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**EFFET DES FACTEURS CLIMATIQUES SUR LA
PHÉNOLOGIE ET LE SUCCÈS DE LA REPRODUCTION
CHEZ LA GRANDE OIE DES NEIGES (*CHEN
CAERULESCENS ATLANTICA*) À L'ÎLE BYLOT, NUNAVUT**

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RÉSUMÉ

Nous avons étudié l'impact des variations climatiques sur la phénologie et le succès de la reproduction chez la Grande Oie des neiges (*Chen caerulescens atlantica*), une espèce nichant en Arctique où le réchauffement climatique est particulièrement prononcé. Nos analyses ont été effectuées sur la base d'une banque de données climatiques et biologiques de 16 ans (1989-2004) récoltées sur l'Île Bylot dans l'Arctique canadien. La variation individuelle de la phénologie de la reproduction était expliquée à environ 50% par des facteurs climatiques printaniers, principalement par la température de l'air et la couverture neigeuse. Au contraire, le succès reproducteur jusqu'à l'envol était davantage influencé par les valeurs extrêmes du climat régional (*i.e.* l'indice de l'OA) au cours de l'été que par les conditions climatiques printanières. La taille et la masse des oisons peu avant l'envol étaient généralement réduites par des températures printanières élevées, vraisemblablement parce que ces conditions diminuaient la synchronisation entre la date d'éclosion des oisons et le pic dans la qualité maximale des plantes en début de saison. Ce décalage est survenu puisque la phénologie des plantes est davantage avancée que celle des oies lors des printemps chauds. Nous concluons que le réchauffement climatique devrait avancer la phénologie de la reproduction des oies, mais que des températures printanières élevées et des valeurs extrêmes de l'indice estival de l'OA pourraient diminuer leur succès reproducteur.

ABSTRACT

We studied the impact of climatic variations on the breeding phenology and the reproductive success of the Greater Snow Goose (*Chen caerulescens atlantica*), a migratory bird breeding in the Arctic where climate warming is most pronounced. Our analysis used a 16-year climatic and biologic database (1989-2004) collected on Bylot Island in the Canadian Arctic. About 50% of the individual variation in reproductive phenology was explained by climatic factors in spring, mostly air temperature and snow cover. In contrast, breeding success up to fledging was more influenced by extreme values of the regional climate (*i.e.* the AO index) during the summer than by the spring climatic conditions. Goslings size and mass near fledging were generally reduced in years with high spring temperatures, likely because these conditions reduced the synchronization between goslings hatching date and the early season peak in plant quality. This mismatch occurred because the advancement in phenology during warm springs is more pronounced in plants than in geese. We conclude that climate warming should advance the reproductive phenology of geese, but that high spring temperatures and extreme values of the summer AO index may decrease their reproductive success.

AVANT-PROPOS

Ce mémoire est constitué de quatre parties. D'abord, l'introduction générale donne un bref aperçu des changements climatiques actuels et prédits ainsi que de ses répercussions sur le monde animal et végétal, particulièrement sur les communautés arctiques et les oiseaux migrateurs. Ensuite, l'importance du climat chez les oies est expliquée et les objectifs et hypothèses de l'étude sont présentés. Le corps du mémoire est constitué de deux chapitres rédigés en anglais sous forme d'insertion d'articles dans l'éventualité d'une publication. Je suis l'auteure principale de ces articles et mon directeur de maîtrise Gilles Gauthier en est le co-auteur. Le premier chapitre est celui qui a le plus de contenu, et il porte sur l'influence des variations climatiques au niveau local et régional sur la phénologie et le succès de la reproduction chez la Grande Oie des neiges, dans le but d'anticiper l'impact des changements climatiques sur ces variables. Le second chapitre se concentre sur l'effet des variations climatiques sur un aspect particulier de la phénologie, c'est-à-dire sur la synchronisation de la reproduction des oies par rapport à la phénologie des plantes consommées par les oisons. La quatrième partie du mémoire est consacrée à la conclusion générale qui rappelle les principaux résultats du mémoire et suggère des avenues de recherche intéressantes suite à la présente étude.

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INTRODUCTION GÉNÉRALE

Au cours des dernières décennies, des changements climatiques, dont plusieurs attribuent une part importante à des effets anthropiques, ont été observés à l'échelle de la planète (Balling, 1997; Walker, 1997). Ces changements se traduisent principalement par une élévation de la température moyenne annuelle du globe qui a déjà augmenté de 0.6°C au cours du vingtième siècle. Une augmentation de 1.4 à 5.8°C de cette température moyenne globale est prévue au cours de la période s'étendant de 1990 à 2100 (IPCC, 2001). De plus, le réchauffement devrait être plus fort dans les régions arctiques, particulièrement en hiver et au printemps. En général, un accroissement des précipitations est également prévu, mais avec moins de certitude que pour le réchauffement climatique. En Arctique, une hausse de 8% des précipitations a déjà eu lieu au cours du dernier siècle, et l'on prévoit une croissance d'environ 20% des précipitations annuelles, principalement sous forme de pluie, avant la fin du siècle (ACIA, 2004). Des changements au niveau de l'étendue de la glace de mer, de la couverture de neige et de la distribution de la végétation y sont déjà observés (Moritz *et al.*, 2002). Comme la structure des communautés est plus étroitement liée aux facteurs climatiques à proximité des pôles qu'aux tropiques, les organismes nordiques pourraient être d'autant plus influencés par les changements climatiques (Hansell *et al.*, 1998).

La détection des changements à long terme est rendue difficile par des phénomènes climatiques cycliques comme El Niño et l'ONA (Oscillation Nord-Atlantique; Hurrell, 2000; Ottersen, 2001). En effet, plusieurs considèrent que les fluctuations de ces phénomènes climatiques agissant à grande échelle peuvent être responsables d'une partie des changements climatiques récents observés et inversement, les changements globaux pourraient contribuer à accentuer l'amplitude de ces phénomènes cycliques ou encore à les dérégler (Hurrell, 2000). Ces «téléconnexions» se définissent comme étant des variations simultanées des conditions météorologiques prévalant sur différentes régions éloignées les unes des autres, mais toutes reliées entre elles (Hurrell, 2000). Par exemple, l'indice de l'ONA représente une fluctuation dans les pressions des masses atmosphériques entre l'Islande et les Açores, ce qui rend ce phénomène climatique indirectement responsable d'une part importante des variations interannuelles des précipitations et des températures hivernales dans une partie de l'hémisphère Nord (Hurrell, 1995, 2000).

Une autre téléconnexion, l'Oscillation Arctique (OA), est semblable à l'ONA mais elle serait de plus grande envergure que l'ONA qui serait en fait une manifestation régionale de l'OA (Hurrell, 2000). L'indice de l'OA représente des fluctuations de pressions entre les latitudes polaires et moyennes (Thompson & Wallace, 1998) et expliquerait une part importante de la variabilité du climat arctique (Rigor *et al.*, 2000; Aanes *et al.*, 2002). Depuis les trois dernières décennies, les indices de l'ONA et de l'OA sont restés anormalement élevés (Hurrell, 1995, 2000). La valeur de l'indice est proportionnelle à la différence de pression atmosphérique entre les régions de haute et de basse pressions. Par exemple, un indice élevé signifie que cette différence est importante, c'est-à-dire que tant la haute pression située aux latitudes moyennes que la dépression située au niveau de la région du Pôle Nord sont prononcées. Ce phénomène génère des effets climatiques différents selon les régions concernées. Par exemple, un indice élevé de l'ONA est associé à des hivers et à des printemps plus chauds que la normale en Europe, ce qui pourrait expliquer le réchauffement climatique actuellement observé. En effet, lorsque les indices de l'ONA et de l'OA sont élevés, la pression atmosphérique au-dessus de l'Atlantique est plus élevée que la normale, entraînant ainsi une augmentation de la force des vents d'ouest passant sur l'Atlantique Nord, déplaçant ainsi de l'air plus chaud et humide au-dessus du nord de l'Europe. De plus, ces vents importants limitent le déplacement d'air froid en provenance du Nord au-dessus de la région Nord-Ouest de l'Atlantique, refroidissant par le fait même cette région et conservant ainsi de l'air chaud au-dessus des États-Unis (Hurrell, 1995; 2000; JISAO, 2004). Plusieurs études ont révélé l'influence de l'ONA, et plus récemment celle de l'OA sur les populations animales et végétales (Post & Stenseth, 1998, 1999; Mysterud *et al.*, 2001; Ottersen *et al.*, 2001; Aanes *et al.*, 2002; Hüppop & Hüppop, 2003; Almaraz & Amat, 2004; Welker *et al.*, 2005).

Impacts des changements climatiques sur les communautés arctiques

Plusieurs conséquences du réchauffement climatique sur les communautés arctiques ont été notées ou proposées. Par exemple, la glace de mer a déjà diminué de 5% au cours des 20 dernières années et cette tendance devrait se poursuivre. Par conséquent, les populations d'ours polaires (*Ursus maritimus*) risquent de diminuer face à une fonte importante des banquises dont ils se servent pour chasser les phoques, ainsi que celle des renards arctiques

(*Alopex lagopus*) qui se nourrissent en partie des restes laissés par les ours en hiver (Hansell *et al.*, 1998; Kerr, 2002). De plus, une augmentation du niveau de la mer découlant d'une fonte partielle des banquises pourrait modifier considérablement la végétation côtière et présenter aussi un danger d'infiltration d'eau salée dans les marais d'eau douce. Ceci risquerait de perturber les populations d'herbivores qui se nourrissent dans ces communautés végétales (Boyd & Madsen, 1997; Hansell *et al.*, 1998).

Un envahissement du nord par des plantes du sud face à la remontée des isothermes vers le nord pourrait menacer la végétation du Haut-Arctique canadien et faire disparaître des variétés tolérantes à la sécheresse et au froid, diminuant ainsi globalement la biodiversité et altérant la disponibilité de nourriture pour les herbivores. De plus, selon Hansell *et al.* (1998), le réchauffement aura des effets importants sur la distribution du pergélisol et la couverture de glace au sol, notamment en déstabilisant la structure des sols et altérant ainsi les communautés végétales de la toundra. Les populations d'herbivores seront probablement les plus influencées par les variations au niveau de la qualité et de la quantité des plantes résultant des changements climatiques (Gauthier *et al.*, 1996). Par exemple, une augmentation de la température est susceptible de réduire la disponibilité en nourriture du caribou (*Rangifer tarandus*; Hansell *et al.*, 1998). En effet, sous l'influence d'un réchauffement climatique expérimental (Chapin *et al.*, 1995), les inflorescences de sept espèces de plantes arctiques importantes dans l'alimentation du caribou pendant la lactation (White & Trudel, 1980) ont disparu ou ont été réduites. Les lichens dont ces animaux se nourrissent à l'hiver ont été également réduits.

Impact des changements climatiques sur la phénologie

Plusieurs études ont démontré un changement dans la phénologie chez une grande variété d'espèces et de populations, principalement en réaction au réchauffement climatique déjà amorcé (Parmesan & Yohe, 2003). La phénologie représente l'initiation des différentes activités essentielles du cycle vital des espèces végétales et animales en fonction des saisons (Berteaux *et al.*, 2004). Une revue d'études réalisées sur 143 espèces animales et végétales révèle que la phénologie de leurs activités printanières a été devancée d'environ

5.1 jours en moyenne au cours des 50 dernières années (Root *et al.*, 2003). De plus, la réponse phénologique des espèces vivant dans les régions de haute latitude, où le réchauffement a été particulièrement important (ACIA, 2004), est plus grande que celle survenue aux basses latitudes (Root *et al.*, 2003).

Les différentes étapes de la phénologie des plantes comme le bourgeonnement et la floraison seront plus hâtives au printemps si la tendance au réchauffement se poursuit (Wookey *et al.*, 1993; Sparks & Carey, 1995; Arft *et al.*, 1999; Hollister *et al.*, 2005). De plus, les résultats obtenus par Arft *et al.* (1999) lors du réchauffement expérimental de 13 sites arctiques et alpins dans le cadre de l'*International Tundra Experiment* indiquent que les plantes herbacées ont répondu à une élévation de la température par une croissance plus forte que celle des plantes ligneuses. Cependant, il est possible que la croissance soit limitée par la faible disponibilité en nutriments dans le sol, ou par les différentes adaptations des plantes arctiques qui pourraient répondre à une augmentation de température en favorisant la reproduction aux dépens d'une croissance végétative plus élevée.

Selon Root *et al.* (2003), la classe aviaire compte parmi les groupes ayant subi les effets les plus importants des changements climatiques. Chez les oiseaux migrateurs, le moment de l'initiation du cycle reproducteur par rapport aux conditions environnementales est déterminant pour leur succès subséquent. Par conséquent, ils doivent être en mesure de s'adapter rapidement lorsque les conditions changent. Plusieurs études ont démontré un avancement de la date d'arrivée au site de nidification et de la date de ponte, ainsi qu'une expansion vers le nord chez plusieurs oiseaux migrateurs au cours des dernières décennies (Richardson, 1990; Crick *et al.*, 1997; Tryjanowski *et al.*, 2002; Dunn, 2004). L'indice de l'ONA, associé à des températures printanières plus élevées, est également associé à un avancement de la phénologie chez quelques espèces aviaires européennes (Przybylo *et al.*, 2000; Hüppop & Hüppop, 2003; Frederiksen *et al.*, 2004).

Les changements dans la phénologie des différentes espèces peuvent progresser à un rythme différent, surtout entre les niveaux trophiques. D'ailleurs, un déphasage entre la

phénologie de certaines populations d'oiseaux et la phénologie des proies consommées par les jeunes pendant l'élevage a déjà été observé en Europe (Visser *et al.*, 1998; Thomas *et al.*, 2001; Sanz *et al.*, 2003). Par exemple, une population de gobemouches noirs (*Ficedula hypoleuca*) des Pays-Bas a devancé sa date de ponte d'environ 10 jours en réponse à une augmentation de température pour la période 1980 à 2000. Puisque cette espèce arrive au site de reproduction avant la date optimale de ponte, elle peut s'ajuster dans une certaine mesure aux variations naturelles de l'arrivée du printemps (Both & Visser, 2001). Cependant, cet ajustement s'est avéré insuffisant pour lui permettre de s'adapter au printemps hâtif observé et une arrivée prématurée au site de nidification aurait été nécessaire pour lui permettre d'exploiter de façon optimale le pic d'abondance des insectes qu'elle consomme. Les individus n'ont donc pas pu modifier cette date suffisamment pour s'ajuster totalement au printemps hâtif parce que la date d'arrivée est surtout influencée par la variation de la longueur du jour au site d'hivernage, laquelle n'est pas affectée par les changements climatiques. En effet, la photopériode détermine la fenêtre de temps au cours de laquelle la migration aura lieu (Gwinner, 1996). Les facteurs météorologiques n'influencent pas la photopériode, mais les conditions prévalant dans l'environnement de l'animal, telles la température et la disponibilité de nourriture, vont déterminer le moment précis du départ à l'intérieur de cette fenêtre de temps (Coppack & Pulido, 2004). Toutefois, chez les grands migrateurs, la réponse aux conditions environnementales est en général plus limitée car ces espèces seraient sous un contrôle endogène encore plus important (Both & Visser, 2001).

Relation entre les variations climatiques et la reproduction des oiseaux arctiques

Les oiseaux migrateurs et les milieux arctiques étant particulièrement touchés par les changements climatiques, le succès reproducteur des oiseaux migrateurs nichant en Arctique risque donc d'être tout spécialement affecté. Ainsi, il a été observé que la croissance des poussins de Bécasseaux Cocorli (*Calidris ferruginea*) est réduite lorsque les températures sont basses et les vents élevés dans l'Arctique sibérien (Schekkerman *et al.*, 1998). De plus, une étude a démontré que l'initiation de la ponte est retardée et le succès reproducteur diminué suite à une fonte des neiges tardive et à des températures printanières

froides chez une population de Lagopèdes des saules (*Lagopus lagopus*) sub-arctique nichant à La Pérouse Bay (Martin & Wiebe, 2004).

Parmi les oiseaux nicheurs en Arctique, les oies comptent parmi les plus gros oiseaux et sont d'importants boteurs des milieux humides arctiques (Gauthier *et al.*, 1996). Elles ne disposent que de peu de temps pour compléter leur cycle reproducteur et ainsi produire des jeunes assez gros pour effectuer la longue migration automnale à la fin du court été arctique.

La phénologie de la reproduction chez les oies

La Grande Oie des neiges (*Chen caerulescens atlantica*) est une des espèces d'oies nichant le plus au nord en Amérique du Nord (Choinière & Gauthier, 1995). L'Île Bylot, située dans le Haut-Arctique canadien, supporte une des plus importantes colonies de Grandes Oies des neiges au monde (Reed *et al.*, 2002).

Les conditions environnementales (couverture de neige principalement) prévalant sur l'aire de reproduction au printemps sont déterminantes pour la disponibilité de la nourriture, ce qui va influencer la date et la taille de ponte des femelles (Cooke *et al.*, 1990; Bêty *et al.*, 2003). En effet, les oies doivent acquérir suffisamment de nutriments afin de concevoir les œufs, et les femelles obtiennent en partie les nutriments nécessaires à la formation des œufs sur le site de reproduction. Chez la Grande Oie des neiges, c'est la presque totalité des graisses et la plupart des protéines qui sont obtenues localement (Choinière & Gauthier, 1995; Gauthier *et al.*, 2003). Les réserves corporelles accumulées au cours de la migration sont surtout utilisées par la femelle durant leur jeûne lors de l'incubation, alors que pour les mâles, elles servent dès leur arrivée sur les aires de reproduction pour leur permettre de maximiser le temps passé en vigilance à protéger leur femelle contre les autres mâles ou les prédateurs (Gauthier & Tardif, 1991; Choinière & Gauthier, 1995).

Étant donné que le principal site d'accumulation des réserves corporelles (sites le long du fleuve et de l'estuaire du St-Laurent; Gauthier *et al.*, 1992) est loin de l'Arctique, la Grande

Oie des neiges peut difficilement prévoir les conditions qu'elle va rencontrer à l'arrivée au site de nidification. De plus, étant donné la très longue migration, elle ne peut pas accumuler de réserves à la fois pour la migration, la ponte et l'incubation, car elle serait vraisemblablement trop lourde au départ et la migration serait alors trop coûteuse (Lindstrom & Alerstam, 1992). Ainsi, la taille de la ponte n'est pas déterminée à l'arrivée au site de nidification, ce qui signifie que les conditions d'alimentation retrouvées sur le site de reproduction sont au moins aussi importantes que les réserves accumulées par les femelles avant leur arrivée (Bêty *et al.*, 2003). Ceci pourrait être adaptatif, car les femelles peuvent initier un développement folliculaire rapide au bon moment, selon la date de fonte des neiges par exemple (Choinière & Gauthier, 1995). De plus, les femelles qui débutent la ponte tardivement peuvent pondre moins d'œufs afin de permettre une éclosion plus hâtive et ainsi assurer un meilleur développement des jeunes et augmenter leur succès reproducteur (Lepage *et al.*, 2000). Les conditions environnementales présentes sur le site de nidification ont donc une influence décisive sur la date et la taille de ponte (Cooke *et al.*, 1990; Bêty *et al.*, 2003), puisque le taux de gain en nutriments semble être un facteur important dans la détermination de la date de ponte des femelles (Rowe *et al.*, 1994).

Les oies disposent donc d'une certaine flexibilité afin de maximiser leur succès reproducteur selon les conditions environnementales. Cependant, cette flexibilité est limitée. En effet, un retard trop important dans la fonte des neiges et le dégagement des sites de nidification entraîne une forte proportion d'échecs de reproduction, la plupart des oies ne tentant même pas de se reproduire (Lepage *et al.*, 1996; Reed *et al.*, 2004). Des précipitations hivernales abondantes ainsi que des températures froides au printemps seraient responsables de ces échecs. D'ailleurs, Bêty *et al.* (2003) ont noté que la date de ponte était reliée au pourcentage de couverture de neige au sol, et que cet effet s'amplifiait dans les années où la fonte des neiges était tardive. Parfois, même si la fonte des neiges n'est pas complétée, les oies vont initier la nidification dans des sites différents que ceux utilisés habituellement, car la saison estivale est tellement courte qu'elles doivent débiter le plus tôt possible (Lepage *et al.*, 1996).

La croissance des oisons

La croissance des oisons s'effectue sous des conditions difficiles dans l'Arctique. De plus, les oisons doivent éclore et initier leur croissance le plus tôt possible afin de réussir à accumuler un peu de réserves avant d'entreprendre la migration d'automne (Lesage & Gauthier, 1997). Puisqu'ils sont exclusivement herbivores, les oisons disposent d'une nourriture de faible qualité. En effet, malgré le fait que les plantes dont ils se nourrissent sont de bonne qualité comparée à d'autres végétaux et à d'autres sites comme ceux des régions tempérées (Manseau & Gauthier, 1993), cette nourriture reste tout de même de faible qualité comparée à de la nourriture animale comme des insectes (Sedinger & Raveling, 1986; Klasing, 1998). Les oies ne pouvant digérer les fibres contenues dans les plantes et n'absorbant environ que le tiers de leur contenu, elles ont alors besoin pendant la croissance de grandes quantités de végétaux de haute qualité, surtout à concentration élevée en azote (Manseau & Gauthier, 1993). Les oies comptent en effet parmi les rares espèces d'oiseaux dont l'alimentation des jeunes est composée uniquement de plantes (Sedinger & Raveling, 1984; Audet, 2006; Cadieux *et al.*, 2005).

Le pic de qualité des plantes dont les oies se nourrissent survient habituellement autour de la date d'éclosion des jeunes. Ainsi, les oisons sont confrontés dès leur naissance à une nourriture dont la qualité est en diminution car la proportion de fibres contenue dans les plantes augmente avec la progression de la saison, tandis que la concentration en azote (élément essentiel pour la croissance) diminue (Manseau & Gauthier, 1993; Piedboeud & Gauthier, 1999; Cadieux *et al.*, 2005). De plus, lorsque la qualité nutritive des plantes diminue, les oisons ne compensent pas en s'alimentant davantage, probablement parce que leur capacité gastro-intestinale est déjà atteinte (Sedinger & Raveling, 1988; Manseau & Gauthier, 1993). Par conséquent, les jeunes ont avantage à se nourrir le plus tôt possible en saison afin d'assurer une croissance maximale. D'ailleurs, dès leur éclosion, les jeunes disposent d'organes digestifs et locomoteurs bien développés afin de pouvoir s'alimenter rapidement et ce, indépendamment de la date d'éclosion (Lesage & Gauthier, 1998). Ces facteurs suggèrent que le taux de croissance des oies est expliqué davantage par des facteurs écologiques (disponibilité et qualité de la nourriture) que par des contraintes embryonnaires (Lesage & Gauthier, 1997).

Lepage *et al.* (1998) ont démontré que la masse et la taille des oisons à 35 jours (peu avant leur envol) sont directement reliées à la disponibilité de nourriture de qualité. Cet effet se manifeste surtout lorsque les oisons sont âgés entre 11 et 25 jours, puisque cette période correspond à un taux de croissance très élevé, leur masse passant de 15 à 50% de celle atteinte à l'envol autour de 43 à 45 jours (Lesage & Gauthier, 1997). Ainsi, les facteurs environnementaux qui pourraient affecter la disponibilité et la qualité des plantes sont déterminants pour la croissance des jeunes. D'ailleurs, les oisons nés plus tard en saison sont désavantagés car ils ont une moins bonne croissance que les jeunes nés plus tôt en saison la plupart des années (Sedinger & Flint, 1991; Lindholm *et al.*, 1994; Lepage *et al.*, 1998; Lesage & Gauthier, 1998). Ceci s'explique par le fait que les oisons nés tard ont accès à de la nourriture de moins bonne qualité (déclin saisonnier) et qui est en moins grande quantité, puisque l'abondance a déjà été réduite par le broutement des oisons nés plus tôt (Gauthier *et al.*, 1995; Lepage *et al.*, 1998). Une différence d'une semaine seulement est déterminante dans la croissance des oies à la fin de l'été et cela peut avoir un impact majeur sur leur survie future et leur chance de recrutement dans la population (Lindholm *et al.*, 1994; Sedinger *et al.*, 1995; Lepage *et al.*, 2000; Reed *et al.*, 2003; Menu *et al.*, 2005). Étant donné que les facteurs climatiques influencent aussi la croissance des plantes et leur période de qualité maximale (Berry & Björkman, 1980; Binkley *et al.*, 1994; Arft *et al.*, 1999; Rustad *et al.*, 2001; Hollister *et al.*, 2005), ceux-ci peuvent donc avoir un impact indirect sur la croissance des jeunes via leur effet sur la nourriture.

Le climat peut également avoir une influence directe sur la croissance des oisons. Les jeunes sont homéothermes dès leur naissance et maintiennent une température corporelle constante (40.6 °C) malgré une température ambiante froide (5.6°C en moyenne durant la croissance, Fortin, 1995), sous leur zone de thermoneutralité (Ratté, 1998). Comme ils ne pratiquent pas l'hypothermie, ils doivent investir beaucoup d'énergie pour conserver leur température corporelle élevée. Selon Fortin *et al.* (2000a), l'utilisation exclusive de l'homéothermie est nécessaire pour maximiser leur capacité métabolique afin de permettre une croissance rapide. D'après Renaud (1999), au cours des 40 premiers jours de vie d'un oison, environ 30% de l'énergie de leur métabolisme de maintien est allouée à la thermorégulation, et ce pourcentage augmente lors des années plus froides. Ceci

correspondrait à environ 12 à 18% du bilan énergétique total des oisons consacré à la thermorégulation, en considérant que le pourcentage d'énergie attribué au métabolisme de maintien chez les oisons est similaire à celui retrouvé chez les adultes (Walsberg, 1983; Renaud, 1999). Une augmentation de la température pourrait donc diminuer les coûts en thermorégulation des oisons (Gauthier *et al.*, 1996).

Des variations saisonnières de l'environnement thermique des oisons ont aussi été observées. En effet, les jeunes qui sont nés tardivement sont soumis à un environnement thermique plus défavorable que les jeunes nés plus tôt (Renaud, 1999). Les oisons nés six jours après le pic d'éclosion dépendent environ 6% plus d'énergie pour la thermorégulation que ceux qui sont nés six jours avant ce pic à cause d'un environnement plus froid à la fin de l'été. Ceci pourrait contribuer à la diminution du taux de croissance observé chez les oisons nés tardivement comparativement à ceux qui ont éclos plus tôt (Lindholm *et al.*, 1994; Lesage & Gauthier, 1998). En effet, selon l'hypothèse d'allocation de l'énergie, les oiseaux ayant des coûts de thermorégulation plus élevés ont un taux de croissance plus faible s'ils ne disposent pas de suffisamment d'énergie pour compenser (Olson, 1992).

Changements climatiques et reproduction des oies dans l'Arctique

Les effets des changements climatiques dans l'Arctique sur la reproduction des oies sont, pour l'instant, difficiles à prédire. Par exemple, un réchauffement climatique pourrait diminuer les coûts de thermorégulation des oies, augmenter la croissance des plantes dont elles se nourrissent et allonger la saison de production végétale. Cependant, si la croissance des plantes est plus rapide au printemps et que le pic de qualité survient plus tôt au cours de la saison, alors la synchronisation entre l'éclosion des jeunes et le pic de qualité des plantes risque d'être moins bonne. Si les adultes ne peuvent pas ajuster leur date de ponte en conséquence, alors l'effet sera négatif sur leur succès reproducteur (Crick *et al.*, 1997). Pour des oiseaux effectuant de longues migrations comme les oies, l'adaptation aux changements climatiques risque d'être plus difficile. En effet, les changements climatiques ayant lieu au site d'hivernage peuvent différer ou progresser à une vitesse différente de ceux survenant au site de reproduction et ainsi empêcher une réponse adéquate de l'espèce aux changements se produisant à son site de nidification. De plus, si leur stratégie de

migration n'est pas affectée par les changements climatiques, alors les oies ne pourront probablement pas ajuster leur date d'arrivée au site de reproduction et ainsi s'adapter à un environnement changeant (Béty *et al.*, 2004; Both & Visser, 2001).

Des études antérieures ont amené à conclure que les conditions climatiques prévalant sur les sites de nidification au début du cycle reproducteur, soit au printemps, étaient les plus déterminantes pour le succès reproducteur des oies (Boyd & Madsen 1997; Skinner *et al.*, 1998). Des études ont démontré que la température en juin était positivement corrélée à la production de jeunes mesurée sur les terrains d'hivernage chez l'Oie rieuse (*Anser albifrons*; Zöckler & Lysenko, 2000), la Bernache du Canada (*Branta canadensis*; Sheaffer & Malecki, 1996) et la Bernache cravant (*Branta bernicla*; Boyd, 1987). L'étude de Skinner *et al.* (1998) sur la population de Petites Oies des neiges (*Chen caerulescens caerulescens*) nichant sur la côte ouest de la Baie d'Hudson a mis en relief l'importance de certains facteurs climatiques sur la reproduction de cette population sub-arctique. En effet, les résultats indiquent que jusqu'à 97% de la variabilité interannuelle moyenne dans certains aspects de la phénologie et du succès reproducteur des oies serait expliquée par des variables climatiques. Les corrélations les plus fortes semblent être celles concernant les variables de phénologie de la reproduction du début de la saison, comme les dates médianes de ponte et d'éclosion. Le climat de la région à l'étude fait partie de celles qui subissent depuis les dernières décennies un réchauffement de la température moyenne globale.

Objectifs de l'étude

L'aire de nidification la plus importante de la Grande Oie des neiges, soit l'Île Bylot, est située dans la partie est du Haut-Arctique canadien (voir Annexe 1). Cette aire est incluse dans une vaste région ayant subi un réchauffement climatique important au cours des 50 dernières années, et qui devrait se poursuivre au cours du présent siècle (ACIA, 2004; voir Annexe 2). Des analyses récentes des données climatiques de Pond Inlet, une localité située à moins de 50 km de l'Île Bylot, démontrent que la région a connu un réchauffement estival de 1.8°C au cours de la période 1976 à 2002 (Gauthier *et al.*, 2005). Des études sont menées depuis plusieurs années à l'Île Bylot et des données sur la biologie reproductive de

cette espèce sont disponibles depuis 1989. Cette population représente donc un bon modèle pour étudier les effets potentiels des changements climatiques sur les espèces arctiques.

La présente étude a pour but de déterminer l'influence des variables climatiques sur les fluctuations interannuelles de la phénologie et du succès de la reproduction chez la Grande Oie des neiges à l'Île Bylot, afin d'évaluer l'impact des changements climatiques anticipés sur la reproduction des oies tout au long du cycle reproducteur. Les objectifs principaux de cette étude sont:

Objectif 1: Évaluer dans quelle proportion les facteurs climatiques expliquent les variations interannuelles de la phénologie de la reproduction et du succès reproducteur de la Grande Oie des neiges à l'Île Bylot de 1989 à 2004;

Objectif 2: Identifier quelles variables climatiques et reproductrices sont le plus fortement reliées;

Étant donné la courte saison estivale, l'initiation de la reproduction doit débiter le plus tôt possible au printemps afin de permettre une croissance suffisante des jeunes avant la migration d'automne et ainsi maximiser le succès reproducteur des femelles. Les oies doivent donc débiter la reproduction à un moment où les conditions climatiques sont encore rigoureuses (température froide, neige encore présente). Par conséquent je propose qu'il y aura:

Hypothèse 1.1: Plus d'effets directs du climat sur la reproduction tôt dans le cycle reproducteur que tard.

Si cette hypothèse est juste, alors je prédis que:

-La réponse aux facteurs climatiques printaniers des paramètres de reproduction en début du cycle reproducteur (*e.g.* date et taille de ponte) sera plus importante que celle des paramètres en fin du cycle reproducteur

(production de jeunes ainsi que leur masse et taille à l'envol) face aux facteurs climatiques de la fin de l'été.

-La réponse aux facteurs climatiques printaniers des paramètres de reproduction associés à la fin du cycle reproducteur sera plus importante que la réponse face aux facteurs climatiques de la fin de l'été.

Objectif 3: Examiner si la phénologie de la reproduction et le succès reproducteur des oies sont influencés par les fluctuations climatiques régionales à grande échelle représentées par l'Oscillation Arctique (OA);

L'importance relative du climat régional par rapport au climat local sur les organismes est peu connue (Moller *et al.*, 2004). Cependant, on peut s'attendre à ce que les individus répondent plus fortement à des facteurs climatiques locaux exprimant davantage les spécificités de leur milieu environnant que des facteurs climatiques plus globaux. Par conséquent, je propose que:

Hypothèse 3.1: Le climat local aura plus d'influence sur les oies que le climat régional (*i.e.* OA).

Si cette hypothèse est juste, alors je prédis que:

- Les paramètres de reproduction des oies seront influencés par l'OA
- L'ensemble des paramètres de reproduction des oies sera davantage influencé par les variables de climat local que par l'OA.

De plus, puisque le phénomène de l'OA est plus fort en hiver qu'en été (Serreze *et al.*, 1997), je suggère que:

Hypothèse 3.2: L'OA aura plus d'influence sur les oies au printemps qu'en été.

Si cette hypothèse s'avère juste, alors je prédis que:

-L'indice printanier de l'OA prédira une plus grande part de variabilité dans les paramètres de reproduction des oies que les indices estivaux.

Objectif 4: Déterminer à quel point le climat peut influencer la synchronisation entre la phénologie de la reproduction chez les oies et la disponibilité en plantes de haute qualité pour les oisons;

Étant donné l'importance de la qualité et de la disponibilité de la nourriture sur la croissance des jeunes et la présence d'un déclin saisonnier de la qualité (Manseau & Gauthier, 1993; Lepage *et al.*, 1998), la synchronie entre la date médiane d'éclosion et le pic de la concentration en azote est importante. Je propose donc que:

Hypothèse 4.1: Durant l'été, les effets du climat sur la croissance des jeunes seront davantage via un effet indirect sur les plantes que sur les oies elles-mêmes.

Si cette hypothèse s'avère vraie, je prédis que:

-La croissance et la qualité des plantes en termes d'azote seront influencées par les conditions climatiques au printemps et en été.

-Les variables climatiques auront une influence sur les écarts entre la date d'éclosion des oisons et la date du pic de la concentration en azote ou du pic de la biomasse d'azote, deux indices de la qualité des plantes.

-Les variables climatiques qui affecteront la taille et la masse des jeunes près de l'envol seront les mêmes que celles qui affecteront les écarts entre la date d'éclosion des oisons et la date du pic de la concentration en azote ou du pic de la biomasse d'azote des plantes.

Hypothèse 4.2: Si le climat se réchauffe, la synchronie entre la date du pic de la qualité (concentration en azote ou biomasse d'azote) de la nourriture et celle de l'éclosion des jeunes sera réduite.

Si cette hypothèse est exacte, alors je prédis que:

-Les écarts entre la date d'éclosion des oisons et la date du pic de la concentration en azote ou du pic de la biomasse d'azote des plantes seront plus grands les années où la température moyenne de l'air est élevée.

CHAPITRE 1

EFFECT OF CLIMATIC FACTORS ON THE BREEDING PHENOLOGY AND REPRODUCTIVE SUCCESS OF GREATER SNOW GEESE

RÉSUMÉ

Le réchauffement climatique est le plus prononcé en Arctique et les oiseaux migrateurs y nichant devraient compter parmi les espèces les plus affectées. Nous avons examiné les effets des variations climatiques interannuelles locales et régionales sur la phénologie et le succès de la reproduction chez la Grande Oie des neiges (*Chen caerulescens atlantica*), une espèce migratrice nichant dans le Haut-Arctique canadien. Nous avons utilisé une banque de données à long terme (1989-2004) sur le suivi de plus de 5447 nids d'oies et sur la mesure de plus de 17496 oisons peu avant l'envol à l'Île Bylot. Nous avons observé qu'environ 50% de la variation individuelle dans la phénologie était expliquée par des facteurs climatiques printaniers. Des températures moyennes élevées ainsi qu'un faible couvert de neige au printemps ont favorisé une augmentation de la densité de nids et étaient associés à des dates de ponte et d'éclosion hâtives. Cependant, des températures maximales élevées au jour le plus chaud du printemps étaient reliées à un léger retard de la ponte et à une diminution du succès de nidification. Des précipitations abondantes au début de l'été étaient également positivement corrélées avec le succès de nidification, ce qui est probablement dû à une augmentation de la disponibilité en eau permettant aux femelles de rester près du nid au cours de leurs absences pendant l'incubation, réduisant ainsi sa vulnérabilité face aux prédateurs. Les valeurs très élevées (températures froides) ou très basses (températures chaudes) de l'indice de l'OA (Oscillation Arctique) étaient associées à une augmentation de la perte totale de couvées et à une réduction de la productivité de jeunes à la fin de l'été. Ceci suggère que ces composantes du succès reproducteur étaient davantage influencées par le climat régional (*i.e.* l'indice de l'OA) que par les conditions climatiques printanières. Au contraire, la taille et la masse des oisons près de l'envol étaient généralement réduites par des précipitations abondantes et des températures élevées au printemps. Ce dernier effet résulterait principalement de la diminution de la disponibilité en nourriture de haute qualité lors des années hâtives, provenant soit d'une diminution de la nourriture causée par une densité élevée de jeunes, ou d'une désynchronisation entre la date d'éclosion des oisons et le pic dans la qualité des plantes. Globalement, nos analyses suggèrent que le réchauffement climatique devrait devancer la phénologie de la reproduction des oies, mais des températures printanières élevées et des valeurs extrêmes de l'indice estival de l'OA pourraient diminuer leur succès reproducteur jusqu'à l'envol.

ABSTRACT

Climate warming is most pronounced in the Arctic and migratory birds breeding there are expected to be among the most affected species. We examined the effects of local and regional interannual climatic variations on the breeding phenology and reproductive success of Greater Snow Geese (*Chen caerulescens atlantica*), a migratory species nesting in the Canadian High-Arctic. We used a long term dataset based on the monitoring of 5,447 goose nests and the measurements of 17,496 goslings near fledging over 16 years (1989 to 2004) on Bylot Island. We found that about 50% of the individual variation in reproductive phenology was explained by climatic factors in spring. High mean temperatures and low snow cover in spring were associated with an increase in nest density in the colony and led to early egg-laying and hatching dates. However, high maximum temperatures on the warmest day in spring were related to a slight delay in egg-laying date and to a reduction in nesting success. High early summer rainfall was also positively associated with nesting success, presumably because increased water availability allowed females to stay close to their nest during incubation recesses, thereby reducing its vulnerability to predators. Total brood loss increased when values of the summer AO (Arctic Oscillation) index were either very high (low temperatures) or very low (high temperatures), and productivity of young was reduced similarly by these same factors. This suggests that these components of the breeding success were more influenced by the regional climate (*i.e.* the AO index) during the summer than by the spring climatic conditions. In contrast, goslings size and mass near fledging were generally reduced in years with high rainfall and high temperatures in spring. We suggest that this negative effect of warm springs on goslings growth is mostly due to a reduced availability of high quality food for goslings in early years, either due to food depletion resulting from high brood density or a mismatch between hatching date of goslings and the peak in plant quality. Globally, our analysis suggests that climate warming should advance the reproductive phenology of geese, but that high spring temperatures and extreme values of the summer AO index may decrease their reproductive success up to fledging.

INTRODUCTION

Global warming is currently progressing at an unprecedented rate, especially in the Arctic where warming rate is about twice as fast as anywhere else on earth. Over the next 100 years, an increase of 4 to 7°C in mean surface temperature and of 20% in annual precipitations is expected in the Arctic (IPCC, 2001; ACIA, 2004). Variations in large-scale climatic phenomena such as teleconnections, which represent variations in weather occurring simultaneously in widely separated areas, are also observed (Hurrell, 2000). For example, the North Atlantic Oscillation (NAO), which represents fluctuations in atmospheric pressures between Iceland and the Azores (Hurrell, 2000), explains a large part of the short-term interannual variability in winter temperatures and precipitations over the North Atlantic region. Another, larger teleconnection that could possibly integrate the NAO is the Arctic Oscillation (AO). The AO index represents fluctuations between atmospheric pressures at polar and middle latitudes (Thompson & Wallace, 1998) and is thought to explain a large portion of the variability in arctic climate. Both the NAO and AO indices have shown an upward trend over the last three decades, in parallel to change in climate of the regions submitted to their influence (Thompson & Wallace, 1998; Hurrell, 2000; Rigor *et al.*, 2000; Aanes *et al.*, 2002). In fact, when the NAO and AO indices are high in winter, atmospheric pressure over the central Atlantic is higher than normal, and thus westerly flow across the North Atlantic are enhanced, carrying relatively warm and moist maritime air over Northern Europe. Besides, these strong winds keep cold Arctic air flowing over the Northwest Atlantic, cooling this area and keeping the United States warm (Hurrell, 1995; 2000; JISAO, 2004).

Biological consequences of climatic change are already observed. Many studies have found shifts in phenology of a wide range of animal and plant species, mostly associated with warming (Parmesan & Yohe, 2003; Root *et al.*, 2003) and positive NAO values (Post & Stenseth, 1998; Otterson *et al.*, 2001). In European birds, high NAO index, which is associated with warm spring temperature, is related to early arrival date on breeding areas, early egg-laying date (Przybylo *et al.*, 2000; Frederiksen *et al.*, 2004), and increase in clutch size and offspring quality (Moller, 2002). However, the relative importance of local

versus large-scale weather phenomena on biological processes is still poorly known (Moller *et al.*, 2004).

Migratory birds are particularly interesting to study because, during their annual cycle, they use different areas of the globe that may be subject to various rate of climate change. Although this is especially true in arctic-nesting birds, few studies have examined the potential impact of climate change on arctic species compared to temperate ones (Moller *et al.*, 2004). Yet, the harsh and unpredictable arctic climate can have a strong influence on birds (Schekkerman *et al.*, 1998; Martin & Wiebe, 2004).

Geese are among the largest arctic-nesting birds and are important grazers of arctic wetlands (Gauthier *et al.*, 1996). They have only a short arctic summer to complete their lengthy breeding cycle and fledge goslings in time for the southward fall migration (Lesage & Gauthier, 1997). Females that nest early achieve the highest reproductive success (Lepage *et al.*, 2000) but egg-laying date is thought to be strongly constrained by climatic factors. Snow cover and cold temperature can limit nesting site and food availability in spring, and thus prevent females from feeding intensively to obtain the nutrients required for egg formation (Choinière & Gauthier 1995; Gauthier *et al.*, 2003). Such conditions are thus usually associated with a high proportion of non-breeding and late laying (Skinner *et al.*, 1998; Bêty *et al.*, 2003; Reed *et al.*, 2004). Skinner *et al.* (1998) showed that the impact of local climate on breeding parameters of the sub-arctic Lesser Snow Geese (*Chen caerulescens caerulescens*) was strong in early season, but decreased considerably later in the breeding cycle.

In this study, we conducted a detailed analysis of the effects of local and regional interannual climatic variations on the breeding phenology and reproductive success of Greater Snow Geese (*Chen caerulescens atlantica*). This High-Arctic sub-species is among the northernmost breeding geese in North America (Gauthier *et al.*, 1995), and thus time constraints on these birds should be especially severe. Our objectives were to (1) evaluate which climatic factors were most important in explaining interannual variations in several components of the breeding phenology and success of Greater Snow Geese, (2) determine

which of local or large-scale (*i.e.* AO index) climatic factors had the most effects on goose reproduction, and (3) verify Skinner's *et al.* (1998) hypothesis that climatic variables have more effects early in the breeding cycle than later on. A corollary of this hypothesis is that the later stages of the breeding cycle are more influenced by early season climatic factors (through a carry over effect) than by late season ones. For these analyses, we used a 16-year dataset.

METHODS

Study area

The study took place on the south plain of Bylot Island (73°08'N, 80°00'W), at the northern tip of Baffin Island, Nunavut Territory, Canada (see Appendix 1). This area supports one of the largest colony of Greater Snow Geese in the world and is estimated at *ca.* 20,000 pairs (Reed *et al.*, 2002). Wet meadows dominated by *Dupontia Fisheri* and *Eriophorum scheuchzeri* are the preferred sites of brood-rearing geese (Hughes *et al.*, 1994). Both wetland and dry upland characterize areas used by geese for nesting (Lepage *et al.*, 1996).

The eastern Canadian Arctic has generally experienced a global warming over the last 50 years (ACIA, 2004) (see Appendix 2). A recent analysis found that summer (May to August) temperatures have increased by 1.8°C over the period 1976 to 2002 at Pond Inlet (72°41'N, 77°59'W) located on Baffin Island, less than 50 km from Bylot Island (Gauthier *et al.*, 2005). This warming trend is expected to increase over the next century (ACIA, 2004).

Goose reproductive data

The breeding biology of Greater Snow Geese has been monitored annually from 1989 to 2004. Every spring, we searched and marked several hundred nests during the laying and early incubation periods. Nests are revisited during incubation and hatching, and goslings are marked at hatch with webtags (see Lepage *et al.*, 2000 for methods). We used spotting scopes to visually determine brood size of goose families during the second half of brood-

rearing (90% of the observations were made between 17 and 41 days of age). At the end of the summer, just before fledging (about five weeks after hatching) and when adults are molting, we conducted from 5 to 15 mass captures of families to band them each year. Only geese that nested successfully were susceptible to be captured because most non-breeders or birds that lost their nest leave the island to molt, or have regained flight capabilities at that time (Reed *et al.*, 2003). A sample of several hundred goslings were weighed and measured (culmen, head, tarsus, and ninth-primary length) during these captures every year, including all web-tagged ones because of their known hatching date (see Menu *et al.*, 2001 for methods).

Variables used to evaluate the effect of climatic variations on the phenology and reproductive success of geese were derived from these data described above (see Table 1). Egg-laying date was the date that the first egg was laid in a nest and hatching date was the date where most eggs in a nest hatched. Total clutch laid was the highest number of eggs recorded in a nest (excluding clutches of 1 and >7 eggs, as recommended by Lepage *et al.*, 2000). Nest density was based on the number of nests found in a small area (9.64 ha) located in the center of the colony and thoroughly searched since 1992. Nesting success was the probability that at least one egg hatched in each nest. Clutch size at hatch (*CSH*) and number of goslings leaving the nest (*GLN*) were determined only in successful nests, and hatching success was the ratio *GLN/CSH*. Because this latter value is numerically limited by the size of the brood, we used deviations between observed and expected values based on the null hypothesis that hatching success is independent of brood size. For each nest i , $E(GLN)_i = CSH_i * \text{Mean}(GLN/CSH)$ (see Rockwell *et al.*, 1993 for more details). The ratio young:adult, an index of the summer production of young, was calculated for each individual capture conducted at the end of the summer during goose banding. The proportion of families that lost all their young was calculated as: $1 - [(N \text{ young caught} / N \text{ adult caught}) / (\text{brood size at the end of summer} / 2)]$, assuming that all goslings are accompanied by two parents.

Because our goal was to examine the relative importance of climatic parameters on geese at various stages of their breeding cycle, the summer season was divided in three periods. The

first one was the spring when geese reach the breeding site and begin egg-laying. The second period (early summer) corresponded to the incubation and hatching period. Finally, the last period (late summer) corresponded to the brood-rearing (see Table 1).

Climatic data

From 1994 to 2004, we used climatic data from an automated weather station installed at our study site (20 m ASL). Air temperature was measured at 2 m above ground with a shielded temperature probe and mean hourly values were stored in a CR-10x data logger (Campbell Scientific, Edmonton, Alberta). From these data, we calculated mean, maximum, and minimum temperatures, number of frost-free days, number of thawing degree-days over 0°C, and temperature of the warmest and coldest day. The last two variables were used to examine the effect of extreme temperatures as extreme positive values could better represent those encountered by geese in the future where climatic warming is expected to increase. We recorded total daily rainfall (mm) manually from 3 June to 15 August with a rain gauge. From 1989 to 2004, we visually evaluated the percentage of snow cover over the study area on 5 June. For the period before our automated weather station (1989-1993), we used data from the Environment Canada weather station located at the Pond Inlet airport (72°41'N, 77°59'W). This station is located at 55 m ASL and records temperature data at 1.5 m above ground on a daily basis. Regression analyses between weather data from our automated station and Pond Inlet over the period 1995-2004 showed very close relationships, and these predictive equations were used to transform Pond Inlet's data for the period 1989-1993.

We obtained values for the AO index from the Climate Prediction Center of the National Weather Service (<http://www.cpc.ncep.noaa.gov>). These values are normalized by the standard deviation of the monthly index. We used the winter AO index based on the mean index value of months commonly used, November through April (Shindell *et al.*, 1999; Hartmann *et al.*, 2000; Aanes *et al.*, 2002), and daily values for the summer AO index. In the North Baffin area, high winter AO index is associated with reduced temperatures and precipitations (Hurrell, 1995). The same pattern is observed in summer (Serreze *et al.*, 1997; JISAO, 2004; see Appendix 3) although the reduction in summer precipitations is

Table 1. Variables of phenology and reproductive success of geese used according to different periods of the breeding cycle.

	Dates (period)	Breeding stage	Reproductive variables
1	20 May to 20 June (spring)	Arrival and egg-laying	Egg-laying date ¹ Total clutch laid (<i>TCL</i>) Nest density
2	21 June to 15 July (early summer)	Incubation and hatching	Hatching date ¹ Goslings leaving the nest (<i>GLN</i>) Nesting success Hatching success
3	16 July to 15 August (late summer)	Brood-rearing	Brood size near fledging Gosling mass and size near fledging Young:adult ratio near fledging Proportion of families loosing all their goslings

¹ Variables of phenology (laying and hatching date) are expressed in Julian days relative to the vernal equinox in order to report phenological data that accurately represent changes to the Earth system (Sagarin, 2001; equinox = 0).

weak (Stone *et al.*, 2000). Intensity and frequency of storms (atmospheric perturbations lasting one week or less; Hurrell, 2000) associated to higher cyclonic activity are enhanced north of 60°N with high AO index values in both seasons (Serreze *et al.*, 1997), and the reverse is true for low AO values.

We averaged daily climatic variables (including summer AO index) for each of our three periods, except maximum and minimum temperatures on the warmest and coldest days (Table 2). For statistical analyses, we used relative values by subtracting annual values from the 16-year mean of each period.

Statistical analyses

In order to avoid multicollinearity, we examined correlation matrices among climatic variables. We validated this primary evaluation by examining factor loadings in a global principal component analysis. We then applied a second principal component analysis to highly correlated variables ($r > 0.75$) to obtain a set of reduced, orthogonal variables. Thus, for each period, a variable number of weather variables (mostly associated with temperature) were combined into a single climatic variable obtained as the PC score on the first principal component axis (see Table 2). For all PC analyses, the first axis explained >76% of variations in the data and variables retained had loadings > 0.34 on this axis.

Since 1999, a spring conservation harvest of geese has been taking place at the Quebec staging area, and this negatively affected some goose reproductive parameters (Mainguy *et al.*, 2002; Bêty *et al.*, 2003; Reed *et al.*, 2004). We accounted for this confounding factor by adding a dummy variable in our analyses (1 = years with harvest; 0 = years with no harvest).

We first ran simple regressions to examine the shape of the relationships linking climatic and goose variables. We modeled non-linear effects with square or logarithmic transformations when required, *i.e.* when simple linear relationships were not significant or when the use of non-linear effects improved the R^2 by at least 5%. We then used hierarchical multiple regressions (Singer, 1998) to evaluate the relative importance of

Table 2. Climatic variables used according to different periods of the breeding cycle.

Date (period)	Climatic variables	Climatic variables combined in the PC index
20 May to 20 June (spring)	PC in spring Maximum temperature of the warmest day Total rainfall Winter AO index Spring AO index	Temperature (mean, maximum, minimum) Minimum temperature of the coldest day Sum of thawing degree-days Number of frost-free days % snow cover on 5 June
21 June to 15 July (early summer)	PC in early summer Minimum temperature of the coldest day Total rainfall AO index	Temperature (mean, maximum, minimum) Maximum temperature of the warmest day
16 July to 15 August (late summer)	PC in late summer Total rainfall AO index	Temperature (mean, maximum, minimum) Maximum temperature of the warmest day Minimum temperature of the coldest day

climatic variables on the breeding phenology and reproductive success of Greater Snow Geese. Hierarchical components of multiple regressions were used to take into account the possible dependence among individuals as all geese were submitted to the same climatic effects each year. For analyses using only one value per year (nest density and percentage of families losing all their young), we ran simple multiple regressions. We used forward stepwise selection to choose the final model that best predicted variations in the dependent variable. P value for variables entry and exit in the model was fixed to 0.05, except for models based on only one data per year, where the threshold was set to 0.10. The partial R^2 of each variable entered in the model was used to show its contribution and the adjusted R^2 was used to evaluate the global fit of the model. For each period, we examined the direct effects of climatic variables during the current period and the indirect effects of climatic variables that prevailed during the previous periods. For example, for dependent variables of the third period in Table 1, we used climatic data of that period as well as those from the previous two periods as independent variables. All analyses were performed with SAS 9.1 and all parameter slopes are reported with SE.

We used the individual scores along the first axis of a principal component analysis (PC1) based on measurements of head, tarsus and culmen lengths as an index of structural size of goslings (see Lepage *et al.*, 1998). To evaluate the impact of climatic variations on gosling's size (PC1 scores) and mass, all goslings had to be adjusted to the same age and hatching date, as late-hatched goslings grow more slowly than early-hatched ones (Lepage *et al.*, 1998). We used the 9th primary length to age goslings based on a predictive equation between this variable and age established in known-age goslings at capture (*i.e.* those that were web-tagged at hatching; $n = 17$ to 162 annually). This estimation is known to be reliable, especially when based on year-specific regressions (Lepage *et al.*, 1998; Cooch *et al.*, 1999). To adjust size and mass of goslings, we first ran an analysis of covariance (ANCOVA) using year, relative hatching date and age as covariates. We then added the residuals (*i.e.* difference between the observed and predicted values) to the mean overall size and mass predicted by the model at mean relative hatching date and mean age of goslings (34 ± 4 days) each year. The effect of climatic variables on these data was then tested using the same procedure as outlined before. However, because we found significant

interactions between hatching date and year, age and year, and hatching date and age, we also examined the sensitivity of our analyses to these interactions. To do so, we built different models where we adjusted goslings mass and size to plus or minus 1 standard deviation relative to mean age, or mean hatching date, or both, each year (Lesage & Gauthier, 1998). This yielded eight additional datasets on which we also tested the effect of climatic variables, allowing us to determine how climatic effects detected on goslings mass and size were sensitive to annual variations in age and hatching date effects.

Nesting success data were analysed using the procedure of Dinsmore *et al.* (2002). In this procedure, the daily survival probability of nests was modeled, and the effect of covariates (*i.e.* climatic data) was examined using linear models in program MARK. The Akaike Information Criterion (AIC) was used to select the best model that explained variation in nesting success. To estimate variability in nesting success explained by climatic variables, we used the ratio in relative deviance (DEV) between models (analogous to a R^2 ; Agresti, 1990) as follow:

$$R^2 = 1 - \frac{(\text{DEV climate - dependent model}) - (\text{DEV year - dependent model})}{(\text{DEV constant model}) - (\text{DEV year - dependent model})}$$

The variable «visit» was included as a linear effect to model the impact of the date that nests were visited, and thus control for possible confounding seasonal effects on nesting success. This effect was included in the models used to find out the approximate R^2 of the final model.

RESULTS

Spring reproductive variables

The combination of local temperature and snow cover (PC in spring; see Table 2) was the climatic variable that explained most variation in spring nesting parameters. Three variables affected egg-laying date ($R^2 = 0.435$, $F = 20.6$, $df = 3$, 5430, $P < 0.001$), the most important effect being a delayed laying in cold spring with high snow cover (*i.e.* low PC in spring

values; Fig. 1A). We also found a residual, negative effect of high spring AO index values (associated with colder than average temperatures in the area) on egg-laying date (Fig. 1B). However, a positive quadratic relationship also linked maximum temperature of the warmest day to egg-laying date, as both extremely low or high maximum temperatures tended to be associated with delayed laying (Fig. 1C).

PC in spring was the only variable that explained variability in nest density ($F = 3.44$, $df = 1, 9$, $P = 0.097$), as density was positively related to warm temperature with low snow cover in spring (Fig. 2).

Interannual variation in total clutch laid (TCL) was weakly explained by two climatic variables ($R^2 = 0.036$, $F = 12.2$, $df = 2$, 5093, $P < 0.001$; 1989-2004). The spring AO index was negatively related to TCL (partial $R^2 = 0.017$, $\beta_x = -0.272 \pm 0.074$, $P < 0.001$), and a negative quadratic relationship linked maximum temperature of the warmest day to TCL , indicating that extremely low or high maximum temperatures were associated with reduced TCL (partial $R^2 = 0.019$, $\beta_{x^2} = -0.046 \pm 0.014$, $P = 0.001$).

Early summer reproductive variables

A large proportion of variation in hatching date was explained by three climatic variables ($R^2 = 0.533$, $F = 20.5$, $df = 3$, 4010, $P < 0.001$). The first and third most important were climatic variables from the previous period (*i.e.* spring). Cold spring with high snow cover (*i.e.* low PC in spring values) was associated with a delay in hatching date (Fig. 3A) whereas the spring AO index was positively related to it (Fig. 3C). The other significant variable was the early summer AO index, which showed a positive quadratic relationship with hatching date, as both extremely low or high AO values tended to be associated with delayed hatching date (Fig. 3B).

Interannual variability in nesting success was well explained by climatic variables and the final model included ten variables from both spring and early summer (Table 3). Maximum temperature on the warmest day in spring was the most important one and was associated

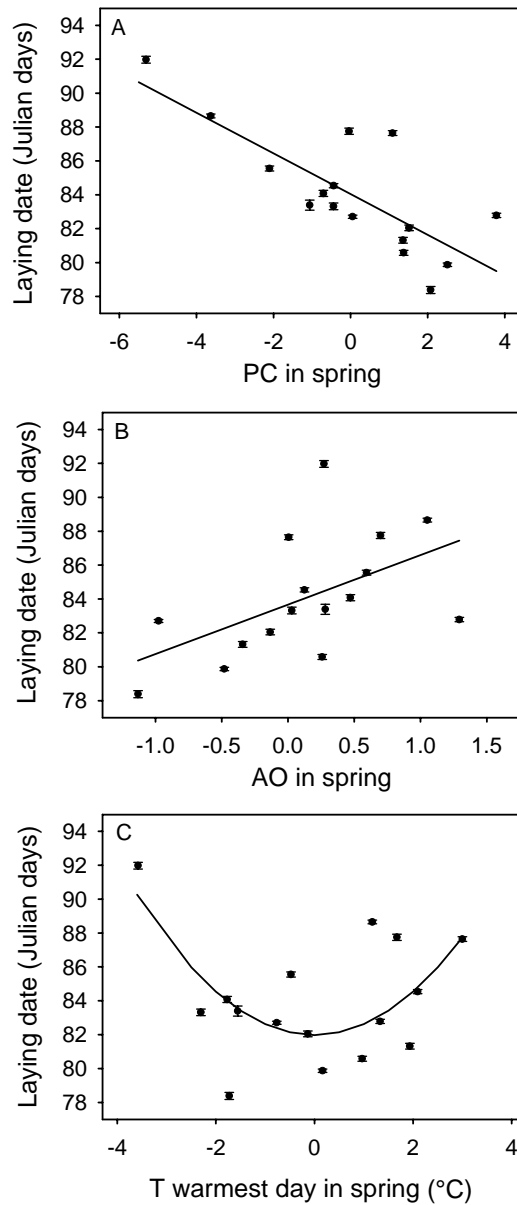


Figure 1. Relationships between egg-laying date of geese (Julian days relative to vernal equinox) and climatic variables retained in the final model, 1989-2004 ($n = 5,447$). A) An index of warm spring temperature and low snow cover (PC in spring; partial $R^2 = 0.282$, $\beta_x = -0.766 \pm 0.210$, $P < 0.001$), B) spring AO index (partial $R^2 = 0.078$, $\beta_x = 2.13 \pm 0.66$, $P = 0.001$), and C) maximum temperature of the warmest day in spring (values are expressed as deviations from the 16-year mean; partial $R^2 = 0.075$, $\beta_x^2 = 0.402 \pm 0.135$, $P = 0.003$). Mean annual values with SE are shown to illustrate the fit of the model.

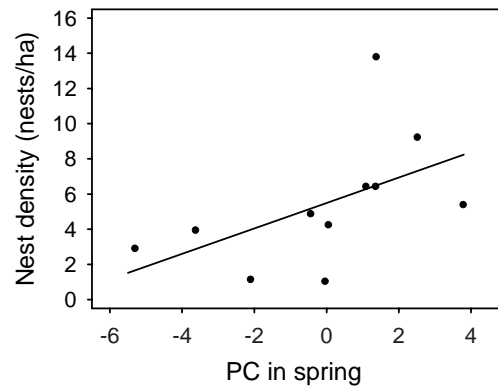


Figure 2. Relationship between nest density of geese and an index of warm spring temperature and low snow cover (PC in spring), 1992 and 1994-2003 ($R^2 = 0.277$, $\beta_x = 0.722 \pm 0.389$, $P = 0.097$, $n = 11$).

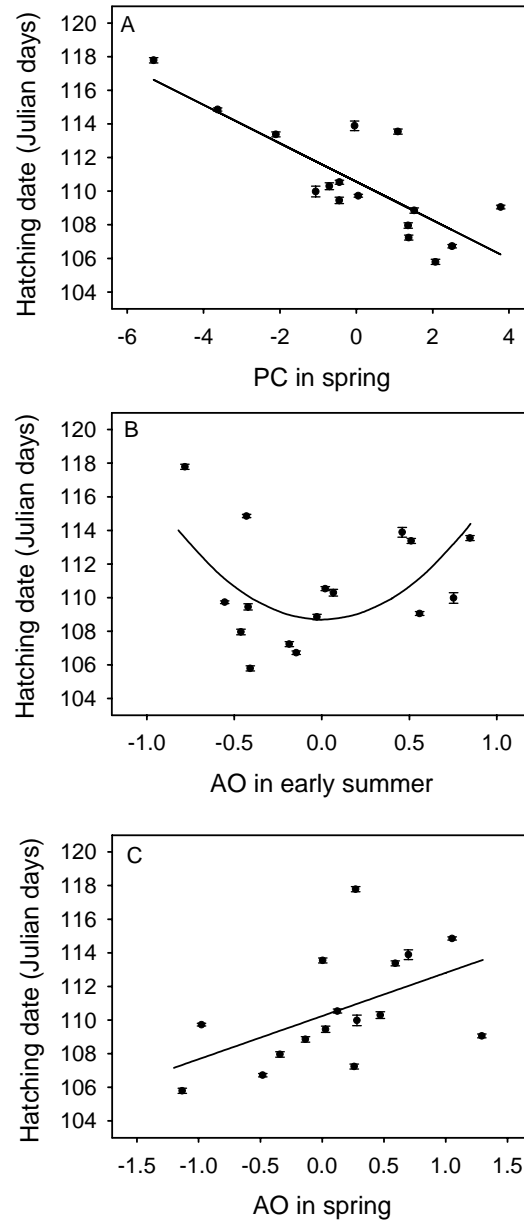


Figure 3. Relationships between hatching date of goose nests (Julian days relative to vernal equinox) and climatic variables retained in the final model, 1989-2004 ($n = 4,027$). A) An index of warm spring temperature and low snow cover (PC in spring; partial $R^2 = 0.370$, $\beta_x = -0.878 \pm 0.180$, $P < 0.001$), B) early summer AO index (partial $R^2 = 0.108$, $\beta_x^2 = 4.71 \pm 1.79$, $P = 0.009$), and C) spring AO index (partial $R^2 = 0.055$, $\beta_x = 1.57 \pm 0.61$, $P = 0.010$). Mean annual values with SE are shown to illustrate the fit of the model.

with a reduction in nesting success, whereas high precipitation during early summer was associated with increased nesting success. Regional climatic variable (*i.e.* AO index) explained more variability in nesting success than local mean temperatures (PC in spring or PC in early summer), as spring AO index was positively related to nesting success and early summer AO index was negatively related to it.

The number of goslings per successful nest was poorly explained by climatic variables. Hatching success was not related to any climatic variations and only one variable was weakly related to *GLN* ($R^2 = 0.019$, $F = 8.01$, $df = 1$, 2323, $P = 0.005$, $\beta_x = -0.345 \pm 0.122$; 1991-2004) as high AO index in spring was associated with reduced number of goslings per family.

Late summer reproductive variables

Variation in the young:adult ratio at the end of the summer was well explained by two climatic variables ($R^2 = 0.497$, $F = 14.4$, $df = 2$, 123, $P < 0.001$, 1990-2004). Regional climate index in summer explained the largest part of variability. Extreme high or low values of both the early and later summer AO indices were associated with a reduced production of young (Fig. 4; only late summer AO is shown as the relationship was identical for early summer; partial $R^2 = 0.143$, $\beta_x^2 = -0.539 \pm 0.190$, $P = 0.005$).

Variation in proportion of families loosing all their young at the end of the summer was generally explained by the same set of climatic variables as production of young ($R^2 = 0.778$, $F = 12.8$, $df = 3$, 11, $P = 0.001$; 1990-1993 and 1995-2004). Extreme low or high values of early and late summer AO indices increased the percentage of families loosing all their goslings (AO in late summer: partial $R^2 = 0.515$, $\beta_x^2 = 0.238 \pm 0.067$, $P = 0.005$. AO in early summer: partial $R^2 = 0.145$, $\beta_x^2 = 0.185 \pm 0.083$, $P = 0.048$). To a lesser extent, high spring temperature and low snow cover (*i.e.* high PC in spring) decreased the proportion of families loosing all their goslings during the summer (partial $R^2 = 0.058$, $\beta_x = -0.015 \pm 0.008$, $P = 0.088$).

Table 3. Climatic variables selected in the final model that best explained goose nesting success variability, 1989-1993 and 1995-2003 ($n = 3,978$). Variables are presented in decreasing order of importance. Final model approximate $R^2 = 0.854$ (for climatic variables only, approximate $R^2 = 0.781$).

Parameters	Beta	Standard error
Intercept	2.920	0.109
T warmest day in spring	-0.549	0.036
Spring harvest	0.863	0.108
Total rainfall in early summer	0.044	0.004
Nest visit	0.040	0.005
AO in spring	0.683	0.161
T coldest day in early summer	-1.294	0.075
AO in early summer	-1.518	0.109
PC in spring	0.898	0.058
AO in winter	0.814	0.079
PC in early summer	0.336	0.045

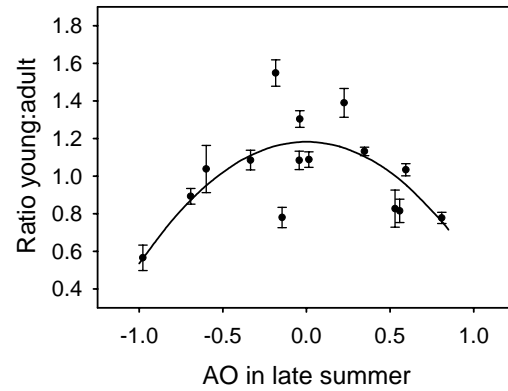


Figure 4. Relationship between the ratio young:adult of geese in individual catches and late summer AO index, 1990-2004 (partial $R^2 = 0.354$, $\beta_{x^2} = -0.598 \pm 0.142$, $P < 0.001$, $n = 138$). Mean annual values with SE are shown to illustrate the fit of the model.

The effect of climatic variables on goslings size was sensitive to the age or hatching date to which data were adjusted across years. In five of the nine datasets, the combination of high spring temperature and low snow cover (*i.e.* high PC in spring) was associated with smaller goslings near fledging above a certain threshold (Fig. 5A). This variable was significant in datasets where goslings age was adjusted to mean value or mean +1 standard deviation (SD). Total rainfall in early summer was also a significant variable in three datasets where goslings age was adjusted to mean +1 SD and was negatively related to gosling size (Fig. 5B). Finally, total rainfall in spring was an additional significant variable in four datasets, mostly those where gosling age was adjusted to mean -1 SD, and high rainfall was associated with reduced goslings size above a certain threshold (Fig. 5C).

The effect of climatic variables on goslings mass was less sensitive to the age or hatching date to which data were adjusted than goslings size. In seven of the nine datasets, the combination of high spring temperature and low snow cover (*i.e.* high PC in spring) was significantly associated with lighter goslings near fledging, but again only above a certain threshold (Fig. 6A). Once PC in spring was accounted for, the spring AO index was significant in five datasets where goslings age was adjusted to mean value or mean + 1 SD, and was positively related to goslings mass (Fig. 6B). Total rainfall in spring was an additional significant variable in three datasets where age was adjusted to mean -1 SD, and had a negative effect on goslings mass near fledging above a certain threshold (Fig. 6C).

Mean brood size in late summer was only weakly explained by variations in climate. Only high early summer AO values were negatively related to brood size ($R^2 = 0.034$, $F = 15.1$, $df = 1, 1883$, $P = 0.001$, $\beta_x = -0.517 \pm 0.133$; 1990-2004).

DISCUSSION

Spring reproductive variables

In spring, the most important climatic variables affecting goose reproductive parameters were those associated with the local climate. Early springs, related to low snow cover and high mean temperatures, are associated with an increase in the reproductive effort (as

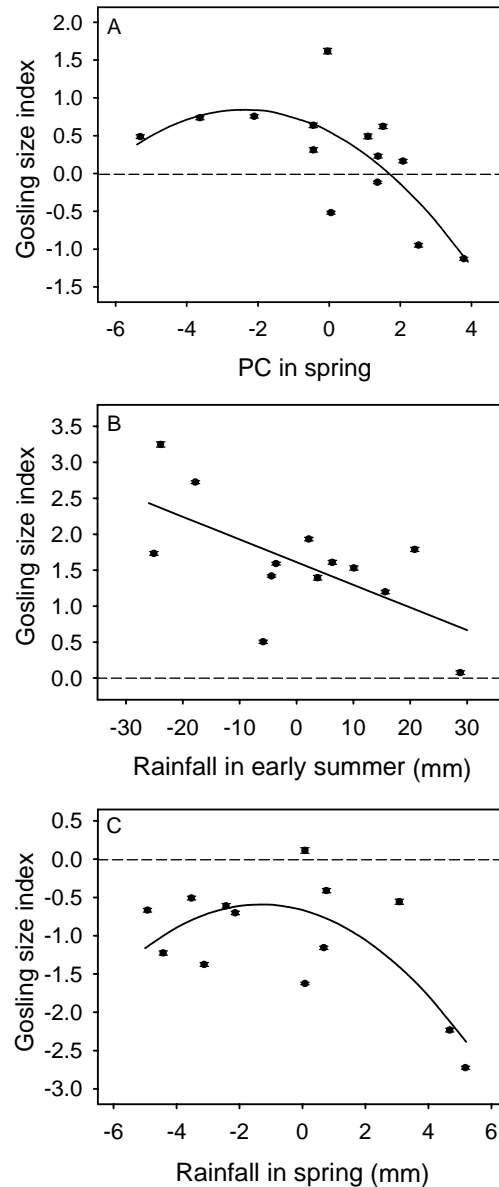


Figure 5. Relationships between goslings size (PC score) and climatic variables retained in models using various datasets. A) An index of warm spring temperature and low snow cover (PC in spring; $R^2 = 0.194$, $\beta_x = -0.243 \pm 0.071$, $\beta_x^2 = -0.051 \pm 0.022$, $P = 0.002$) for the dataset adjusted to mean age and hatching date, 1991-2004 ($n = 19,332$), B) total rainfall in early summer (partial $R^2 = 0.141$, $\beta_x = -0.023 \pm 0.005$, $P < 0.001$) for the dataset adjusted to mean age +1 SD and mean hatching date +1 SD, and C) total rainfall in spring ($R^2 = 0.259$, $\beta_x = -0.111 \pm 0.051$, $\beta_x^2 = -0.042 \pm 0.017$, $P = 0.003$) for the dataset adjusted to mean age -1 SD and mean hatching date, both 1991-1993 and 1995-2004 ($n = 17,496$). Rainfall values are expressed as deviations from the 16-year mean. Mean annual values with SE are shown to illustrate the fit of the model. The dashed line indicates the mean goslings size at capture.

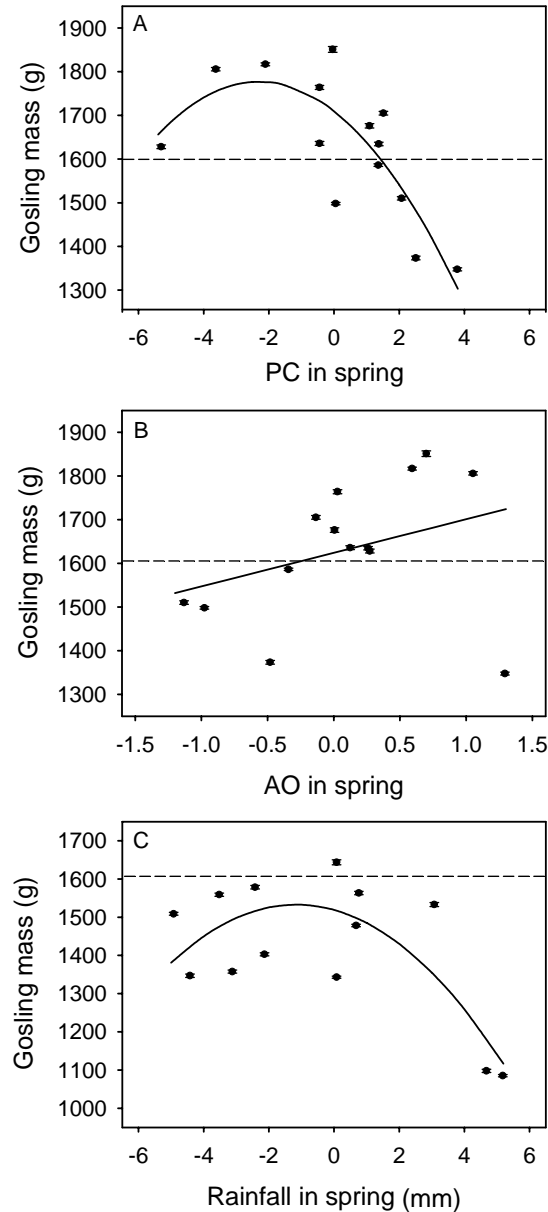


Figure 6. Relationships between goslings mass and climatic variables retained in models using various datasets. A) An index of warm spring temperature and low snow cover (PC in spring; partial $R^2 = 0.342$, $\beta_x = -56.2 \pm 10.5$, $\beta_x^2 = -15.4 \pm 3.4$, $P < 0.001$), and B) spring AO index (partial $R^2 = 0.076$, $\beta_x = 92.0 \pm 34.6$, $P = 0.008$), both for the dataset adjusted to mean age and hatching date, 1991-2004 ($n = 19,234$), and C) total rainfall in spring (values are expressed as deviations from the 16-year mean; $R^2 = 0.361$, $\beta_x = -23.8 \pm 10.9$, $\beta_x^2 = -10.3 \pm 3.7$, $P = 0.001$) for the dataset adjusted to mean age -1 SD and mean hatching date, 1991-1993 and 1995-2004 ($n = 17,400$). Mean annual values with SE are shown to illustrate the fit of the model. The dashed line indicates the mean goslings mass at capture.

indexed by nest density) and lead to early egg-laying. Others studies have shown that laying date and breeding propensity are negatively related to spring snow cover in this species (Bêty *et al.*, 2003; Reed *et al.*, 2004). However, our analysis indicates that it is not possible to clearly disentangle the effects of snow cover and air temperature per se as both are highly correlated. Low snow cover on the ground increases nest site availability and access to food by females during egg formation (Gauthier, 1993; Choinière & Gauthier, 1995; Gauthier *et al.*, 2003; Reed *et al.*, 2004). Many studies have found that migratory birds advance laying in warm spring (Richardson, 1990; Crick *et al.*, 1997; Skinner *et al.*, 1998; Both & Visser, 2001; Tryjanowski *et al.*, 2002). Laying date is important for birds because it determines the timing of the rest of the breeding cycle. When breeding is initiated early, females can lay more eggs and fledge young earlier in the summer (Cooke *et al.*, 1990; Lepage *et al.*, 2000; Bêty *et al.*, 2003). Climatic indices at the regional scale were much less important than those at the local scale in explaining variations in goose reproductive effort and laying date, although a high spring AO index, which is associated with colder temperature than normal, had an additional negative effect on laying date. Despite the beneficial effect of warm spring, we found evidence that extremely high temperature (indexed by the maximum temperature recorded on the warmest day) may be stressful for birds and delay somewhat laying, though the exact mechanism remains to be elucidated.

The weak effect of climatic variables on clutch size may be surprising because early laying, which is induced by warm spring temperature, is generally associated with large clutch sizes (Lepage *et al.*, 2000; Bêty *et al.*, 2003). However, only about half of individual variation in laying date was explained by climatic variables in our study, and clutch size is much less variable than laying date (Williams & Cooch, 1996; Dunn, 2004). Studies on Passerines have also shown that warm spring temperatures advance laying date but has no effect on clutch size (Winkel & Hudde, 1997; Winkler *et al.*, 2002; Weatherhead, 2005). This suggests little direct effect of climate on clutch size, which may be primarily determined by the individuals themselves and by laying date as suggested by Rowe *et al.* (1994) and Bêty *et al.* (2003).

Early summer reproductive variables

It is not surprising that hatching date was primarily influenced by the same climatic variables than laying date because, of the three main parameters that determine hatching date (*i.e.* laying date, clutch size, and incubation length), laying date is the most variable. However, by affecting the thermal regime of eggs, climatic factors could theoretically influence incubation time, and thus hatching date, especially in the Arctic where air temperature is much colder than egg temperature (Poussart *et al.*, 2000). Frequency and duration of incubation recesses are partly influenced by air temperature in Greater Snow Geese, although the impact of air temperature on egg-cooling rates was found to be low (Poussart *et al.*, 2000). A longer incubation due to increased egg cooling rate during female recesses could nonetheless explain the slight delay in hatching date when the AO index is high, as this is associated with cold temperature and more frequent and intense storms, which could increase wind-driven egg-cooling (Poussart *et al.*, 2000). However, we also found that, at the other extreme, a low AO index in early summer (*i.e.* warmer and sunnier conditions than average) was associated with a delay in hatching date, suggesting an increase in incubation length. We suggest that this effect may be mediated mostly through females hydration status. The primary need fulfilled by female Greater Snow Geese during incubation recesses appears to be drinking (Reed *et al.*, 1995; Nicolas Lecomte, unpubl. data). High temperature may increase water loss and enhance the need to drink more often, thereby increasing recesses frequency and egg-cooling rate because, even under warm conditions, air temperature is still lower than egg temperature in the Arctic (Poussart *et al.*, 2000).

The primary cause of nest failure in geese is egg predation (Bêty *et al.*, 2001, 2002). Therefore, we suggest that the climatic effects found on nesting success may also be mediated through an effect on the behaviour of incubating females, which would affect the vulnerability of eggs to predation, rather than through a direct effect of temperature or rain on the eggs. Vulnerability of goose eggs to predation increases considerably when females move greater than 10 m from the nest to drink or feed during incubation recesses (Inglis, 1977; Thompson & Raveling, 1987; Samelius & Alisauskas, 2001; Bêty *et al.*, 2002). Thus, if females have to leave nests more often to drink under very warm temperature, this may

increase egg predation rate and account for a negative effect of the high temperature during egg-laying and incubation on nesting success. In contrast, high rainfall during incubation may fill small tundra depressions with water and allow females to drink close to the nest, thereby reducing vulnerability of eggs to predators and accounting for the positive effect of rainfall on nesting success. Recently, an experimental manipulation showed that females stayed closer to their nest during incubation recesses and had a reduced egg predation rate when water availability was increased (Nicolas Lecomte, unpubl. data). This may also explain why low values of the maximum temperature and high AO values in spring, which are associated to cold temperatures, improved nesting success as cold temperatures may delay snowmelt and evaporation on the tundra, thereby increasing water supply for females later during incubation.

Late summer reproductive variables

The production of young at the end of the summer was mostly affected by climatic factors at the regional scale, and these effects were often non-linear. These effects were apparently primarily mediated through climatic effects on total brood loss during the summer rather than on brood attrition. Because high summer AO values are associated with low temperature and increased storms, such conditions may increase the thermoregulatory costs of young goslings (as suggested by Ratté, 1998; Renaud, 1999) and their probability of death due to cold exposure (Green, 1984; Beintema & Visser, 1989; Schekkerman *et al.*, 1998). At the other extreme, low summer AO values also had a negative effect on production of young, which is somewhat surprising. As suggested before, this negative effect may result from heat stress caused by sunny, hot, and windless conditions. Fortin *et al.* (2000b) showed that exposure to high solar radiation in the absence of wind can considerably increase heat gain of goslings even in the Arctic. Under such conditions, the standard operative temperature (Bakken, 1992) of goslings may reach 37°C and signs of heat stress have been observed (Fortin, 1995). Goslings must also walk for long periods while foraging or to reach feeding sites (Cooch *et al.*, 1993; Sedinger *et al.*, 2001; Mainguy *et al.*, 2006), and their metabolism is well adapted to function under cold temperatures. Indeed, walking does not increase energetic costs under cold conditions, since the heat produced by locomotor movements replaces the one that would be produced by

thermogenesis (Otis, 2002). Furthermore, goslings forced to walk for extended periods under experimental conditions had a reduced growth at 20°C compared to 8°C (Ouellet, 2006). All of this suggest that goslings may be sensitive to heat stress even in the Arctic and that it may occasionally have a negative impact on their survival.

In contrast to the previous index of survival and reproductive success, goslings size and mass near fledging were mostly influenced by local climatic conditions prevailing in spring. Previous studies have showed that availability of high quality plants is a major factor affecting goslings growth in geese (Cooch *et al.*, 1993; Aubin *et al.*, 1993; Lindholm *et al.*, 1994; Leafloor *et al.*, 1998; Lepage *et al.*, 1998). As high spring temperature and low snow cover are associated with a high breeding effort (see above; also Reed *et al.*, 2004), such conditions should lead to high brood density during the summer. This should in turn increase the proportion of plant biomass grazed by geese (Gauthier *et al.*, 2004), leading to a reduced food availability for goslings due to density-dependent effects, and hence a reduced growth. Alternatively, a mismatch between goose and plant phenology may explain why high spring temperature and low snow cover decrease goslings mass and size. We showed elsewhere that, because plant phenology responds more quickly than goose phenology to high spring temperature, hatching of goslings tends to occur later than the peak of high quality food in early, warm springs (see Chapter 2).

Generally, rainfall had a negative effect on goslings growth but this effect varied with gosling age and the period of the season when rain fell. Heavy spring rainfall had a negative effect on mass and size of young goslings (*ca.* 30 days). High rainfall occurring during snowmelt may swell run off water and flood wetlands for several days, causing a delay in the onset of plant growth. In many tundra plants, too little or too much water may both depress growth (Hodkinson *et al.*, 1999). In contrast, it was the size of older goslings (*ca.* 38 days) that was depressed by high rainfall in early summer. We showed elsewhere (Chapter 2) that early summer rainfall had a positive effect on plant growth up to a certain point and sped up their phenology. Such conditions may also increase the mismatch between goose and plant phenology, and hence depress goslings' growth. Alternatively, heavy rainfall during or soon after hatch can expose goslings to chilling and create

problems in maintaining their body temperature because their plumage is not totally waterproof yet (Fortin *et al.*, 2000a). Goslings may then need to be brooded more often by the parents, causing a reduction in foraging time at a crucial period when plant quality is highest.

CONCLUSION

Local, early season climate, mostly spring temperature and snow cover, had the greatest impact on the breeding phenology and reproductive effort of Greater Snow Geese, as observed in other studies (Boyd, 1987; Sheaffer & Malecki, 1996; Skinner *et al.*, 1998). However, breeding success at the end of the season was more influenced by the regional climate (*i.e.* the AO index) prevailing during the summer than by the spring climatic conditions. Therefore, our results partly reject Skinner's *et al.* (1998) hypothesis that the breeding cycle of arctic geese is mostly influenced by early season climatic variables. They also show the importance of teleconnections such as the AO in explaining variability in biological parameters of some arctic species, as previously shown in temperate species with the NAO index (Przybylo *et al.*, 2000; Frederikson *et al.*, 2004). Moreover, the fact that this global index was generally a better predictor of goose breeding success than several local climatic variables suggests that it may integrate well the overall climatic conditions encountered by geese.

We also detected several non-linear effects where extreme positive or negative values both had a negative effect on goose reproduction. This was especially true of the spring highest temperature recorded and extreme summer AO index values. Finally, our results suggest that the primary effect of climate on goslings growth was more indirect rather than direct, through an effect of spring climate on the availability and quality of food plants for goslings.

We conclude that, although arctic climate warming could advance goose breeding phenology, it could nonetheless result in a reduction of their breeding success. We suggest that future studies should focus on the effects of extreme in weather variables and large

scale climatic phenomena such as the Arctic Oscillation. Long time-series are also essential to obtain interannual variations as large as possible in climatic parameters.

CHAPITRE 2

EFFECT OF CLIMATIC FACTORS ON THE SYNCHRONIZATION BETWEEN REPRODUCTION AND PLANT PHENOLOGY IN GREATER SNOW GEESE

RÉSUMÉ

Les changements dans la phénologie des organismes en réponse au réchauffement climatique peuvent varier à travers le réseau trophique, entraînant un découplage des événements entre les niveaux trophiques. Si la réponse phénologique des plantes est plus rapide que celle de la phénologie de la reproduction des herbivores, alors ceci pourrait causer une désynchronisation entre les périodes les plus intenses de demande énergétique des jeunes et la disponibilité de nourriture de haute qualité. Nous avons testé cette hypothèse chez la Grande Oie des neiges (*Chen caerulescens atlantica*), une espèce herbivore nichant en Arctique où le réchauffement climatique devrait être particulièrement important, en examinant l'influence des variations climatiques interannuelles sur la synchronisation entre la phénologie de leur reproduction et la disponibilité saisonnière de nourriture de haute qualité. Des études antérieures ont permis de démontrer que la croissance des oisons est hautement sensible à la quantité d'azote disponible dans la nourriture consommée. Nous avons observé que des températures élevées ainsi qu'un faible couvert de neige au printemps étaient associés à une diminution de la synchronisation entre la date d'éclosion des oisons et la date où les plantes consommées par les oisons atteignent leur concentration maximale en azote. Ceci s'explique par l'avancement plus prononcé de la phénologie des plantes par rapport à celle des oies lors des printemps chauds. De plus, la valeur maximale de la biomasse d'azote était réduite au cours des printemps chauds puisque la concentration maximale des plantes en azote était atteinte à un niveau de biomasse plus faible que lors des printemps frais. Des précipitations très faibles et très fortes au début de l'été étaient aussi reliées à une diminution de la synchronisation entre le pic de biomasse d'azote et la période de haute demande énergétique des oisons. Nos résultats appuient donc l'hypothèse voulant que le réchauffement climatique anticipé conduise à un déphasage entre la reproduction des oies et le pic de disponibilité maximale en azote des plantes, ce qui devrait réduire la croissance des oisons. Ceci pourrait expliquer les effets négatifs précédemment observés des printemps chauds et des précipitations élevées au début de l'été sur la croissance des oisons.

ABSTRACT

Change in the phenology of organisms in response to climate warming can vary through the food web, leading to an uncoupling of events between trophic levels. If plant phenology responds more quickly than herbivore breeding phenology, this may cause a mismatch between the periods of highest energetic demand of young and of high quality food supply. We tested this hypothesis in the Greater Snow Goose (*Chen caerulescens atlantica*), a herbivorous species breeding in the Arctic where climate warming is expected to be strongest, by examining the influence of interannual climatic variations on the synchronization between their reproductive phenology and the seasonal availability of high quality food. Previous studies have shown that goslings growth is highly sensitive to the amount of nitrogen available in their food plants. We found that high temperatures and low snow cover in spring were associated with a decrease in the synchronization between goslings hatching date and the early season peak in nitrogen concentration in plants consumed by goslings. This occurred because the advancement in phenology during warm springs was more pronounced in plants than in geese. Peak nitrogen biomass was also reduced during warm springs because peak nitrogen concentration occurred at a lower plant biomass than in cool springs. Furthermore, very low and high rainfall during early summer were both related to a decrease in the synchronization between peak nitrogen biomass and the period of high energetic demand of goslings. Our results thus support the hypothesis that future climatic warming should lead to a mismatch between goose reproduction and peak nitrogen availability in plants, which should reduce the growth of goslings. This may explain the negative effects of warm springs and heavy early summer rainfall on goslings growth previously reported.

INTRODUCTION

Phenology is one of the first biological processes affected by climate change. Phenology can be defined as the timing of activities of living organisms in relation to the progress of the season (Berteaux *et al.*, 2004). Parmesan & Yohe (2003) found that 62% of 677 species reviewed showed trends towards earlier phenology in response to warmer spring. Over the period 1990-2100, an increase of 1.4 to 5.8°C of mean global surface temperature is anticipated (IPCC, 2001), and this should have a considerable impact on phenology. Already, Root *et al.*'s (2003) review of 143 studies revealed that spring phenology of species was advanced by an average of 5.1 days over the past 50 years, and birds were among the species showing the greatest shift. Early season change in phenology induced by climate change can have an effect on all subsequent activities of an organism. Large-scale climatic phenomena such as the North Atlantic Oscillation (NAO) can also affect phenology, as found in European birds (Przybylo *et al.*, 2000; Hüppop & Hüppop, 2003; Frederiksen *et al.*, 2004). The NAO index represents fluctuations of atmospheric pressures between Iceland and the Azores (Hurrell, 2000) and it explains a large part of the short-term interannual variability in winter temperatures and precipitations over the North Atlantic region. Over the last thirty years, NAO index have shown an upward trend, which is associated with warmer spring in Europe (Hurrell, 2000).

Effects of climate change on the phenology of organisms can also vary through the food web, leading to an uncoupling of events between trophic levels (Winder & Schindler, 2004). For instance, it has been shown that warmer temperatures may cause a mismatch between the peak in chicks energy requirements and peak in food availability in Blue and Great Tits (*Parus caeruleus* and *P. major*; Visser *et al.*, 1998; Buse *et al.*, 1999; Thomas *et al.*, 2001) and Pied Flycatchers (*Ficedula hypoleuca*; Both & Visser 2001; Sanz *et al.*, 2003). This occurs because climate change may shift the phenology of various species (in this case, birds and their insect food) at different rates. Moreover, in long-distant migrant birds, change occurring on the wintering and breeding grounds may progress at different rates, making it difficult for these species to adapt to climate change (Visser *et al.*, 2004). Indeed, phenological responses of species living at high latitudes, where warming has been

most important (ACIA, 2004), are stronger than for those living at lower latitudes (Root *et al.*, 2003).

Migratory birds breeding in the Arctic, where warming is expected to be strongest, should be among the species the most affected in terms of phenology, and should thus be susceptible to mismatch with their food supply. Geese, which are a prominent herbivore of arctic wetlands, are one example (Gauthier *et al.*, 1996). Geese are among the few avian species whose chicks are strictly herbivorous (Sedinger & Raveling, 1984; Manseau & Gauthier, 1993), and goslings growth is highly sensitive to variation in food quality during the summer (Aubin *et al.*, 1993; Lindholm *et al.*, 1994; Gadallah & Jefferies, 1995; Lepage *et al.*, 1998). As plants grow over the summer, their quality decline (*i.e.* nitrogen content decreases and fiber content increases), and goslings can not compensate for low plant quality by increasing their food intake rate due to gastrointestinal capacity limitations (Sedinger & Raveling 1988; Manseau & Gauthier, 1993). Therefore, the timing of hatch of goslings in relation to the early season peak in food quality is critical (Sedinger & Raveling, 1986; Lepage *et al.*, 1998). Goslings hatched just a few days later have a lower growth rate and reduced survival probabilities compared to those hatched earlier (Lindholm *et al.*, 1994; Sedinger *et al.*, 1995; Lesage & Gauthier, 1998; Lepage *et al.*, 2000). Nitrogen biomass availability during the period when goslings are between 11 and 25 days old (*i.e.* when their energetic demand is very high; Lesage & Gauthier, 1997) appears to be most critical for their growth (Lepage *et al.*, 1998).

If plant phenology responds more quickly than goose breeding phenology to climate warming, this may lead to a mismatch between the periods of highest energetic demand of goslings and of high quality food supply (*mismatch hypothesis*). Our aim was to test this hypothesis in the Greater Snow Goose (*Chen caerulescens atlantica*), one of the northernmost breeding geese in North America. In order to do so, we examined the effects of climatic variations on seasonal phenology of plant quality (*i.e.*, nitrogen) and biomass, and on the synchronization between goose reproductive and plant phenology over a 6-year period in order to evaluate the potential impact of future climate change on the timing of these events.

METHODS

Study area

The study took place on the south plain of Bylot Island (73°08'N, 80°00'W), at the northern tip of Baffin Island, Nunavut Territory, Canada (see Appendix 1). This area supports one of the largest colony of Greater Snow Geese in the world (Reed *et al.*, 2002). This area is characterized by polygon tundra (Tarnocai & Zoltai, 1988). Shallow ponds formed by sunken polygons develop into wet meadows where *Carex aquatilis* var. *stans*, *Dupontia fisheri*, and *Eriophorum scheuchzeri* dominate (Gauthier *et al.*, 1995), and these are the preferred sites used by brood-rearing geese (Hughes *et al.*, 1994). Nesting geese use both wetland and dry upland areas (Lepage *et al.*, 1996).

The eastern Canadian Arctic has generally experienced a global warming over the last 50 years, though not as strong as in the western Canadian Arctic (ACIA, 2004; see Appendix 2). A recent analysis found that summer (May to August) temperatures have increased by 1.8°C over the period 1976 to 2002 at Pond Inlet (72°41'N, 77°59'W) located on Baffin Island, <50 km from Bylot Island (Gauthier *et al.*, 2005). The warming trend is expected to increase in this area for the next century (ACIA, 2004).

Plant and goose reproductive data

From 1990 to 2004, we erected 12 seasonal exclosures every year in wet meadows after snowmelt (mid-June), before any significant goose grazing had occurred. Exclosures were 1 x 1-m and made of chicken wire 30 cm high supported by wooden stakes at each corner. A randomly chosen piece of turf 20 x 20-cm was taken in each exclosure at the end of the growing season around mid-August. Above-ground biomass included all green material and white basal stems buried in the mosses, and live plants were sorted into grass (mostly *Dupontia fisheri*), *Eriophorum* spp, *Carex* spp, and dicotyledons. Plants were oven-dried at 45°C and then weighed (see Gauthier *et al.*, 1995). This provided an estimate of total above-ground dry biomass/m² (excluding dicotyledons, which accounted for <2% of biomass) in the absence of goose grazing.

From 1991 to 1996, the same sampling was also carried out every two weeks from mid-June to mid-August, both inside exclosures (ungrazed plants) and outside (grazed plants). We determined the nitrogen concentration of *Eriophorum* and *Dupontia* separately on the dried samples of above-ground biomass of these plants (green material only; see Gauthier *et al.*, 1995 for details). Samples collected on the same dates but coming from different exclosures were often pooled in order to get enough material for nitrogen analyses. Nitrogen concentration of ground samples was determined with an automated macro-Kjeldahl analyser (Kjell-Foss, model 16210) following the AOAC (1984:154) method (see Gauthier *et al.*, 1995).

We first calculated the mean nitrogen concentration within species on each sampling date, and then a weighted mean nitrogen concentration across both species at each sampling date to determine the nitrogen concentration of goslings food. We also calculated an index of total nitrogen biomass available to goslings on each sampling date (g/m^2) as the product of plant biomass by nitrogen concentration within each species (see Lepage *et al.*, 1998). The summation of these indices provided an estimate of total nitrogen biomass/ m^2 available for each sampling date. These data were used to determine the date of peak nitrogen concentration and of peak total nitrogen biomass, and the value of these parameters at the peak each year. These calculations were made separately for ungrazed plants (*i.e.* inside exclosures) and grazed ones (*i.e.* outside exclosures). Data presented in the results are always for ungrazed plants, unless mentioned otherwise.

The breeding biology of Greater Snow Geese has been monitored from 1989 to 2004 on a sample of several hundred nests annually (see Chapter 1). We determined hatching dates by either visiting nests regularly during the hatching period, or based on clutch size and a fixed incubation length of 24 days when laying date of the first egg was known. We calculated the difference between the hatching date of each nest and the date of peak nitrogen concentration or peak total nitrogen biomass of plants in order to find the difference in synchrony between goslings hatch and the quality of their food plants. Zero would indicate that goslings hatched on the day of peak nitrogen concentration (or nitrogen biomass),

positive values would indicate that hatching occurred after the peak in quality, and negative values would indicate that hatching occurred before.

Climatic data

Climatic data used for the analyses came from either an automated weather station installed at our study site (most years), or from predictive equations of the climate at our study site based on climatic data obtained from the Environment Canada weather station located at the Pond Inlet airport (for details, see Chapter 1). We used variables derived from temperature data for our analyses. Variables were daily air temperature (mean, maximum, and minimum) measured at 2 m above ground, number of frost-free days in spring, number of thawing degrees days over 0°C in spring, maximum temperature of the warmest day, and minimum temperature of the coldest day. We recorded daily rainfall (mm) manually from 3 June to late August with a rain gauge, and we visually estimated percentage of snow cover over the study area on 5 June.

We used the winter and summer values of the Arctic Oscillation (AO) as an index of climate at the regional scale. The AO is similar to the NAO and has also shown an upward trend over the last thirty years. It represents fluctuations between atmospheric pressures at polar and middle latitudes and is thought to explain a large portion of the variability in arctic climate (Thompson & Wallace, 1998; Rigor *et al.*, 2000; Aanes *et al.*, 2002). We obtained values for the AO index from the Climate Prediction Center of the National Weather Service (<http://www.cpc.ncep.noaa.gov>). These values are normalized by the standard deviation of the monthly index. For the winter, we used mean AO index values of the commonly used months, November through April (Shindell *et al.*, 1999; Hartmann *et al.*, 2000; Aanes *et al.*, 2002), and daily values during the summer. In the North Baffin area, high AO index values are associated with reduced winter and summer temperatures and precipitations, although the reduction in summer precipitations is weak (Hurrell, 1995; Serreze *et al.*, 1997; Stone *et al.*, 2000; JISAO, 2004; see Appendix 3 for summer temperature trends). Intensity and frequency of storms (atmospheric perturbations lasting one week or less; Hurrell, 2000) associated to high cyclonic activity are also enhanced in

the region north of 60°N during years with high AO index in both seasons (Serreze *et al.*, 1997). The reverse is true for low AO index years.

Statistical analyses

Because we were interested in the direct and indirect effects of climatic factors on biological variables (*i.e.* the effect of current climatic conditions and those that prevailed earlier in the season), we divided the breeding season in three periods. The first one was the spring period (20 May to 20 June) when geese arrive on the breeding ground and start egg-laying, and included the onset of plant growth toward the end. The second period was the early summer (21 June to 15 July) and corresponded to incubation and hatching periods for geese, and the early growth season of plants. The last period was the late summer (16 July to 15 August) and corresponded to the brood-rearing period of geese and late growth season of plants. Biological and climatic data associated with each of these periods are presented in Table 1.

Daily climatic variables were averaged within each period, except maximum and minimum temperature on the warmest and coldest days. Annual values were expressed as deviations from the long-term average (period 1989-2004) for each variable. In order to avoid multicollinearity problems among climatic variables, we applied principal component analyses to highly correlated variables ($r > 0.75$) to obtain a set of reduced, orthogonal variables within each period. Thus, for each period, a variable number of weather variables (mostly associated with temperature) were combined into a single climatic variable obtained as the PC score on the first principal component axis (Table 1; see chapter 1 for more details).

We used simple regressions to evaluate the effects of each climatic variable on the date and value of peak nitrogen concentration and nitrogen biomass in plants. To examine the direct effects of current climatic conditions on biological parameters and the indirect effects of conditions that prevailed earlier, we used both climatic data of the current period and those from the previous periods as independent variables. We also modeled non-linear effects

Table 1. Biological and climatic data used according to the different periods of the breeding cycle.

Period	Climatic data	Biological data
1 20 May to 20 June (spring)	PC in spring ^a Temperature of the warmest day Total rainfall Spring AO index Winter AO index	
2 21 June to 15 July (early summer)	PC in early summer ^b Temperature of the coldest day Total rainfall Early summer AO index	Date of peak nitrogen concentration Value of peak nitrogen concentration Difference between hatching date and date of peak nitrogen concentration
3 16 July to 15 August (late summer)	PC in late summer ^c Total rainfall Late summer AO index	Date of peak nitrogen biomass Value of peak nitrogen biomass Difference between hatching date and date of peak nitrogen biomass Total plant biomass

^a This variable is obtained from a principal component analysis combining mean, maximum, and minimum temperatures, temperature of the coldest day, sum of thawing degree-days and number of frost-free days in spring, and % snow cover on 5 June.

^b This variable is obtained from a principal component analysis combining mean, maximum, and minimum temperatures, and temperature of the warmest day in early summer.

^c This variable is obtained from a principal component analysis combining mean, maximum, and minimum temperatures, and temperatures of the coldest and warmest day in late summer.

with square or logarithmic transformations when required, *i.e.* when simple linear relationships were not significant or when the use of non-linear effects improved the R^2 by at least 5%. Because sample sizes were small ($n = 6$ years in most cases), we used $P < 0.1$ as significance level.

We used hierarchical multiple regressions (Singer, 1998) to evaluate the influence of climatic variables on deviations of goslings hatching date from dates of peak nitrogen concentration and biomass in plants, and on total plant biomass at the end of the summer. In these analyses, sampling units were respectively individual nests and plant exclosures. Hierarchical components of multiple regressions were used to take into account that all geese and plant samples were exposed to the same climatic effect each year. This considers the possible dependence among individual geese or plant samples. Non-linear effects were also examined using x^2 terms in the model when simple linear relationships were not significant or when the use of non-linear effects improved the R^2 by at least 5%, and total plant biomass values at the end of the summer were log-transformed for normality. We used forward stepwise selection to choose the final model that best predicted variations in each dependent variable. The P value threshold for variables to enter and exit the model was fixed to 0.05. The partial R^2 of each variable entered in the model was used to show its contribution and the adjusted R^2 was used to evaluate the global fit of the model. All analyses were performed with SAS 9.1 and all parameter slopes are reported with SE.

RESULTS

The date of peak nitrogen concentration in plants was negatively associated with two climatic variables in spring, and two in early summer. The nitrogen concentration peak was delayed in springs with cool temperature and high snow cover (PC in spring; Fig. 1A, $R^2 = 0.816$, $F = 17.7$, $df = 1, 4$, $P = 0.014$), and to a lesser extent in springs where maximum temperature on the warmest day was low (Fig. 1B, $R^2 = 0.531$, $F = 4.53$, $df = 1, 4$, $P = 0.101$). Similarly, it was delayed when temperature on the coldest day in early summer was low (Fig. 1C, $R^2 = 0.632$, $F = 6.88$, $df = 1, 4$, $P = 0.059$). Finally, years where rainfall during early summer was very low (*i.e.* drought) or very high (*i.e.* flooding) were

both associated with a delay in the date of peak nitrogen concentration (Fig. 1D, $R^2 = 0.905$, $F = 28.7$, $df = 1, 3$, $P = 0.013$). However, the peak value of nitrogen concentration in plants was not significantly explained by any of the climatic variables.

Total plant biomass at the end of the summer was explained by three climatic variables, mostly of the late summer period ($R^2 = 0.241$, $F = 9.18$, $df = 3, 153$, $P < 0.001$). The most important effect was an increase in plant biomass with warm temperature in late summer (PC in late summer; Fig. 2). Once this variable was accounted for in the model, two more climatic variables were retained. Plant biomass decreased slightly when minimum temperature on the coldest day in early summer was high (partial $R^2 = 0.041$, $\beta_x = -0.055 \pm 0.024$, $P = 0.023$), and decreased when the late summer AO index was high (partial $R^2 = 0.032$, $\beta_x = -0.096 \pm 0.049$, $P = 0.050$), but these relationships were weak.

The date of peak nitrogen biomass in plants was only influenced by two early summer climatic variables. The nitrogen biomass peak occurred later when early summer rainfall was low (Fig. 3A, $R^2 = 0.918$, $F = 33.8$, $df = 1, 3$, $P = 0.010$) and when minimum temperature on the coldest day in early summer was low (Fig. 3B, $R^2 = 0.895$, $F = 34.1$, $df = 1, 4$, $P = 0.004$).

The value of peak nitrogen biomass in plants was affected by several spring, early summer, and late summer climatic variables. Peak nitrogen biomass was reduced when the maximum temperature on the warmest day in spring was high (Fig. 4A, $R^2 = 0.678$, $F = 6.30$, $df = 1, 3$, $P = 0.087$). The peak in nitrogen biomass was reduced by both extreme cold or warm temperatures in early summer (Fig. 4B, $R^2 = 0.925$, $F = 37.1$, $df = 1, 3$, $P = 0.009$), and also decreased linearly with increasing values of the late summer AO index (Fig. 4C, $R^2 = 0.853$, $F = 17.4$, $df = 1, 3$, $P = 0.025$).

The synchrony between peak hatching date of goose nests and the date of peak nitrogen concentration in plants was strongly influenced by spring climatic variables. The synchrony between these two variables was good in springs with cool temperature and high snow cover (*i.e.* low PC in spring). However, in years with warm temperature and low snow

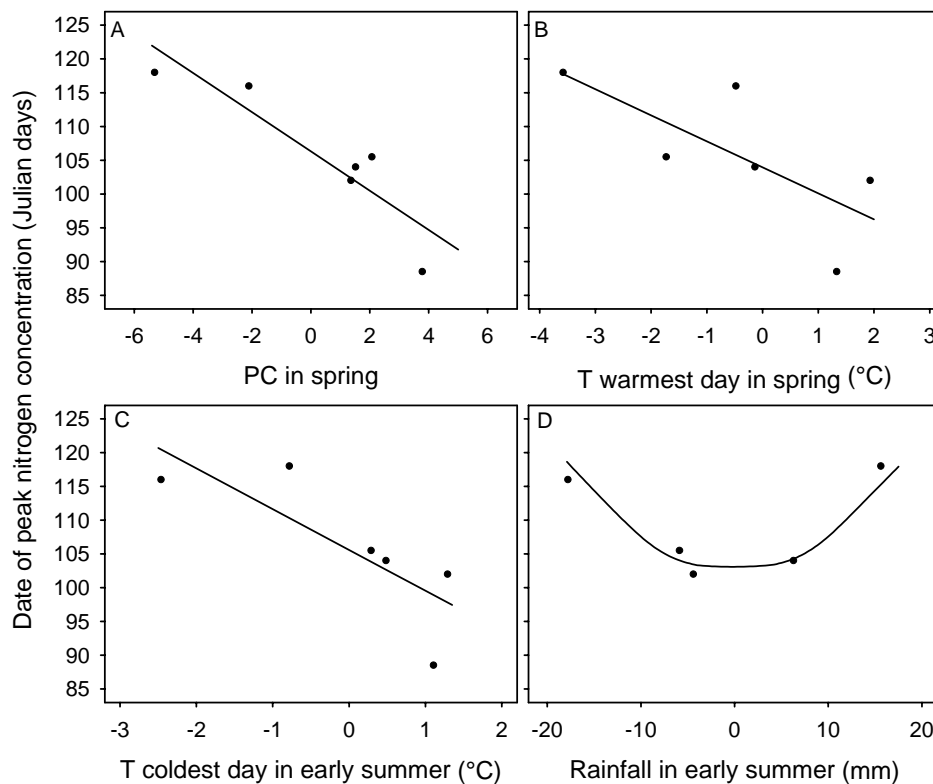


Figure 1. Relationships between date of peak nitrogen concentration in plants (Julian days relative to vernal equinox) and A) an index of warm spring temperature and low snow cover (PC in spring; $\beta_x = -2.90 \pm 0.69$; 1991-1996), B) maximum temperature of the warmest day in spring ($\beta_x = -3.85 \pm 1.81$; 1991-1996), C) minimum temperature of the coldest day in early summer ($\beta_x = -6.04 \pm 2.30$; 1991-1996), and D) total rainfall in early summer ($\beta_x^2 = 0.050 \pm 0.009$; 1991-1993 and 1995-1996). Temperature and rainfall values are expressed as deviations from the mean.

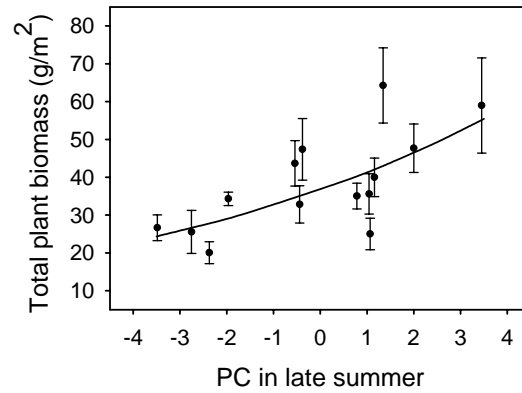


Figure 2. Relationship between total plant biomass at the end of the summer from 1990 to 2003 and an index of warm late summer temperature (PC in late summer; partial $R^2 = 0.168$, $\beta_x = 0.059 \pm 0.013$ on a log scale, $P < 0.001$, $n = 167$). Mean annual values with SE are shown to illustrate the fit of the model.

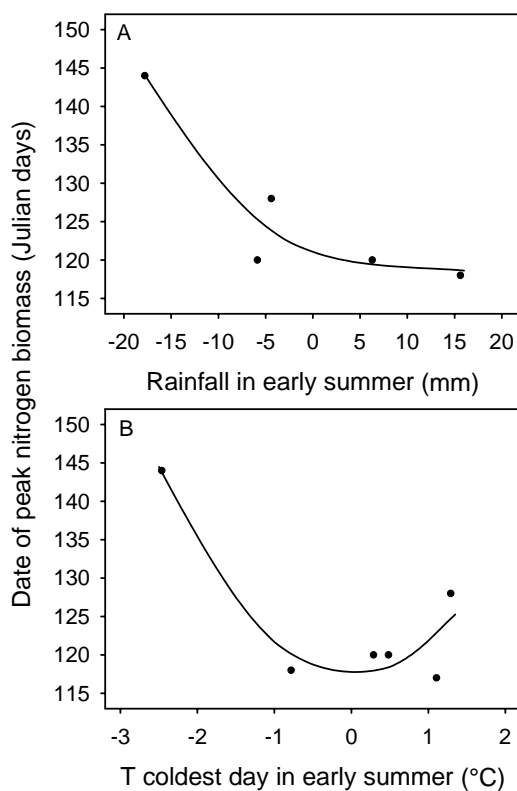


Figure 3. Relationships between date of peak nitrogen biomass in plants (Julian days relative to vernal equinox) and A) early summer total rainfall ($\beta_{\log(x+18)} = -11.4 \pm 2.0$; 1991-1993 and 1995-1996), and B) minimum temperature of the coldest day in early summer ($\beta_x^2 = 4.34 \pm 0.74$; 1991-1996). Temperature and rainfall values are expressed as deviations from the mean.

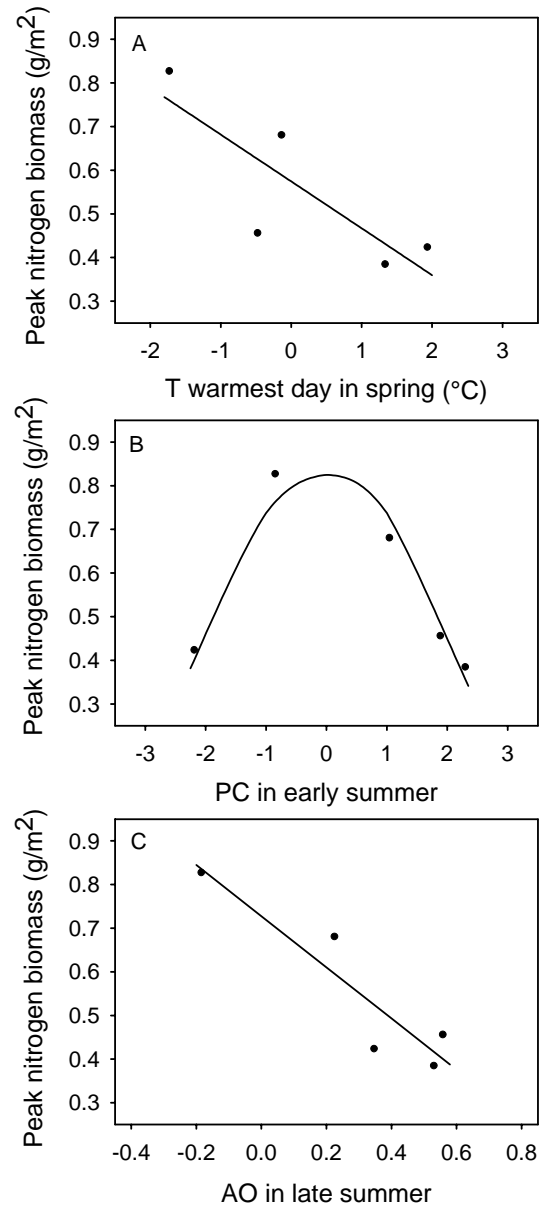


Figure 4. Relationships between peak nitrogen biomass in plants in 1991 and 1993-1996 and A) maximum temperature of the warmest day in spring (expressed as deviations from the mean; $\beta_x = -0.107 \pm 0.043$), B) an index of warm early summer temperature (PC in early summer; $\beta_x^2 = -0.088 \pm 0.014$), and C) the late summer AO index ($\beta_x = -0.586 \pm 0.141$).

cover, goslings hatched later than the peak in nitrogen concentration in plants (Fig. 5, $R^2 = 0.866$, $F = 6.76$, $df = 2$, 1398, $P = 0.001$). Because goose grazing can affect the nitrogen concentration of plants (Gauthier *et al.*, 1995), geese could potentially modify the synchrony between peak nitrogen concentration and hatching dates. To test for that, we repeated the analysis using nitrogen concentration data from grazed swards. However, the results of the analysis were very similar to the one with ungrazed plants ($R^2 = 0.831$, $F = 4.46$, $df = 2$, 1398, $P = 0.012$) because the date of peak nitrogen concentration of grazed swards was delayed in only one out of six years.

The synchrony between peak hatching date of goose nests and the date of peak nitrogen biomass in plants was also influenced by climatic variables, but this time by early summer conditions. The difference between hatching and peak nitrogen biomass dates was not influenced by temperature but was reduced with increasing rainfall in early summer (Fig. 6, $R^2 = 0.896$, $F = 38.2$, $df = 1$, 866, $P < 0.001$). Because goslings growth is highest and most sensitive to the nitrogen biomass available between the ages of 11 and 25 days (Lepage *et al.*, 1998), the peak in nitrogen biomass should occur between 11 and 25 days after hatch for optimum growth conditions. Our analysis thus suggests that peak nitrogen biomass could occur too early in very wet years or too late in very dry years (Fig. 6). This effect, however, disappeared when the difference with hatching date was calculated using the data of peak nitrogen biomass in grazed swards.

DISCUSSION

Effect of climatic factors on plant phenology and biomass

Phenological events and growth (*i.e.* biomass) of arctic plants appear to be affected by different climatic factors operating at different times of the season. The phenology of plant quality (*i.e.* nitrogen concentration) was mostly driven by spring and early summer climatic factors. In arctic plants, nitrogen concentration is usually highest in young shoots shortly after the onset of plant growth and decreases slowly throughout the summer (Manseau &

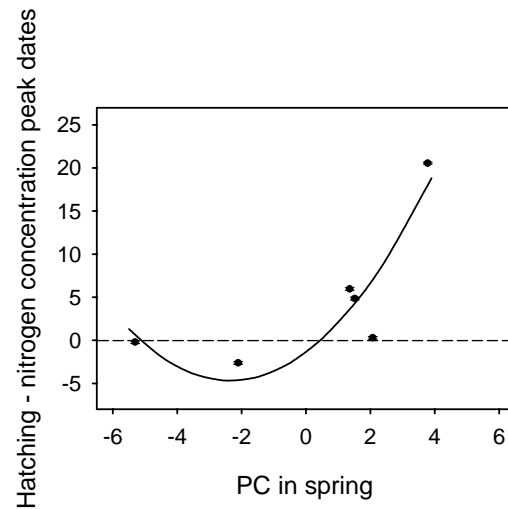


Figure 5. Relationship between the difference in hatching date of goose nests and date of peak nitrogen concentration in plants, and an index of warm spring temperature and low snow cover (PC in spring), 1991-1996 ($\beta_x = 2.83 \pm 0.77$, $\beta_x^2 = 0.603 \pm 0.248$, $n = 1,404$). The dashed line indicates no difference between hatching and peak nitrogen concentration dates. Mean annual values with SE are shown to illustrate the fit of the model.

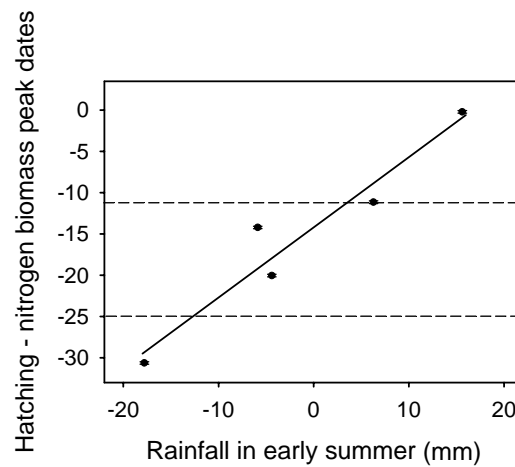


Figure 6. Relationship between the difference in hatching date of goose nests and peak nitrogen biomass in plants, and total rainfall in early summer, 1991-1993 and 1995-1996 ($\beta_x = 0.850 \pm 0.138$, $n = 871$). Rainfall values are expressed as deviations from the mean. The dashed lines set the interval where growth rate of goslings is highest and most sensitive to nitrogen biomass available (from Lepage *et al.*, 1998). Mean annual values with SE are shown to illustrate the fit of the model.

Gauthier, 1993; Gauthier *et al.*, 1995; Lepage *et al.*, 1998; Larter & Nagy, 2001; Cadieux *et al.*, 2005). The advancement of the peak in nitrogen concentration of *Eriophorum* and *Dupontia* in years with high spring and early summer temperatures and a low snow cover in spring is presumably due to an early onset of plant growth in those years. This is supported by many studies that demonstrated an advancement in phenology of arctic plants in response to experimental warming (Wookey *et al.*, 1993; Sparks & Carey, 1995; Arft *et al.*, 1999; Hollister *et al.*, 2005). Despite this phenological effect of warm spring, the value of the peak nitrogen concentration itself was not affected by climatic factors.

Our results also suggest that intermediate amount of rainfall during the early summer is required to avoid delay in plant phenology. In many species of tundra plants, growth response is highest under specific soil moisture range and decreases when soil is wetter or drier than this optimal range (Hodkinson *et al.*, 1999). On one hand, water flow may accelerate nitrogen mineralization (Chapin *et al.*, 1988; Binkley *et al.*, 1994) and nutrients diffusion in plants roots (Chapin *et al.*, 1988). On the other hand, heavy rainfall may prolong the flooding period following snowmelt and lead to anoxic conditions where nutrient availability is reduced due to a decrease in mineralization and nitrification rates and an increase in denitrification rates (Ponnamperuma, 1972; Reddy *et al.*, 1986). Soil oxygen depletion may also have a direct impact on plant growth by changing metabolic and physiological functions (Gebauer *et al.*, 1995) and by reducing nitrogen uptake by plants (Drew, 1990).

Unlike the phenology of nitrogen concentration, total plant biomass was mostly influenced by mid to late summer climatic variables, as cold temperatures at both the local and regional scales (high AO index) reduced biomass. Previous studies have suggested that low temperature is the main growth regulating factor of high-arctic plants (Havström *et al.*, 1993; Rustad *et al.*, 2001) and many others have shown an increase in plant growth in response to experimental warming despite some site-specific differences (Henry & Molau, 1997; Arft *et al.*, 1999; Dormann & Woodin, 2002; Hollister *et al.*, 2005). Plant biomass is largely the product of the accumulation of carbon resulting from photosynthetic activity. Total photosynthetic activity is both dependent of ambient temperature and total leaf area

of the plant (Berry & Björkman, 1980; Poorter & Remkes, 1990). Our results suggest that biomass accumulation is more affected by low temperatures occurring in periods (*i.e.* late summer) when leaf area is highest and thus the total photosynthetic potential of the plant high, than in spring when leaf area is still reduced.

Because nitrogen biomass is the product of nitrogen concentration and plant biomass, it is not surprising that its phenology and level were affected by a combination of factors affecting each of these components. For instance, if warm spring temperature advances peak nitrogen concentration because of an early onset of plant growth but has little effect on biomass due to a low total photosynthetic capacity at that time, then the nitrogen concentration would start to decline when total plant biomass is still low, resulting in low peak nitrogen biomass. This could explain the lower value of peak nitrogen biomass observed in warm spring and early summer temperatures. In contrast, when cold temperature persist during early summer, both the peak in nitrogen concentration and plant growth may be delayed, and thus nitrogen concentration could again start to decline when total plant biomass is still low. This could explain why very cold temperature during early summer delayed peak nitrogen biomass and reduced its value.

Effect of climatic factors on the synchronization between hatching date and plant quality

Warm springs with low snow cover are associated with early hatching date in geese, mostly because females lay their eggs earlier (see Chapter 1), and also with an advancement of the peak nitrogen concentration in plants consumed by geese. However, because goslings hatching occurred later after this peak than in normal or cool springs, this suggests that the advancement in phenology in warm springs is more pronounced in plants than in geese. Moreover, extremely high temperature (indexed by the warmest temperature recorded each spring) can have the opposite effect and delay egg-laying (hence, hatching date) of goose nests (see Chapter 1), but these conditions still enhanced plant phenology. The best timing for goslings would be to hatch at the peak in nitrogen concentration, or slightly before, to benefit from the highest quality food during early growth (Sedinger & Raveling, 1986; Lepage *et al.*, 1998). However, our results show that in warm springs, goslings hatch when

the seasonal decline in plant quality is well under way, thus supporting the hypothesis of a mismatch between goslings growth and the peak in food quality. Although the onset of egg laying by geese and of plant growth are both advanced in warm springs, the clutch size and incubation length of geese, which determine hatching date, are little affected by temperature. In contrast, plant phenology and growth are not constrained and can speed up under warm conditions, leading to the observed mismatch. Springs with cool or near average temperature lead to a better synchronization between geese and plants because plant growth is slowed down during the laying and incubation periods of geese. This mismatch can explain in part the reduction in goslings mass and size at fledging observed in warm springs (see Chapter 1), and thus can have serious fitness consequences. Indeed, small and light goslings near fledging have a much reduced survival during the fall migration (Schmutz, 1993; Sedinger *et al.*, 1995; Reed *et al.*, 2003; Menu *et al.*, 2005). The mismatch hypothesis has already been supported in several species of European passerines where spring warming speed up the development of their insect food more than the bird's breeding cycle, leading to a mismatch between the period of high energetic requirement of chicks and their food supply (Visser *et al.*, 1998; Buse *et al.*, 1999; Both & Visser, 2001; Thomas *et al.*, 2001; Sanz *et al.*, 2003). Our study is the first to provide support for this hypothesis in a herbivorous bird.

Rainfall in early summer influenced the phenology of plants but had no effect on hatching date of nests (see Chapter 1), and thus is another climatic factors that can affect the synchronization between goslings hatch and high quality food. Lepage *et al.* (1998) found that the cumulative biomass of nitrogen encountered by goslings between the ages of 11 to 25 days, when they grow from 15 to 50 % of their fledging mass (Lesage & Gauthier, 1997), is the best predictor of mass near fledging. Therefore, it would be optimal for goslings to be exposed to the peak in nitrogen biomass during this interval. Our results suggest that too little or too much rain during the early summer can both lead to a poor synchronization between the period of peak growth of goslings and of peak nitrogen biomass. Under heavy rain conditions, the peak in nitrogen biomass would occur near the hatching date, which is too early, and under drought conditions, it would occur too late in the growth period of goslings. This mechanism may explain why we found that heavy early

summer rainfall reduced the size of goslings near fledging (see Chapter 1). However, we found no negative effect of low early summer rainfall on goslings size (see Chapter 1). Complex interactions could affect this result if, for instance, low early summer rainfall is associated with warm springs, which advance plant phenology and thus could compensate the opposite effect of low rainfall on synchronization. Moreover, the effect of rainfall on synchronization disappeared when we used nitrogen biomass in grazed swards. This occurred because heavy goose grazing reduces plant biomass (Gauthier *et al.*, 1995, 2004) and thus the peak in nitrogen biomass occurs earlier than in ungrazed swards. However, heavy grazing also has a negative effect on goslings growth (Lepage *et al.*, 1998).

CONCLUSION

We found that climatic conditions influenced the synchronization between hatching and early growth of goslings, when energetic requirements are highest, and the availability of high quality food. Springs with warm temperature and low snow cover lead to a mismatch between goslings hatching date and peak nitrogen concentration in plants that they consumed. Our results suggest that warming and increase in summer precipitations of arctic regions due to climate change should amplify this mismatch in the future, and thus may have negative fitness consequences for geese. Although climate warming may prolong the summer season, benefits for goslings may be marginal because, in late summer, food quality is at the lowest for them (Manseau & Gauthier, 1993; Cadieux *et al.*, 2005). More studies on the vulnerability of the synchronization between the phenology of arctic-breeding birds and their food supply are required.

CONCLUSION GÉNÉRALE

Notre étude met en relief l'importance des conditions climatiques dans la détermination de la phénologie et du succès reproducteur chez un grand oiseau migrateur nichant en Arctique. L'indice de température printanier au site d'étude (PC in spring) explique une part importante des variations interannuelles dans la reproduction des oies tout au long du cycle reproducteur. Nos résultats démontrent que des températures plus élevées que la moyenne et un faible couvert de neige au printemps sont associés à une augmentation de l'effort de reproduction et devancent la phénologie de la reproduction chez la Grande Oie des neiges. Par contre, contrairement à d'autres études évaluant l'importance du climat sur la reproduction des oies (Boyd, 1987; Sheaffer & Malecki, 1996; Boyd & Madsen 1997; Skinner *et al.*, 1998; Zöckler & Lysenko, 2000), notre étude révèle que non seulement les facteurs climatiques printaniers mais également ceux prévalant durant l'été, surtout à l'échelle régionale, sont déterminants pour le succès reproducteur de la Grande Oie des neiges. Ainsi, l'hypothèse voulant qu'il y ait plus d'effets directs du climat sur la reproduction tôt dans le cycle reproducteur que tard est infirmée. En effet, une part importante de la variabilité dans la perte totale de jeunes au cours de l'élevage et le nombre de jeunes par adulte est prédite principalement par l'entremise de l'indice de l'OA estival avec un impact négatif des valeurs extrêmes de l'indice.

L'impact du climat régional sur les paramètres de reproduction des oies est donc parfois plus important que le climat local et il est présent tout au long du cycle reproducteur, ce qui nous permet d'infirmier l'hypothèse voulant que le climat local ait plus d'influence sur l'ensemble des paramètres de reproduction des oies que le climat régional (OA). De plus, le fait que cet indice global prédise davantage le succès reproducteur des oies que les variables climatiques locales suggèrent qu'il intègre bien les conditions climatiques générales rencontrées par les oies au cours de l'été. Cette propriété globalisante de l'OA, qui constitue un des avantages majeurs de l'utilisation des téléconnexions comme variables climatiques (Stenseth *et al.*, 2003), pourrait expliquer pourquoi l'indice estival est plus important pour prédire la variation des paramètres de reproduction des oies que l'indice printanier, ce qui est contraire à nos attentes. En effet, ce dernier reflète davantage les conditions climatiques qui ont contribué à préparer l'environnement rencontré par les oies à leur arrivée en Arctique et au début du cycle reproducteur, plutôt que les conditions

climatiques générales rencontrées par les oies au cours du cycle reproducteur. Également, c'est le climat printanier local (*i.e.* indice de température local et de couverture de neige; PC in spring) qui explique davantage de variabilité dans les paramètres de reproduction des oies, surtout au niveau de la phénologie. Ceci peut être expliqué par le fait qu'un des facteurs importants intégrés dans l'indice de température printanier (PC in spring) est le pourcentage de couverture de neige retrouvé sur le site d'étude et que ce facteur est très important pour déterminer l'initiation de la ponte chez la Grande Oie des neiges (Chapitre 1 de la présente étude; Bêty *et al.*, 2003).

De plus, le succès de nidification compte parmi les paramètres de reproduction dont la variabilité interannuelle est fortement expliquée par les facteurs climatiques. Dans ce cas-ci, des pluies abondantes au cours de la période d'incubation et d'éclosion seraient favorables pour le succès de nidification. Nous avons émis l'hypothèse qu'une forte disponibilité en eau autour des nids limiterait l'absence des femelles et leur éloignement du nid pendant l'incubation, et par le fait même réduirait la prédation sur les oeufs qui est la cause première d'échec de nidification chez les oies (Bêty *et al.*, 2001, 2002). De plus, nos résultats suggèrent que des températures maximales très élevées au printemps, et dans une moindre mesure au début de l'été, seraient néfastes pour le succès de nidification puisqu'elles contribueraient à augmenter les absences au nid dues à une déshydratation accrue des femelles. Quant aux tailles de ponte et de couvée, elles sont très peu influencées par les variables climatiques sélectionnées.

De plus, nous avons détecté quelques effets non linéaires pour lesquels les valeurs extrêmes positives ou négatives avaient des effets négatifs sur les paramètres de reproduction des oies, particulièrement au niveau de la température du jour le plus chaud au printemps et les indices estivaux de l'Oscillation Arctique. Ceci démontre l'importance de considérer non seulement la valeur moyenne des variables climatiques, mais également les valeurs extrêmes puisque leurs effets sur les organismes peuvent être encore plus importants (Moller *et al.*, 2004).

Les conditions climatiques ont une influence sur la croissance et la qualité des plantes au printemps et en été, et sur l'écart entre la date d'éclosion des jeunes et la date du pic de la concentration en azote et du pic de biomasse d'azote. Les variables climatiques qui influencent ces écarts correspondent principalement à celles qui influencent aussi la taille et la masse des oisons près de l'envol. Ainsi, la synchronisation entre la date du pic de la concentration en azote et l'éclosion des jeunes, de même que la masse et la taille des oisons peu avant l'envol, sont réduites lors des printemps chauds. Nous pouvons donc confirmer l'influence indirecte plutôt que directe du climat sur la croissance des oisons par l'entremise de son effet sur les plantes. En effet, un printemps hâtif devance la phénologie de la reproduction, mais à un rythme moins élevé que celui de la phénologie des plantes consommées par les oisons. Même si des températures printanières élevées permettent aux oisons de bénéficier d'une saison plus longue pour leur croissance, cela diminue également leur accès à une nourriture de haute qualité qui est essentielle à leur croissance (Aubin *et al.*, 1993; Lindholm *et al.*, 1994; Lepage *et al.*, 1998). Cette désynchronisation pourrait ainsi expliquer en partie la réduction de la taille et la masse des oisons à l'envol lors des printemps chauds. De plus, des précipitations très faibles ou très abondantes au début de l'été contribuent à diminuer la synchronisation entre la biomasse d'azote disponible pour les oisons et la période où leur besoin en nutriments est le plus grand durant la croissance. L'impact de cette désynchronisation a aussi été détectée sur la taille des oisons.

Globalement, des températures printanières élevées devancent la phénologie des oies, tel qu'observé chez plusieurs espèces végétales et animales en réaction au réchauffement climatique actuel (Parmesan & Yohe, 2003; Root *et al.*, 2003), mais elles diminuent néanmoins leur succès reproducteur jusqu'à l'envol, surtout en réduisant la synchronisation entre la phénologie de la reproduction et celle des plantes essentielles à la croissance des oisons. Par conséquent, le réchauffement climatique actuel et anticipé pourrait être néfaste pour le succès reproducteur de la Grande Oie des neiges dans l'Arctique. Quant à l'augmentation généralement prévue des précipitations en Arctique, son influence sur la phénologie de la reproduction et le succès reproducteur des oies demeure incertain. Au printemps, des précipitations abondantes seraient néfastes pour le succès reproducteur des oies puisqu'elles sont associées à une réduction de la taille et de la masse des oisons près de

l'envol. Des précipitations printanières importantes peuvent en effet causer l'inondation des milieux humides et ralentir l'initiation de la croissance des plantes. Plus tard en été, des précipitations abondantes ont plutôt un effet positif sur le succès de nidification, mais peuvent conduire à une désynchronisation entre la période de haute demande énergétique des oisons et le pic dans la disponibilité en plantes de haute qualité qu'ils consomment.

Notre étude démontre également la contribution importante d'un phénomène climatique à grande échelle comme l'Oscillation Arctique pour expliquer les variations interannuelles de la reproduction chez un grand oiseau migrateur nichant en Arctique, tel que démontré avec l'indice hivernal de l'ONA chez des espèces en milieux tempérés (Przybylo *et al.*, 2000; Frederikson *et al.*, 2004). Nous appuyons et suggérons l'intégration des téléconnexions dans l'étude des impacts du climat sur les espèces animales et végétales, particulièrement de l'indice de l'OA estival qui est sous utilisé comparativement à l'indice hivernal, même si son importance pendant la saison estival a aussi été démontrée (Serreze *et al.*, 1997; Aanes *et al.*, 2002). De même, nous proposons que les prochaines études incluent des variables mesurant le rayonnement (solaire et atmosphérique) et la vitesse des vents, puisque ces variables pourraient jouer un rôle important dans la reproduction des espèces arctiques.

La désynchronisation que nous avons remarquée entre la phénologie de la reproduction chez les oies et celle des plantes qu'elles consomment suite à des températures printanières élevées, ainsi que les conséquences observées sur leur succès reproducteur, constituent un résultat original et significatif dans le contexte de l'étude de l'impact des changements climatiques. Plusieurs études ont déjà permis de démontrer l'impact négatif d'un tel décalage sur le succès reproducteur d'espèces européennes, mais dont les jeunes ne sont pas herbivores (Visser *et al.*, 1998; Buse *et al.*, 1999; Both & Visser, 2001; Thomas *et al.*, 2001; Sanz *et al.*, 2003). Par contre, il s'agit d'une étude plutôt préliminaire utilisant une banque de données de seulement six ans. Il serait intéressant de poursuivre la prise de données au niveau de la phénologie de la qualité des plantes et de mettre en place des dispositifs expérimentaux afin de valider les présentes conclusions. Par exemple, il serait préférable de simuler expérimentalement le réchauffement climatique anticipé à l'aide de chambres à toit ouvert (OTCs: open topped-chambers) afin de mesurer en conditions

contrôlées son impact sur la phénologie des plantes, plutôt que d'étudier uniquement la réponse phénologique des plantes à partir de données sur les variations interannuelles des températures actuelles. Plusieurs études ont déjà prouvé l'efficacité de ces méthodes et leur importance étant donné la diversité des réponses des différentes espèces et des divers milieux arctiques (Henry & Molau, 1997; Arft *et al.*, 1999; Dormann & Woodin, 2002; Hollister *et al.*, 2005).

Puisque le succès reproducteur des oies est aussi affecté par la date d'arrivée au site de reproduction (Bêty *et al.*, 2004), il serait également intéressant d'étudier l'impact des variations climatiques sur les dates de départ des sites d'hivernage et des haltes migratoires durant la migration printanière. De telles études permettraient aussi de vérifier si les changements climatiques ayant lieu sur les aires d'hivernage, migratoires et de nidification progressent à un rythme différent, et d'en évaluer les conséquences sur les possibilités d'adaptation des populations qui se reproduisent dans l'Arctique et hivernent dans les régions tempérées.

RÉFÉRENCES

- Aanes R, Saether B-E, Smith FM, Cooper EJ, Wookey PA, Oritsland NA (2002) The Arctic Oscillation predicts effects of climate change in two trophic levels in a high-arctic ecosystem. *Ecology Letters*, **5**, 445-453.
- ACIA (2004) *Impacts of a warming climate: Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge, 146 pp.
- Agresti A (1990) *Categorical data analysis*. John Wiley, New York, New York, USA, 558 pp.
- Almaraz P, Amat JA (2004) Complex structural effects of two hemispheric climatic oscillators on the regional spatio-temporal expansion of a threatened bird. *Ecology letters*, **7**, 547-556.
- Arft AM, Walker MD, Gurevitch J, *et al.* (1999) Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491-511.
- Aubin AE, Dzubin A, Dunn EH, MacInnes CD (1993) Effects of summer feeding area on gosling growth in Snow Geese. *Ornis Scandinavia*, **24**, 255-260.
- Audet B (2006) *Écologie alimentaire des oisons de la Grande Oie des neiges (Chen caerulescens atlantica) en milieux mésiques sur l'Île Bylot, Nunavut*. Mémoire de maîtrise, Université Laval, Sainte-Foy, Québec, Canada.
- Bakken GS (1992) Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist*, **32**, 194-216.
- Balling RC Jr (1997) Analysis of daily and monthly spatial variance components in historical temperature records. *Physical geography*, **18**, 544-552.
- Beintema AJ, Visser GH (1989) Growth parameters in chicks of charadriiform birds. *Ardea*, **77**, 169-180.
- Berry J, Björkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*, **31**, 491-543.
- Berteaux D, Réale D, McAdam AG, Boutin S (2004) Keeping pace with fast climate change: can Arctic life count on evolution? *Integrative and Comparative Biology*, **44**, 140-151.
- Bêty J, Gauthier G, Giroux J-F (2003) Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. *American Naturalist*, **162**, 110-121.

- Bêty J, Gauthier G, Giroux J-F, Korpimäki E (2001) Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos*, **93**, 388-400.
- Bêty J, Gauthier G, Korpimäki E, Giroux J-F (2002) Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *Journal of Animal Ecology*, **71**, 88-98.
- Bêty J, Giroux J-F, Gauthier G (2004) Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology*, **57**, 1-8.
- Binkley D, Stottleyer R, Suarez F, Cortina J (1994) Soil nitrogen availability in some Arctic ecosystems in northwest Alaska: Responses to temperature and moisture. *Écoscience*, **1**, 64-70.
- Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296-298.
- Boyd H (1987) Do June temperatures affect the breeding success of dark-bellied brent geese *Branta b. bernicla*? *Bird Study*, **34**, 155-159.
- Boyd H, Madsen J (1997) Impacts of global change on arctic-breeding birds. Dans: *Global change and arctic terrestrial ecosystems, Ecological studies* (eds Oechel WC, Callaghan T, Gilmanov T, Holten JJ, Maxwell B, Molau U, Sveinbjörnsson B), **124**, 201-217. Springer, Berlin.
- Buse A, Dury SJ, Woodburn RJW, Perrins CM, Good EG (1999) Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology*, **13** (suppl.1), 74-82.
- Cadieux M-C, Gauthier G, Hughes RJ (2005) Feeding ecology of Canada Geese (*Branta Canadensis interior*) in sub-arctic inland tundra during brood-rearing. *Auk*, **122**, 144-157.
- Chapin FS III, Fetcher N, Kielland K, Everett KR, Linkins AE (1988) Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology*, **69**, 693-702.
- Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.
- Choinière L, Gauthier G (1995) Energetics of reproduction in female and male greater snow geese. *Oecologia*, **103**, 379-389.

- Cooch EG, Dzubin A, Rockwell RF (1999) Using body size to estimate gosling age. *Journal of Field Ornithology*, **70**, 214-229.
- Cooch E, Jefferies GRL, Rockwell RF, Cooke F (1993) Environmental change and the cost of philopatry: an example in the lesser snow goose. *Oecologia*, **93**, 128-138.
- Cooke F, Taylor PD, Francis CM, Rockwell RF (1990) Directional selection and clutch size in birds. *American Naturalist*, **136**, 261-267.
- Coppack T, Pulido F (2004) Photoperiodic response and the adaptability of avian life cycles to environmental change. Dans: *Birds and Climate Change, Advances in Ecological Research* (eds Moller AP, Fiedler W, Berthold P), **35**, 131-150. Academic Press, London.
- Crick QP, Dudley C, Glue DE, Thompson DL (1997) UK birds are laying eggs earlier. *Nature*, **388**, 526-526.
- Dinsmore SJ, White GC, Knopf FL (2002) Advanced techniques for modeling avian nest survival. *Ecology*, **83**, 3476-3488.
- Dormann CF, Woodin SJ (2002) Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology*, **16**, 4-17.
- Drew MC (1990) Sensing soil oxygen. *Plant, Cell and Environment*, **13**, 681-693.
- Dunn P (2004) Breeding dates and reproductive performance. Dans: *Birds and Climate Change, Advances in Ecological Research* (eds Moller AP, Fiedler W, Berthold P), **35**, 69-87. Academic Press, London.
- Fortin D (1995) *L'environnement thermique des oisons de la Grande Oie des neiges (Chen caerulescens atlantica) dans l'Arctique canadien*. Mémoire de maîtrise, Université Laval, Sainte-Foy, Québec, Canada.
- Fortin D, Gauthier G, Larochelle J (2000a) Body temperature and resting behavior of Greater Snow Goose goslings in the High Arctic. *Condor*, **102**, 163-171.
- Fortin D, Larochelle J, Gauthier G (2000b) The effect of wind, radiation and body orientation on the thermal environment of Greater Snow goose goslings. *Journal of Thermal Biology*, **25**, 227-238.
- Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004) Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology*, **10**, 1214-1221.
- Gadallah FL, Jefferies RL (1995) Forage quality in brood rearing areas of the lesser snow goose and the growth of captive goslings. *Journal of Applied Ecology*, **32**, 276-287.

- Gauthier G (1993) Feeding ecology of nesting greater snow geese. *Journal of Wildlife Management*, **57**, 216-223.
- Gauthier G, Bêty J, Giroux J-F, Rochefort L (2004) Trophic interactions in a High Arctic Snow Goose colony. *Integrative and Comparative Biology*, **44**, 119-129.
- Gauthier G, Bêty J, Hobson KA (2003) Are Greater Snow Geese capital breeders? New evidence from a stable-isotope model. *Ecology*, **84**, 3250-3264.
- Gauthier G, Giroux J-F, Bédard J (1992) Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. *Canadian Journal of Zoology*, **70**, 2077-2087.
- Gauthier G, Giroux J-F, Reed A, Béchet A, Bélanger L (2005) Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? *Global Change Biology*, **11**, 856-868.
- Gauthier G, Hugues RJ, Reed A, Beaulieu J, Rochefort L (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.
- Gauthier G, Rochefort L, Reed A (1996) The exploitation of wetland ecosystems by herbivores on Bylot Island. *Geoscience Canada*, **23**, 253-259.
- Gauthier G, Tardif J (1991) Female feeding and male vigilance during nesting in Greater Snow Geese. *Condor*, **93**, 701-711.
- Gebauer RLE, Reynolds JF, Tenhunen JD (1995) Growth and allocation of the Arctic sedges *Eriophorum angustifolium* and *E. vaginatum*: effects of variable soil oxygen and nutrient availability. *Oecologia*, **104**, 330-339
- Green RE (1984) The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in east Anglia. *Journal of Applied Ecology*, **21**, 817-830
- Gwinner E (1996) Circannual clocks in avian reproduction and migration. *Ibis*, **138**, 47-63.
- Hansell RIC, Malcom JR, Welch H, Jefferies RL, Scott PA (1998) Atmospheric change and biodiversity in the Arctic. *Environmental Monitoring and Assessment*, **49**, 303-325.
- Hartmann DL, Wallace JM, Limpasuvan V, Thompson DWJ, Holton JRB (2000) Can ozone depletion and global warming interact to produce rapid climate change? *Proceedings of the National Academy of Science of the United States of America*, **97**, 1412-1417.

- Havström M, Callaghan TV, Jonasson S (1993) Differential growth responses of *Cassiope tetragona*, an arctic dwarf-shrub, to environmental perturbations among three contrasting high- and subarctic sites. *Oikos*, **66**, 389-402.
- Henry GHR, Molau U (1997) Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology*, **3** (Suppl. 1), 1-9.
- Hodkinson ID, Webb NR, Bale JS, Block W (1999) Hydrology, water availability and tundra ecosystem function in a changing climate: the need for a closer integration of ideas? *Global Change Biology*, **5**, 359-369.
- Hollister RD, Webber PJ, Bay C (2005) Plant response to temperature in Northern Alaska: Implications for predicting vegetation change. *Ecology*, **86**, 1562-1570.
- Hughes RJ, Gauthier G, Reed A (1994) Summer habitat use and behaviour of greater snow geese *Anser caerulescens*. *Wildfowl*, **45**, 49-64.
- Huppöp O, Huppöp K (2003) North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London, Series B*, **270**, 233-240.
- Hurrell JW (1995) Decadal trends in the North Atlantic Oscillations: Regional temperatures and precipitation. *Science*, **269**, 676-679.
- Hurrell JW (2000) *Climate: North Atlantic and Arctic Oscillation (NAO/AO)*. Prepared for the National Academy of Sciences, 12th Annual Symposium on Frontiers of Science, Irvine, CA, 21 pp.
- Inglis I (1977) The breeding behaviour of the pink-footed goose: behavioural correlates of nesting success. *Animal Behaviour*, **25**, 747-764.
- IPCC (2001) *Climate Change 2001: The scientific basis*. Contribution of working group I to the third assessment report of the intergovernmental panel on climate change (eds Houghton JT, Ding Y, Griggs DJ, *et al.*), Cambridge University Press, Cambridge, 881 pp.
- JISAO: Joint Institute for the Study of the Atmosphere and Ocean (2004), site web: <http://jisao.washington.edu/ao/>.
- Kerr RA (2002) A warmer Arctic means change for all. *Science*, **297**, 1490-1492.
- Klasing KC (1998) *Comparative avian nutrition*. CAB International, New York, 350 pp.
- Larter NC, Nagy JA (2001) Seasonal and annual variability in the quality of important forage plants on Banks Island, Canadian High Arctic. *Applied Vegetation Science*, **4**, 115-128.

- Leafloor JO, Ankney CD, Rusch DH (1998) Environmental effects on body size of Canada Geese. *Auk*, **115**, 26-33.
- Lepage D, Gauthier G, Menu S (2000) Reproductive consequences of egg-laying decisions in snow geese. *Journal of Animal Ecology*, **69**, 414-427.
- Lepage D, Gauthier G, Reed A (1996) Breeding-site infidelity in greater snow geese: a consequence of constraints on laying date? *Canadian Journal of Zoology*, **74**, 1866-1875.
- Lepage D, Gauthier G, Reed A (1998) Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia*, **114**, 226-235.
- Lesage L, Gauthier G (1997) Growth and organ development in greater snow goose goslings. *Auk*, **114**, 229-241.
- Lesage L, Gauthier G (1998) Effect of hatching date on body and organ development in greater snow goose goslings. *Condor*, **100**, 316-325.
- Lindholm A, Gauthier G, Desrochers A (1994) Effects of hatch date and food supply on gosling growth in arctic-nesting greater snow geese. *Condor*, **96**, 898-908.
- Lindstrom A, Alerstam T (1992) Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *American Naturalist*, **140**, 477-491.
- Mainguy J, Bêty J, Gauthier G, Giroux J-F (2002) Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? *Condor*, **104**, 156-161.
- Mainguy J, Gauthier G, Giroux J-F, Bêty J (2006) Gosling growth and survival in relation to brood movements in greater snow geese. *Auk* (sous presse).
- Manseau M, Gauthier G (1993) Interactions between Greater Snow Geese and their rearing habitat. *Ecology*, **74**, 2045-2055.
- Martin K, Wiebe KL (2004) Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. *Integrative and comparative biology*, **44**, 177-185.
- Menu S, Gauthier G, Reed A (2001) Survival of juvenile greater snow geese immediately after banding. *Journal of Field Ornithology*, **72**, 282-290.
- Menu S, Gauthier G, Reed A (2005) Survival of young Greater Snow Geese (*Chen caerulescens atlantica*) during fall migration. *Auk*, **122**, 479-496.

- Moller AP (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology*, **71**, 201-210.
- Moller AP, Berthold P, Fiedler W (2004) The challenge of future research on climate change and avian biology. Dans: *Birds and Climate Change, Advances in Ecological Research* (eds Moller AP, Fiedler W, Berthold P), **35**, 237-245. Academic Press, London.
- Moritz RE, Bitz CM, Steig EJ (2002) Dynamics of recent climate change in the Arctic. *Science*, **297**, 1497-1502.
- Mysterud A, Stenseth NC, Yoccoz NG, Langvatn R, Steinheim G (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature*, **410**, 1096-1099.
- Olson JM (1992) Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. *Physiological Zoology*, **65**, 124-152.
- Otis P (2002) *Adaptations au froid chez les oisons, juvéniles et adultes et modèles de croissance chez la grande oie des neiges*. Mémoire de maîtrise, Université Laval, Sainte-Foy, Canada.
- Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia*, **128**, 1-14.
- Ouellet N (2006) *Effet des activités locomotrices sur la croissance des oisons de la Grande Oie des neiges*. Mémoire de maîtrise non publié, Université Laval, Sainte-Foy, Québec, Canada.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.
- Piedboeuf N, Gauthier G (1999) Nutritive quality of forage plants for greater snow goose goslings: when is it advantageous to feed on grazed plants? *Canadian Journal of Zoology*, **77**, 1908-1918.
- Ponnamperuma FN (1972) The chemistry of submerged soils. *Advances in Agronomy*, **24**, 29-96.
- Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, **83**, 553-559.
- Post E, Stenseth NC (1998) Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. *Ecology*, **67**, 537-543.

- Post E, Stenseth NC (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**, 1322-1339.
- Poussart C, Larochelle J, Gauthier G (2000) The thermal regime of eggs during laying and incubation in greater snow geese. *Condor*, **102**, 292-300.
- Przybylo R, Sheldon BC, Merilä J (2000) Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *Journal of Animal Ecology*, **69**, 395-403.
- Ratté J (1998) *Thermorégulation et croissance chez les oisons de la Grande Oie des neiges, Anser caerulescens atlantica*. Mémoire de maîtrise, Université Laval, Sainte-Foy, Québec, Canada.
- Reddy KR, Feijtel TC, Patrick WH Jr (1986) Effect of soil redox conditions on microbial oxidation of organic matter. Dans: *The role of organic matter in modern agriculture* (eds Chen Y, Avnimelech Y), pp. 117-156. Nijhoff, Dordrecht.
- Reed A, Hughes RJ, Boyd H (2002) Patterns of distribution and abundance of Greater Snow Geese on Bylot Island, Nunavut, Canada 1983-1998. *Wildfowl*, **53**, 53-65.
- Reed A, Hughes RJ, Gauthier G (1995) Incubation behavior and body mass of female greater snow geese. *Condor*, **97**, 993-1001.
- Reed E, Gauthier G, Giroux J-F (2004) Effects of spring conditions on breeding propensity of Greater Snow Goose females. *Animal Biodiversity and Conservation*, **27.1**, 35-46.
- Reed ET, Gauthier G, Pradel R, Lebreton J-D (2003) Age and environmental conditions affect recruitment in Greater Snow Geese. *Ecology*, **84**, 219-230.
- Renaud M (1999) *Coûts énergétiques de la thermorégulation chez les jeunes de la grande oie des neiges en milieu naturel*. Mémoire de maîtrise, Université Laval, Sainte-Foy, Canada.
- Richardson WJ (1990) Timing of bird migration in relation to weather: updated review. Dans: *Bird migration* (eds Gwinner E), pp. 78-101. Berlin, Springer Verlag.
- Rigor I, Colony GRL, Martin S (2000) Variations in surface air temperature observations in the Arctic, 1979-97. *Journal of Climate*, **13**, 896-914.
- Rockwell RF, Thompson EG, Thompson CB, Cooke F (1993) Age and reproductive success in female lesser snow geese: experience, senescence and the cost of philopatry. *Journal of Animal Ecology*, **62**, 323-333.
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-60.

- Rowe L, Ludwig D, Schluter D (1994) Time, condition, and the seasonal decline of avian clutch size. *American Naturalist*, **143**, 698-722.
- Rustad LE, Campbell JL, Marion GM, *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543-562.
- Sagarin R (2001) Phenology - False estimates of the advance of spring. *Nature*, **414**, 600.
- Samelius G, Alisauskas RT (2001) Detering arctic fox predation: the role of parental nest attendance by lesser snow geese. *Canadian Journal of Zoology*, **79**, 861-866.
- Sanz JJ, Potti J, Moreno J, Merino S, Frías O (2003) Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology*, **9**, 461-472.
- SAS institute. (2002-2003) *SAS/STAT User's Guide Version 9.1*. SAS Institute, Cary, NC, USA.
- Schekkerman H, Van Roomen MWJ, Underhill LG (1998) Growth, behaviour of broods and weather-related variation in breeding productivity of curlew sandpipers *calidris ferruginea*. *Ardea*, **86**, 153-168.
- Schmutz JA (1993) Survival and pre-fledging body mass in juvenile Emperor Geese. *Condor*, **95**, 222-225.
- Sedinger JS, Flint PL (1991) Growth rate is negatively correlated with hatch date in Black Brant. *Ecology* **72**:496-502.
- Sedinger JS, Flint PL, Lindberg MS (1995) Environmental influence on life-history traits: growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology*, **76**, 2404-2414.
- Sedinger JS, Herzog MP, Person BT, Kirk MT, Obritchkewitch T, Martin PP, Stickney AA (2001) Large-scale variation in growth of Black Brant goslings related to food availability. *Auk*, **118**, 1088-1095.
- Sedinger JS, Raveling DG (1984) Dietary selectivity in relation to availability and quality of food for goslings of Cackling Geese. *Auk*, **101**, 295-306.
- Sedinger JS, Raveling DG (1986) Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. *Journal of Animal Ecology*, **55**, 1083-1102.
- Sedinger JS, Raveling DG (1988) Foraging behavior of cackling Canada Goose goslings: implications for the roles of food availability and processing rate. *Oecologia*, **75**, 119-124.

- Serreze MC, Carse F, Barry RG (1997) Icelandic low cyclone activity: climatological features, linkages with the NAO, and relationships with recent changes in the northern hemisphere circulation. *American Meteorological Society*, **10**, 453-464.
- Sheaffer SE, Malecki RA (1996) Predicting breeding success of Atlantic population Canada geese from meteorological variables. *Journal of Wildlife Management*, **60**, 882-890.
- Shindell D, Miller RL, Schmidt GA, Pandolfo L (1999) Simulation of recent northern winter climate trends by greenhouse-gas forcing. *Nature*, **399**, 452-455.
- Singer JD (1998) Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *Journal of Educational and Behavioral Statistics*, **24**, 323-355.
- Skinner WR, Jefferies RL, Carleton TJ, Rockwell RF, Abraham KF (1998) Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. *Global Change Biology*, **4**, 3-16.
- Sparks TH, Carey PD (1995) The responses of species to climate over two centuries: an analysis of the Marsham phenological record, 1736-1947. *Journal of Ecology*, **83**, 321-329.
- Stenseth NC, Ottersen G, Hurrell JW, *et al.* (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 2087-2096.
- Stone DA, Weaver AJ, Zwiers FW (2000) Trends in Canadian precipitation intensity. *Atmosphere-Ocean*, **2**, 321-347.
- Tarnocai C, Zoltai SC (1988) Wetlands of Arctic Canada. Dans: *Wetlands of Canada* (ed National Wetlands Working group), pp. 27-53. Ecological Land Classification Series, no. 24. Environnement Canada, Ottawa, Ontario et Polyscience Publications Inc., Montréal, Québec.
- Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, **291**, 2598-2600.
- Thompson DWJ, Wallace JM (1998) The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters*, **25**, 1297-1300.
- Thompson SC, Raveling DG (1987) Incubation behaviour of Emperor Geese compared with other geese: interactions of predation, body size, and energetics. *Auk*, **104**, 707-716.

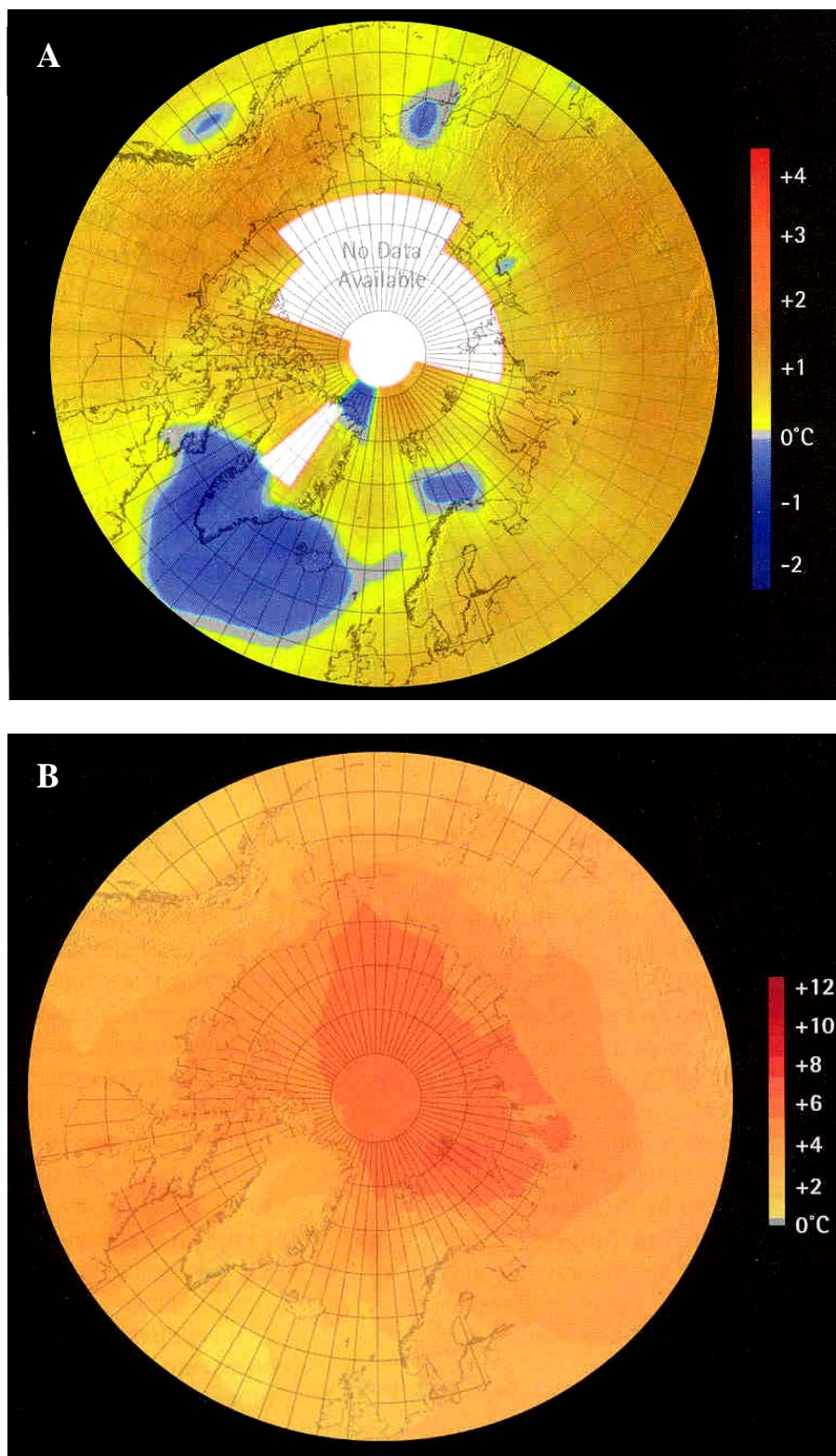
- Tryjanowski P, Kuzniak S, Sparks T (2002) Earlier arrival of some farmland migrants in western Poland. *Ibis*, **144**, 62-68.
- Visser ME, Both C, Lambrechts MM (2004) Global climate change leads to mistimed avian reproduction. Dans: *Birds and Climate Change, Advances in Ecological Research* (eds Moller AP, Fiedler W, Berthold P), **35**, 89-109. Academic Press, London.
- Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1867-1870.
- Walker BH (1997) Global change and terrestrial ecosystems: the GCTE research program for the arctic. Dans: *Global change and arctic terrestrial ecosystems, Ecological studies* (eds Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, Sveinbjörnsson B), **124**, v-xii. Springer, Berlin.
- Walsberg GE (1983) Avian ecological energetics. Dans: *Avian Biology* (eds King Farner DS et JR), **7**, 161-220. Academic Press, New York.
- Weatherhead PJ (2005) Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. *Oecologia*, **144**, 168-175.
- Welker JM, Rayback S, Henry GHR (2005) Arctic and North Atlantic Oscillation phase changes are recorded in the isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) of *Cassiope tetragona* plants. *Global Change Biology*, **11**, 997-1002.
- White RG, Trudell J (1980) Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. *Arctic and Alpine Research*, **12**, 511.
- Williams TD, Cooch EG (1996) Egg size, temperature and laying sequence: why do snow geese lay big eggs when it's cold? *Functional Ecology*, **10**, 112-118.
- Winder M, Schindler DE (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, **85**, 2100-2106.
- Winkel W, Hudde H (1997) Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and Pied Flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology*, **28**, 187-190.
- Winkler DW, Dunn PO, McCulloch CE (2002) Predicting the effects of climate change on avian life-history traits. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 13595-13599.
- Wookey PA, Parsons AN, Welker JM, Potter JA, Callaghan TV, Lee JA, Press MC (1993) Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. *Oikos*, **67**, 490-502.

Zöckler C, Lysenko I (2000) *Water Birds on the Edge: First circumpolar assessment of climate change impact on Arctic breeding water birds*. WCMC - World Conservation Press. WCMC Biodiversity Series No. 11, 28 pp.

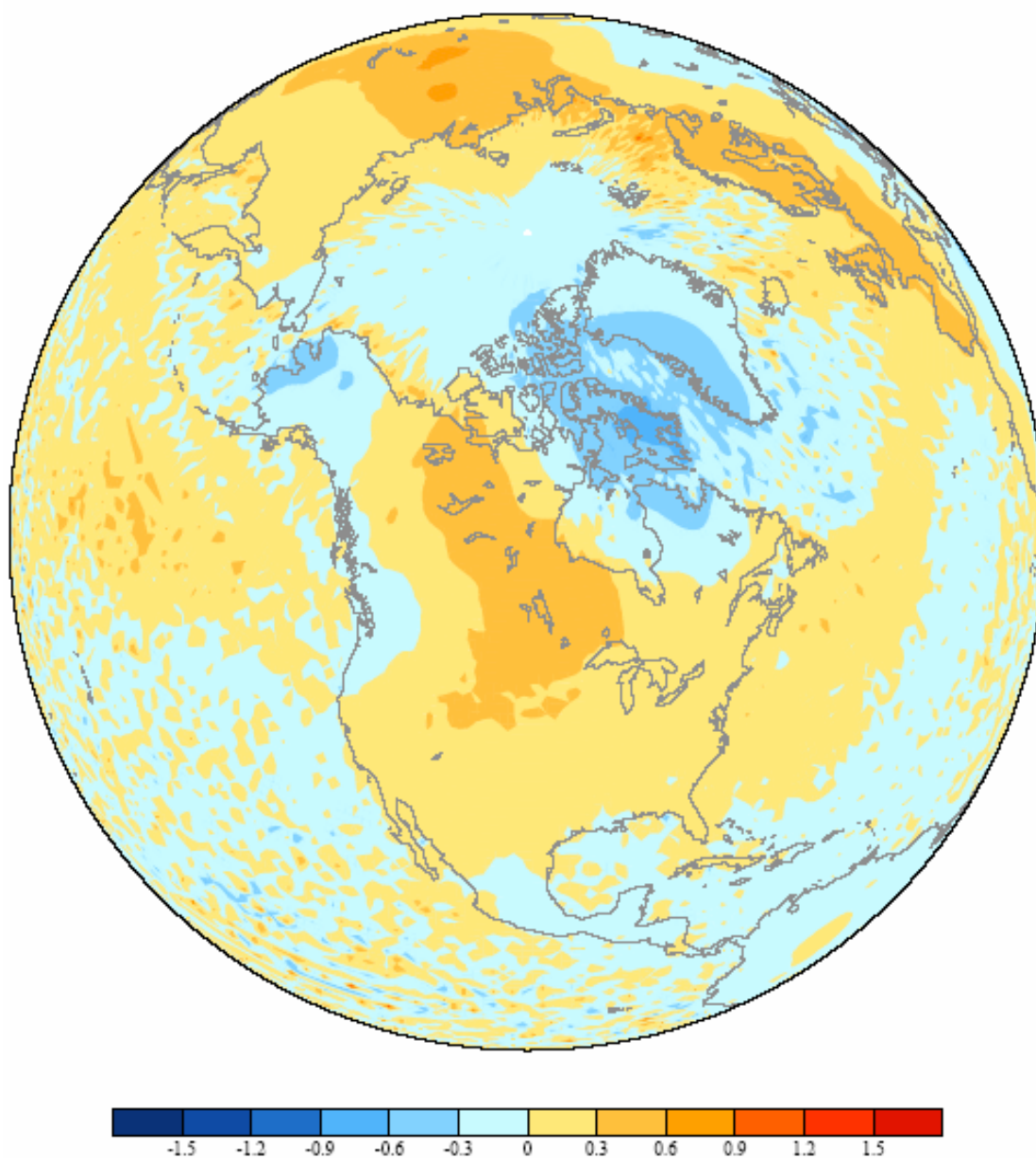
ANNEXES



Annexe 1. Localisation de l'aire d'étude, Île Bylot, Nunavut, Canada



Annexe 2. Changements annuels de la température de l'air (°C), A) observés de 1954 à 2003 et B) prévus pour 1990-2090 selon le scénario B2 (ce scénario d'émissions des gaz à effet de serre prévoit que le monde futur sera axé sur la protection environnementale et l'équité sociale) (tiré de ACIA, 2004).



Annexe 3. Anomalies de températures de l'indice estival de l'Oscillation Arctique (OA) correspondant à plus ou moins un écart-type de l'OA, de 1979 à 1997. Le signe de l'anomalie sur la carte est corrélée positivement à l'indice de l'OA (Tiré du site web du JISAO, 2004).