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Thick-billed Murres on an ice pan
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Introduction

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The Thick-billed Murre *Uria lomvia* is one of the most numerous seabirds breeding in the northern hemisphere. In the North Atlantic and adjacent part of the Arctic Ocean, it breeds in large numbers in Novaya Zemlya, Franz Josef Land, Spitsbergen, Bear Island, Iceland, and Greenland and over most of the Arctic coasts of eastern Canada (Tuck 1961). All of these populations winter in Arctic or sub-Arctic waters of the North Atlantic. They have been harvested for centuries over most of their range: by native peoples in the western Atlantic at breeding colonies in Greenland and the eastern Canadian Arctic, and by local nonnatives on their wintering grounds off Newfoundland and Labrador. In West Greenland, in parts of the eastern Canadian Arctic, and in parts of Newfoundland, they still form an important part of the local diet at certain seasons.

Since the 1960s, when the introduction of a gill-net fishery for salmon off West Greenland resulted in the drowning of hundreds of thousands of Thick-billed Murres, there have been concerns about the status of the species in the Northwest Atlantic (Tull et al. 1972; Christensen and Lear 1977; Nettleship 1977; Evans and Nettleship 1985). In addition to death by hunting and drowning in gill nets, Thick-billed Murres suffer heavy unnatural mortality from oiling, especially around southern Newfoundland. Our knowledge of the demography of the Thick-billed Murre is fairly fragmentary, but what we know, combined with extrapolations from the closely related Common Murre *Uria aalge*, suggests that mortality from various unnatural causes may exceed the sustainable yield. A number of projects are currently under way in Canada and Greenland to evaluate the status, the levels of unnatural mortality, and the present population dynamics of the species.

Because Thick-billed Murres probably live a long time under natural conditions, any study of their population dynamics necessarily extends over many years. We are very fortunate that two individuals, Leslie Tuck and Finn Salomonsen, had the foresight, more than four decades ago, to initiate (and, in Tuck's case, to undertake personally) the large-scale banding of Thick-billed Murres. Without their pioneering work, in Canada and Greenland, respectively, we would be much farther than we are from understanding the dynamics of Thick-billed Murre populations.

This collection of papers derives from a symposium held at Memorial University of Newfoundland, St. John's, in April 1989. Contributions by Evans and Kampp and by Kampp deal with the current dynamics of the Thick-billed Murre population in West Greenland. Evans and Kampp provide clear evidence of a substantial decline in numbers over the past 50 years. Kampp's detailed analysis of band recoveries points to shooting at breeding colonies as a major cause of mortality, and one that affects the most demographically valuable segment of the population — the breeders. He also examines the weaknesses of haphazard banding in attempting to answer certain demographic questions. His results provide a convincing explanation for the differences, documented by Evans and Kampp, between the southern colonies, many of which have all but disappeared, and the northern colonies, where declines have been less drastic. The paper by Falk and Durinck addresses the question of the threat posed to Thick-billed Murres by the salmon drift-net fishery of Greenland, which appears to be small at present.

Turning to Canada, Elliot reviews the history and socioeconomic context of the winter harvest of Thick-billed Murres in Newfoundland. Evidence of harvest levels before the 1970s is weak, but it appears that the total kill increased considerably with the advent of faster boats and better weapons. Elliot, Collins, Hayakawa, and Métras show that participation in the Newfoundland hunt remains steady, and harvest levels remain high. Their results indicate that the Newfoundland hunt is probably the main cause of mortality for all age-classes of Thick-billed Murres in the Northwest Atlantic.

There are indications that Thick-billed Murre populations in the eastern Canadian Arctic declined between the 1950s and the 1970s (Evans and Nettleship 1985). Unfortunately, there is no consensus among those active in the field about the magnitude of the decline or about the current status of the species at Canadian Arctic colonies. However, there probably has been no decline in numbers at some colonies since the 1970s (AJG, pers. obs.).

For Coats Island, a fairly small colony in northern Hudson Bay, where numbers of Thick-billed Murres have not declined since 1981, Noble, Gaston, and Elliot describe some preliminary demographic parameters. These may eventually provide an understanding of how current populations are being maintained. The authors also present evidence that, in addition to the effects of hunting mortality, year-to-year variation in conditions on the wintering grounds may affect the recruitment of young Thick-billed Murres. Despite the promising level of recruitment at this colony over the past few years, recent population modeling shows that even a slight deterioration in any demographic parameter could initiate a decline in the population (Nettleship and Chardine 1989).

In West Greenland, recent changes in regulations and in the economics of hunting give some hope that the decline of Thick-billed Murre populations there can be arrested and perhaps reversed. Elliot argues for a similar reduction in the kill in Newfoundland, partly by better enforcement of current laws prohibiting sale, and partly by the imposition of bag limits and a reduction in the legal season. Because of the complexity of altering the Migratory Birds Convention between Canada and the United States, progress on introducing new regulations in Newfoundland is slow, and there is a possibility that the strong consensus now established among hunters in support of harvest reductions may weaken before new regulations are in place.

Although we believe that Canadian Thick-billed Murre populations are mainly stable at present, this may be no more than a breathing space provided by a period of highly favourable environmental conditions. In the concluding paper, Harris describes changes in populations of Atlantic Puffins *Fratercula arctica* and Common Murres in the United Kingdom, basing his work on more detailed monitoring than is available for Thick-billed Murres. He demonstrates that underlying environmental changes, causing changes in food availability to auks and operating on a scale of decades, may ultimately determine the dynamics of seabird populations.

If conditions for Thick-billed Murres in the western Atlantic deteriorate over the next few years, as they did recently in the Barent's Sea, we have inadequate regulatory tools with which to protect the population. This is a distressing prospect for hunters and managers alike.

This Occasional Paper is the second of three to be focused on research on high-latitude seabirds. An earlier volume dealt with seabird feeding ecology. A large-scale energetics model, which estimates the spatial and temporal prey harvests of seabirds throughout the year, was also presented during the symposium and will be published as a subsequent contribution in this series.

Recent changes in Thick-billed Murre populations in West Greenland

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Abstract

Numbers of Thick-billed Murres *Uria lomvia* breeding in West Greenland have decreased over the past several decades. The decline has been most severe between Disko Bay and southern Upernavik District, where formerly large colonies were situated close to major settlements. Hunting of breeding birds at their colonies during the breeding season has probably been a major factor in the observed decline. The recent Game Act, adopted by the Greenland Home Rule government in 1988, prohibits hunting at most colonies during June through August. The successful rehabilitation of the Thick-billed Murre population in West Greenland may depend on the success of this management strategy.

Résumé

Le nombre de Marmettes de Brünnich *Uria lomvia*, qui nichent dans l'Ouest du Groënland a diminué au cours des dernières décennies. C'est dans la région qui s'étend entre Disko Bay et le sud du district d'Upernavik que la baisse a été la plus prononcée, précisément là où il y avait auparavant de grandes colonies, à proximité des grandes collectivités. La chasse des oiseaux nicheurs, dans leurs colonies, pendant la saison de nidification, a probablement été un des grands facteurs responsables de cette baisse. La Loi sur la chasse, récemment adoptée par l'Administration du Groënland, en 1988, interdit la chasse dans la plupart des colonies, entre juin et août. La réussite du rétablissement des populations de Marmettes de Brünnich dans l'Ouest du Groënland pourrait dépendre du succès de cette mesure de gestion.

1. Introduction

West Greenland has long held large populations of Thick-billed Murres (Brünnich's Guillemot) *Uria lomvia*. Although early population estimates were crude, they nevertheless give some indication of former population size. On the basis of visits, mainly in 1925 and 1936, supplemented by discussions with local people, Finn Salomonsen estimated that about 2 million pairs bred in Greenland, with about 63% concentrated in Upernavik District of Northwest Greenland (Salomonsen 1950). Substantial declines in the population were noted by Evans and Waterston (1976), and these may have continued until recently (Evans 1984; Kampp 1988c). In this paper, we summarize information on trends in Thick-billed Murre populations in West Greenland, as well as biological data obtained by the 1987 joint U.K./Denmark/Greenland/Canada survey (Evans 1987).

Because many Greenland murre colonies are very remote, they have been visited rarely, and most have been censused only three or four times this century. Combined with the difficulty of accurately enumerating breeding populations, this has hindered the monitoring of changes in status. Some observers did not describe their census methods, and it is sometimes unclear how their population estimates were derived. Moreover, some observers used "pairs" and "individuals" interchangeably, assuming off-duty birds to be absent during the count. Salomonsen (pers. commun.) did this, and it is likely that earlier authors, such as Bertelsen (1921) and Pedersen (1930), did likewise. Today, some observers convert counts of individuals on the colony to pairs by applying a correction factor (k), generally taken to be about 0.75 (Gaston and Nettleship 1981). However, the use of such a correction factor needs to be stated explicitly; otherwise, the basis for the estimate is unclear (Nettleship and Evans 1985; Evans 1986). In this paper, we express numbers throughout as individuals counted or estimated on the colony.

With Greenland Home Rule, there is a general trend towards the adoption of Greenlandic names instead of the previous Danish or English names. To avoid confusion, the alternative names for each colony are listed in Appendix 1, together with coordinates; these are cross-referenced to two maps. As local maps of Greenland still use older spellings, these have been retained in the text.

2. Evidence for population change

Some colonies have clearly declined over the past 50 years (Table 1). Several colonies (e.g., Angissoq, Kingigtuarssuk III, Umiasugssuk, Qõrnoq Kitdleq), each formerly numbering 100–1500, are now extinct. The colony at Sagdleq, Umanaq District, thought to number "hardly less than 500,000 pairs" during the 1910s (Bertelsen 1921), is now virtually extinct, with only a handful of birds present in 1987 (T. Lash, pers. commun.). Counts made in the early part of this century may have been less reliable than more recent counts because census techniques had not been developed. Consequently, some early figures may be overestimates. However, in the case of colonies in Upernavik District, apparent declines have been greatest in the last 25 years (Fig. 1). Population changes are considered below by district.

Table 1
Thick-billed Murre colonies in West Greenland (expressed as individuals)

Area	Year of surveys				
Thule District				1936[a]	1987[b]
Hakluyt Island				"Fairly large"	37 000
Carey Islands				20 000	6 700
Saunders Island				200 000	143 000
Parker Snow Bay				"Small colonies"	50 000
Agpat agpai				100 000	48 000
Upernavik District	1936[a]	1965[c]	1974[d]	1983[e]	1987–88[f]
(North)					
Agparssuit	1 000 000	970 000	—	112 000	187 000
Kípako	30 000	17 500	5 700	11 250	13 000
Torqussâq	8 000	2 150	—	400	600
(South)					
Kingigtuarssuk III	100–1 500	1 000	0	0	0
Kingigtuarssuk II	10 000	3 500	500	25	39
Angissoq	100–1 500	200	0	0	0
Upernavik Agparssuit	100 000	27 200	18 000	5 000	3 800
Kingigtoq Agparssuit	100 000	6 415	13 000[f]	9 700	8 450
Agpatsiait	10 000	8 700	5 300	1 200	917
Qôrnoq Kitdleq	100–1 500	525	0	0	0
Tingmiakulugssuit	5 000	6 800	6 100[f]	400	369
Ùmánaq	—	50	0	0	0
Umanaq District		1921[g]	1949[a]	1984[e]	1987[h]
Sagdleq		500 000	>130 000	0	50
7 colonies near Umanaq		14 000	Present	0	—
Jakobshavn District			1946[a]	1980[i]	1984[j]
Ivnaq (Ritenbenk)			50 000	~5 000–6 000	4 500
5 colonies near Arveprinsen's Island			10–200	0	0
Sukkertoppen District		1925[a]	1946[a]	1977[k]	1987–88[e]
Sermilínguaq		100 000	5 000	13 600	11 500
Tâterât		—	—	9 000	9 000
Søndre Isortoq		—	—	370	2 200
Godthåb District			?1830s/1920s[a]	?1949[a]	1977–78[k]
Qeqertarsuaq			—	—	50
Núngarússuit			—	—	1 000
Simiútat Islands			Small colony	0	
Ravn's Storø			Small colony	0	
Utorqarmiut			—	30	
Kingigtuarssuk (Hellefiske Island)			—	+	

Frederikshåb District	1949[a]	1971[l]	1973[l]	1974[m]	1975[l]	1976[l]	1983[e]	1986[j]
Kangeq Peninsula	4 000	0	—	—	—	—	—	—
Agpat, Sermersût Island	1 000	0	—	—	—	—	—	—
Foxfaldet, Arsuk Fjord	—	0	100	250	2 000	5 000–10 000	3 300	2 300

Julianehåb District	1949[a]	1971[l]	1981[n]	1983[e]	1985[j]
Ydre Kitsigsut	—	61 200	—	4 500	7 700
Qioqê, Nunârssuit Foreland	1 000	—	0	—	—

Note: All counts are presented here as number of individuals attending the colony. Some of these were originally expressed as pairs but, at least in the case of Salomonsen's figures, had been directly converted from counts of individuals (see text).

[a] Salomonsen 1950
[b] Kampp 1990
[c] Joensen and Preuss 1972
[d] Evans and Waterston 1976
[e] K. Kampp, unpubl. data
[f] Evans 1987
[g] Bertelsen 1921
[h] T. Lash, pers. commun.
[i] N. Andersen, in Evans 1984
[j] Kampp 1988a, 1988c
[k] F. Salomonsen, unpubl. data
[l] Salomonsen 1979
[m] Boertmann 1979
[n] Kampp 1982

2.1. Thule (Avanersuaq) District

The Thick-billed Murre population was estimated at 350 000 in 1936, although Parker Snow Bay was not visited, and the colony on Hakluyt Island was simply described as "fairly large" (Salomonsen 1950). Counts made from photographs taken in 1987 estimated the population at 285 000 (Kampp 1990), suggesting little change over the past 50 years.

2.2. Upernavik District

Counts are available for colonies in this district from 1936, 1965, 1974, 1983, and 1987-88, making it the best-surveyed region of Greenland. In 1936, Salomonsen (1950) estimated the population at 1.3 million. By far the largest colony was at Kap Shackleton, or Agparssuit, where he estimated 1 million birds. In 1965, Joensen and Preuss (1972) counted a similar number: 970 000.

The next count, from photographs taken from the sea, was made by Kampp (unpubl. data) in July 1983, giving 112 000 birds. Because the distribution of the birds remained unchanged from earlier counts, Kampp considered that previous estimates must have exaggerated the number present. A direct count from a boat in July 1987 gave 187 000 birds (Evans 1987). However, the observers considered that some birds were missed by surveys from a boat and, on the basis of additional land-based counts, estimated the total present to be about 200 000.

Salomonsen's count is hard to evaluate, but Joensen and Preuss (1972) provided a clear breakdown of their counts, marked on photographs. When counts for individual sites are compared with those made in 1987, the resulting regression line departs significantly from that expected if there had been no change (Fig. 2). Moreover, the linear relationship suggests that rates of change were similar at different sites. Unfortunately, one site holds the bulk of the population, so a counting error for that site would have a disproportionate effect on the total estimate.

Changes in population have probably occurred at different rates in different parts of the district (Table 2). In northern Upernavik, there was little change between 1936 and 1965; however, if Agparssuit was correctly estimated in 1965, a steep decline occurred thereafter. The apparent increase during the 1980s may be due to differences in counting methods. Nevertheless, the earlier decline has probably halted.

In southern Upernavik, the major decline took place during the 1970s, averaging a little over 10% per annum between 1974 and 1983. Since then, the decline seems to have slowed. Counts given in Table 2 for 1987-88 are those given by Evans (1987), except at Upernavik Agparssuit (Sanderson's Hope), just south of Upernavik town, where we use a figure of 3800, obtained by Kampp in 1988. The resulting 1987-88 estimate for the whole district is 214 000, suggesting a decline of approximately 83% over the past 50 years and an 80% decline over the past 25 years. The number of colonies has been reduced from 12 in 1936 to eight in 1987.

2.3. Umanaq (Ũmánaq) District

Formerly, most murres bred at Sagdleq, close to the settlement of Umanaq, where Bertelsen (1921) reported 500 000 pairs. Salomonsen was told by locals in 1949 that the colony had decreased by 50%. He recorded 130 000 in his field notes, later rounded to 150 000, but many chicks had already departed — hence his figure of 150 000-250 000 (Salomonsen 1950). In 1984, no birds were seen on the cliffs, and only about 50 were seen in 1987. Salomonsen (1950) also noted seven other colonies of up to 3000 pairs, all of which are now believed to be extinct. Thus, the population of Umanaq has fallen from a total in excess of 100 000 to zero in less than 40 years, with a decline already having occurred over the previous 30 years.

2.4. Jakobshavn (Ilulissat) District

Several colonies existed in Disko Bay, the largest being at Ivnaq, on Arveprinsen's Island. Salomonsen (1950) reported 50 000 birds at Ivnaq in 1946 and noted five other small colonies of from 10 to 200 pairs nearby. His unpublished field notes record that all the small colonies later disappeared. In 1980, Ivnaq was reduced to no more than 10 000 birds, probably 5000-6000 (N. Andersen, in Evans

Figure 1
Population estimates for selected colonies in Upernavik District, 1930s-1980s

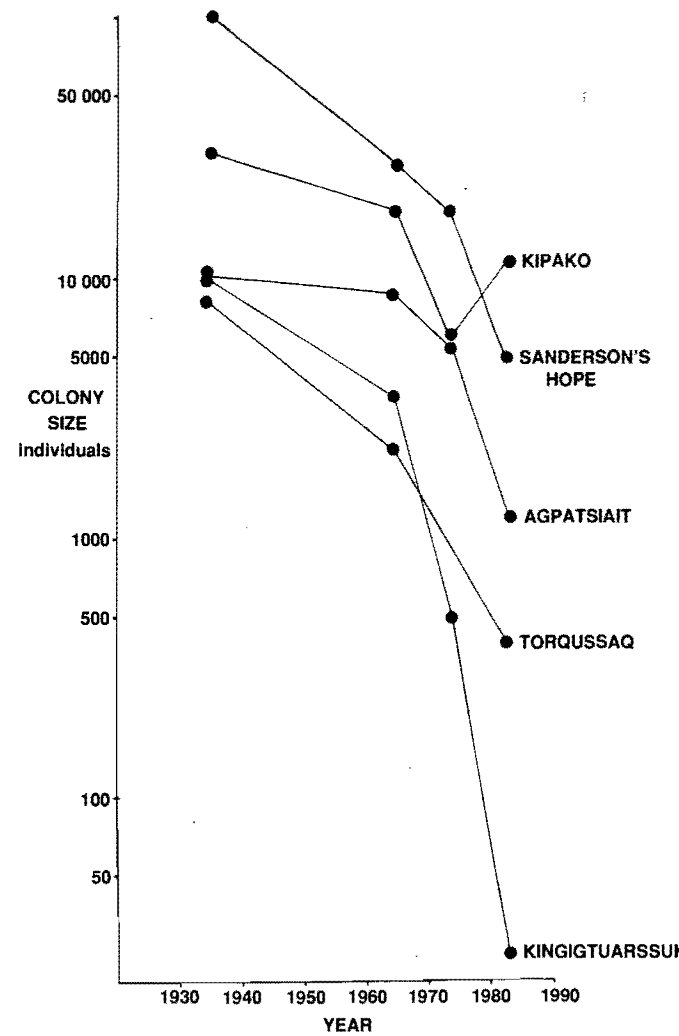


Figure 2
Counts of selected areas of the Agparssuit (Kap Shackleton) colony in 1965 and 1987, showing the actual regression (solid line) and the expected regression if there had been no change in numbers (dashed line)

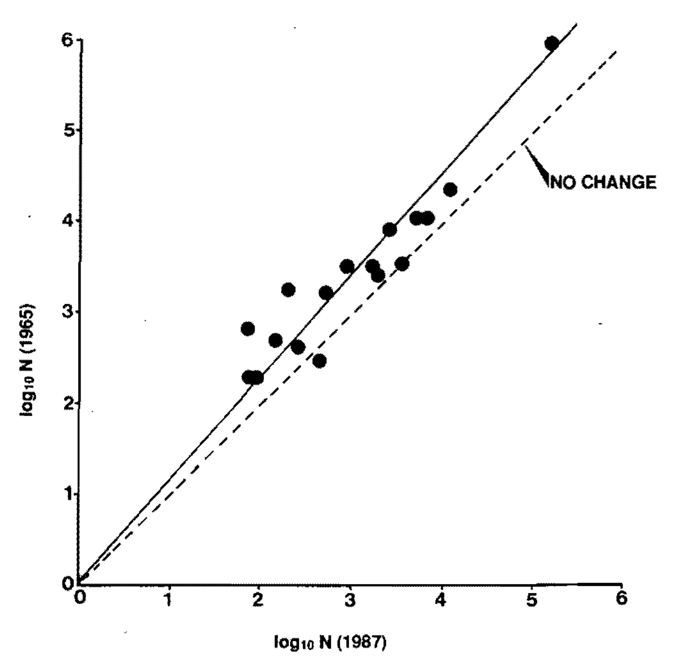


Table 2
Estimated sizes of Thick-billed Murre populations in Upernavik District (expressed as individuals)

	Count year				
Location	1936	1965	1974	1983	1987-88
Southern Upernavik	229 500	54 300	42 900	16 300	13 500
Annual rate of change	-5%	-3%	-10%	-5%	
Northern Upernavik					
Kípako	30 000	17 500	5 700	11 250	13 000
Agparssuit	1 000 000	970 000	—	112 000	187 000
Torqussâq	8 000	2 150	—	400	500
Total	1 038 000	989 650		123 650	200 500
Annual rate of change					
Kípako	-2%	-12%	+8%	+4%	
All three colonies	<-1%		-11%	+13%	

1984); in 1984, Kampp (1988a, 1988c) counted 4500 birds. Hence, the population of the district declined by 91% in 40 years.

2.5. Sukkertoppen (Manîtsoq) District

The main colony, at Sermilínguaq, supported 100 000 birds in 1925 but only 5000 in 1946 (Salomonsen 1950). Other colonies existed at Evighedsfjorden and Søndre Isortoq, although counts were not reported (Salomonsen 1967). Since then, counts by Kampp (unpubl. data), from photographs taken by F. Wille in 1987-88, indicate 9000 birds at Tâterât in Evighedsfjorden, 11 500 at Sermilínguaq, and 2200 at Søndre Isortoq. These estimates correspond fairly well with notes made by Salomonsen in 1960 and 1977. The total population apparently declined by about 80% over 60 years, with most of the decline occurring prior to 1946.

2.6. Godthåb (Nûk) District

Small colonies were reported in this district by Salomonsen (1950), Holbøll (1846), and Oldendow (1935). Salomonsen's field notes for 1977-78 indicate about 1000 at Núngarússuit and 50 at Qeqertarsuaq. These may be the only colonies existing at present.

2.7. Frederikshåb (Pâmiut) District

On the basis of secondhand observations, Salomonsen (1950) estimated the colony at Kangeq South (but possibly referring to Agparssuit inât on Kangeq North) at 4000, and that on a small islet just west of Sermersût Island at 1000 birds in 1949. In 1971, both colonies were extinct, but a new colony had become established at Foxfaldet, in Arsuk Fjord (Ilorput), where local sources reported 100 present in 1973, increasing to 250 in 1974 (Salomonsen 1979; Boertmann 1979). Kampp (1988c, and unpubl. data) counted 3300 in 1983 and 2300 in 1986. This total for the district represents an overall decline of about 46% in 37 years.

2.8. Julianehåb (Qaqortoq) District

The southernmost Thick-billed Murre colony in Greenland used to be on Qioqê Islet, just south of Nunârssuit Foreland, where Salomonsen (1950) estimated 1000 birds in 1949. It has since become extinct (Kampp 1982).

Other colonies occur on at least 11 islands in the group known as Ydre Kitsigsut. This site has been occupied only since 1950. Salomonsen (1979) estimated 61 200 birds in 1971, but, on the basis of his photographs and the amount of available cliff, it seems unlikely that numbers could have been so large. Kampp (unpubl. data) counted 4500 birds on 12 June 1983, when many ledges were still covered in snow. In 1985, the colony was estimated at about 7700 Thick-billed Murres and 1300 Common Murres *Uria aalge* (Kampp 1988a, 1988c). Salomonsen misplaced the colony locations, probably as a result of foggy conditions at the time, and he may have combined both species in his estimates.

2.9. Scoresbysund (Ittoqqortoormiit) District

Salomonsen (1950) gave estimates for two colonies in this district, based on reports by local people given in Pedersen (1930): Raffles Island, off the Liverpool coast (5000), and Kap Brewster (10 000), including the coast south of there. Meltofte (1976) estimated about 33 000 birds at Kap Brewster in 1974 and, from secondhand information, reported a small colony on Stewart Island. Korte (1973) estimated 4000 birds on Raffles Island in 1973. The recent estimates suggest a total population for the district of about 35 000, with little evidence of a change in status during this century.

2.10. Total population estimate

The current distribution of the Thick-billed Murre population of West Greenland is summarized in Figure 3. The total of colony estimates is a little over half a million individuals, indicating about 400 000 breeding pairs. An additional few tens of thousands breed in East Greenland.

3. The current situation in Upernavik District

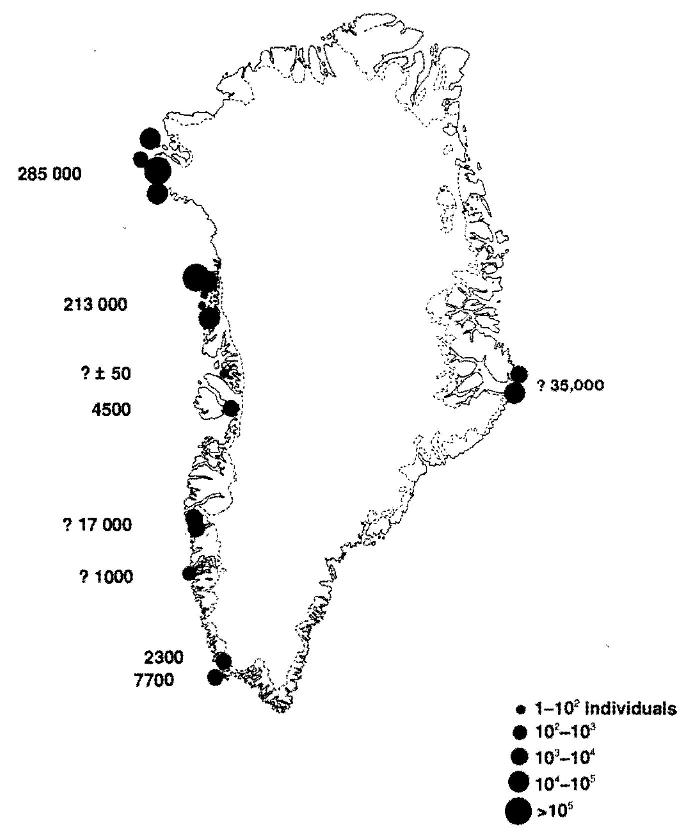
3.1. Biological studies in Upernavik District

Between 1 July and 8 September 1987, studies of Thick-billed Murres were carried out in Upernavik District by a team of 13 (mainly from the United Kingdom, but including members from Denmark and Canada, as well as two Greenlanders). All colonies in the district were censused, and studies of attendance, reproductive success, diet, and feeding rates were carried out simultaneously at two colonies: Agparssuit (7 July – 25 August), where there was little human disturbance, and Kípako (7 July – 2 September), which suffered moderate disturbance from egging and other sources. Boat surveys were carried out to collect information on foraging ranges.

Reproductive success was studied at 10 study plots (six on Agparssuit, four on Kípako), each comprising about 100 site-holding pairs. Because a few birds could have laid eggs and lost them before the start of observations, we assumed that all sites occupied on more than 85% of daily checks were used for breeding (Gaston et al. 1983). Eggs were seen on practically all sites that qualified by this criterion. Correction factors (k) for converting counts of individuals to breeding pairs were derived from daily counts of the breeding study plots (i.e., k = breeding pairs/count). Average and extreme values for Agparssuit and Kípako are given in Table 3 and are similar to those obtained in the eastern Canadian Arctic by Gaston and Nettleship (1981). It is worth noting that the most disturbed plot (No. 2 at Kípako) gave the rather low value of 0.58.

Reproductive success was determined by checks made every 1–2 d (see Evans 1987 for details). Most eggs were laid in the fourth week of June, and the young departed in the third week of August, although a few, probably replacement layings, remained until early September. Hatching success was higher on Agparssuit than on Kípako, but fledging success was similar on both. Overall reproductive success was 0.82 chicks/pair at

Figure 3
The current breeding distribution of the Thick-billed Murres in Greenland (c. mid-1980s)



Agparssuit and 0.73 chicks/pair at Kípako (Table 4), again similar to values obtained in the eastern Canadian Arctic (Gaston and Nettleship 1981). These values are used to derive estimates of total annual production for Upernavik District. Our estimates for reproductive success and k-ratios suggest that 160 000 breeding pairs in Upernavik District produced 128 000 chicks to the age of departure from the colony. If 100 pairs produce 80 fledged young and annual adult mortality is 10%, then 25% (2 × 10/0.8) of fledged young must be recruited to the breeding population to maintain stability.

3.2. Hunting in Upernavik District

During July–September 1987, we made visits to practically all settlements in Upernavik District to interview hunters about the importance of murres in their diet, the main periods and areas of hunting, and the annual number taken. Detailed results are given by M. Heubeck in Evans (1987).

Intensive hunting occurs from mid-May to mid-June, especially in late May. Fewer birds are shot in July and August. Most birds are shot at sea, near settlements. In spring, they may be shot at the edge of land-fast ice. Most hunting is opportunistic and incidental to seal hunting, except at three settlements in southern Upernavik, where people make special trips to hunt murres in spring. Most are eaten locally, but a cooperative at Ivnârssuit freezes murres for export to Nûk; about 1000 were sent in 1987. Some selling also takes place in Upernavik town, mainly of birds shot in spring in excess of hunters' needs. On the basis of our interviews, we estimated that 400 permit-holding hunters shoot an average of four or five murres

Table 3
Proportion of breeders among birds attending colonies (k-ratio)

Study plot	Mean k	Range
Agparssuit		
1	0.70	0.63–0.83
2	0.79	0.70–0.87
3	0.82	0.70–0.96
4	0.74	0.63–0.81
5	0.72	0.62–0.87
6	0.83	0.75–0.93
Overall mean	0.77	
Kípako		
1	0.73	0.59–0.98
2	0.58	0.48–0.65
3	0.82	0.74–1.00
4	0.80	0.67–0.98
Overall mean	0.73	

Table 4
Reproductive success at two colonies in 1987

Study plot	Sites occupied	% hatch	% fledge	% success
Agparssuit				
1	81	89	89	79
2	97	95	85	80
3	107	93	83	77
4	87	91	83	76
5	84	94	94	88
6	94	95	85	81
Total	550	93	88	82
Kípako				
1	126	85	85	72
2	111	77	99	76
3	97	80	90	72
Total	334	81	91	73

each per week during spring and summer. This yields a minimum estimate of 20 000–30 000 murres harvested per year but takes no account of fall hunting, hunting by persons without permits, or birds hit but not retrieved. The upper limit may be about 50 000.

Additional mortality occurs from egg collecting. This activity is much less important than in the past, when colonies were larger and eggs constituted a greater proportion of family diet. A combined total of about 1000 eggs was estimated to be taken annually, now mainly from Upernavik Agparssuit and Kípako, although some had also been taken from Kap Shackleton. Re-laying often takes place, although the resulting young fledge late in the season and so may have reduced survival in their first winter.

We estimate the number of breeding adults in Upernavik District at about 320 000, with an additional 130 000 nonbreeding subadults (40% of the breeding population). A summer harvest of 20 000–50 000 murres represents 4–11% of the population. Band recoveries suggest that 72–79% of the birds shot are of breeding age (Kampp 1982), in which case the harvest represents 3–8% of the breeding population. This compares with average annual mortality rates of 6% per annum for murre populations not subject to hunting (Mead 1974; Harris, this volume).

4. Causes of population changes

4.1. Hunting

Thick-billed Murre populations in West Greenland have declined substantially over the past 50 years. In Upernavik District, most of the decline has taken place in the last 25 years, but some colonies in Central and Southwest Greenland were declining before then (e.g., Sagdleq in Umanaq District).

Salomonsen (1955, 1970) was the first to draw attention to the population declines, attributing them to overhunting. Although murres were probably harvested for meat over the last 4000 years, it is unlikely that the harvest had any great impact until this century. Local communities were small and scattered, and hunting was by the traditional method of bow and arrow from a kayak. During this century, the human population increased rapidly, and motorboats and firearms were introduced. Human impact on major prey species, such as Thick-billed Murres, must have increased greatly. By 1974, many formerly large colonies had decreased drastically, leading to serious concern with respect to the effects of hunting and the associated disturbance (Evans and Waterston 1976).

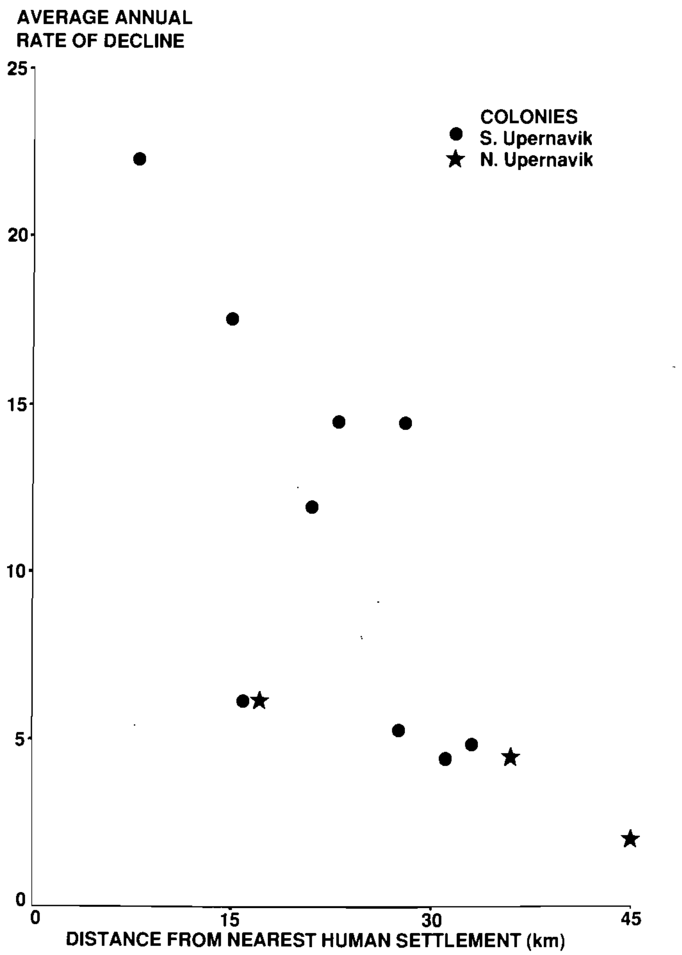
Kampp (1982, and this volume) presents evidence, from band recovery data, that hunting at the breeding colonies is the most important source of adult mortality. In Upernavik, between 1.3% (northern colonies) and 4.0% (southern colonies) of breeders were recovered in summer, indicating that a similar or somewhat higher percentage was being killed. The hunting pressure in Jakobshavn seemed similar to that in southern Upernavik, whereas it was much higher in Umanaq. In comparison, only 0.5% of banded adult murres were recovered in winter. Comparisons with other districts are not possible, as birds were not banded at other colonies.

The differing rates of kill correspond fairly well with the rates of decline in different districts. The major discrepancy concerns northern Upernavik, perhaps because the size of Agparssuit, and hence overall decline rates, was overestimated in the past. If Agparssuit did decline by more than 80% between 1965 and 1983, it seems unlikely that hunting was the main cause, and it is still uncertain what has occurred to the murres at this colony.

Other evidence that summer hunting has been important in colony declines comes from differences in rates of decline among colonies. Data from Upernavik District, which has the largest number of available counts, show a significant negative relationship between the average annual rate of decline and the distance from the colony to the nearest settlement (Fig. 4). Colonies in southern Upernavik, especially those near Upernavik town, have suffered the worst. During the period 1965–75, murres were traded commercially in Upernavik, where a freezer was in operation, processing about 15 000 murres annually at the peak. The additional pressure on the local murre population created by the commercial operation was reflected both in the banding recoveries (Kampp, this volume) and in the timing of major colony declines in the district (see Fig. 1).

Until 1978, hunting regulations in Greenland were chiefly the responsibility of local authorities, and they differed among districts. Salomonsen (1955, 1970) campaigned for improved regulations and influenced local rules in many communities, although these were rarely observed (Evans and Waterston 1976; Salomonsen 1979). A major breakthrough occurred in 1977, when general regulations were adopted for West Greenland, largely as a result of Salomonsen's perseverance. Murres were protected during the period 15 June – 15 August, except in Upernavik and Umanaq districts. The harvesting of eggs was allowed in Upernavik District until 10 July.

Figure 4
Rates of decline (% per annum) of Thick-billed Murre colonies in Upernavik District in relation to distance from the nearest permanent settlement



4.2. Drowning in gill nets

Large numbers of Thick-billed Murres are known to have been killed by a drift-net fishery for salmon and cod, which began in 1965. Most birds were caught during night fishing, particularly in September and October, in the Disko Bay area (Christensen and Lear 1977). Tull et al. (1972) estimated annual mortality at 500 000 birds and expressed concern that this might exceed production. Christensen and Lear (1977), using a larger data set, revised this estimate down to 215 000–350 000.

Analysis of band recoveries showed that birds killed by drift nets included many from outside West Greenland, including the eastern Canadian Arctic, Spitsbergen, and the European Arctic, with the area of origin related to the timing of the by-catch (Salomonsen 1967; Kampp 1982). Moreover, Kampp (1982, and this volume) showed that most of those drowned belonged to the prebreeding age-classes (less than five years old).

In 1976, fishing by foreign vessels was terminated, and salmon quotas were set to regulate the fishery. This effectively ended the fishing season in mid-September, reducing the incidental mortality of murres (Evans and Waterston 1977; Kampp 1982; Evans 1984). The current situation is reviewed by Falk and Durinck (this volume). As indicated by the analysis of banding recoveries (Kampp 1982, and this volume), it seems unlikely that net drowning has had more than a negligible impact on Greenland murre populations, outside the period 1965–75.

5. Recommendations and conclusions

As a result of the biological studies and hunter surveys carried out in Upernavik District, several recommendations were formulated that contributed to a new Game Act adopted by the Greenland Home Rule in May 1988. Thick-billed Murres are now protected south of Disko Bay between 15 March and 15 October. In northern Greenland (Disko Bay and Umanaq and Upernavik districts), the closed season is restricted to 1 June – 31 August, but this includes most of the period when the murres are present in these areas. Only in Thule and Scoresbysund districts is there a year-round open season. Hunting is reserved for residents with subsistence as a primary or secondary occupation, and all egg collecting is banned. There are also special stipulations for activities within 5 km of bird cliffs, compared with a previous limit of 2 km.

Breeding reserves will be set up at Agparssuit, Torqussâq, Kingigtuarssuk, and Upernavik Agparssuit (Upernavik District). Other reserves include Sagdleq, Ivnaq, and Ydre Kitsigsut. At those sites, all trespassing and traffic within 500 m of the reserves will be illegal from 1 June to 31 August.

These regulations are welcome, but their success depends on the extent to which they are observed. This is where problems have occurred in the past. Continued monitoring of hunting, together with status changes at the murre colonies themselves, will be essential.

Acknowledgements

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Appendix 1
List of Thick-billed Murre colonies with locations and Greenlandic and English/Danish names[a]

Colony	Location
Thule (Avanersuaq) District	
1. Appaarsuit (Hakluyt Island), Agpârssuit	77°26′N, 72°40′W
2. Kitsissut (Carey Islands), Kitsigsut	76°44′N, 73°05′W
3. Appat (Saunders Island), Agpat	76°34′N, 70°00′W
4. Issuvissuup appai, Parker Snow Bay	76°10′N, 68°40′W
5. Appat appai, Agpat agpai	76°05′N, 68°25′W
Upernavik District	
6. Kuup apparsui, Agparssuit, Kap Shackleton	73°48′N, 56°47′W
7. Kippaku, Kípako	73°43′N, 56°38′W
8. Toqqussaaq, Torqussâq	73°26′N, 56°35′W
9. Kingittuarsuk (III), Kingigtuarssuk	73°15′N, 56°51′W
10. Kingittuarsuk (II), Kingigtuarssuk	72°56′N, 56°38′W
11. Angissoq	72°54′N, 56°25′W
12. Upernaviup apparsui, Upernavik Agparssuit, Sanderson's Hope	72°42′N, 56°20′W
13. Kingittup apparsui, Kingigtoq Agparssuit	72°40′N, 55°53′W
14. Appatsiaat, Agpatsiait	72°42′N, 55°49′W
15. Qoornoq Killeq, Qôrnoq Kitdleq	72°41′N, 55°45′W
16. Timmiakulussuit, Tingmiakulugssuit	72°39′N, 55°38′W
17. Uummannaq, Ũmânaq	72°38′N, 55°53′W
Umanaq (Uummannaq) District	
18. Salleq, Sagdleq	70°58′N, 52°17′W
Jakobshavn (Ilulissat) District	
19. Appat, Agpat, Innaq, Ivnaq (Ritenbenk)	69°48′N, 51°13′W
20. Other colonies near Arveprinsen's Island	
Sukkertoppen (Maniitsoq) District	
21. Sermilinnguaq, Sermilínguaq	65°40′N, 52°38′W
	65°41′N, 52°35′W
22. Taateraat, Tâterât	66°00′N, 52°22′W
23. Søndre Isortoq	65°27′N, 52°09′W
Godthåb (Nuuk) District	
24. Qeqertarsuaq, Qeqertarssuaq	63°54′N, 51°32′W
25. Nunngarussuit, Núngarússuit	63°46′N, 51°43′W
26. Simiútat Islands	63°47′N, 51°42′W
27. Ravn's Storø	~62°41′N, 50°25′W
28. Utorqarmiut	63°40′N, 51°28′W
29. Kingittuarsuk (off Hellefiske Island), Kingigtuarssuk	63°05′N, 50°40′W
Frederikshåb (Paamiut) District	
30. Søndre Kangeq	61°21′N, 48°59′W
31. Appat, Agpat (Sermersût Island)	61°16′N, 48°57′W
32. Foxfaldet (Arsuk Fjord)	61°20′N, 48°00′W
Julianehåb (Qaqortoq) District	
33. Kitsissut avalliit, Ydre Kitsissut, Ydre Kitsigsut	60°46′N, 48°28′W
34. Qiioqit, Qioqê (Nunârssuit Foreland)	60°41′N, 47°45′W
Scoresbysund District	
35. Appalik, Raffles Island	70°36′N, 21°31′W
36. Kangikajik, Kap Brewster	70°09′N, 22°06′W
37. Stewart Island	69°52′N, 22°47′W

[a] See Figures A.1 and A.2 for locations of colonies.

Figure A.1
Map showing the location of Thick-billed Murre colonies in Greenland (numbers refer to Appendix 1)

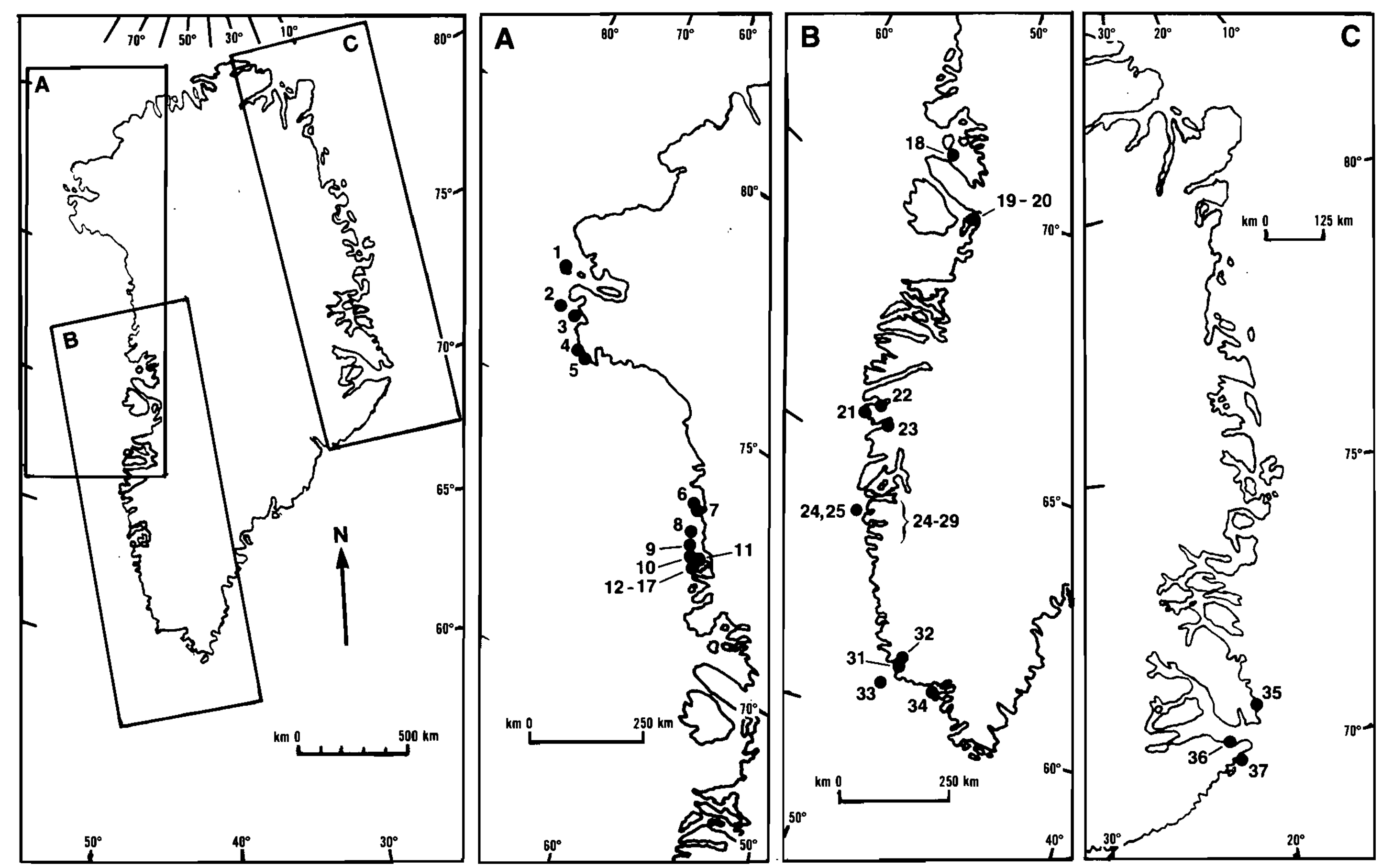
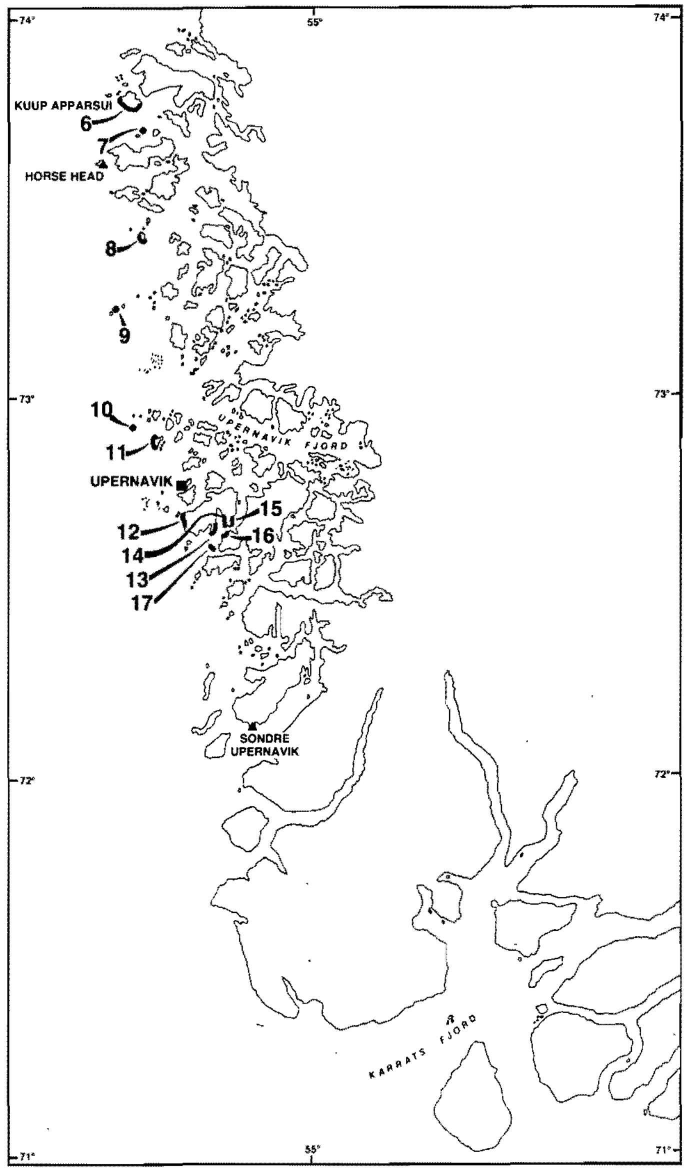


Figure A.2
Map showing the location of Thick-billed Murre colonies in Upernavik District (numbers refer to Appendix 1)



Mortality of Thick-billed Murres in Greenland inferred from band recovery data

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Abstract

Data on 2453 recoveries from 38 119 Thick-billed Murres *Uria lomvia* banded in four regions of West Greenland in 1946–80 were analyzed to extract information on mortality and recovery rates for different age-classes and populations. The structure of the data was not very well suited for this purpose; the methods used to estimate the parameters are therefore explained and discussed at some length, and the uncertainties of the estimates are stressed. Nonetheless, it seems safe to conclude that hunting had a measurable effect on mortality, particularly hunting during summer near the breeding colonies, where from 1.3% to perhaps 12% of the adult birds were recovered annually. In winter, hunters took mainly birds in their first year of life (recovery rate about 1.5%, but this is certainly an underestimate) and relatively few adults (recovery rate about 0.5%). The conclusions are consistent with regional differences in observed population declines during the last 50 years. Qualitatively, they undoubtedly hold true even today, but recently introduced legal regulations may gradually reduce the hunting pressure and reverse the negative population trends.

Résumé

Les données tirées de la récupération de 2 453 des 38 119 bagues de Marmettes de Brünnich *Uria lomvia*, quatre régions de baguées dans l'Ouest du Groënland entre 1946 et 1980, ont été analysées afin d'évaluer les taux de mortalité et de récupération des différentes populations et classes d'âge. La structure des données se prêtait mal à cette fin; nous avons donc expliqué et décrit assez longuement les méthodes utilisées pour évaluer les paramètres, et expliqué dans quelle mesure les évaluations étaient imprécises. Néanmoins, on peut conclure avec une certaine certitude que la chasse a eu un effet mesurable sur la mortalité, en particulier la chasse en été près des colonies de nicheurs, prélevant entre 1,3 % et peut-être 12 % des adultes, chaque année. En hiver, les chasseurs ont capturé principalement les oiseaux de moins d'un an (taux de récupération d'environ 1,5 %, mais ce pourcentage est certainement sous-estimé) et peu d'adultes (taux de récupération d'environ 0,5 %). Les conclusions concordent avec les différences régionales dans les baisses de populations observées au cours des cinquante dernières années. Qualitativement, elles sont toujours valables, même aujourd'hui, mais des règlements récemment adoptés pourraient faire diminuer les pressions exercées par la chasse et renverser les tendances à la baisse chez les populations.

1. Introduction

The Thick-billed Murre *Uria lomvia* breeds along most of the coast of West Greenland, in the Thule area in North Greenland, and at Scoresby Sound in East Greenland (Fig. 1). Many of these birds stay in Greenland waters during the winter. In addition, many murres of western (Canadian high Arctic) and eastern (mainly Spitsbergen) origin occur in Greenland outside the breeding season (cf. Kampp 1988b).

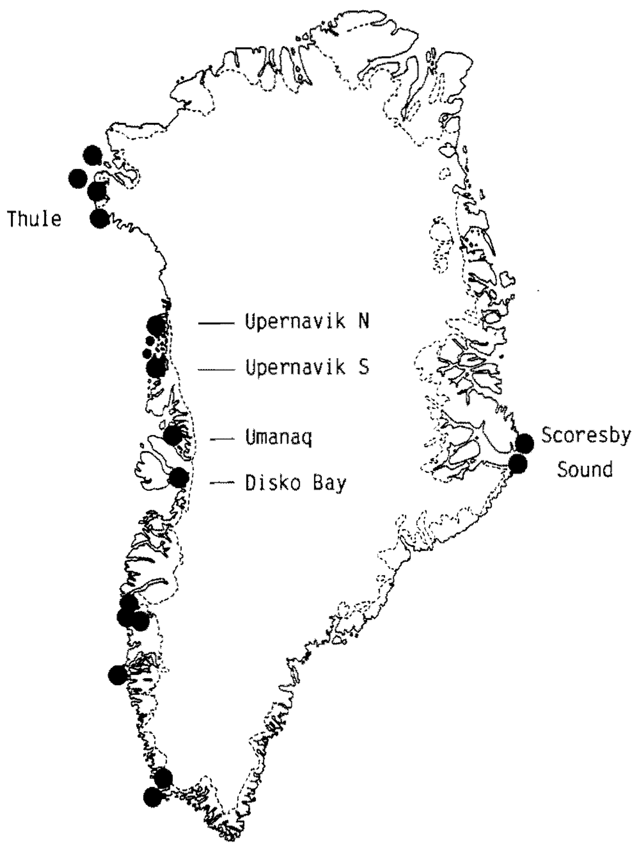
The murres in Greenland provide a reliable and important meat resource for the human population. This has been so since the first Eskimos settled in the country more than 4000 years ago. Despite the rapid modernization of the community since World War II, many people still live as full-time hunters, and almost everyone does at least some hunting.

Murre populations are characterized by very slow turnover rates, which limit the hunting pressure they are capable of sustaining. Until this century, the human population was quite small, and their mobility and fire-power were limited. Consequently, the risk of overexploiting murre populations was low. During the last 50 years, the number of Greenlanders has increased almost threefold to more than 50 000, and they are now equipped with modern firearms and outboard-powered dinghies. This development has jeopardized the murre population. Hunting in the breeding season near the colonies is particularly harmful, as most birds killed are adults. Also, no relationship between kill per unit effort and population size exists to regulate the "harvest" when hunting occurs in the immediate vicinity of the colonies.

Legal regulations aimed at protecting murre populations were introduced in Greenland in 1978. These regulations remained in force after Greenland obtained Home Rule in 1979, but they have not been sufficient to halt the decline of murre numbers. In the spring of 1988, the regulations were revised, and stricter limitations were placed on murre hunting both within and outside the breeding season. Among other things, murre hunting was banned between 15 March and 15 October in West Greenland south of Disko Bay, and between 1 June and 31 August farther north (including Umanaq and Upernavik districts, where no restrictions were in force previously). By that time, however, the formerly large murre population in Umanaq district was virtually extinct, and other populations were much reduced (in particular in Disko Bay and the southern parts of Upernavik district).

Rational management of Thick-billed Murres in Greenland requires reliable data on population sizes, harvest levels, and population dynamics. Population sizes

Figure 1
Breeding distribution of the Thick-billed Murre in Greenland



have been dealt with elsewhere (Evans 1984; Kampp 1988a; Evans and Kampp, this volume); in the present paper, the existing banding data are examined to extract information on survival rates and hunting pressure. Much of the contents has previously appeared in an informal report of limited distribution (Kampp 1982) but has here been reexamined and revised.

2. Material

2.1. The Greenland bird-banding system

The Greenland bird-banding system, as it existed between 1946 and 1984, was essentially the accomplishment of one person: the late Dr. Finn Salomonsen. Before World War II, only about 1000 birds (of 20 species) had been banded (Bertelsen 1948). After 1946, under the system devised and organized by Salomonsen, banding increased enormously; by 1984, about 240 000 birds of 50 species had been reported banded, with the number of recoveries totaling more than 12 000.

The system producing these impressive figures was described by Salomonsen (1956) and Mattox (1970). Local Greenlanders were recruited to do the actual banding, for which they received payment according to numbers and species banded. The local representatives of the government (later the Greenland Trade Department KNI, formerly KGH) forwarded banding reports and recovered bands to the Zoological Museum in Copenhagen, which managed the program. A modest reward was given for bands delivered with the bird's foot and relevant data. The practice of returning both the band and the leg of the bird helped to correct errors that unavoidably occur when banders are nonprofessional and often inexperienced.

Payments and rewards were paid by the Ministry for Greenland, together with costs needed to maintain the system (e.g., travel expenses). Bands and routine management were paid for by the Carlsberg Foundation.

The existence of this system also enhanced the reporting of foreign-banded birds recovered in Greenland. However, knowledge of the system among Greenlanders dwindled from the 1960s onwards, by which time a transition from a subsistence to a cash-based economy had taken place in the country. Consequently, the payment for banding birds became rather insignificant. Under these changed circumstances, banding efforts could be sustained only in a few places and were directed mainly towards colonially breeding species, of which many birds could be banded rapidly. In 1984, after banding for cash had practically ceased, the system was abandoned. Banding in Greenland now takes place only at a modest level when opportunities arise. Rewards for recovered bands are still paid by the Home Rule government.

2.2. Murre bandings

Thick-billed Murres were banded, mostly as chicks, throughout the period in which the banding system existed (Table 1). From the start in 1946, murres were banded at the Ritenbenk colony in Disko Bay, and soon afterwards banding was initiated in Umanaq district. Banding activities later concentrated on the murre population in southern Upernavik district (Upernavik S); from the mid-1960s on, large numbers of murres were banded in northern Upernavik district (Upernavik N), whereas efforts were slight or discontinued elsewhere. Banding efforts in all areas varied greatly among years. Apart from Scoresby Sound in 1970, no banding of murres took place in other parts of the country until after the termination of the cash banding system (southernmost West Greenland, 1985; Thule district, 1987), and these bandings have not yet produced recoveries useful in the present context.

Unfortunately, the reported numbers of murres banded are far from accurate. Almost all murres were banded as chicks, and the scarcity of recoveries from certain band series suggests that bands were used on chicks too small to retain them. To some extent, this may have been the case even in band series displaying more normal recovery patterns (on which the present analysis is based). Furthermore, particularly during the later years, many band series produced few or no recoveries, presumably because most or all of the bands were never used. Problems of this sort are to be expected under such a banding system. On the other hand, it was the only way to achieve large-scale bandings in remote and inaccessible places.

In addition to chicks, a limited number of adult murres were also banded (Table 1), and the recoveries from these play a major role in calculations of harvest levels. These calculations are necessarily rough but will probably yield estimates within reasonable orders of magnitude.

3. Methods

3.1. Adult annual survival

During the past 10–15 years, several sophisticated models for calculating survival and recovery rates from bird-banding data have been developed, most notably those of Brownie et al. (1985). Nevertheless, studies using simpler methods are still frequently published, because most data sets do not meet the standards required by more advanced schemes. To obtain reasonably accurate age-specific parameter values, the number of bands recovered must be

Table 1
Banding totals and recoveries of Thick-billed Murres in four regions of West Greenland (cf. Fig. 1)[a]

Region	No. banded	Season	Year of recovery 1	2	3	4	5	6	7	8	9	10	>10
Disko Bay, 1946–63													
Chicks	2 424	Summer	19	54	36	14	17	17	7	14	12	6	38
		Winter	41	9	4	1	1	0	1	3	0	0	10
Umanaq, 1949–62													
Chicks	5 027	Summer	17	52	40	33	35	29	19	15	12	14	23
		Winter	28	9	0	4	3	1	0	2	1	1	2
Upernavik S, 1952–73													
Chicks	11 306	Summer	42	82	117	82	44	55	38	28	21	34	70
		Winter	169	30	13	5	4	4	4	6	3	0	7
Adults	318	Summer	6	6	9	4	15	4	4	4	7	5	4
		Winter	2	0	1	0	0	2	1	1	1	1	1
Upernavik N, 1961–80													
Chicks	18 654	Summer	55	80	56	35	27	30	18	18	18	18	48
		Winter	321	28	21	9	9	4	5	6	3	3	8
Adults	390	Summer	1	5	5	3	3	1	1	7	1	3	6
		Winter	5	4	1	3	0	0	0	1	0	0	3

[a] The recoveries (shot birds only) are given separately for summer (May–September) and winter (October–April) for the first 10 years after banding, and all later years (max. 28) combined. Excluded are bandings that have produced no or abnormally few recoveries.

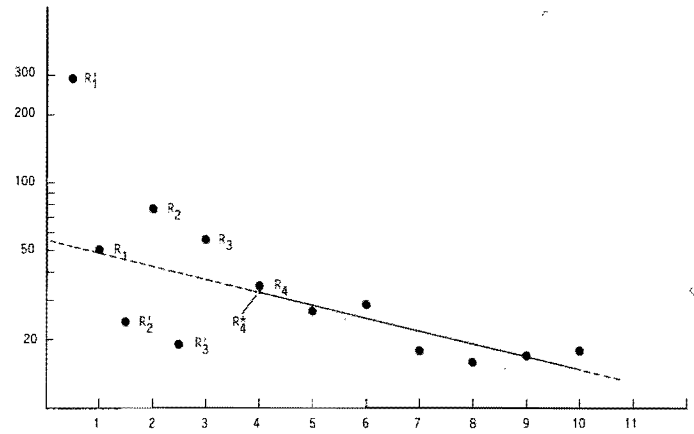
fairly large, which will normally be the case only in hunted species. Furthermore, accurate banding numbers from bandings of adults as well as chicks through several consecutive years are required. The need for banding adults must be stressed, because age-specific survival and recovery rates cannot be estimated from the banding of young only unless some very restrictive and unrealistic assumptions are made, as fully discussed by Brownie et al. (1985).

The present data do not meet the criteria for applying advanced methods. Almost all data are from birds banded as chicks, the number of birds banded is very imperfectly known, and some banded chicks probably died during the banding operations (losses occur even when banders are highly experienced). Of the simpler methods that might be considered, Haldane's (1955) classic formula appears most satisfactory from a theoretical point of view. It is also fairly robust. Unfortunately, it allows the calculation of adult survival rate only; survival of young birds and recovery rates for all age-classes are not obtainable. The consideration of these parameters has to be based on the limited data from birds banded as adults following methods explained under Results.

Haldane's method assumes age- and year-independent survival and recovery rates. These requirements are not likely to be met precisely in any real cases, but they may be approximately fulfilled for adult birds. The assumption of a constant recovery rate is probably the most doubtful, and the consequences of relaxing it are investigated in the discussion, supported by simulated recovery data.

As the Haldane scheme assumes that all parameters are constant, it naturally follows that recoveries from different banding years can be combined, provided that no further recoveries from any of them can be expected. This procedure can be combined neatly with another modification: truncating the recoveries by ignoring those made after a certain number of years. This is necessary when dealing with long-lived species like murres in order to correct for band loss. Inspection of the Greenland murre data suggests that band loss becomes important after 11–12 years. This is further supported by the weight loss of the bands (Kampp 1982).

Figure 2
Semilogarithmic plot of recoveries from Upernavik N (1961–78). The line connects expected numbers of recoveries according to Haldane's model. Some numbers used in calculating recovery rates are defined.



Common experience and inspection of the present data show that survival and recovery rates (vulnerability to hunting) differ between young and adult birds. It is therefore necessary to exclude the first few years of recovery when applying Haldane's method to data from birds banded as chicks. By trial and error, it appears that at least the first three years should be excluded from the Greenland murre data.

To summarize, the calculation of adult survival is here based on Haldane's method, modified for "truncated" recovery data, applied to a single row of recovery numbers (different banding years combined) including the fourth to 10th year after banding. This very conservative use of the data is an unavoidable consequence of their poor quality. Only shot birds (the vast majority of recoveries; cf. Kampp 1988b) are included.

3.2. Symbols and definitions

In the present context, "year" means "year of life" (or "year after banding") reckoned from September to August. "Summer" includes the months May–September, i.e., the part of the year when adult and most immature murres are found near the breeding colonies (Kampp 1988b); "winter" includes the months October–April. Symbols used in formulas are as follows:

- s — Adult annual survival rate, i.e., the probability that a bird alive at the beginning of the year survives to the beginning of the following year
- s_i — Annual survival rate for the i'th age-class
- f — Adult seasonal recovery rate during summer, i.e., the probability that a banded bird alive at the beginning of the summer will be shot and the band returned during the same summer
- f' — Adult seasonal recovery rate during winter
- f_i, f_i' — Seasonal recovery rates during summer and winter, respectively, for the i'th age-class
- N, N_a — Number of birds banded as chicks and adults, respectively
- R_i, R_i' — Number of banded birds recovered during the i'th year after banding (summer and winter, respectively; cf. Fig. 2)

Table 2
Adult survival rate for Disko Bay, Umanaq, Upernavik S, and Upernavik N[a]

Region	No. of birds shot 4	5	6	7	8	9	10	s	SE	χ_5^2	P
Disko Bay	14	17	17	7	14	12	6	0.898	0.049	6.04	0.30
Umanaq	33	35	29	19	15	12	14	0.825	0.034	2.86	0.72
Upernavik S[b]	82	44	55	38	28	21	34	0.831	0.025	14.18	0.01
Upernavik S[c]	54	35	41	33	22	21	32	0.887	0.029	8.73	0.12
Upernavik N[d]	35	27	29	18	16	17	18	0.875	0.035	2.83	0.73

[a] Shown are the number of chick-ringed birds shot during the 4th–10th summers, annual survival and standard error (Haldane estimates), and result of goodness-of-fit test.
[b] All bandings included.
[c] 1966 bandings excluded.
[d] 1979–80 bandings excluded because they may still produce recoveries.

Table 3
Recovery rates of adult-banded murres, together with figures used to compute them (see text): number banded N_a, recoveries R_i and R_i' through the first 10 years, and estimated annual survival

Region	N_a	ΣR_i summer	$\Sigma R_i'$ winter	s	Recovery rate (%) Summer	Winter
Upernavik S	318	64	9	0.83	4.05	0.47
Upernavik N	390	30	14	0.87	1.33	0.54

With these symbols, Haldane's formulas in the present modification become (see Appendix 1 for derivation of formulas 1 and 2):

$$\sum_{i=1}^{n} iR_i/R - 1/(1-s) + ns^n/(1-s^n) = 0 \quad (1)$$

$$SE^{-2} = R[1/(s[1-s]^2) - n^2s^{n-2}/(1-s^n)^2] \quad (2)$$

where SE = the standard error of the estimate,
R = the total number of recoveries (ΣR_i), and
n = the number of terms in the sums (n=7 in the present case).

4. Results

The recoveries of banded Thick-billed Murres for the four regions where banding has been performed are given in Table 1, and the corresponding Haldane estimates of adult survival rates are given in Table 2. The recovery rates of adult murres can be tentatively estimated from the recoveries of birds banded as adults. Recoveries from single years are very few; in order to utilize a larger part of the recoveries, the recovery rates are calculated as:

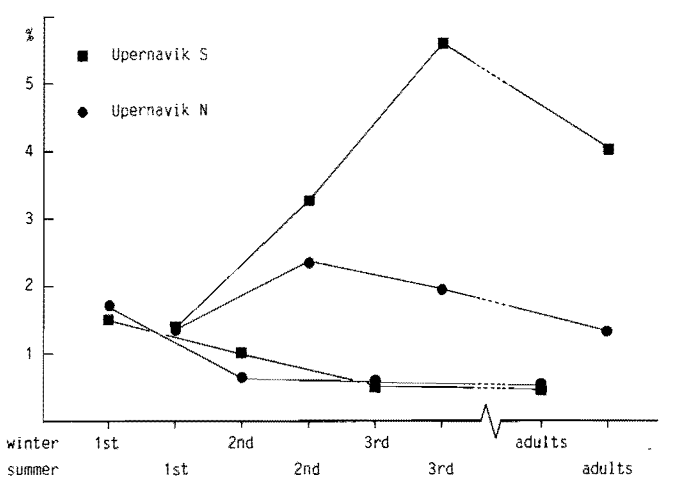
$$f = \sum_{i=1}^{n} R_i / \sum_{i=1}^{n} N_a \cdot s^i = (\sum_{i=1}^{n} R_i/N_a)\cdot[(1-s)/(s\cdot[1-s^n])] \quad (3)$$

$$f' = \sum_{i=1}^{n} R_i' / \sum_{i=0}^{n-1} N_a \cdot s^i = (\sum_{i=1}^{n} R_i' N_a)\cdot[(1-s)/(1-s^n)] \quad (4)$$

where recoveries from the summer of banding are excluded. Only 10 years are included to avoid the effects of band loss. The results are given in Table 3. Similar estimates cannot be obtained for Umanaq and Disko Bay, because no adults were banded there.

Recovery rates during winter ought to be equal for all four regions and might be used to correct for different banding "efficiencies" (i.e., the proportion of bands put on chicks of the correct age). From this it appears that efficiencies have been roughly equal in all areas except Umanaq, where it was only about half as good. Assuming equal reporting probabilities in all regions and correcting for efficiencies in this way, it appears that summer recovery rates in Upernavik S and Disko Bay have been similar, about 4%, or three times the rate in Upernavik N, and that the recovery rate in Umanaq may have been as much as three times as high again.

Figure 3
Estimated recovery rates for murres banded in Upernavik. First-winter rates are underestimated (see text).



Of the 297 adult murres that I banded in Disko Bay in 1984, 12 were shot during the summers of 1985–88, indicating a recovery rate of about 1.5%. This suggests that hunting pressure or reporting probability, or both, have decreased during the past 30 years.

The expected number of recoveries in the fourth summer after banding of chicks is given by:

$$R_4 = Ns_1s_2s_3s_4f \quad (5)$$

Hence, the total survival through the first four years of life is:

$$s_1s_2s_3s_4 = R_4^*/Nf \quad (6)$$

(cf. Fig. 2; the "smoothed" number of recoveries R_4^* is used instead of the actual number R_4 in order to reduce the effect of random fluctuations). Because the number of banded birds is not accurately known, this estimate is burdened with a substantial uncertainty but may provide a minimum value.

The expected numbers of first-, second-, and third-summer recoveries are Ns_1f_1, $Ns_1s_2f_2$, and $Ns_1s_2s_3f_3$, respectively. The corresponding winter recovery expectations are Nf', Ns_1f', and Ns_1s_2f'. Taking ratios, and using the not unreasonable assumption that

$$s_2 \approx s_3 \approx s_4 \approx s \quad (7)$$

estimates may even be obtained for the recovery rates of immatures:

$$f_1 = (R_1/R_4^*)\cdot s^3\cdot f \quad (8)$$
$$f_2 = (R_2/R_4^*)\cdot s^2\cdot f \quad (9)$$
$$f_3 = (R_3/R_4^*)\cdot s\cdot f \quad (10)$$
$$f_1' = R_1'/N = (R_1'/R_4^*)\cdot s_1s^3\cdot f \quad (11)$$
$$f_2' = (R_2'/R_4^*)\cdot s^3\cdot f \quad (12)$$
$$f_3' = (R_3'/R_4^*)\cdot s^2\cdot f \quad (13)$$

In this approximation, only the estimate of first-winter recovery rate (formula 11) depends on the banding total N (or, equivalently, the undetermined parameter s_1) and should therefore be regarded as a minimum value. If formula 7 is a poor approximation for s_2 (second-year survival appreciably less than adult survival), even f_1 and f_2' are underestimated, but this is probably rather unimportant considering the rough character of the calculations.

Table 4
Recovery rates during summer (f) and winter (f') for young murres (1st–3rd years), together with numbers banded and recovery numbers used to compute the recovery rate estimates (defined in Fig. 2)[a]

Region	N	R_4^* (= Ns_1s^3f)	R_1 (= Ns_1f_1)	R_2 (= Ns_1sf_2)	R_3 (= $Ns_1s^2f_3$)	R_1' (= Nf_1')	R_2' (= Ns_1f_2')	R_3' (= Ns_1sf_3')	Recovery rates (%) f_1	f_2	f_3	f_1'	f_2'	f_3'
Upernavik S	11 306	70.2	51	77	56	291	24	19	1.4	3.3	5.6	1.5	1.0	0.5
Upernavik N	17 304	32.9	42	82	117	169	30	13	1.4	2.4	2.0	1.7	0.6	0.6

[a] Also used are s and f (from Table 3).

The values obtained for survival up to an age of four years (formula 6) are 0.143 and 0.153 for Upernavik N and S, respectively. The estimated recovery rates are summarized in Figure 3, with numbers used to compute them given in Table 4.

5. Discussion

5.1. Adult survival rate

I tested the goodness of fit between the recovery data and Haldane's model (Table 1). Only in Upernavik S was the deviation significant, and that result can be altered by omitting a single banding year (1966); a possible reason for this is discussed below.

Because Haldane's model is a robust one, the correspondence between data and model may be misleading; the test has low power. In particular, the data suggest some variation in recovery rate from year to year, which is only partly "smoothed out" by combining data from different banding years.

In order to obtain some idea of how varying recovery rates influence recovery patterns, a number of simulations were run on a micro-computer. In these simulations, a cohort banded and alive at the beginning of its fourth summer was followed through seven years, with probability $p_s \cdot p_r$ of being recovered *and* reported each year, and probability $(1-p_s)\cdot s_0$ of surviving to the next year. The values of s_0 and p_r (probability of being reported if recovered) were kept constant at 0.90 and 0.50, respectively. The value of p_s (probability of being shot) was obtained for each summer from a gamma distribution with parameters giving the desired expectation and a coefficient of variation (CV) of 50%.

The initial numbers of banded birds were chosen to approximately reproduce the actual summer recovery patterns from the four regions. The results from 100 simulations for each region, together with similar simulations where p_s was kept constant, are summarized in Table 5 and Figure 4.

For runs where the recovery rate (hunting pressure) was kept constant from year to year, the standard deviation naturally approximates the Haldane estimate (mainly determined by the model structure and sample size), and the percentage of significant deviations is close to the chosen significance level. As expected, the introduction of an additional component of stochastic variation increases the variance on the calculated survival rates. At the same time, most runs still give patterns consistent with the Haldane model, although this tendency is weakened as the extent to which the recovery data are dominated by a single year increases (in the following sequence: Disko Bay, Umanaq, Upernavik N, Upernavik S). There is no relationship between goodness of fit and survival estimate.

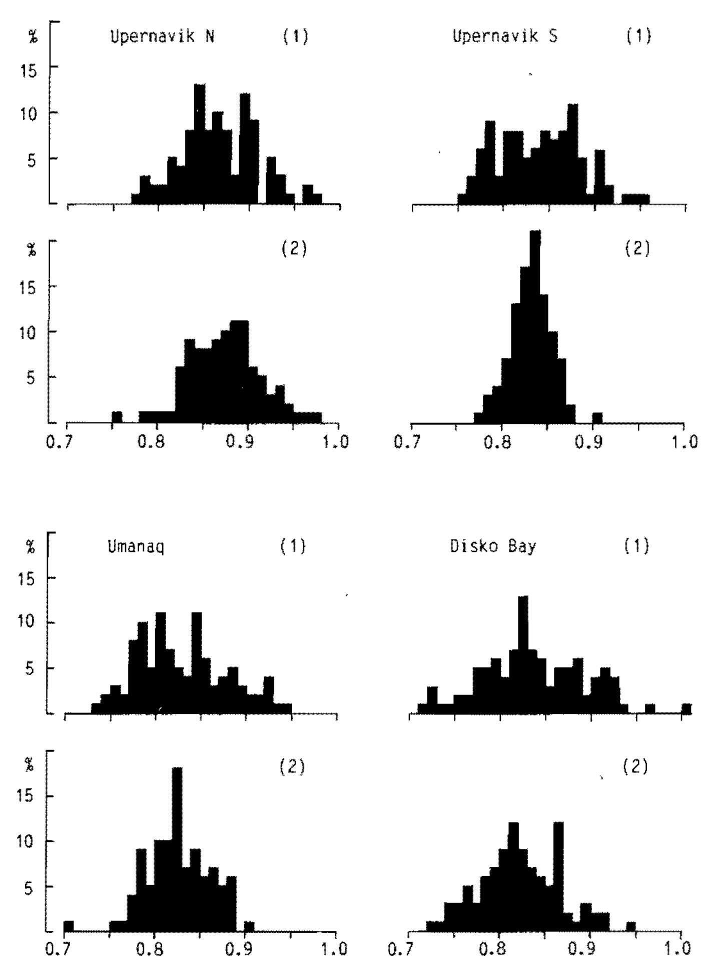
These results confirm that the Haldane method is robust and that the standard error of the estimated survival rate may well be too low, making the estimate appear more accurate than is actually the case. However, they also

Table 5
Summary of eight simulations,[a] each of 100 runs

Region		Expectation of p_s	CV of p_s (%)	s_{model}	s ± SD	% runs deviating from model (5% level)
Upernavik N	(1)	0.03	50	0.873	0.867 ± 0.042	24
	(2)	0.03	0	0.873	0.875 ± 0.039	2
Upernavik S	(1)	0.07	50	0.837	0.840 ± 0.047	48
	(2)	0.07	0	0.837	0.832 ± 0.022	5
Umanaq	(1)	0.08	50	0.828	0.829 ± 0.049	19
	(2)	0.08	0	0.828	0.826 ± 0.033	6
Disko Bay	(1)	0.08	50	0.828	0.837 ± 0.057	9
	(2)	0.08	0	0.828	0.823 ± 0.044	5

[a] In the model, a number of banded cohorts are followed through seven years, with initial numbers of birds chosen so that recovery matrices from simulations resemble those observed. Birds are recovered with probability $0.5\cdot p_s$ and survive to next year with probability $s_{model} = (1 - p_s)\cdot 0.9$. The probability that a bird will be shot during the summer (p_s) is for each year taken from a gamma distribution with a coefficient of variation (CV) of either 50% or 0% (constant hunting pressure and recovery rate).

Figure 4
Distributions of survival rates obtained from the simulations summarized in Table 5



suggest that the estimated survival rate may be quite good even if the model's assumptions are violated, particularly if such violations involve only the random fluctuation of parameters and if recoveries are combined from different banding years.

A systematic trend in parameter values could seriously bias the estimate. Such a trend, specifically an increasing recovery rate in the late 1960s and early 1970s, may have occurred for Upernavik S because murres were utilized commercially during 1965–75, when a freezer operated in the town. Most of the approximately 15 000 birds processed annually (Kampp 1988a) were undoubtedly taken near the town, i.e., in the southern part of the district. Furthermore, even though birds from the northern part were involved, banding in Upernavik N took place later than in Upernavik S, so recoveries from most banding years were not affected. The effect would be more recoveries of "old" birds banded some years before and of "young" birds banded shortly before/during this period; this might explain the poor fit between data and model, the improved fit when 1966 (or 1965 and 1966) is omitted, and the simultaneous increase in apparent survival (Table 2).

One further complication adds to uncertainty about the validity of the estimated survival rates. Estimates based on band recoveries tend to be low when compared with "safer" methods. In the past, this tendency was commonly caused by applying demonstrably faulty estimating techniques (cf. Seber 1972). In the present case, the failure of a general assumption underlying all estimating schemes — the assumption of homogeneous parameter values (probabilities) — could be a problem. It appears quite likely that individual birds differ in "quality" and that this even affects survival. If so, the population segment that has supplied the present data — i.e., birds at most 10 years old — will have lower average survival than the adult population in general (note that the average age of breeders is k + s/(1-s) for a stable population with homogeneous survival s and age at first breeding k). This is another difficulty caused by banding chicks only.

Estimates of survival rates for adult Common Murres *Uria aalge* have been obtained from banding data (Birkhead 1974; Mead 1974), from controls of individually marked birds (Birkhead and Hudson 1977), and from the turnover at sites of birds belonging to the bridled morph (Birkhead et al. 1985). The results lie between 0.88 and 0.94, with the more reliable estimates in the upper half of this range. The populations involved were exposed to little, or no, hunting.

A comparison of these values with those obtained here suggests that Thick-billed Murres in Greenland suffer reduced adult survival rates, i.e., higher than normal mortality. For reasons discussed above, this cannot be tested rigorously but accords with expectations, considering the extent of murre hunting in Greenland and the observed population declines.

5.2. Survival of young birds

The total survival from banding through to the start of the fourth summer was estimated above for the two parts of Upernavik district, using recovery rates obtained from bandings of adults. The estimated four-year survivals, about 15% in both cases, appear very low. To maintain the population, total survival β through to breeding age in the present model is given by:

$$\beta = (1-s)/m \qquad (14)$$

where m is production of young per adult. Breeding probably first takes place in the fifth summer (cf. Birkhead and Hudson 1977 for *U. aalge*), so if $2m \approx 0.7$ (Gaston and Nettleship 1981), β should be 0.37–0.49 with the s values obtained here (0.87 and 0.83). In unexploited murre populations, with $s \approx 0.92$, β should be at least as high as 0.23 to balance adult mortality. With $s_5 \approx s$, the estimated values here become 0.13 for both populations.

It is very probable that recruitment in Greenland's murre populations does *not* balance losses of adults — after all, the populations have gone down. Nonetheless, the estimated values probably represent serious underestimates, mainly because effective banding numbers are much lower than reported numbers. This could be caused, for example, by banding chicks too young to retain the bands, or by heavy mortality in the banded sample owing to disturbance from the banding activities.

Another point is that survival and reporting rates in young birds, at least during the first year of life, may be much more variable than corresponding parameters for adults; in that case, a simple model as used here would be less suited to describe this part of the population process. There are strong indications that the recovery rate during the first winter is far from being constant (Kampp 1988b); that first-year survival in some years may be very poor is suggested by the recovery pattern of the 1970 cohort (Upernavik N), showing "normal" recovery numbers through to February 1971 but very few later on, even in subsequent years.

All factors taken together, immature survival is the most elusive of parameters describing the population dynamics of wild bird species. Owing to confounding with dispersal, mortality of young birds cannot be derived from studies of individually marked birds either, and the survival through to the third summer found by Birkhead and Hudson (1977) (recalculated at 0.23) is therefore a minimum value. Only under special circumstances can the effect of dispersal be approximately corrected for (e.g., Harris 1983, for the Atlantic Puffin *Fratercula arctica*).

One reason to stress the problems in obtaining good or even approximate estimates of immature survival rates is that a very simple scheme to make such estimations from banding data has been published (Birkhead and Hudson 1977; Hudson 1985). The method was simply to put recovery numbers, for the first five years alone, into Lack's classical formula (Lack and Schifferli 1948):

$$s = 1 - \sum_{i=1}^{\infty} R_i / \sum_{i=1}^{\infty} iR_i$$

However, this formula demands complete data and is supposed to yield annual survival (not total survival through five years). It also assumes constant survival and recovery rates. So, for three separate reasons, the method will not produce useful estimates, even in an approximate sense.

5.3. Recovery rates

Like immature survival, recovery rates (see Fig. 3) were obtained for Upernavik N and S by use of the meagre data on murres banded as adults. The estimates could therefore be poor; except for the first-winter recovery rate, however, the estimates do not depend on banding numbers, so there is no reason to regard them as grave underestimates.

If all recovered bands were reported, recovery rate would be equal to the proportion of birds shot seasonally. But the reporting probability must surely be less than one; it may also vary somewhat between different parts of the country, so summer and winter rates are not strictly comparable. It is comforting that the two independent data sets, from Upernavik N and S, respectively, produce similar winter recovery rates, as the two murre populations probably share the same winter range.

Despite the stated reservations, it is likely that Figure 3, in relative terms, approximately reflects the actual situation, which could then be summarized as follows: the hunting pressure is higher in summer than in winter, and higher in the southern colonies near the town of Upernavik than in the more remote northern colonies. Summer hunting affects mainly adult murres, with relatively little impact on yearlings, which do not concentrate in any particular area at this time. Winter hunting takes mainly young-of-the-year, for which the rates in Figure 3 are certainly underestimated, but relatively few older birds. Young birds appear to be more vulnerable to hunting than older birds; this is known to be the case even in other hunted species. The depicted pattern of heavy shooting mortality in the breeding season is consistent with the observed pattern of geographically differentiated population decline rates, with colonies in densely inhabited areas faring worse than those situated farther from densely inhabited areas.

For Umanaq and Disko Bay, summer recovery rates were very roughly estimated relative to the Upernavik estimates. In Disko Bay, the magnitude was apparently similar to that in Upernavik S; in Umanaq, it was much higher, perhaps about 12%, which would suggest that about 15–20% of the birds were shot annually. It is not surprising that this population was wiped out.

The age distribution of shot birds cannot be calculated from the recovery rates, because the age-distribution in the population is not known with any precision. The distribution cannot be found directly from the recovery data either, because, owing to loss of older bands, adults will be underrepresented. By using only the ages up to 10 years and correcting the number of adults using the survival rate s = 0.85, the proportions of first-year birds, older immatures, and adults become 8:40:52 in summer and 71:19:10 in winter; the proportions are rather sensitive to the value of s adopted in the correction.

Thick-billed Murres from Greenland winter both in central West Greenland and off Newfoundland (Salomonsen 1967; Gaston 1980; Kampp 1988b). The recoveries from Newfoundland are included in the calculations above. They comprise 40% of all winter recoveries. If reporting probabilities from Newfoundland and Greenland were similar, this would imply that winter hunting in the two regions killed similar proportions of the Greenland murre population. Considering that a reward system exists in Greenland, however, it may well be that recoveries from Newfoundland are underrepresented. If so, hunting of murres in Newfoundland has a somewhat larger impact on the populations in Greenland than is apparent immediately from the numbers available.

6. Conclusions

The Ministry for Greenland supported bird banding in order to obtain information useful in managing the living resources of the country. However, banding is not a very efficient method to obtain such data unless the project is carefully designed. Considering the magnitude of the present material, the conclusions that can be drawn are surprisingly vague. Excluding migrants and visitors, it seems certain that more murres are shot in summer than in winter, albeit with regional differences in hunting pressure during summer; and that summer hunting takes mainly adults and winter hunting mainly immatures (in particular young-of-the-year). Quantitative estimates are less certain. Hunting seems to have a measurable effect on survival; harvest levels amount to at least a few percent of the murres annually and, depending on reporting probabilities, may exceed 10% for some populations. These conclusions are consistent with observed population declines.

Acknowledgements

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Appendix 1

Derivation of formulas 1 and 2

The modified Haldane formulas 1 and 2 may be derived in several ways. If one follows the original derivation by Haldane (1955), all that is needed is that the (conditional) probability of recovery through the i'th year

$$s^{i-1}(1-s) \qquad (i = 1, 2, \ldots)$$

must be normalized so as to add up to unity:

$$\frac{s^{i-1}(1-s)}{1-s^n} \qquad (i = 1, 2, \ldots, n)$$

yielding the log-likelihood:

$$L = \sum_{i=1}^{n} R_i \ln \frac{s^{i-1}(1-s)}{1-s^n} \qquad (A1)$$

The ML-estimate of s is obtained by solving:

$$\frac{dL}{ds} = \sum_{i=1}^{n} R_i \left(\frac{i-1}{s} - \frac{1}{1-s} + \frac{ns^{n-1}}{1-s^n} \right) = 0 \qquad (A2)$$

i.e. (with $\sum_{i=1}^{n} R_i = R$):

$$\frac{1}{s} \left(\sum_{i=1}^{n} iR_i - R \right) - \frac{R}{1-s} + \frac{Rns^{n-1}}{1-s^n} = 0 \qquad (A3)$$

or, after multiplication by s/R (and using the identity 1 + s/[1-s] = 1/[1-s]):

$$\frac{\sum_{i=1}^{n} iR_i}{R} - \frac{1}{1-s} + \frac{ns^n}{1-s^n} = 0 \qquad (A4)$$

which is formula 1.

The standard error is estimated by:

$$SE^{-2} = \frac{-d^2L}{ds^2} = -\sum_{i=1}^{n} R_i \left(-\frac{i-1}{s^2} - \frac{1}{(1-s)^2} + \frac{n(n-1)s^{n-2}(1-s^n) + (ns^{n-1})^2}{(1-s^n)^2} \right) \qquad (A5)$$

Formula A2 may be rewritten as:

$$\sum_{i=1}^{n} R_i \frac{i-1}{s^2} = \frac{R}{s} \left(\frac{1}{1-s} - \frac{ns^{n-1}}{1-s^n} \right) \qquad (A6)$$

which, inserted in formula A5, yields:

$$SE^{-2} = \frac{R}{s}\left(\frac{1}{1-s} - \frac{ns^{n-1}}{1-s^n} + \frac{s}{(1-s)^2} - \frac{n(n-1)s^{n-1}-n^2s^{2n-1}+ns^{2n-1}+n^2s^{2n-1}}{(1-s^n)^2}\right),$$

$$= R\left(\frac{1}{s(1-s)^2} - \frac{ns^{n-2}-ns^{2n-2}+n(n-1)s^{n-2}+ns^{2n-2}}{(1-s^n)^2}\right) \qquad (A7)$$

which is equivalent with:

$$SE^{-2} = R\left(\frac{1}{s(1-s)^2} - \frac{n^2s^{n-2}}{(1-s^n)^2}\right) \qquad (A8)$$

which is formula 2.

In this paper, the method was applied to birds banded as chicks, and the first few years of recovery had to be excluded. When the recoveries so included are from birds belonging to the n age-classes m to m+n-1, R_i should be replaced by R_{i+m-1}, with everything else being unchanged.

In the present case, only a single row of recoveries was considered, and the method might just as well be called a modified Lack formula. Haldane's more general scheme for incomplete recovery data may be modified for truncation in a similar way.

The by-catch of Thick-billed Murres in salmon drift nets off West Greenland in 1988

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Abstract

The by-catch of Thick-billed Murres *Uria lomvia* in the domestic salmon fishery in West Greenland was surveyed in 1988. Based on interviews with 51 fishermen (of 893 licensees), by-catch rates, fishing effort, and fishing areas for large (>9 m) and small (≤9 m) vessels were determined. Among the large vessels, 56% fished outside the baseline ("offshore," max. 9–10 km), whereas only 12% of the small boats fished in this area. Most (65%) of the fish were landed by small vessels. Fishing effort had two peaks: late August - early September, and early October. Because of a new quota system in 1988, this pattern differs from that of earlier years, when fishing effort was concentrated at the beginning of the salmon season, i.e., before mid-September. Monofilament drift nets set in long chains were the most common gear.

About 1150 murres were reported drowned. Seven of 27 drowned murres were Common Murres *Uria aalge*, probably of local origin. By-catch was almost exclusively observed in the northern part of the fishing area, between Nuuk and Disko Bay. It is estimated that less than 3000 murres were entangled in 1988. This crude estimate is 100 times less than the losses estimated in the early 1970s. The problem has been reduced because large foreign ocean-going vessels were excluded from salmon fishing in Greenlandic waters after 1975, and because the domestic Greenland fleet never shifted significantly towards larger vessels and offshore fishery. Furthermore, the reduced salmon quotas are usually met early in the autumn before the murres approach the coast and enter the fjords.

Résumé

On a étudié les prises accidentelles de Marmettes de Brünnich *Uria lomvia*, dans le cadre de la pêche nationale du saumon de l'Ouest du Groënland, en 1988. On a pu déterminer, d'après les entrevues avec 51 pêcheurs (sur 893 titulaires de permis), les taux de prises accidentelles, l'effort de pêche et les zones de pêche des grands (>9 m) et des petits (≤9 m) bateaux. Une proportion de 56 % des grands bateaux ont pêché en dehors de la limite de base («en haute mer», max. 9–10 km), tandis que seulement 12 % des petits bateaux ont pêché dans cette zone. La grande partie (65 %) du poisson est débarqué par les petits bateaux. L'effort de pêche a connu deux périodes de pointe: fin août/début septembre, et début octobre. Un nouveau système de contingents ayant été introduit en 1988, ces dates diffèrent de celles des années précédentes, alors que l'activité était concentrée au début de la saison de pêche du saumon, soit avant la mi-septembre. L'engin de pêche le plus commun est le filet dérivant en monofilament rattaché à d'autres pour former une longue chaîne.

Les données recueillies font état d'environ 1150 marmettes noyées. Sept d'un groupe de 27 marmettes noyées étaient des Marmettes de Troïl *Uria aalge*, probablement d'origine locale. Les prises accidentelles ont lieu presque exclusivement dans le nord de la zone de pêche, entre Nuuk et Disko Bay. Il semble que moins de 3 000 marmettes se seraient prises dans les filets en 1988. Cette évaluation approximative est cent fois moins grande qu'au début des années soixante-dix. Le problème a diminué à la suite de l'exclusion des grands navires océaniques étrangers de la pêche du saumon dans les eaux du Groënland, après 1975, et parce que la flottille nationale du Groënland ne s'est jamais réorientée véritablement vers les gros bateaux et la pêche hauturière. De plus, les contingents de saumon sont réduits et sont atteints au début de l'automne, avant que les marmettes s'approchent de la côte et entrent dans les fjords.

1. Introduction

In the early 1970s, huge numbers of seabirds, mainly Thick-billed Murres *Uria lomvia*, were killed annually in the intense drift-net fishery for salmon *Salmo salar* off West Greenland. Tull et al. (1972) estimated that 230 000–820 000 murres drowned annually between 1969 and 1971. In a more rigorous study, Christensen and Lear (1977) estimated a by-catch of approximately 200 000 murres in 1972 for the nondomestic fishing fleet. This high gill-net mortality probably contributed to marked declines in the populations of murres in West Greenland (Evans and Waterston 1976; Evans 1984).

The non-Greenlandic (Norwegian, Faroese, and Danish) fishing fleet was phased out by 1975, and that largely eliminated the net-mortality problem (Evans and Waterston 1977). However, it was later predicted that changes in the domestic fishery would lead to an increase in the by-catch of murres off West Greenland (Piatt and Reddin 1984).

Because no fieldwork on the mortality of murres due to net entanglement had been conducted in West Greenland since 1972 (Christensen and Lear 1977), a survey of the seabird by-catch in the domestic salmon fishery was carried out by the authors in 1988. In this paper, we report on the entanglement of murres in fishing nets and estimate the total by-catch in 1988. The domestic salmon fishery as practised in recent years is described in detail to aid in the interpretation of the by-catch data obtained in 1988 and to explain changes in the potential risk of the fishery to the murres.

2. Methods

Fieldwork was conducted during the autumn of 1988 and the winter of 1989. Information on the salmon fishery was obtained from licence and trade statistics from the Greenland Fishing Licence Control Authority (GFLCA). The GFLCA supplied data on salmon quotas distributed in 1988, daily trade of salmon reported from the salmon processors, and fishery development during the 1980s. Throughout this paper, quotas and amounts of salmon landed are given in tonnes.

Inuit place names are used throughout this paper, but readers may be more familiar with the Danish names, which are listed in Appendix 1.

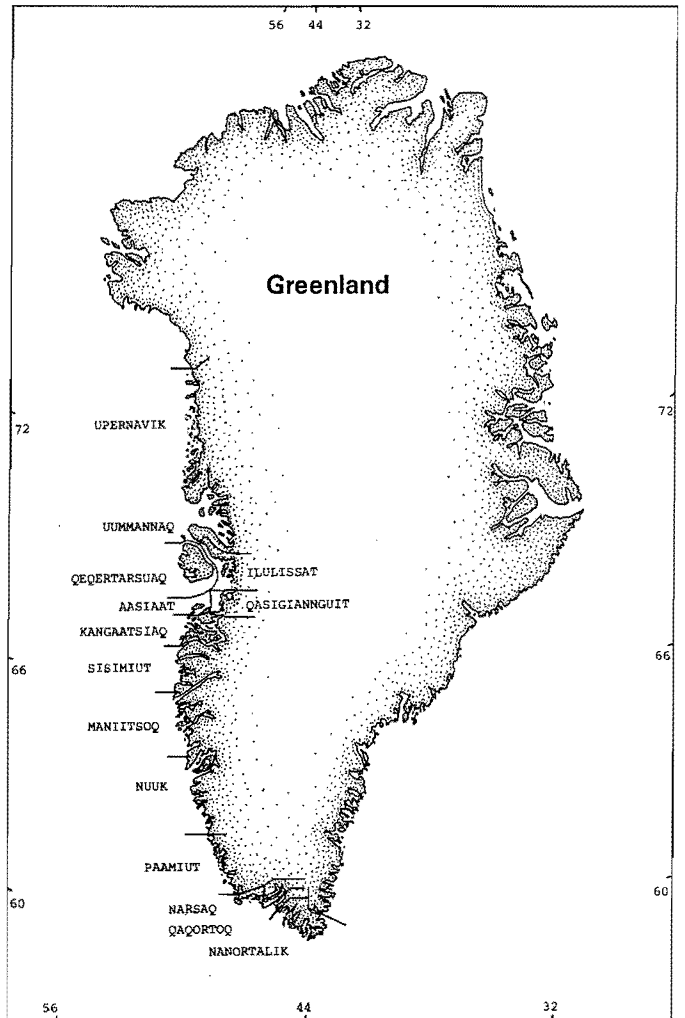
Data on murre by-catch in fishing gear were obtained by interviewing fishermen at fishing wharves or by telephone at the end of the season. With help from a Greenlandic interpreter, we called fishermen in the following districts: Qaqortoq, Paamiut, Nuuk, Maniitsoq, Kangaatsiaq, Sisimiut, Aasiaat, and Qeqertarsuaq (Fig. 1). Fifty-one fishermen supplied information included in this paper. The fishermen were asked to provide details on:
(1) numbers of murres drowned in their nets;
(2) number and length of nets used;
(3) number of fishing days in the periods before (period 1) and after (period 2) 25 September (see Results); and
(4) location of fishing effort inside or outside baseline (cf. Christensen and Lear 1977; in this paper, called "inshore" and "offshore," respectively); fishermen who fished offshore were asked to specify distance from the coast.

The sample of interviewed licensees was biased in favour of those fishermen using larger vessels. To minimize the influence of this bias on the estimate of total by-catch, large- and small-vessel by-catch rates were calculated separately. The term "large" vessels is applied here to boats longer than 9 m, whereas "small" vessels are those ≤9 m long.

On three occasions, we boarded salmon boats to investigate by-catch: JD fished on a 14-m cutter in Paamiut district during 24–25 August, and KF fished from dinghies at Qeqertarsuaq on 5 September and at Nuuk on 4 October. Vessels landing their catch were observed in the harbours of Arsuk (Paamiut district) on 24–26 August, Nuuk on 24–26 August, Maniitsoq on 16–22 October, Sisimiut on 30 August – 4 September, and Qeqertarsuaq on 5–8 September.

Christensen and Lear (1977) and Piatt et al. (1984) estimated total by-catch from the total fishing effort and number of birds caught per unit effort in different areas. In calculating the by-catch in West Greenland, Tull et al. (1972) used the ratio of salmon to murres caught on research vessels. A similar approach is necessary here, and extrapolations are based on data supplied by the interviewed fishermen on murre by-catch rates, fishing effort, catch of salmon per unit effort, and the trade statistics on fish landed in each district and period. Estimates were made by multiplying the murre by-catch rates (birds/net·km·d) by the fishing effort per tonne of salmon (net·km·d/t), by the amount of salmon caught (t), and by the share of the quotas taken by large and small vessels inshore and offshore, respectively. Specific by-catch rates for small and large boats for inshore and offshore fisheries in each of the two fishing periods were applied.

Figure 1
Districts in West Greenland. Greenlandic and Danish names are listed in Appendix 1.



3. Results

3.1. Regulation and timing of the salmon fishery

After 1975, only fishermen living or registered in a Greenlandic community could obtain a licence. Since 1974, the annual salmon quota has been divided into a "free" quota, which all licensees can exploit in free competition, and "local" quotas, reserved for fishermen with small vessels (Table 1). The total quota has been almost halved since foreign vessels were excluded from the salmon fishery in West Greenland in 1975.

Since 1979, there has been an upper limit to the size of vessels allowed to fish salmon, and the legal limit has gradually decreased to the present 50 Gross Register Tonnage (GRT, Table 1).

Since the introduction of an official salmon season in 1975, the opening date has varied between 1 and 25 August, with no clear trend (Table 1).

In 1988, 893 fishermen had a personal or "boat" quota, to be met before 25 September. After that date, the licensees could fish for the remaining local quota in free competition. The largest proportions of quotas in each district (except Narsaq) were distributed among fishermen

Table 1
Summary of regulations for the Greenlandic salmon fishery, 1973–88[a]

Year	Opening date (August)	Maximum size of boat (GRT)	Quotas (t)			
			Local			
			Free	District[b]	Foreign	Total
1973	—	—	1100		852	1952
1974	—	—	1050	50	846	1946
1975	20	—	841	350	731	1922
1976	10	—	900	291		1191
1977	10	—	900	291		1191
1978	10	—	959	232		1191
1979	1	150[c]	959	232		1270
1980	1	150	958	232		1253
1981	25	150	1038	232		1270
1982	25	150	1021	232		1253
1983	10	150	958	232		1190
1984	18	150	638	232		870
1985	1	150	620	232		852
1986	15	80	649	260		909
1987	25	50	533	356		889
1988	25[d]	50	800[e]	104		904

[a] Data are from the Ministry for Greenland and the Greenland Home Rule official regulations.
[b] After the free quota was fished out, only vessels with a total length less than 8–9 m were allowed to continue fishing for the district quotas.
[c] Vessels between 80 and 150 GRT that had shrimp quotas as well were limited to a total salmon catch of 15 t.
[d] Opening date for salmon fishery is 1 August for the three southernmost districts (see Fig. 1).
[e] In 1988, there were no free quotas, just personal quotas to each licensee.

with small vessels, and most of those were outboard-powered dinghies. Overall, about 72% of the personal quotas were given to "small-boat" fishermen, who comprised about 90% of all licensees.

The introduction of "personal" quotas in 1988 resulted in a shift in fishing effort to later in the year (October) and has prolonged the fishing season (Fig. 2). In 1985 and 1986, when the seasons started earlier (Table 1), the fishery ended by late August in some districts and during early September in others (Bøllehus 1986; Thorsøe 1989). In some years, the fishery failed. For example, in 1983 and 1984, only 33% and 26%, respectively, of the total quotas for those years were met. This also prolonged the season, but the later fishing effort was probably minimal (Pedersen 1984).

3.2. Fishing areas and gear

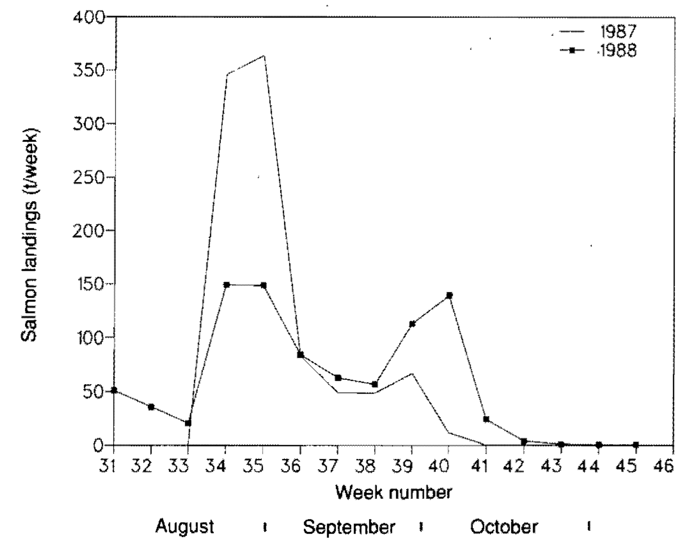
The southern region of the west coast between Maniitsoq and Nanortalik (Fig. 1) is the main salmon fishing area, and 86% of the total catch of salmon in 1988 was taken in this region.

From Paamiut, the composition of the fishing fleet is known: salmon licences were given to 49 outboard-powered dinghies, 14 cutters of 20–22 feet, nine cutters of 23–29 feet, 18 cutters 30 feet long, and 20 vessels longer than 30 feet. Among 362 fishermen from all along the west coast, 65% of the total landings derived from small vessels.

About half (44%) of the interviewed fishermen operating from large vessels fished offshore (Table 2). The remaining large vessels fished within the outer skerries or in fjords, which is also where most small vessels and dinghies fished. In total, 88% of small vessels fished in inshore waters. Offshore fishing was more common in northern areas and usually took place within about 3.5 km of the coast, although a few fishermen fished up to 9–10 km offshore.

A few fishermen used multifilament gill nets, but monofilament nets were much more common. Since 1982, the mesh size has been set at 140 mm stretched length. Most nets had a length of about 30 m (range 15–60 m). For drift-netting, many nets were linked together in a chain. Large vessels used an average of 101 nets (SD = 38, n = 15) per chain, for an average total length of about 2800 m (SD = 1400 m). Small vessels and dinghies used an average of 55 nets (SD = 29, n = 24) totaling about 1850 m (SD = 930 m), excluding six that used single nets fixed to the shore.

Figure 2
Landings of salmon in the West Greenland fishery, 1987 and 1988. In the three southernmost districts (Fig. 1), the season opened 1 August 1988 (Table 1). The year 1987 represents a "normal" year in which fishing effort is concentrated in the beginning of the season. The year 1988 differs because of the introduction of personal quotas.



3.3. Reported murre by-catch

The fishermen we interviewed reported a total of 848 murres drowned during the entire salmon fishing season in 1988. Only two vessels reported catching more than 100 birds (Table 3), but we know of one other vessel that caught about 300 birds, giving a total known by-catch of about 1150 birds. In South Greenland, by-catch was minimal: only one large vessel in Paamiut reported 30 murres, and no birds were reported taken in the three southernmost districts by the two interviewed fishermen. Other sources confirmed the absence of birds on salmon vessels in southern districts.

During our visits to fishing harbours, we saw only 27 drowned murres: eight in Sisimiut at the beginning of the salmon season, and 19 in Nuuk in early October. Seven of the 27 observed drowned murres were Common Murres *Uria aalge*. Except for two Common Eiders *Somateria mollissima*, no other species were observed entangled, but some fishermen reported that nets fixed to the shore caught Black Guillemots *Cepphus grylle* foraging along the coastline.

All of the "major" incidents of net entanglement occurred in the two northernmost of the important salmon fishing districts — Maniitsoq and Sisimiut. Two-thirds of the birds were caught offshore (Table 3). The murres caught inshore derived mainly from a single vessel from Sisimiut, which caught 200 birds in October. Calculated by-catch rates were thus low. For those by-catch incidents for which we have data on timing, the number of murres caught per unit effort was higher after 25 September and was especially high for the large vessels fishing offshore (Table 4).

Table 2
Numbers and proportions of salmon licensees interviewed, in relation to boat size and distance from shore[a]

Boat size/ fishing zone	District QAQ	PAM	NUK	MAN	SIS	QEQ	Total
Boats > 9 m							
Inshore							
No.	1	5	2	2	0	0	10
%	100	100	67	33	—	—	56
Offshore							
No.	0	0	1	4	3	0	8
%	—	—	33	67	100	—	44
Boats ≤ 9 m							
Inshore							
No.	1	8	4	11	3	1	28
%	100	100	80	100	100	25	88
Offshore							
No.	0	0	1	0	0	3	4
%	—	—	20	—	—	75	13

[a] For district abbreviations, see Appendix 1.

Table 3
By-catch of murres reported by fishermen in West Greenland, 1988

District	No. of licensees: Inter-viewed	No. of licensees: Reporting by-catch	% of licensees reporting by-catch	No. of murres in by-catch: Offshore	Inshore	Total	% of total murres in by-catch
QAQ	2	0	0.0	0	0	0	—
PAM	13	1	7.7	30	0	30	3.5
NUK	8	3	37.5	50	20	70	8.3
MAN	19	7	36.8	430	48	478	56.4
SIS	6	4	66.7	18	200	218	25.7
QEQ	3	2	66.7	52	0	52	6.1
Total	51	17	33.3	580	268	848	100.0

Table 4
By-catch rates of murres (murres/net·km·d)

Boat size/ fishing zone	Period 1	Period 2
Boats > 9 m		
Offshore	0.65	6.48
Inshore	0.15	0
Boats ≤ 9 m		
Offshore	NA[a]	NA
Inshore	0.23	0.90

[a]NA = not applicable.

Table 5
Total estimated by-catch of murres in West Greenland, 1988[a]

District/ fishing zone	Estimated murre by-catch: Period 1	Period 2	Total
PAM			
Offshore			0
Inshore			30
NUK			
Offshore	21	72	93
Inshore	143	192	335
MAN			
Offshore	30	190	220
Inshore	380	947	1327
SIS			
Offshore	50	162	212
Inshore	116	148	264
QEQ			
Offshore			300
Inshore			0
Total	740	1711	2780

[a] Based on by-catch rates (Table 4) and proportion of quotas fished inshore and offshore by large and small vessels in each period and area, respectively.

3.4. Estimated total murre mortality

Because most murre by-catch occurred in Nuuk, Maniitsoq, and Sisimiut districts, only these areas are included in the extrapolation. In those districts, about 2500 murres were drowned in salmon gill nets in 1988 (Table 5). The sample of interviewed fishermen in Paamiut and Qeqertarsuaq is too small to warrant extrapolation, but the data from Qeqertarsuaq suggest that about 300 birds were drowned west of the island Disko.

4. Discussion

Among the few drowned birds observed, a rather large proportion (7/27) were Common Murres, all recorded in Sisimiut in late August. We believe this is fortuitous, as only about 0.1% of murres identified on ship surveys along West Greenland during September were Common Murres (Falk and Durinck 1989). In the offshore by-catch survey in 1972, only two of 926 identified murres were Common Murres (Christensen and Lear 1977).

The presence of Common Murres may give a hint about the origin of the birds drowned in the early salmon fishery season. In Greenland, the Common Murre breeds only in small numbers near Maniitsoq and Paamiut, and murres (both species) from those colonies may be vulnerable as they move northwards along the coast, after leaving the cliffs just before the salmon fishery starts. At present, net entanglement may be a greater problem to the small Greenlandic population of the Common Murre than to the Thick-billed Murre.

Besides this information, we obtained no clues on the origin of the drowned murres that can update the summary by Evans and Nettleship (1985).

In some areas, stationary nets at skerries and along shores may take some Black Guillemots, as pointed out by Christensen and Lear (1977). Our fieldwork focused on the murres and did not intend to quantify all seabird mortality. Our conclusions relate only to Thick-billed Murres.

Because of our limited data on fishing and by-catch rates, the by-catch estimate determines only the order of magnitude of the problem. Our evidence indicates that a reduction in murre by-catch by two orders of magnitude, from 10^5 to 10^3 murres, has occurred in Greenlandic waters since the early 1970s. It might be suspected that fishermen underreported by-catches because they considered it prudent not to emphasize the problem. However, most fishermen seemed open to the issue, and, in a few cases where double-checking was possible, their by-catch reports were generally confirmed. Furthermore, our observations in the harbours revealed few drowned birds, and we saw none in the nets we helped to haul.

Other anecdotal information supports our conclusion. In Nuuk, many of the large foreign salmon boats used to have a number of special metal forks installed on the deck to which the murres were attached while they were being disentangled from the nets. Today, no vessels have similar gear. Residents of Sisimiut and Qeqertarsuaq informed us that in the early 1970s, truckloads of drowned murres were fed to the numerous sled dogs, whereas in recent years only birds shot for human consumption have been obtainable at high prices in local markets.

What accounts for the dramatic decline in by-catch over the last 20 years? The main factor appears to be the very reduced fishing activity in offshore waters. Further, owing to reduced quotas, the fishery stops earlier in the autumn, although the 1988 season was a slight exception because of the new quota system. Even in years with late opening dates, the fishing effort has been concentrated in August and early September. At that time, most murres are offshore and have not yet entered inshore waters where most salmon are caught. This is consistent with the conclusion of Piatt and Reddin (1984) who, based on the data from Christensen and Lear (1977), considered the timing of the season to be "probably the most significant (change in domestic fishery) in terms of murre net-mortality." In the southernmost districts, few birds occur offshore even in late September (Falk and Durinck 1989), as the murres from East Greenland and the Northeast Atlantic have not yet reached their wintering quarters (Kampp 1988b).

Besides time shift of fishing effort, Piatt and Reddin (1984) listed a number of changes in the domestic fishery that could lead to an increased murre by-catch:

(1) a shift from multifilament nets set in fjords and nearshore to monofilament nets set inshore as well as offshore;
(2) a shift from small "open boat" fishing vessels to many mid-sized and some large ocean-going vessels;
(3) a shift from daylight fishing to day and night fishing; and
(4) a northward displacement of fishery instead of a fishing effort widely distributed along the coast.

Below we will address each of these four points.

(1) *Shift to monofilament nets* — Light-coloured monofilament nets certainly are the most common gear used today. However, because the murres and the salmon drift-net fishery generally have become separated in time and space since the mid-1970s (see below), the shift in fishing gear towards monofilament nets does not seem to have had the negative effect that had been expected, although these effects are known from other areas, such as the North Pacific, coastal California, and Newfoundland (Piatt et al. 1984; Evans and Nettleship 1985; Atkins and Heinemann 1987; Piatt and Nettleship 1987). Further, "ghost nets" are unlikely to cause many problems because fishermen have to keep a relatively close watch on nets set in coastal waters.

(2) *Shift to larger vessels* — In accordance with legislation, large vessels were allowed to fish salmon until recently. However, few large Greenlandic vessels ever participated in the fishery. In 1981, 1982, and 1983, vessels of more than 80 GRT took less than 2% of the total catch each year. Therefore, the reduced maximum size of vessels set by regulations has not significantly altered the composition of the domestic fishing fleet (Pedersen 1983; Thorsøe 1989). It is unknown to what extent small cutters have replaced dinghies since the 1970s, but most boats are still small cutters and dinghies.

(3) *Shift to day and night fishing* — The vessels operating offshore in large fjords and bays usually fish overnight. However, most fishermen still fish inshore, so there is no reason to suspect that day and night fishing has become significantly more widespread in the domestic fishery than previously.

(4) *Northward displacement of fishery* — Based mainly on data from 1973 and 1979, when 67% and 29% of the salmon, respectively, was landed south of Nuuk, Piatt and Reddin (1984) concluded that fishing effort had shifted considerably northward, which is significant in terms of murre net entanglement. In the years between 1985 and 1988, 51%, 56%, 59%, and 62%, respectively, of the salmon was landed in Nuuk and southwards. One exception was the very bad salmon season of 1984, when only 27% of salmon was landed south of Nuuk. In general, however, the southern and central part of the west coast is the main fishing area. From Sisimiut northwards, the small quotas are rarely met.

Fortunately, most of the predictions made by Piatt and Reddin (1984) did not materialize. Although the domestic fishery did change in some respects, the anticipated expansion to an offshore, large-vessel fishery has not occurred, and, consequently, the by-catch of murres in gill nets is at present a relatively minor source of mortality. The observed by-catch is minimal compared with that in other areas. For example, off eastern Newfoundland, more than 22 000 murres, mostly Common Murres, were estimated drowned annually in fishing gear between 1981 and 1984 (Piatt and Nettleship 1987). Our estimated mortality from net entanglement is almost negligible compared with the numbers that are currently harvested in the intensive winter hunt along the West Greenland and Newfoundland coasts (Elliot 1987; Falk and Durinck 1990).

It appears that the regulations for the 1988 fishery were an experiment, because the personal quotas were abandoned for 1989 and 1990. This switched peak fishing effort back to the start of the season. As the salmon is a resource reserved for the small fishermen, most of the fishing probably will continue to take place in inshore waters. If fishing regulations ensure that the season is not shifted towards a later date, we expect that net entanglement will not become a serious source of mortality for Thick-billed Murres.

Acknowledgements

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Appendix 1
Greenlandic and Danish geographic names and their abbreviations used in the tables

Greenlandic name	Abbreviation	Danish name
Nanortalik		Nanortalik
Qaqortoq	QAQ	Julianehåb
Narsaq		Narsaq
Arsuk		Arsuk
Paamiut	PAM	Frederikshåb
Nuuk	NUK	Godthåb
Maniitsoq	MAN	Sukkertoppen
Sisimiut	SIS	Holsteinsborg
Kangaatsiaq		Kangaatsiaq
Aasiaat		Egedesminde
Qasigiannguit		Christianshåb
Ilulissat		Jakobshavn
Qeqertarsuaq	QEQ	Godhavn
Uummannaq		Umanak
Upernavik		Upernavik

The management of the Newfoundland turr hunt

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Abstract

Thick-billed Murres *Uria lomvia*, known locally as turrs, are harvested during the late fall and winter in coastal waters of Newfoundland by hunters in small boats powered by outboard motors. The hunt was historically a valuable subsistence source of winter meat and remains an important winter activity. Present regulations that limit the season to seven months but do not restrict the daily harvest permitted the development of substantial illegal commercial sale. Harvest levels apparently increased until the 1980s as hunting equipment and access improved, and current harvest estimates of between 600 000 and 900 000 birds appear to exceed the sustainable yield. Although population declines have occurred at Greenland colonies affected by additional summer hunting, recent decreases have not been confirmed at major Canadian colonies. A public information program explaining the numbers, sources, and reproductive characteristics of the murres has resulted in widespread support among Newfoundland hunters for practical harvest restrictions, such as daily and season bag limits and shorter open seasons. Enforcement agencies and wildlife conservation groups also back the need for effective controls to be developed with input from concerned parties.

Résumé

La Marmette de Brünnich *Uria lomvia* est chassée, vers la fin de l'automne et en hiver, dans les eaux côtières de Terre-Neuve à partir de petites embarcations munies de moteurs hors-bord. Historiquement, la chasse était une importante source de subsistance pendant l'hiver et elle demeure une importante activité de cette saison. Le règlement actuel, qui restreint la saison de chasse à sept mois, sans toutefois limiter les prises quotidiennes, a permis l'établissement d'un important commerce illégal. Les niveaux de captures ont augmenté apparemment jusqu'aux années quatre-vingt, grâce à l'amélioration du matériel de chasse et de l'accès, et les prises actuelles, qui seraient de l'ordre de 600 000 à 900 000 oiseaux, semblent dépasser le rendement soutenu. Bien que les populations de certaines colonies du Groënland où la chasse est aussi autorisée en été aient diminué, on n'a pas confirmé de baisse récente des principales colonies canadiennes. Un programme d'information publique, décrivant le nombre, les sources et les caractéristiques de reproduction des marmettes a suscité chez les chasseurs de Terre-Neuve un soutien général aux restrictions pratiques de la chasse, telles que les limites de prises quotidiennes et saisonnières et le raccourcissement des saisons de chasse. Les organismes d'application des règlements et les groupes de conservation de la faune sont aussi en faveur de la mise en place de moyens de contrôle efficaces avec la participation des parties concernées.

1. Introduction

Large numbers of murres, locally called turrs, are traditionally harvested for winter food from small boats in Newfoundland's coastal waters. Their winter distribution is primarily affected by the movements of pack ice and the availability of food (Elliot et al. 1990). Most birds shot are Thick-billed Murres *Uria lomvia* (known locally as Arctic or northern turrs), although smaller numbers of Common Murres *U. aalge* (Newfoundland turrs, murres, or Baccalieu birds) are also taken. I refer to populations of murres and harvests of turrs in keeping with the terminology used by the people primarily concerned with the birds — the biologists and hunters, respectively.

Most hunters leave small outport communities at dawn, in crews of two or three men, one of whom drives while the others shoot. They encounter murres in loose flocks that collect to feed on small fish or crustaceans (Elliot et al. 1990). Hunters shoot most birds on the surface of the water and pick them up with dip nets. They spend the afternoon or evening in a shed or basement, "picking" (plucking) or skinning the birds, cleaning them, and dividing up the harvest among the crew. The turrs are usually gutted and the feathers removed after loosening in boiling water. Most turrs are either consumed fresh by the hunter's family or frozen for later use, although some are illegally sold.

Although the hunting season extends from September to March inclusive, murres are present in appreciable numbers only for two or three months in most areas. Turrs are taken in Labrador in October–November, along the Northern Peninsula of Newfoundland and Notre Dame Bay in November–December, from Bonavista Bay to the Avalon Peninsula in January–March, and from about December to February along the south coast (Fig. 1).

The long season and a lack of other harvest restrictions reflect the present classification of murres as nongame birds under the Migratory Birds Convention. However, current harvest levels appear to be close to the sustainable yields of the populations (Nettleship and

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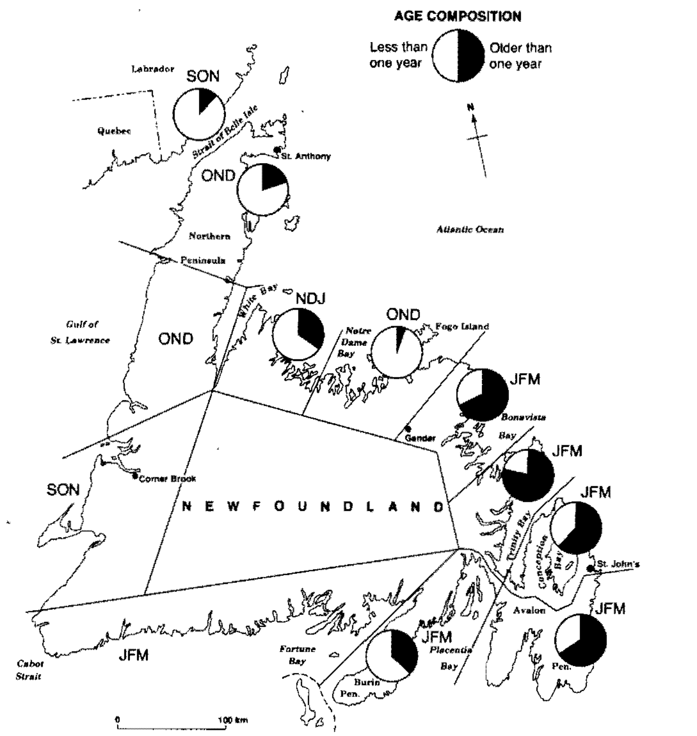
Figure 1
Map of Newfoundland showing the three main hunting months for each of 12 zones based on harvest survey results (O = October, N = November, D = December, J = January, F = February, M = March) and the proportion of first-year birds and older birds in the harvest of Thick-billed Murres from nine zones in 1984-85 (n = 660) and 1985-86 (n = 550) combined (Elliot 1989)



Chardine 1989), and new regulations are being considered to reduce the annual kill. This paper discusses the historical background and cultural role of the turr hunt, the characteristics of the hunt, and its effects on murre populations, all of which must be considered in managing the harvest.

2. The history of Newfoundland turr hunting and management

2.1. Prior to Confederation with Canada in 1949

Newfoundlanders traditionally harvested a variety of seabirds, including Common Murres, Black-legged Kittiwakes *Rissa tridactyla*, and Atlantic Puffins *Fratercula arctica* from local colonies, Sooty Shearwaters *Puffinus griseus* and Greater Shearwaters *P. gravis* when fishing inshore and on the Grand Banks, and Thick-billed Murres along with smaller numbers of Common Murres, Black Guillemots *Cepphus grylle*, Razorbills *Alca torda*, puffins, and Dovekies *Alle alle* during the winter months (Montevecchi and Tuck 1987). These were part of an annual cycle of harvest of wild food, along with waterfowl, caribou, hares, seals, and fish. The hunting of seabirds was legal, with some restrictions, until Newfoundland joined Canada in 1949 (Montevecchi and Tuck 1987), and murres and their eggs were specifically protected from 1 June to 31 August (Tuck 1953).

In most outport communities, Thick-billed Murres were a staple for two or three months in late fall or winter because of their large size (about 1 kg) and relative abundance when other meat was scarce. The turr harvest was relatively low in areas where large sea ducks, such as Common Eiders *Somateria mollissima*, were available (Tuck 1953). Where turrs were plentiful, they were sometimes used as food for sled dogs and bait for codfish.

As recently as the early 1940s, turrs were harvested by fishermen who rowed out in small wooden boats. These trips often lasted most of the day, with risks to the hunter of being caught by shifting pack ice or changes in weather. However, older hunters who used these techniques suggest that the birds then fed closer to land, often within several hundred metres of the shore, so that the distances that hunters traveled were usually shorter than today.

Motorboats powered by two-cycle motors became common in the mid-1940s and had largely supplanted the smaller hand-rowed dories by the early 1950s (Tuck 1953). Four men usually hunted from each boat as a community activity. Although slow in comparison with today's boats, they were faster than rowing or sailing boats and very reliable, and they extended the turr hunter's range and harvesting capacity.

Prior to the 1960s, most turrs were killed with large muzzle-loading shotguns. Although reports of many birds being killed in one shot are common, it is likely that few shots were fired on each trip. The number of turrs taken was limited by such factors as the time needed to locate and approach feeding birds and collect the shot turrs from the water. Most older hunters say they averaged 15–30 birds per boat on a successful day and that kills of over 100 turrs were rare, although this varied among regions.

Tuck (1953) quoted newspaper articles to indicate the extent of the daily kill. Some examples: extraordinary numbers on the northeast coast with up to 150 per day (14 December 1945); 400 on one expedition from Wesleyville (13 February 1947); up to 1000 per boat during the fall shooting in Notre Dame Bay (16 January 1948); plentiful with up to 30–48 per trip near Nipper's Harbour (19 December 1951); fairly good supplies in Conception Bay, with two boats bagging 40 per day (9 April 1952); and Tuck's observations of 64 men in 18 boats shooting an average of 23 birds per boat from Hants Harbour on 28 March 1952.

Although some turrs were cooked fresh, most were preserved in a brine solution, by cooking and bottling in glass jars, or by freezing in a shed, a snowbank, or the open air. Preservation meant turrs could be consumed beyond the period that birds were present and could be accumulated for sale. Salted and canned turrs were sold legally and supported a minor canning industry, with one company selling up to 300 cases of Newfoundland turr annually, representing about 15 000 murres (Tuck 1953). Turrs were customarily bartered for other food or services within communities, and some were sold to those who were unable to hunt.

The relative isolation of most outports on the northeast coast because of winter ice suggests that the number of birds sold may have been relatively small in the first half of this century, before winter road connections had been established. However, Tuck (1953) reported an instance in 1947 of 8000 turrs shipped to large settlements by steamer to sell for 50 cents each, and he estimated that up to 50 000 were sold annually this way.

2.2. The effects of Newfoundland joining Canada: 1949–56

On 1 April 1949, Newfoundland became the 10th Canadian province and subject to the restrictions of the Migratory Birds Convention Act (MBCA) enacted in 1917. The Act implemented the Migratory Birds Convention agreed between the United States and Canada in 1916 to conserve populations of birds shared between the two countries. It prohibited the hunting of murres, which it classified as migratory nongame birds, except by native people.

Continued access to the turr harvest by Newfoundlanders was not a condition of entering Confederation, and the change in the status of murres was not discussed prior to the union (Higgins, in Hansard 1951:1241). L.M. Tuck, the first federal wildlife biologist in Newfoundland, stated in November 1949 that MBCA regulations prohibiting the shooting of turrs would not be enforced "for the present," although the sale of turrs and the hunting of other nongame seabirds would be prohibited (*St. John's Evening Telegram*, 8 November 1949). Murres were apparently singled out because they were the most valued group in providing fresh meat in the winter when it was most needed.

Turr-hunting privileges were to be removed in southern Newfoundland beginning with the 1950-51 season (*St. John's Daily News*, 20 October 1950). This area, which contained most of the large communities, had little winter ice and thus had access to steamship service and fishing in winter. The hunt was to stop around the northeastern part of the island the next year. This plan resulted in much anger, little compliance among hunters, and an intensive petitioning campaign with over 15 000 signatures (Hansard 1951:1244). An unsuccessful motion was presented in the Canadian House of Commons in March 1951 to amend the MBCA to permit the taking of seabirds in Newfoundland (Hansard 1951). Arguments centred on the need of rural Newfoundlanders to hunt turrs for winter meat. Most hunters assumed that murre populations could not be hurt because their numbers were so great. As a result of the campaign, the prohibition of the hunting of murres was not enforced pending further study (*St. John's Daily News*, 22 June 1951).

Tuck set out to investigate the hunt, and the biology, distribution, and population size of the murres, to provide information on which regulations could be based. He concluded that almost all turrs harvested were Thick-billed Murres, and that the United States had little at stake in the management of the hunt, as few wintered south of Nova Scotia (e.g., Tuck 1953). He later showed that breeding numbers were high at the Arctic colonies he visited, including Akpatok Island, Digges Island, and Cape Hay (e.g., Tuck 1955, 1957). He estimated an annual Newfoundland harvest of about 200 000 birds in the early 1950s, from about 5 million wintering off Newfoundland (Tuck 1953, 1961). This would have been within the sustainable yield of the population of Thick-billed Murres in the eastern Canadian Arctic and western Greenland, then estimated at 10 million individuals (Tuck 1961).

As a result of Tuck's work and continued pressure from rural Newfoundlanders, an agreement was reached to authorize subsistence hunting of murres. A federal order-in-council passed on 29 November 1956 specified that residents of Newfoundland and Labrador could hunt turrs if they resided and hunted in rural areas, if they were "in need," and if they took them for human food only and did not offer them for sale, between 1 September and 31 March inclusive. This gave protection to breeding birds and set the guidelines for the hunt as it is today.

2.3. Changes since 1956

The requirement to demonstrate "need" was removed by the late 1950s, and the restriction to rural areas was removed in 1969, thus enabling all Newfoundland residents to hunt turrs. As murres were still technically nongame birds, turr hunters were not required to purchase the Migratory Game Bird Hunting (MGBH) Permit when it was introduced in 1966. This exception has since made it difficult to monitor the turr harvest.

The equipment used to hunt turrs has improved steadily since 1949. By the early 1970s, motorboats were largely replaced by 4.5- to 6-m wooden speedboats powered by 10- to 30-horsepower outboard motors, with advantages of increased range and speed. Many of these were replaced in the mid-1980s by larger 5.5- to 6.5-m fibreglass speedboats with more powerful 30- to 50-horsepower motors. These boats can operate almost unimpeded through thin slob or new ice and can travel up to 50 km from the home port in search of turrs. In calm water conditions, hunters can now travel almost as fast as turrs can fly.

The ammunition and guns used to hunt turrs have also improved. By the early 1950s, shotguns were used with inexpensive homemade cartridges that made loading much easier (Tuck 1953). The plastic shells available since the 1970s have resulted in versatile water-resistant ammunition well suited for use in open boats. Most hunters now use pump-action or semiautomatic shotguns and, as they are not restricted to the game bird maximum of three shells at a time, often have five shells ready to fire.

The subsistence need that had formed the basis of the argument to maintain the hunt became less important through the 1970s. All-weather roads now connect all but a dozen or so Newfoundland communities. Thus, alternatives to eating turr meat exist, and, as all families have access to at least unemployment or welfare benefits, they can buy adequate food in local stores. The costs of hunting trips have increased so much that turrs are seldom the cheapest meat available, after considering expenses for gasoline, shotgun shells, and equipment maintenance. The subsistence value of wild game is greater in southern Labrador, but turrs play a minor role there in comparison with other game (Northland Associates Ltd. 1986).

However, turrs are sought after as preferred meat and still contribute significant amounts of high-quality protein to the diets of many rural Newfoundlanders. The hunt also has an important cultural and social role in maintaining traditional links with the sea. It remains an important winter activity, eagerly anticipated by many Newfoundland men.

Some Newfoundlanders have come to rely on turrs as a source of revenue, and illegal selling has become big business in some outports. Although local bartering and selling continue, most turrs are sold now to people from large communities and cities. The resettlement of isolated outports in the 1960s and the movement of people to cities in search of jobs have created an urban market of people with money but little opportunity to hunt. Many obtain turrs from family members in outports, whereas others visit coastal communities especially to buy turrs. Turrs are also shipped directly to the major towns and cities for sale.

Although it is well known that selling is illegal, sellers defend it as a traditional way to supply those who are unable to get birds themselves. They ignore the volume of birds sold and are reluctant to believe the consequent effects on murre populations. They now fear that impending harvest restrictions will adversely affect their activities.

The present magnitude of selling is difficult to determine because of its illegal nature. However, some hunters admit to selling 1000–2000 turrs a year. At many community meetings I presented my estimate that one-third of all turrs shot are sold, and the only serious argument from hunters was that in some outposts this was too low.

3. Current harvest characteristics and trends

3.1. The species of concern

The conservation of Thick-billed Murres is of primary concern, although Common Murres are also hunted in Newfoundland. Tuck (1953) estimated that Common Murres made up about 2% of the kill in the early 1950s, and they now comprise about 5% of the harvest (Elliot 1987, 1989). Field observations, particularly in 1984-85 and 1985-86, indicated that proportions of Common Murres were highest in harvests in northern areas in October and November (up to about 15%) and through the winter along the south coast (up to 30%) (Elliot 1985, 1986). Few Common Murres are taken during the peak of the season in major hunting areas, such as Bonavista Bay.

In the fall, hunters who can identify Common Murres avoid them, as they are likely to be moulting. However, the relative harvest primarily reflects the availability of the two species, as Common Murres generally winter farther south (Tuck 1961; Brown 1986). Band returns suggest that many of those shot come from only a few large or northern colonies, such as Funk Island or the Gannet Islands, although insufficient banding has been done to confirm this.

Canadian Wildlife Service surveys show that Common Murre breeding numbers have increased dramatically at major Canadian colonies, such as Witless Bay (77 000 pairs in 1979) and Funk Island (396 000 pairs in 1972), especially since about 1940 (Nettleship and Evans 1985; D.N. Nettleship, pers. commun.). This is despite large numbers being killed annually in fishing nets (Piatt et al. 1984) and by oil at sea (Piatt et al. 1985). Consequently, the following sections address the management of Thick-billed Murre populations only.

Small numbers of other seabirds are still taken illegally by turr hunters (Gaston et al. 1984). Although difficult to assess, I estimate that the overall numbers are less than 5% of the turr harvest. Different species are favoured in different areas — e.g., guillemots in southern Labrador, puffins in the Northern Peninsula and Notre Dame Bay, Dovekies in the Northern and Avalon peninsulas, and kittiwakes in Bonavista Bay. The numbers killed are probably not high enough to affect most populations. However, Razorbills are taken unintentionally wherever they overwinter, as they are difficult to distinguish from murres. This harvest could affect the small Canadian population if Razorbills from certain colonies make up a large proportion of those killed.

3.2. The magnitude of the Newfoundland turr harvest

The Canadian Wildlife Service conducted eight mailed questionnaire surveys of murre hunters holding MGBH Permits from 1977-78 to 1987-88 (Wendt and Cooch 1984; Elliot et al., this volume).Their results indicate that about 300 000-725 000 Thick-billed Murres were shot annually by permit holders, with no overall upward or downward trend.

Preliminary surveys in 1985-86 and 1987-88, to account for the harvest by murre hunters who do not purchase permits, suggest that the total harvest may be about double that by permit holders. This does not include estimates for crippling losses, which are difficult to estimate but may be in the order of 5-10%. Revised surveys that more accurately estimate the harvest by hunters without permits are needed to confirm these overall harvest levels. An index of harvest per unit effort did not indicate clear trends in the availability of murres (Elliot et al., this volume).

Changes in harvest levels prior to the survey period are difficult to evaluate. Tuck (1961:214-215) stated that "it was estimated in 1949 that approximately 200,000 murres were shot annually for food in Newfoundland. In consequence of a more favourable economic situation since confederation with Canada, only half that number are now shot annually." The level of 200 000 was probably based on an estimate of 202 000 that Tuck derived for the 1951-52 season from discussions, educated guesses, and interviews, aggregated from estimates for 15 districts (Tuck 1953). Tuck's second estimate was interpreted by Inder and Gillespie (1974) to refer to years just prior to 1959.

The only subsequent harvest estimate was for 1960-61, when murres were included on the list sampled from provincial small game licence stubs; Inder and Gillespie (1974) estimated that 82 000 turrs were killed in Newfoundland in that season. I believe that they greatly underestimated the harvest, as many turr hunters would not have been sampled by their methods, and the survey response rate was low. All estimates prior to 1977-78 may be low, as band return data suggest no increase in harvest level since the 1950s, assuming that the likelihood of hunters reporting banded birds has not changed (A.J. Gaston, pers. commun.). It is significant that all previous estimates were well below both the unadjusted and adjusted estimates from recent surveys.

The levels of Thick-billed Murre mortality from hunting must be considered in comparison with other causes of death, even though these are much harder to estimate. The number shot in Newfoundland is in the order of three times the total that die from oil pollution, Greenland and Inuit hunting, gill-netting, predation, and other natural sources (Table 1). Despite the great uncertainty in these estimates, it is evident that reducing the turr harvest could greatly lower annual mortality.

3.3. Age structure of the turr harvest

First-year murres can be separated from older birds by the degree of development of superorbital ridges on the skull (Gaston 1984) and by four measurements of bill and skull (Elliot and Gaston 1986). Thick-billed Murres less than one year old made up about 53% of samples of Thick-billed Murres harvested in 1984-85 and 1985-86 (n = 1261) (Elliot and Gaston 1986). First-year birds predominated in northern areas before 1 January, and older birds predominated in harvests from areas in the southeast later in the season (Fig. 1). The inexperienced young birds are apparently at greater risk of being harvested; they may winter close to the coast in higher proportions than do older murres, as first-year birds probably make up less than 20% of the murres present off Newfoundland (Table 2).

4. Effects of the harvest on Thick-billed Murre populations

4.1. Current estimates of Thick-billed Murre colony sizes

Banding recoveries in Newfoundland suggest that most harvested Thick-billed Murres come from colonies in northeastern Canada, with smaller numbers from West Greenland (Tuck 1961; Gaston 1980; Kampp 1982, 1988b).

Table 1
Estimated annual levels of mortality, from major sources, of approximately 5 000 000 Thick-billed Murres that winter off Newfoundland[a]

Source	Approximate level of mortality (%)	Main reference
Oil pollution	50 000 (<10%)	Piatt et al. 1985
Hunters in West Greenland	50 000 (<10%)	Evans and Kampp, this volume
Inuit hunters in Canada	5 000 (<1%)	Gaston et al. 1985
Greenland gill nets	5 000 (<1%)	Falk and Durinck, this volume
Predation of adults	10 000 (<5%)	Gaston et al. 1985
Other natural mortality	50 000 (<10%)	Estimated for this study
Newfoundland hunters	800 000 (>75%)	Elliot et al., this volume
Total[b]	1 000 000	

[a] These rough estimates have been derived in different ways, using data from these references and other sources, and may not be more accurate than to order of magnitude.
[b] This is in addition to a rough estimate that about 300 000 juveniles (25%) die of natural causes soon after leaving their colonies and before reaching Newfoundland.

Table 2
Calculations of the number of individual Thick-billed Murres arriving through the fall to winter off the coast of Newfoundland, assuming that 25% of chicks die before reaching Newfoundland[a]

Age	Calculation	No.[b] leaving colonies	No.[b] reaching Newfoundland
Hudson Strait, Minarets, and Labrador (all murres of all ages)			
Year 1	1030 × 70% (fledging rate)	721	541
Year 2-4	2060 × 40%	824	824
Year 5+	1030 (pairs in colonies) × 2	2060	2060
			3425
Lancaster Sound (75% of murres of all ages)			
Year 1	406 × 70% (fledging rate)	284	213
Year 2-4	812 × 40%	325	244
Year 5+	406 (pairs in colonies) × 2	812	609
			1066
West Greenland (50% of murres of all ages)			
Year 1	410 × 70% (fledging rate)	287	144
Year 2-4	820 × 40%	328	164
Year 5+	410 (pairs in colonies) × 2	820	410
			718

Newfoundland age distribution		**Proportion from main breeding areas**	
Year 1	898 (17%)	Hudson Strait, Minarets, and Labrador	66%
Year 2-4	1232 (24%)	Lancaster Sound	20%
Year 5+	3079 (59%)	West Greenland	14%
	5209		

[a] Colony sizes are from Nettleship and Evans (1985), A.J. Gaston (pers. commun.), and Evans and Kampp (this volume), and the proportions of each age-group are based on Gaston (1980) and Kampp (1988b, and this volume).
[b] All numbers refer to thousands of birds.

The most recent colony surveys indicate that about 1 440 000 pairs breed in the eastern Canadian Arctic and Labrador (Nettleship and Evans 1985; A.J. Gaston, pers. commun.) and 410 000 pairs breed in West Greenland (Evans and Kampp, this volume). More precise photo surveys and ground-truthing have resulted recently in higher population estimates for colonies such as Akpatok Island (Chapdelaine et al. 1986), and these may be needed at several other colonies to determine whether past estimates were low.

The estimate of 1 850 000 pairs is the equivalent of about 3 700 000 breeders, plus 1 470 000 subadult non-breeders and 1 290 000 juvenile murres in late summer, for a total of about 6 450 000 birds. This assumes that the average age of first successful breeding is five years (Noble et al., this volume).

4.2. The numbers and sources of murres wintering off Newfoundland

About 5 million Thick-billed Murres are probably present at some time during the winter in coastal or offshore Newfoundland waters (Table 2). Only about 17% of these are first-year birds, and 60% are of breeding age of more than five years. This assumes that 25% of chicks that fledge die before reaching Newfoundland. The estimate of 60% calculated by Gaston and Nettleship (1981) has been rejected, as it was based on unsound assumptions (A.J. Gaston, pers. commun.), and more research is needed to determine the actual proportion.

I estimate that about two-thirds of all Thick-billed Murres that currently winter off Newfoundland are from Canadian low-Arctic colonies in Hudson Strait, the Minarets (Reid Bay), and Labrador, 20% are from high-Arctic colonies in Lancaster Sound, and only about 14% are from West Greenland.

Band recoveries in Newfoundland indicate that most of the murres from Hudson Strait and the Canadian low Arctic are harvested from December to March. Those from the Canadian high Arctic and West Greenland are apparently harvested over a longer period, from October to March (A.J. Gaston, pers. commun.). About 40 000 pairs of Thick-billed Murres from Labrador and Newfoundland colonies probably all overwinter in Newfoundland waters.

One Thick-billed Murre shot in Bonavista Bay in January 1986 had been banded as a breeding adult in Iceland in 1983 (pers. obs.), and a second one found oiled on Miquelon in March 1990 had been banded as a breeding adult in Iceland the preceding year (Etcheberry 1990). About 1.6 million pairs, close to the combined breeding population of Canada and Greenland, may breed there (Nettleship and Evans 1985). Additional banding is needed at Iceland colonies to determine whether they are important sources of murres wintering off Newfoundland.

A first-year Thick-billed Murre shot in Twillingate in November 1989 had been banded in Spitsbergen three months previously (J.W. Chardine, pers. commun.). This is the first indication that birds from the large colonies there, roughly estimated to include 1 million breeding pairs (Nettleship and Evans 1985), occasionally reach Newfoundland waters.

4.3. Recent population trends

Breeding numbers of Canadian Thick-billed Murres may have declined between the early 1950s and 1970s (Nettleship and Evans 1985). Colony monitoring programs initiated from 1971 onwards suggest that those in Hudson Strait and Lancaster Sound are stable at present (A.J. Gaston, pers. commun.).

Most West Greenland colonies have declined severely in the last 50 years, with estimated decreases of 20-100% at some colonies (e.g., Nettleship and Evans 1985; Evans and Kampp, this volume). Declines were probably caused primarily by hunting and egging at colonies (Kampp 1990; Evans and Kampp, this volume). Hunting in Greenland outside the breeding period and losses in salmon gill nets (Kampp, this volume) also contributed to declines. These sources of mortality have been addressed by policy and regulatory changes in Greenland (Evans and Kampp, this volume).

Continued hunting in Newfoundland would also have contributed to the decline, as up to 40-50% of Newfoundland turrs may have come from Greenland at a time when populations were high. The turr harvest may now be limiting the rate at which these populations can recover. Continued declines in Greenland mean that fewer turrs are available to be shot in Newfoundland waters, and that the overall sustainable yield has decreased.

5. Public awareness of the effects of the turr hunt

By the early 1980s, it was apparent that harvest levels could be contributing to declines in Canadian and Greenland breeding populations of Thick-billed Murres, and that realistic harvest restrictions could help to halt a decline. Such a change would require the understanding and support of the Newfoundland hunters. In late 1983, the Canadian Wildlife Service began a program to give hunters accurate information about the murres and the turr hunt. Most hunters had misconceptions about the birds but were interested to find out more. With better information, their attitudes towards hunting changed, and many now support harvest controls to conserve the turrs and maintain the hunt.

Prior to this program, most rural Newfoundlanders had assumed that hunting had little effect on the huge populations of turrs. The effects of oil pollution and gull predation were often considered more important as causes of mortality. Few people understood the differences between Thick-billed Murres and Common Murres and concluded that turr numbers were increasing, as local Common Murre colonies had grown through the 20th century. Apparent declines were often dismissed as changes in behaviour in response to boat activity, changing distribution, or simply year-to-year variation. Most hunters were unaware that murres do not breed until they are five years of age and lay only one egg per year.

The gradual change from a subsistence harvest to a sport hunt (and even a market hunt) was rarely acknowledged, and selling turrs was tolerated in most hunting communities. The differences between the regulations governing turr hunting and those that apply to the hunting of migratory game birds were seldom clearly understood. The lack of bag limits was often interpreted to mean that the turr hunt had little effect on murre populations.

The information program was designed to take several years of open exchange to modify the traditional attitudes of Newfoundlanders. Over five winter seasons, I visited more than 175 coastal communities with an assistant, spoke to over 1900 hunters individually and in small groups, and gave about 40 illustrated talks to communities and schools. We left information booklets (Gaston and Jones 1984) and fact sheets to maintain contact, solicit for band recoveries, and continue the information exchange. We reinforced our messages with posters in stores and post offices, radio and television interviews, newspaper articles, announcements of upcoming meetings, and letters to 300 hunters who sent in turr bands.

We emphasized the importance of knowing hunters' perceptions of trends in turr numbers, the cultural value of the hunt, their uses of the birds, the effects of selling, and ways to resolve the problems. This allowed hunters to contribute to the management process. We concentrated on exchanging information in the first two seasons, on soliciting their suggestions for reducing the harvest the next two years, and on presenting the approach of daily bag limits and shorter seasons in the final year.

Among the important information we conveyed were the differences between Thick-billed Murres and Common Murres, and why most turrs shot were Thick-billed Murres; the age of first breeding; the clutch size of only one egg; the number wintering off Newfoundland, and the proportion shot each year; and evidence for population declines in Greenland and Canada. This was balanced with details of the birds' movements and feeding and breeding habits, and of our experiences banding and studying the murres, to emphasize how we obtained this information.

Most hunters were fishermen with a basic knowledge of fish population dynamics and sustainable yields. Once they knew the correct turr population parameters, they usually concluded for themselves that they were shooting too many birds. We spoke in nonscientific terms and used comparisons with familiar subjects and local returns of our colour-banded turrs to help explain aspects of wintering and breeding areas, migration patterns, age-specific mortality, and breeding age.

Suggestions from hunters to reduce the harvest included issuing numbered turr tags to each hunter annually, closing the season for one to five years to let populations rebuild, shortening the season, and bringing in season or daily bag limits. After discussing each option, most hunters concluded that a solution involving shorter seasons and bag limits, similar to those for other game birds, would be the most practical and effective.

As a result of this public information program, most turr hunters are now better informed about the characteristics of the birds they shoot and the concerns of overharvesting. Those who hunt turrs for enjoyment, tradition, and food generally agree that restrictions are needed, if only to prevent future population declines and to maintain the turr hunt for their children. However, up to 10% feel they have a right to shoot large numbers of turrs, despite the effects this could have on populations, and are reluctant to accept the need for restrictions. Many of these hunters sell many birds and could lose considerable income if harvests were controlled.

Reduced harvests are favoured by most community leaders and older respected hunters, who serve as influential allies in carrying public opinion. Many admit they are unlikely to reduce their personal harvests voluntarily if their neighbours continue to kill many turrs and thus ask for firmly enforced bag limits. This has become the option preferred by most hunters, as well as by wildlife managers.

The information program also extended to local and Canadian nongovernment conservation and wildlife organizations, to gain their support and input in developing a management framework. Consultations were also conducted to gain the backing of the Royal Canadian Mounted Police and other agencies that enforce the Migratory Bird Regulations. Their task would be easier and more effective if turr hunters were required to purchase a hunting licence and adhere to restrictions such as those that apply to migratory game bird hunters, including daily bag and possession limits.

Details of proposed harvest restrictions will be discussed with the public as they are developed, ensuring that hunters understand the reasons for the regulations and emphasizing the input that hunters had in their development. Proposed restrictions may be modified in response to legitimate concerns of those involved, again increasing the chances of widespread compliance.

6. Turr management requirements

A goal of the Canadian Wildlife Service is to rebuild and conserve the affected Thick-billed Murre populations. Population modeling exercises using available parameters suggest that the current harvest exceeds the maximum sustainable yield (Nettleship and Chardine 1989). However, population changes occur slowly because of the longevity of these birds. Because of their low reproductive potential, it is prudent to reduce the harvest immediately while these inconsistencies are investigated.

Target harvest levels must be sufficiently below the sustainable yield to prevent excessive mortality when overall rates may increase as a result of such factors as extreme winter conditions, poor breeding seasons, or high net drowning or oiling losses. The effects of these poorly documented mortality sources may exceed the estimates presented earlier. Harvest levels also must be low enough for depleted Greenland populations to rebuild, rather than just to stabilize, to prevent future declines.

The turr hunt is one of the last major unregulated wildlife harvests in North America. Conservation groups, as well as management agencies and the hunters themselves, agree that this incongruity must be resolved. The lack of effective regulations has contributed to inadequate control of the harvest and reduced perceptions of the value of turrs, leading to excessive sale and occasional shooting of birds for target practice. Practical restrictions would thus add to the quality of the hunt while protecting populations of murres.

The overall harvest could be reduced most effectively through daily bag limits and restrictions on the number of birds in a hunter's possession. Limits should be adequate to permit most hunters to shoot enough turrs to justify the effort of hunting and to meet family needs, while making it no longer profitable to sell excess birds.

Further limitations could be achieved by shortening the season to the few months when most murres are present. This would effectively reduce the illegal kill of other seabirds, most of which are now taken in early fall before the arrival of most of the murres. It would also greatly reduce the period when sea duck seasons are closed but turr hunting is permissible, with corresponding benefits to ducks, especially Newfoundland-breeding Common Eiders, whose numbers have decreased greatly in some areas. Different seasons and bag limits should be set for distinct hunting zones to reflect local differences in the periods when murres are available and in the importance of turrs to the needs of local hunters.

Hunters should be required to purchase a hunting permit to enable wildlife agencies to monitor hunter numbers and conduct representative surveys to assess harvest levels. The understanding and compliance of hunters could be improved by ensuring that turr hunting regulations are similar to those governing migratory game birds, such as the sea ducks. This would also increase the involvement and effectiveness of enforcement agencies.

These objectives could be achieved by effectively treating murres as migratory game birds, using a regulatory regime familiar to most Newfoundland hunters. Although such a change would likely require an amendment to the Migratory Birds Convention, which may be difficult to achieve (Thompson 1991), a regime using comparable regulations would be supported by most hunters and could satisfy management and conservation goals.

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The harvest of murres in Newfoundland from 1977-78 to 1987-88

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Abstract

Eight questionnaire surveys were conducted during the period 1977-88 to assess the characteristics and harvest levels of the Newfoundland murre hunt. Samples were selected from lists of hunters who purchased Migratory Game Bird Hunting (MGBH) Permits. As murre hunters are not required to buy MGBH Permits, special surveys were conducted in 1985-86 and 1986-87 to assess the error caused by sampling permit holders only. We estimate that a mean of about 7300 permit holders hunted murres, shooting approximately 300 000 - 725 000 murres annually, with each hunter averaging about 6.3 murres per hunting day or 60 murres each season. Although based on small samples that were not selected representatively, the special surveys indicated that 40-50% of murre hunters did not purchase permits, and that overall harvest levels could therefore be twice those estimated for permit holders. Results are presented to show hunting trends through the survey period and to describe the characteristics of an average hunting season.

Résumé

Huit enquêtes ont été réalisées au moyen de questionnaires entre 1977 et 1988, en vue d'évaluer les caractéristiques et les niveaux de prises de la chasse de la marmette à Terre-Neuve. Pour les enquêtes, les chasseurs ont été sélectionnés au hasard des listes de détenteurs de permis de chasse aux oiseaux migrateurs considérés comme gibier. Étant donné que les chasseurs de marmettes ne sont pas tenus de se procurer ce permis, on a fait des enquêtes spéciales, en 1985-1986 et en 1986-1987, afin de déterminer le pourcentage d'erreur causé par l'échantillonnage des détenteurs de permis seulement. Nous évaluons à environ 7 300, en moyenne, les détenteurs de permis qui ont chassé les marmettes, les prises ayant varié entre 300 000 et 725 000 par année, ce qui représente une moyenne de 6,3 marmettes par jour de chasse par chasseur, ou 60 marmettes par saison. Bien qu'elles aient été basées sur un échantillonnage restreint qui n'était pas nécessairement représentatif, les enquêtes spéciales ont révélé que 40 à 50 % des chasseurs de marmettes ne se sont pas procuré de permis et que le total des prises pouvait donc atteindre le double de ce qui a été évalué pour les détenteurs de permis. Les résultats présentés servent à illustrer les tendances de la chasse pendant la période d'enquête et à décrire les caractéristiques d'une saison de chasse moyenne.

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1. Introduction

Thick-billed Murres *Uria lomvia* and Common Murres *U. aalge* are harvested in a traditional fall and winter hunt off the coasts of Newfoundland and Labrador. Tuck (1961) concluded that about 5 million murres wintered off the Newfoundland coast, based on the results of banding at colonies in the eastern Canadian Arctic and West Greenland, and showed that most birds shot were Thick-billed Murres. Recent field observations in Newfoundland have confirmed that Common Murres make up only about 5% of the total harvest (Elliot, this volume). Thick-billed Murres reach southern Labrador and the northern portions of the island of Newfoundland by October and November (Gaston 1980) and move south through the winter as pack ice advancing from the north reduces the amount of open water, until the ice breaks up in March and April. Inshore distribution of murres is also influenced by local ice formation and ice movements.

Tuck (1961) calculated that between 100 000 and 200 000 murres were harvested annually in Newfoundland. The first figure probably referred to the years just prior to 1959 (Inder and Gillespie 1974) and the second to 1951-52 (Tuck 1953). Tuck considered those levels to be within the sustainable yield of populations. The only other estimate of the Newfoundland harvest, of 82 000 birds, calculated from reports of hunters who returned provincial small game licence stubs for 1960-61 (Inder and Gillespie 1974), probably greatly underestimated the actual harvest. These data were subject to reporting bias, as they were collected incidentally rather than in a well-designed survey, and murre hunters would have been poorly represented, as they were not required to buy the small game licence. As knowledge of population sizes and trends expanded during the 1970s, and with it information on breeding biology and postbreeding distribution of murres, concern was expressed about the unknown magnitude of this harvest and its possible effects on source populations.

A standardized survey was initiated in 1977-78 to assess the timing, extent, and characteristics of the harvest and to monitor annual trends (Wendt and Cooch 1984). This questionnaire survey used as a sampling frame the list of purchasers of the Migratory Game Bird Hunting (MGBH) Permit, required to hunt migratory game birds in Canada. The survey was conducted for three years with additional questions on the sea duck harvest, and for five years on the murre harvest alone. As murre hunters are not specifically required to purchase the MGBH Permit, the standard survey was supplemented by an experimental one in two seasons to evaluate the effect of sampling only from the MGBH Permit sales file. An assessment of the questionnaire surveys is presented by Elliot et al. (1991).

We present estimates of hunter numbers, hunting effort, and harvest levels of murres in Newfoundland and Labrador, based on these questionnaire surveys. The results are interpreted in the context of field studies and interviews with hunters conducted in Newfoundland from 1983-84 to 1987-88 (Elliot 1989, and this volume).

2. Methods

2.1. Standard surveys

A questionnaire was mailed to a stratified sample selected from purchasers of MGBH Permits in the province of Newfoundland for eight seasons over an 11-year period (Table 1). The questionnaire asked about both sea duck and murre hunting through 1979-80 (Wendt and Couling 1978; Wendt and Cooch 1984; Elliot et al. 1991). Several additional questions were added in 1981-82 when the survey addressed only murre hunting, and the format then remained essentially the same through to 1987-88 (Elliot et al. 1991). Places where differences in the wording of questions between years may have affected the responses are noted below.

The province was divided into 13 geographical zones, based largely on inshore fisheries surveys areas, to stratify the permit sales lists to account for presumed differences in hunting characteristics between sample zones. A further stratification by date of purchase was included for 1977-78 and 1978-79, as it was expected that those purchasing permits after the 30 November end of provincial sport duck hunting seasons were more likely to be active murre hunters. However, as the kill by late purchasers accounted for only 3% of the total harvest, this group was not sampled separately in subsequent surveys (Wendt and Cooch 1984). Samples were selected systematically by taking permit numbers at regular intervals from the list of hunters within each stratum. The number selected from each stratum was roughly in proportion to the number of permits sold, with some adjustments made to ensure enhanced representation from coastal zones with low permit sales. This procedure was modified after 1978-79 to optimize the allocation of the sample among strata, based on the results from the first two surveys (Cochran 1977).

Samples were selected from the current year's MGBH Permit sales list for the first five surveys, with the stratification by date in the first two years noted above, although late permit purchasers would have been underrepresented because the permit sales file was often incomplete when the sample was selected. Beginning in 1985-86, samples were selected from the previous year's list to ensure the inclusion of some late purchasers, although this meant those who did not hunt the previous year were not sampled.

The questionnaires were mailed in April for the first three years (Wendt and Cooch 1984) and in mid- to late March in subsequent years. Second questionnaires were sent to those who did not respond to the first one within about six weeks. A covering letter explaining the need for the survey was included in the first three years, after which the survey forms themselves were considered self-explanatory.

Responses were analyzed on the assumption that hunters who did not specify their hunting locations hunted in the zones where they bought permits. Field observations confirm that this assumption is generally valid, except for the small proportion of murre hunters who live inland (e.g., sample zone 5) or in the city of St. John's (sample zone 9).

Field observations have shown that some of the sample zones grouped areas with quite different hunting characteristics, such as the north and south portions of zone 1, the east and west segments of zone 4, and the portions of zone 7 on opposite sides of the Northern Peninsula (RDE, pers. obs.) (Fig. 1). The results are therefore presented by nine more appropriate management zones that were selected to group communities and hunting areas with similar characteristics for the harvests of both murres and sea ducks, based on field observations during the 1980s (RDE and R.I. Goudie, pers. obs.) (Fig. 2). They were defined for this analysis by regrouping subdivisions of the sample zones.

Sample zone 5 is included in management zone IV to the north, and sample zone 9 (St. John's) is part of management zone VI. Results from management zone I (northern Labrador) are combined here with those from management zone II (southern Labrador), as few responses were received from zone I, where relatively few murres were harvested, and the timing of hunting was similar along the whole Labrador coast.

The survey samples were selected from the MGBH Permit sales files on a simple stratified random basis. The numbers of hunters, hunting days, and birds harvested were estimated using standard survey procedures, except that special techniques were required for incomplete questionnaires (Elliot et al. 1991). These arose when a respondent reported hunting murres but did not provide information on the number of days spent hunting or the number of murres harvested. The harvest of each of these hunters was assumed to equal the average for hunters from the same sample strata. The assumption increased the variance of the final estimate (Elliot et al. 1991). The estimation by management zone was done using the theory of domains of study (Cochran 1977).

2.2. Special surveys

Although murre hunters are not legally required to hold MGBH Permits, it was initially unknown whether the number of hunters not purchasing permits was large enough to result in a significant underestimate of the total number of murre hunters. It was thought that the downward bias in harvest estimates resulting from the incomplete sampling frame might have been reduced by an opposing upward bias resulting from difficulties in separating individual kill from party kill (Wendt and Cooch 1984).

However, field observations indicated that many hunters did not buy permits. The likelihood of purchase was related to such factors as the local popularity of sea duck hunting, for which a permit is required, and the degree to which local enforcement officers encouraged possession of a permit. Elliot (1987) found only 19 of 46 murre hunters' names in permit sales files in 1983-84, 132 of 267 in 1984-85, and 138 of 293 in 1985-86, an indication that only about 44% of murre hunters may have purchased permits (corrected for hunters sampled in more than one year). Although he considered this to be a minimum estimate, owing to inabilities to match misspelled names, it indicated that the initial sampling frame was inadequate.

Table 1
Characteristics of the survey samples and responses by survey year, and the standard errors associated with estimates (in parentheses)

Survey year	Size of permit file sampled	Sample selected	Sample intensity (%)	No. responding	Response as % of sample	No. of active murre hunters responding	Est. no. of permit holders hunting murres	Est. no. of hunting days by permit holders	Est. no. of murres killed by permit holders	No. of permits sold	Est. % of all permit holders hunting murres
1977-78	36 458	4 693	12.9	2 681	57.1	—	9 005	113 913	541 764	36 188	25
							—	(8 307)	(38 030)		
1978-79	37 523	4 695	12.5	2 345	49.9	—	6 829	81 972	353 559	37 297	18
							—	(7 242)	(39 539)		
1979-80	37 155	3 990	11.2	1 990	49.9	—	8 025	83 982	478 391	35 490	22
							—	(7 163)	(44 989)		
1981-82	31 330	3 000	9.6	1 182	39.4	300	7 020	58 733	379 560	31 406	22
							(430)	(5 509)	(37 149)		
1982-83	31 163	3 000	9.6	1 020	34.0	305	8 798	98 710	725 287	31 215	28
							(547)	(17 035)	(78 646)		
1985-86	25 616	3 000	11.7	1 257	41.9	381	7 182	66 112	412 483	25 652	28
							(386)	(7 015)	(49 125)		
1986-87	25 616	3 000	11.7	1 194	39.8	376	6 963	59 470	298 976	25 498	27
							(382)	(5 384)	(24 913)		
1987-88	20 394	3 000	14.7	1 175	39.2	370	6 868	61 325	375 919	21 080	34
							(360)	(8 234)	(46 973)		

Additional special surveys were conducted in 1985-86 and 1987-88 to assess how seriously the incomplete sampling frame affected the estimates. Questionnaires were sent to all hunters contacted during fieldwork in hunting communities in years immediately preceding these surveys whose names, addresses, and approximate ages were known (Table 2). The sample in 1987-88 was not selected independently but included most of the hunters sampled in 1985-86. The samples selected for the regular survey were checked to ensure that hunters were not sent two questionnaires. The names and ages of those responding were matched with lists of current purchasers of MGBH Permits, to divide responses into those for permit holders and those for non-permit holders. The data were then analyzed as for permit holders to estimate overall harvest characteristics based on these small samples.

The sample used in the special survey was assumed to be a simple random selection from the murre hunters in each management zone. The special survey provided estimates of the proportion of murre hunters with MGBH Permits and the number of hunting days and size of the harvest for hunters without permits. Details of the estimation procedures are given by Elliot et al. (1991).

2.3. Characteristics of an average hunting season

The five surveys conducted during the 1980s were analyzed in more detail to give a picture of specific characteristics of the murre hunt needed to make appropriate conservation decisions on regulations to manage the harvest. The characteristics of the distribution of the harvest, both temporally and geographically, and of the activity and success of murre hunters were averaged for these surveys and presented on the basis of management zones.

The information from the survey is presented in the context of possible management restrictions, such as the obligatory 10 March end of migratory game bird hunting seasons, and relevant biological information, such as the distribution of the age structure of harvested murres through the season (Elliot, this volume).

3. Results

3.1. Response to the surveys

In 1977-78, 1978-79, and 1979-80, the combined sea duck and murre harvest questionnaires were sent to approximately 4000-4700 permit holders, for a sampling intensity of over 10% of permit holders (Table 1). All subsequent questionnaires were sent to 3000 permit holders, giving a sampling intensity that rose from just under 10% in the early 1980s to a maximum of 14.7% in 1987-88, as permit sales declined.

The response rate averaged above 50% in the three combined surveys, dropping to about 40% in subsequent years, when questions on sea ducks were omitted (Table 1). The response rate to the special surveys was in the same range (Table 2). There was no indication of a declining response rate through the 1980s as a result of response fatigue, even though about 4000-7000 Newfoundland hunters were being sampled annually for the National Harvest Survey (e.g., Dickson 1989).

The questionnaires for 1978-79, 1979-80, and 1980-81 asked whether the respondent hunted sea ducks or murres, whereas later questionnaires asked about murres only. Thus, the estimates of the numbers of permit-holding murre hunters for the first three seasons (Tables 1 and 3, Fig. 3) are inflated by unknown amounts, reflecting respondents who hunted sea ducks but not murres.

3.2. Standard surveys

A comparison of the harvest estimated from responses to the first questionnaire only with that estimated from responses to either the first or second (reminder) questionnaire gives an indication of the effect of nonresponse bias. This was investigated for the 1977-78 returns, and extrapolation to a theoretical 100% response rate gave an estimate of nonresponse bias of -1% for murre kill (Wendt and Cooch 1984). This low value suggested that this source of bias could be ignored in comparison with sampling errors.

Although the estimated numbers of permit holders hunting murres varied annually within management zones, particularly in those with few hunters (Table 3), the total numbers varied comparatively little (Table 1, Fig. 3), with estimates in the range of about 6800-9000 hunters. However, the proportion of all MGBH Permit holders that they represented increased gradually after 1978-79, from about 18% to 34% (Table 1). The figures for the three combined surveys in the late 1970s averaged about 8% higher than those in the 1980s, probably due in part to the inclusion of respondents who hunted sea ducks but not murres.

Figure 1
Map of Newfoundland and Labrador showing the boundaries of murre harvest survey sample zones

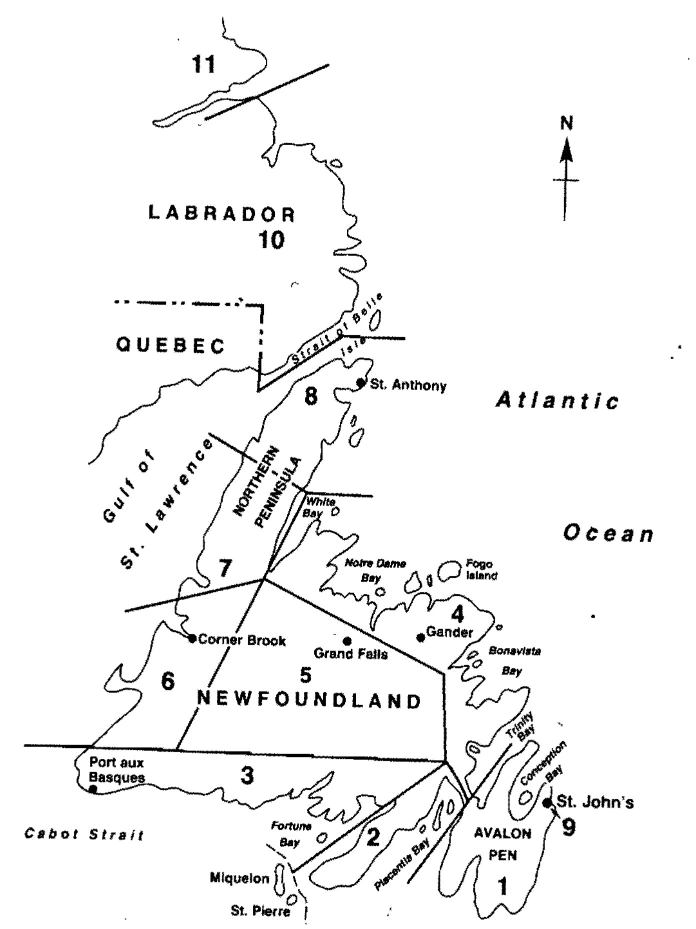
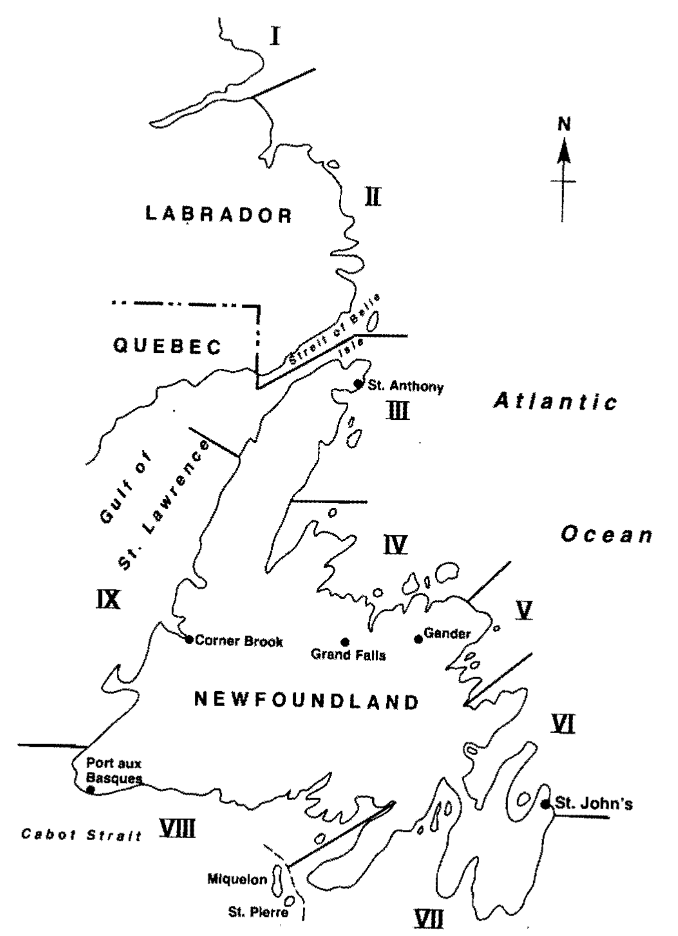


Figure 2
Map of Newfoundland and Labrador showing the boundaries of murre and sea duck harvest management zones



The number of days spent hunting by permit holders, an indication of the amount of effort expended in this activity, varied markedly from year to year within management zones, even between consecutive years and in zones where murre hunting was an important activity (Table 4). The annual estimates for the number of hunting days appear to have declined somewhat since 1977-78 (Fig. 4). As with the estimated number of hunters, estimates of hunting days are highest for 1977-78 and 1982-83 (Table 1).

The estimated kill of murres by permit holders varied appreciably without an overall trend (Table 5). The highest harvest estimate was about 725 000 (SE = 79 000) murres in 1982-83, about twice the level estimated for the previous year (Table 1, Fig. 5). This was also the peak harvest year in six of the eight management zones during the 1980s surveys (Table 5). The greatest numbers of murres were shot in zones IV, V, and VII, in different years, with large between-year fluctuations in all zones (Table 5).

The index of harvest per unit effort, obtained by dividing estimated annual harvest by the estimated total number of hunting days each year, does not show a consistent rising or falling trend over the complete survey period, although it appeared to rise gradually in the early survey years (Fig. 6).

3.3. Special surveys

The special surveys were sent to comparatively small samples (Table 2), which were not selected representatively; some management zones were sampled poorly (e.g., south coast) or not at all (west coast). Thus, the resulting estimates are not very precise but indicate the type of effects

Table 2
Characteristics of the samples and responses to the special surveys conducted in 1985-86 and 1987-88

Survey year	No. sampled	No. responding	Response as % of sample	No. of active murre hunters responding	No. of active murre hunters with permits responding	% of active murre hunters responding who held permits
1985-86	483	220	45.5	171	98	57.3
1987-88	585	258	37.6	199	116	58.3

that can be attributed to the present sampling frame. In both years, the overall estimate of the number of murre hunters was close to twice that derived using permit holders only (Table 6). The estimated proportion of hunters who bought permits ranged from 37% in Bonavista Bay in 1987-88 to 86% on the south coast in 1985-86. The estimates of the proportion buying permits were within 10% of each other in both years, in all zones except for Trinity-Conception bays and the south coast, where estimates were markedly lower in 1987-88.

There was corresponding variation among management zones in the proportion of total days that were spent hunting by permit holders (Table 7). The proportion of days spent hunting by permit holders was slightly higher than the estimated proportion that they made up of all hunters. This suggests that permit holders may tend to hunt on more days than non-permit holders.

The estimated proportion of the harvest taken by permit holders also varied markedly among zones, and between years in zones such as Bonavista Bay (Table 8).

Table 3
The estimated numbers of permit holders hunting murres annually in each management zone, and the standard error associated with the estimate (in parentheses)

Management zone	Survey year 1981–82	1982–83	1985–86	1986–87	1987–88
I&II. Labrador	301 (71)	426 (73)	405 (55)	339 (56)	357 (55)
III. Northern Peninsula	914 (95)	1074 (118)	907 (88)	1064 (83)	834 (90)
IV. White-Notre Dame bays	1759 (184)	1815 (207)	1211 (140)	1793 (192)	1748 (197)
V. Bonavista Bay	1423 (297)	1788 (386)	881 (220)	1080 (252)	1487 (272)
VI. Trinity-Conception bays	442 (104)	547 (122)	471 (97)	235 (71)	549 (92)
VII. Southern Avalon-Burin	1012 (169)	1333 (291)	1628 (224)	1021 (132)	1143 (215)
VIII. South coast	954 (160)	1482 (202)	1315 (178)	1251 (171)	696 (102)
IX. West coast	180 (59)	177 (65)	195 (50)	181 (50)	54 (25)

Table 4
The estimated numbers of days spent hunting annually by permit holders in each management zone, and the standard error associated with the estimate (in parentheses)

Management zone	Survey year 1981–82	1982–83	1985–86	1986–87	1987–88
I&II. Labrador	2 306 (840)	6 271 (1 972)	3 954 (723)	2 756 (677)	3 145 (741)
III. Northern Peninsula	7 460 (1 040)	9 463 (1 713)	8 040 (1 311)	8 249 (1 094)	4 417 (669)
IV. White-Notre Dame bays	15 713 (2 415)	13 699 (2 453)	8 885 (1 572)	11 465 (1 489)	13 244 (1 975)
V. Bonavista Bay	6 963 (1 749)	10 481 (2 716)	6 672 (3 025)	6 493 (1 904)	13 163 (3 937)
VI. Trinity-Conception bays	3 359 (1 030)	5 626 (1 672)	2 092 (683)	4 173 (2 399)	3 137 (818)
VII. Southern Avalon-Burin	7 049 (1 437)	28 586 (15 506)	18 825 (5 139)	10 991 (1 989)	16 064 (6 708)
VIII. South coast	11 874 (3 441)	20 884 (5 467)	13 511 (2 678)	11 345 (3 126)	6 836 (1 417)
IX. West coast	3 690 (2 145)	3 781 (3 640)	2 987 (1 340)	4 124 (1 650)	950 (309)

Figure 3
The estimated numbers of permit holders hunting murres in Newfoundland in eight survey years (± 1 SE)

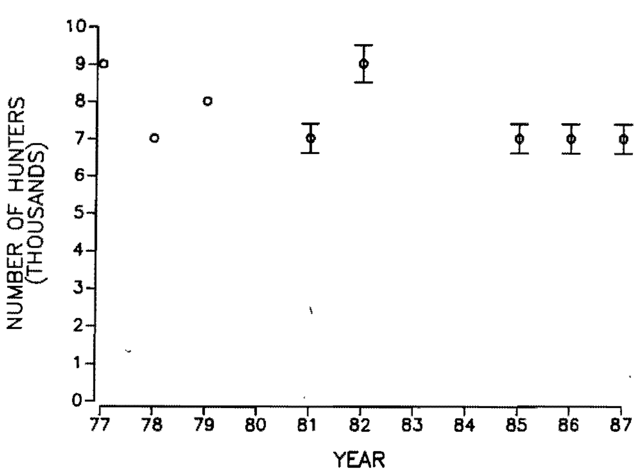
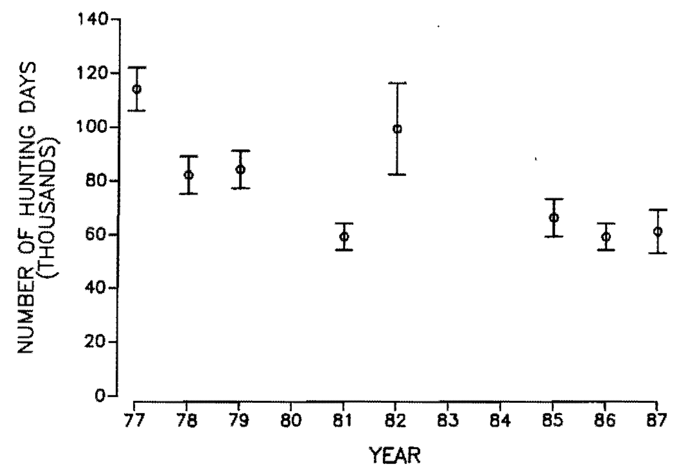


Figure 4
The estimated numbers of days spent hunting murres by permit holders in Newfoundland in eight survey years (± 1 SE)



The overall proportion of the estimated harvest apparently taken by permit holders was appreciably lower than the proportion they made up of all hunters. This suggests that although non-permit holders may have hunted on fewer days, their overall harvest rates were higher than those for permit holders. In both years, the overall harvest estimated from the special surveys was more than twice that of permit holders only, although the standard errors of these estimates are high.

3.4. Characteristics of an average hunting season

The characteristics of hunting activity and harvests by permit holders, shown in Table 9 by management zones, give a general picture of an average hunting year during the 1980s. However, the additional effects of activity by non-permit holders, which vary between zones (e.g., Tables 6, 7, and 8), must be kept in mind when considering these data.

The peak hunting period occurred in late fall in northern zones (I&II, III, and IV) and was earliest in Labrador (Table 9). Along the east and south coasts (zones V, VI, VII, and VIII), most hunting activity took place after 1 January. The timing of activity of the small number of hunters on the west coast (zone IX) was intermediate, with hunting occurring in late fall and March (Table 9). The periods of peak harvest were similar, although the peak month occurred later than the peak of hunting effort in zones I&II, V, and VIII.

The mean monthly estimated harvest for all zones combined shows the general pattern of annual harvest during the 1980s (Fig. 7). The harvest peaked in November and leveled off at lower numbers through the rest of the season. The approximate proportions of first-winter murres in the harvest each month (from Elliot 1989) show that juveniles made up the majority of the kill before 1 January, and that older birds comprised most of the harvest from January to March (Fig. 7).

The proportion of hunting effort and harvest that occurred after 10 March, the last allowable date for a migratory game bird hunting season, is presented to consider the effect that adhering to the existing timing of game bird seasons could have on murre hunting. About 9% of all hunting effort and 12% of the overall harvest (Table 9) occurred after this date. The proportions were highest in the three eastern zones (V, VI, and VII) and in the relatively insignificant west coast zone (IX).

The degree to which the harvest was concentrated in a short period is indicated by the number of months taken to kill 60% of the harvest (Table 9). Labrador (zones I&II) and the northeastern zones (IV, V, and VI) had relatively

Table 5
The estimated numbers of murres killed annually by permit holders in each management zone, and the standard error associated with the estimate (in parentheses)

Management zone	Survey year 1981–82	1982–83	1985–86	1986–87	1987–88
I&II. Labrador	10 139 (2 708)	23 336 (5 947)	21 978 (4 485)	13 201 (3 116)	18 561 (5 117)
III. Northern Peninsula	58 556 (9 781)	73 519 (11 543)	72 200 (17 550)	48 607 (5 409)	41 814 (5 987)
IV. White-Notre Dame bays	120 241 (22 502)	127 747 (21 369)	58 354 (11 600)	68 020 (11 508)	80 853 (11 016)
V. Bonavista Bay	30 713 (8 212)	133 691 (37 887)	20 679 (5 669)	38 660 (13 031)	93 975 (45 897)
VI. Trinity-Conception bays	28 684 (8 406)	85 331 (38 928)	32 877 (10 742)	14 555 (8 786)	52 401 (12 653)
VII. Southern Avalon-Burin	49 328 (10 218)	100 057 (27 774)	114 177 (41 196)	55 595 (8 752)	57 803 (13 007)
VIII. South coast	71 006 (23 030)	158 473 (36 882)	78 367 (19 388)	56 187 (12 144)	28 285 (6 407)
IX. West coast	4 694 (2 399)	6 163 (2 677)	4 061 (2 710)	3 361 (1 331)	3 099 (1 888)

Figure 6
The estimated kill of murres per unit effort in eight survey years, derived by dividing the total estimated harvest for permit holders by the overall number of days they spent hunting murres

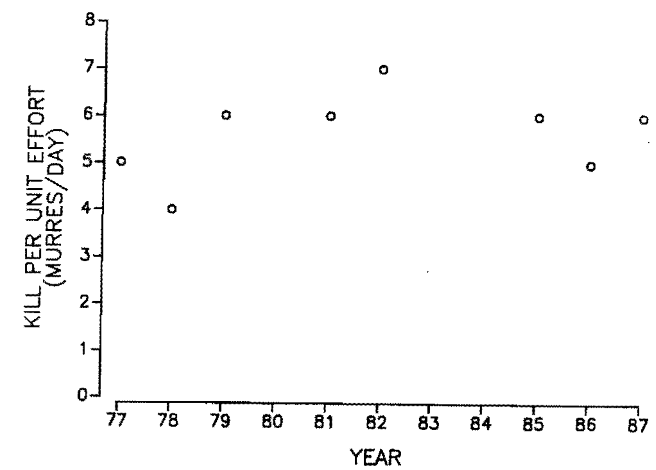


Figure 5
The estimated numbers of murres killed by permit holders in Newfoundland in eight survey years (± 1 SE)

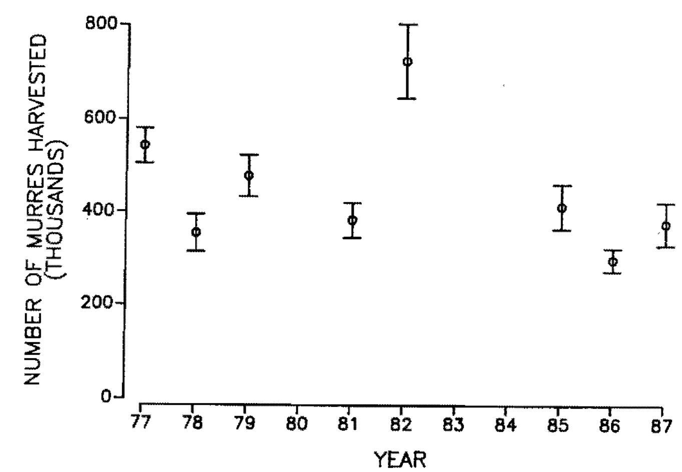


Table 6
The estimated total numbers of murre hunters in each management zone, derived from special surveys in 1985-86 and 1987-88, and the estimated proportions of hunters with permits

Management zone	1985–86 Total no. of hunters (SE)	1985–86 No. with permits as % of total	1987–88 Total no. of hunters (SE)	1987–88 No. with permits as % of total
I&II. Labrador	479 (88)	85	476 (90)	75
III. Northern Peninsula	1 269 (218)	71	1 154 (174)	72
IV. White-Notre Dame bays	2 967 (619)	41	3 440 (584)	51
V. Bonavista Bay	2 115 (743)	42	4 014 (1 263)	37
VI. Trinity-Conception bays	660 (165)	71	1 200 (302)	46
VII. Southern Avalon-Burin	2 664 (513)	61	2 130 (508)	54
VIII. South coast	1 534 (330)	86	1 114 (242)	62
IX. West coast	195[a] (50)	[100]	54[a] (25)	[100]
Provincial total	11 883 (1 139)	60	13 583 (1 447)	51

[a] As no hunters were sampled in management zone IX in either special survey, it is assumed here that the total number of murre hunters in that zone equals the number with permits.

brief hunting seasons, whereas the Northern Peninsula (zone III) and southern and western zones (VI, VIII, and IX) had access to murres for several months.

Overall hunting success is shown by the overall annual kill per hunter (Table 9) and averaged almost 60 murres/hunter. There was no general pattern among the zones, where annual kill ranged from less than 30 murres/hunter on the west coast (zone IX) to about 95 murres/hunter in Trinity-Conception bays (zone VI).

Harvest per unit effort, as indicated by overall kill/day in Figure 6, is shown by management zone in Table 9. The rate was above the average level of 6.3 birds/day in the northeastern zones (III, IV, and V), particularly in Trinity-Conception bays (zone VI). Comparable estimates for kill/day during the peak hunting month in each zone followed a similar pattern (Table 9).

4. Discussion

4.1. Sampling frame limitations

The relatively high response rate and low likelihood of nonresponse bias together suggest that the respondents are valid representatives of Newfoundland hunters who buy permits. The low variance of the estimates for the number of permit holders hunting murres (95% confidence interval of about 10–13%) indicates that an estimated annual mean of about 7300 hunters is valid. The estimate of about 11 000 hunters, with and without permits, for each of the two special survey years is also relatively reliable, as confidence intervals were about 19–21%, despite the small sample size and variation between zones. Similarly, the confidence limits on estimates for the overall number of hunting days by permit holders (about 15–35%) indicated that they are quite reliable, although the estimates for all hunters had relatively large degrees of error (confidence intervals of about 40%).

Unfortunately, the harvest estimates, which are most important from a biological point of view, showed the least precision. The confidence intervals for the harvest of all permit holders ranged from about 14% to 25% and were much higher within management zones (Table 8), whereas those that included harvests of non-permit holders were about 67% in 1985-86 and just over 100% in 1987-88. As the

Table 7
The estimated total numbers of days spent hunting murres by all hunters in each management zone, derived from special surveys in 1985-86 and 1987-88, and the estimated proportions of hunting days used by permit holders

Management zone	1985-86 Total days by all hunters (SE)	1985-86 Days by permit holders as % of total	1987-88 Total days by all hunters (SE)	1987-88 Days by permit holders as % of total
I&II. Labrador	4 359 (1 857)	91	4 002 (1 619)	79
III. Northern Peninsula	11 969 (4 373)	67	7 046 (4 078)	63
IV. White-Notre Dame bays	24 315 (9 971)	37	26 975 (13 953)	49
V. Bonavista Bay	20 434 (13 772)	33	29 380 (13 845)	45
VI. Trinity-Conception bays	2 720 (1 251)	77	9 202 (5 411)	34
VII. Southern Avalon-Burin	26 150 (8 666)	72	21 988 (7 977)	73
VIII. South coast	14 387 (5 147)	94	11 222 (6 833)	61
IX. West coast	2 987[a] (1 340)	[100]	950[a] (309)	[100]
Provincial total	107 320 (20 331)	62	110 764 (23 269)	55

[a] As no hunters were sampled in management zone IX in either special survey, it is assumed here that the total number of days spent hunting in that zone equals the number of days spent hunting by permit holders.

Table 8
The estimated total numbers of murres killed by all hunters in each management zone, derived from special surveys in 1985-86 and 1987-88, and the estimated proportions killed by permit holders

Management zone	1985-86 Total harvest by all hunters (SE)	1985-86 Harvest by permit holders as % of total	1987-88 Total harvest by all hunters (SE)	1987-88 Harvest by permit holders as % of total
I&II. Labrador	22 420 (4 857)	98	21 605 (7 104)	86
III. Northern Peninsula	118 377 (41 185)	61	50 114 (14 160)	83
IV. White-Notre Dame bays	158 150 (102 832)	37	192 579 (89 354)	42
V. Bonavista Bay	163 187 (148 820)	13	387 616 (449 037)	24
VI. Trinity-Conception bays	44 281 (21 471)	74	129 354 (118 984)	41
VII. Southern Avalon-Burin	288 037 (221 555)	40	132 940 (153 178)	43
VIII. South coast	93 272 (77 193)	84	48 010 (23 999)	59
IX. West coast	4 061[a] (2 710)	[100]	3 099[a] (1 888)	[100]
Provincial total	891 786 (299 434)	46	965 317 (497 382)	39

[a] As no hunters were sampled in management zone IX in either special survey, it is assumed here that the total murre harvest in that zone equals the harvest by hunters with permits.

survey was stratified on the basis of permit sales, the effects of extrapolating the results for non-permit holders to estimate harvests for the whole province are uncertain. Although the values for permit holders provide useful trend data and an indication of their actual harvest, the estimates for all hunters merely point out that the total annual harvest is very high, and that more accurate approximations are needed.

A better control over the bias introduced by the incomplete sampling frame could be achieved by sending the regular survey to both a sample of permit holders and a sample selected from another universe containing appreciable proportions of murre hunters who do and who do not purchase permits. This will soon be undertaken using a sample from a file of applicants for Newfoundland big game hunting licences, which is likely to include most murre hunters. This should quantify the effects that the sampling frame has had on the results to date, but a requirement that all murre hunters purchase permits would provide a better long-term sampling frame.

4.2. Management implications of murre hunt characteristics

Since the reports on the murre hunt by Gaston et al. (1984) and Wendt and Cooch (1984), much additional information has been gained on the murre harvest and on the breeding characteristics and population sizes of source populations. The survey results are interpreted here in light of this knowledge and the need to manage the hunt to regulate the harvest.

The number of permit holders who hunt murres remained quite constant through the survey period. However, they represented an increasing proportion of all permit holders, as the overall numbers of MGBH Permit sales in Newfoundland fell by 43% from a peak in 1978 to 1987 (Dickson 1989). If indications from the special surveys are correct, about equal numbers of Newfoundlanders actively hunted murres and waterfowl by 1987 (Table 10 in Dickson 1989; Table 6). Together with the consistently high effort spent hunting murres (the number of hunting days), these data confirm that interest in this activity remains high, despite concerns about the status of murre populations (Elliot 1989).

Newfoundland has twice the Canadian average participation in wildlife hunting (Filion et al. 1989). Although the population of the province comprises only about 2.2% of the Canadian population, the harvest of murres there is one of the largest harvests of any species taken in the country. Harvest levels by permit holders alone during the survey period consistently exceeded the estimated harvest of all waterfowl in the Atlantic provinces (e.g., Wendt and Hyslop 1981; Métras and Wendt 1986; Dickson 1989). At the national level, the murre harvest by permit holders averaged higher than the total Canadian take of Canada Geese *Branta canadensis*, a migratory game bird whose harvest levels in recent years have been exceeded only by those of the Mallard *Anas platyrhynchos*.

Total murre harvest levels are less certain but are likely comparable with the Canadian kill of Mallards in years such as 1982, when the estimated Mallard harvest was 1.2 million (Métras and Wendt 1986) and the estimated murre harvest by permit holders was about 725 000 (SE = 79 000, Table 1), although both are subject to the effects of biases and incomplete sampling frames. Doubling the latter value, as suggested by the special surveys, would indicate an overall kill by all hunters in the order of 1.5 million murres that season.

Elliot's (1987) estimate that only 5% of murres harvested were Common Murres is smaller than the degree of error in the harvest estimates, so we assume here that these estimates approximate the kill of Thick-billed Murres. Recent population modeling by Nettleship and Chardine (1989) suggests that harvest levels of Thick-billed Murres should not exceed 400 000 if populations are to be maintained. The consistently higher harvest levels estimated over the survey period suggest that some inputs into the models, such as breeding numbers of source populations, the numbers dying outside the hunting season, or adult survival, may be too conservative; that the biases in these surveys have combined to produce

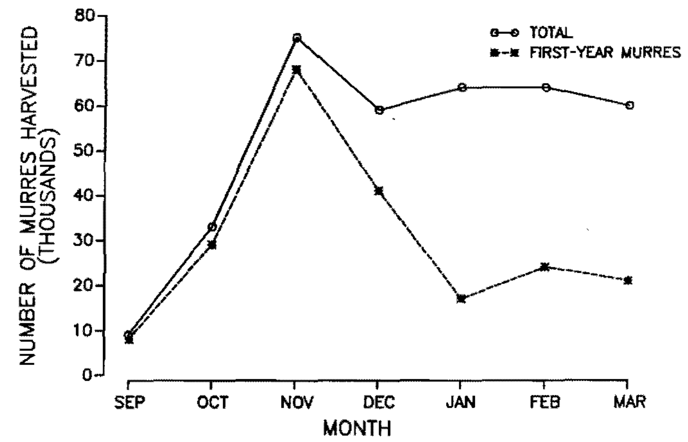
Table 9
The main characteristics of hunting activity and murre harvest of permit-holding hunters by management zone, based on means of results from the five surveys conducted in the 1980s

Management zone	(1) Est. % of permits	(2) Peak hunting months[a]	(3) % hunting days > 10 March	(4) Overall kill/ hunter	(5) Est. % of kill	(6) Peak kill months[a]	(7) % kill > 10 March	(8) No. of months to kill 60%	(9) Overall kill/ day	(10) Peak month kill/day
I&II. Labrador	5	sO*N*	5	48	4	sO*N*	6	1.8	5	6
III. Northern Peninsula	13	O*N*d	<3	60	14	O*N*d	4	2.2	8	8
IV. White-Notre Dame bays	23	o*N*D	1	55	21	o*N*D	1	1.5	7	8
V. Bonavista Bay	18	*J*Fm	15	48	15	jF*M*	26	1.8	7	12
VI. Trinity-Conception bays	6	jF*M*	16	95	10	jF*M*	24	1.7	12	18
VII. Southern Avalon-Burin	17	*J*Fm	14	61	17	j*F*M	16	2.4	5	6
VIII. South coast	16	d*J*F	9	69	18	d*J*F	11	2.5	6	9
IX. West coast	2	o*N*M	12	17	1	*N*dM	17	3.9[b]	2	2
Provincial total	100	—	9	59	100	—	12	—	6.3	—

(1) Percentage of mean total estimate of 7293 permit holders
(2) Months with highest mean number of hunting days: *HIGHEST*, SECOND, third
(3) Estimated percentage of mean number of hunting days after 10 March
(4) Mean total annual kill/mean total number of active hunters
(5) Percentage of mean total estimated harvest of 431 870 birds
(6) Months with highest mean kill: *HIGHEST*, SECOND, third
(7) Estimated percentage of mean kill shot after 10 March
(8) Minimum number of consecutive months to shoot 60% of mean total harvest
(9) Mean total annual kill/mean total number of hunter-days
(10) Mean total kill in peak month/mean number of hunter-days in month

[a] j/J = January, m/M = March.
[b] 2.5 months if not consecutive.

Figure 7
The mean numbers of murres harvested by permit holders each month, based on the five surveys conducted in the 1980s (solid line). The dashed line represents the approximate mean numbers of first-year murres in the monthly harvest, based on proportions derived by Elliot and Gaston (1986).



appreciable overestimates; or that the harvests are indeed excessive.

Kill per unit effort is often a useful index of population change, with declines indicated by either an increase in the amount of effort needed to take the same harvest or a reduction in harvest with constant hunting effort. Although harvest per unit effort appeared to increase until 1982-83 and then decline (Fig. 6), it should not be assumed that the availability of murres followed the same pattern. This index of availability is valid only if the characteristics of effort do not change. It seems likely that hunters' efficiency increased through the 1980s as a consequence of a continued move to larger boats and motors (Elliot, this volume). Many hunters also reported that they hunted only when they knew that murres were within range, as they perceived that birds were becoming scarcer (Elliot 1989, and pers. obs.). The 1982-83 hunting season was acknowledged to be exceptional in many areas, when weather and ice conditions combined with large numbers of murres quite close to shore likely resulted in a reduction in the effort needed to shoot murres.

Thus, kill-per-unit-effort data do not preclude the possibility that the harvested populations are declining. Severe declines have occurred in West Greenland (Evans and Kampp, this volume), and smaller declines may have taken place in the eastern Canadian Arctic (Nettleship and Evans 1985). Murres from both areas make up most of the birds harvested in Newfoundland (Gaston 1980; Elliot, this volume). Data from the harvest surveys are useful in describing the present hunt and pointing to ways to reach effective reductions to conserve breeding populations.

The timing and other characteristics of the hunt varied appreciably among management zones. This is in keeping with Gaston's (1980) interpretation, from banding data, of the movement of birds south through the winter and Elliot et al.'s (1990) interpretation of the effects of ice and water temperature on the distribution of important food species. Management zones can be further grouped into three areas on the basis of timing and characteristics of the hunt during the survey periods (Table 9). The age structure of the murres taken also varies among these areas.

The peak of harvest occurs along the coast of Labrador (zones I&II) in early fall (September - early November), and most murres taken are birds-of-the-year (Elliot, this volume). The length of the peak hunting period — the time required to take 60% of the harvest — is less than two months here, as murres are often pushed south of the area by advancing pack ice in mid-fall. Labrador hunters account for only about 5% of the total provincial harvest.

In mid- to late fall (late October - December), most hunting takes place along northern and western parts of the island of Newfoundland, including the Northern Peninsula, White Bay, Notre Dame Bay, and the west coast (zones III, IV, and IX). About 35% of the total harvest is taken in these zones. The hunting peak is less than two months in White and Notre Dame bays but longer on the Northern Peninsula, where it extends into early winter in some years, and first-year birds are again predominantly taken. Common Murres are recorded in early harvests in zone IV, before this species has moved out of northern coastal waters (Elliot, this volume).

The hunt then shifts to the south and east coasts in winter (January-March), along Bonavista, Trinity, and Conception bays, the Avalon and Burin peninsulas, and the south coast of the island (zones V, VI, VII, and VIII). The south coast and southern peninsulas have a relatively long hunting season, with murres present from late fall on and a 2.5-month hunting peak. The peak is less than two months long in Bonavista, Trinity, and Conception bays, where murres arrive well into the winter and are still present when the season ends on 31 March. The latter zones would be most affected if the season closing were advanced to 10 March, in line with migratory game bird seasons, as about 15% of the hunting days and 25% of the harvest occur there after that date. Most murres shot on the east coast and southern peninsulas are older than one year (Elliot, this volume), and thus a 10 March closing date would preferentially conserve older birds, including many Thick-billed Murres of breeding age.

Hunting success (kill/day) was highest in the eastern zones in both the peak month and through the season (Table 9). Although Trinity and Conception bays accounted for only about 6% of permit holders, the high success rates there brought their harvest share to about 10%. Field observations showed that these zones near Common Murre colonies had quite high proportions of this species in the March harvests as birds returned to breeding areas. That species also occurred in harvests along the south coast and Burin Peninsula through much of the winter (Elliot 1987).

When a murre harvest management regime is developed, data from these surveys will enable managers to select practical zones and hunting seasons to meet harvest reduction target levels, considering the numbers of murres taken in each zone and, to a lesser extent, their age and species composition. Although not reported here, the comments noted in these surveys document the attitudes of murre hunters and show that most now support practical harvest limits. If the harvest by non-permit holders can be successfully estimated using an amended sample selection process, these surveys will continue to provide important data to monitor the activities, harvests, and attitudes of murre hunters and the possible effects of their harvests on murre populations.

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Preliminary estimates of survivorship and recruitment for Thick-billed Murres at Coats Island

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Abstract

Recruitment by Thick-billed Murres *Uria lomvia* was investigated at a colony on Coats Island in northern Hudson Bay. We used resightings of birds banded as chicks at the colony to estimate survivorship. The influences of emigration, site attachment of prospectors, band loss, and banding mortality on the estimates are discussed. A minimum of 2% of the three-year-olds and 16% of the four-year-olds attempted to breed in 1988, almost all unsuccessfully. In 1989, at least 8% of the four-year-olds and 31% of the five-year-olds attempted to breed. Rates of resightings at the colony were compared with rates of recoveries of banded birds in Newfoundland and Labrador. We conclude that differences in winter conditions between years have a significant effect on cohort-specific survivorship curves.

Résumé

Le recrutement de la Marmette de Brünnich *Uria lomvia* a été étudié dans une colonie de l'île Coats, dans le nord de la baie d'Hudson. De nouvelles observations d'oiseaux bagués au stade d'oisillons, dans la colonie, ont servi à évaluer le taux de survie. On décrit les influences, sur les évaluations, de l'émigration, de la préférence accordée au lieu par les prospecteurs, de la perte de bagues et de la mortalité des oiseaux bagués. Au moins 2 % des oiseaux de trois ans et 16 % des oiseaux de quatre ans ont tenté de se reproduire en 1988, presque tous sans succès. En 1989, au moins 8 % des oiseaux de quatre ans et 31 % des oiseaux de cinq ans ont tenté de se reproduire. Les taux des nouvelles observations à la colonie ont ensuite été comparés au taux de récupération des oiseaux bagués à Terre-Neuve et au Labrador. Nous en concluons que les différences des conditions météorologiques en hiver, d'une année à l'autre, ont des incidences marquées sur les courbes de survie des différentes cohortes.

1. Introduction

Thick-billed Murres *Uria lomvia*, like other alcids, do not breed for several years after their initial return to the colony. The age of first breeding in other alcids ranges from two to three years in Cassin's Auklet *Ptychoramphus aleuticus* (Speich and Manuwal 1974) and Black Guillemots *Cepphus grylle* (Asbirk, in Hudson 1985) to five to eight years in the Atlantic Puffin *Fratercula arctica* (Harris 1981). Although there have been some preliminary estimates of survival to recruitment (reviewed in Hudson 1985), very little is known of age-specific survival rates in alcids.

Thick-billed Murre populations in the eastern Canadian Arctic are subject to significant mortality through the traditional winter murre hunts in Newfoundland, Labrador, and Greenland (Elliot et al., this volume). The annual kill in Canada is likely between 500 000 and 1 000 000 birds, close to half of which are in their first winter. Goodman (1974) showed theoretically that demographic variables such as survivorship and fecundity should respond to changes in other demographic variables. Hence, we anticipate that the high adult mortality sustained by western Atlantic Thick-billed Murres may have resulted in compensatory adjustments in other demographic parameters, such as the age of first breeding.

In this paper, we report the age of first return and recruitment to breeding status of Thick-billed Murres at Coats Island. Our main aims are:

(1) to demonstrate the degree of philopatry among young birds returning to Coats Island;
(2) to use resightings in a fraction of the colony to estimate survivorship for each age cohort;
(3) to estimate the minimum proportion of each age cohort that attempts to breed; and
(4) to examine the evidence for age-specific or cohort-specific mortality patterns provided by comparing the resightings of banded birds at the colony with the rates of banded birds recovered from Newfoundland and Labrador.

2. Methods

2.1. Field methods

Each year from 1984 to 1989, we banded between 1454 and 2686 Thick-billed Murre chicks at Coats Island, Northwest Territories (62°57′N, 82°00′W). This relatively small colony is divided into two subcolonies separated by 1 km of unsuitable coast. The west colony supports about 18 000 pairs, the east colony about 7000 pairs (Gaston et al. 1987). All banding was carried out within a well-defined area including about one-quarter of the population of the west subcolony. All birds in 1984 and 50% of chicks in 1985 were banded with standard stainless steel U.S. Fish and Wildlife Service (USFWS) bands, the inscriptions of which are difficult to read, even at close range. In 1985, half of the chicks and all of the adults were banded with special stainless steel murre bands. These have the number upright on both sides of the band, making it comparatively easy to read with a telescope at distances up to 30 m. After 1985, we used only the special bands. Each chick also received a coloured darvic band indicating the year of banding. All bands were placed on the right leg.

During the 1988 and 1989 breeding seasons, we attempted to read the band numbers of as many birds of known age as possible, concentrating our efforts on specific parts of the colony, all of which were necessarily close to the top of the cliff. Different areas were identified by letters and individual ledges by numbers, so that the position of each observation could be located. In 1988, observations were made daily from 10 June to 17 August. The exact time spent in recording band numbers was not recorded but was in excess of 350 person-hours. In 1989, observations were made daily from 28 July to 19 August in watches of 1 h, amounting to 45 person-hours. We recorded the behaviour of all known-age individuals (i.e., those banded as chicks), their breeding status where possible, and whether the colour-band was present.

From 1986 onwards, we conducted periodic counts of known-age birds during the period from 23 July to 14 August. These were made simultaneously by four observers, using observation points spread along the entire west subcolony, two within and two outside the banding area. Observers counted all visible right tarsi every 10 min, recording the total number seen and the numbers of each year-class. Proportions of different year-classes were averaged over an hour or more of counting.

Most birds for which the right tarsus was visible were standing up; hence, this sample included a disproportionately high number of prospecting birds. Consequently, these counts cannot be used to compare the strengths of different cohorts in a single year. However, they can be used to compare cohorts of the same age among years and the relative abundance of given cohorts within and outside the banding area.

2.2. Estimating survival

It was possible to read bands only over a fraction of the banding area. Moreover, our banding efforts varied in their extent from year to year (see Table 1). Consequently, we have based our survival estimates on the numbers of survivors of a given cohort that returned to two areas: "NG" in 1988 and 1989, and "S" in 1989. All of the ledges in these two areas were included in banding operations between 1984 and 1989.

Survival (S_i) was estimated by comparing the estimate of the total number of survivors (N_s) with the number of chicks originally banded that fledged (C), as follows.

2.2.1. *The original cohort*

The initial size of the cohort (C) was estimated by the equation:

$$C = [N \cdot k \cdot RS \cdot p \cdot (1 - M_i)] \quad (1)$$

where N = mean count of adult murres in the specified area,
k = k-ratio (ratio of breeding pairs to counts of individuals, as described in Birkhead and Nettleship 1980),
RS = reproductive success (chicks reared per breeding pair),
p = proportion of chicks that were of bandable age, and
M_i = chick mortality during banding.

The estimate of C depends on the assumption that the number of adults breeding in the area has not changed since the hatching year of the cohort in question. In area NG, the number of breeding pairs was determined by the product of the count of adult murres (N) and the mean k-ratio determined at a breeding plot D during the same time period. The actual count (N) has no error attached; the error is incorporated into the k-ratio, which, at a colony on Digges Island (200 km east of Coats Island), has been found to vary slightly during the chick-rearing period and among plots (Gaston et al. 1985).

In area S, the number of breeding pairs was calculated differently, by counting eggs and chicks present just after the start of hatching and assuming a 20% loss of eggs to that stage (Gaston and Nettleship 1981).

As the reproductive success (RS) of birds breeding in the NG and S areas was not monitored in any year of the Coats Island study, we used the RS determined for breeding plot D in 1988. The range of breeding success found among plots and years on Digges Island was used to estimate the error.

The p represents the proportion of chicks in the area that were banded. We banded only once on each ledge; some chicks were too small to band, and a few eggs remained unhatched at the time of banding. Although never measured directly, we believe that the proportion marked ranged between 85% and 95%.

Banding mortality for each year (M_i) was estimated, based on the impressions of the banders, in order to correct the estimate of the number of chicks banded for the proportion surviving to fledge ($1 - M_i$).

2.2.2. *Number of survivors*

The number of survivors (N_s) was derived from an estimate of the number of site-attached birds (N_{sa}) in a particular area, corrected for the proportion (E_i) that "emigrated" outside the banding area, as follows:

$$N_s = N_{sa} \cdot (1 + E_i) \quad (2)$$

We defined birds as "site attached" if they were recorded at least twice in one of these areas (which consisted of about 10 ledges each) and not more than once elsewhere. Although the total period of observations was 68 d in 1988, we modified the criteria for three-year-olds to account for an initial lack of site attachment. As many three-year-olds do not arrive until early July (Noble 1990), we considered only the period between 14 July and 17 August.

In order to test the criteria for site attachment, we plotted the cumulative totals of first sightings of individuals of a particular cohort fitting those criteria against date. An asymptote was interpreted as evidence that all members of that age cohort occupying the defined area had been seen.

As the 1985 cohort was banded alternately with USFWS and special bands, we compared the number of site-attached individuals of each band type seen within the defined area to obtain a correction factor for the readability of the two band types. This method assumes that all surviving members of a given cohort were visiting the colony that year and were attached to a particular area. A certain proportion of each cohort appeared to be occupying sites outside the banding area (which we defined as emigration whether or not the individuals subsequently bred there), and this varied with age. We corrected the number of site-attached birds (N_{sa}) for this fraction.

The emigration rate (E_{ij}) for a given age i in year j was calculated from the ratio (R_{ij}) of known-age birds recorded within versus outside the banding area during the simultaneous counts. As the nonbanding area contains three times as many birds as the banding area, we estimated the proportion (E_i) of a given age-class that was settled outside the banding area as:

Table 1
Numbers of Thick-billed Murre chicks banded annually at Coats Island, and the number recovered each winter in Newfoundland and Greenland

Banding year	No. banded	No. recovered each winter				
		1984–85	1985–86	1986–87	1987–88	1988–89
1984	1454	35	22	2	3	2
1985	1619	—	32	11	9	2
1986	2237	—	—	21	18	11
1987	2250	—	—	—	55	16
1988	2686	—	—	—	—	40

Table 2
Ages at which colour-banded murres first returned to the colony and first attempted to breed

Age in years	No. banded	Seen at the colony		Known to attempt breeding	
		No. seen	% of murres banded as chicks	No. known to breed	% of total no. seen
1988					
One	2250	0	—	0	—
Two	2237	97	4.3	0	—
Three	1619	150	9.3	3	2.0
Four	1454	45	3.1	7	15.5
1989					
One	2686	0	—	0	—
Two	2250	48	2.1	0	—
Three	2237	103	4.6	0	—
Four	1619	57	3.5	4	7.0
Five	1454	16	1.1	5	31.2

$$E_i = 3 / (3 + R_i) \quad (3)$$

An important assumption of the previous step is that our watch areas are representative of the entire banding area, and that they are not subject to an abnormal amount of emigration or immigration.

Thus, survival of a particular cohort to a given age i, corrected for emigration and mortality during banding (M_i), was determined by:

$$S_i = [N_{sa} \cdot (1 + E_i)] / [(N \cdot k \cdot RS \cdot p) \cdot (1 - M_i)] \quad (4)$$

2.3. Evidence of cohort-specific mortality

In order to investigate cohort-specific patterns of survival, we analyzed data from the simultaneous watches from 1986 to 1989. Only counts between 23 July and 16 August, a period represented in all four years, were included. Although we report data from the GH area only, the proportions of known-age birds seen from the two vantage points (GH and I) within the banding area did not differ.

The attendance rates of known-age birds at the colony were estimated from the proportions of colour-banded right tarsi counted during the simultaneous watches. The estimates were corrected for the total number of chicks banded each year (Table 1) and year-specific band loss rates.

Band loss was assessed by two methods. We determined the proportion of a sample of specimens recovered in Newfoundland that had lost their colour-band and the proportion of colour-band loss in individuals resighted at the colony in 1988. As we have found no evidence of band wear on Coats Island since banding began in 1981, we have assumed that all band loss occurs early in life (i.e., the bands fell off the chicks before their legs grew to full size).

We tested for differences in the proportions (arcsine square-root transformed) of known-age birds present among years using the Fisher PLSD multiple range test in the ANOVA procedures of STATVIEW. The pattern of return rates at the colony was compared with the pattern of recovery rates of known-age birds shot in Newfoundland.

3. Results

3.1. Age and timing of return

No first-year birds were observed at the colony (Table 2). In 1988, when observations commenced early in the season (10 June), two-year-olds were first seen on 28 June. Three-year-olds were first seen on 14 June and four-year-olds on 11 June, a few days before egg laying began. In 1989, birds of all ages from two to five were present on our arrival at the colony on 28 July.

3.2. Recruitment

Only three (2%) of 150 three-year-olds seen in 1988 were observed breeding, and all three lost their egg within two weeks of laying (Table 2). Two-year-olds did not arrive until midway through the incubation period, and none attempted to breed.

Seven of the 45 four-year-olds (16%) whose band numbers were recorded in 1988 attempted to breed (Table 2). Only one of the total of eight breeding four-year-olds was successful in raising a chick to fledging age in that year. Our presence probably contributed to the failure of at least two of the attempts. Of the seven failures, one egg did not hatch and five eggs and one chick disappeared, perhaps taken by Glaucous Gulls *Larus hyperboreus*, major predators of eggs and chicks at Coats Island.

In 1989, only four (7.0%) of 57 identified four-year-olds and five (31%) of 16 identified five-year-olds were known to breed (Table 2). Another three five-year-olds bred on plot S, but their band numbers were not read. There was no evidence of breeding by three-year-olds in 1989.

3.3. Emigration

Birds banded as chicks that regularly visited areas outside the banding area provided evidence of dispersal. The proportions of two-year-olds among birds whose tarsi were seen within the banding area between 1987 and 1989 ranged from five to 21 times the proportions outside, and the proportions of three-year-olds ranged from nine to 28 times as high (Table 3). The mean ratios for all years combined (R_i) were 10.7 for two-year-olds, 15.1 for three-year-olds, 14.3 for four-year-olds, and 19.4 for five-year-olds. This yielded estimates for emigration from the banding area of 26% for two-year-olds, 17% for three- and four-year-olds, and 13% for five-year-olds.

Only one banded bird (a three-year-old) was ever seen at the east subcolony, of more than 1000 birds examined there. We have therefore ignored emigration to other colonies, although some may occur.

3.4. Survival

3.4.1. *Estimate of the number of site-attached individuals*

The criteria for site attachment were tested by plotting the cumulative total of sightings in 1988. Observations were carried out every day until day 76 (1 June = 1). The total number of site-attached three-year-olds banded with the special bands approached an asymptote of just over 30, suggesting that we recorded practically all individuals attached to sites in NG. Similar plots of the cumulative first sightings of three- and four-year-olds banded with the USFWS bands (Figs. 1 and 2) were not asymptotic.

Table 3
Ratios of known-age murres counted within:outside the banding area during simultaneous watches on Coats Island

	Age in years				No. of murres counted	
Year	Two	Three	Four	Five	Within	Outside
1987	5.0	8.6	—	—	9994	7175
1988	6.2	8.6	10.9	—	7608	11174
1989	20.8	28.0	17.7	19.4	2262	6726
Mean ratio	10.7	15.1	14.3	19.4		

Thirty of the three-year-olds banded with special bands were site-attached in the NG area in 1988, as well as 15 banded with USFWS bands. Return rates should not be affected by band type, so we assumed that the difference in numbers sighted related to the readability of the inscriptions. Fifty percent of the 1985 cohort were banded with the special bands; hence, we estimated that there were 60 site-attached three-year-olds in the NG area in 1988 (Table 4). Ten four-year-olds were site-attached in NG in 1988. All chicks banded in 1984 received the USFWS bands, so, using the above correction, we estimated that there were 20 site-attached four-year-olds in total (Table 4).

Correcting for the 1988 age-specific emigration rates, we estimated that there were 76 surviving three-year-olds and 24 surviving four-year-olds of the original cohorts from NG are at the colony in 1988 (Table 4).

3.4.2. Estimate of the original banded cohort

The mean count of adults (N) in plot NG in August 1988 was 372, and the mean August k-ratio (k) was 0.67. We assumed an error of ± 0.05, which was the range in k-ratio found by Gaston et al. (1985) on nearby Digges Island.

Reproductive success at plot D was 0.66 in 1988; variation in breeding success among years and plots at Digges Island (Gaston et al. 1985) suggested an error of approximately ±0.12. Chick mortality during banding (M_i) was estimated as 10% in 1984 and 5% in 1985 and subsequently. Hence, we estimated that 143 and 135 banded chicks successfully fledged from the NG area in 1985 and 1984, respectively (Table 4).

3.4.3. Survival estimate

Substituting the parameters above into equation 1 yielded a survival estimate of 53% to age three for the 1985 cohort, which provided the best data set (Table 4). By substituting the upper and lower limits of the error estimates of each parameter used to calculate survival, we obtained a range of survival to third year of 36–74%. By the same method, survival of the 1984 cohort to fourth year was estimated to be 18% (Table 4).

The number of resightings in the NG area in 1989 was much lower than in 1988 because of the shorter duration of the field season. Hence, the estimates of survival based on data from that year are probably underestimates. The S area was much smaller than the NG area, with an estimated 119 breeding pairs.

In 1989, based on resightings at the colony, survival to third year was estimated as 19% in area NG and 16% on plot S. Survival to fourth year was 17% in both areas NG and S, and survival to fifth year was 3% in both areas (Table 4). We did not estimate the error in these estimates.

3.5. Evidence for cohort-specific survival rates

The proportions of known-age birds detected in the simultaneous counts were corrected for year-specific colour-band loss rates and the total numbers of chicks banded each year.

Figure 1
Comparison of the cumulative number of site-attached three-year-olds, banded with special bands or USFWS bands, seen in the NG area in 1988

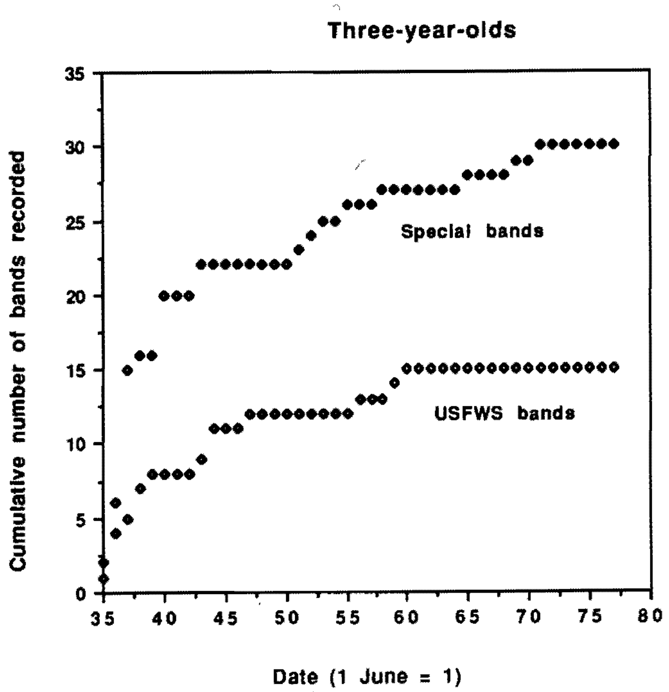
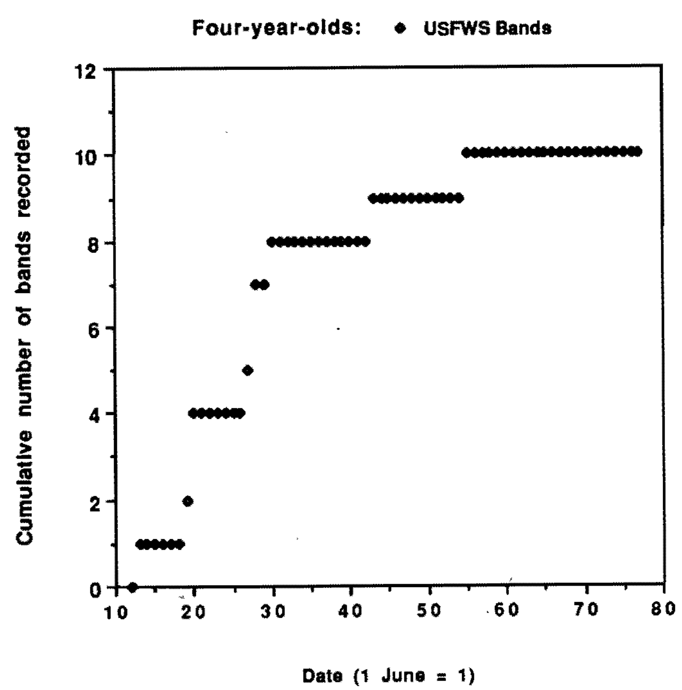


Figure 2
Cumulative number of site-attached four-year-olds seen in the NG area in 1988 (all banded with USFWS bands)



3.5.1. Colour-band loss

Colour-band loss rates varied among years, based on two sources of data: resightings at the colony, and recoveries of banded birds in Newfoundland (Table 5). Although the two sources suggested different overall loss rates, birds banded with the special bands appeared to retain their colour-bands longer than those banded with USFWS bands. Mean colour-band loss rates were 16.2%, 3.8%, and 0.5% for 1984, 1985, and 1986, respectively.

Table 4
Steps in the calculation of survival rates to three, four, and five years

Age in years (cohort)	Study area	Initial no. in banded cohort[a]	No. seen site-attached[b]	Ratio of banded murres counted within:outside banding area	Emigration rate (%)	No. alive at colony	Estimated survival rate (%)
1988							
Three (1985)	NG	143	60	8.6	25.9	76	53
Four (1984)	NG	153	20	10.9	21.6	24	18
1989							
Three (1986)	NG	143	25	28.0	9.7	28	19
	S	81	12			13	16
Four (1985)	NG	143	20	17.7	14.5	25	17
	S	81	12			14	17
Five (1984)	NG	135	4	19.4	13.4	4.5	3
	S	77	2			2	3

[a] Corrected for banding mortality.
[b] Corrected for band type.

3.5.2. Comparisons of attendance at the colony

Multiple comparisons of the proportions of two-year-olds detected in the simultaneous counts (corrected for colour-band loss rates and the number of chicks originally banded) showed that the proportions were significantly influenced by banding year ($F = 6.585$, $p = 0.004$). A significantly greater proportion of the 1984 cohort was present as two-year-olds compared with the 1986 or 1987 cohorts. The proportion of the 1986 cohort present at age two was also significantly less than that of the 1985 cohort (Fig. 3).

The proportions of three-year-olds present, corrected in the same way, were not significantly influenced by banding year ($F = 1.839$, $p = 0.195$), although the 1985 cohort was better represented than either the 1984 or 1986 cohort (Fig. 3). Comparison of the four-year-olds showed that the proportion of the 1985 cohort present was significantly greater than the proportion of the 1984 cohort present at the same age ($F = 5.735$, $p = 0.037$).

4. Discussion

4.1. Age of return and recruitment

As found for most other alcids (Petersen 1976; Lloyd and Perrins 1977; Birkhead and Hudson 1977; Ashcroft 1979), no first-year birds were ever seen at the colony. The arrival of two-year-olds midway through the incubation period at Coats Island is also consistent with those studies. We assumed that all three- and four-year-olds visited the colony. However, the fact that the proportion of three-year-olds detected in the simultaneous watches was consistently greater than that of two-year-olds suggested that not all two-year-olds visited the colony (Fig. 3).

In 1988, only a very small proportion of three-year-olds and slightly larger numbers of four- and five-year-olds attempted to breed. Mean lay date was relatively early and chicks reached high weights, which suggest that conditions in 1988 may have been particularly favourable (AJG and DGN, unpubl. data).

This pattern of recruitment is consistent with previous observations at Coats and Digges islands, where one possible four-year-old and six five-year-olds were found brooding chicks (Gaston et al. 1987). These data are also similar to ages of first breeding reported for Common Murres *Uria aalge*: three years at an expanding colony in Scotland (Swann and Ramsay 1983) and four years at an expanding colony on Skomer Island (Hudson 1985). However, breeding attempts by young birds at Coats Island were probably more common than recorded. We know little

Table 5
Estimated rate of colour-band loss, assuming no loss of metal bands

Banding year	Type of metal band	Method of estimation	No. checked	No. with no colour-band (%)
1984	USFWS	Recoveries in Nfld.	34	8 (23)
1984	USFWS	Resightings at the colony (1988)	45	4 (9)
1985	USFWS	Recoveries in Nfld.	10	1 (10)
1985	USFWS	Resightings at the colony (1988)	49	2 (4)
1985–86	Special	Recoveries in Nfld.	23	0
1985–86	Special	Resightings at the colony (1988)	198	1 (0.5)

about many individuals that were seen only rarely. First-time breeders appear to have very poor reproductive success, and our chances of observing quickly lost eggs were very low.

4.2. Emigration and philopatry

Observations of returning known-age birds suggest that Thick-billed Murres at Coats Island are relatively philopatric. Known-age birds seen outside the banding area amounted to less than 10% of those seen within the banding area.

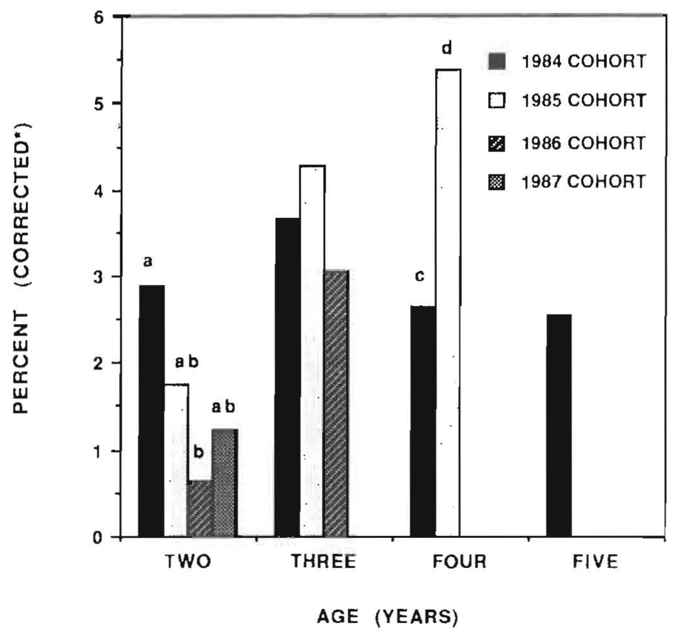
Although the banding locations of chicks banded prior to 1986 were not recorded, resightings of birds banded in 1986 showed that most returned very close to their natal site. In 1988, 35 (52%) of 67 two-year-olds resighted were seen only in the area where they were banded.

We know that some known-age birds did settle far outside the banding area. For example, in 1988, one four-year-old regularly occupied a site at the far end of the colony. The gradual tendency to be found within the banded area with increasing age probably reflects the closer site attachment of older birds as their prospecting range decreases.

Few two-year-olds were site-attached, and this age cohort had the greatest proportion of birds seen outside the banding area (Table 3). It appears that two-year-olds that arrive during the incubation period usually visit several areas before settling in a particular location.

There are no published records of visits to a nonnatal colony by Thick-billed Murres, but extensive colony interchange has been reported in other alcids (Lloyd and Perrins 1977)—up to 50% among surviving Atlantic Puffin recruits (Harris 1983). Although one visit to the other Coats Island subcolony was recorded, recruitment to other colonies was considered negligible.

Figure 3
Comparison of attendance at the colony as seen from the GH vantage point (corrected to per 1000 birds banded and adjusted for band loss) of four cohorts. Different letters within an age-class indicate significant differences among the percentages of those cohorts present.



* Corrected for band loss and per 1000 birds banded

4.3. Survival estimates

Our best estimate of survival of prebreeding Thick-billed Murres at Coats Island is 53% to age three, with a range of error (based on errors in the components of equation 2) from 36% to 74%. Survival to age four was estimated to be 18% in 1988 and 17% in 1989. The latter are almost certainly underestimates, because cumulative plots of first sightings of site-attached individuals showed no sign of approaching an asymptote.

Low percent return rates based on observations of colour-marked birds have been reported in most studies of recruitment in alcids (Birkhead and Hudson 1977; Lloyd and Perrins 1977; Ashcroft 1979; Harris and Wanless 1988). Return rates for Common Murres and Razorbills *Alca torda* were generally lower than those reported here, ranging from 10% to 20% for survival to three, four, and five years of age. Return rates for Atlantic Puffins were even lower, attributed partly to emigration (Harris 1983).

Judging from the adult survival rates listed in Table 5.4 in Hudson (1985), estimates obtained by analyses of band recoveries consistently yield higher survival estimates than those based on resightings. Survival rates based on rates of return to the colony can be regarded as minima only, because of the difficulties in recording all of the individuals present.

Although the data presented here are based on incomplete knowledge of some of the important parameters (and hence our estimates are preliminary), they illustrate a method of estimating survival rates with a small subset of birds in a large seabird colony. Colony- or year-specific differences in emigration rates, site attachment, or band loss can be incorporated.

Another possible method of estimating survival is the modified capture-recapture model used by Harris (1983) to calculate survival of Atlantic Puffins to fifth year by retrapping them at the colony. However, catch effort techniques are not appropriate at Coats Island, because the assumptions of a closed population and a constant probability of capture or resighting (Davies and Winstead 1980) are violated. Our efforts at capturing prebreeders and reading band numbers varied considerably over the season and between years and were difficult to quantify.

We did compare our survivorship estimates with one obtained from all resightings of members of a group of chicks banded on one readily identifiable ledge in the NG area in 1985. Of 53 chicks banded with the special bands, 15 were resighted at the colony in 1988 and an additional three in 1989, suggesting that the survival of this group to third year was at least 34%. As only a small number of these were seen in 1989, presumably due to the reduction in observer effort then, we did not estimate survival to fourth year.

The derived survival estimates required a number of assumptions, some of which were discussed earlier. First, we assumed that there was no preference for particular areas. However, observations of the breeding plots suggest that recruits tend to colonize ledges on the periphery (AJG and DGN, unpubl. data). Moreover, we noted that many prebreeders congregrated on broad or unoccupied ledges, presumably because breeders on narrower ledges usually repel prospectors.

Another consideration is the extent to which prebreeders visit several areas of the colony and the criteria we use to assign site-attached status. We know that many individuals, even breeders, will visit other areas occasionally. A plot of the best set of data, the cumulative total of the number of site-attached three-year-olds with special bands seen, was asymptotic. Therefore, although the "two visit" criterion is somewhat arbitrary, it is probably the most appropriate in these circumstances.

4.4. Cohort-specific differences in survival rates: the effects of hunting and climatic conditions

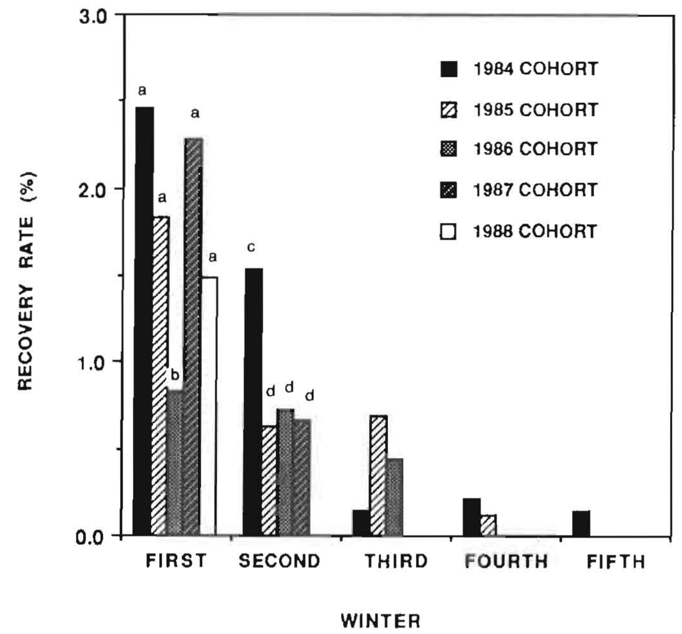
The large difference in the mean estimates of survival to third and fourth years may represent a low survivorship from three to four years. However, it is more likely that there are significant differences in the age-specific survival rates of the 1984 and 1985 cohorts. Climatic conditions and hunting activity in Newfoundland and Labrador vary from year to year and are likely to affect different-aged cohorts differently.

A greater proportion of the 1984 cohort returned to the colony as two-year-olds, compared with the 1985 cohort. However, more of the 1985 cohort returned at the ages of three and four years (Fig. 3). The reversal suggests that mortality of the 1984 cohort was particularly high in their third winter (1986–87), affecting them more than it did the 1985 cohort in their third winter (1987–88).

This scenario is consistent with data from band recoveries in Newfoundland and Labrador (Table 1). All of the recoveries included in these analyses are of birds shot by hunters. The recovery rate of the 1984 cohort was higher than that of the 1985 cohort during their first two winters (Fig. 4), significantly so in their second winter ($\chi^2 = 10.72$, $p = 0.013$). However, by the third winter, the pattern had reversed, with the 1985 cohort recovery rate higher (although not significantly so) than the 1984 cohort recovery rate in their third winter ($\chi^2 = 3.12$, $p = 0.209$) (Fig. 4).

In both cohorts, recovery rate declined most dramatically in the winter of 1986–87. Furthermore, the

Figure 4
Comparison of rates of recovery in Newfoundland of different cohorts and different ages of Thick-billed Murres banded on Coats Island between 1984 and 1988. Different letters within an age-class indicate significant differences in recovery rates among those cohorts.



recovery rate of the 1986 cohort in their first winter (1986–87) was significantly lower than all other cohorts ($\chi^2 = 21.25$, $p = 0.0003$) (Fig. 4). Recoveries of birds that were in at least their fourth winter also declined abruptly in 1986–87 (Table 6).

We consider several possibilities. Relatively low recovery rates of all cohorts over the winter of 1986–87 may have been due to reduced hunting pressure. There may have been a major source of mortality sometime between the winters of 1985–86 and 1986–87. It is also possible that a single factor such as extensive ice cover could simultaneously increase natural mortality and reduce hunting activity.

The reduced-hunting-pressure hypothesis is supported by the fact that recovery rates of both the 1984 and 1985 cohorts increased in the season following the winter of 1986–87. It also agrees with observations that relatively few murres were harvested during the winter of 1986–87 (Elliot et al. 1991; RDE, unpubl. data). Some hunters said that the few birds present during the winter of 1986–87 were in such poor condition that they were not worth shooting. This suggests that it may have been low food availability in combination with weather conditions affecting hunting activity that reduced the kill as well as overwinter survival during that winter.

Counts at the colony show that although significantly more of the 1984 cohort attended the colony as three-year-olds than as two-year-olds (Fig. 3), the increase with age was much less pronounced than for the 1985 cohort. It appears that the 1984 cohort, despite being older, was more adversely affected by conditions during the winter of 1986–87 than was the 1985 cohort.

We speculate that the poor survival of the 1984 cohort in that winter, compared with the younger 1985 cohort, was due to differences in wintering area and timing of southward migration. A.J. Gaston et al. (unpubl. data) noted that first- and second-year birds have similar temporal patterns of recovery in Newfoundland, differing from the timing of recoveries of birds aged three years or more, which have spent their summer in the north.

Table 6
Numbers of murres banded as chicks and recovered in at least their fourth winter (Digges Island, 1980–81), and numbers banded as adults and recovered each winter (Digges Island, 1979–82; Coats Island, 1981, 1984–88)

Year	No. banded as chicks	No. banded as adults
1984–85	13	3
1985–86	17	7
1986–87	4	1
1987–88	2	0
1988–89	0	0

We suggest that the 1984 cohort, although initially doing well, was affected to a greater extent than the 1985 cohort by heavy ice or weather conditions during the winter of 1986–87 as a result of temporal or spatial differences in wintering behaviour. The 1986 cohort, in its first winter, was also particularly vulnerable to those conditions, and relatively few returned to the colony in their second year.

5. Summary

At Coats Island, many individuals return to the colony at the age of two years, and probably most surviving birds are attending the colony by their third year. Our best estimates of survivorship are 53% to third year and 18% to fourth year, but these estimates are cohort-specific. We speculate that the difference in the survival of the 1985 cohort relative to the 1984 cohort is due mainly to differences in wintering behaviour. Poor weather or ice conditions during the winter of 1986–87 may have increased mortality directly or by reducing the availability of food, resulting in higher natural mortality, although with fewer recoveries because of the reduction in hunting. Philopatry to colony appears to be very high, and emigration from the natal area to areas outside the banding area exhibited a gradual decline between the ages of two and five. A small number of three-year-olds and larger numbers of four- and five-year-olds attempted breeding, most unsuccessfully.

Acknowledgements

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Population changes in British Common Murres and Atlantic Puffins, 1969-88

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Abstract

The number of Common Murres *Uria aalge* in Britain and Ireland more than doubled, to 1.2 million, between 1969-70 and 1985-88. However, many populations started to decline by the early 1980s. In the North Sea, this decline started earliest in the north and gradually spread south, while the southern populations were still increasing. The decrease at an intensively studied colony appeared to be due to poor recruitment, which probably indicates poor survival of immatures. The number of Atlantic Puffins *Fratercula arctica* in Britain and Ireland increased, but by a smaller proportion, over the same period. The rate of increase in the population of Isle of May decreased after 1981, and by 1988 the population appeared stable. Survival of both adults and immatures was reduced. "Natural" factors were probably responsible for these changes, and there is nothing obvious that can be done in the way of management.

Résumé

Le nombre de Marmettes de Troïl *Uria aalge*, en Angleterre et en Irlande, a plus que doublé, atteignant 1,2 million, entre 1969-1970 et 1985-1988. Cependant, de nombreuses populations ont commencé à diminuer au début des années quatre-vingt. Dans la mer du Nord, cette baisse a commencé par le nord s'étendant graduellement vers le sud, tandis que les populations du sud continuaient de s'accroître. La diminution, dans une colonie qui fait l'objet d'études intensives, semble attribuable à une diminution du recrutement, qui reflète probablement une baisse du taux de survie des jeunes oiseaux. Le nombre de Macareux moines *Fratercula arctica*, en Angleterre et en Irlande a augmenté, quoique dans une faible proportion, au cours de la même période. Le rythme d'augmentation de la population de l'île de May a ralenti après 1981 et, en 1988, la population semblait stable. Par ailleurs, la survie des adultes et des jeunes a diminué. Des facteurs «naturels» sont probablement à la base de ces changements, de sorte qu'aucune mesure particulière de gestion ne semble appropriée.

1. Introduction

Britain and Ireland have large and internationally important populations of seabirds, and during the last 20 years much effort has been put into monitoring changes in their numbers. Auks have figured prominently in this work because:

(1) they are numerous and obvious;
(2) they are peculiarly susceptible to a whole range of pollutants, including oil and chemicals (Bourne 1976);
(3) they are potential competitors with expanding human fisheries for small fish such as sand lance *Ammodytes* spp. (Evans and Nettleship 1985);
(4) various species feed in different ecological zones, which allows interesting ecological comparisons to be made; and
(5) they have great appeal to the general public so that, if they are threatened, funds are often made available for research.

Much attention has focused on the Common Murre *Uria aalge* and the Atlantic Puffin *Fratercula arctica*, although for different reasons: the former is common, obvious, easily counted, and susceptible to oil pollution, whereas the latter has great public appeal and was at one time thought to be endangered.

Most monitoring schemes were originally set up solely to monitor changes in the numbers of seabirds. A recent review of the results of annual counting of murres at sample areas of British colonies concluded that the techniques used provided adequate descriptions of long-term changes in numbers but did not lead to a greater understanding of either the biological process involved or the factors that might be influencing the numbers of birds at the colonies (Rothery et al. 1988). Recent work has, therefore, concentrated on developing schemes to monitor various aspects of the demography and breeding biology of seabirds in an attempt to remedy this shortcoming.

The present paper reports on recent changes in the numbers of murres in Britain and on breeding output and survival at a single Scottish colony, where numbers were increasing rapidly until recently but are now declining. Some comparative data are also presented for the Atlantic Puffin from the same areas, although the results of the detailed studies are reported more fully elsewhere (Harris and Wanless 1991).

2. Methods

2.1. Common Murre

The numbers of individual murres ashore at all British and Irish colonies were counted in 1969-70 (Operation Seafarer) and in 1985-87 (Nature Conservancy Council - Seabird Group Seabird Colony Register). In these counts, it was impossible to separate breeding and nonbreeding birds. At most colonies, only single counts were made, so that the totals are of unknown accuracy. Counts at the same place made on different days can vary by up to 26% (Lloyd 1975), but, on the Isle of May during each June from 1981 to 1989, the mean error of single counts was 12% (95% confidence interval 7-17%, n = 9 years).

Commencing in 1969, numbers of murres at several colonies have been monitored annually by counting the individuals present in clearly defined areas on 5-10 d during the chick-rearing period in June (Seabird Group 1981; Stowe 1982). The representativeness of the sample plots used to determine population trends has been questioned (Harris et al. 1983; Heubeck et al. 1986; Mudge 1988), but, during the 1980s, attempts were made to overcome this by siting plots in some objective way (e.g., at random or stratified) or by counting all the birds in the colony (which may again cause problems if it is possible to make only a single count each year). As I am concerned here with long-term changes in numbers and not with year-to-year variation, I have given equal weight to complete and sample counts. The clear patterns that emerge suggest that the approach was justified. The colonies considered are shown in Figure 1 and listed in Table 1. In the Firth of Forth, murres on the Isle of May and all five nearby colonies have been counted regularly, and consequently I have pooled the counts and treated the colonies as a unit (Harris et al. 1987).

The results of complete surveys of all British and Irish murre and puffin colonies come from the reports and data files of Operation Seafarer (Cramp et al. 1974) and the Seabird Colony Register (C.S. Lloyd, pers. commun.). Monitoring of seabirds is carried out by a number of organizations, and there is, as yet, no complete data base of counts. My information included all counts stored in the Seabird Colony Register, with additional published and solicited unpublished data from Benn et al. (1987), Birkhead and Ashcroft (1975), Evans (1989), Harris et al. (1987), Hatchwell (1988), P. Hawkey (unpubl. data), Heubeck (1989a, and pers. commun.), Mudge (1986), K. Rideout (pers. commun.), Royal Society for the Protection of Birds (unpubl. data), Thomas (1988), Wanless et al. (1982), Ward (1987), and reports of the Nature Conservancy Council.

For each colony, counts (ln) were plotted against year, and any obvious trends in numbers and turning points were assessed visually. All apparent trends involving counts in at least five years were tested using linear regression analysis, and only those significant at the 5% level are included here. Where a significant trend was found, all the years involved were included in the regression; thus, when a trend was reversed, a single year could be included in both a significant decline and a significant increase.

2.2. Atlantic Puffin

Puffins are much harder to census than murres, but the total population was assessed in 1969-70 and 1985-87, whereas that in east Britain (from the Moray Firth to the

Figure 1
Locations of colonies of Common Murres and Atlantic Puffins mentioned in the text. Numbers refer to the colonies listed in Table 1. The arrows indicate the limits of the east British population.

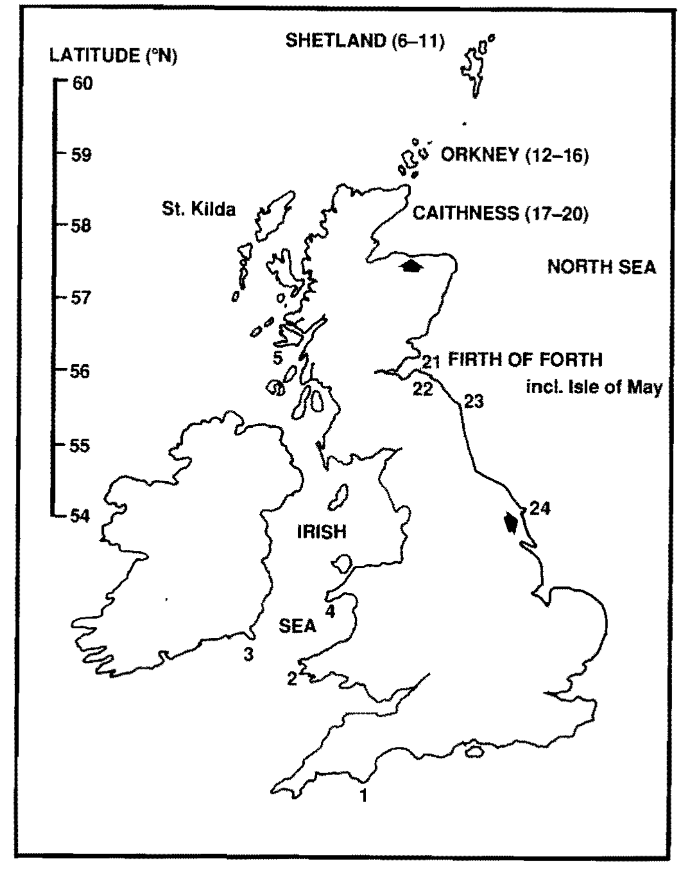
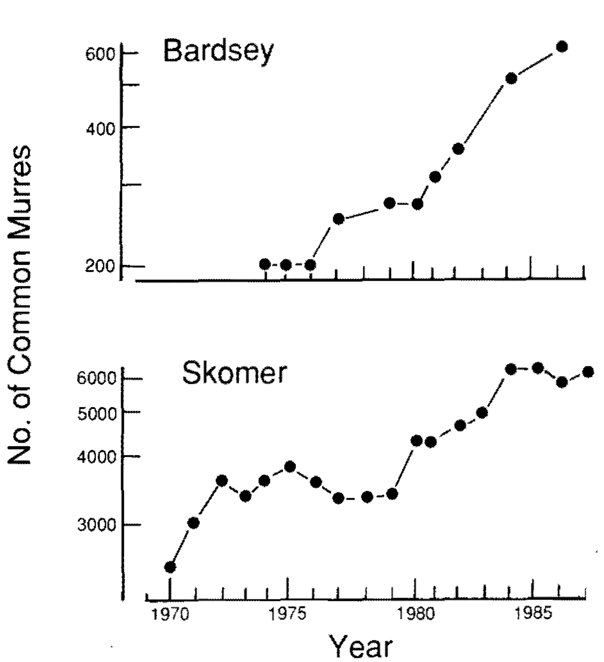


Table 1
Rate of change in the numbers of Common Murres at some British colonies[a]

	Colony[b]	Period	Type of count	No. of annual counts over which the trend extended	Mean change per annum (%)
1	Berry Head	1976-87	Total	6	+13
2	Skomer	1978-87	Total	9	+7
3	Great Saltee	1978-87	Total	5	+4
4	Bardsey	1976-87	Total	8	+10
5	Canna	1974-83	Sample	9	+11
6	Hermaness	1982-88	Sample	7	-8
7	Noss	1981-88	Sample	8	-7
8	Burravoe	1982-88	Total	7	-28
9	Eshaness	1981-88	Total	8	-11
10	Troswickness	1976-82	Sample	7	+3
		1982-88	Sample	7	-12
11	Sumburgh Head	1977-84	Sample	8	+6
		1984-88	Sample	5	-5.5
12	Costa Head	1976-81	Sample	5	+5
13	Marwick Head	1976-80	Sample	5	+6
14	Row Head	1976-80	Sample	6	+6
15	Mull Head	1976-80	Sample	5	+13
	Mull Head	1981-88	Sample	8	-3
16	Gultak	1976-82	Sample	6	+4
	Gultak	1981-88	Sample	8	-3
17	Skirza	1980-84	Sample	5	-3
	Skirza	1984-88	Sample	5	+4
18	Inver Hill	1980-86	Sample	6	-6
19	Badbea	1980-87	Sample	8	-2
20	An Dun	1980-88	Sample	9	-3
21	Firth of Forth	1969-83	Total	5	+7
22	St. Abb's Head	1969-88	Total	10	+7.5
23	Farne Islands	1972-88	Total	16	+14
24	Bempton	1975-87	Sample	11	+4

[a] Only instances in which there was a significant ($P < 0.05$) linear change over at least five counts are included.
[b] Numbers refer to Figure 1. At another Caithness colony, Iresgoe, there was no significant linear change.

Figure 2
Complete colony counts of Common Murres on Bardsey and Skomer, Irish Sea. Note log scale of y axis.



River Humber) was estimated every four to six years. Where possible, counts were made in terms of occupied burrows, but at some colonies estimates were based on counts of the numbers of birds present. The numbers of occupied burrows on Dun, part of Britain's largest colony on St. Kilda (Fig. 1), have been assessed every four to five years, and those at Hermaness and Isle of May, Firth of Forth, have been assessed annually (Harris 1984; Harris and Rothery 1988; Martin 1989).

2.3. Breeding and numbers of Common Murres and Atlantic Puffins on the Isle of May

These data were collected in standardized ways (Harris 1984; Harris and Wanless 1985, 1988). Adult survival rates were based on resightings of colour-banded birds, and immature survival rates come from large-scale resighting and retrapping of birds colour-banded as chicks at the natal and other colonies. Breeding success was taken to be the proportion of young leaving the colony from a known number of eggs laid, assessed without handling the adults. The diet and feeding frequency of young were assessed by observations from blinds and the collection of fish retrieved from adults, chicks on the breeding ledges, or burrows. The energy values of loads were calculated using relationships in Harris and Hislop (1978), up to the maximum values determined from fish taken from auks on the Isle of May.

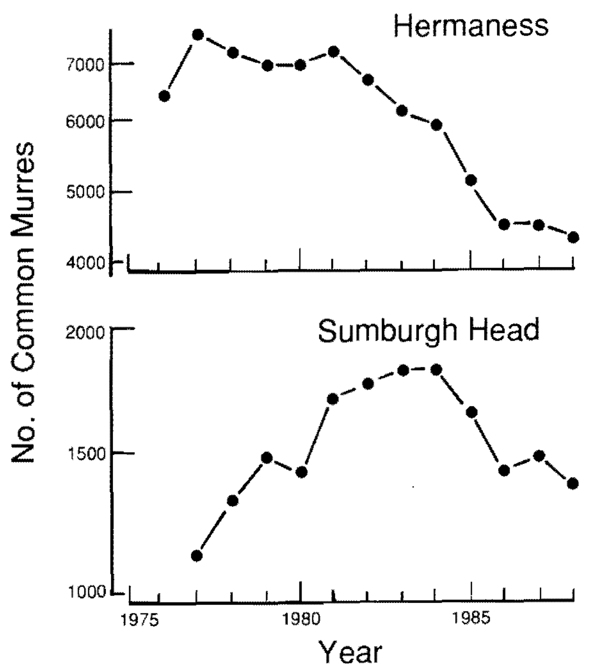
3. Results

3.1. Population changes

3.1.1. *Common Murre*

The total British and Irish population increased from about 540 000 individuals in 1969–70 to 1 200 000 in 1985–88. In both surveys, 80% of the birds were at Scottish colonies. In 1982, Stowe and Harris (1984) estimated the population at 1 100 000 individuals by using counts made at 120 (of about 200 known) colonies and the 1969–70 distribution of birds. Increases between 1969–70 and 1985–88 were largest (490%) in southwest Scotland (totaling all colonies) and smallest (50%) in southwest Ireland and southwest England (C.S. Lloyd, pers. commun.).

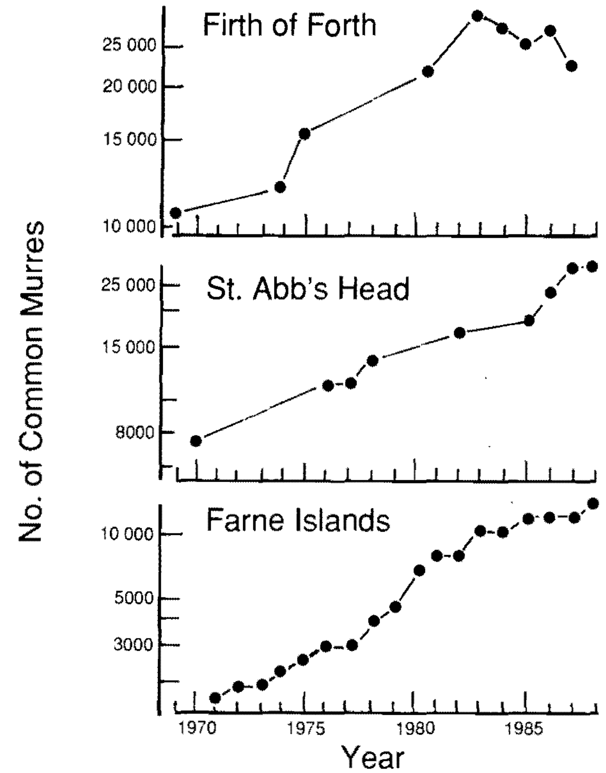
Figure 3
Counts of Common Murres in sample plots at Hermaness and Sumburgh, Shetland Islands. Note log scale of y axis.



Where additional counts were available for intervening years, it was obvious that numbers at some colonies had increased and then declined while still being above the 1969–70 level, and that patterns of change varied greatly between colonies. Murres at Irish Sea colonies were badly affected during a severe national wreck of seabirds in the autumn of 1969, and numbers at many colonies subsequently declined — for example, by 40% on Skomer (Birkhead and Ashcroft 1975). Numbers recovered slightly in the following years and then stabilized, but it was not until the late 1970s that counts indicated a sustained increase, which continued to at least 1987 (Table 1, Fig. 2). Farther north in the Inner Hebrides, numbers on Canna increased at 11% per year between 1974 and 1983 but have since declined slightly (Swann and Ramsay 1984; Swann et al. 1989).

A series of 18 colonies or areas arranged from north to south from the northern tip of Shetland down the east side of Scotland to the Farne Islands has been counted regularly. Numbers increased at all colonies during the 1960s and 1970s, but the most northern colonies started to decline in the late 1970s and early 1980s (Fig. 3); by 1988, all but the most southern colonies counted — those at St. Abb's Head and the Farne Islands — were declining (Fig. 4). Overall, there was a significant negative correlation between the year when numbers were highest and the latitude of the colony (Fig. 5) ($r = -0.60$, $n = 20$, $P < 0.01$). Numbers at some colonies were still declining at the time of the most recent available counts. At others, recent counts were higher than those recorded when counting was initiated. However, in general, the lowest counts in the last 15–20 years occurred much earlier in the southern colonies. Counts at the colony on Helgoland, Germany, which is at the same latitude as the southernmost British North Sea colony that is monitored, showed similar trends, with numbers very low in 1967 and 1973–74 and then increasing steadily up to 1985 before remaining stable in 1986 and 1987 (Vauk-Hentzelt et al. 1986; Kleist and Werner 1987; Meyer 1988). Outside the North Sea, the small population farther south in Brittany has increased from about 250 pairs in 1981 to 350+ pairs in 1988 (P. Yesou, pers. commun.). The

Figure 4
Complete colony counts of Common Murres in the Firth of Forth (total of six colonies), St. Abb's Head, and Farne Islands. Note log scale of y axis.



population in Iberia declined dramatically, from 20 000 birds in the 1950s to 300 in the early 1980s, apparently due to predation and pollution (Barcena et al. 1984), and there are few signs of recovery.

The annual rates of increase and decrease at the various British colonies that showed significant sustained linear changes are given in Table 1. The mean rate of increase at 17 colonies was 7.3% per year (SE = 0.9). Excluding Burravoe, a small colony where some adults were shot by vandals (M. Heubeck, pers. commun.), the mean rate of decline was 5.8% ($n = 11$, SE = 1.03). All declines occurred at colonies in or near the North Sea during the 1980s, and there was a significant relationship between the rate of decrease and latitude, the numbers at northern colonies decreasing most rapidly (Fig. 6) ($r = 0.78$, $P < 0.01$). There was no significant relationship between the rates of increase and latitude.

3.1.2. *Atlantic Puffin*

The total British and Irish population in 1984–88 was about 600 000 occupied burrows, with approximately 90% in Scotland. This figure suggests an overall increase of about 20% since 1969–70. In part, this could be an artifact resulting from improved coverage of some of the large isolated colonies, but the increase is supported by the regular monitoring counts on Dun, St. Kilda, which show an increase of 18% between 1977 and 1987 (Harris and Rothery 1988). Numbers at the large colony at Hermaness have remained fairly stable through 1973–88 (A.R. Martin, pers. commun.).

There have been proportionally large increases at some small southern colonies in England and Wales. In northeast Britain, the total number of pairs of puffins between Troup Head (Grampian) and Bempton (Humberside) (Fig. 1) was estimated at 10 000 in 1969, 17 000 in 1974, 24 000 in 1979, and 49 000 in 1984, which indicates a steady rate of increase of 10% per year.

Figure 5
Year of recent maximum count of Common Murres at 19 British colonies in relation to latitude. All the colonies were in northeast Britain. Arrows indicate where the maximum count was at the start or end of the period of counts.

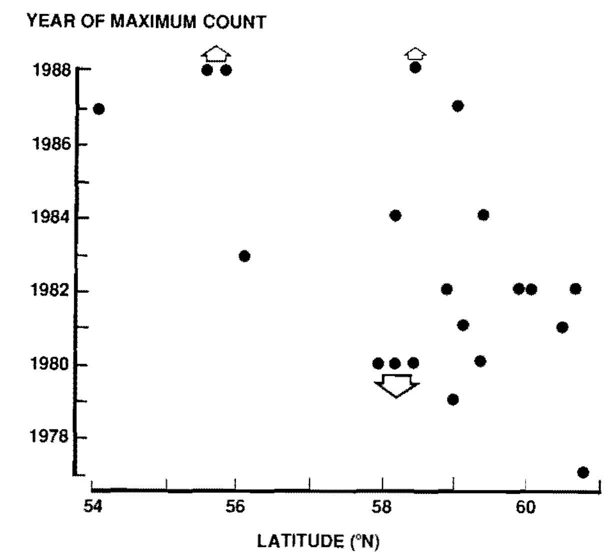
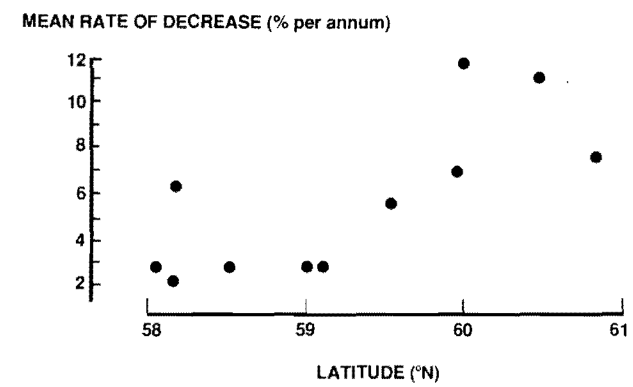


Figure 6
Rates of decrease of the numbers of Common Murres at 11 colonies in northeast Britain in relation to latitude



3.2. Demography and breeding on the Isle of May

3.2.1. *Common Murre*

Counts increased during the 1970s and early 1980s (Harris and Galbraith 1983), stabilized about 1983, and declined significantly from 1986 onwards (Fig. 7). The numbers of pairs known to breed in study plots stabilized slightly later and did not decline. The reduction in total numbers was attributed to a combination of fewer nonbreeding birds and changes in attendance behaviour of breeding adults.

Adult survival and most measures of breeding output remained very high from 1981 to 1988 (Table 2). Two murres of known age had been found breeding on the Isle of May up to 1988; one was three years old (and was brooding a small chick when caught), and the other was six (and had been present for the two previous seasons but had certainly not bred). Of 133 chicks colour-banded in 1983, 11 (8%) were identified during intensive daily searches of the breeding areas and loafing rocks, and only four (3%) were known to have definitely survived until five years of age. Of 250 chicks marked in 1984, 11 (4.5%) were present at four years of age. Despite thorough searches of other colonies in east Britain, only two chicks reared at the Isle of May have been found elsewhere, both on the Farne Islands; one of these was subsequently seen back on the Isle of May.

3.2.2. Atlantic Puffin

The annual counts of burrows in about a quarter of the colony showed that the population increased at 19% per year between 1973 and 1981, after which the increase slowed; for the first time, numbers declined slightly between 1987 and 1988 (Fig. 8). There was little variation in breeding success or the mass of food fed to chicks during the 16 years (Table 3), but fledging weight declined ($r = 0.812$, $n = 15$, $P < 0.001$). The population increased each year until 1987, so it is unclear whether the decrease in fledging weight was due to increasing intraspecific competition for food (Gaston 1985) or to changes in the overall food supply.

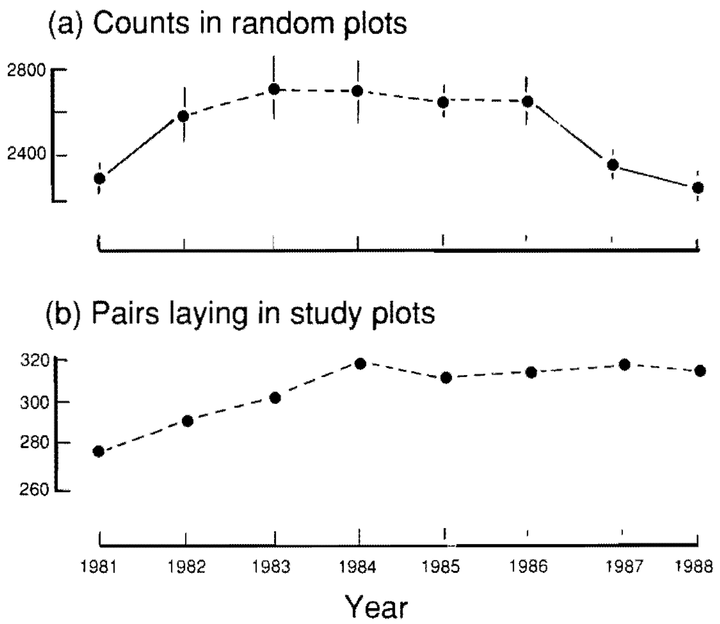
Adult survival decreased quite abruptly after the winter of 1980-81, at exactly the same time that the rate of population increase slowed down. The most recent survival estimates could be too low, as not every adult is recorded every year, so that some missing birds could still be alive. However, recalculating the survival rates using Leslie models (Leslie and Chitty 1951) to allow for this confirmed the reduction in survival: the mean of nine estimates from 1973 to 1981 was 96.0% (SE = 1.8), and the mean of five estimates from 1981 to 1987 was 91.4% (SE = 1.8). The survival of adult puffins is also monitored on Skomer, where survival declined from a mean of 95.8% per year in 1973-78 to a mean of 88.4% per year in 1978-86 (C.M. Perrins, unpubl. data).

Estimates of immature survival (calculated from fledging until the median age of first breeding at five years for birds returning to the island) are available for chicks fledging each year from 1973 to 1978. The mean survival of the 1973-77 cohorts was 28%; that of the 1978 cohort was 18% (Harris and Wanless 1991). Large-scale colour-banding and subsequent checking of many British colonies indicated that at least 46% of young puffins recruited to colonies away from where they hatched, which suggests that about one-half of the young survived to breeding age from the cohorts produced during the 1970s. Immature puffins can be separated from adults by bill characters, and the proportions of such birds present on the Isle of May declined from 37% in 1980 to 0-10% in 1985-88, which also suggests that survival of immatures had decreased in recent years (or that more birds were emigrating and fewer were immigrating).

4. Discussion

The most likely reason for the decrease in total numbers of Common Murres while the numbers breeding remained constant is a reduction in the numbers of immature murres returning to the colony. Hudson (1985) listed 10 estimates of the survival of chicks until breeding age; the mean of these was 30% (SE = 2), and even the lowest estimate (17%) was far in excess of the numbers found back on the Isle of May. Most of these published estimates were based on banding returns and so are probably not directly comparable with sight records. However, on Skomer, similar methodology indicated that 17-23% of young survived to return to the colony between 1973 and 1977 when numbers were stable (Hudson 1979); in 1987, 13 (9%) of 148 chicks ringed in 1985 were seen, compared with only 10 (1.2%) of 796 young recorded on the Isle of May at a similar age (Hatchwell 1988; pers. obs.). On the Isle of May in 1989, 33 (17%) of 199 young colour-banded in the main study colony in 1986 were seen at the colony, which suggested that survival of that cohort was high and supported the conclusion that most of the young

Figure 7
Mean counts (± 2 SE) of (a) individual Common Murres in monitoring plots, and (b) pairs laying in study plots on the Isle of May, 1981-88. Solid lines joining points indicate significant differences (t-tests; $P < 0.05$).



ringed in 1983-85 had died, rather than been overlooked on the Isle of May or elsewhere.

Immature murres are known to visit other colonies, but there are no quantitative estimates available on the rates of emigration or immigration. It is possible that some young reared on the Isle of May have recruited into the nearby colonies at St. Abb's Head or the Farne Islands, as these are still expanding, but careful searches have failed to locate any. Details of this aspect of murre biology are needed urgently.

Banding recoveries provide some indication on the age and cause of death of murres from the Isle of May. Of 45 recoveries of murres ringed as chicks in 1981-87, 29 (64%) were reported in the first year after leaving the colony, 13 (29%) in the second year, and only three (7%) when older. Although more older birds will doubtless be reported in the future, there is obviously a large mortality in the first year and, to a lesser extent, second year. There have been wrecks involving large numbers of immature murres found dead or dying, apparently of starvation, in the North Sea in several winters during the 1980s (e.g., Underwood and Stowe 1984). Of 73 recoveries of murres of all ages banded on the Isle of May, 51 (70%) occurred between November and February, which coincided with the timing of these wrecks. Most recoveries were of birds found dead on the shore (47%), whereas fewer were oiled (25%), tangled in fishing nets (25%), or shot (3%).

Although breeding output was high right up to 1988, there was evidence that in the later years the duration of feeding trips for adults with young had increased (MPH and S. Wanless, unpubl. data), suggesting that birds were having to travel farther to feed or taking longer to catch prey in the feeding area. There is, therefore, some evidence of a recent reduction in food availability during the chick-rearing period, which would result in lower counts, as fewer off-duty adults would be present (Gaston and Noble 1986). So far this has not been reflected in a reduction in the daily energy intake of the young. However, adults appear to be approaching the time when they cannot extend their

Table 2
Details of breeding, food of young, and adult survival for Common Murres on the Isle of May, 1981-88

Year	Median laying date (May)	Lost eggs replaced (%)	Young fledged/pair	Leaving weight (g)[a]	Feeds/day	Value of fish (kJ)	Daily intake g	Daily intake kJ	Adult survival[b]
1981	8	60	0.81	?	5.2	113	61	590	?
1982	8	39	0.79	249	3.4	104	45	354	93.0
1983	7	52	0.77	250	4.1	94	44	386	93.2
1984	5	43	0.70	262	3.6	82	36	295	93.5
1985	7	41	0.86	262	3.8	64	30	244	93.7
1986	10	52	0.81	264	3.9	69	33	269	97.3
1987	8	45	0.80	252	3.7	86	37	319	92.6
1988	6	86	0.86	252	3.5	113	39	396	92.4

[a] Leaving weight is the mean weight of chicks with wing lengths of more than 60 mm.
[b] Survival refers to survival over winter between year n and year n + 1.

Figure 8
Counts of occupied Atlantic Puffin burrows in sample areas on the Isle of May, 1973-88

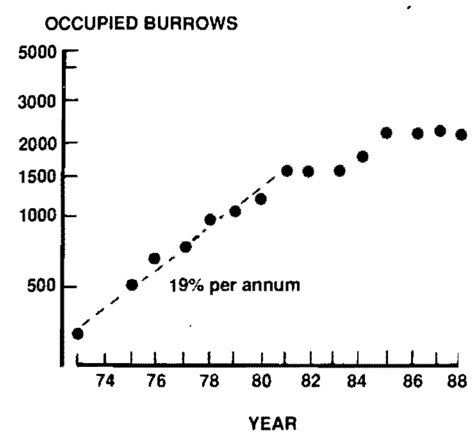


Table 3
Details of adult survival, breeding success, food intake, and fledging weights of chicks and immatures present for Atlantic Puffins on the Isle of May, 1973-88

Year	Adult survival[a] (%)	Chicks fledged per pair	Intake of chicks per day g	Intake of chicks per day kJ	Fledging weight (g)	% immatures[b]
1973	94.6	0.74	?	?	?	?
1974	98.4	?	?	?	289	?
1975	94.7	?	57	435	293	?
1976	97.9	?	37	249	304	12
1977	95.0	0.73	65	513	281	15
1978	93.6	0.87	42	310	289	28
1979	95.5	0.90	46	348	278	22
1980	95.0	0.76	27	194	285	37
1981	86.1	0.89	43	330	272	15
1982	87.5	0.92	40	284	279	15
1983	86.0	0.79	47	316	273	22
1984	93.9	0.88	49	353	270	14
1985	89.2	0.79	47	330	270	5
1986	84.3[b]	0.80	36	259	281	10
1987	76.1[b]	0.93	43	315	270	0
1988	?	0.88	47	310	264	0

Note: See Harris (1984) and Harris and Wanless (1991) for methods and sample sizes.
[a] Survival from year n to year n + 1.
[b] In mist-net catches during the chick-rearing period.

feeding trips farther and still guard the chick, and, if conditions become worse, chick production could be affected.

The Isle of May is the only British colony for which detailed information on numbers and ecology is available for the Atlantic Puffin. During the 1970s, numbers increased at an average rate of 19% per year compared with the 16% per year expected from the demographic data, indicating that the colony must have been receiving recruits from other colonies (Harris 1984). During the 1980s, a less complete data set indicated that although the proportion of birds breeding and breeding success remained high, adult and immature survival had both decreased, and that this should result in the stabilization of the population, a prediction borne out by counts of the colony (Harris and Wanless 1991).

4.1. Implications for management

A period of rapid increase for British murre and puffin populations appears to have ended recently. Numbers in 1988 were more or less stable or declining. Young auks disperse widely (Mead 1974), and birds from different natal areas occur in the same areas. Immature murres banded on the Isle of May have been recovered all around Britain. It is, therefore, difficult to envisage a regular latitudinal ranking of wintering areas, although critical data are lacking. The sequential latitudinal trend in the timing of this change among colonies in the North Sea points to a cause operating during the breeding season. However, whereas murres on the Isle of May had been making longer feeding trips during the chick-rearing period in the later few years, this was not reflected in a reduced breeding output. Similarly, at none of the many colonies visited each year during monitoring counts or chick banding did observers report any serious breeding failures. The same appeared to be true for puffins up to 1986; however, during the last three breeding seasons, pairs at two of the largest colonies in Shetland, Hermaness and Foula, reared very few chicks, apparently because the adults were unable to obtain small sand lance (Furness 1989; Martin 1989). This food shortage also resulted in breeding failures of Arctic Tern *Sterna paradisaea* and Black-legged Kittiwake *Rissa tridactyla* (Monaghan et al. 1989; Heubeck 1989b). The reduction in numbers of sand lance around Shetland appears to be a natural event (perhaps exacerbated by a human fishery) and part of a widespread change in the marine environment of the northern North Sea (Kunzlik 1989; Harris and Wanless 1990).

Thus, although there is some evidence that conditions during the breeding season have deteriorated recently, and a possibility that this occurred first in northern colonies, it is difficult to reconcile these findings with the observed population changes. All the evidence suggests that a reduction in immature survival and also, in the case of the puffin, in adult survival outside the breeding season has been responsible for the leveling off or decline in numbers, but with this explanation it is hard to see why systematic, geographic differences should have arisen.

The similar declines in the annual survival rates of puffins nesting on Skomer, which winter to the south and east of Britain, and birds on the Isle of May, which winter mainly in the North Sea, suggest that recent changes must be acting over a wide area. Further, the coincidence in changes of population trends of Isle of May puffins, which winter well offshore, and murres, which winter closer to land (Tasker et al. 1987), suggests that a range of habitats may be affected. Despite recent advances in our knowledge of auks at sea, we still know almost nothing of their ecology in winter. Auks in Britain get oiled, get caught in fishing nets, accumulate heavy metals, PCBs, and other chemicals, and are (rarely) shot, but present knowledge suggests that these threats are now fairly minor (Evans and Nettleship 1985), although there is increasing concern about the numbers of auks drowned in fishing nets (Mead 1989). Changes in the marine environment are the most likely reasons for recent changes. We can fairly easily protect the birds while they are at their breeding sites, but it is difficult to protect them at sea, except by reducing the pollution of the sea and managing fish stocks sensibly.

Attaining these aims will be no small achievement. Rigorous population studies will probably do little to help the birds directly but must continue, as they will enable us to identify the magnitude of problems once they become apparent. The detailed work on the puffins on Røst, Norway, and their repeated failures to rear young (Lid 1981) is a good example of a problem being highlighted before the population declined noticeably. However, care must be exercised not to claim a species as endangered or threatened after a minor decline in numbers or breeding success. Auks are much more resilient species than they sometimes appear.

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Literature cited

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

Atkins, N.; Heinemann, B. 1987. The dangers of gill netting to seabirds. Am. Birds 41:1395-1403.

Barcena, F.; Teixeira, A.M.; Bermejo, A. 1984. Breeding seabird populations in the Atlantic sector of the Iberian Peninsula. Pages 335-345 *in* Croxall, J.P.; Evans, P.G.H; Schreiber, R.W. (eds.), Status and conservation of the world's seabirds. Int. Counc. Bird Preserv. Tech. Rep. No. 2, Cambridge, U.K.

Benn, S.; Tasker, M.L.; Reid, A. 1987. Changes in numbers of cliff-nesting seabirds in Orkney, 1976-1985. Seabird 10:51-57.

Bertelsen, A. 1921. Fuglene i Umanaq Distrikt. Medd. Groenl. 33:141-214.

Bertelsen, A. 1948. Fuglemærkningen i Vest-Grønland i Aarene 1926-1945. Medd. Groenl. 142(4):1-34.

Birkhead, T.R. 1974. Movement and mortality rates of British Guillemots. Bird Study 21:241-254.

Birkhead, T.R.; Ashcroft, R.E. 1975. Auk numbers on Skomer Island. Nat. Wales 14:222-223.

Birkhead, T.R.; Hudson, P.J. 1977. Population parameters for the Common Guillemot *Uria aalge*. Ornis Scand. 8:145-154.

Birkhead, T.R.; Nettleship, D.N. 1980. Census methods for murres, *Uria* species: a unified approach. Can. Wildl. Serv. Occas. Pap. No. 43. 25 pp.

Birkhead, T.R.; Kay, R.; Nettleship, D.N. 1985. A new method for estimating the survival rates of the Common Murre. J. Wildl. Manage. 49:496-502.

Boertmann, D. 1979. Ornithologiske øbservationer i Vestgrønland i somrene 1972-77. Dan. Ornithol. Foren. Tidsskr. 73:171-176.

Bøllehus, B. 1986. Redegorelse for laksefiskeriet 1986. Notat fra Grønlands Fiskerilicenskontrol [Review of the salmon fishery 1986]. Unpubl. report, Greenland Fishing Licence Control Authority.

Bourne, W.R.P. 1976. Seabirds and pollution. Pages 403-502 *in* Johnson, R. (ed.), Marine pollution. Academic Press, London, U.K.

Brown, R.G.B. 1986. Revised atlas of eastern Canadian seabirds — 1. Shipboard surveys. Can. Wildl. Serv., Ottawa. 111 pp.

Brownie, C.; Anderson, D.R.; Burnham, K.P.; Robson, D.S. 1985. Statistical inference from band recovery data — a handbook. 2nd ed. U.S. Fish Wildl. Serv., Resour. Publ. No. 156. 305 pp.

Chapdelaine, G.; Gaston, A.J.; Brosseau, P. 1986. Censusing the thick-billed murre colonies of Akpatok Island, Northwest Territories. Can. Wildl. Serv. Prog. Notes No. 163. 9 pp.

Christensen, O.; Lear, W.H. 1977. Bycatches in salmon drift-nets at West Greenland in 1972. Medd. Groenl. 205:1-38.

Cochran, W.G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, New York, NY. 428 pp.

Cramp, S.; Bourne, W.R.P.; Saunders, D. 1974. The seabirds of Britain and Ireland. Collins, London, U.K. 287 pp.

Davies, D.E.; Winstead, R.L. 1980. Estimating the numbers of wildlife populations. Pages 221-246 *in* Schemnitz, S. (ed.), Wildlife management techniques manual. 4th ed. The Wildlife Society, Washington, DC.

Dickson, K.M. 1989. Migratory game birds killed in Canada during the 1987 hunting season. Can. Wildl. Serv. Prog. Notes No. 179. 41 pp.

Elliot, R.D. 1985. Preliminary field investigations of the Newfoundland turr hunt in 1983-84. Unpubl. report, Can. Wildl. Serv., St. John's. 23 pp.

Elliot, R.D. 1986. Preliminary field investigations of the Newfoundland turr hunt in 1984-85. Unpubl. report, Can. Wildl. Serv., St. John's. 27 pp.

Elliot, R.D. 1987. Field investigations of the Newfoundland turr hunt in 1985-86. Unpubl. report, Can. Wildl. Serv., St. John's. 54 pp.

Elliot, R.D. 1989. Background for a Newfoundland turr harvest management strategy. Unpubl. report, Can. Wildl. Serv., St. John's. 69 pp.

Elliot, R.D.; Gaston, A.J. 1986. The age structure of the Newfoundland Thick-billed Murre harvest. Poster paper presented at the 19th Int. Ornithol. Congr., Ottawa. 10 pp.

Elliot, R.D.; Ryan, P.C.; Lidster, W.L. 1990. Winter diet of Thick-billed Murres in coastal Newfoundland waters. Stud. Avian Biol. 14:125-138.

Elliot, R.D.; Hayakawa, E.G.; Collins, B.T.; Métras, L. 1991. Surveys of murre hunting in Newfoundland from 1977-78 to 1987-88. Can. Wildl. Serv. Tech. Rep. (in press).

Etcheberry, R. 1990. The spring migration (1990) in St. Pierre and Miquelon Islands. Osprey 21:78-87.

Evans, P.G.H. 1984. The seabirds of Greenland: their status and conservation. Pages 49-84 *in* Croxall, J.P.; Evans, P.G.H; Schreiber, R.W. (eds.), Status and conservation of the world's seabirds. Int. Counc. Bird Preserv. Tech. Publ. No. 2, Cambridge, U.K.

Evans, P.G.H. 1986. Monitoring seabirds in the North Atlantic. Pages 179-206 *in* MEDMARAVIS [Mediterranean Seabird Group]; Montbailliu, X. (eds.), Mediterranean marine avifauna. Springer-Verlag, Berlin.

Evans, P.G.H. 1987. Project studying ways to reduce the impact of hunting upon the Brunnich's Guillemot *Uria lomvia* populations of Upernavik District, West Greenland, July 1st - September 8th 1987. Unpubl. report, Upernavik, Greenland. 41 pp.

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

Evans, P.G.H.; Waterston, G. 1976. The decline of the Thick-billed Murre in Greenland. Polar Rec. 18:283-287.

Evans, P.G.H.; Waterston, G. 1977. Recent salmon netting restrictions in South-West Greenland. Polar Rec. 18:507-508.

Evans, R.J. 1989. Seabird studies in east Caithness, summer 1988. Royal Society for the Protection of Birds report to Britoil, Sandy, Bedfordshire, U.K. 19 pp.

Falk, K.; Durinck, J. 1989. Polarlomvien ved Vestgrønland, efteraret 1988: Pelagisk udbredelse samt vurdering af omfanget af drukning i laksegarn [The Thick-billed Murre in West Greenland, autumn 1988: pelagic distribution and the extent of net entanglement in salmon drift nets]. Greenland Home Rule, Department of Wildlife Management Tech. Rep. No. 9. 38 pp. (In Danish with English summary.)

Falk, K.; Durinck, J. 1990. Lomviejagten i Vestgrønland 1988-89 [Thick-billed Murre hunting in West Greenland 1988-89]. Greenland Home Rule, Department of Wildlife Management Tech. Rep. No. 15. 40 pp. (In Danish with English summary.)

Filion, F.L.; DuWors, E.; Jaquemot, A.; Bouchard, P.; Boxall, P.; Gray, P.A.; Reid, R. 1989. The importance of wildlife to Canadians: highlights of a national survey. Can. Wildl. Serv. Spec. Publ., Ottawa. 43 pp.

Furness, R.W. 1989. Changes in diet and breeding ecology of seabirds on Foula 1971-88. Pages 22-25 *in* Heubeck, M. (ed.), Seabirds and sandeels: Proceedings of a seminar in Lerwick, 15-16 October 1988. Shetland Bird Club, Lerwick, U.K.

Gaston, A.J. 1980. Populations, movements and wintering areas of Thick-billed Murres (*Uria lomvia*) in eastern Canada. Can. Wildl. Serv. Prog. Notes No. 110. 10 pp.

Gaston, A.J. 1984. How to distinguish first-year murres, *Uria* spp., from older birds in winter. Can. Field-Nat. 98:52-55.

Gaston, A.J. 1985. Development of the young in the Atlantic Alcidae. Pages 319-352 *in* Nettleship, D.N.; Birkhead, T.R. (eds.), The Atlantic Alcidae. Academic Press, Orlando, FL.

Gaston, A.J.; Cairns, D.K.; Elliot, R.D.; Noble, D.G. 1985. Natural history of Digges Sound. Can. Wildl. Serv. Rep. Ser. No. 46. 67 pp.

Gaston, A.J.; Elliot, R.D.; Noble, D.G. 1987. Studies of Thick-billed Murres on Coats Island, Northwest Territories, in 1981, 1984, 1985 and 1986. Can. Wildl. Serv. Prog. Notes No. 167.

Gaston, A.J.; Goudie, R.I.; Noble, D.G.; Macfarlane, A. 1984. Observations on "turr" hunting in Newfoundland: age, body condition and diet of thick-billed murres (*Uria lomvia*), and proportions of other seabirds killed off Newfoundland in winter. Can. Wildl. Serv. Prog. Notes No. 141. 7 pp.

Gaston, A.J.; Jones, I.L. 1984. Guide to the seabirds of eastern Canada. Can. Wildl. Serv., Ottawa. 53 pp.

Gaston, A.J.; Nettleship, D.N. 1981. The Thick-billed Murres of Prince Leopold Island — a study of the breeding ecology of a high arctic seabird. Can. Wildl. Serv. Monogr. No. 6, Ottawa. 350 pp.

Gaston, A.J.; Noble, D.G. 1986. The possible effect of food availability on incubation and breeding shifts of Brunnich's Guillemot *Uria lomvia* at Digges Island, Northwest Territories. Seabird 9:47–51.

Gaston A.J.; Noble, D.G.; Purdy, M.A. 1983. Monitoring breeding biology parameters for murres *Uria* spp.: levels of accuracy and sources of bias. J. Field Ornithol. 54:275–282.

Goodman, D. 1974. Natural selection and a cost ceiling on reproductive effort. Am. Nat. 108:247–268.

Haldane, J.B.S. 1955. The calculation of mortality rates from ringing data. Proc. 11th Int. Ornithol. Congr. 1954:454–458.

Hansard. 1951. Record of the proceedings of the House of Commons of Canada, 14 March 1951; the Migratory Birds Convention Act. pp. 1239–1261.

Harris, M.P. 1981. Age determination and age of first breeding of British puffins. Br. Birds 74:246–256.

Harris, M.P. 1983. Biology and survival of the immature puffin, *Fratercula arctica*. Ibis 125:109–114.

Harris, M.P. 1984. The puffin. Poyser, Calton, U.K. 224 pp.

Harris, M.P.; Galbraith, H. 1983. Seabird populations of the Isle of May. Scott. Birds 12:174–180.

Harris, M.P.; Hislop, J.R.C. 1978. The food of young puffins. J. Zool. (London) 185:213–236.

Harris, M.P.; Rothery, P. 1988. Monitoring of puffin burrows on Dun, St. Kilda, 1977–1987. Bird Study 35:97–99.

Harris, M.P.; Wanless, S. 1985. Fish fed to young Guillemots, *Uria aalge*, and used in display on the Isle of May, Scotland. J. Zool. (London) 207A:441–458.

Harris, M.P.; Wanless, S. 1988. The breeding biology of Guillemots *Uria aalge* on the Isle of May over a six year period. Ibis 130:172–192.

Harris, M.P.; Wanless, S. 1990. Breeding success of British kittiwakes *Rissa tridactyla* in 1986–1988: evidence for changing conditions in the northern North Sea. J. Appl. Ecol. 27:172–187.

Harris, M.P.; Wanless, S. 1991. Population studies and conservation of Puffins *Fratercula arctica*. Pages 230–248 *in* Perrins, C.M.; Lebreton, J.D.; Hirons, G. (eds.), Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, U.K.

Harris, M.P.; Wanless, S.; Rothery, P. 1983. Assessing changes in the numbers of Guillemots *Uria aalge* at breeding colonies. Bird Study 30:57–66.

Harris, M.P.; Wanless, S.; Smith, R.W.J. 1987. The breeding seabirds of the Firth of Forth, Scotland. Proc. R. Soc. Edinburgh 93B:521–533.

Hatchwell, B.J. 1988. Population biology and coloniality of Common Guillemots *Uria aalge*. Ph.D. thesis, University of Sheffield, Yorkshire, U.K. 222 pp.

Heubeck, M. 1989a. Monitoring of breeding seabirds in Shetland in 1988. Report to Shetland Oil Terminal Environmental Advisory Group, University of Aberdeen, Scotland, U.K. 125 pp.

Heubeck, M. 1989b. Breeding success of Shetland's seabirds: Arctic Skua, Kittiwake, Guillemot, Razorbill and Puffin. Pages 11–18 *in* Heubeck, M. (ed.), Seabirds and sandeels: Proceedings of a seminar in Lerwick, 15–16 October 1988. Shetland Bird Club, Lerwick, U.K.

Heubeck, M.; Richardson, M.C.; Dore, C.P. 1986. Monitoring numbers of Kittiwake *Rissa tridactyla* in Shetland. Seabird 9:32–42.

Holbøll, C. 1846. Ornithologischer Beitrag zuer Fauna Grönlands. Uebersetzt und mit einem Anhange versehen von J.H. Poulsen, Leipzig.

Hudson, P.J. 1979. The behaviour and survival of auks. Ph.D. thesis, University of Oxford, Oxford, U.K. 110 pp.

Hudson, P.J. 1985. Population parameters for the Atlantic Alcidae. Pages 233–261 *in* Nettleship, D.N.; Birkhead, T.R. (eds.), The Atlantic Alcidae. Academic Press, Orlando, FL.

Inder, J.G.; Gillespie, D.I. 1974. Estimates of the kill of migratory game birds in the province of Newfoundland 1959–1965; analysis of small game licence returns. Nfld. Wildl. Div. Tech. Bull. No. 1. 19 pp.

Joensen, A.H.; Preuss, N.O. 1972. Report on the ornithological expedition to North-West Greenland 1965. Medd. Groenl. 191:1–58.

Kampp, K. 1982. Den Kortnæbbede Lomvie *Uria lomvia* i Grønland [The Thick-billed Murre in Greenland]. Unpubl. dissertation, Zoological Museum, University of Copenhagen, Copenhagen. 148 pp. (Translated from Danish by R.G.B. Brown as "Studies on northern seabirds," Can. Wildl. Serv. Rep. No. 164, 1983.)

Kampp, K. 1988a. Lomvien i Grønland [The guillemot in Greenland]. Tusaat 1988(1):2–15. (In Danish, with a Greenlandic translation by R. Hard.)

Kampp, K. 1988b. Migration and winter ranges of Brünnich's Guillemots *Uria lomvia* breeding or occurring in Greenland. Dan. Ornithol. Foren. Tidsskr. 82:117–130.

Kampp, K. 1988c. Grønlands lomvier [Greenland's murres]. Tidsskr. Groenl. 1:13–27.

Kampp, K. 1990. Thick-billed Murre populations of the Thule District, Greenland. Arctic 43:115–120.

Kleist, G.; Werner, R. 1987. Brutpaaraufstellung aus unseren Schutzgebeiten 1986. Seevogel 8:L–L1.

Korte, J. de. 1973. Nederlandse Groenland Expeditie Scorsebysond 1973. Unpublished preliminary avifaunistical report. 10 pp.

Kunzlik, P.A. 1989. Small fish around Shetland. Pages 38–47 *in* Heubeck, M. (ed.), Seabirds and sandeels: Proceedings of a seminar in Lerwick, 15–16 October 1988. Shetland Bird Club, Lerwick, U.K.

Lack, D.; Schifferli, A. 1948. Die Lebensdauer des Stares. Ornithol. Beob. 45:107–114.

Leslie, P.H.; Chitty, D. 1951. The estimation of population parameters from data obtained by means of capture-recapture methods. Biometrika 38:269–292.

Lid, G. 1981. Reproduction of the Puffin at Rost, in the Lofoten Islands in 1964–1980. Fauna Norv. Ser. C, Cinclus 4:30–39.

Lloyd, C.S. 1975. Timing and frequency of census counts of cliff-nesting auks. Br. Birds 68:507–513.

Lloyd, C.S.; Perrins, C.M. 1977. Survival and age of first breeding in the Razorbill (*Alca torda*). Bird-Banding 48:239–252.

Martin, A.R. 1989. Diet of the Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* at a Shetland colony during a period of changing prey availability. Bird Study 36:170–180.

Mattox, W.G. 1970. Bird-banding in Greenland. Arctic 23:217–228.

Mead, C.J. 1974. The results of ringing auks in Britain and Ireland. Bird Study 21:45–86.

Mead, C.J. 1989. Mono-kill. Br. Trust Ornithol. News 163:1.

Meltofte, H. 1976. Ornithological observations from the Scoresby Sund areas, East Greenland, 1974. Dan. Ornithol. Foren. Tidsskr. 70:107–122.

Métras, L.; Wendt, J.S. 1986. Migratory birds killed in Canada during the 1984 season. Can. Wildl. Serv. Prog. Notes No. 161. 39 pp.

Meyer, A. 1988. Brutpaaraufstellung aus unseren Schutzgebieten 1987. Seevogel 9:31–32.

Monaghan, P.; Uttley, J.D.; Burns, M.D.; Thaine, C.; Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in arctic terns *Sterna paradisaea*. J. Anim. Ecol. 58:261–274.

Montevecchi, W.A.; Tuck, L.M. 1987. Newfoundland birds: exploitation, study, conservation. Publ. Nuttall Ornithol. Club 21, Cambridge, MA. 273 pp.

Mudge, C. 1986. Trends of population change at colonies of cliff-nesting seabirds in the Moray Firth. Proc. R. Soc. Edinburgh 91B:73–80.

Mudge, C. 1988. An evaluation of current methodology for monitoring changes in the breeding populations of Guillemots *Uria aalge*. Bird Study 35:1–9.

Nettleship, D.N. 1977. Seabird resources of eastern Canada: status, problems and prospects. Pages 96–108 *in* Mosquin, T.; Suchal, C. (eds.), Proceedings of a symposium on Canada's endangered species and habitats. Can. Nat. Fed. Spec. Publ. 6, Ottawa.

Nettleship, D.N.; Chardine, J. 1989. A simulation model for the management of Thick-billed Murres in the northwest Atlantic. Unpubl. report, Can. Wildl. Serv., Dartmouth.

Nettleship, D.N.; Evans, P.G.H. 1985. Distribution and status of the Atlantic Alcidae. Pages 54–154 *in* Nettleship, D.N.; Birkhead, T.R. (eds.), The Atlantic Alcidae. Academic Press, Orlando, FL.

Noble, D.G. 1990. Factors affecting recruitment in Thick-billed Murres (*Uria lomvia*) on Coats Island, N.W.T. M.Sc. thesis, Queen's University, Kingston. 121 pp.

Northland Associates Ltd. 1986. Native waterfowl harvest in coastal Labrador. Unpubl. report to Can. Wildl. Serv., St. John's. 77 pp.

Oldendow, K. 1935. Naturfredning i Grønland. Groenl. elskabs Skr. 9:1–309.

Pedersen, A. 1930. Der Scorsbysund. Drei Jahre Forschungsreisen an der Ostkuste Gronlands. Berlin. 157 pp.

Pedersen, T.H. 1983. Redegørelse for laksefiskeriet 1983. Notat fra Rigsombudsmanden i Grønland [Review of the salmon fishery 1983]. Unpubl. report, Prefect of Greenland.

Pedersen, T.H. 1984. Redegørelse for laksefiskeriet 1984. Notat fra Rigsombudsmanden i Grønland [Review of the salmon fishery 1984]. Unpubl. report, Prefect of Greenland.

Petersen, A. 1976. Age of first breeding in puffin, *Fratercula arctica*. Astarte 9:43–50.

Piatt, J.F.; Nettleship, D.N. 1987. Incidental catches of marine birds and mammals in fishing nets off Newfoundland, Canada. Mar. Pollut. Bull. 18:344–349.

Piatt, J.F.; Reddin, D.G. 1984. Recent trends in the West Greenland salmon fishery, and implications for Thick-billed Murres. Pages 208–210 *in* Nettleship, D.N.; Sanger, G.A.; Springer, P.F. (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Piatt, J.F.; Nettleship, D.N.; Threlfall, W. 1984. Net-mortality of Common Murres and Atlantic Puffins in Newfoundland, 1951–81. Pages 196–206 in Nettleship, D.N.; Sanger, G.A.; Springer, P.F. (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Piatt, J.F.; Elliot, R.D.; MacCharles, A. 1985. Marine birds and oil pollution in Newfoundland, 1951–1984. Newfoundland Institute for Cold Ocean Science Rep. 105, Memorial University, St. John's. 54 pp.

Rothery, P.; Wanless, S.; Harris, M.P. 1988. Analysis of counts from monitoring Guillemots in Britain and Ireland. J. Anim. Ecol. 57:1–19.

Salomonsen, F. 1950. Grønlands Fugle — The birds of Greenland. Ejnar Munksgaard, Copenhagen. 604 pp.

Salomonsen, F. 1955. Fredning af fuglivet i Grønland [Bird preservation in Greenland]. Dan. Ornithol. Foren. Tidsskr. 49:3–11. (In Danish with English summary.)

Salomonsen, F. 1956. The Greenland bird-banding system. Arctic 9:258–264.

Salomonsen, F. 1967. Fuglene på Grønland [The birds of Greenland]. Rhodos, Copenhagen. 343 pp. (The chapters on seabirds translated from Danish by R.G.B. Brown as "Studies on northern seabirds," Can. Wildl. Serv. Rep. No. 100, 1981.)

Salomonsen, F. 1970. Birds useful to man in Greenland. Pages 169–175 *in* Productivity and conservation in northern circumpolar lands. IUCN (Int. Union Conserv. Nat. Nat. Resour.), Morges, Switzerland.

Salomonsen, F. 1979. Ornithological and ecological studies in South-West Greenland (50°46′–62°27′N lat.). Medd. Groenl. 204:1–214.

Seabird Group. 1981. Auk censusing manual. The Seabird Group, Oxford, U.K.

Seber, G.A.F. 1972. Estimating survival rates from bird-band returns. J. Wildl. Manage. 36:405–413.

Speich, S.; Manuwal, D.A. 1974. Gular pouch development and population structure of Cassin's Auklet. Auk 91:291–306.

Stowe, T.J. 1982. Recent population trends in cliff-nesting seabirds in Britain and Ireland. Ibis 124:502–510.

Stowe, T.J.; Harris, M.P. 1984. Status of Guillemots and Razorbills in Britain and Ireland. Seabird 7:5–18.

Swann, R.L.; Ramsay, A.D.K. 1983. Movements from and age of return to an expanding Scottish Guillemot colony. Bird Study 30:207–214.

Swann, R.L.; Ramsay, A.D.K. 1984. Long-term seabird monitoring on the Isle of Canna. Scott. Birds 13:40–47.

Swann, R.L.; Aiton, D.G.; Carruthers, J.; Graham, R.; Ramsay, A.D.K. 1989. Changes in recovery and retrap patterns of Guillemots ringed on Canna 1974–1985. Ringing Migr. 10:35–40.

Tasker, M.L.; Webb, A.; Hall, A.J.; Pienkowski, M.W.; Langslow, D.R. 1987. Seabirds in the North Sea. Nature Conservancy Council, Peterborough, U.K. 336 pp.

Thomas, C.J. 1988. Surveillance of cliff-nesting seabirds in Orkney 1988. Nature Conservancy Council Chief Scientist Directorate Rep. No. 872, Peterborough, U.K. 53 pp.

Thompson, J.G. 1991. Current perspectives on the management of migratory birds in northern Canada and Newfoundland. Trans. 56th North Am. Wildl. Nat. Resour. Conf. (in press).

Thorsøe, E.W. 1989. Redegørelse for det erhvervsmaessige fiskeri efter laks i 1988 og dettes indhandling. Notat fra Grønlands Fiskerilicenskontrol [Review of the commercial salmon fishery and trade in 1988]. Unpubl. report, Greenland Fish Licence Control Authority.

Tuck, L.M. 1953. A murre investigation with special reference to Newfoundland (preliminary). Unpubl. report, Can. Wildl. Serv., St. John's. 38 pp.

Tuck, L.M. 1955. The murre colonies in Digges Sound, Hudson Bay — a report on summer's field work — 1955. Unpubl. report, Can. Wildl. Serv., St. John's. 15 pp.

Tuck, L.M. 1957. Wildlife investigations in the Cape Hay region, Lancaster Sound, 1957. Unpubl. report, Can. Wildl. Serv., St. John's. 74 pp.

Tuck, L.M. 1961. The murres — their distribution, populations and biology, a study of the genus *Uria*. Can. Wildl. Serv. Monogr. 1, Ottawa. 260 pp.

Tull, C.E.; Germain, P.; May, A.W. 1972. Mortality of Thick-billed Murres in the West Greenland salmon fishery. Nature (London) 237:42–44.

Underwood, L.A.; Stowe, T.J. 1984. Massive wrecks of seabirds in eastern Britain, 1983. Bird Study 31:79–88.

Vauk-Hentzelt, E.; Schrey, E.; Vauk, G. 1986. Bestandsentwicklung der Trottellumme (*Uria aalge*) auf Helgoland 1956–1984. Seevogel 7:40–45.

Wanless, S.; French, D.D.; Harris, M.P.; Langslow, D.R. 1982. Detection of annual changes in the numbers of cliff-nesting seabirds in Orkney 1976–80. J. Anim. Ecol. 51:585–595.

Ward, R.M. 1987. Surveillance of cliff-nesting seabirds in Orkney 1987. Nature Conservancy Council Chief Scientist Directorate Rep. No. 759, Peterborough, U.K. 82 pp.

Wendt, J.S.; Cooch, F.G. 1984. The kill of murres in Newfoundland in the 1977–78, 1978–79 and 1979–80 hunting seasons. Can. Wildl. Serv. Prog. Notes No. 146. 10 pp.

Wendt, J.S.; Couling, L. 1978. Preliminary report — the kill of sea ducks and murres in Newfoundland. Unpubl. rep., Can. Wildl. Serv., Ottawa. 5 pp.

Wendt, J.S.; Hyslop, C. 1981. Migratory birds killed in Canada during the 1980 season. Can. Wildl. Serv. Prog. Notes No. 126. 42 pp.

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