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The Role of Lichens, Reindeer, and Climate in Ecosystem Change on a Bering Sea Island

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ABSTRACT. Archived reports from an international controversy in the early 1890s over management of the harvest of fur seals, *Callorhinus ursinus*, on the Pribilof Islands in the southeastern Bering Sea provided an unanticipated record of observations on the growth of lichens in association with the prevailing climatic conditions. The abundance of lichens observed in plant communities on the Pribilof Islands prompted the introduction of reindeer, *Rangifer tarandus*, in 1911. Grazing pressure by the introduced reindeer brought changes to lichen presence in the plant communities of St. Paul Island of the Pribilofs: lichens were depleted, and vascular plants expanded to replace the depleted lichens in a climate that became markedly warmer and drier in comparison to that of the late 19th century. These changes are described primarily through the use of historical documentation. Dominance of lichens in the plant communities on the Pribilof Islands at the time of their discovery and settlement appears to have been a relict of their development in the cooler and moister climate that characterized the southern Bering Sea in the mid-Holocene.

Key words: lichens, reindeer, Pribilof Islands, grazing pressure, climate change, island ecosystem, lichenometry, fur seals

RÉSUMÉ. Des rapports archivés se rapportant à une controverse d'envergure internationale ayant eu lieu au début des années 1890 à propos de la récolte de l'otarie à fourrure, *Callorhinus ursinus*, sur les îles Pribilov dans le sud-est de la mer de Béring, ont permis de recueillir, par hasard, des observations sur la croissance des lichens en fonction des conditions climatiques en vigueur. L'abondance de lichens observée au sein de peuplements végétaux des îles Pribilov a favorisé l'implantation du renne, *Rangifer tarandus*, en 1911. Le taux de charge des pâturages résultant de la présence du renne a entraîné des changements sur le plan des lichens au sein des peuplements végétaux de l'île Saint-Paul des îles Pribilov. Ainsi, les lichens ont été appauvris et remplacés par des plantes vasculaires dans un climat qui se réchauffait et s'asséchait manifestement comparativement au climat de la fin du XIX[e] siècle. Ces changements sont principalement décrits au moyen de documentation historique. La dominance des lichens au sein des peuplements végétaux des îles Pribilov au moment de leur découverte, de même que leur établissement, semble être une relique de leur développement dans un climat plus frais et plus humide qui caractérisait le sud de la mer de Béring vers le milieu de l'Holocène.

Mots clés : lichen, renne, îles Pribilov, taux de charge des pâturages, changement climatique, écosystème de l'île, lichenométrie, otarie à fourrure

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INTRODUCTION

The Pribilof Islands, located in the southeastern Bering Sea, comprise St. Paul Island (103.6 km²), St. George Island (90.7 km²), and adjacent small islets (Fig. 1). Their discovery in 1786 by the Russian navigator Pribylov terminated the search for the primary breeding grounds of the northern fur seal, *Callorhinus ursinus*, whose pelts were among the most valued in the international fur trade at that time. The Pribilof Islands were uninhabited at the time of their discovery (Torrey and Krukoff, 1978). A Russian fur company relocated Unungan (Aleut) natives from the Aleutian Islands to the Pribilof Islands to aid in the harvest of northern fur seals, which returned annually to these islands to breed and bear their young. St. Paul, the only community on the island of St. Paul, currently has a population of about 500 people, and about 100 people live in the community on St. George. A National Weather Service (NWS) office is currently located on St. Paul Island at the airport (57˚10′ N, 170˚13′ W). Continuous weather observations have been recorded at St. Paul since 1949.

This paper reviews the history of the relationship between lichens and reindeer (*Rangifer tarandus* includes both reindeer and caribou) on the Pribilof Islands. A major source of information has been historical archives relating to the harvest and management of fur seals, which include information and photographs that allow interpretation of the relative presence and growth of lichens before

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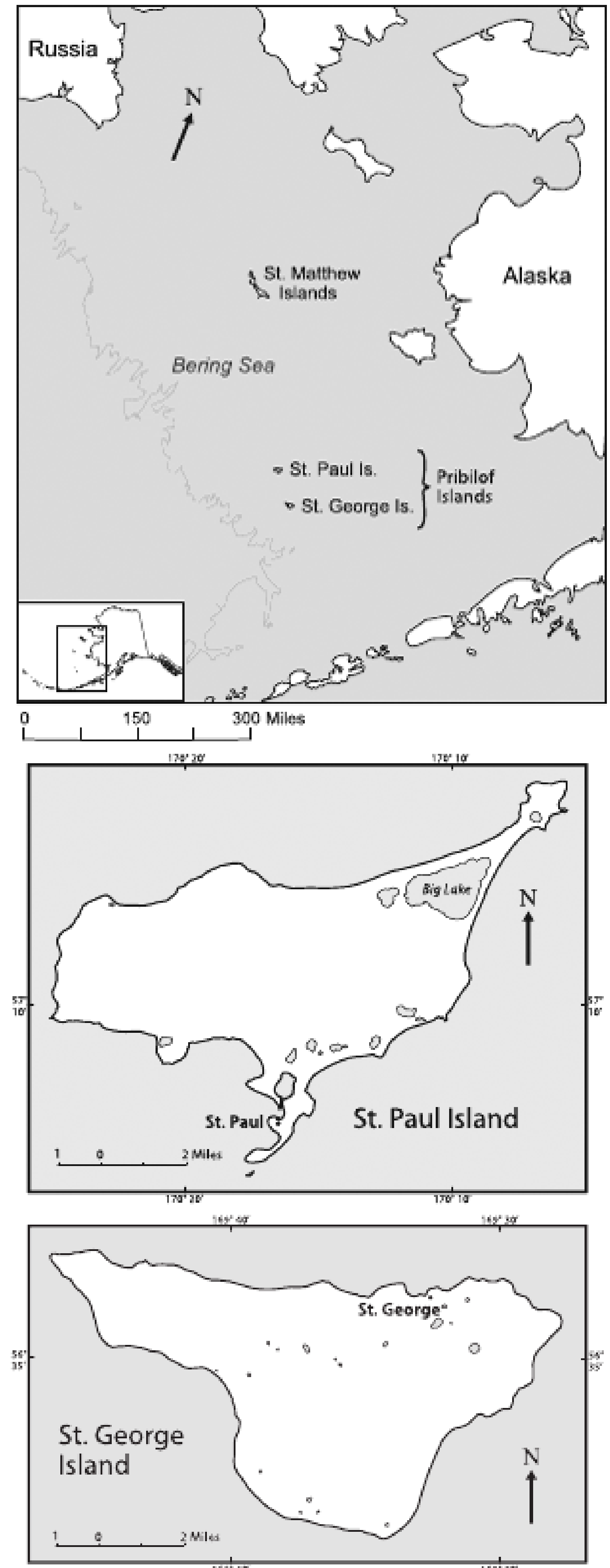

FIG. 1. Location in the southern Bering Sea of the Pribilof Islands, with accompanying maps of St. Paul and St. George Islands.

reindeer were introduced (Healy, 1889; TAFSC, 1892). These archives deal primarily with conditions on St. Paul Island, where the major fur harvest facilities, administrative headquarters, and harbor have been located. Similarly, detailed information on the reindeer, their numbers, and the effects of their introduction on vegetation has been limited mainly to St. Paul Island (Scheffer, 1951; Wilke and Hajny, 1965; Swanson and Baker, 1992). During visits to the Pribilofs by Klein, field reconnaissance surveys in plant communities used by the reindeer were carried out on St. Paul in 1985 and 2005 and on St. George in 2001. After their introduction, the reindeer were allowed to range freely over the island, and no attempts were made to move them seasonally in relation to optimal sustained production of forage types. On St. Paul, reindeer numbers have been monitored and associated range conditions assessed only occasionally, in years when federal agencies primarily responsible for management of the fur seals were able to arrange for such herd and range monitoring efforts. On St. George, which has been much more difficult to access, comparatively little effort has been directed toward the reindeer and their relation to the island vegetation. The limited information available on lichen and reindeer interaction on St. George Island has, necessarily, limited the primary focus of this paper to St. Paul Island.

FUR SEALS, LICHENS, AND REINDEER ON THE PRIBILOF ISLANDS

The Pribilof Islands, noted from the time of their discovery for persistent summer fog, support treeless maritime tundra. Visitors to the islands in the 1800s, before reindeer were introduced, noted the abundance there of lichens (Healy, 1889; Merriam, 1901–10), which are an important component of the winter diet of most reindeer and caribou. Their abundance in the tundra vegetation of the island at that time is evident in a photograph included in the report on a visit to the island in 1884 by Lieutenant J.E. Lutz of the U.S. Revenue Marine Service (Fig. 2a, Healy, 1889). Lichens, formerly included as cryptogams along with ferns, mosses, fungi, and algae, are a unique “plant” group involving a symbiotic fungal and algal or cyanobacterial relationship. Unlike most green plants, lichens lack roots and vascular systems to transport water and nutrients, so they derive moisture and other mineral requirements for growth directly from the atmosphere. On St. Paul, lichens were especially abundant on the rocky surfaces of lava fields, products of an earlier period of volcanism on the island (Hopkins and Einarsson, 1966). Scientists on the Harriman Expedition that visited the islands in 1899 described the landscape and the vegetation of the islands, commenting on the high abundance of lichens among their flora (Merriam, 1901–10).

After purchasing Alaska from Russia in 1867, the United States government assumed responsibility for the harvest of fur seals on the Pribilof Islands. However, it leased the rights to harvest seals to private corporations, under a quota system. The total population of fur seals present at the Pribilof Islands in the summer of 1873 was estimated at more than 4.5 million (Elliot, 1882). A decline in the numbers of fur seals returning annually, however, continued after the Alaska purchase. Harvest quotas were substantially reduced on the seal islands, but pelagic hunting of the seals, which resulted primarily in the killing of females, as well as illegal raids on the breeding grounds by crews from sealing schooners, accelerated the decline in the seal population (TAFSC, 1892). In 1892, the United States declared pelagic sealing in the eastern Bering Sea off limits to vessels of any nation. This action was challenged by Great Britain, representing Canada, where the majority of the pelagic sealers were based, and the attempt to resolve the controversy culminated in an international tribunal. The British disputed American claims of major declines in fur seal numbers on the Pribilofs and challenged the accuracy of their methods of estimating population trends. It was in this regard that the growth rates and abundance of lichens at that time played a major role in the method of assessing changes in fur seal numbers on the Pribilofs.

The absence of lichens on rocky surfaces within the seal haul-out areas of the Pribilofs was found to be a consequence of the seals' dragging themselves to and from the sea during their summer presence on the islands (Fig. 2b). American authorities on the Pribilofs in the late 1800s assessed the rate of recovery of the lichens in haul-out areas that seals had abandoned in order to verify the timing of abandonment. Thus, the time required for lichen regrowth in the old seal haul-out areas provided a basis for determining the timing and magnitude of the suspected decline in the seal population. The British, who questioned the reliability of this technique, arranged for Jason Macoun, a Canadian university botanist who had received his botanical training in England, to visit the Pribilofs in 1892, along with the Americans who were assessing the age of previously used seal haul-out areas. Macoun was able to assess rates of growth of lichens on the Pribilofs by observing their growth on the surface of rocks used in retaining walls and building foundations with known construction dates. These investigations convinced him that the atmospheric and substrate conditions on St. Paul Island were uniquely propitious for lichen growth. After his visit to the Pribilofs, Macoun was quoted in a report of the trip, which is included in the Appendix to the Counter Case of Great Britain of the Tribunal of Arbitration of the Fur Seal Controversy (TAFSC, 1892:503):

> I noticed at the time of my first visit to a rookery [abandoned] on St. Paul Island in 1892 [1st July] that much of this grass-covered ground was dotted with boulders of various sizes, upon which were mature lichens. Even small stones that were less than a foot above the ground were completely encrusted by them. … The climate of the Pribiloff [sic] Islands is in every way suited for the rapid growth of lichens, and every rock and stone that has been undisturbed for a sufficient length of time is covered with them. … It is thus evident that under the most favorable conditions, at least 20 years are necessary for the full development of lichens growing on these islands. The same or closely allied species on the coast of England have been found to require at least twice that length of time to fully mature.

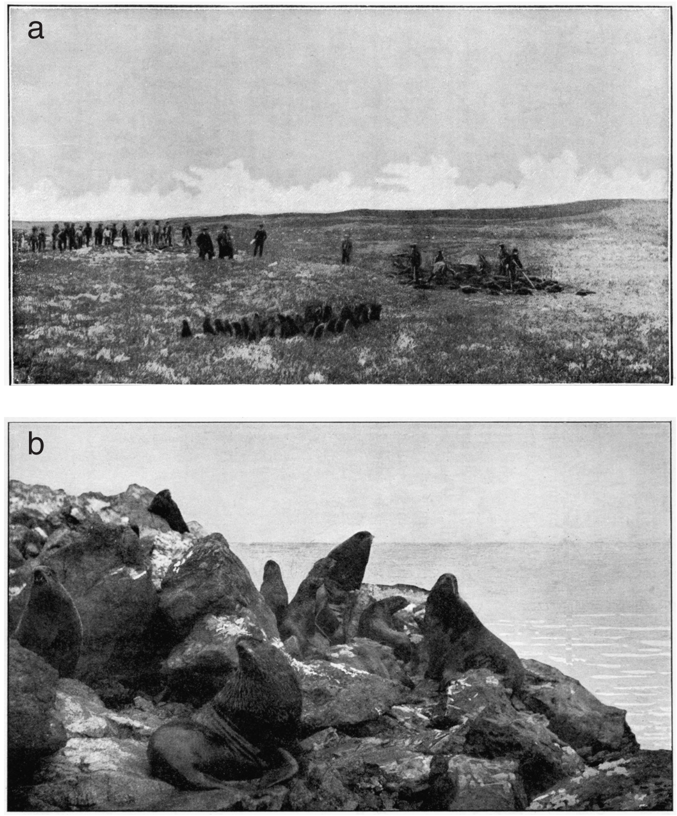

FIG. 2. a) The abundance of light-colored ground lichens is evident in the tundra of St. Paul Island in this 1884 photo taken at a fur seal slaughtering ground (Healy, 1889). b) An 1899 photo of fur seals on a rocky portion of a haul-out area on St. Paul Island. The light-colored lichens, presumably *Ramalina* sp., are evident only on surfaces of the larger rocks where they had not been rubbed off by the seals (Jordan, 1903).

PRIBILOF WEATHER FAVORS LICHEN GROWTH

Lichens, like all green plants, require heat, sunlight, and moisture for growth. In high latitudes, these are available only in summer. This region has a characteristically maritime summer climate, with frequent fog or low cloud cover, moderate temperatures, and light but persistent precipitation. Pegau (1969) recorded rates of growth of fruticose lichens on the foggy Bering Sea coast of the Seward Peninsula that exceeded those of tundra regions of Canada and Russia. Computer models developed recently to predict lichen growth in relation to hydration and desiccation rates in northern Sweden also emphasize the importance of sustained high ambient humidity for optimum lichen growth (Čabrajić, 2009). During May to September, the primary season for lichen growth on the Pribilofs, fog is present nearly 30% of the time, temperatures average 6.4˚C, and rainfall totals more than 260 mm, as determined using the most recent climatologically normal period (1971 – 2000) for St. Paul. This region of the Bering Sea is close to the Aleutian Low, a semi-permanent feature in the pressure field that persists during the cold season from October to March (Wang et al., 2006). Therefore, the stormy part of the year generally does not occur during the growing season. Snowfall normally occurs from October to May, with average seasonal totals of 145 cm (Shulski and Wendler, 2007).

We recovered 19th-century weather observations for May through November on St. Paul Island from the fur seal tribunal publication (TAFSC, 1892). These observations, available for the years 1872 – 83, were made by members of the U.S. Signal Service, the military agency responsible for meteorological observations at that time. They include monthly summaries of total precipitation, days with precipitation, mean temperatures, and percent of daily fog at St. Paul. Table 1 shows a comparison of these 19th-century data with May through September data for the years 1971 to 2000 (National Climatic Data Center, 2005). The differences between the two time periods illustrate a shift to warmer and drier conditions for the recent period. Daily percent fog in the 19th century during May through September, the months of primary growth potential for lichens and vascular plants, varied from a high of 41% in July to 8.5% in September. Although directly comparable data on fogginess were not collected during the 20th century, declining trends in both relative humidity and frequency of low cloud ceiling are apparent in the 1949 – 2000 climate record. This climate shift for the region has been documented by Shulski and Wendler (2007) and Klein and Shulski (2009). May through September is the primary growth season for both vascular plants and lichens on the Pribilof Islands; however, the increased warming and drying of recent decades have been much less favorable for lichen growth than the cooler, moister climate of the 19th century. During the 1800s, when the Pribilofs were reachable only by ship, the islands were noteworthy for their extreme fogginess in summer and were frequently referred to in ships' logs as "The Misty Islands." The maritime climate of St. Paul was presumably optimal for the growth of lichens in the 19th century when Macoun was there, as noted above.

REINDEER ENTER THE PRIBILOFS

The declining trend in population numbers of fur seals on the Pribilof Islands during the late 19th and early 20th centuries ultimately led to an International Fur Seal Treaty in 1911 between the United States, Great Britain (representing Canada), Russia, and Japan (U.S. Fish and Wildlife Service, 1961). The treaty and its subsequent modifications ultimately resulted in pronounced curtailment of the commercial seal harvest (Scheffer, 1955). The United States' oversight responsibility for managing the harvest of fur seals on the Pribilofs also extended to assuring the wellbeing of the Unungan (Aleut) residents of the islands, who played an essential role in harvesting the seals and preparing the seal skins for shipment to the fur-processing companies. Because of the continuing decline in numbers of seals on the breeding grounds, concern had also been expressed at that time over the heavy reliance of Pribilof islanders on fur seals as a subsistence food source. Additionally, since the annual cycle of the seals results in their absence from the islands in winter, seals were not available to the islanders as subsistence food in that season. In this context, government managers in the early 1900s considered introducing reindeer to the Pribilofs to provide an additional source of subsistence food for the islanders. Reindeer from Russian Chukotka had been successfully established on Alaska's Seward Peninsula during 1892 – 1902, only a short time earlier. Those involved with the transfer of the reindeer from Chukotka to the Seward Peninsula understood that lichens were the primary winter forage of the reindeer both in Chukotka and on the Seward Peninsula (Lantis, 1950). To government managers of the Pribilofs, the abundance of lichens on the islands at that time, the absence of large grazing animals, and the lack of natural predators appeared as optimal conditions for establishment of reindeer. In the short time that reindeer had been in Alaska, however, little experience had been gained on the response of lichens or the native vascular plants to grazing pressure by reindeer. Accordingly, desirable stocking levels necessary for sustainable production of lichens and other forage species in the presence of the reindeer had not been established.

Reindeer were introduced to the Pribilofs in 1911, when 25 animals were released on St. Paul Island and 15 on St. George (Scheffer, 1951). On St. Paul, those 25 reindeer increased to over 2000 by 1938; however, they then underwent a precipitous decline, and in 1951 only two remained. At that time, 31 reindeer from Nunivak Island were released on St. Paul (Wilke and Hajny, 1965). The reestablished population increased to a high of about 700 in 1962, and since then it has fluctuated widely below this level. Major population reductions have occurred periodically after large control harvests. Such harvests were designed to hold the population at a level thought to be sustainable, allowing continued production of sufficient suitable forage for the reindeer on the island. Substantial losses of animals have also occurred during occasional severe winters, when snow conditions (including icing on the snow surface and within the snow column) limited reindeer access to forage (Scheffer, 1951; Hanson, 1952; Wilke and Hajny, 1965).

The reindeer of St. George Island, in contrast to those on St. Paul, were poorly monitored following their introduction; however, they appear to have fluctuated differently than the St. Paul reindeer. After reaching an initial peak of 222 animals 11 years after its establishment, the St. George population declined markedly. During the next 15 years, while the St. Paul herd increased exponentially to a peak of 2000 animals before its precipitous decline, the St. George herd remained at a lower and more stable level of 40 – 60

TABLE 1. St. Paul precipitation and temperature data for March through September from 19th century archives (1872–83) (TAFSC, 1892) are compared with similar data from the 20th century (1971–2000) (National Climatic Data Center, 2005).

Month	Precipitation total (mm)		Days with precipitation		Average temperature (°C)	
	1872–83	1971–2000	1872–83	1971–2000	1872–83	1971–2000
May	46	31	25	14	0.9	2.0
June	54	36	20	13	4.7	5.5
July	85	49	24	15	7.3	8.1
August	90	75	28	18	8.4	9.1
September	111	71	27	19	7.2	7.2

animals (Scheffer, 1951). Little attention was paid to the St. George reindeer after they failed to follow the pattern of increase shown by those on St. Paul. They persisted at close to minimal levels for survival of the herd until additional animals were brought from the reestablished St. Paul herd in 1980 (Swanson and Barker, 1992). Subsequently, the St. George herd began slowly to increase, reaching more than 300 in 2009 (M. St. Martin, Natural Resources and Agricultural Sciences, University of Alaska Fairbanks, pers comm. 2009). On a visit to St. George Island in 2001, Klein walked through the southern portion of the island, south of the road from St. George village to the airport, which has always been the primary grazing area for the St. George reindeer. Fruticose lichens, which covered much of the relatively smooth substrate on the rolling hills of the landscape, had been heavily grazed and shattered. North of the road, the terrain is geologically younger, with extensive, poorly eroded lava fields. The extremely rough terrain is patchily vegetated with vascular plants in troughs between the ridges of lava, which often support an abundant mix of crustose, foliose, and fruticose lichens. The lichens showed little evidence of use by reindeer, and few fresh or winter fecal droppings were present in the limited area visited in 2001. Local residents explained that the northern portion of the island receives only light reindeer use, primarily by adult males in summer. The proximity of St. George reindeer to the village and the road throughout the year has given residents of this island easier access for hunting than has been the case on St. Paul. This factor has likely contributed to the differing patterns of reindeer population growth on the two islands.

REINDEER AND LICHENS ON ISLAND ECOSYSTEMS

Successful management of grazing lands in the North, as elsewhere, requires an understanding of the requirements for growth of the primary forage plants and their response to the grazing pressures of the herbivores that are present. Lichens have long been known to be the major component of the winter diet of most reindeer and caribou throughout their distribution in the Arctic and Subarctic regions of the world. In summer, however, these herbivores feed primarily on green plant material (Ahti, 1961; Zhigunov, 1968; Skuncke, 1969; Klein, 1970, 1982). In grazing systems at lower latitudes, large herbivores, both domestic and wild, feed almost exclusively on the tissues of green plants throughout the year, selecting the growing tissues when available in summer or the rainy season, and consuming the dormant or senesced above-ground portions of plants in winter or the dry season.

In the past, especially in North America, botanists or wildlife managers have expended relatively little effort, beyond gaining knowledge from indigenous herders or hunters of reindeer and caribou, to increase their understanding of the life processes of lichens (in contrast to rooted vascular plants) as components of northern grazing systems. Consequently, until recently relatively little has been known about the physiology, growth, and ecology of the lichens—a strange, symbiotic complex of fungal and algal forms of life, unrelated to the vascular plants—that dominate most grazing systems. We now know that thick mats of ground lichens tend to inhibit warming of the underlying soil in summer through their insulating effect, as well as their albedo effect (lichens reflect a higher proportion of incoming solar radiation than green plants). Lichens are able to grow over a wider temperature range than vascular plants; they can grow even under snow cover at temperatures slightly below freezing if sufficient light penetrates the snow to permit photosynthesis. However, lichens must remain moist in order for photosynthesis and growth to occur. Warmer summer temperatures with less fog and associated bright sunlight increase the frequency and duration of dry periods, which in turn stimulate dormancy of the lichens. The net effect for lichens, in contrast to green vascular plants, is reduced annual growth (Fig. 3).

It is not surprising that in 1911 there was little awareness of the potential consequences of introducing reindeer to the Pribilofs, or of how the presence of introduced reindeer might result in changes to the plant community structure on these islands. This naïveté is reflected in the following comments made in 1914 by E.L. Jones, an agent of the U.S. Bureau of Fisheries, following his visit to the Pribilof Islands (Jones, 1915:136):

> There is nothing that will prove more beneficial to both islands than the already established reindeer. … The fact that reindeer do not disturb or eat it [he presumably was referring to both grasses and sedges], subsisting principally on the reindeer or white moss, suggested the question as to whether this grass could not be utilized in summer for feeding to a number of cattle.

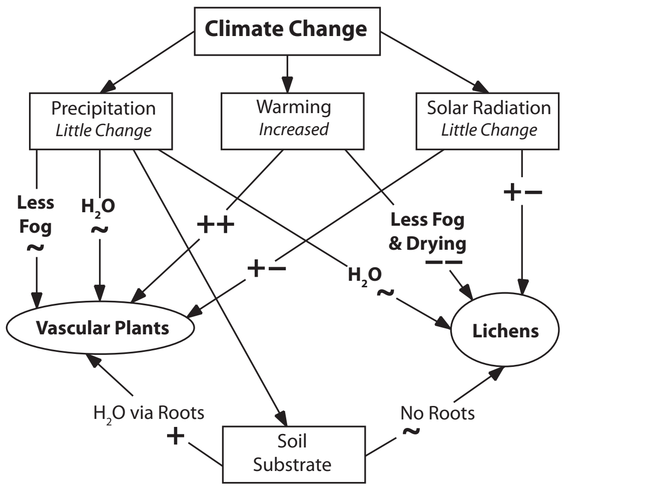

FIG. 3. Flow diagram showing positive, neutral, and negative influences of climate change on growth of lichens versus vascular plants on the Pribilof Islands during recent decades. The diagram is based on weather data from Table 1 and recent publications on lichen ecology and modeling of parameters of lichen growth described in the text (Klein, 1972; Čabrajić, 2009; Klein and Shulski, 2009).

FIG. 4. A July 2005 view of an enclosure erected in the 1960s on St. Paul Island when the reindeer had again increased to high density and lichens had been eliminated as significant components of the island's plant communities. Lupine, wild celery, and other vascular plants were quick to expand into the previously lichen-dominated communities following removal of the lichens and trampling disturbance by the grazing reindeer. The lush and dense growth of the vascular plants, through their shading effect, precluded reestablishment of lichens both inside and outside of the enclosure. (Photo by D.R. Klein.)

Jones obviously was familiar with the importance of grass to cattle on grazing lands in the western states, but he had no understanding of the seasonal variability in the diet of reindeer or the different responses of lichens and grasses to grazing pressure.

By the early 1940s, after the St. Paul reindeer had reached their peak population of 2000 animals and had begun a precipitous decline, the earlier presumption that the lichen-rich maritime tundra of the Pribilof Islands portended an auspicious future for the reindeer was being challenged. The biologist Ford Wilke, reporting on a visit to St. Paul in late November of 1942, observed that, "The lichen commonly called reindeer moss is practically gone from the Island…and none was seen in the stomachs [of autopsied reindeer]" (F. Wilke in Scheffer, 1951:358). Scheffer had pointed out, on the basis of L.J. Palmer's investigations in the lichen-dominated grazing areas used by reindeer in northwestern Alaska (Palmer and Rouse, 1945), that the St. Paul herd, at its peak population, was at least three times the recommended carrying capacity for the range. The plant ecologist H.C. Hanson (1952) observed that the lichens were severely overused on St. Paul when he did a reconnaissance of the reindeer range there in 1952.

Talbot et al. (2001), during their study of lichen species diversity on St. Paul in 1997, found it necessary to make a "concerted effort" to sample sites where the reindeer could not graze, such as high on rock surfaces and deep among boulders, because of the heavy grazing and trampling effect of the reindeer on lichens elsewhere. As a consequence of the damage and removal of lichens through grazing and trampling by the large populations of reindeer, several vascular plant species, especially lupine (*Lupinus nootkatensis*), wild celery (*Angelica lucida*), and sedges (*Carex* spp.), have readily expanded into the areas of exposed soil vacated by the lichens. Many residents of St. Paul, on observing the increase of vascular plants at the expense of lichens, presciently suggested that the causes were too many reindeer and climate warming (V. Merculieff, TDX Corporation, St. Paul, Alaska, pers. comm. 2008). Although reindeer also consume vascular plants, at least seasonally, once these plants are established where lichens had previously been present, they preclude reestablishment of the lichens through their shading effect (Fig. 4).

DISCUSSION AND CONCLUSIONS

It was the lush growth of lichens on the Pribilofs, as observed by visitors to these islands in the 19th century, and the documented evidence of their rapid growth, that provided encouragement for the establishment of reindeer there. Climate warming and the associated drier conditions in recent decades have slowed regrowth of the lichens on St. Matthew Island, about 370 km north of St. Paul, which had been severely overgrazed by introduced reindeer (Klein and Shulski, 2009). During the same climate regime, lichens in caribou wintering areas of northwestern Alaska have shown a similar pattern of reduced growth, whereas increased growth of vascular plants has brought about a greening of the landscape at the expense of the lichens (Joly et al., 2009).

Since the time of the discovery and settlement of St. George and St. Paul islands in the 18th century, differences between the two islands in geology, climate, structure of plant communities, and the presence of bird and mammal species have been observed (Macoun, 1899; Gabrielson and Lincoln, 1959; Hopkins and Einarsson, 1966; MacDonald and Cook, 2009). The complex of plants and animals on St. George show stronger affinities with the Aleutians, whereas the flora and fauna of St. Paul reflect a stronger influence of the Arctic system. An increase in Arctic species with increasing latitude is apparent in the flora of St. Matthew Island (Klein, 1968, 1987) and St. Lawrence Island (Young, 1971), ca. 370 and 660 km respectively to the north of St. Paul in the Bering Sea. Although St. Paul and St. George are separated by only 40 miles, the mean southern limit of winter sea ice lies midway between the two islands, and the mean annual temperature on St. George is a few degrees warmer than on St. Paul. Monthly weather during the summer plant growth season (May through September) was recorded at St. Paul from the early 1870s through the early 1880s. These data indicate that a cooler, moister, and presumably foggier climate existed at that time in comparison to the subsequent and continuous 20th-century record of more than 50 years. The difference is most pronounced when compared to recent decades following the step increase in climate warming in the Bering Sea region in the mid-1970s (Luchin et al., 2002). The cooler, moister climate and associated foggy conditions in the 1800s clearly would have favored the growth of lichens at the expense of vascular plants.

Ground lichens, formerly dominant in plant communities of the maritime tundra of St. Paul Island, were virtually eliminated through grazing pressure by introduced reindeer. The rapid growth and peak population numbers reached by the reindeer following their introduction were achieved through their winter reliance on reserves of lichen biomass that had accumulated when no reindeer or other large herbivores were present on the island. In some island ecosystems outside of the Arctic, introduced reindeer left to roam freely have essentially eliminated lichens that were present as significant components of the plant community structure, replacing them in the winter diet with graminoid species that have proved resistant to grazing pressure (Leader-Williams, 1988). In West Greenland, where they have no natural predators, caribou depleted lichens (but not grasses and sedges) in the drier interior regions of their habitat, though not in the moister coastal wintering areas (Thing, 1984). An additional influence on vegetation in such cases is the fertilization effect of recycling nutrients to the soil via the feces and urine of these herbivores, which would benefit rooted vascular plants, but not lichens. Similarly, when Svalbard reindeer, *Rangifer tarandus platyrhincus*, regained access to "insular" and lichen-rich habitats that had been vacated for nearly a century, they increased rapidly, and the lichens were eliminated as a forage resource for the reindeer (Van der Wal et al., 2001). Similar patterns of island hopping by caribou and wild reindeer to exploit accumulated lichen forage reserves, followed by disappearance of these island populations after those reserves are depleted, have been reported (Kishchinskii, 1971; Klein, 1999) or reconstructed from fossil evidence (Forman et al., 2000) on Franz Josef Land. In these insular systems, the annual growth of lichens cannot compensate for the selective removal of their tissues by the caribou or reindeer in winter, especially where these herbivores lack natural predators, are constrained in their movements, and may continue to forage on lichens in summer because vascular plant biomass suitable as forage is limited. Trampling of the lichens in summer also impedes recovery from tissue lost to grazing. The abundance and lush growth of lichens observed by visitors to the Pribilof Islands in the 1800s were a product of a cooler and more moist climate, which was more favorable for lichens and less so for most vascular plants than at present. The Pribilof Islands lie at the southern limit of seasonal ice in the Bering Sea, so the maritime tundra supports more prolific growth of vascular plants on the Pribilofs than on the St. Matthew Islands to the north (Klein and Shulski, 2009).

Management of reindeer population levels on St. Paul Island since their introduction has suffered from a lack of understanding of the ecology of lichens in the maritime tundra communities of the island. And of particular importance was the lack of appreciation of the constraints imposed by small islands on sustaining lichens as a forage component without close control of reindeer numbers. Since reindeer were introduced on these remote islands in 1911, efforts directed toward their management by government agencies have been limited and sporadic, since the primary responsibilities assigned to these agencies were toward the fur seals and other marine resources of the islands. As a consequence of the substantial climatic change, the introduction of reindeer to St. Paul Island, and the associated changes in plant community structure involving replacement of lichens by lupine, wild celery, and sedges, recovery of lichens to their former presence is an unlikely possibility even with complete removal of the reindeer.

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