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Decadal changes in vegetation of a subarctic salt marsh used by lesser snow and Canada geese

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Abstract: In the Hudson-James Bay system, grubbing and grazing by lesser snow geese have resulted in severe devegetation of coastal marshes. These changes likely represent an example of an alternative stable state; however, long-term datasets documenting whether revegetation is occurring are scarce. Here, we report results of a 10-year study investigating changes in the state of a degraded salt marsh system on the north coast of Akimiski Island, Nunavut. Four transects were intensively sampled in 1998 and 2008, two within the dense nesting and brood-rearing area of a snow geese colony, one on the colony edge, and one outside it; all of these sites were also used by broods of Canada geese. Key forage species (*Puccinellia phryganodes*, *Festuca rubra*, *Carex subspathacea*) were less common near the colony centre than elsewhere; biomass of *Puccinellia* also tended to be lower in more central areas. Forage species often increased in abundance between samplings, but the magnitude of changes was small. In contrast, non-forage species (*Salicornia*, *Spergularia*, *Glaux*) often reached high abundance within the colony centre; some (*Salicornia*) decreased while others (*Spergularia*) increased. We argue the degraded state was initiated by foraging damage from an exceptional stopover of 295,000 staging birds in 1972 and that the combined foraging pressure of relatively small numbers of nesting and migrant geese since then, coupled with soil changes, has been sufficient to maintain devegetated areas as a persistent alternative state. Whether or not this state is truly stable, further recovery is likely to be very slow.

Key words: alternative states; *Festuca rubra*; foraging; Hudson-James Bay; *Puccinellia phryganodes*.

Introduction

Vertebrate herbivores are important components of northern ecosystems and have significant effects on the structure and functioning of plant communities, including species composition, nutrient cycling, and other ecosystem characteristics (Jefferies et al. 1994). For instance, consumption of forage plants (primarily grasses and sedges) by geese has important impacts at many arctic and subarctic coastal wetland sites (e.g., lesser snow geese: Jefferies et al. 2003; black brant: Person et al. 2003; greater snow geese: Gauthier et al. 2004; pink-footed geese: van der Wal et. al 2007). Grazing by moderate densities of geese can sustain or even stimulate plant community productivity in a positive feedback through increased nutrient cycling, resulting in a grazing lawn (Cargill and Jefferies 1984; Hik and Jefferies 1990; Hik et al. 1991; Jefferies et al. 2003). However, a second feedback involving grubbing for shoots and rhizomes by dense aggregations of spring migrating or pre-nesting birds can have devastating effects on northern plant communities, especially when coupled with intense summer grazing by local resident birds (Jefferies 1988). For instance, at La Pérouse Bay, Manitoba, sporadic spring staging events by northbound lesser snow goose (*Chen caerulescens caerulescens*) migrants (Jefferies and Rockwell 2002) and a rapid increase in the size of the local nesting colony over two decades led to extensive devegetation of intertidal grazing flats and loss of graminoid vegetation from fresh-water supratidal areas (Jefferies et al. 2003; Abraham et al. 2005). Effects of foraging by large numbers of lesser snow geese similar to those at La Pérouse Bay have now been observed at multiple locations in the Hudson-James Bay system, including Southampton Island, the Nunavut coast of Hudson Bay, Cape Henrietta Maria (Ontario) and Akimiski Island in James Bay (Abraham and Jefferies 1997; Didiuk and Ferguson 2005; Alisauskas et al. 2006; Jefferies et al. 2006; Abraham et al. 2012).

Herbivory is capable of shifting sensitive systems into alternative stable states (van de Koppel et al. 1997; Beisner et al 2003; Suding et al. 2004). For example, the introduction of cattle and European rabbits into Chile is believed to have stably converted sclerophyllous matorral forest to savanna (Holmgren 2002), a change now very difficult to reverse even with protection from grazing. The available evidence indicates that devegetation of northern wetlands due to goose foraging also is very difficult to reverse. In intertidal and supratidal sites, changes to soil including increased salinity and anoxia can severely restrict recolonization by plants other than halophytes such as *Salicornia* (Srivastava and Jefferies 1995, 1996; Handa et al. 2002; McLaren and Jefferies 2004). In freshwater sites, graminoids such as *Carex* and *Eriophorum* apparently have difficulty recolonizing the moss carpets that develop in areas from which vascular plant cover has been removed (Kerbes et al. 1990; Kotanen and Jefferies 1997). Revegetation may be possible if foraging pressure is reduced (Handa et al. 2002); however, as vegetation cover declines, pressure may be sustained or even increased in remaining patches of forage plants.

Despite their importance for understanding the trajectories of dynamically slow northern plant communities, multi-year datasets documenting vegetation change are rare for sites seriously impacted by geese; La Pérouse Bay (Jefferies and Rockwell 2002; Jefferies et al. 2003) provides the most extensive exception. As a result, evidence that foraging geese have created alternative stable states usually has been inferred from descriptions of existing vegetation (e.g., Kerbes et al. 1990) or remote sensing (e.g., Jefferies et al. 2006), rather than being directly demonstrated by repeated observations of affected communities. In this paper, we present the first analysis of a dataset from Akimiski Island, Nunavut, a location about 1000 km away from La Pérouse Bay. The north shore of this island has been severely affected by geese (Jefferies et al. 2006). Much of the devegetation at this site may have resulted from a single event in 1972,

when an estimated 295,000 birds were delayed at this site during their northward migration (Curtis 1973). Since that event, these salt marshes have been exposed to continuous foraging by lesser snow geese from a small breeding colony and breeding Canada geese of the Southern James Bay Population (*Branta canadensis interior*). In 1998, we intensively sampled supratidal-intertidal sites; in 2008, we re-sampled the same locations, providing a record of vegetation change over the intervening decade. Our dataset allows us to determine whether substantial recovery has occurred at these coastal sites, or whether sustained foraging pressure from the relatively small local goose population, coupled with soil changes, has been sufficient to slow or prevent revegetation.

Methods

Study Site

Akimiski Island, Nunavut Territory, Canada (53°N, 81°W, 3800 km²) is the largest island in James Bay. During this study, lesser snow geese nested in a relatively dense, discrete colony of about 4000 birds along a 35 km stretch of the north shore of this island (Abraham et al. 1999), while nesting Canada geese occurred at lower densities throughout the island (Leafloor et al. 1996, 2000), including the areas used by snow geese (Fig. 1). These species intensively graze leaves of forage plants in intertidal and supratidal areas during the breeding season, as well as in the freshwater fens adjacent to the supratidal areas. Nesting and brood rearing snow geese as well as nesting and brood-rearing Canada geese are responsible for most summer grazing close to the snow goose colony, so this area is the most intensively used segment of the north shore. Snow geese also extensively grub roots and shoots of forage plants in early spring as do Canada geese, to a lesser extent.

Intertidal vegetation on Akimiski is dominated by the highly palatable forage grass, *Puccinellia phryganodes*, in the lower marsh, with the forage sedge *Carex subspathacea* in the upper marsh in areas more influenced by fresh water, including streams that drain the interior of the island, and seepage areas near supratidal zone (Martini and Glooschenko 1983). However, intense grazing pressure in the area of the snow goose colony has depleted these species (Figs 2a-c), largely replacing them with unvegetated mudflats (O et al. 2005; Jefferies et al. 2006). The forage grass *Festuca rubra* has also been reduced in extent, but still locally occurs in nearly pure pastures in supratidal areas used by nesting and brood-rearing snow geese and Canada geese. Patches of short, intensely grazed plants are interspersed with infrequently grazed taller plants and exposed formerly-vegetated mudflats (Fig. 2b; O et al. 2006).

Sampling

Five permanent transects were established along the north shore of Akimiski Island in 1998 at intervals of 6-10 km (Fig. 1). Those near the Thompson and Stitt rivers were located within the dense nesting area and principal brood rearing area of the current snow goose nesting colony; the Lumsden River transect was beyond the west edge of the dense nesting colony but within the brood rearing area; the Ministik River transect was east of the colony and the brood-rearing area (all place names unofficial). All of these areas were also used by pre-breeding snow geese, by broods of Canada geese, spring migrant brant, and moult migrant Canada geese. Transects extended from near the end of vegetation in the lower intertidal zone to the upper end of the supratidal zone traversing the zones roughly perpendicular to the shoreline; they ranged in length from approximately 850m to 1550m, and were marked at both ends with angle iron posts driven into the sediment.

These transects were sampled between 14-22 July 1998 and again between 19-22 July 2008, when annual growth and flowering of most species was well advanced. A measuring tape

was laid along the transect and the presence or absence of all vascular plant species was noted at 1m intervals (within a "quadrat" approximately 10 cm in diameter). Sites with no plant cover included mudflats where plants may or may not previously have occurred, as well as sites unsuitable for forage plant growth, such as ponds, unstable gravel bars, large rocks, and drainage channels; it often was difficult to distinguish among these categories.

In 2008, transects were re-located using landmarks, GPS co-ordinates, and compass bearings. The original seaward end stakes were found for the Stitt, Lumsden, and Ministik transects; no end stake was found for the Thompson transect, but the transect passed close to an observation tower that was used for alignment to the GPS end point. We do not assume exactly the same points were sampled in both years; however, the 1998 and 2008 transects represent samples of very closely proximate areas.

We also sampled above ground standing crop in one *Puccinellia*- and one *Festuca*-dominated area at the Thompson, Stitt, and Ministik sites in 1998 and 2008. The Lumsden site also was sampled in 1998, but not 2008; this site was last sampled in 2006. On each date, we deliberately chose sampling locations with the best available vegetation, to describe the maximum potential forage at that site. Three to five 100cm² turfs were collected in each vegetation type and clipped, washed, and dried to constant weight in a drying oven. Biomass was recorded to the nearest 0.01g. Sampling dates (23 July 1998, 26 July 2006, 26 July 2008) corresponded to late brood rearing stage for geese and was near the peak of the growing season. This technique sets an upper limit to potential forage availability in surviving grazed vegetation, but should not be taken as an average value; a random quadrat in most of our study area would contain little to no green biomass (see below). Thus, these values also should not be taken as a measure of average change between samplings, but rather a comparison of best conditions at each sampling.

Analysis

Data were analyzed with JMP 10 (2010, SAS Institute Inc., Cary, NC, USA). For each transect, data were grouped by 100m sections, beginning at the most seaward point. As there were obvious differences between transects, and because our principal goal was to describe changes in each transect over time, we analyzed each transect separately. Data were analyzed using generalized linear models with a binomial distribution and a logit link, and Firth bias-adjusted estimates. We compared the number of occurrences of each species among different segments of the same transect, and between the same segment at different sampling dates, using a factorial design (position $\times$ year); we treated both year and position on the transect as fixed factors. A significant "position" term means a species was not evenly distributed along a transect; a significant "year" term indicates a species' overall abundance changed between years; a significant interaction means that a species' position shifted between years. In some cases a full analysis was not possible, usually because a species was very rare or absent in one year, leading to inestimable parameters. In response, we dropped the interaction terms from such models to separately test whether the overall frequency of a species differed between years and among locations along a transect; such tests should be treated with caution since they ignore position $\times$ year interactions. Species with a total of fewer than 60 occurrences in either year gave unreliable estimates and conservatively were excluded from analysis.

Biomass was analyzed in a 2-way standard least squares ANOVA (site $\times$ year) for the Thompson, Stitt, and Ministik sites. The Lumsden site was excluded from this analysis, since 2008 data were not available; however, we separately calculated mean and SEM values for this site for 1998 and 2006.

Results

Extent of sampling

We sampled a total of more than 6000 quadrats (6 km) along our transects in 1998, and more than 5400 in 2008. As we ended sampling of transects at slightly different lengths in each year, we discarded any positions not represented in both samplings to equalize transect length. We then truncated each transect at the nearest 100m point, so that all sections within each transect were equally sized. As transects extended from the lower intertidal to the beginning of freshwater vegetation, these deletions meant losing some information on freshwater areas, but little from the intertidal or supratidal zones, which were the focus of this study. Our final sample size was 5200 quadrats in both 1998 and 2008; our shortest transect (Stitt) was 700m long, while our longest (Lumsden) was 1500m long (Fig. 1).

Overall patterns

In the intertidal zone, our most commonly occurring species were *Puccinellia phryganodes*, *Carex subspathacea*, *Spergularia* spp., *Salicornia* cf. *borealis*, and *Glaux maritima*; in the supratidal, we also frequently recorded *Festuca rubra*. Mosses were rare or absent in the areas sampled. In addition to these common species, we infrequently encountered several other grasses (e.g., *Dupontia fisheri*, *Calamagrostis* spp., *Hierochlœe odorata*), sedges (*Carex* spp., *Eleocharis* spp.), herbaceous dicots (e.g., *Senecio congestus*, *Honkenya peploides*, *Hippuris* spp.), and woody species (*Shepherdia canadensis*, *Myrica gale*). Most of these occurred in freshwater areas, which our transects barely entered; therefore, we made the decision to restrict analyses to the principal intertidal and supratidal species. See Blaney and Kotanen (2001) for a complete species list for this site.

The primary intertidal forage species *Puccinellia phryganodes* and *Carex subspathacea* (hereafter *Puccinellia* and *Carex*) were found at all transect sites, as was the primary supratidal

forage species *Festuca rubra* (hereafter *Festuca*) (Figs 3,4). However, at both samplings there was a tendency for these species to be less frequent at transects within the snow goose colony than in surrounding areas (Fig. 4). For instance, *Puccinellia* was much more frequent at the Ministik than at sites within the snow goose colony (Thompson, Stitt). Similarly, *Carex* was much scarcer within the colony than to the east (Ministik), possibly reflecting a greater freshwater input at this site; *Carex* also was more abundant west of the dense colony (Lumsden) in 2008, though not in 1998. *Festuca* was more abundant west of the colony than inside it; *Festuca* also was more abundant east of the colony than within it in 1998, though not in 2008. No forage species reached peak abundance within the snow goose nesting area.

In contrast to forage species, non-forage species often reached high abundances inside the snow goose colony, as well as outside it (Figs. 5,6). The highly halophytic *Salicornia* occurred abundantly at the Lumsden River in 1998, but otherwise was scarce. *Spergularia* similarly was restricted to the Lumsden transect in 1998, but had spread east by 2008, when it was abundant at the Thompson, present at the Stitt, and frequent at the Ministik. *Glaux* was frequent at transects both inside and outside the colony, but especially at the Thompson.

Changes in individual species

The overall frequency of all forage species tended to increase between 1998 and 2008 (Figs 3,4), though the absolute magnitude of these changes usually was small ($\leq 10\%$ of quadrats per transect, or 1% / year; Fig. 4) and often nonsignificant (Table 1). *Puccinellia* generally was significantly less frequent at the inland end than in the middle or seaward end of transects (Fig. 3; Table 1). This species increased in overall frequency between samplings at all sites, except to the west of the colony at the Lumsden River, where there still was a nonsignificant increasing trend (Fig. 4; Table 1). At both sites where estimation was possible, a position $\times$ year interaction

indicated that the distribution of this species along the transect changed between samplings: it tended to shift inland both outside the snow goose colony (at the Lumsden River) and within it (at the Stitt River) (Fig. 3; Table 1). In contrast, *Carex* usually was more abundant at the inland end of transects (Fig. 3; Table 1), reflecting the presence of freshwater seepage areas or streams. Abundance was too low within the snow goose colony to meaningfully test for changes between years, though it tended to occur more frequently in 2008 than 1998 (Fig. 4; Table 1); outside the colony, *Carex* increased at the Ministik site, where an interaction also indicated a change in distribution between samplings: frequency increased seaward (Fig. 3). Like *Carex*, *Festuca* also was significantly more common at the inland end of transects (Fig. 3; Table 1). Changes in abundance between samplings were significant at some but not all sites: outside the colony, the frequency of *Festuca* increased slightly at the Ministik and did not change at the Lumsden, though the trend was positive; inside the colony, it increased at the Stitt but not the Thompson, though again there was a non-significant increasing trend (Fig. 4; Table 1).

Changes also occurred between samplings in the distribution and abundance of non-forage species (Figs 5,6; Table 2); in most cases, these also tended to increase in overall abundance (Fig. 6). In contrast, the occurrence of bare mud usually declined (Fig. 6; Table 2), reflecting increases in both forage and non-forage species. *Salicornia* was only present in the seaward and middle portions of the Lumsden transect (Fig. 5), where it greatly declined in abundance between samplings (Fig. 6; Table 2); as indicated by a significant position $\times$ year interaction, the few plants that survived were disproportionately concentrated at the seaward end of the transect. In 1998, *Spergularia* occurred only at the Lumsden; in contrast, it was present at all sites in 2008, though it still was too scarce to analyze statistically at the Stitt (Figs 5,6). This increase was especially striking at the Thompson, where it was found in 49% of all quadrats in

2008 (Fig. 6), and was statistically significant at the Thompson and the Ministik (Table 2), while there was a nonsignificant increasing trend at the Lumsden (Fig. 6; Table 2). As well, a significant interaction indicates *Spergularia* moved seaward at the Lumsden, the only site where it was observed in both years (Fig. 5; Table 2). Finally, *Glaux* occurred at all sites, where it was most frequent at mid-intertidal levels (Fig. 5; Table 2). This species increased significantly at the Thompson and showed an increasing trend at the Lumsden and Ministik, though not at the Stitt (Fig. 6; Table 2); as well, a shift in distribution occurred at the Thompson, where it expanded both seaward and landward.

Biomass

Biomass of the best remaining grazed patches of *Puccinellia* (Fig. 7) differed among the Thompson, Stitt, and Ministik sites ($F_{2,17} = 5.48$; $p = 0.01$); the Lumsden transect was excluded from these analyses since 2008 data were not available. Biomass was lower in the centre of the colony at the Thompson than outside it at the Ministik ($p < 0.05$: Tukey HSD). Biomass did not change significantly between samplings ($F_{1,17} = 0.19$; $p = 0.67$), and there was no site $\times$ year interaction ($F_{2,17} = 0.52$; $p = 0.60$). Mean biomass values at these sites ranged from 20-35 gm^{-2} ; values at the Lumsden in 1998 (mean $\pm$ SEM: $33 \pm 2.3 \text{ gm}^{-2}$) and 2006 ($29 \pm 3.2 \text{ gm}^{-2}$) were within this range.

Biomass of the best remaining *Festuca* (Fig. 7) did not differ among the Thompson, Stitt, and Ministik sites ($F_{2,18} = 2.10$; $p = 0.15$); again, the Lumsden was excluded from these analyses. There was an increase in biomass between years ($F_{1,18} = 6.31$; $p = 0.02$). These results likely were influenced by an anomalously low mean and variance for the Thompson River in 1998 (Fig. 7); nonetheless, there was no significant site $\times$ year interaction ($F_{2,18} = 1.35$; $p = 0.28$). The low value at the Thompson may reflect sampling of an especially heavily grazed site: *Festuca*

typically exists as a mosaic of patches (Fig. 2b) differing in grazing intensity (O et al. 2006). Biomass values at these sites were considerably greater than for *Puccinellia*, reflecting the larger stature of *Festuca*: means ranged from 7-87 gm⁻² (Fig. 7). Values at the Lumsden tended to be higher than these values in both 1998 (97 ± 19.6 gm⁻²) and 2006 (94 ± 29.7 gm⁻²).

Discussion

Effects of geese on vegetation

Our results are consistent with a past and continuing effect of foraging by geese. Forage species were scarce compared to values expected in undegraded sites (Jefferies et al. 1979; Hik et al. 1992; Jefferies and Rockwell 2002), and generally were less frequent within than outside the colony, where only Canada geese stage and nest. This agrees with biomass estimates which even in the few relatively intact areas remaining tended to be lower at more central sites, though this was significant only for *Puccinellia*. In contrast, non-forage species often were equally or more frequent inside the colony than outside, as might be expected for species that are not susceptible to goose damage and/or can tolerate the high salinity of devegetated areas. Positions of species along individual transects likely often reflected gradients in physical conditions (Martini and Glooschenko 1983); for instance, the tendency of *Carex* to occur at slightly higher elevations and often closer to the freshwater (upper marsh boundary and streams) than *Puccinellia* is expected given its lower salt tolerance, as also observed at La Pérouse Bay (Jefferies et al. 1979; Jefferies and Rockwell 2002); similarly, the tendency of *Festuca* to occur on the inland end of transects is consistent with its usual position in the supratidal zone (Jefferies et al. 1979; Srivastava and Jefferies 2002).

Changes in forage species between samplings provided some evidence of recovery from 1998 conditions, but the magnitude of these changes was small. In particular, by 2008 the preferred forage species *Puccinellia* increased both within the snow goose colony (at the

Thompson and Stitt Rivers) and to the east (at the Ministik River), but remained far from the near-continuous vegetation possible in good-quality sites (Fig. 2a), such as pre-collapse La Pérouse Bay (Jefferies et al. 1979; Jefferies and Rockwell 2002). Because we measured frequency rather than cover, these increases often reflected the establishment of small isolated colonists (Fig. 2d) rather than continuous vegetation. This is reflected by the fact that biomass values showed no significant increase, and instead remained low in both years even in the best patches available ($\sim 30 \text{ gm}^{-2}$). This is less than the 40-60 gm^{-2} values typical in pre-decline grazing lawns at La Pérouse Bay, but similar to post-decline values (Cargill and Jefferies 1984; Jefferies and Rockwell 2002). It should be remembered that these are best-case estimates; in fact, the biomass of *Puccinellia* in most of our 10 cm quadrat samples was zero, as indicated by its low frequency along most transects. Similarly, though *Carex subspathacea* and *Festuca* showed some tendency to increase, their cover remained far from the near-continuous swards possible in undamaged or protected sites; high biomass values for *Festuca* reflect the fact that isolated patches of good-quality vegetation may remain even in severely damaged areas (O et al. 2006).

Some non-forage species showed large changes in abundance between samplings. In particular, *Salicornia* nearly vanished between samplings, while *Spergularia* greatly increased in abundance and distribution. These halophytes have similar ecological requirements and (at least at the Lumsden River) occur in similar positions along the intertidal gradient; it is unclear why this replacement occurred. Although it has been suggested that germination and therefore population size of this annual *Salicornia* may be very vulnerable to year-to-year variation in weather (Jefferies et al. 1983); the same principle may apply to the annual *Spergularia*.

Despite these changes, unvegetated ground remained common at all sites. Again, our frequency measurements underestimate the amount of surface area actually occupied by bare mud. For instance, the lower values at the Lumsden and Thompson Rivers in 2008 reflect the

proliferation of *Spergularia*, rather than a large decline in bare space, which still was by far the largest fraction of surface area.

Stability of goose-damaged systems

In springs when thaw is delayed on northern Hudson Bay-Foxe Basin nesting areas (Boyd et al. 1982), interrupted migration puts unexpected foraging pressure on the vegetation of staging areas in southern Hudson Bay and James Bay (Jefferies et al. 2003), because geese are in a hyperphagic state at this time of pre-breeding as they accumulate reserves for egg production and the final stages of migration (Wypkema and Ankney 1979). In the case of Akimiski Island, the lower intertidal marshes are the communities most vulnerable to staging geese because melting snow from higher elevations floods these flats, saturating the graminoid mats and warming the soil, conducive to grubbing of below ground plant parts. We propose that the state of the salt marsh in 1998 was likely the result of a combination of one such episode of staging and foraging by a large number of snow geese in 1972 (Curtis 1973), and two succeeding decades of cumulative spring grubbing and grazing damage by geese in lesser numbers.

Together, our results suggest that goose-damaged communities on Akimiski are very slow to recover, consistent with suggestions that these sites can represent an alternative state for arctic salt marsh vegetation (Abraham et al. 2005; Srivastava and Jefferies 1996; Srivastava and Jefferies 2002). Despite a small, relatively stable local snow goose population and 40 elapsed years since the original migratory stopover event believed to have initiated much of the current devegetation, coverage by forage species at this site remains sparse compared to other less-damaged locations, or to pre-degradation La Pérouse Bay (Jefferies and Rockwell 2002). This suggests that a single severe impact may have been sufficient to trigger a switch of these coastal wetlands into a new, persistent alternative state (van de Koppel et al. 1997; Beisner et al. 2003). Although forage species did increase in frequency over our study, the rate of recovery was very

low (~1%/year); since the colonists contributing to this increase typically were isolated or small (Fig. 2d), recovery of biomass is likely to be even slower. Thus, while affected areas on Akimiski technically might represent alternative transient states rather than true alternative stable states (Fukami and Nakajima 2011), current evidence suggests that their persistence will be prolonged.

Since the loss of vegetation cover, these conditions likely are being maintained in part by increased surface salinity, decreased redox, and erosion of surface sediments, as also has been well documented elsewhere (Srivastava and Jefferies 1996; McLaren and Jefferies 2004). Experimental work at La Pérouse Bay (Handa and Jefferies 2000) and at Akimiski Island (O et al. 2005, McLaren et al. unpublished) has confirmed that revegetation of such sites is difficult; for instance, *Festuca* usually dies if transplanted into degraded sites (O et al. 2005). As well, continuing foraging pressure on the remaining intertidal vegetation likely is working against recovery, consistent with both models of alternative states (van de Koppel et al 1997) and results of manipulative trials (Handa and Jefferies 2000). Although few in relative number compared to the migrants that may have initiated the decline in 1972, nesting Akimiski Island geese are able to exert significant grazing pressure on the diminished vegetation that remains (Jefferies, RL, 1992, unpublished report; O et al. 2006), slowing recovery; conversely, exclosure experiments at La Pérouse Bay have shown recovery of intertidal vegetation can be improved by fencing damaged sites (Handa et al. 2002). The slight increase we observed in forage species does suggest recovery is possible even in the presence of geese, but future changes seem likely to be slow, as previously predicted (Abraham et al. 2005; Jefferies et al. 2006). Clearly demonstrating alternative stable states is difficult (Connell and Sousa 1983; Scheffer and Carpenter 2003; Schröder et al. 2005), and Akimiski may indeed be in a process of prolonged recovery, but as at

La Pérouse Bay, the combination of long-term data and field experiments indicates geese are capable of triggering significant and lasting changes in northern coastal ecosystems.

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Table 1: Generalized linear model analyses of the distribution of forage species. Shown are results of a factorial analysis (Year, Position, Position $\times$ Year). The Thompson River and Stitt River transects were located within the dense snow goose nesting area; the Lumsden River transect was near the west edge of the nesting colony; the Ministik River transect was east of the colony. Values shown are likelihood ratio X^2 ; ns: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; -: sample size insufficient for analysis.

Species	Factor ^a	Lumsden	Thompson	Stitt	Ministik
<i>Puccinellia</i>	Year	0.900 ^{ns}	41.016***	19.952***	31.911***
	Position	170.182***	65.069***	68.366***	191.579***
	Position $\times$ Year	103.906***	-	23.894***	-
<i>Carex</i>	Year	0.334 ^{ns}	-	-	16.412***
	Position	29.039*	-	-	153.012***
	Position $\times$ Year	8.583 ^{ns}	-	-	68.925***
<i>Festuca</i>	Year	2.191 ^{ns}	2.039 ^{ns}	22.573***	6.055*
	Position	719.517***	284.263***	278.606***	634.307***
	Position $\times$ Year	-	13.471 ^{ns}	-	-

^a df for Year = 1; df for Position, Position $\times$ Year = 14 (Lumsden), 10 (Thompson), 6 (Stitt), 8 (Ministik).

Table 2: Generalized linear model analyses of the distribution of non-forage species. Shown are results of a factorial analysis (Year, Position, Position $\times$ Year). The Thompson River and Stitt River transects were located within the dense snow goose nesting area; the Lumsden River transect was near the west edge of the nesting colony; the Ministik River transect was east of the colony. Values shown are likelihood ratio X^2 ; n; ns: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; -: sample size insufficient for analysis. "Mud" includes intertidal and supratidal exposed mud and seaweed-covered sediments.

Species	Factor ^a	Lumsden	Thompson	Stitt	Ministik
<i>Salicornia</i>	Year	80.299***	-	-	-
	Position	214.074***	-	-	-
	Position $\times$ Year	128.012***	-	-	-
<i>Spergularia</i>	Year	0.311 ^{ns}	973.906***	-	220.216***
	Position	1072.455***	135.372***	-	257.123***
	Position $\times$ Year	535.048***	-	-	-
<i>Glaux</i>	Year	2.585 ^{ns}	229.107***	0.792 ^{ns}	0.992 ^{ns}
	Position	235.487***	241.080***	199.816***	322.378***
	Position $\times$ Year	-	167.564***	-	-
Mud	Year	30.288***	1304.504***	1.243 ^{ns}	124.323***
	Position	238.797***	147.504***	167.343***	433.269***
	Position $\times$ Year	209.996***	65.053***	191.729***	61.063***

^a df for Year = 1; df for Position, Position $\times$ Year = 14 (Lumsden), 10 (Thompson), 6 (Stitt), 8 (Ministik).

List of Figure Captions

Figure 1: Map of Akimiski Island, indicating position of snow goose nesting and brood-rearing areas, and of transect sampling sites. Locations of transects (seaward end, uncorrected magnetic compass bearing, and length): L (Lumsden) 53°11.88'N, 81°36.28'W, 200°, 1500m; S (Stitt) 53°12.68'N, 81°18.10'W, 215°, 700m; M (Ministik): 53°11.47'N, 81°12.83'W, 200°, 900m. The Lumsden, Stitt, and Ministik endpoints are associated with metal stakes; the Thompson (T) endpoint is back-calculated as approximately 1163m at 55° from an observation tower located at 53°11.94'N, 81° 26.29'W.

Figure 2: **a)** Excellent quality *Puccinellia* marsh (to the right) on an island in Akimiski Strait with no evidence of goose nesting or brood-rearing (2006). Note the continuous plant cover. **b)** Heavily used Akimiski Island brood-rearing area, 1994. Higher areas show grubbed former *Festuca rubra* and vegetation there is dominated by remaining patches of *Festuca rubra*; lower areas contain *Puccinellia phryganodes*, *Carex subspathacea*, and bare sediments. **c)** Severely devegetated intertidal flats on Akimiski Island, 2008. The tall plant is *Senecio congestus*. **d)** Typical colonizing individual of *Puccinellia phryganodes*, 2008; note the low cover and biomass.

Figure 3: Spatial distribution of forage species; 0m represents the seaward end of each transect. The Thompson River and Stitt River transects were located within the dense snow goose nesting area; the Lumsden River transect was near the west edge of the nesting colony; the Ministik River transect was east of the colony. Each bar represents the number of observations of that species per 100m transect segment, out of a possible total of 100 datapoints. Note the differences in horizontal scale.

Figure 4: Overall frequency of forage species in 1998 and 2008. The Thompson River and Stitt River transects were located within the dense snow goose nesting area; the Lumsden River transect was near the west edge of the nesting colony; the Ministik River transect was east of the colony. Also shown is the number of points sampled (n); note the differences in scale.

Figure 5: Spatial distribution of non-forage species; 0m represents the seaward end of each transect. The Thompson River and Stitt River transects were located within the dense snow goose nesting area; the Lumsden River transect was near the west edge of the nesting colony; the Ministik River transect was east of the colony. Each bar represents the number of observations of that species per 100m transect segment, out of a possible total of 100 data points. Note the differences in horizontal scale.

Figure 6: Overall frequency of non-forage species in 1998 and 2008. The Thompson River and Stitt River transects were located within the dense snow goose nesting area; the Lumsden River transect was near the west edge of the nesting colony; the Ministik River transect was east of the colony. Also shown is the number of points sampled (n); note the differences in scale.

Figure 7: Biomass (mean $\pm$ SEM) of best remaining *Puccinellia* and *Festuca* at the Lumsden (diamond), Thompson (square), Stitt (circle), and Ministik (triangle) sites. The Thompson River and Stitt River transects were located within the dense snow goose nesting area; the Lumsden River transect was near the west edge of the nesting colony; the Ministik River transect was east of the colony.

Figure 1.

Figure 2.

a)

b)

c)

d)

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.