Optimal control of Atlantic population Canada geese

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ABSTRACT

Management of Canada geese (*Branta canadensis*) can be a balance between providing sustained harvest opportunity while not allowing populations to become overabundant and cause damage. In this paper, we focus on the Atlantic population of Canada geese and use stochastic dynamic programming to determine the optimal harvest strategy over a range of plausible models for population dynamics. There is evidence to suggest that the population exhibits significant age structure, and it is possible to reconstruct age structure from surveys. Consequently the harvest strategy is a function of the age composition, as well as the abundance, of the population. The objective is to maximize harvest while maintaining the number of breeding adults in the population between specified upper and lower limits. In addition, the total harvest capacity is limited and there is uncertainty about the strength of density-dependence. We find that under a density-independent model, harvest is maximized by maintaining the breeding population at the highest acceptable abundance. However if harvest capacity is limited, then the optimal long-term breeding population size is lower than the highest acceptable level, to reduce the risk of the population growing to an unacceptably large size. Under the proposed density-dependent model, harvest is maximized by maintaining the breeding population at an intermediate level between the bounds on acceptable population size; limits to harvest capacity have little effect on the optimal long-term population size. It is clear that the strength of density-dependence and constraints on harvest significantly affect the optimal harvest strategy for this population. Model discrimination might be achieved in the long term, while continuing to meet management goals, by adopting an adaptive management strategy.

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1. Introduction

The sustainable use of wild populations, such as fish and forests, poses significant challenges (Ludwig et al., 1993; Rosenberg et al., 1993). In addition to social, political and economic issues, there are a number of scientific uncertainties that inhibit our ability to identify sustainable exploitation strategies. Populations are influenced by environmental variation, which is unpredictable and uncontrollable. While managers may estimate population size and other relevant information, such as environmental variables, it is impossible to measure the state of the system without error. The harvest rates and other regulations set by managers will not be executed exactly as intended. Finally, the understanding of

the population that is used to set regulations (the model) is not a perfect representation of actual population dynamics (Williams et al., 1996).

In representing population dynamics, one of the critical questions is how much structural detail to include. There must be sufficient detail to capture key dynamics, but not so much that estimation issues undermine the predictive ability of the model. One common structural detail that can play a significant role in sustainable harvest is the age composition of the population. Individuals of different ages may contribute differently to the population growth rate through reproduction (motivating the study of reproductive value; McArthur, 1960), thus the age structure of the population can affect growth rate and harvest potential. The consideration of age structure, however, brings added uncertainties. First, the modeling process becomes more complicated by including the size of each age group within the population. This increases the number of population processes that must be described, and the number of parameters to be estimated. Second, it is common for harvest regulations to be set using an estimate of total population size, but it is usually much more difficult to measure the proportion of the population belonging to each age group. Third, the optimal harvest will have age structure, but it is unlikely that the individuals to be harvested can be selected according to age (Hauser et al., 2006).

In North America, Canada geese (*Branta canadensis*) are an important harvested species that exhibit considerable population structure. The Atlantic population, to be modeled in this paper, has a range covering eastern parts of the United States and Canada. Like many species of waterfowl, Canada geese are hunted for sport, an activity circulating millions of dollars each year (Henderson, 2005). Resident (non-migratory) populations of geese and migratory populations during the non-breeding season can damage crops and cause public nuisance complaints. Thus, management of goose populations can be a balance between providing high harvest opportunity while not allowing populations to get so large as to cause damage (Hindman et al., 2004).

Canada geese in the Atlantic population, like other goose populations, exhibit life-history attributes that differ by age. The age at first reproduction is typically greater than 3 years (Hardy and Tacha, 1989). There is reason to believe that birds of different ages may have different survival rates, including a different vulnerability to harvest (Mowbray et al., 2002). Thus, a structured model may be necessary to fully capture the dynamics of this population, and hence, to derive an appropriate harvest policy.

Before hunting regulations for Atlantic population Canada geese are set, an aerial survey of breeding grounds is conducted annually in June to estimate the number of breeding pairs of birds. In addition, annual reproduction is estimated from the age-ratio of birds banded in the late summer (Hindman et al., 2004). The abundance of non-breeding birds in several age classes can be reconstructed from these two data series. Thus, observation of the system state can support decision-making that depends on the age structure of the population.

The objective of harvest management in the past has most commonly been to maximize the value of the harvest taken over some time horizon. Increasingly, there is concern about overabundance for some species in conjunction with the desire to maintain the population rather than eradicate it. Recent examples include raccoons (Rosatte, 2000), gulls (Brooks and Lebreton, 2001), deer (Doerr et al., 2001; Giles and Findlay, 2004), moose (Nilsen et al., 2005), and a variety of species of geese (Ankney, 1996). Maintaining population size above a set level has also emerged as a goal for waterfowl management (Nichols et al., 1995; Williams and Johnson, 1995). For example, the objective applied to mallards has been to maximize the value of harvest, with harvest devalued when population size falls below some threshold (Johnson et al., 1997). Given that Canada geese potentially have negative effects on society at very high numbers as well as very low numbers, we will adapt this objective to incorporate lower and upper thresholds, between which population size is deemed to be acceptable. Demographic structure has not been considered an important influence on population dynamics for other waterfowl, and so previous management strategies have been dependent only on total population size, along with an environmental state variable (Williams, 1996a; Johnson et al., 1997, 2002).

We use stochastic dynamic programming (SDP) to find the optimal harvest strategy for this population of Canada geese, based on the estimated dynamics and the management objectives. This technique has been used for optimizing harvest in the past (e.g., Walters, 1975; Williams, 2001). However, demographic structure (age, size and/or sex) has rarely been considered, probably due to the increased number of dimensions in the state space (exceptions are Stocker, 1983; Milner-Gulland, 1997). Thus, the optimization of harvest for an age-structured population with an objective that incorporates both harvest value and population size is a novel study that may develop new rules of thumb pertinent to the management of Canada geese.

In this paper, we explore the impact of two key uncertainties on the optimal harvest strategy. First, there is a limited ability to control the population. Given a finite number of hunters, there is an upper limit on the total harvest that can be taken each year. Part of the management objective is to maintain population size below a certain upper bound, so limited control can lead to a risk-averse strategy that foregoes harvest opportunity to ensure the population remains within the desired bounds.

Second, there is some uncertainty about the strength of density-dependence. Over the range of abundance observed for this species, there is no clear information about the carrying capacity of the population. General models of harvested populations indicate that the optimal harvest strategy is sensitive to the strength of density-dependence (Reed, 1979; Lande et al., 1995), and so we pose two models of reproduction to investigate the potential effects of density-dependence.

2. Model and methods

As the basis of this study, we used the decision framework and population model developed by the Atlantic Population Canada Goose Adaptive Harvest Management (APCG AHM) working group, on which all of the authors serve. The working group intends to describe the rationale for the decision frame-

work and the development and parameterization of the model structure in a future publication. These elements, but not their development, are described below, along with the methods used to derive optimal strategies, investigate the properties of such strategies, and explore the effects of uncertainty.

2.1. Management objective

While the Atlantic population of Canada geese is not currently considered to be overabundant, experience with other goose populations raises some concern about the future status of this population (Ankney, 1996). For this reason we set an upper limit on acceptable population size, N^{MAX}. In addition to this objective, there is a desire to maintain population size above a minimum level needed to sustain a satisfactory level of hunting, N^{MIN}, and to maximize the opportunity for harvest, H_t.

To represent these objectives, we seek to maximize

$$\sum_{t=0}^{\infty} u(N_t^{(B)})H_t, \tag{1}$$

where

$$u(N) = \begin{cases} 1, & N^{MIN} < N < N^{MAX} \\ 0, & \text{otherwise.} \end{cases}$$

We use $N_t^{(B)}$ to denote the number of breeding adult birds at time t, and H_t to denote the total harvest taken at time t. Harvest is valued by a utility function $u(N)$, indicating whether or not the current population size N is acceptable. The number of breeding adult birds must be kept between N^{MIN} and N^{MAX} for management to be completely acceptable, and harvest is of no value when the number of breeding adults is outside these limits. Thus, the objective aims to maximize the harvest taken over an infinite time horizon, while keeping the number of breeding adults between N^{MIN} and N^{MAX}.

2.2. Decision and state variables

There is evidence to suggest that there are four significantly different demographic groups within the Canada goose population. These are the 1-year-olds (1), 2-year-olds (2), non-breeding adults (NB), and breeding adults (B). The state of the population is assessed just before the breeding season, so that the youngest individuals are nearing their first birthday and are classified as 1-year-old. Adult birds are 3 or more years of age, and individuals may or may not breed in a given year.

The control available to management is to set a harvest rate on the breeding adult population, $h_t^{(B)}$. Other groups within the population will be harvested subject to their vulnerability to harvest, relative to breeding adult birds. Young birds are considered to be inexperienced and therefore more easily hunted. Thus, the age classes respond to the set harvest rate in different ways. The harvest rate is limited by the total number of birds that can possibly be taken in 1 year. We set H^{MAX} to be the maximum total harvest that can be taken annually.
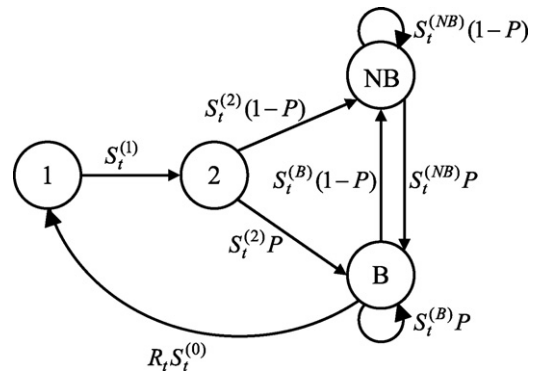

Fig. 1 – The life cycle of the Canada goose. Nodes represent 1-year-olds (1), 2-year-olds (2), non-breeding adults (NB), and breeding adults (B). Arrows pointing left-to-right give stage-specific survival rates, the arrow pointing right-to-left gives stage-specific fertility.

2.3. State dynamics

Fig. 1 shows the life cycle of the Canada goose, as modeled in this paper. In a given year, a proportion of 1-year-olds will survive to become 2-year-olds. A proportion of 2-year-olds will survive to become adults. A proportion P of these individuals will breed in the next year, with the remainder being classed as non-breeding adults. For every breeding adult, R offspring are hatched. These offspring undergo natural mortality and harvest before becoming 1-year-olds in the following year.

The number of offspring hatched in spring fluctuates from year to year. There is evidence that it is a function of the timing of the snow melt on breeding grounds (Hindman et al., 2004). There is uncertainty as to whether there is density-dependence. We will pose two possible models for breeding productivity R_t in year t that reflect different hypotheses regarding density dependence.

In the first model, we assume breeding productivity is a uniformly distributed random variable that is independent of total population size. Stochasticity in R_t represents the influence of the timing of the snow melt and process error.

In the second model, we assume that the impact of the timing of snow melt, z_t, can be described as a standard Normal random variable. Breeding productivity has the density-dependent function

$$R_t = \frac{\exp(a + bz_t + \varepsilon_t)}{1 + \exp[c(N_t^{TOT} - d)]}, \tag{2}$$

where ε_t is a Normal process error term, and N_t^{TOT} is the total population size at time t. We assume that $a, b, c, d > 0$ are known constants and that ε_t has a mean of zero and known variance σ_ε^2. Conditional on knowing total population size, breeding productivity R_t has a lognormal distribution, with parameters

$$\mu = a - \ln(1 + \exp[c(N_t^{TOT} - d)]) \tag{3}$$

and

$$\sigma^2 = b^2 + \sigma_\varepsilon^2. \tag{4}$$

After using one of the above models to calculate breeding productivity, we calculate the number of offspring in year t as

$$N_t^{(0)} = R_t N_t^{(B)},$$

the number of offspring hatched per breeding adult multiplied by the number of breeding adults.

The control variable is the harvest rate on breeding adults, $h_t^{(B)}$. Let the relative vulnerability of offspring and non-breeding birds be $d^{(0)}$ and $d^{(NB)}$, respectively. Then the harvest rates on offspring and non-breeding birds are

$$h_t^{(0)} = \min\{d^{(0)} h_t^{(B)}, 1\}$$

and

$$h_t^{(NB)} = \min\{d^{(NB)} h_t^{(B)}, 1\},$$

so that the harvest rate on each class is constrained to be no more than one (total removal of the class). Thus, the harvest rate applied to the total population is likely to be different from the control variable $h_t^{(B)}$.

The total harvest prescribed for each group then becomes

$$H_t^{(0)} = h_t^{(0)} N_t^{(0)}, \tag{5}$$

$$H_t^{(NB)} = h_t^{(NB)}[N_t^{(1)} + N_t^{(2)} + N_t^{(NB)}], \tag{6}$$

and

$$H_t^{(B)} = h_t^{(B)} N_t^{(B)}. \tag{7}$$

However, we are limited to removing at most H^{MAX} birds from the population. If the total harvest prescribed by our harvest rate $h_t^{(B)}$ exceeds H^{MAX}, then we set the total harvest to be H^{MAX}:

$$H_t = \min\{H_t^{(0)} + H_t^{(NB)} + H_t^{(B)}, H^{MAX}\}.$$

If $H_t = H^{MAX}$, then we must also rescale our actual harvest rates by multiplying $h_t^{(0)}$, $h_t^{(NB)}$ and $h_t^{(B)}$ by $H^{MAX}/[H_t^{(0)} + H_t^{(NB)} + H_t^{(B)}]$.

The survival rates of birds in each demographic group are calculated by combining natural mortality with the harvest rates:

$$S_t^{(0)} = s^{(0)}(1 - h_t^{(0)}),$$

$$S_t^{(1)} = s^{(1)}(1 - h_t^{(NB)}),$$

$$S_t^{(2)} = s^{(2)}(1 - h_t^{(NB)}),$$

$$S_t^{(NB)} = s^{(NB)}(1 - h_t^{(NB)}),$$

and

$$S_t^{(B)} = s^{(B)}(1 - h_t^{(B)}),$$

where $s^{(i)}$ is the proportion of birds in demographic group i that survive natural mortality, and $S_t^{(i)}$ is the proportion of birds in demographic group i that survive both natural mortality and harvest during year t. It is assumed that harvest occurs over a sufficiently short season that natural mortality is negligible during this time.

Then the population at the beginning of year $t + 1$ is composed of

$$N_{t+1}^{(1)} = S_t^{(0)} N_t^{(0)}, \tag{8}$$

$$N_{t+1}^{(2)} = S_t^{(1)} N_t^{(1)}, \tag{9}$$

$$N_{t+1}^{(NB)} = (1 - P)(S_t^{(2)} N_t^{(2)} + S_t^{(NB)} N_t^{(NB)} + S_t^{(B)} N_t^{(B)}), \tag{10}$$

and

$$N_{t+1}^{(B)} = P(S_t^{(2)} N_t^{(2)} + S_t^{(NB)} N_t^{(NB)} + S_t^{(B)} N_t^{(B)}), \tag{11}$$

where P is the proportion of adults that breed in a given year.

Thus, the state dynamics link management (setting $h_t^{(B)}$) to the state variables $\{N^{(1)}, N^{(2)}, N^{(NB)}, N^{(B)}\}$, which in turn contribute to the objective (expression (1)).

2.4. Optimization

We used stochastic dynamic programming to find the optimal state-dependent harvest policy. For a system with Markovian dynamics such as this one, SDP uses Bellman's equation recursively, backwards through time, to determine the optimal harvest decision as a function of the system state (Puterman, 1994). For this management problem, Bellman's equation is:

$$V(\mathbf{x}, t) = \max_h \{u(x_4)H(h, \mathbf{x}) + E_{x'}[V(\mathbf{x}', t + 1)]\}, \tag{12}$$

where $V(\mathbf{x}, t)$ is the value of using the optimal harvest strategy from year t into the future, given the population is in state $\mathbf{x}$ at time t. State $\mathbf{x}$ is a vector of four state variables $(N_t^{(1)}, N_t^{(2)}, N_t^{(NB)}, N_t^{(B)})$. This value V is found by determining the value of using harvest rate h on breeding adults in year t, followed by the optimal strategy from year $t + 1$ onwards, then choosing the harvest rate h that gives the highest value. Since the model of state dynamics is Markovian, then the decision h only directly affects returns during the year t and then the system state in year $t + 1$, denoted $\mathbf{x}'$. The returns generated during this year are $u(x_4)H(h, \mathbf{x})$, which is the term in expression (1) that refers to year t. The value of the utility function depends on the fourth state variable, breeding population size $N_t^{(B)}$. The total harvest taken, H, depends on the harvest decision h and the population state $\mathbf{x}$. The expected future value of the strategy is the value of using the optimal harvest strategy from year $t + 1$ into the future, given the population is in state $\mathbf{x}'$ at time $t + 1$. However the future state $\mathbf{x}'$ is uncertain, and so we must integrate over all possible future states, weighted by their probability of occurrence, which is determined from the state dynamics.

The optimal strategy over an infinite time horizon can be determined by the methods of value iteration and policy iteration (Puterman, 1994). Alternatively, SDP can be used over increasingly long time horizons, eventually reaching a stationary state-dependent strategy which does not depend on the time period or the terminal reward condition (Williams, 1996b). We take this approach and set a zero-reward terminal condition at time horizon T:

$$V(\mathbf{x}, T) = 0, \quad \text{for all } \mathbf{x}.$$

Then we work backwards through time using the recursive Eq. (12) to determine the optimal state-dependent strategy over increasingly long time horizons. This was carried out in the ASDP software package (Lubow, 1995).

Table 1 – Values taken by state, decision and random variables for the optimization

Variable	Values
Density-independent model	
$N^{(1)}$, $N^{(2)}$, $N^{(B)}$	0:100000:1000000[a]
$N^{(NB)}$	0:50000:500000[a]
$h_t^{(B)}$	0:0.1:0.6[a]
R_t	1, 1.5, 2, 2.5, or 3 with equal probability
Ceiling in Eqs. (6)–(9)	800000
H^{MAX}	200000:100000:1500000[a]
Density-dependent model	
$N^{(1)}$, $N^{(2)}$, $N^{(NB)}$	0:50000:550000[a]
$N^{(B)}$	0:100000:1000000[a]
$h_t^{(B)}$	0:0.1:0.6[a]
Discretized standard	$\Pr(x = -2) = 0.0400$
Normal distribution	$\Pr(x = -1.5) = 0.0656$
	$\Pr(x = -1) = 0.1210$
	$\Pr(x = -0.5) = 0.1747$
	$\Pr(x = 0) = 0.1974$
	$\Pr(x = 0.5) = 0.1747$
	$\Pr(x = 1) = 0.1210$
	$\Pr(x = 1.5) = 0.0656$
	$\Pr(x = 2) = 0.0400$
R_t	$\exp(\mu + \sigma x)$, for x above and μ, σ from Eqs. (1) and (2)
H^{MAX}	200000:100000:1500000[a]

[a] Notation X:Y:Z indicates that the minimum value considered is X, increasing in steps of size Y to a maximum value Z.

Table 2 – Values for parameters in the optimization

Parameter	Value
N^{MIN}	120000
N^{MAX}	500000
a	0.7
b	0.15
c	3.0×10^{-6}
d	800000
σ_ε	0.2
P	0.8
$d^{(0)}$	2.0
$d^{(NB)}$	1.0
$s^{(0)}$	0.65
$s^{(1)}$	0.86
$s^{(2)}$	0.86
$s^{(NB)}$	0.86
$s^{(B)}$	0.86

The method of SDP requires us to discretize the state, decision and random variables. The values used in this paper are listed in Table 1. To prevent inappropriate extrapolation, a ceiling was placed on population size in Eqs. (8)–(11) in the case of density-independent breeding productivity. Other parameter values required for the model are listed in Table 2.

3. Results

We will look briefly at population dynamics in the absence of harvest, under both the density-dependent and density-
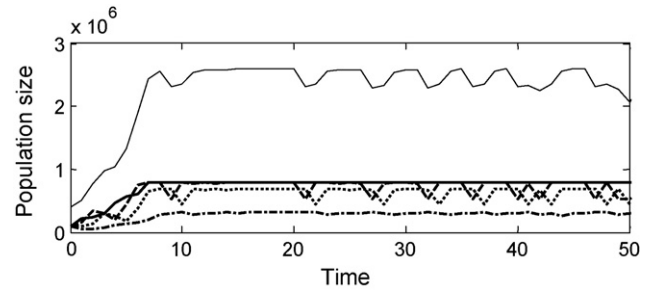

Fig. 2 – A simulation of the population using the density-independent model, in the absence of harvest. All classes have an initial abundance of 100,000; lines give total abundance (thin solid), abundance of 1-year-olds (dash), abundance of 2-year-olds (dot), abundance of non-breeding adults (dash-dot) and abundance of breeding adults (thick solid).

independent models. The optimal harvest strategy is a function of four state variables, and is therefore very difficult to visualize. Instead we will focus on the equilibrium population size when the optimal harvest strategy is used under each hypothesis for density-dependence and harvest limitation. We do this by simulating populations subject to harvest and recording the long-term population fluctuation. In particular we look at the number of breeding adults in the population, since their abundance contributes directly to the objective.

3.1. Density-independent model

In the absence of harvest, the density-independent model for breeding productivity causes the number of breeding adults in the population to grow without bound. For computational reasons our model is not truly density-independent, as we impose a ceiling on each age group (Table 1). Therefore, the number of breeding adults maintains this ceiling over time (Fig. 2) rather than increasing without bound. Other age groups fluctuate below their ceiling, although the number of 1-year-old birds frequently reaches its ceiling also. The total population size fluctuates between 2 and 2.6 million birds.

The optimal harvest strategy was derived for a variety of values of maximum harvest H^{MAX} (Table 1). An example run with a maximum harvest of 500,000 is shown in Fig. 3. In Fig. 4 we display the mean number of breeding adults in the population and the fluctuation around the mean for the remaining observations. Each harvest strategy was simulated for 100 runs, each 200 years in length. The first 100 years in each run were discarded.

When H^{MAX} was set to 200,000, the population was not always successfully held within the desired range, i.e. a breeding population size between N^{MIN} and N^{MAX}. In 90 of the 100 runs, the population grew until the number of breeding adults reached its ceiling. Since the ceiling was constructed for computational convenience and has no biological relevance, these runs were discarded from the data plotted in Fig. 4. However, this information does indicate the likelihood that the breeding population will not be maintained in the desired range over the long term, when total annual harvest is severely limited.
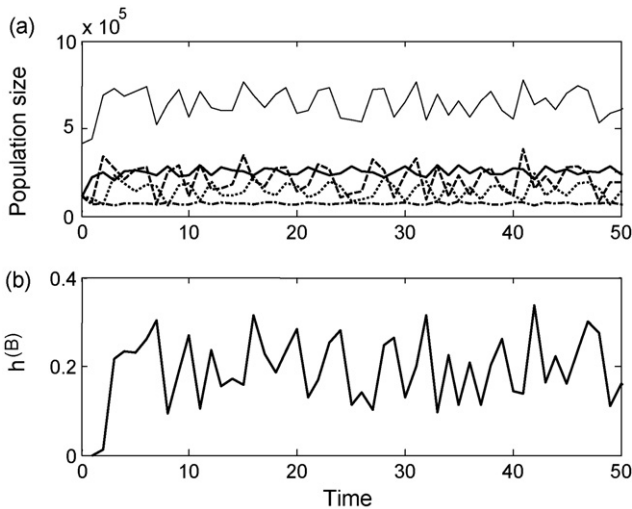
Fig. 3 – A simulation of the population using the density-independent model, under the optimal harvest strategy with maximum harvest $H^{MAX} = 500,000$: (a) population abundance and structure over time, lines give total abundance (thin solid), abundance of 1-year-olds (dash), abundance of 2-year-olds (dot), abundance of non-breeding adults (dash-dot) and abundance of breeding adults (thick solid); (b) the harvest rate set for breeding adult birds over time. All classes have an initial abundance of 100,000.

Since population growth is independent of density in the range of interest, harvest (and hence the objective) is maximized when the population is large. We see in Fig. 4 that when there is a great capacity to harvest the population (H^{MAX} is
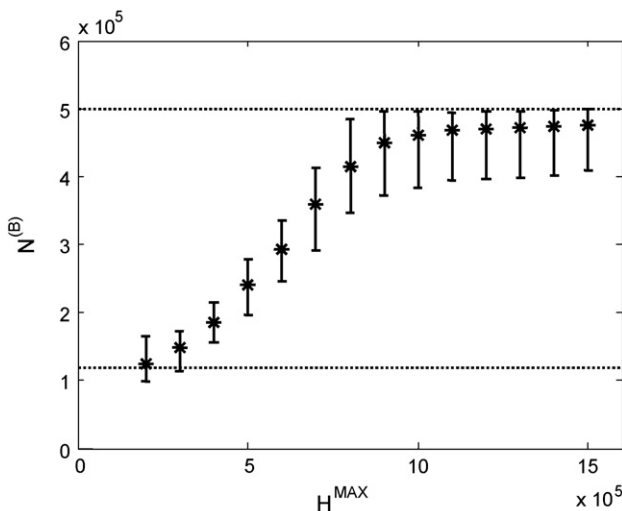

Fig. 4 – Long-term breeding population size under the optimal harvest strategy, as a function of maximum annual harvest H^{MAX}, using the density-independent model for breeding productivity. Asterisks denote the mean population size over 100 simulations; error bars indicate the interval that covers 95% of observations. Dotted lines show the lower and upper acceptable thresholds N^{MIN} and N^{MAX}, respectively.

large), then the population is maintained at a level close to the upper acceptable threshold, N^{MAX}. Stochasticity in breeding productivity, R, means that population size will fluctuate, and the mean breeding population size is held a little below the upper threshold to reduce the risk of the breeding population exceeding the threshold. Fluctuations above the mean breeding population size are smaller than fluctuations below the mean. The optimal strategy is able to avoid increases in abundance above the upper threshold N^{MAX} by increasing the harvest rate. However the only available response to population declines is to reduce harvest until the breeding population increases of its own accord. These declines incur some harvest loss but this is of less consequence than allowing the breeding population to exceed the upper threshold N^{MAX}, which completely eliminates the value of harvest to the objective.

When ability to control is limited (H^{MAX} is low), then the breeding population size is held well below the maximum acceptable level. If the population were permitted to grow nearer to the upper threshold, the maximum possible harvest could not prevent the population from exceeding the upper threshold, so that the objective is not achieved in the long term. When control is extremely limited (H^{MAX} is 200,000 or 300,000), random population fluctuations below the minimum acceptable size N^{MIN} occasionally occur. These are caused by random fluctuation in breeding productivity R, and are permitted because the alternative is increasing the risk that the manager will 'lose control' of the population and will be unable to prevent it from exceeding the upper threshold indefinitely.

Thus, limited control can have a significant effect on the optimal harvest strategy if breeding productivity is density-independent over the range of interest. There is a trade-off between maintaining the population at a high abundance to maximize harvest, while ensuring that the maximum harvest capacity can maintain breeding population size below the maximum acceptable level.

3.2. Density-dependent model

In the absence of harvest, the population under density-dependent breeding productivity approaches a stochastic carrying capacity above the maximum acceptable population size N^{MAX}. Using the parameters given in Table 2, the breeding population fluctuates around 700–800 thousand birds, while the total population size is 1.2–1.4 million birds (see Fig. 5 for an example simulation).

Given that breeding productivity is density-dependent in the manner of Eq. (2), there should be a particular target breeding population size that maximizes the stochastic annual harvest. We investigate this by simulating the population at a variety of fixed harvest rates, assuming that there is no upper limit on total harvest (H^{MAX} is infinite). In Fig. 6 we present the maximum sustainable yield for this population and the equilibrium breeding population size at which this occurs. These plots were created by simulating the population under a fixed harvest rate $h^{(B)}$, making 100 runs, each 200 years in length, and discarding the first 100 observations, but they also could have been derived by solving the equations numerically, using the methods of Runge and Johnson (2002). The annual yield and breeding population size were recorded. Fig. 6(a) indicates that annual yield is maximized for a harvest rate of about 13%,
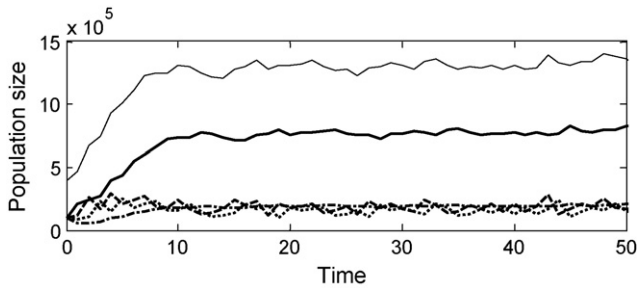
Fig. 5 – A simulation of the population using the density-dependent model, in the absence of harvest. All classes have an initial abundance of 100,000; lines give total abundance (thin solid), abundance of 1-year-olds (dash), abundance of 2-year-olds (dot), abundance of non-breeding adults (dash-dot) and abundance of breeding adults (thick solid).

which holds the long term breeding population size at a little over 300,000 birds, although there is some stochastic fluctuation in abundance (Fig. 6(b)).

To determine the effect of limited control on the optimal harvest strategy, we ran state-dependent optimizations and simulations in the same manner as for the density-independent model. (Variable levels and parameter values are listed in Tables 1 and 2, respectively.) Fig. 7 gives an example run of the optimal harvest strategy when maximum harvest is 500,000. The number of breeding adults did not exceed the maximum acceptable size N^{MAX} in any simulation.

Fig. 8 displays the mean breeding population size and fluctuation around the mean, under a variety of levels of maximum harvest H^{MAX} (Table 1). For all levels of control above $H^{MAX} = 500,000$, the breeding population is held at about 300,000 birds with some fluctuation due to stochasticity in breeding productivity. When maximum total harvest is 300,000 or 400,000 the population is held slightly lower to ensure that control is maintained. When maximum har-

vest is 200,000, population fluctuations have greater amplitude than when larger harvests are possible. With such limited control it is difficult to maintain the population at the level giving maximum sustainable yield. However the density-dependent function for breeding productivity ensures that the population never exceeds its upper acceptable threshold. This result depends critically on the fact that the population size that achieves maximum sustainable harvest falls within the desired bounds. If the nature of density-dependence in the population did not have this property, then there would be tension between the different components of the objective, and the limits to control could play a more central role.

3.3. Management implications

In this paper we have explored a variety of models for the optimal control of Canada geese, all of which may reasonably describe the dynamics of the Atlantic population and the constraints on harvest. We posed two models for stochastic breeding productivity, and investigated a variety of values for the upper limit on annual harvest. The objective was to maximize harvest, while maintaining the breeding population size between specified upper and lower bounds.

The optimal harvest strategy looks markedly different over the range of alternative models chosen. Under the density-independent model, sustainable annual harvest increases with breeding population size. When there is sufficient control available it is optimal to maintain the breeding population as close to the upper acceptable limit as possible, while ensuring that fluctuations rarely exceed this value. When control is limited then the population is optimally maintained at a lower level, to ensure that it does not exceed harvest capacity and the upper acceptable limit on population size, indefinitely.

Under the density-dependent model for breeding productivity, the maximum sustainable yield is obtained by keeping the breeding population size well below the maximum acceptable level. This equilibrium population size appears to be optimal for almost all levels of harvest control. However
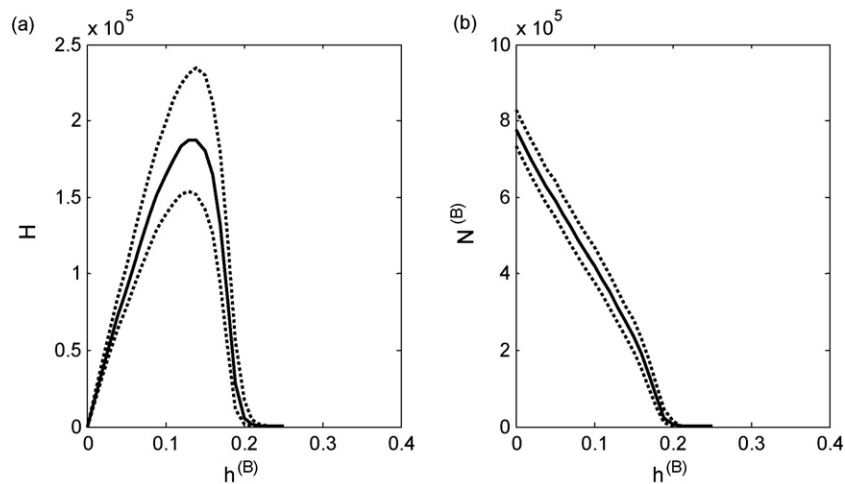

Fig. 6 – Simulation of the population with density-dependent breeding productivity under a constant harvest rate: (a) annual harvest, and (b) breeding population size, as a function of harvest rate $h^{(B)}$. Mean values are given by solid lines, 95% of observations fall between the dotted lines.
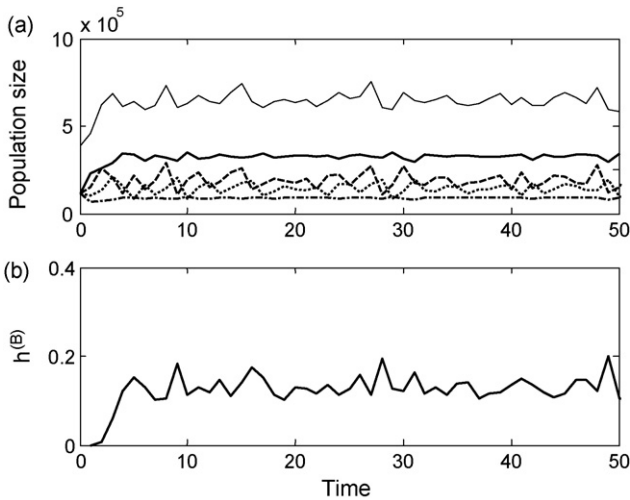
Fig. 7 – A simulation of the population using the density-dependent model, under the optimal harvest strategy with maximum harvest $H^{MAX} = 500,000$: (a) population abundance and structure over time, lines give total abundance (thin solid), abundance of 1-year-olds (dash), abundance of 2-year-olds (dot), abundance of non-breeding adults (dash-dot) and abundance of breeding adults (thick solid); (b) the harvest rate set for breeding adult birds over time. All classes have an initial abundance of 100,000.

the amplitude of fluctuations may increase under very limited control. If the breeding population size at which annual harvest is maximized exceeds the upper acceptable limit then we expect that a trade-off between maximizing harvest and
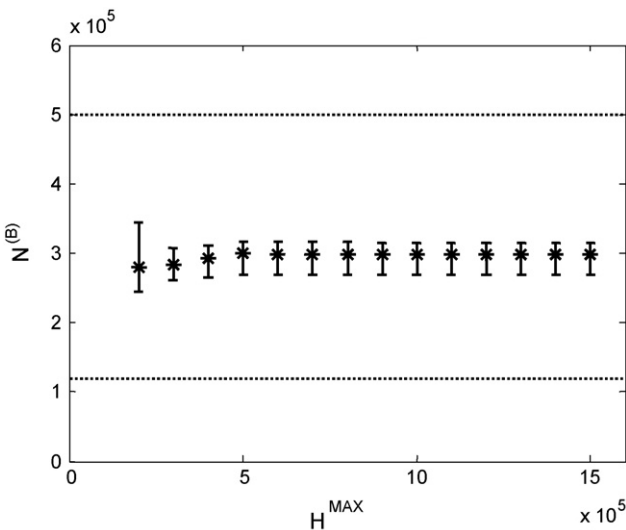

Fig. 8 – Long-term breeding population size under the optimal harvest strategy, as a function of maximum annual harvest H^{MAX}, using the density-dependent model for breeding productivity. Asterisks denote the mean population size over 100 simulations; error bars indicate the interval that covers 95% of observations. Dotted lines show the lower and upper acceptable thresholds N^{MIN} and N^{MAX}, respectively.

controlling abundance will arise, as previously seen for the density-independent model.

These results are consistent with other studies. The strength and form of density-dependence are well known to affect the optimal harvest strategy when the objective is to maximize yield (Saether et al., 1996; Johnson et al., 1997; Runge and Johnson, 2002). When breeding productivity is density-independent then harvest is maximized by letting the population grow as large as possible, whereas a particular finite population size maximizes harvest under density-dependent breeding productivity. Our additional objective of maintaining population size within set limits, which has rarely been investigated, places additional constraints on the target population size.

Reduction of target population size when harvesting capacity is limited has been observed previously (Lande et al., 1995; Saether et al., 1996), but this applied only to a density-dependent model. Keeping in mind our additional objective regarding population size, results for both density-dependent and density-independent models consider the risk of being unable to harvest a very large population down to the level that best achieves the objective, whether the objective is a function of harvest value, population size, or both.

Optimizing harvest with an objective that incorporates both harvest yield and population size has only been seen for other waterfowl management (Johnson et al., 1997, 2002). In particular, two different hypotheses regarding the strength of density-dependence were also considered for the management of mallards. The optimal strategy for a population with strong density-dependence had more liberal regulations than the optimal strategy under weak density-dependence. We also found this to be the case when breeding population size is low to moderate. However, we found that the optimal strategy under the density-independent model is more liberal when breeding population size exceeds the maximum acceptable size. In this scenario a population under the density-independent model has a higher growth rate than under the density-dependent model, and requires a higher harvest rate to ensure that the population returns to an acceptable size. Johnson et al. (1997, 2002) did not impose an upper limit on acceptable population size. These results may not apply generally to other studies since the optimal equilibrium population size, harvest rate and harvest yield are dependent upon the parameter values and functional form governing dynamics (Saether et al., 1996; Runge and Johnson, 2002).

Given that the optimal harvest strategy varies markedly between hypotheses, achievement of management goals could clearly be improved with a better understanding of population dynamics and limits to annual harvest. The data collection required to discriminate between these alternative models is a very slow process, but might be sped up by experimental management. The use of adaptive management techniques (Walters, 1986; Williams et al., 1996) can find the optimal trade-off between meeting management goals in the short term and experimenting for learning in the long term.

A number of previous studies have investigated optimal passive and active adaptive management when the strength of density-dependence regulating a population is uncertain (Walters, 1981; Ludwig and Walters, 1982; Johnson et al., 1997). If all models are weighted evenly, then the optimal passive

adaptive harvest strategy is likely to be a smooth weighted average of the optimal harvest strategies under each model. Learning about the strength of density-dependence can be accelerated by forgoing harvest in the short term (active adaptive management). This allows the population to increase to an abundance where the alternative models of density-dependence make very different predictions of future population size, so that subsequent monitoring will indicate which model best supports the observed population dynamics. However, limited harvesting capacity was not considered in these studies and this poses an additional risk of 'losing control' of the population if it is permitted to grow too large. It remains to be seen whether the potential benefits of allowing the population to grow large (while still within the acceptable bounds of the objective) outweigh the short-term sacrifice of harvest and the risk of the population explosion.

Acknowledgments

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