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 goose containing approximately 3300 pairs in 10 km². 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 km² in the early 1970s to 175 km² in 1997 (Kerby, 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 goose; 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 Jeffries, 1991; Srivastava and Jeffries, 1996; Handa et al., 2002; Jeffries 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
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 deschampsiioides. 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. deschampsiioides 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; Jefferyes et al., 1979; Srivastava and Jefferyes, 2002), and these plant assemblages are widespread in coastal areas of the Hudson Bay Lowland (e.g., Kernhaw, 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
### TABLE 1
Vegetation and land-cover classes used in the surveys in 1976–1977 and 1997 at La Pèrouse 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.

<table>
<thead>
<tr>
<th>Class</th>
<th>Class name</th>
<th>Dominant species and environmental description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class 1</td>
<td>Hippuris</td>
<td><em>Hippuris teretifolia</em> and <em>Hippuris vulgariis</em>, found in shallow water in unconsolidated sediment and at the land-water interface in eutrophic and slow-moving waters.</td>
</tr>
<tr>
<td>Class 2</td>
<td>Carex aquatilis</td>
<td><em>Carex aquatilis</em>, sometimes with <em>Poa annua</em>, found at margins of freshwater streams or shallow ponds and at land edges in these water bodies grading into saturated soils.</td>
</tr>
<tr>
<td>Class 3</td>
<td>Wet graminoids</td>
<td>Mixtures of sedges including <em>Elymus acris</em>, <em>Elymus repens</em>, and <em>Elymus repens var. glaucus</em>, found in better drained soils and sandy and gravelly areas, including elevated hummock tops, and beach ridges.</td>
</tr>
<tr>
<td>Class 4</td>
<td>Dry grasses</td>
<td><em>Salsola brachycarpa</em> and <em>S. serpyllifolia</em>, found in dry, exposed areas.</td>
</tr>
<tr>
<td>Class 5</td>
<td>Mixed shrubs</td>
<td><em>Salix brevifolia</em> and <em>S. serpyllifolia</em>, found in dry, exposed areas.</td>
</tr>
<tr>
<td>Class 6</td>
<td>Exposed sediments</td>
<td><em>Salix brevifolia</em> and <em>S. serpyllifolia</em>, found in dry, exposed areas.</td>
</tr>
<tr>
<td>Class 7</td>
<td>Salt marsh</td>
<td><em>Spartina pectinata</em> and <em>S. alterniflora</em>, occurring in nearly monotypic stands in disturbed, wet, sandy areas.</td>
</tr>
<tr>
<td>Class 8</td>
<td>Dried mosses</td>
<td><em>Bryum cinereum</em> and <em>Campylium stellatum</em>, in areas where former graminoid or dicotyledonous vegetation has been stripped away.</td>
</tr>
<tr>
<td>Class 9</td>
<td>Senecio</td>
<td><em>Senecio congeria</em>, occurring in nearly monotypic stands in disturbed, wet, weedy areas.</td>
</tr>
<tr>
<td>Class 10</td>
<td>Mixed sedges</td>
<td><em>Carex aquatilis</em>, <em>Carex rostrata</em>, and <em>Carex pensylvanica</em>, occurring in flooded areas.</td>
</tr>
<tr>
<td>Class 11</td>
<td>Grassy sedge</td>
<td><em>Carex aquatilis</em>, <em>Carex rostrata</em>, and <em>Carex pensylvanica</em>, occurring in flooded areas.</td>
</tr>
<tr>
<td>Class 12</td>
<td>Salt marsh</td>
<td><em>Spartina pectinata</em> and <em>S. alterniflora</em>, occurring in nearly monotypic stands in disturbed, wet, sandy areas.</td>
</tr>
<tr>
<td>Class 13</td>
<td>Dried mosses</td>
<td><em>Bryum cinereum</em> and <em>Campylium stellatum</em>, in areas where former graminoid or dicotyledonous vegetation has been stripped away.</td>
</tr>
<tr>
<td>Class 14</td>
<td>Senecio</td>
<td><em>Senecio congeria</em>, occurring in nearly monotypic stands in disturbed, wet, weedy areas.</td>
</tr>
<tr>
<td>Class 15</td>
<td>Mixed sedges</td>
<td><em>Carex aquatilis</em>, <em>Carex rostrata</em>, and <em>Carex pensylvanica</em>, occurring in flooded areas.</td>
</tr>
</tbody>
</table>

*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).*

### TABLE 1 (Cont.)
Dominant species and environmental description.

<table>
<thead>
<tr>
<th>Class</th>
<th>Class name</th>
<th>Dominant species and environmental description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class 16</td>
<td><em>Atriplex paniculata</em> and <em>A. glauca</em></td>
<td>occurring in monotypic stands in disturbed, low-lying intertidal areas.</td>
</tr>
<tr>
<td>Class 17</td>
<td>Honckenya</td>
<td><em>Honckenya peploides</em>, found in sandy and gravelly areas on near-coast beach ridges and dunes.</td>
</tr>
<tr>
<td>Class 18*</td>
<td>Water</td>
<td>Open water present at the time of the survey, including permanent ponds, streams, and lagoons.</td>
</tr>
</tbody>
</table>

1976–1977, but their densities and cover 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 25203). The original photographs were taken on 6 August 1960 at a height of 12,600 ft (3850 m) above sea level. Contiguous photographic enlargements, each representing an area of 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 coast were surveyed in an area where nests occurred on the east side of La Pèrouse Bay (region 5 in Fig. 1). In 1997, 48 of the original 62 transects in regions 1–4 were resurveyed. Fourteen replacement transects (200–400 m) were surveyed in 1997 (6 oriented north-south in the southern supratidal marsh south of La Pèrouse 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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Source</th>
<th>df</th>
<th>Wald statistic</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Third-order</td>
<td>vegetation class × year</td>
<td>10</td>
<td>6745.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>vegetation class × region</td>
<td>38*</td>
<td>7893.48</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>vegetation class × year ×</td>
<td>25*</td>
<td>1434.19</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>region</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second-order by region</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Beach Ridge</td>
<td>vegetation class × year</td>
<td>7*</td>
<td>1614.32</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2. Lagoons and Ridges</td>
<td>vegetation class × year</td>
<td>8*</td>
<td>1362.76</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>3. Mast River Delta</td>
<td>vegetation class × year</td>
<td>8*</td>
<td>1725.49</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>4. Southern Supratidal</td>
<td>vegetation class × year</td>
<td>9*</td>
<td>4721.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>5. Eastern Supratidal</td>
<td>vegetation class × year</td>
<td>3*</td>
<td>1611.76</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Marsh</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marsh</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second-order for initial</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year 1976</td>
<td>vegetation class × region</td>
<td>35</td>
<td>5679.95</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

* 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 < 0.001.
‡ Log-ratio chi-square of the second-order terms are (in order): 3357.17, 2682.17, 2762.50, 6818.30, 2103.40.
§ Log-ratio of second term 9.159.44.

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 re-
duced 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. phragmites and C. sub-
spathacea (Class 5), but other graminoid communities such as
Leymus, Festuca, and Calamagrostis also have been severely affected
(Class 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 grazing led to a more fragmented vegetation cover. Mono-
specific stands of one or two species present in 1976 either broke up
or lost entirely (e.g., P. phragmites 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 condi-
tions (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 Wolf and Jeffries. 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 Jeffries, 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 glabriscapulata* and *A. patula*, *Bryum inclination*, *Matricaria ambigua*, and *Parnassia palustris* colonized former *Leymus* sites (Jeffries 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 Jeffries, 1984; Barey and Jeffries, 1986; Jeffries, 1988a; Iacobell and Jeffries, 1991; Srivastava and Jeffries, 1996; Jano et al., 1998; Jeffries 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 (Jeffries 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; Jeffries and Rockwell, 2002). Much of the loss of vegetation induced by the geese is associated directly or indirectly with grubbing (Jeffries, 1988b) and shoot pulling (Kotanen and Jeffries, 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, 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 goose in early spring (Ganter et al., 1996). This species was formerly common in nearly pure swards on coastal ridges throughout La Pérouse Bay when the goose population was low (Heagy, 1976; Jeffries 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

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The other vegetation classes that showed an increase, except in the eastern intertidal marsh, were low willow and/or mixed shrubs. Where
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 Jeffries, 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 goose 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 Jeffries, 1991; Srivastava and Jeffries, 1996). The resultant loss of shrubs has led to severe habitat alteration comparable to that of the near total loss of graminoid stands in the intertidal marsh (Jeffries and Rockwell, 2002; McLaren and Jeffries, 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. phyrgioides and C. subspathacea) and in the beach ridges (e.g., large monotypic stands 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 Jeffries, 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 Senecon 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 (Jeffries, unpublished) and by the late 1990s, plants of this species had become fugitive (Jeffries, unpublished). Salicornia borealis and Arctium glabratissima and A. pomela 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 Campylipium 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 xerophytic 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. phyrgioides and C. subspathacea, the dominant intertidal graminoids, must spread by clonal growth, because the grass is isoeukaryotic (sterile tripod; 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.

Acknowledgments

We wish to thank the students and staff at La Pérouse Bay Field Station for their support and especially Diana Pollak, Graham Baug, Marjorie Boufield, Roger Healey, and Judy Smith for help in collecting vegetation and land cover data and Andrew Jano for producing the map. The area surveyed is now part of Wapusk National Park and we acknowledge the interest and cooperation of Parks Canada. We are grateful for the financial support for the study, which was received from the Arctic Goose Joint Venture, the Natural Sciences and Engineering Research Council of Canada, the Mississippi and Central Flyway Councils, the Ontario Ministry of Natural Resources (OMNR), and Queen’s University. This is an OMNR Wildlife Research and Development Section contribution.

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Revised ms submitted October 2004