

## Agricultural Food Subsidies, Migratory Connectivity and Large-Scale Disturbance in Arctic Coastal Systems: A Case Study<sup>1</sup>

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**SYNOPSIS.** An allochthonous input can modify trophic relationships, by providing an external resource that is normally limiting within a system. The subsidy may not only elicit a growth response of the primary producers via a bottom-up effect, but it also may lead to runaway herbivore growth in the absence of increased predation. If the consumer is migratory and predation is similarly dampened in the alternative system, the increased numbers may produce a top-down cascade of direct and indirect effects on an ecosystem that may be a great distance from the source of the subsidy. In an extreme case, it can lead to a catastrophic shift in ecosystem functioning as a result of biotic exploitation that produces an alternative stable state. The loss of resilience is particularly sensitive to herbivore density which can result in two different outcomes to the vegetation on which the consumer feeds. Over-compensatory growth of above-ground biomass gives way to sward destruction and near irreversible changes in soil properties as density of a herbivore increases. A striking temporal asymmetry exists between a reduction in the consumer population and recovery of damaged vegetation and degraded soils.

### INTRODUCTION

Arctic and sub-Arctic regions are open to the exchange of energy and materials from other biomes. These exchanges are not unidirectional, but represent movement between systems. Such exchanges are usually thought of in terms of atmospheric or oceanic events, that can lead to habitat fragmentation in northern systems, as a result of fire and paludification (Payette *et al.*, 2001; Crawford *et al.*, 2002). However, fragmentation can also be driven by biological events, whose ultimate causes also may have their origins in distant biomes. Events in temperate or tropical biomes can indirectly impact Arctic and sub-Arctic environments via their effect on migratory species. A very high percentage of the breeding birds of northern landscapes (>85%), for example, spend the winter in southern latitudes (Schmiegelow and Mönkkönen, 2002). This regular seasonal movement between breeding and non-breeding sites has been termed migratory connectivity (Webster *et al.*, 2002). Events that occur thousands of kilometres from Arctic breeding sites may change winter survival of individuals, which not only affects the breeding success of a population but also the stability of Arctic coastal ecosystems themselves. When foraging pressure is intense and sustained on the breeding grounds, this connectivity can result in a cumulative loss of vegetation, the development of a mosaic and increased fragmentation of the remaining patches of vegetation (*sensu* Andrén, 1994; Fahrig, 1997). Overtime, the newly created patches of exposed sediment coalesce to produce open flats nearly devoid of vegetation.

This paper provides an overview of the ecological consequences of a dramatic increase in the sizes of breeding colonies of lesser snow geese (*Chen caerulescens caerulescens*) especially the one at La Pérouse Bay, Manitoba (58°04'N, 94°03'W) on the Hudson Bay coast which is located on the Arctic/sub-Arctic boundary. The colony has been studied since 1968 (Cooke *et al.*, 1995) and is part of the Mid-Continent Population which has increased in numbers geometrically in recent decades, most probably a consequence of birds foraging in agricultural fields on the wintering grounds and along flyways (*cf.*, Abraham *et al.*, 1996; Ankney, 1996; Abraham and Jefferies, 1997; and references therein). The increases are not confined to the above population, indeed most populations of Arctic goose species that feed on agricultural land in North America and Europe in winter have shown a substantial rise in numbers (Alisauskas *et al.*, 1988; Van Eerden, 1998; Madsen *et al.*, 1999; Jefferies *et al.*, 2003). Initially, the impact of modern agriculture on the Mid-Continent and other populations of lesser snow geese is discussed, followed by an examination of the ecological consequences of increasing numbers of birds on breeding and staging grounds in northern coastal environments, particularly those associated with the Hudson Bay lowlands of Ontario, Manitoba and Nunavut.

### THE IMPACT OF AGRICULTURE ON THE MID-CONTINENT POPULATION OF LESSER SNOW GESE

Before the 1920s lesser snow geese from this population wintered in the Gulf coastal marshes of the United States (Bent, 1925; McIlhenny, 1932; Lynch, 1975) which at that time stretched from Port Lavaca, Texas to the Pearl River, Louisiana, a distance of 800 km (Bateman *et al.*, 1988). In the 1930s and 1940s snow geese began feeding in irrigated rice prairies ad-

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adjacent to the coastal marshes of Texas, coincident with rapid changes in agriculture and the development of the Gulf coast (Robertson and Slack, 1995). The geographical expansion of agricultural lands used by the geese accelerated in the 1950s and 1960s (Stutzenbaker and Buller, 1974; Hobaugh *et al.*, 1989). In Louisiana similar changes occurred and snow geese expanded their winter range to include rice fields and other crop lands, which led to a decline in their use of traditional coastal areas (Lynch, 1975). The geographical expansion into agricultural lands has continued unabated as the population has grown, and now includes Arkansas (Widner and Yaich, 1990), the Missouri River valley (Missouri, Iowa, Kansas, Nebraska) that is both a spring and fall staging area and a winter feeding area (Burgess, 1980) and the Rainwater Basin in west-central Nebraska. The valley lies at the boundaries of the Mississippi and Central flyways and provides resources for populations of both flyways. Increases in numbers and in the distribution of lesser snow geese along these flyways appear to be closely linked to increases in crop production and to changes in agricultural practices (Jefferies *et al.*, 2003). For example, correlation coefficients between snow goose counts and production of rice and wheat are 0.91 and 0.90 respectively. The yield of rice, wheat, maize and soybean in states through which the flyways pass and amounts of nitrogen fertilizers applied to these crops in these states rose substantially from 1955 to 1990. This was especially evident from 1965 to 1975 when high yielding crops were introduced. In 1990, almost 40% of the total amount of nitrogenous fertilizer used in the United States was applied to agricultural land in the Mid-Western states and Texas, a substantial percentage increase compared to the period from 1940 to 1954 (Lanyon, 1995).

Overall, approximately 70% of the Mid-Continent population of lesser snow geese are resident in the Gulf States in mid-winter but they are not necessarily feeding on salt-marsh vegetation. The birds forage on spilt and wasted grain, sprouted seed, green stubble, and young seedlings and rye grass; preferences depend on seasonal crop phenologies (Stutzenbaker and Buller, 1974; Hobaugh *et al.*, 1989). The rise in the lesser snow goose population appears to be inextricably linked to overall changes in crop production, fertilizer and land use, although within different areas food availability and diet selection vary greatly (Alisauskas *et al.*, 1988).

Increases in numbers have occurred in other populations of "white" geese, including populations of lesser snow geese, greater snow geese (*A.c. atlantica*) and Ross's geese (*A. rossii*) (Abraham *et al.*, 1996; Reed *et al.*, 1998). In addition, populations of Canada geese (*Branta canadensis*) have increased (Ankney, 1996). In all cases the increases appear linked to the use of agricultural crops or grasslands. Significantly, geese that winter in maritime habitats, such as emperor geese (*Chen canagica*) or brant geese (*Branta bernicla*), have not shown a similar increase in numbers

TABLE 1. Average annual kills from hunting of lesser snow geese for the designated years between 1962 and 1999 along the Mississippi and Central Flyways of the United States, and Canada.

Years	Mississippi Flyway	Central Flyway	Canada
1962–1969	102,494	134,042	49,958*
1970–1979	154,968	258,649	106,501
1980–1989	104,854	244,128	164,787
1990–1999	185,051	296,502	182,646

Source of data: Central Flyway Harvest and Population Survey Data Book compiled by K.L. Kruse and D.E. Sharp (2002).

\* This average is based on the 3 years from 1967–1969.

(Abraham *et al.*, 1996; Abraham and Jefferies, 1997). Comparable changes in agricultural practice in the Netherlands also have led to long-term shifts in the abundance of Anatidae (Van Eerden, 1998). From 1939 to 1992 there was a six-fold increase in the annual amount of nitrogenous fertilizer applied to grassland in which the different species of Anatidae fed.

The Mid-Continent population of lesser snow geese increased at least three- to four-fold from the early 1970s to the mid-1990s (Abraham and Jefferies, 1997). From 1970 until 1994 the annual number of birds harvested fluctuated between 300,000 and 700,000 with no clear trend (Cooke *et al.*, 1999). Years of low harvest were often linked to weather-related low recruitment on the breeding grounds, such as in 1972, 1978, 1982, 1983 and 1992 (Boyd and Madsen, 1997; Ganter and Boyd, 2000). Over the same period (1970 to 1997) numbers of hunters declined in the United States (Abraham *et al.*, 1996). However, the data in Table 1 indicate that the rise in the Mid-Continent population has not been caused by a significant reduction in harvesting, as there is no discernable trend in the total harvest for the Mississippi and Central flyways and for Canada since 1970 when the population size increased dramatically. Although the average annual number of kills from 1970 to 1999 was substantially higher than that from 1960 to 1969, it did not continue to rise in proportion with the population growth. With the increase in bird numbers, the harvest rate fell and it was insufficient to contain the population growth. Because of a "fixed number" of kills and a decline in the overall harvest rate, bird numbers continued to increase when the hunting pressure did not respond to the change. As a result the replacement rate ( $\lambda$ ) rose above one. Since 1999, however, the harvest pattern has changed as a result of the introduction of a spring hunt which is discussed later.

#### THEORETICAL CONSTRUCTS

A conservative estimate of the geometric increase in the Mid-Continent population in recent decades is about 5% to 7% per annum (Cooke *et al.*, 1995; Abraham *et al.*, 1996). and the current population size in late fall is in excess of 5 million, possibly as high as 7 million. The breeding colony at La Pérouse Bay has grown from about 1,300 pairs in 1967 to an estimated 44,500 pairs in 1997 (Cooke *et al.*, 1995; Abraham,

Rockwell and Ross, unpublished aerial survey) and the geographical extent of the colony has increased substantially, similar to that of other colonies in the coastal zone of the Hudson Bay lowlands. Such a large increase in numbers in the different colonies may be expected to have a substantial effect on these coastal ecosystems. The recorded outcome (see later) can be placed within theoretical constructs. de Roos *et al.* (1998) and Richards and de Roos (2001) have developed patch models which examine interactions of consumers (*e.g.*, geese) and their prey (*e.g.*, plants) that are characterized by scale differences in their use of space. Prey are assumed to occupy patches, with low migration rates between patches, whereas consumers are homogeneously distributed over these patches, and thus they exert a global influence as a result of broad-scale foraging behaviour at the local level. It is possible to incorporate in the models a high consumer density that can be caused by mobile, widely dispersed consumers flocking to local areas where the density of prey patches is high. The outcomes of their models indicate that although multiple equilibria are possible, equilibria with a large number of barren prey patches are more stable and give rise to an alternative stable state (*cf.*, Holling, 1973; Noy-Meir, 1975; May, 1977; Westoby *et al.*, 1989). Abrupt and rapid changes between stable states are often caused by positive feedbacks (Maruyama, 1963; DeAngelis *et al.*, 1986; Oksanen, 1990). As indicated in the next section, these theoretical constructs describe changes that have occurred in different habitats at La Pérouse Bay leading to loss of vegetation as the goose population has increased in size.

Two major constraints on the growth of herbivore populations are resource limitation and predation. When predators are absent, herbivore populations can increase dramatically resulting in a true trophic cascade characterized by a sustained reduction in the biomass of the primary producers and changes in plant and animal community assemblages (Paine, 1969; Power, 1992; Strong, 1992; Polis and Strong, 1996). The same effect also may occur if consumers increase in number as a result of an external food subsidy without a concomitant increase in predation (Polis, 1999). We have used the term apparent trophic cascade to describe the cascading effects of a burgeoning population of snow geese on coastal vegetation and soils that have led to ecosystem changes (Jefferies and Rockwell, 2002). The consumer (herbivore) has increased in numbers in response to a trophic subsidy triggered by the bottom-up effect of the application of fertilizers to high-yielding crops (Fig. 1).

As a first approximation, trophic relations at La Pérouse Bay can be represented as a trophic ladder dominated by the breeding colony of lesser snow geese and the preferred coastal forage plants on which they feed. The primary predators of eggs and goslings at the above study site are herring gulls (*Larus argentatus*), parasitic jaegers (*Stercorarius parasiticus*), ravens (*Corvus corax*) and Arctic foxes (*Alopex lagopus*). In

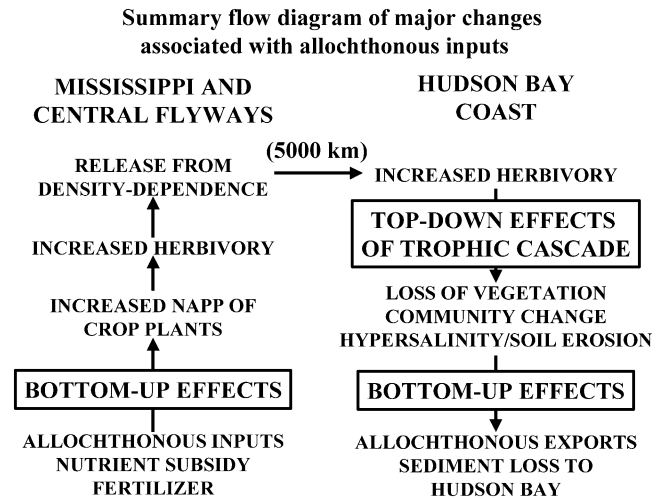


FIG. 1. Summary of allochthonous inputs and bottom-up and top-down effects in different ecosystems linked to the seasonal movements of the Mid-Continent Population of Lesser Snow Geese.

recent years polar bears (*Ursus maritimus*) and Arctic fox have become an important predator of both adults and goslings during the post-hatch molt period, particularly in the inter- and supratidal zones of La Pérouse Bay, but the effects appear to be local as far as we can assess and there have been no systematic changes in numbers of predators in response to increased numbers of geese (Cooke *et al.*, 1995). Although we have made no quantitative studies of the non-migratory predators, their population sizes are probably regulated by the availability of local winter food supplies so that population growth is unable to increase rapidly in response to a transient summer food spike.

#### A TALE OF TWO FEEDBACKS

The effect of the interaction between the herbivore and the preferred forage species on the plant community and the soil system is inherently unstable and is sensitive to goose numbers. The two outcomes, which are described by positive feedbacks (Jefferies *et al.*, 1985; Srivastava and Jefferies, 1996), lead either to increased above-ground primary production of intertidal graminoid forage species (Cargill and Jefferies, 1984b; Hik and Jefferies, 1990), or else to destruction of salt-marsh grazing lawns (*sensu* McNaughton, 1984) and exposure of intertidal sediment (Jefferies, 1988). The two feedbacks are sensitive to numbers of geese, the intensity of grazing and the extent and quality of the graminoid resource base. The outcome of the second positive feedback is detrimental to gosling growth, as it results in the loss of graminoid swards and the unavailability of high quality forage. The negative feedback that acts to stop this positive feedback is the development of hypersaline sediment which is inimical to plant growth. The preferred prostrate forage species in the inter- and supratidal salt marshes on which the geese feed are an asexual triploid stoloniferous grass, *Puccinellia phryganodes*, and a rhizoma-

tous sedge, *Carex subspathacea*, which flowers and fruits very infrequently, especially when grazed (Jefferies, 1988). Both species are widespread in Arctic coastal systems. In the adjacent freshwater sedge meadows, the dominant forage species is *Carex aquatilis* which can grow up to 50 cm or more and increasingly has become an important forage plant of the geese with the loss of salt-marsh vegetation (Kotanen and Jefferies, 1997). There are three types of goose foraging that are recorded in these coastal marshes: grubbing of roots and rhizomes beneath salt-marsh swards which takes place in spring immediately after the upper layer of soil has thawed, but before the above-ground growth of the graminoid species has commenced; grazing of these swards once above-ground growth is initiated, that is the preferred mode of foraging during the period of gosling growth and gain in adult body weight (late June to mid-August), and lastly shoot-pulling of *Carex aquatilis* and *Leymus mollis* (Ganter and Cooke, 1996) that occurs in spring (and in early autumn in some years) after the ground has thawed (Abraham and Jefferies, 1997). Shoots of these plants are pulled up, the basal portion that has high amounts of nitrogen and soluble sugars is eaten and the remainder is discarded. If this continues during successive springs the parent plant weakens and dies. Likewise, where grubbing occurs, the sward rarely recovers within 5 years (see later).

The breeding colony of lesser snow geese removes up to 90% of the net above-ground primary production when they graze intertidal swards in summer during the post-hatch period (Cargill and Jefferies, 1984b). Goslings increase in weight from about 80 g at hatch to about 1,500 g at fledging (Cooke *et al.*, 1995). In the absence of grazing, growth of the salt-marsh swards is nitrogen-limited (Cargill and Jefferies, 1984a). Moderate goose grazing increases nitrogen availability and net above-ground primary production (NAPP) via the first of the positive feedback mechanisms (Fig. 2). Within a season, nitrogen is increased by a rapid recycling of this element from goose faeces. Passage of food through the gut is fast (45–60 min) and geese defaecate, on average, every four to five minutes. When experimental additions of fresh goose droppings rich in soluble nitrogen are made to swards, there is an increase in NAPP compared to that of control plots (Bazely and Jefferies, 1985; Ruess *et al.*, 1989). Thus, goose grazing initiates a positive feedback in which increased growth of salt-marsh swards is driven by improved nitrogen availability derived from faecal inputs.

Intense grazing also maintains open swards with bare microsites which are colonized by nitrogen-fixing cyanobacteria, particularly early in the season (Bazely and Jefferies, 1989). Results from nutrient budgets indicate that these inputs of nitrogen from fixation balance nitrogen incorporated in the body mass of the geese when swards are intact and pseudo-steady state conditions prevail (Wilson and Jefferies, 1996; Walker *et al.*, 2003).

A series of late spring thaws during the last 20 years in the Hudson Bay region, coincident with the increasing goose population, has resulted in large numbers of staging geese at La Pérouse Bay during the pre- and early nesting period (Jefferies *et al.*, 1995; Skinner *et al.*, 1998), in addition to the presence of the breeding population of birds. At this time the birds grub for roots and rhizomes of their preferred salt-marsh graminoids which initiates the second positive feedback process (Fig. 2) that has led to the destruction of the intertidal salt-marsh swards and the death of willow bushes in the supratidal marsh, the latter largely from the effects of hypersalinity (Jefferies, 1988; Kerbes *et al.*, 1990; Iacobelli and Jefferies, 1991; Srivastava and Jefferies, 1995, 1996). Grubbing acts as a trigger that results in near-irreversible changes in sediment properties in the intertidal marsh, including the development of hypersalinity in summer, compaction of sediment, changes in infiltration rate, loss of soil nitrogen and organic matter and the depletion of the soil seed bank (Iacobelli and Jefferies, 1991; Srivastava and Jefferies, 1996; Chang *et al.*, 2001; McLaren, 2002). On occasions, the salinity of the soil solution can reach 120 g of solutes per liter in mid-summer (Iacobelli and Jefferies, 1991). The loss of a seed bank is associated with a decline in seed viability, an absence of a seed rain and erosion of the thin veneer of organic matter (*ca.* 2.5 cm) immediately below the surface of the sediment (Chang *et al.*, 2001). Hence, the second feedback is composed of coupled biotic and abiotic components. Once the vegetation has been lost as a result of grubbing, increased evaporation from the exposed sediment occurs, which draws inorganic salts to the surface from the underlying marine clays deposited when this region was the Tyrell Sea (*i.e.*, the effect of isostatic uplift, *cf.*, Hansell *et al.*, 1983). These salts give rise to hypersalinity that develops in summer. In spring when the salinity is lower, extensive biocrusts composed of a community of cyanobacteria, diatoms and mites develop on exposed soil surfaces in the intertidal zone where the thin organic layer still remains. The community is transitory, it rapidly dries out in summer as aridity and hypersalinity develop and either it remains as a salt-encrusted hardened layer, or it may be blown away with the remaining soil organic matter exposing underlying mineral sediments. The hostile soil conditions depress the clonal growth of the two salt-marsh graminoids and the ability of individuals to establish from vegetative fragments (remember seed set does not occur in one species and is a rare event in the other species) (Chou *et al.*, 1992; Srivastava and Jefferies, 1995, 1996; McLaren, 2002). Experimental studies indicate that if the diameter of circular areas of exposed soil exceeds 20 cm, re-colonization of the sediment by inward clonal growth of *Puccinellia* from an adjacent intact sward is very slow, on account of deleterious changes in soil properties (McLaren, 2002). In addition, developing shoots of these graminoids cannot penetrate the hardened thick algal crust below which anaerobic conditions often develop. As a

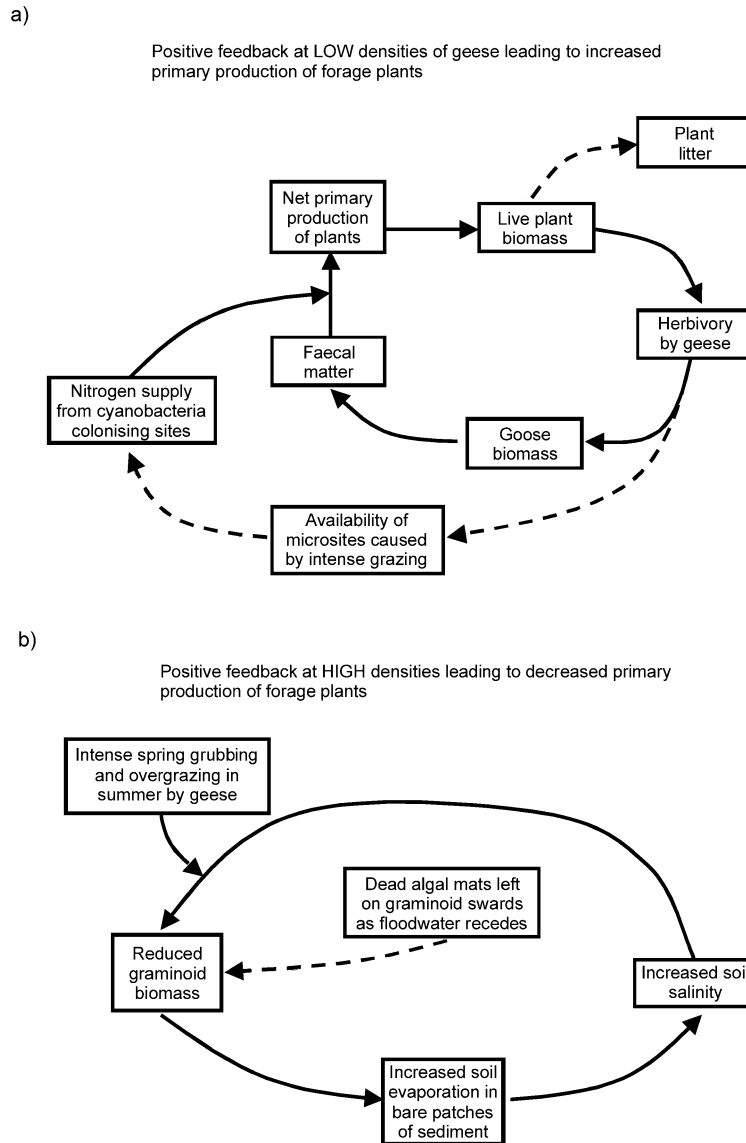


FIG. 2. Positive feedbacks in the intertidal salt marshes at La Pérouse Bay that occur under a) low densities and b) high densities of foraging lesser snow geese.

result, it is very difficult to re-establish tillers of *Puccinellia phryganodes* in these consolidated, degraded soils without first amending the soil with mulch and fertilizer (Handa and Jefferies, 2000). Over time, remaining patches of intact vegetation become smaller and smaller as the effects of spring grubbing and the subsequent abiotic processes reduce their area. In the intertidal zone and to a lesser extent the supratidal marsh, the highly fragmented vegetative mosaic is ultimately lost to give an alternative stable state of exposed hypersaline sediment in which re-establishment of vegetation is long-term (>30 years) (Hik *et al.*, 1992; Handa *et al.*, 2002; Jefferies and Rockwell, 2002). The outcome of these processes is that an ecological sere (the intertidal zone) has been lost, similar to the process of desertification in the Sahel (*cf.*, Graetz, 1991). An abrupt transition is created from ex-

posed tidal flats to freshwater sedge meadows or willow and heathland communities, where formerly salt-marsh communities existed seaward of the transition. Loss of vegetation results in an increase in bulk density, and salinity, and decreases in infiltration rate, in organic matter and in soil nitrogen of exposed sediments (McLaren, 2002). The sediments have remained in this state, both on the west coast of Hudson Bay near the estuary of the McConnell River and at La Pérouse Bay for 30 years or more. Transient algal mats or patches of the annual, *Salicornia borealis*, may develop on the surface, but the necromass is wind-blown, together with the attached dried sediment that contains some organic matter. Eroded sediment borne away by wind and water is re-deposited as unconsolidated sediment along the sides of drainage channels and lagoons. Re-establishment of vegetation in unamended

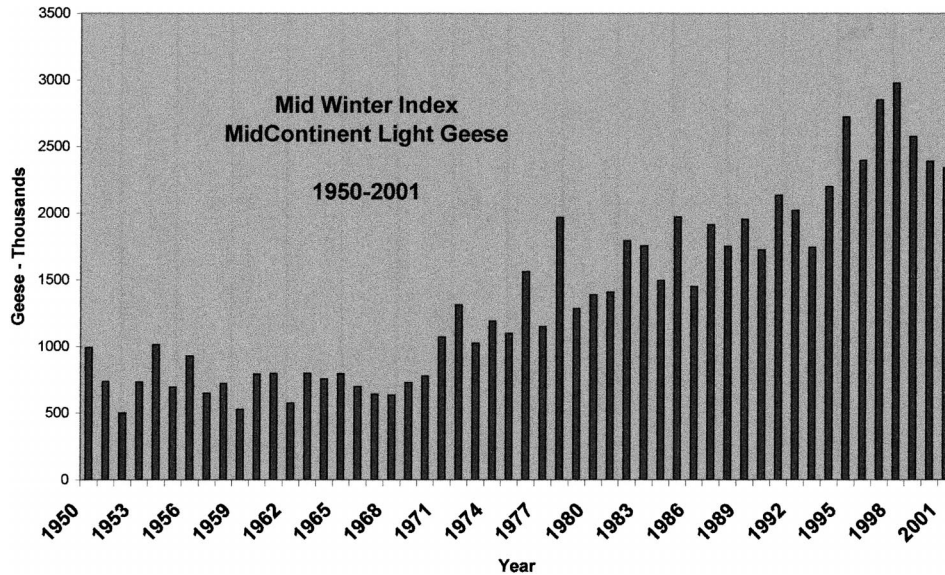


Fig. 3. Population index of the mid-continent population of light geese (primarily lesser snow geese) based on winter counts from 1950 to 2001. Source: U.S. Fish and Wildlife Annual Reports. The spring hunt in the United States and southern Canada started in 1999.

soils requires the availability of this unconsolidated soft sediment in which plant fragments (generated by goose foraging) can root and colonize sediment (Handa *et al.*, 2002). At present, however, colonization is incipient but transitory, as geese remove the developing vegetation and this situation is likely to continue in the foreseeable future.

Loss of the small patches of vegetation (<10 m<sup>2</sup>) creates a homogeneous landscape at a larger scale, as a result of the coalescence of areas of exposed sediment in the intertidal zone. This can be detected with the use of LANDSAT imagery, not just at La Pérouse Bay, but elsewhere around the shores of the Hudson Bay lowlands where the effects of grubbing are clearly evident associated with the presence of nesting geese (Jano *et al.*, 1998; Jano, unpublished).

#### AN APPARENT TROPHIC CASCADE

It is important to stress that the effect of the consumer on these coastal ecosystems is not confined solely to changes in vegetation and soils of the inter- and supratidal marshes and the adjacent freshwater sedge meadows. All types of habitat are adversely affected leading to a loss of vegetation and changes in species abundances throughout the coastal lowlands (Abraham, unpublished data). The long-term decline in forage availability has impacted directly the different fitness components of the goose population (Cooke *et al.*, 1995; Cooch *et al.*, 2001). From 1973 to 1992 there was a long-term decline (adjusted for laying date) in clutch size from approximately 4.25 to 3.4. Food availability on migration and locally is the likely prime proximate mechanism influencing clutch size (Cooke *et al.*, 1995). Mean annual body mass, tarsus and culmen length of pre-fledging goslings declined significantly by approximately 16%, 4% and 2% respectively in cohorts hatching between 1976 and 1988.

The decline led to a decrease in size of locally hatched adults (Cooch *et al.*, 1991). Goslings reared by individual adult females also showed a decline in size over time, suggesting that the decline reflected a non-genetic change in gosling growth rates during the fledging period (Cooch *et al.*, 1991). The decrease was not dependent on mean hatch date, egg or hatch mass, or post-hatch weather. Total brood failure, which is the probability that a female loses her entire brood of goslings from hatching to fledging, has increased from 10% during the early 1970s to 20 to 40% during the late 1980s (Cooke *et al.*, 1995) and in all likelihood it has probably increased further in the 1990s. The mean annual survival of young banded just before fledging was about 0.42 over the period 1970 to 1988, but this value disguises a long term decline from 0.57 to 0.35 (Francis *et al.*, 1992) that probably has continued to the present. Most surviving females return to their natal colony and it is assumed that the cohort-specific return rate to the colony is proportional to the immature survival rate (Cooke *et al.*, 1995). Thus, there is a cost to philopatry with respect to clutch size and survival and body mass of goslings. In dramatic contrast with the decreased survival of immature birds, adult survival rate has increased commensurate with the increase in the size of the population and a decline in the rate of deaths attributable to hunters (Francis, 1999; Cooke *et al.*, 1999; Cooch *et al.*, 2001). While the reduction in reproductive success that has occurred during the growth of the colony in the traditional nesting and brood-rearing area of La Pérouse Bay and the decline in density conforms to a density-dependent response, the recovery phase represented by an increase in density fails to conform. In normal density-dependent models when a reduction in density occurs, reproductive success increases immediately. However, in this coastal marsh there is a delayed recovery of veg-

etation and the geese are forced to move elsewhere to maintain reproductive success. Because of changes in soil conditions, the recovery may be incomplete, or protracted, and this creates instability in the system. The data relate to birds present within the tidal marshes of La Pérouse Bay and their immediate vicinity. During the last decade, the breeding population has become widely dispersed, both during the nesting phase and the post-hatch period, and few data are available on the reproductive success of the birds in these alternative habitats. In addition, since the 1980s, those birds that remained to nest at La Pérouse Bay mostly used the relatively intact salt and freshwater marshes on the east coast of the Cape Churchill Peninsula during brood rearing. The body mass of goslings from these marshes, as distinct from those remaining at La Pérouse Bay, was high and similar to the mean weight of goslings at the latter site in the 1970s (Cooch *et al.*, 1993). Recently, however, on-going destructive foraging has depleted these alternative resource bases, so that salt-marsh vegetation, in particular, has been lost from most sites on the Peninsula. Geese no longer nest in any numbers at La Pérouse Bay, and in 2000 and 2001 Ross's geese and Canada geese often out-numbered snow geese and their families on the degraded intertidal flats during the post-hatch period (Pezzanite, 2003). As this has occurred, the snow goose population has expanded geographically, especially during the post-hatch period, and small family groups are widely scattered throughout the northern section of the Peninsula where they forage primarily on freshwater sedges. This doughnut effect, marked by a resource loss and an absence of snow geese in the core area, characterizes the changes that have taken place in the 1990s.

Loss of vegetation and the deterioration in the condition of coastal habitats have affected other taxa besides flowering plants and geese. As mentioned earlier, hypersalinity destroys willow bushes in grubbed areas in the supratidal marsh and only the woody skeletons remain. Savannah sparrows (*Passerculus sandwichensis*) nest at the base of live bushes where there is ample grass for nest construction and concealment. The 63% decline in vegetative cover over the last 25 years, coincides with a decline of 77% in the number of nesting pairs of this local population that is linked to processes associated with the destructive foraging by geese (Rockwell *et al.*, 2003). Other passerines, such as blackpoll warblers (*Dendroica striata*), American tree sparrows (*Spizella arborea*) and lapland longspurs (*Calcarius lapponicus*), may be similarly affected.

The changes have led both to a sharp decline in the abundance of soil invertebrate species and a loss of some species in the supratidal marsh, particularly spiders and beetles that are an important food source for passerines and shore birds (Milakovic and Jefferies, 2003). The same trend is evident in midge (Chironomidae) populations that occur in shallow vernal ponds in this marsh. Brackish ponds in the undamaged

salt marsh contained five species from five genera, while only the large-bodied *Cricotopus* sp., most likely *ornatus*, was represented in the hypersaline ponds in the degraded marsh (Milakovic *et al.*, 2001). This loss of aquatic invertebrates is also likely to affect populations of shore birds. Declines in the nesting densities of semi-palmated sandpipers (*Calidris pusilla*) and other shore birds have occurred, although nesting densities of semi-palmated plovers (*Charadrius semipalmatus*) and horned larks (*Eremophila alpestris*) have increased in open, degraded areas where little vegetation remains (Rockwell, unpublished data).

Overall, the field data indicate large-scale changes in the species composition and abundances of different taxa in response to the top-down effect of the consumer on these coastal ecosystems. Although initially the effects are local, over time damaged areas coalesce to produce an alternative stable state at the meso-scale level.

#### THE SPRING HUNT

Before 1999 in North America the non-aboriginal hunting season of lesser snow geese was restricted to autumn and early winter by the Migratory Birds Convention of 1916 that was jointly signed by the Governments of Canada and the United States (Francis, 1999). Because the Mid-Continent population has increased several fold in recent decades and the birds are severely damaging vegetation at different Arctic breeding sites, including that at La Pérouse Bay, a spring hunt was introduced in 1999 in both Canada (Canadian Wildlife Service) and the United States (U.S. Fish and Wildlife Service) in an effort to reduce the size of the goose population and to allow recovery of the vegetation (*c.f.*, Fig. 3). Regulations governing the spring hunt differ depending on the authority responsible for changing the laws. Although this represents a change in hunting practices at southern locations, the harvesting of waterfowl in both autumn and spring has long been practiced by the aboriginal peoples of Canada. Traditionally, the spring harvest is important because it represents the first available fresh food after the long winter.

The stated goal of the Arctic Goose Habitat Working Group, which advises the Canadian Wildlife Service and the U.S. Fish and Wildlife Service, is to reduce the population growth rate to some sustained level with  $\lambda < 1.0$  (the replacement rate) (Rockwell *et al.*, 1997). The rationale for the introduction of a spring hunt in order to reduce  $\lambda$  to less than one, was based on the following arguments. Individuals of this species are long-lived with a mean life expectancy of about 7 years, and the birds do not breed until they are two or more years old. Rockwell *et al.* (1997) showed in their model of the projected impacts of reductions in survival and fertility on population growth rates, that adult survival had the greatest impact on the growth rate. Therefore, shooting a young bird has substantially less impact on population growth than shooting a breeding adult female goose (Rockwell *et al.*,

1997). Although there has been considerable debate on the actual harvest rate necessary to achieve a reduction because of uncertainty of current population values (*cf.*, Cooke *et al.*, 1999; Rockwell and Ankney, 1999), if the population is reduced by a fixed number (1.41 million) each year for 5 years the output of the model predicts that the annual growth rate should fall from 0.94 in 1999 to 0.71 in 2005 and the total fall flight population should decline from an estimated 8.33 million to 3 million (Rockwell and Ankney, 1999). It is significant that the number of birds harvested has increased from 0.6 million in 1998 to 1.4 million in 2001 (U.S. Fish & Wildlife Annual Reports). If this level of harvesting can be sustained and current unpublished estimates of survival and fecundity in the different local populations of the Mid-Continent population are correct, the target population size (50% or less) will be achieved in 2005 or 2006.

#### CONCLUSIONS

The results of the fate of this local population on the Arctic/sub-Arctic boundary during the last 35 years indicate a highly dynamic and unpredictable course of events. The changes to the coastal wetlands are the indirect outcome of bottom-up perturbations to agricultural lands and the availability of food supplies in refugia. These changes in resource supply attract a herbivore that has not only resulted in increased numbers of individuals, but has also led to large-scale disturbance of Arctic coastal and inland wetlands that are 5,000 km distant from the perturbations—a consequence of migratory connectivity (*cf.*, Webster *et al.*, 2002) via a biotic agent. Although the direct and indirect effects on these Arctic ecosystems can be placed in a series of theoretical constructs, such as over-compensation of above-ground primary production, desertification, loss of an ecological sere, an alternative stable state, an apparent trophic cascade, positive feedbacks with opposing outcomes, and loss of species richness and diversity, there is no over-arching construct. The highly unstable, non-equilibrium conditions and the spatial complexity of these coastal wetlands defies the application of a simple construct that is all encompassing to describe this plant-herbivore interaction at the different ecological hierarchical scales. In addition, there is a striking temporal asymmetry between the time required to achieve a substantial reduction in the lesser snow goose population and the re-vegetation of the degraded exposed sediment and peats. Highly consolidated hypersaline mineral sediment devoid of a seed bank provides a poor template for plant re-establishment. In ecological time (<15 years) it represents an alternative stable state.

Although other species of Arctic breeding geese have increased in number in recent decades, an increase that can be linked to their use of agricultural crops, the overall deleterious effects of these birds on northern ecosystems are less evident than in the case of the lesser snow goose. This excludes Ross's geese and molting Canada geese that often associate with

lesser snow geese in the post-hatch period (Alisauskas and Boyd 1994; Abraham and Jefferies, 1997). Additional factors are involved in the case of other species that limit their ability to trigger large-scale landscape changes (Drent *et al.*, 2003; Mainguy *et al.*, 2002; Drent and Jefferies, in preparation). The population of lesser snow geese, therefore, are at one end of a continuum of responses of the different Arctic goose species to the direct and indirect effects of modern agriculture. They have shown a high degree of plasticity in coping with change. The effects of agriculture on this and other species represents biomanipulation of wild populations on a continental scale (Bazely and Jefferies, 1997), the ecological outcome of which is still unfolding.

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