

Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling

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Abstract. Determining the manner in which food webs will respond to environmental changes is difficult because the relative importance of top-down vs. bottom-up forces in controlling ecosystems is still debated. This is especially true in the Arctic tundra where, despite relatively simple food webs, it is still unclear which forces dominate in this ecosystem. Our primary goal was to assess the extent to which a tundra food web was dominated by plant–herbivore or predator–prey interactions. Based on a 17-year (1993–2009) study of terrestrial wildlife on Bylot Island, Nunavut, Canada, we developed trophic mass balance models to address this question. Snow Geese were the dominant herbivores in this ecosystem, followed by two sympatric lemming species (brown and collared lemmings). Arctic foxes, weasels, and several species of birds of prey were the dominant predators. Results of our trophic models encompassing 19 functional groups showed that <10% of the annual primary production was consumed by herbivores in most years despite the presence of a large Snow Goose colony, but that 20–100% of the annual herbivore production was consumed by predators. The impact of herbivores on vegetation has also weakened over time, probably due to an increase in primary production. The impact of predators was highest on lemmings, intermediate on passerines, and lowest on geese and shorebirds, but it varied with lemming abundance. Predation of collared lemmings exceeded production in most years and may explain why this species remained at low density. In contrast, the predation rate on brown lemmings varied with prey density and may have contributed to the high-amplitude, periodic fluctuations in the abundance of this species. Our analysis provided little evidence that herbivores are limited by primary production on Bylot Island. In contrast, we measured strong predator–prey interactions, which supports the hypothesis that this food web is primarily controlled by top-down forces. The presence of allochthonous resources subsidizing top predators and the absence of large herbivores may partly explain the predominant role of predation in this low-productivity ecosystem.

Key words: Bylot Island, Canada; *Chen caerulescens atlantica*; climate change; Ecopath; lemmings; mass balance trophic models; predation; Snow Geese; top-down control.

INTRODUCTION

Determining whether food webs are primarily controlled by top-down (consumer-driven) or bottom-up (resource-driven) forces has long been a central question in ecology (Power 1992, Elmhagen and Rushton 2007, Fritz et al. 2011). Knowing which forces dominate is crucial to predict the manner in which ecosystems will react to anticipated global environmental changes. According to the bottom-up view, organisms at each trophic level are food-limited (Hunter and Price 1992, Polis and Strong 1996). On the other hand, the top-

down view states that organisms at higher trophic levels regulate the abundance of lower level organisms (Menge and Sutherland 1976, Power 1992), a form of control that may lead to trophic cascades (Paine 1980, Fretwell 1987, Estes et al. 1998, Anthony et al. 2008). The relative importance of these forces can depend on productivity gradients (Oksanen et al. 1981, Aunapuu et al. 2008), body size (Yodzis and Innes 1992, Borer et al. 2005), or the presence of allochthonous food subsidies (Leroux and Loreau 2008).

The relative strength of top-down vs. bottom-up forces in controlling food webs may also affect conservation efforts aimed at mitigating or reversing the impacts of environmental changes (Post and Pedersen 2008). Climate change is one of the most

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serious environmental perturbations that will alter the distribution and abundance of species and disrupt trophic linkages (Thomas et al. 2004, Berteaux et al. 2006, Post et al. 2009). Of all the regions on Earth, it is in the Arctic that the current global warming trend is occurring at the fastest rate (ACIA 2005). Even though Arctic food webs are less complex than those encountered at lower latitudes (Elton 1927, Gauthier et al. 2012), determining how they will respond to those changes is difficult because the relative importance of top-down vs. bottom-up forces in this ecosystem is still unclear and may vary across regions (e.g., Oksanen et al. 2008, 2009, Gauthier et al. 2009). In Fennoscandia and northern Alaska, there is evidence that tundra ecosystems are controlled by primary production, with herbivores being resource-limited (Ims and Fuglei 2005, Pitelka and Batzli 2007, Oksanen et al. 2008). However, in several areas of the Nearctic, the reverse pattern seems more prevalent, with herbivores being mainly controlled by their predators (Reid et al. 1995, Wilson et al. 1999, Gilg et al. 2003, Krebs et al. 2003, Gauthier et al. 2004).

As highlighted by Ims and Fuglei (2005), there is a strong need to address these questions using large-scale integrated monitoring, which is rare in the Arctic. To date, only one study (Krebs et al. 2003) has attempted to investigate the forces structuring terrestrial Arctic ecosystems using a complete food web approach. This study was based on mass balance ecosystem modeling of 12 sites across the Canadian Arctic. This first attempt provided a quantitative framework for studying trophic interactions in the Arctic and suggested that top-down regulation was more prevalent than bottom-up regulation in those Canadian tundra sites. Despite the spatial replicates, a major limitation of the Krebs et al. (2003) study was the scarcity of empirical data. Indeed, each study site was visited once and only for a few days. This short-term study was thus unable to explore the effects of lemming cycles, a major feature of tundra ecosystems (Ims and Fuglei 2005), on food web dynamics.

In the present study, we expanded upon the work of Krebs et al. (2003) by applying the same modeling approach to a comprehensive, long-term ecological monitoring program conducted on Bylot Island, Nunavut, Canada (Gauthier et al. 2004). This High Arctic site is characterized by high-amplitude fluctuations of lemming populations (brown and collared lemmings), with peaks occurring every 3–4 years, and by the presence of a large breeding colony of Snow Geese (see Table 1 for scientific names). Our primary goal was to assess the extent to which this food web was dominated by top-down or bottom-up trophic interactions. Specifically, we developed mass balance trophic models to determine: (1) the fraction of plant production that is consumed by herbivores, (2) the fraction of herbivore production that is consumed by predators, and (3) whether the answers to these questions have changed

over time, given that this region is experiencing a strong warming trend (Gauthier et al. 2012).

METHODS

Study system and field monitoring

This long-term study was conducted on the southwest plain of Bylot Island, Nunavut, Canada (73° N, 80° W). This region is characterized by upland plateaus dissected by numerous valleys with extensive flat lowlands at an elevation generally below 350 m above sea level. The 520-km² study area is dominated by mesic tundra in the upland and a mixture of mesic tundra and wetlands (primarily polygonal tundra) in the lowlands (see Gauthier et al. 2012 for details). Mesic tundra and wetlands represent a large percentage (>95%) of the study area, the remaining 5% being xeric tundra, which is almost devoid of plants and animals and was not considered here. Wetlands are dominated by graminoids and mosses and mesic tundra is dominated by forbs, low shrubs, and some graminoids and mosses. The percentages of wetland and mesic habitats in the study area (15% and 85%, respectively; Massé et al. 2001) were taken into account to calculate plant and animal biomasses.

The key terrestrial wildlife species and plant production (Table 1) have been monitored at this site from 1993 to 2009 (Gauthier et al. 2004, 2012). The main features of Bylot Island are the absence of large mammalian herbivores (caribou [*Rangifer tarandus*] or muskoxen [*Ovibos moschatus*]) and the presence of a relatively large (>10 000 breeding pairs) Snow Goose colony. Field data were collected yearly from early June to mid-August. Monitoring of plants, lemmings, Snow Geese, passerines, Snowy Owls, and Arctic foxes began in the first years of the study (Gauthier et al. 2004). Other functional groups were progressively added, including shorebirds, arthropods, other avian predators (initiated in 2005), and weasels (in 2009 only). The 19 functional groups used in the ecosystem models (Table 1) represent the vast majority of the terrestrial organisms of Bylot Island. Field methods used to sample annual abundance and other parameters relevant for ecosystem modeling (e.g., diet, food consumption rate, annual production) are presented in detail for each functional group in the Appendix.

Mass balance modeling

We used a mass balance ecosystem modeling software, Ecopath with Ecosim (EwE), that has been used extensively to study marine and aquatic food webs (Christensen et al. 2008) as well as terrestrial ones (Ruesink et al. 2002, Krebs et al. 2003). Ecopath with Ecosim combines software for ecosystem mass balance analysis (Ecopath) with a dynamic modeling capability (Ecosim) to forecast species abundance in exploited ecosystems. It provides a quantitative overview of how species interact in the system. The main equation of EwE models (Christensen et al. 2008) is as follows:

TABLE 1. Functional groups used in Ecopath with Ecosim (EwE) modeling of the tundra ecosystem of Bylot Island, Nunavut, Canada.

Functional group	Taxa
Mosses	<i>Polytrichum</i> spp., <i>Meesia triquetra</i>
Forbs	<i>Luzula</i> spp., <i>Saxifraga</i> spp., <i>Oxytropis maydelliana</i> , <i>Polygonum viviparum</i>
Shrubs	<i>Salix</i> spp., <i>Cassiope tetragona</i> , <i>Dryas integrifolia</i> , <i>Vaccinium uliginosum</i>
Sedges/grasses	<i>Carex aquatilis</i> , <i>Eriophorum scheuchzeri</i> , <i>Dupontia fisheri</i> , <i>Arctagrostis latifolia</i>
Snow Goose	<i>Chen caerulescens atlantica</i>
Brown lemming	<i>Lemmus trimucronatus</i>
Collared lemming	<i>Dicrostonyx groenlandicus</i>
Arthropods	Chironomidae, Muscidae, Aranea, Lepidoptera, Ichneumonidae, Carabidae
Shorebirds	<i>Calidris bairdii</i> , <i>C. fuscicollis</i> , <i>C. melanotos</i> , <i>Pluvialis dominica</i> , <i>P. squatarola</i> , <i>Phalaropus fulicarius</i>
Passerines	<i>Calcarius lapponicus</i> , <i>Plectrophenax nivalis</i> , <i>Eremophila alpestris</i> , <i>Anthus rubescens</i>
Weasel	<i>Mustela erminea</i>
Arctic fox	<i>Vulpes lagopus</i>
Snowy Owl	<i>Bubo scandiaca</i>
Rough-legged Hawk	<i>Buteo lagopus</i>
Glaucous Gull	<i>Larus hyperboreus</i>
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>
Parasitic Jaeger	<i>Stercorarius parasiticus</i>
Peregrine Falcon	<i>Falco peregrinus</i>
Detritus	Dead materials from plants and animals as well as marine subsidies (e.g., beached marine seals)

Note: For plants and arthropods, only the dominant taxa are listed.

$$B_r \times \left(\frac{P_r}{B_r} \right) \times EE_r = \sum \left[B_c \times \left(\frac{Q_c}{B_c} \right) \times d_{rc} \right] + \Delta B_r \quad (1)$$

where B is biomass (in kilograms per square kilometer per year), P is net production in kilograms per year, Q is consumption (ingested biomass based on food intake in kilograms per year), EE is the ecotrophic efficiency (a proportion), and d_{rc} is the proportion of resource r in the diet of consumer c . Assuming equilibrium ($\Delta B_r = 0$), the algorithm (Eq. 1) requires that three of the four listed parameters (B , Q , P , and EE) are entered into the model for each functional group. At equilibrium (i.e., $\Delta B_r = 0$), a taxon's EE is the proportion of its net annual production consumed by higher trophic levels, expressed as a ratio. In other words, EE represents the fraction of the production that is used in the system to satisfy the consumers' energetic demands. Because EE estimates the flow of biomass across trophic levels, it was the parameter of primary interest in this study and thus we entered values for B , Q , and P (either derived empirically or allometrically) in Eq. 1 in order to estimate this parameter. An $EE > 1$ indicates resource overconsumption, hence that the system is unbalanced. Biomass was assessed empirically at our study site for all functional groups using density estimates based on counts or capture-recapture and radio-tracking of marked animals, and values were compared to those in the literature to ensure their validity (see details in the Appendix). Weasel density was the only parameter that had to be derived from estimates taken from the literature. For the vegetation, B was determined by sampling plants at the end of the growing season (i.e., between 12 and 15 August) inside annual exclosures (1×1 m fenced areas) to prevent summer grazing by geese in wetlands and by geese and lemmings in mesic tundra (see details in the Appendix).

Data on diet were obtained from local field data using a variety of techniques including regurgitation pellet analyses, automated cameras, direct field observations, and stable-isotope analyses (see details in the Appendix). However, diet had to be derived from the literature for lemmings, weasels, and arthropods. For predators, different diet matrices were used depending on the phase of the lemming cycle (peak, intermediate, or crash). The phase of the cycle was assigned based on lemming abundance obtained by trapping (see the Appendix) following B ty et al. (2002). Intermediate years typically occurred "post-peak" (Gruyer et al. 2008), which differs from other cycles in which intermediate years often occur before peaks (i.e., increase phase; Ruesink et al. 2002, Gilg et al. 2003). Consumption Q and production P were assessed both empirically and allometrically, using primarily the equations of Banse and Mosher (1980) and Nagy (1987) in the latter case. Empirical values of P (number of eggs and/or young produced for animals) were available for most functional groups (plants, fox, and all birds except the Peregrine Falcon) based on fieldwork conducted at our study area. Empirical values of Q determined at our study area were available for avian predators and geese. Published values on the consumption rate measured empirically were used as empirical estimates of Q for the remaining species (see details in the Appendix). These values take into account that not all ingested food is assimilated, especially for herbivores. When calculating Q values, we also accounted for the time spent by each species on Bylot Island.

For each year, we computed three food web models: empirical, allometric, and Monte Carlo simulations (sensitivity analysis). The empirical model almost exclusively used values of Q and P that were determined empirically for each functional group (allometric values were used when empirical values were not available; two

times for P and four times for Q ; see Appendix), whereas the allometric model used only values derived from allometric equations (except for plant production, which was based on data from the literature). Parameter values used in each model are listed in Appendix Tables A1–A4.

Uncertainty

Ecopath with Ecosim can provide an instantaneous estimate of trophic flow and instantaneous mortality rates for some reference years or multi-year averaging windows. Calculations assumed mass balance, but in a number of cases we recognize that biomasses were in fact changing over the period for which EwE reference data (B , P/B , Q/B , diet composition) were provided (Christensen et al. 2008). In these cases, assuming equilibrium for the reference period would lead to overly optimistic estimates of sustainable mortality rates. Indeed, the “steady-state” requirement of EwE means that the model outputs apply only to the period for which inputs are deemed valid (Christensen and Pauly 1992). Specification of the period for which these models are expected to have predictive power is therefore critical (Plaganyi and Butterworth 2004). To address this, we built independent models for each year of the study because within-year biomass variation is expected to be much lower than among-year variation.

We conducted a sensitivity analysis based on Monte Carlo simulations on balanced models. When EE values were >1 , which sometimes occurred for lemmings, we artificially increased the biomass B of lemmings to reach an $EE = 0.95$. On average, this required an increase of 55% ($\pm 20\%$ [mean \pm SE]; $N = 7$) and 21% ($N = 1$) of collared and brown lemming biomass, respectively. Considering that lemming densities were estimated with large confidence intervals (CI), especially at low densities (CI = 69% for brown and 101% for collared lemming), balanced models were still based on parameter values within the range of uncertainty of the biomass estimates. We thus argue that although the steady-state assumption was sometimes violated, it was in an “acceptable” manner that is unlikely to affect the interpretation of the results and modeling outcomes. We performed sensitivity analyses using Ecoranger, a resampling routine implemented in EwE based on the probability distribution of parameters B , P , Q , and d . Confidence intervals were calculated based on the variance of empirically derived parameters B , P , and Q (see Appendix: Table A4). From the balanced models, we calculated EE repeatedly (1000 models per year were generated assuming a uniform distribution of parameters values within the CI in Monte Carlo simulations).

Statistical analyses

We compared annual EE values estimated from the empirical model among functional groups and phases of the lemming cycle using linear models in R 2.11 (R Development Core Team 2010). The EEs were log-

transformed to meet normality and homoscedasticity assumptions. All means are presented with SE.

RESULTS

The food web of Bylot Island is relatively simple (Fig. 1). At the landscape level, primary producers are dominated by mosses (90% of all biomass; Appendix: Table A1), whereas vascular plants are split among graminoids, shrubs (5% each), and forbs ($<1\%$). The herbivore trophic level is dominated by the Snow Goose (88% of the total biomass on average), whereas lemmings account for 25% of the total herbivore biomass in a peak year but only 2% in a low year. The carnivore biomass is dominated by the Arctic fox (range = 11–40%), followed by the Glaucous Gull and the Long-tailed Jaeger (11–22% and 0–27%, respectively), the Snowy Owl (0–47%), and the weasel (<1 –15%). These proportions are based on summer population estimates and resident species (lemmings, weasel, and fox) are thus far more abundant in winter (this aspect is taken into account in the models since Q is adjusted to the time spent on site; see the Appendix).

The EEs of all functional groups were <1 except for lemmings, which were >1 in one and seven out of the 17 years for brown and collared lemmings, respectively (empirical parameterization; Fig. 2). For all functional groups, EE estimates from the three models were very similar, although parameterization with allometric data resulted in more violations of mass balance constraints (12 of the 17 years had EEs of lemmings >1 with this parameterization).

While important variations were found among years, most of the variation depended on the phase of the lemming cycle (Fig. 2). The EE values varied among plants, herbivores, and insectivores in concert with the phase of the lemming cycle (interaction functional group \times lemming phase, $F_{23,112} = 40.7$, $P < 0.001$). Predators and mosses were excluded because EEs were equal or close to 0. The EEs of vascular plants (forbs, sedges, and shrubs) were very low (88% of annual values were ≤ 0.1) compared to those of the other groups but were slightly greater in years of high lemming abundance than in other years due to increased consumption by lemmings and geese ($F_{2,48} = 8.60$, $P < 0.001$; Fig. 2a and Fig. 3). The EEs of mosses were overall negligible (≤ 0.02) but lack of long-term data precluded an assessment of temporal variation. Snow Geese EEs tended to be higher during lemming crash years ($EE = 0.55 \pm 0.11$) compared to other years ($EE = 0.36 \pm 0.06$; $F_{2,14} = 2.66$, $P = 0.12$; Fig. 2b). The EEs of brown lemmings also tended to change according to the phase of their cycle ($F_{2,14} = 3.04$, $P = 0.10$; Fig. 2c): they were higher during years of low abundance ($EE = 0.77 \pm 0.08$) than in years of intermediate ($EE = 0.54 \pm 0.18$) and high ($EE = 0.53 \pm 0.15$) abundance. In contrast, EEs of collared lemmings remained high (overall $EE = 1.04 \pm 0.12$) independently of the phase of the lemming cycle ($F_{2,14} = 0.28$, $P = 0.76$; Fig. 2d). The EEs of passerines and

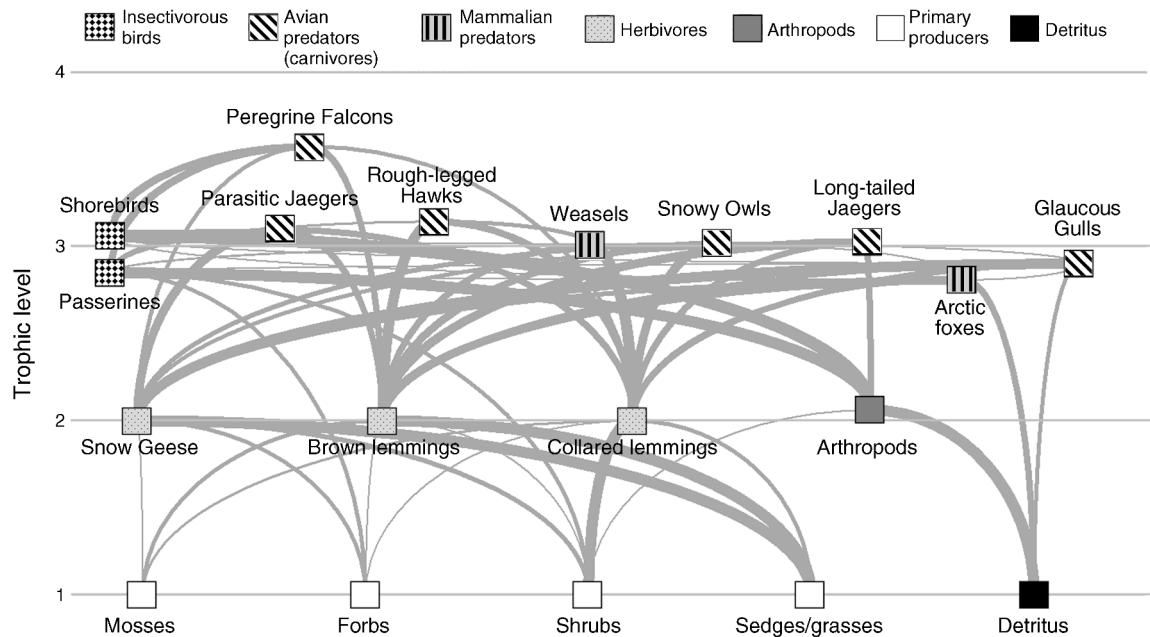


FIG. 1. Schematic representation of the tundra food web of Bylot Island, Nunavut, Canada, showing interactions among functional groups in 2008, a year of high lemming abundance. Line width is scaled to the relative importance of each group in the diet. Detritus includes marine subsidies.

shorebirds ranged widely from 0.2 to 0.8 (Fig. 2e and f). The EEs of passerines were reduced during lemming crash years compared with other years ($F_{2,14} = 21.8$, $P < 0.001$). Lemming phase had little effect on shorebird EEs ($F_{2,14} = 0.81$, $P = 0.47$), but shorebird production was monitored only during five years and was considered constant for the remaining years for which we had no data. The sensitivity analysis (based on Monte Carlo simulations) revealed that the uncertainty associated with empirical measurements for the different input parameters used in the models did not alter the main patterns found for any of the functional groups (black triangles in Fig. 2).

Finally, the EE of vascular plants decreased over time ($\beta = -0.04$, $F_{1,49} = 9.90$, $P = 0.003$, adjusted $R^2 = 0.25$; Fig. 3). This decrease was found for all plant groups but was statistically significant only in shrubs (shrubs, $F_{1,15} = 10.7$, $P = 0.005$, adjusted $R^2 = 0.42$; sedges, $F_{1,15} = 4.0$, $P = 0.06$, adjusted $R^2 = 0.16$; forbs, $F_{1,15} = 2.5$, $P = 0.13$, adjusted $R^2 = 0.11$). For herbivores (lemmings and geese) monitored throughout the 17 years, no temporal trend was detected (all $F_{1,15} < 1.95$, $P > 0.18$).

DISCUSSION

The role of predator–prey interactions in the functioning of food webs in general, and in controlling lemming cycles in particular, is still controversial (e.g., Oksanen et al. 2008, 2009, Gauthier et al. 2009, Ims et al. 2011, Krebs 2011). We addressed this question using a very detailed and exhaustive data set spanning almost two decades and found that predation played a

dominant role in the tundra food web of Bylot Island. In the present study, $\leq 10\%$ of the annual vascular plant production was consumed by herbivores in most years, whereas 20% to $>100\%$ of the annual production of all vertebrate herbivores and insectivores was consumed by predators. Krebs et al. (2003), who used the same approach to quantify trophic interactions at 17 sites scattered across the Canadian Arctic (excluding Bylot Island), also found that predator–prey interactions were more important than plant–herbivore interactions in those food webs. Although the Krebs et al. (2003) study was based on a limited data set collected over a single year, the similarities between their conclusions and ours suggest that the situation encountered on Bylot Island may be representative of a large portion of the Nearctic tundra (but see, for instance, Turchin and Batzli 2001).

Plant–herbivore interactions

Snow Geese were the dominant herbivores in the food web even in years of high lemming abundance. Despite the presence of a large Snow Goose colony at our study site, the proportion of the total vascular plant production consumed annually was small. Nonetheless, this proportion more than doubled during years of peak lemming abundance. However, this impact was not solely due to the higher abundance of lemmings but also to a higher grazing impact of geese in those years due to indirect interactions between lemmings and geese. Predation rates on goose eggs are low in high lemming years, which leads to a good production of goslings

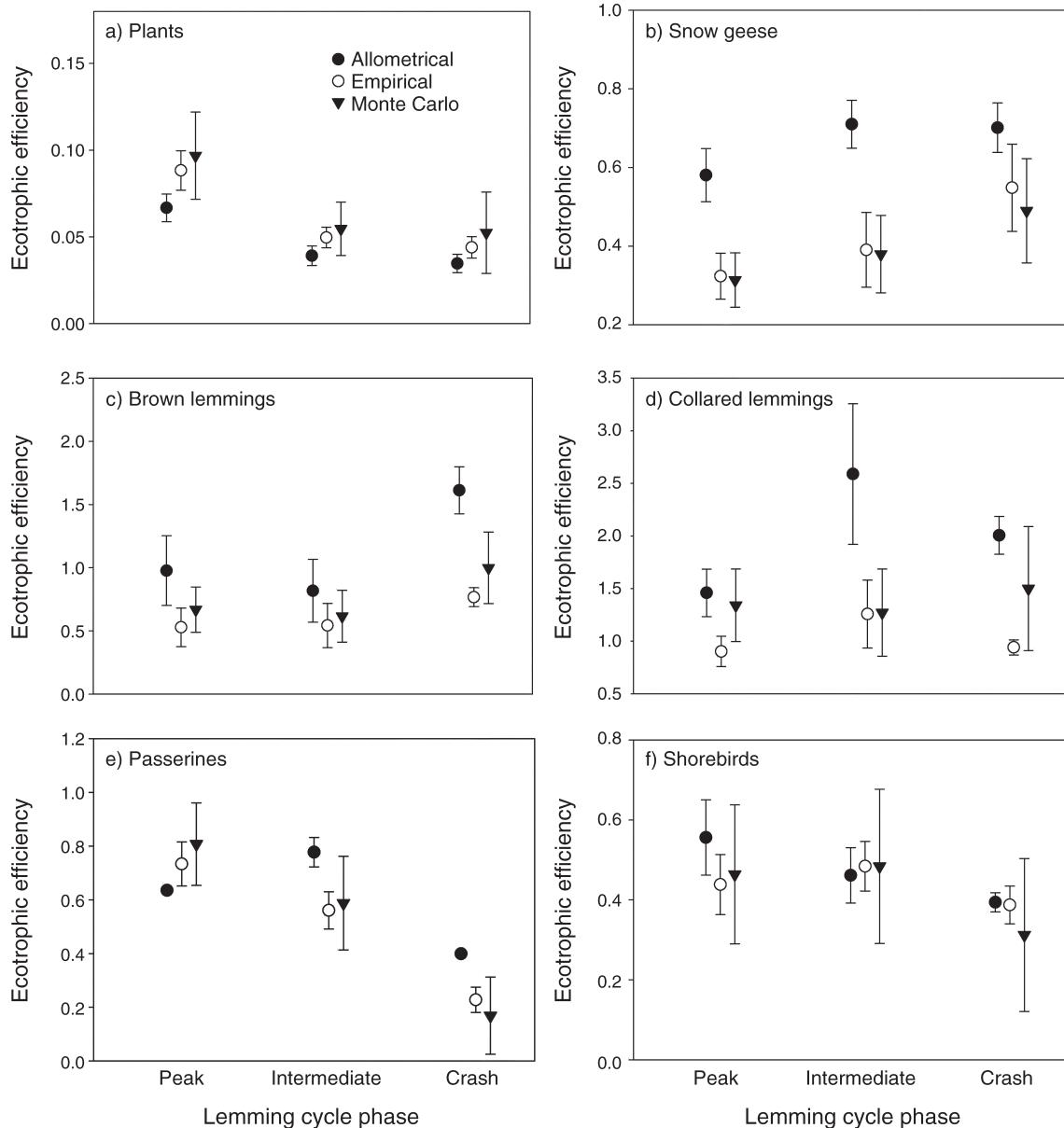


FIG. 2. Ecotrophic efficiency (the proportion of the net annual production consumed by higher trophic levels) of several functional groups according to the phase of the lemming cycle (peak, intermediate, and crash years) and different parameterization: allometric (solid circle), empirical (open circle), and Monte Carlo (solid triangle; see *Methods* for details). Functional groups are: (a) vascular plants (forbs, shrubs, and sedges/grasses combined); (b) Snow Geese; (c) brown lemmings; (d) collared lemmings; (e) passerines, and (f) shorebirds. Data points represent means \pm SE. Note that scale of the y -axis differs among groups. $EE > 1$ indicates resource overconsumption (unbalanced system).

(Morrisette et al. 2010) and increases the local grazing pressure by geese (Gauthier et al. 2004).

Previous studies had reported that Snow Geese consumed, on average, 30% of the annual production of graminoids on Bylot Island and up to 60% in some years (Massé et al. 2001, Gauthier et al. 2004, Valéry et al. 2010), which may appear to contradict our results. However, these estimates apply solely to wetlands dominated by grasses and sedges, the habitat preferred

by geese. This habitat occupies only 15% of the landscape on Bylot Island compared to 85% for the mesic tundra, which is only lightly used by geese. This explains why grazing impact at the landscape level is relatively low.

A problem inherent to the kind of models that we used is that all the annual primary production is considered available to herbivores, which is unlikely to be true. For instance, the presence of feeding deterrents

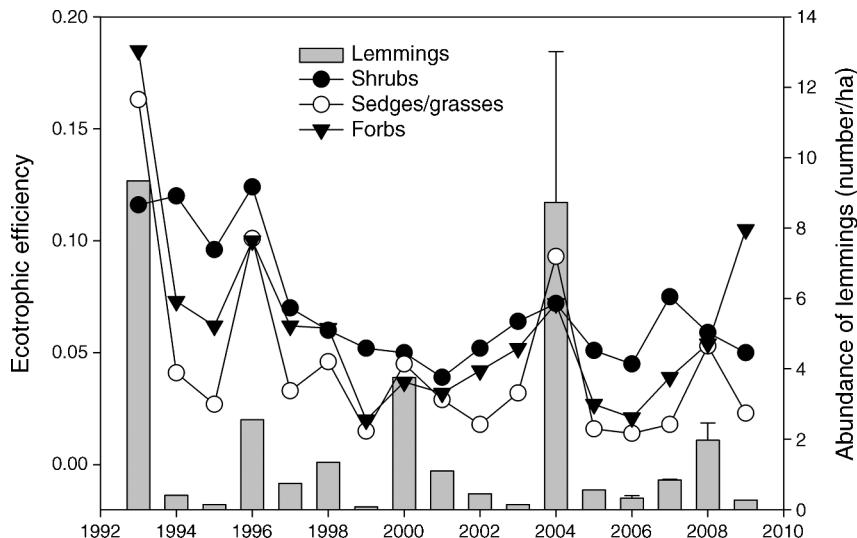


FIG. 3. Ecotrophic efficiency (the proportion of the net annual production consumed by herbivores) of vascular plants (forbs, shrubs, and sedges/grasses; lines) based on the empirical parameterization according to years. Gray bars represent annual abundance of lemmings (both species pooled; mean + SE).

such as phenolic compounds in some plants or, more importantly, plant senescence in fall will reduce availability for resident herbivores in winter. In several Arctic plants, when senescence begins in fall, some material is lost but most soluble nutrients are translocated (up to 80–90%; see Jonasson and Chapin 1991, Jonasson and Shaver 1999) to basal stems or belowground reserves as an adaptation to the harsh environment. The consequence of this is that the portion of plant EE due to lemming consumption may have been underestimated. However, if we take an extreme situation and consider that only 10% of vascular plant production remains available for lemmings over a nine-month long winter period (equivalent to increasing the portion of plant EE due to lemmings by a factor 3), overall EE of vascular plants would still be at a relatively low level ($EE = 0.19 \pm 0.10$ in lemming peak years). During winter, brown lemmings also consume mosses (Batzli 1993) but the EE of this group is even lower (<0.02) as mosses are almost 10 times more abundant than vascular plants on Bylot Island, which is typical of the Nearctic tundra (Turchin and Batzli 2001, Krebs et al. 2003). Therefore, applying the same correction to mosses would still result in a very low EE value. In summary, even if plant EE was underestimated in our study, any realistic correction applied to these estimates would still result in a low overall plant consumption by herbivores because our values are so low to start with. Of course, this statement would not necessarily apply to other tundra systems where uncorrected EE values could be higher than ours.

Predator–prey interactions

Predators had a strong impact on all vertebrates, though the impact was strongest on lemmings and lowest on geese and shorebirds. Moreover, the two

sympatric lemming species show different patterns of predation rates. At all phases of the cycle, collared lemmings are heavily predated and consumption was always equal to or higher than production ($EE \geq 1$). In contrast, consumption of brown lemmings was always lower than production although EE approached 1 in crash years. The consistently high predation rate on collared lemmings is probably due to the preference exhibited for this species by many predators such as weasels (Duchesne et al. 2011) and birds of prey (J.-F. Therrien, *unpublished data*). Interestingly, fluctuations of collared lemmings on Bylot Island are weak, with population sizes remaining relatively low most of the time (four- to sevenfold difference between crash and peak years) in contrast to brown lemmings, which show population fluctuations of high amplitude (≥ 40 -fold difference between crash and peak years; Gruyer et al. 2008). Even though collared lemmings can exhibit cyclic fluctuations of high amplitude elsewhere (e.g., on west Greenland, where brown lemming is absent; Gilg 2002), we suggest that predation limits collared lemming abundance on Bylot Island and prevents the occurrence of high-amplitude cycles there. Limitation of collared lemmings at low density also occurs at some sites in the western Canadian Arctic (Pearce Point, NWT; Reid et al. 1995).

The decrease in consumption rate of brown lemmings with increasing population size is similar to the pattern found by Ruesink et al. (2002) in cyclic snowshoe hare (*Lepus americanus*) populations in the boreal forest. The high predation rate at low population size may limit population growth of brown lemmings but, under some conditions, they appear to be able to escape predation, leading to outbreaks. Although predation may slow down population growth, a proportion of lemming

production still escapes from predation during outbreaks, and thus other factors are required to stop growth and initiate a decline. In cyclic snowshoe hare, Sheriff et al. (2010) showed that intergenerationally inherited stress caused by high predation risk could reduce fecundity sufficiently to initiate a population decline, in accordance with the maternal effect hypothesis (see Inchausti and Ginzburg 2009 for a review). In addition, our model does not take into account seasonality (i.e., differential predation and reproductive rate between the summer and winter period under the snow). In Norwegian lemming (*Lemmus lemmus*), Ims et al. (2011) showed that favorable winter conditions enabling high reproductive rate under the snow could hinder predator control and lead to lemming population outbreaks.

Generally, geese, shorebirds, and passerines constitute alternative prey to lemmings for many predators on Bylot Island (Béty et al. 2002, McKinnon 2011). This creates the potential for indirect interaction between lemmings and these species (Holt and Kotler 1987) because predators switch to alternative prey when lemmings are scarce, as previously documented with geese (Béty et al. 2002, Lecomte et al. 2008). This mechanism can explain why a greater proportion of goose production is consumed by predators (primarily Arctic foxes and Glaucous Gulls) during years of low lemming abundance. In contrast, passerines were less consumed by predators in years of low lemming abundance. A possible explanation may be that eggs and young of these species are prey of low profitability due to their small size and sparse distribution, which makes them difficult to find. In addition, some predators (e.g., Long-tailed Jaegers, Snowy Owls) may forego breeding and leave the system in lemming crash years (J.-F. Therrien, *unpublished data*). Passerines and shorebirds could thus be more incidental prey than alternative prey (McKinnon 2011).

Control of the tundra food web

Our analysis provided little evidence that herbivores are limited by primary production on Bylot Island. In addition, the temporal decrease in plant EE observed during the study indicates that the impact of herbivores is not only weak, but has lessened over time. In contrast, the strength of the predator–prey interactions that we measured is consistent with the hypothesis that the system is primarily controlled top-down. The temporal decrease in plant EE was probably due to an increase in vascular plant production over time due to climate warming (Gauthier et al. 2012; see also Appendix: Fig. A1) without any concomitant change in herbivore abundance. This may be additional evidence that the system is controlled by predators.

The control of the tundra food web by predators, though frequent (Reid et al. 1995, Wilson et al. 1999, Gilg et al. 2003, 2006), is not ubiquitous. For instance, lemming populations in northern Fennoscandia and

northern Alaska may be largely controlled by plant–herbivore interactions (Turchin et al. 2000, Oksanen et al. 2008, but see Ims et al. 2011). Along the western coast of Hudson Bay in Canada, Snow Goose density has exceeded the local carrying capacity of coastal marshes, leading to overgrazing and significant habitat degradation, and thus an ecosystem also dominated by plant–herbivore interactions (Jefferies and Rockwell 2002, Jefferies et al. 2004). An important question is therefore what factors are likely to favor bottom-up over top-down control of the tundra ecosystem. One such factor may be the presence of allochthonous resources generated by the flow of organic and inorganic matter across ecosystem boundaries (Leroux and Loreau 2008). For instance, resources acquired in the Arctic marine ecosystem by some tundra predators or in temperate areas by migratory birds may subsidize the populations of top predators and strengthen top-down control (Tarroux 2011, Therrien et al. 2011, Gauthier et al. 2012, Giroux et al. 2012). Anthropogenic influences may be another factor. The demographic explosion of the Snow Goose population along Hudson Bay is largely due to a food subsidy provided by human agriculture in winter (Jefferies et al. 2003), which may have allowed the population to escape from predator control in the Arctic, a phenomenon referred to as an apparent trophic cascade (Jefferies et al. 2003). Finally, Bylot Island is characterized by the absence of large mammals (caribou/reindeer and muskox) and their associated predator, the wolf. The presence of large herbivores in an ecosystem can induce strong direct and indirect effects (Ripple and Beschta 2005, Pringle et al. 2007) and their presence could change the patterns of trophic interactions reported here.

CONCLUSION

The use of a trophic mass balance model proved useful in assessing the relative importance of top-down vs. bottom-up forces in controlling a relatively simple tundra food web despite some limitations in quantifying plant–herbivore interactions. Some of these limitations could be alleviated by combining this approach with experimental manipulations (e.g., herbivore exclosures). Mass balance models should be especially useful in comparing the relative intensities of plant–herbivore vs. predator–prey interactions across different ecosystems. Future studies should aim at examining the generalities of the patterns that we documented and elucidating factors favoring top-down over bottom-up control in different tundra ecosystems. Allochthonous subsidies, the body size range of herbivores, and anthropogenic influences are likely to be some of the key factors.

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SUPPLEMENTAL MATERIAL

Appendix

Biomass, diet, production, and consumption data used in the ECOPATH modeling for each functional group and details of the methods used to collect the data (*Ecological Archives* E093-148-A1).