



Impacts of chronic marine oil pollution and the murre hunt in Newfoundland on thick-billed murre *Uria lomvia* populations in the eastern Canadian Arctic

Francis K. Wiese^{a,*}, Gregory J. Robertson^b, Anthony J. Gaston^c

^aDepartment of Biology, Atlantic Cooperative Wildlife Ecology Research Network, Memorial University of Newfoundland, St. John's, NF, Canada A1B 3X9

^bCanadian Wildlife Service, Environment Canada, Mount Pearl, NF, Canada A1N 4T3

^cCanadian Wildlife Service, Environment Canada, National Wildlife Research Centre, Hull, Quebec Canada, K1A 0H3

Received 5 November 2002; received in revised form 22 April 2003; accepted 2 May 2003

Abstract

We developed a deterministic and stochastic age-based matrix projection population model to assess and quantify the impact of mortality caused by chronic oil pollution and legal hunting on thick-billed murre *Uria lomvia* populations breeding and wintering in eastern Canada. We calculate the potential population growth rate in the absence of anthropogenic mortality sources using a modeling technique that translates absolute number of birds killed from anthropogenic mortality to potential survival rates in the absence of these anthropogenic impacts. The intrinsic growth rate of the deterministic matrix based on vital rates from Coats Island ($\lambda_d = 1.0102$), as well as the stochastic growth rate ($\lambda_s = 1.0098$, 95% C.I. 0.9969–1.0226), matched observed population trends. Hunting mortality reduced population growth rate by 0.020 (0.012–0.039), oiling mortality reduced population growth rate by 0.025 (0.012–0.039). Combined these sources reduced the population growth rate by 0.047 (0.033–0.610). Although thick-billed murre populations are stable or slowly growing in eastern Canada, anthropogenic sources of mortality are reducing the ability of the population to grow, and increase vulnerability in these populations to changes in their environment and other pulse perturbations. Our modeling technique could be used to assess specific anthropogenic impacts on populations where a vital rates and numbers killed are known, but no long-term trend information is available.

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Keywords: Murres; Oil pollution; Hunt; Newfoundland; Canada; Conservation; Population dynamics

1. Introduction

Much concern has been voiced over the potential impacts of chronic oil pollution on seabird populations (Bourne, 1968; Croxall, 1975; Camphuysen, 1989; Dunnet, 1982; Albers, 1995; Newton, 1998), and several authors have suggested that it may be more detrimental to long-term population stability than occasional large spills (Hunt, 1987; Burger and Fry, 1993; Oka et al., 1999). Unequivocal demonstration of a direct cause and effect relationship between oil pollution and fluctuations in populations sizes is difficult because: (1) estimates of

the magnitude of mortality from acute or chronic spills are often imprecise; (2) seabird colonies are difficult to census because they are often widely dispersed or sensitive to disturbance; (3) it is often difficult to ascribe changes in abundance to specific causes in light of other anthropogenic pressures (e.g. hunt, by-catch), normal year-to-year variations in populations, the presence of large non-breeding cohorts, and the occurrence of natural phenomena (e.g. El Niño); and (4) most mortality from oil occurs in winter, when breeding populations from different regions may be impacted simultaneously (Piatt et al., 1991; Burger and Fry, 1993).

Despite the difficulties, attempts have been made to link large oil spills to observed seabird population declines (Hope-Jones et al., 1970; Baillie and Mead, 1982; Stowe, 1982; Hunt, 1987; Page et al., 1990; Piatt et al., 1991; Takekawa et al., 1990; Edwards and White,

* Corresponding author. Present address: School of Fishery and Aquatic Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA.

E-mail address: wiesef@u.washington.edu (F.K. Wiese).

1999; Irons et al. 2000). Many of these studies have accumulated evidence that immediate, and in some cases long-term, population effects occur after large oil spills. Regardless, some debates continue (Baker et al., 1990; Piatt et al., 1991; Murphy et al., 1997; Lance et al., 2001), perhaps because the focus often lies only on decreasing populations (Hunt, 1987; Burger, 1993; Burger and Fry, 1993) or on the disappearance of small local colonies (Piatt et al., 1991). Yet more subtle effects can occur, such as reductions in population growth (Hunt, 1987), declines in numbers of non-breeders, reduced adult survival (Esler et al., 2000) or reduced reproductive success (Ainley et al., 1981), that do not necessarily lead to detectable population declines.

In Newfoundland, Canada, it has been estimated that on average, about 300,000 murre and dovekeys are killed every winter due to the illegal discharges of oily waste from ships (Wiese, 2002a). One of most numerous seabirds in the northern hemisphere (Gaston and Hipfner, 2000), the thick-billed murre *Uria lomvia* is the most frequent and vulnerable victim of chronic marine oil spills in Atlantic Canada (Wiese and Ryan, in press). In addition to the mortality caused by oil pollution, about 200,000 thick-billed murre are killed every year during the traditional Newfoundland winter hunt (Chardine et al., 1999).

Fluctuations in numbers of breeders at two thick-billed murre colonies at opposite ends of their range in the eastern Arctic, suggest that population changes may be determined by events on the common wintering grounds (Gaston, in press). Although thick-billed murre populations in the eastern Canadian Arctic appear to have been stable or increasing since the 1970s (Gaston, 2002), it is important that the impacts of these anthropogenic causes of mortality on thick-billed murre populations be examined. We developed a population model to examine the relative and cumulative effects of mortality due to oil and harvest that occur in Newfoundland waters on the population of thick-billed murre that breed in the eastern Canadian Arctic.

2. Methods

2.1. Demography

Thick-billed murre, like all auks, are characterized by a low fecundity–high survival life history strategy: clutch size is one, age of first breeding is 4–6 years, adult survival is 90% or higher, and individuals live up to 30 years of age (Gaston and Hipfner, 2000). The current population size is estimated at about 1.95 million breeding pairs in the eastern Canadian Arctic (Gaston and Jones, 1998, A.J. Gaston, unpublished data). Demographic parameters of thick-billed murre in the

Canadian Arctic have been reported by Nettleship and Birkhead (1985) but are best and most recently known for Coats Island, northern Hudson Bay (Table 1; Gaston et al., 1994; Donaldson, 1995; Gaston, 2002).

2.2. Migration

In the North Atlantic, thick-billed murre breed in the eastern Canadian Arctic, Greenland, Iceland, Svalbard and several other locations in Northern Europe (Gaston and Hipfner, 2000, Fig. 1). In August and early September, chicks and adults leave their colonies and migrate to their wintering areas (Fig. 1). Although the relative proportion of each breeding area that make up the winter population encountered off Newfoundland has not been clearly quantified, results from banding studies in the eastern Canadian Arctic and Greenland indicate that roughly 80% of thick-billed murre that

Table 1
Summary of demographic parameters used for the pre-breeding population model for thick-billed murre breeding in the eastern Canadian Arctic

Parameter	Value	Source
Population size N (breeding pairs)	1,950,000	Nettleship and Evans (1985), Gaston and Jones (1998), A. J. Gaston personal communication.
Survival of juveniles S_0	0.52	Donaldson (1995)
Adult survival (2+ years old) S_a	0.91	Nettleship and Birkhead (1985), Gaston et al. (1994), Gaston (2002), Gaston and Hipfner (2000), A. J. Gaston personal communication.
Proportion breeders Pb_a		Gaston et al. (1994), Gaston unpublished data
1 year-old	0.000	
2 year-old	0.000	
3 year-old	0.025	
4 year-old	0.367	
5 year-old	0.700	
6 year-old	0.931	
> 6 year-old	0.980	
Fecundity m_a		Gaston et al. (1994), Gaston unpublished data
1 year-old	0	
2 year-old	0	
3 year-old	0.17	
4 year-old	0.20	
5 year-old	0.33	
6 year-old	0.46	
7 year-old	0.41	
8 year-old	0.54	
9 year-old	0.52	
10 year-old	0.58	
11 year-old	0.65	
> 11 year-old	0.73	

Fertilities calculated as $F_a = Pb_a \times m_a \times S_0 \times 0.5$.

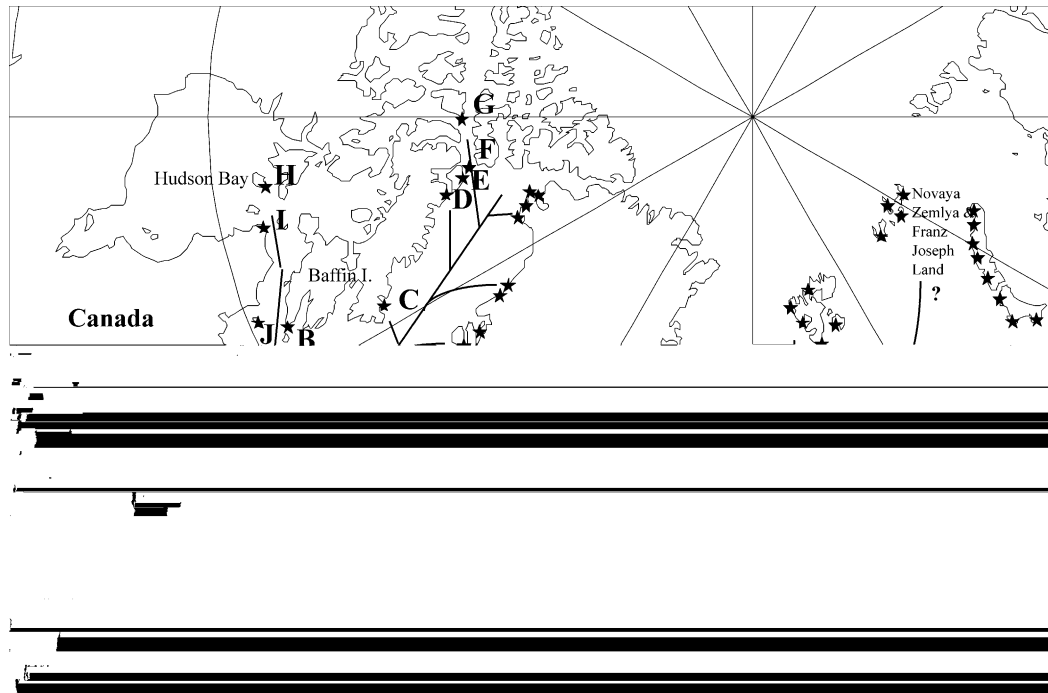


Fig. 1. Location of thick-billed murre colonies in the North Atlantic and eastern Canadian Arctic. Canadian colonies are (A) Gannet Islands, (B) Hantzsch Island, (C) Reid Bay (The Minarets), (D) Cape Graham Moore, (E) Cape Haye, (F) Coburg Island, (G) Prince Leopold Island, (H) Coats Island, (I) Digges Island, and (J) Akpatok Island. Approximate direction of fall migration is shown. Adapted from Gaston (1980), Kampp (1988), and Donaldson et al. (1997).

overwinter off Newfoundland and Labrador originate from the eastern Canadian Arctic and about 20% from western Greenland (Tuck, 1961; Gaston, 1980; Kampp, 1988; Donaldson et al., 1997), with very few individuals from Iceland, Svalbard or further east (Gaston and Hipfner, 2000). A few thick-billed murres, mostly non-breeders and a small number of breeders, can be found in Newfoundland year-round (Tuck, 1971; Montevecchi and Tuck, 1987), but large numbers are only present between November and April, with a peak in January and February (Tuck, 1961; Brown et al., 1975; Gaston, 1980).

2.3. Mortality due to chronic oil pollution

Thick-billed murres are the most frequent and vulnerable victim of chronic oil pollution in Newfoundland and comprised 56.3–87.5% (160,735–274,877) of the estimated annual kill 1998–2001 (Wiese 2002a). We are not aware of any conclusive evidence that indicates that chronic oil pollution affects certain age classes differentially, and assume oil mortality is not age-specific.

2.4. Mortality due to hunt

The most recent estimates of annual hunter kill in Newfoundland and Labrador average 227,000 birds (173,000–287,000) during the period 1995–1998 (Chardine

et al., 1999). Thick-billed murres make up 95% of these birds, while the remainder are common murres *Uria aalge* (Elliot, 1991). First-year birds, which are about 10% of the population (Eq. 1) appear to be at a greater risk of being shot than older birds, because they comprised 50–58% of murres killed (Gaston et al., 1983; Elliot 1991; Donaldson et al., 1997). Recent studies (Gaston, 2002) indicate no significant changes in the proportion of 1 year olds killed in the hunt over time, but significant decreases for older birds. Most markedly, recoveries of birds banded as breeders virtually ceased between 1990 and 2001. Based on these findings, we assumed that 50% of thick-billed murres killed in the Newfoundland hunt are in their first year, and that the rest of the harvest is spread among the other age classes according to their abundance.

2.5. Population model

We developed a stochastic (demographic and environmental), age-structured, pre-breeding, Lefkovich population projection matrix to model population dynamics (Lefkovich, 1965; McDonald and Caswell, 1993; Caswell, 2001). This model was based mainly on information from the breeding population at Coats Island (Gaston et al., 1994; Gaston and Hipfner, 2000). The computer model written in Matlab consisted of 12 age classes, and only females were considered. We

assumed a sex ratio of 1:1 (Tuck, 1961), so fecundity parameters from Table 1 were divided by 0.5 for the model. We define breeding birds as 5 years and older (Gaston and Hipfner, 2000), although a few 3 and 4 year olds breed. Stochasticity in survival rates, as well as in fecundity, was assumed to be $\pm 5\%$ of the observed values for each age class (Gaston et al., 1994; Donaldson, 1995). No estimates of variance were available for the proportion breeding per age class, so these values were held constant. Stochasticity in mortality due to oil and harvest was based on the observed range of values described above. Harvest values were multiplied by 0.95 in order to eliminate Common Murres from the hunt, by 0.8 to take into account only birds from Canadian colonies, and by 0.5 to consider only females. This resulted in a range of 65,705–109,010 female thick-billed murres from Canadian colonies killed annually in the hunt. Similarly, oil mortality values were multiplied by 0.8 and 0.5 to give an effective range of 64,294–109,951 female thick-billed murres from Canadian colonies killed by chronic oil pollution. For all runs, random uniform numbers within each range were drawn for each projection. A uniform distribution was chosen because mortality estimates come only from 3 years of data, and in order to increase variance.

The effects of anthropogenic mortality on a population are most easily determined by comparing survival rates between affected and unaffected populations. In the case of thick-billed murres, however, we are not aware of any populations that are not subjected to anthropogenic mortality to some extent, and we were interested in quantifying the relative effects on this particular population. As a result, we evaluated the cumulative and individual effects of anthropogenic mortality due to oil and hunting on population dynamics in three phases. Phase one determined baseline growth rates from vital rates obtained from Coats Island (an impacted population). In phase two, birds killed by explicit anthropogenic mortality due to oil and hunting (actual number of birds killed) were removed from the population, and the reduction this caused in the population growth rate was determined. In essence, birds were killed twice: once explicitly due to anthropogenic causes and once implicitly by using observed survival rates of a population that is already impacted by anthropogenic mortality. In phase three, we increased survival rates sufficiently to compensate for the anthropogenic mortality (oil and hunting) and to return to the population growth rate calculated in phase one. In essence we translated the anthropogenic mortality expressed as an absolute number into a reduction in survival rate. To assess potential population growth in the absence to hunting and chronic oil pollution we ran the model with increased survival rates but without the explicit mortality.

In phase one, we determined the stable age distribution, the elasticity matrix (e), and the intrinsic growth

rate of the deterministic matrix (λ_d ; Caswell, 2001). Elasticity analysis of matrix projection models examines the effects of proportional changes in demographic transitions (survival, growth, and reproductive parameters) on the asymptotic population growth rate λ (Heppell et al., 2000). Elasticities are useful in identifying vital rates that have large impacts on population growth rates. We calculated the initial population vector (\mathbf{n}) by distributing the estimated female breeding population according to the stable age distribution (\mathbf{w}) and based on the known proportion of breeders (Pb_a) in each age class. The number of non-breeders were calculated once the number of breeders in each age-class was assigned.

These calculations resulted in the base values used for comparison during phase three. We also used the Heyde–Cohen equation to calculate the growth rate (with 95% confidence intervals) for the stochastic matrix (λ_s), based on a 20 year projection period (Heyde and Cohen, 1985), and compared our model to observed values for λ . A 20 year projection time was chosen because we considered it a relevant time frame for management purposes, and because we did not want to consider density dependent processes that may apply with a long-term projections.

In phase two, using \mathbf{n} as the initial vector, we projected the stochastic population matrix over 20 years in half-year stages (Fig. 2). The first stage was the breeding season to the middle of winter, and second stage was the middle of winter to pre-breeding phase at the colony. During stage one, young were produced, and individuals from each age class were removed based

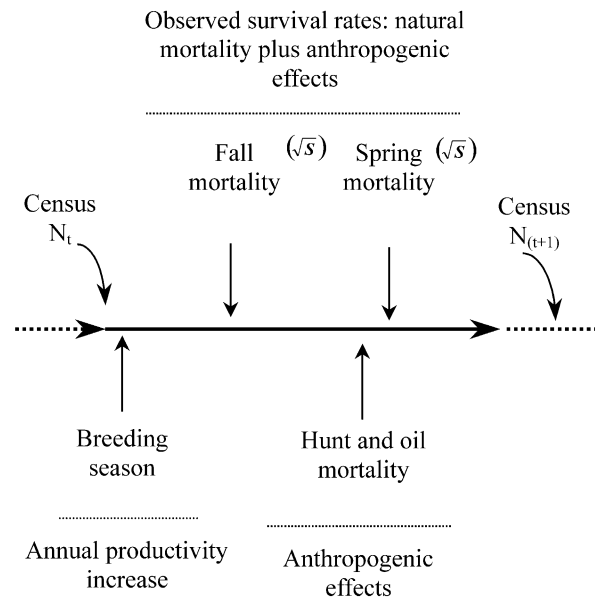


Fig. 2. Schematic of two-staged population projection during phase two (see Section 2 for details) for thick-billed murres breeding in the eastern Canadian Arctic.

on the square root of observed annual survival rates (\sqrt{S}). Between stages, birds dying from stochastic, but density-independent, age-class specific, hunt and oil mortality were explicitly removed from the population. During stage two, this population was further reduced based on the square root of observed annual survival rates to model winter and spring mortalities. The overall growth rate after these two projections was calculated by running 10,000 simulations, or until the mean and median stochastic growth rates were equal.

In phase three, we examined the relative impact of anthropogenic mortality on population dynamics by adding to the juvenile survival rate, to the adult survival rate, and to both survival rates simultaneously, until the growth rate again matched the baseline λ_s determined during phase one. In order to estimate population growth in the absence of the hunt and mortality due to oil, the explicit anthropogenic mortality introduced between stages in phase two was removed, and the stochastic matrix was projected with the increased survival rates. Phases two and three were carried out using oiling mortality and hunting separately and in combination. Relative decreases in potential population growth caused by each mortality factor were calculated, as were the cumulative effects of both impacts.

3. Results

3.1. Baseline values

The intrinsic growth rate of the deterministic matrix was $\lambda_d = 1.0102$, while $\lambda_s = 1.0098$ (95% C.I. 0.9969–1.0226). Assuming stable age structure (w), 90% of individuals in the populations were more than 1 year old, while 55% were breeders [Eq. (1)]. Proportional changes in survival of non-juvenile birds (> 1 year) had the largest influence on population trends (93.7%), whereas proportional changes in juvenile survival and fecundity had weaker influence on population growth [6.3%, (Eq. 2)]. Proportional changes in survival rates of breeding age birds (> 4 years) contributed 68.8% of the growth rate.

3.2. Mortality and survival rates

Proportional increases in survival rates, which were required to offset the explicitly added mortality in order to return to the baseline level of λ_s , were greatest for juveniles (Table 2). Increases for adults, and for adults and juveniles combined, were almost equal. The increase in survival rate needed to compensate for oiling mortality was greater than that needed to compensate for hunting (Table 2). The cumulative effect of anthropogenic mortality on survival rates was slightly

greater than simply adding the effects of oil and hunting.

$$w = \begin{bmatrix} 0.0992 \\ 0.0894 \\ 0.0805 \\ 0.0725 \\ 0.0653 \\ 0.0588 \\ 0.0530 \\ 0.0477 \\ 0.0430 \\ 0.0387 \\ 0.0349 \\ 0.3169 \end{bmatrix} \quad (1)$$

$$e = \begin{bmatrix} 0 & 0 & 0.000 & 0.001 & 0.002 & 0.004 \\ 0.063 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.063 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.063 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.062 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.059 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.055 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$\begin{bmatrix} 0.003 & 0.004 & 0.004 & 0.004 & 0.004 & 0.037 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0.052 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.048 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.046 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.041 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.037 & 0.350 \end{bmatrix} \quad (2)$$

3.3. Effects of anthropogenic mortality on population growth

In the absence of a hunt, adult and juvenile survival would be 0.928 and 0.531, respectively, and it is estimated that the thick-billed murre populations would grow at $\lambda = 1.030$ per annum. In the absence of mortality

Table 2
Stochastic growth rates for three different models projected over 20 years

Explicit mortality model	% Increase in S to compensate	Potential population growth	Effect
Oil	S_a :	2.8	
	S_0 :	41.0	
	$S_a + S_0$:	2.6	1.035 (1.009–1.062) –0.025 (0.012–0.039)
Hunt	S_a :	2.0	
	S_0 :	34.0	
	$S_a + S_0$:	2.0	1.030 (1.004–1.057) –0.020 (0.007–0.340)
Hunt and oil	S_a :	5.1	
	S_0 :	77.5	
	$S_a + S_0$:	4.7	1.057 (1.030–1.084) –0.047 (0.033–0.610)

due to chronic oil pollution, adult and juvenile survival would be 0.933 and 0.533, respectively, and populations would grow at $\lambda = 1.035$ per annum. If both types of anthropogenic mortality were removed, adult and juvenile survival would be 0.953 and 0.544, respectively, and thick-billed murre populations would grow substantially at $\lambda = 1.057$ per annum (Fig. 3).

4. Discussion

Chronic marine oil pollution and hunting off the Newfoundland coast have a significant effect on thick-billed murre populations breeding in the eastern Canadian Arctic. Our study supports the interpretation that events on the common wintering grounds may cause

population changes in thick-billed murres (Gaston, in press). Despite the absence of observed population declines, anthropogenic sources of winter mortality have decreased annual survival rates and have led to slower population growth. As expected, the cumulative effect of chronic oil pollution and harvest together had the largest impact, lowering adult survival by more than 0.043, and population growth by 4.7%. Although similar numbers may be killed by both sources of mortality, population growth and survival rates were decreased by a correspondingly larger extent by oil pollution. This was because oiling affected age classes according to their abundance, while the hunt preferentially impacted juveniles, whose survival has less importance in determining population growth.

4.1. Model assumptions

Recent surveys at colonies in the Canadian Arctic indicate that thick-billed murre populations are stable to moderately growing, with average growth rates between 0.4 and 2.1% during 1975–2001 (Gaston, 2002). Our baseline λ of 1.01 falls in the mid-range of these observed conditions, suggesting our model was performing well overall. In the model we assumed density-dependent processes were not occurring, and now evaluate this assumption.

Thick-billed murre populations in the Canadian High Arctic (about half of the Canadian population) declined between the 1950s and 1970s (Nettleship and Evans, 1985). Annual influxes of first-year thick-billed murres to the Great Lakes and northeastern United States common during the early part of the twentieth century, have not occurred since 1952 (Gaston, 1988). Despite

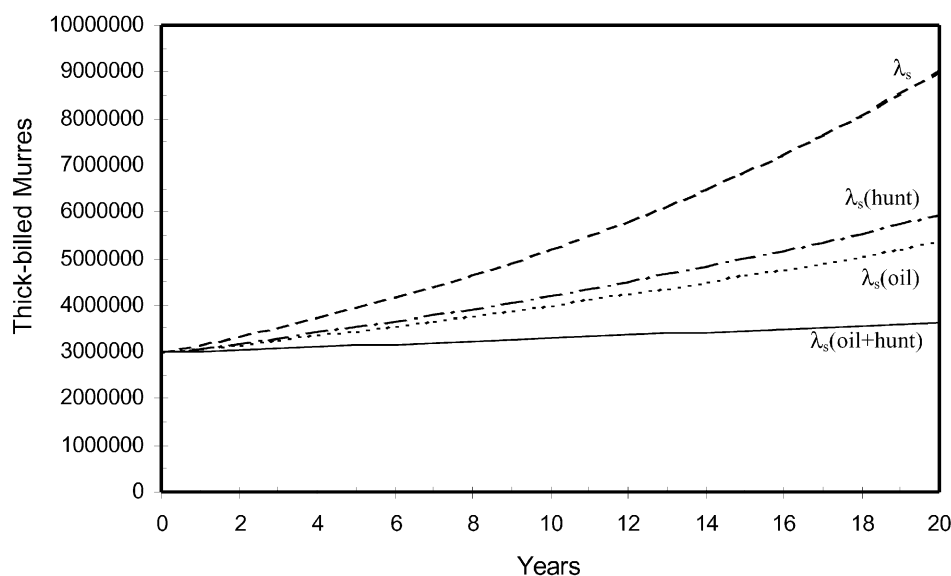


Fig. 3. Mean stochastic, density independent growth curves during a 20 year projection for thick-billed murre populations breeding in the eastern Canadian Arctic affected by both oil and hunt [$\lambda_s(\text{oil} + \text{hunt})$], for the same population affected only by harvest [$\lambda_s(\text{hunt})$], affected only by chronic oil pollution [$\lambda_s(\text{oil})$], and in the absence of both harvest and mortality due to oil (λ_s). Population size relates to females only.

overall population increases since the 1980s, a return to pre-1950 population levels has probably not happened (Gaston, in press). These observations support the assumption that thick-billed murre populations are not currently at carrying capacity in their wintering grounds, and that density-dependent processes do not appear to be at play, at least not in the short-term. In addition, given current population sizes and trends, it seems most reasonable to assume density independent mortality (for oil and hunt) for the time periods considered in the model.

Anthropogenic causes of mortality must be, at least in part, additive, and not simply compensatory to natural mortality to have an effect on populations (Fox, 2000). Compensatory mortality assumes that anthropogenic causes kill the “doomed surplus”, the annual proportion of the population that would have died due to natural causes (Singer et al., 1997; Banks, 1999; Boyce et al., 1999). In general, it is assumed that all or part of the “doomed-surplus” is killed when density-dependent factors are present, which is most likely to occur when populations are near carrying capacity (Allen et al., 1998; Boyce et al., 1999). As described above, this does not seem to be the case for thick-billed murre. In addition, relatively constant natural mortality of long-lived species does not provide a mechanism for compensation to occur (Hellgren et al., 1995; Boyce et al., 1999; Gauthier et al., 2001). Therefore, we consider the thick-billed murre harvest and the mortality due to chronic oil pollution, especially in the older age classes, to be additive to natural mortality (Boyd, 2000). Further, compensatory mechanisms are generally only effective to counter-balance temporary disturbances, and rarely effective enough to withstand high sustained increases in adult and juvenile mortality (Weimerskirch et al., 1997). Additional work is needed to determine the presence and plasticity of compensatory mechanisms in thick-billed murre populations.

4.2. Murre hunt

Murres have been hunted in Newfoundland and Labrador for centuries, and surveys in the late 1970s and early 1980s, after the introduction of speed boats and modern shotguns, estimated between 600,000 and 900,000 birds were killed every winter (Wendt and Cooch, 1984; Elliot, 1991). Simple population models indicated that those levels of harvest were unsustainable and needed to be reduced by 50% to maintain a stable population (Chardine, 1988). Although no declines at colonies in Canada had been detected at the time (Gaston, 1999), restrictive hunting regulations (shorter season, reduced daily bag limit) were introduced in 1993 that effectively reduced the harvest to its current levels of approximately 173,000–287,000 per winter season (Chardine et al., 1999).

Despite expectations, it is difficult to detect whether this reduction in the hunt had an effect on populations in the eastern Canadian Arctic. The thick-billed murre population at Coats Island was increasing between 1991 and 1993 (Gaston, 2002), and continued to increase as these hunting restrictions were implemented. At the same time, unfavorable environmental conditions on thick-billed murre wintering grounds between 1989 and 1990 in the form of an abrupt onset of cold water, slowly returned to pre-1989 conditions (Montevocchi and Myers, 1996, 1997; Carscadden et al., 2001). However, an improvement in the rate of recruitment of 4 and 5 year olds was observed at Coats Island after 1996, cohorts which were reared subsequent to the implementation of hunting regulations in 1993 (Gaston, 2002). This suggests a positive effect of increasing recruitment.

Gaston (2002) reported similar adult survival rates at Coats Island before and after hunting restriction came into place. However, no banded breeding-age birds were recovered in the hunt during the 1990s, suggesting that older birds now comprise a small proportion of the hunt. If this pattern holds true, we could have overestimated the impact of the hunt on thick-billed murre populations by overestimating the impact on older (breeding) age-classes. Sufficient data to measure impacts on adult and juvenile survival rates and recruitment only exists for Coats Island, which comprises only 1% of the population (Gaston, 1999). There are also no data to assess whether changes in age structure may have taken place, while leaving population sizes unaffected.

4.3. Oil pollution

Millions of seabirds have died from oil pollution in recent decades, the majority recorded only after large catastrophic spills (Newton, 1998). The effects of chronic marine oil pollution on adult and juvenile survival and reproductive success has gained little emphasis in comparison, despite the fact that several studies have indicated that it may be equally or more detrimental to long-term population stability than occasional large spills (Hunt, 1987; Burger and Fry, 1993; Oka et al., 1999).

Chronic oil pollution off the Newfoundland coast is among the highest recorded in the world (Wiese and Ryan, in press). The best estimate of annual seabird mortality due to this pollution is equivalent to an *Exxon Valdez*-sized spill every year (Wiese 2002a). Our study estimates that these current levels of mortality have reduced population growth of thick-billed murres by 2.5% (1.3–3.9%). These values are higher than those estimated for common murres in Britain (0.9–1.5%) after a winter of severe chronic spills (Baillie and Mead, 1982), are comparable with reduced growth rates calculated by Nur et al. (1997) for common murres exposed

to chronic oil pollution on the Farallon Islands (3%). They are lower than the estimated impacts of a winter of severe chronic spills on razorbill *Alca torda* populations in Britain (3.4–5.6%; Baillie and Mead, 1982).

We estimate that the annual adult survival has been reduced by sustained mortality from chronic oil pollution by 2.75%. This value is higher than calculated for common murres (1.7%) by Nur et al. (1997), but lower than that for female harlequin ducks *Histrionicus histrionicus* (5.7%) after continued chronic exposure to oil residues from the Exxon Valdez oil spill (Esler et al., 2000), certainly a determinant of the annual 5.4% decrease in that population.

Our estimates of a potential adult survival rate of 0.933 in the absence of mortality due to chronic oil pollution, or 0.953 in the absence of mortality due to both oil and harvest, is well within survival rates recorded elsewhere for other auks, especially common murres, (Table 3). However, our estimate of the impacts of chronic oil pollution on this population could be biased for several reasons. Effects could have been over-estimated if, during an average winter, young birds are more affected than adults than their abundance would suggest. Also, because the fecundity estimates for birds > 11 years old of 0.73 (Table 1) is generally lower than those measured at High Arctic colonies (0.8; Gaston and Nettleship, 1981; Birkhead et al., 1985) we may be underestimating the global productivity of thick-billed murres in the eastern Canada Arctic. On the other hand, we could have under-estimated the impact of oil mortality because these absolute mortality estimates were considered conservative (Wiese 2002a), and because no chronic, sub-lethal effects of oil on thick-billed murres

populations due to contaminated prey were considered (Croxall, 1977; Peakall et al., 1981; Culik et al., 1991; Holmes, 1984; Leighton, 1995). Overall, the estimated impact of these two sources of anthropogenic mortality on thick-billed murres appear to be reasonable, and substantial enough to raise conservation concerns.

4.4. Conservation implications

Murres have been hunted in Newfoundland and Greenland for centuries and are considered a culturally important food source. Hunting regulations are now in place in Canada that have reduced the mortality by 50%, and the hunt kills mostly juveniles. Thus, we are more concerned about the mortality caused by chronic oil pollution off the Newfoundland coast (Wiese, 2002a), and its implications for the long-term population trends of thick-billed murres that breed in the eastern Canadian Arctic. The high annual kill due to negligent, illegal behaviour by ship operators is unacceptable in itself.

In addition to oil pollution and hunt, by-catch of murres in commercial fisheries is also a potential threat to thick-billed murre populations from the Canadian Arctic, and one that was not considered here. Very large numbers of thick-billed murres died in a salmon drift-net fishery in 1960s in western Greenland (Tull et al., 1972; Falk and Durnick, 1992). Inshore gill-net fisheries in Newfoundland substantially affected common murres in the 1970s and 1980s (up to 20% of the local breeding population drowned in 1 year; Piatt et al., 1984). Since a groundfish moratorium sharply reduced fishing effort in 1992, seabird by-catch is thought to have plummeted,

Table 3
Adult survival rates (S_a) for different auk species in Europe and North America

Species	Location	S_a	Reference
Common murre (<i>Uria aalge</i>)	Isle of May, Scotland	0.93–0.97	Harris and Bailey (1992) Harris and Wanless (1995)
	Skomer, Wales	0.94	Hatchwell and Birkhead (1991)
	United Kingdom	0.94	Mead (1974)
	Farallon Island, California	0.94	Sydemann (1993)
	Gannet Island, Labrador	0.94	Birkhead et al. (1985)
	Great Island, Newfoundland	0.98	Wilhelm and Storey (unpublished data)
Razorbill (<i>Alca torda</i>)	Skomer, Wales	0.92	Lloyd and Perrins (1977)
	United Kingdom	0.91	Mead (1974)
	Quebec, Canada	0.90	Chapdelaine (1997)
Atlantic Puffin (<i>Fratercula arctica</i>)	Isle of May, Scotland	0.89–0.96	Harris (1983), Harris et al. (1997)
	Skomer, Wales	0.95	Ashcroft (1979)
Thick-billed murre (<i>Uria lomvia</i>)	Coats Island, Canada	0.89	Gaston et al. (1994)
	Greenland	0.85	Kampp (1991)

Model descriptions refer to explicitly added anthropogenic mortalities. Survival rates (S) are proportional increases needed to offset added mortality back to baseline levels $\lambda_s = 1.010$ (0.997–1.023). S_a = adult survival, S_0 = first year survival. Potential population growth is defined as λ_s in the absence of specified additional mortality, but with added survival. Effect is defined as the estimated absolute effect of the specified anthropogenic mortality on the potential population growth rate. Where applicable, 95% confidence intervals are given in parentheses.

although a limited fishery was re-opened in Atlantic Canada in 1997 (Chardine, 1998). Seabird by-catch is not regularly monitored in Atlantic Canada. Some data suggest that by-catch mortality also occurs offshore at murre wintering areas (Piatt et al., 1984; Chardine, 1998) and other observations indicate that current inshore by-catch incidents are under-reported (Davoren 2001). At present levels of hunting and oil mortality, our model indicates that thick-billed murre populations are probably stable. If by-catch or other levels of anthropogenic mortality reach that level of mortality, population increases would most likely stop or change to declines. We concur with Chardine (1998), that seabird by-catch monitoring should become an integral part of fisheries management activities in all Canadian waters.

5. Conclusions

We present a model that allows the quantification of effects on seabird populations of sources of anthropogenic mortality. The model is especially useful in the absence of detectable population declines or where logistical considerations do not allow sufficient data collection to measure potential impacts. This is especially critical in light of natural variation in demographic parameters, and confounding environmental impacts that may make it difficult to detect population changes in the field, or to attribute them to a specific cause (Eppley, 1992). In essence, however, such models cannot be built in the absence of data from long-term demographic monitoring studies, such as that ongoing at Coats Island since 1984.

There is no doubt that sustained adult mortality inflicted by human activities can cause severe population declines in seabirds (Moloney et al., 1994; Weimerskirch et al., 1997; Tasker et al., 2000; Tuck et al., 2001; Ainley et al., 2001), and that these sustained impacts are generally more detrimental to populations in the long-term than single large kills. Even some very abundant bird species have not escaped these impacts (e.g. great auk *Pinguinus impennis*; Montevecchi and Kirk, 1996; passenger pigeon

- sportfish populations. *Lakes and Reservoirs: Research and Management* 3, 67–79.
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