based on observations of birds seen initially in their second year. Akaike information criterion (AIC) and a G statistic comparing the simplest model (constant survival and recapture probabilities) with other models introducing effects of age or year on survival and/or recapture estimates.

Model		np	s (95% CI)	R (95% CI)	
Surv.	Rcap.				
const	const	2	0.82 (0.76-0.87)	0.73	(0.65-0.80)
const	year	6	0.83 (0.77-0.88)	0.56	(0.32-0.77)
				0.67	(0.48-0.81)
				0.77	(0.63-0.87)
				0.92	(0.79-0.97)
const	age ¹	6	0.83 (0.76-0.88)	0.59	(0.46-0.72)
				0.79	(0.68-0.87)
				0.67	(0.53-0.79)
				0.66	(0.48-0.80)
				0.79	(0.41-0.96)
const	age ²	5	0.83 (0.76-0.88)	0.61	(0.25-0.88)
				0.79	(0.68-0.87)
				0.67	(0.54-0.78)
				0.66	(0.48-0.80)
const	age ³	4	0.83 (0.76-0.88)	0.74	(0.45-0.90)
				0.79	(0.68-0.87)
				0.67	(0.54-0.78)
				0.68	(0.52-0.80)
const	age ⁴	3	0.83 (0.76-0.88)	0.78	(0.68-0.87)
age ¹	year	10	0.86 (0.74-0.93)	0.54	(0.30-0.75)
			0.78 (0.64-0.88)	0.66	(0.48-0.81)
			0.85 (0.64-0.95)	0.76	(0.62-0.86)
			0.84 (0.50-0.97)	0.92	(0.79-0.97)
			0.89 (0.03-1.00)	0.59	(0.44-0.72)

cont/...

Table B.2 (continued)

Model		np	s (95% CI)		R (95% CI)	
Surv.	Rcap.					
age ²	year	9	0.86	(0.75-0.93)	0.54	(0.30-0.75)
			0.78	(0.64-0.88)	0.66	(0.48-0.81)
			0.86	(0.63-0.95)	0.76	(0.62-0.87)
			0.85	(0.54-0.96)	0.92	(0.79-0.97)
age ³	year	8	0.86	(0.74-0.93)	0.54	(0.30-0.75)
			0.78	(0.63-0.88)	0.66	(0.47-0.81)
			0.85	(0.69-0.94)	0.76	(0.62-0.87)
					0.92	(0.79-0.97)
age ⁴	year	7	0.86	(0.75-0.92)	0.54	(0.31-0.76)
			0.81	(0.72-0.89)	0.66	(0.46-0.82)
					0.77	(0.62-0.86)
					0.92	(0.79-0.97)
age ¹	age ¹	10	0.82	(0.70-0.89)	0.80	(0.69-0.88)
			0.84	(0.66-0.94)	0.67	(0.53-0.79)
			0.93	(0.32-1.00)	0.60	(0.39-0.77)
			0.59	(0.37-0.78)	1.00	(0.00-1.00)
age ²	age ²	8	0.74	(0.33-0.94)	0.74	(0.33-0.94)
			0.82	(0.71-0.89)	0.80	(0.68-0.88)
			0.84	(0.63-0.94)	0.67	(0.53-0.79)
			0.94	(0.17-1.00)	0.59	(0.39-0.77)
age ³	age ³	6	0.57	(0.41-0.72)	1.00	(0.00-1.00)
			0.82	(0.71-0.89)	0.80	(0.68-0.88)
			0.85	(0.63-0.95)	0.67	(0.51-0.79)
age ⁴	age ⁴	4	0.85	(0.57-0.96)	0.66	(0.46-0.82)
			0.82	(0.71-0.89)	0.80	(0.68-0.87)
			0.85	(0.73-0.92)	0.67	(0.54-0.77)

2-3
3-4
4-4

- 1 - 5 age groups; all ages separate (2 to 7 years)
- 2 - 4 age groups; 2, 3 and 4 year olds separate, all older ages combined
- 3 - 3 age groups; 2 and 3 year olds separate, all older ages combined
- 4 - 2 age groups; 2 year olds separate, all older ages combined

Table B.3 Survival and recapture estimates for a selection of models based on observations of birds seen on at least two occasions in their third year. Akaike information criterion (AIC) and a G statistic comparing the simplest model (constant survival and recapture probabilities) with other models introducing effects of age and/or year in the survival or recapture estimates.

Model		np	s (95% CI)	R (95% CI)
Surv.	Rcap.			
const	const	2	0.76 (0.72-0.80)	0.70 (0.64-0.77)
const	year	6	0.78 (0.74-0.81)	0.26 (0.15-0.41)
				0.72 (0.60-0.82)
				0.76 (0.67-0.84)
				0.90 (0.83-0.94)
				0.58 (0.51-0.64)
const	age ¹	6	0.76 (0.71-0.80)	0.67 (0.62-0.73)
				0.76 (0.67-0.83)
				0.73 (0.60-0.82)
				0.81 (0.55-0.93)
				0.41 (0.19-0.67)
const	age ²	4	0.76 (0.72-0.80)	0.68 (0.62-0.73)
				0.76 (0.67-0.83)
				0.72 (0.61-0.81)
const	age ³	3	0.76 (0.72-0.80)	0.68 (0.62-0.73)
				0.74 (0.67-0.81)
age ¹	year	10	0.73 (0.68-0.78)	0.28 (0.17-0.44)
			0.84 (0.76-0.91)	0.73 (0.61-0.83)
			0.83 (0.69-0.92)	0.77 (0.68-0.84)
			0.78 (0.58-0.90)	0.91 (0.84-0.95)
			0.54 (0.23-0.83)	0.59 (0.52-0.65)
age ²	year	8	0.74 (0.68-0.79)	0.28 (0.16-0.44)
			0.86 (0.77-0.91)	0.73 (0.60-0.83)
			0.80 (0.70-0.87)	0.77 (0.68-0.84)
				0.91 (0.84-0.95)
				0.58 (0.52-0.65)
age ³	year	7	0.78 (0.73-0.82)	0.26 (0.15-0.41)
			0.81 (0.71-0.88)	0.73 (0.60-0.82)
				0.77 (0.68-0.83)
			0.90 (0.83-0.94)	
			0.58 (0.51-0.64)	

cont...

<u>Model</u>					
<u>Surv.</u>	<u>Rcap.</u>	<u>np</u>	<u>s (95% CI)</u>	<u>R (95% CI)</u>	
age ¹	age ¹	10	0.71 (0.64-0.76)	0.76 (0.64-0.76)	
			0.83 (0.70-0.91)	0.91 (0.70-0.91)	
			0.88 (0.57-0.98)	0.98 (0.57-0.98)	
			0.69 (0.38-0.89)	0.89 (0.38-0.89)	
			0.56 (0.21-0.86)	0.86 (0.21-0.86)	
age ²	age ²	6	0.71 (0.64-0.76)	0.72 (0.65-0.78)	
			0.85 (0.70-0.93)	0.72 (0.61-0.81)	
			0.79 (0.65-0.89)	0.69 (0.54-0.80)	
age ³	age ³	4	0.76 (0.71-0.80)	0.70 (0.65-0.75)	
			0.80 (0.66-0.89)	0.69 (0.55-0.80)	

-
- 1 - 5 age groups; all ages separate (3 to 8 years)
 - 2 - 3 age groups; 3 and 4 year olds separate, all older ages combined
 - 3 - 2 age groups; 3 year olds separate, all older ages combined