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The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems[1]

Gilles GAUTHIER[2], Département de biologie and Centre d'études nordiques, Université Laval, Québec, Québec G1V 0A6, Canada.
Dominique BERTEAUX, Joël BÊTY & Arnaud TARROUX, Canada Research Chair in Conservation of Northern Ecosystems and Centre d'études nordiques, Université du Québec à Rimouski, Rimouski, Québec G5L 3A1, Canada.
Jean-François THERRIEN, Département de biologie and Centre d'études nordiques, Université Laval, Québec, Québec G1V 0A6, Canada.
Laura MCKINNON, Canada Research Chair in Conservation of Northern Ecosystems and Centre d'études nordiques, Université du Québec à Rimouski, Rimouski, Québec G5L 3A1, Canada.
Pierre LEGAGNEUX & Marie-Christine CADIEUX, Département de biologie and Centre d'études nordiques, Université Laval, Québec, Québec G1V 0A6, Canada.

Abstract: It is increasingly recognized that ecosystems are not closed systems and that exchanges of resources across ecosystem boundaries can have repercussions on food webs, especially in low productivity systems such as the terrestrial Arctic. However, because these exchanges can take multiple forms, assessing their significance in the functioning of the tundra food web is difficult. In this paper, we first review some important concepts related to resource exchanges between ecosystems and examine their relevance to the study of trophic interactions in the arctic tundra. An analysis of the Bylot Island food web in the Canadian Arctic using a mass-balance trophic model suggests that predators are the dominant force controlling this food web. However, an important feature of this ecosystem is that several top predators benefit from allochthonous inputs, either through the presence of migratory birds during the summer or the use of the marine environment as a foraging ground in winter. We also show that migratory birds may act as autochthonous resource exporters for lower trophic levels, for instance by removing nitrogen from the nutrient pool when young produced locally migrate south and die away from the system. Although these resource exchanges may be a general feature of several arctic terrestrial ecosystems, their importance in the functioning of the tundra food web remains to be determined. Through long-term monitoring, we found that primary production in wetlands of Bylot Island increased by 85% over a 20-y period, likely a consequence of the warming trend observed in the area. However, we have not detected any changes at higher trophic levels, which is consistent with a top-down control of this food web. Given the importance of resource exchanges between ecosystems in the dynamics of the tundra food web, a full investigation of the effects of climate change will require a broader cross-ecosystem perspective.
Keywords: allochthonous input, arctic predator, climate change, cross-ecosystem resource exchange, trophic interaction, tundra food web.

Résumé : On reconnaît de plus en plus que les écosystèmes ne sont pas des systèmes fermés et que les échanges de ressources entre écosystèmes peuvent avoir des répercussions sur les réseaux trophiques, surtout dans les systèmes peu productifs comme le milieu terrestre arctique. Ces échanges peuvent prendre des formes multiples, ce qui rend difficile l'évaluation de leur importance pour le fonctionnement du réseau trophique de la toundra. Dans cet article, nous passons d'abord en revue des concepts importants reliés aux échanges entre écosystèmes et nous évaluons ensuite leur pertinence pour l'étude des interactions trophiques dans la toundra arctique. Une analyse du réseau trophique de l'île Bylot dans l'Arctique canadien réalisée à l'aide d'un modèle de bilan de masse indique que les prédateurs sont la force dominante structurant ce réseau. Cependant, un aspect important de cet écosystème est que plusieurs prédateurs utilisent des ressources allochtones grâce à la présence d'oiseaux migrateurs durant l'été ou en s'alimentant dans l'environnement marin en hiver. Nous démontrons également que les oiseaux migrateurs peuvent agir comme des exportateurs de ressources autochtones pour les niveaux trophiques inférieurs, par exemple en retirant de l'azote du réservoir de nutriments lorsque les jeunes produits localement migrent vers le sud et meurent à l'extérieur du système. Bien que ces échanges puissent être une caractéristique générale de plusieurs écosystèmes terrestres arctiques, leur importance reste à déterminer pour le fonctionnement du réseau trophique de la toundra. Grâce à un suivi à long terme, nous avons mesuré une augmentation de 85 % de la production primaire des milieux humides de l'île Bylot en 20 ans, vraisemblablement due au réchauffement observé dans cette région. Toutefois, nous n'avons détecté aucun changement dans les niveaux trophiques supérieurs, ce qui est en accord avec l'hypothèse d'un contrôle descendant de ce réseau trophique. Considérant l'importance des échanges entre écosystèmes dans la dynamique du réseau trophique de la toundra, une investigation complète des effets des changements climatiques nécessitera une perspective plus large englobant plusieurs écosystèmes.
Mots-clés : changement climatique, échange entre écosystèmes, interaction trophique, prédateur arctique, réseau trophique de la toundra, ressource allochtone.

Nomenclature: Porsild & Cody, 1980; American Ornithologists' Union, 1998; Wilson & Reeder, 2005.

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[2]Author for correspondence.
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Introduction

The tundra is characterized by low primary production primarily because of the harsh climate that prevails most of the year. Because of this low productivity, tundra food webs generally have a low biodiversity and a relatively simple structure (Krebs *et al.*, 2003). Oksanen *et al.* (1981) proposed the exploitation ecosystem hypothesis (EEH), according to which the primary production of an ecosystem influences the length of the food chain that it can sustain and hence determines whether plant–herbivore or predator–prey interactions will dominate the system. According to the EEH, primary production of the tundra should be sufficient to support herbivore populations but should generally be too low to support viable predator populations dependent upon these herbivores; hence, the system should be dominated by the plant–herbivore interactions (Oksanen, 1983; Oksanen & Oksanen, 2000). Under such conditions, herbivores could impose a strong control on plant biomass but predators should be relatively unimportant. When moving south through a latitudinal gradient of primary production (*e.g.*, from the tundra to the boreal forest), primary production will eventually be high enough to support viable populations of both herbivores and predators. Predator–prey interactions should then become significant and could allow predators to depress or even control herbivore populations (Oksanen, 1992; Crête, 1999; Oksanen & Oksanen, 2000).

It is clear that herbivores can have, under some circumstances, a strong impact on the tundra vegetation. Examples include several caribou (*Rangifer tarandus*) herds in North America (Jefferies, Klein & Shaver, 1994; Manseau, Huot & Crête, 1996), snow geese (*Chen caerulescens*) in coastal marshes of Hudson Bay (Kotanen & Jefferies, 1997; Jefferies, Jano & Abraham, 2006), and small mammals in northern Fennoscandia (Moen, Lundberg & Oksanen, 1993; Hambäck *et al.*, 2004). However, in contradiction to the EEH, there is increasing evidence that predators may also play an important role in some tundra food webs. For instance, predators can depress small mammal populations in several areas of North America and Greenland and perhaps sometimes drive their population cycles (Reid, Krebs & Kenney, 1995; Wilson, Krebs & Sinclair, 1999; Gilg, Hanski & Sittler, 2003; Gauthier *et al.*, 2004). It thus appears that the control of the tundra food web may be more complex than the simple view of the EEH model.

A limitation of the EEH model is that it considers the tundra as a closed system. However, an ecosystem cannot be understood in isolation (Polis, Anderson & Holt, 1997; Jefferies, 2000; Polis *et al.*, 2004). Frequently, species belonging to a given ecosystem can be subsidized by resources coming from other ecosystems (allochthonous inputs). This can have considerable direct effects on the dynamics of some populations of the receiving ecosystem, with additional indirect effects on prey or predators of the subsidized populations (Polis, Anderson & Holt, 1997; Polis *et al.*, 2004; Leroux & Loreau, 2008). Although the occurrence of allochthonous subsidies in the tundra ecosystem has been recognized before (Oksanen, 1990; Jefferies, 2000; Oksanen *et al.*, 2008), we argue that its significance for the functioning of the tundra food web has been underestimated.

The Arctic is currently experiencing rapid changes, most notably due to the strong warming trend affecting the circumpolar world (Moritz, Bitz & Steig, 2002; ACIA, 2005; Kaufman *et al.*, 2009). This has considerable impacts on both physical and biological systems, including retreat of the sea ice (Kerr, 2007), shortening of the snow season (Post *et al.*, 2009), warming and thawing of the permafrost (Smith, *et al.*, 2010), and "greening up" of the Arctic (Sturm, Racine & Tape, 2001; Tape, Sturm & Racine, 2006). However, the consequences of climate change on the tundra food webs remain poorly documented. How food webs will be affected by these changes will depend in part on whether they are primarily controlled by resources (bottom-up control) or predators (top-down control). The amplitude of allochthonous subsidies may also play a key role, because they can either amplify or dampen the effects of changing environmental conditions on different trophic levels (Leroux & Loreau, 2008).

In this paper, we first explain some basic concepts related to exchanges between ecosystems and examine their relevance to the tundra. We then describe the long-term study of the tundra food web of Bylot Island (Nunavut, Canada), draw examples from this study to illustrate the various forms that allochthonous subsidies can take, and make a preliminary assessment of their role in the functioning of the food web. Finally, we use data from the long-term monitoring program conducted at this site to show current impacts of climate warming on some trophic levels, and we discuss how these impacts should interact with exchanges between ecosystems in affecting the arctic terrestrial food web.

Resource exchanges between ecosystems: Some basic concepts

"Allochthonous" means "originating in a place other than where it is found". In ecology, allochthonous inputs in a given ecosystem occur via movement of organic or inorganic resources across habitat or ecosystem boundaries, thereby establishing trophic connectivity (Polis, Anderson & Holt, 1997; Huxel & McCann, 1998; Spiller *et al.*, 2010). Movements of resources across ecosystems can take several forms, subsidize multiple trophic levels in the receiving ecosystem (Polis *et al.*, 1996), and lead to so-called trophic cascades (Polis, Anderson & Holt, 1997; Leroux & Loreau, 2008). Nutrients and detritus can flow both passively via gravity, wind and currents (Hodkinson *et al.*, 2001; Rose & Polis, 1998) and actively via mobile animals (Nowlin *et al.*, 2007; Hahn, Bauer & Klaassen, 2008; Hocking & Reimchen, 2009). For instance, prey can move from one ecosystem to another, providing resources for local consumers (*e.g.*, migratory birds; Gauthier *et al.*, 2004).

The spatial flow of resources among ecosystems can be considered a driving force in the food web dynamic of the receiving ecosystem, especially when the difference in productivity between ecosystems is high (Polis & Hurd, 1996; Polis *et al.*, 1996). Arctic tundra ecosystems exhibit low productivity compared to the surrounding marine ecosystems or to temperate terrestrial ecosystems

(Oksanen, 1983; Springer, McRoy & Flint, 1996). Therefore, we can predict that trophic dynamics of the arctic tundra will be influenced by the strength of allochthonous inputs from these more productive systems. Although we expect relatively little passive input of nutrients from other terrestrial ecosystems or of detritus from the neighbouring marine ecosystem, movements of consumers and prey are of particular interest in the insular and coastal arctic tundra ecosystem. Indeed, several consumers and prey can move from the tundra to other ecosystems.

Marine allochthonous resources are generally acquired at the boundary between marine and terrestrial ecosystems (Rose & Polis, 1998; Barrett *et al*., 2005; Spiller *et al*., 2010) or when prey such as salmon move upstream and become accessible to terrestrial predators (Ben-David, Flynn & Schell, 1997; Darimont & Reimchen, 2002). In the Arctic, however, presence of the sea ice allows terrestrial predators that are sufficiently mobile to move across ecosystem boundaries and acquire allochthonous resources during most of the year. In some areas, Inuit experts have reported seasonal and short-term movements of arctic foxes (*Vulpes lagopus*) on the sea ice, particularly in spring when seal pups are available (Gagnon & Berteaux, 2009). Satellite-tracking of adults and juveniles revealed that individuals can spend several months on the ice (Pamperin, Follmann & Person, 2008; Tarroux, Berteaux & Bêty, 2010), and other studies have documented the use of marine resources by adults in winter and spring (Roth, 2002).

In the arctic tundra, migratory birds provide a multi-faceted example of exchange between ecosystems as they can simultaneously represent consumers and prey moving across ecosystem boundaries. Even though migratory birds belong to the arctic terrestrial ecosystem in the sense that they breed there every year, their populations are maintained by resources obtained in distant temperate or tropical ecosystems during migration and winter. Therefore, these species can generate allochthonous inputs into the tundra food web for higher trophic levels. An example is provided by arctic-nesting geese, whose eggs and young are heavily predated by tundra predators such as the arctic fox (Samelius & Lee, 1998; Samelius & Alisauskas, 2000; Bêty *et al*., 2002). The subsidizing effect of goose eggs on fox populations is extended due to the egg caching/hoarding behaviour of the arctic fox (Careau, Giroux & Berteaux, 2007; Samelius *et al*., 2007; Careau *et al*., 2008a,b), which enables foxes to access eggs well after the geese have departed. However, if an herbivore population increases in abundance due to an allochthonous input without a concomitant increase in predation, this can have a strong influence on lower trophic levels. An example is the effect of snow geese on primary production in the coastal, sub-arctic ecosystem of West Hudson Bay, a phenomenon that has been referred to as an apparent trophic cascade (Jefferies, Rockwell & Abraham, 2004). The increase in agricultural food subsidies available during winter caused a demographic explosion of this snow goose population, which led to intense over-grazing on their arctic breeding grounds and severe impacts on plant communities, with large-scale habitat degradation (Jefferies, Rockwell & Abraham, 2004; Jefferies, Jano & Abraham, 2006).

Much of the discussion on resource flow concerning arctic migratory birds has focused on allochthonous inputs. Considerably less attention has been paid to the potential importance of nutrient uptake and its subsequent export when the offspring of these organisms depart at the end of the breeding season. In years of high reproductive output, millions of juvenile birds will depart from the arctic breeding grounds on their first southward migration. Given that the body mass of these juveniles is derived almost entirely from arctic resources, and that a great majority of these birds will not survive their first year due to high juvenile mortality, this could represent a considerable net export of biomass and nutrients from the arctic tundra. We examine this question in greater detail below.

Methods

Study site

Bylot Island is an 11 100 km^2 island located at the northern tip of Baffin Island, Nunavut, Canada (Figure 1). The 1600 km^2 south plain, which is bordered to the north by mountains (up to 2000 m) and an ice cap and to the south by the sea (Navy Board Inlet and Eclipse Sound), is covered by relatively lush tundra vegetation for this latitude. This region is characterized by flat lowlands and upland plateaus dissected by valleys, with elevations generally below 350 m above sea level. Average annual temperature is –14.5 °C (Cadieux *et al*., 2008). During the summer months (June to August), the average temperature is 4.5 °C and the average number of thawing degree-days is 438. Snow cover is present on the ground typically from late September to mid-June.

We can recognize 3 main plant communities on Bylot Island, which are largely determined by soil moisture. Wetlands occur in low-lying areas such as along streams and shallow ponds and, most commonly, in low-centre tundra polygons created by the growth of ice wedges in the permafrost. These sites are typically moss-covered fens dominated by grasses and sedges such as *Dupontia fisheri*, *Carex aquatilis*, and *Eriophorum scheuchzeri*. Mesic tundra covers most of the landscape on plateaus and gentle slopes. Common plants of these communities include shrubs (*Salix* spp., *Vaccinium uliginosum*), forbs (*Luzula* spp., *Cassiope tetragona, Oxytropis maydelliana*, *Astragalus alpinus*, *Oxyria digina*, *Polygonum viviparum*), grasses (*Arctagrostis latifolia, Poa arctica*), and some mosses. Finally, exposed areas with dry, gravel soil such as ridges or high-elevation sites have a very sparse vegetative cover consisting of only a few plant species, such as *Dryas integrifolia* or *Saxifraga oppositifolia* (Gauthier, Rochefort & Reed, 1996; Duclos, 2002).

Our activities are conducted primarily at 2 sites on the island, the Qarlikturvik Valley (*ca* 50 km^2; 73° 08' N, 80° 00' W) and a secondary site 30 km to the south (*ca* 30 km^2; 72° 53' N, 79° 55' W), where a large snow goose nesting colony is present. However, some of the monitoring activities (*e.g*., for arctic foxes and some avian predators) encompass the entire coastal area between these 2 sites (up to 520 km^2).

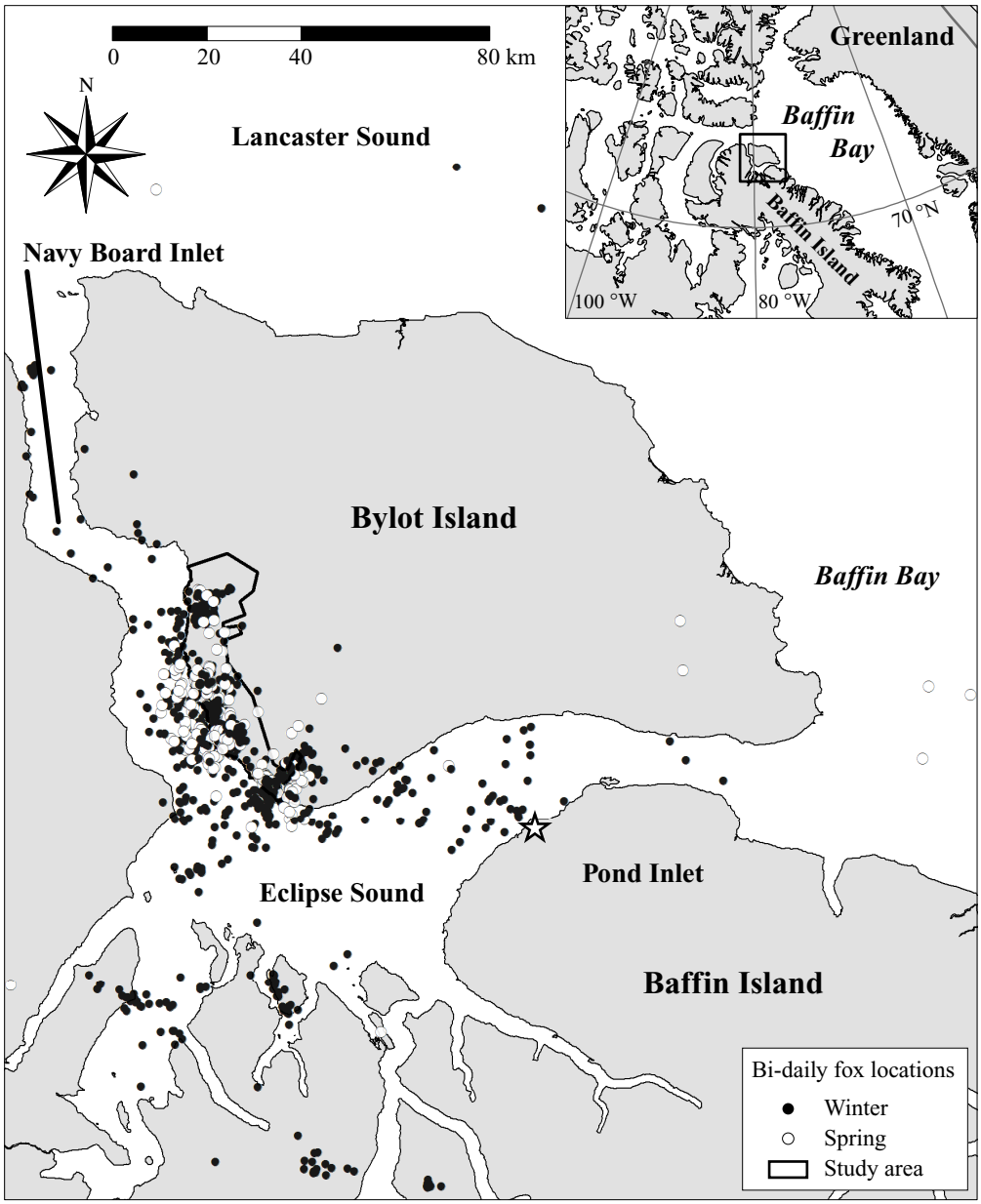

FIGURE 1. Winter (black dots; November to March) and spring (white dots; April–May) bi-daily locations (*i.e.*, 1 location every 48 h) of adult arctic foxes marked on Bylot Island and tracked by satellite from 2007 to 2009. Data from all individuals and both years were pooled by season to better illustrate global utilization of sea ice (n = 1700 locations, 18 individuals, including 6 in 2007-2008 and 15 in 2008-2009). Precision of locations is typically ≤ 1.5 km, based on information delivered by the Argos system (for details about precision of Argos locations see Tarroux, Berteaux & Bêty, 2010). A few individuals wandered outside the area shown on this map.

FIELD METHODS

We have maintained since 1994 a fully automated weather station operating year-round in the Qarlikturvik Valley (located at 20 m above sea level). The station records on an hourly basis air temperature and humidity (at 2 m), soil temperature (at depths of 2 and 10 cm), wind speed and direction (at 3 m), snow depth, and solar radiation. Daily precipitation is recorded manually during the summer (1 June to 20 August) using a pluviometer. Snowmelt is monitored manually from 1 June until snow disappearance by measuring snow depth along transects and by visually estimating snow cover over the study area at 2-d intervals. We also retrieved weather data from the Environment Canada weather station located at the Pond Inlet airport on Baffin Island (72° 41' N, 77° 59' W; 80 km southeast of the Qarlikturvik Valley weather station). Weather data from our automated station and Pond Inlet over the period 1995-2004 were highly correlated and thus could be used to extend the time series of climatic data from our station (once properly adjusted; see Dickey, Gauthier & Cadieux, 2008 for statistical analyses).

We have monitored the annual plant production in wetlands of the Qarlikturvik Valley since 1990. Each year, 12 new exclosures (1 × 1 m) made of chicken wire are installed in late June to prevent goose grazing. At the end of the plant-growing season (*i.e*., mid-August), we sample the vegetation inside exclosures by removing a piece of turf of 20 × 20 cm in each exclosure. All live aboveground plant biomass is cut, sorted into sedges (*Eriophorum scheuchzeri* or *Carex aquatilis*), grasses (mostly *Dupontia fisheri*), and forbs, dried, and weighed. Live aboveground biomass in mid-August is a good measure of annual graminoid plant production (Gauthier *et al*., 1995).

An annual index of lemming abundance has been obtained with snap-traps since 1993 in the Qarlikturvik Valley and since 1997 at our secondary study site. Since 2004, monthly density of brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings has been estimated via capture–mark–recapture methods using live-trapping data from two 11-ha grids in the Qarlikturvik Valley during the summer (see Gruyer, Gauthier & Berteaux, 2008; 2010 for details).

We have monitored annually the reproductive activity of a large number of birds. These species include the snow goose (since 1990), snowy owl (*Bubo scandiacus*, since 1993), Lapland longspur (*Calcarius lapponicus*, since 1995), long-tailed jaeger (*Stercorarius longicaudus*), parasitic jaeger (*Stercorarius parasiticus*), and glaucous gull (*Larus hyperboreus*, all 3 since 2004), shorebirds (since 2005), and rough-legged hawk (*Buteo lagopus*, since 2007). For most of these species, nests are found during systematic searches of the study area (though in some cases, *e.g*., longspurs, nests are found opportunistically). Nests are revisited periodically to determine their content (clutch size), phenology (laying date), and success (number of young hatched or fledged) (see Lepage, Gauthier & Menu, 2000; Gauthier *et al*., 2004; and McKinnon & Bêty, 2009 for methods). These data provide information on annual abundance and reproductive success of these species. Satellite-tracking of snowy owls was also conducted over the period 2007-2010 (Therrien, Gauthier & Bêty, 2011).

We monitored arctic fox dens opportunistically from 1993 to 2002 and systematically throughout the study area since 2003. Known fox dens are checked for breeding activity every year in summer (Szor, Berteaux & Gauthier, 2008). Since 2003, adult and juvenile arctic foxes are captured, marked with ear-tags, and sampled for carbon–nitrogen isotopic analyses (Tarroux *et al*., 2010). Finally, intensive satellite-tracking of adults was started in 2007 to monitor their year-round movements (Tarroux, Berteaux & Bêty, 2010).

Results

Bylot Island food web

The food web of Bylot Island is relatively diverse for its latitude (Figure 2). We have divided the species into 3 main categories. Resident species are those that are present year-round. Migrants are present only during the brief summer and leave for distant, southerly locations during winter. Finally, partial migrants form an intermediate category as

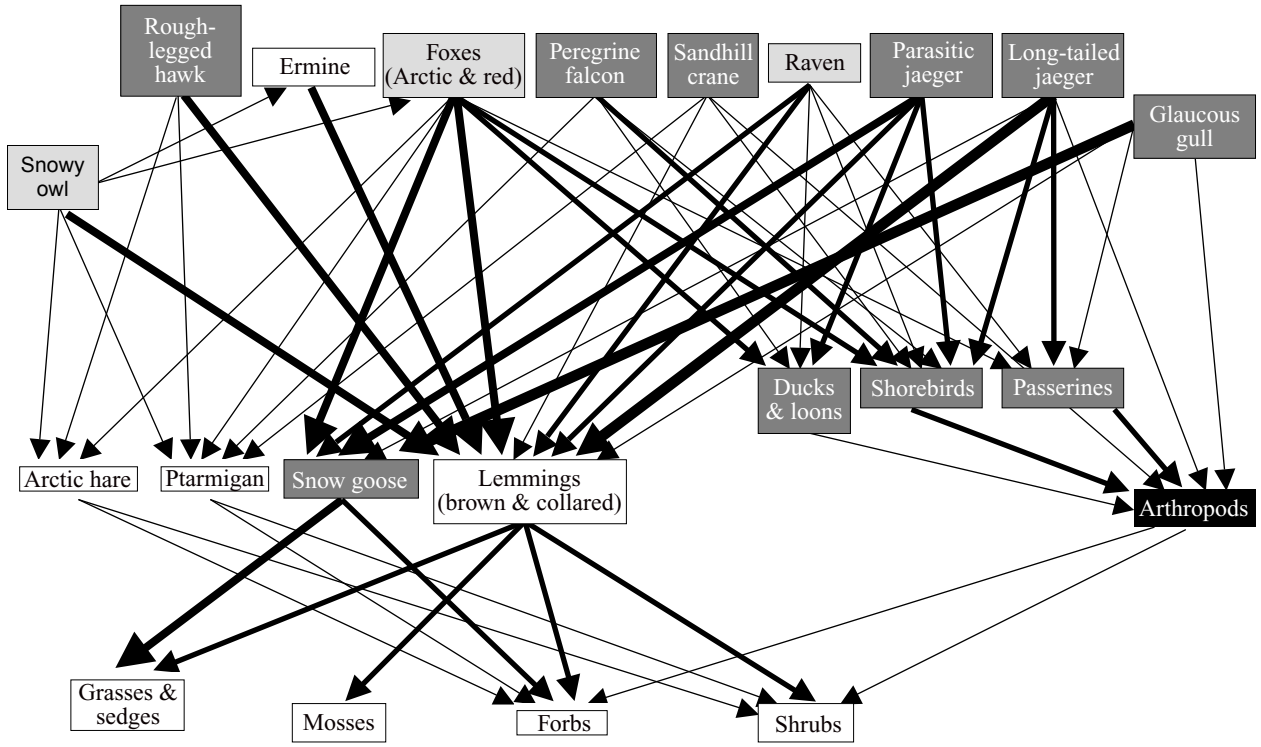

Figure 2. Bylot Island food web illustrated using 4 species categories: migrant (dark grey), partial migrant (light grey), resident (white), and resident frozen in the soil during winter (black). Line thickness indicates relative strength of interactions between species.

their winter presence is variable among individuals, years, or winter periods. When they leave Bylot, partial migrants move shorter distances than full migrants and generally remain in the Arctic during the winter, though often in a different ecosystem such as the marine ecosystem. Some residents, such as arthropods, remain at the site year-round but escape the food web in winter as they remain inactive in the frozen soil. Because of the strong seasonality of the arctic tundra, the food web is a lot more complex in summer than during the rest of the year (Figure 2).

A large colony of snow geese is present at the study site (Reed, Hughes & Boyd, 2002). Geese are the most important herbivore during the summer, especially in wetlands, their preferred habitat (Gauthier *et al*., 1995; Gauthier, Rochefort & Reed, 1996). The other important herbivores are brown and collared lemmings. The brown lemming has regular, high-amplitude cycles of abundance with a 3- to 4-y periodicity, whereas the collared has weak, low-amplitude cycles (Gruyer, Gauthier & Berteaux, 2008; 2010). Other herbivores, such as the rock ptarmigan (*Lagopus mutus*) and arctic hare (*Lepus arcticus*), are also present, but in low numbers. Insectivorous birds, which are abundant, are all migratory and include a few passerines (mostly Lapland longspur and snow bunting, *Plectrophenax nivalis*) and several shorebirds, such as white-rumped, Baird's, and pectoral sandpipers (*Calidris fuscicollis*, *C. bairdii*, and *C. melanotos*), American golden, black-bellied, and common-ringed plovers (*Pluvialis dominica, P. Squatarola*, and *Charadrius hiaticula*; Lepage, Nettleship & Reed, 1998). Ducks such as the long-tailed duck (*Clangula hyemalis*) and king eider (*Somateria spectabilis*) mostly use aquatic rather than terrestrial arthropods, and loons (*Gavia* spp.) feed on aquatic arthropods and fishes. Both groups are present in low numbers.

The diverse predator community present on Bylot Island is almost completely dominated by migrants or partially migrant species, the only permanent year-round resident being the ermine (*Mustela erminea*). The arctic fox, the other important mammalian predator, is usually present year-round, but winter residency may vary with local lemming abundance. The red fox (*Vulpes vulpes*), a newcomer in this system (Gagnon & Berteaux, 2009), is at the northern limit of its range and is present in very low numbers. Numerous avian predators are present during the summer, but the abundance of several of them varies with the lemming cycle. This is the case for the rough-legged hawk, the long-tailed jaeger, and especially the snowy owl, which are very abundant in years of peak lemming abundance (Gauthier *et al*., 2004). Other avian predators, such as the glaucous gull, parasitic jaeger, common raven (*Corvus corax*), peregrine falcon (*Falco peregrinus*), and sandhill crane (*Grus canadensis*), are present every year in low numbers.

Legagneux, P., G. Gauthier, D. Berteaux, J. Bêty, M. C. Cadieux, F. Bilodeau, E. Bolduc, L. McKinnon, A. Tarroux, J.-F. Therrien, L. Morissette and C. J. Krebs (unpubl. data) used the software ECOPATH (Christensen & Pauly, 1992) to build a trophic mass-balance model assessing the strength of various trophic interactions in this ecosystem over a 17-y period. Results indicate that whereas < 13% of annual primary production is consumed by herbivores at the landscape level, 20 to 100% of annual herbivore production is consumed by predators. This suggests that predation may be the dominant force in this food web.

ECOSYSTEM EXCHANGES ON BYLOT ISLAND

As with many other populations of arctic-nesting geese, the snow goose population breeding on Bylot Island has increased considerably in recent decades (Reed, Hughes & Boyd, 2002), in part due to southern agricultural food subsidies acquired during winter (Gauthier *et al*., 2005). Although the high goose population has impacted some plant communities by decreasing primary production and changing specific composition on Bylot Island, it has not yet resulted in any large-scale habitat degradation (Gauthier *et al*., 1995; 2004). We explored whether juvenile snow geese dying away from the breeding grounds represent a significant net export of nitrogen from the arctic tundra. Based on the calculations provided in Appendix I, we estimate that in a good year of production of young such as 1993, young snow geese dying away from Bylot Island were removing 3582 kg of nitrogen from this tundra ecosystem. This represents 10% of the nitrogen deposited in the annual aboveground vascular plant biomass produced in local wetlands. Although this habitat occupies only 11% of the south plain of Bylot Island, it is the most productive and the preferred feeding habitat of geese on the island (Gauthier, Rochefort & Reed, 1996; Massé, Rochefort & Gauthier, 2001). Therefore, geese are removing a sizeable amount of nitrogen from this ecosystem every year.

Migratory birds and their eggs (mainly snow geese) represent a significant allochthonous input for arctic foxes on Bylot Island (Giroux, 2007; Careau *et al*., 2008b). However, marine resources (mainly ringed seals, *Phoca hispida*; Gagnon & Berteaux, 2009) are another important allochthonous resource for foxes. From the consumers' point of view, migratory birds represent a direct import of resources within their ecosystem, whereas the use of marine resources implies active predator movements and foraging outside the tundra. Data from satellite-tracking and stable isotope-based diet analysis of arctic foxes on Bylot Island show that resources are acquired on the sea ice in both winter and spring by many individuals (Tarroux, 2011). Most foxes appear to travel on the sea ice very early in fall, as soon as it is completely formed, while individual patterns of sea ice use are more variable later in winter (Tarroux, 2011). For the years 2007-2008 and 2008-2009, 27% of all bi-daily locations between November and May were situated on the sea ice (Figure 1).

We recently documented that winter use of sea ice is a strategy used by other tundra predators besides arctic foxes. Satellite-tracking of snowy owls marked on Bylot Island revealed that most individuals breeding there overwinter at high latitudes in the eastern Canadian Arctic and spend several weeks (up to 101 d) on the sea ice between December and April (Therrien, Gauthier & Bêty, 2011). Owls concentrated their activity in the Hudson and Davis straits and in Hudson Bay at a median distance of 40 km from the coast but sometimes as far as 210 km. Analysis of high-resolution satellite images of sea ice indicated that

owls were primarily gathering around open water patches (Therrien, Gauthier & Bêty, 2011), which are commonly used by wintering seabirds (especially eiders), their potential prey in these areas (Robertson & Gilchrist, 2003). This extensive use of sea ice by owls was unexpected and suggests that marine resources can potentially subsidize populations of this tundra predator when its primary prey (small mammals) declines or becomes less accessible, for instance due to snow cover in winter.

Consequences of climate warming on the food web

Like many other regions in the Arctic, the Bylot Island area has been warming rapidly in recent decades (Figure 3). The average air temperature during the spring and summer seasons has warmed by 2.8 °C in Pond Inlet over the past 35 y. Recent summers have been especially warm. However, the strongest warming trend has occurred during the fall (4.3 °C over the same period). In contrast, no change has been observed during the winter months.

The most significant temporal trend detected in the Bylot Island food web has been an increase in primary production. Over a 20-y period, plant biomass in wetlands has increased by 85% at the peak of summer production (Figure 4). This increase is likely a consequence of the warming trend observed during the summer, because the number of thawing degree-days during the summer is a significant determinant of annual variation in plant biomass ($F = 4.91$, $P = 0.041$, df = 1, 17, $R^2 = 0.22$). However, this increase has not yet affected higher levels of the food web as we have not detected significant changes in herbivore or predator abundance over the same period (Cadieux *et al*., 2008).

Annual variations in climatic conditions are substantial at this site, and we have shown that this has had a considerable impact on several species. In snow geese, high temperatures and low snow cover in spring result in early egg-laying, an increase in nest density and nesting success, and ultimately high reproductive success

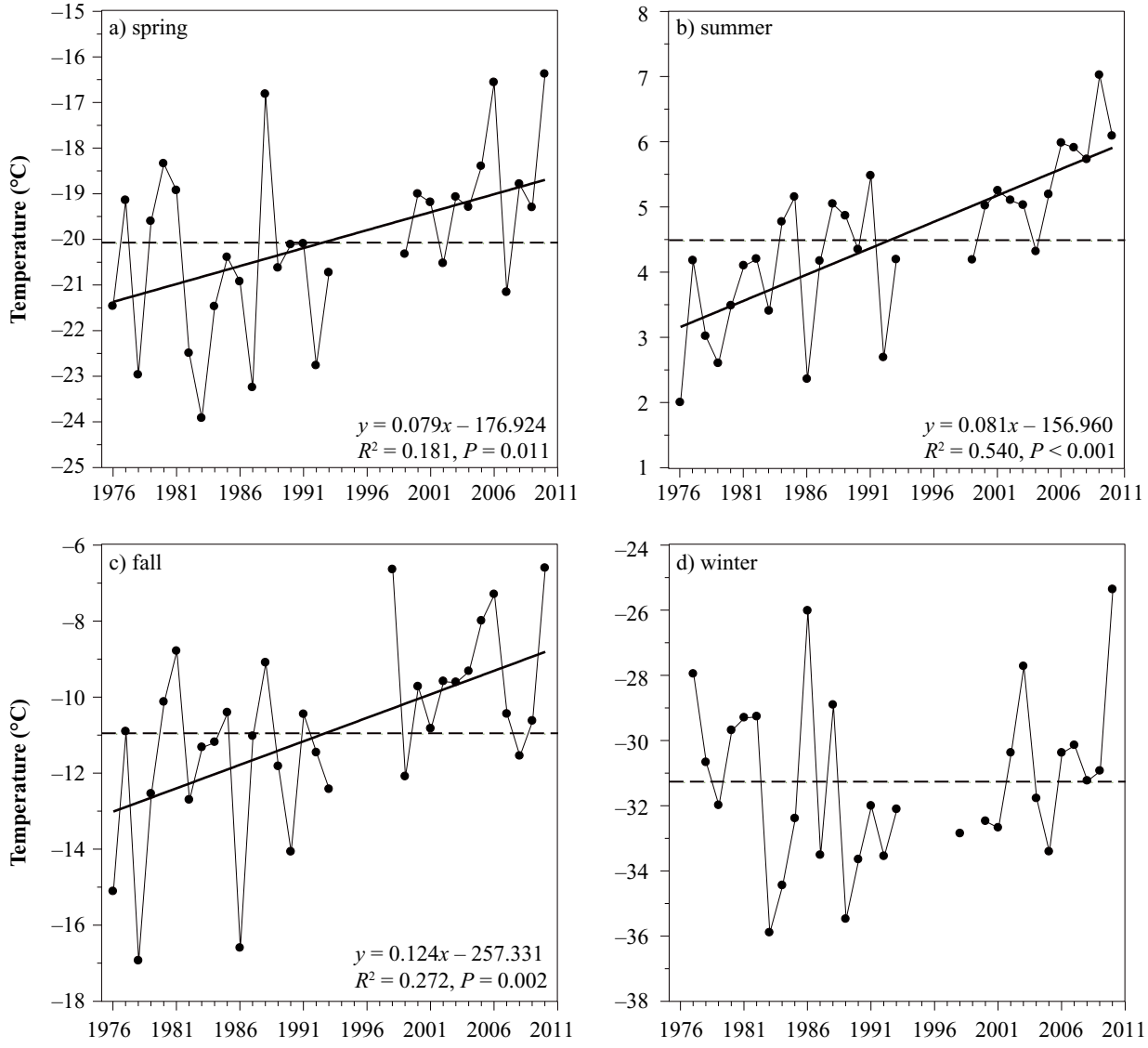

FIGURE 3. Seasonal temperature trend from Pond Inlet, Nunavut, over the period 1976–2010. Spring = March to May, Summer = June to August, Fall = September to November, Winter = December to February. Dashed line = mean.

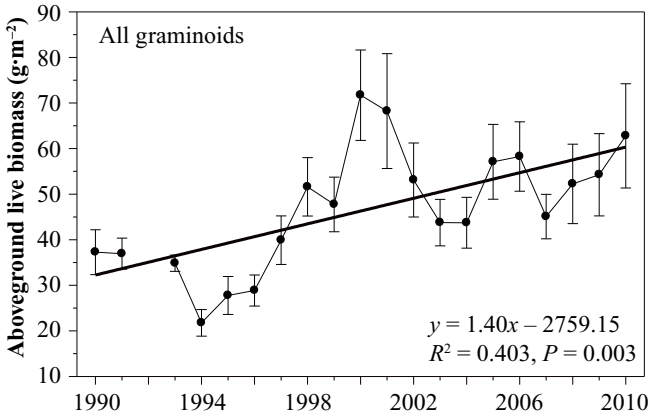

FIGURE 4. Temporal trend in primary production in the wetlands of Bylot Island, Nunavut, 1990–2010. Error bars = standard error.

(Dickey, Gauthier & Cadieux, 2008; Morrissette *et al*., 2010). In brown lemmings, a recent analysis conducted by F. Bilodeau (unpubl. data) shows that the amplitude of the cycle is affected by winter snow cover, as snow depth and the dates of fall onset of snow and spring melt have a positive effect on population size during years of peak abundance. However, despite such tight links between climatic variables and some demographic parameters, we have not yet detected any long-term trend in the reproductive success or phenology of any bird or mammal species that we monitor in this ecosystem.

During the period 1971-2000, average break-up dates for ice around Bylot Island were 2 July and 30 July on the northwest and southeast sides of the island, respectively, while average freeze-up dates were 22 October and 24 September (Canadian Ice Service, 2002). Between 1979 and 2007, the length of the melt season (from melt onset to early freeze onset; Markus, Stroeve & Miller, 2009) over the Canadian Arctic Archipelago increased by 14 d. This is the consequence of earlier melt onset (–2.3 d per decade) and later early freeze onset (2.8 d per decade; Table III in Markus, Stroeve & Miller, 2009). Because sea ice is a foraging habitat for arctic fox (see above), sea ice reduction has direct effects on the availability of this habitat to foxes.

Discussion

FUNCTIONING OF THE TUNDRA FOOD WEB AND THE ROLE OF ECOSYSTEM EXCHANGES

An emerging pattern of our analysis of the Bylot Island data is the strong impact of top predators on this food web. These results echo those of Krebs *et al*. (2003) for several other sites across the Canadian Arctic and suggest that predators may sometimes be a dominant force controlling the tundra food web. This contradicts the EEH of Oksanen *et al*. (1981) but is consistent with a growing body of literature. For instance, there is increasing evidence that lemming populations may be controlled by predators rather than by their food supply in several areas of the Arctic (Reid, Krebs & Kenney, 1995; Wilson, Krebs & Sinclair, 1999; Gilg, Hanski & Sittler, 2003; Gauthier *et al*., 2009; Ims, Yoccoz & Killengreen, 2011). However, some caveats apply to this conclusion.

A prominent feature of the Bylot Island food web is the near absence of large mammalian herbivores such as the caribou and muskox (*Ovibos moschatus*) and of their main predator, the gray wolf (*Canis lupus*). Legagneux *et al*. (unpubl. data) applied the same modelling approach used on Bylot Island (*i.e*., trophic mass-balance model) to the food web of Herschel Island along the northern coast of Yukon, a site where these large mammalian species are present. Their preliminary analysis indicates that a much higher proportion of the primary production (especially mosses and lichens) is consumed by these herbivores compared to Bylot Island. This suggests that plant–herbivore interactions may be more important at this site, possibly due to the presence of these large mammals. Body size may indeed play a key role in the control of the tundra food web. In the African savanna, the extent to which herbivores are regulated by resources (bottom-up) or predators (top-down) appears largely determined by body size, with small herbivores being controlled by predators and large herbivores by resources (Sinclair, Mduma & Brashares, 2003; Hopcraft, Olff & Sinclair, 2010). This pattern is consistent with what we have observed so far in the Canadian Arctic.

A second important feature of the Bylot Island food web is that several predators benefit from allochthonous inputs, either through the presence of migratory birds during the summer (*e.g*., predation of geese by foxes) or through use of the marine environment in winter (*e.g*., sea ice by foxes, open-water patches by snowy owls). These resources likely subsidize predator populations, especially during the lean winter period, and may allow them to maintain higher or more stable populations than would be possible based solely on autochthonous prey. The EEH considers the tundra as a closed system and does not take into account allochthonous inputs. Although exchanges among ecosystems have been known for a long time (Polis, Anderson & Holt, 1997), including in the Arctic (Oksanen, 1990), Oksanen *et al*. (2008) considered such exchanges to be limited to immediate coastal areas, and thus very limited spatially. However, the presence of migratory birds is widespread across the arctic tundra. Moreover, Walker *et al*. (2005) estimated that approximately 80% of non-alpine tundra is located within 100 km of a coastline, a distance that mobile predators like foxes and owls can cover (Tarroux, Berteaux & Bêty, 2010; Therrien, Gauthier & Bêty, 2011). Therefore, occurrence of allochthonous inputs may be relatively common across a large proportion of the tundra and thus needs to be considered in trophic models. It has been shown that exchanges across ecosystems can indeed have a strong impact on the dynamics of the recipient food web (Leroux & Loreau, 2008).

The export of nutrients from an ecosystem by migratory birds is a topic that has received very little attention to date. On Bylot Island, we have shown that up to 10% of the nitrogen deposited annually by vascular plants in their aboveground tissues may be transferred into the body tissue of growing goslings and removed from the system when young migrate and die away from the

arctic breeding grounds. This estimate is crude and is not a genuine estimate of net nitrogen loss in this ecosystem because it does not account for other possible losses (*e.g*., due to leaching to streams) or for additions due to nitrogen fixation by soil microbes (Chapin & Bledsoe, 1992; Deslippe, Egger & Henry, 2005). Moreover, the amount of nitrogen removed by geese in this system is likely variable because annual production of young is highly variable in geese, being influenced by climatic factors (most notably those reflected in the North Atlantic Oscillation) and indirect trophic interactions with cycling lemmings due to shared predators (Morrissette *et al*., 2010). Nonetheless, nitrogen loss due to geese may have important consequences for an ecosystem where nitrogen availability limits plant production (Pouliot, Rochefort & Gauthier, 2009). This example further highlights the complex role played by migratory animals in ecosystem exchanges where a group like geese can simultaneously be an allochthonous resource input for higher trophic levels (*i.e*., predators) and an autochthonous resource exporter for lower trophic levels (*i.e*., plants and the nutrient pool). Because the trophic level (*i.e*., nutrients, plants, herbivores, or predators) at which ecosystem exchange occurs can have contrasting effects on the functioning of the food web and the strength of trophic cascades, it must be considered when modelling trophic dynamics (Leroux & Loreau, 2008). Despite their importance, the impact of these complex interactions on food web control remains largely unexplored.

Impact of climate change on the tundra food web

Though documenting impacts of climate change on arctic ecosystems is difficult and requires long-term data sets, there is already increasing evidence that several tundra species are currently impacted worldwide (Post *et al*., 2009). Our study and the one by Hudson and Henry (2009) are among the first field-based studies showing a temporal increase in plant production in the High Arctic, most likely a direct consequence of the strong warming trend currently affecting this region, including at our study site (Figure 3). However, we have failed to detect any significant change in higher trophic levels that could be linked to the observed warming trend or change in primary production. For instance, we have yet to detect any change in lemming cycles at our site (Gruyer, Gauthier & Berteaux, 2008; G. Gauthier, unpubl. data) despite evidence of collapsing cycles elsewhere in the Arctic, possibly in response to warmer winter conditions (Ims, Henden & Killengreen, 2008; Kausrud *et al*., 2008; Gilg, Sittler & Hanski, 2009; Ims, Yoccoz & Killengreen, 2011). As a consequence, the proportion of biomass consumed by herbivores has decreased over time in our ecosystem (P. Legagneux, G. Gauthier, D. Berteaux, J. Bêty, M. C. Cadieux, F. Bilodeau, E. Bolduc, L. McKinnon, A. Tarroux, J.-F. Therrien, L. Morissette & C. J. Krebs, unpubl. data). This is consistent with our conclusion that the Bylot Island food web is primarily a top-down controlled system (*i.e*., herbivores are mostly controlled by predators). However, it is also possible that arctic herbivores and predators simply show more inertia than plants in responding to climate warming. Indeed, because wildlife species are warm-blooded animals, they should be less sensitive than plants to the direct effects of temperature increases but more sensitive to the indirect effects (*e.g*., due to change in food supply).

The strong ecosystem exchanges that we documented in the Bylot Island food web will inevitably affect our ability to assess the effects of climate change on the tundra. Indeed, we must consider the impact of climate warming not only on the terrestrial ecosystem, but also on other ecosystems, such as the marine environment, which is seasonally used by tundra predators. For instance, change in the sea ice regimes due to climate warming (Johannesen *et al*., 2004) may negatively affect tundra predators. Because arctic foxes seem to use the sea ice as soon as it is completely formed in fall, changes in the timing of sea ice formation such as those currently occurring in the Canadian Arctic could potentially impact their food base during this shoulder season. However, no data are available yet to quantify such effects. For snowy owls, change in the sea ice regimes will likely alter the abundance and distribution of wintering seabirds (Mallory *et al*., 2010), which will undoubtedly affect the wintering strategy of this top predator. However, it is yet unclear if this will have positive effects on its prey base (*e.g*., more open water leading to more wintering seabirds) or negative effects (*e.g*., more open water spreading prey over a wider area, thereby reducing local concentrations).

Given the importance of ecosystem exchange in the trophic dynamic of the arctic tundra food web, future studies investigating the effects of climate change on arctic organisms will need to adopt a broader cross-ecosystem perspective. Further investigation of these complex issues will be challenging as it will require a combination of long-term data sets and intensive field studies from cross-connected ecosystems, including during the elusive winter period.

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Appendix I

Snow geese nesting on Bylot Island hatch around 9 July and depart the island on their southward migration around 1 September (Lepage, Gauthier & Menu, 2000; Gauthier *et al*., unpubl. data), meaning that the young leave the island at about 54 d of age. Lesage and Gauthier (1997) determined the parameters of the logistic growth curve for whole body protein of male and female juvenile snow geese at this site. Assuming an equal sex ratio among young, we can estimate that the whole body protein of a 54-d gosling is 431 g and that its nitrogen content is 69 g (considering that protein tissues are composed of 16% nitrogen on average; Robbins, 1983). In 1993, a good reproduction year for geese on Bylot Island, Reed, Hughes, and Boyd (2002) estimated that 86 470 goslings were present in late July, 3 weeks after hatch. Lepage, Gauthier, and Menu (2000) estimated gosling survival until fledging at 39%, but most of the mortality occurs during the first 2 weeks of hatch. Therefore, we assume that 60% of the young surveyed in late July would leave the island on 1 September, a conservative estimate. We can thus estimate that 3582 kg of nitrogen would leave the island with the geese. Many of the young produced on the island will recruit in the population and eventually return to breed. Some of these resulting individuals may die on the island, and thus their nitrogen return to the system. However, survival of adults during the summer is high, and probably fewer than 3% of them die over this 3-month period annually (Gauthier *et al*., 2001), a negligible proportion.

Massé, Rochefort, and Gauthier (2001) estimated aboveground vascular plant production in wetlands of the south plain of Bylot Island at 2685×10^3 kg·y^{-1} (dry mass) on average. From Gauthier *et al*. (1995), we can assess the average nitrogen concentration in wetland plants at peak production to be 1.82% (these wetlands are dominated in a 2:1 ratio by *Dupontia fisheri* [1.5% nitrogen] and *Eriophorum scheuchzeri* [2.45% nitrogen]). Therefore, the total nitrogen biomass in aboveground tissues of wetland plants can be estimated at 35 171 kg. The amount exported annually by geese in a year of good reproduction thus represents about 10.1% of the annual nitrogen deposited in wetland vascular plants.