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# Goose-induced Changes in Vegetation and Land Cover between 1976 and 1997 in an Arctic Coastal Marsh

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## Abstract

Since the 1970s, a breeding colony of lesser snow geese (*Chen caerulescens caerulescens* L.) at La Pérouse Bay, Manitoba, has grown 8% annually. This increase has led to significant loss of plant cover in all major salt- and freshwater coastal habitats between 1976 and 1997. A series of transects established in 1976 was resurveyed in 1997. Exposed sediment, extent and type of vegetative cover, and aquatic areas were recorded along transects using a classification of 12 a priori classes. Five regions within the colony were identified, and changes in vegetation cover differed among these and depended on unique combinations of vegetation class and year. Grubbing by geese has led to loss of graminoid plants, especially in intertidal and supratidal marshes. Exposed sediments have largely replaced previously vegetated areas since 1976. Species characteristic of disturbed sites have colonized exposed sediment with the most abundant species varying according to soil conditions. In intertidal marshes, willow cover declined in association with the development of hypersalinity after loss of the graminoid mat, but willow cover increased at the base of well-drained beach ridges and in a river delta with ample winter snow accumulation and freshwater flow in spring that protected ground vegetation. Most of the expected successional trends associated with isostatic uplift and changes in soil organic matter failed to occur because of intense goose foraging throughout the 20 years. The likelihood of sustained recovery of plant communities in the immediate coastal zone is very low, as long as goose numbers continue to increase. Indirect effects of vegetation loss (e.g., hypersalinity) and subsequent erosion of exposed sediments following grubbing will delay plant colonization and retard succession.

## Introduction

Herbivores exert a strong control on vegetation dynamics in terrestrial systems and can bring about major changes in species richness leading to the establishment of alternative stable states (cf. Noy-Meir 1975; May 1977; Westoby et al., 1989). When the consumption rate of forage plants exceeds their growth rate, herbivores may trigger rapid, nonlinear shifts of species assemblages toward alternate stable states, often characterized by loss of vegetation and low species richness (Van de Koppel et al., 1997). Over the last three decades the intense foraging activities of increasing numbers of lesser snow goose have severely altered soils and plant assemblages in the intertidal and supratidal marshes of the Hudson Bay Lowland. The foraging has led to loss of vegetation and exposure of sediment that represents an alternate stable state (Hik et al., 1992; Handa et al., 2002).

In 1976–1977, the vegetation in coastal habitats at La Pérouse Bay, Manitoba, was surveyed in all known nesting and brood-rearing areas of a small breeding colony of lesser snow geese containing approximately 3300 pairs in 10 $km^2$. The survey was made in all habitats and took place before extensive loss of vegetation had occurred as a result of goose foraging. Since then, the nesting colony at La Pérouse Bay has grown in numbers at a rate of 8% per year (Cooke et al., 1995). By 1997, the number of pairs was estimated to be 44,500, and the geographical extent of the colony had grown from 10 $km^2$ in the early 1970s to 175 $km^2$ in 1997 (Kerbes, 1975; K. F. Abraham, R. F. Rockwell, and R. K. Ross, unpublished aerial survey). The nesting geese and thousands of geese that stage there during migration, but which nest further north, are part of the Mid-Continent Population of lesser snow geese; this population has grown at an average rate of at least 5% per year in recent decades (Rockwell et al., 1997). The growth of the La Pérouse Bay colony has been linked directly to loss of vegetation, alteration of soils, and habitat fragmentation in the intertidal and supratidal marshes (Iacobelli and Jefferies, 1991; Srivastava and Jefferies, 1996; Handa et al., 2002; Jefferies and Rockwell, 2002).

The objectives of this study were to determine the frequencies of all coastal vegetation types and their contribution to land cover before and after the period of rapid colony growth. The survey was not limited to the inter- and supratidal areas which have been intensively studied, because the geese also nest and forage in riverine marshes, on beach ridges, and at the margins of coastal lagoons. A classification scheme was developed to describe and quantify the vegetation associations and goose use of these areas (Abraham, 1980) and was used in both 1976 and 1997 surveys. The present study complements the more intensive studies of the inter- and supratidal marshes, enabling the effects of goose foraging on vegetation to be placed in a wider spatial context.

## Materials and Methods

### *STUDY AREA*

The study area at La Pérouse Bay, Manitoba (58°44′N, 94°28′W), which is now within Wapusk National Park, was occupied by a nesting colony of the lesser snow goose in the mid-1970s. Abraham (1980) described the major vegetation types, the dominant types of land cover, and the history of use of the area by snow geese at that time. Our first

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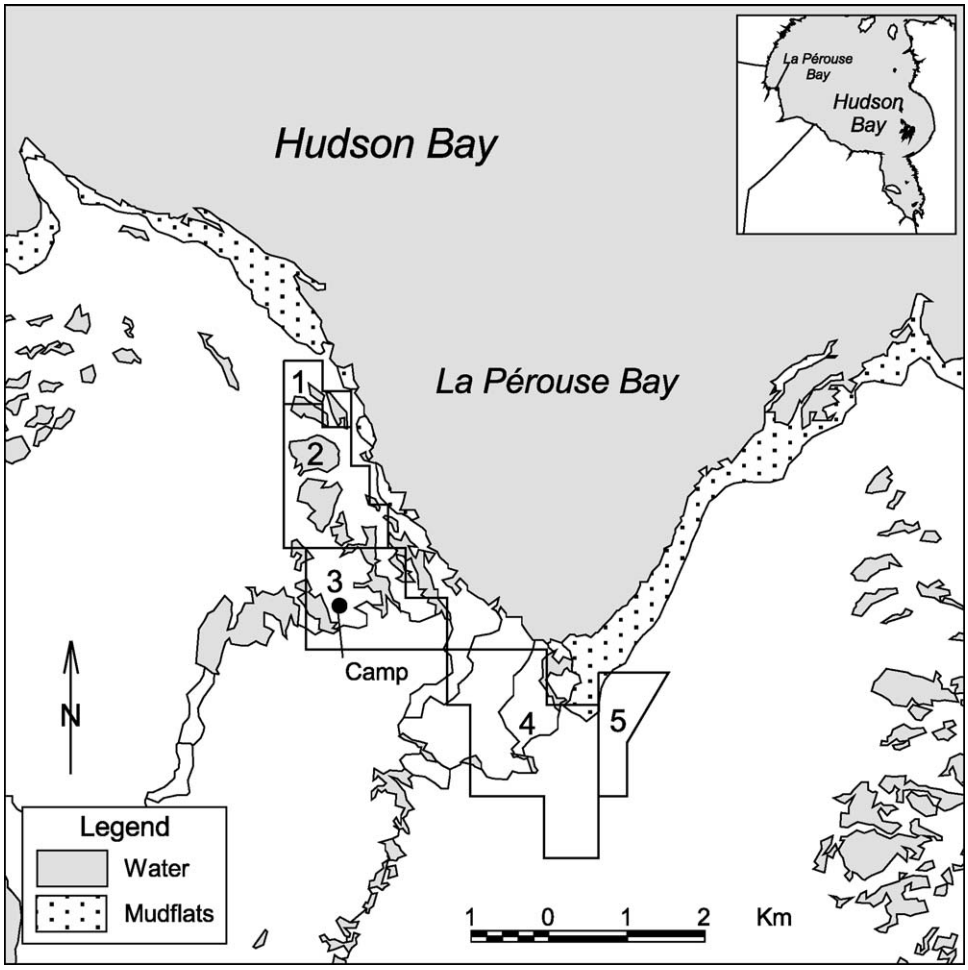



**FIGURE 1. Map of La Pérouse Bay, Manitoba (58°44′N, 94°28′W), showing the five regions where transects were located: (1) Beach Ridge, (2) Lagoons and Ridges, (3) Mast River Delta, (4) Southern Supratidal Marsh, and (5) Eastern Intertidal Marsh. An arrow on the inset map indicates position of La Pérouse Bay on the Hudson Bay coast, approximately 40 km east of Churchill, Manitoba.**

survey of the plant assemblages in the study area took place in late July and early August 1976 and 1977, while the second was completed in the same months in 1997. The surveys were made in five regions in the immediate coastal strip (Fig. 1), and include (1) coastal beach ridge, (2) lagoons and ridges in the lacustrine area of the Mast River delta, (3) braided channels of the Mast River delta, (4) supratidal marsh south of the southern V-shaped point of La Pérouse Bay where the frequency of tidal coverage is 2–3 times every 3 years, and (5) intertidal marsh on the east side of La Pérouse Bay.

The regions were highly heterogeneous with respect to types of land cover represented and goose use (Abraham, 1980; Cooke and Abraham, 1980). In 1976, the vegetation on the beach ridge (1) was dominated by *Leymus mollis* (Trin.) Pilger, with low-lying areas dominated by *Puccinellia phryganodes* and *Carex subspathacea* (unless otherwise indicated, plant nomenclature follows Porsild and Cody, 1980). The ridge, which is in the northwest region of La Pérouse Bay, extends westward and runs parallel to the coast. Formerly, it was used extensively by staging geese and by breeding geese and their goslings from spring until late summer. Low ridges (2) dominated by *Salix* spp. and *Betula glandulosa* separate the four largest lagoons in the lacustrine portion of the Mast River. In low-lying areas between these ridges, moss carpets and freshwater sedges, including *Carex aquatilis*, are present. Relict beaches with willow-dominated ridges also impound the braided delta of the Mast River (3) with its numerous small islands. At the time of the initial surveys, the ridges of both the lagoon/ridges and delta had moderate to high densities of nesting geese, but the use of these regions was relatively low during the post-hatch period. In the 1970s, the supratidal marsh to the south (4) was an area of low willows, *Salix brachycarpa*, and grasses, *Festuca rubra* and *Calamagrostis deschampsioides*. These species grew on frost-heave hummocks, but again, in low-lying parts of the area, *P. phryganodes* and *C. subspathacea* were abundant. Because of relatively early spring melt, this region had notably high early season use by spring migrants and had the highest goose nesting densities in the colony in the 1970s; further, it had relatively high post-hatch use because the graminoids grew rapidly after early thaw. Extensive lawns of *P. phryganodes* and *C. subspathacea* dominated the eastern intertidal marsh (5), but in the zone above the limit of mean spring tides *F. rubra* and *C. deschampsioides* replaced these two graminoids. In the 1970s, the upper marsh had a low density of nesting geese, but brood-rearing adults and their goslings intensively grazed the lower marsh. By the 1990s, virtually no snow geese nested in the five regions, and pre-nesting and post-hatch use were severely reduced.

### *VEGETATION CLASSIFICATION*

The classes of plant assemblages and land cover that were recognized subjectively a priori in 1976 are given in Table 1 (hereafter, vegetation class and class are used interchangeably). The classes identified were formally described independently (cf. Heagy and Cooke, 1979; Jefferies et al., 1979; Srivastava and Jefferies, 2002), and these plant assemblages are widespread in coastal areas of the Hudson Bay Lowland (e.g., Kershaw, 1976, Ringius, 1980). The species named in Table 1 are the visual dominants. Classes 1–11 and 18 were used in both the surveys of 1976–1977 and 1997 and are the only ones included in the analyses. Classes 12–17 were variants of some of the original classes and were recognized only in the second survey. Species that characterize these latter classes were recorded in



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**TABLE 1**

**Vegetation and land-cover classes used in the surveys in 1976–1977 and 1997 at La Pérouse Bay, Manitoba. Classes 12–17 inclusive were recognized only in 1997, and data from these classes were pooled with the original 12 classes (see text) in the statistical analysis.**

| Class | Class name | Dominant species and environmental description |
|---|---|---|
| Class 1 | Hippuris | *Hippuris tetraphylla* and *Hippuris vulgaris*, found in shallow water in unconsolidated sediment and at the land-water interface in estuarine and slow moving waters. |
| Class 2 | Carex aquatilis | *Carex aquatilis*, sometimes with *Potentilla palustris*, found at margins of freshwater streams or shallow ponds and at land edges in these water bodies grading into saturated soils. |
| Class 3 | Wet graminoids | Mixtures of sedges including *Eleocharis acicularis* and *Eriophorum angustifolium*, characteristic of wetland areas, often covering pond basins or reworked sediment deposits. |
| Class 4 | Dupontia-Carex | *Dupontia fisheri* and *Carex glareosa*, found in very moist or saturated soils, often at the land-water interface. |
| Class 5 | Puccinellia-Carex | *Puccinellia phryganodes* and *Carex subspathacea*, found on the lowest elevation land, the latter often in moss substrates. |
| Class 6 | Mixed short grass | A mixture of grasses, notably *Calamagrostis deschampsioides* and *Festuca rubra*, found at slightly higher elevations than Puccinellia-Carex. |
| Class 7 | Elymus | *Leymus mollis* (formerly *Elymus arenarius* var. *mollis*), found in better drained soils and sandy and gravelly areas, including elevated hummock tops, and beach ridges. |
| Class 8 | Low willow | *Salix brachycarpa* and *S. myrtillifolia*, found on beach ridges and hummocks in lower lying ares. |
| Class 9 | Mixed shrubs | Mixed, taller shrubs including several species of *Salix* (*candida, planifolia, lanata*), *Betula glandulosa*, and *Myrica gala*, found at higher elevations than "Low willow". |
| Class 10 | Dry hummocks | Relatively open areas at local elevation peaks with a variety of species including *Pyrola* spp., *Castilleja raupii*, *Leymus mollis*, and mosses and lichens. |
| Class 11 | Exposed sediments | Terrestrial soils with no vegetation or sometimes with remnant individual plants (<5% of area) and dry land-water margins indistinguishable from exposed sediments at the time of the survey. |
| Class 12 | Salicornia | *Salicornia borealis*, occuring in nearly monotypic stands, in low-lying hypersaline areas. |
| Class 13 | Dried mosses | *Bryum inclinatum* and *Campylium stellatum*, in areas where former graminoid or dicotyledonous vegetation has been stripped away. |
| Class 14 | Senecio | *Senecio congestus*, occuring in nearly monotypic stands in disturbed, wet seepage areas. |
| Class 15 | Mixed dicotyledons | *Matricaria ambigua*, *Parnassia palustris*, *Primula stricta*, occurring in beach ridge areas formely dominated by *Leymus*. |
| Class 16 | Atriplex | *Atriplex patula*, *A. glabriuscula*, occurring in monotypic stands in disturbed, low-lying intertidal areas. |
| Class 17 | Honckenya | *Honckenya peploides*, found in sandy and gravelly areas on near coast beach ridges and dunes. |
| Class 18* | Water | Open water present at the time of the survey, including permanent ponds, streams, and lagoons. |

* This class was one of the original twelve 1976 classes. It was recorded in the field in both survey periods, but was not included in the analysis on vegetation-land cover (see Methods, Statistical Analyses for explanation).

1976–1977, but their densities and coverage were very low, consequently they were not ranked as separate classes at that time. Even in 1997, total records in Classes 12–17 were only 231, 54, 192, 358, 111, and 64, respectively, compared to a grand total of 26,790 records for Classes 1–11 (i.e., only 3.7%). Therefore, values for Classes 12, 13, 14, and 16 were added to Class 11 (exposed sediment with little plant cover) and results for Classes 15 and 17 were pooled with Classes 3 and 7, respectively, in the statistical analyses. Some classes reflect vegetation characteristic of shorelines, pond margins, and very wet soils, e.g., Classes 1–5. Other classes reflect vegetation growing on sites at higher elevations, or which have more well-drained and drier soils, e.g., Classes 6–10.

### *VEGETATION AND LAND COVER TRANSECTS*

Black and white aerial photographs were obtained from the National Air Photo Library, Ottawa (scale 2520:1). The original photographs were taken on 6 August 1960 at a height of 12,600 ft (3850 m) AASL. Contiguous photographic enlargements, each representing an area 600 m × 600 m, provided coverage of most of the nesting colony in 1976. In 1976, a total of 62 transects, each 600 m in length, were marked on transparent overlays on the photographs. These were oriented in a north-south direction and placed at intervals of 100 m or 200 m in areas where snow goose nests were found in regions 1–4 (Fig. 1). In 1977, an additional 6 transects of variable length (300–500 m) oriented in a northwest-southeast direction perpendicular to the coastline were surveyed in an area where nests occurred on the east side of La Pérouse Bay (region 5 in Fig. 1). In 1997, 48 of the original 62 transects in regions 1–4 were resurveyed. Fourteen replacement transects (200–800 m) were surveyed in 1997 (6 oriented north-south in the southern supratidal marsh south of La Pérouse Bay [region 4 in Fig. 1] and 8 oriented west-east crossing the eastern intertidal marsh [region 5 in Fig. 1]). These were needed because some 1976 transect overlays of region 4 had been lost and because the 1977 original transects in region 5 were plotted on field maps with local landmarks, but not on photographs. In each year the vegetation and land cover along transects were surveyed by the same person (Abraham) who assigned each pace along a transect to a vegetation or land cover class. In 1997, the original 12 classes were used, but as discussed earlier, 6 others that reflected the foraging impact of the geese over the intervening 20 years were added.

### *STATISTICAL ANALYSES*

Data for each transect were summarized as the number of paces assigned to each of the vegetation and land cover classes encountered.



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**TABLE 2**

**Results of log-linear modeling of cross-classified vegetation and land cover data (excluding water areas) from 1976–1977 and 1977 surveys of a snow goose colony at La Pérouse Bay, Manitoba.**

| Model | Source | df | Wald statistic | $p$ |
|---|---|---|---|---|
| Third-order | vegetation class × year | 10 | 6475.39 | <0.001 |
| | vegetation class × region | 38* | 7893.48 | <0.001 |
| | vegetation class × year × region | 25* | 1434.19† | <0.001 |
| Second-order by region | | | | |
| 1. Beach Ridge | vegetation class × year | 7* | 1614.32‡ | <0.001 |
| 2. Lagoons and Ridges | vegetation class × year | 8* | 1362.76‡ | <0.001 |
| 3. Mast River Delta | vegetation class × year | 8* | 1725.49‡ | <0.001 |
| 4. Southern Supratidal Marsh | vegetation class × year | 9* | 4721.55‡ | <0.001 |
| 5. Eastern Supratidal Marsh | vegetation class × year | 3* | 1611.70‡ | <0.001 |
| Second-order for initial year 1976 | vegetation class × region | 35 | 5679.95§ | <0.001 |

* Degrees of freedom depart from expectation owing to cells containing zeros.

† Log-ratio chi-square of the third-order term is 1916.18, which is significant at $p < 0.0001$.

‡ Log-ratio chi-square of the second-order terms are (in order): 3357.17, 2682.17, 2767.58, 6818.30, 2103.40.

§ Log-ratio chi-square is 9159.44.

These summaries provide absolute frequency distributions of the class composition of the transects and are independent of the pattern of those classes across the transects. We pooled data across transects within each of the five regions to reduce statistical limitations imposed by small sample sizes for some vegetation classes (Fienberg, 1989). Because our primary purpose was to determine whether the relative composition of vegetation and land cover classes changed during the time between the two surveys, we evaluated the data with log-linear models of the absolute frequencies, cross-classified by transect and year, a procedure sometimes referred to as multidimensional contingency analysis (Bishop et al., 1975; Jefferies and Rockwell, 2002; Rockwell et al., 2003). The procedure requires only that transects be assigned without prior knowledge of vegetation and land class composition, that paces be taken along the transect without reference to the classes and that any variation in pace length be random with respect to those classes. As explained above, every attempt was made to satisfy these requirements.

In our evaluation, we treated the distributions of vegetation and land cover classes as response variables, while year and/or space (set of pooled transects referred to as a Region in Fig. 1) were considered to be classification variables. Because our objective was to determine changes in the relative response variable distribution over time and/or space, we only consider models that included the second- and third-order terms involving vegetation and year and/or space, and only the values associated with those terms are given in the Results. This constraint is consistent with the nearly fixed nature of each transect over time (cf. Fienberg, 1989; Everitt, 1992; Jefferies and Rockwell, 2002). The log-linear models used to determine dependency of the vegetation response variables on year, region, or unique combinations of year and region (3-way tables) were generated using the CATMOD procedure from SAS® 8.02 (SAS Institute, 2001). Effects were evaluated statistically using the Wald statistic, and the log-ratio chi-square statistic was used to confirm the significance of the second- and third-order terms (Stokes et al., 2000). Because the nature of the analysis of hierarchical models requires repeated evaluation of subsets of data (9 in this case), we have reduced inflation of our overall $\alpha$-error rate using a Bonferroni approach that requires $p < 0.006$ for significance.

Several vegetation classes were so rare that they were not recorded along transects in some regions. These classes represent sampling zeros in the cross-classification of data, and they can lead to difficulties when evaluating data with log-linear models. As indicated in Table 2, the degrees of freedom of the class × year × region term of the third-order model and of the class × year terms in the second-order model were adjusted below expectation based on standard procedures. This reduces the power of the Wald statistic to detect significant dependency of the response variable on both class × year × region and class × year. However, because those tests were significant, the reduced power from the analysis does not affect our general conclusions. As a check, however, we repeated the analyses after setting each 0 to 1 (Stokes et al., 2000). The results did not differ from those summarized in Table 2.

## Results

The results of the log-linear evaluations of the 1976–1977 and 1997 vegetation-land cover class data are summarized in Table 2. The significant third-order term (class × year × region) indicates that the distribution of the vegetation classes depends on unique combinations of year and region. In the second-order models (Table 2), this is examined further by evaluating the changes in vegetation and land cover over the two decades for each of the 5 regions separately. While all five analyses are highly significant, indicating that the distributions of vegetation classes changed in each region over the two decades, the precise pattern and extent of change varied among regions (Fig. 2).

These regional differences depend, in part, on initial vegetation differences among the regions (significant region × vegetation class term for 1976 in Table 2). The relative magnitudes of the Wald statistics suggest that the extent of change was most extreme in the southern supratidal marsh of La Pérouse Bay (Table 2). Exposed sediment (Class 11, Table 1) increased in all regions, largely at the expense of the graminoid community *P. phryganodes* and *C. subspathacea* (Class 5), but other graminoid communities such as *Leymus*, *Festuca*, *and Calamagrostis* also have been severely affected (Classes 3, 4, 6, 7) (Fig. 2). Changes in the low willow (Class 8) and mixed shrub (Class 9) assemblages, in contrast, differed depending on the region. In the beach ridge, the lagoons and ridges, the Mast River delta, and the southern supratidal marsh (areas of freshwater and/or locally elevated frost-heave islands with good drainage), the frequency of these classes increased during the 20 years, whereas their frequencies declined over the period in the eastern intertidal marshes. Strong clonal growth from bushes present in 1976 accounted for much of the increase in the frequencies of these woody shrubs on ridges in the lagoon and delta areas where freshwater was present and where spring flooding regularly washed the soils and limited goose access to the graminoid classes.

In general, vegetation characteristic of low-lying areas was the most severely altered over the period between the two surveys. The effect of grubbing led to a more fragmented vegetation cover. Monospecific stands of one or two species present in 1976 either were broken up or lost entirely (e.g., *P. phryganodes* in the intertidal areas and *Leymus mollis* in the beach ridge area).

The survey in 1997 resulted in the recognition of six new vegetation classes, most of which represented goose-disturbed conditions (Classes 12–17, Table 1). Annuals, tolerant of the hypersaline conditions that occurred in the eastern intertidal marsh and in the supratidal marsh, represented two of the new classes. The first is *Salicornia borealis* Wolff and Jefferies. In 1976, this annual was present at high frequencies in two small areas of Region 4. Although the species is at the northern limit of its distribution in Manitoba (Johnson, 1987; Wolff and Jefferies, 1987), *S. borealis* has become more widespread in recent years in goose-disturbed coastal marshes.



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A second new class was represented by *Senecio congestus*, a species that, following grubbing, became abundant in the exposed sediments which were formerly colonized by *P. phryganodes* and *C. subspathacea*. Other disturbed areas in the upper intertidal marsh were also colonized by *Atriplex glabriuscula* and *A. patula*. *Bryum inclinatum*, *Matricaria ambigua*, and *Parnassia palustris* colonized former *Leymus* sites (Jefferies et al., 1979; Handa et al. 2002).

## Discussion

Population increases of the lesser snow goose in the mid-continent of North America have resulted in increased forage demands over larger and larger subarctic and Arctic staging and nesting areas during recent decades. Changes in the vegetation at the nesting colony at La Pérouse Bay between 1976 and 1997 that are described in this paper are the outcome of this increase. Although results from monitoring and experimental studies during the intervening two decades provide strong evidence to support these conclusions (Cargill and Jefferies, 1984; Bazely and Jefferies, 1986; Jefferies, 1988a; Iacobelli and Jefferies, 1991; Srivastava and Jefferies, 1996; Jano et al., 1998; Jefferies and Rockwell, 2002), data from this study indicate that goose foraging results in changes to plant assemblages and land cover classes of *all* coastal habitats, not just intertidal and supratidal marshes and sedge meadows. This affects reproductive and foraging habitats of all organisms that co-inhabit these coastal lowlands. Differences in the changes of vegetation classes over the entire coastal system during the two decades suggest that the cumulative direct and indirect effects of the foraging activities of the geese were not synchronous across all regions, similar to the finding for the intertidal salt marshes (Jefferies and Rockwell, 2002). The regional differences depended on annual and within-season variation in snow, ice, and water cover, and numbers and dispersion of geese within and between regions in spring, as well as edaphic conditions at the different spatial scales (Abraham, 1980; Cooch et al., 2001; Jefferies and Rockwell; 2002). Much of the loss of vegetation induced by the geese is associated directly or indirectly with grubbing (Jefferies, 1988b) and shoot pulling (Kotanen and Jefferies, 1997). The prevalence of these foraging behaviors depends on the absence of snow cover and the presence of thawed ground in early spring before the above-ground growth of vegetation has started. Patterns of snow, ice, and meltwater cover and thawed ground vary, depending on local conditions, precipitation, and the prevailing wind direction at that time of year (Abraham, 1980), hence the location of accessible foraging sites in early spring varies each year.

In spite of the different composition of plant assemblages in the five regions, graminoid vegetation, in particular, declined along nearly all transects as a result of grubbing, grazing, and shoot pulling. A good example is the disappearance of *Leymus* as a result of shoot pulling by geese in early spring (Ganter et al., 1996). This species was formerly common in nearly pure swards on coastal beach ridges throughout La Pérouse Bay when the goose population was low (Heagy, 1976; Jefferies et al., 1979; Ganter et al., 1996). In the beach ridge region, the frequency of *Leymus* dropped from 16.6% to 1.8% (Class 7, Fig. 2). *Salix* bushes may establish at the base of the slopes of beach ridges or in the supratidal marsh gradually displacing *Leymus* and other species from these sites over time. However, where *Salix* bushes are of sufficient size, they afford protection from foraging and the grass may persist as a fugitive species under bushes. Even in more open areas, small shoots of *Leymus* that are prostrate and less than 10 cm in length persist despite heavy goose foraging (Handa et al., 2002). Salt-marsh plants in East Coast marshes of North America show similar fugitive responses to both abiotic and biotic conditions (Bertness and Shumway, 1993).

An exception to this trend of loss of graminoid classes was the *Carex aquatilis* class (Class 2, Fig. 2) in the lagoons and ridges, and in the Mast River delta regions. In these two regions of the study area, this species is found predominantly in wetland basins and on the margins of rapidly flowing freshwater streams, which are often ice-bound or deeply flooded in spring, and as a consequence are inaccessible to geese when they engage in shoot pulling. *Carex aquatilis* readily establishes in submerged areas with mineral substrates that are not subject to tidal immersion (Handa et al., 2002).

The other vegetation classes that showed an increase, except in the eastern intertidal marsh, were low willow and/or mixed shrubs. Where

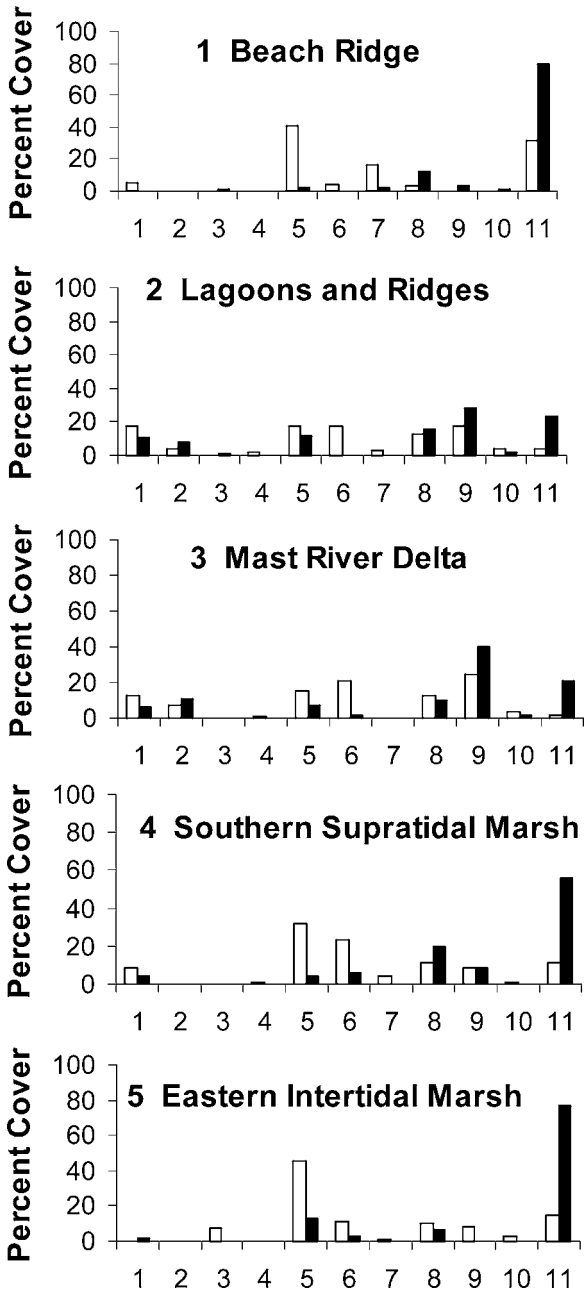



**FIGURE 2. Percentage contributions of vegetation/land cover classes to the total land surface cover in 1976–1977 (white) and 1997 (black) for five different regions of coastal habitats of La Pérouse Bay, Manitoba (58°44′N, 94°28′W). Vegetation/land cover classes are: (1) Hippuris, (2) Carex aquatilis, (3) Wet graminoids, (4) Dupontia-Carex, (5) Puccinellia-Carex, (6) Mixed short grass, (7) Elymus, (8) Low willow, (9) Mixed shrubs, (10) Dry hummocks, (11) Exposed sediments. See Table 1 and text for description of vegetation and land cover classes. Class 12 (water) is not shown.**



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high densities of these shrubs occur, sites are often snow-bound in early spring because snow accumulates around shrubs during winter. The initial obstruction to snow movement acts as a positive feedback leading to further accumulation throughout the winter. Hence, ground vegetation is relatively well protected from access by geese in spring and therefore from the effects of grubbing that lead to soil hypersalinity and the death of willow plants (Iacobelli and Jefferies, 1991). Additionally, the shrubs undergo clonal growth where they are undamaged, so bushes tend to coalesce and form dense stands, which further enhances snow accumulation. In the upper intertidal and supratidal marshes, dense stands of willows often occur on elevated frost-heave mounds that are separated by low-lying areas along which water drains. The geese grub along these low-lying, snow-free corridors in spring where the wet surface soil is thawed. Since 1976, much of the graminoid vegetation on these terraces and in the incipient shallow drainage channels has been lost as a result of grubbing. Decreased frequency of willow in the eastern intertidal marsh and some sections of the southern supratidal marsh was associated with the effects of grubbing: exposure of roots and development of soil hypersalinity leading to low survival of shrubs (Iacobelli and Jefferies, 1991; Srivastava and Jefferies, 1996). The resultant loss of shrubs has led to severe habitat alteration comparable to that of the near total loss of graminoid swards in the intertidal marsh (Jefferies and Rockwell, 2002; McLaren and Jefferies, 2004). However, in four of five regions, percentage cover of willows and mixed shrubs increased between 1976 and 1997 and hence at the larger spatial scale shrub frequency is increasing.

Relatively homogeneous stands of graminoid vegetation in the eastern intertidal marsh (e.g., large intact grazing lawns of *P. phryganodes* and *C. subspathacea*) and in the beach ridges (e.g., large monotypic swards of *Leymus mollis*) have become increasingly spatially heterogeneous since 1976 as goose foraging has resulted in a mosaic of small, remnant intact graminoid patches interspersed with larger patches of exposed sediment. In the Mast River delta, the local loss of shrubs and associated ground cover also has increased spatial heterogeneity which has led to a decrease in terrestrial invertebrate species (Milakovic and Jefferies, 2003) and nesting passerines, such as Savannah sparrows (*Passerculus sandwichensis*) (Rockwell et al., 2003).

Some species that readily establish in disturbed intertidal habitats were widely recorded in 1997 and were dominant in some classes (Table 1, classes 12, 13, 14, 16). One example is *Senecio congestus*, which was recorded in 1976, but at a very low frequency. Subsequently, it rapidly colonized areas disturbed by geese and was common in 1997. The geese feed intensively on the swollen leaf bases of the basal rosettes in early spring (Jefferies, unpublished) and by the late 1990s, plants of this species had become fugitive (Jefferies, unpublished). *Salicornia borealis* and *Atriplex glabriuscula* and *A. patula* also have become increasingly abundant in exposed sediments in depressions, especially in upper intertidal and supratidal marshes. *Bryum inclinatum* (Brid.) Bland. has invaded some open sandy sites and *Campylium stellatum* (Hedw.) C. Jens. has become widespread in many habitats. Geese do not eat these plants. These examples indicate the abrupt changes in the densities and dispersion of these local ruderal species that may occur in response to disturbance. Necromass of these species is washed away by meltwater or blown by the wind, so that organic litter does not accumulate in disturbed sediments.

Recolonization of disturbed intertidal graminoid sites is long-term (>10 years), even in the absence of geese, as vegetation change is out of phase with on-going changes in disturbed soils. Once a sward is destroyed, the soil seed bank is depleted within a few years (Chang et al., 2001). *P. phryganodes* and *C. subspathacea*, the dominant intertidal graminoids, must spread by clonal growth, because the grass is asexual (sterile triploid; Bowden, 1961), and the sedge rarely sets seed when grazed. As a result, conditions for plant re-establishment are poor. In short, the intertidal system has moved to an alternative stable state represented by a state and transition model (Handa et al., 2002). Whether the other habitats shown here to be severely altered will respond similarly to the continued impact of intense goose foraging can only be determined over time.

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