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A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay

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Summary

1 Herbivores may initiate small changes to plant-soil systems that trigger positive feedbacks leading to rapid catastrophic shifts in vegetative states, including irreversible changes in soil properties. In the coastal marshes of Hudson and James bays, foraging by increasing numbers of lesser snow geese (*Chen caerulescens caerulescens* A.O.U.) has led to loss of vegetation, and exposure and partial erosion of sediment.

2 Multi-temporal analysis of LANDSAT data has been carried out to detect vegetation change from 1973 to 1999 or later at nine sites in the coastal marshes of these bays where staging and/or breeding geese are present annually.

3 Images were co-registered, and for each image NDVI (Normalized Differential Vegetation Index) channels were generated. For each location, pairwise normalized differences were calculated between these NDVI images for each successive period defined by the imagery acquisition dates. The resulting secondary NDVI difference images expressed changes in NDVI values for each time interval and yielded three well-defined classes: water, vegetation decline and no detectable change in vegetation.

4 At the nine widely separated study sites, the intertidal saltmarsh (an ecological sere) has been lost (to a total of 35 000 ha) and an alternative stable state (exposed sediment) established. Similar changes have occurred elsewhere along the 2000-km coastline where the geese breed or stage.

5 Re-vegetation of these coastal marshes will take decades because of near-irreversible changes in soil properties that require erosion and re-deposition of unconsolidated sediment before large-scale plant colonization can occur, and because large numbers of geese continue to forage annually producing this dramatic top-down effect.

Keywords: alternative vegetative states; LANDSAT imagery; population numbers of lesser snow geese; soil salinity, self-organized patchiness.

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Introduction

The Mid-Continent Population of lesser snow geese (*Chen caerulescens caerulescens* A.O.U.) breeds in the coastal areas of Hudson Bay, Foxe Basin and Queen Maud Gulf in Arctic Canada, and mostly winters in the southern United States (Fig. 1). The geometric increase in this population since the late 1960s is estimated to be between 5% and 7% per year and the adult population size in 1997 was in excess of 5 million, and possibly as high as 7 million (Abraham & Jefferies 1997). However, the introduction of greatly liberalized

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hunting regulations in 1999 may have slowed population growth in recent years. Likely causes for the population increase include an agricultural food subsidy on the wintering grounds and along the flyways, a decline in the hunting harvest rate and the establishment in an agricultural landscape of refugia that birds can use as a sanctuary from hunting (Abraham *et al.* 1996). Climatic change and a shift in the nesting location of birds may also have contributed to the increase in numbers (MacInnes *et al.* 1990). However, the readily available food subsidy is thought to be the major contributor accounting for much of the increase (Abraham *et al.* 2005a).

Alternate stable states in plant communities result from abrupt changes in vegetation and soils that are 235 Biotically induced soil–vegetation change



Fig. 1 Hudson Bay region, indicating the location of the study sites.

effectively irreversible (Holling 1973; May 1977; Westoby et al. 1989). Interactions between snow geese and their preferred forage species on the Arctic breeding grounds are inherently unstable and are sensitive to goose numbers and the intensity and type of foraging. In spring, large numbers of geese initiate a positive feedback that results in the removal of vegetation of the coastal saltmarsh grazing lawns (sensu McNaughton 1979) and exposure of intertidal sediment, giving rise to an alternative stable state (Hik et al. 1992; Srivastava & Jefferies 1996). The geese grub for roots and rhizomes in the saltmarsh swards where the ground is thawed, leading to loss of vegetation and triggering nearirreversible changes in sediment properties, including the development of hypersalinity in summer, compaction of sediment, decrease in infiltration rate, loss of soil nitrogen and organic matter, and depletion of the soil seed bank (Kerbes et al. 1990; Iacobelli & Jefferies 1991; Srivastava & Jefferies 1996; Chang et al. 2001; McLaren & Jefferies 2004). Biocrusts of diatoms and cyanobacteria develop where a thin veneer of organic soil remains, but the crusts are transitory - they dry out and are blown away together with organic matter, as aridity and hypersalinity develop (Handa et al. 2002; McLaren & Jefferies 2004). Ultimately, the vegetative mosaic in the intertidal zone disappears (the loss of an ecological sere - the early successional vegetated intertidal marsh - is similar to the process of desertification in the Sahel; Graetz 1991), creating an abrupt transition from exposed

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 234–242 tidal flats to freshwater communities (Handa *et al.* 2002). Re-establishment of vegetation on the hypersaline sediment is long-term (> 20 years).

We use LANDSAT imagery to report on the loss of vegetation and exposure of sediment, not only in coastal marshes at La Pérouse Bay (Jano *et al.* 1998; Gadallah 2002) where many of previous studies have been conducted, but also in similar marshes elsewhere in Hudson Bay and James Bay where geese breed or stage. This regional change, as distinct from a local event, can also be linked to increases in numbers of lesser snow geese at breeding and staging areas within the region as a whole.

Materials and methods

Marshes in Nunavut, Manitoba and Ontario were selected for the study. They were located along the western and southern coasts of Hudson Bay, including James Bay, from the Maguse River, north of Arviat, to Moosonee, a distance of approximately 2000 km (Fig. 1, Table 1). The entire region is undergoing isostatic uplift. Local breeding lesser snow geese are known to have been present each summer from 1973 to 2003 at six of the nine locations investigated (La Pérouse Bay, McConnell River, Maguse River, Seal-Knife River, Pen Islands and Akimiski Island) but breeding was negligible or intermittent at the other three localities (Table 1, including references). In spring, snow geese stage at all locations while migrating to more northerly breeding areas (Thomas 236 R. L. Jefferies, A. P. Jano & K. F. Abraham

 Table 1
 Vegetation loss and goose numbers at different coastal sites along western and southern Hudson Bay, including James

 Bay. Vegetation loss represents declines based on NDVI. Note that satellite imagery was not available for matching years among sites and that goose estimates were not available for the same years as the images

Site	Loss (ha)	Breeding adult geese	Source of goose numbers
La Perouse Bay (58°44'	N, 94°28' W) (Group 1)		
1973-1984	1038	5600 in 1973	Kerbes (1975)
1984-1993	525	17 000 in 1984	Cooke <i>et al.</i> (1995)
1993-2000	197	45 000+ in 1990	Cooke <i>et al.</i> (1995)
		58 700 in 1997	R. H. Kerbes et al. (unpublished data)
Total:	1761		
McConnell River (60°50)' N 94°25' W) (Group 1		
1974–1988	519	326 000 in 1973	Kerbes (1975)
1988-1997	266	184 400 in 1985	MacInnes & Kerbes (1987)
1997-2001	198	65 500 in 1997	R H Kerbes <i>et al</i> (unpublished data)
Total area affected	945	00 000 m 1997	it. II. Iterees er ur. (unpublished dutu)
Magusa Divor (62°48' N	$0.0^{\circ}10' W$ (Group 1)		
1074 1088	, 94 10 W) (Gloup I)	1000 in 1072	$V_{\text{orbos}}(1075)$
19/4-1900	1877	14 200 in 1975	Kerbes(1975)
1900-1997	4/8	14 300 III 1979 80 000 in 1007	B H Karbas at al (uppublished data)
Total area officiated	2256	80 900 III 1997	K. H. Kerbes <i>et al.</i> (unpublished data)
Total alea allected.	2550		
Little Cape (55°14' N, 83	3°35′ W) (Group 2)		
1974–1987	261	none in 1979	Angehrn (1979)
1987–2000	3733	<3000 in 1996–2001	K. F. Abraham et al. (unpublished data)
Total:	3994		
Lake River* (54°20' N,	82°26' W) (Group 2)		
1974-1981	1787	negligible	K. F. Abraham et al. (unpublished data)
1981–1984	79	negligible	K. F. Abraham et al. (unpublished data)
1984-1990	3726	negligible	K. F. Abraham et al. (unpublished data)
1990-2000	5249	7500 in 1994	K. F. Abraham et al. (unpublished data)
Total:	10841		
Pen Islands (56°45' N. 8	8°38' W) (Group 3)		
1974–1984	1565	negligible	K. F. Abraham <i>et al.</i> (unpublished data)
1984–1997	112	<1000 in 1985	K F Abraham <i>et al.</i> (unpublished data)
1997-2000	1282	16 500 in 1997	R. H. Kerbes <i>et al.</i> (unpublished data)
Total:	2959		
Winial (55010' NI 05007	(W) (Crown 2)		
1075 1085	724	nagligibla	Lumsdon (1087)
1975-1985	210	600 in 1004	K E Abraham <i>et al</i> (unpublished data)
1907 2000	400	nogligible	K. F. Abraham <i>et al.</i> (unpublished data)
2000 2002	499	negligible	K. F. Abraham <i>et al.</i> (unpublished data)
2000-2002 Total:	200	negligible	K. F. Abraham <i>et al.</i> (unpublished data)
	1830		
Seal–Knife River (58°57	" N, 94°35' W) (Group 4	·)	
1973–1984	586	900 in 1979	R. H. Kerbes <i>et al.</i> (unpublished data)
1984–1996	1471		
1996–1999	215	4700 in 1997	R. H. Kerbes et al. (unpublished data)
Total:	2272		
Akimiski† (53°12' N, 81	l°33' W) (Group 4)		
1976-1985	2250	<400	Abraham et al. (1999)
1985-1993	5621	<400	Abraham et al. (1999)
1993-2000	2364	2200 in 1993	Abraham et al. (1999)
		1800 in 2000	K. F. Abraham et al. (unpublished data)
Total:	10235		· · · /

*Lake River has been a major staging area for over 25 years. Single day counts were made of 45 000 birds in 1972 (Curtis 1973) and 69 000 in 1994 (K. F. Abraham *et al.*, unpublished data).

†Akimiski Island was a major staging area in the 1970s and a lesser one in recent years. Single day counts were made of of 295 000 birds in 1972 (Curtis 1973) and 20 000 in 1994 (K. F. Abraham *et al.*, unpublished data).

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& Prevett 1982; Berkes *et al.* 1994, 1995), but estimates of staging goose numbers at Lake River and Akimiski Island are available only for two individual years (Table 1, including references). Because of the lack of annual quantitative estimates of numbers of breeding and staging birds, it is not possible to correlate loss of vegetation directly with goose numbers at these remote sites.

Areas were selected for study because they represented a range of intensity of use and length of occupancy by either or both staging and nesting snow geese and 237 Biotically induced soil-vegetation change because suitable LANDSAT imagery of temporal changes in vegetation was obtainable. Estimates of numbers of geese were based on visual and photographic aerial surveys made at irregular intervals at the different locations. In addition, ground surveys were conducted in some years at La Pérouse Bay (Cooke *et al.* 1995) and on Akimiski Island (Abraham *et al.* 1999). Plant nomenclature follows Porsild & Cody (1980).

Photographs of the loss of vegetation and classified NDVI (Normalized Differential Vegetation Index) images are available on the Hudson Bay Project website (http://research.amnh.org/users/rfr/hbp/main.html). LANDSAT imagery (available since 1973) can be used to detect vegetation changes (Barrett & Curtis 1992; Lunetta & Elvidge 1998; Jano et al. 1998), subject to availability. From 1973 to 1993, the sensor used was a multispectral scanner (MSS); thereafter, LANDSAT 4 used thematic mapper (TM) scanners and LANDSAT 7 an enhanced thematic mapper (ETM). All images were 8-bit and the NDVI values were scaled between 0 and 225. For each study area, cloud-free, good-quality, summer LANDSAT imagery from 12 July to 24 August was obtained for each year/on several occasions between 1973 and 2002, except the image of Akimiski Island in 1976 which was recorded on 18 September. Images of the same site were co-registered. Depending on the size of the study area and the number of recognizable features, 19-69 ground control points were selected. The images were reprojected to UTM (North American Datum 1983) projection to a pixel size of 25 m using a first-order polynomial with cubic convolution resampling. The registration error between images varied between 0.17 pixels and 0.49 pixels. For each image, NDVI channels were generated. The NDVI is closely linked to biomass values. For each location, pairwise normalized differences were calculated between these NDVI images for each successive period defined by the image acquisition dates. This step resulted in secondary NDVI difference images expressing changes in the NDVI values for each time interval. To avoid confusion with apparent changes caused by different water levels, all image processing was confined to a common land area defined by the highest water level found in the imagery set. Classification of these secondary images yielded three well-defined classes: water, vegetation decline and no detectable change in the vegetation. The values in Table 1 reflect areas where there has been a decline in vegetational cover based on a decrease in NDVI and ground-truthing of two of the sites (La Pérouse Bay and Akimiski Island). Visits to the other sites indicate that similar declines are associated with destructive foraging of graminoid swards by geese (Kotanen & Jefferies 1997; Jefferies & Rockwell 2002; O et al. 2005; Abraham et al. 2005b). To eliminate small artefacts caused by co-registration errors, a 15pixel minimum area filter was applied to the classified image; this step left areas of large contiguous vegetation loss (typical of the decline of coastal saltmarsh, Jefferies & Rockwell 2002) unchanged. The vegetation

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 234–242 decline class was not subdivided further into severity classes over this wide geographical area because extensive ground-truthing was not possible and was not available for the earlier dates. To distinguish vegetation loss occurring in the coastal marsh zone from those in the immediate interior (e.g. forest fires, flooding), masks were developed for the coastal zone and reports of the vegetation loss under the mask were generated for each period. The resolution of the early LANDSAT images from the 1970s is only 0.5 ha, and hence reporting to the nearest hectare is satisfactory. For each study area, a set of classified maps was created displaying the extent and also the distribution of vegetation change. The total difference between the earliest and the latest date was calculated by adding together vegetation loss files created for this purpose. Areas of overlap between successive periods (i.e. showing decline in more than one period) were assigned to the earlier period, so that the total area affected over the entire period was calculated without double- or triple-counting. Hence, the areas of loss in successive periods in Table 1 do not add up to the value for the total area affected from the earliest to the latest image. It would be misleading to report total area of vegetation decline as a percentage of the total area examined at each location, because some types of vegetation (e.g. willow and birch shrubs and mosses) are not eaten by snow geese. The extent of these vegetation types varies at each site and cannot be detected directly from remote-sensing imagery.

Results

The results of the vegetation loss calculations are given in Table 1. Although the timing of the changes was different at each of the nine locations examined, the various locations can be assigned to four groups based on the similarity of patterns of spatial and temporal changes of vegetation in the classified images.

The first group includes locations where damage to coastal vegetation is long-term, but the extent of the newly affected areas has declined steeply in recent years because intact swards are no longer available to be converted (i.e. further vegetation loss is limited by past events). Data for La Pérouse Bay are shown in Fig. 2; snow



Fig. 2 Numbers of nesting geese from 1963 to 1997 (solid squares) and the proportion of total area of saltmarsh as exposed sediment from 1986 to 1997 (open triangles) at La Pérouse Bay, Manitoba.

238 R. L. Jefferies, A. P. Jano & K. F. Abraham geese have staged and/or nested here and on coastal marshes in the vicinity of the McConnell and Maguse Rivers for at least 50–60 years (Fig. 1, Table 1) (Hanson *et al.* 1972; MacInnes & Kerbes 1987; Cooke *et al.* 1995). Large numbers of adult snow geese and goslings were recorded during the post-hatch period at La Pérouse Bay in the 1970s and early 1980s, but in the last 15 years the local post-hatch population has declined concurrent with the near total loss of intertidal vegetation and exposure of sediment. Adult females are strongly philopatric and the declining numbers of birds in the 1990s probably reflects an aging cohort (Cooke *et al.* 1995; Jefferies & Rockwell 2002; Pezzanite 2003). Ultimately, when the systems are exhausted (e.g. McConnell River colony; Table 1), snow geese no longer use the sites in any numbers.

Although damage to vegetation, especially at McConnell River (Lieff 1973), occurred before the availability of LANDSAT imagery (prior to 1973), the

intertidal zone at all three of the locations above is nearly devoid of vegetation and exposed sediment occurs over a wide area. In the exposed sediments on the intertidal flats close to the estuary of the McConnell River, the remains of *Puccinellia* swards were visible in the mineral substratum in 1987 (Kerbes et al. 1990). Damage during the last three decades includes changes not only to intertidal and supratidal saltmarshes, but also to the adjacent inland freshwater marshes. In the freshwater marshes, much of the damage is associated with shoot-pulling in spring by both nesting birds and north-bound staging birds. The removal of the graminoid ground cover has also led to the death of shallow-rooted willow bushes, especially in the supratidal marshes, as a result of the development of soil hypersalinity (Iacobelli & Jefferies 1991). The geographical extent of the damage now includes all major vegetation types, at least in the coastal zone of La Pérouse Bay (Fig. 3)



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239 Biotically induced soil-vegetation change (Abraham et al. 2005b). Before the steep decline in numbers in the late 1990s, geese foraged over a wide area during their residency at this location. Initially, mostly areas of intertidal saltmarsh vegetation were adversely affected (shown in red in Fig. 3). From the mid 1980s to the early 1990s, the primary loss of vegetation occurred in graminoid communities in the supratidal marshes and inland relict saltmarshes (shown in dark blue in Fig. 3). During both these periods, some damage occurred to freshwater sedge communities as a result of shoot-pulling, especially in early spring in the vicinity of thermokarst lakes and ponds (Kotanen & Jefferies 1997). This has continued, but recent damage (indicated in yellow) has also included riverine plant communities and beach ridge communities, often dominated by lyme grass, Leymus mollis var. arenarius.

The nesting colony near Cape Henrietta Maria at the confluence of Hudson Bay and James Bay and the staging site at Lake River on the James Bay coast (Fig. 1) make up the second group. The average size of the colony of nesting snow geese at the Cape between 1996 and 2001 was 134 000 pairs of birds (K.F. Abraham & R.K. Ross, unpublished survey data), but it was over 200 000 pairs at its peak. As it grew in numbers from under 40 000 pairs in 1973, the geographical extent of the nesting colony extended eastwards and westwards to include the whole coast from Little Cape to Cape Henrietta Maria (Fig. 1, Table 1) (Abraham et al. 1998). Between 1974 and 1987, in the absence of nesting and apparently few staging birds, little damage to vegetation was evident at Little Cape, whereas a substantial loss of vegetation occurred from 1987 to 2000 as the Mid-Continent Population and the local nesting colony grew rapidly and both breeding and staging birds grubbed in the marshes. Vegetation surveys in this area in 1993-95 indicated that saltmarsh plant communities dominated by Puccinellia phryganodes and Carex subspathacea were only lightly grazed during the post-hatch period (Abraham & Jefferies 1997), but by 2000-01 extensive grubbing had exposed large areas of sediment and surveys showed heavy grazing on remaining swards.

Lake River is primarily a staging area where there is incidental nesting in some years and it is representative of the coastal marshes from Lake River to Ekwan Point, which have been used by tens to hundreds of thousands of snow geese for spring staging for at least four decades (Curtis 1973, 1976; Thomas & Prevett 1982; Prevett et al. 1983; Abraham et al. 1998; Ontario Ministry of Natural Resources, unpublished data). Where areas are snow-free and the ground has thawed, both freshwater marshes and saltmarshes are adversely affected by foraging geese. Within the immediate coastal saltmarsh zone, loss is evident since 1985. There is no clear pattern of progressive loss of vegetation in the freshwater sedge meadows and riverine marshes, but there, too, staging birds pull up shoots of freshwater sedges where the ground is not frozen and is free of snow and ice. During late springs when ice and snow cover persist, these foraging activities of the geese are spatially restricted and

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 234–242 some local recovery of freshwater vegetation in areas used in previous years may occur as a consequence (e.g. 1981–84, Table 1).

The third group of marshes includes those where the rate of vegetation loss slowed in the late 1980s and early 1990s, but subsequently increased. Two locations, Winisk River and the Pen Islands on the northern Ontario coastline (Fig. 1, Table 1), show this pattern of loss. Before 1986, the town of Winisk was located near the river mouth and Cree hunters from the community had ready access to the coastal strip (Ontario Ministry of Natural Resources 1985; Berkes et al. 1995). Their presence influenced the distribution of spring staging geese, probably forcing them to freshwater marshes away from the immediate coastline: between 1975 and 1985 the saltmarshes near Winisk were relatively unaffected. However, the loss of the town due to a flood at spring melt in 1986, and the establishment of a new community at Peawanuck 40 km upstream from the coast (Stewart & Lockhart 2005), probably led to diminished hunting pressure near the river mouth. The coastal saltmarshes north-west of the estuary were subsequently adversely affected by increased goose foraging in spring from 1985 to 1997. Since then, further loss of vegetation has occurred in both intertidal marshes and the immediate coastal freshwater areas. At the Pen Islands on the Ontario-Manitoba border (Fig. 1), considerable loss of vegetation took place between 1974 and 1984, approximately at the time of establishment of the nesting colony there. Between 1984 and 1997, there was no net loss of vegetation, strongly suggesting that marshes were little used as a major staging area and that some recovery of vegetation may have occurred. Recent loss (between 1997 and 2000) is extensive, particularly in the brackish marshes between the mainland and the East Pen Island, and to a lesser extent on the island itself, and on the mainland coast close to the Manitoba border, just west of West Pen Island. The area is now used by large numbers of staging and breeding snow geese (Table 1).

The last group of sites includes the Seal and Knife River estuaries on the west coast of Hudson Bay and the intertidal marshes on the northern shore of Akimiski Island in James Bay (Figs 1 & 4, Table 1). These locations are, or were, used both as staging and as breeding areas and numbers of breeding geese have increased considerably since 1993. The increase in the population of lesser snow geese on Akimiski Island is well documented (Abraham et al. 1999). The large number of birds feeding (grubbing and grazing) at the two sites has severely reduced the availability of vegetation. Undamaged graminoid swards occupy an increasingly small area as a percentage of the total area and this has led to a recent decline in the rate of vegetation loss compared with the period from the mid 1980s to the mid 1990s, as the birds find sources of vegetation elsewhere in response to the alternative stable state (O et al. 2005).

The total area where some loss of vegetation has taken place at the nine sites is approximately 35 000 ha



Fig. 4 Akimiski Island, Nunavut, indicating areas of vegetation loss for three successive periods between 1976 and 2000. Most vegetation loss occurred in the intertidal saltmarsh between 1976 and 1985. From 1985 to 1993, the majority of the vegetation loss was in the inland freshwater sedge meadows, while from 1993 to 2000 the loss was in brackish and supratidal marsh communities.

of intertidal and supratidal marsh (Table 1). Damage to vegetation is cumulative and there is little evidence of recovery of vegetation in intertidal habitats at any of the nine locations, largely because hypersaline conditions develop where exposed marine sediments occur, precluding rapid re-colonization of vegetation. Seasonal shifts in soil salinity also occur, with minimum and maximum values, respectively, recorded at spring melt and in mid–late July in most years.

Discussion

The dominant intertidal marsh species on this coast are Puccinellia phryganodes, an asexual grass, and the sedge Carex subspathacea, which rarely sets seed in grazed swards. Hence, re-establishment after grubbing is strongly dependent on clonal reproduction, which is minimal under hypersaline conditions (Srivastava & Jefferies 1995; Handa & Jefferies 2000). Erosion of consolidated hypersaline sediments and the build up of unconsolidated, less saline sediments are necessary before re-establishment of these species can occur (Handa et al. 2002). The time required for these geomorphological changes to take place is the order of decades on these coasts, which are characterized by isostatic uplift, the presence of permafrost and the action of sea ice on the lower shore. Hence, the recovery of the vegetation from the effects of goose foraging is slow. Even when vegetative units colonize unconsolidated sediment, geese quickly remove plants.

© 2006 The Authors Journal compilation © 2006 British Ecological Society, *Journal of Ecology*, **94**, 234–242 In contrast to processes at the saltmarshes, the recurrent and episodic loss of vegetation in the freshwater sedge meadows can potentially be followed by recovery within 5–10 years. Subsequently, there may be a further loss of vegetation as a result of a new episode of shoot-pulling by the geese. In these non-saline peaty habitats, there is little or no development of hypersalinity following loss of vegetation, so a potentially much faster rate of recolonization is possible. However, if erosion of the thin veneer of organic matter occurs, then underlying saline clays and glacial gravels are exposed and different plant communities establish on these soils compared with those characteristic of peaty soils (Handa *et al.* 2002).

Although a number of species of geese breed in coastal habitats in the eastern Canadian Arctic, only populations of the lesser snow geese and Ross's geese (*Chen rossii*) (Ryder & Alisauskas 1995) appear to have initiated such large-scale catastrophic landscape changes. This is because these species are colonial and gregarious, so high densities of birds may be anticipated. The overall population size (7 million) is high relative to population numbers of other Arctic-breeding geese, such as Canada geese (*Branta canadensis*) (1 million) and brant geese (*B. bernicla*) (300 000).

The presence of nesting snow geese at some intertidal and estuarine sites appears to have a finite life. Within colonies at such sites, there is a shift in the nesting distribution over time (MacInnes & Kerbes 1987; Cooke et al. 1995) that is linked to the loss of vegetation at a local scale. Central areas are abandoned, as older philopatric breeders die and as new breeders fail to nest and rear broods in these locations. Over a longer period, loss of vegetation and a steep decline in primary productivity occur throughout the entire system and the nesting and brood rearing birds increase in numbers elsewhere. This process took place at the estuaries of the two arms of the McConnell River at least 2-3 decades ago and it is recently evident at La Pérouse Bay. At least in southern Hudson Bay, snow goose colonies appear to establish, grow and then decline at a given geographical location over a period of 60-100 years, reflecting a long-term alteration in the patterns of resource availability and ecosystem structure at the meso-scale (order of 100s of km²).

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Recently, Rietkerk et al. (2004) have used the term 'local bistability' to describe the outcome of sudden catastrophic change on the structure and functioning of an ecosystem leading to an alternative stable state that is a consequence of positive feedbacks between consumers and limiting resources. Where such changes occur at larger spatial scales ('global bistability'), selforganized patchiness of the landscape may be evident, as a result of fine-scale interactions that occur within systems when a sudden transition to an alternative state occurs (Rietkerk et al. 2004). Within the coastal marshes of southern Hudson Bay, the underlying biotic and abiotic processes leading to local bistability have been well documented (cf. Jefferies 1988; Jefferies et al. 2003). Interactions between producers and high numbers of consumers trigger the onset of the alternative states in the grazed intertidal marshes. In the ungrazed state, the nutritional quality of the vegetation is poor (high C: N ratio, Cargill & Jefferies 1984; Wilson & Jefferies 1996), and the mat of plant litter in early spring insulates the ground and delays the onset of the thaw, so that the geese are unable to grub. Soil condition in the intertidal marshes is the ecological indicator of each of the alternative stable states on both spatial and temporal scales. Self-organized patchiness of soil hypersalinity in summer on the intertidal flats following loss of vegetation (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995, 1996; McLaren & Jefferies 2004) is an internal property of the system and develops in response to evaporative demand (Srivastava & Jefferies 1995). Seasonal shifts in soil salinity occur with minimum and maximum values, respectively, recorded at spring melt and in mid-late July in most years.

The combination of experimental field studies, population surveys of the biotic agent triggering these changes and the use of remote sensing imagery provides a powerful approach to examine the mechanisms as well as the outcomes of these biotic and abiotic interactions in these coastal Arctic marshes. The nine study sites represent only a small fraction of the coastline that has been affected (Abraham & Jefferies 1997) but they are typical of the broad spatial continuity of change that is evident along 2000 km of coastline.

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