



Impacts des changements climatiques sur les relations plantes-herbivores dans l'Arctique

Thèse

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RÉSUMÉ

Lorsque des espèces à différents niveaux trophiques répondent aux changements climatiques à des rythmes différents, il peut en résulter une désynchronisation entre la phénologie des consommateurs et celle de leurs ressources. Les oiseaux migrateurs qui se reproduisent dans l'Arctique pourraient être parmi les espèces les plus touchées par une telle désynchronisation. Cette étude examine l'impact du réchauffement climatique sur les interactions entre la grande oie des neiges (*Chen caerulesens atlantica*) et les plantes dont elle s'alimente sur l'Île Bylot, Nunavut. À l'aide de petites serres, nous avons examiné l'impact d'un réchauffement sur la biomasse et la concentration en azote (un indice de qualité nutritive) des plantes utilisées par les oies. Nos résultats montrent qu'un réchauffement annuel mène à une augmentation de la biomasse végétale, mais que cette hausse est accompagnée d'un déclin plus rapide de la qualité nutritive des plantes. En effet, la concentration en azote des plantes des parcelles réchauffées était jusqu'à 14% plus faible que celle des parcelles témoins, et ce pendant la période de croissance des jeunes oies. Nous avons également montré qu'un indice satellitaire, le *Normalized Difference Vegetation Index* (NDVI) peut être utilisé comme proxy afin de déterminer la date du pic de concentration en azote des plantes. En utilisant le NDVI, nous avons donc pu estimer la date de pic d'azote des années pour lesquelles nous n'avions pas de données empiriques sur la végétation. Finalement, nous avons analysé des données à long-terme sur le climat, la phénologie des plantes et la reproduction des oies afin d'examiner l'impact potentiel de la désynchronisation trophique sur la croissance des jeunes. Selon nos résultats, les oies ajustent seulement partiellement leur reproduction en fonction des changements annuels dans la disponibilité de nourriture de haute qualité. En conséquence, la masse et la taille structurelle des jeunes oies à l'envol étaient réduites lorsque la reproduction des oies était moins bien synchronisée avec le pic de qualité nutritive des plantes. Nos résultats supportent l'hypothèse que la désynchronisation trophique peut avoir des effets négatifs sur l'aptitude phénotypique des herbivores arctiques, et que ces effets pourraient s'accroître avec l'augmentation prévue des températures à l'échelle globale.

ABSTRACT

When species at different trophic levels respond to climate change at different rates, this may lead to a trophic mismatch between the phenology of consumers and that of their resources. As polar regions are warming more rapidly than the rest of the planet, migratory birds breeding in the Arctic are expected to be among the species most affected by trophic mismatch in the wake of rapid climate change. This study examines the impact of climate warming on the interactions between an arctic herbivore, the greater snow goose (*Chen caerulescens atlantica*), and its food plants on Bylot Island, Nunavut, Canada. Using small greenhouses, we examined the impact of increased temperatures on plant biomass and a proxy of nutritive quality, nitrogen concentration, of graminoid plants used by geese during the brood-rearing period. This experiment showed that annual warming significantly increased biomass of graminoids but also led to an acceleration of the seasonal decline in plant nutritive quality and resulted in a decrease in the nitrogen concentration of plants by up to 14% during the period of gosling growth. We also showed that satellite-derived Normalized Difference Vegetation Index (NDVI) can be used as a proxy to determine date of peak nitrogen concentration in some tundra plants, and can thus be a reliable measure of the early changes in the timing of the availability of high quality food for herbivores. Using NDVI, we were then able to estimate the date of peak nitrogen in years when we had no empirical data on plant phenology. Finally, we analysed long-term data on climate, plant phenology and the reproduction of geese in order to examine the potential impact of mismatched reproduction on the growth of young. We found that geese are only partially able to adjust their breeding phenology to compensate for annual changes in the timing of high quality food plants, and that gosling body mass and structural size at fledging was reduced when trophic mismatch was high. Our results support the hypothesis that trophic mismatch can negatively affect the fitness of arctic herbivores, and that it is likely to be exacerbated by rising global temperatures.

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À mes parents

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AVANT-PROPOS

Cette thèse est composée d'une introduction générale suivie de trois chapitres rédigés sous forme d'article scientifique et se termine par une conclusion générale. Bien que chacun des chapitres fait partie de la même thématique générale, ils ont été préparés pour publication individuelle dans trois revues différentes, et peuvent donc être lus indépendamment. Je suis l'auteur principal de tous les chapitres, mais leur réalisation n'aurait pas été possible sans l'aide et le soutien de mes co-auteurs. Gilles Gauthier (mon directeur de thèse) et Esther Lévesque (ma co-directrice) ont grandement contribué à chaque étape de leur préparation, de l'élaboration des objectifs et du protocole expérimental jusqu'à la toute fin de la rédaction. Pierre Legagneux a également contribué à l'analyse des données NDVI et a participé à la rédaction du deuxième chapitre. De par sa contribution importante à ce chapitre, il en est donc co-auteur. Le premier chapitre a été publié dans la revue *Journal of Ecology*, le deuxième chapitre publié dans la revue *Applied Vegetation Science*, et le troisième chapitre sera soumis à la revue *Global Change Biology*.

INTRODUCTION GÉNÉRALE

Impacts des changements climatiques sur les écosystèmes

Au cours du dernier siècle (1880-2012), la température moyenne globale de la planète a augmenté d'environ 0.85°C, accompagnée d'une diminution dans le couvert de neige et de glace à l'échelle globale (IPCC 2013). Ces changements de température sont associés à une hausse dans la concentration atmosphérique de gaz à effets de serre d'origine anthropique, et les modèles climatiques globaux produits par le Groupe intergouvernemental d'experts sur le climat (GIEC/IPCC) prédisent que cette augmentation de température continuera au cours du prochain siècle, pouvant atteindre une augmentation de 1.0 à 3.7°C d'ici 2100 (IPCC 2013).

Le réchauffement climatique est plus prononcé dans les régions polaires comparativement au reste de la planète (ACIA 2004, Barber *et al.* 2008, Serreze & Barry 2011). Au nord du 60^e parallèle, la température a augmenté d'environ 1.36°C au cours du dernier siècle, soit environ le double de la moyenne globale (Bekryaev *et al.* 2010), avec une augmentation encore plus dramatique depuis 1979 (0.5°C par décennie; IPCC 2013). Les températures du pergélisol ont augmenté dans la plupart des régions arctiques au cours des 30 dernières années, pour atteindre un réchauffement de 2 à 3°C dans certaines régions du nord de l'Alaska et de la Russie (IPCC 2013). De plus, des analyses satellitaires effectuées depuis 1979 montrent que la période de fonte de neige s'est raccourcie à la grandeur de l'Arctique et que la fonte de neige a été devancée de 5 à 10 jours par décennie (Tedesco *et al.* 2009). Selon les modèles climatiques du GIEC, le réchauffement de l'Arctique sera encore plus important d'ici la fin du siècle, et connaîtra une augmentation de température de 2.2 à 2.4 fois celle de la moyenne globale, le tout accompagné d'une augmentation considérable de précipitations pouvant atteindre de 15 à 25% selon la saison (IPCC 2013).

Le réchauffement climatique global est un phénomène environnemental ayant des conséquences importantes sur un grand nombre d'écosystèmes. Au cours des dernières décennies, une multitude d'études et de méta-analyses ont rapporté des changements dans le cycle vital et la physiologie des espèces, et ce en lien avec le réchauffement du climat (Root *et al.* 2003). Ces études montrent que l'augmentation de température d'origine anthropique a déjà eu un impact mesurable sur de nombreux écosystèmes (Walther *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 2003, Parmesan 2006), et représente probablement la plus grande menace à la biodiversité à l'échelle planétaire (Thomas *et al.* 2004).

Le réchauffement climatique peut affecter les espèces animales de nombreuses façons, par exemple en modifiant leurs aires de répartition géographique ou leurs abondances (Hannah 2010). Toutefois, la phénologie est souvent un des premiers processus biologiques touché par les changements climatiques. La phénologie se définit comme étant l'initiation des activités essentielles du cycle vital d'une espèce selon les saisons (Berteaux *et al.* 2004). Selon Parmesan & Yohe (2003), plus de 50% des espèces étudiées ont connu des changements dans leur phénologie et/ou leur distribution au cours du dernier siècle, et une méta-analyse a révélé que 143 espèces animales et végétales ont devancé leur phénologie de 5.1 jours par décennie au cours de 50 dernières années (Root *et al.* 2003). Plus récemment, une autre méta-analyse effectuée en Grande-Bretagne sur 726 espèces terrestres et aquatiques a montré que la majorité des espèces ont devancé leur phénologie de façon cohérente avec l'augmentation de température, et que ces changements dans la phénologie peuvent se produire à des rythmes différents selon le niveau trophique (Thackeray *et al.* 2010).

Changements climatiques et interactions trophiques

Les interactions trophiques (prédateurs-proies, plantes-herbivores) jouent un rôle clé dans la dynamique des écosystèmes. Chez les espèces vivant dans des habitats saisonniers, les variations annuelles dans les conditions environnementales ainsi que la disponibilité des ressources déterminent la période idéale pour l'initiation d'événements comme la migration, la reproduction ou la mue (Futuyma 1998). Comme la reproduction est souvent une période où le besoin en ressources est très élevé, l'initiation de celle-ci a généralement lieu lors du pic annuel d'abondance et/ou de qualité de nourriture (Perrins 1970). Or, si la période de forte abondance de nourriture est modifiée par des changements dans l'environnement et que les consommateurs ne réussissent pas à s'adapter en modifiant leur période de reproduction (i.e. leur phénologie), il peut en résulter une désynchronisation trophique entre le pic de besoin en ressources et la disponibilité de celles-ci.

L'idée d'une désynchronisation dans la phénologie de deux espèces (ou groupes d'espèces) n'est pas nouvelle et porte le nom de « *match/mismatch hypothesis* » (Durant *et al.* 2007). Cette hypothèse tente d'expliquer les variations dans le recrutement au sein d'une population

par le biais de la relation entre la phénologie de cette espèce (i.e. consommateur) et celle de l'espèce ou groupe fonctionnel du niveau inférieur dans la chaîne trophique (i.e. proie). Le terme « *match/mismatch* » fut utilisé pour la première fois dans les écosystèmes aquatiques pour expliquer les variations extrêmes dans le recrutement de populations de morues (*Gadus* spp.) (Cushing 1974). Dans ce système, l'intensité du recrutement dépend du degré de chevauchement dans le temps entre la période critique du développement des larves et le pic d'abondance de leur nourriture, le zooplancton. Le degré de chevauchement, qui peut être illustré par deux courbes normales représentant l'abondance de deux niveaux trophiques en fonction du temps (voir Figure 1), peut varier entre un chevauchement presque total (synchronisation, « *match* ») ou un chevauchement presque nul (désynchronisation, « *mismatch* ») (Cushing 1990).

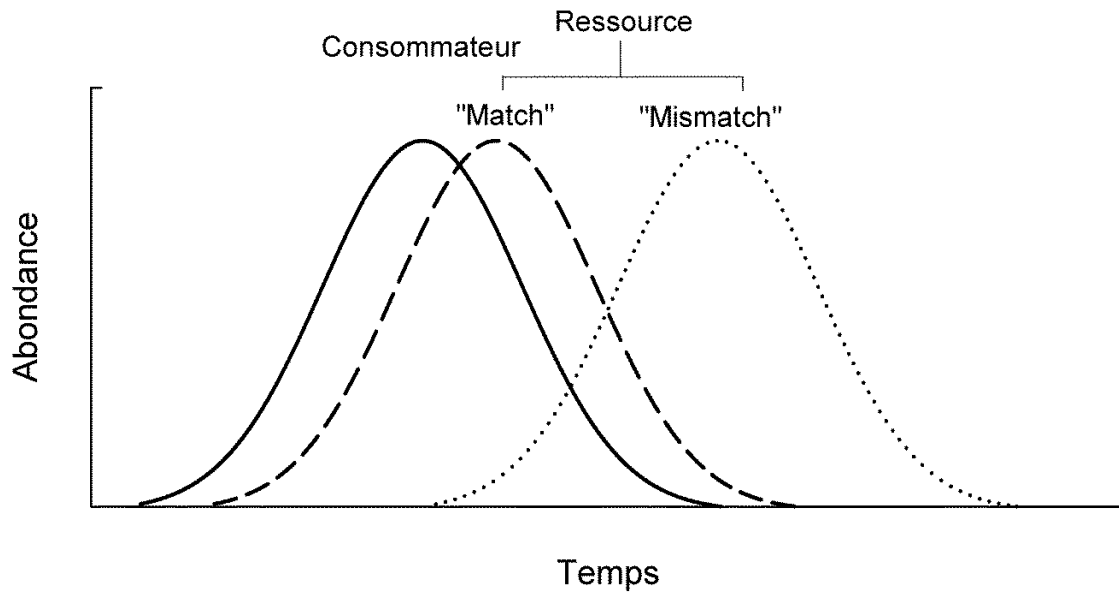


Figure 1. L'hypothèse « *match/mismatch* ». L'abondance des consommateurs (ex. poissons; ligne pleine) et de leur ressource (ex. plancton; lignes pointillées) à travers le temps. Le degré de chevauchement entre la courbe du consommateur et la courbe de sa ressource représente un « *match* » (synchronisation) ou « *mismatch* » (désynchronisation). Figure modifiée de Durant *et al.* 2007.

Selon Durant *et al.* (2007), une désynchronisation trophique peut avoir lieu si a) les proies et les prédateurs présentent chacun un certain degré de saisonnalité (i.e. leur effort de reproduction est concentré à une seule période de l'année), et b) le recrutement ou la survie des prédateurs est régulé par l'accès aux proies (contrôle du bas vers le haut). Chez des espèces principalement contrôlée par les prédateurs (contrôle du haut vers le bas), l'impact d'une désynchronisation sur la survie et la croissance des jeunes pourrait être négligeable comparativement à l'impact de la prédation (voir Sinclair *et al.* 2000). Selon Cushing (1990), le climat joue un rôle important dans ce degré de chevauchement puisque les conditions environnementales peuvent modifier la phénologie de ces espèces, parfois à des rythmes différents selon le niveau trophique. L'ampleur des effets d'un réchauffement climatique sur une espèce pourrait donc dépendre de la capacité de celle-ci à devancer (ou reculer) l'initiation de sa période de reproduction pour maintenir une bonne synchronie avec la phénologie de ses proies. Depuis la publication des travaux originaux de Cushing (1974), l'hypothèse « *match/mismatch* » a été appliquée à de nombreux systèmes dans le contexte des changements climatiques.

Un des groupes les plus étudiés en lien avec l'impact du réchauffement sur la phénologie est celui des oiseaux forestiers insectivores en Europe, particulièrement la mésange charbonnière (*Parus major*) et le gobe-mouche noir (*Ficedula hypoleuca*). Ces deux espèces nidicoles nourrissent leurs jeunes de chenilles folivores dont l'abondance atteint un pic très élevé pendant l'été, mais seulement pour une courte période de temps. Des suivis effectués depuis les années 1980 ont montré que ces oiseaux ont devancé leur date de ponte suite à une augmentation des températures printanières, mais à des rythmes différents selon la population (Visser *et al.* 1998, Slater 1999, Both *et al.* 2004, Visser *et al.* 2009). Les chenilles ont elles aussi devancé leur pic d'abondance en lien avec le climat mais à un rythme supérieur à celui de plusieurs populations d'oiseaux, menant à une désynchronisation trophique dans ces populations (Visser *et al.* 2006, Both *et al.* 2009). Lorsque la date de reproduction des oiseaux a peu changé comparativement au pic des chenilles, le manque de synchronie qui en résulte a été relié à une augmentation de la mortalité juvénile et une diminution du nombre de jeunes produits (Visser *et al.* 1998, Both 2012, Reed *et al.* 2013).

Un autre exemple de désynchronisation trophique ayant lieu suite aux changements climatiques est celui du caribou migrateur (*Rangifer tarandus*) et des plantes dont il s'alimente au Groenland (Post & Forchhammer 2008, Kerby & Post 2013b). Selon ces études, la date d'émergence des plantes a avancé d'environ 16 jours sur une période de 10 ans, alors que la période de reproduction du caribou a peu changé, faisant en sorte que la naissance des jeunes a lieu après le pic de qualité nutritive des plantes. En conséquence, la mortalité juvénile a augmenté et la production de jeunes a chuté. Dans le même système, une étude a également montré que les traits d'histoire de vie d'une espèce peuvent moduler leur vulnérabilité aux effets de la désynchronisation trophique. Les espèces qui dépendent principalement des ressources acquise dans l'environnement local pendant la période de reproduction (« *income breeders* », par exemple le caribou) sont plus sensibles au manque de synchronie trophique que les espèces qui utilisent principalement des réserves corporelles acquises plus tôt dans l'année (« *capital breeders* », le bœuf musqué, *Ovibos moschatus*) (Kerby & Post 2013a).

Au cours de la dernière décennie, les changements climatiques ont mené à un désynchronisation trophique dans de nombreux autres systèmes, dont les oiseaux marins (Gaston *et al.* 2009), les limicoles (Pearce-Higgins *et al.* 2009, McKinnon *et al.* 2012), les poissons d'eau douce et d'eau salée (Edwards & Richardson 2004, Winder & Schindler 2004), les insectes (Memmott *et al.* 2007, Høye *et al.* 2013, Schwartzberg *et al.* 2014), les rongeurs (Lane *et al.* 2012), et les grands herbivores en milieu tempéré (Plard *et al.* 2014). Il semble donc qu'un grand nombre d'espèces animales soient exposées à ce phénomène partout sur la planète.

Chez les populations migratrices qui sont caractérisées par une courte période de temps entre l'arrivée sur le site et le début de la reproduction, la capacité de devancer sa reproduction doit en grande partie passer par un devancement ou une accélération de la migration (Ahola *et al.* 2004, Both *et al.* 2004). Or, chez plusieurs espèces, l'initiation de la migration est déterminée surtout par la longueur du jour (Gwinner 1996), la photopériode représentant un indice temporel qui reflète le changement des saisons. Lorsque les changements climatiques modifient rapidement la relation entre la photopériode et les conditions environnementales (ex. printemps plus chauds, fonte de neige hâtive ou encore augmentation du nombre de

tempêtes), la longueur du jour peut devenir un indice de mauvaise qualité pour prédire la période optimale de migration. Les espèces migratrices de longue distance seraient particulièrement limitées dans leur capacité d'adaptation à des changements se produisant sur leurs aires de reproduction car elles doivent se baser sur une série d'indices environnementaux à l'échelle locale pour prendre leurs décisions au cours de la migration. Or ces indices peuvent devenir inefficaces lorsque les changements climatiques ont lieu à des rythmes différents tout le long du parcours migratoire (Both *et al.* 2010, Winkler *et al.* 2014). Ceci peut être particulièrement dommageable pour les espèces aviaires qui nichent dans l'Arctique car au printemps elles doivent quitter des régions relativement stables du point de vue climatique (régions tempérées) pour aller se reproduire des milliers de kilomètres plus loin, à des latitudes où les conditions climatiques sont beaucoup plus variables et davantage affectées par les changements climatiques. Étant donné la vitesse à laquelle ces changements ont lieu (IPCC 2013), certaines espèces animales ne possèdent peut-être pas la plasticité phénotypique nécessaire pour s'adapter rapidement à ces perturbations (Kerby *et al.* 2012).

Relations plantes-herbivores dans l'Arctique

Dû à la rigueur du climat et aux étés courts, la distribution et l'abondance des espèces dans les écosystèmes arctiques sont fortement contraintes par les conditions abiotiques (telles la température et le couvert nival), ce qui les rend particulièrement vulnérables à ces changements rapides de l'environnement physique (Post *et al.* 2009, Gilg *et al.* 2012). La toundra arctique est un écosystème relativement pauvre en espèces végétales. Vu la simplicité du réseau trophique (comparativement aux écosystèmes retrouvés en milieux tempérés ou tropicaux), toute modification de la communauté végétale peut avoir des répercussions importantes sur les espèces occupant les niveaux trophiques supérieurs. Afin de bien comprendre les effets des changements du climat sur le fonctionnement des écosystèmes terrestres arctiques, il est donc nécessaire d'évaluer de quelle façon les producteurs primaires sont touchés.

Les plantes arctiques sont un groupe qui a reçu beaucoup d'attention dans le contexte de l'effet des changements climatiques sur les écosystèmes arctiques grâce notamment à des

suivis à long terme et des expériences de réchauffement réalisées sur le terrain. Ces études, menées entre autres par le groupe circumpolaire « *International Tundra Experiment* », ont démontré que le réchauffement entraîne des changements dans la composition floristique des communautés (Walker *et al.* 2006, Elmendorf *et al.* 2012b, Post 2013), notamment par une présence accrue d'arbustes (Myers-Smith *et al.* 2011), ainsi qu'à une augmentation de la biomasse végétale, une augmentation de l'effort de reproduction des plantes et une accélération de la phénologie (Arft *et al.* 1999, Aerts *et al.* 2006, Jia *et al.* 2009, Forbes *et al.* 2010, Elmendorf *et al.* 2012a, Elmendorf *et al.* 2012b, Oberbauer *et al.* 2013).

Du point de vue des herbivores, les plantes les plus nutritives sont celles avec une forte teneur en protéines (souvent indexée par le contenu en azote) et une faible concentration en fibres (Robbins 1993). Dans l'Arctique, le taux d'azote disponible dans la végétation atteint son maximum peu après la fonte de la neige et connaît ensuite une diminution saisonnière abrupte (Chapin 1980, Klein 1990, Manseau & Gauthier 1993). Par conséquent, à mesure que la période de croissance des plantes avance, les plantes deviennent de moins en moins nutritives, surtout pour les jeunes herbivores en croissance dont les besoins en protéines sont très élevés (Mattson Jr 1980, Albon & Langvatn 1992, Sedinger 1997). Puisque la disponibilité de nourriture de haute qualité est très limitée dans le temps, une bonne synchronie entre la reproduction et le pic de qualité nutritive des plantes est essentielle pour les herbivores arctiques. Afin de pouvoir évaluer de quelle façon les changements climatiques pourraient affecter ces espèces, il est donc important de pouvoir mesurer l'effet de ces changements sur la concentration en nutriments des plantes ainsi que sur le patron saisonnier de celle-ci (i.e. le « *timing* » du pic d'abondance de nourriture de haute qualité, voir Figure 1).

Cependant, relativement peu d'études jusqu'à présent se sont attardées spécifiquement sur l'impact potentiel d'un réchauffement sur la qualité nutritive des plantes broutées par les herbivores. Les plantes des régions polaires et alpines ont typiquement des concentrations plus élevées en nutriments que les plantes de milieux tempérés, un phénomène qui semble être lié aux températures plus froides retrouvées dans ces régions (Kudo *et al.* 2001, Weih & Karlsson 2001). On pourrait donc supposer qu'une augmentation de la température pourrait causer une diminution de la teneur en nutriment des plantes arctiques, mais il ne semble pas y

avoir de consensus à cet effet parmi les études précédentes qui se sont penchées sur la question. Selon le site ou les espèces étudiées, on observe soit une diminution (Shaver *et al.* 1986, Welker *et al.* 1997, Jonsdottir *et al.* 2005a), une augmentation (Chapin *et al.* 1995, Welker *et al.* 2005) ou pas d'effet significatif (Lenart *et al.* 2002, Natali *et al.* 2012) sur la concentration en azote des plantes suite à un réchauffement expérimental. Ces différences pourraient être liées entre autres aux conditions climatiques et édaphiques à l'échelle locale, à la période d'échantillonnage, au type de réchauffement ou à l'ampleur de ce dernier (Jonsdottir *et al.* 2005a). Il devient alors difficile de généraliser quant à l'impact potentiel d'un réchauffement sur la concentration en nutriment des plantes pour les herbivores.

Le cas des oies migratrices

Les oies sont des herbivores importants dans la toundra, la majorité des espèces effectuant une longue migration printanière pour se reproduire dans les régions arctiques. Leur reproduction est hautement saisonnière et elles disposent d'une courte période au cours de laquelle elles peuvent nicher et élever leurs jeunes. Dû à la combinaison de ces facteurs, les oies pourraient être particulièrement vulnérables au phénomène de la désynchronisation trophique, d'autant plus lorsqu'on considère la rapidité à laquelle l'Arctique se réchauffe.

Bien que la taille corporelle des oies ait une composante génétique (Larsson & Forslund 1991), le taux de croissance des oisons demeure très variable et est directement relié à la qualité et la quantité de nourriture disponible lors de la période de croissance (Davies *et al.* 1988, Cooch *et al.* 1991, Sedinger & Flint 1991, Lepage *et al.* 1998, Lindholm *et al.* 1994). Les oisons nés plus tard en saison ont généralement une croissance plus lente et un taux de survie réduit, et ces différences seraient reliées au déclin rapide de la qualité nutritive des plantes retrouvées en milieu arctique pendant l'été (Larsson & Forslund 1991, Lindholm *et al.* 1994, Lepage *et al.* 1998). Des différences aussi faibles que 5-7 jours dans les dates d'éclosion peuvent avoir des conséquences majeures sur la croissance des individus (Lindholm *et al.* 1994).

La période d'élevage est une période critique dans la vie des oies parce que leur taille et leur condition corporelle à la fin de leur premier été ont une influence importante sur leurs

chances de survivre leur première année, une période où la mortalité juvénile est élevée (Owen & Black 1989, Schmutz 1993, Menu *et al.* 2005). Une étude de Sedinger *et al.* (1995) menée sur la Bernache cravant (*Branta bernicla*) en Alaska a montré qu'il y avait une relation positive entre la taille corporelle des oisons et leur taux de survie. La taille des oisons était également positivement corrélée à leur taille adulte, et les oisons les plus gros avaient de meilleures chances de se reproduire à l'âge de 2 ou 3 ans que des oisons de plus petite taille. De plus, les adultes les plus gros produisaient des couvées avec un volume total et un nombre d'œufs plus élevé que les adultes de plus petite taille, ce qui laisse entendre que la taille corporelle influence également la fécondité. Des changements dans la croissance des oisons pourraient donc avoir des conséquences importantes dans la dynamique des populations des oies migratrices en modifiant la survie, le succès reproducteur et le recrutement des individus dans la population.

On pourrait penser à prime abord que les oies pourraient bénéficier du réchauffement climatique arctique de façon directe (coûts réduits de thermorégulation, Renaud 1999) ou de façon indirecte via la nourriture (augmentation de la biomasse des plantes, saison de croissance végétale plus longue) ou les sites de reproduction (expansion latitudinale des sites propices à la reproduction, Jensen *et al.* 2008). Cependant, si la croissance plus rapide des plantes devance le pic de qualité nutritive de la végétation, comme cela a été rapporté chez le caribou au Groenland (Post & Forchhammer 2008), il est possible que la synchronisation entre l'éclosion des jeunes et le pic de qualité de plantes soit menacée. Puisque les oies arrivent sur les aires de reproduction peu de temps avant le début de la ponte, leur capacité d'ajuster leur date de ponte en fonction des conditions locales une fois sur le site est très limitée (Bêty *et al.* 2003). De plus, le temps d'incubation pour produire et incuber une couvée étant fixe (Poussart *et al.* 2000), les oies peuvent difficilement ajuster la phénologie de leur reproduction pour devancer l'éclosion des jeunes face à des changements rapides dans la phénologie de la croissance des plantes dont elles s'alimentent (Gauthier *et al.* 2013).

Objectifs de la thèse

La grande oie des neiges (*Chen caerulescens atlantica*) est une sous-espèce migratrice qui se reproduit dans l'est de l'Arctique canadien et hiverne sur côte est américaine. L'une des plus grandes colonies au monde est située sur la plaine sud de l'île Bylot, au Nunavut (73°08'N, 80°00'W; Figure 2). Cette colonie fait l'objet d'un suivi depuis 1989, et il existe maintenant une base de donnée à long-terme sur la reproduction de la grande oie des neiges (dates de ponte, dates d'éclosion, tailles de couvées, croissance et alimentation des jeunes, utilisation de l'habitat, démographie), ainsi que sur une série d'autres facteurs biotiques (production primaire, effets du broutement, prédation) et abiotiques (variables climatiques). Au cours des 35 dernières années, les températures à l'Île Bylot ont augmenté en moyenne de 2.8°C au printemps (Gauthier *et al.* 2011), et la valeur annuelle cumulative de degrés-jours au dessus de zéro a augmenté de 381 à 521 entre 1989 et 2011 (Gauthier *et al.* 2013).

L'objectif global de cette thèse est de vérifier si l'hypothèse du « *match/mismatch* » s'applique à l'interaction entre la grande oie des neiges et sa nourriture dans un contexte de réchauffement du climat arctique, et de mesurer ses conséquences potentielles sur les oies via son impact sur la croissance des jeunes. Pour ce faire, j'ai utilisé une combinaison de manipulations expérimentales et de données à long terme. Lors de sa maîtrise, Marie-Hélène Dickey a étudié la relation entre la phénologie de la reproduction des oies et plusieurs variables climatiques sur l'île. Selon ses travaux, les facteurs climatiques printaniers expliquent 50% de la variation individuelle dans la phénologie, et des températures élevées ainsi qu'un faible couvert de neige sont associés à une reproduction hâtive (Dickey *et al.* 2008). Cependant, les analyses préliminaires effectuées dans son deuxième chapitre suggèrent que des températures élevées et un faible couvert de neige au printemps étaient également associés à une désynchronisation entre la date d'éclosion et le pic de qualité des plantes (Dickey 2006). Ses travaux ont donc servi de point de départ pour les questions abordées dans cette thèse.

Organisation de la thèse

Le premier chapitre de cette thèse se penche sur l'impact du réchauffement climatique sur la qualité nutritive et la disponibilité des plantes broutées par les oies. Pour ce faire, j'ai utilisé un dispositif expérimental sur le terrain (serres de polycarbonate; Figure 3) afin d'augmenter la température dans deux habitats utilisés par les oies pendant la période d'élevage des jeunes. Cette expérience m'a permis de tester l'hypothèse selon laquelle un réchauffement (1) augmente la biomasse aérienne des plantes, et (2) accélère le déclin saisonnier dans la concentration en azote, un indice de la qualité nutritive des plantes pour les herbivores (Sedinger & Raveling 1984).

Le deuxième chapitre est plus méthodologique. Afin de pouvoir mesurer l'impact de la désynchronisation trophique sur les oies, je devais être en mesure d'évaluer à quelle date avait lieu le pic de qualité nutritive des plantes (i.e. la concentration en azote). Or, comme il est difficile d'obtenir de longues séries de données sur la phénologie des plantes arctiques, nous disposons seulement de 10 années de données pour cette mesure (vs 20 années de données pour les oies). Nous avons donc voulu vérifier si l'indice de végétation par différence normalisée (*Normalized Difference Vegetation Index* ou NDVI; voir Annexe 1 pour plus de détails), est un indice approprié pour estimer (1) la date de pic d'azote des plantes, et (2) la biomasse aérienne à différentes périodes de l'été. Ce chapitre était essentiel aux analyses du chapitre suivant puisqu'il m'a permis de doubler le jeu de données utilisé.

Le troisième chapitre porte directement sur le phénomène du « *match/mismatch* » chez les oies. Le but de ce chapitre était de déterminer quels facteurs climatiques influencent la date de pic d'azote des plantes ainsi que la synchronie entre cette dernière et la date d'éclosion des jeunes, et enfin d'examiner de quelle façon un manque de synchronie pourrait affecter la croissance des jeunes. J'ai voulu tester les hypothèses suivantes : (1) la date de pic d'azote des plantes a lieu plus tôt lors d'années chaudes avec fonte de neige hâtive, (2) le « *mismatch* » entre la phénologie de la reproduction des oies et le date de pic d'azote des plantes est plus important lors d'années chaudes avec fonte de neige hâtive, et (3) ce manque de synchronisation a des effets négatifs sur la masse corporelle et la taille structurelle des jeunes oies juste avant l'envol.

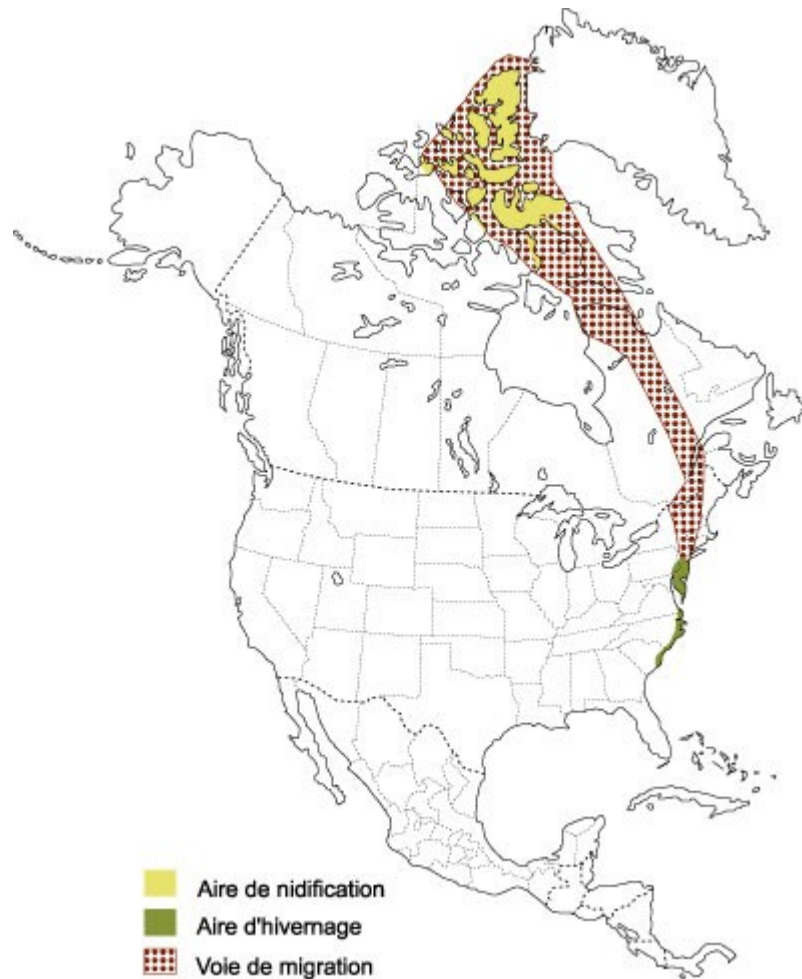


Figure 2. Aires de répartition (en rouge) de la grande oie des neiges (*Chen caerulescens atlantica*). Figure tirée de <http://www.hww.ca/fr/especes/oiseaux/la-grande-oie-des-neiges.html>

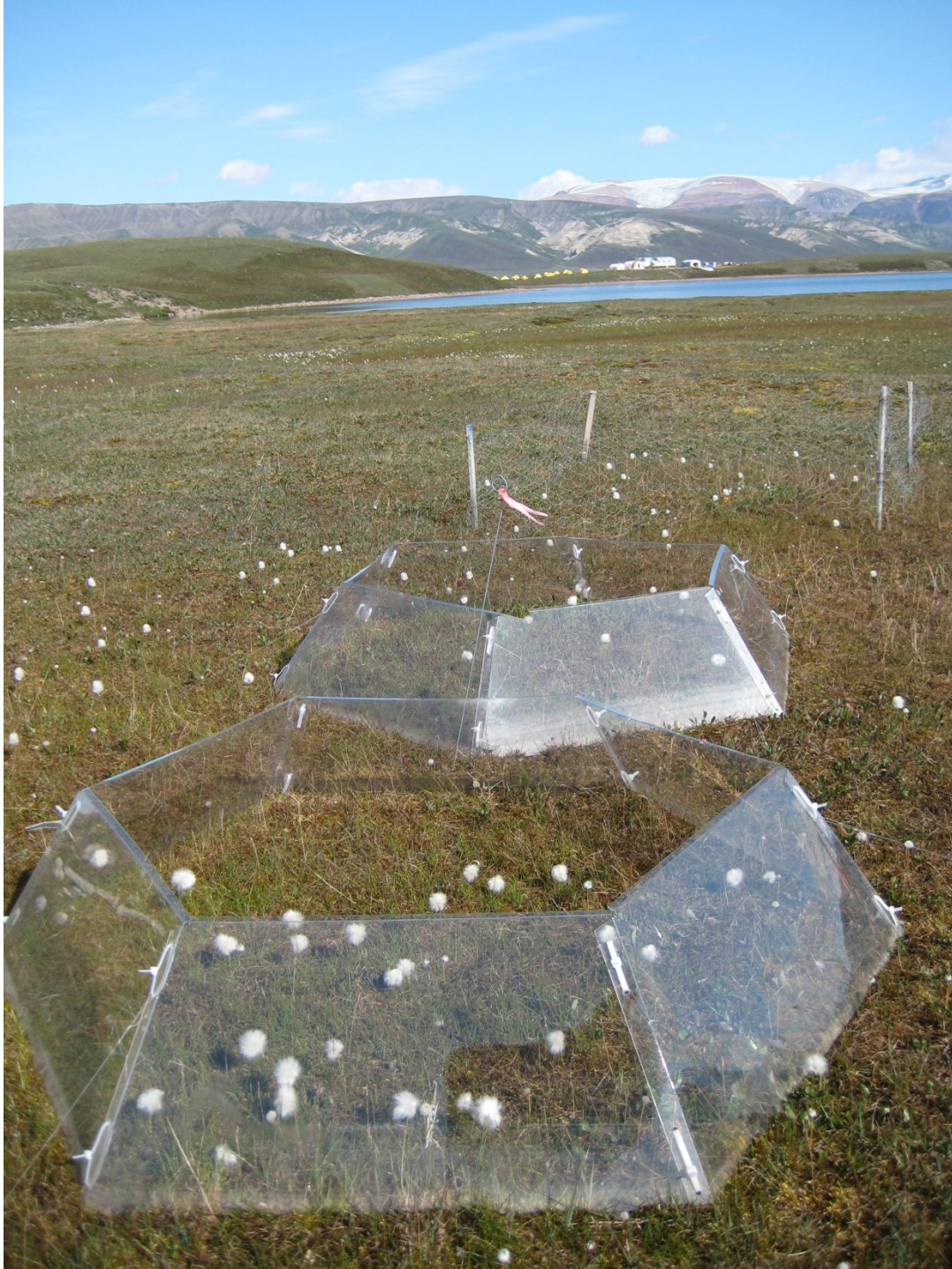


Figure 3. Serres de polycarbonate utilisées dans le protocole expérimental du Chapitre 1. Ces serres augmentent la température à laquelle les plantes sont exposées pendant la période de croissance tout en permettant des précipitations normales. Le design de ces serres est basé sur les travaux du groupe *International Tundra Experiment* (Marion *et al.* 1997).

CHAPITRE 1

Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore

Doiron, M., Gauthier, G. & Lévesque, E. (2014) Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *Journal of Ecology*, **102**, 508-517.

Résumé

Chez plusieurs herbivores de l'Arctique, la croissance des jeunes dépend d'une bonne synchronie entre la date de naissance/d'éclosion et le changement saisonnier de la qualité nutritive des plantes. Si les plantes répondent plus rapidement que les herbivores au réchauffement climatique, il pourrait en résulter une désynchronisation entre la disponibilité de nourriture de haute qualité et l'éclosion des jeunes. Cette étude examine l'impact d'un réchauffement expérimental sur les plantes dont s'alimentent un herbivore de l'Arctique, la grande oie des neiges (*Chen caerulescens atlantica*) se reproduisant sur l'Île Bylot, Nunavut, Canada. Pendant les étés 2007-2009, nous avons augmenté la température à l'aide de petite serres (« *open-top chambers* », OTC) dans deux habitats, les milieux humides et les prairies mésiques. À chaque 10 jours, nous avons mesuré la biomasse aérienne des plantes ainsi qu'un indice de qualité nutritive, la concentration en azote, des plantes herbacées se trouvant dans les parcelles réchauffées et les parcelles témoin, et ce à partir de la fonte de la neige en juin jusqu'à la fin juillet. Les OTCs ont mené à une augmentation des températures maximales pouvant atteindre 2,0°C dans les milieux humides et 4,6°C dans les prairies mésiques. Tôt en saison, il n'y avait pas de différence dans la concentration en azote des quatre espèces échantillonnées (*Dupontia fisheri*, *Eriophorum scheuchzeri*, *Arctagrostis latifolia* and *Luzula* spp.), mais le déclin saisonnier de l'azote a eu lieu plus tôt dans les parcelles réchauffées que dans les parcelles témoins (10% à 14% moins d'azote dans les parcelles réchauffées en juillet). Cet effet était consistant pour les trois années de l'expérience et était indépendant des variations annuelles dans la phénologie des plantes. Il y avait soit un faible effet positif ou pas d'effet du réchauffement sur la biomasse en azote des plantes dépendant de l'espèce échantillonnée ou de la période de la saison. Nos résultats montrent que le réchauffement mène à une accélération de la phénologie des plantes et du déclin saisonnier dans la qualité nutritive des plantes pour les herbivores arctiques. Puisque les jeunes herbivores comme les oies sont très sensibles à la concentration en azote de leur nourriture, un climat plus chaud pourrait donc diminuer leur croissance. En conséquence, le réchauffement climatique pourrait avoir des impacts négatifs sur les effectifs de population des herbivores arctiques en réduisant la qualité nutritive des plantes dont ils s'alimentent pendant la période de reproduction.

Abstract

In many arctic herbivores, the growth of young depends upon a synchrony between hatch date and seasonal change in plant nutritive quality. If plants respond more quickly than herbivores to climate warming, this may cause a mismatch between the availability of high quality food and the hatching of young. This study examines the impact of experimental warming on the main food plants of an arctic herbivore, the greater snow goose (*Chen caerulescens atlantica*) breeding on Bylot Island, Nunavut, Canada. During summers 2007-2009, we increased temperature using small greenhouses (open-top chambers, OTC) in two habitats, wetlands and mesic tundra. Every 10 days, we measured aboveground plant biomass and a proxy of nutritive quality, nitrogen concentration, of graminoid plants in warmed and control plots from snow-melt in June until late July. OTCs increased mean maximum temperature by up to 2.0°C in wetlands and 4.6°C in mesic tundra. Annual warming significantly increased biomass of graminoids by up to 29% in wetlands and 20% in mesic tundra. There was no difference in nitrogen concentration of the four plant species sampled (*Dupontia fisheri*, *Eriophorum scheuchzeri*, *Arctagrostis latifolia* and *Luzula* spp.) early in the season, but the seasonal decline in nitrogen occurred more rapidly in warmed than in control plots (10% to 14% less nitrogen in warmed plots in July). This effect was consistent across the three years of the experiment and independent of annual variation in plant phenology. There was either a weak positive effect or no effect of the warming treatment on the nitrogen biomass of plants depending on species or period of the season. Our results show that warming speeds up plant phenology and the seasonal decline in nutritive quality for arctic herbivores. Because young herbivores like geese are highly sensitive to the nitrogen concentration of their food, a warmer climate will likely reduce their growth. Climate warming may therefore have a negative impact on the population dynamic of arctic herbivores by reducing the quality of their summer forage.

Introduction

Mean global temperature has increased by approximately 0.74°C over the last century (1906-2005) and global climatic models predict that this will continue over the next century and reach an increase of 1.8 to 4.0°C before 2099 (IPCC 2007). This warming has already had major impacts on ecosystems by altering not only the distribution of species but also their phenology (Walther *et al.* 2002, Parmesan & Yohe 2003, Oberbauer *et al.* 2013). Phenology, defined as the seasonal initiation of essential life-cycle activities (Berteaux *et al.* 2004), is the parameter most often affected by climate change (Parmesan 2006). Changes in phenology can affect trophic interactions through a phenomenon known as trophic mismatch, which occurs when species at different trophic levels exhibit differential change in phenology in response to changes in their environment (Durant *et al.* 2007, Kerby & Post 2013b). Trophic mismatch between predators and their prey can reduce reproductive success and/or recruitment, leading in some cases to population declines (Post & Forchhammer 2008, Both *et al.* 2010). Moreover, in long-distant migrants, changes in climate occurring on the wintering and breeding grounds may progress at different rates, hindering their adaptation to warming and making them more susceptible to trophic mismatch (Visser *et al.* 2004, Møller *et al.* 2010).

Polar regions are warming at a faster rate than the rest of the planet and arctic ecosystems are among the most vulnerable to climate change (Post *et al.* 2009, Gilg *et al.* 2012). Reproduction of arctic herbivores is highly seasonal and typically timed to coincide with the period when food quality and availability is at its peak (Lepage *et al.* 1998, Post *et al.* 2003). For these reasons, goose populations that breed in arctic regions should be highly susceptible to trophic mismatch. Migratory geese, which are major herbivores in many tundra regions, have a short time-window to reproduce during the summer, leading to synchronized reproduction (Lepage *et al.* 2000). Gosling growth is highly sensitive to environmental conditions (Gauthier *et al.* 2006) and is directly related to quality and availability of food plants, primarily protein content, on the brood-rearing areas (Larsson & Forslund 1991, Lindholm *et al.* 1994, Lepage *et al.* 1998).

In recent years, numerous studies have examined the response of plants to experimental warming, most notably by the International Tundra Experiment (ITEX) group in polar and

alpine regions. These studies have demonstrated that plants respond to warming by an accelerated phenology, increased growth and a greater reproductive effort in the form of increased flower production (Henry & Molau 1997, Arft *et al.* 1999, Aerts *et al.* 2004, Aerts *et al.* 2006, Elmendorf *et al.* 2012a, Oberbauer *et al.* 2013). While these studies show how warming affects plant phenology, it is unclear how temperature increases could affect the nutrient content of plants for herbivores. Plants at high latitudes and high elevation generally have high nutrient concentrations (Kudo *et al.* 2001), possibly as an adaptation to low air temperature (Weih & Karlsson 2001), and thus we would expect warming to have a negative impact on nitrogen content. However, previous warming experiments show decreases, increases, or no effect on the nitrogen content of plants (Lenart *et al.* 2002, Jonsdottir *et al.* 2005a, Welker *et al.* 2005, Aerts *et al.* 2009, Natali *et al.* 2012; see Table 1 in Annexe 2 for a review). These discrepancies may be due to differences in species sampled, climatic and edaphic conditions, type of warming experiment or timing of sampling (Jonsdottir *et al.* 2005a). It is therefore not possible to make generalizations on how future increases in temperature should affect forage quality of arctic herbivores.

Proteins, generally measured by the nitrogen concentration of plants, are known to be the most limiting nutrient for the growth of arctic herbivores like geese (Sedinger & Raveling 1986, Lepage *et al.* 1998). Nitrogen concentration of arctic plants, which is typically highest shortly after the onset of plant growth, decreases slowly throughout the summer, and the hatching of goslings is generally timed to coincide with the period of peak food quality (Manseau & Gauthier 1993, Lepage *et al.* 1998, Larter & Nagy 2001, Cadieux *et al.* 2005). If warming was to change this pattern by advancing the date of peak nitrogen or accelerating the seasonal decline in plant quality, this may lead to a mismatch between the hatching of goslings and the availability of high quality food, with potential negative impacts on gosling growth and survival.

The aim of this study is to examine the effect of short-term experimental warming on the availability and quality of forage plants for an arctic herbivore. To accomplish this, we used small polycarbonate greenhouses to increase air temperature in two different habitat types used by geese during three summers (2007-2009) in order to evaluate the effects of warming on i) total aboveground biomass and ii) the timing of the seasonal decline in plant nutritive

quality, an important phenological event for growing herbivores during the summer. In this study, nitrogen concentration was the proxy used for nutritive quality of forage for goslings. We predicted that i) warming would increase the total forage plant biomass but ii) that this increase would be accompanied by a more rapid decline in plant nitrogen concentration in warmed plots.

Material and methods

Study area

This study was conducted on the south plain of Bylot Island (73°08'N, 80°00'W), north of Baffin Island, Nunavut, Canada. This region is one of the most important breeding areas for the greater snow goose (Reed *et al.* 2002). Habitats used by geese can be divided in two broad categories (Gauthier *et al.* 1996). The first habitat type consists of wetlands characterized by wet polygon fens (Tarnocai & Zoltai 1988). Vascular plant communities in this habitat are dominated by graminoids and sedges, such as *Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe and *Carex aquatilis* Wahlenb., growing through a thick carpet of moss. These 3 species account for >90% of the vascular plant biomass in this habitat (Manseau & Gauthier 1993). The second habitat type consists of upland mesic tundra, characterized by rolling hills and better drained soil. Vascular plant communities are more diversified and dominated, in decreasing order of abundance, by prostrate shrubs (*Salix arctica* Pall. and *Cassiope tetragona* D. Don), graminoids (*Arctagrostis latifolia* (R. Br.) Griseb., *Luzula nivalis* (Laest.) Beurling, *Luzula confusa* Lindeberg, *Poa arctica* R. Br.) and other small herbaceous species (e.g. *Stellaria longipes* Goldie, *Oxytropis maydelliana* Trautv., *Polygonum viviparum* L.) (Duclos 2002, Audet *et al.* 2007). Though less preferred by geese, mesic tundra vegetation covers approximately 90% of the landscape and is used at low densities throughout the nesting and brood-rearing periods (Hughes *et al.* 1994).

The annual average air temperature on Bylot Island over the period 1994 and 2007 was -14.5°C (4.5°C in the summer and -32.8°C in the winter; Cadieux *et al.* 2008). Over the past 35 years, temperature in the area has warmed on average by 2.8°C in spring and summer and

by 4.3°C in fall (Gauthier *et al.* 2011). The annual cumulative number of thawing degree-days has also increased from 381 in 1989 to 521 in 2011 (Gauthier *et al.* 2013).

Experimental design and sampling

Air temperature was increased using hexagonal, conical open-top chambers (OTC) made of polycarbonate according to the specifications of the ITEX protocol (Molau & Mølgaard 1996). They measured approximately 1.6 m in diameter at the base, 83 cm at the top and 24 cm high. Design was modified slightly to increase rigidity by bending the top 1cm of each panel. This allowed the use of thinner polycarbonate (2 mm thick) and reduced their weight and the impact of the chambers on light quality. These warming devices have been used in numerous studies to increase temperature on a small scale (Marion *et al.* 1997, Hollister & Webber 2000, Hollister *et al.* 2005, Hollister *et al.* 2006, Elmendorf *et al.* 2012a). OTCs allow for normal precipitations, but they alter light conditions and wind patterns around the plants and can advance snow melt by up to 14 days (Marion *et al.* 1997). Most of the heating by OTCs occurs when radiation peaks and thus the strongest impact of warming relates to daily maximum temperatures. In previous studies, daily maximums were increased by ~3.5°C in OTCs and the change in mean soil temperature (at -3cm) ranged from -0.2°C to 1.3°C (see Marion *et al.* 1997 for further details concerning OTC performance). Each OTC was paired with an adjacent unwarmed control plot (2m²) protected from goose grazing by a 30-cm high, 2.5 cm mesh chicken wire (exclosure). This experiment was conducted over three summers (2007-2009) in the two habitat types described above (wetlands and mesic tundra).

OTCs and exclosures were set up at the end of the summer preceding plant sampling at 6 different sites per habitat type and spaced from each other by >200m. The same general sites were reused every year but OTCs and exclosures were moved 10 to 20 meters each year due to destructive plant sampling. In summers 2007 and 2008, we used 3 OTCs and 3 control plots per site (each spaced out by a few meters), for a total of 18 OTCs and 18 control plots per habitat type. In 2009, the sampling was downscaled to one OTC and one control plot per site, for a total of six OTCs and six control plots per habitat type. The effect of treatments on the microclimate of growing plants was monitored in a subsample of each treatment

(typically three to five plots) in 2007 and 2008 using two types of automated temperature loggers: Onset HOBO® Pendant probes (Onset Computer Corporation, Bourne, MA, USA; ~0.5°C precision) or Model 107 Campbell Scientific temperature probes (Campbell Scientific, Edmonton, AB, Canada; ~0.2°C precision). In 2007, most temperature loggers in control plots of mesic tundra habitats were destroyed by foxes over the course of the summer, so data from control plots were obtained from a single logger until the end of July. The loggers were buried approximately 2-3 cm under the surface and recorded the temperature every 20 minutes for the duration of the experiment.

We collected aboveground plant biomass of two common species in each habitat type four times per season (approximately every 10-14 days) from shortly after snow melt in mid-June until the end of July. Plant species were: *Arctagrostis latifolia* and *Luzula* spp. (*L. nivalis* or *L. confusa*) in mesic tundra and *Eriophorum scheuchzeri* and *Dupontia fisheri* in wetlands. These species were chosen for their abundance and their importance in the diet of goslings (Manseau & Gauthier 1993; Duclos 2002; Audet *et al.* 2007). In wetlands, sampling was done by removing a 20 x 20 cm piece of turf at random within OTCs or exclosures, avoiding sampling directly adjacent to previous sampling. We cut all vegetation present on the pieces of turf at the base of the white basal stem buried in the moss. In mesic tundra, we marked a random 25 x 50 cm area in each plot and removed each shoot of *Arctagrostis* and *Luzula* present in this area by pulling it from the root. The size of the sampling area differed between the two habitat types to ensure that we collected sufficient plant material to conduct the nitrogen analyses (stem density was higher in wetland than in mesic tundra). Markers were left in the plots after each sampling to avoid subsequent sampling over the same area. Samples were sorted to separate vegetative green parts (i.e. leaves), flowers (including stems) and dead matter, dried at 45-50 °C for 24 to 36 hours and weighed to the nearest 0.001g. Green parts (i.e. leaves) of *Eriophorum*, *Dupontia*, *Arctagrostis* and *Luzula* were ground to a fine powder and analysed for nitrogen concentration using a QuickChem Lachat nutrient auto-analyser (Zellweger Analytic, Milwaukee, WI, USA, QuickChem 4000 Series).

Data analysis

For temperatures, we averaged values across loggers at each sampling time and extracted daily maximum temperatures. We calculated mean daily maximum temperature over four time periods corresponding to our plant sampling periods.

Linear mixed models were used to determine the impact of treatment (warming v.s. control) on aboveground green biomass and on nitrogen concentration (%) and biomass (g/m²). Because the same experimental units were repeatedly sampled over a period of time within years (but differed between years), our model consisted of a split-block ANOVA with repeated measures. The year effects appeared in the main part of the model with the random factor site as the blocking factor, while the treatment effect appeared in the subpart of the model. Measures were repeated over sampling periods in experimental units within each site × year × treatment combination. The correlation structure that best fitted the data, based on the Akaike information criteria, was the first-order autoregressive structure (Crowder & Hand 1990). Distributions of continuous variables were tested for normality, and, if appropriate, log or square root transformations of skewed variables were used in the analyses. For plant biomass, we summed both plant species within each sampling unit but each species was treated separately for the nitrogen analyses. Nitrogen biomass was calculated as the product of green biomass by nitrogen concentration in each individual sample. Samples with fewer than 20 shoots were excluded from the biomass analyses. Following significant effects in the ANOVA table, we used the protected LSD multiple comparison method to identify differences among treatments. Statistical analyses were performed with SAS (procedure PROC MIXED of SAS 9.3; SAS Institute, 2010, Cary, NC, USA) and R (R Development Core Team 2006). Conditional r^2 values were calculated following the procedure outlined by Nakagawa & Schielzeth (2013).

Results

Temperature

Temperature in warmed plots was higher than in control plots in both habitat types, but the difference was most pronounced in mesic tundra (Figure 1). In wetlands, OTCs increased

maximum daily soil temperatures by $0.2 \pm 1.0^\circ\text{C}$ (95% CI) for 10-18 June, $1.4 \pm 0.6^\circ\text{C}$ for 26 June-2 July, $2.0 \pm 2.3^\circ\text{C}$ for 8-14 July and $1.1 \pm 1.1^\circ\text{C}$ for 22-28 July. In mesic tundra, OTCs increased maximum daily soil temperatures by $3.9 \pm 0.9^\circ\text{C}$ for 15-24 June, $4.6 \pm 0.9^\circ\text{C}$ for 27 June-5 July, $1.9 \pm 0.7^\circ\text{C}$ for 13-19 July and $1.4 \pm 1.2^\circ\text{C}$ for 26-29 July.

Aboveground biomass

Warming increased live aboveground biomass of the sampled plants in both wetlands ($F_{1,15} = 11.6$, $P = 0.004$; r^2 of the full model = 0.72) and mesic tundra ($F_{1,15} = 9.32$, $P = 0.008$; r^2 of the full model = 0.65). In wetlands, biomass was 21%, 29% and 17% higher in warmed plots in late June, mid-July and late July, respectively (Figure 2a). In mesic tundra, biomass was 20% higher in warmed plots in mid-July and 15% higher in late July but the trend was already apparent in early July (Figure 2b). Although there were annual variations in live aboveground biomass (wetlands: $F_{2,10} = 5.35$, $P = 0.026$; mesic tundra : $F_{2,10} = 34.0$, $P < 0.001$), there were no significant interactions between year and the warming treatment ($P > 0.28$), indicating that the effect of warming was consistent across all three years of the experiment.

Nitrogen concentration

In wetlands, plants reached a peak in nitrogen concentration in late June/early July, after which nitrogen declined rapidly (Figure 3a,b). The same decline was found in mesic tundra but the peak in nitrogen concentration possibly occurred earlier because the highest nitrogen values were recorded during the first sampling period in mid-June (Figure 3c,d; note that the first sampling date was slightly later in mesic tundra than in wetlands due to logistical constraints). Overall, warming affected the nitrogen concentration of all four plant species but the effect of the treatment changed over the season as the interaction period \times treatment was always significant (Table 1). Warming had no effect on the nitrogen concentration of *Dupontia* early in the growing season but there was a significant negative impact of warming in mid- and late July (Figure 3a). In *Eriophorum*, nitrogen concentration was significantly higher in warmed plots at the first sampling period but this effect was reversed in mid- and

late July (Figure 3b). Nitrogen concentration of *Dupontia* was 14% and 10% lower in warmed plots than in the control in mid- and late July, respectively and 13% and 14% lower in *Eriophorum* over the same periods. We found similar results in mesic tundra, but the effect of warming on nitrogen concentration occurred earlier during the season (Figure 3c,d). Nitrogen concentration of warmed *Arctagrostis* samples was 12%, 14% and 14% lower than control and that of warmed *Luzula* samples was 11%, 10% and 7% lower at the three sampling dates in July.

There were significant interactions between sampling periods and year for all four species sampled (Table 1), which suggests annual variations in plant phenology (i.e. the seasonal decline in nitrogen concentration occurred earlier in some years and later in others). However, there was no significant interaction between the warming treatment and year for any species, indicating that the decline in nitrogen concentration was consistently steeper in warmed plots than in the control for all three years regardless of annual differences in phenology.

Nitrogen biomass

In wetlands, nitrogen biomass (g/m^2) of plants showed a sharp increase at the beginning of the season in late June, continued to increase at a slower rate in the first half of July and tended to decrease at the end of July (Figure 4a,b). In mesic tundra, nitrogen biomass of *Arctagrostis* increased in late June but reached a plateau in July with little change thereafter (Figure 4c). Nitrogen biomass of *Luzula* was very low compared to the three other species and showed a weak increase over time (Figure 4d). In wetlands, there was no significant effect of the warming treatment on the nitrogen biomass of *Dupontia*, but the effect was nearly significant for *Eriophorum* ($P = 0.055$; Table 2). Generally, warming had a positive effect on nitrogen biomass of wetland plants but a significant difference was only found for *Dupontia* in late June when it was 17% higher in warmed plots than in the control (Figure 4a,b). There was no effect of warming on plant nitrogen biomass in mesic tundra (Table 2 and Figure 4c,d). Overall, there was no change in the impact (or lack thereof) of warming over the season (interaction period \times treatment was not significant for any plant species) and there was no evidence that the effect of warming changed between years (treatment \times year

interaction was never significant; Table 2). Finally, nitrogen biomass varied annually in all plant species except *Dupontia*.

Discussion

Effects of warming on plant growth

Differences in temperature between warmed and control plots were similar to those found by previous studies using OTCs in arctic or sub-arctic systems (Marion *et al.* 1997, Jonsdottir *et al.* 2005b, Hollister *et al.* 2006). As temperature was recorded 2-3 cm in the soil, the temperature increase experienced by plants at the ground level or slightly above was probably higher. This temperature increase was within the lower range of the warming predicted for polar regions over the next century (IPCC 2007). Wetland soils were saturated in water for most of the growing season and this probably explains why the impact of OTCs on temperatures was more pronounced in mesic tundra than in wetlands, since water has a relatively high thermal inertia.

Our plots were warmed for only one growing season and thus we were unable to measure the cumulative effect of warming on plants. Nonetheless, short-term experiments are relevant to feeding conditions encountered by herbivores, at least during the initial stages of warming, because seasonal changes in nutrients result from physiological processes that are expected to be sensitive to temperature. Moreover, by repeating our experiment over 3 growing seasons, we were able to show that the effects of warming were consistent across all years despite annual variations in weather conditions.

As predicted, aboveground live biomass of plants was higher in warmed plots in both wetlands and mesic tundra, which is in agreement with previous studies using similar manipulations (Wookey *et al.* 1994, Wookey *et al.* 1995, Arft *et al.* 1999, Rustad *et al.* 2001, Hollister *et al.* 2005). This increase may be an effect of increased photosynthetic activity at higher temperatures and/or an effect of increased nutrient availability due to higher rates of mineralization in the soil. A recent, multisite analysis of warming experiments (combining 61 tundra warming experiments) showed that the response of tundra vegetation to warming

shows strong regional variations, but that linear increases in effect size were common, with little evidence of acceleration or saturation over time (Elmendorf *et al.* 2012a). This meta-analysis also suggests that graminoids are more responsive to warming at colder sites, with a larger response of sedges in wet habitats and of grasses in dry habitats. Nonetheless, other studies reported that vegetative growth was only significantly higher in the early years of experimental warming and that after four years of warming, increases were no longer significant at some sites, possibly due to nutrient depletion (Arft *et al.* 1999). Therefore, under some circumstances, the short term response of plants to temperature may have long-term costs if increased growth occurs at the expense of below-ground stored reserves. Although an increase in temperature typically leads to increased mineralization of nitrogen, this may not fully compensate for nutrient depletion because a large percentage of the nitrogen released is quickly taken up and stored by the microbial community, especially in nutrient-poor sites (Rustad *et al.* 2001).

Although the concentration of nitrogen varied among species and sometimes by year, possibly in relation to annual climatic variations in the latter case, the same seasonal pattern was observed in all plant taxa and years. We did not observe an initial increase in nitrogen concentration in mesic tundra, but this is probably because our first sampling period occurred too late to capture it. The seasonal decline in plant nutritive quality is ubiquitous in high latitude plants and may be caused in part by an increase in structural material (fiber) during the growing season, as previously shown in wetland plants at our study site (Manseau & Gauthier 1993, Piedboeuf & Gauthier 2000). This increase results in a decline in nitrogen concentrations even though total nitrogen biomass may be increasing (Chapin 1980). In our study, total nitrogen biomass generally increased initially, but this increase quickly levelled off and nitrogen biomass tended to decrease after mid-July. This late summer decline is probably due to translocation of nitrogen to the roots, leading to a decrease in total nitrogen content of green parts (Jonasson & Chapin 1991, Jonasson & Shaver 1999).

Nitrogen concentration of plants in warmed plots decreased more rapidly than in control plots, which supports our second prediction. This is possibly because the dilution effect caused by the seasonal increase in carbon-rich tissues (i.e. fiber) occurred more rapidly in warmed plots due to the speeding up of plant growth, a result consistent with other warming

experiments conducted in polar regions (Tolvanen & Henry 2001, Day *et al.* 2008). However, the reduction in nitrogen concentration in warmed plots lagged behind the concomitant increase in biomass, which started earlier in the season. A possible explanation is that fibre accumulation is typically more important during mid-summer in arctic graminoids (Manseau & Gauthier 1993), when plants become taller and presumably require more structural support. Alternatively, plants could perhaps partly adjust their nitrogen uptake to initially match the increase in biomass production but only up to a certain limit. When we combine the opposite trends of increased biomass but reduced nitrogen concentration in warmed plots, we found that warming tended to increase total nitrogen biomass. However, this potential positive effect of warming on total plant nitrogen was only present in wetland plants in the first half of the growing season as it weakened or disappeared later on.

Consequences of warming on herbivore food quality

For herbivores like geese, nitrogen concentration is probably more important than total nitrogen biomass in determining plant nutritive quality, especially in growing goslings. Unlike most herbivores, geese have a rapid passage time of food in their gut, are unable to digest most of the cellulose and have low nitrogen retention efficiency (Mattocks 1971, Sedinger 1997). They must therefore select food with a high nitrogen concentration to meet their nutrient requirements, a constraint that is exacerbated in goslings by the synthesis of new tissues during growth (Sedinger 1997). The guts of goslings already operate at their maximum capacity and any decrease in nitrogen concentration of their food (plants) cannot be compensated by an increase in total food intake and thus results in a reduction in their growth, as shown by experiments conducted in captivity and in the wild (Lindholm *et al.* 1994, McWilliams & Leafloor 2005, Gauthier *et al.* 2006). The natural, seasonal decline in plant nitrogen can have major consequences on growth rate of goslings, especially in those hatched late in the season, which suffer from an increased mismatch between the timing of hatch and the period of highest food quality (Sedinger & Raveling 1986, Lindholm *et al.* 1994, Lepage *et al.* 1998). Indeed, Lepage *et al.* (1998) have shown that nitrogen availability when goslings are 11-25 days old was the best predictor of structural size and body mass of

greater snow goose goslings near fledging at our study site. This period of gosling growth coincides with the 3rd and 4th sampling periods in our study, where the negative impact of warming on plant quality was most pronounced. Therefore, an acceleration of the seasonal decline in plant quality due to climate warming, as documented here, can have serious consequences for gosling growth, regardless of concurrent increases in plant biomass. Additionally, as the negative impacts of warming on plant nitrogen occurred relatively early in the season (July), geese are apparently not able to adjust for a steeper decline in plant nutritive quality by advancing their breeding phenology (Gauthier *et al.* 2013).

Body size and body condition of goslings at the end of summer are strongly linked to their first year survival and future reproductive success (Owen & Black 1989, Schmutz 1993, Sedinger *et al.* 1995, Menu *et al.* 2005). Such effects are not unique to geese, as annual productivity of other arctic herbivores such as caribous (*Rangifer tarandus*) are also affected by their body condition and quality of their summer forage (Post & Klein 1999, Post & Forchhammer 2008). Thus, a reduction in growth of young arctic herbivores due to a climate-induced mismatch with the phenology of their food plants could have important consequences on their population dynamics (Dickey *et al.* 2008, Kerby & Post 2013a). While arctic herbivores may benefit from climate change in other ways (i.e. latitudinal and altitudinal expansion of breeding grounds, longer summers, higher forage biomass; Jensen *et al.* 2008, Gilg *et al.* 2012), our results show that these benefits may be counterbalanced by a loss in forage quality, at least in the short-term. To get a more complete understanding of how climate change may affect arctic herbivore populations, further studies are needed to better evaluate the demographic consequences of trophic mismatch and the long-term impact of warming on plant phenology and community composition.

Table 1. Effects of sampling period, year and treatment (warming v.s. control) on nitrogen concentration (%) of four plant taxa on Bylot Island, Nunavut during three summers (2007-2009). The F -values for the main effects and the interactions (ANOVA for repeated measures) are presented with their level of significance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Conditional r^2 values were calculated following the procedure outlined by Nakagawa & Schielzeth (2013).

	<i>df</i>	<i>Dupontia</i> (<i>n</i> = 320)	<i>Eriophorum</i> (<i>n</i> = 300)	<i>Arctagrostis</i> (<i>n</i> = 321)	<i>Luzula</i> (<i>n</i> = 309)
Period ¹	3	150.5***	73.8***	214.0***	151.0***
Treatment ²	1	10.4**	7.7*	24.3**	13.3**
Year ³	2	1.8	2.6	17.5**	1.8
Period x Treatment ¹	3	4.4**	8.7***	2.6*	2.9*
Period x Year ¹	6	7.0***	4.2**	10.9***	17.6***
Treatment x Year ²	2	0.2	0.9	1.2	1.6
r^2 of the model		0.73	0.64	0.80	0.76

¹ df of error term = 272 (*Dupontia*), 252 (*Eriophorum*), 273 (*Arctagrostis*), 261 (*Luzula*)

² df of error term = 15

³ df of error term = 10

Table 2. Effects of sampling period, year and treatment (warming v.s. control) on nitrogen biomass (g/m²) of four plant taxa on Bylot Island, Nunavut during three summers (2007-2009). The *F*-values for the main effects and their interactions are presented, together with their level of significance (+ 0.05 < *P* < 0.10; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001). Conditional *r*² values were calculated following the procedure outlined by Nakagawa & Schielzeth (2013).

	<i>df</i>	<i>Dupontia</i> (<i>n</i> = 307)	<i>Eriophorum</i> (<i>n</i> = 242)	<i>Arctagrostis</i> (<i>n</i> = 278)	<i>Luzula</i> (<i>n</i> = 248)
Period ¹	3	70.3***	14.3***	7.2**	5.7**
Treatment ²	1	2.3	4.4+	2.5	0.7
Year ³	2	0.4	5.9*	29.5***	4.6*
Period x Treatment ¹	3	2.5+	0.4	0.4	0.8
Period x Year ¹	6	3.6**	2.2*	1.8	2.7*
Treatment x Year ²	2	1.4	0.4	0.3	1.9
<i>r</i> ² of the model		0.65	0.57	0.56	0.19

¹ *df* of error term = 259 (*Dupontia*), 194 (*Eriophorum*), 230 (*Arctagrostis*), 200 (*Luzula*)

² *df* of error term = 15

³ *df* of error term = 10

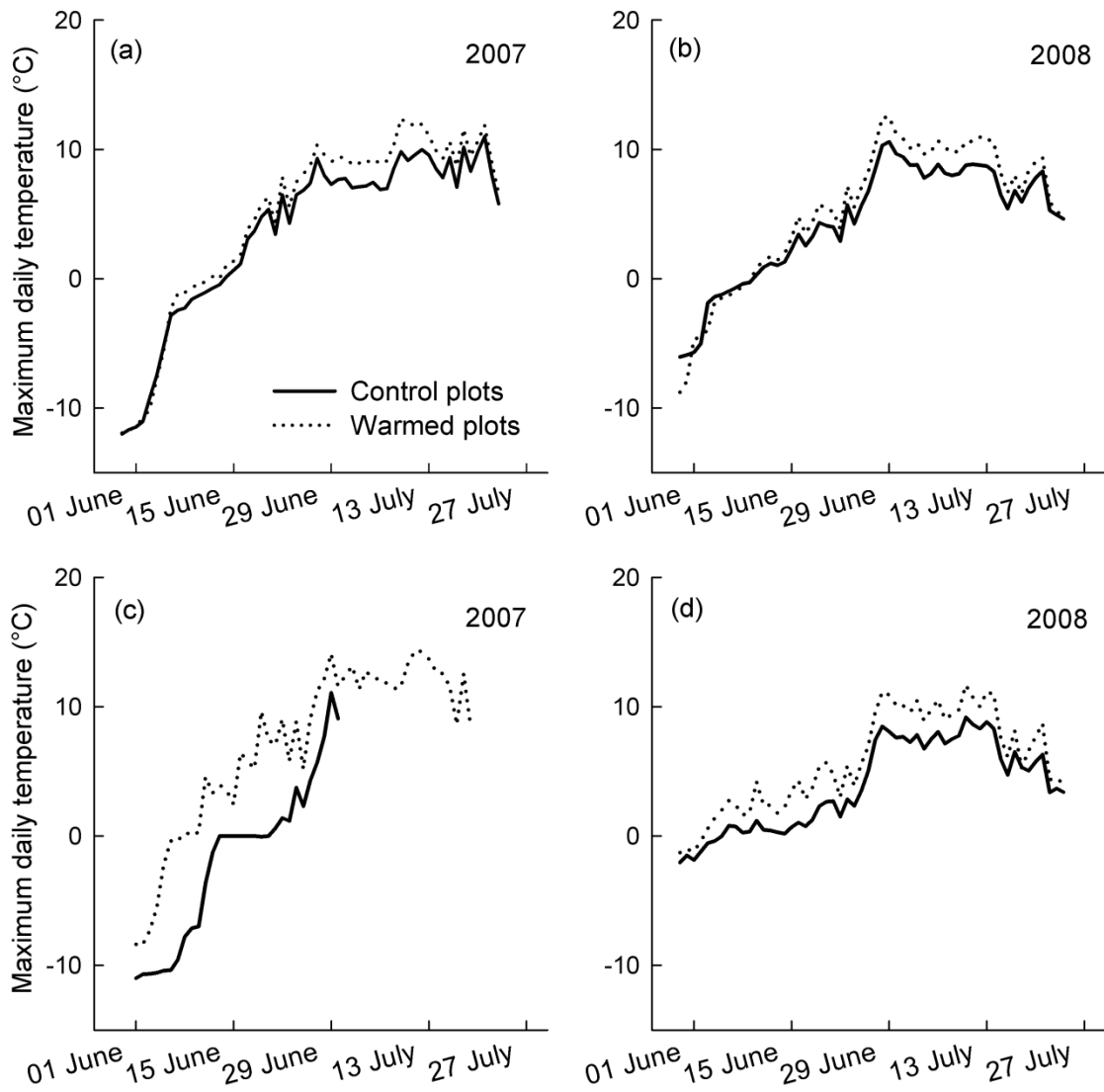


Figure 1. Mean maximum daily soil temperature ($^{\circ}\text{C}$) in (a,b) wetlands and (c,d) mesic tundra in control and warmed plots during summers 2007 and 2008 on Bylot Island, Nunavut. Temperatures were recorded 2-3 cm under the surface. Data points were obtained by averaging temperatures across loggers and calculating the daily maximum from these averaged values.

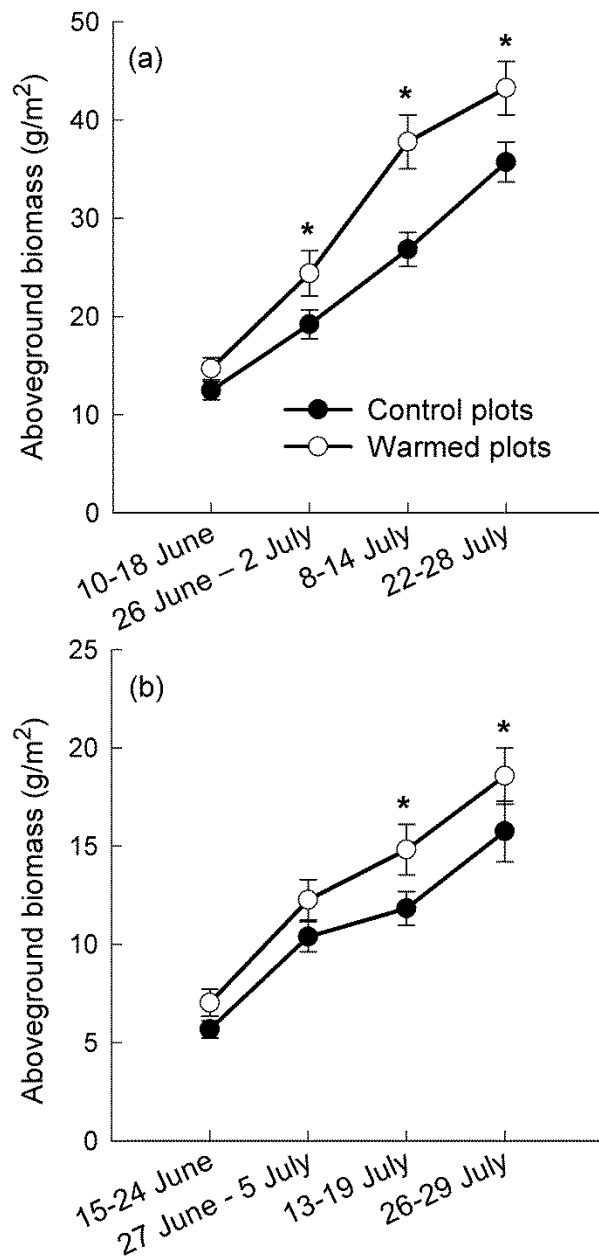


Figure 2. Dry aboveground green biomass of two species of goose forage plants in (a) wetlands and (b) mesic tundra in control and warmed plots on Bylot Island, Nunavut. Each data point is based on 42 replicate plots over 3 summers (2007-2009). Asterisks indicate significance ($P < 0.05$) based on individual Least-Square Means comparisons. Error bars represent ± 1 SE.

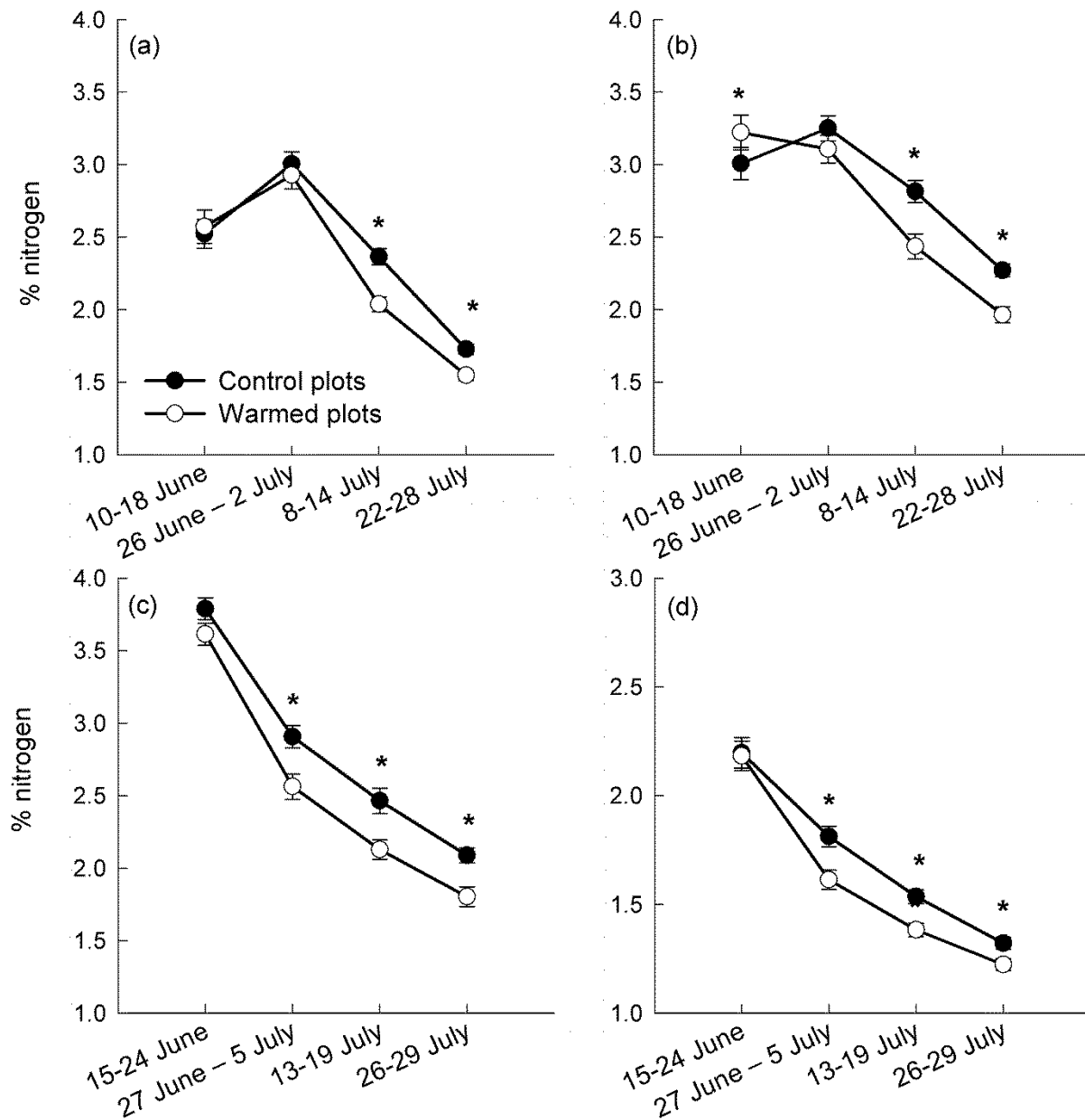


Figure 3. Nitrogen concentration of aboveground green parts of (a) *Dupontia fisheri*, (b) *Eriophorum scheuchzeri*, (c) *Arctagrostis latifolia*, and (d) *Luzula* spp. in control and warmed plots on Bylot Island, Nunavut. Each data point is based on 42 replicate plots over three summers (2007-2009). Asterisks indicate significance ($P < 0.05$) based on individual Least-Square Means comparisons. Error bars represent ± 1 SE.

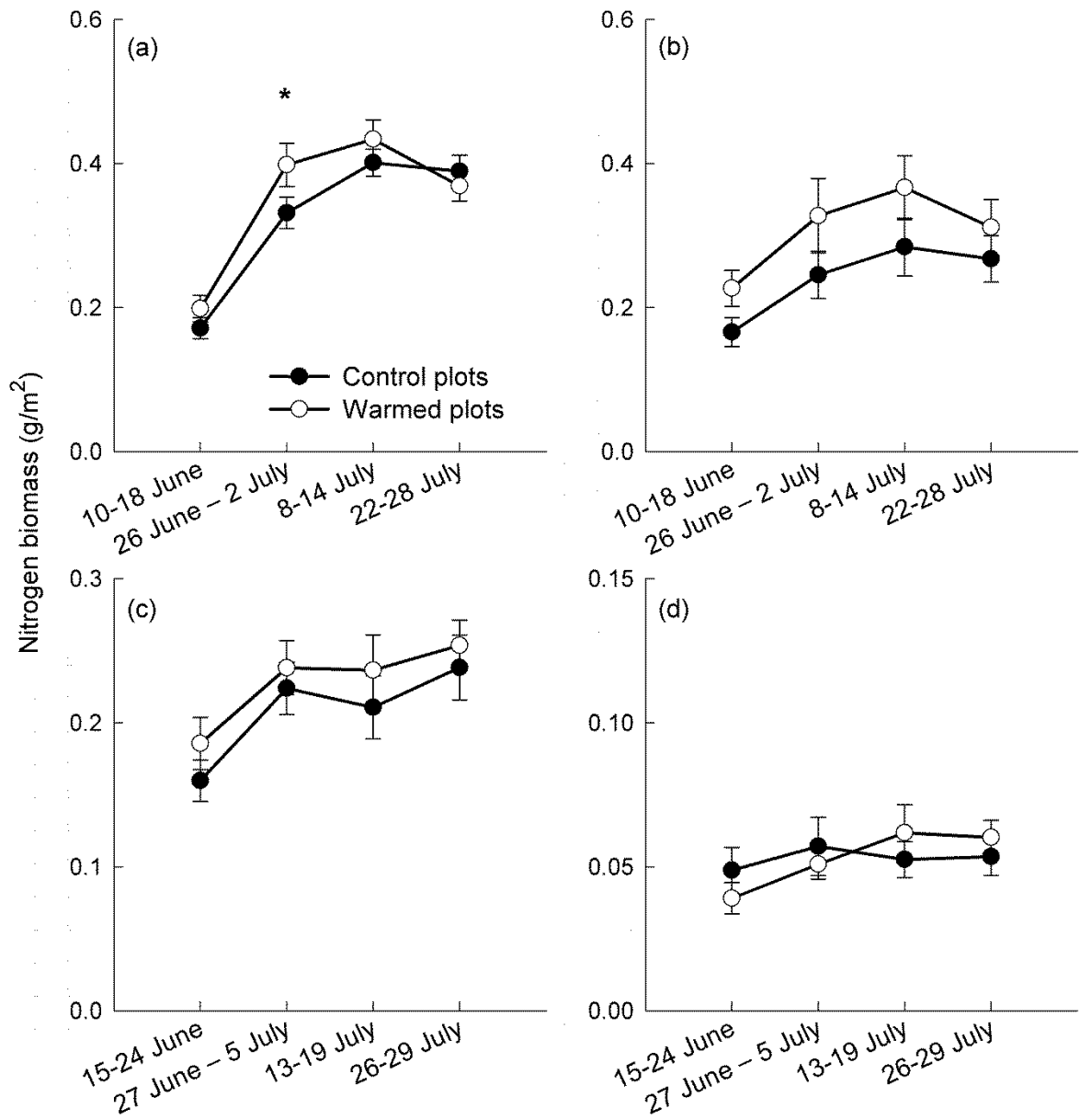


Figure 4. Nitrogen biomass (g/m²) of aboveground green parts of (a) *Dupontia fisheri*, (b) *Eriophorum scheuchzeri*, (c) *Arctagrostis latifolia*, and (d) *Luzula* spp. in control and warmed plots on Bylot Island, Nunavut. Each data point is based on 42 replicate plots over three summers (2007-2009). Asterisks indicate significance ($P < 0.05$) based on individual Least-Square Means comparisons. Error bars represent ± 1 SE.

CHAPITRE 2

Broad-scale satellite Normalized Difference Vegetation Index (NDVI) data predict plant biomass and peak date of nitrogen concentration in Arctic tundra vegetation

Doiron, M., Legagneux, P., Gauthier, G. & Lévesque, E. (2013) Broad-scale satellite Normalized Difference Vegetation Index data predict plant biomass and peak date of nitrogen concentration in Arctic tundra vegetation. *Applied Vegetation Science*, **16**, 343-351.

Résumé

Dans les écosystèmes terrestres, un indice satellitaire appelé le *Normalized Difference Vegetation Index* (NDVI) est fréquemment utilisé comme proxy afin d'estimer à quel moment a lieu le début de la croissance des plantes au printemps, et d'évaluer la qualité d'un habitat pour les herbivores. De plus en plus souvent, l'utilisation du NDVI remplace donc la récolte de données directement sur le terrain. Plusieurs études ont montré que le NDVI est un bon indice pour prédire la production primaire dans une variété d'écosystèmes, mais très peu ont validé la relation entre le NDVI et les changements annuels dans la qualité de la végétation avec des données prises au sol. Pendant les étés 1991, 1993-1996 et 2006-2008, nous avons échantillonné les plantes herbacées des milieux humides dans un écosystème de toundra arctique sur l'Île Bylot, Nunavut, Canada. Par la suite, nous avons examiné la relation entre quatre indices NDVI (données satellites AVHRR à une résolution spatiale de 1 km²) et la date de pic d'azote des plantes, un indice de la variabilité saisonnière dans la qualité des plantes. Nous avons également évalué la relation entre le NDVI et les changements saisonniers dans la biomasse aérienne des plantes. Nos résultats montrent qu'il y avait une relation linéaire significative entre la date de pic d'azote des plantes et trois des quatre indices NDVI que nous avons testés, la relation la plus forte étant celle avec la date à laquelle le NDVI atteint 50% de sa valeur maximale annuelle ($r^2 = 0.87$). Il y avait également une relation exponentielle positive entre la biomasse aérienne des plantes et le NDVI ($r^2 = 0.58$), mais cette relation était plus forte tôt en saison. Nos résultats montrent que le NDVI peut être utilisé comme proxy afin d'estimer la date du pic dans la concentration en azote de certaines plantes arctiques, et reflète donc bien les changements saisonniers dans la disponibilité de nourriture de haute qualité pour les herbivores. Nous avons également montré qu'en début de saison, le NDVI peut aussi être utilisé pour estimer la biomasse aérienne végétale. Notre étude sert donc de validation additionnelle quant à l'utilisation du NDVI calculé à partir de données satellitaires afin d'estimer les changements annuels dans la qualité d'un habitat pour les herbivores.

Abstract

In terrestrial ecosystems, the satellite-derived Normalized Difference Vegetation Index (NDVI) is increasingly used as a proxy to estimate the timing of spring green-up and habitat quality for herbivores, thus circumventing the need for direct vegetation sampling. While NDVI has been shown to be a good predictor of primary production in a variety of ecosystems, very few studies have validated the relationship between NDVI and the annual changes in vegetation quality using ground data. During the summers 1991, 1993-1996 and 2006-2008, we sampled graminoid plants every two weeks in tundra wetlands of Bylot Island, Nunavut, Canada. We then assessed the relationship between four NDVI indices (AVHRR satellite data at 1 km² spatial resolution) and the date of peak nitrogen concentration of plants, an index of seasonal variability in plant quality. We also examined the relationship between NDVI and the seasonal changes in aboveground live plant biomass. Three out of the four NDVI metrics that we tested were significantly related to date of peak nitrogen concentration. The strongest relationship was found with the date at which NDVI values reached 50% of their annual maximum ($r^2 = 0.87$). We also found a positive exponential relationship between aboveground biomass of plants and NDVI ($r^2 = 0.58$), though this relationship was strongest early in the growing season. Our results show that NDVI can be used as a proxy to determine date of peak nitrogen concentration in some tundra plants, and can thus be a reliable measure of the yearly changes in the timing of the availability of high quality food for herbivores. To a lesser extent, NDVI can also be used to assess seasonal change in plant biomass. This study provides additional support for the use of satellite-derived NDVI to assess seasonal changes in habitat quality for herbivores.

Introduction

Plant standing crop and phenology are parameters of prime interest for ecologists because they strongly influence herbivores and have direct impacts on their distribution and reproduction. In seasonal environments, accurately measuring the abundance and timing in availability of high-quality plant food is essential. Indeed, these factors will not only influence timing of reproduction, but also habitat use, timing of migration, feeding ecology, survival and recruitment of herbivores, and indirectly of higher trophic levels (Albon & Langvatn 1992, Lepage *et al.* 1998, Van der Wal *et al.* 2000, Mysterud *et al.* 2001, Visser & Holleman 2001, van der Graaf *et al.* 2006, Van der Putten *et al.* 2010). Plants of high nutritive value for herbivores are those with high protein (typically indexed by nitrogen) and low fiber contents (Robbins 1993). As the season advances, plant nutritive quality typically declines because the nitrogen concentration, which is highest at the beginning of plant growth, decreases and tissues become less digestible as their fiber content increases (Manseau & Gauthier 1993).

Monitoring seasonal variations in aboveground plant biomass and nutrient content requires repeated measurements. Methods for estimating the abundance and nutritive quality of plants available to herbivores in the field are traditionally based on biomass harvesting, which is expensive, time-consuming and restricted both spatially and temporally (Pineiro *et al.* 2006). For these reasons, ecologists are increasingly turning to large-scale indices to infer habitat quality, rather than directly measuring biomass and nutrient content in the field. In terrestrial ecosystems, the Normalized Difference Vegetation Index (NDVI) has been used in numerous studies to circumvent the limitations associated with the harvesting of plant biomass. NDVI is a global vegetation indicator obtained by remote sensing, which combines signals from the red (RED) and near-infrared (NIR) reflectance of Earth's objects ($NDVI = (NIR-RED)/(NIR + RED)$) and is a good measure of absorbed photosynthetically active radiation (Tucker & Sellers 1986). NDVI is a widely available index that covers all terrestrial biomes and thus represents an attractive tool in a wide variety of ecological studies (e.g. Kerr & Ostrovsky 2003, Pettorelli *et al.* 2005, Chamaille-Jammes & Fritz 2009, Pettorelli *et al.* 2011).

The relationship between NDVI and vegetation productivity is well documented over large temporal and geographical scales (Running 1990, Reed *et al.* 1994, Myneni *et al.* 1995,

Myneni *et al.* 1997, Paruelo *et al.* 1997, Zhou *et al.* 2001, Wang *et al.* 2004). Because the rate of greening is correlated with plant nutritive quality, NDVI is increasingly used as a proxy to estimate the timing of spring green-up in studies of herbivore behavior and habitat use (Griffith *et al.* 2002, Pettorelli *et al.* 2005, Garel *et al.* 2006, Pettorelli *et al.* 2006, Ryan *et al.* 2007, see Pettorelli *et al.* 2011 for a review). While studies using portable spectroradiometers have shown that NDVI is correlated to plant nitrogen content at fine scales (Chen & Brutsaert 1998, Cabrera-Bosquet *et al.* 2011), few studies have validated the reliability of satellite-derived NDVI as a proxy for measuring timing of high-quality vegetation using ground data (but see Hamel *et al.* 2009 for an example in an alpine system). Satellite-derived NDVI can be a useful tool to monitor seasonal changes in vegetation but is subject to errors, especially in highly heterogeneous habitats such as mountain ranges (Box *et al.* 1989) and in sparsely vegetated areas, where soil reflectance can bias the relationship between NDVI and vegetation (Huete 1988). However, White *et al.* (2009) found that broad-scale NDVI was a better predictor of the start of spring at northern latitudes than in other regions, and recent studies in the sub-Antarctic Kerguelen archipelago (Santin-Janin *et al.* 2009) and in semiarid regions of Chile (De La Maza *et al.* 2009) have shown that NDVI can still provide useful information on plant biomass and phenology in low-vegetation areas. However, they also highlighted the need to adequately validate such indices in these environments and to assess the biological significance of the many indices that can be derived from NDVI data.

In the Arctic tundra, nitrogen is the plant nutrient that shows the strongest seasonal variation, and is thus of primary importance for herbivores and their growing young such as geese (Manseau & Gauthier 1993, Lindholm *et al.* 1994, Lepage *et al.* 1998, van der Graaf *et al.* 2006). The timing of the onset of plant growth and especially of the peak in nitrogen concentration is critical for the reproduction of several arctic herbivores (Sedinger & Raveling 1986, Lepage *et al.* 1998, Post & Forchhammer 2008, Post *et al.* 2008). In the context of climate change, the need to adequately measure phenological changes in ecosystems has never been greater because this is one of the first biological processes affected by climate warming (Parmesan & Yohe 2003). This is especially true in Arctic ecosystems where climate change is occurring at a faster pace than anywhere else on Earth (IPCC 2007). Using remote-sensing tools such as NDVI to predict plant biomass and

seasonal changes in nitrogen concentration would thus be extremely useful in the Arctic, where field logistic constraints limit the acquisition of long time series of plant data. Because NDVI measures the photosynthetic capacity of plants (i.e. their “greenness”), we expected that it could also be a good predictor of the timing in peak nitrogen concentration because both change rapidly in spring and are constrained by the onset of plant growth.

In this study, we used long-term data on seasonal variation in plant aboveground biomass and nutritive quality in a High Arctic tundra system to 1) evaluate whether NDVI values can be used as a proxy to estimate the date of peak nitrogen concentration in plants, a critical phenological event for herbivores, and 2) test whether NDVI values can be used to predict plant aboveground biomass. Plants were sampled seasonally in freshwater wetlands used by greater snow geese (*Chen caerulescens atlantica*), an important herbivore in the High Arctic (Gauthier *et al.* 2004).

Methods

Study site

This study was conducted in a 50 km² valley located on the south plain of Bylot Island (73°08'N, 80°00'W), north of Baffin Island, Sirmilik National Park, Nunavut, Canada. This region of Bylot Island is one of the most important breeding areas for the greater snow goose (Reed *et al.* 2002). The area is characterized by tundra polygon wetlands (Ellis *et al.* 2008) dominated by graminoids and sedges, such as *Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe and *Carex aquatilis* Wahl. var. *minor* Boott, growing through a thick moss carpet. These wetlands, though representing only approximately 10% of the landscape, are the preferred habitat for brood-rearing geese, the most abundant herbivores of this system (Hughes *et al.* 1994, Gauthier *et al.* 2004).

Plant sampling

We sampled aboveground live biomass in wetlands (polygon fens) in 1991, 1993-1996 and 2006-2008. Each year, 12 new goose exclosures (1 m²) were set up at each site just after

snow melt in June, before any significant grazing by geese had occurred. Exclosures were made of 30 cm high chicken wire (2.5 cm mesh) and were set up over an area of ~1 km².

Plant samples were collected inside exclosures at least 4 times per season from mid-June to mid-August (roughly every two weeks). In most years, the first sampling date occurred shortly after snow-melt. Each time we removed a 20 cm x 20 cm piece of turf at random but avoided to collect samples adjacent to previously-removed pieces of turf to prevent edge effect. We cut all vegetation present on the pieces of turf at the base of the white basal stem buried in the moss. We retained only live vascular plants and sorted them into four categories: grasses (mainly *D. fisheri*), cottongrass sedges (*E. scheuchzeri*), *Carex* sedges (*Carex* spp.) and dicotyledonous plants (<2%; mostly *Stellaria longipes s.l.*, *Saxifraga* sp. and *Salix* spp.). Plants were oven-dried at 45°C for 24 to 36 hours and weighed to the nearest 0.001 g (see Gauthier *et al.* (1995) for details).

The samples of *Dupontia* and *Eriophorum*, the two dominant plants, were ground to a fine powder and analysed separately for total nitrogen concentration. Between 1991 and 1996, the samples were analysed using an automated macro-Kjeldahl analyser (Kjell-Foss, model 16210) following the AOAC (1984: 154) method (Gauthier *et al.* 1995). From 2006 onwards, nitrogen concentration was determined using a QuickChem Lachat nutrient auto-analyser (Zellweger Analytic, Milwaukee, WI, USA, QuickChem 4000 Series). In some cases, it was necessary to pool samples from different exclosures (but collected at the same date) to obtain sufficient material for the nitrogen analyses.

NDVI data

NDVI data were derived from the Advanced Very High Resolution Radiometer (AVHRR) / National Oceanic and Atmospheric Administration (NOAA) satellites (Brown *et al.* 2006). We extracted the maximum value encountered in each pixel over 10-day periods using composite images at 1 km² spatial resolution made available by the Canada Centre for Remote Sensing (Pouliot *et al.* 2009) from 1991 to 2008. We selected pixels covering 48 km² (i.e. the whole study area) and calculated the median NDVI value across all pixels, thus obtaining a single NDVI value for each 10-day period for the entire study area. We chose to use the median in order to obtain an estimate of NDVI representative of the whole study area

and to minimize the influence of extreme and potentially biased values. Because NDVI values used for each pixel were the highest value encountered within 10-day windows, these values were more likely to be encountered toward the end of the interval during spring growth. We thus assigned the date of the end of the interval for each composite NDVI value and interpolated daily values from there. From these NDVI values, we computed four indices: a) the date at which NDVI values first reached 50% of their annual maximum, b) the date at which NDVI values reached 100% of their annual maximum, c) the maximum NDVI value of the period between 11 June and 20 June (i.e. just after the average snow-melt date), and d) the sum of 10-day NDVI values during the month of June.

Data analyses

To calculate the date of peak nitrogen (DPN), we first calculated the mean nitrogen concentration within each plant species (i.e. *Dupontia* and *Eriophorum*) on each sampling date and then calculated a mean value across both species, giving equal weight to each. Although *Dupontia* is more abundant than *Eriophorum* in wetlands of Bylot Island (Gauthier *et al.* 1995), geese preferentially feed on the latter species (Manseau & Gauthier 1993). We fitted Gaussian, Weibull and log-normal regressions to our data of nitrogen concentration v.s. date for each year of the study and estimated DPN from the function peak. Although each equation yielded similar results, the Gaussian function gave, on average, a better fit to our data and worked well even in years with small sample sizes ($n = 5$). For these reasons, we estimated DPN with this function for the rest of the analyses (see Figure 1 for the Gaussian curves obtained each year). We used DPN rather than absolute nitrogen concentration because we were interested in yearly variation in the timing of peak nitrogen concentration rather than in the nitrogen values themselves.

We fitted linear regression models to test the relationship between each of our four NDVI indices and date of peak nitrogen concentration in wetland graminoids. We used linear models to test the relationship between seasonal aboveground biomass values and the median NDVI values at the corresponding dates. We tested for the effect of sampling period (5 two-week periods) and season (*spring* for sampling dates ranging from the beginning of the growing season up to early July and *summer* for later sampling) to determine whether this

relationship changed over the course of the summer. We also tested for exponential and quadratic relationships between aboveground biomass and NDVI. In all cases, we used regression analyses to find out which NDVI index could best predict our variables of interest and not to explore possible causal relationships among those variables. Model selection was based on the AICc statistics (Burnham & Anderson 2002). Statistical analysis was performed using SigmaPlot version 11.0 (Systat Software Inc, Chicago, IL) and R (R Development Core Team 2006).

Results

Nitrogen concentration in wetland graminoids showed a slight increase early in the season in most years followed by a steep seasonal decline in all years (Figure 1). In two years out of eight, we did not observe this initial increase but it may have happened before our sampling began. In those cases, we arbitrarily fixed the DPN at the first sampling date. Date of peak nitrogen concentration ranged from 17 June to 14 July.

Three out of our four NDVI metrics were significantly related to DPN (Figure 2). The strongest relationship was found with the date at which NDVI values reached 50% of their annual maximum (Figure 2a; $F_{1,7} = 39.8$, $P < 0.001$, $r^2 = 0.87$), indicating that this NDVI metric accurately predicted the timing of peak nitrogen concentration in plants. There was no significant relationship between DPN and date at which NDVI values reached 100% of their annual maximum (Figure 2b; $F_{1,7} = 0.07$, $P = 0.79$). DPN was negatively related to the maximum NDVI value between 11-20 June (Figure 2c; $F_{1,7} = 17.7$, $P = 0.006$) and to the sum of 10-day NDVI values in June (Figure 2d; $F_{1,7} = 15.27$, $P = 0.008$), but the fit was lower than with the date at which NDVI values reached 50% of their annual maximum. Therefore, the best equation to predict the date of peak nitrogen is: $DPN = -10.1 + 1.07 * \text{date } 50\% \text{ NDVI}$ (95% CI of slope: 0.65, 1.48).

There was a significant positive relationship between aboveground biomass of wetland plants and the median NDVI values at the corresponding dates (Figure 3). The best model to explain seasonal variation in aboveground biomass included an exponential transformation of NDVI with sampling season (summer or spring) as an additive factor (Table 1). The variable

sampling period (mid-June, early July, mid-July, early August and mid-August) was not selected in any of the best models. The second model suggested that this relationship may have varied with year. Despite this positive relationship, there was still a considerable scatter around the regression as shown by the moderate r^2 (Figure 3).

Discussion

We showed that broad-scale NDVI can be a very good proxy to estimate the date of peak nitrogen concentration and, to a lesser extent, seasonal change in aboveground biomass of some tundra plants. The robust nature of these broad-scale results is remarkable considering that our sampling was spatially very restricted and limited to a particular habitat type (wet tundra polygons) that represented ~10% of the landscape in our study area. Moreover, the plants we sampled only account for 5-10% of the total aboveground biomass as most (~90%) of the plant biomass in this system comes from non-vascular plants (i.e. mosses; Gauthier *et al.* 2004, Legagneux *et al.* 2012). However, our results suggest that the “greenness” signal coming from the entire landscape and captured by the NDVI values can still act as a good proxy for the specific species we sampled, and that the seasonal changes observed in these plants are representative of the changes occurring in the vegetation of the entire study area. Finally, in the same study area (Sirmilik National Park), Fraser *et al.* (2011) recently showed that coarse (NOAA-AVHRR) and finer (Landsat) resolution NDVI were able to detect long term changes in vegetation. This also suggests that the “greenness” presents similar trends whatever the vegetation type.

Among the NDVI metrics that we tested, the date at which NDVI reaches 50% of its annual maximum was the best predictor of the date of peak nitrogen in wetland graminoids, an important phenological event for herbivores in highly seasonal environments such as the Arctic (Sedinger & Raveling 1986, Lepage *et al.* 1998, van der Graaf *et al.* 2006). This period coincides with a sharp increase in the greenness of the landscape and reflects the seasonal availability of high-quality food.

There was no significant relation between date of maximum NDVI value and date of peak nitrogen. This is not surprising considering that the date of maximum NDVI in most years

occurred between late July and early August whereas, in Arctic systems, the nitrogen concentration of plants is typically highest shortly after the onset of plant growth in June and decreases slowly throughout the summer (Manseau & Gauthier 1993, Gauthier *et al.* 1995, Lepage *et al.* 1998, Larter & Nagy 2001, Cadieux *et al.* 2005; this study). The date of maximum NDVI value is presumably most affected by the total plant biomass, which largely results from carbon accumulation and leads to a dilution of nitrogen concentration in plant tissues.

Although metrics that used absolute NDVI values (such as maximum NDVI value between 11-20 June and cumulative June NDVI values) were also related to the date of peak nitrogen in wetland graminoids, they were poorer predictors than the one based on the date of 50% of maximum NDVI value. A possible explanation for that may be that those metrics are more sensitive to false highs and noise correction than a temporal metric based on relative change in NDVI (Pettorelli *et al.* 2005). In addition, date at which 50% of the seasonal maximum is attained incorporates the timing of annual maximum NDVI as well as the slope of the increase, which may be more ecologically relevant. Therefore, when attempting to determine the timing of peak nitrogen concentration, metrics that incorporate temporal components such as the date of 50% of maximum NDVI value appear more appropriate to use than those based on absolute NDVI values.

We found a non-linear relationship between NDVI and aboveground biomass. NDVI is expected to saturate at high biomass values, and NDVI has a tendency to reach a plateau at high Leaf Area Index (LAI) values (Tucker & Sellers 1986, Hobbs 1995). In our study, there was a greater yearly variation in the biomass of samples taken late in the summer than in those taken early in the growing season, and the inclusion of a seasonal factor (spring vs. summer) significantly improved our models. The shape of the relationship between biomass and NDVI suggests a temporary saturation of reflectance before the onset of senescence, indicating that NDVI may be a reliable predictor of biomass early in the growing season, but that its accuracy decreases as the season advances. At the peak of the growing season, there may be greater variation in plant biomass among the various habitat types than at the onset of plant growth. Moreover, NDVI values integrate all habitats and plants in the landscape but our plant sampling was limited to a single habitat (wet polygon fens) and vascular plants,

which may explain the increased variability in the relationship between NDVI and aboveground biomass later in the summer. Huete (1988) has also shown that, in sparsely vegetated areas, NDVI can be sensitive to soil humidity. The spatial variation in soil moisture is likely higher at the end of the growing season (cool and wet in some areas, warm and dry in others) than at the onset, when most areas are saturated in water due to snowmelt, thereby adding another source of noise to the NDVI data during the summer. Thus, while NDVI appears to be highly relevant to estimate the onset of plant growth and its yearly variation in this system, it may provide a noisier estimate of peak plant biomass measured at the end of the growing season for specific plant sub-groups. Additionally, because the range of aboveground biomass and NDVI values from the onset of plant growth to peak plant production is lower in the High Arctic than in more productive systems, this may increase the ratio of noise to signal and reduce the fit of the model.

NDVI has previously been used in Arctic systems to map vegetation types (Walker *et al.* 2005, Reynolds *et al.* 2006), to compare seasonal and regional variation of tundra vegetation biomass (Jia *et al.* 2004, Riedel *et al.* 2005), and to track changes in plant productivity and vegetation types in relation to climate (Myneni *et al.* 1997, Zhou *et al.* 2001, Olthof & Latifovic 2007, Fraser *et al.* 2011). Because empirical vegetation data are very difficult to come by in the Arctic over large spatial and temporal scales, the use of satellite data to monitor changes in Arctic vegetation offers the potential to overcome such limitations. In one of the few studies that links ground-based plant productivity measurements to NDVI in an Arctic system, Riedel *et al.* (2005) have shown that seasonal LAI and NDVI were only related in one of four tundra vegetation types examined, and that vegetation types with different phytomass values can exhibit similar NDVI values, especially towards the beginning and the end of the growing season. These results highlight the importance of properly validating satellite data with empirical vegetation data whenever possible. Intra-seasonal measures of plant biomass and plant quality are rare in tundra systems, and our data set provided a unique opportunity to examine the relation between NDVI and seasonal changes in plant biomass and quality. Our findings suggest that NDVI is an accurate tool to determine the timing of high quality vegetation for herbivores.

The proxy tested in this study could have significant applications for the study of plant-herbivore interactions in the Arctic tundra ecosystem. In many herbivores, the growth of young is dependent upon a good synchrony between timing of reproduction and the seasonal change in plant nutritive quality. This is especially critical for herbivores in arctic systems due to the short summers, leading to a high seasonality of plant quality and availability. If plants respond more quickly than herbivores to climate change, this may lead to a mismatch between the phenology of breeding and availability of high quality food (expected to occur earlier with warming), with negative impacts for herbivores (Dickey *et al.* 2008, Post & Forchhammer 2008). At many study sites, the reproductive activity and phenology of animals is closely monitored but, due to time constraints, data on plant nutritive quality and phenology is sparse. Since we showed that the date at which NDVI reaches 50% of its maximum value can adequately predict the timing of peak nutritive quality of wetland graminoids at a large spatial scale, this should provide a useful tool to examine the occurrence of phenological mismatches. For example, by allowing us to backtrack through time and estimate annual dates of peak nitrogen using pre-existing NDVI data, we should be able to greatly increase the temporal scale over which we can study the relationship between the timing of reproduction and plant growth in many Arctic herbivores, and how this relationship could have changed over time.

Previous studies by Hamel *et al.* (2009) and Ryan (2006) have found positive relations between NDVI and faecal crude protein in ungulates living in alpine and savanna systems respectively. To our knowledge, this study is the first to show that broad-scale NDVI can accurately predict the timing of plant nutritive quality for herbivores in an Arctic tundra system. Nevertheless, as NDVI is becoming more widely used in population ecology and wildlife management (Pettorelli *et al.* 2011), such relationships should be validated at other sites.

Table 1. Model selection statistics of the effect of NDVI, SEASON (spring and summer; see methods for definition), sampling PERIOD (mid-June, early July, mid-July, early August and mid-August) and YEAR on seasonal aboveground plant biomass on Bylot Island, Nunavut, in 1991, 1993-1996 and 2006-2008. Only the best ranked models ($\Delta\text{AICc} < 7$) and the null model are presented. K = number of parameters, LL = Log-Likelihood, exp = exponential transformation.

Model	ΔAICc	AICc Weight	LL	K
exp(NDVI)+SEASON	0	0.25	-101.8	4
exp(NDVI)+SEASON+YEAR	0.26	0.22	-89.6	11
NDVI+SEASON	0.36	0.21	-102.0	4
NDVI+SEASON+YEAR	1.17	0.14	-90.1	11
exp(NDVI)*SEASON	2.57	0.07	-101.7	5
NDVI*SEASON	2.67	0.07	-101.8	5
Null Model	27.06	0.00	-117.84	2

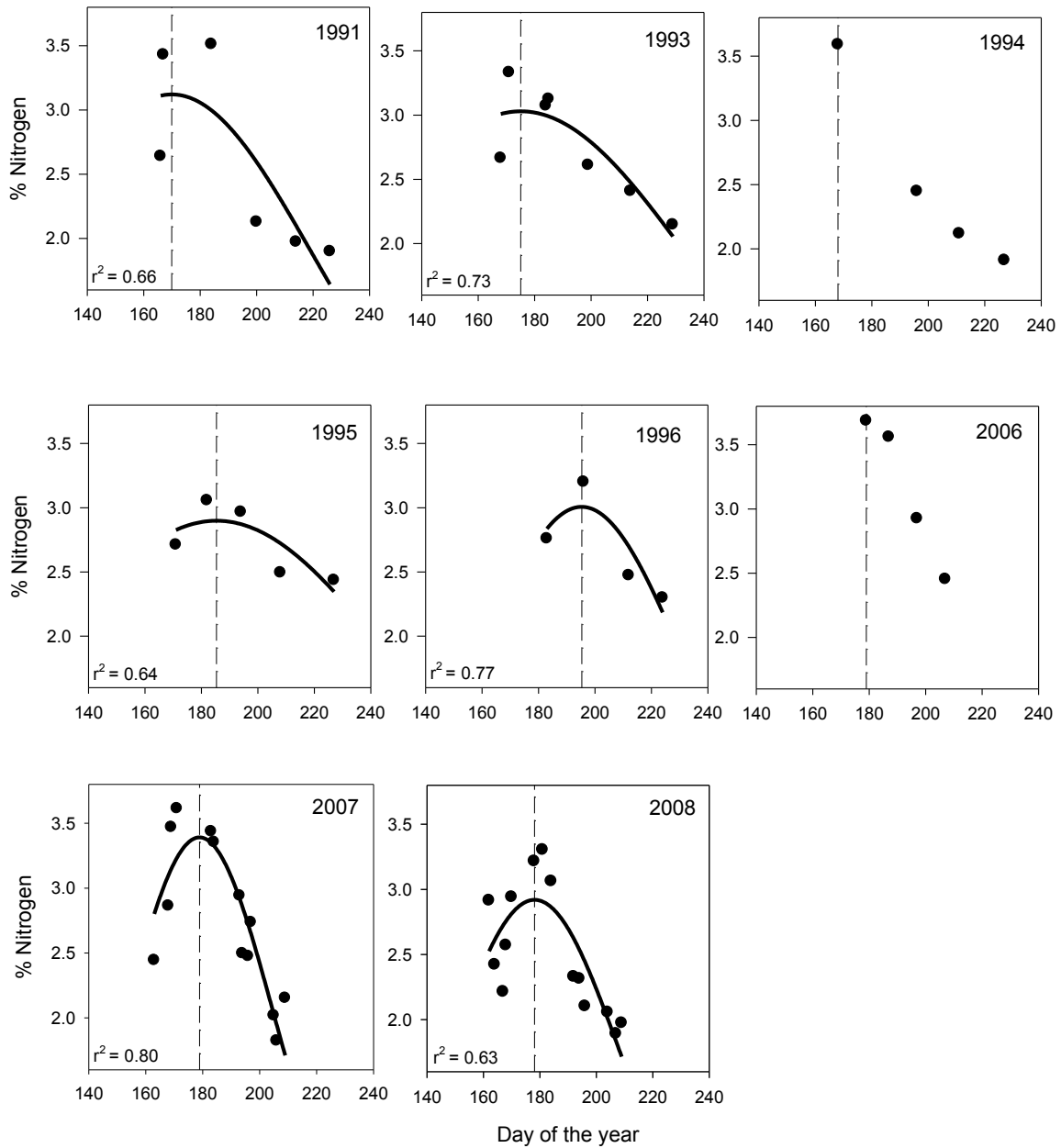


Figure 1. Seasonal variations in percentage of nitrogen found in graminoid plants in wetlands of Bylot Island, Nunavut, during 8 years. Each dot represents observed percentage of nitrogen averaged from 1 to 6 samples taken on the same day. The dashed line represents the estimated date of peak nitrogen. This date was estimated by fitting a Gaussian function to the data (represented by the solid line) except in 1994 and 2006 (see methods for details).

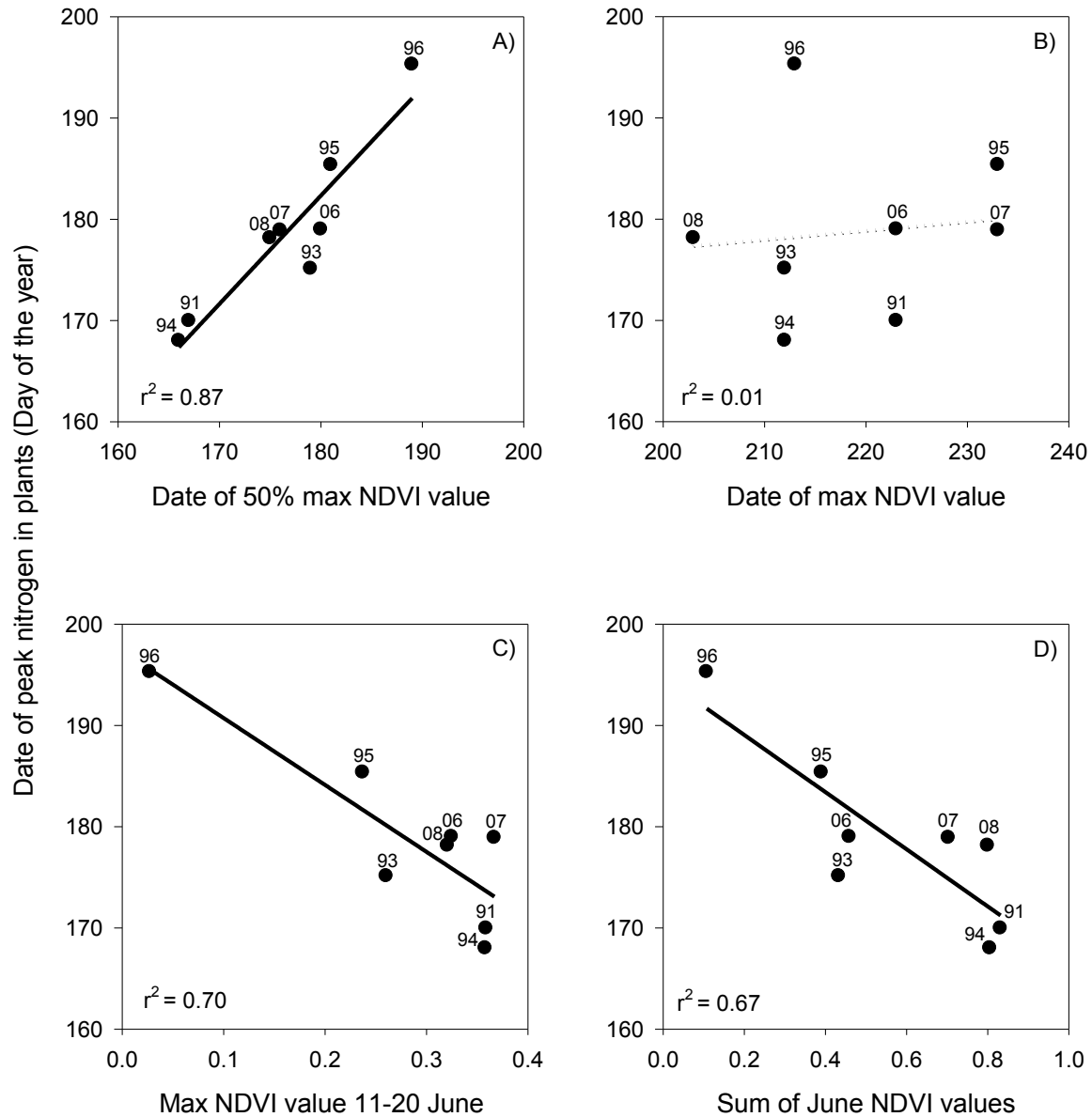


Figure 2. Relationships between estimated date of peak nitrogen concentration (Day of the year) in plants sampled in wetlands of Bylot Island, Nunavut and 4 different NDVI metrics: A) date at which 50% of the seasonal maximum value is attained, B) date at which 100% of the seasonal maximum value is attained, C) maximum NDVI value between 11 and 20 June, and D) cumulative 10-day NDVI values for the month of June. Dashed lines represent non-significant trends ($p > 0.05$). Numbers refer to the last 2 digits of years.

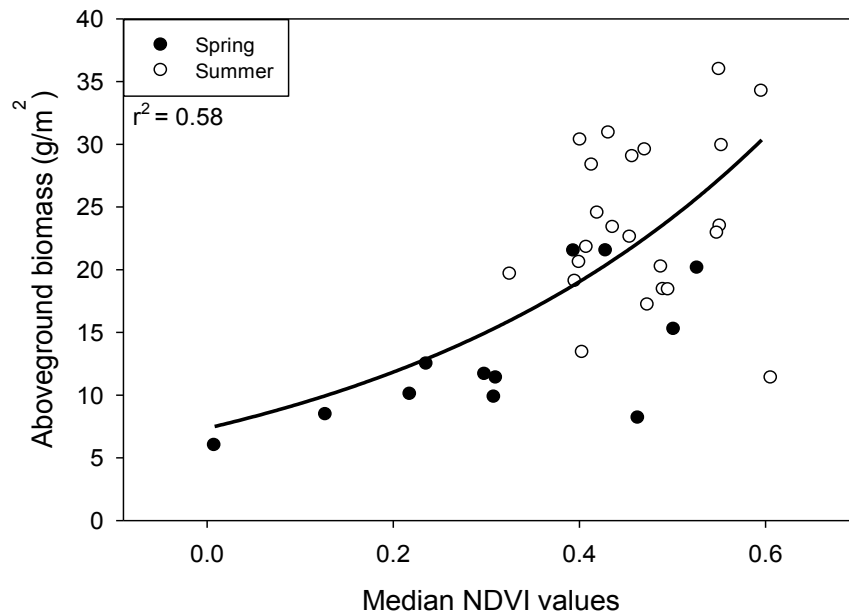


Figure 3. Relationship between aboveground live biomass of plants sampled in wetlands on Bylot Island, Nunavut and the corresponding median NDVI values in 1991, 1993-1996 and 2006-2008. Each dot represents a biomass value averaged from 1 to 6 samples taken during the same sampling period during a particular year. Black circles represent spring samples (mid-June to early July) and white circles represent summer samples (mid-July to early August).

CHAPITRE 3

Trophic mismatch and its effects on the growth of young in an Arctic herbivore

Doiron, M., Gauthier, G. & Lévesque, E. Ce manuscrit sera soumis à *Global Change Biology*.

Résumé

Dans les environnements saisonniers, la période de reproduction des animaux coïncide généralement avec la période où les ressources sont les plus abondantes. Cependant, vu la rapidité à laquelle a lieu le réchauffement planétaire, il est possible que les animaux ne réussissent pas à modifier suffisamment leur phénologie pour tenir compte des changements dans leur environnement. Ceci pourrait avoir comme effet de rompre la synchronie entre la phénologie des consommateurs et celle de leurs ressources, un phénomène connu sous le nom désynchronisation trophic (ou « *trophic mismatch* »), et peut avoir des conséquences majeures sur le succès reproducteur des animaux. Dans cette étude, nous avons analysé des données à long-terme (1991-2010) sur le climat, sur la phénologie des plantes ainsi que sur la reproduction d'un oiseau migrateur de longue-distance nichant dans l'Arctique, la grande oie des neiges (*Chen caerulescens atlantica*), et ce dans le but d'examiner l'impact potentiel d'une désynchronisation trophique sur la croissance des jeunes oies. Nos résultats montrent que les oies ajustent seulement partiellement leur reproduction en fonction des changements annuels dans la disponibilité de nourriture de haute qualité, ce qui mène à une désynchronisation trophique pouvant atteindre jusqu'à 19 jours. Le pic de concentration en azote des plantes, un indice de qualité nutritive pour les jeunes oies, avait lieu plus tôt lors de printemps chauds avec une fonte de neige hâtive. De plus, la désynchronisation entre les dates d'éclosion des jeunes et la date du pic d'azote avait tendance à être plus importante lors des années où la fonte de neige avait lieu tôt en saison. La masse corporelle et la taille structurelle des oisons à l'envol étaient plus faibles lorsque que le manque de synchronie était important, particulièrement lorsque le délai entre la date du pic d'azote et l'éclosion était de plus de 10 jours. Nos résultats supportent l'hypothèse que la désynchronisation trophique peut avoir des effets négatifs sur l'aptitude phénotypique des herbivores de l'Arctique, et que cet effet risque d'être exacerbé par la hausse continue des températures à l'échelle globale.

Abstract

In highly seasonal environments, timing of breeding of organisms is typically set to coincide with the period of highest resource availability. However, breeding phenology may not change at a rate sufficient to keep up with the rapid changes in the environment in the wake of climate change. This lack of synchrony between the phenology of consumers and that of their resources leads to a phenomenon called trophic mismatch, which may have important consequences on reproductive success of herbivores. We analysed long-term data (1991-2010) on climate, plant phenology and the reproduction of a long-distance arctic migrant, the greater snow goose (*Chen caerulescens atlantica*), in order to examine the potential impact of mismatched reproduction on the growth of young. We found that geese are only partially able to adjust their breeding phenology to compensate for annual changes in the timing of high quality food plants, leading to mismatches of up to 19 days between the two. The peak of nitrogen concentration in plants, an index of the nutritive quality of plants for young, occurred earlier in warm springs with an early snowmelt. Likewise, mismatch between hatch dates of young and date of peak nitrogen tended to be more important in years with early snow melt. Gosling body mass and structural size at fledging was reduced when trophic mismatch was high, particularly when the delay between date of peak nitrogen concentration and hatching was greater than 10 days. Our results support the hypothesis that trophic mismatch can negatively affect the fitness of arctic herbivores, and that this is likely to be exacerbated by rising global temperatures.

Introduction

The fast pace at which climate change is occurring (IPCC 2013) has had measurable impacts on ecosystems and organisms by altering not only the distribution of species but also their phenology (Walther *et al.* 2002, Root *et al.* 2003). Indeed, phenology, defined as the seasonal initiation of essential life-cycle activities such as reproduction or migration (Berteaux *et al.* 2004), is probably the parameter most often affected by climate warming (Parmesan 2006). Changes in phenology can have important consequences on trophic interactions when species at different trophic levels react to changes in their environment at different rates, a phenomenon known as trophic mismatch (Durant *et al.* 2007, Kerby *et al.* 2012). A lack of temporal synchrony between periods of high resource requirement by the consumer and periods of high food abundance can have serious population-level consequences by negatively affecting reproductive success and/or recruitment (Post & Forchhammer 2008, Both *et al.* 2010, Miller-Rushing *et al.* 2010). Trophic mismatch has been documented across multiple taxa and environments as a result of climate change (Thackeray *et al.* 2010), most notably in temperate passerine birds (Visser *et al.* 1998, Both *et al.* 2006), caribou (*Rangifer tarandus*; Post & Forchhammer 2008, Post *et al.* 2008) defoliating insects (Visser & Holleman 2001, Schwartzberg *et al.* 2014) and aquatic ecosystems (Edwards & Richardson 2004, Winder & Schindler 2004).

Polar regions are warming at a faster pace than the rest of the planet (ACIA 2004, Barber *et al.* 2008, Walsh *et al.* 2011), and plant phenology in many arctic regions is expected to change due to earlier snowmelt and/or higher temperatures during the growing season (Cleland *et al.* 2007). Warming experiments conducted in arctic and alpine regions have shown that plants can respond rapidly to increased temperatures by an accelerated phenology, increased growth and a greater reproductive effort (Henry & Molau 1997, Arft *et al.* 1999, Aerts *et al.* 2004, Elmendorf *et al.* 2012a, Oberbauer *et al.* 2013), which could in turn affect herbivores that feed upon them. As summers are short in the tundra, animals have a small time window to reproduce and rear young, making them highly susceptible to trophic mismatch. This effect can be compounded in long-distance migrants because changes in climate occurring on the wintering grounds may occur at a different speed than those on the

breeding grounds, thereby limiting their potential for adaptation to warming (Both *et al.* 2010, Møller *et al.* 2010).

Arctic-nesting geese are major herbivores in many tundra regions and these long-distance migrants may be vulnerable to trophic mismatch during reproduction. Gosling growth is known to be highly sensitive to environmental conditions during the pre-fledging period (Gauthier *et al.* 2006), and is directly related to the quality and availability of food plants during brood-rearing (Larsson & Forslund 1991, Lindholm *et al.* 1994, Lepage *et al.* 1998). Growth of goslings is limited by protein, which is generally measured by the nitrogen concentration of plants (Sedinger & Raveling 1986, Lepage *et al.* 1998). Nitrogen concentration of arctic plants typically reaches a peak shortly after the onset of plant growth followed by a constant decline throughout the summer until senescence (Chapin 1980, Manseau & Gauthier 1993, Piedboeuf & Gauthier 2000). Goose reproduction is highly synchronized within the population and is timed so that hatching coincides with peak nitrogen concentration in plants (Manseau & Gauthier 1993, Lepage *et al.* 1998, Larter & Nagy 2001, Cadieux *et al.* 2005). Should this synchrony be disrupted, growth of goslings may be negatively affected, with potentially severe consequences for population dynamics (Aubry *et al.* 2013). A mismatch between hatching and peak food availability has been shown to negatively affect growth in arctic-nesting insectivorous shorebirds (McKinnon *et al.* 2012).

We previously showed that short-term warming had a negative impact on the main food plants of geese in the Canadian Arctic. An experimental increase of 1 to 2°C caused an acceleration of the seasonal decline in plant nutritive quality and resulted in a decrease in the nitrogen concentration of plants by up to 14% during the period of gosling growth (Doiron *et al.* 2014). Moreover, at the same study site, Dickey *et al.* (2008) have shown that gosling mass and size near fledging were reduced in years with high spring temperature. They suggested that this resulted from a reduced availability of high quality food during growth due to a lack of synchrony between hatch dates and peak nitrogen concentration in plants.

In this study, we use a 20-year dataset on climate, plant nutritive quality, goose breeding phenology and gosling growth to test the hypothesis that trophic mismatch negatively affects the reproduction of greater snow geese (*Chen caerulescens atlantica*) in the Arctic. Our aims are to determine which climatic factors affect date of peak nitrogen in plants and the synchrony between hatching and date of peak nitrogen, and to evaluate the effects of a mismatch between the two on gosling growth. We predict that (i) date of peak nitrogen will occur earlier in warm years with an early spring snow-melt, (ii) the mismatch between goose breeding phenology and date of peak nitrogen concentration will increase in warm years with an early snow-melt, and (iii) this mismatch negatively impacts body mass and size of goslings at fledging.

Methods

Study area

This study took place on the South Plain of Bylot Island (73°08'N, 80°00'W), north of Baffin Island, Nunavut, Canada. This region is characterised by flat lowlands surrounded by extensive upland plateaus covered with lush tundra vegetation for its latitude. The South Plain of Bylot Island is one of the most important breeding areas for the greater snow goose, a colonial nester (Reed *et al.* 2002). During nesting, geese are mainly localised in a relatively small area (ca 50 km²), but during brood-rearing adults with goslings disperse throughout most of the South Plain (ca 1600 km²). The habitats used by geese can be divided in two broad categories (Gauthier *et al.* 1996). The first habitat type consists of freshwater wetlands characterized by wet polygon fens (Tarnocai & Zoltai 1988) dominated by grasses and sedges, such as *Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe and *Carex aquatilis* Wahlenb., growing through a thick carpet of brown mosses. The second habitat type consists of upland mesic tundra, characterized by rolling hills and better drained soil where vegetation is more diversified and dominated by prostrate shrubs, graminoids and other small herbaceous species. Though comprising only about 15% of the landscape, wetland polygon fens are preferred by geese and are used at high density throughout the nesting and brood-rearing periods (Hughes *et al.* 1994). Over the past 35 years, temperatures on the study site

have increased on average by 2.8°C in spring (Gauthier *et al.* 2011), and the annual cumulative number of thawing degree-days has increased from 381 to 521 between 1989 and 2011 (Gauthier *et al.* 2013).

Climatic data

Since 1994, a fully automated weather station located in the Qarlikturvik Valley, a large glacial valley near the north end of the South Plain, has been recording air temperature at 2-m above the ground on an hourly basis (CEN 2013). Daily rainfall was collected manually with a rain gauge from 1 June to 15 August from 1995 to 2010. We also obtained temperature and rainfall data from the Environment Canada weather station located at the Pond Inlet airport on Baffin Island, approximately 80 km southeast of the Qarlikturvik Valley. Weather data from those two stations were highly correlated over the period of 1995-2004, which allowed us to estimate local temperatures and rainfall between the years 1991-1993 (see Dickey *et al.* 2008), thus extending our data to cover 1991 to 2010. Each year, snow-melt was monitored by visually estimating percent snow cover from a vantage point from 1 June until complete snow melt at two-day intervals.

From the snow-melt data, we extracted the date at which snow cover first reached 50%. From the temperature data, we defined two periods, *Spring* (20 May to 20 June), which corresponds to the arrival, pre-laying and laying period of geese, and *Summer* (20 June to 15 August), which corresponds mostly to the incubation and brood-rearing period. We extracted the following variables: average, maximum and minimum temperature (expressed as mean of daily average, maximum and minimum values for each period), and sum of thawing degree-days. For each time period (Spring and Summer), we performed a principal component (PC) analysis based on the aforementioned temperature variables and extracted individual scores along the first axis as an index (PC score) of temperature. In all PC analyses, the first axis explained > 71% of variation and the variables had loadings of > 0.69 on this axis (see Annexe 3, Table 1). A high PC score was associated with warm conditions and a low one with cool conditions. Total annual rainfall was also calculated for spring (1 June to 20 June, as no rain data was available for earlier dates) and summer (20 June to 15 August) for all years except 1994 (no data available for that year).

We retrieved daily Arctic Oscillation (AO) and North Atlantic Oscillation (NAO) values from the Climate Prediction Center of the National Weather Service (<http://www.crp.ncep.noaa.gov>) and calculated annual average values for Spring (20 May to 20 June) and Summer (20 June to 15 August). The AO is a nearly axisymmetric spatial pattern of sea-level pressure centred over the Arctic (Thompson & Wallace 1998). NAO can be considered a regional manifestation of AO, and both have been linked to climate and biological processes at our site (Dickey *et al.* 2008, Morrissette *et al.* 2010, Bêty *et al.* 2014). NAO and AO values were strongly correlated within each time period ($r > 0.70$), and in this study we used the AO index for all analyses. In our study area, the AO explains more than half of the increase in winter surface air temperature (Rigor *et al.* 2000), and positive AO values are associated with low temperatures and precipitations in winter (Hurrell 1995, JISAO 2004). Although the AO is primarily viewed as a winter phenomenon, it shows similar patterns of change in atmospheric pressure in the summer months but with less vigorous variation (Serreze *et al.* 1997, Aanes *et al.* 2002).

Plant biomass and nitrogen data

Aboveground live biomass in wetlands (polygon fens) was sampled at roughly two-week intervals in 1991, 1993-1996 and 2006-2010. Each year, 12 new goose exclosures (1 m² or 4 m² depending on year) were set up in the Qarlikturvik Valley just after snow melt in June, before any significant grazing by geese had occurred. Exclosures were made of 30 cm high chicken wire (2.5 cm mesh) and were set up over an area of ~1 km². Plant samples were collected inside exclosures at least 4 times per season from mid-June to mid-August. In most years, the first sampling date occurred shortly after snow-melt. Each time we removed a 20 cm x 20 cm piece of turf at random but avoided to collect samples adjacent to previously-removed pieces of turf to prevent edge effect. Vascular plants were cut at the base of the white basal stem buried in the moss. Plants were sorted into four categories: grasses (mainly *D. fisheri*), cottongrass sedges (*E. scheuchzeri*), *Carex* sedges (*Carex* spp.) and dicotyledonous plants (<2%; mostly *Stellaria longipes*, *Saxifraga* sp. and *Salix* spp.). Samples were sorted out into vegetative green parts (i.e. leaves), flowers (including stems)

and dead matter (which was discarded), oven-dried at 45°C for 36 hours and weighed to the nearest 0.001 g (see Gauthier *et al.* (1995) for details).

The vegetative green parts of *Dupontia* and *Eriophorum*, the two preferred plants of geese at our study site (Manseau & Gauthier 1993, Gauthier *et al.* 1995), were ground to a fine powder and analysed separately for total nitrogen concentration. Between 1991 and 1996, the samples were analysed using an automated macro-Kjeldahl analyser (Kjell-Foss, model 16210) following the AOAC (1984, p.154) method (Gauthier *et al.* 1995). From 2006 onwards, nitrogen concentration was determined using a QuickChem Lachat nutrient auto-analyser (QuickChem 4000 Series, Zellweger Analytics, Milwaukee, WI, USA). In some cases, it was necessary to pool samples from different exclosures (but collected at the same date) to obtain sufficient material for the nitrogen analyses. Date of peak nitrogen was extracted from the relationship between plant nitrogen concentration and date of the season (see Doiron *et al.* 2013 for details). For each sampling date, we used the mean nitrogen concentration measured in both plant species (i.e. *Dupontia* and *Eriophorum*), giving equal weight to each species in the calculation. Nitrogen biomass was calculated as the product of green biomass by nitrogen concentration in each individual sample.

A previous study by Doiron *et al.* (2013) showed that the date at which 50% of the annual maximum Normalized Difference Vegetation Index (NDVI) is attained is a good predictor of the date of peak nitrogen concentration in graminoid plants at our study site. As nitrogen was only directly measured during 10 years (1991, 1993-1996, 2006-2010), we used the equation of Doiron *et al.* (2013) to predict peak nitrogen date for an additional 10 years, extending our time series to cover the entire time period of 1991 to 2010. NDVI data were obtained from the Canada Centre for Remote Sensing (Pouliot *et al.* 2009) and were derived from the Advanced Very High Resolution Radiometer of the National Oceanic and Atmospheric Administration (NOAA) satellites (see Doiron *et al.* 2013 for details). Since NDVI was not an accurate predictor of actual maximum nitrogen concentration (%) or maximum nitrogen biomass (g/m²) in plants, our time series for these two variables are comprised of only 10 years.

Goose reproductive data

Goose breeding biology has been monitored in our study area since 1989. Each spring, several hundred nests (> 350 in all years but one) initiated throughout the laying period are found in the colony and monitored. Nests are revisited near hatching to determine hatch date (defined as the date when $\geq 50\%$ of the eggs hatched) and to mark goslings in the nest with web-tags (see Lepage *et al.* 2000 for details). Approximately 5 weeks after hatching, before fledging, goose families were captured in mass banding drives over a 7-10 day period. The majority of captures were made in the Qarlikturvik Valley, although in most years some captures were also made in neighbouring valleys. Captured goslings were sexed by cloacal examination and the majority of them, including all web-tagged goslings recaptured, were weighed (nearest 25g in 1991-1994, nearest 1g from 1995 onward) and measured with callipers (culmen, head and tarsus length to the nearest 0.1mm). An average of 105 (ranging from 17 to 275) web-tagged goslings were recaptured and measured each year, for a total of 2,096 individuals from 1,115 different families. All captured adults and goslings were released together at the end of each banding drive.

Statistical analyses

Using simple linear regressions, we first examined the relationship between median hatch date of goslings and annual date of peak nitrogen concentration in plants. We defined the mismatch between geese and plants as the difference (in days) between hatch date of goslings and date of peak nitrogen concentration. We also determined which climatic variables best explained the annual variation in four variables related to plant nitrogen: date of peak nitrogen concentration, maximum nitrogen concentration, maximum nitrogen biomass, and mismatch. The seven climatic variables tested (along with their Pearson's r values) are presented in Table 2 of Annexe 3. As we used annual values, sample sizes were small ($n = 9-20$) and thus we were limited in the number of climatic variables we could simultaneously test in our linear models. To counter this, we did not include in the model more than three variables together in cases when $n = 19-20$ and two variables when $n = 9-10$, and re-tested them along with their interactions in several combinations of the variables.

We further examined the combined effects of plant nitrogen and climatic variables on the body mass and size of goslings. To determine structural size of goslings, we performed a principal component analysis based on the measurements of head, culmen and tarsus length and used the individual scores as an index of size (see Lepage *et al.* 1998). The first axis explained > 92% of total variation and all variables had loadings of > 0.9 on this axis (see Table 3 of Annexe 3). To compare the mass and size of goslings, it was necessary to correct for the age at which they were measured. Indeed, both year and age as well as their interaction explained a significant amount of variation in goslings mass and size ($P < 0.001$ in both cases). For each individual, we thus added the residuals (i.e. the difference between observed and predicted values) to the mean overall mass and body size measurements predicted by the model for each year at 35 days (average age at capture) and used these values for subsequent analysis.

We proceeded in two steps to determine variables affecting body mass and size of goslings. First, we ran simple regressions using annual means of gosling mass and size to examine the shape of the relationships between these variables and the independent variables of interest (see Table 2 of Annexe 3 for the full list), using linear or second degree polynomial models when appropriate (x^2 terms were included when they improved the AICs of the model). In the second step, we used hierarchical mixed models to determine which variables had an effect on individual measures of gosling mass and size (procedure PROC MIXED of SAS 9.3; following the method outlined in Bell *et al.* 2013). Multi-level models were necessary because of the hierarchical nature of our data set: the dependent variables (gosling mass and size) and mismatch (number of days between hatch date and annual date of peak nitrogen) were at the individual level (level 1) whereas the other variables (nitrogen and climatic variables) were single annual values (level 2). This approach allowed us to account for the possible dependence among individuals, as all goslings hatched each year were exposed to the same climatic conditions. Additionally, the variable ‘family’ was included in the models as a random effect to account for the dependence (genetic and environmental) between goslings originating from the same nest. Because some of the variables were highly correlated (Table 2, Annexe 3), we reran the same analyses multiple times using only one of the correlated variables at a time (when $r \geq 0.70$). As rainfall and snow cover values were missing in 1994, this year was excluded from the multi-level models.

Model selection was based on the AICc statistics, starting from the most complex models and removing variables to obtain the models that best explained the variation in each dependent variable. The model with the lowest AICc value was considered the most parsimonious, and those with differences of <2 AICc units were considered well supported by the data (Burnham & Anderson 2002). As we only had 9 years of data for maximum nitrogen concentration and maximum nitrogen biomass (vs. 19 years for all other variables), we repeated the previous analysis with only 9 years of data in order to include these variables. For these years, mismatch with the date of peak nitrogen concentration was calculated solely from empirical data rather than with a mixture of empirical data and values estimated from the linear equation with NDVI (described above). Therefore, this smaller data set also served to validate the results obtained with the 19-year data set. We used model averaging (multimodel inference) to obtain parameter estimates (Burnham & Anderson 2002). Conditional r^2 values were calculated following the procedure outlined by Nakagawa & Schielzeth (2013). Statistical analyses were performed with R (R Development Core Team 2006) and SAS (SAS Institute, 2010, Cary, NC, USA).

Results

Annual variations in plant and goose phenology

Over the 20-year period, the date of peak nitrogen concentration in plants showed considerable variation. Peak nitrogen occurred over a 27-day period, ranging from 17 June to 14 July, with a mean date of 29 June (day of the year [DOY] 180 ± 6.9 ; Figure 1a). Goose breeding phenology showed much less variation, as annual median hatch date spanned a 13-day period from 3 to 16 July, with a mean median date of 9 July (DOY 190 ± 3.2 days; Figure 1a). There was little overlap between these two variables and in all but two years, median hatch date occurred after date of peak nitrogen in plants. There was a significant positive relationship between median hatch date and date of peak nitrogen (Figure 1b), with a regression slope of 0.25 (CI 95%: 0.06, 0.44). The annual gap between median hatch date of goslings and date of peak nitrogen (*i.e.* mismatch) varied from -2 to 19 days, with a mean value of 8.9 ± 5.4 days.

Maximum nitrogen concentration in plants varied from 2.7 to 3.7% (mean = $3.3 \pm 0.3\%$) over the 10 years it was measured. Maximum nitrogen biomass varied from 0.5 to 1.1 g/m² (mean = 0.8 ± 0.2 g/m²) and occurred on average on 19 July \pm 9 days. There was a weak negative relationship between peak nitrogen concentration and date of peak nitrogen in plants ($\beta_x = -0.02$; $r^2 = 0.25$; $F = 4.09$; $df = 9$; $P = 0.078$) suggesting that maximum nitrogen concentration (%) in plants tended to be higher in years when the date of the peak occurred earlier in the season. Maximum nitrogen biomass was not related to date of peak nitrogen ($P = 0.74$).

Effects of climate on plant nitrogen and mismatch

Only two climatic variables explained a significant proportion of variation in date of peak nitrogen concentration in plants. Date of peak nitrogen was negatively related to the spring temperature index (Figure 2a) but positively related to the date of 50% snow cover (Figure 2b). These two climatic variables were correlated ($r = -0.66$) and the model with date of 50% snow cover provided the best fit to our data ($\Delta AICc = 14.9$ vs spring temperature index). The annual mismatch tended to be related to date of 50% snow cover ($r^2 = 0.16$; $F = 3.27$; $df = 18$; $P = 0.088$) with mismatch tending to be larger in years with earlier snowmelt (Figure 3). Annual maximum nitrogen biomass was significantly related to two climatic variables: summer temperature (Figure 4a; $y = 0.10x + 0.74$; $r^2 = 0.68$; $F = 17.40$; $df = 9$; $P = 0.003$) and summer AO (Figure 4b; $y = -0.31x + 0.77$; $r^2 = 0.57$; $F = 10.47$; $df = 9$; $P = 0.012$). Maximum nitrogen concentration was not related to any of the climatic variables.

Effect of mismatch on gosling growth

The annual mean body mass of goslings near fledging was significantly related to the date of peak nitrogen, but this relationship was non-linear. In years with an early nitrogen peak, goslings were smaller, but this effect leveled off in years with a late nitrogen peak (Figure 5a; $r^2 = 0.47$; $F = 7.61$; $df = 18$; $P = 0.004$). There was also a quadratic effect of mismatch on body mass; when annual mismatch between hatch date and date of peak nitrogen was greater

than 10 days, body mass of goslings was lower (Figure 5b; $r^2 = 0.31$; $F = 3.87$; $df = 18$; $P = 0.041$). Annual body mass of goslings was not related ($P > 0.24$) to maximum nitrogen concentration (%) and maximum nitrogen biomass (g/m^2). The best-supported hierarchical model explaining individual body mass of goslings included mismatch as well summer rain, spring AO and summer AO (Table 1). Individual body mass was negatively related to the mismatch but the presence of a quadratic effect in the second model, a close competitor, supported the pattern observed in Figure 5b. Body mass was also negatively related to summer rain and summer AO values but positively related to spring AO values (Table 1). Models where mismatch was replaced by date of peak nitrogen concentration performed more poorly ($\Delta\text{AICc} > 44.5$). Conditional r^2 values of the top-ranked models were > 0.68 . When we reran the analysis with only 9 years of data (the years for which we had empirical nitrogen values), the same variables (with similar parameter estimates) were selected in the best-supported models, with the exception of summer AO which was replaced by summer temperature (Table 3a).

Annual mean body size of goslings was also significantly related to both date of peak nitrogen and mismatch (Figure 6). Goslings had smaller body size (PC score) in years with early dates of peak nitrogen, but this effect was non-linear (Figure 6a; $r^2 = 0.38$; $F = 5.19$; $df = 18$; $P = 0.017$). Similarly, body size of goslings was lowest in years when mismatch was greater than 10-12 days (Figure 6b; $r^2 = 0.32$; $F = 4.08$; $df = 18$; $P = 0.036$). Body size was also positively related to maximum nitrogen biomass (Figure 5c; $r^2 = 0.53$; $F = 8.89$; $df = 9$; $P = 0.018$). The best-supported hierarchical model explaining individual body size of goslings included a negative, second degree effect of mismatch, as well negative effects of summer rain and summer AO and a positive effect of spring AO (Table 2). Results are thus very similar than those with body mass. Competing models ($\Delta\text{AICc} < 2$) generally retained the same effects (with mismatch as a linear negative effect in two out of the five models), and conditional r^2 values of top-ranked models were > 0.65 . Models where mismatch was replaced by date of peak nitrogen concentration performed more poorly ($\Delta\text{AICc} > 30.2$). In the analysis based on only 9 years of data, the best-supported model again included a negative effect of mismatch and a negative effect of summer rain, but also a positive effect of summer temperature whereas summer and spring AO were not retained (Table 3b).

Discussion

Our results provided support for all our initial predictions: date of peak nitrogen concentration occurred earlier in warm years with early snow-melt; in those years, the mismatch between goose and plant phenology increased; finally, gosling growth was negatively affected by this trophic mismatch.

Annual variations in goose and plant phenology

The phenology of plants (date of peak nitrogen concentration) and geese (median hatch date) in our study area both showed important inter-annual variability. Although there was a positive relationship between the two, the slope of 0.25 shows that geese are only partially able to adjust their breeding phenology to compensate for annual changes in the timing of high quality food, leading to trophic mismatches of up to 19 days in early years. This was expected as long-distance migrants are known to be relatively inflexible in their response to advances in spring phenology, and are thus potentially the most susceptible to trophic mismatch among avian species (Both *et al.* 2010). As climate change can occur at different speeds or even in opposite directions at different stages along the migratory route, the ability of these birds to adapt to changes in their environment may be limited.

The migration of geese is composed of several long-distance flights divided by stopover periods when they accumulate fat reserves, and environmental conditions encountered on these sites can affect the migratory decisions of individuals (Bêty *et al.* 2003, Bauer *et al.* 2008, Duriez *et al.* 2009). If they are unable to acquire sufficient nutrients at stopover sites or if the weather is inclement, birds may be delayed in arriving on the breeding sites at the optimal period for breeding, and may be further delayed in laying eggs if they need to replenish energy on the breeding site (Gauthier *et al.* 2003). As geese are long-lived birds, the timing of egg-laying may also be partly determined by learned or inherited mechanisms related to photoperiod or other invariant cues, which has been suggested as a potential cause for mismatch in thick-billed murres (*Uria lomvia*) breeding in Hudson Bay (Gaston *et al.* 2009). In our study population, breeding females tracked by radio-transmitters showed relatively high repeatability in their arrival dates on the breeding site, which implies that this

trait may be characteristic of individuals in this species (Bêty *et al.* 2004). Moreover, the time for incubating eggs is fixed (24 days in snow geese), and thus breeding individuals are unable to advance their phenology once eggs are laid, whereas plant phenology can continue to be affected by increased temperatures during that time window (Doiron *et al.* 2014).

The advancement in the date of peak nitrogen concentration of plants in warm years was presumably due to an early onset of plant growth, as warm temperatures and early snow melt have previously been linked to advanced phenology of arctic plants (Wipf & Rixen 2010, Oberbauer *et al.* 2013, Doiron *et al.* 2014). Warm temperatures have also been shown to accelerate plant growth: at our study site, aboveground biomass of plants was correlated to sum of thawing degree-days (Gauthier *et al.* 2013), and warming experiments at other sites throughout the High Arctic have demonstrated that warm temperatures increase plant production (Rustad *et al.* 2001, Elmendorf *et al.* 2012a, Elmendorf *et al.* 2012b). A large mismatch typically occurred in years when the date of peak nitrogen was reached earlier than the long term average, and mismatch tended to be greater in years of early snow melt. Both egg laying (Dickey *et al.* 2008) and the onset of plant growth (Wipf & Rixen 2010) are limited by snow cover in spring. However, plants appear to track the disappearance of snow more quickly than geese as they adjust their laying date by only 0.38 days for every day of advance in snow-melt (Gauthier *et al.* 2013).

Although the date of peak nitrogen concentration was highly variable, the value of the peak itself changed very little between years, reaching 3 to 3.5% and declining sharply thereafter (Doiron *et al.* 2013). Maximum nitrogen biomass (the product of nitrogen concentration and plant biomass) was lower in years with cool summer temperatures (both at the local and regional scales, as indexed by high AO values), probably as a result of lower vegetative growth in those years (Gauthier *et al.* 2013). However, for growing goslings, nitrogen concentration is thought to be more important than total nitrogen biomass, which is supported by our results. Unlike most other herbivores, geese have a rapid throughput time in their gut resulting in a low digestive efficiency (i.e. they do not digest plant fiber) and a low nitrogen retention rate (Mattocks 1971, Sedinger 1997). Growing goslings thus depend on food with high nitrogen concentration to meet their high nutrient requirements as they must synthesize a large amount of new tissues (Sedinger 1997).

Effect of mismatch on growth of young

Gosling body mass and structural size near fledging was reduced in years of high mismatch between date of peak nitrogen concentration and median hatch date. Body mass and structural size started to decline rapidly when mismatch exceeded ~10 days, probably because feeding conditions of goslings deteriorate rapidly after that. Indeed, we showed in a previous study that (1) the nitrogen concentration of graminoid plants at our study site reaches a peak in late-June/early-July, after which it decreases rapidly to about half its peak levels 15 to 20 days later, and (2) this decline is more abrupt when the temperature is increased (Doiron *et al.* 2014). Thus, goslings hatched late in the season have access to food of much lower quality (i.e. lower nitrogen concentration, more fiber content). The effect of this mismatch on the mass and size of gosling near fledging can have major fitness consequences, as smaller goslings have lower chances of surviving the fall migration, a period of high mortality (Owen & Black 1989, Francis *et al.* 1992, Schmutz 1993, Menu *et al.* 2005). In addition, size of goslings at fledging is correlated to their final adult size (Cooch *et al.* 1991, Sedinger *et al.* 1995), which is in turn related to their fecundity (Sedinger *et al.* 1995).

Gosling growth was also related to spring and summer AO, though the sign of the effect changed from positive in the spring to negative in the summer. This global index appeared to be a better predictor of gosling mass and size at fledgling than the temperature index calculated from a local weather station, which suggests that AO may succeed at capturing a wider range of climatic conditions on the breeding grounds than local measurements (Hallett *et al.* 2004). Negative AO values are associated with warm temperatures at our study site (JISAO 2004). Thus, a positive relationship between gosling growth and spring AO supports the idea that warm and dry conditions cause plant phenology to accelerate in spring, leading to an increased mismatch between hatching and plant nutritive quality. The effect of the AO was reversed later in the summer (i.e. negative relationship between gosling growth and summer AO) presumably because cold summer temperatures (and increased rainfall) negatively impact young during the brood-rearing period, either due to increased thermoregulatory costs (Renaud 1999), reduced foraging time due to a greater need for

brooding (Fortin *et al.* 2000) or a reduced late summer growth of their forage plants. Therefore, conditions that will maximize gosling growth in the High Arctic appear to be cool spring temperatures and relatively late snow melt to ensure a good synchrony between hatch and plant nutritive quality, combined with warm temperatures and dry conditions during brood-rearing to reduce energy expenditure and maximize food intake. However, populations breeding at different latitudes may be affected differently as gosling growth in sub-Arctic snow geese, which have a relatively short migration, appears to be favoured by warm spring and cool summers, an opposite situation to ours (Aubry *et al.* 2013).

Climate change and mismatch

Arctic warming is expected to continue at a faster pace than the rest of the planet and temperature should increase by 3-5°C at the end of the century (IPCC 2013). This range of warming has already been shown to advance the phenology of plants and to reduce the quality of forage for arctic herbivores (Post *et al.* 2008, Doiron *et al.* 2014). Unless herbivores are able to advance their phenology to keep up with such important changes in their breeding environment, they are likely to become increasingly mismatched with the period of high-quality food on the breeding grounds, and our study shows how this could have negative consequences for individuals. Although climate warming may increase total plant production and prolong the summer season, this may not be sufficient to offset the risk of hatching well after the peak in nitrogen concentration, as food quality is low at the end of the summer (Manseau & Gauthier 1993, Cadieux *et al.* 2005). Geese, like other long-distance migrants, appear to have a limited ability to track inter-annual variations in spring phenology on their breeding ground, which is likely to impede their capacity to adapt to increases in spring temperature in the wake of rapid global warming.

The phenomenon of trophic mismatch is widespread and has been shown to have negative impacts on species in multiple biomes (Visser *et al.* 1998, Winder & Schindler 2004, Lane *et al.* 2012, Plard *et al.* 2014). However, its impacts can be amplified in Arctic systems due to the extreme seasonality of resources, the short breeding seasons, the long distance travelled by most migratory species and the rapid pace of climate change, as it has been reported in Arctic-nesting shorebirds (McKinnon *et al.* 2012) and caribous (Post & Forschhammer 2008,

Post *et al.* 2008). Moreover, complex feedbacks between climate and the physical environment may have important consequences in Arctic ecosystems. For instance, accelerated decline of the Arctic sea ice due to warming has led to temporal changes in the availability of prey for seabirds (Gaston *et al.* 2009), but this rapid decline may also affect terrestrial herbivores. Indeed, Kerby & Post (2013b) have shown that sea ice loss can be linked to the ongoing advance in plant phenology in West Greenland and has contributed to the decline of caribou reproductive success via a trophic mismatch.

Our study provides additional evidence that trophic mismatch could have important consequences on the population dynamics of long-distance migrants by affecting the quality of food supply. This adds to the growing body of evidence that some of the most severe impacts of climate warming on Arctic species may be indirect, through disruptions of the synchrony in the phenology of species at different trophic levels (Miller-Rushing *et al.* 2010). This emphasizes the importance of taking a multi-species food web approach when examining the consequences of environmental change on organisms. In order to fully understand how climate change may affect long-distance migrants, it will be useful to track these species during their entire annual cycle (van Oudenhove *et al.* 2014). By examining how changes in climate on stopover sites and on wintering grounds influences the timing of migration, we could gain a better understanding of which specific constraints are preventing migratory birds from adjusting to the rapid warming on their breeding grounds.

Table 1. Parameters along with sign of the effect, Log-Likelihood value (LL), number of estimated parameters (k), ΔAICc values, AICc weights (ω_i) and conditional r^2 values of the most parsimonious models explaining variation in gosling body mass at 35 days on Bylot Island, NU from 1991 to 1993 and 1995 to 2010 (19 years, $n = 2025$). Goose family ID was used as a random factor in the analysis. Model-averaged parameter estimates are presented along with their standard error (SE).

Model	k	LL	ΔAICc	ω_i	r^2	Parameter	Estimate	SE
-Mismatch +SpringAO -SummerAO -SummerRain	9	-13164	0.00	0.24	0.69	Mismatch	-11.4	1.8
-Mismatch -Mismatch ² +SpringAO -SummerAO -SummerRain	10	-13163	0.23	0.21	0.68	Mismatch ²	-0.37	0.24
-Mismatch +SpringAO -SummerAO -SummerRain +SummerTemp	10	-13164	1.13	0.13	0.68	SpringAO	118.0	26.7
-Mismatch ² +SpringAO -SummerAO -SummerRain	9	-13165	1.30	0.12	0.68	SummerAO	-131.4	45.1
-Mismatch -Mismatch ² +SpringAO -SummerAO -SummerRain +SummerTemp	11	-13163	1.54	0.11	0.68	SummerRain	-1.47	0.52
-Mismatch +SpringAO -SummerAO -SummerRain -SnowCover	10	-13164	1.84	0.09	0.69	SummerTemp	8.16	8.91
-Mismatch +SpringAO -SummerAO -SummerRain -SpringTemp	10	-13164	1.87	0.09	0.69	SnowCover	-1.47	3.54
Null model	3	-13336	331.94	0.00		SpringTemp	-4.1	10.5

Table 2. Parameters along with sign of the effect, Log-Likelihood value (LL), number of estimated parameters (k), ΔAICc values, AICc weights (ω_i) and conditional r^2 values of the most parsimonious models explaining variation in gosling body size at 35 days on Bylot Island, NU from 1991 to 1993 and 1995 to 2010 (19 years, $n = 2019$). Goose family ID was used as a random factor in the analysis. Model-averaged parameter estimates are presented along with their standard error (SE). Body size was obtained from the PC score of head, culmen and tarsus length measurements.

Model	k	LL	ΔAICc	ω_i	r^2	Parameter	Estimate	SE
-Mismatch ² +SpringAO -SummerAO -SummerRain	9	-3328	0.00	0.20	0.65	Mismatch	-0.08	0.02
-Mismatch -Mismatch ² +SpringAO -SummerAO -SummerRain	10	-3328	0.54	0.15	0.66	Mismatch ²	-0.003	0.002
-Mismatch +SpringAO -SummerAO -SummerRain -SnowCover	10	-3328	0.57	0.15	0.66	SpringAO	0.71	0.26
-Mismatch -Mismatch ² +SpringAO -SummerAO -SummerRain -SnowCover	11	-3327	0.68	0.14	0.65	SummerAO	-1.05	0.38
-Mismatch +SpringAO -SummerAO -SummerRain	9	-3329	0.71	0.14	0.67	SummerRain	-0.01	0.001
-Mismatch ² +SpringAO -SummerAO -SummerRain -SnowCover	10	-3328	0.75	0.14	0.65	SnowCover	-0.04	0.03
-Mismatch ² +SpringAO -SummerAO -SummerRain +SummerTemp	10	-3328	1.71	0.08	0.65	SummerTemp	0.04	0.07
Null model	3	-3504	340.05	0.00				

Table 3. Parameters along with sign of the effect, Log-Likelihood value (LL), number of estimated parameters (k), ΔAICc values, AICc weights (ω_i) and conditional r^2 values of the most parsimonious models explaining variations in gosling (a) body mass ($n = 883$) and (b) body size ($n = 887$) in 1991, 1993, 1995, 1996 and 2006 to 2010 (9 years) at 35 days. Goose family ID was used as a random factor in the analysis. Model-averaged parameter estimates are presented along with their standard error (SE). Body size was obtained from the PC score of head, culmen and tarsus length.

(a)

Model	k	LL	ΔAICc	ω_i	r^2	Parameter	Estimate	SE
-Mismatch +SpringAO -SummerRain +SummerTemp	9	-5737	0.00	0.31	0.64	Mismatch	-12.3	2.8
-Mismatch -SummerRain +SummerTemp	8	-5738	0.07	0.30	0.63	SpringAO	61.8	39.3
-Mismatch -SummerRain +SummerTemp -SnowCover	9	-5738	1.34	0.16	0.64	SummerRain	-2.05	0.83
-Mismatch +SpringAO +SummerTemp	10	-5737	1.88	0.12	0.63	SummerTemp	43.8	15.3
-Mismatch -Mismatch ² +SpringAO -SummerRain +SummerTemp	10	-5737	2.02	0.11	0.64	SnowCover	-7.23	6.19
Null model	3	-5799	112.29	0.00				

(b)

Model	k	LL	ΔAICc	ω_i	r^2	Parameter	Estimate	SE
-Mismatch -SummerRain +SummerTemp	8	-1425	0.00	0.40	0.60	Mismatch	-0.06	0.02
-Mismatch -SummerRain +SummerTemp -SnowCover	9	-1425	0.74	0.28	0.60	SpringAO	0.55	0.52
-Mismatch +SpringAO -SummerRain +SummerTemp -SnowCover	10	-1424	1.76	0.17	0.59	SummerRain	-0.01	0.001
-Mismatch +SpringAO -SummerRain +SummerTemp	9	-1425	1.94	0.15	0.60	SummerTemp	0.36	0.12
-Mismatch -SummerRain +NitrogenBiomass	8	-1426	2.07	0.12	0.61	SnowCover	-0.05	0.04
Null model	3	-1485	108.62	0.00		NitrogenBiomass	0.39	0.39

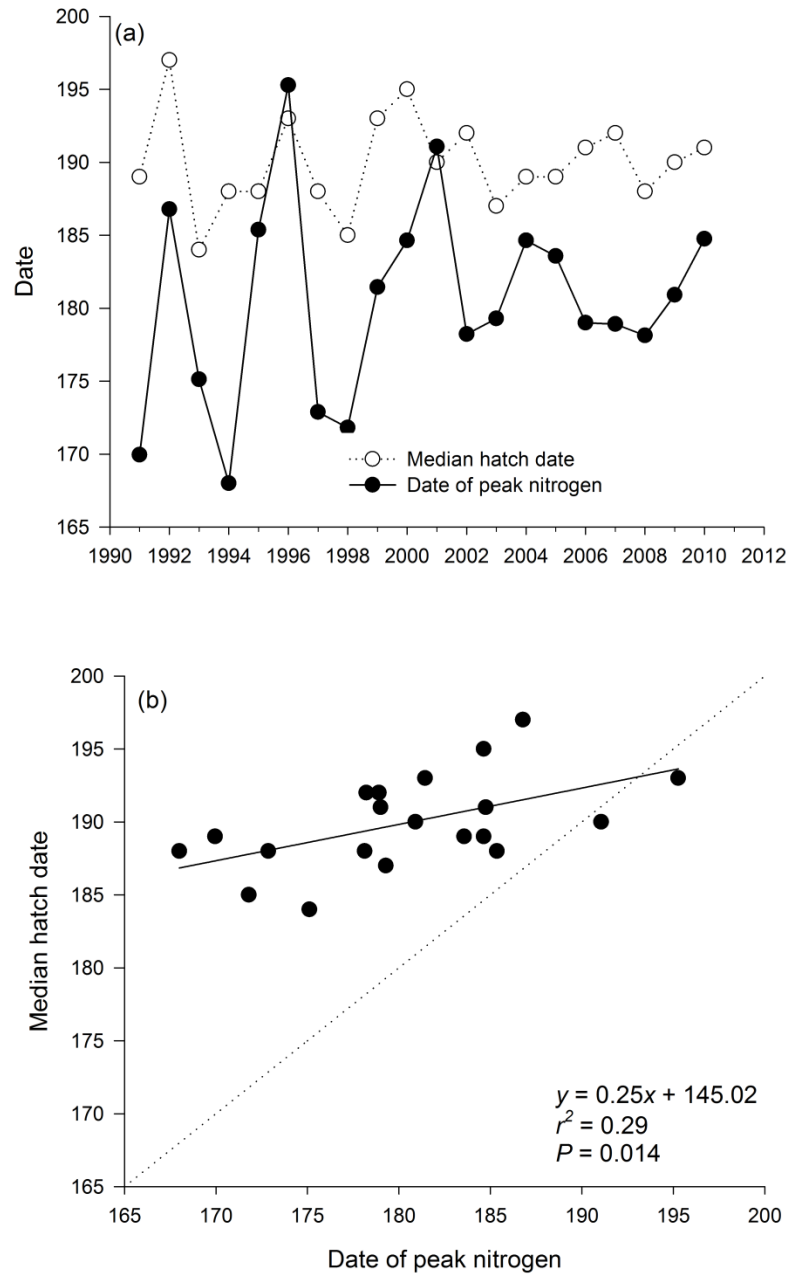


Figure 1. (a) Annual variation in median hatch date of snow goose goslings and date of peak nitrogen concentration in their food plants on Bylot Island, NU, from 1991 to 2010. (b) Linear relationship between median hatch date and date of peak nitrogen concentration in plants. The dotted line represents a 1:1 line. If gosling hatch date perfectly tracked plant phenology, the data points would fall on the dotted line. Dates are in day of the year.

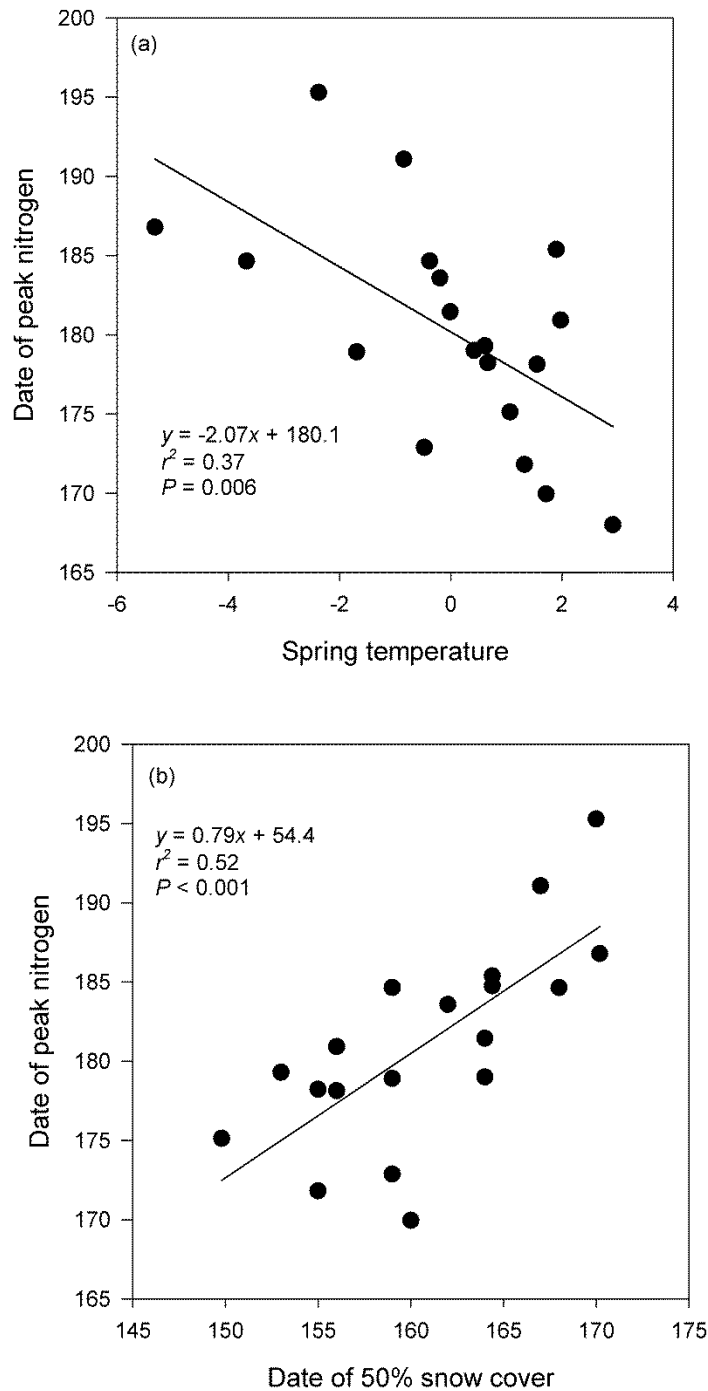


Figure 2. Relationships between date of peak nitrogen concentration in plants and (a) spring temperature and (b) date of 50% snow cover on Bylot Island, NU from 1991 to 2010. Spring Temperature was an index obtained from a principal component analysis combining temperature data (mean, maximum and minimum temperature and sum of thawing degree-days) between 20 May and 20 June. Dates are in day of the year.

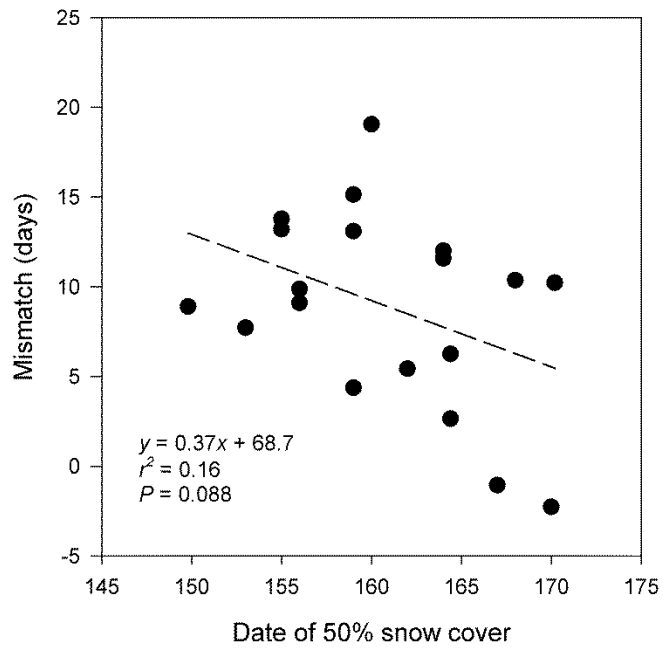


Figure 3. Relationship between mismatch (annual median hatch date of snow goose goslings -date of peak nitrogen concentration) and date of 50% snow cover on Bylot Island, NU, from 1991 to 2010. Dates are in day of the year.

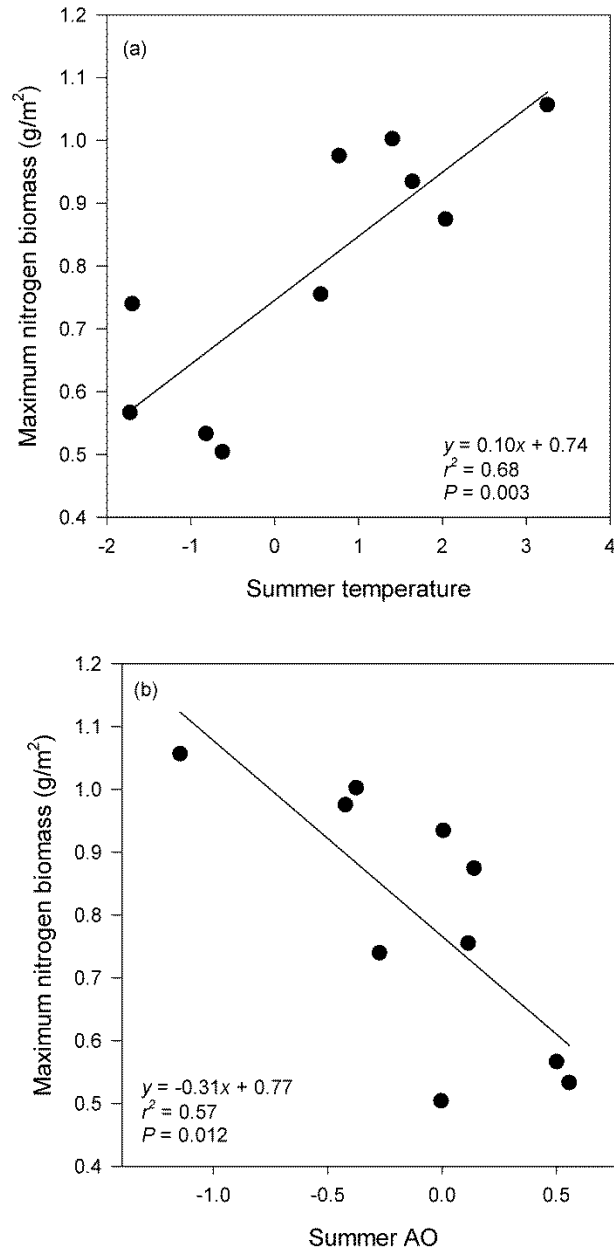


Figure 4. Relationships between maximum nitrogen biomass and (a) summer temperature and (b) summer AO (Arctic Oscillation) on Bylot Island, NU from 1991 to 2010. Summer temperature was an index obtained from a principal component analysis combining temperature data (mean, maximum and minimum temperature and sum of thawing degree-days) between 20 June and 15 August.

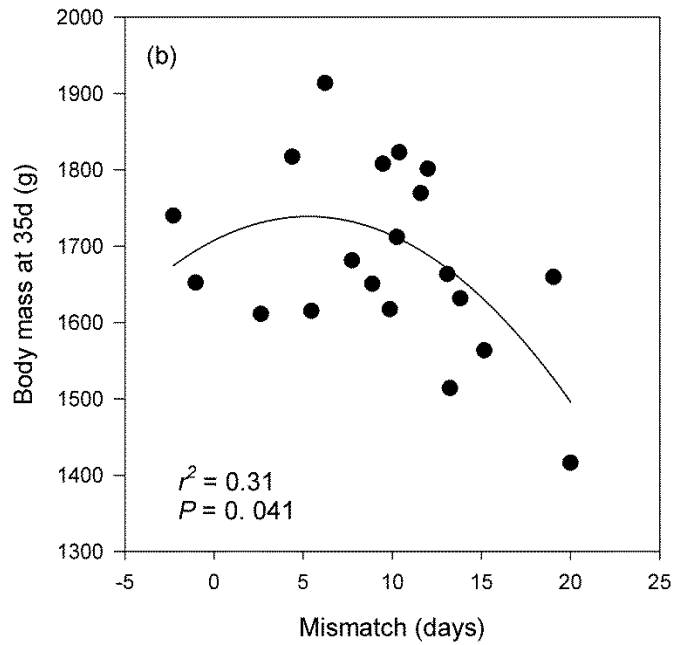
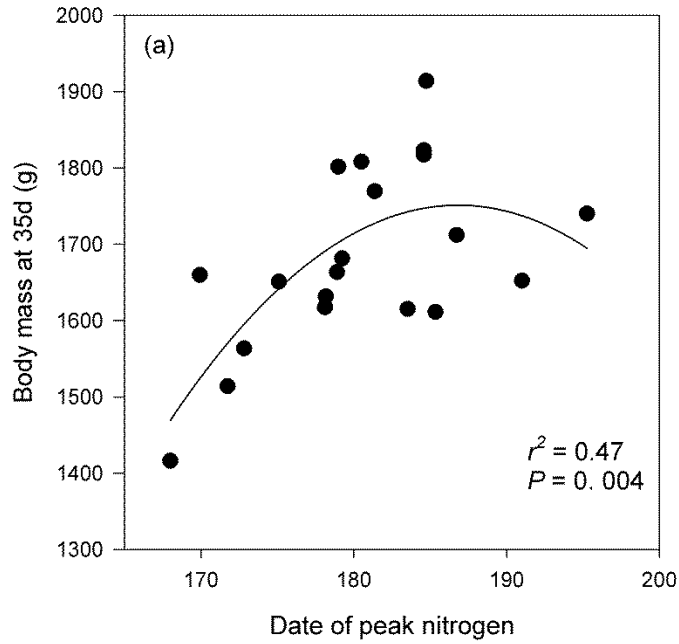


Figure 5. Relationships between annual mean body mass of goslings adjusted at 35 days and (a) date of peak nitrogen concentration in plants and (b) mismatch between median hatch date and date of peak nitrogen concentration in plants on Bylot Island, NU, from 1991 to 2010. Dates are in day of the year.

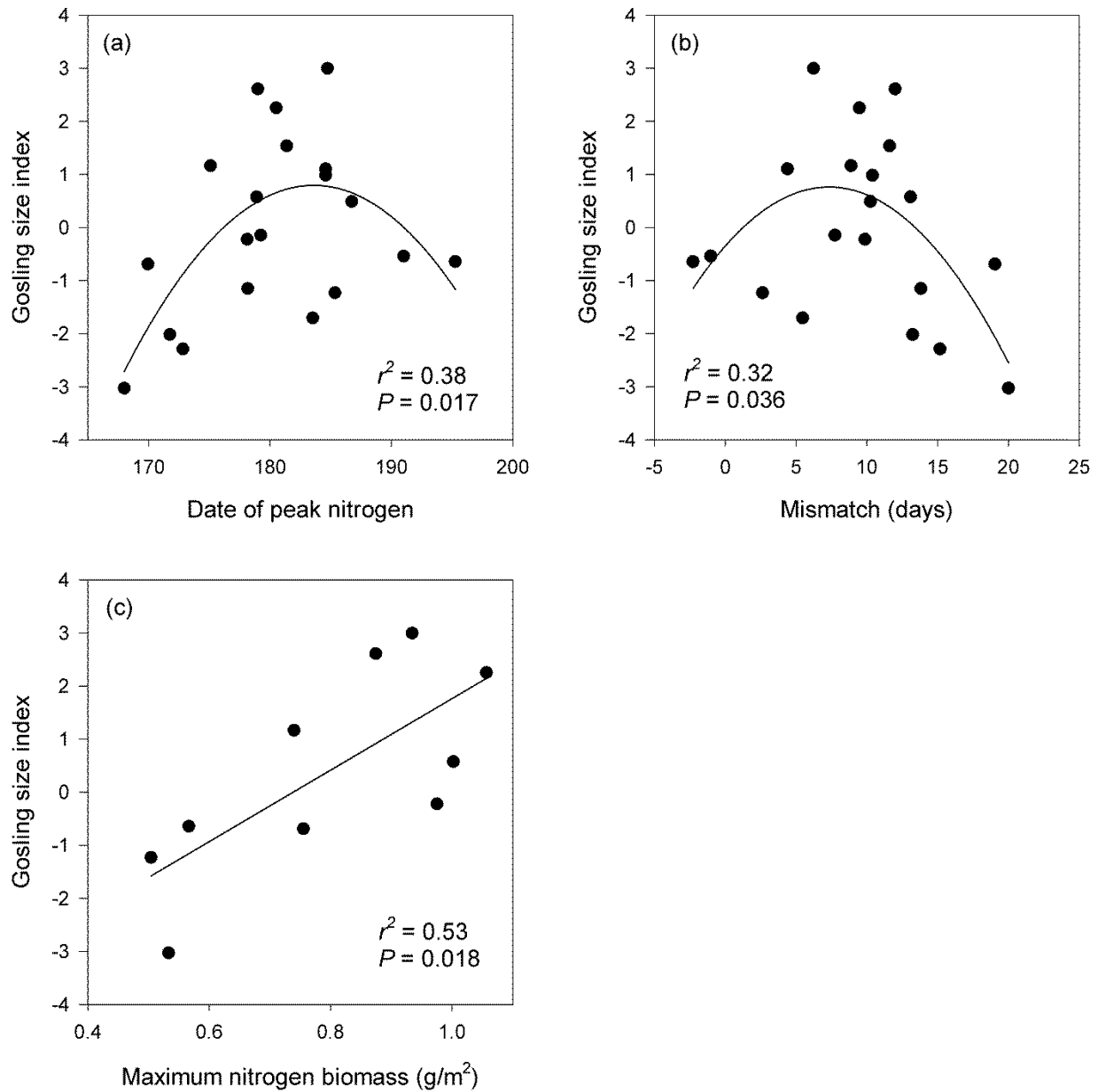


Figure 6. Relationships between annual mean body size (PC score of head, culmen and tarsus length measurements) of goslings adjusted at 35 days and (a) date of peak nitrogen concentration in plants, (b) mismatch between median hatch date and date of peak nitrogen concentration in plants, and (c) annual maximum nitrogen biomass in plants on Bylot Island, NU from 1991 to 2010. Nitrogen biomass values were only available for 10 years over this time period (1991, 1993-1996 and 2006-2010). Dates are in day of the year.

CONCLUSION GÉNÉRALE

Afin de maximiser leur succès reproducteur, les espèces vivant dans des environnements saisonniers doivent se reproduire pendant la période où les conditions environnementales sont les plus favorables (Lepage *et al.* 1998, Post *et al.* 2003, Visser *et al.* 2006). Une bonne synchronie entre la reproduction et le pic d'abondance et/ou de qualité de nourriture est particulièrement importante dans les régions polaires, où les étés courts et les hivers rigoureux signifient que la période propice à la reproduction est très courte. En utilisant une combinaison de manipulations expérimentales, de données à long terme récoltées sur le terrain et d'images satellitaires, j'ai examiné divers aspects de la relation entre les oies et les plantes dont elles s'alimentent dans l'Arctique dans un contexte de changements climatiques. Mes travaux de thèse démontrent l'importance de la synchronie trophique pour la grande oie des neiges et mes résultats permettent de mieux comprendre comment le réchauffement rapide de l'Arctique pourrait menacer cette synchronie.

Impact du réchauffement sur la qualité nutritive des plantes

Dans mon premier chapitre, j'ai réalisé une expérience de réchauffement afin d'évaluer l'influence d'une hausse de la température sur la qualité nutritive des plantes broutées par les oies. Les serres hexagonales ouvertes (« *Open-Top Chambers* », ou OTC) que nous avons utilisées furent une façon simple et efficace de manipuler la température à petite échelle. Bien que tout dispositif de réchauffement passif ait nécessairement des effets non-désirés, comme par exemple une perturbation du vent au niveau du sol ou une modification de la qualité de la lumière qui traverse les parois de la serre, les OTC étaient suffisamment ouvertes pour permettre des précipitations normales et avaient un impact minime sur la fonte de neige au printemps.

Des serres de ce genre ont été utilisées à maintes reprises et à long terme en milieu arctique, subarctique et alpin (Marion *et al.* 1997, Arft *et al.* 1999, Elmendorf *et al.* 2012a), mais peu d'études jusqu'à présent l'ont fait dans l'optique d'examiner directement les changements dans la qualité nutritive des plantes pour les herbivores. Dans les quelques cas où la concentration en nutriments des plantes fut mesurée, il ne semblait pas exister de consensus quant à l'impact d'un réchauffement expérimental sur cette concentration. En effet, selon le site et les espèces végétales étudiées, une augmentation de température avait comme effet

soit d'augmenter, de diminuer, ou de ne pas changer la concentration en azote des plantes (Shaver *et al.* 1986, Chapin *et al.* 1995, Tolvanen & Henry 2001, Jónsdóttir *et al.* 2005), ce qui rendait difficile la tâche de prévoir quel serait l'impact sur les espèces broutées par les oies dans l'Arctique. L'expérience que j'ai effectuée pendant trois étés consécutifs à l'Île Bylot au Nunavut nous a permis de répondre à cette question de façon claire et sans équivoque : une augmentation de la température maximale allant de 2 à 4°C, soit un réchauffement cohérent avec les modèles climatiques globaux les plus conservateurs pour l'Arctique, mène à une accélération du déclin de la concentration en azote des plantes au cours de l'été. La baisse dans la qualité nutritive des plantes pour les oies peut atteindre jusqu'à 14% comparé aux sites témoins et est mesurable dès le début juillet, une période qui correspond à l'éclosion et aux premières semaines de vie des jeunes oies, où les besoins en nutriments sont critiques. Ce chapitre représente donc une étape cruciale et une contribution significative à la question de l'impact potentiel d'une désynchronisation trophique chez les oies, un herbivore important des régions arctiques et subarctiques, dans un contexte de réchauffement climatique.

Développement d'un indice de qualité nutritive avec le NDVI

Dans les régions éloignées comme l'Arctique, les séries de données à long-terme sur la qualité de la végétation pour les herbivores sont plutôt rares. Afin d'obtenir des données sur les changements saisonniers dans la concentration en azote des plantes, tel qu'effectué lors de mon premier chapitre, il est nécessaire d'effectuer un échantillonnage destructif et ce à de nombreuses reprises au cours de l'été. Ce processus peut être coûteux, autant en temps sur le terrain qu'en argent nécessaire pour les analyses en laboratoire de plusieurs centaines d'échantillons de plantes. Dans mon deuxième chapitre, j'ai montré qu'un index calculé à partir d'images satellites, le *Normalized Difference Vegetation Index* (NDVI), pouvait être utilisé pour estimer la date du pic d'azote des plantes sur notre aire d'étude. Bien que le NDVI soit fréquemment utilisé en écologie animale pour évaluer la qualité d'un habitat ou les changements saisonniers dans la croissance de la végétation pour les herbivores, peu d'études ont validé cet index avec des données empiriques récoltées sur le terrain. Puisque

nous avons en main 10 années de données sur la concentration en azote et la biomasse des plantes, nous avons une opportunité unique de le faire.

La relation établie dans le deuxième chapitre a été fort utile dans les analyses du troisième chapitre, mais son utilité ne s'arrête pas là. Même si les changements climatiques de l'Arctique ont lieu à une vitesse presque sans précédent, les espèces animales peuvent être lentes à réagir à ces changements, ce qui nécessite des suivis à long-terme couvrant plusieurs générations. L'index NDVI que nous avons identifié nous permettra d'estimer la date du pic d'azote des plantes au cours des années à venir, et ce à faible coût, ce qui sera d'une grande utilité afin d'évaluer l'impact du réchauffement sur les réseaux trophiques de l'Arctique. De plus, comme mes résultats (Chapitre 3) démontrent que la date du pic d'azote des plantes est un paramètre fortement lié à l'avancement du printemps, tel que mesuré par les températures printanières et la fonte de la neige, notre index pourrait se révéler être une méthode simple et efficace pour estimer la date de début de la croissance végétale à chaque année. Le NDVI est une mesure de la verdure d'un paysage (Tucker & Sellers 1986), ce qui en fait un index qui intègre bien toutes les conditions environnementales printanières importantes pour la croissance des plantes, et par conséquent la période optimale pour la reproduction des herbivores. Dans certains cas, le NDVI pourrait donc être plus approprié que des données climatiques mesurées à l'échelle locale afin d'effectuer des comparaisons interannuelles des conditions environnementales printanières et ainsi déterminer à quel point un printemps est hâtif par rapport à un autre.

La désynchronisation trophique chez les oies

Dans mon troisième chapitre, j'ai montré que les oies, comme d'autres migrateurs de longue-distance, semblent limitées dans leur capacité d'ajustement aux changements globaux rapides qui ont lieu sur leurs aires de nidification. Les dates d'éclosion varient peu d'une année à l'autre malgré des différences importantes dans les conditions climatiques printanières, ce qui pourrait être expliqué par : a) des contraintes encourues au cours de la migration et liées, par exemple, aux conditions climatiques et/ou à l'abondance de nourriture sur les aires d'hivernage et les haltes migratoires, ou b) un manque de plasticité phénotypique nécessaire pour changer leurs patrons annuels de migration et/ou de reproduction, lesquels pourraient

être davantage contrôlés par la photopériode, du moins à court terme. Ces deux hypothèses (la contrainte environnementale et la plasticité phénotypique) ne sont pas nécessairement mutuellement exclusives et pourraient agir en tandem pour faire en sorte que la phénologie de la reproduction des oies demeure relativement invariable. Par exemple, des études menées sur le gobe-mouche noir (*Ficedula hypoleuca*) en Europe ont montré que ces oiseaux peuvent démontrer une certaine flexibilité dans l'initiation de leur migration printanière, mais que cette stratégie est efficace seulement si les conditions environnementales sont favorables pendant tout leur parcours (Both 2010). En contrepartie, chez la même espèce, la date de ponte dans certaines populations n'est pas contrainte par la date d'arrivée sur le site car les oiseaux sont présents sur les aires de reproduction plusieurs semaines avant le début de la ponte. Ces individus n'ont malgré tout pas modifié leurs dates de ponte suivant une augmentation de la température, menant à une désynchronisation trophique avec leur proie sur une période de 15 ans (Goodenough *et al.* 2011). Ce manque de flexibilité est probablement dû à un manque de plasticité phénotypique, mais pourrait également être lié à des contraintes génétiques ou encore à d'autres pressions sélectives allant dans le sens contraire, comme un effet néfaste d'une reproduction trop hâtive sur la survie des adultes (Both 2012). Chez la grande oie des neiges, les travaux de Bêty *et al.* (2004) ont montré que les femelles reproductrices font preuve d'une certaine constance dans leurs dates d'arrivée lors de la migration printanière, mais il serait pertinent de réexaminer ce phénomène à plus long terme, dans un contexte d'adaptation aux changements climatiques.

En plus de montrer que le climat peut modifier la synchronie entre la date de ponte et la date d'un pic de qualité des plantes, j'ai démontré dans ce chapitre qu'un manque de synchronie entre l'éclosion et la date de pic d'azote des plantes a des effets néfastes sur la masse et la taille structurelle des jeunes juste avant l'envol. Plusieurs études portant sur la désynchronisation trophique ont utilisé la mortalité juvénile et/ou la production de jeune comme variables réponses (Visser *et al.* 1998, Post & Forchhammer 2008). Cependant, chez les espèces longévives, les conditions environnementales pendant la période de croissance des jeunes peuvent avoir des effets à long-terme, bien au-delà de la saison de reproduction. Par exemple, des conditions défavorables sur les aires d'élevage des jeunes peuvent affecter la taille adulte des individus produits, ce qui peut ensuite affecter leur succès reproducteur à

long-terme en diminuant leur fécondité (Cooch *et al.* 1991, Sedinger *et al.* 1995). Pour ces raisons, une mesure comme la taille ou la condition corporelle des juvéniles pourrait s'avérer très utile lorsque l'on désire mesurer l'impact d'une désynchronisation trophique sur la dynamique d'une population comme celle de l'oie des neiges.

Message final et apport de la thèse

En conclusion, cette thèse présente des résultats qui appuient l'hypothèse que les oies de l'Arctique sont vulnérables à la désynchronisation trophique suite à des changements dans la phénologie des plantes dont elles s'alimentent. Ces changements risquent d'ailleurs de s'accroître au cours des prochaines décennies dû au réchauffement climatique causé par l'émission de gaz à effets de serre d'origine anthropique (IPCC 2013). Mon étude s'ajoute au nombre croissant de travaux (Saino *et al.* 2011, Visser *et al.* 2011, Both 2012, Kerby *et al.* 2012) qui suggèrent que certains des impacts les plus importants des changements climatiques sur les écosystèmes pourraient être indirects, via les interactions entre les espèces à divers niveaux trophiques.

De plus, ma thèse ouvre la porte à de nouvelles avenues de recherche. Dans mon premier chapitre, j'ai mesuré l'impact d'une hausse de la température sur la qualité nutritive des plantes pour les herbivores. Cependant, ce réchauffement était à court terme seulement : pour chaque année de l'expérience, les plantes subissaient un réchauffement pour une seule saison de croissance. Bien que cette méthode fut utile car elle nous a permis de déterminer que le réchauffement avait un effet consistant lors des trois années, et ce malgré des différences dans les conditions climatiques annuelles, il serait pertinent d'examiner quel serait l'effet d'un réchauffement à plus long-terme. Par exemple, une étude précédente a montré que certains effets du réchauffement sur la croissance des plantes peuvent s'estomper après quelques années, possiblement dû à une déplétion des nutriments (Arft *et al.* 1999). Les serres mises en place lors de mon projet pourront être utilisées à l'avenir pour examiner l'impact d'un réchauffement continu sur plusieurs saisons de croissance.

Afin de mieux comprendre les impacts potentiels à long-terme des changements climatiques sur les oies, il serait également important de déterminer quels facteurs influencent la

flexibilité dans la phénologie de leur migration, de leur arrivée au site de nidification et de leur ponte. Pour ce faire, il faudrait étudier de quelle façon les conditions climatiques rencontrées pendant tout le cycle vital d'un individu affectent le « timing » de la migration, des aires d'hivernage jusqu'au site de nidification. Il pourrait également être utile de comparer la population que nous avons étudiée avec d'autres populations d'oies migratrices afin d'évaluer si des facteurs comme la longueur et la durée de la migration jouent un rôle sur la capacité d'adaptation des oies aux changements dans la phénologie de leur nourriture.

À l'aide d'un suivi à long-terme d'individus marqués, il serait également possible d'évaluer la flexibilité individuelle dans les dates de pontes. Si certains individus sont plus flexibles que d'autres dans leurs dates de pontes, on pourrait imaginer que ceux-ci auraient tendance à être mieux synchronisés avec la phénologie des plantes d'une année à l'autre comparativement à la moyenne de la population, et que les jeunes produits par ces individus plus flexibles seraient en moyenne plus gros à la fin de l'été.

Les populations d'oies à l'échelle globale ne sont pas en danger d'extinction : au contraire, la plupart des populations d'oies en Amérique du Nord ont connu une augmentation exponentielle au cours des 60 dernières années (Menu *et al.* 2002). Cependant, il est possible que la population de la grande oie des neiges soit en train de se stabiliser, et cette diminution du taux de croissance a été attribué principalement à des mesures de chasses instaurées sur les aires d'hivernage et les haltes migratoire (Reed & Calvert 2006). Il reste que même pour des espèces qui ne semblent pas menacée dans l'immédiat, il est nécessaire de bien comprendre les mécanismes qui peuvent réguler ou affecter leur démographie. En acquérant une meilleure compréhension du rôle potentiel des changements climatiques sur les espèces, il devient possible de prendre des décisions plus éclairées en ce qui concerne la gestion des ressources fauniques, ce qui est d'autant plus important chez une espèce chassée comme l'oie des neiges.

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ANNEXE 1

L'indice de végétation par différence normalisée *(Normalized Difference Vegetation Index)*

L'indice de végétation par différence normalisée

Au cours des 20 dernières années, de plus en plus d'écologistes se sont tournés vers la télédétection afin de pouvoir mesurer les caractéristiques de la surface de la planète et ainsi évaluer les propriétés physiques et biologiques des écosystèmes (Kerr & Ostrovsky 2003). Certains satellites utilisés en télédétection sont équipés de senseurs qui mesurent les ondes de lumières absorbées et réfléchies par la végétation, et sont donc utilisés pour calculer des indices reliés à la végétation.

L'indice de végétation le mieux connu et le plus utilisé est sans doute l'indice de végétation par différence normalisée (« *Normalized Difference Vegetation Index* », ou NDVI), un indice numérique qui utilise les proportions de lumière reflétées dans les bandes visibles et proche-infrarouge du spectre électromagnétique (Rouse Jr *et al.* 1974) et calculé selon l'équation suivante :

$$NDVI = \frac{(Proche\ infrarouge - Visible)}{(Proche\ infrarouge + Visible)}$$

Généralement, la végétation saine (i.e. verte) absorbe la majorité de la lumière visible qui la touche, mais reflète une grande proportion des rayons dans le proche-infrarouge, ce qui lui donne des valeurs de NDVI élevées (Knipling 1970, Jensen 2007). Lorsque la végétation s'assèche ou meurt en fin de saison, ses propriétés d'absorption et de réflectance changent, avec pour effet de diminuer les valeurs de NDVI (Jensen 2007; Annexe 1, Figure 1). Les sols nus, la neige et le couvert nuageux ont quant à eux des valeurs de NDVI proches de zéro (Neigh *et al.* 2008).

Ces différences dans l'absorption de la lumière font du NDVI une bonne mesure de la verdure d'un paysage. Le NDVI a été corrélé à l'activité photosynthétique des plantes ainsi qu'à la production primaire nette, et ce à une variété d'échelles spatiales et temporelles (Reed *et al.* 1994, Paruelo *et al.* 1997, Zhou *et al.* 2001, Wang *et al.* 2004). Cet indice devient alors très utile pour cartographier la végétation, évaluer l'impact de perturbations sur les paysages, ou mesurer le changement des saisons (Pettorelli *et al.* 2005).

Le NDVI a cependant certaines limites : les valeurs ont tendance à se saturer lorsque la végétation est très dense (Huete 1988), et peut être contaminé par le couvert nuageux, la fumée ou la présence de polluants dans l'atmosphère (Pettorelli *et al.* 2005). De plus, la plupart des jeux de données sur le NDVI ont une résolution temporelle de 10 à 15 jours, et une résolution spatiale allant de 250 m à 8 km, ce qui peut limiter la précision des mesures (Pettorelli *et al.* 2011).

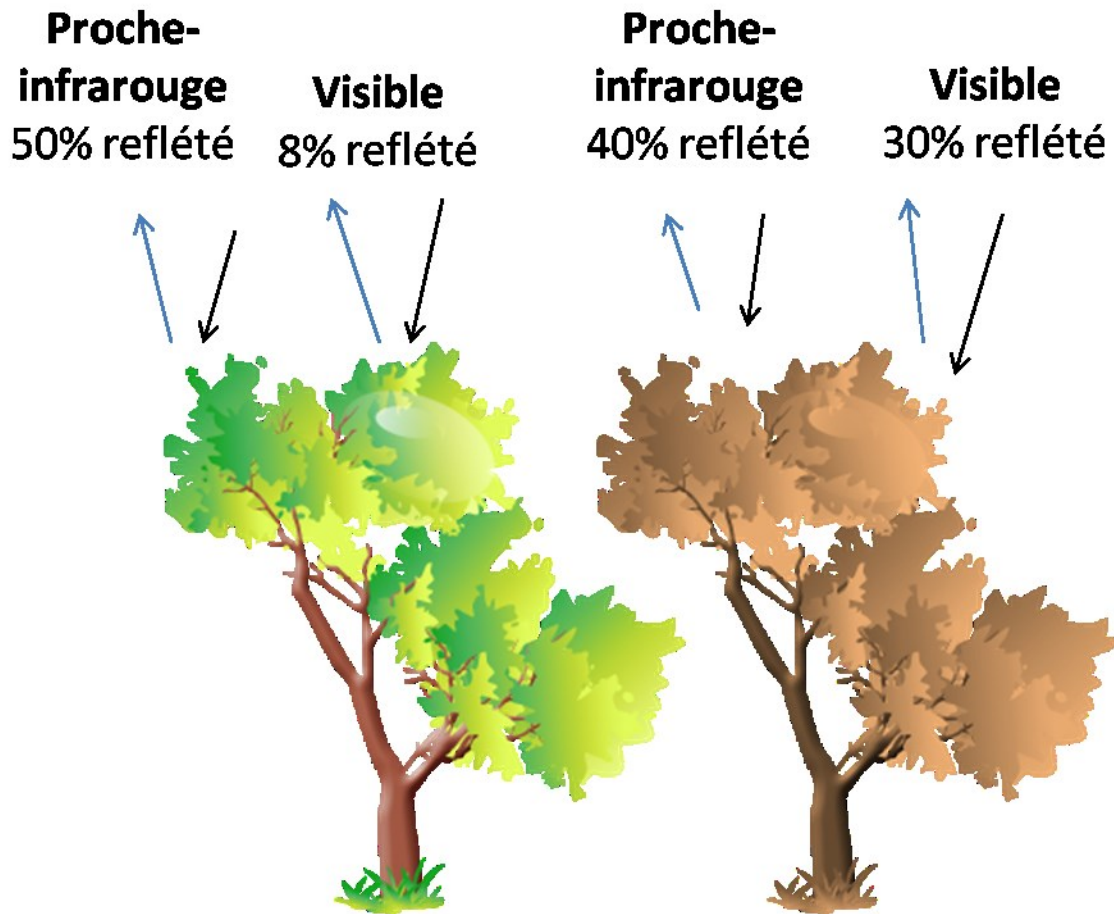


Figure 1. Calcul de l'indice de végétation par différence normalisée (NDVI). La végétation verte (à gauche) absorbe la majorité de la lumière visible, mais reflète une grande proportion de la lumière dans le proche-infrarouge, ce qui lui donne un indice NDVI élevé (0.72) La végétation sénescence, morte ou éparse (à droite) reflète une plus grande proportion de la lumière visible et une plus faible proportion de la lumière dans le proche-infrarouge comparativement à la végétation verte, ce qui lui donne un indice NDVI plus faible (0.14).

ANNEXE 2

Matériel supplémentaire du Chapitre 1

Table 1. Synthesis of the results of previous studies that examined the effects of warming experiments on nitrogen content of various vascular plants in arctic and alpine sites.

Source	Duration	Study site	Species	Effect of warming on nitrogen content
Shaver <i>et al.</i> 1986	3 years	Toolik Lake, Alaska	<i>Eriophorum vaginatum</i>	Negative; warming treatment caused a significant decrease in nitrogen concentration of leaf blades.
Chapin <i>et al.</i> 1995	3 years and 9 years	Toolik Lake, Alaska	<i>Eriophorum vaginatum</i> <i>Carex bigelowii</i> <i>Betula nana</i> <i>Rubus chamaemorus</i> <i>Ledum palustre</i> <i>Vaccinium vitis-idaea</i>	Positive; nitrogen availability tended to increase with elevated temperatures.
Welker <i>et al.</i> 1997	5-15 years	Niwot Ridge, Colorado Toolik Lake, Alaska Svalbard, Norway	<i>Dryas octopetala</i>	Negative; leaf nitrogen was lowered under warmer conditions.
Jonasson <i>et al.</i> 1999	5 years	Abisko, Sweden	All species present (sorted into deciduous shrubs, evergreen shrubs, forbs and graminoids, mosses)	Variable; warming tended to reduce nitrogen concentration in aboveground parts, but this varied by plant group & habitat sampled.

Source	Duration	Study site	Species	Effect of warming on nitrogen content
Tolvanen & Henry 2001	1 year	Alexandra Fjord, Canada	<i>Cassiope tetragona</i> <i>Dryas integrifolia</i> <i>Salix arctica</i> <i>Oxyria digyna</i> <i>Carex stans</i>	Negative or no effect; nitrogen concentration decreased with warming for <i>C. tetragona</i> , <i>D. integrifolia</i> and <i>S. arctica</i> , but no effect of warming on <i>O. digyna</i> and <i>Carex stans</i> .
Weih & Karlsson 2001	1 year	Abisko, Sweden	<i>Betula pubescens</i>	Negative; leaf nitrogen content decreased with warming.
Lenart <i>et al.</i> 2002	2 years	Wrangell mountain, Alaska	All vascular plants present (sorted into forbs, graminoids and prostrate willows)	Negative or no effect; nitrogen concentration of graminoids and forbs tended to be lower in warmed plots, but no consistent effect between years & sampling periods.
Welker <i>et al.</i> 2005	7 years	Toolik Lake, Alaska	All vascular plants present (sorted into deciduous shrubs, evergreen shrubs and graminoids)	Positive or no effect; warming resulted in higher leaf nitrogen in moist tundra sites, but no impact of warming on leaf nitrogen in dry tundra sites.
Jonsdottir <i>et al.</i> 2005a	5 years	Latnjajaure, Sweden	<i>Carex bigelowii</i>	Negative; green tissue concentration of nitrogen was lower in warmed plots.

Source	Duration	Study site	Species	Effect of warming on nitrogen content
Aerts <i>et al.</i> 2009	5 years	Abisko, Sweden	<i>Empetrum hermaphroditum</i> <i>Andromeda polifolia</i> <i>Betula nana</i> <i>Vaccinium uliginosum</i> <i>Calamagrostis lapponica</i> <i>Rubus chamaemorus</i>	Negative or no effect; leaf nitrogen concentrations decreased with warming in the grass and forb species, but there was little to no effect for the woody evergreen and deciduous species.
Natali <i>et al.</i> 2012	2 years	Eight Mile Lake, Alaska	<i>Betula nana</i> <i>Carex bigelowii</i> <i>Eriophorum vaginatum</i> <i>Rhododendron subarcticum</i> <i>Rubus chamaemorus</i> <i>Vaccinium uliginosum</i>	No effect; summer warming had no detected effect on canopy nitrogen.

ANNEXE 3

Matériel supplémentaire du Chapitre 3

Table 1. Results of the principal component analyses (PCA) of four temperature variables during Spring (20 May-20 June) and Summer (20 June-15 Aug) on Bylot Island, Nunavut, Canada. (a) Eigenvalue and percentage of variation explained by each factor, and b) loading of each variable on the first axis of the PCA.

(a)

<i>Factor</i>	Spring		Summer	
	<i>Eigenvalue</i>	%	<i>Eigenvalue</i>	%
		<i>variation</i>		<i>variation</i>
1	2.83	71.2	2.95	73.7
2	0.63	15.7	0.99	24.8
3	0.49	12.2	0.05	1.2
4	0.04	0.9	0.01	0.3

(b)

<i>Variable</i>	Factor loading	
	<i>Spring</i>	<i>Summer</i>
Average Temperature	0.98	0.99
Sum of thawing degree-days	0.80	0.99
Minimum Temperature	0.86	0.69
Maximum Temperature	0.71	0.71

Table 2. Correlation coefficients (Pearson's r values) among the climatic and plant nitrogen (N) variables used in the analyses. $n = 19-20$ for all variables, except maximum nitrogen biomass and maximum nitrogen concentration ($n = 10$). Highly correlated variables (i.e. $r > 0.7$) are shown in bold.

	Spring Temp*	Summer Temp*	Spring Rain	Summer Rain	Snow Cover**	Spring AO	Summer AO	Date of peak N	Mismatch	Max N biomass	Max N concentration
Spring Temp*	1	0.25	-0.10	0.13	-0.66	-0.22	-0.07	-0.58	0.27	-0.13	0.03
Summer Temp*		1	-0.09	-0.06	-0.02	0.12	-0.26	-0.03	0.01	0.82	0.02
Spring Rain			1	0.01	0.08	-0.26	0.16	-0.03	0.02	-0.05	0.47
Summer Rain				1	-0.08	-0.01	-0.12	0.11	-0.29	0.18	-0.21
Snow Cover**					1	0.57	0.42	0.72	-0.40	-0.44	-0.24
Spring AO						1	0.34	0.17	0.10	-0.26	0.40
Summer AO							1	0.07	-0.02	-0.75	0.13
Date of peak N								1	-0.89	-0.07	-0.58
Mismatch									1	0.17	0.66
Max N biomass										1	0.03
Max N concentration											1

* Scores from a principal component analysis combining average, minimum and maximum temperature and cumulative thawing degree-days (see Annexe 3, Table 1).

**Measured as date at which snow cover reached 50%.

Table 3. Results of the principal component analysis (PCA) of three body size measurements (culmen, head and tarsus length) of goslings captured on Bylot Island, Nunavut, Canada. a) eigenvalue and percentage of variation explained by each factor, and b) loading of each variable on the first axis of the PCA.

(a)			(b)	
<i>Factor</i>	<i>Eigenvalue</i>	<i>% variation</i>	<i>Variable</i>	<i>Factor Loading</i>
1	2.78	92.7	Head length	0.96
2	1.15	4.9	Culmen length	0.97
3	0.07	2.4	Tarsus length	0.90