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Winter distributions of Thick-billed Murres from the eastern Canadian Arctic and western Greenland in relation to age and time of year

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Abstract

Thick-billed Murres *Uria lomvia* from colonies in the eastern Canadian Arctic and West Greenland winter in large numbers off the coast of Newfoundland, where they are subjected to heavy hunting pressure. Some of these colonies, especially in Greenland, have declined over the past 50 years, and this has raised concerns over the effects of current harvest levels in Newfoundland. We analyzed the recoveries of birds banded at Canadian and Greenland colonies to determine where and when birds of different ages and from different colonies were killed. We dealt with recoveries for the period prior to recent restrictions (winter of 1993–1994 onwards), which allowed us to compare recoveries from different geographical areas over the whole period when the birds are present off Newfoundland.

The majority of recoveries of murres banded at Canadian colonies came from Newfoundland, except for birds banded at Cape Hay and Prince Leopold Island, the majority of which were recovered in Greenland. Among recoveries from Newfoundland, most first-year birds from high Arctic and Greenland colonies were recovered before the end of January, whereas most third-year or older birds were recovered later in the year. First-year birds from the Hudson Strait colonies generally were recovered later than those from the high Arctic. The timing of recoveries of second-year birds was intermediate between that of the other two age-classes. Overall, recoveries from high Arctic and Greenland colonies were spread over a greater part of the hunting season and were less concentrated in particular areas than those from colonies in Hudson Strait. Our results suggest that high Arctic populations are exposed to hunting for a longer period than those from Hudson Strait, indicating a need for more intensive population monitoring in the high Arctic.

The main area of recovery of first-year birds banded at Coats Island varied from year to year, perhaps because of environmental factors. Even allowing for interyear variation, significant differences were found among colonies in the temporal and spatial distributions of recoveries. The proportion of recoveries of first- and second-year birds from Digges Island was lower than that of birds from Coats Island, suggesting that many birds from Digges Island do not visit Newfoundland waters in their first two winters. Moreover, there was a sharp difference between two high Arctic colonies in the proportion of recoveries coming from Greenland. Those from the high Arctic colonies and from Greenland tended to be concentrated off the Northern Peninsula and in Notre Dame Bay, probably because hunting there occurs mainly in the first half of the season. After December, most recoveries of older birds from the Hudson Strait colonies were in Bonavista, Trinity, and Conception bays, whereas many of those from the high Arctic were from Placentia and Fortune bays. Hence, there is some evidence of segregation on the wintering grounds, and adjacent colonies may behave in different ways. We predict that reductions in hunting in Notre Dame Bay will affect mainly first-year birds, especially from the high Arctic; reductions in Bonavista, Trinity, and Conception bays could reduce mortality of birds of breeding age from Hudson Strait; whereas reductions for the Avalon Peninsula and south coast are more likely to affect birds of breeding age from the Canadian high Arctic. The geographical spread of recoveries from Greenland colonies was more even than that of recoveries from Canadian colonies, so we were unable to suggest a time or area where a reduction in hunting would be especially likely to benefit this depleted population. Additional information is required for colonies where little or no banding has been carried out, both in Canada and elsewhere. Because of the international movements of murre populations, an international approach to managing the population wintering off Newfoundland is required.

Résumé

Les marmettes de Brünnich *Uria lomvia* provenant de colonies de la région est de l'Arctique canadien et de la région ouest du Groenland passent l'hiver en grands nombres au large de la côte de Terre-Neuve, où elles sont très exposées à des activités de chasse. Certaines de ces colonies, surtout au Groenland, sont en baisse depuis une cinquantaine d'années et cette situation soulève des préoccupations quant aux effets des niveaux actuels de prises à Terre-Neuve. Nous avons analysé les récupérations d'oiseaux bagués dans les colonies du Canada et du Groenland afin d'établir où et quand les oiseaux de différents groupes d'âge et de différentes colonies ont été abattus. Nous nous sommes intéressés aux récupérations renvoyant à la période qui a précédé les récentes restrictions (à partir de l'hiver de 1993–1994), et nous avons pu ainsi comparer entre elles les récupérations effectuées dans différentes zones géographiques pendant toute la période où les oiseaux sont présents au large de Terre-Neuve.

La majorité des récupérations de marmettes de Brünnich baguées dans les colonies canadiennes provenaient de Terre-Neuve, sauf dans le cas des oiseaux bagués à Cap Hay et à l'île Prince Leopold, dont la plus grande partie ont été récupérés au Groenland. Quant aux récupérations effectuées à Terre-Neuve, la plupart des oiseaux de première année des colonies de l'Extrême-Arctique et du Groenland ont été récupérés avant la fin de janvier, tandis que la plupart des oiseaux de troisième année et plus ont été récupérés plus tard dans l'année. En général, les oiseaux de première année des colonies du détroit d'Hudson ont été récupérés plus tard dans l'année que ceux de l'Extrême-Arctique. Les récupérations d'oiseaux de deuxième année ont été effectuées pendant une période intermédiaire entre celles des deux autres groupes d'âge. Dans l'ensemble, les récupérations provenant des colonies de l'Extrême-Arctique et du Groenland s'échelonnaient sur une plus grande partie de la saison de chasse et étaient moins concentrées dans une zone particulière que celles provenant des colonies du détroit d'Hudson. Nos résultats donnent à penser que les populations de l'Extrême-Arctique sont exposées à la chasse pendant une plus grande période que celles du détroit d'Hudson et donc, qu'une surveillance plus poussée des populations serait nécessaire dans l'Extrême-Arctique.

Pour des raisons qui tiennent peut-être à des facteurs environnementaux, le lieu où s'effectuaient la plupart des récupérations d'oiseaux de première année bagués à l'île Coats n'était pas le même d'une année à l'autre. Même en tenant compte de la variation annuelle qui pouvait intervenir, on a constaté d'importantes différences d'une colonie à l'autre dans les distributions temporelles et spatiales des récupérations. La proportion des récupérations d'oiseaux de première et de deuxième année de l'île Digges était moins élevée que celle des oiseaux de l'île Coats, ce qui donne à penser qu'un grand nombre d'oiseaux de l'île Digges ne se rendent pas jusqu'aux eaux de Terre-Neuve pendant leurs deux premiers hivers. De plus, il y avait une différence marquée entre deux colonies de l'Extrême-Arctique du point de vue de la proportion des récupérations d'oiseaux provenant du Groenland. Les récupérations d'oiseaux provenant des colonies de l'Extrême-Arctique et du Groenland avaient tendance à être plus nombreuses au large de la péninsule Northern et dans la baie Notre-Dame; la raison à cela tient sans doute au fait que la chasse dans ces régions a lieu surtout pendant la première moitié de la saison. Après décembre, la plupart des récupérations d'oiseaux plus âgés des colonies du détroit d'Hudson ont été effectuées dans les baies de Bonavista, de la Trinité et de la Conception, tandis qu'un grand nombre des récupérations d'oiseaux provenant de l'Extrême-Arctique ont été effectuées dans les baies de Plaisance et de Fortune. Il y a donc des raisons de croire qu'une ségrégation s'opère dans les zones d'hivernage et que des colonies voisines peuvent se comporter de manière différente. Nous prédisons que les réductions de la chasse dans la baie Notre-Dame auront surtout un effet dans le cas des oiseaux de première année, surtout ceux provenant de l'Extrême-Arctique. Les réductions imposées dans les baies de Bonavista, de la Trinité et de la Conception pourraient faire baisser la mortalité des oiseaux du détroit d'Hudson ayant atteint l'âge de reproduction. Les réductions visant la péninsule Avalon et la côte sud auront vraisemblablement surtout des conséquences pour les oiseaux de l'Extrême-Arctique canadien ayant atteint l'âge de reproduction. La répartition géographique des

récupérations effectuées dans les colonies du Groenland était plus uniforme que celle des récupérations effectuées dans les colonies canadiennes; pour cette raison, nous ne sommes pas en mesure de dire à quelle époque de l'année ou dans quelle zone une réduction de la chasse serait vraisemblablement le plus utile pour cette population en déclin. Des renseignements supplémentaires sont nécessaires dans le cas des colonies où il n'y a pas ou presque pas eu de baguage, aussi bien au Canada qu'ailleurs. À cause des déplacements des populations de marmettes de Brünnich au-delà des frontières nationales, la gestion de la population qui passe l'hiver au large de Terre-Neuve doit se faire dans un contexte international.

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Contents

1. Introduction

The Thick-billed Murre *Uria lomvia* is the most numerous species of seabird breeding in the eastern Canadian Arctic (6.8 million in eastern Canada and West Greenland; Chardine 1994) and is hunted in large numbers by residents of Newfoundland and Labrador. In some years, it is the second most hunted migratory bird in Canada, after the Mallard *Anas platyrhynchos* (Filion et al. 1993; Lévesque et al. 1993). Murres are long-lived birds with low annual productivity and thus are vulnerable to chronic mortality affecting adults, such as that caused by marine pollution or unsustainable harvesting.

Murres are legally hunted in Canada only by residents of Newfoundland and Labrador and by Native peoples. They are of special importance to residents of Newfoundland, where seabirds have been hunted for centuries and where murres (known locally as "turrs"; the word is also applied to Common Murres *Uria aalge*, but these form only a small proportion of those killed and will not be dealt with here) have been a major item of the winter diet in many coastal outport communities. This hunt occurs predominantly in winter. Until Newfoundland joined Canada, in 1949, it was not governed by the regulations of the *Migratory Birds Convention Act*, which protect other migratory bird species in Canada. In 1956, a provision for the legal hunting of murres in Newfoundland and Labrador was created within the *Migratory Birds Convention Act* to allow the legal continuation of the murre hunt with no requirement for a permit and a seven-month open season with no bag limit.

The annual hunt in Newfoundland and Labrador is believed to have been the most significant source of adult mortality for the northwestern Atlantic population of Thick-billed Murres prior to 1993–1994. It may have been responsible for more than 75% of winter mortality (Elliot 1991). Comparison of mortality rates among Thick-billed Murres in Canada and Greenland (Kampp 1991; Gaston et al. 1994) with the mortality rates of Common Murres in populations unaffected by hunting suggests that hunting adds 50% or more to natural mortality rates (Gaston et al. 1994). Between 600 000 and 900 000 murres were harvested annually during the 1980s (Elliot 1991; Elliot et al. 1991). However, with the relocation of remote communities since the 1950s and the increased accessibility of market foods in most places, there has been a reduction in subsistence need for the hunt.

Practically all hunting mortality in Canada occurs off Newfoundland and Labrador. A small number of murres are hunted by Native Canadians near their colonies, but with insignificant effects on local breeding populations (Gaston et al. 1985). The level of harvesting, combined with some evidence of declines in Canadian breeding populations (Nettleship and Evans 1985) and steep declines in some Greenland colonies (Evans and Kampp 1991; Kampp et al. 1994), created an apprehension that populations might be threatened. Consequently, in recent years, additional hunting restrictions have been imposed. Restrictions introduced in 1993 include a shortened season, a daily bag limit, and a possession limit. In 1991 and 1992, the hunt was closed early in some areas of Newfoundland under section 37 of the *Migratory Birds Convention Act*, which allows the Minister of the Environment to vary hunting quotas and seasons for conservation purposes (Chardine 1994). This closure was instituted because hunting levels were considered excessive and significant numbers of murres were being sold illegally. Section 37 has since been used in the 1993–1994 hunting season and subsequently to impose new restrictions province-wide (Chardine 1994).

As a result of an extensive public education program during the 1980s (Elliot 1991), the new restrictions were implemented with the participation and support of the majority of hunters. Harvest reductions were achieved by shortening the open season to about three months in three separate management zones, which have since been redivided into four. The timing of the hunt in each zone was chosen with the help of a hunter opinion survey, to coincide with the times of year when murres were plentiful. In addition to the shortened season length, daily bag limits of 20 murres per hunter and a possession limit of 40 murres were set (Chardine 1994). These measures, along with better control of illegal market hunting, are expected to reduce the annual harvest of murres by 50%, to between 300 000 and 450 000 birds (JWC, unpubl. data).

The new hunting restrictions are intended to be temporary, pending the amendment of the Migratory Birds Convention, the international agreement with the United States that the Canadian act ratifies. This amendment was signed by both governments in 1995, but its entrenchment in law is still awaiting its ratification by the U.S. Senate. The successful implementation of the amendment to the

Migratory Birds Convention Act, if and when it is achieved, will require population monitoring and, if necessary, alterations in hunting pressure to ameliorate adverse effects caused by the hunt or any other threat to population size.

The new management strategy for murres has created a need for better information on the population dynamics of the species. In Greenland, hunting of adult Thick-billed Murres has caused a severe decline in numbers, to the point of extirpation in some places (Salomonsen 1979; Evans and Kampp 1991; Falk and Durinck 1992; Kampp et al. 1994). However, Canadian populations show no signs of decrease at colonies that have been monitored in the recent past. The colony at Coats Island has expanded since 1972, although this may not be representative of the Canadian population as a whole (Gaston et al. 1993).

Thick-billed Murres breed in a few widely separated colonies, and each colony may require unique management strategies. Given the broad geographical spread of colonies contributing to the hunted population off Newfoundland in winter and the likelihood that yearling birds may arrive in Newfoundland before older birds (Gaston 1980), it is possible that there may be a partitioning on the wintering grounds with respect to age and colony of origin. To create a better understanding of the implications of current hunting restrictions for population dynamics, we analyzed available band recovery data from Canada and West Greenland to determine the geographical and temporal distribution around Newfoundland of murres of different ages and from different colonies. Knowledge of variation in the winter distributions of birds from different colonies will allow a better assessment of the impact of hunting in specific areas in Newfoundland at particular times of the year. For Thick-billed Murres, individuals of breeding age are the most valuable to the population, because experienced breeders have a much higher reproductive success than first-time breeders (de Forest and Gaston 1996). A clear understanding of when and where breeders are likely to be hunted is key for effective management of the hunt.

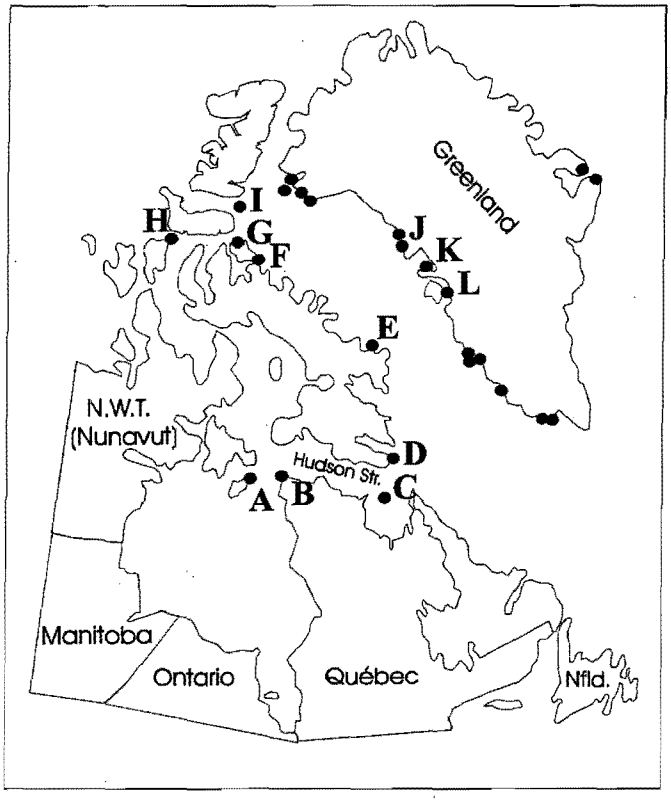
2. Methods

The Canadian Wildlife Service (CWS) has banded Thick-billed Murres at colonies across the eastern Canadian Arctic since 1955. The largest banding effort was at Coats Island (62°N, 82°W; Fig. 1, "A") in northern Hudson Bay. Banding has also been carried out at Digges Island (62°N, 77°W; "B"), Hantzsch Island (61°N, 65°W; "D"), The Minarets (Reid Bay, 67°N, 62°W; "E"), Cape Hay, Bylot Island (73°N, 80°W; "G"), Prince Leopold Island (70°N, 90°W; "H"), and Coburg Island (75°N, 79°W; "I") (Table 1, Fig. 1). In the 1950s, large numbers of chicks and adults were banded by L.M. Tuck at Digges Island and Cape Hay, Bylot Island. Following his efforts, little banding was carried out until 1979, when large-scale banding, mainly of chicks, was recommenced at Digges Island, and 1981, when banding was conducted at Coats, Digges, and Coburg islands.

Murres banded prior to the mid-1970s received circular aluminum bands, supplied by the joint U.S. Fish and Wildlife Service (USFWS)/CWS banding program. However, the bands were found to wear and corrode if in place for a number of years, which caused significant problems with band loss. After the mid-1970s, murres from all Canadian colonies were banded with stainless steel USFWS bands; this greatly reduced the risk of band loss, as stainless steel bands show little sign of wear even after many years (AJG, pers. obs.).

At Coats Island, banding of both chicks (Table 2) and adult birds has been carried out annually since 1984. In 1985, special stainless steel murre bands were introduced there. These bands are triangular in shape, with the number repeated on both sides to improve readability. In addition, the special bands carried the address "CWS, Box 9158, St. John's, NF," in the hope that hunters would be more willing to report recoveries to a local address. Reports of these birds received by the St. John's CWS office were then transferred to the Bird Banding Laboratory of the USFWS in Washington, D.C. The regular USFWS bands instruct the finder to "AVISE BIRD BAND, WRITE WASHINGTON D.C. USA." In 1985, all adults and half the chicks banded received the special bands, whereas the remaining chicks received normal, circular, stainless steel bands. After 1985, all murres from Coats Island received the special bands. Comparison of recovery rates for the two band types used in 1985 suggests that recovery rates may have been slightly higher for those with the Newfoundland address, of which 5.4%

Figure 1
Distribution of Thick-billed Murre breeding colonies in the eastern Canadian Arctic and Greenland. Canadian colonies are (A) Coats Island, (B) Digges Island, (C) Akpatok Island, (D) Hantzsch Island, (E) Reid Bay (The Minarets), (F) Cape Graham Moore, (G) Cape Hay, (H) Prince Leopold Island, and (I) Coburg Island. Greenland colonies used in this analysis are indicated by district: (J) Upernavik, (K) Uummannaq, and (L) Ilulissat.



have been recovered to date, compared with 3.4% for the standard bands ($\chi^2 = 3.43$, 1-tailed $p < 0.05$).

Recoveries contained in the USFWS/CWS database up to and including the winter of 1991–1992 were used for these analyses, which therefore deal with recoveries prior to the institution of recent hunting restrictions (1993–1994). Only recoveries from Newfoundland and Labrador and Greenland were considered in our analyses, because our main aim is to provide data relevant to the management of the murre hunt. Very few murres were recovered outside these areas (Table 3); consequently, few data were discarded because of this constraint. Wherever possible, the data in the USFWS database were checked against information from the CWS office in St. John's. The small number of discrepancies were corrected in favour of the CWS information, as this was the original data source and is therefore less likely to contain transcription errors.

Recovery information for murres banded in Greenland and recovered in Newfoundland was supplied by the Danish Zoological Museum in Copenhagen. The exact number of individuals banded during this period is not known because of incomplete information from banders (Kampp 1988). Because data exist for birds banded in Greenland over a long period (1946–1988), the effects of time on recovery distribution were tested using first-winter recoveries of birds banded in Upernavik District. This offered a data set of 206 recoveries during

Table 1
Banding efforts in the eastern Canadian Arctic by the Canadian Wildlife Service, up to 1991

Colony	Banding years	No. of adults banded	No. of chicks banded
Cape Hay	1957	1 363	1 137
Coats Island	1981, 1984–1991	1 231	17 654
Coburg Island	1981, 1987	0	4 756
Digges Island	1955	2 002	8 027
	1979–1982	594	5 080
Hantzsch Island	1982	72	448
Prince Leopold Island	1975–1977	42	150
The Minarets	1985	17	35
Total		5 321	37 287

Table 2
Numbers of Thick-billed Murres banded as chicks at Coats Island in 1981 and 1984–1991. The number of birds recovered in Newfoundland categorized by age at recovery is also indicated.

Banding year	No. of chicks banded	Recoveries at age (years) 1	2	3	4	5	6	7	≥8
1981	1584	10	9	5	5	4	2	1	0
1982	0								
1983	0								
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							

1955–1979 from a single banding area — sufficient to look at recoveries by five-year periods and test for changes in the temporal and spatial distributions in Newfoundland. No significant trends were found (Appendix 1); consequently, recoveries from all time periods were combined.

Recovered Greenland murres were banded primarily at colonies in Upernavik District (85.3%). Other recoveries came from colonies in Ilulissat (7.7%), Uummannaq (6.2%), Qaqortoq (0.5%), and Scoresbysund (0.2%) districts. Recovery distributions of birds from colonies in Upernavik, Ilulissat, and Uummannaq districts were not statistically distinct (Appendix 1). As a result of this, and given the close proximity of these colonies (Fig. 1), data from the three districts were combined for statistical analysis. Data from Qaqortoq and Scoresbysund were not included.

2.1 Selection of data

The majority of recoveries dealt with were reported as shot. Others were classified as "found dead," "oiled," or "recovered by unknown means": the value of these latter classifications is difficult to assess, because birds may have been floating dead for some time or transported by scavengers before being found. These categories accounted for less than 2% of recoveries and were excluded from the analyses.

In analyzing data from Coats Island with respect to age, we selected only five cohorts for analysis. This

Table 3
Recovery locations of Thick-billed Murres banded at colonies in the Canadian Arctic

Colony	No. of recoveries	% recovered		
		Newfoundland	Greenland	Other
Cape Hay	192	23.0	76.5	0.5[a]
Coats Island	515	93.6	1.9	4.5[b]
Coburg Island	176	80.1	15.3	4.5[b]
Digges Island	199	79.9	7.5	12.6[a]
Hantzsch Island	11	81.8	9.1	9.1[a]
Prince Leopold Island	6	0.0	100.0	0.0

[a] Predominantly birds hunted by residents of communities adjacent to the colonies.
[b] Birds recovered on eastern seaboard south of Newfoundland.

selection was made to ensure that all cohorts considered had experienced a minimum of two potential recovery winters prior to the institution of bag and season limits in 1993 and to omit data obtained before the 1984–1985 winter, when CWS initiated a recovery enhancement program to increase the number of data available. Thus, for Coats Island, recoveries were included from 1987 to 1991 only (representing five hunting seasons).

Banding at other colonies in the eastern Canadian Arctic was carried out in only a few years; consequently, all recoveries from birds banded at Cape Hay and on Coburg Island, Digges Island, Prince Leopold Island, and Hantzsch Island were used.

Recoveries were categorized by month and by age. Before 1993, the hunting season for murres off Newfoundland extended from 1 September to 31 March. Only three recoveries were reported in September, and these have been omitted from our analyses, which were restricted to the period from October to March. For some analyses relating to time of year, small samples in the fall and early winter required the pooling of data across months of recovery. Where possible, three categories were formed: October–November, December–January, and February–March. Where data were still too sparse to analyze, months were combined into two categories: "early" (October–November–December) and "late" (January–February–March).

Preliminary analysis by year suggested that there was no significant difference in the pattern of recovery of murres older than two years. Consequently, age-classes were combined in all cases to create three categories: first year (banded as chicks the previous summer and < 1 year old), second year (>1 and < 2 years old), and birds in their third year or older. The latter category included any recovered birds that were banded as breeding adults on the colony. This categorization seems realistic on the basis of current biological knowledge, because one-year-olds do not visit the breeding colony, whereas many two-year-olds do (Noble et al. 1991). Hence, we might expect the behaviour of second-year birds to differ from that of breeders more than that of third-year birds.

Because of cell counts that produced an unacceptable number of expected values that were too low (Bishop et al. 1975), a multivariate approach, categorizing recoveries according to age, month of recovery, and year of recovery, was not possible. Instead, a series of two-dimensional contingency tables, usually collapsed among years, was used. Given the large number of comparisons without a priori hypotheses, an adjusted alpha = 0.025 was adopted in order to reduce the possibility of type I errors (wrongly rejecting the null hypothesis) resulting from multiple comparisons. However, considering the large number of comparisons made, results close to the 0.025 probability level should be treated with caution. Where comparisons among more than two areas, time periods, or colonies were significant at a low probability (<0.01), we subdivided data tables into pairwise comparisons in order to determine those pairs contributing most to the overall significance (Zar 1984).

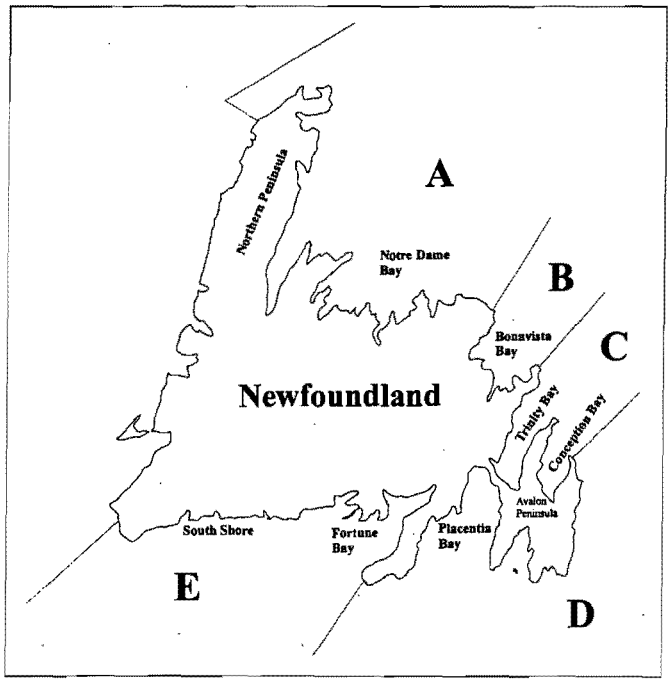
Data were analyzed by geographical area, using areas corresponding as closely as possible to the murre management zones described by Elliot et al. (1991), but treating Bonavista Bay separately from the rest of management zone 4, because of the large number of recoveries from this area. The zones were derived from those used for fisheries management in coastal waters off Newfoundland, modified to reflect the biology of the Thick-billed Murre and local variations in hunting pressures. For some of the areas described by Elliot et al. (1991), there were too few recoveries to permit analysis. Consequently, our area A combines the data from Labrador, the west coast of the Northern Peninsula, and Notre Dame Bay (Fig. 2), all of which were treated separately by Elliot et al. (1991). Bonavista Bay makes up murre recovery area 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, where murre hunting is not common (P. Ryan, pers. commun.). Recoveries from this part of Newfoundland were not considered in these analyses.

Although some information on the amount of hunting activity has been obtained from hunter questionnaires (Elliot et al. 1991), it is available for only a few winters. Consequently, rather than try to correct our results for hunter effort, we have sought, as far as possible, to use within-season comparisons that avoid the possible confounding effects of changes in effort and reporting rates.

2.2 Intercolony comparisons

In almost all cases, the recovery patterns of second-year murres were intermediate between those of first- and third-year or older murres and were never significantly different from either distribution on its own (see below). Because sample sizes for second-year birds were generally small, we restricted intercolony

Figure 2
Areas used to describe spatial distributions of recoveries (after Elliot et al. 1991). Detailed description of areas included in text; "A" included recoveries in Labrador (not shown).



comparisons to two age categories: first-years and third-years or older. However, samples of first-year recoveries from Digges Island and Cape Hay were also considered too small for inclusion in intercolony comparisons. Murres at Coburg Island were banded only in 1981 and 1987; in order to minimize biases introduced by interyear variation, data from Coats Island for those two years only were used for intercolony comparisons.

For comparisons with birds banded in Greenland, all recoveries from Canadian colonies were included. Because birds three years or older were recovered over several hunting seasons, the effects of year were necessarily averaged over the number of years in which data were available. Thus, for older birds, all years of data available for analysis were combined to increase sample sizes.

3. Results

3.1 Recovery rates

Between 5 and 90 recoveries of birds banded as chicks from Coats Island were reported each year since 1981 (Table 2). 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 ranged between 0.7% (1990) and 2.7% (1984) of chicks banded (Table 4). Taking the recoveries of birds in their fifth year or younger for the banding years 1984–1987 (N = 262), 58% were in the first year, 25% in the second, 8% in the third, 6% in the fourth, and 2% in the fifth (Table 2). Proportions of first-year birds recovered were often much greater than the number of older birds in all seasons except 1990–1991 and 1986–1987 (Table 4). A general decline over time in recovery rates was detected for first- and second-year birds (Fig. 3). This decline was significant for first-year birds only (first-year: $f = 6.46$, $p < 0.05$; second-year: $f = 5.48$, $p < 0.07$).

3.2 Seasonal distribution of recoveries

3.2.1 Coats Island

The number of birds banded at Coats Island and subsequently recovered in Newfoundland increased over the hunting season (Fig. 4). The peak of recoveries for first-year birds was in January–March; second-year and older birds were recovered most often in February. Although all age-classes tended to be recovered more frequently in the latter part of the hunting season, significant differences among them were detected using three time periods (October–November, December–January, and February–March; $\chi^2_4 = 13.93$, $p = 0.008$), indicating that the significance was probably the result of differences between third-year or older murres and the two younger 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+: $\chi^2_2 = 7.16$, $p = 0.028$).

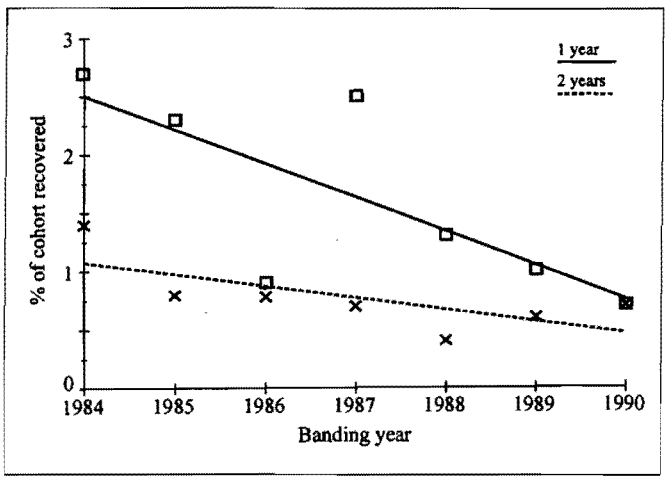
3.2.2 Digges Island

Based on 5080 chicks banded at Digges Island 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. The age

Table 4
Percentage of murre chicks banded at Coats Island and recovered in Newfoundland at ages ranging from their first to their fifth year

	% recovered at age (years)				
Banding year	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	0.1
1987	2.5	0.7	0.0	0.4	0.0
1988	1.3	0.4	0.5	0.1	
1989	1.0	0.6	0.1		
1990	0.7	0.7			
1991	1.0				

Figure 3
Percentage of initial cohort recovered as first-year (box) and second-year (cross) murres. Birds banded at Coats Island as chicks between 1984 and 1990 were included.



at recovery of chicks banded at Digges Island was quite different from the pattern seen for Coats Island: only 0.2% were recovered in both their first and second years, whereas 0.7% were recovered in their third year or later (Fig. 5).

A substantial sample of Thick-billed Murres was banded at Digges Island in 1955 by L.M. Tuck. As with the recoveries in the 1980s, relatively few first- and second-year birds were recovered from this sample, compared with birds in their third year or older. Most murres in the older age category were recovered in January–March, with the highest number in January (Fig. 6). The proportions of early and late recoveries did not differ significantly among age-classes ($\chi^2_3 = 6.83$, $p = 0.03$). No difference was found between the decades in the timing of recoveries of third-year or older birds ($\chi^2_1 = 2.85$, ns; Fig. 7).

3.2.3 Coburg Island

At Coburg Island, 3073 chicks were banded in 1981 and 1683 in 1987. The peak of recoveries of first-year birds in Newfoundland occurred in November, with another, smaller peak in February–March (Fig. 8). Second-year birds were most often recovered in January and February, whereas recoveries of older birds were more evenly distributed over the winter but peaked in February–

Figure 4
Temporal distribution of recoveries of first-, second-, and third-year or older murres banded on Coats Island

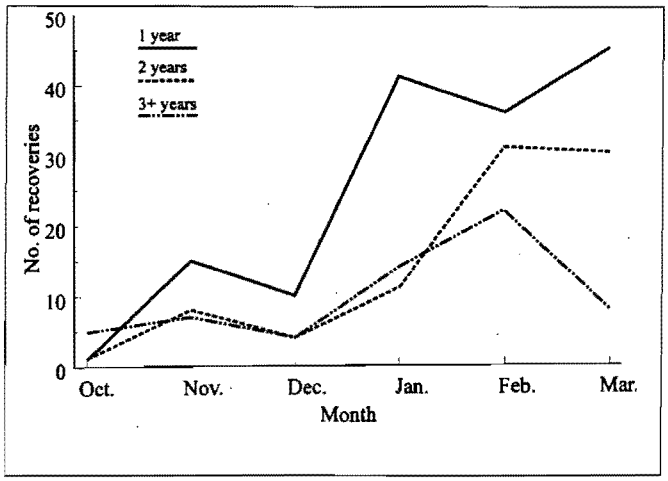
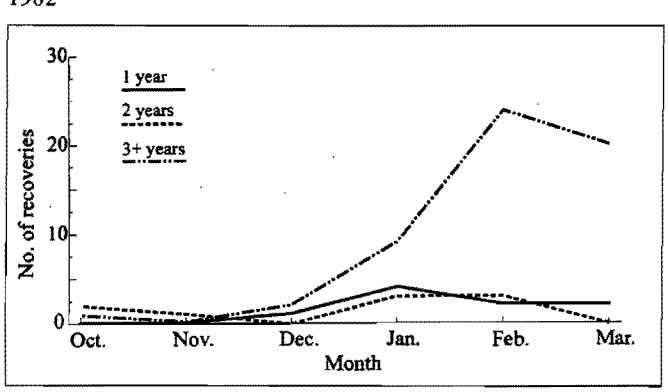


Figure 5
Temporal distribution of recoveries of first-, second-, and third-year or older murres banded on Digges Island from 1979 to 1982



March. The proportions of the three age-classes recovered before and after 31 December differed significantly ($\chi^2_4 = 11.88$, $p = 0.018$), with the main difference being between first-year birds and third-year or older murres ($\chi^2_2 = 10.34$, $p = 0.006$).

3.2.4 Cape Hay

In total, 2500 adults and chicks were banded in 1957 at Cape Hay, Bylot Island. First-year birds were most commonly recovered in Newfoundland in November, whereas the older age-classes were recovered more often later in the hunting season (Fig. 9), the difference being significant using two time periods ($\chi^2_2 = 13.72$, $p < 0.001$). The distribution of first-year birds did not differ significantly from that of second-year birds but differed from the distribution of third-year or older birds (1 vs. 2: 2-tailed Fisher exact test, $p = 0.049$; 1 vs. 3+: $\chi^2_1 = 12.11$, $p = 0.0005$). The difference between second-year and older birds was 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 may be an important wintering area for Cape Hay birds. Most birds recovered in Greenland were

Figure 6
Temporal distribution of recoveries of first-, second-, and third-year or older murres banded on Digges Island in 1955

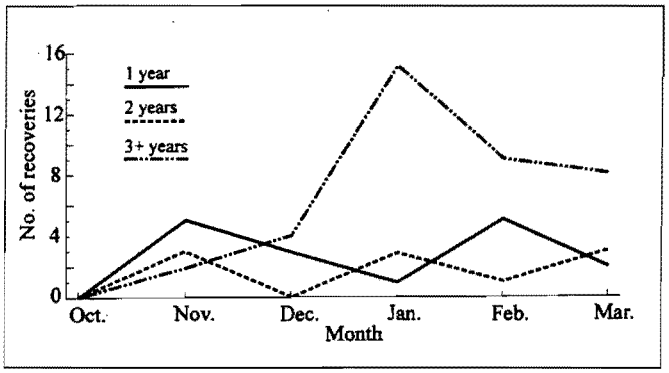
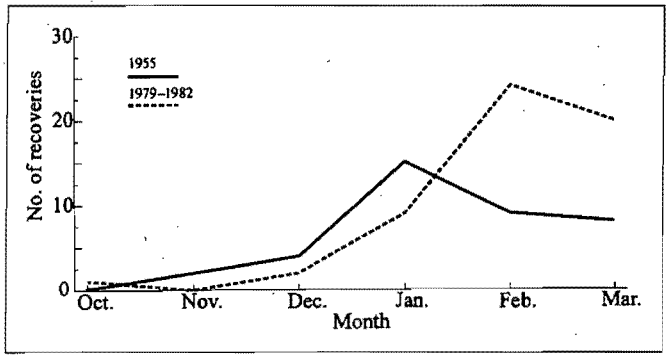


Figure 7
Comparison of temporal distribution of recoveries of third-year or older murres from banding efforts on Digges Island in 1955 and 1979–1982



shot (86%, N = 153), some were entangled in fishing gear (3%), and the means of recovery was unknown for the remainder (11%). In addition, all six recoveries of murres banded on Prince Leopold Island, farther to the west in Lancaster Sound, occurred in Greenland. A comparison of the temporal distributions in Greenland and Newfoundland of murres banded at Cape Hay suggests no difference for birds in their first year ($\chi^2_2 = 3.10$, $p = 0.212$); recoveries peaked in November in both areas (Fig. 9). However, in Greenland, older birds showed a gradual decline from a peak in October; in Newfoundland, on the other hand, they increased gradually to a peak in February ($\chi^2_2 = 17.50$, $p = 0.0002$). 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%). This lends further support to the idea that some adults from Cape Hay remain off Greenland for the winter.

3.2.5 Greenland

First-year birds were recovered most frequently in Newfoundland in November, whereas recoveries of second-year birds peaked in January, and those of older birds in February. The temporal distribution of recoveries for second-year and older birds was similar to the distributions noted from the Coats Island data, whereas the pattern for first-years appeared intermediate between

Figure 8
Temporal distribution of recoveries of first-, second-, and third-year or older murres banded on Coburg Island

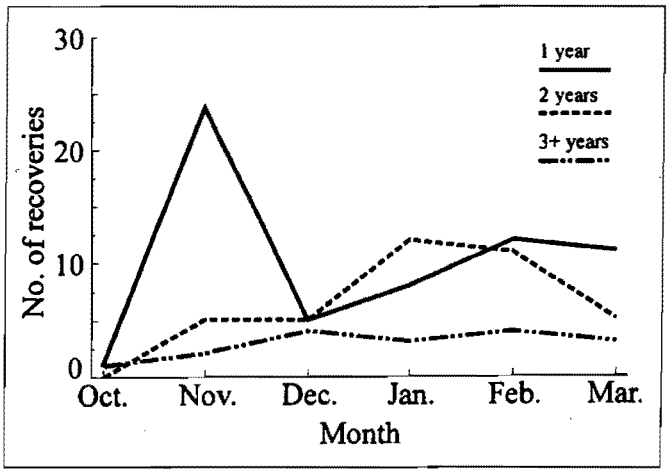
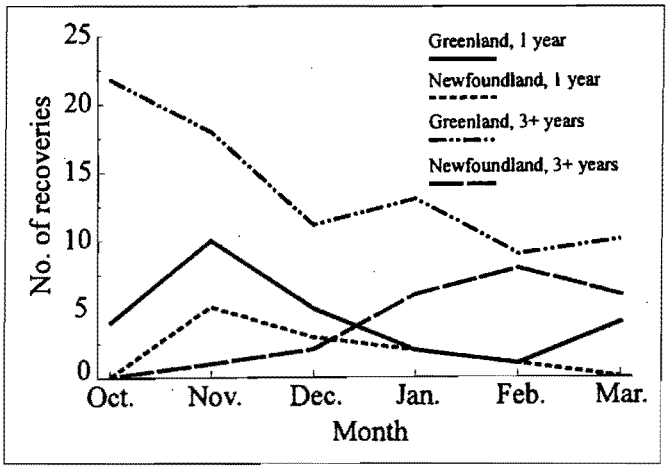


Figure 9
Temporal distribution of recoveries of murres banded at Cape Hay. Recoveries in Greenland and Newfoundland are indicated for first-year and third-year or older birds.



those of Coburg Island and Coats Island birds (Fig. 10). The proportion of first-year birds from Greenland recovered in October–December (49%) was higher than the corresponding proportion from Coats Island (19%). Significant differences were detected among age categories ($\chi^2_4 = 34.96$, $p < 0.0001$), based on a three time category analysis. The recovery distribution of first-year birds differed significantly from those of the two older age categories (1 vs. 2: $\chi^2_2 = 13.18$, $p = 0.001$; 1 vs. 3+: $\chi^2_2 = 25.95$, $p < 0.0001$), whereas the difference between the two older age categories was not significant ($\chi^2_1 = 4.08$, ns).

3.2.6 Intercolony comparisons

Recoveries of first- and second-year birds from Digges Island were proportionately lower than recoveries of the same age-classes from Coats Island, although this was not true for older birds (Table 5). Older birds from Digges Island, like those from Coats Island, were recovered mainly after December (Fig. 5). There was no significant difference among age-classes in the propor-

Figure 10
Temporal distribution of recoveries of first-, second-, and third-year or older murres banded in Greenland and recovered in Newfoundland

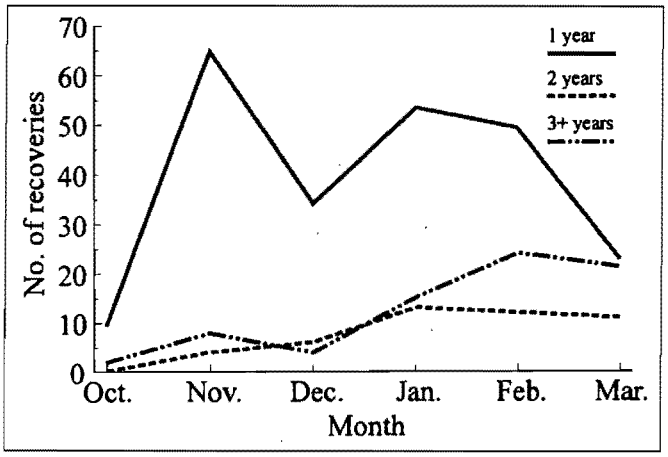


Table 5
Comparison of the proportion of murres recovered from Coats and Digges islands

	% recovered			
Age (years)	Coats	Digges	χ^2	p
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

tions recovered before and after 31 December ($\chi^2_2 = 7.12$, ns).

The seasonal distribution of recoveries of first-years differed significantly among Coats Island, Coburg Island, and Greenland samples ($\chi^2_{10} = 34.43$, $p = 0.0002$; only 1981 and 1987 samples from Coats Island considered), the significance being largely due to the difference between the Coats Island and Greenland samples ($\chi^2_5 = 27.75$, $p < 0.0001$). Coats Island and Coburg Island recoveries did not differ significantly ($\chi^2_5 = 10.50$, ns; Fig. 11). There was a tendency for recoveries from all three colonies to be lower in December than in November or January. November was the peak month for both Coburg Island and Greenland birds. Highest numbers from Coats Island were recovered in February and March.

For birds in their third year or older, most recoveries from all colonies occurred after December (Fig. 12), but differences in temporal distributions among colonies were detected ($\chi^2_4 = 11.57$, $p = 0.021$). In paired comparisons, recoveries from Digges and Coburg islands differed significantly ($\chi^2_1 = 10.84$, $p = 0.001$), but no others did. However, this pairing was merely the most extreme example of the tendency for the two Hudson Strait colonies (Coats and Digges islands) to be recovered proportionately more often than the others in February and March.

Figure 11
Intercolony comparison of the temporal distribution of recoveries of first-year murres from Coats Island, Coburg Island, and Greenland

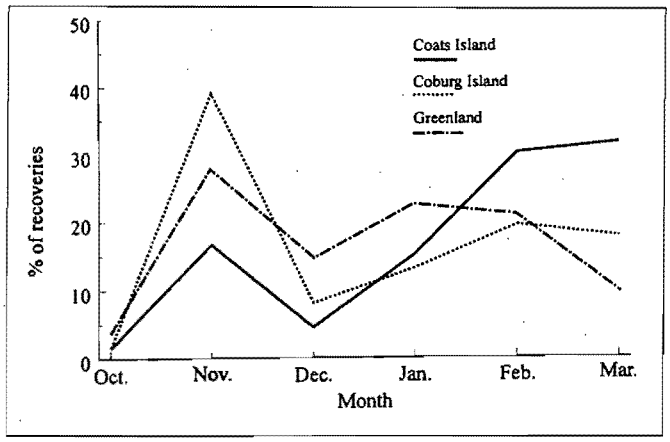
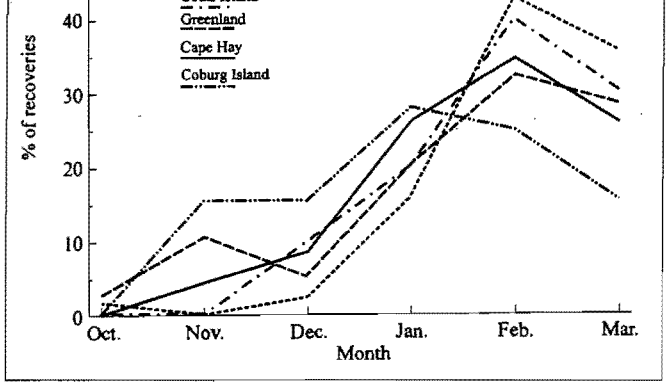


Figure 12
Intercolony comparison of the temporal distribution of recoveries of third-year or older murres from Coats Island, Digges Island, Cape Hay, Coburg Island, and Greenland



3.3 Geographical distribution of recoveries

3.3.1 Coats Island

Large numbers of first-year birds from Coats Island (80%) were recovered in areas from the Northern Peninsula to Bonavista Bay and in Fortune Bay (areas A, B, and E; see Fig. 2), whereas second-year birds were more evenly spread over the whole Newfoundland coast, and older birds were recovered mainly in the Bonavista Bay – Trinity Bay area (B and C, 71%; Fig. 13; comparing age categories, $\chi^2_8 = 48.90$, $p < 0.0001$). There was a highly significant difference between first-year birds and birds in their third year or older ($\chi^2_4 = 47.39$, $p < 0.0001$). Birds recovered in their second year appeared to be intermediate in their geographical distribution between first-year and older birds. The proportions of second-years recovered in Notre Dame Bay (A, 23%) and Fortune Bay (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 Trinity and Conception bays (C, 20%) was higher than that of first-years (7%), but lower than that of older birds (38%). Separate compari-

Figure 13
Spatial distribution of recoveries of Coats Island murres in three age categories (see Fig. 2 for area details)

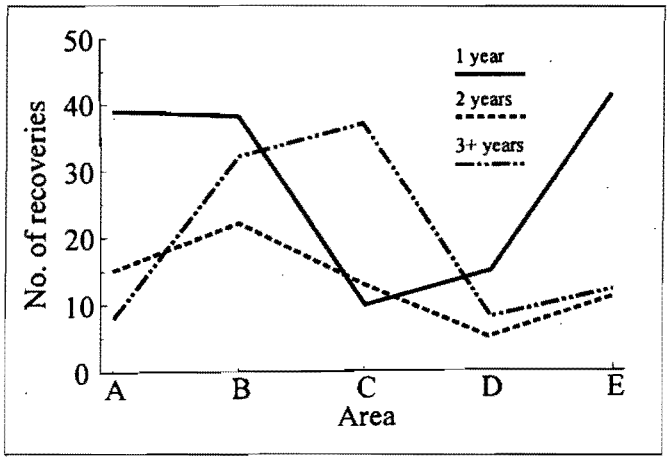
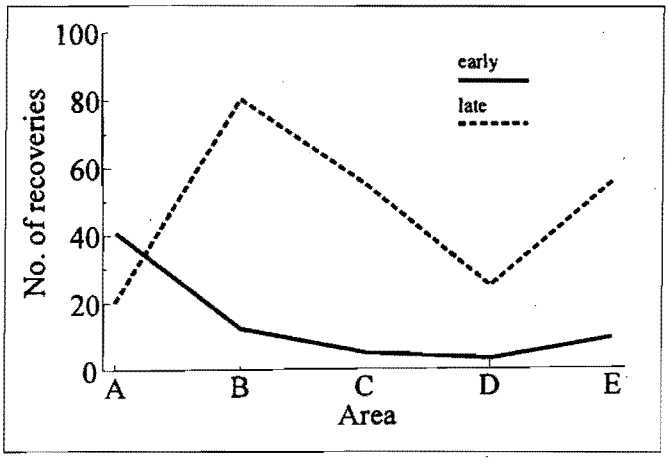


Figure 14
Recovery of all Coats Island murres by area (see Fig. 2 for area details), for the "early" (October–December) and "late" (January–March) part of the turr hunting season, 1987–1992



sons of second-year birds with first-year and older birds were not significant ($\chi^2_4 = 10.72$, ns; $\chi^2_4 = 10.73$, ns).

Most Coats Island recoveries in all areas except the northeast coast (area A) occurred after 31 December (Fig. 14), with a significant difference in the geographical distribution of recoveries in the early and late periods ($\chi^2_4 = 83.14$, $p < 0.0001$). The area of peak recoveries differed significantly from year to year ($\chi^2_{16} = 84.61$, $p < 0.0001$; Fig. 15). With the exception of the Avalon Peninsula and Placentia Bay (area D), which produced the fewest recoveries overall, each of the other areas had the most recoveries in at least one of the hunting seasons considered. Fortune Bay and the south coast (area E) had the largest number of recoveries in two hunting seasons.

3.3.2 Digges Island

Most recoveries of older Digges Island birds banded in 1979–1982 occurred in Bonavista, Trinity, and Conception bays (areas B and C; Fig. 16). This pattern is similar to that observed for older birds from Coats Island. The few first- and second-year recoveries reported were

Figure 15
Annual variation in number of recoveries of Coats Island murres among hunting areas (see Fig. 2 for area details)

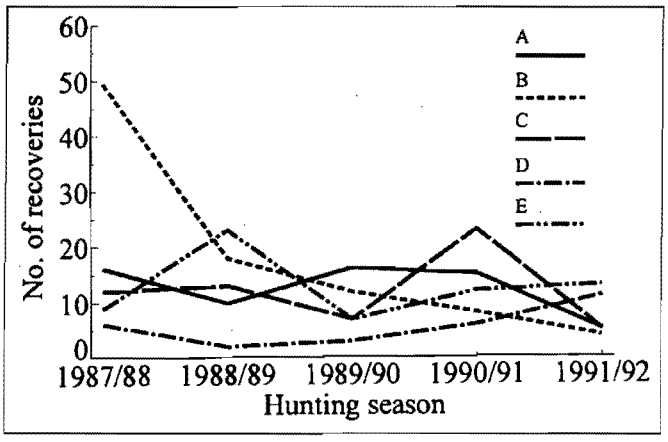
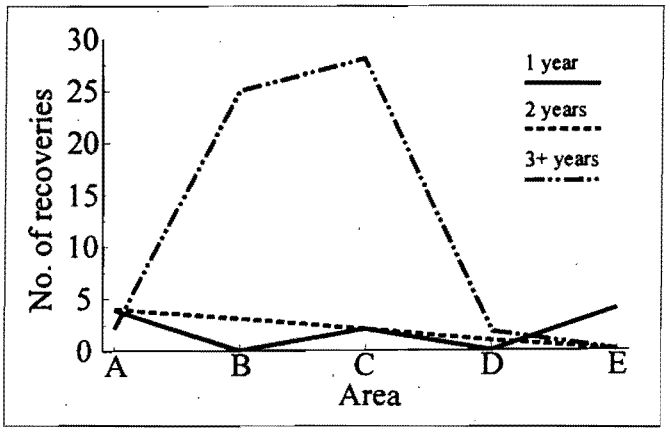


Figure 16
Spatial distribution of recoveries of murres banded on Digges Island, 1979–1982 (see Fig. 2 for area details)



more or less evenly distributed among areas. Most first- and second-year birds from the 1955 banding were recovered in the northeast (area A), and most older birds in Trinity and Conception bays (area C; Fig. 17), although the difference was not significant ($\chi^2_8 = 11.83$, ns). Fewer birds from the 1955 banding were recovered in Bonavista Bay (area B) and more in the northeast (area A) than was found for birds banded in 1979–1982 ($\chi^2_4 = 29.55$, $p < 0.0001$; Fig. 18).

3.3.3 Coburg Island

First-year birds banded at 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 (Fig. 19). Second-year birds were recovered in small numbers in all areas, whereas older birds were most often recovered along the Northern Peninsula and Notre Dame Bay (area A), Bonavista Bay (area B), and Fortune Bay (area E). Differences among age categories were not significant ($\chi^2_8 = 14.60$, ns).

Figure 17
Spatial distribution of recoveries of murres banded on Digges Island in 1955

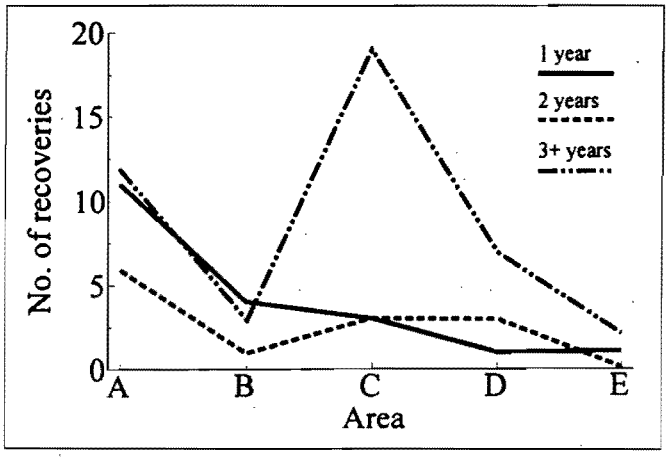


Figure 18
Comparison of spatial distribution of recoveries of third-year or older murres from banding efforts on Digges Island in 1955 and in 1979–1982

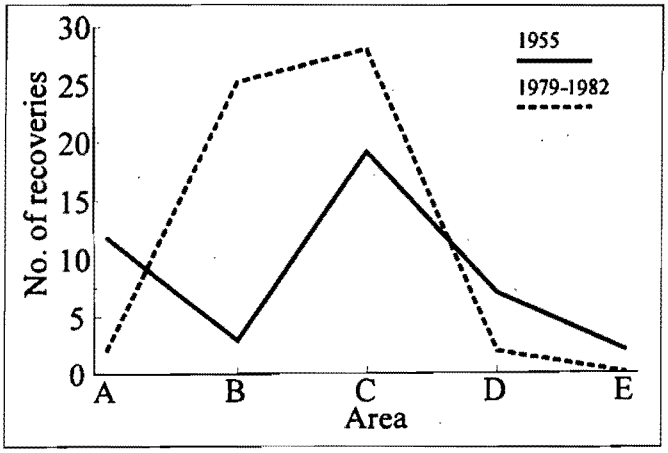


Figure 19
Recovery distribution by area for murres in three age categories from Coburg Island (see Fig. 2 for area details)

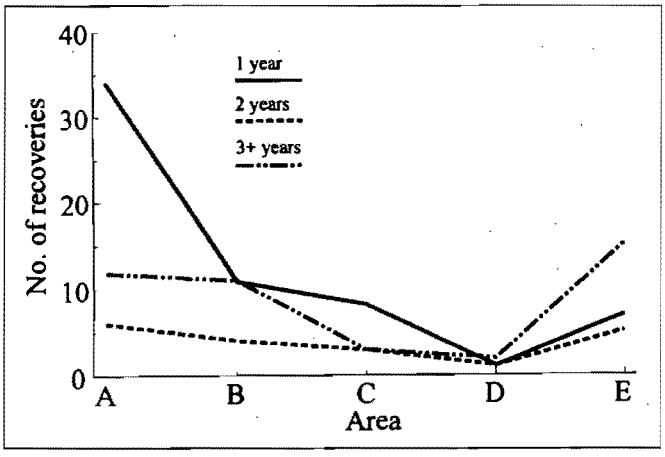


Figure 20
Recovery distribution by area for murres in three age categories from Cape Hay, Bylot Island

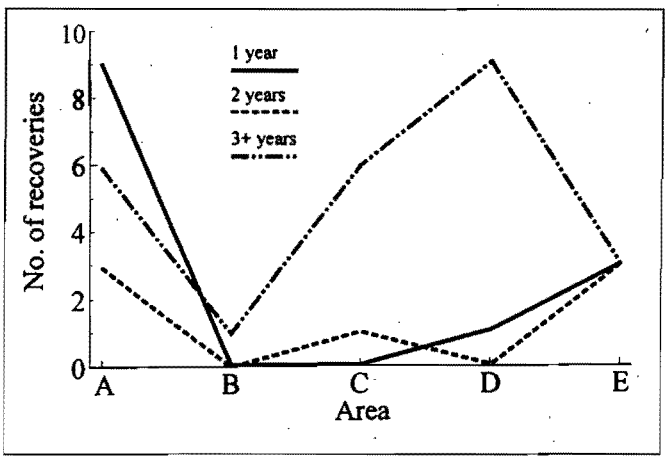
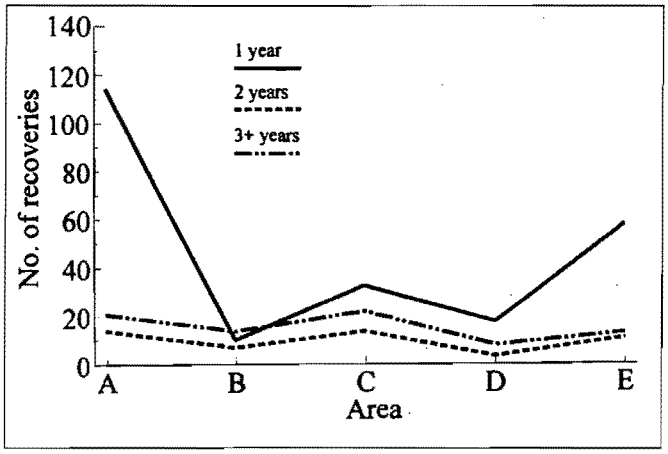


Figure 21
Recovery distribution by area for murres in three age categories from Greenland



3.3.4 Cape Hay

Of the few birds banded in 1957 at Cape Hay and recovered in Newfoundland (Fig. 20), most first-year birds were recovered in the northeast (area A, 67%). Third-year or older birds were most often recovered around the Avalon Peninsula and in Placentia Bay (area D), a pattern not seen for any other sample.

3.3.5 Greenland

Nearly one-third (32%) of all birds banded in Greenland and recovered in Newfoundland were shot as first-year birds in the northeast (area A; Fig. 21). Very few first-year birds (3%) were recovered in Bonavista Bay (area B). The distribution of older recoveries was rather evenly spread. The distribution of age-classes differed significantly, with many more first-years than older birds recovered in areas A and E ($\chi^2_8 = 32.73$, $p < 0.0001$; 1 vs. 2: $\chi^2_4 = 12.13$, $p = 0.016$; 1 vs. 3+: $\chi^2_4 = 27.73$, $p < 0.0001$). Distributions of second-year and older murres were not significantly different ($\chi^2_4 = 2.47$, ns).

Figure 22
Intercolony comparison of the spatial distribution of recoveries of first-year murres from Coats Island, Coburg Island, and Greenland

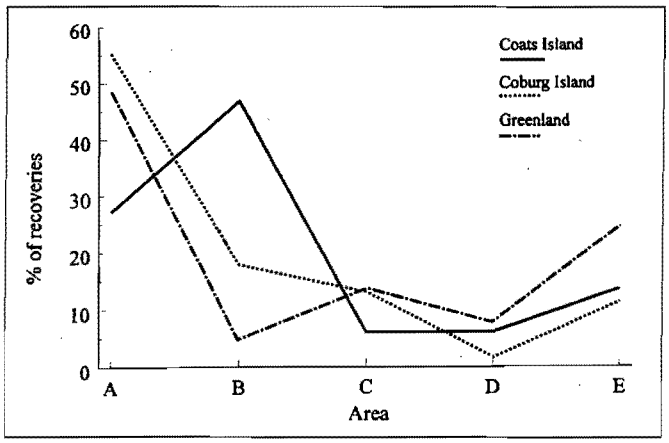
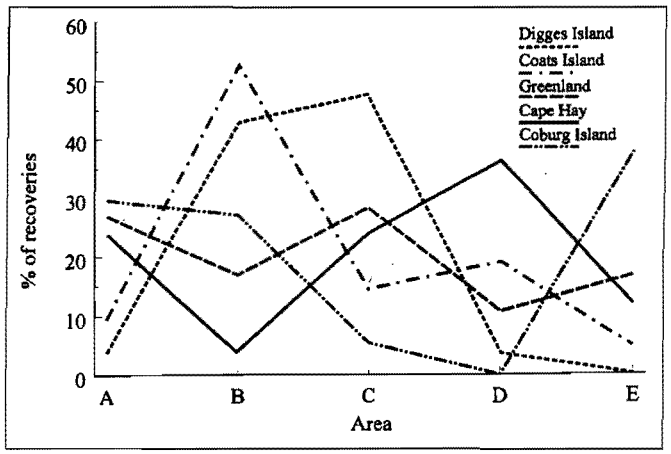


Figure 23
Intercolony comparison of the spatial distribution of recoveries of third-year or older murres from Coats Island, Digges Island, Cape Hay, Coburg Island, and Greenland



3.3.6 Intercolony comparisons

The distribution of recoveries for first-year birds from different colonies showed highly significant differences, with most Coats Island recoveries coming from area B, whereas those from Coburg Island and Greenland came largely from area A ($\chi^2_8 = 81.63$, $p < 0.0001$; Fig. 22). All colonies differed significantly in paired comparisons (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: $\chi^2_4 = 18.67$, $p = 0.0009$). Although samples were small, recoveries from Cape Hay showed a distribution similar to those from Coburg Island and Greenland. Like seasonal distributions, the geographical distribution of recoveries of older birds differed significantly among Cape Hay, Coats, Digges, and Coburg islands and Greenland; recoveries from the Hudson Strait colonies came mainly from areas B and C, whereas those from other colonies came predominantly from areas A, D, and E ($\chi^2_{16} = 92.95$, $p < 0.0001$; Fig. 23). All pairwise comparisons were significant, with the exception of that between Cape Hay and Greenland (Table 6).

Table 6
Pairwise comparisons of spatial distributions of third-year or older murres in Newfoundland

Colony comparison	χ^2	p
Cape Hay vs. Greenland	9.66	0.047
Coburg vs. Greenland	13.16	0.011
Coats vs. Digges	11.71	0.020
Coats vs. Greenland	14.62	0.006
Cape Hay vs. Coburg	20.46	<0.001
Cape Hay vs. Coats	22.59	<0.001
Cape Hay vs. Digges	39.35	<0.001
Coburg vs. Coats	27.09	<0.001
Coburg vs. Digges	46.70	<0.001
Digges vs. Greenland	34.78	<0.001

4. Discussion

Simple demographic models have shown that, in K-selected species like seabirds, trends in populations are most sensitive to changes in adult survival (Croxall and Rothery 1991). Consequently, the age composition of the murres killed in Newfoundland, and how that varies in space and time, has important implications for the demographic effects of the hunt.

The gradual decline in the proportion of Coats Island birds recovered in their first year (Fig. 3) may relate to a general trend towards lower harvests, or lower reporting rates, over the period of the study. The decline is particularly striking because the relative recovery rates of the two band types used in 1985 suggest that the special bands used since 1985 may be reported more frequently than the old-style bands used in 1984 and for the sample of adults and half the chicks in 1985. It is possible that some "reporting exhaustion" is occurring, with hunters who have already reported a band being less likely to report subsequent bands. The large interyear variation in the proportion and area of recoveries observed for successive cohorts banded at Coats Island indicates that year-to-year changes are substantial. Interyear variation may relate to variation in the presence and accessibility of the birds caused by weather, ice conditions, or the movements of suitable food organisms. We have attempted to reduce the potential effects of interyear variation by combining several seasons' data, where possible.

Extrapolation from the geographical and temporal distributions of band recoveries to the entire population can be done only with a detailed knowledge of hunting pressure and reporting rates. Unfortunately, this is not yet practicable for Thick-billed Murres. The long season without bag limits and the lack of requirement for a hunting permit make an accurate assessment of hunting pressure difficult and prevent us from distinguishing the effects of changes in hunting pressure from those of changes in reporting rates. Consequently, some of the following conclusions are speculative.

4.1 Temporal segregation

We confirmed, for a larger number of colonies, the result obtained by Gaston (1980), who showed that the majority of recoveries of first-year birds occurred before the end of December, whereas recoveries of older birds occurred mainly later in the winter. Our finding that recoveries of second-year birds show a pattern intermediate between those of first-years and third-year or older murres is new and suggests that demographic treatments of the effects of hunting need to consider at least three age-classes. The predominance of first-year recoveries before January applied to all colonies except Coats Island, where all age-classes were recovered mainly after December, and possibly Digges Island, where first-year recoveries were too few to allow conclusions to be drawn. Among older birds, a higher proportion of those banded at the northern colonies were recovered before February than was true for birds banded at the two Hudson Strait colonies. Those from the most northerly colony, Coburg Island, were the earliest to be recovered, being the least well represented after January, whereas those from Digges Island were the latest, with hardly any recovered before January.

4.2 Spatial segregation

The substantial interyear variation in the spatial distribution of recoveries from Coats Island and the overlap in recoveries from different colonies indicate that there is no sharp segregation among populations during winter. However, the highly significant differences among colonies in the distributions of recoveries for older birds indicate that the proportion of birds from different colonies differs among hunting areas around Newfoundland.

Variation in the geographical distribution of recoveries is clearly influenced by recovery date. Hunting in northeastern Newfoundland takes place mainly in October–December, after which ice conditions usually prevent hunters from putting to sea. Consequently, only those birds that arrive before January are likely to be recovered in area A. This presumably explains the great importance of area A for recoveries of first-year birds, especially those from the northern colonies; this area has produced more than half of the first-year recoveries of birds banded at Coburg Island, Cape Hay, and Greenland. In contrast, very few recoveries of older birds from the Hudson Strait colonies came from this area.

Hunting may occur in other areas more or less throughout the season; on the south coast (area E), however, it takes place mostly after January, because large

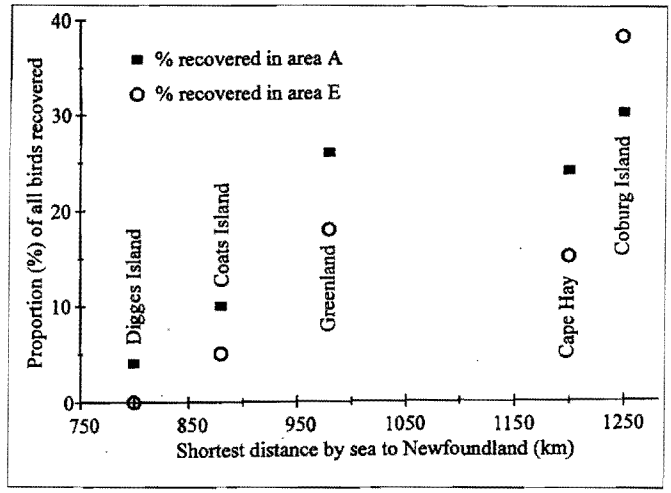
numbers of murres do not appear there until then in most winters. We do not know whether murres remain off the north coast of Newfoundland throughout the winter but are recovered only in the first half because hunting becomes impossible later, or whether heavy ice conditions force birds out of that area in the new year. The proportions of recoveries in areas A and E are both positively correlated with the shortest sea route distances from the colonies of origin to Newfoundland (Fig. 24). This suggests that birds arriving in the early part of the winter (mostly from the northern colonies) are more likely to move to the south coast than those arriving later (mostly from Hudson Strait), which remain mainly in areas B and C.

Because hunting outside area A is not necessarily restricted by ice conditions to the first half of the winter, the distribution of recoveries among other areas is less affected by the timing of arrival. Consequently, the variation apparent in the recovery areas of older birds (Fig. 23) may reflect real intercolony differences in wintering areas. Even if we except the recoveries from Cape Hay, which, being based entirely on banding in 1957, may have been obtained at a period when the distribution of hunting pressure was very different from that of recent decades, the variation among colonies is striking. Peak recoveries from Coats (area B), Digges (C), and Coburg (E) islands and from Greenland (A) all fell in different areas. Very few recoveries from either of the Hudson Strait colonies came from area E, and very few recoveries from Digges Island came from area D. Of the birds from Cape Hay that were recovered in Newfoundland, many came from Placentia Bay (area D). Few older birds from any other colony were recovered in this bay, which was consistently the area of fewest recoveries for Coats Island birds over a number of years (Fig. 15). Moreover, few recoveries from the 1955 banding at Digges Island came from area D. Hunting in Placentia Bay may therefore affect birds from Cape Hay more than those from other colonies.

Despite the difference in their timing, recoveries of first-year and older birds from Coats Island show some similarity in their spatial distributions, with 48% of first-years and 53% of older birds coming from area B. Likewise, for Coburg Island, the patterns of recoveries for the two age-classes are similar, the first-year and older birds being least common in areas C and D. Recoveries of older birds from Greenland are spread rather evenly throughout the five areas, perhaps reflecting their origin from a number of different colonies, albeit in a restricted area.

A comparison of the pattern of first-year and third-year or older birds from Cape Hay recovered in Greenland and Newfoundland shows that more older birds than first-year birds were being shot in Greenland at a time of year when the reverse was true in Newfoundland. This suggests that older birds lingered longer than first-years off Greenland and that the absence of older birds in the Newfoundland kill in November was due not to a greater susceptibility of young birds to hunting, but rather to a real difference in the timing of migration of the two age-classes. However, this result, being based on a single year's banding, must be treated with caution. The much smaller proportion of recoveries from Greenland observed for the Coburg Island birds banded in the 1980s may

Figure 24
Proportions of birds recovered in areas A and E as a function of the minimum distance between the colonies and Newfoundland



relate to a difference in the migration and wintering patterns of birds from the two colonies or to a change in hunting pressure in Greenland. The fact that all six recoveries from banding at Prince Leopold Island in 1975–1977 came from Greenland suggests that hunting pressure there was substantial until the 1970s, at least. Further banding at the high Arctic colonies, especially Cape Hay and Prince Leopold Island, would be desirable to elucidate variation among colonies.

Although there is substantial overlap among older birds from different colonies in their wintering areas around Newfoundland, it is clear that in the early winter there is considerable spatial segregation among first-year birds. Those from Greenland and the Canadian high Arctic colonies are abundant around Newfoundland at that time, but few birds are found from the Hudson Strait colonies. This seems to be the most dramatic spatial segregation demonstrated by the recoveries. The lack of first-year recoveries from Digges Island suggests that a substantial proportion of these birds do not reach Newfoundland at all in their first year, or, if they do, they remain in areas far offshore that are not subject to hunting. The same is apparently true of second-year birds from Digges Island, which were recovered much less frequently than those from Coats Island, although older birds from both colonies were recovered in similar proportions. As most Thick-billed Murres have left Hudson Strait by the end of September (Gaston 1980), it seems likely that birds from that population spend October and November in the Labrador Sea. Some Thick-billed Murres are known to winter in the Labrador Sea (Brown 1989), and these may include a disproportionate number of birds from Digges Island.

4.3 Implications for management of murre hunting in Newfoundland

Eastern Canada and western Greenland are estimated to support 4 million breeders out of a total population of 6.8 million birds (Chardine 1994). If breeding success is 0.65 chicks/pair (Birkhead and Nettleship 1981; Gaston and Nettleship 1981; Gaston et

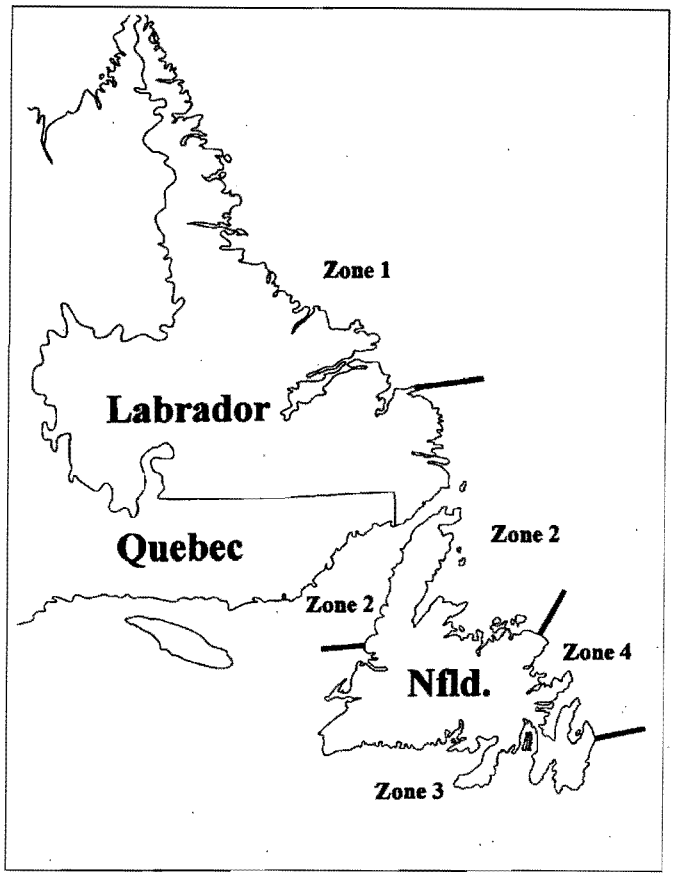
al. 1994), annual production is 1.3 million chicks. Estimates of harvest levels in the 1980s ranged between 600 000 and 900 000 birds, of which approximately 50% are assumed to be first-years (Elliot 1991); consequently, 23–35% of young produced were being harvested in Newfoundland. As significant mortality may occur soon after fledging (Tuck 1961; Birkhead and Nettleship 1981), the actual number of first-year birds reaching Newfoundland may be considerably less than the number of chicks departing successfully from their colonies. Consequently, an even higher proportion of those reaching Newfoundland waters may have been taken. Although the proportion of older age-classes killed is smaller than that of first-year birds, the effect of the hunt on these older birds may have a greater demographic impact. Gaston et al. (1994) estimated that mortality of breeding adults at Coats Island during 1989–1993 was significantly greater than the mortality of Common Murres in populations unaffected by hunting, which suggests that hunting mortality is not compensated by density-dependent factors. This increased mortality affects reproductive performance by reducing the proportion of breeding pairs in which both members are experienced.

Currently, the mortality generated by hunting does not appear to be causing declines in Canadian murre populations, as there is no evidence that Canadian colonies declined significantly between the 1970s and the early 1990s (Gaston et al. 1993; AJG and DNN, unpubl. data). The same is not true for murres breeding in Greenland, where hunting mortality in Newfoundland would have affected recruitment to some degree. Restrictions on the hunt in Newfoundland–Labrador, imposed in the 1993–1994 hunting season, were aimed at halving the annual harvest. The new restrictions are believed to have resulted in a substantial reduction in the harvest. This reduction in a significant source of mortality should have a positive influence on population size, in the absence of strong density-dependent effects.

Elliot et al. (1991), using hunter questionnaires from the 1980s, found that the total monthly harvest of murres in Newfoundland remained relatively constant from November to March. Inspection of hunter-killed samples being brought to wharves throughout Newfoundland showed that the proportion of first-year birds in the harvest fell from more than 90% in November to less than 30% in March, the sharpest change being between December and January. Our results suggest that most first-years shot in the early part of the season are from colonies in Greenland and the Canadian high Arctic. In addition, many older birds are shot in January (Elliot et al. 1991), when relatively few recoveries from Hudson Strait colonies occur. Consequently, most of these birds must originate from farther north. Added to the fact that most older birds recovered in area E, where a substantial amount of hunting occurs, are from northern colonies, these data suggest that hunting pressure overall may be heavier on birds from northern colonies than on those from Hudson Strait. This indicates a need for careful monitoring of the high Arctic colonies, especially when the largest colony in Hudson Strait for which information is available has probably been stable, rather than expanding, over the past two decades (Gaston et al. 1993).

The zonation currently being used to manage the hunt in Newfoundland–Labrador is shown in Figure 25.

Figure 25
Zones currently used for the management of the Newfoundland murre hunt



Numbers of birds killed and numbers of bands recovered in Labrador suggest that activity in zone 1 is not likely to have a noticeable effect on populations. Hunting in zone 2 (roughly our area A) occurs in October–December and thus affects mainly first-year birds, especially those from Greenland and the high Arctic. Alterations to season length or bag limits in zone 2 are therefore likely to affect recruitment and to have a delayed impact on the breeding population (as birds start to breed at 4–5 years; Gaston et al. 1994). Hunting activity in zone 3 (our areas D and E) and zone 4 (our B and C) occurs mainly later in the winter (January–March). It affects some first-year birds, but, more importantly, the zones include the main area for recoveries of older birds. Evidence from the recoveries suggests that changes in zone 3 will have their greatest impact on colonies in Hudson Strait, whereas changes in zone 4 are more likely to affect high Arctic colonies.

4.4 Future research

To date, recovery information from some of the largest Canadian Thick-billed Murre colonies at Akpatok Island, The Minarets (Reid Bay), and Prince Leopold Island is inadequate. Given the differences detected among other colonies, knowledge of temporal and spatial distributions of different age-classes from these colonies may prove important in the future. The fact that no recoveries from Prince Leopold Island came from Newfoundland, although based on a small sample,

suggests that the wintering area for this population may differ from that for Coburg Island birds. Banding efforts in the coming years should focus on colonies other than those where substantial numbers have already been banded, especially at Akpatok Island, the largest Thick-billed Murre colony in the region. Only small numbers of chicks have been banded there to date.

4.5 Management relating to breeding populations in Greenland

Dramatic declines at colonies in Greenland have been attributed largely to hunting at the colonies during the breeding season (Kampp 1988; Falk and Durinck 1992; Kampp et al. 1994). However, restoration of colonies there may require measures beyond the changes to hunting restrictions adopted by the Greenland Home Rule government. Recoveries in Newfoundland of older birds banded in Greenland showed a relatively even distribution among areas. This suggests that there is no specific area or time period for which additional restrictions on hunting in Newfoundland might benefit Greenland populations. Rather, an overall reduction in numbers killed over the entire season seems to hold the best hope of improving adult survival rates for Greenland birds. However, large numbers of first-year Greenland birds are shot in Notre Dame Bay (zone 2), and it is here that management efforts in Canada might help enhance Greenland populations. A reduction in the hunt in Notre Dame Bay might increase the number of Greenland birds available to be recruited into the breeding population. However, for such a reduction to be effective, international cooperation with Greenland would be needed to ensure that efforts to conserve shared murre populations were bilateral. Canada and Greenland are both members of the Conservation of Arctic Flora and Fauna (CAFF) working group and the Circumpolar Seabird Working Group. Under CAFF, Canada has taken the lead in producing an International Murre Conservation Strategy and Action Plan, which is expected to be adopted by all eight circumpolar nations. This development is an indication that managers are taking an international approach to conserving northwest Atlantic murre populations.

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Appendices

Appendix 1

Distribution of recoveries for Thick-billed Murres banded in Greenland and recovered in Newfoundland: analyses to detect differences in distributions of birds banded in different time periods and in different districts.

1. Analysis of spatial and temporal distributions of Thick-billed Murres banded in Greenland in Upernavik District between 1955 and 1979. For this analysis, Newfoundland recoveries of first-year birds were used, as they represented the best sample set over such a lengthy period of time.

Spatial segregation:

	No. of birds recovered, by recovery area				
Banding years	A	B	C	D	E
1955–1959	6	3	2	4	9
1960–1964	7	1	1	1	3
1965–1969	40	3	16	5	8
1970–1974	29	3	4	5	13
1975–1979	21	0	5	4	13

$\chi^2_{16} = 25.06, p < 0.07$

Temporal segregation:

	No. of recoveries, by month of recovery					
Banding years	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1955–1959	0	3	2	8	6	2
1960–1964	0	3	3	5	2	0
1965–1969	0	19	13	11	15	6
1970–1974	3	19	5	12	6	7
1975–1979	2	11	8	8	9	4

$\chi^2_8 = 8.98, p < 0.34$

2. Analysis of spatial and temporal distributions of Thick-billed Murres banded in Greenland in Upernavik, Uummannaq, and Ilulissat districts. Too few second-year recoveries were obtained to conduct this analysis; hence, Newfoundland recoveries of first- and third-year or older murres were considered.

Spatial segregation:

		No. of recoveries, by recovery area				
Age	Colony	A	B	C	D	E
1	Upernavik	110	10	30	19	49
	Uummannaq	7	1	1	0	6
	Ilulissat	8	1	5	0	5
3+	Upernavik	19	10	20	8	14
	Uummannaq	1	0	2	1	0
	Ilulissat	1	2	3	0	0

First-year: $\chi^2_8 = 7.82, p < 0.45$
Third-year or older: $\chi^2_8 = 10.26, p < 0.30$

Temporal segregation:

		No. of recoveries, by month of recovery					
Age	Colony	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1	Upernavik	6	68	32	45	41	20
	Uummannaq	3	2	0	1	4	2
	Ilulissat	0	5	2	5	3	1
3+	Upernavik	2	7	4	13	23	16
	Uummannaq	0	0	0	0	1	2
	Ilulissat	0	1	0	1	0	3

First-year: $\chi^2_4 = 4.92, p < 0.30$
Third-year or older: $\chi^2_4 = 2.78, p < 0.60$

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