

Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands?

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Abstract

The North American greater snow goose population has increased dramatically during the last 40 years. We evaluated whether refuge creation, changes in land use on the wintering and staging grounds, and climate warming have contributed to this expansion by affecting the distribution, habitat use, body condition, and migration phenology of birds. We also reviewed the effects of the increasing population on marshes on the wintering grounds, along the migratory routes and on the tundra in summer. Refuges established before 1970 may have contributed to the initial demographic increase. The most important change, however, was the switch from a diet entirely based on marsh plants in spring and winter (rhizomes of *Scirpus/Spartina*) to one dominated by crops (corn/young grass shoots) during the 1970s and 1980s. Geese now winter further north along the US Atlantic coast, leading to reduced hunting mortality. Their migratory routes now include portions of southwestern Québec where corn production has increased exponentially. Since the mid-1960s, average temperatures have increased by 1–2.4 °C throughout the geographic range of geese, which may have contributed to the northward shift in wintering range and an earlier migration in spring. Access to spilled corn in spring improved fat reserves upon departure for the Arctic and may have contributed to a high fecundity. The population increase has led to intense grazing of natural wetlands used by geese although these habitats are still largely undamaged. The foraging in fields allowed the population to exceed limits imposed by natural marshes in winter and spring, but also prevented permanent damage because of their overgrazing.

Keywords: agriculture land, greater snow geese, habitat use, population increase, wetland

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Introduction

Populations of several wildlife species have increased dramatically in recent decades, such that their habitats are threatened and the populations are in conflict with human activities. Snow geese (*Chen caerulescens*) are a prominent example of exploding populations in North America (Ankney, 1996). During the last century, the greater snow goose (*C. c. atlantica*) population, which breeds in the eastern Canadian Arctic archipelago and

winters along the Atlantic coast of the US, has increased from a few thousands birds to more than 800 000 (Menu *et al.*, 2002; Béchet *et al.*, 2004b). A similar increase has occurred in the lesser snow goose population (*C. c. caerulescens*) breeding in the central Canadian Arctic and wintering along the Gulf of Mexico coast (Abraham & Jefferies, 1997; Abraham *et al.*, 2005).

The causes of these increases are complex and not well understood. The consensus among wildlife specialists is that human activities along the migration routes and on the wintering range of geese were responsible for the increase. Changes in hunting regulations, creation of refuges for wintering and migrating

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birds, changes in agricultural practices, and climate change have all been invoked as potential causes (Abraham & Jefferies, 1997; Menu *et al.*, 2002; Jefferies *et al.*, 2004). However, there have been few attempts to examine how these factors could have affected the population ecology of geese (distribution, habitat use, body condition), and contributed to the increase. Although population growth of greater snow geese since the late 1960s appears well correlated with variations in sport harvest (Menu *et al.*, 2002), changes in hunting regulations explain only some of the variations in population development during this period (Calvert *et al.*, 2005).

The consequences of population increases in geese are better documented than their causes. Numerous studies have shown that large densities of geese can severely impact wetland vegetation in both lesser (Kerbes *et al.*, 1990; Jano *et al.*, 1998; Abraham *et al.*, 2005) and greater snow geese (Smith & Odum, 1981; Giroux & Bédard, 1987; Bélanger & Bédard, 1994; Gauthier *et al.*, 1995). However, these impacts and the responses of the vegetation to intense grazing of aerial shoots and grubbing of rhizomes are variable (Gauthier *et al.*, 2005).

In this paper, we study the potential causes and consequences of the population increase in greater snow

geese from 1965 onwards when scientific data are available. We examine the hypotheses that refuge creation, changes in land use, and climate warming also contributed to the population development. We look at temporal trends of these factors and their potential influence on the population ecology of geese (their distribution, habitat use, diet, body condition, and migration phenology). We focus on the winter and spring periods in temperate areas because this is where human activities are concentrated and where conditions presumably have changed most. Finally, we review the effects of increasing number of geese on wetland habitats during winter and spring/autumn staging in temperate areas and during summer in the Arctic.

Methods

Study area

The greater snow goose breeds from North-Central Baffin Island to North Ellesmere Island and in Western Greenland (Fig. 1). Despite this large breeding range, detailed information is available only from a single breeding colony, Bylot Island, which accounts for ca. 15% of the total breeding population (Reed *et al.*, 2002).

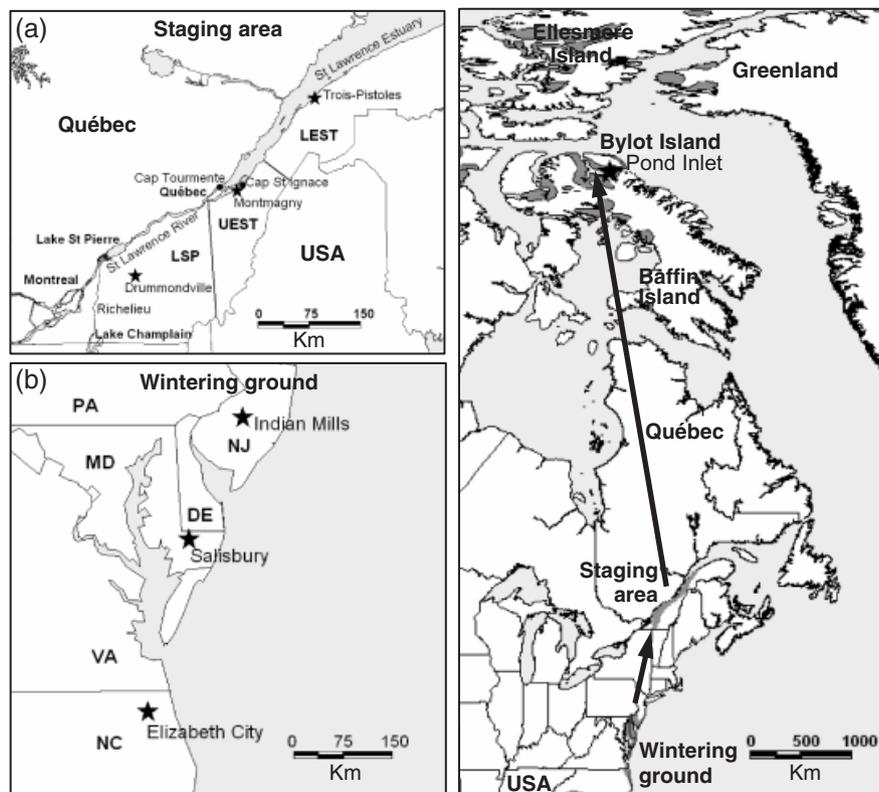


Fig. 1. Map showing the wintering, spring staging and breeding range (gray areas) of greater snow geese, and migratory route (arrows). (a) Limits of the Lac-St-Pierre (LSP), Upper estuary (UEST) and Lower estuary (LEST) regions of the St Lawrence River, Québec. (b) Close-up of wintering range. Localities from where we obtained weather data are shown with a star.

Birds migrate through central Québec and stage for 6–8 weeks in spring and autumn along the St Lawrence River in southern Québec. We divided this area into three regions: the upper estuary (UEST; the traditional area used by geese), the lower estuary (LEST) to the east, and the Lac-St-Pierre area (LSP – which includes the south shore of the St Lawrence, up-river from Québec City) to the west (Fig. 1). Greater snow geese winter in the mid-Atlantic states of the Atlantic Flyway, which we divided into three regions: (i) southern (South (SC) and North Carolina (NC), and Virginia (VA)), (ii) central (Delaware (DE) and Maryland (MD)), and (iii) northern (New Jersey (NJ), Pennsylvania (PA), and New York (NY)) states.

Data

Since 1965, the Canadian Wildlife Service (CWS) has conducted an annual photographic survey of greater snow geese during spring staging when the entire population is confined to the shores of the St Lawrence River in Québec (see Béchet *et al.*, 2004b for methods and Reed *et al.*, 1998 for data). The US Fish and Wildlife Service (USFWS) has also conducted mid-winter aerial surveys since 1950 that can be used to document the spatial distribution of geese in winter (see Reed *et al.*, 1998). We calculated the proportion of geese wintering in each of the three regions and transformed these data into total goose-days using the annual population size determined in spring, assuming that winter lasted 120 days (15 November to 15 March). Mean goose-day values over 5-year periods were used to minimize year-to-year variations. Data on the use of the three Québec regions in spring were available for three periods. In 1971–1975, we calculated the average number of geese counted in the UEST and LEST regions ($n = 6–9$ aerial surveys per year) each year (no geese used the LSP region at that time). We transformed these data into total goose-days as done in winter. The same procedure was applied in 1990–1991, except at LSP, a region used earlier in the season by geese before the aerial surveys took place, but where daily ground counts were conducted at the main roosting site (De Koster, 1993). The total number of goose-days from ground counts was added to those calculated from the aerial survey to determine use of the three regions. Finally, in 1997–1998, goose-days during spring staging were obtained from daily ground counts conducted at all major roosting sites in the three regions (see Béchet *et al.*, 2003 for methods).

Habitat use by geese in spring is available from three studies. In 1975–1976 and 1979–1980, regular scans of geese feeding in various habitats were conducted from the ground at two sites in the UEST and two in the

LEST (A. Reed, unpublished results; Gauthier *et al.*, 1988). In 1990–1991, presence of geese on agricultural lands at LSP was obtained by multiple scans of goose flocks (De Koster, 1993). In 1997–1998, tracking of radiomarked geese occurred in the three regions (Béchet *et al.*, 2004a), from which the proportion of time spent foraging in marshes, hayfields, and cornfields was determined.

Dates at which the largest number of arriving and departing geese were counted were available for several years in the UEST (1971–1975, 1990–1994, and 1997–1998) and at LSP (1990–1991, 1997–1998). These data came from regular counts conducted at the Cap Tourmente National Wildlife Area (CWS, unpublished results) or from our own work (Gauthier *et al.*, 1992; Béchet *et al.*, 2003). Duration of staging was the difference between departure and arrival dates.

Data on total body fat of geese arriving and departing from the UEST were obtained from Gauthier *et al.* (1984) for 1979–1980 and from Gauthier *et al.* (1992) for 1989–1990. In 1999–2000, geese departing from the LSP (April) and the UEST (May) were also collected using cannon-nets. We weighed the abdominal fat mass, an index of total body fat (Gauthier & Bédard, 1985), and determined the stable-carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$, expressed in delta notation, $\delta^{13}\text{C}$) of fat (see Féret *et al.*, 2003 for methods). Because corn is the only plant eaten by geese at LSP and in the UEST with a high $\delta^{13}\text{C}$ value typical of C_4 plants, this value provides an index of the intensity of corn feeding by individual birds (i.e. percentage of corn in the diet) at these sites (see Féret *et al.*, 2003).

Within the wintering range of greater snow geese, we tallied the number of National Wildlife Refuges (NWR), their date of creation, and area covered (excluding large areas of open water) from the USFWS web site (<http://refuges.fws.gov/>). Most refuges are a mixture of marshes and farmlands. This represents a minimum number of protected areas as additional state wildlife management areas also exist. Within the staging range in Québec, we obtained similar information on Migratory Bird Sanctuaries and the National Wildlife Area (NWA) of Cap Tourmente from the CWS web site (<http://www.qc.ec.gc.ca/faune/faune/html/rom.html>). Although some US NWR and the Cap Tourmente NWA allow controlled snow goose hunting, they always provided significant hunting-free areas for geese.

Agricultural data were obtained from 1965 to 2002 for the wintering (USDA-NASS, 2003) and the staging areas (Statistics Canada, 1966–1986, Statistics Canada, 2003). We examined surface area of harvested crops usable by geese (corn, barley, oats, winter wheat (US only) and hay (including alfalfa)). We limited our compilation to the geographical range occupied by geese. In

winter, this included the northern coast of NC and the southeastern coast of VA and its peninsula (southern states), DE and the upper and lower eastern shores of MD (central states), and central and south NJ (northern states). For Québec, we used the same three regions as defined above.

We obtained long-term temperature records from 1965 to 2001 from representative weather stations away from large cities within the geographical range of the species. In the US, the sites were Elisabeth City (NC) in the southern, Salisbury (MD) in the central, and Indian Mills (NJ) in the northern states for the months of December to February (Fig. 1; NCDC, 2002). In Québec, the sites were Drummondville (LSP region), Montmagny (UEST) and Trois-Pistoles (LEST) for the months of March to May (Environment Canada, 2003). In the Arctic, we used data from Pond Inlet (NU), the community located closest to Bylot Island (data available from 1975; Environment Canada, 2003). At all sites we used daily mean temperature to calculate mean temperature for the season of interest each year. These annual temperatures were then expressed as deviations from the mean temperature for the period considered.

We used data from several long-term studies to assess the impact of population increase on natural habitats. In the Arctic, Gauthier *et al.* (1995, 2004) have monitored the impact of goose grazing in wet meadows of Bylot Island by measuring the biomass at peak production in August in 1 m × 1 m goose exclosures set up annually at different sites since 1990. The plots enabled us to determine the annual production of areas continuously grazed until the current year. Along the St Lawrence River, monitoring has been conducted in three *Scirpus* tidal marshes. Production of the main macrophytes is estimated using stem density evaluated in 25 cm × 25 cm (Montmagny and Cap St-Ignace) or 30.5 cm × 30.5 cm (Cap Tourmente NWA) quadrats, and biomass estimates based on allometric equations using plant heights (Giroux & Bédard, 1988a; Reed, 1989).

Results

Population size

Reliable information on population size prior to the first year in which a photographic survey was conducted (1965) is scarce. Between 1900 and 1906, the autumn population was thought to be as low as 2000–4000 birds (Lemieux, 1959; Anonymous, 1981), but in the first year of the photographic survey, the spring population was estimated at 25 400 (Fig. 2). Assuming a population of 2000, the average population growth rate from 1900 to 1965 was 4% yr⁻¹. Between 1965 and 1998, the popu-

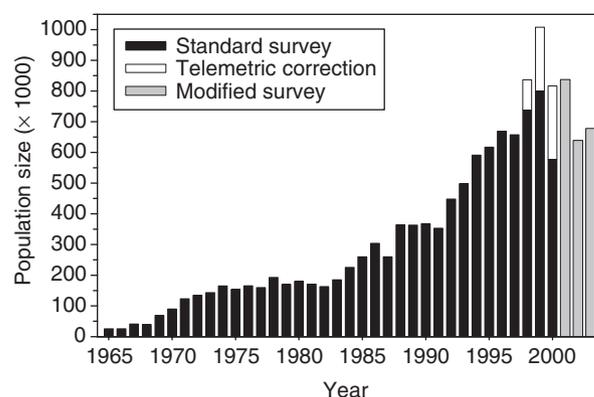


Fig. 2. Greater snow goose spring population size, 1965–2003 (Reed *et al.*, 1998; CWS unpublished results). The survey coverage was increased in 2001 to correct for the underestimation revealed by a telemetry study (Béchet *et al.*, 2004b).

lation grew at an average rate of 9% yr⁻¹, although we can recognize three growth phases. Until 1974, the population grew very rapidly (15% yr⁻¹), from 1975 to 1983 it was nearly stable (1% yr⁻¹), and from 1984 to 1998 rapid growth resumed (9% yr⁻¹, Fig. 2; Menu *et al.*, 2002). Change in the sport harvest over this period explained the cessation of population growth from 1975 to 1983: harvest rate doubled with the reopening of the US hunting season in 1975 but abruptly decreased around 1984 (see Fig. 5 in Menu *et al.*, 2002), possibly because of movements of geese to less heavily hunted areas in winter (Calvert *et al.*, 2005). With the introduction of the special conservation measures to limit population growth in 1999, harvest rate increased again and the population declined at an average rate of 8% yr⁻¹ until 2003 (Fig. 2).

Changes observed in the population

Distribution and migration route. The mid-winter surveys show a major northern shift in the distribution of geese since 1965. Until 1979, wintering geese were concentrated in the southern states, with NC and VA accounting for 81% of geese censused (Fig. 3). However, the number of geese wintering in the central states has risen dramatically since 1980, and a similar increase has been noted more recently in the northern states, whereas, the number in the southern states has declined. From 1990 to 1998, the northern, central, and southern states accounted for 30%, 58%, and 12% of wintering geese, respectively.

Major changes also occurred in the distribution of spring migrating geese in southern Québec. Up to the 1960s, geese were restricted to the traditional area of the upper St Lawrence estuary marshes (UEST, Lemieux,

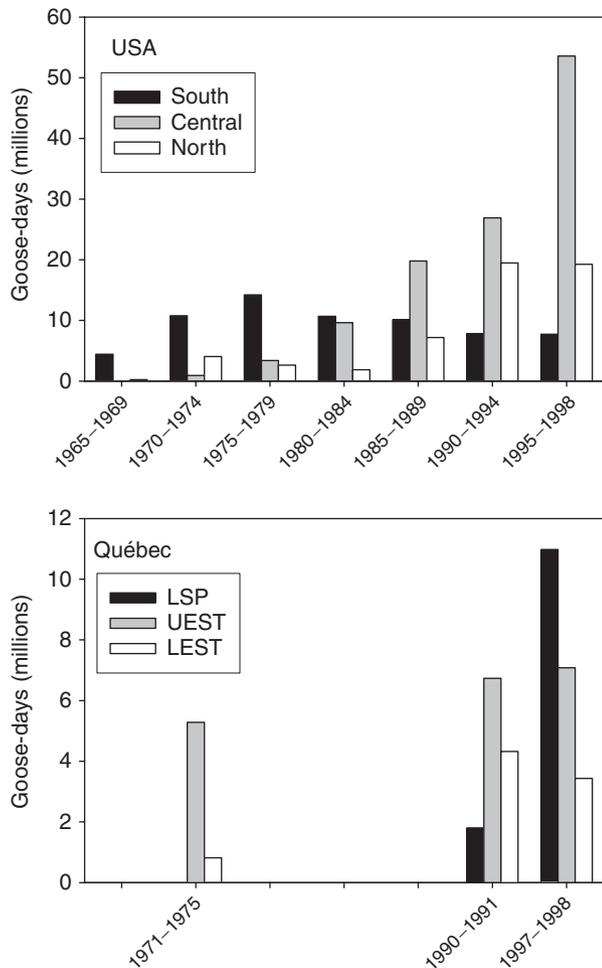


Fig. 3. Change in the use of three regions of the US Atlantic Flyway in winter and of 3 regions of Québec (Lac-St-Pierre LSP, Upper estuary UEST and Lower estuary LEST) during spring staging by greater snow geese between 1965 and 1998. Each bar group is the annual mean of 2–5 years.

1959). By the early 1970s, geese had expanded their range to the LEST, which then accounted for 13% of goose use, and continued to do so until the 1990s (Fig. 3). However, the most dramatic increase has been in the use of the LSP region where geese started to appear in the 1980s. In the early 1990s, 14% of total goose use in spring occurred there, but by 1997–1998 this proportion had risen to 51%. Despite the large increase in population size since the 1970s, use of the traditional staging area in spring (UEST) has increased only marginally (Fig. 3). These changes in distribution actually reflect a change in migration route. Previously, geese flew directly from wintering areas along the Atlantic coast to the St Lawrence estuary across the Appalachian Mountains (Lemieux, 1959). Now, geese move up the Hudson/Richelieu River

valleys to reach the LSP first, before moving down to the St Lawrence estuary later on (Béchet *et al.*, 2003, Fig. 1).

Habitat use and diet. In winter, the only quantitative data on habitat use by geese comes from the study of Hill & Frederick (1997) conducted in Delaware in 1990. Although geese roosted in marshes where some feeding occurred, daytime feeding was almost entirely confined to agricultural habitats. Harvested cornfields were the dominant feeding habitat (~50% of use), followed by small-grain cereals (~20%) and hayfields (pastures, ~15%). Use of cornfields decreased over winter whereas use of small-grain cereals increased. However, before the 1970s, when the population was much smaller, feeding in *Spartina* marshes was apparently more common than in 1990. Smith & Odum (1981) summarized numerous early reports that indicated extensive use of these marshes throughout the wintering range of snow geese.

In spring, goose feeding in the traditional, UEST region was formerly limited to marshes (Lemieux, 1959) and their diet was almost entirely *Scirpus pungens* (formerly *S. americanus*) rhizomes (>95%, Bédard & Gauthier, 1989). During the 1970s, geese started to feed on farmland along the St Lawrence estuary (Fig. 4). Geese used hayfields and fed on grass leaves (65%, mostly *Phleum pratense*) and spilled small-grain cereals (25%, barley and oats). Use of farmlands increased along the estuary at the expense of marsh feeding, but most dramatically in the LEST: in 1997–1998, 90% of feeding activity occurred in farmlands in the LEST compared with 46% in the UEST. The LEST is a saltwater marsh where *Scirpus pungens* is replaced by *Spartina alterniflora*, a plant with low quality rhizomes for foraging geese (Bédard & Gauthier, 1989). By 1997–1998, a small amount of feeding also occurred in cornfields along the estuary, a new crop in this area at the time. At LSP, goose feeding occurred entirely in farmlands, mostly cornfields (Fig. 4) where geese feed almost exclusively on spilled corn (98%, Giroux & Bergeron, 1996).

Migration phenology and body condition. Departure dates of geese from staging areas for the Arctic have not changed (1971–1975 vs. 1992–1998, mean departure date of flocks from the UEST was 20 May). However, changes in arrival dates have occurred in Québec. During 1971–1975, geese first arrived in the UEST region around 4 April, on average. From 1990 to 1998, geese arrived earlier (around 25 March) at LSP ($t_7 = 3.03$, $P = 0.02$), but later (around 16 April) in the UEST ($t_8 = 2.76$, $P = 0.03$). Thus, geese now arrive earlier and stage longer in Québec than formerly

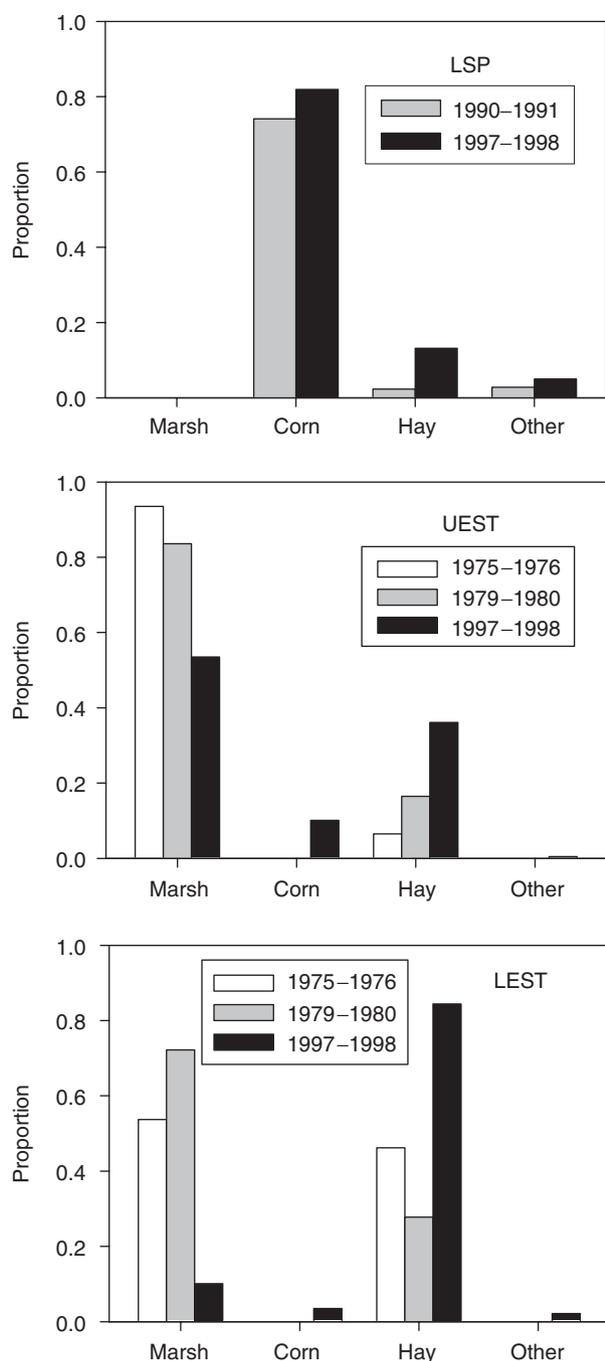


Fig. 4. Habitat use by greater snow geese for daytime feeding during spring staging in the Lac-St-Pierre (LSP), Upper estuary (UEST) and Lower estuary (LEST) regions of the St Lawrence River, Québec, for different periods between 1975 and 1998. Marsh = *Scirpus* marsh in UEST and *Spartina* marsh in LEST, corn = cornfields, hay = hayfields, other = unidentified crops or abandoned fields.

when they flew directly to the estuary from the wintering grounds.

Body condition of geese leaving Québec for the Arctic has increased over time. In 1989–1990, the fat

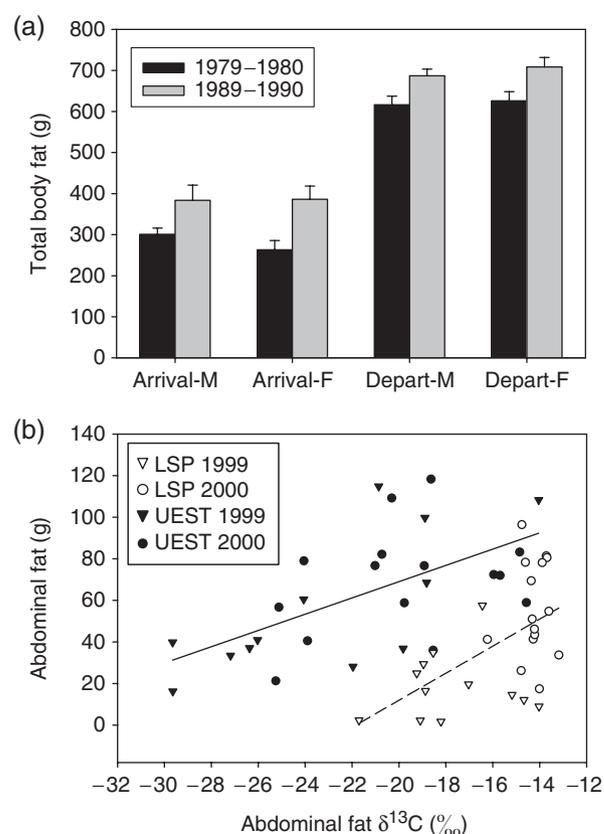


Fig. 5. (a) Total body fat (mean \pm SE) of male (M) and female (F) greater snow geese at arrival (1–16 April) and departure (9–16 May) in the upper St Lawrence estuary (data from Gauthier *et al.*, 1984, 1992). Factorial ANOVA with variables year (1979–1980 vs 1989–1990), sex and date (arriving or departing geese); year effect, $F_{1,184} = 27.5$, $P < 0.001$ (interactions year \times sex and year \times date were discarded, $P > 0.41$). (b) Relationship between abdominal fat mass and $\delta^{13}\text{C}$ signature of abdominal fat of geese departing from Lac-St-Pierre (LSP, 19 April, dotted line) and the upper estuary (UEST, 11–13 May, solid line) in 1999–2000. Factorial ANCOVA with variables sex, year, and $\delta^{13}\text{C}$ (covariate). Abdominal fat vs. $\delta^{13}\text{C}$, $F_{1,50} = 11.7$, $P = 0.001$, $R^2 = 0.45$ (interactions $\delta^{13}\text{C} \times$ site and $\delta^{13}\text{C} \times$ year were discarded, $P > 0.24$).

stores of geese departing from the UEST were 12% higher than in 1979–1980 (Fig. 5a). However, fat accumulation by geese staging in the estuary (i.e. the difference between fat at departure and arrival) actually decreased slightly during that period (by 4% in females and 11% in males) because geese arrived in the estuary with fat stores 35% higher in 1989–1990 than in 1979–1980 (Fig. 5a). Therefore, geese now accumulate large amounts of fat before arriving in the traditional area of the St Lawrence estuary (i.e. while staging at LSP). We found a positive relationship between the $\delta^{13}\text{C}$ signature of abdominal fat, an index of corn consumption, and the amount of abdominal fat accumulated by individual geese at both the LSP and

the UEST (Fig. 5b). Geese leaving LSP move to the estuary region to complete their fattening and thus have not yet reached their final departure condition, which explains their lower abdominal fat than geese departing from the UEST. Since we are dealing with two point samples, the spread in values reflects the large individual variation in fat accumulation. These data suggest that individuals that favour corn (as deduced from the isotope signature) in their spring feeding end up with higher fat stores.

Factors associated with the population increase

Creation of refuges. Between 1934 and 1967, 12 NWR (total area: 55 140 ha) were created, in part, for geese on the wintering area. Although another refuge created in 1990 (Pocosin Lake) was large (38 600 ha), it is located in NC, a region that by then was used by a very small fraction of the wintering population. In southern Québec, one NWA and four Migratory Bird Sanctuaries were created for geese between 1967 and 1972, and three Sanctuaries between 1980 and 1986 (total area: 6361 ha). Although the Cap Tourmente NWA, the most important protected area for geese, was created in 1971, it previously already had a very low hunting pressure. Total protected areas for geese are about 10 times smaller on the staging than on the wintering areas.

Change in agricultural practices. Changes in land use occurred on the wintering range of geese but these varied among regions. Corn is the dominant crop, especially in the southern and central states (Fig. 6). However, crop surface area available to geese has decreased by half in the southern states since 1976, largely because of corn, which decreased by 62% from 1976 to 2000. In the central states, total crop surface area showed no long-term trend although corn decreased slightly after a peak in 1981, concomitant to an increase in winter wheat (Fig. 6). In the north, area of corn showed no temporal trend, but total crop surface area was about six times smaller (eight times when considering only corn) compared with central or southern states. Reduction of use of southern states by geese in winter (Fig. 3) was correlated with the decrease in corn surface area ($r_{33} = 0.55$, $P < 0.001$) but the increased use in central states was negatively related to corn surface area ($r_{33} = -0.52$, $P = 0.002$) and no relation was found in the north ($r_{33} = -0.24$, $P = 0.17$).

On the staging grounds, total crop surface area available to geese has decreased slightly since 1966 in southern Québec where the dominant crop is hay (Fig. 6). There was little temporal change in the surface area

of various crops in the LEST, except for a gradual substitution of oats for barley, as observed in the other Québec regions (Fig. 6). In the UEST, area of corn increased rapidly since 1991 at the expense of hayfields, accounting for 17% of crops in 2001. However, major changes occurred at LSP with a dramatic increase in corn production at the expense of hayfields. Corn, which occupied only 3% of surface area in 1966, had become the most important crop by 2001 (49% of the area; Fig. 6).

Climate change. The climate has warmed up over the past four decades throughout the range of greater snow geese. During the winter, mean temperature has increased by $0.67\text{ }^{\circ}\text{C } 10\text{-yr}^{-1}$ in NJ ($P = 0.004$, Fig. 7), $0.36\text{ }^{\circ}\text{C } 10\text{-yr}^{-1}$ in coastal MD ($P = 0.129$) and $0.56\text{ }^{\circ}\text{C } 10\text{-yr}^{-1}$ in coastal NC ($P = 0.027$) since 1965. The warming trend during winter was most pronounced from 1978 to 1999. In spring, mean temperature has increased by $0.49\text{ }^{\circ}\text{C } 10\text{-yr}^{-1}$ at LSP ($P = 0.033$), $0.45\text{ }^{\circ}\text{C } 10\text{-yr}^{-1}$ in the UEST ($P = 0.031$, Fig. 7) and $0.26\text{ }^{\circ}\text{C } 10\text{-yr}^{-1}$ in the LEST ($P = 0.15$) since 1965. During summer, mean temperature has increased by $0.67\text{ }^{\circ}\text{C } 10\text{-yr}^{-1}$ in North Baffin ($P = 0.021$, Fig. 7) since 1976.

Strength of associations. We explored the strength of associations between annual population size (Fig. 2) and some environmental factors using multiple regression. Population size was positively related to total corn surface area on staging ground (partial $R^2 = 0.70$, $F_{1,27} = 37.4$, $P < 0.001$) but showed a curvilinear relationship with corn surface area in winter, being positive until the late 1970s but negative afterward (corn: partial $R^2 = 0.14$, $F_{1,27} = 18.8$, $P = 0.002$; corn²: partial $R^2 = 0.04$, $F_{1,27} = 15.5$, $P = 0.005$). Population was also positively related to winter temperature (partial $R^2 = 0.02$, $F_{1,27} = 5.0$, $P = 0.035$) but other variables (surface area of refuges and spring temperature) were not retained in the model ($P > 0.15$; summer temperature was not considered because data only started in 1976). Globally, the model explained 88.4% of the variation (adjusted R^2).

Consequences of population expansion on habitats

Temperate wintering salt marshes. On the wintering grounds, greater snow geese have reduced the primary production of *Spartina alterniflora* in some parts of wildlife refuges along the US Atlantic coast. These areas referred to as 'eat-outs' require several years without grubbing to recover (Smith & Odum, 1981, Smith, 1983). They represent, however, a small proportion of the total area of salt marshes on the eastern seaboard of the US and the extent of these

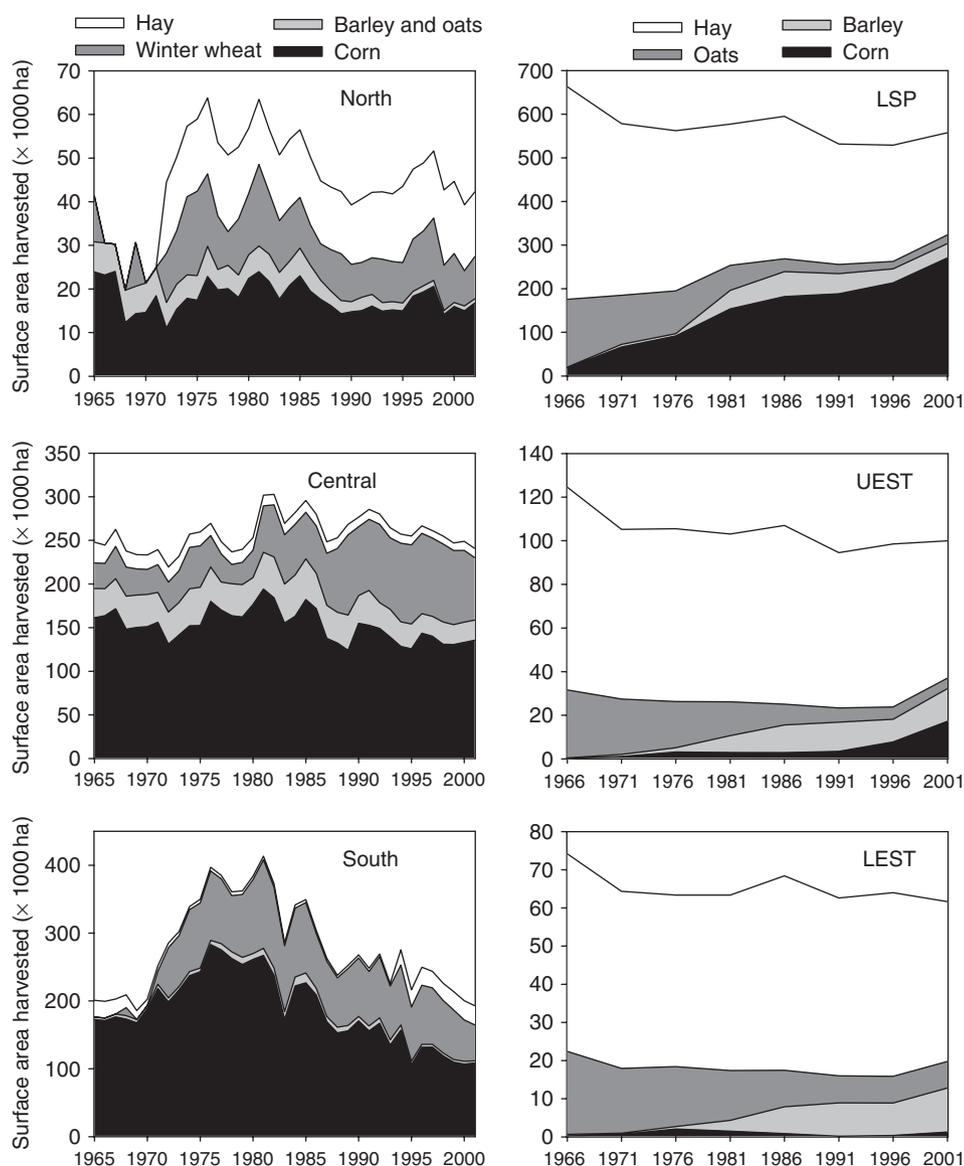


Fig. 6. Harvested surface area of various crops used by greater snow geese on their wintering (US) and staging (Québec) range from 1965 to 2001. US Wintering regions are coastal North Carolina and coastal Virginia (south), coastal Maryland and Delaware (central) and southern New Jersey (north; no data for hay prior to 1972 in NJ). Québec staging regions are Lac-St-Pierre (LSP), Upper estuary (UEST) and Lower estuary (LEST).

eat-outs has not increased over the past decade because of the increased use of cultivated land by geese and the implementation of hunting on refuges (Giroux *et al.*, 1998).

Temperate staging brackish wetlands. The tidal brackish marshes of the St Lawrence estuary are exposed to two episodes of herbivory annually when geese feed intensively on *Scirpus pungens* rhizomes during their spring and autumn staging (Giroux & Bédard, 1988b; Bédard & Gauthier, 1989). In the heavily used marshes of Montmagny and Cap St-Ignace located along the

south shore, Giroux & Bédard (1987) found a lower *Scirpus* rhizome biomass than in lightly used areas. However, *Scirpus* production in plots where goose grazing had been prevented for 2 years in intensively used marshes reached levels similar to those measured in exclosures located in lightly used areas. Despite the continuous population increase, we did not observe any significant changes in *Scirpus* aboveground biomass between 1983 and 1999 (Fig. 8). In contrast, on the north shore, a 47% decline in *Scirpus* stem density has been observed at the Cap Tourmente NWA since 1971 ($1.5\% \text{ yr}^{-1}$, $R^2 = 0.39$, $F_{1,21} = 13.7$, $P = 0.001$;

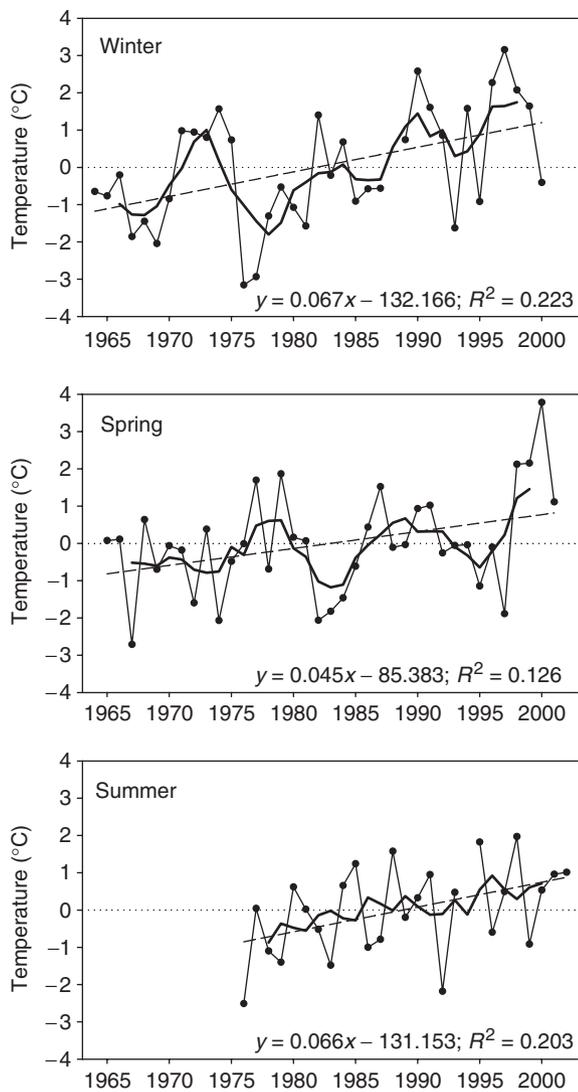


Fig. 7. Change in winter (December–February; Indian Mills, NJ) and spring (March–May; Montmagny, QC) temperature from 1965 to 2000, and in summer temperature (May–August; Pond Inlet, NU) from 1976 to 2002. Each graph shows annual deviations from the mean for the whole period (thin line with dots), the 5-year running mean (thick line) and the regression line of annual deviations.

Reed, 1989 and Fig. 8). Although the goose grazing in these marshes is the most obvious factor, the total use of the NWA by geese has also declined over the same period (A. Reed, unpublished results).

Arctic breeding freshwater wetlands. On the breeding grounds at Bylot Island, the grass *Dupontia fisheri* and the sedge *Eriophorum scheuchzeri* are the preferred species consumed by geese in wetlands (Manseau & Gauthier, 1993). Goose grazing reduced standing crop in those wetlands every summer, sometimes by as much as 60% (Gauthier *et al.*, 1995, 2005). Nonetheless,

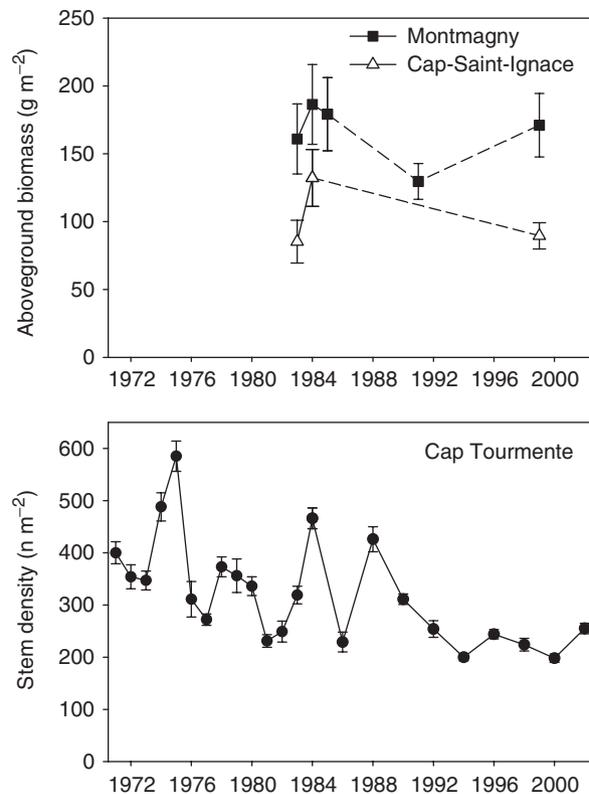


Fig. 8. Aboveground production (\pm SE) of *Scirpus pungens* expressed as peak biomass in August at Montmagny and Cap St-Ignace, 1983–1999, and stem density at Cap Tourmente NWA, 1971–2002.

the annual production of *Dupontia* increased between 1990 and 2003 ($R^2 = 0.32$, $F_{1,12} = 5.07$, $P = 0.046$), mostly during the period 1994–1997 (Gauthier *et al.*, 2004, 2005). There was a similar trend for *Eriophorum* ($R^2 = 0.28$, $F_{1,12} = 4.29$, $P = 0.063$), although in this case the increase occurred abruptly following a year of poor reproduction for geese (1999), and tended to decline afterwards.

Discussion

The greater snow goose population grew twice as fast in the last third of the 20th century than in the previous two-thirds, and our analysis sought factors that could explain this pattern. Over the last 40 years, only two changes in hunting regulations had an impact on the demography: the reopening of hunting in the US in 1975 (Menu *et al.*, 2002) temporarily reduced population growth, and introduction of the special conservation measures in 1999 (including a spring harvest) stopped it (Calvert *et al.*, 2005). Hence, between the 1960s and the late 1990s, population growth persisted, even though hunting regulations were increasingly permissive. Therefore, restrictive hunting regulations cannot

explain why the population grew so much throughout this period.

Most protected areas were established before 1972, which coincided with a period of rapid growth. This may have resulted in reduced disturbance, lower local harvest rates, and improved feeding areas, and thus probably contributed to the initial population increase. However, very few new refuges were created for geese afterward while the use of some of them (e.g. Cap Tourmente NWA) decreased. Thus, the relative impact of refuges on goose populations may have lessened thereafter.

We showed that numerous changes in distribution, migratory routes and habitat use occurred in greater snow geese since the late 1960s. Wintering geese, formerly largely confined to *Spartina* marshes, now heavily feed in farmlands, especially on spilled corn (Hill & Frederick, 1997), a highly energetic source of food for geese (Alisauskas *et al.*, 1988). This habitat shift apparently occurred during the 1970s (Anonymous, 1981), and was followed by a northward change in wintering distribution in the 1980s. Abandonment of the southern states by wintering geese may in part be because of the observed reduction in the area of corn cultivation in these states as both events were correlated. The greater concentration of geese in the central states compared with the northern ones in the 1990s may be because NJ is a more urbanized state with much less cultivated areas than DE and coastal MD. The warming trend that occurred in winter (between 1.3 and 2.4 °C since 1965 depending on the state) may have also contributed to the northern shift in goose distribution. Total corn surface area in winter was initially related to population size but the relationship became negative afterward. However, the recent negative relationship was largely driven by the decline in corn in southern states, a region that geese had mostly deserted by then. A problem with this analysis is that corn surface area is only a surrogate of food available to geese. Thus, other important variables such as yield per hectare, which actually increased over time because of selection for high yield varieties, increased use of fertilizers in the US (Jefferies *et al.*, 2004), or variation in proportion of grains spilled during harvest are not considered.

The northern shift in distribution of wintering geese in the 1980s led to a reduction in hunting mortality, apparently because of a reduced hunting pressure in the central and northern states (Calvert *et al.*, 2005). This was probably the principal demographic cause for the resumption of rapid population growth in the 1980s. It is also possible that reduced natural mortality in winter because of use of farmlands and warmer temperature contributed to the population increase, as found in pink-footed geese (*Anser brachyrhynchus*; Fox *et al.*,

2005). Use of farmlands may have been especially critical in the very cold winters of 1976 and 1977 (Fig. 7) when marshes froze for long periods and caused die-offs in Atlantic brant (*Branta bernicla*) but not in snow geese (Kirby & Ferrigno, 1980; Ward *et al.*, 2005).

Changes in habitat use and distribution of spring staging geese also started in the early 1970s. The invasion of farmlands by geese in the St Lawrence estuary was not associated with any obvious change in the types of agricultural crops in this region. However, it is possible that geese were already approaching the carrying capacity of the *Scirpus* marshes in the 1970s, and thus a decreasing per capita food supply may have prompted this habitat shift. Intense grubbing can reduce standing crop (Giroux & Bédard, 1987) and foraging geese leave bare patches when a minimal threshold of rhizome density is reached (Bélanger & Bédard, 1995; Boyd, 1995). Improvement in hay quality also may have encouraged the movement of geese to hayfields at that time. From 1966 to 1986, sales of nitrogen fertilizers increased sevenfold in Québec from 12 800 to 89 400 tons (AAFC, 1997). Although some of this increase may be because of crop changes (e.g. increase use of corn, which requires high fertilizer levels), use of fertilizers probably also increased in hayfields, thus improving the quality (e.g. protein) and quantity of forage plants for geese (Van Eerden *et al.*, 2005).

The subsequent invasion of the LSP region by geese in the 1980s is undoubtedly a consequence of the dramatic increase of cornfields in this region (15-fold between 1966 and 2001). There are no marshes suitable for goose feeding in this region and all feeding is restricted to farmlands, mostly cornfields (Giroux & Bergeron, 1996; Béchet *et al.*, 2004a). The progression of corn in southern Québec is because of the development of new varieties that require fewer degree-days to mature, which is essential where the growing season is short. The expansion of hog farming in Québec also contributed to the increase of corn (number of pigs sold in Québec increased from 2.1 millions in 1965 to 15.1 in 1999; Statistics Canada, 2003). Corn is a staple food for pigs and this plant can absorb more nutrients from the highly concentrated hog manure than any other crop.

The warming trend observed in Québec may have contributed to the earlier arrival of geese in spring, and also favoured the expansion of corn at LSP, further benefiting geese. In late April and May, staging geese move from LSP to the UEST and LEST regions, possibly because corn availability is reduced because of depletion and ploughing of fields, while young shoots of grass are at their best in the estuary region because of the delayed onset of spring there. Surprisingly, unlike arrival dates, departure dates of geese for the Arctic have not changed over time even though both the estuary region in spring

and the Arctic breeding ground in summer have experienced a similar warming trend.

Corn surface area in Québec was the variable that explained by far the most variation in total population size. We provided evidence that use of corn in spring was responsible for increased fat reserves of geese at departure for the Arctic, both at the population and individual levels. Because endogenous reserves are a determinant of reproductive success in geese (Ebbinge & Spaans, 1995; Bêty *et al.*, 2003; Drent *et al.*, 2003), we would have expected a concomitant increase in reproductive success over time, but Menu *et al.* (2002) found no change in annual production of young between 1970 and 1998. However, considering that the population has increased eightfold during this period, a reduction in fecundity because of density-dependent effect should have occurred, as found in other species (Cooch *et al.*, 1989; Cooch & Cooke 1991; Pettifor *et al.*, 1998). Improved body condition upon arrival in the Arctic because of agricultural food subsidy in spring may have allowed greater snow geese to 'escape' density-dependent effects on fecundity and maintain a high population growth rate, as suggested in Greenland white-fronted geese (*Anser albifrons flavirostris*, Fox *et al.*, 2005). The recent warming trend observed on the breeding ground may also have contributed to high productivity during that period because spring temperature can have a considerable impact on reproductive success of Arctic geese (Skinner *et al.*, 1998; Reed *et al.*, 2004).

In the St Lawrence estuary marshes, conflicting trends in plant production were noted with a continuous decline in *Scirpus* production along the north shore (Cap Tourmente) but no similar trend on the south shore. Giroux & Bédard (1987) showed with enclosures that when goose grubbing is stopped, *Scirpus* production bounced back very rapidly on the south shore. It remains to be seen if goose grazing at Cap Tourmente has reached a threshold beyond which recovery is more difficult or if other natural factors are involved. The levelling off in the use of the UEST region by geese combined with the increasing use of farmlands throughout southern Québec may also explain why the impact of geese on some *Scirpus* marshes has apparently not increased with the population expansion. However, the long-term impact of goose grazing on *Scirpus* marshes remain unclear.

We have no evidence of a continuous decline in plant production on the Arctic breeding grounds in the 1990s even though the population on Bylot Island followed the same increasing trend as the total population (Reed *et al.*, 2002). Although goose grazing reduced production on Bylot Island, the vegetation came back rapidly within a few years in areas where geese were excluded (Gauthier *et al.*, 2004). The system thus appears stable so

far, unlike the situation observed in the salt marshes of west Hudson Bay where intense grazing and grubbing by lesser snow geese damaged the vegetation and moved the system toward an alternative, desert-like stable state (Srivastava & Jefferies, 1996; Jefferies *et al.*, 2004). It is unknown if these differences are because goose density on Bylot Island, unlike along west Hudson Bay, has simply not exceeded the carrying capacity of the habitat (Massé *et al.*, 2001).

Although little information is available on the long-term response of *Spartina* marshes to intense goose grazing in winter, the short-term experiments of Smith & Odum (1981) suggest that they may not be able to sustain high, repeated grazing pressure as well as *Scirpus* marshes in Québec. This, in combination with the poor nutritive quality of *Spartina* rhizomes, may have been important factors limiting the goose population in the past. However, the switch to farmland feeding in winter has presumably released the population from these limiting factors, while lessening any negative impact of geese on these marshes. It is thus possible that the population has never been as high as it has been since the mid-1970s.

Conclusion

There is evidence that a switch to agricultural lands and a concomitant change in winter and spring distribution are the primary causes for population increase of greater snow geese in recent decades. These changes enhanced winter survival through a reduction in hunting mortality and possibly natural mortality, and enabled geese to arrive in the Arctic with improved body condition, apparently allowing them to attenuate density-dependent effects. A similar link between increased use of fertilizers, increased farmland feeding, and population expansion has been made in lesser snow geese (Jefferies *et al.*, 2004; Abraham *et al.*, 2005). A warming trend experienced by greater snow geese throughout the year likely contributed to the population increase, possibly by lowering natural mortality in winter. The foraging in fields allowed the population to exceed limits imposed by natural marshes in winter and spring, but also prevented overgrazing and may explain why we have no evidence yet of permanent damage to these habitats.

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