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EVALUATING THE SUSTAINABILITY OF HARVEST AMONG NORTHERN COMMON EIDERS IN GREENLAND AND CANADA

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Abstract: Sustainable harvest, the extraction of game without affecting population viability, is a desirable approach to the use of wildlife. However, over-harvest has been responsible for the decline of many wildlife populations globally, so there is an urgent need to balance human requirements while avoiding the severe depletion of wild populations. Northern common eiders (*Somateria mollissima borealis*) are heavily hunted in Canada and Greenland, but the effect of this intensive harvest has not been examined. We developed a population model to investigate the sustainability of the reported harvest, which consisted of two wintering areas in Greenland and Atlantic Canada and three breeding populations. The model indicated that harvest in Atlantic Canada was sustainable, but a number of conditions could lead to slow declines. In contrast, the annual winter harvest of 55000-70000 eiders reported between 1993 and 2000 in Greenland was not sustainable, and this conclusion held under a wide range of alternate conditions. The model indicated that harvest during late winter may have a greater effect on populations than harvest in early winter. We further refined the model to assume that at some low population level the success of hunters would decline and that harvest became a function of population size (a rate). This scenario had the expected and undesirable result of stabilizing populations at very low levels. Overall, our model suggests that the high harvest reported in Greenland from 1993-2000 endanger the sustainable use of the northern common eider population and that management actions are required. Common eider harvest levels in Greenland should be reduced by at least 40% of the 1993-2000 levels to stop projected declines, and allow for recovery of the decimated Greenland breeding population. Encouragingly, new hunting regulations were introduced in Greenland in 2002-2004, and harvest levels appear to be

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decreasing. If these harvest reductions continue, our population model could be used to re-evaluate the status of populations in the two countries.

Introduction

Throughout the world, wildlife is harvested for subsistence, recreation, and income. Over-exploitation has been identified as a contributing factor among nearly one-third of the bird and mammal species that are threatened with extinction (Peres 2001, Rosser & Mainka 2002, Rao & McGowan 2002). To maintain global biodiversity, there is an urgent need to find ways to satisfy human requirements while avoiding the decimation of wild populations (Pims et al. 1995, Johannes 1998). Arguably, the ability to balance human requirements for food while maintaining wildlife populations requires the development of practical and reliable models of sustainable wildlife harvest (Hilborn & Walters 1992, Lele & Norgaard 1996). Simulation models of wildlife populations are useful tools to explore the relative importance of demographic parameters, and to help identify gaps in existing knowledge (Caswell 2001). Among exploited wildlife populations, demographic models also provide the opportunity to compare the effectiveness of alternative conservation approaches (Hilborn & Walters 1992, Fieberg & Ellner 2001).

The northern common eider (*Somateria mollissima borealis*) breeds in the eastern Canadian Arctic and west Greenland, and winters in large flocks along the coasts of southwest Greenland and Atlantic Canada (Goudie et al. 2000). It is an important component of subsistence harvests in Arctic Canada and west Greenland (Piniarneq 2003), and also the recreational harvest in southern wintering areas including Atlantic Canada

(Reed & Erskine 1986), making it one of the most heavily hunted birds in the circumpolar arctic (Circumpolar Seabird Working Group 1997). Despite this, there has been a pervasive lack of available information to assess the population status of northern common eider populations. Among northern eiders breeding and wintering in west Greenland, declines have apparently occurred (Merkel 2004a), and harvest of adult birds and disturbance at breeding colonies are thought to be contributing factors (Boertmann et al. 1996). The effects of harvest on population dynamics of northern common eiders have never been assessed, although magnitude of the Greenland harvest has recently generated international concern (Circumpolar Seabird Working Group 1997, Hansen 2002).

New information on the size, trend, and geographic delineation of northern eider populations make it possible for the first time to assess the sustainability of reported harvest levels. We developed a population model to explore the relative importance of demographic parameters and harvest to population dynamics and predicted trends, and to identify gaps in existing knowledge. To account for migration flyways and different hunting scenarios in Greenland and Canada, we constructed projection matrices for 3 different breeding populations that winter in the two countries. Here, we describe how existing demographic data were integrated in the model and explore the effects of timing of harvest, density-dependent harvest and dispersal between sub-populations on model output. We evaluate the sustainability of reported harvest levels, assess how uncertainty in the model affects the assessment of the sustainability of the harvest, and discuss the management implications of model forecasts for both Canada and Greenland.

Methods

Population delineation

Northern common eiders were recently tracked using satellite telemetry and two main wintering areas and three major migration flyways were identified (Mosbech et al. 2006). Eiders tracked from a breeding colony in west Greenland migrated south along the Greenland coast to winter exclusively in southwest Greenland, and all migrated north again in spring to breed in Greenland (Greenland flyway). Of the eiders tracked from a colony near Southampton Island, in northern Hudson Bay, Canada, some migrated through Hudson Strait then south along coasts of Labrador, Newfoundland and Québec, to winter in Atlantic Canada (Canadian Flyway). However, most crossed the Davis Strait to winter in southwest Greenland and returned in spring to breed in Canada; thus linking the two north-south flyways (Canadian-Greenland flyway). Seven of 8 eiders marked in southwest Greenland in winter also migrated west across Davis Strait in spring, apparently to breed in Canada (Mosbech et al. 2006). The importance of this east-west flyway was unknown and not considered in previous population assessments which assumed that all eiders breeding in Arctic Canada wintered in Atlantic Canada (Reed & Erskine 1986).

Model components

To account for different hunting scenarios in Greenland and Canada and the three flyways described above, the model treated these three populations separately (Fig. 1). Because age can influence vital rates of common eiders (Baillie & Milne 1982, Coulson

1984, Goudie et al. 2000), we used an age-structured projection matrix that included four age classes (McDonald & Caswell 1993, Caswell 2001). Only females were considered in the model. In addition, the model was constructed using a seasonal matrix approach that divided the annual population projection into a series of seasonal transitions corresponding to ecologically relevant periods (Schmutz et al. 1997, Cooch et al. 2003). Since eiders reproduce once per year and population counts are generally obtained in late winter, we started by building a projection matrix configured for a population census during the pre-breeding season. The first transition allowed for the production of young (M_a in Fig. 2, Table 1, where a is the age class), and removed females killed by natural breeding season mortality (S_{sa}, Fig. 2, Table 1). The second transition removed females killed by natural fall mortality first (S_{fa}), then removed females killed in the fall harvest (H_{af}). Similarly, the third projection removed females dying from natural winter mortality (S_{wa}) and then removed females killed in the late-winter harvest (H_{aw}). Figure 3 provides a simplified general time line of these annual events.

Model parameter estimates

When possible, vital rates were based upon existing field data specific to the northern common eider. For those rates for which no data existed, we extracted values from the published literature on other subspecies of common eiders. There are no estimates of breeding propensity for northern common eiders, or how this may vary annually (see Coulson 1984). Therefore, we used age-specific breeding propensity values reported for common eiders breeding in Scotland (*S. m. mollissima;* Baillie & Milne 1982), and assumed all females bred by age 4. Reproductive variables included clutch size (cs_a), nest success (ns_a), hatch success (hs_a) were based on published results and ongoing field studies of northern common eiders (Table 1), while duckling survival (ds_a) and post-fledging survival (S_{s1}) were based on *S. m. mollissima* (Swennen 1991), as no data for northern common eiders was available. We partitioned the annual cycle into three equal 4-month long periods (called summer (or breeding), and fall and winter (or early and late non-breeding), and partitioned annual survival rates among these three periods for each age class. In the absence of harvest or periodic catastrophic events, we set annual adult survival rates near the maximum reported for common eiders (~95%, Swennen 1991). Common eider females occasional fall victim to predators while nesting, so survival for the breeding period was set slightly lower than the two non-breeding periods for breeding-age females, while summer survival was set higher in 2-year old birds, as they breed only rarely and we assumed that summer is a relatively benign time for non-breeding individuals (Table 1).

As a starting point, we assumed that the populations were well below carrying capacity and there were no stresses on the populations; that is, there were no periodic catastrophic events, stochasticity in demographic parameters, or hunting mortality. Under these conditions, the values we used forecasted an intrinsic population growth rate (hereafter λ) of 1.068. This population growth rate was similar to the rate observed during the period of expansion of common eiders in the Dutch Wadden Sea (1.07 see Swennen 1991), so we increased the immature survival rate slightly to achieve Swennen's observed λ of 1.07. The stable age distribution of this projection had 23.5% percent of the population less than, or equal to, two-years-old just before the breeding season.

Population estimates

Starting population sizes for the model were based on estimates of the number of northern eiders wintering in southwest Greenland and Atlantic Canada. The number of females wintering in Greenland (231500) was half the number of wintering eiders surveyed in 1999 (463000 birds, 95% CI 342000-627000; Merkel et al. 2002, Boertmann et al. 2004). Limited ground surveys during the past 25 years produced a minimum estimate of 10000 breeding pairs of common eiders in west Greenland (Boertmann et al. 1996), although more extensive surveys in 1997-2001 suggest a breeding population of 15000 pairs (Frich et al. 1998, Christensen & Falk 2001, Merkel 2002). Eiders breeding in northeast Greenland winter in Iceland while the wintering area of the relatively few eiders breeding in southeast Greenland is unknown (Lyngs 2003). Thus, Greenland itself may contribute only 30000 of the adult eiders wintering in southwest Greenland; 15000 of them female (Table 2).

Canadian over-winter estimates were based on aerial surveys conducted in 2003 using methods developed by Bordage et al. (1998), which estimated 203922 (±15478 SE) eiders wintered in the Gulf of St. Lawrence, Québec and along coasts of Newfoundland. In the Gulf of St. Lawrence, Québec all wintering common eiders and thought to be the northern subspecies (J.-P. L. Savard, unpubl. data), while 87% in northern, and 39% in southern Newfoundland are northern common eiders (the remainder are the American race, *S. m. dresseri*; Gilliland & Robertson submitted). Half of the wintering populations in both Newfoundland and Québec are female (Gilliland & Robertson submitted). Using these values we estimated that 93500 northern common eider females wintered in Atlantic Canada in 2003.

Because the number of female eiders breeding in northern Canada is unknown, we calculated this value based on the other estimates. There are 15000 females breeding in Greenland (age classes 3 and older; Merkel 2002), and adding another 23.5% for the younger age classes, we calculated that 19600 females wintering in Greenland are Greenlandic breeding stock. Thus, the remaining 211900 (231500-19600) female eiders wintering in Greenland were assumed to originate from Canada. When combined with all females estimated to winter in Newfoundland and Québec (93500) the estimate for northern common eiders breeding in Canada is 305400 females.

Harvest

Mean harvest estimates in Greenland (H_{af} and H_{aw}; Table 2), was based upon 8 years of data from surveys of hunters (1993-2000; Piniarneq 2003). However, female eiders are rarely identified to species by hunters so that both female common and king eiders (*Somateria spectabilis*) are reported as common eiders. To address this, we applied a correction factor developed by examining eiders at the community market in Nuuk, Greenland, in the winters of 1988/89, 1995/96 (Frich & Falk 1997) and 2000/2001 (Merkel 2004b). The mean corrected harvest of common eiders was estimated at 60500 annually in west Greenland of which about 50% were females (Frich & Falk 1997, Merkel 2004b).

Canadian sport harvest was estimated from both the National Waterfowl Harvest Survey and a targeted Sea Duck Harvest Survey (B. Collins & H. Lévesque, Canadian Wildlife Service, unpubl. data). Harvest estimates for Newfoundland and Québec for 1996-2001 were corrected for unreported late season harvest and the proportion of northern eiders in the harvest (75% in Newfoundland, Gilliland & Robertson submitted, 20% in

Québec, J.-P. Savard, unpubl. data). This calculation yielded an average of 13000 northern eiders harvested annually. Equal numbers of females and males are harvested in Newfoundland (Gilliland & Robertson submitted), yielding a final estimate of 6500 northern eider females killed annually in Atlantic Canada (Table 2). We estimated subsistence harvest of female eiders in Nunavut, Canada as half of the mean harvest reported for the years 1999-2001 (i.e. 1200 females; Nunavut Wildlife Harvest Study, unpubl. data). We also assumed that only breeding adults (3 or 4+ age classes) were taken in this summer hunt.

Juvenile eiders are typically 2 to 3 times more vulnerable to hunting than adults (Joensen 1974). Thus, we used a vulnerability index that made hatch-year birds 3.5 (age class 1) and second-year birds 2.0 (age class 2) times more vulnerable to harvest than adults. These vulnerability indices produced an age distribution harvested birds in the model that were similar to those reported in both Greenlandic and Canadian harvests (60% young, Frich & Falk 1997, Merkel 2004b, Gilliland & Robertson submitted).

Dispersal

To consider how harvest levels in each of the two wintering areas could effect the overall population and each population segment individually, we included a dispersal component in the model. We assumed that adult females showed total fidelity to their breeding and wintering areas (Robertson & Cooke 1999). For young however, the model allowed for different dispersal scenarios because it is not known how juveniles disperse to their first wintering areas. At one extreme, we assumed that juveniles wintered at the same area as their mothers (i.e. D = 0). This scenario assumes that dispersal is either culturally or genetically transmitted from the mother to the juvenile, as seen in some harlequin ducks (*Histrionicus histrionicus*; Regehr et al. 2001). At the other extreme, we assumed that the probability of a juvenile dispersing to a wintering area depended on the proportion of adult females in the breeding population that came from that wintering area (D = 1). This scenario models a situation where juveniles would randomly mix with the breeding female population, and simply follow adults to their wintering grounds, as seen in mallards (*Anas platyrhynchos*; Nichols & Hines 1987). We explored other scenarios by varying the dispersal factor to intermediate values, but once a juvenile wintered at an area, the model assumed that they always returned there.

Harvest: timing and population size relationships

We incorporated two harvest periods in the model so that we could apportion the harvest between them (i.e. 'Fall' before 1 January; 'Winter' after 1 January). In Canada, 51% of the harvest occurred before 1 January (B. Collins & H. Lévesque, Canadian Wildlife Service, unpubl. data), while in Greenland 41% of the harvest occurred before 1 January (Greenland Department of Fishing and Hunting, unpubl. data).

Initially, we assumed that the number of eiders harvested each year was constant. Unlike the regulated sport hunting of migratory game birds by non-aboriginal people in North America, harvests of eiders in parts of Atlantic Canada and particularly in Greenland are to some extent for subsistence; suggesting that hunters require a certain harvest each year. Further, the tendency of eiders to congregate in large flocks along coastlines (often near communities) helps ensure that hunters are efficient even if bird numbers decline. But at some low threshold harvest should eventually decline before eiders were completely extirpated, as hunter efficiency declines. We modeled this scenario by adding a term for strength of the inverse linear relationship between winter numbers and harvest and by adjusting the threshold population size where the reduction in hunter efficiency occurred.

Perturbation analyses and uncertainty

As both fixed and density-dependent harvest relationships lead to changing population growth rates over time, standard asymptotic elasticity analyses were not possible (Caswell 2001). Instead, we used perturbation analysis to estimate the relative effects of changes in the vital rates on population growth (following MacDonald & Caswell 1993, Schmutz et al. 1997). Each vital rate was reduced by 1% and the resulting population growth rate was calculated. We used a 20-year projection, extracted population size at 15 and 20 years, and calculated λ using the Heyde-Cohen equation (Heyde & Cohen 1985; $\ln\lambda = (\ln N_t - \ln N_0)/t$) based on these 5 years to avoid problems associated with early transient dynamics. These estimates are synonymous with lower level elasticities of the vital rates (Schmutz et al. 1997).

To explore uncertainty in harvest levels and population sizes on our general conclusions, we explored plausible harvest levels and population sizes that would lead to declining or growing populations. Plausible population sizes were based simply on the variance calculated with each estimate. For harvest, however, we felt bias from under- or non-reporting was the most important source of uncertainty, so we assigned upper and lower ranges of what we felt the harvest could have been. For both countries, harvest is not likely to be overestimated (maximum 5%), and we decided that the harvest in Greenland could plausibly be 25% higher, while in Canada, it could be up to double of the recorded values. In addition, to account for uncertainty in the vital rates used in the projection matrix, we considered scenarios where λ in the absence of harvest was increased to 1.089 (by raising duckling survival by 20% from 0.3 to 0.36) and reduced to 1.051 (by decreasing nest success 20% from 0.9 to 0.72).

Results

Initial conditions

In the absence of harvest, initial parameter values were set to yield a growth rate of 1.07 for all three populations with a stable age distribution $\mathbf{w}$ of 0.25, 0.11, 0.07, 0.57. The reproductive value vector $\mathbf{v}$ was 0.10, 0.23, 0.323, 0.35, indicating that adult females contributed about 3.5 times more to the population than juveniles each year in the model.

Harvest

With harvest included in the model the age distribution of birds wintering in Canada was 0.14, 0.10, 0.08, 0.68, after 20 years and indicated a higher portion of adults in the population. Projections including harvest resulted in declines in the number of eiders wintering in Greenland (Fig. 4A). Thus, even with reproduction and survival rates set at relatively high levels for this species, the model suggested that harvest of common eiders in west Greenland is not sustainable if maintained at levels reported between 1993-2000. Harvest would have to be reduced by approximately 40% in Greenland to halt projected declines. The Canadian harvest appears to be just below sustainable levels, and is projected to allow modest population growth.

The seasonality of harvest strongly influenced population projections. For eiders wintering in Canada, moving all of the harvest into the fall increased the population growth rate. In Greenland, the numbers continued to decline, but this decline occurred more slowly if the harvest occurred entirely in the fall (Fig. 4B).

Model structure: dispersal and density-dependent hunting

Changes in patterns of dispersal had little impact on the overall dynamics of the two wintering populations. When dispersal was proportional to population sizes the number of Greenland wintering birds declined slightly faster at the expense of Canadian wintering birds. Given the lack of any significant effect on overall dynamics, dispersal was not considered further.

Adjusting the strength of harvest density-dependence and raising the threshold value at which harvest becomes density-dependent, had similar influences on the dynamics of the declining Greenland population (Fig. 5). Both increased the level and the time to reach equilibrium (Fig. 5). However, if the threshold was too low or the strength of the density dependence of harvest was too weak, the Greenland wintering population still went extinct.

Perturbation analyses and uncertainty

The most sensitive component of the model was adult survival, as would be expected in a long-lived species (Nur & Sydeman 1999). A proportional change in adult survival had 7-10 times more impact on the population than a change in fecundity or immature survival rates (recognizing that adult survival rate includes the sum of the elasticities of all birds four or more years old).

Uncertainty in population size estimates, harvest levels and population growth rates are explored in Figure 6. Only under a high population growth rate, a population size in the high range of the estimate and low harvest levels could the current wintering numbers be maintained in Greenland. In Canada, where harvest levels were calculated to be sustainable, there still was a wide range of plausible conditions that could lead to population decline, especially if harvest is being underestimated as expected. Poor breeding conditions alone could also lead to declines in Canada, under the current population size and harvest levels.

Discussion

Uncertainty existed in several parameter values and model assumptions; a situation shared among many sea duck species in North America. The northern common eider occurs in remote areas of the Arctic and does not follow flyways traditionally considered by waterfowl management programs in North America, making it particularly poorly known. The expense and logistical difficulties associated with Arctic field studies also explains the lack of monitoring and research efforts. In addition, harvest estimates for sea ducks are generally poor and are not precise enough for effective management (Wendt & Silieff 1986, Caithamer et al. 1998).

Regardless of these uncertainties, growing conservation concern necessitated evaluation of northern common eider management regimes in both Canada and Greenland

(Circumpolar Seabird Working Group 1997, Sea Duck Joint Venture Management Board 2001, Hansen 2002). Here, we used a demographic model that integrated existing information of the northern common eider to, 1) evaluate the sustainability of reported harvest, 2) for projected declining populations suggest harvest levels that would stabilize the populations and 3) identify and rank knowledge gaps hampering the ability to assess appropriate harvest levels. Throughout we evaluate the role of uncertainty, in both parameter estimates and model structure, on our conclusions.

Sustainability of the eider harvest

When reported rates of harvest were introduced into the model, and despite survival and reproductive rates both set at favourable levels, the number of eiders wintering in Greenland quickly declined. This suggests that harvest of northern common eiders wintering in Greenland is not sustainable at levels reported between 1993 and 2000, whereas the Canadian harvest apparently was close to, our below, levels that would lead to population declines. The conclusion that the Greenlandic harvest is well above sustainable levels held under a wide range of plausible population sizes and harvest levels, and only under a combination of the most favourable conditions with very high vital rates and underestimated population sizes could the Greenlandic harvest be conceivably sustained. In Canada, the model suggests that current harvest levels could be sustained, but a wide variety of conditions could lead to population declines. As one example, the model did not include stochastic events occurring naturally that could cause reduced breeding and success or increased mortality (e.g. years of heavy sea; Robertson & Gilchrist 1998).

This model output was generally supported by recently observed conditions. First, surveys of Greenlandic breeding colonies indicate that there has been a significant decline over the past 40 years (λ=0.96; Merkel 2004a). Second, and in contrast, breeding numbers of eiders occurring at southern limits of the breeding range in Canada, from where eiders are assumed to winter mainly in Atlantic Canada, have increased between 1980 and 2003 (Goudie et al. 2000, Falardeau et al. 2003, Chaulk et al. 2005). Third, when harvest mortality was included, the model calculated an annual adult survival rate of 0.84 among female eiders wintering in west Greenland (see methods in Wiese et al. 2004). Survival has recently been estimated for adult female common eiders breeding in northern Hudson Bay, Canada at 0.80 (1996-2005; H.G. Gilchrist & E. Reed, unpubl. data); a site where 75% of the eiders winter in Greenland (Mosbech et al. 2006). Both the survival rate generated by the model and observed at the Canadian colony suggest a declining population and are low when compared to other hunted eider populations whose adult survival rates can exceed 0.90 (Wakeley & Mendall 1976, Krementz et al. 1996, Goudie et al. 2000).

We did not include density dependence in our model, and in so doing, assumed that all hunting mortality was additive to natural mortality. We felt this assumption was appropriate for a number of reasons. First, the population size of common eiders wintering in both Canada and Greenland appear to be much reduced from historical levels, and is well documented for Greenland (Merkel 2004a). In Canada, older information is sparse and not as well documented; Gillespie and Learning (1974) quote Les Tuck as suggesting up to 2 million eiders wintered in Newfoundland alone in the 1950s, and Gillespie (1968) reports their visual estimates for eider flock size were seriously underestimated and that "... several hundred thousand ...' eiders wintered in eastern Newfoundland in 1968. Other studies of longer-lived species, such as geese, show that most hunting mortality is additive (Gauthier et al. 2001); especially that of adults as there little variation in adult survival to allow for compensation (Lebreton 2005). Finally, without any meaningful sense of what carrying capacity may be for eiders in the Northwest Atlantic, and which population processes regulate numbers in common eiders, we felt that modeling density-dependence would not further our understanding of the impact of harvest. However, it must be recognized that the predictions of the model are based on complete additivity, and that if some compensatory mechanisms exist at the current population sizes, then more birds could be harvested.

Dispersal

Little is known about how young disperse in many species of sea ducks, and further work is required to understand how juvenile ducks select their first wintering grounds, and how faithful adults are to these sites (Robertson & Cooke 1999). Harlequin duck females occasionally migrate with their brood to their wintering grounds (Regehr et al. 2001), providing a mechanism for the location of the mother's winter site to be transmitted to the young. Extensive brood parasitism, crèching and brood abandonment suggest that young eiders would not necessarily migrate with their mothers to wintering grounds. Regardless, a range of dispersal scenarios was considered in our model because dispersal provided a possible mechanism to link the sympatric populations breeding in the Canadian Arctic with those that winter in Greenland and Canada. The model suggested that dispersal of young eiders between populations did not greatly influence the overall dynamics in the model, and that an intensive Greenland harvest will not strongly affect eiders that both breed and winter in Canada. Similarly, a conservative harvest management regime in Canada that results in an increasing Canadian winter population is not likely to increase numbers of eiders wintering in Greenland.

Timing of harvest

Our model indicated that a late winter harvest would have a greater effect on populations than early winter harvest, although the level of this effect depended on population size and the number of birds harvested. This occurred because harvests later in the winter are taken from a smaller population reduced by natural mortality, resulting in a higher harvest rate (the proportion of birds harvested in the population). However, under the current Greenlandic harvest levels; a shift from late to early winter harvest only slowed inevitable declines. Adjusting the timing of harvest could be a more useful management tool when harvest levels are closer to sustainable levels and earlier harvests could help to ensure harvest levels remain below sustainable levels.

A summer harvest will have the greatest detrimental effect on populations because it targets the adult cohort that has the highest reproductive value. The harvest of adult northern eiders during summer has extirpated regional breeding populations in both Arctic Canada (Cooch 1986), and west Greenland (Salomonsen 1951, Merkel 2002a). Despite the potential effect of summer harvest, it was numerically small and so had little influence on the overall trajectories of the populations.

Conservation implications

At some low population size, harvest of eiders should decrease when it becomes difficult for hunters to encounter and kill them. In the model, the level at which eider numbers stabilized was a function of where we arbitrarily set the level of this density-dependence. The sooner harvest became proportional to population size (i.e. a rate) rather than a fixed-number, the higher the equilibrium population size became. Complete extirpation of a wild population is unlikely to occur from harvest alone (but see, Rosser & Mainka 2002). In many cases, natural refuges exist where remnants of a population can persist in areas inaccessible to hunters (Merkel 2004b). However, populations can be driven to extremely low levels before the equilibrium between population size and harvest levels is reached (Ludwig et al. 1993), and clearly, a population that persists at low equilibrium levels is an undesirable outcome of harvest. Small wildlife populations are also more vulnerable to stochastic environmental and demographic events that increase mortality or reduce natality (Lande 1993).

Recommendations

It is often recommended that harvest levels should be adjusted each year in relation to population size and the yearly production of young (Hilborn & Walters 1992). However, this management approach is only possible if good annual estimates of harvest, population size, and annual production exist, as occurs for many North American and European waterfowl species. This is not feasible for northern eiders breeding in Arctic Canada and west Greenland due largely to the expense and logistical complexity of monitoring this remote population.

Northern common eiders in west Greenland, which apparently consists of ~90% Canadian breeding birds, remains one of the most heavily hunted birds in Greenland (Piniarneq 2003); perhaps because eiders occur in concentrated flocks at predictable locations and in close proximity to coastal communities (Merkel 2004a). Despite a lack of information and infrequent population surveys, our findings suggest that there is an urgent need to prevent declines projected by the model. The model indicates that the most efficient way to do so is to lower adult mortality by reducing harvest levels in Greenland by at least 40%, particularly in spring. However, given the continued uncertainty associated with some estimates of population size and harvest, we cannot yet determine precise harvest levels that would allow eider populations to be maintained or to grow.

Favourable vital rates were used in the model, and eiders can show successive years of high population growth in certain conditions (e.g. Coulson 1994, Chaulk et al. 2005). However, other factors not yet considered in this model could lower calculated sustainable harvest levels even further (Fieberg & Ellner 2001). For example, environmental factors such as heavy sea ice conditions in winter could lower juvenile and adult survival rates (Robertson & Gilchrist 1998). Occasionally, breeding failure occurs among common eiders, particularly at high latitudes (Goudie et al. 2000), and this, or any other, source of stochasticity can reduce intrinsic growth rates further (Tuljapurkar 1997). Given these uncertainties, conservative harvest rates lower than those generated by the model should be sought, particularly in Greenland where a number of professional hunters rely on eider ducks for food and income (Christensen 2001, Pars et al. 2001), and where they have few economic alternatives if sources of wild meats are extirpated.

Recently, the Greenland Home Rule has decided to take action on the recommendation to reduce the spring harvest of eiders. Over the period 2002–2004 new bird hunting regulations were introduced in Greenland. Among other things, eider hunting in March and April was prohibited and it appears that harvest levels are now declining (Piniarneq 2007). If future years confirm this development we recommend to repeat the current modelling exercise to revise projections and to evaluate sustainability based on the new harvest levels. Ideally, more data will be available from breeding grounds in Greenland and Canada at this point, including population growth rates, making it possible to compare growth rates projected by the model and growth rates measured in the field.

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Table 1. Age-specific vital rates used in the model to simulate northern common eider populations.

	Year	class			
Paramenter	1	2	3	≥4	Source
Breeding propensity (bp_a)	0	0.22	0.40	1.00	Baille & Milne 1982
Clutch size (cs_a)	0	3.6	3.6	3.6	Joensen and Preuss 1972, Chapdelaine et al. 1986, Cooch 1986, Prach et al. 1986, Gilchrist unpubl, Nyegaard 2004
Nest success (ns_a)	0	0.9	0.9	0.9	Nyegaard 2004, Gilchrist unpubl.
Hatch success (hs_a)	0	0.9	0.9	0.9	Nyegaard 2004, Gilchrist unpubl.
Duckling survival (ds_a)	0	0.3	0.3	0.3	Swennen 1991
Relative vulnerability to hunting	3.5	2.0	1.0	1.0	Joensen 1974, Frich and Falk 1997, Gilliland & Robertson submitted
Summer survival (S_{sa})	-	0.92	0.98	0.98	
Fall survival (S_{fa})	0.707	0.866	0.985	0.985	
Winter survival (S_{wa})	0.707	0.866	0.985	0.985	
Annual survival†	0.5	0.69	0.95	0.95	Swennen 1991

† Annual survival of non-hunted common eider population, survival post-fledging for first year-birds

Overall fecundity: $M_a = bp_a * cs_a * ns_a * hs_a * ds_a$

Table 2. Initial values for population sizes, harvest levels and seasonality of harvests for the Canadian and Greenland subcomponents used in the model to simulate northern common eider populations.

Parameter	Definition	Value	Years data collected	Source
Ncwc	Number of Canadian females wintering in Canada	93500	2003	Canadian Wildlife Service
Ncwg	Number of Canadian females wintering in Greenland	211900	1999	Mosbech & Johnson 1999, Merkel et al., 2002
Ngwg	Number of Greenlandic females wintering in Greenland	19600	1998-2001	Frich et al., 1998; Christensen & Falk 2001; Merkel 2004b
Hcw	Canadian winter harvest of females	6500	1996-2001	Canadian National Harvest Survey
Hcs	Canadian summer harvest of Females	1200	1999-2001	Nunavut Harvest Study Final Report
Hg	Greenlandic harvest of females	30250	1993- 2001	Frich & Falk 1997, Piniarneq 2003, Merkel 2004a
Pfc	Proportion of Canadian harvest occurring in fall	0.51	1997-1999	B. Collins & H. Levesque, unpubl. data
Pfg	Proportion of Greenlandic harvest occurring in fall	0.41	2000, 2001	Merkel 2004b

Fig. 1. Schematic of the population structure for northern common eiders showing linkages among the sub-populations. Eiders that breed and winter in eastern North America are represented by open circles, while eiders that breed in eastern North America and winter in Greenland are represented by closed circles, and eiders that breed and winter in Greenland are represented by hatched circles. Arrows represent population connections, with the arrow showing a connection between the two breeding populations in Canada representing the possibility of changing wintering grounds through juvenile dispersal.

Fig. 2. Life-cycle diagram for the northern common eider population model. Eiders that breed and winter in eastern North America are represented by open circles, while eiders that breed in eastern North America, and winter in Greenland are represented by closed circles and eiders that breed and winter in Greenland are represented by hatched circles.

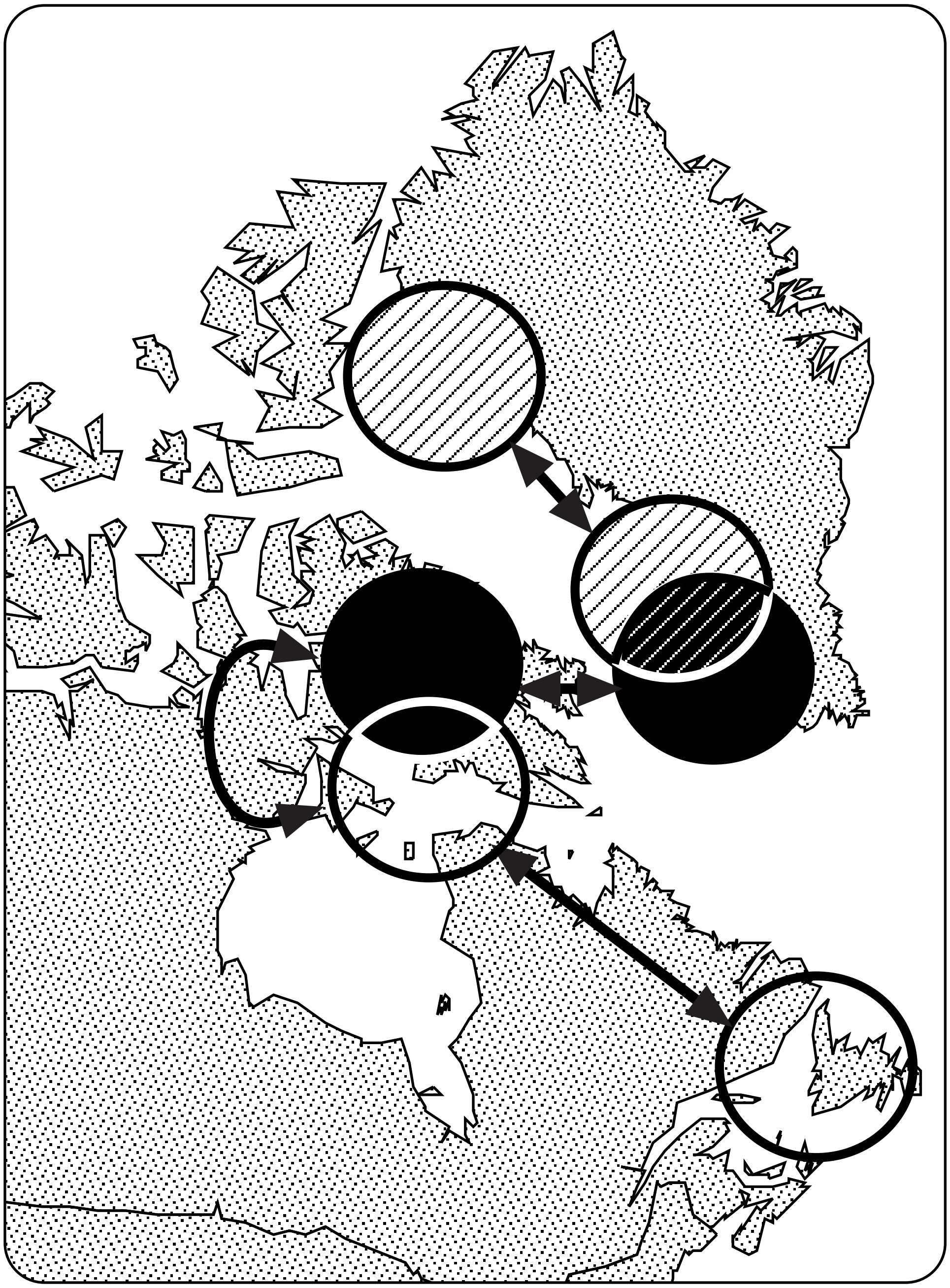
Fig. 3. General time line of annual events of the demographic model.

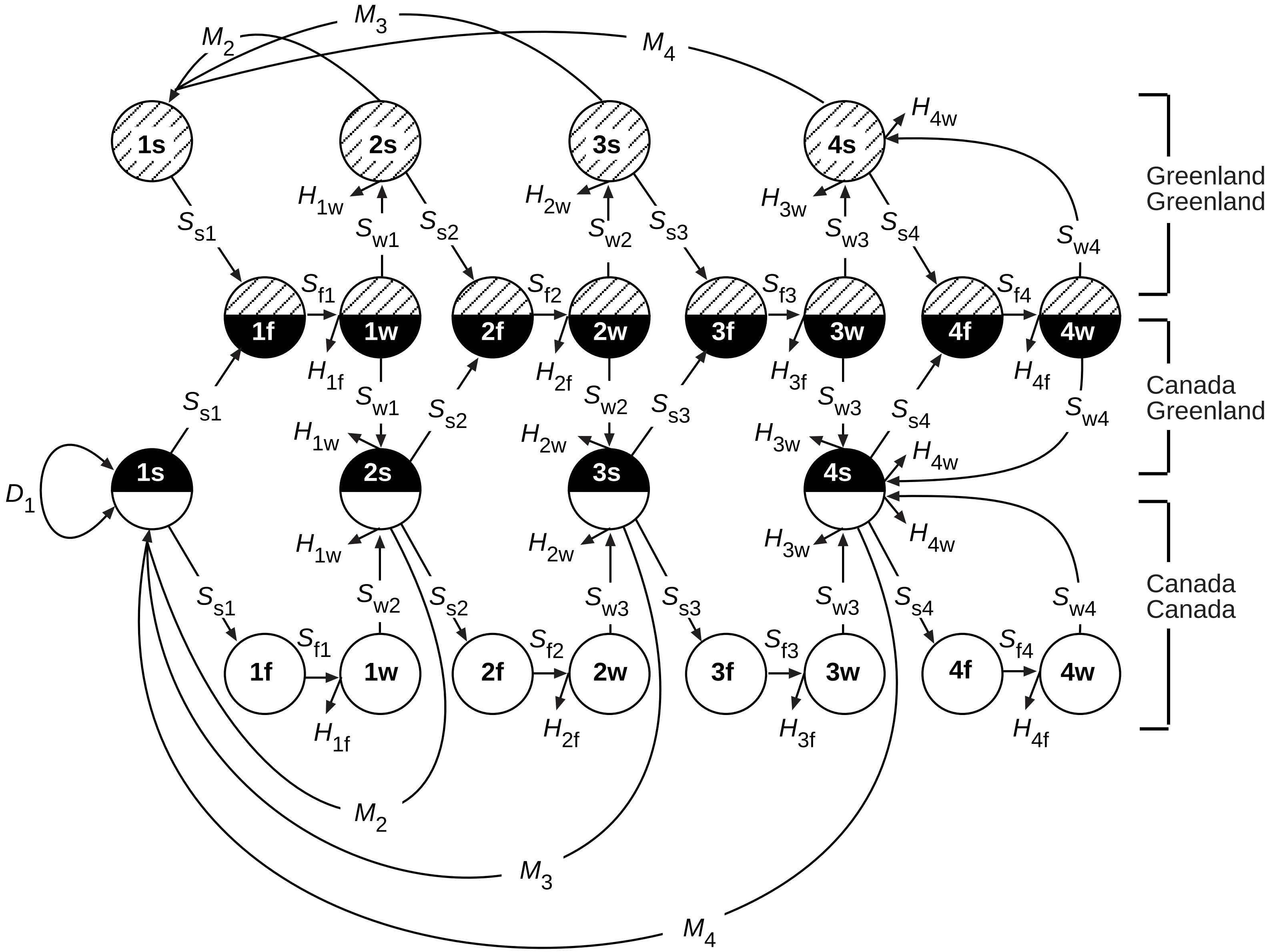
Fig. 4. Population projections of female northern common eiders over 50 years under current harvest regimes (A), and with harvest allocated to be entirely focussed in the fall or spring (B).

Fig. 5. Population projections of female northern common eiders over 50 years with different threshold values of where density-dependent reductions in harvest begin (A) and different strengthes of density-dependence reductions in harvest (B). High and low

thresholds and strength of the dependence are 50% increases and decreases of both, respectively.

Fig. 6. Relationships among population size, harvest levels and population trajectories of northern common eiders in the Northwest Atlantic. Points are population sizes and harvest levels used in the model, error bars represent ±1 SE on the population size estimates (or 68% of the probability mass), while the height of the boxes for Canada and Greenland indicate the range of plausible values for harvest levels. Population size and harvest levels combinations above and to the left of a line indicate declining populations; below and to the right, growing populations.




M_3
M_2
M_4
1s
2s
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H_{4w}
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S_{s1}
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Greenland
Greenland
S_{f1}
S_{f2}
S_{f3}
S_{f4}
1f
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4w
H_{1f}
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S_{s1}
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S_{s2}
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S_{s3}
S_{w3}
S_{s4}
S_{w4}
Canada
Greenland
H_{1w}
H_{2w}
H_{3w}
H_{4w}
D_1
1s
2s
3s
4s
H_{1w}
H_{2w}
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S_{s1}
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S_{w3}
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S_{w4}
Canada
Canada
S_{f1}
S_{f2}
S_{f3}
S_{f4}
1f
1w
2f
2w
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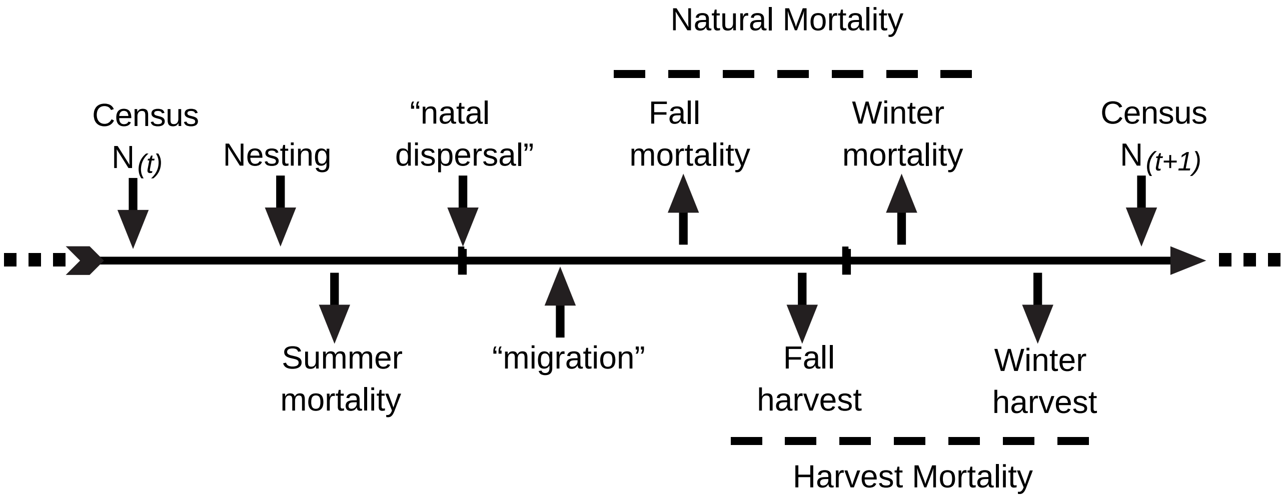
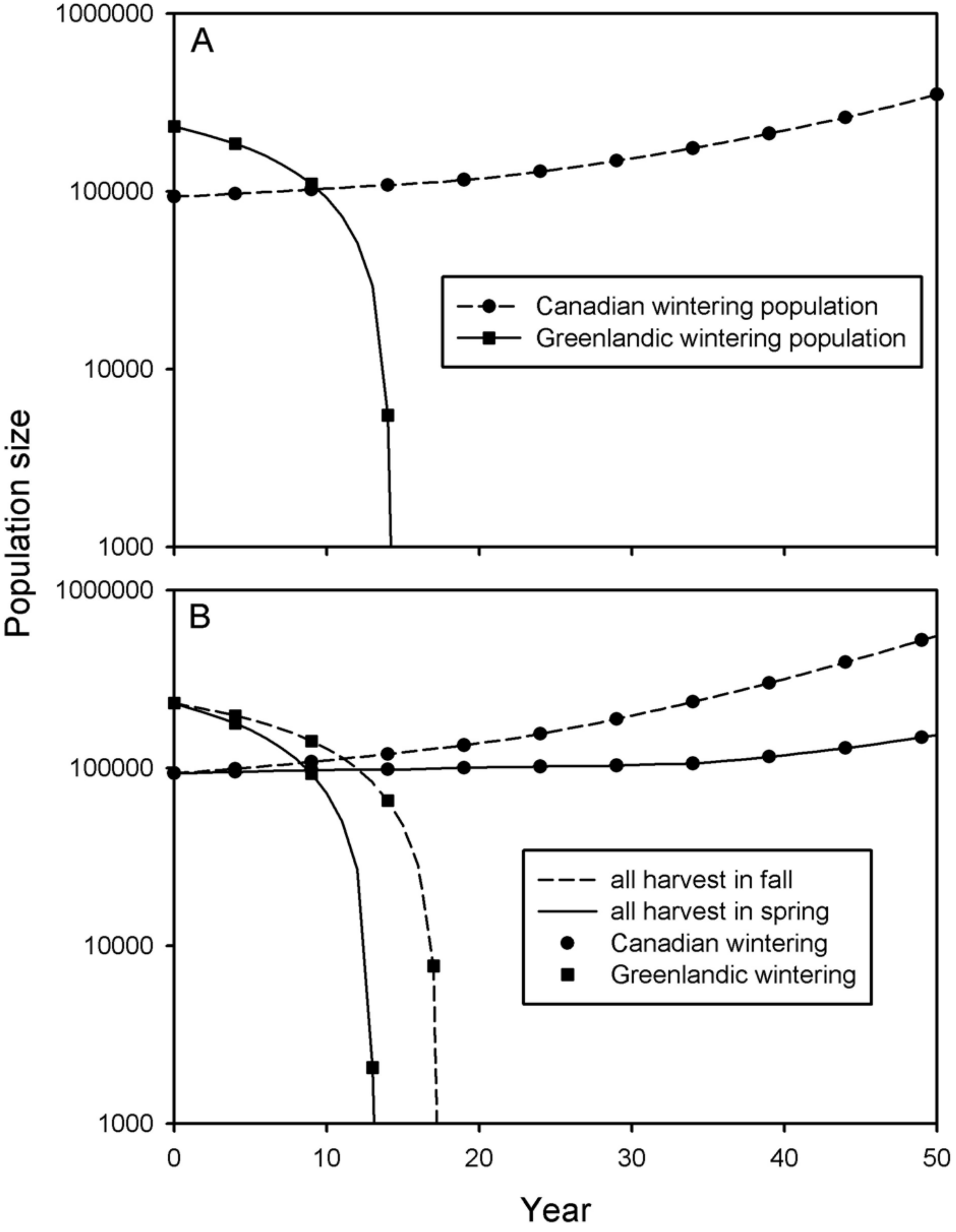
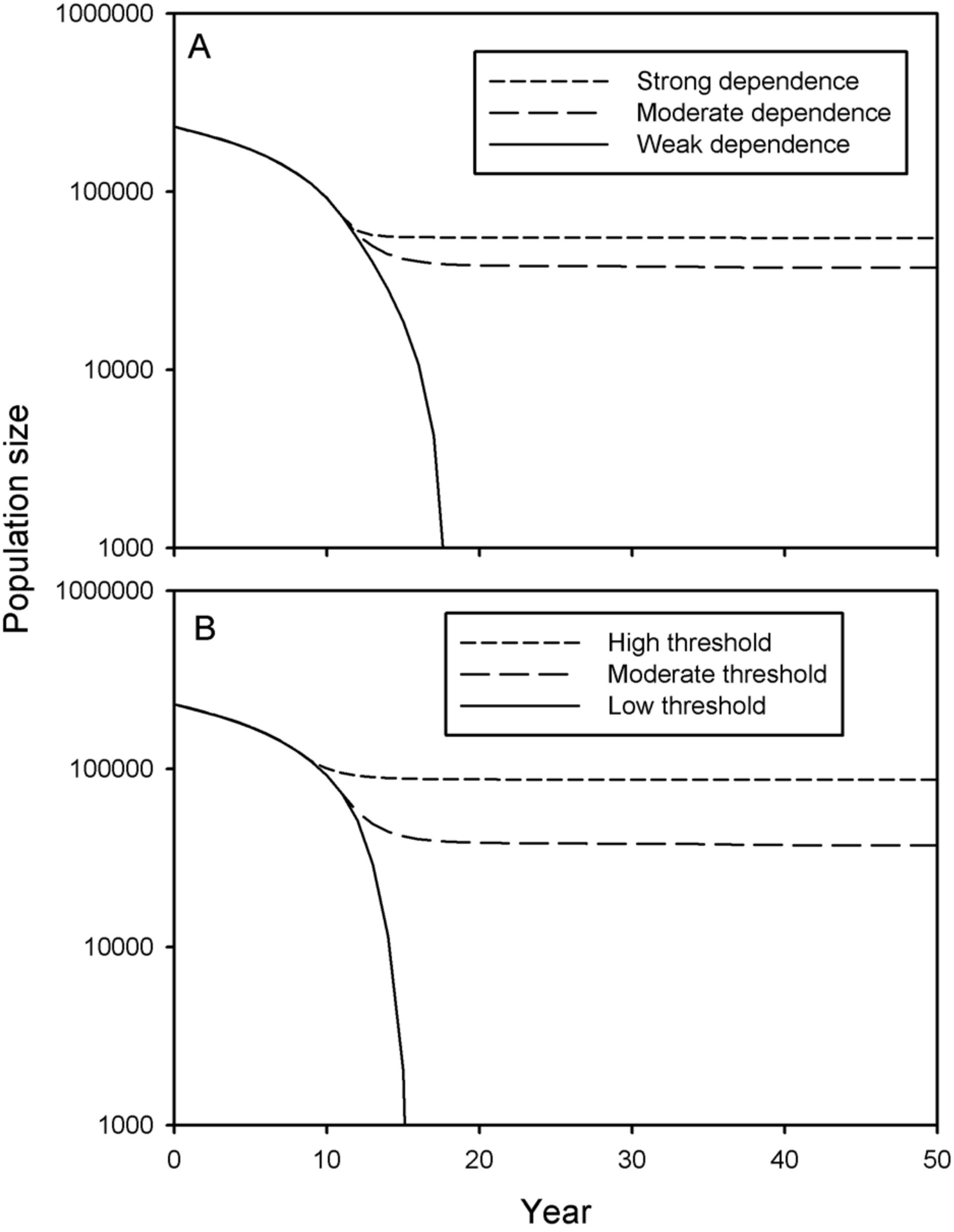
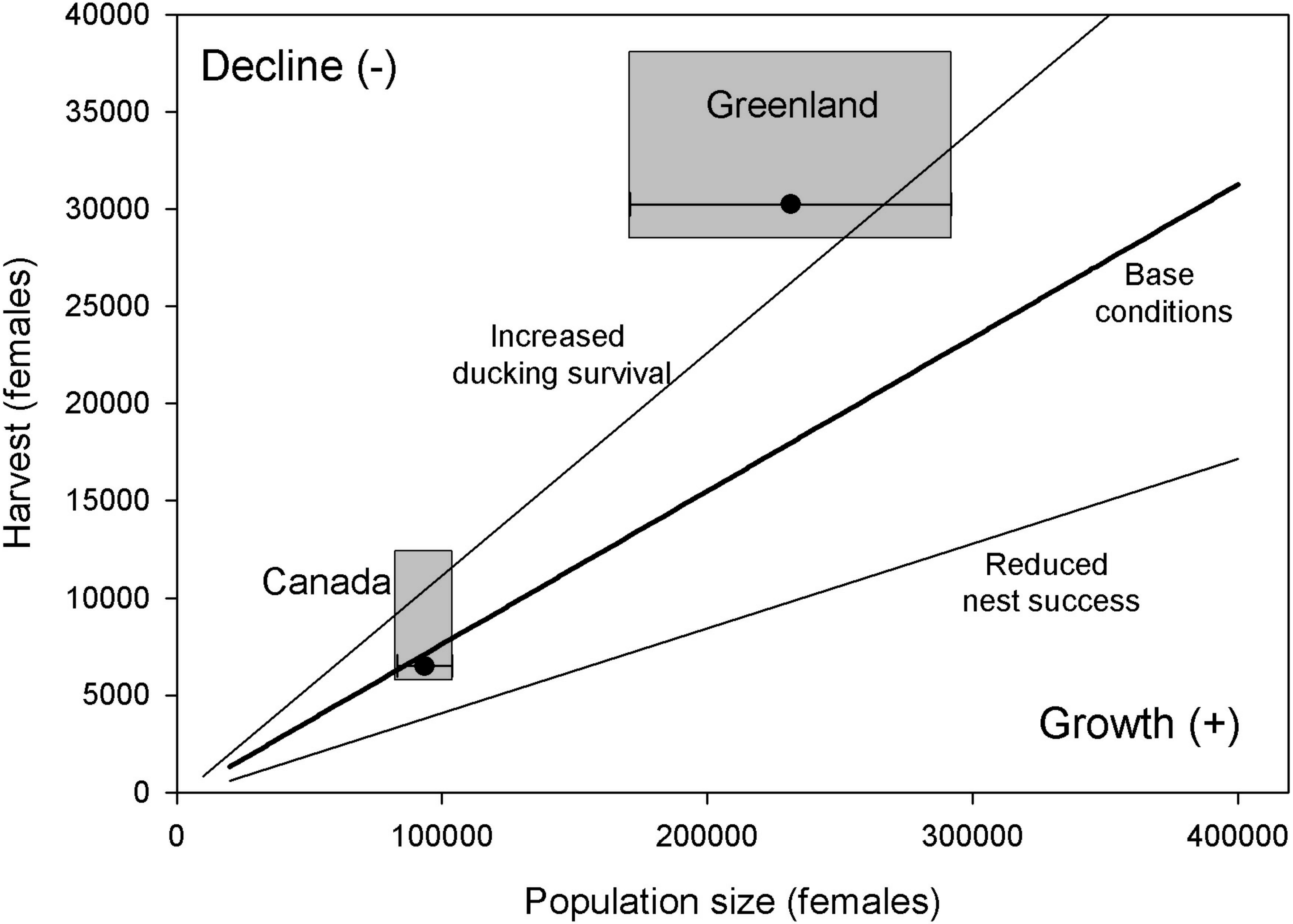
4w
H_{1f}
H_{2f}
H_{3f}
H_{4f}
M_2
M_3
M_4


Natural Mortality
Census
N(t)
Nesting
"natal dispersal"
Fall mortality
Winter mortality
Census
N(t+1)
Summer mortality
"migration"
Fall harvest
Winter harvest
Harvest Mortality



A
B
Canadian wintering population
Greenlandic wintering population
all harvest in fall
all harvest in spring
Canadian wintering
Greenlandic wintering
Population size
1000000
100000
10000
1000
Year
0
10
20
30
40
50


A
Strong dependence
Moderate dependence
Weak dependence
B
High threshold
Moderate threshold
Low threshold
1000000
100000
10000
1000
Population size
0
10
20
30
40
50
Year


40000
35000
30000
25000
20000
15000
10000
5000
0
Harvest (females)
0
100000
200000
300000
400000
Population size (females)
Decline (-)
Greenland
Base conditions
Increased ducking survival
Canada
Reduced nest success
Growth (+)