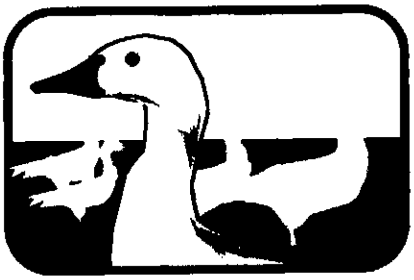

The Exploitation of Wetland Ecosystems by Herbivores on Bylot Island

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SUMMARY

We examine the interactions between herbivores, plants and climatic factors in arctic wetlands using, as a case study, results of our research on grazing by snow geese on Bylot Island. During the summer, geese are the most important herbivore on the island and consume a high proportion of the annual graminoid production (grasses and sedges). Herbivores can sometimes enhance plant production by increasing the turnover rate of nitrogen, a nutrient which commonly limits growth of arctic plants. However, we found no evidence of positive feedback of grazing on plant growth and, on the contrary, chronic goose grazing tended to decrease production of these ecosystems in the long term. Geese need large quantities of high-quality plants to breed successfully, and negative effects on goose reproduction as a result of lack of food were detected. Herbivore populations are also influenced by climatic factors, either directly or indirectly through effects on plant growth. It is likely that tundra plant–herbivore systems will be strongly affected by future climatic changes.

RÉSUMÉ

Nous examinons les interactions entre les herbivores, les plantes et les facteurs climatiques dans les terres humides arctiques en utilisant nos recherches sur le broutement par les oies des neiges à l'Île Bylot comme étude de cas. Durant l'été, les oies sont les herbivores les plus importants de l'île et elles consomment une forte proportion de la production annuelle de graminoides. Les herbivores peuvent parfois stimuler la production végétale en augmentant le taux de recyclage de l'azote, un nutriment qui limite fréquemment la croissance des plantes arctiques. Cependant, nous n'avons pas trouvé d'évidence de rétroaction positive du broutement sur la croissance des plantes et, au contraire, le broutement chronique par les oies semblait diminuer la production de ces écosystèmes. Les oies ont besoin d'une grande quantité de plantes de haute qualité pour se reproduire avec succès, et des effets dépendants de la densité sur leur succès reproducteur suite à un manque de nourriture ont été détectés. Les populations d'herbivores sont aussi influencées par des facteurs climatiques, soit directement ou indirectement par les effets sur la croissance des plantes. Il est probable que les systèmes plantes/herbivores de la toundra seront fortement affectés par les changements climatiques futurs.

INTRODUCTION

The plant-herbivore interaction is usually the dominant trophic interaction of arctic terrestrial ecosystems. Although predation may be important locally, it is believed that the abundance of arctic herbivores is limited largely by resource availability, *i.e.*, plants (Oksanen *et al.*, 1981; Messier *et al.*, 1988; Jefferies *et al.* 1992). In contrast, plant productivity and distribution appears to be little affected by herbivores at the landscape level, although herbivores locally may have a high impact on plant communities (Jefferies *et al.* 1994b). Abiotic factors (water, temperature, nutrients) appear to be more important than herbivory in limiting arctic plants.

In this paper, we examine the nature of the interactions between herbivores, plants and climatic factors in the Arctic. This review focusses on the plant and herbivore communities found on northern Baffin Island. We use research that we have conducted over the past eight years on grazing by snow geese (*Chen caerulescens*) in the wetlands of Bylot Island as a case study. Nutrient cycling through the herbivore occupies a prominent place in our review as this is thought to be a key process in this system. The role of climatic factors will also be discussed in the context of global warming.

PLANT-HERBIVORE INTERACTIONS

The abundance and distribution of herbivores depend upon their foraging efficiency and on forage availability. Thus, in order to understand fluctuations of herbivore populations, it is necessary to have a good knowledge of 1) the foraging behaviour of the animal, 2) the interaction between the herbivore and the plants, and 3) the factors that limit plant production. Herbivores vary in body size, digestive efficiency, and locomotor abilities, all factors which will affect their use of resources (Klein and Bay, 1994). Herbivores are selective in their use of food plants and typically select plants high in nutrients such as soluble carbohydrates and nitrogen, and low in compounds such as fibre or phenols that reduce digestibility (Gauthier and Bédard, 1990; Manseau and Gauthier, 1993; Gauthier and Hughes 1995). Therefore, temporal and spatial variations in both plant abundance and quality will influence herbivore performance.

In the Arctic, the combination of the short growing season, cold temperature, and reduced availability of nutrients and water limit primary productivity of terrestrial ecosystems to relatively low levels (Bliss, 1986). However, grazing by herbivores also influences the abundance and quality of the vegetation (Cargill and Jefferies, 1984b; Gauthier *et al.*, 1995; Manseau *et al.*, 1996). Although grazing reduces standing crop, some forage plants produce new foliage following defoliation which is often of higher quality (high nitrogen, low fibre) than ungrazed plants. However, the ability of plants to recover from grazing is variable, both among and within plant species, and is influenced by many factors, including the timing of grazing, its intensity and the availability of nutrients (Beaulieu *et al.*, 1996). Thus, the dynamics of feedback processes between herbivores and plants will have a strong influence on the herbivore.

PLANT COMMUNITIES OF NORTHERN BAFFIN ISLAND

Tundra vegetation is extensive in low-elevation areas (<300 m) surrounding Eclipse Sound on Bylot and Baffin islands. At a small scale, the spatial heterogeneity of the vegetation is considerable, mostly in response to the moisture gradient. Because permafrost blocks much of the underground water movement, poorly drained areas readily develop into wetlands. Topography features that contribute to wetland formation include patterned ground (polygons), thermokarst pits, or any depression. Wetlands that do not retain standing water during the summer are commonly covered by a rich and diverse community of mosses. These wetlands develop into fens, *i.e.*, peat-accumulating systems. A lush vascular plant community also occupies these wetlands and is composed mostly of sedges (*Carex aquatilis, Eriophorum scheuchzeri, E. angustifo-lium*), grasses (*Dupontia fisheri* and *Pleuropogon sabinei*), and a few forbs (herbaceous plants) (*e.g., Pedicularis* spp.; Zoltai *et al.*, 1983; Gauthier *et al.*, 1995). These fens are often called wet sedge or cottongrass meadow because of the abundance of graminoids (grasses and sedges).

Moist areas with fine soil material also have a rich and diverse vegetative cover, although plant abundance generally decreases along a decreasing soil moisture gradient. Polygon rims, sloping terrain, and hummocky tundra are examples of this habitat. In this paper, we refer to these areas as uplands. Common plants of this habitat include shrubs (*Salix* spp, *Vaccinium uliginosum*), forbs (*Cassiope tetragona, Oxytropis maydelliana*), grasses (*Arctagrostis latifolia, Alopecurus alpinus, Poa glauca, Luzula confusa*), and some mosses (Zoltai *et al.*, 1983). Finally, exposed areas with dry, gravel soil such as ridges have a very sparse vegetative cover consisting of only a few plant species (*e.g., Dryas integrifolia, Saxifraga oppositifolia*).

THE HERBIVORE COMMUNITY OF NORTHERN BAFFIN ISLAND

Northern Baffin Island supports six species of vertebrate herbivores. One conspicuous absence is the muskox (*Ovibos moschatus*). This species has been absent from the area possibly since the last glaciation (Zoltai *et al.*, 1983). The herbivore community of northern Baffin Island is summarized in Table 1. All herbivores but one, the snow goose, are permanent residents.

Even though geese are present for only part of the year, they are certainly the most abundant herbivore from late May to early September on Bylot Island, and probably over much of northern Baffin Island. This whole area holds large breeding colonies of greater snow geese (subspecies *atlantica*) and may account for half of the subspecies' total breeding population. Based on censuses conducted on the spring staging ground along the St. Lawrence estuary in Quebec, this population has increased considerably over the past three decades. The total population expanded from 25,000 birds in 1965 to 669,000 birds in 1996, an average annual rate of increase of 11% (Reed, 1990; unpubl. data). During the period 1983-1993, the breeding population of the south plain of Bylot Island experienced the same increase, $11\%\cdot a^{-1}$ (Fig. 1). In 1993, the brood-rearing population of Bylot Island was composed of 69,500 adults and 86,500 goslings.

The caribou is the most important mammalian herbivore. Although it is locally abundant over parts of northern

Table 1 Habitat, abundance and population trends of vertebrate herbivore species present on northern Baffin Island.

Species	Habitat	Abundance	Population Trend
Caribou *Rangifer tarandus*	Upland, wetland	Low to moderate	Increasing
Arctic hare *Lepus arcticus*	Dry upland, slopes	Low	Unknown
Brown lemming *Lemmus sibiricus*	Wetland (polygon fen)	Low (except in peak years)	Populations with irregular cycles
Collared lemming *Dicrostonyx groenlandicus*	Dry upland	Low (except in peak years)	Populations with irregular cycles
Greater snow goose *Chen caerulescens atlantica*	Wetland (polygon fen)	Moderate to high	Increasing
Rock ptarmigan *Lagopus mutus*	Dry upland	Low	Unknown

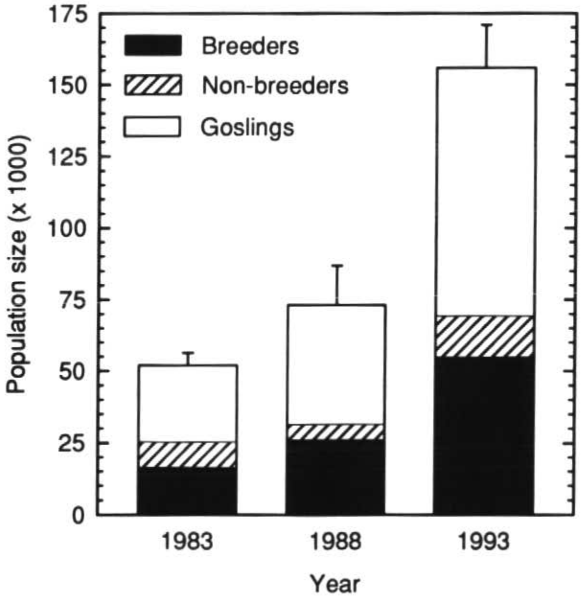

Figure 1 *Population size of greater snow goose on the south plain of Bylot Island partitioned by adult breeders and non-breeders, and goslings. Censuses were conducted in late July. Standard error of total estimate is given (from Reed and Chagnon, 1987; Reed* et al., *1992; Reed, unpubl. data).*

Baffin Island, it is rare on Bylot Island. Caribou were extirpated from the island in 1943 (Zoltai *et al.*, 1983) although over the past few years small numbers have moved back to the island in summer. Caribou migrate seasonally over a large area of Baffin Island and use a variety of habitats, including both wetlands and uplands (Ferguson, 1996).

Two species of lemmings occur on northern Baffin Island, each species preferring slightly different habitats (Table 1). In most years, lemmings occur at low density. However, their populations undergo cyclic fluctuations, periodically increasing to very high density for a short period, typically one year. Difference in lemming abundance between the high and low phases of the cycle can be more than one order of magnitude. Population cycles of lemmings in the high Arctic appear to be longer and more erratic than the regular 3-4 year cycle commonly observed in the low Arctic (Fuller *et al.*, 1975; Krebs *et al.*, 1995; Gauthier, unpubl. data). Reasons for this are unclear, but may be related to the shorter growing season of higher latitudes, which allows fewer breeding cycles per year (Jefferies *et al.*, 1992). The last two species of herbivores, the arctic hare and rock ptarmigan, are present in low numbers in the area (Zoltai *et al.*, 1983).

Many herbivore species depend either mostly (snow geese, brown lemmings) or partly (caribou) on wetland graminoids for their food (Table 1). Yet, wetlands occupy only a small proportion of the tundra around Eclipse Sound. In our 70 km^2 study area on Bylot Island, wetlands (ponds and wet meadows) occupy only 23% of the land area even though the site includes some of the most extensive wetland complexes on the island (Hughes *et al.*, 1994). This stresses the importance of this habitat for arctic herbivores.

NITROGEN CYCLING BY HERBIVORES

In the Arctic, nutrient availability is often deficient and limits plant growth (Babb and Whitfield, 1977; Ulrich and Gersper, 1978; Jefferies *et al.*, 1994b). Fertilization experiments have shown that nitrogen is often the most limiting nutrient for tundra plants (McKendrick *et al.*, 1978; Cargill and Jefferies, 1984a; Shaver and Chapin, 1995). At Bylot Island, growth of wetland graminoids was enhanced by addition of nitrogen, either alone or in combination with phosphorus, but not by phosphorus added alone (Pineau *et al.*, unpubl. data).

Soil nitrogen for plant growth usually comes from three sources: microbial decomposition, fixation of aerial nitrogen by bacteria, and from precipitation. In the Arctic, turnover of nutrients is slow because the cold temperature considerably slows microbial decomposition of litter in the soil (Nadelhoffer *et al.*, 1992), by far the most important source of soil nitrogen (Chapin and Bledsoe, 1992). Herbivores may play a key role in increasing the turnover rate of nitrogen in the Arctic: fecal material contains a high proportion of soluble nitrogen that can be readily absorbed by plants, and hence enriches the soil (Bazely and Jefferies, 1985). Thus, the passage of plants through the gut of an herbivore can replace the rate-limiting process of soil microbial decomposition. A speeding up of nitrogen recycling through the herbivore can, therefore, have the same effect as fertilization and enhances the primary production of forage species.

Enhanced primary production following grazing — a process referred to by botanists as overcompensation — has been observed in coastal salt marshes of Hudson Bay grazed by lesser snow geese (*Chen caerulescens caerulescens*; Cargill and Jefferies, 1984b; Hik and Jefferies, 1990; Jefferies *et al.*, 1992). Jefferies and co-workers have shown that the positive response of graminoids (*Puccinellia phryganodes* and *Carex subspathacea*) to grazing in this ecosystem is largely a consequence of an increase in the availability of nitrogen to plants *via* the deposition of feces by the herbivore (Bazely and Jefferies, 1985; Hik and Jefferies, 1990). A second, positive effect of the herbivore on nitrogen recycling is that, by preventing the accumulation of litter on the ground, it promotes the colonization of bare sediments in grazed swards by nitrogen-fixing cyanobacteria (Bazely and Jefferies, 1989).

Overcompensation in response to herbivory has been reported in only a few arctic plant–herbivore systems. Several conditions must be met to obtain such response, including a rapid turnover of nutrients in the rooting zone, continuous and rapid regrowth of the plants, presence of basal meristems, intensive grazing without destruction of meristems and rapid return of fecal nitrogen to the soil (see Jefferies *et al.*, 1994b for a complete list of characteristics). In contrast to the situation prevailing in the coastal marshes of Hudson Bay, we have failed to detect any evidence of overcompensation in graminoid plants grazed by snow geese in wet meadows on Bylot Island (Gauthier *et al.*, 1995). In this ecosystem, the presence of goose feces does not seem to have any fertilization effect on the plants (Beaulieu *et al.*, 1996), even though fertilization experiments showed that lack of nitrogen is limiting plant growth.

This is a surprising result because many of the conditions enumerated by Jefferies *et al.* (1994b) are met on Bylot Island. One important difference, however, with coastal marshes of Hudson Bay is the presence of a thick layer of moss in the wet meadows used by snow geese on Bylot Island. We have hypothesized that most nutrients leaching from goose feces are absorbed by mosses rather than graminoids because mosses have a higher ion exchange capacity than vascular plants (Clymo, 1963; Graigie and Maass, 1966; Glime *et al.*, 1982). Preliminary results from fertilization experiments show that mosses respond positively to nitrogen addition at lower concentration than graminoids (Pineau *et al.*, unpubl. data). This suggests that mosses act like a sponge, soaking up most of the nutrients released from feces. It thus appears that nitrogen cycling in this ecosystem is more complex and involves three levels (graminoids, mosses and herbivore) rather than only two. More information is needed, however, to better understand the nature of this interaction.

PLANT PRODUCTION AND THE IMPACT OF GOOSE GRAZING ON BYLOT ISLAND

Compared to other arctic ecosystems, primary production of wetlands is high, partly because of the high availability of water (Webber, 1978). However, compared to temperate biomes, production of arctic wetlands is modest. Average annual above-ground primary production of graminoids in arctic wetlands ranges from 20-100 g·m^2 (Table 2). Although high arctic sites tend to have the lowest production values, there is considerable variability among plant communities and years at the same site. Climatic factors (timing of snow-melt, precipitation, temperature) are most likely involved in annual variation in production. Production data from Bylot Island tend to be at the lower end of the range for wet arctic graminoid communities. It is not known whether this reflects site-specific differ-

Table 2 Above-ground primary production (dry mass) of various types of wetland dominated by graminoids in the Arctic.

Site	Species	Production (g m^2 year)	Reference
West Hudson Bay (58°N)	*Puccinellia phryganodes, Carex subspathacea*	55-100	Cargill and Jefferies, 1984b Hik *et al.*, 1991
Victoria Island (69°N)	—	52	Henry *et al.*, 1994
Barrow, Alaska (70°N)	*Carex aquatilis, Dupontia fisheri, Eriophorum angustifolium*	101	Tieszen, 1972
Barrow, Alaska (70°N)	*Dupontia fisheri, Eriophorum angustifolium*	51	Webber, 1978
Barrow, Alaska (70°N)	*Carex aquatilis*	44-45	Webber, 1978
East Greenland (71°N)	*Carex aquatilis*	38	Madsen and Mortensen, 1987
Bylot Island (73°N)	*Dupontia fisheri, Eriophorum scheuchzeri*	20-35	Gauthier *et al.*, 1995; unpubl. data
Banks Island (72-74°N)	—	16-37	Henry *et al.*, 1994
Devon Island (75°N)	*Carex aquatilis*	38	Muc, 1977
Alexandra Fjord (78°N)	*Carex membranacea, Eriophorum angustifolium, Carex aquatilis*	36	Henry *et al.*, 1994

ences in net primary production or is a consequence of the intense, chronic grazing by geese on Bylot Island.

When grazing is too intense, damage to the plants may occur. Damage due to overgrazing by geese has already been reported in coastal salt-marsh habitats along west Hudson Bay (Kerbes *et al.*, 1990; Jefferies *et al.*, 1994a). We have been monitoring the impact of goose grazing at our study area on Bylot Island since 1990. Grazing significantly reduced the above-ground biomass of graminoids at the end of the season. In preferred feeding areas, we estimated that geese consumed from 65-100% of the annual above-ground production of *Eriophorum*, and from 30-78% for *Dupontia* (Gauthier *et al.*, 1995). Despite this intense grazing pressure, plants were able to grow back some of the lost foliage, although the production of *Dupontia* was slightly reduced in grazed areas. Accumulation of soluble carbohydrates in rhizomes was also lower in grazed than in ungrazed plants (Beaulieu *et al.* 1996). As below-ground reserves are important to sustain production of new tillers in arctic graminoids (Mattheis *et al.* 1976), chronic grazing eventually could lead to a decrease in both tiller density and overall production.

Preliminary results from the monitoring of long-term goose exclosures showed that, indeed, both the production and composition of the community may be affected by geese. After 5 years of goose exclusion, the peak biomass of *Eriophorum*, the preferred food plant of geese, was 3 times higher than in sites protected from goose grazing only in the current year (23 g·m^2 *versus* 8 g·m^2, respectively; Gauthier and Rochefort, unpubl. data), and the number of tillers was twice as high (2048 tillers·m^2 *versus* 1081 tillers·m^2). Although *Eriophorum* was less abundant than *Dupontia* in the first year of goose exclusion (37% of total graminoid biomass), it had become the dominant species 5 years later (55% of biomass). The shoot-pulling habit of geese is another factor that may contribute to the decrease in tiller numbers in grazed areas. In early spring and late summer, geese often excavate basal stems and rhizomes of graminoids (Gauthier, 1993), thereby killing individual shoots. These results suggest that chronic, intense grazing by geese may lead to a low-level production equilibrium between the herbivore and the plants. Response of the community to the absence of goose grazing needs to be evaluated over a longer period than 5 years, and at the landscape level (*i.e.*, over the whole tundra of Bylot Island).

THE ROLE OF FOOD IN SNOW GOOSE REPRODUCTION

Because the breeding cycle of geese is relatively long compared to the short arctic summer, all activities are compressed in time in order for the goslings to fledge before the end of the summer. One of the most important reproductive decisions facing snow geese is when to start breeding. Even though breeding is highly synchronized among individuals (90% of the clutches hatch within 1 week; Lindholm *et al.*, 1994), the timing of hatching is critical for the growth and subsequent survival of goslings. A difference of as little as 4-6 days between early and late-hatched goslings may have major consequences on their growth.

Timing of hatch affects gosling growth for two reasons. First, geese have a low digestive efficiency (they cannot digest plant fibre and therefore absorb only about one-third of the plant material that they ingest) and need large quantities of high-quality forage. When plant quality decreases, their digestive system is unable to compensate by increasing food intake; hence, rate of nutrient assimilation decreases (Sedinger and Raveling, 1988; Manseau and Gauthier, 1993; Piedboeuf, 1996). Food addition experiments have confirmed that gosling growth is sensitive to slight variations in food quality (Lindholm *et al.*, 1994). During summer, there is a seasonal decline in plant quality (decrease in nitrogen, increase in fibre) which starts at the time goslings hatch (Manseau and Gauthier, 1993). Hence, late-hatched goslings have a slower growth rate than early-hatched ones because they miss the period when plant quality is highest (Lindholm *et al.*, 1994; Lepage and Gauthier, unpubl. data).

Food depletion in preferred feeding areas by early-hatched goslings is a second reason for the slower growth rate of late-hatched goslings: by the time they hatch, the most nutritive species (*Eriophorum*) or plant parts (leaf tips) are already partly consumed (Gauthier *et al.*, 1995). Even though plant regrowth after grazing is of higher quality (more nitrogen) than ungrazed plants, this is probably not sufficient to compensate for the decrease in biomass (Piedboeuf, 1996). Seasonal movements of broods from pond margins and wet meadows dominated by *Dupontia/Eriophorum* to drier upland areas (Hughes *et al.*, 1994; Gauthier, pers. obs.) also suggest that less forage is available for geese in wetland habitats later in the season.

About 10 days after fledging, goslings must start a migration of 3000 km to southern Quebec even though their growth is not entirely completed and they have little fat reserves to meet the energy demand of the migration (Lesage, 1995). Goslings that grow more slowly will fledge later in the season or will be smaller at fledging, and are likely to experience higher mortality during the fall migration (Owen and Black, 1989; Cooch and Cooke, 1991; Cooch *et al.*, 1993; Menu *et al.*, unpubl. data). This could be a density-dependent regulation factor in this population: as population density increases, gosling growth will be depressed through increased competition for high-quality food, and mortality during fall migration will increase. We have already detected evidence of density-dependent effects on gosling growth. Over the past 20 years, birds shot at Cap Tourmente in Quebec have shown a significant decline in body size (Reed and Plante, in press). Since 1991, we have also detected a negative trend in body mass of goslings at fledging on Bylot Island (Lepage *et al.*, unpubl. data).

CLIMATIC EVENTS

Climatic effects on herbivore populations can be either direct and/or indirect through their influence on plant growth. Timing of snow-melt in spring is probably one of the most important direct climatic effects on goose populations. Although there are considerable pressures for the birds to lay their eggs as early as possible in spring to maximize gosling growth, and hence their reproductive success, snow cover often prevents geese from doing so. Date of nest initiation by geese is correlated with both snow-melt date and average temperature in late May and early June (Lepage *et al.*, 1996). Snow-melt affects goose nesting in two ways. First, snow-free areas in relatively dry sites must be available for the geese to initiate their nest. Second, suitable feeding areas must also be available to geese before and during laying. Because egg-laying is energetically costly for geese, they need to feed intensively during this period to acquire enough nutrients to form the eggs (Gauthier and Tardif, 1991; Choinière and Gauthier, 1995). Even though geese are flexible in their choice of feeding areas and nesting sites in spring (Gauthier, 1993; Lepage *et al.*, 1996), late snow-melt will delay nesting and reduce reproductive success.

Episodic climatic events can also have a major impact on the population dynamics of arctic animals, as shown by the variation in annual production of young in greater snow geese. Since 1973, the proportion of young in the fall flock has been monitored when they pass through southern Quebec in migration. The production of young shows considerable annual variation with periodic breeding failure observed (when the proportion of young is <10%) in 1974, 1986 and 1992 (Fig. 2). These three summers were characterized by extreme weather conditions in the Arctic: snow-melt was severely delayed because of high winter precipitation and cold spring temperatures (Heyland, 1974; Lepage *et al.*, 1996; Reed unpubl. data). Most geese did not even attempt to breed in these years, presumably because not enough time was available to complete their breeding cycle when the snow finally melted. These periodic breeding failures could increase in the future if global warming increases the frequency of these climatic anomalies.

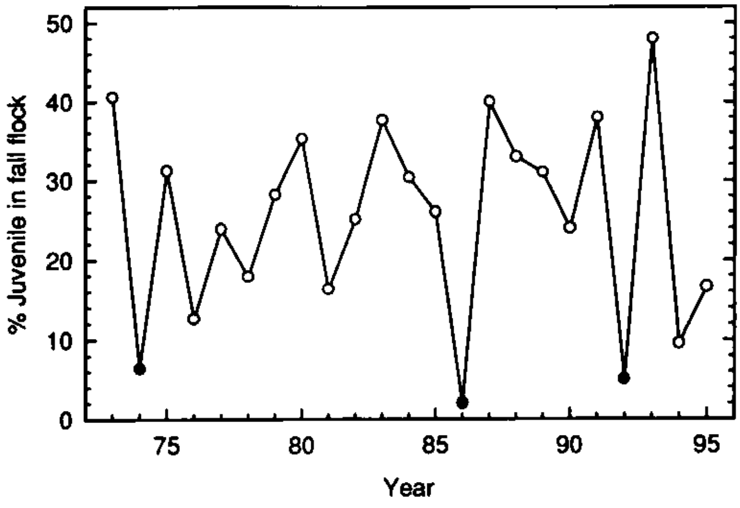

Figure 2 *Proportion of juveniles in the fall flock of greater snow geese along the St. Lawrence estuary. Filled dots are years of breeding failure (when proportion of juveniles is < 10%; from Gauvin and Reed, 1987; Reed unpubl. data).*

Another example of a direct effect is the influence of climatic conditions on the thermoregulatory costs of growing goslings. The amount of energy expended by goslings for thermoregulation, a major component of their internal energy budget, is sensitive to variations in temperature, wind speed, and solar radiation (Fortin, 1995). Increased cost of thermoregulation will decrease energy available for growth, and hence may affect gosling survival.

An interesting example of indirect climatic effect on an arctic herbivore population is provided by the snow goose population of west Hudson Bay. The cooling trend recently observed over southern Baffin Island (Findlay and Deptuch-Stapf, 1991; Allard *et al.*, 1995) has delayed snow melt at the very large snow goose colonies located on Southampton Island and the Great Plain of the Koukdjuak. This has forced birds nesting in these areas to prolong their staging along west Hudson Bay in spring where they feed by grubbing for rhizomes, thereby destroying salt-marsh plants (Jefferies *et al.*, 1994a). This destruction has had an adverse effect on the local population of snow geese that nest and raise their goslings in the salt marshes of west Hudson Bay.

Late snow melt, flooding, drought or cold temperature are all climatic events that can negatively affect growth of tundra plants during the summer, and hence indirectly influence herbivore populations. Because the hatch of goslings on Bylot Island must coincide with the period of maximum plant quality in order for them to achieve optimal growth, any reduction or delay in plant growth will have an impact on goslings.

CONCLUSION

From the previous discussion, it is clear that population dynamics of arctic herbivores, and geese in particular, are strongly influenced by their food supply. The nature of the interaction between herbivores and plants is affected by the behaviour and physiology of the herbivore, the intensity of grazing, the role of the herbivore in cycling nitrogen, and the growth characteristics of plants. All these processes are modulated by both the overall climatic conditions as well as by episodic events. In the context of global warming, it is difficult to anticipate the effects of predicted climatic changes on these populations since climate acts at many different levels, including soil microbial processes, plant growth, and the herbivores themselves.

The effect of climatic changes on tundra grazing systems was discussed by Jefferies *et al.* (1992). Predicted increase in temperature may enhance the production of arctic plants. However, modifications to the water regime are more complex and could have both positive and negative impacts on plants as increased winter precipitation will delay snow-melt and the onset of plant growth in spring, but increased summer precipitation could enhance it. Changes in plant production through global warming will affect herbivores. Direct effects on animals could also be positive or negative: higher temperatures may reduce thermoregulatory costs of goslings but late snow-melt will delay nesting by geese. Because tundra plant–herbivore systems are tightly coupled with climate, it is likely that they will be affected by future climatic changes and that they will in turn respond to these changes.

ACKNOWLEDGEMENTS

The goose research on Bylot Island was supported by the Natural Sciences and Engineering Research Council of Canada, the Arctic Goose Joint Venture (Environment Canada), the Fonds pour la Formation de chercheurs et d'aide à la recherche of the Quebec Government, Ducks Unlimited (Canada), Polar Continental Shelf Project, and the Department of Indian Affairs and Northern Development of Canada. We thank the Pond Inlet Hunters and Trappers Association for their support, and Bob Jefferies and Bill Montevecchi for their comments on this paper.

REFERENCES

Allard, M., Wang, B. and Pilon, J., 1995, Recent cooling along the southern shore of Hudson Strait, Québec, Canada, documented from permafrost temperature measurements: Arctic and Alpine Research, v. 27, p. 157-166.

Babb, T.A. and Whitfield, D.W.A., 1977, Mineral nutrient cycling and limitation of plant growth in the Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem: University of Alberta Press, Edmonton, Alberta, p. 589-606.

Bazely, D.R. and Jefferies, R.L., 1985, Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh: Journal of Applied Ecology, v. 22, p. 693-703.

Bazely, D.R. and Jefferies, R.L., 1989, Lesser snow geese and the nitrogen economy of a grazed salt marsh: Journal of Ecology, v. 77, p. 24-34.

Beaulieu, J., Gauthier, G. and Rochefort, L., 1996, The growth response of graminoid plants to goose grazing in a High Arctic environment: Journal of Ecology, v. 84, p. 905-914.

Bliss, L.C., 1986, Arctic ecosystems: Their structure, functions, and herbivore carrying capacity, *in* Gudmundsson, O., ed., Grazing Research at Northern Latitudes: Plenum Press, New York, p. 5-26.

Cargill, S.M. and Jefferies, R.L., 1984a, Nutrient limitation of primary production in a sub-arctic salt marsh: Journal of Applied Ecology, v. 21, p. 657-668.

Cargill, S.M. and Jefferies, R.L., 1984b, The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh: Journal of Applied Ecology, v. 21, p. 669-686.

Chapin, D.M. and Bledsoe, C.S., 1992, Nitrogen fixation in arctic plant communities, *in* Chapin III, F.S., Jefferies, R.L., Reynolds, J.F., Shaver, G.R., Svoboda, J. and Chu, E.W., eds., Arctic Ecosystems in a Changing Climate: Academic Press, Inc., New York, p. 301-319.

Choinière, L. and Gauthier, G., 1995, Energetics of reproduction in female and male greater snow geese: Oecologia, v. 103, p. 379-389.

Clymo, R.S., 1963, Ion exchange in *Sphagnum* and its relation to bog ecology: Annals of Botany, v. 27, p. 309-324.

Cooch, E.G. and Cooke, F., 1991, Demographic changes in a snow goose population: biological and management implications, *in* Perrins, C.M., Lebreton, J.D. and Hirons, G.J.M., eds., Population studies: relevance to conservation and management: Oxford University Press, Oxford, p. 168-189.

Cooch, E.G., Jefferies, B., Rockwell, R.F. and Cooke, F., 1993, Environmental change and the cost of philopatry: an example in the lesser snow goose: Oecologia, v. 93, p. 128-138.

Ferguson, M.A.D., 1996, Arctic tundra caribou and climatic change: questions of temporal and spatial scales: Geoscience Canada, v. 23, n. 4, p. 245-252.

Findlay, B.F. and Deptuch-Stapf, A., 1991, Colder than normal temperature over north eastern Canada during the 1980's: Climatic Perspectives, 13 April Issue, p. 9-12.

Fortin, D., 1995, L'environnement thermique des oisons de la grande oie des neiges (*Chen caerulescens atlantica*) dans l'Arctique canadien: M.Sc. thesis, Université Laval, Sainte Foy, Québec, 135 p.

Fuller, W.A., Martell, A.M., Smith, R.F.C. and Speller, S.W., 1975, High arctic lemmings (*Dicrostonyx groenlandicus*) II. Demography: Canadian Journal of Zoology, v. 53, p. 867-878.

Gauthier, G., 1993, Feeding ecology of nesting greater snow geese: Journal of Wildlife Management, v. 57, p. 216-223.

Gauthier, G. and Bédard, J., 1990, The role of phenolic compounds and nutrients in determining food preference in greater snow geese: Oecologia, v. 84, p. 553-558.

Gauthier, G. and Hughes, R.J., 1995, The palatability of arctic willow for greater snow geese: the role of nutrients and deterring factors: Oecologia, v. 103, p. 390-392.

Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J. and Rochefort, L., 1995, Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada): Journal of Ecology, v. 83, p. 653-664.

Gauthier, G. and Tardif, J., 1991, Female feeding and male vigilance during nesting in greater snow geese: Condor, v. 93, p. 701-711.

Gauvin, J. and Reed, A., 1987, A simulation model for the greater snow goose population: Occasional Paper No 64, Canadian Wildlife Service, Ottawa, 28p.

Glime, J.M., Wetzel, R.G. and Kennedy, B.J., 1982, The effects of bryophytes on succession from alkaline marsh to *Sphagnum* bog: The American Midland Naturalist, v. 108, p. 209-223.

Graigie, J.S. and Maass, W.S.G., 1966, The cation-exchanger in *Sphagnum* spp.: Annals of Botany, v. 30, p. 153-154.

Henry, G.H.R., Svoboda, J. and Freedman, B., 1994, Standing crop and net production of non-grazed sedge meadows of a polar desert oasis, *in* Svoboda, J. and Freedman, B., eds., Ecology of a Polar Oasis: Captus Printer Inc., York University Campus, North York, Ontario, p. 85-95.

Heyland, J.D., 1974, Preliminary report on studies of greater snow geese on Bylot Island, May 28 to June 20, 1974: unpublished manuscript, Québec Fish and Wildlife Service, Québec.

Hik, D.S. and Jefferies, R.L., 1990, Increases in net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model: Journal of Ecology, v. 78, p. 180-195.

Hik, D.S., Sadul, H.A. and Jefferies, R.L., 1991, Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*: Journal of Ecology, v. 79, p. 715-730.

Hughes, R.J., Reed, A. and Gauthier, G., 1994, Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories: Journal of Wildlife Management, v. 58, p. 536-545.

Jefferies, R.L., Gadallah, F.L., Srivastava, D.S. and Wilson, D.J., 1994a, Desertification and trophic cascades in arctic coastal ecosystems: a potential climatic change scenario?, *in* Callaghan, T.V., ed., Global Changes and Arctic Terrestrial Ecosystems: Ecosystem Report no 10, European Community, Luxembourg, p. 206-210.

Jefferies, R.L., Klein, D.R. and Shaver, G.R., 1994b, Vertebrate herbivores and northern plant communities: reciprocal influences and responses: Oikos, v. 71, p. 193-206.

Jefferies, R.L., Svoboda, J., Henry, G., Raillard, M. and Ruess, R., 1992, Tundra grazing systems and climatic change, *in* Chapin III, F.S., Jefferies, R.L., Reynolds, J.F., Shaver, G.R., Svoboda, J. and Chu, E.W., eds., Arctic Ecosystems in a Changing Climate: Academic Press, Inc., New York, p. 391-412.

Kerbes, R.H., Kotanen, P.M. and Jefferies, R.L., 1990, Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson bay: Journal of Applied Ecology, v. 27, p. 242-258.

Klein, D.R. and Bay, C., 1994, Resource partitioning by mammalian herbivores in the high arctic: Oecologia, v. 97, p. 439-450.

Krebs, C.J., Boonstra, R. and Kenney, A.J., 1995, Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada: Oecologia, v. 103, p. 481-489.

Lepage, D., Gauthier, G. and Reed, A., 1996, Breeding site infidelity in greater snow geese: a consequence of constraints on laying date?: Canadian Journal of Zoology, v. 74, p. 1866-1875.

Lesage, L., 1995, La croissance corporelle, et l'influence de la date d'éclosion et du site d'élevage sur le développement tissulaire chez les oisons de la grande oie des neiges: M.Sc. thesis, Université Laval, Sainte Foy, Québec, 99 p.

Lindholm, A., Gauthier, G. and Desrochers, A., 1994, Effects of hatch date and food supply on gosling growth in arctic-nesting greater snow geese: Condor, v. 96, p. 898-908.

Madsen, J. and Mortensen, C.E., 1987, Habitat exploitation and interspecific competition of moulting geese in east Greenland: Ibis, v. 129, p. 25-44.

Manseau, M. and Gauthier, G., 1993, Interactions between greater snow geese and their rearing habitat: Ecology, v. 74, p. 2045-2055.

Manseau, M., Huot, J. and Crête, M. 1996, Effects of summer grazing by caribou on community and productivity of vegetation: community and landscape level: Journal of Ecology, v. 84, p. 503-513.

Mattheis, P.J., Tieszen, L.L. and Lewis, M.C., 1976, Responses of *Dupontia fisheri* to simulated lemming grazing in an Alaskan Arctic tundra: Annals of Botany, v. 40, p. 179-197.

McKendrick, J.D., Ott, V.J. and Mitchell, G.A., 1978, Effects of nitrogen and phosphorus fertilization on carbohydrate and nutrient levels in *Dupontia fisheri* and *Arctagrostis latifolia*, *in* Tieszen, L.L., eds., Vegetation and Production Ecology of an Alaskan Tundra: Springer-Verlag, New York, p. 509-537.

Messier, F., LeHénaff, D. and Luttich, S., 1988, Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion: Arctic, v. 41, p. 79-87.

Muc, M., 1977, Ecology and primary production of sedge-moss meadow communities, Truelove Lowland, *in* Bliss, L.C., eds., Truelove Lowland, Devon Island, Canada: a High Arctic Ecosystem: University of Alberta Press, Edmonton, AB, p. 157-184.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R. and Linkins, A.E., 1992, Microbial processes and plant nutrient availability in arctic soils, *in* Chapin III, F.S., Jefferies, R.L., Reynolds, J.F., Shaver, G.R., Svoboda, J. and Chu, E.W., eds., Arctic Ecosystems in a Changing Climate: Academic Press, Inc., New York, p. 281-300.

Oksanen, L., Fretwell, D.S., Arruda, J. and Niemela, P., 1981, Exploitation ecosystems in gradients of primary productivity: American Naturalist, v. 118, p. 240-261.

Owen, M. and Black, J.M., 1989, Factors affecting the survival of barnacle geese on migration from the breeding grounds: Journal of Animal Ecology, v. 58, p. 603-617.

Piedboeuf, N., 1996, Qualité nutritive des sites d'alimentation des oisons de la grande oie des neiges: est-il avantageux d'utiliser des sites déjà broutés?: M.Sc. thesis, Université Laval, Sainte Foy, PQ, 69 p.

Reed, A., 1990, Population dynamics in a successful species: challenge in managing the increasing population of greater snow geese: Transactions of the International Union of Game Biologists Congress, v. 19, p. 136-142.

Reed, A., Boyd, H., Chagnon, P. and Hawkings, J., 1992, The numbers and distribution of greater snow geese on Bylot Island and near Jungersen Bay, Baffin Island, in 1988 and 1983: Arctic, v. 45, p. 115-119.

Reed, A. and Chagnon, P., 1987, Greater snow geese on Bylot Island, Northwest Territories, 1983: Journal of Wildlife Management, v. 51, p. 128-131.

Reed, A. and Plante, N., 1997, Decline in body mass, size, and condition of greater snow geese, 1975-1994: Journal of Wildlife Management, v. 61, p. 413-419.

Sedinger, J.S. and Raveling, D.G., 1988, Foraging behaviour of cackling Canada goose goslings: implications for the roles of food availability and processing rate: Oecologia, v. 75, p. 119-124.

Shaver, G.R. and Chapin, F.S., 1995, Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species: Ecography, v. 18, p. 259-275.

Tieszen, L.L., 1972, The seasonal course of aboveground production and chlorophyll distribution in a wet arctic tundra at Barrow, Alaska: Arctic and Alpine Research, v. 4, p. 307-324.

Ulrich, A. and Gersper, P.L., 1978, Plant nutrient limitations of tundra plant growth, *in* Tieszen, L.L., ed., Vegetation and Production Ecology of an Alaskan Tundra: Springer-Verlag, New York, p. 457-481.

Webber, P.J., 1978, Spatial and temporal variation of the vegetation and its production, Barrow, Alaska, *in* Tieszen, L.L., ed., Vegetation and Production Ecology of an Alaskan Tundra: Springer-Verlag, New York, p. 37-112.

Zoltai, S.C., McCormick, K.J. and Scotter, G.W., 1983, A natural resource survey of Bylot Island and adjacent Baffin Island, Northwest Territories: Parks Canada, Ottawa, ON, 176 p.

Accepted as revised 18 November 1996.