ANNA M. CALVERT

VARIATIONS SPATIALES ET TEMPORELLES DE LA MORTALITÉ DUE À LA CHASSE ET LES EFFETS DES MESURES DE GESTION CHEZ LA GRANDE OIE DES NEIGES (*Chen caerulescens atlantica*)

Mémoire présenté
à la Faculté des études supérieures de l'Université Laval
dans le cadre du programme de maîtrise en biologie
pour l'obtention du grade de maître ès sciences (M.Sc.)

FACULTÉ DES SCIENCES ET DE GÉNIE
UNIVERSITÉ LAVAL
QUÉBEC

MARS 2004

RÉSUMÉ

L'objectif principal de ce mémoire était d'examiner les caractéristiques à long terme de la récolte sportive de la Grande Oie des neiges (*Chen caerulescens atlantica*), afin d'améliorer nos connaissances des effets de l'exploitation sur la démographie des populations de sauvagine. Une analyse des variations temporelles et géographiques de la récolte pendant 30 ans a indiqué que des changements dans la distribution pendant la halte migratoire et surtout sur les aires d'hivernage ont probablement contribué au déclin du taux de récolte, ce qui a permis la croissance rapide de la population dans les années 1980. Des analyses de récupérations de bagues ont démontré une augmentation de la mortalité à la chasse chez les adultes avec l'initiation de mesures de gestion spéciales en 1999, et un déclin correspondant dans la survie adulte a aussi été noté. Sur une base saisonnière, la nouvelle chasse printanière et la libéralisation des règlements de la chasse hivernale semblaient contribuer à l'augmentation de la mortalité annuelle, mais aucun effet n'a été observé en automne. Ces résultats suggèrent qu'une manipulation de la récolte pendant les saisons régulières d'automne et d'hiver pourrait être utile pour la gestion future si la chasse printanière est arrêtée.

ANNA CALVERT, étudiante graduée

GILLES GAUTHIER, directeur de recherche

ABSTRACT

The main objective of this thesis was to examine long-term characteristics of the sport harvest of greater snow geese (*Chen caerulescens atlantica*) to improve our understanding of how exploitation impacts the demography of waterfowl populations. Analysis of temporal and geographic trends in the harvest over 30 years indicated that changes in distribution on staging and especially wintering grounds may have contributed to a decline in harvest rate that allowed for rapid growth of the population in the 1980s. Band recovery analyses demonstrated an increase in adult hunting mortality with the initiation of special conservation measures in 1999, and a corresponding decline in adult survival was also noted. On a seasonal basis, the new spring hunt and the liberalisation of winter hunting regulations appeared to contribute to the increase in annual hunting mortality, but no effect of relaxed fall hunting regulations was observed. The results suggest that harvest manipulations during the regular fall and winter hunting seasons could be effective for future management if the spring hunt is discontinued.

ANNA CALVERT, graduate student

GILLES GAUTHIER, supervisor

AVANT-PROPOS

Ce mémoire est divisé en quatre sections principales. Premièrement, l'introduction générale présente le domaine de ma recherche, soit la gestion de populations animales exploitées, et explique la problématique de la surpopulation de la Grande Oie des neiges. Cette première partie inclut aussi une discussion de l'approche méthodologique suivie au cours de mon étude, et une description des objectifs principaux du projet. Ensuite, le corps du mémoire est composé de deux chapitres sous la forme d'articles scientifiques écrits en anglais, afin de les publier dans des revues avec comité de lecture. J'ai été l'auteur principal des deux articles, en faisant toutes les analyses et la rédaction. Le premier, qui concerne les variations spatiales et temporelles de la récolte sportive de cette espèce, a été soumis à la revue « Journal of Wildlife Management » en septembre 2003, mais une réponse est toujours attendue. Pour cet article, mes co-auteurs étaient mon directeur Gilles Gauthier ainsi que Austin Reed, un membre de mon comité qui a beaucoup contribué à la collecte des données. Le deuxième article, concernant les effets des changements de règlements de chasse sur la survie et la mortalité à la chasse, sera bientôt soumis à une revue (pas encore spécifiée), ayant comme auteurs Gilles Gauthier et moi. Finalement, le mémoire se termine avec une conclusion générale qui résume les résultats importants de mon étude en suggérant des implications pour la gestion de cette population dans l'avenir.

modélisation et de m'impliquer dans des questions importantes pour la gestion de la faune. Il m'a engagée comme étudiante quand je connaissais très peu le domaine, et quand mon français était loin d'être parfait. Il m'a donné la chance d'utiliser une très grande base de données et m'a encouragée à travailler indépendamment. En même temps, il a répondu à toutes mes questions et m'a fourni des suggestions approfondies pendant les analyses et la rédaction. Je me considère très chanceuse d'avoir participé à son programme de recherche, et cela va certainement influencer mes travaux dans l'avenir, donc merci Gilles!

Je veux aussi remercier les membres de mon comité, Steeve Côté et Austin Reed, de m'avoir aidée à améliorer ma recherche dès le début et de m'avoir aidé à améliorer mon mémoire. Austin a aussi fréquemment répondu à des questions par rapport aux données que j'utilisais et a ajouté des informations historiques importantes, en plus de participer à la rédaction du premier article, et je lui en suis très reconnaissante.

Ici à l'Université, j'ai eu la chance de connaître beaucoup de personnes intéressantes, y compris des étudiants dans notre labo et d'autres qui ont beaucoup amélioré mon ambiance de travail. Ceux-ci incluent : Morgane Lamote (la folle - merci encore pour toutes tes corrections!), Marie-Christine Cadieux (ma jumelle), Hélène Sénéchal (Crazy Chicken), Niko Lecomte, David Veliz (Oh No!), Eric Reed, Isabelle Duclos, Miguel Pardo, Grég Bourguelat, Mathieu Féret, Julien Mainguy, Joël Béty, Catherine Gagnon, Marie-Hélène Dickey, Benoit Audet, Annie Langlois, Guy Perry, Sean Rogers et Andy Casper, pour en mentionner seulement quelques-uns. En plus, Gérald Picard (il n'est pas étudiant, même qu'il adore les stats!) a ajouté beaucoup de fun au labo, en plus d'aider la recherche de données et le travail de terrain. Aussi, Eric Reed a non seulement été un ami de labo, mais aussi m'a souvent donné des conseils au cours de la modélisation avec cher MARK, et durant la rédaction. Sans l'aide de tous ces gens, ça aurait été une expérience beaucoup moins le fun!

Mon travail de terrain pendant l'été 2002 m'a permis de découvrir la beauté de l'Arctique canadien, une région merveilleuse où j'ai passé trois mois inoubliables qui vont influencer mes intérêts de recherche et ma vie future. Ça m'a aussi donné l'opportunité de travailler avec un groupe de personnes magnifiques, qui sont vite devenues des amis : Catherine Gagnon, Olivier Mathieu, Vincent Préfontaine, Niko Lecomte, Marie-Claire Bédard, Claudia St-Arnaud, Isabelle Duclos, Julien Mainguy et Kelly Akpaleapik ont tous amélioré cette expérience.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

INTRODUCTION GÉNÉRALE

INTRODUCTION

Une meilleure compréhension des impacts humains sur les populations animales est essentielle pour une saine conservation et gestion de la faune. Nous affectons la survie et la persistance des animaux dans notre environnement via la destruction d'habitat, la pollution, les changements climatiques et l'exploitation de la faune. Pour les espèces exploitées en particulier, les effets anthropiques tels que la chasse et la pêche sportives ou la création de refuges peuvent amener des changements extrêmes, non naturels d'abondance.

Il existe probablement de nombreux exemples où l'étendue de nos impacts sur les populations animales n'est pas bien connue, mais pour certaines situations l'ampleur de ces impacts a pu être établi. Par exemple, la majorité des populations mondiales de grands poissons marins ont subi une forte pression de la part des pêcheries industrielles (Pauly et al. 2002), ce qui a réduit leur abondance d'environ 90% (Myers et Worm 2003). Certaines populations sont tellement décimées qu'il semble impossible qu'elles se rétablissent d'elles mêmes dans leur milieu naturel. Un bon exemple est le cas de la morue Atlantique (*Gadus morhua*) qui ne démontre aucune évidence de rétablissement malgré une forte réduction de la pression de pêche (Hutchings 2000). De nombreuses espèces de grands mammifères sont aussi gravement menacées à cause de la chasse et du braconnage à tel point que l'extinction de ces espèces est à prévoir dans un avenir proche (e.g. Rabinowitz 1995, Wikramanayake et al. 1998).

Par contre, il y a des situations où les impacts anthropiques ont eu un effet opposé sur les populations animales en favorisant une explosion démographique. Par exemple, plusieurs populations d'oies en Amérique du Nord sujettes à la chasse sportive ont démontré une croissance sans précédent, encouragée par la présence de refuges où la chasse est interdite et par une disponibilité accrue de nourriture dans les terres agricoles (Ankney 1996). De même, une surabondance de cerfs de Virginie (*Odocoileus virginianus*) dans l'est de l'Amérique du Nord, provoquée par leur adaptabilité aux changements d'habitat et l'élimination de leurs prédateurs par l'homme (Halls 1984), a causé des craintes pour le bien-être des plantes et des animaux avec qui les cerfs partagent les mêmes habitats. Cet excès de grands mammifères est d'ailleurs à l'origine d'un vif débat sur les stratégies à employer afin de réduire leur abondance (e.g. Warren 1991). Dans de nombreux cas où les effets anthropiques ont sévèrement perturbé les niveaux de populations animales, l'exploitation par

la chasse est souvent manipulée par les gestionnaires afin d'essayer d'augmenter ou de diminuer la mortalité, et ultimement de ramener la taille de la population à un niveau désiré.

Afin d'éviter des situations où l'abondance d'une espèce exploitée atteint un niveau problématique, le concept de gestion adaptative ou "adaptive harvest management" a été développé. Ce concept appelle à une réévaluation fréquente de l'impact des mesures de gestion dans le but de maximiser la probabilité d'arriver aux résultats visés (Walters 1986). En mettant en place des systèmes de gestion adaptative, les gestionnaires cherchent alors à mieux comprendre les liens entre la biologie des populations et les effets de l'exploitation par la chasse, en reconnaissant l'incertitude associée à toute décision de gestion (Williams et al. 1996). Spécifiquement, la manipulation des règlements de chasse et le suivi des effets qui en découlent est recommandée comme une manière active de comprendre pleinement les impacts de l'exploitation (Walters et Holling 1990, Williams et Johnson 1995).

HYPOTHÈSES DE MORTALITÉ ADDITIVE ET COMPENSATOIRE

Une question importante par rapport à la gestion d'espèces exploitées concerne la possibilité que la mortalité naturelle puisse compenser la mortalité due à la chasse. Anderson et Burnham (1976) ont proposé deux hypothèses alternatives : (1) que la mortalité par la chasse et la mortalité naturelle sont inversement reliées jusqu'à un certain seuil, toute mortalité causée par la chasse sous ce seuil étant compensée par une réduction de la mortalité naturelle (compensation complète; Figure 1); ou (2) que la mortalité naturelle est indépendante de la mortalité causée par la chasse, la mortalité par la chasse s'additionnant à la mortalité naturelle pour augmenter la mortalité totale (additivité complète; Figure 1).

Il est important de savoir laquelle de ces deux alternatives s'applique pour la gestion des populations exploitées, car l'utilité de la chasse comme outil de gestion dépend de cette relation. L'hypothèse de mortalité compensatoire nécessite une forme de régulation dépendante de la densité, où les individus tués à la chasse seraient quand même morts naturellement car la capacité de support était dépassée; une augmentation de mortalité à la chasse apporte alors une diminution de la mortalité naturelle (Anderson et Burnham 1976). En particulier, des processus dépendants de la densité qui sont saisonniers et qui ne s'appliquent qu'à certaines périodes de l'année peuvent être importants dans la compensation (Kokko et Lindstrom 1998). Par exemple, des facteurs dépendants de la
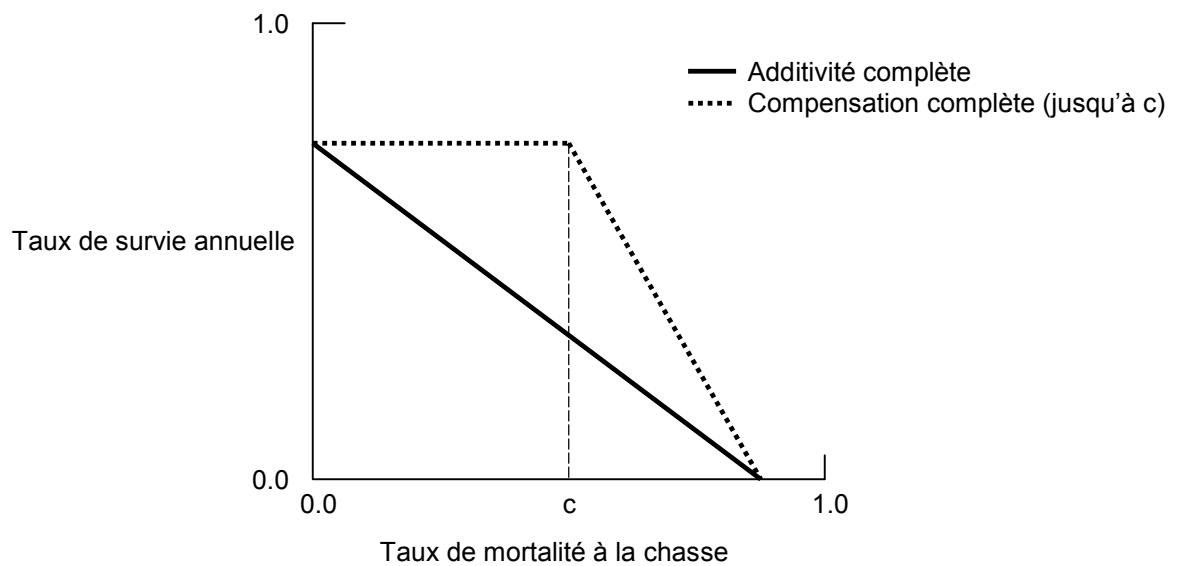
Figure 1. La relation entre le taux de survie annuelle et le taux de mortalité à la chasse, selon la relation d'additivité ou de compensation. Pour la compensation, toute augmentation de mortalité à la chasse jusqu'à un seuil (noté c) n'apporte aucun impact sur la survie; pour l'additivité, par contre, la relation est directe et négative (d'après Anderson et Burnham 1976, Nichols 1991a).

densité qui sont importants seulement après la saison de chasse, et donc qui opèrent seulement quand la population est réduite, peuvent ainsi permettre une augmentation de la survie qui compense la mortalité provenant de la chasse (Boyce et al. 1999). À cause de cette régulation dépendante de la densité, les manipulations de la chasse pour ces espèces ont peu d'effet sur la mortalité totale, et ainsi ne sont pas avantageuses pour gérer les populations. Par contre, la mortalité additive se retrouve souvent chez des espèces ne démontrant aucune ou peu d'évidence de régulation dépendante de la densité, et dans ces cas la mortalité à la chasse tue surtout des animaux qui auraient autrement survécus (Anderson et Burnham 1976). Par conséquent, pour ces populations la manipulation de règlements de chasse peut être très utile pour leur gestion si elle apporte des changements dans la mortalité à la chasse, car la survie totale sera affectée.

Bien que ces hypothèses ont été testées chez d'autres espèces telles que les poissons (e.g. Allen et al. 1998) et les mammifères (e.g. Dusek et al. 1992), les questions de mortalité additive et compensatoire ont été examinées plus en détails chez la sauvagine. Dans leurs études sur les Mallards (*Anas platyrhynchos*), Anderson et Burnham (1976, 1978) ont démontré que la mortalité à la chasse était surtout compensatoire, et donc que les changements des règlements de chasse (et du nombre d'oiseaux tués) avaient relativement peu d'effets sur la mortalité totale. Depuis ce temps, les hypothèses de mortalité compensatoire et additive ont été examinées chez plusieurs espèces, avec des résultats variables. En effet, les résultats obtenus par d'autres études chez diverses espèces exploitées sont partagés entre les hypothèses de mortalité additive (Barker et al. 1991, Dusek et al. 1992, Hestbeck 1994, Longcore et al. 2000) et compensatoire (Halse et al. 1993, Boyce et al. 1999), ou sont ambiguës (Krementz et al. 1988, Conroy et Krementz 1990, Allen et al. 1998, Francis et al. 1998). Devant ces résultats contradictoires, plusieurs chercheurs suggèrent que les effets de la chasse sont spécifiques à chaque population, et donc que les décisions de gestion doivent être prises avec prudence (Nichols et al. 1984, Conroy et Krementz 1986, Krementz et al. 1988, Nichols 1991a).

Le Canard Noir (*Anas rubripes*), une espèce exploitée et en déclin, a souvent servi comme modèle pour tester ces hypothèses de mortalité. Depuis les années 1950, les populations de Canards Noirs ont montré une décroissance marquée et inquiétante (Anderson et al. 1987). Ceci a d'abord été attribué à des niveaux de chasse trop élevés, mais même après l'établissement de règlements plus stricts, la population a continué à diminuer (Anderson et

al. 1987, Conroy et Krementz 1990). Plusieurs études, ayant pour but de déterminer la relation entre la mortalité par la chasse et la mortalité totale, ont été entreprises avec des résultats contradictoires (Conroy et Krementz 1990, Francis et al. 1998, Longcore et al. 2000). Anderson et al. (1987) et Nichols (1991a, b) ont suggéré que la seule façon de régler ce débat, et d'acquérir les connaissances nécessaires pour mieux gérer la population, serait d'utiliser des manipulations expérimentales. Ils ont suggéré qu'une comparaison des taux de survie et de mortalité entre années consécutives avec et sans chasse, ou entre années où on a fait varier la pression de chasse selon des niveaux fixés *a priori*, serait la meilleure façon d'établir la relation entre la chasse et la mortalité totale des espèces exploitées (Anderson et al. 1987, Nichols 1991a, b), mais de telles opportunités sont rares.

En plus de la question de mortalité à la chasse additive versus compensatoire, la gestion de populations de sauvagine peut être compliquée par la présence de sous-populations présentant des tendances différentes parmi des populations d'une même espèce. Chez la Bernache du Canada (*Branta canadensis*) de la voie migratoire de l'Atlantique, deux tendances opposées ont été démontrées dans les années 1980: alors que les populations migratrices diminuaient considérablement, les populations résidentes, qui ne migrent pas du tout, augmentaient rapidement (Lindberg et Malecki 1994, Heusmann 1999, Malecki et al. 2001). En conséquence, des restrictions ont été mises en place sur la chasse des bernaches migratrices pendant que des saisons de chasse spéciales étaient établies pour essayer de contrôler le nombre de résidentes (Heusmann 1999, Malecki et al. 2001). Cependant, la capacité des chasseurs à distinguer les oiseaux des deux populations étant douteuse, le succès de chacune de ces mesures de gestion a été remis en question (Lindberg et Malecki 1994, Heusmann 1999). En plus, la relation entre la mortalité totale et la pression de chasse pour cette espèce n'a pas été entièrement établie, compliquant encore plus la gestion de ces deux populations. D'une part, une étude suggère que chez les Bernaches il n'y a pas de lien entre la survie et les règlements de chasse (Rexstad 1992), tandis que d'autres études ont trouvé un effet mineur (Raveling et al. 1992) ou significatif de la pression de chasse sur la mortalité, et recommandent donc des changements des règlements de chasse pour gérer ces populations (Hestbeck et Malecki 1989a, Hestbeck 1994).

LA PROBLÉMATIQUE DE SURPOPULATION DES OIES DES NEIGES
Un exemple pertinent d'un problème de gestion de la sauvagine est celui des nombreuses populations d'oies dans l'hémisphère Nord. Plusieurs de ces populations ont démontré une

forte croissance démographique pendant la deuxième moitié du vingtième siècle (Madsen 1991, Ankney 1996, Abraham et Jefferies 1997, mais voir King et Derkson 1986). La possibilité d'une régulation dépendante de la densité en relation avec la capacité de support des milieux naturels chez les oies est contestée (Owen et Black 1989, Loonen et al. 1997, Massé et al. 2001, Menu et al. 2002), et les populations en Amérique du Nord en particulier démontrent une croissance exponentielle qui ne semble pas ralentir (Ankney 1996). Ceci a été attribuée à une disponibilité accrue et presque illimitée de nourriture dans les champs agricoles pendant la migration et sur les aires d'hivernage, leur permettant ainsi d'atteindre un taux de survie plus élevé pendant l'hiver (Owen et Black 1991), et à leur capacité de se disperser vers d'autres aires de reproduction pour éviter les régions qui ont été sur-broutées (Abraham et Jefferies 1997). De plus, le taux de mortalité par la chasse a apparemment diminué à mesure que les populations augmentaient (Ankney 1996, Abraham et Jefferies 1997). Les deux sous-espèces d'Oie des neiges en particulier ont atteint une telle surabondance que cela peut causer des risques à la fois pour les populations elles-mêmes ainsi que pour leurs écosystèmes.

Chez les Oies des neiges, les études ont montré que la mortalité à la chasse est additive à la mortalité naturelle (Francis et al. 1992, Gauthier et al. 2001, Menu et al. 2002). En dépit de leur grande abondance, ces populations semblent peu affectées par des facteurs dépendants de la densité pendant les saisons de chasse, un élément essentiel pour que la mortalité à la chasse soit compensatoire. Dans ce contexte, des changements de la pression de chasse pourraient être utiles pour limiter la croissance de ces populations (Menu et al. 2002). De plus, la compensation est difficile chez de telles espèces car leur longue durée de vie et leur faible taux de mortalité naturelle laissent peu de marge de manœuvre pour un abaissement de la mortalité naturelle en présence de chasse (Anderson et Burnham 1976, Gauthier et al. 2001). Par conséquent, la manipulation de la chasse est devenue un facteur important dans la gestion de ces populations.

La Petite Oie des neiges a démontré une forte croissance depuis plusieurs décennies (récemment, au moins 5 % par an), surtout chez les populations de la région de la Baie d'Hudson (Kerbes et al. 1990, Cooch et Cooke 1991, Boyd 2000, Cooke et al. 2000). On a détecté quelques évidences d'effets dépendants de la densité pendant la saison reproductive, comme une diminution de la masse des oisons et de la production d'œufs et une augmentation de la mortalité des jeunes (Cooch et Cooke 1991, Abraham et Jefferies

1997), mais les populations continuent néanmoins à croître. Les communautés de plantes dont les oies sont dépendantes pour se nourrir pendant l'été ont été beaucoup affectées par la surabondance et l'extension des aires de reproduction; la surexploitation des ressources par ces oies pourrait ainsi affecter d'autres espèces utilisant le même habitat (Kerbes et al. 1990, Abraham et Jefferies 1997). Plusieurs mesures de gestion ont été évaluées comme des solutions possibles à ce problème de surabondance. Rockwell et al. (1997) ont conclu que pour diminuer la population à un niveau raisonnable et la maintenir à cette taille, une réduction substantielle de la survie des adultes était nécessaire. Pour atteindre cet objectif, ils ont calculé que le nombre d'oies tuées par la chasse devrait être augmenté par un facteur de 2 ou 3 (Rockwell et al. 1997). Cet objectif pourrait être atteint avec des changements de la durée des saisons de chasse, des méthodes permises et des limites de prises (Johnson 1997). Cependant, d'autres auteurs ont soutenu que la libéralisation seule des règlements de chasse n'était peut-être pas suffisante (Francis 2000) car, selon leurs calculs, c'est plutôt une augmentation de 3 à 7 fois du niveau d'exploitation qui serait requis pour réduire la survie à un niveau permettant une réduction de la population (Cooke et al. 2000). Toutefois, le consensus était qu'une forte augmentation du taux d'exploitation par la chasse était nécessaire pour une meilleure gestion de cette population.

La Grande Oie des neiges a aussi démontré des tendances inquiétantes depuis les années 1960, semblables à celles de la Petite Oie des neiges. Entre 1965 et 1997, la taille de la population printanière a augmenté par un facteur 12, et le taux de croissance entre 1983 et 1997 était de 9.7% par an (Reed et al. 1998). On a aussi observé une augmentation de l'utilisation des terres agricoles pendant la migration provoquant ainsi des dommages aux récoltes, et une diminution du taux de récolte par la chasse (Filion et al. 1998, Reed et al. 1998, Giroux et al. 1998a, Menu et al. 2002). Le broutement des oies a également réduit la production végétale de la colonie de l'Île Bylot (Giroux et al. 1998a), bien que la population ne semble pas encore avoir atteint la capacité de support théorique de ces terrains d'été dans l'Arctique (Massé et al. 2001). En plus, la distribution des oies au Québec pendant les haltes migratoires s'est beaucoup étendue depuis les années 1970, les oies se retrouvant maintenant plus à l'ouest et à l'est de leur aire habituelle dans le haut estuaire du St-Laurent (Reed et al. 1998). Parce que la tradition de chasse de l'Oie des neiges est beaucoup plus forte dans la région de l'estuaire du St-Laurent que dans les régions aux alentours (Freemark et Cooch 1978), il est possible que la mortalité par la chasse ait diminué à mesure que les oies s'éloignaient de leurs aires traditionnelles, contribuant ainsi à la croissance de la

population. D'ailleurs, le taux de récolte des oies calculé d'après des enquêtes auprès des chasseurs a démontré une diminution marquée dans le milieu des années 1980 (Menu et al. 2002), ce qui a coïncidé avec la croissance accélérée de la population. Ceci suggère donc qu'une baisse de la mortalité à la chasse aurait fortement contribué au problème de surabondance.

Face à cette situation, les membres du Arctic Goose Habitat Working Group ont aussi recommandé une augmentation des taux de récolte à la chasse pour cette population (Batt 1998, Giroux et al. 1998b). La Grande Oie des neiges, comme d'autres espèces à longue durée de vie, démontre une mortalité à la chasse additive à la mortalité naturelle (Gauthier et al. 2001), ce qui suggère que la chasse pourrait être utile comme outil de gestion pour diminuer l'abondance. De plus, les variations du taux de chasse expliquent assez bien les variations du taux de croissance de cette population depuis 30 ans (Menu et al. 2002). En conséquence, plusieurs modifications des règlements de chasse ont été proposées, comme l'établissement d'une chasse de conservation hors de la saison régulière, afin d'arrêter la croissance de cette population (Giroux et al. 1998b). Des simulations ont indiqué que, parce que la survie des adultes était le facteur qui affectait le plus la croissance, la chasse devrait augmenter de 1.6 à 2 fois pour stabiliser la population (Gauthier et Brault 1998). Suite à ces recommandations, les règlements de chasse ont changé en 1998-99. Depuis ce temps, une saison de chasse de conservation printanière a été instaurée chaque année pendant la halte migratoire, et les méthodes de chasse permises ont été libéralisées, permettant l'utilisation de méthodes auparavant interdites telles que les appeaux électroniques et la technique d'approche (CWS Waterfowl Committee 2001a,b).

Ces changements dans les règlements de chasse avaient pour but premier de réduire la survie des adultes afin d'arrêter la croissance de la population le plus rapidement possible. Cependant, l'introduction d'une nouvelle saison de chasse, une action unique dans le domaine de gestion de la sauvagine depuis la promulgation de la « loi sur la Convention concernant les oiseaux migrateurs » en 1916, a aussi apporté d'autres effets qu'une simple augmentation de la mortalité. La chasse printanière a augmenté le dérangement des oies, ce qui a amené des changements dans leur déplacement en halte migratoire (Béchet et al. 2003); en se déplaçant plus souvent, elles ont aussi passé moins de temps à s'alimenter (Béchet et al. sous presse). Ce dérangement a diminué l'accumulation de graisses et de protéines (Féret et al. 2003), apportant un impact négatif sur la reproduction (Mainguy et al.

2002, Bêty et al. 2003). Ces impacts additionnels n'étaient pas anticipés dans le plan d'action pour stabiliser la population, ce qui souligne l'importance d'une bonne compréhension de tous les effets biologiques possibles de ces mesures de gestion. C'est donc seulement en étant conscients de l'étendue des implications de leurs actions que les gestionnaires pourront prédire les effets de modifications importantes aux règlements de chasse dans l'avenir.

CONTEXTE DE L'ÉTUDE

La Grande Oie des neiges fournit un excellent modèle d'étude du rôle de la chasse comme outil de gestion de la faune. En particulier, la croissance récente de la population et les modifications des règlements de chasse qui ont été mises en place pour la contrôler offrent une opportunité unique pour évaluer les effets de telles mesures de gestion sur une espèce animale. Tout changement du taux de mortalité résultant de ces nouvelles mesures pourrait confirmer si la chasse a bien les effets attendus sur la dynamique de population des Grandes Oies des neiges.

Le concept de gestion adaptative encourage l'utilisation des changements de règlements pour mieux comprendre les effets de la chasse, et le cas de la Grande Oie des neiges en fournit un exemple. Les manipulations expérimentales sont un outil puissant pour évaluer les conséquences démographiques de différents régimes d'exploitation (Nichols 1991a). Or, l'instauration des mesures de gestion exceptionnelles en 1999 fournit une sorte d'expérience naturelle à grande échelle sur la population entière, où la période avant 1999 constitue le témoin et la période après, le traitement. Une telle expérience pourrait aider à mieux distinguer les effets anthropiques de ceux dus aux fluctuations démographiques naturelles, une séparation qui n'est pas toujours évidente (e.g. Nichols 1991b, Smith et Reynolds 1992, Sedinger et Rexstad 1994). En plus, cette situation est caractérisée par des circonstances uniques dans la gestion de la faune, soit l'addition d'une saison entière de chasse nouvelle, ce qui fournit un exemple rare et extrême. Souvent, l'évaluation des effets de la chasse sur la démographie des populations de sauvagine s'est faite en analysant l'impact de changements moins importants de régime de chasse (e.g. Francis et al. 1998, Otis et White 2002), ou avec des suivis démographiques où les variations temporelles dues à des facteurs externes peuvent être difficiles à distinguer des effets de la chasse (e.g. Smith et Reynolds 1992, Giudice 2003). Par contre, notre analyse des impacts de changements réglementaires radicaux appliqués à l'Oie des neiges pourrait servir comme outil prédictif pour des effets de changements moins extrêmes qui sont plus communs dans la gestion de sauvagine. L'impact

de mesures aussi radicales n'ayant jamais été examiné avec des méthodes d'analyse modernes, notre étude présente donc une opportunité unique pour l'écologie appliquée.

APPROCHE MÉTHODOLOGIQUE

Nos connaissances de la mortalité due à la chasse chez les oiseaux sont basées soit sur le retour d'oiseaux bagués qui sont tués à la chasse (Conroy et Eberhardt 1983, Burnham et Anderson 1984, Hestbeck et al. 1990, Caithness et al. 1991), soit sur des enquêtes menées par les gestionnaires de la faune auprès des chasseurs (Boyd et Finney 1978). Ces informations sont les plus utiles quand elles sont récoltées à long terme sur une même population, ce qui est le cas chez la Grande Oie des neiges. La disponibilité de telles informations, provenant d'une trentaine années avant les mesures de gestion exceptionnelles et de 4 années depuis leur instauration, nous a offert une opportunité de différencier les impacts des mesures récentes par rapport aux tendances à long terme.

L'analyse de données provenant d'animaux marqués trouve son origine dans les modèles de Lincoln (1930) et Petersen (1896), lesquels visaient à estimer l'abondance des populations. Au cours des dernières décennies, les possibilités offertes par ces modèles se sont accrues considérablement, au point de faciliter l'étude de nombreux autres paramètres démographiques (Cormack 1964, Jolly 1965, Seber 1965, Brownie et al 1985, Pollock et al. 1990). Ces méthodes permettent maintenant d'estimer avec une bonne précision des paramètres tels que le mouvement, la survie et le recrutement. Les récupérations de bagues d'oiseaux tués à la chasse sont particulièrement utiles pour examiner les effets de l'exploitation sur la démographie, car la mortalité causée par la chasse peut ainsi être séparée d'autres sources de mortalité. Les données provenant des animaux marqués qui sont tués permettent alors d'estimer deux paramètres : la survie et le taux de récupération. Ce dernier paramètre est fonction des probabilités qu'un animal marqué soit tué, ramassé et rapporté par le chasseur (Brownie et al. 1985).

Cependant, toute estimation basée sur des données provenant d'animaux marqués dépend de suppositions importantes qui doivent être satisfaites pour que les résultats soient crédibles (Brownie et al. 1985, Cooch et White 2001). Ces suppositions sont les suivantes : 1) tous les animaux marqués qui sont présents dans la population à un moment donné ont la même probabilité d'être rencontré (soit observé, capturé, ou tué) durant cette période de temps; 2) tous les animaux marqués ont la même probabilité de survivre pendant une période de temps

donnée; 3) aucune marque sur un animal n'est perdue; et 4) la période de marquage est très courte par rapport à la durée de la période entre les marquages (Cooch et White 2001). Cependant, les deux premières suppositions étant rarement satisfaites, les modèles considérés doivent souvent inclure des variables additionnelles pour essayer de corriger les sources d'hétérogénéité présentes.

Les données provenant d'enquêtes auprès des chasseurs ne peuvent pas fournir les mêmes informations démographiques que celles obtenues avec les individus marqués, mais elles peuvent néanmoins fournir des renseignements précieux sur la récolte totale des oies, et sur la composition et distribution géographique de celle-ci. Il existe des enquêtes nationales menées au Canada et aux États-Unis depuis plus d'une trentaine d'années par le Service canadien de la faune et le US Fish and Wildlife Service. Des formulaires sont envoyés aux chasseurs chaque année, et ceux-ci doivent y indiquer leur récolte totale pour l'année, ainsi que la région géographique où les oiseaux ont été tués. Les chasseurs doivent aussi retourner les queues des oies et les ailes des canards qu'ils ont tués. À partir de ces échantillons, les services de la faune peuvent déterminer l'espèce et l'âge (jeune de l'année ou adulte) de chaque oiseau abattu (Boyd et Finney 1978). Les enquêtes ajoutent donc des renseignements complémentaires à celles provenant des récupérations de bagues et permettent de compléter nos connaissances des effets de l'exploitation. Habituellement, seulement l'une ou l'autre des sources de données est utilisée à la fois. Pourtant, une comparaison entre les taux de mortalité à la chasse estimés par chacune des deux méthodes pourrait être très informative, mais cela a rarement été fait (mais voir Cooke et al. 2000).

La disponibilité de ces deux bases de données à long terme pour la Grande Oie des neiges nous a donné l'opportunité de faire une analyse comparative et exhaustive des effets de la chasse. Les deux types d'information ont pu être analysés avec des méthodes de maximum de vraisemblance, basées sur la théorie de l'information et le principe de sélection de modèles (Burnham et Anderson 1998). Cette approche, contrairement aux tests d'hypothèses, recherche le modèle le plus complexe que peut supporter nos données, tout en minimisant l'incertitude des estimations des paramètres dans ce modèle (Burnham et Anderson 1998). En particulier, on s'est servi du critère d'information d'Akaike comme critère de sélection de modèles, une valeur qui fait le compromis entre le maximum d'information retenue dans un modèle et le minimum de paramètres requis pour y parvenir (Akaike 1973). L'application de cette méthode nous a permis d'estimer des paramètres démographiques et

d'examiner l'effet d'un certain nombre de variables à partir des bases de données que nous disposions, pour en arriver à des conclusions pertinentes pour la gestion.

OBJECTIFS DE L'ÉTUDE

L'objectif principal de cette étude était d'examiner les tendances à long terme de la récolte sportive de la Grande Oie des neiges, et de savoir comment celle-ci avait changé depuis l'instauration des mesures de conservation spéciales. On désirait établir les variations dans le taux de mortalité provenant de la chasse et ses impacts sur la survie des oies, ainsi que les changements temporels survenus dans la distribution de la récolte sur les aires de halte migratoire et d'hivernage. À court terme, de telles informations pourraient contribuer à la gestion de cette population abondante afin de mieux protéger son habitat et d'atténuer les problèmes de surabondance. Ultimement, une telle compréhension améliorée pourrait servir au développement de plans de gestion et à l'établissement de règlements de chasse dans l'avenir.

Dans le premier chapitre, on s'est intéressé aux variations spatiales et temporelles de la récolte d'oies par la chasse depuis une trentaine d'années afin de déterminer comment les effets récents des mesures de conservation se distinguent des variations à long terme. Les objectifs étaient : 1) de déterminer si des changements temporels dans la distribution géographique de la récolte au Québec et aux États-Unis étaient associés aux changements observés dans le taux de récolte; 2) d'identifier des différences possibles entre les groupes d'âge ou les sexes dans la distribution temporelle et géographique de la récolte; et 3) d'établir si la distribution géographique et la composition de la récolte printanière différaient de celles d'automne. Ce faisant, on voulait tenter d'identifier si des changements dans la chasse sportive auraient pu contribuer à la baisse du taux de récolte observée au cours des années 1980, une baisse qui a contribué fortement à la croissance rapide de la population (Menu et al. 2002). De plus, on désirait mieux comprendre les effets des mesures de conservation spéciales sur la distribution de la récolte de différents segments de la population pour pouvoir prédire les impacts de la gestion future.

Dans le deuxième chapitre, on a examiné les tendances dans les taux de survie et de mortalité à la chasse afin d'élucider les effets des mesures de gestion spéciales introduites en 1999 par rapport aux tendances démographiques historiques. On avait comme prédictions que depuis l'initiation des mesures spéciales: 1) la mortalité annuelle due à la

chasse a augmenté; 2) la survie annuelle a diminué; et 3) la mortalité a augmenté dans toutes les saisons de chasse. En général, on désirait évaluer si les mesures de conservation ont apporté les effets démographiques désirés par les gestionnaires. Étant donné que ces mesures de gestion ne sont qu'une solution temporaire au problème d'abondance élevée, une telle évaluation était nécessaire pour que les règlements de chasse futurs soient les plus appropriés. Plus globalement, on a utilisé un système qui a connu des changements exceptionnels et uniques en terme de régime de chasse sportive comme une expérience naturelle de manipulation anthropique de la démographie d'une population animale.

La forte croissance démographique de la population de la Grande Oie des neiges à été encouragée par des influences anthropiques, entre autres la création de refuges et une baisse dans le taux de récolte par la chasse. Une évaluation approfondie des effets des mesures qui ont été prises pour régler ces problèmes suit un des principes proposés par le concept de gestion adaptative, soit de réévaluer fréquemment les impacts de nos actions sur la population gérée. Notre étude contribue donc aux efforts d'évaluer les impacts des mesures de gestion exceptionnelles sur cette population exploitée, ainsi qu'au développement des connaissances plus générales des impacts de l'exploitation de la faune par l'homme.

RÉFÉRENCES

Abraham, K. F. et R. L. Jefferies. 1997. High goose populations: causes, impacts and implications. Pages 7-72 *dans* Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *dans* Second International Symposium on Information Theory (B. N. Petrov et F. Csaki, Eds.). Akademiai Kiado, Budapest, Hungary.

Allen, M. S., L. E. Miranda, et R. E. Brock. 1998. Implications of compensatory and additive mortality to the management of selected sportfish populations. Lakes and Reservoirs Research and Management **3**:67-79.

Anderson, D. R. et K. P. Burnham. 1978. Effect of restrictive and liberal hunting regulations on annual survival rates of the mallard in North America. Transactions of the North American Wildlife and Natural Resources Conference **43**:181-186.

Anderson, D. R. et K. P. Burnham. 1976. Population ecology of the mallard IV: The effect of exploitation on survival. US Department of the Interior, Fish and Wildlife Service Resource Publication **128**:45 pp.

Anderson, D. R., K. P. Burnham, J. D. Nichols, et M. J. Conroy. 1987. The need for experiments to understand population dynamics of American black ducks. Wildlife Society Bulletin **15**:282-284.

Ankney, C. D. 1996. An embarrassment of riches: too many geese. Journal of Wildlife Management **60**:217-223.

Barker, R. J. 1991. Nonresponse bias in New Zealand waterfowl harvest surveys. Journal of Wildlife Management **55**:126-131.

Batt, B. D. J. 1998. The greater snow goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Béchet, A., J.-F. Giroux, G. Gauthier, J. D. Nichols, et J. E. Hines. 2003. Spring hunting changes the regional movements of migrating greater snow geese. Journal of Applied Ecology **40**:553-564.

Béchet, A., J.-F. Giroux, et G. Gauthier. Sous presse. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. Journal of Applied Ecology.

Bêty, J., G. Gauthier, et J.-F. Giroux. 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.

Boyce, M. S., A. R. E. Sinclair, et G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos **87**:419-426.

Boyd, H. 2000. Population modelling and management of snow geese. Occasional Paper No. 102. Canadian Wildlife Service, Ottawa, ON.

Boyd, H. et G. H. Finney. 1978. Migratory game hunters and hunting in Canada. Canadian Wildlife Service, Ottawa, ON.

Brownie, C., D. R. Anderson, K. P. Burnham, et D. S. Robson. 1985. Statistical Inference from Band-recovery Data: a Handbook. Second ed. U.S. Fish and Wildlife Service.

Burnham, K. P. et D. R. Anderson. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag New York Inc., New York, NY.

Burnham, K. P. et D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology **65**:105-112.

Caithness, T., M. Williams, et J. D. Nichols. 1991. Survival and band recovery rates of sympatric grey ducks and mallards in New Zealand. Journal of Wildlife Management **55**:111-118.

Canadian Wildlife Service (CWS) Waterfowl Committee. 2001a. Migratory Game Bird Hunting Regulations in Canada: July 2001. CWS Migratory Birds Regulations Report No. 3.

Canadian Wildlife Service (CWS) Waterfowl Committee. 2001b. Population Status of Migratory Game Birds in Canada: November 2001. CWS Migratory Birds Regulations Report No. 4.

Conroy, M. J. et R. T. Eberhardt. 1983. Variation in survival and recovery rates of ring-necked ducks. Journal of Wildlife Management **47**:127-137.

Conroy, M. J. et D. G. Krementz. 1986. Incorrect inferences regarding the effects of hunting on survival rates of American black ducks. Wildlife Society Bulletin **14**:326-328.

Conroy, M. J. et D. G. Krementz. 1990. A review of the evidence for the effects of hunting on American black duck populations. Transactions of the North American Wildlife and Natural Resources Conference **55**:501-517.

Cooch, E. et G. White. 2001. Program MARK: A gentle introduction. Second edition.

Cooch, E. G. et F. Cooke. 1991. Demographic changes in a snow goose population: biological and management implications. Pages 168-189 *dans* Bird Population Studies: relevance to conservation and management (C. M. Perrins, J.-D. Lebreton, et G. J. M. Hirons, Eds.). Oxford University Press, Oxford.

Cooch, F. G. 1978. Distribution between Canada and the United States of the retrieved waterfowl kill by sport hunters. Pages 78-81 *dans* Migratory game bird hunters and hunting in Canada (H. Boyd et G. H. Finney, Eds.). Canadian Wildlife Service, Ottawa, ON.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika **51**:429-438.

Dusek, G. L., A. K. Wood, et S. T. Stewart. 1992. Spatial and temporal patterns of mortality among female white-tailed deer. Journal of Wildlife Management **56**:645-650.

Féret, M., G. Gauthier, A. Béchet, J.-F. Giroux, et K. A. Hobson. 2003. Effect of a spring hunt on nutrient storage by greater snow geese in southern Quebec. Journal of Wildlife Management **67**:796-807.

Filion, B., D. Luszcz, et M. Allard. 1998. Impact of geese on farmlands. Pages 58-64 *dans* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic

Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Francis, C. M. 2000. The relative impact of a spring hunt on snow goose population dynamics. Pages 6-16 *dans* Population modelling and management of Snow Geese (H. Boyd, Ed.). Canadian Wildlife Service, Ottawa, ON.

Francis, C. M., M. H. Richards, F. Cooke, et R. F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology **73**:1346-1362.

Francis, C. M., J. R. Sauer, et J. R. Serie. 1998. Effect of restrictive harvest regulations on survival and recovery rates of American black ducks. Journal of Wildlife Management **62**:1544-1577.

Freemark, K. E. et F. G. Cooch. 1978. Geographic analysis of waterfowl kill in Canada. Pages 66-77 *dans* Migratory game bird hunters and hunting in Canada (H. Boyd et G. H. Finney, Eds.). Canadian Wildlife Service, Ottawa, ON.

Gauthier, G. et S. Brault. 1998. Population model of the greater snow goose: projected impacts of reduction in survival on population growth rate. Pages 65-80 *dans* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Gauthier, G., R. Pradel, S. Menu, et J.-D. Lebreton. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology **82**:3105-3119.

Giroux, J.-F., G. Gauthier, G. Costanzo, et A. Reed. 1998a. Impact of geese on natural habitats. Pages 32-57 *dans* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Giroux, J.-F., B. Batt, S. Brault, G. Costanzo, B. Filion, G. Gauthier, D. Luszcz, A. Reed. 1998b. Conclusions and management recommendations. Pages 81-88 *dans* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose

Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Giudice, J. H. 2003. Survival and recovery of mallards and gadwalls banded in eastern Washington, 1981-1998. Journal of Field Ornithology **74**:1-11.

Halls, L. K. 1984. White-tailed deer: Ecology and management. Stackpole Books, Harrisburg, Pennsylvania.

Halse, S. A., I. R. James, P. E. Fitzgerald, D. A. Diepeveen, et D. R. Munro. 1993. Survival and hunting mortality of Pacific black ducks and grey teal. Journal of Wildlife Management **57**:42-48.

Hestbeck, J. B. 1994. Survival of Canada geese banded in winter in the Atlantic flyway. Journal of Wildlife Management **58**:748-756.

Hestbeck, J. B. et R. A. Malecki. 1989. Estimated survival rates of Canada geese within the Atlantic flyway. Journal of Wildlife Management **53**:91-96.

Hestbeck, J. B., D. H. Rusch, et R. A. Malecki. 1990. Estimating population parameters for geese from band-recovery and mark-recapture data. Transactions of the North American Wildlife and Natural Resources Conference **55**:350-373.

Heusmann, H. W. 1999. Special hunting seasons and resident Canada goose populations. Wildlife Society Bulletin **27**:456-464.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature **406**:882-885.

Johnson, M. A. 1997. Management strategies to address the mid-continent lesser snow goose overpopulation problem. Pages 101-111 *dans* Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika **52**:225-247.

Kerbes, R. H., P. M. Kotanen, et R. L. Jefferies. 1990. Destruction of wetland habitats by

lesser snow geese: a keystone species on the west coast of Hudson Bay. Journal of Applied Ecology **27**:242-258.

King, J. G. et D. V. Derksen. 1986. Alaska goose populations: past, present and future. Transactions of the North American Wildlife and Natural Resources Conference **51**:464-479.

Kokko, H. et J. Lindstrom. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. Oikos **110**:293-304.

Krementz, D. G., M. J. Conroy, J. E. Kines, et H. F. Percival. 1988. The effects of hunting on survival rates of American black ducks. Journal of Wildlife Management **52**:214-226.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. US Department of Agriculture Circular **188**:1-4.

Lindberg, M. S. et R. A. Malecki. 1994. Hunting vulnerability of local and migrant Canada geese in Pennsylvania. Journal of Wildlife Management **58**:740-747.

Longcore, J. R., D. G. McAuley, D. A. Clugston, C. M. Bunck, J.-F. Giroux, C. Ouellet, G. R. Parker, P. Dupuis, D. B. Stotts, et J. R. Goldsberry. 2000. Survival of American black ducks radiomarked in Québec, Nova Scotia, and Vermont. Journal of Wildlife Management **64**:238-252.

Loonen, M. J. J. E., K. Oosterbeek, et R. H. Drent. 1997. Variation in growth of young and adult size in barnacle geese *Branta leucopsis*: evidence for density dependence. Ardea **85**:177-192.

Madsen, J. 1991. Geese of the Western Palearctic: present status and challenges for research and management in the '90s. Transactions of the North American Wildlife and Natural Resources Conference **56**:453-461.

Mainguy, J., J. Bety, G. Gauthier, et J.-F. Giroux. 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? Condor **104**:156-161.

Malecki, R. A., B. D. J. Batt, et A. E. Shaeffer. 2001. Spatial and temporal distribution of Atlantic population Canada geese. Journal of Wildlife Management **65**:242-247.

Massé, H., L. Rochefort, et G. Gauthier. 2001. Carrying capacity of wetland habitats used by breeding greater snow geese. Journal of Wildlife Management **65**:271-281.

Menu, S., G. Gauthier, et A. Reed. 2002. Changes in survival rates and population dynamics of greater snow geese over a 30-year period: implications for hunting regulations. Journal of Applied Ecology **39**:91-102.

Myers, R. A. et B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423**:280-283.

Nichols, J. D. 1991a. Responses of North American duck populations to exploitation. Pages 498-525 *dans* Bird Population Studies: relevance to conservation and management (C. M. Perrins, J.-D. Lebreton, et G. J. M. Hirons, Eds.). Oxford University Press, Oxford.

Nichols, J. D. 1991b. Science, population ecology, and the management of the American black duck. Journal of Wildlife Management **55**:790-799.

Nichols, J. D., M. J. Conroy, D. R. Anderson, et K. P. Burnham. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Transactions of the North American Wildlife and Natural Resources Conference **49**:535-554.

Otis, D. L. et G. C. White. 2002. Re-analysis of a banding study to test the effects of an experimental increase in bag limits of mourning doves. Pages 479-495 *dans* Statistical Analysis of Data from Marked Bird Populations (B. J. T. Morgan et D. L. Thomson, Eds.). Journal of Applied Statistics **29**.

Owen, M. et J. M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology **58**:603-617.

Owen, M. et J. M. Black. 1991. The importance of migration mortality in non-passerine birds. Pages 360-372 *dans* Bird Population Studies: relevance to conservation and management (C. M. Perrins, J.-D. Lebreton, et G. J. M. Hirons, Eds.). Oxford University Press, Oxford.

Pauly, D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson,

et D. Zeller. 2002. Towards sustainability in world fisheries. Nature **418**:689-695.

Petersen, C. G. J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. Report of the Danish Biological Station 1895 **6**:5-84.

Pollock, K. H., Nichols, J. D., Brownie, C., et Hines, J. E. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs No. 107, The Wildlife Society.

Rabinowitz, A. 1995. Helping a species go extinct: the Sumatran rhino in Borneo. Conservation Biology **9**:482-488.

Raveling, D. G., J. D. Nichols, J. E. Hines, D. S. Zezulak, J. G. Silveira, J. C. Johnson, T. W. Aldrich, et J. A. Weldon. 1992. Survival of cackling Canada geese, 1982-1988. Journal of Wildlife Management **56**:63-73.

Reed, A., J.-F. Giroux, et G. Gauthier. 1998. Population size, productivity, harvest and distribution. Pages 5-31 *dans* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Rexstad, E. A. 1992. Effect of hunting on annual survival of Canada geese in Utah. Journal of Wildlife Management **56**:297-305.

Rockwell, R., E. Cooch, et S. Brault. 1997. Dynamics of the mid-continent population of lesser snow geese - projected impacts of reductions in survival and fertility on population growth rates. Pages 73-100 *dans* Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika **52**: 249-259.

Sedinger, J. S. et E. A. Rexstad. 1994. Do restrictive harvest regulations result in higher survival rates in mallards? A comment. Journal of Wildlife Management **58**:571-577.

Smith, G. W. et R. E. Reynolds. 1994. Hunting and mallard survival: a reply. Journal of Wildlife Management **58**:578-581.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan Publishing Co., New York, NY.

Walters, C. J. et C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

Warren, R. J. 1991. Ecological justification for controlling deer populations in eastern national parks. Transactions of the North American Wildlife and Natural Resources Conference **56**:56-66.

Wikramanayake, E. D., E. Dinerstein, J. G. Robinson, U. Karanth, A. Rabinowitz, D. Olson, T. Mathew, P. Hedao, M. Conner, G. Hemley, et D. Bolze. 1998. An ecology-based method for definiting priorities for large mammal conservation: the tiger as a case study. Conservation Biology **12**:865-878.

Williams, B. K. et F.A. Johnson. 1995. Adaptive management and the regulation of waterfowl harvests. Wildlife Society Bulletin **23**:430-436.

Williams, B. K., F. A. Johnson, et K. Wilkins. 1996. Uncertainty and the adaptive management of waterfowl harvests. Journal of Wildlife Management **60**:223-232.

CHAPITRE 1

SPATIOTEMPORAL HETEROGENEITY OF GREATER SNOW GOOSE HARVEST AND IMPLICATIONS FOR HUNTING REGULATIONS

ANNA M. CALVERT, GILLES GAUTHIER, AUSTIN REED[1]

RÉSUMÉ

Nous avons utilisé les données de récupération de bagues et d'enquêtes nationales pour étudier les variations à long terme dans la distribution géographique et la composition de la récolte de la Grande Oie des neiges (*Chen caerulescens atlantica*), et pour étudier comment celles-ci ont varié depuis l'initiation des mesures de conservation de 1999. Nous avons observé un élargissement progressif de la répartition spatiale de la récolte automnale, allant de l'estuaire vers le sud-ouest du Québec. En hiver, un soudain déplacement de la distribution de la récolte vers le nord au milieu des années 1980 a pu conduire à une réduction de la pression de chasse des oies des neiges, et pourrait être une cause majeure du soudain déclin du taux de récolte qui a encouragé la croissance récente de la population. Nous avons aussi mis en évidence une proportion décroissante de juvéniles tués au cours de la chasse automnale, et une représentation accrue d'adultes dans la récolte printanière par rapport à l'automne. Nous suggérons que la gestion future vise à une augmentation de la récolte dans les états au milieu de la voie migratoire de l'Atlantique si un contrôle supplémentaire de la population est désiré.

ABSTRACT

We used band-recovery and harvest survey data to study long-term variations in geographic harvest distribution and composition for greater snow geese (*Chen caerulescens atlantica*) and how these may have differed with the implementation of conservation measures in 1999. We detected a gradual spreading of the fall harvest from the St. Lawrence estuary toward southwestern Québec. During winter, a sudden northward shift in the distribution of the USA harvest in the mid-1980s may have led to a reduction of hunting pressure on greater snow geese, and could be a principal cause of the sudden decline in harvest rate that fuelled the most recent population increase. We also present evidence for a decreasing proportion of juveniles in the kill throughout the hunting season within fall staging grounds, and a much higher proportion of adults in the spring harvest than in the fall. We recommend that management actions be focused on increasing harvest in mid-Atlantic Flyway states if further control of population growth is desired.

INTRODUCTION

Hunting mortality appears to be a key factor influencing waterfowl demography (Burnham and Anderson 1984, Smith and Reynolds 1992, Francis et al. 1998), especially for long-lived species with low natural mortality rates, such as geese (Hestbeck 1994, Francis et al. 1992a, Gauthier et al. 2001). However, hunting intensity may change over time and among regions, and harvest may not equally affect all groups within a population; such variations require consideration in the development of management schemes.

Many hunted goose populations in the Northern hemisphere have shown strong growth in recent years (Ankney 1996, Abraham and Jefferies 1997, Madsen et al. 1999). These increases have been attributed to advantages gained from the use of hunting-free refuges and extra food available in agricultural fields (Krapu et al. 1995, Abraham and Jefferies 1997, Reed et al. 1998). Most populations of lesser snow geese (LSG; *Chen c. caerulescens*) have grown to levels where they have severely degraded several staging and breeding habitats (Abraham and Jefferies 1997). Greater snow geese (GSG) have had similar though lesser negative impacts during their more-than-12-fold increase in abundance since 1965 (Giroux et al. 1998a, Reed et al. 1998).

Due to the growth in abundance, hunting regulations for snow geese have been continually liberalised over the past three decades. Daily bag limits for GSG during fall and winter increased in southern Québec from 5 in the 1980s to 20 in 1999, and in the Atlantic Flyway (AF) states from 5 in the late 1970s to 15 in the late 1990s (Canadian Wildlife Service (CWS) annual Migratory Birds Hunting Regulations Summaries, J. Kelley US Fish and Wildlife Service (USFWS) personal communication). Despite this increase in allowable kill, harvest rates of GSG dropped sharply in the mid-1980s and remained relatively low through the 1990s (Menu et al. 2002), and similar tendencies were observed for LSG harvest rates (Francis et al. 1992a, Cooke et al. 2000), contributing to the population growth of both sub-species. The period of snow goose population increase was also associated with a variety of changes in habitat use, migration timing and migration routes (Alisauskas 1998, Reed et al. 1998). In particular, fall staging GSG, which were traditionally concentrated in marshes of the upper St. Lawrence estuary, increasingly used farmlands and considerably expanded their range into south-western Québec, away from natural marshes (Olson 2001). A northerly shift in snow goose wintering distribution was also noted in the AF states (Reed et al. 1998).

These changes could have contributed to the decline in harvest rate if geese were less exposed to hunting in the newly occupied areas (Freemark and Cooch 1978).

In response to the perceived threat to natural habitats posed by the rapid population growth and low harvest rates, the Arctic Goose Habitat Working Group recommended that aggressive conservation measures be implemented in order to stabilize the population size of GSG (Giroux et al. 1998b) and to reduce the abundance of LSG (Johnson 1997). These measures included the introduction of a spring hunt (April and May) in agricultural habitats in Québec for GSG, and the relaxation of existing fall and winter hunting regulations for both sub-species, beginning in winter 1998-99 (CWS Waterfowl Committee 2001a, b).

We examined long-term variations in GSG harvest using two sources of data: returns of metal leg-bands by sport hunters, and national sport harvest surveys conducted by the CWS and USFWS. Specifically, our main objectives were to: 1) determine whether geographic variation in harvest in Canada and the United States over 32 years was associated with temporal trends in harvest rates observed during this period; 2) uncover any differences in temporal and geographic distributions of harvest between adults and juveniles, and between sexes; and 3) establish whether harvest distribution and composition differed between the spring conservation hunt and the traditional fall hunt in Québec.

METHODS

Data Base

Greater snow geese were leg-banded in several locations and at varying intensities during the period 1970-2001 (n = 54,421; very few bandings before 1970). The majority of banding occurred from 1970-1974 (7,191) and 1990-2001 (43,141); geese were banded primarily during the summer in Nunavut (44,132), with most others during staging in southern Québec (8,881) and winter in the USA portion of the Atlantic Flyway (AF) (1,399). All birds were marked with USFWS metal bands, and some birds (mainly adult females; Menu et al. 2000) were affixed with plastic neck collars. We could not determine whether birds marked with a collar had retained it until time of harvest, but collar loss is low in this population (3-5%/year; Gauthier et al. 2001, Reed 2003). Banding and recovery records (n = 6,571 recoveries) were obtained from the Bird Banding Laboratory (USFWS). For our analyses, we used data on recoveries of all individuals killed and retrieved by hunters; recovery data only began in 1975 for the USA, prior to which there was no legal snow goose hunt in the AF states.

Our additional source of data for Canada was the Species Composition Survey (SCS) database compiled by CWS. Because the fall migration of GSG in Canada is largely limited to the province of Québec (Reed et al. 1998), we used SCS data for all snow geese reported in Québec only (*n* = 7,568 tails; snow geese reported from neighbouring Atlantic provinces and eastern Ontario represented only 1.5% of the total reported for eastern Canada). The CWS distinguished between GSG and LSG in the harvest based on tail measurements; however, the annual proportion of LSG reported in the Québec harvest based on this index (mean = 0.26; annual range 0.00-1.00) was unrealistically high relative to the annual proportion of blue phase geese in the harvest (mean = 0.01; annual range 0-0.06). Presence of blue geese is a useful marker to distinguish these two sub-species because blues are very rare in GSG (<1 %, A. Reed and G. Gauthier, unpublished data), while eastern LSG populations contain a very large proportion of blues (>70%, Cooke et al. 1995). We thus concluded that tail measurements were unreliable to distinguish the 2 sub-species. In the AF as well, proportion of blue geese in the harvest was minimal (mean = 0.02; annual range 0-0.04). Based on these indices, we concluded that the true proportion of LSG in the reported harvest from Québec and the AF states was negligible, and like Reed et al. (1998) we did not correct for their presence in our data.

Statistical Analyses

In order to examine spatial and temporal variations in harvest distribution and composition, and to determine how the spring and fall hunting seasons differed, we compared series of models in several different data sets based on band recoveries and tail returns (Table 1). Band recoveries were split between Canada and the USA to permit within-country regional analyses. Total recoveries (all recoveries of hunter-shot geese over all years) were used for analyses of temporal and geographic variations in harvest over the last 32 years. Direct recoveries (only those that were recovered within one calendar year after banding) were used to examine questions pertaining to age representation in the harvest. Both total and direct recovery data sets were analysed to determine whether birds with and without collars differed in their harvest distribution. In addition, a subset of the direct recoveries was used to compare spring and fall hunts in Québec for 1999-2001, and a data set consisting of the direct recoveries from both countries combined was used to look for large-scale differences in the harvest between Canada and the USA. Finally, indirect recoveries (>1 yr post-banding) of geese banded as young were used to verify sex differences in recovery locations once they had been separated from their parents (note that in this case the "age" factor considered was

age at banding, which differed from age at recovery used in the analyses with direct recoveries). This was done to determine whether males were more likely than females to be recovered in areas away from the AF after their first year, as might be expected given the tendencies for female philopatry and pairing during winter (Francis and Cooke 1992, Robertson and Cooke 1999), and the potential for pairing with LSG that winter close to GSG wintering grounds (Cooke et al. 1995). Tail return data (available for Canada only) were used in temporal, geographic, and age-related analyses and for comparison with band recoveries but, unlike band recoveries, tail returns did not cover harvest from the spring hunt.

We conducted loglinear analyses for each data set in PROC CATMOD (SAS Institute 1999). Reported harvest was the dependent variable, so counts of the number of harvested geese (tail returns or band recoveries) were organised according to the independent variables: region (for Québec, we defined five functional geographic areas (Fig. 1), and for the AF we combined pairs of adjacent states: Vermont & New York, Pennsylvania & New Jersey, Delaware & Maryland, and Virginia & North Carolina), age (young of the year, hereafter juveniles, vs. adults ≥1 yr), and sex (band returns only), as well as season (spring and fall), neck collar presence and country for some data sets. Data were further grouped into time blocks of 5 years starting in 1970, except for 1995-98 (4 years) and 1999-2001 (3 years), thus separated to distinguish pre- and post-spring hunt years. Because of unequal interval length, the annual average number of harvested geese reported per time period was used as the dependent variable instead of the total count. While some variables were of little interest by themselves (e.g. variations in the number of recoveries over time or region may simply reflect variations in the number of birds banded or differences in the size of regions, respectively), 2- or 3-way interactions among variables were often the parameters of interest to addressing our specific research questions. We did not construct and compare all potential models but only those that we considered biologically appropriate following the principle of parsimony (Burnham and Anderson 1998). For each candidate model, we calculated the AIC_c (Akaike Information Criterion corrected for small sample size), where the model with the smallest AIC_c value for that data set, and the largest AIC_c weight (ωAIC_c, the weight of evidence for each model where the sum of model weights=1) provides the most parsimonious fit to the data(Burnham and Anderson 1998). For the most general model of each data set we also calculated the $\hat{c}$, a measure of overdispersion of the data equal to the ratio of the χ^2-value to its degrees of freedom (Burnham and Anderson 1998). In all cases $\hat{c} < 1$ and therefore we made no correction for overdispersion.
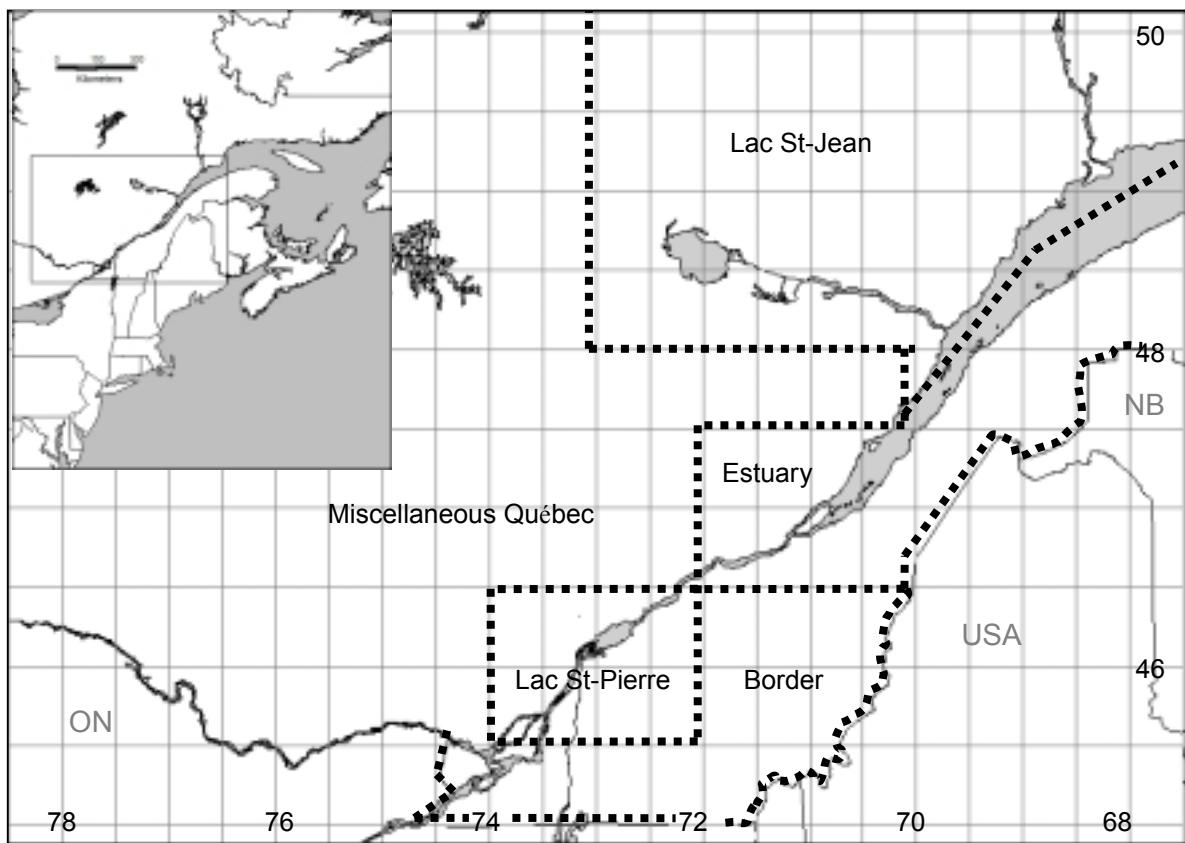
Figure 1. Limits of the geographic regions of southern Québec (stippled lines) used to group band recoveries and tail returns for geographic comparisons of greater snow goose harvest distributions. Regional boundaries continue past the edge of the enlarged map to the political boundaries of the province of Québec. Grid lines show latitudes and longitudes.

Additional Harvest Calculations

Harvest rates for 1970-1998 were calculated as in Menu et al. (2002). For the 1999-2001 seasons, we calculated harvest rate as the total annual harvest (Canada + USA) divided by fall population size, following the procedure of Menu et al. (2002). Harvest estimates for Québec were obtained from the Canadian National Harvest Survey (NHS, CWS unpublished data) and for the AF states from the USA survey (Martin and Padding 1999, 2000, 2001, 2002). Spring harvest data were obtained from a special harvest survey conducted by the CWS and informal age-ratio surveys conducted by P. Brousseau (CWS, personal communication); the spring harvest was included with the previous fall/winter harvest (e.g. the 2000 spring harvest was part of the 1999-2000 hunting season).

RESULTS

Collar effects

Analyses of band recovery data (both total and direct recoveries) showed no evidence of differential geographic harvest distribution between birds with and without collars (interaction region*collar was never present in the preferred models, Table 1). The interaction time*collar was retained but not biologically meaningful, as collars were rarely used before 1990. As a result, the two groups were pooled for other analyses that relied on subsets of recovery data.

Spatiotemporal Variation in Harvest

The geographic harvest distribution changed over time in both Canada and the USA, as the region*time interaction was present in the best models (Table 1; the sum of AIC_c weights (Σ ωAIC_c) of all models containing this effect was >0.999 for both Canadian and American total band recoveries). The proportion of Canadian band recoveries coming from the St. Lawrence estuary declined gradually from 96% in the early 1970s to 52% in 1999-2001, with an increasing trend in all other regions, particularly in the Lac-St-Pierre and border areas (Figs. 2A and 3). Canadian tail returns (which do not include spring harvest data) showed the same spatiotemporal trends (the interaction region * time was also present in the best model, Table 1; Σ ωAIC_c for this effect >0.999). The only differences were a lower contribution of the estuary to the total harvest in 1999-2001 (41%) than in band recoveries, and a slightly higher contribution of the Lac-St-Jean area during the same period. Note that in absolute terms, harvest increased in all parts of the province (Reed et al. 1998), but while the mean annual number of bands recovered in the estuary increased by a factor of 3 between the 1970s and 1995-2001, it showed a 30-fold increase in the Lac St-Pierre and Border areas (Fig. 3).

Table 1. Best-fit models of each band recovery and tail return data set for greater snow geese from 1970-2001, based on AIC_c. The variables retained in the model, the difference between a model's AIC_c value and the smallest one for that data set (ΔAIC_c), the number of model parameters (k), and the model's AIC_c weight relative to all models in the data set (ωAIC_c) are shown.

Data set	Best-fit models [a]	ΔAIC_c	k	ωAIC_c
CAN all recoveries	Region, age, time, collar, region*time, age*time, time*collar	0.00	64	0.758
USA all recoveries	Region, sex, age, time, collar, region*time, age*time, time*collar	0.00	49	0.325
	Region, sex, age, time, collar, region*time, time*collar	0.05	39	0.317
	Region, sex, age, time, collar, region*time, age*time, time*collar, age*sex	0.24	50	0.289
CAN/USA direct recoveries (country comparison)	Country, sex, age, time, country*time, country*age, age*time, age*sex	0.00	21	0.449
	Country, sex, age, time, country*time, country*age, age*time	1.99	20	0.166
CAN direct recoveries	Region, age, time, collar, region*age, time*collar	0.00	23	0.728
USA direct recoveries	Region, age, time	0.00	11	0.330
	Region, age, time, collar	1.76	12	0.137
	Region, age, time, region*time	1.82	15	0.133
CAN indirect recoveries	Region, age, time	0.00	13	0.687
USA indirect recoveries	Region, age, sex, time	0.00	12	0.376
	Region, age, time	0.37	11	0.312
CAN direct recoveries (spring hunt 1999-2001)	Region, age, season, age*season	0.00	8	0.625
CAN tail returns	Region, age, time, region*time, age*time, region*age	0.00	46	0.996

[a] Additional models are shown if the best-fit model had ωAIC_c <0.50 or when several models were very close in ωAIC_c.
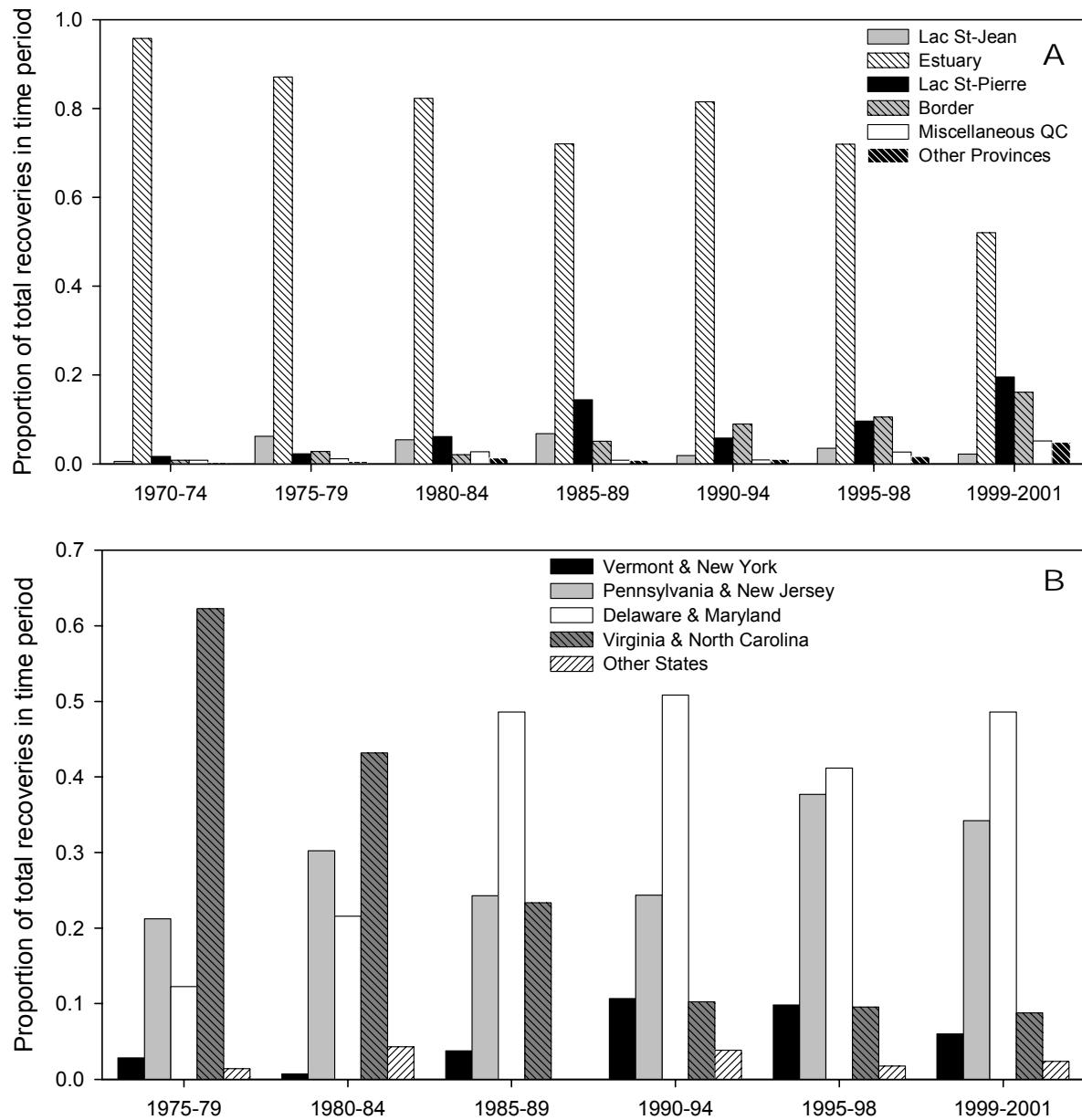
Figure 2. Proportional distribution of total band recoveries of greater snow geese across Québec regions (A, n = 3,779) and Atlantic Flyway states (B, n = 2,542) within each time period, 1970-2001. There was no hunting in the USA before 1975. The period 1999-2001 includes the spring hunt in Québec.
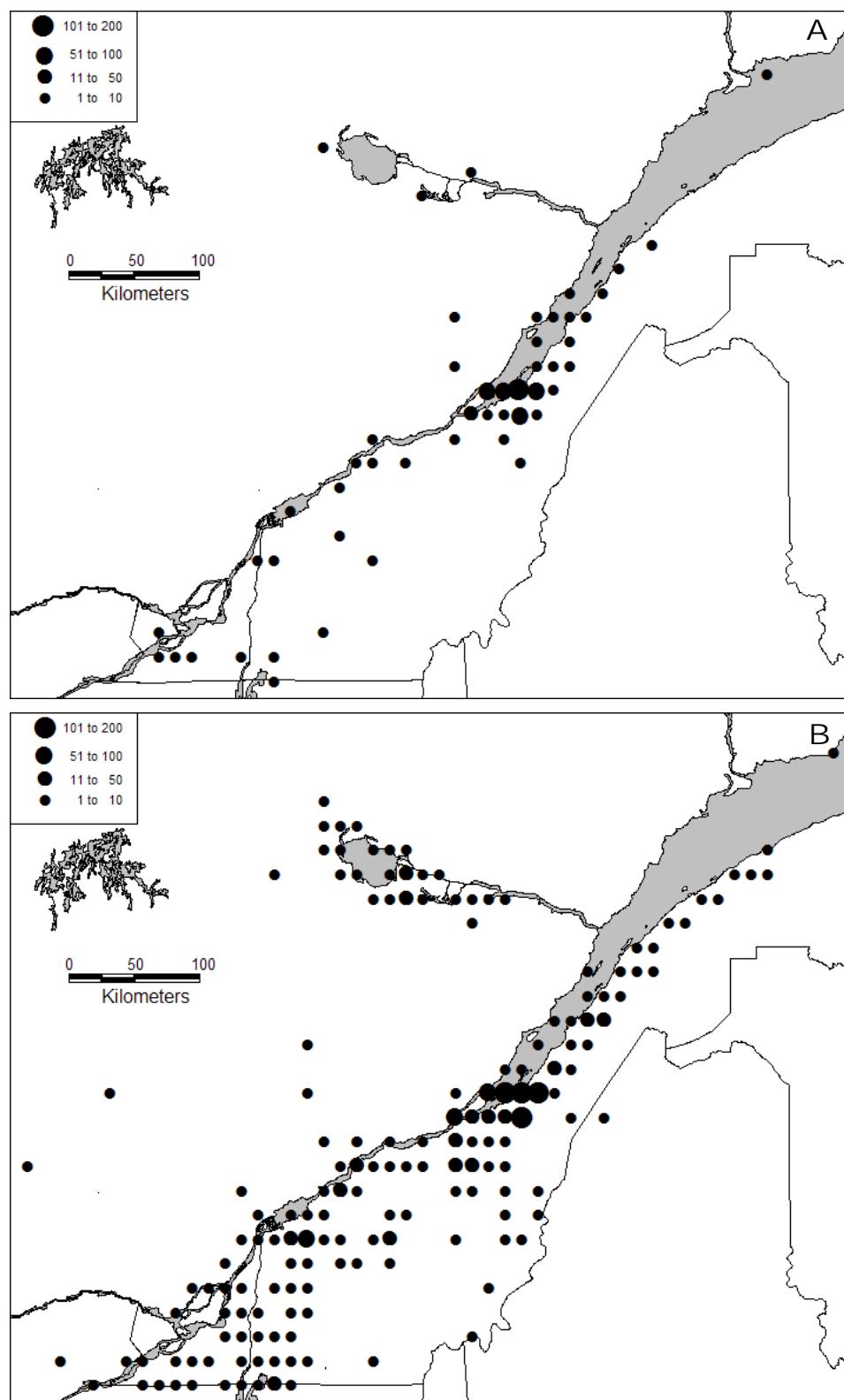
Figure 3. Distribution of greater snow goose band recoveries (precise to 10 degree-minutes) in Québec at the beginning (1970-79, A) and at the end (1995-2001, B) of the study period. The second period includes the spring hunt in Québec (1999-2001).

In the AF states, winter band recoveries showed a marked and abrupt shift toward the north in the mid 1980s (Fig. 2B). The proportion of bands coming from Virginia & North Carolina decreased from 62% in the late 1970s to less than 9% in 1999-2001, and the proportions from Delaware & Maryland and Pennsylvania & New Jersey increased accordingly (Fig. 4). In absolute terms, the mean annual number of bands recovered was reduced by more than half in Virginia and North Carolina but increased by a factor of 10 in Delaware & Maryland and by a factor of 4 to 6 in more northern states.

The relative proportion of band recoveries between the two countries also varied over the years since the AF states hunt opened in 1975 (the country*time interaction was present in the best model for the combined Canada/USA dataset, Table 1; $\Sigma \, \omega AIC_c$ for this effect = 0.875). Band recoveries were higher in the USA (63%) than Canada from 1975-79, and also slightly higher in the USA in 1985-89 (51%), but the majority came from Canada in all other time periods (56-77%).

Age and Sex Representation in the Harvest

We found evidence that age distribution of the harvest varied spatiotemporally. On a large spatial scale, the proportion of juveniles in the band recoveries was much higher in Canada (69%) than in the USA (44%; the country*age interaction was present in the best model for the combined Canada/USA dataset, Table 1; $\Sigma \, \omega AIC_c$ for this effect > 0.999). Spatial differences in age distribution were also found among regions within Québec (the region*age interaction was present in the best models for Canadian direct recoveries and for tail returns, Table 1; $\Sigma \, \omega AIC_c$ for this effect = 0.810 and > 0.999, respectively), but not among AF regions (the region*age interaction was not present for USA direct recoveries, Table 1; $\Sigma \, \omega AIC_c$ for this effect = 0.135). The juvenile proportion of band recoveries decreased from north to south in Québec, being highest (>70%) in the estuary and Lac St-Jean areas, and lowest (52%) along the Québec-USA border (Fig. 5); tail returns showed a very similar pattern. There was also evidence for temporal change in the age representation in the Québec fall harvest (age*time interaction present in the best model for tail returns, Table 1; $\Sigma \, \omega AIC_c$ for this effect = 0.996), with adults accounting for a progressively larger share of the harvest, especially during 1999-2001 (Fig. 6). The age*time effect could not be interpreted with band recoveries because in some time periods virtually no young were banded.
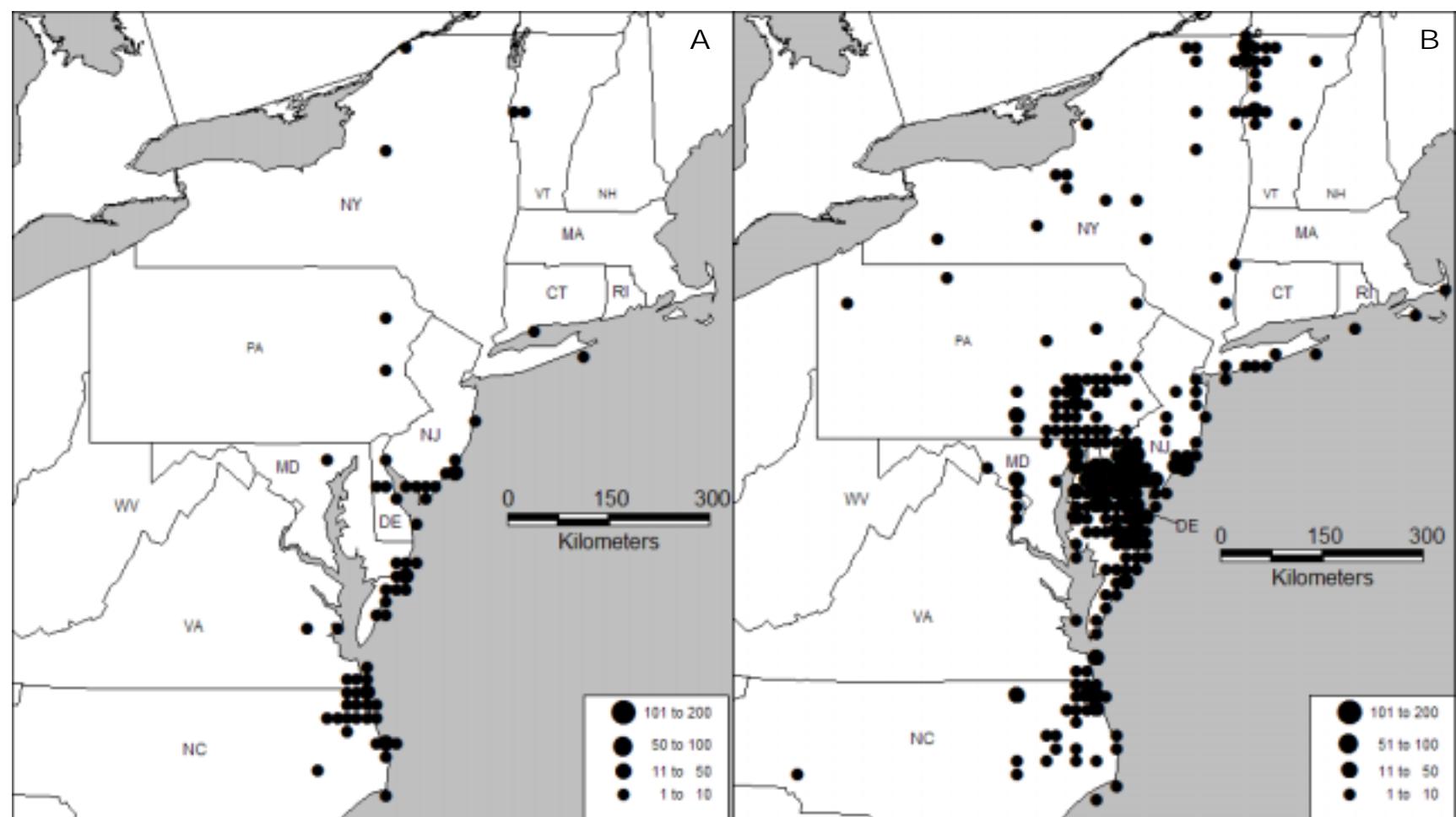
Figure 4. Distribution of greater snow goose band recoveries (precise to 10 degree-minutes) in the Atlantic Flyway states at the beginning (1975-79, A) and the end (1995-2001, B) of the study period (note that hunting only opened in 1975).

Overall, there were few indications of sex-related differences in harvest. The factor sex and the interaction age*sex were present in the best model only in the Canada/USA direct band recoveries and the USA band recoveries datasets (Table 1). In the country comparison, juvenile recoveries showed very similar proportions of each sex (51.1% females), while for adults more females were recovered (57.4%) than males. For USA recoveries the differences were small, with males (52.3%) represented slightly more than females among juveniles, and females (54.3%) more frequently among adults. There was no evidence that young male geese were recovered in areas away from the traditional migration routes more often than other sex-age groups for either Canadian or USA indirect recoveries (the region*age*sex interaction was not present in the best models, Table 1; $\Sigma\ \omega AIC_c$ for this effect = 0.002 for Canada and 0.010 for the USA).

Comparison of Regular and Conservation Harvests

Analyses of recoveries during years with a spring hunt (1999-2001) in Québec provided no indication that geographic harvest distribution differed between fall and spring (the region*season interaction was not present in the best model, Table 1; $\Sigma\ \omega AIC_c$ for this effect = 0.016). There was, however, evidence that the representation of age groups in the harvest differed between spring and fall hunting seasons (the age*season interaction was present in the best model, Table 1; $\Sigma\ \omega AIC_c$ for this effect = 0.925), with a much higher proportion of adults in the spring (59%) than in the fall recoveries (34%).

Harvest Rates

Mean harvest rate for 1998-2001 (since the special conservation measures) was estimated at 0.135 ± 0.006 (SE) for adults and 0.513 ± 0.083 for juveniles. This represented a large increase in harvest rate for adults compared to the previous period of stability (1985-1997, 0.061 ± 0.004; $t = -8.64$, df = 15, $P < 0.001$) but not for juveniles (1985-1997, 0.422 ± 0.026; $t = -1.42$, df = 15, $P = 0.18$).
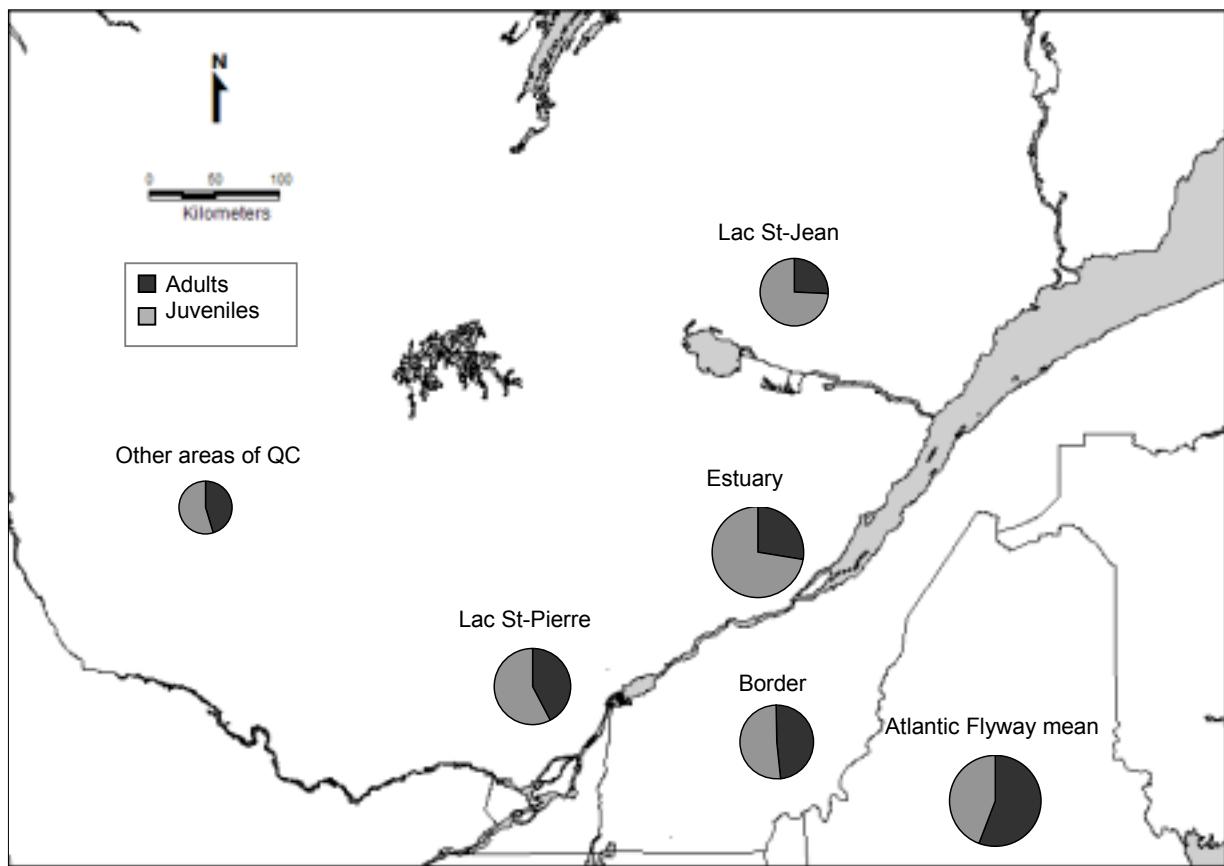
Figure 5. Proportional representation of age classes in the harvest, by region, for direct band recoveries of greater snow geese in Québec, 1970-2001 (n = 1,734), and for the whole Atlantic Flyway (n = 845). Circle size is proportional to sample size on a logarithmic scale.
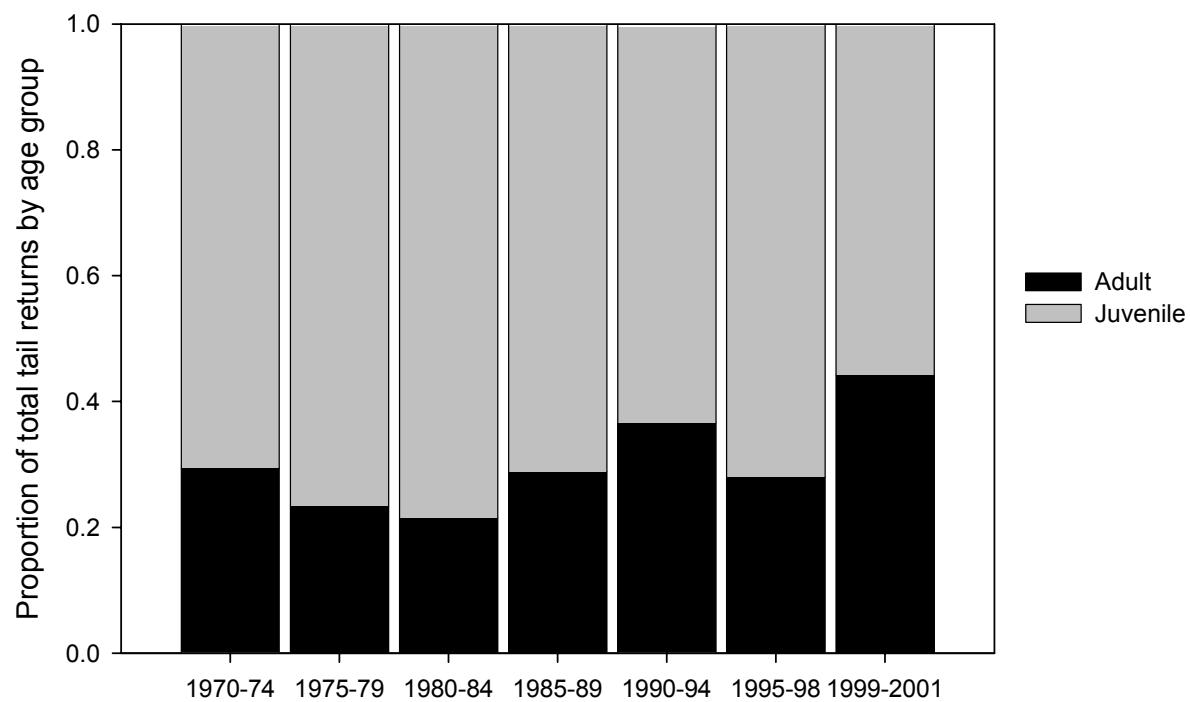
Figure 6. Proportional representation of age classes in the greater snow goose fall harvest in Québec from 1970-2001, based on returns of goose tails as part of the Canadian Wildlife Service Species Composition Survey (total *n* = 9,739).

DISCUSSION

Spatial Heterogeneity of Harvest Distribution Over 32 Years

The GSG harvest increased in 1975 with the opening of the hunt in the AF states, and the resulting combined Canadian and American harvest was apparently sufficient to stop the population growth for close to a decade (Reed 1990, Gauthier and Brault 1998). However, an abrupt drop in harvest rate occurred in the mid-1980s and the population began to increase again despite harvest regulations remaining liberal (Menu et al. 2002). Spatial variation of waterfowl harvest is difficult to analyse (Royle and Dubovsky 2001), but Menu et al. (2002) hypothesized that a change in the migratory route and habitat use of geese, especially in Québec, might explain this rapid decline in harvest rate.

Over three decades, we detected a gradual spreading in the reported harvest in Québec from the central region of the St. Lawrence estuary toward the south-western area of the province (Lac St-Pierre and along the Québec-USA border). This closely followed the observed changes in staging distribution of geese during the period of population growth and their increased use of agricultural fields for feeding, particularly in south-western Québec (Filion et al. 1998, Reed et al. 1998). The expansion of the distribution was associated with an increase in the proportion of the population using areas outside the upper estuary in fall (Olson 2001), the region traditionally used by snow goose sport hunters (Freemark and Cooch 1978), and may have been amplified by the spring hunt beginning in 1999 (Béchet et al. 2003). However, the harvest distribution changes we noted have been occurring slowly since 1970 with no sudden shifts, and thus were likely too gradual to fully explain the sudden harvest rate decline in the mid-1980s.

Alteration in the spatial harvest distribution was also observed on wintering grounds, characterised by a major northward shift in the mid-1980s and a concentration of the harvest in mid-AF states. The observed redistribution of the winter harvest appears to be associated with changes in migratory behaviour of the geese, and may explain the decline in harvest rate that occurred in the 1980s. A similar shift in snow goose wintering distribution in the AF was revealed by the mid-winter counts, where numbers in the south decreased slightly, while the numbers in New Jersey, Delaware and Maryland increased dramatically (Reed et al. 1998). This change in wintering distribution could be due to "short-stopping", where the distance travelled southward is shortened over time in favour of remaining further north, as has been observed in LSG (Alisauskas 1998). Such changes in wintering location in other species have

been associated with changes in refuge and food availability (e.g. increase in corn; Malecki et al. 1988, Abraham and Jefferies 1997, Hill and Frederick 1997), population size (Williams and Bishop 1990, Alisauskas 1998), or temperatures (Rogers 1979, Hestbeck et al. 1991, Clausen et al. 1998), all of which may have contributed to the redistribution of GSG as well.

The shift in winter distribution of GSG probably affected the harvest in several ways. First, by short-stopping in mid-AF states, geese were exposed to a smaller pool of hunters than in the past when they continued through this area to southern AF states. Duck stamp sales in the mid-AF states also decreased in recent decades (Serie 1996, Boyd et al. 2002), and thus the high density of geese now wintering in mid-AF states may have "swamped" the shrinking pool of hunters, as is the case in ecological "predator swamping" (Hamilton 1971). Second, mid-AF states have a strong tradition of hunting Canada geese and therefore interest in snow goose hunting may have been limited (e.g. there was little increase in GSG kill in this area between 1995 and 1998 during the Canada goose harvest closure; J. Kelley, USFWS, personal communication). Consequently, the GSG harvest did not increase in the AF states during the period of population growth of the 1980s and 1990s (Reed et al. 1998). Thus, while the harvest rate remained stable in Canada, the harvest rate in the USA was decreasing.

To summarize, the evidence implies that wintering GSG are now concentrated in mid-AF states, where snow geese are not the preferred hunting target and where hunters have been unable to maintain harvest rates as high as in other areas. We therefore suggest that a sudden change in the wintering distribution of snow geese, possibly in combination with other distributional changes on staging areas in Québec, may explain the shifts in harvest distribution and the ensuing decline in harvest rate observed in the mid-1980s.

Spatiotemporal Variation of Harvest Composition

We found that the overall proportion of juveniles in the harvest within a given year was greatest in the areas reached earliest on the fall migration. It has been suggested that juveniles are more susceptible to hunting mortality than adults, especially early in their exposure to hunters (Prevett and MacInnes 1980, Francis et al. 1992b). The change we observed in age representation within the fall hunting season is concordant with this hypothesis, and may be due to a rapid "learning curve" of juveniles. Repeated experience with hunters likely influences the behaviour of geese, which quickly learn to avoid risky areas such as the edges of refuges (Giroux and Bédard 1986, Fox and Madsen 1997), or learn to

fly and feed in larger groups (Prevett and MacInnes 1980). Reduction in the number of juveniles in the fall flight due to a high early fall hunting mortality will also result in fewer of these individuals being available for hunters in regions reached later on the migration, and those remaining in the population would by then likely be less vulnerable (van der Jeugd and Larsson 1998, Lemoine 2003).

In some analyses, we found a female bias in the adult harvest but equal or slightly male-biased (AF only) ratios among juveniles. Menu et al. (2002) found no differences in recovery rates between sexes in leg-banded adults in this population, but the female bias we detected may be due to the use of neck-collars almost exclusively in females since 1990. While collars do not affect survival of GSG (Menu et al. 2000, Reed 2003), collared birds are generally characterised by a higher reporting rate than those wearing only a metal band (Samuel et al. 1990, Castelli and Trost 1996, Schmutz and Morse 2000, Menu et al. 2002). The larger proportion of adult females recovered compared to males could therefore be a reflection of a higher reporting rate. Female bias could also be enhanced in direct recoveries given that newly banded geese are predominantly successful breeders (Reed et al. 2003) and mothers with juveniles may experience elevated hunting vulnerability (Giroux and Bédard 1986).

In geese, life-long pairing occurs on wintering grounds (Cooke et al. 1975, Owen et al. 1988, Robertson and Cooke 1999). The presence of small populations of LSG wintering in areas adjacent to those of GSG (Cooke et al. 1995) raises the potential for mixed pairing to occur. Given the pattern of female geese to be philopatric to their breeding area (Francis and Cooke 1992, Robertson and Cooke 1999) and the possibility of exchanges between the small AF LSG population and the much larger Mississippi Flyway population, we expected that male GSG banded as young would be more likely to disperse away from the AF than other age-sex classes. However, we found no indication of any differential distribution of recoveries of young males after their first year, suggesting that mixed pairing with populations from other flyways may be quite rare.

Effects of Changes in Hunting Regulations on Harvest Composition and Distribution

The implementation of conservation measures in 1999 was associated with an increase in total harvest rates, as well as changes in the harvest composition. The main difference between the regular and conservation harvests in Québec was a much higher proportion of adults killed in the spring than in the fall. The spring hunt was introduced with the intention of

further reducing adult survival, the parameter to which population growth rate is most sensitive (Gauthier and Brault 1998), and the predominance of adults in the spring harvest implies that the conservation measures are working toward this goal. We found no difference in the geographic distribution of spring and fall harvests even though spring and fall staging distributions of geese in Québec are not identical (Reed et al. 1998). This suggests that hunter activities are similar between the two seasons, and is supported by CWS data indicating that 79-88% of the spring permit holders each year were those who had purchased permits for the previous fall (CWS unpublished data 1999-2002).

At the same time as the spring conservation hunt was implemented, regulations were also liberalized for the fall and, to a lesser extent, winter hunts (CWS Waterfowl Committee 2001b). Tail return data, which are restricted to the fall season, were useful in examining changes in the Québec fall harvest brought about by these regulation changes. The spatial distribution of the harvest in the 1999-2001 time period was similar to previous years with a further proportional decline in estuary harvest. The proportion of adults in the fall harvest was also highest during this time period, following a general increasing trend. The increased representation of the Lac St-Pierre and border regions in the harvest, where juveniles appear less vulnerable than elsewhere in Québec, could have contributed to this high adult kill in recent years. In addition, relaxed fall regulations since 1999 that allowed the use of baiting, electronic calls and stalking techniques (CWS Waterfowl Committee 2001a,b) may have increased the adult kill, as observed in the spring hunt. In contrast to Canada, we found no evidence for changes in AF states geographical harvest distribution or age representation for the 1999-2001 period relative to previous years.

Validity of Data Used for Analyses

Band recoveries and harvest surveys are key sources of data for waterfowl studies, but potential biases are not always considered. Our use of parallel data sets allowed their cross-validation and provided more robust inferences than had we relied on only one source of data. Cooke et al. (2000) also made use of both band recovery and NHS data. They found that band recoveries resulted in lower harvest rate estimates than obtained from survey data, likely due to biases in survey responses, population size estimates, or band reporting rates (Cooke et al. 2000). Survey data, such as the goose tail returns of the SCS used in our analyses, may be prone to biases because they rely on hunters properly reporting their kill, and non-response bias or inaccurate responses may be a problem (Filion 1981, Barker 1991,

Lemoine 2003). Perhaps even more critical is the dependency of band recoveries on reporting rate. Our conclusions drawn from band recovery data make the assumption that variation in band-reporting rate was not the cause of observed patterns. For instance, GSG reporting rates may have increased in recent years due to heightened public awareness, band solicitation, and the introduction of toll-free-number bands in 1995 (J. Dubovsky, USFWS, personal communication). Reporting rates may also vary among regions; in particular, rates might be higher in the AF states because French is the predominant language in Québec and band inscriptions are in English. This is supported by the majority of bands reported in 1975-79 and 1985-89 coming from AF states, even though the Canadian harvest was larger than the USA harvest in virtually all years based on survey data (Reed et al. 1998).

While these factors could have influenced our analyses, they are unlikely to have affected the interactions we examined (e.g. presumably any regional differences in reporting rate did not change over time, and temporal changes in reporting rate were consistent among regions and age-sex groups). Moreover, we found that band recoveries and tail returns indicated the same overall tendencies for the Canadian harvest, implying that any biases in the data sets were minor and did not affect our general inferences.

MANAGEMENT IMPLICATIONS

Conservation measures implemented in 1999 to control GSG abundance have resulted in increased harvest rates and stabilisation of population sizes (CWS unpublished data). However, these actions were not intended to be permanent, and they did not resolve the original cause of rapid population growth. Our analyses suggest that a major cause of the decrease in harvest rates in the 1980s was a northward shift of wintering GSG in the AF, and possibly a redistribution on fall staging grounds. The increase in numbers of geese wintering in the mid-AF states probably resulted in a reduction in the hunting pressure on this population. We suggest that if sufficient harvest is to be maintained in order to prevent further population growth once the spring hunt is closed, agencies should focus their efforts on encouraging increased hunting in mid-AF states, the area where harvest has not kept pace with increases in population size during the 1980s and 1990s. We also recommend a similar assessment of potential causes of harvest rate decline in other expanding waterfowl populations.

LITERATURE CITED

Abraham, K. F., and R. L. Jefferies. 1997. High goose populations: causes, impacts and implications. Pages 7-72 *in* Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., and Ottawa, ON.

Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. Auk **115**:851-862.

Ankney, C. D. 1996. An embarrassment of riches: too many geese. Journal of Wildlife Management **60**:217-223.

Barker, R. J. 1991. Nonresponse bias in New Zealand waterfowl harvest surveys. Journal of Wildlife Management **55**:126-131.

Béchet, A., J.-F. Giroux, G. Gauthier, J. D. Nichols, and J. E. Hines. 2003. Spring hunting changes the regional movements of migrating greater snow geese. Journal of Applied Ecology **40**:553-564.

Boyd, H., H. Levesque, and K. M. Dickson. 2002. Changes in reported waterfowl hunting activity and kill in Canada and the Unites States, 1985-1998. Occasional Paper No. 107. Canadian Wildlife Service, Ottawa, ON.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology **65**:105-112.

Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag New York Inc., New York, NY.

Canadian Wildlife Service (CWS) Waterfowl Committee. 2001a. Migratory Game Bird Hunting Regulations in Canada: July 2001. CWS Migratory Birds Regulations Report No. 3.

Canadian Wildlife Service (CWS) Waterfowl Committee. 2001b. Population Status of Migratory Game Birds in Canada: November 2001. CWS Migratory Birds Regulations Report No. 4.

Castelli, P. M., and R. E. Trost. 1996. Neck bands reduce survival of Canada geese in New Jersey. Journal of Wildlife Management **60**:891-898.

Clausen, P., J. Madsen, S. M. Percival, D. O'Connor, and G. Q. A. Anderson. 1998. Population development and changes in winter site use by the Svalbard light-bellied brent goose, *Branta bernicla hrota* 1980-1994. Biological Conservation **84**:157-165.

Cooke, F., C. M. Francis, E. G. Cooch, and R. Alisauskas. 2000. Impact of hunting on population growth of mid-continent lesser snow geese. Pages 17-31 *in* H. Boyd, editor. Population modelling and management of Snow Geese. Occasional Paper No. 102. Canadian Wildlife Service, Ottawa, ON.

Cooke, F., C. D. MacInnes, and J. P. Prevett. 1975. Gene flow between breeding populations of lesser snow geese. Auk **93**:493-510.

Cooke, F., R. F. Rockwell, and D. B. Lank. 1995. The Snow Geese of La Perouse Bay: Natural Selection in the Wild. Oxford University Press, New York, NY.

Filion, B., D. Luszcz, and M. Allard. 1998. Impact of geese on farmlands. Pages 58-64 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., and Ottawa, ON.

Filion, F. L. 1981. Importance of question wording and response burden in hunter surveys. Journal of Wildlife Management **45**:873-882.

Fox, A. D., and J. Madsen. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology **34**:1-13.

Francis, C. M., and F. Cooke. 1992. Sexual differences in survival and recovery rates of lesser snow geese. Journal of Wildlife Management **56**:287-296.

Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992a. Long-term changes in survival rates of lesser snow geese. Ecology **73**:1346-1362.

Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992b. Changes in survival rates of lesser snow geese with age and breeding status. Auk **109**:731-747.

Francis, C. M., J. R. Sauer, and J. R. Serie. 1998. Effect of restrictive harvest regulations on survival and recovery rates of American black ducks. Journal of Wildlife Management **62**:1544-1557.

Freemark, K. E., and F. G. Cooch. 1978. Geographic analysis of waterfowl kill in Canada. Pages 66-77 *in* H. Boyd and G. H. Finney, editors. Migratory game bird hunters and hunting in Canada. Report Series No. 43. Canadian Wildlife Service, Ottawa, ON.

Gauthier, G., and S. Brault. 1998. Population model of the greater snow goose: projected impacts of reduction in survival on population growth rate. Pages 65-80 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., and Ottawa, ON.

Gauthier, G., R. Pradel, S. Menu, and J.-D. Lebreton. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology **82**:3105-3119.

Giroux, J.-F., B. Batt, S. Brault, G. Costanzo, B. Filion, G. Gauthier, D. Luszcz, and A. Reed. 1998b. Conclusions and management recommendations. Pages 81-88 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Giroux, J.-F., and J. Bédard. 1986. Sex-specific hunting mortality of greater snow geese

along firing lines in Québec. Journal of Wildlife Management **50**:416-419.

Giroux, J.-F., G. Gauthier, G. Costanzo, and A. Reed. 1998a. Impact of geese on natural habitats. Pages 32-57 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology **31**: 295-311.

Hestbeck, J. B. 1994. Survival of Canada geese banded in winter in the Atlantic flyway. Journal of Wildlife Management **58**:748-756.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site-fidelity using mark-resight data of wintering Canada geese. Ecology **72**:523-533.

Hill, M. R. J., and R. B. Frederick. 1997. Winter movements and habitat use by greater snow geese. Journal of Wildlife Management **61**:1213-1221.

Johnson, M. A. 1997. Management strategies to address the mid-continent lesser snow goose overpopulation problem. Pages 101-111 *in* Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, Ontario.

Krapu, G. L., K. J. Reinecke, D. G. Jorde, and S. G. Simpson. 1995. Spring-staging ecology of midcontinent greater white-fronted geese. Journal of Wildlife Management **59**:736-746.

Lemoine, V. 2003. Évaluation de la chasse de conservation printanière à la Grande Oie des neiges : Comportement, succès des chasseurs, et effets sur la survie des oies. MSc Thesis, Université de Québec à Montréal, Montréal, Québec.

Madsen, J., G. Cracknell, and T. Fox, editors. 1999. Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publication No 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rönde, Denmark. 344pp.

Malecki, R. A., S. E. Shaeffer, and J. W. Enck. 1988. Influence of agricultural land use changes on wintering Canada geese in the Atlantic Flyway. Transactions of the North American Wildlife and Natural Resources Conference **45**:8-17.

Martin, E. M., and P. I. Padding. 1999. Preliminary Estimates of Waterfowl Harvest and Hunter Activity in the United States during the 1998 Hunting Season. U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, MD.

Martin, E. M., and P. I. Padding. 2000. Preliminary Estimates of Waterfowl Harvest and Hunter Activity in the United States during the 1999 Hunting Season. U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, MD.

Martin, E. M., and P. I. Padding. 2001. Preliminary Estimates of Waterfowl Harvest and Hunter Activity in the United States during the 2000 Hunting Season. U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, MD.

Martin, E. M., and P. I. Padding. 2002. Preliminary Estimates of Waterfowl Harvest and Hunter Activity in the United States during the 2001 Hunting Season. U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, MD.

Menu, S., G. Gauthier, and A. Reed. 2002. Changes in survival rates and population dynamics of greater snow geese over a 30-year period: implications for hunting regulations. Journal of Applied Ecology **39**:91-102.

Menu, S., J. B. Hestbeck, G. Gauthier, and A. Reed. 2000. Effects of neck bands on survival of greater snow geese. Journal of Wildlife Management **64**:544-552.

Olson, J. 2001. Comportement migratoire automnal de la Grande Oie des neiges dans le Québec méridional. MSc Thesis, Université de Québec à Montréal, Montréal, Québec.

Owen, M., J. M. Black and H. Liber. 1988. Pair bond duration and timing of its formation in Barnacle geese (*Branta leucopsis*). Pages 23-38. *in* Waterfowl in Winter (M. W. Weller, Ed.). University of Minnesota Press, Minneapolis, MN.

Prevett, J. P. and MacInnes, C. D. 1980. Family and other social groups in snow geese. Wildlife Monographs No. 71, The Wildlife Society.

Reed, A. 1990. Population dynamics in a successful species: challenges in managing the increasing population of greater snow geese. Transactions of the 19th IUGB Congress, Trondheim 1989, Norway.

Reed, A., J.-F. Giroux, and G. Gauthier. 1998. Population size, productivity, harvest and distribution. Pages 5-31 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., and Ottawa, ON.

Reed, E. T. 2003. Coûts des soins parentaux et effets des conditions environnementales sur la reproduction de la Grande Oie des neiges. PhD Dissertation, Université Laval, Ste-Foy, Québec.

Reed, E. T., J. Bêty, J. Mainguy, G. Gauthier, and J.-F. Giroux. 2003. Molt migration in relation to breeding success in Greater Snow Geese. Arctic **56**:76-81.

Robertson, G. J., and F. Cooke. 1999. Winter philopatry in migratory waterfowl. Auk **116**:20-34.

Rogers, J. P. 1979. *Branta bernicla hrota* in the USA – a management review. Pages 198-207 *in* Proceedings of the First Technical Meeting on Western Palearctic Migratory Bird Management: *Branta bernicla bernicla*. International Waterfowl Research Bureau, UK.

Royle, J. A., and J. A. Dubovsky. 2001. Modeling spatial variation in waterfowl band-recovery

data. Journal of Wildlife Management **65**:726-737.

Samuel, M. D., D. H. Rusch, and S. Craven. 1990. Influence of neck bands on recovery and survival rates of Canada geese. Journal of Wildlife Management **54**:45-54.

SAS Version 8.0. SAS Institute Inc. 1999. Cary, NC.

Schmutz, J. A., and J. A. Morse. 2000. Effects of neck collars and radiotransmitters on survival and reproduction on emperor geese. Journal of Wildlife Management **64**:231-237.

Serie, J. 1996. Atlantic Flyway Waterfowl Harvest and Population Survey Data. U.S. Fish and Wildlife Service, Patuxent Environmental Science Center, Laurel, MD.

Smith, G. W., and R. E. Reynolds. 1992. Hunting and mallard survival, 1979-88. Journal of Wildlife Management **56**:306-316.

van der Jeugd, H. P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology **67**:953-966.

Williams, B. K., and R. Bishop. 1990. Perspectives on goose management in North America: challenges and opportunities for the '90s. Transactions of the North American Wildlife and Natural Resources Conference **55**:283-285.

CHAPITRE 2

IMPACTS OF EXCEPTIONAL CONSERVATION MEASURES ON SURVIVAL AND HUNTING MORTALITY: A NATURAL EXPERIMENT WITH GREATER SNOW GEESE

ANNA M. CALVERT et GILLES GAUTHIER

RÉSUMÉ

Nous avons évalué les effets d'une nouvelle chasse printanière et d'une libéralisation dans les règlements de chasse d'automne et d'hiver, des mesures introduites en 1998-99 pour contrôler l'abondance de la Grande Oie des neiges (*Chen caerulescens atlantica*). Plus spécifiquement, nous avons testé des hypothèses concernant les impacts de ces changements sur les taux de survie et de récupération de bagues, ainsi que sur les taux de mortalité due à la chasse, en analysant des données de 1990-2001. Les taux de survie et de récupération annuels ont été estimés à partir de modèles de récupérations dans le logiciel MARK, et nous avons développé une structure de modèle flexible dans le logiciel SURVIV afin de déterminer les implications des changements à chacune des trois saisons de chasse. Les taux de récupération et de mortalité adulte ont augmenté depuis 1999, principalement dus à l'ajout de la chasse printanière et aux modifications des règlements d'hiver, alors que les taux de récupération et de mortalité des juvéniles étaient hautement variables. Nous avons aussi observé un déclin dans la survie adulte annuelle moyenne de 83.5% avant les nouvelles mesures à 71.9% après, bien que l'initiation des mesures spéciales de conservation n'explique pas entièrement la variation temporelle de survie. Globalement, nos résultats suggèrent que les taux de survie et de mortalité ont été affectés comme prédites par les mesures de gestion spéciales, et que des manipulations des règlements pendant les saisons régulières pourraient être utilisées pour un contrôle de la population future dès que la chasse printanière est suspendue.

ABSTRACT

We assessed the effects of a new spring hunting season and more liberal autumn and winter regulations introduced in 1998-99 to control population growth of greater snow geese (*Chen caerulescens atlantica*). Specifically, we tested hypotheses regarding the impacts of these changes on survival and recovery probabilities and on kill rates by analysing data from 1990-2001. Annual survival and recovery probabilities were estimated using band recovery models in program MARK, and we developed a flexible model structure in program SURVIV to determine the implications of changes to each of the three hunting seasons. Adult recovery rates and kill rates increased since 1999, mainly because of the addition of the spring hunt and the liberalised winter regulations, while juvenile recovery rates were highly variable. We also observed a decline in mean annual adult survival rate, from 83.5% before the addition of the special measures to 71.9% afterward, although the implementation of conservation measures did not explain all temporal variability in survival. Overall, our results suggest that survival and hunting mortality rates were affected as expected by the special conservation measures, and that regular season regulations could be manipulated for future population control once the spring hunt is discontinued.

INTRODUCTION

An understanding of the impacts of human actions upon animal population growth is critical to management of wildlife. Despite increasing recognition of the value of frequent re-evaluations in the context of adaptive management (Walters and Holling 1990, Williams and Johnson 1995), anthropogenic actions such as refuge creation and sport harvest have often allowed populations to reach exceptionally high or low abundances. The rapid growth of many North American goose populations (Ankney 1996) and the worldwide decline of commercially harvested fish populations (Hutchings 2000, Myers and Worm 2003) are current examples of such extreme management problems.

Traditionally, studies have considered the effects of hunting on game-birds by monitoring long-term variations in survival and recovery rates (e.g. Smith and Reynolds 1992, Krementz et al. 1996, Giudice 2003), or by evaluating the consequences of local or regional variations in harvest regime (e.g. Anderson and Burnham 1978, Kirby et al. 1983, Francis et al. 1998, Otis and White 2002). In many cases, though, it has been difficult to distinguish the effects due to changes in harvest from naturally-occurring environmental and demographic stochasticity (Nichols 1991b, Smith and Reynolds 1992, Sedinger and Rexstad 1994, Williams and Johnson 1995). Evaluation of the impacts of large-scale or extreme management actions, which may become more frequent as human influence on wildlife populations continues to increase, has seldom been made. Yet, analysis of drastic changes to exploitation regimes could clarify the demographic impacts of harvest better than has been possible in the past.

For waterfowl, the relationship between natural and hunting mortality may depend on the species or on environmental conditions (Conroy and Krementz 1990, Jensen 1991, Nichols 1991a, Francis et al. 1998). Long-lived species with high natural survival rates, such as geese, experience hunting mortality that is primarily additive to natural mortality (Hestbeck 1994, Gauthier et al. 2001). Consequently, changes in harvest should directly affect survival of these species, and hunting regulations could be used to manipulate vital rates (Cooke et al. 2000, Menu et al. 2002). Because population growth is highly sensitive to changes in survival rate for many birds (Sæther and Bakke 2000, Gauthier and Brault 1998, Hoekman et al. 2002), manipulating the harvest should directly affect their abundance.

The rapid population growth of greater snow geese (*Chen caerulescens atlantica*) during the late 20th century (Reed et al. 1998) prompted managers to implement exceptional conservation measures beginning in winter 1998-99, in response to the threat posed to natural habitats (Giroux et al. 1998b). Introduced with the intention of reducing adult survival and ultimately stabilising abundance, these actions included the liberalisation of existing sport hunting regulations, strongly in autumn and to a lesser degree in winter. Most significantly, these actions included also the initiation of a special spring hunting season on staging grounds in Québec (CWS Waterfowl Committee 2001). The annual population survey indicates that, globally, these measures led to a reduction in abundance from 938,000 in 1999 to 639,000 in 2002 (CWS unpublished data); however, the relative effectiveness of the different seasonal measures is yet unknown. Furthermore, changes in migratory route and wintering range over the past two decades (Reed et al. 1998, Olson 2001, Béchet et al. 2003) have led to a redistribution of the harvest (Chapter 1). Such changes may have altered seasonal harvest impacts and ultimately affected the efficiency of hunting in controlling abundance.

In this study, we took advantage of the changes to hunting regulations for greater snow geese to assess the implications of radical alterations to harvest strategy throughout the range of a population. Although not designed as an *a priori* experiment, this situation can be considered a large-scale natural quasi-experiment affecting the entire population, where the period prior to 1999 is the control, and the period since then the treatment. Moreover, the spring hunt is a unique management initiative and there are no previous studies of the impacts of such actions using modern analytical tools. Our main objective was therefore to conduct an integrative evaluation of the impacts of the measures implemented in 1999 by comparing the magnitude of these effects to base-line temporal variability in survival and recovery rates. To achieve this, we tested three predictions concerning the potential impacts of regular and special hunting seasons on the population. We predicted that since the implementation of the special conservation measures, for all age-sex groups: 1) annual recovery rates and kill rates have increased; 2) annual survival rates have declined; and 3) seasonal recovery and kill rates have increased with the regulation changes in each hunting season. In testing these predictions, we aimed to evaluate the effects of important and previously unexamined changes to the management regime of a waterfowl population.

METHODS

Data Collection

Greater snow geese were leg-banded on breeding grounds every August from 1990-2001 (total n = 42,226 banded) on Bylot Island, Nunavut (73° N, 80° W). Sex was determined by cloacal eversion and age by plumage characteristics; hereafter all first-year birds are referred to as "juveniles", and all birds ≥1 year as "adults". All birds were marked with USFWS metal bands; some adult birds (mainly females) were affixed also with plastic neck collars (see Menu et al. 2000 for details). We could not determine whether birds marked with a collar had retained it until the time of harvest, but collar loss is low in this population (3-5%/year; Gauthier et al. 2001, Reed 2003). Some juveniles were marked also with plastic leg-bands since 1998, but a separate analysis showed that these did not affect survival or recovery rates (Appendix A) and they were therefore ignored.

Banding and recovery records (n = 4,333 recoveries from August 1990-July 2002) were obtained from the Bird Banding Laboratory (USFWS), and we used only data from hunter-shot birds. Recoveries came principally from sport hunting seasons during autumn in Canada and winter in the Atlantic Flyway states of the US, as well as from the spring conservation hunt in Québec (Canada) since 1999. Estimates of annual harvest rate (H) were taken from Menu et al. (2002) and Chapter 1 as the ratio between the total number of greater snow geese reported killed by hunters to the CWS and USFWS divided by the total autumn population size. Seasonal harvest rates were estimated following the same procedure, giving a rate relative to the autumn population size.

Models of annual survival and recovery rates

Data on bandings and recoveries were structured into 12-month periods from 1 August to 30 July each year, resulting in 12 recovery periods and 11 survival intervals. Hereafter, a year (e.g. 1998) will refer to the 12-month period beginning with banding in August that year and ending the following July prior to the next banding period (i.e. August 1998-July 1999). We separated banding and recovery totals into five groups for our initial analyses: juvenile males and females, adult males and females, and adult females marked with neck collars; the few adult males (<300) marked with collars were eliminated from the data set, as were all radio-marked birds. We used program MARK (White and Burnham 1999) to run Brownie-type (Brownie et al. 1985) dead recovery models and followed their terminology. Survival rate (S_i) is the probability that a bird banded in year i survives to time of banding in year $i+1$, and

recovery rate (f_i) is the probability that a banded bird alive at the time of banding in year i will be shot by a hunter during that year's hunting season, retrieved and reported. Recovery rate f is therefore the product of K (kill rate, probability of being killed by a hunter), c (retrieval rate, the probability that a hunter retrieves a bird that is shot), and λ (reporting rate, the probability that a hunter who shoots and retrieves a banded bird will report the band to wildlife agencies); the product of K and c is known as harvest rate (H) (Brownie et al. 1985).

Candidate models were constructed with different sets of factors affecting survival and recovery rates. Survival and recovery rates were both allowed to vary with year (t in model notation), age group ($a2$, a 2-class structure where juveniles = birds <1yr old, adults = birds ≥1yr) and sex (s, applied to both age groups or to one only). Recovery rates were also modelled with a direct-recovery effect ($f\,^\wedge$, where recovery rates are different in the first year following marking, which could represent the fact that the banded sample is not random but instead represents successful breeders, who might differ in hunting vulnerability from non-breeders; in models with the 2-age-class structure, this only applied to adults) and with a collar effect (col, where collared females differed from non-collared females; collars do not affect survival in this population, Menu et al. 2000, Reed 2003). We further modelled recovery rates using three different external covariates: 1) annual harvest rates for adults and juveniles (H); 2) conservation measures implemented beginning in 1998-999 (m); and 3) the introduction of toll-free-number bands beginning in 1996 (b; toll-free-number bands were placed on birds beginning in 1996; these bands apparently increased reporting rates for other waterfowl species, CWS unpublished data and J. Dubovsky USFWS, personal communication). The former was modelled as a linear constraint on survival and recovery rates using the actual harvest rate values. The latter two factors affected recovery rate only and were modelled as "dummy variables" (i.e. a binary coding for presence or absence of the effect). Parentheses with capital letters following a factor indicate the only group(s) to which it was applied (e.g. $s(A)$ signifies a sex-effect on adults only), while * and + symbols represent interactive and additive effects, respectively. Note that unless otherwise stated, interactions were always between (t) and another factor, and not between two other factors, e.g. a model notation of $fa2*t+s*col$ signifies interactions time*age, and time*collar, and an additive effect of time and sex. We constructed also *a posteriori* models including an effect of band solicitation between 1990-1993 (o; during this period, a technician regularly made bags checks among outfitters in Québec and recorded banded birds shot), based partly on parameter estimates obtained from initial model selection.

The more general models were tested first; reduced models were then constructed by constraining some parameters in order to determine which parameters were the most parsimonious for modelling our data. We tested the fit of our data using goodness-of-fit tests in programs BROWNIE and ESTIMATE (Brownie et al. 1985) because the bootstrap goodness-of-fit procedure available in MARK may generate biased $\hat{c}$ estimates (White 2002). We pooled χ^2 values and degrees of freedom from male and female age-group comparisons and from collared geese, estimated with model H1 (time variation in survival and recovery rates), to obtain an overall $\hat{c}$ value. This value was used in MARK to correct for overdispersion in our data by adjusting the deviance in the AIC_c calculation to become $QAIC_c$ (the quasi-likelihood Akaike Information Criterion, Burnham and Anderson 1998). We then used the $QAIC_c$ to select the best model (i.e. the model with the smallest $QAIC_c$ value); all other models were relatively ranked. The $QAIC_c$ weights ($\omega QAIC_c$, where the sum of all model weights = 1) were also used to evaluate the importance of particular factors.

Models of seasonal recovery rates

In order to determine how recovery rates differed between hunting seasons and locations, we separated each year's total recoveries into two (1990-97) or three (1998-2001) seasons. These were defined as "autumn" (all geese recovered between September and December in Québec), "winter" (all geese recovered between October and March in the Atlantic Flyway (AF) states; while some of these came from autumn months, we grouped them with winter recoveries based on their location, i.e. they had already passed through Québec), and "spring" (all geese recovered in April and May of 1999-2001 in Québec). Recoveries that did not fit into any one of these categories (n = 47) were excluded, with resulting recovery totals of 1716, 1926 and 644 for autumn, winter and spring, respectively.

Because this seasonal separation resulted in two or three recovery periods for each banding period, we had to use the more flexible program SURVIV instead of MARK to analyse these data (White 1983). Based on preliminary model selection in MARK, we used four groups for this modelling: adult males, adult females, collared adult females, and juveniles (sexes combined). For each group we built recovery matrices with two or three periods for each year, relying on two main simplifying assumptions: 1) natural mortality between hunting seasons within a banding year was negligible; and 2) reporting rate was equal among seasons/regions within each year. We considered recovery rate in autumn (f_i^a) as simply the probability of a bird being recovered in autumn of year i, whereas the probability of recovery in subsequent

seasons was the product of the seasonal recovery rate (f_i^w or f_i^p for winter and spring, respectively) and the proportion of the population remaining after the previous season's harvest (1 minus the harvest rate from the previous season, i.e. f_i/λ_i). For example, the probability of recovery in autumn 2001 would be [f_{01}^a], in winter 2001 [$f_{01}^w \cdot (1 - f_{01}^a/\lambda_{01})$], and in spring 2001 [$f_{01}^p \cdot (1 - f_{01}^w/\lambda_{01}) \cdot (1 - f_{01}^a/\lambda_{01})$] (for full parameterisation see Appendix B). Annual survival rates were included in the matrix in the same way as in the Brownie-type models (modelling of seasonal survival rates was not possible because banding occurred only on an annual basis). A general model and a series of constrained models were constructed to determine how seasonal recovery rates differed from one another and among groups. The fit of the data was tested using the ratio of the χ^2-value to its degrees of freedom for the most general model, and this was used as described above to correct AIC_c values to $QAIC_c$ values, which were used in model selection.

In order to avoid problems of parameter identifiability (Brownie et al. 1985) in our SURVIV models, we had to fix annual reporting rates (λ_i) to reasonable values for this population. We estimated reporting rate from the equation $f = \lambda H$ where f is the annual recovery rate estimated in MARK and H the annual harvest rate calculated from independent survey data. The slope of this relationship provided an estimate of λ.

RESULTS

Annual recovery rate estimates

Pooled contingency test results from BROWNIE and ESTIMATE resulted in a $\hat{c}$ estimate of 1.294 ($\chi^2 = 324.66$, df = 251, P<0.001). The best-fit model ($S_{a2*t}\ f^\wedge_{a2*t*s(A)*col}$) retained age, time, sex (adults only), and collar effects on recovery rate, and consistently higher direct than indirect recovery rates (Table 1). For recovery rate calculations, we relied upon parameter estimates from the second model ($S_{a2*t}f_{a2*t+s(A)+col}$), as the large number of parameters in the best-fit model confused the evaluation of our hypotheses, and patterns found in direct vs. indirect recovery rates were very similar (survival estimates were also very similar between these 2 models). Overall, annual recovery rates gradually declined in the first few years of the study but increased abruptly from 1998 onward (Fig. 1). Recovery rates were about twice as high in juveniles and adult females with collars as in adult males or females without collars. A model where recovery rates were constrained to be dependent on our external variable

Table 1. The ten best-fit models among the initial candidate model set, and the most general model (in bold), for band-recovery data of greater snow geese from 1990-2001, with an overdispersion correction factor of $\hat{c}$ = 1.326. Each model is shown with its number of parameters, the deviance, the difference in $QAIC_c$ between the current and best model ($\Delta QAIC_c$), and its $QAIC_c$ weight ($\omega QAIC_c$). The models include five groups (adult males, adult females, adult collared females, juvenile males, juvenile females). Parentheses with a capital letter after an effect refer to that effect being applied only to the group mentioned (e.g. *s(A)* indicates a sex-effect on adults only).

Model Name	# Parameters	Deviance	$\Delta QAIC_c$	$\omega QAIC_c$
$S_{a2*t}\ f^{\wedge}{}_{a2*t*s(A)*col}$	103	439.3	0.00	0.768
$S_{a2*t}\ f_{a2*t+s(A)+col}$	48	589.8	3.09	0.164
$S_{a2*t+s(A)}\ f_{a2*t+s(A)+col}$	49	589.8	5.10	0.060
$S_{a2*t*s}\ f_{a2*t*s(A)*col}$	92	482.1	10.15	0.005
$S_{a2*t}\ f_{a2*t*s(A)+col}$	59	573.8	13.06	0.001
$S_{a2*t*s(A)}\ f^{\wedge}{}_{a2*t*s(A)*col}$	114	428.9	14.27	<0.001
$S_{a2*t*s(A)}\ f_{a2*t+s(A)+col}$	59	575.5	14.35	<0.001
$S_{a2*t+s(A)}\ f_{a2*t*s(A)+col}$	60	573.7	15.01	<0.001
$S_{a2*t}\ f_{a2*t+s(A)*col}$	59	578.6	16.65	<0.001
$S_{a2*t}\ f_{a2*t*s(A)*col}$	70	549.8	17.08	<0.001
$\boldsymbol{S_{a2*t*s}\ f^{\wedge}{}_{a2*t*s*col}}$	**137**	**380.4**	**23.99**	**<0.001**

S: survival rate

f: recovery rate

a2: age effect (juveniles <1yr and adults)

t: time effect (annual)

s: sex effect

col: neck-collar effect

^: direct recovery effect
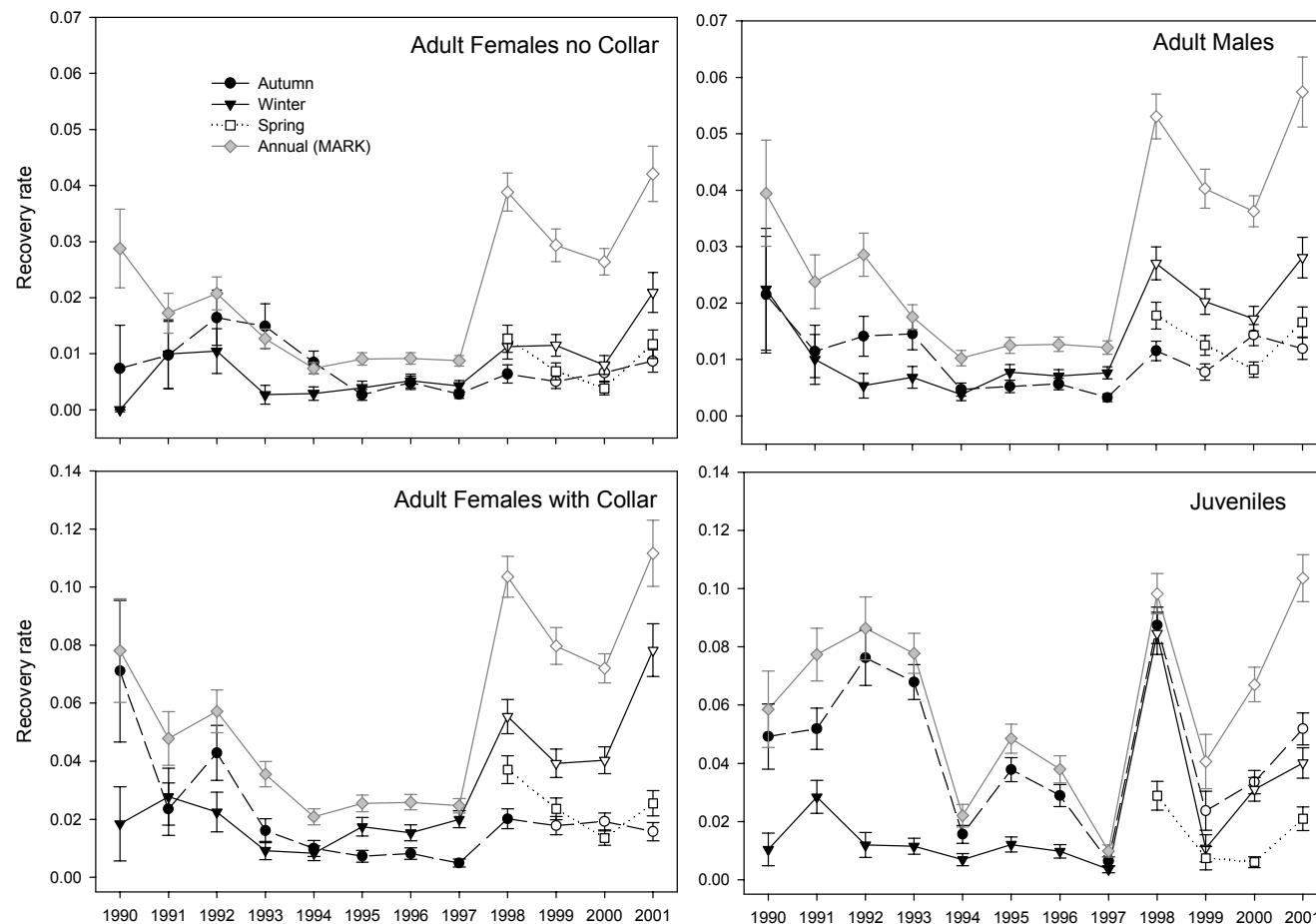
Figure 1. Annual and seasonal recovery rate estimates (mean ± SE) for adult female with and without collars, adult male, and juvenile greater snow geese from 1990-2001. Annual estimates are derived from model $S_{a2*t}\ f_{a2*t+s(A)+col}$ in program MARK, and seasonal estimates from the unconstrained model in program SURVIV (see Table 3). Autumn recoveries come from harvest in Québec, winter recoveries from harvest in Atlantic Flyway states, and spring recoveries from the conservation hunt implemented in Québec from 1999-2001. Annual rates are not equal to the sum of seasonal rates, as seasonal rates are based on the number of banded birds still alive (i.e. adjusted for the previous season's harvest), while annual rates are based on the total number of banded birds at the time of banding. Empty dots refer to years/seasons after the implementation of conservation measures.

harvest rate (different estimates for adults and young, but same between sexes) was not preferred (model $S_{a2*t}\ f_{a2*H+s(A)+col}$, $\Delta QAIC_c$ = 203.8). Nevertheless, the slope of this relationship was significant (β = 3.69, 95% CI: 3.08 - 4.29 for birds without collars). A plot of annual recovery rate estimates based on the second-ranked model ($S_{a2*t}\ f_{a2*t+s(A)+col}$) and annual harvest rates revealed a good fit between these 2 variables, especially in adults (Fig. 2). This suggested that while harvest rate did not fully account for time variation in recovery rate, they were well correlated.

To evaluate the effect of the special conservation measures on recovery rate, we built a model ($S_{a2*t}\ f\hat{}_{a2*m(A)*s(A)*c}$) contrasting recovery rate before 1998 vs. afterward, but this model was not preferred ($\Delta QAIC_c$ = 20.0). However, we further divided the period 1990-1997 in two: 1990-1993, which corresponds to the period where some band solicitation took place in Québec, and 1994-1997. The *a posteriori* model $S_{a2*t}\ f\hat{}_{a2*m(A)o(A)+s(A)+col}$ (Table 2) that included band-solicitation and conservation measure effects on adult recovery rates only was as good as our previous best model (Table 2). Recovery rates were much higher after the introduction of conservation measures in 1998 than during the previous periods with or without band solicitation. Direct recovery rate estimates (±SE) for periods 1990-93, 1994-97 and 1998-2001, respectively, were: adult collared females [0.052 (0.004), 0.030 (0.002) and 0.099 (0.005)], adult females without collars [0.019 (0.002), 0.011 (0.001) and 0.037 (0.003)], and adult males [0.026 (0.002), 0.015 (0.001) and 0.051 (0.003)]. These estimates therefore suggest an increase in adult annual recovery rate since the initiation of conservation measures, supporting our first prediction for adults but not for juveniles. Addition of effects of toll-free number bands on recovery rate did not improve model ranking (best model with this effect, $\Delta QAIC_c$ = 23.2).

Annual survival rate estimates

The best-fit models all retained age and full time effects on survival (Table 1). Survival did not differ between sexes, but was much higher and generally less variable in adults than in juveniles (Fig. 3). In some years, adult survival rates were estimated at or near 1 whereas in other years (e.g. 1997-98), adult survival was unrealistically low. The best-fit models were rerun in a dataset made of adults only, in an attempt to isolate the cause of these aberrant estimates, but with the same results.
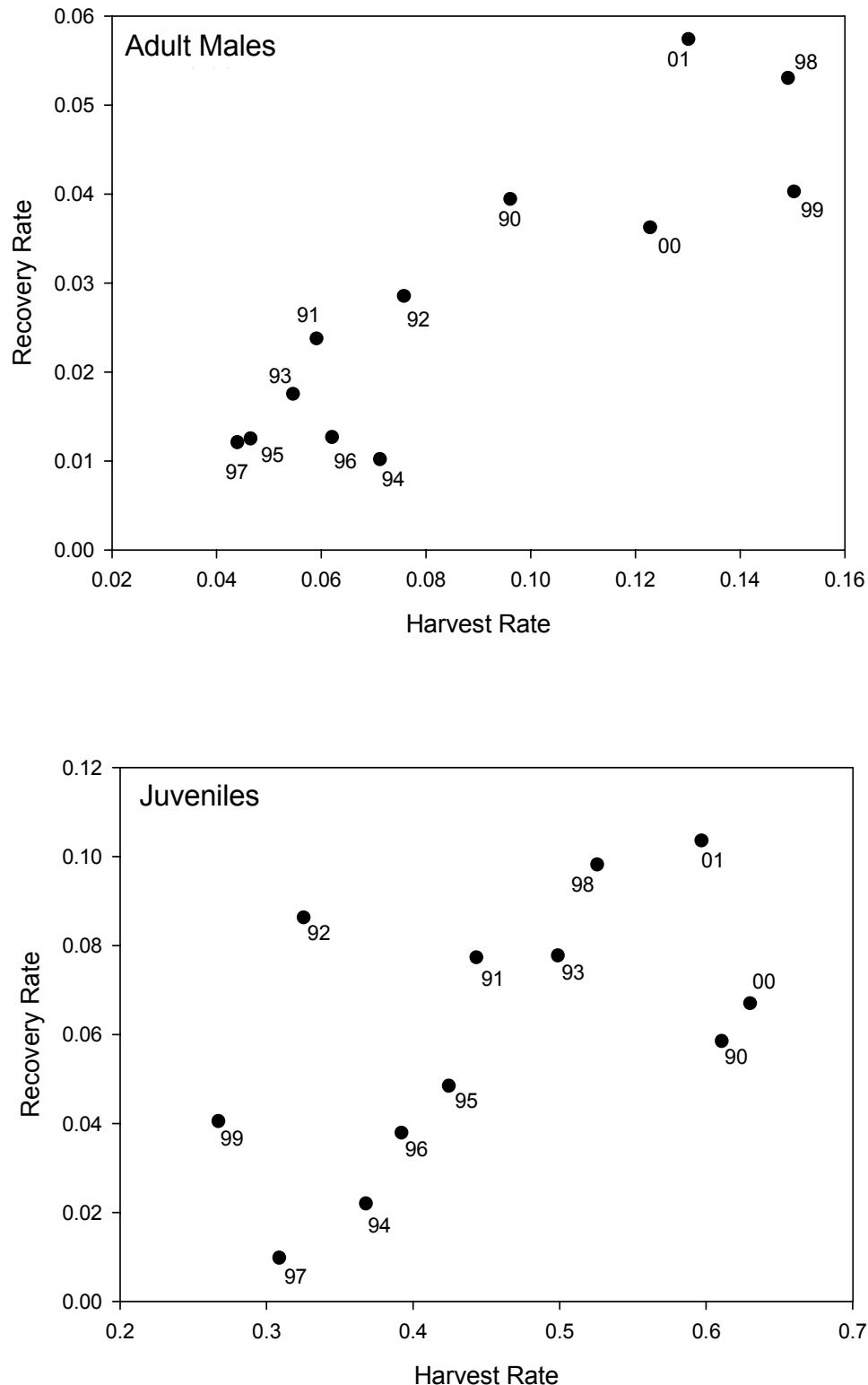
Figure 2. Recovery rate (estimated from MARK model $S_{a2*t}\ f_{a2*t+s(A)+col}$) vs. harvest rate (estimated from survey data) for adult male and juvenile greater snow geese from 1990-2001. Because of additive effects of sex and collar on recovery rates of adults in this model, we only present adult males for simplicity. Numbers next to data points indicate the year.

Table 2. The seven best-fit models of the *a posteriori* candidate model set (i.e. including a band-solicitation effect for the early 1990s) for band-recovery data of greater snow geese from 1990-2001. Each model is shown with its number of parameters, its deviance, the difference in $QAIC_c$ between the current and best model ($\Delta QAIC_c$), and its $QAIC_c$ weight ($\omega QAIC_c$). See Table 1 for further details.

Model Name	# Parameters	Deviance	ΔQAIC$_c$	ωQAIC$_c$
S_{a2*t} $f^{\wedge}_{a2*t*s(A)*col}$	103	439.3	0.00	0.443
S_{a2*t} $f^{\wedge}_{a2*m(A)o(A)+s(A)+col}$	40	608.1	0.86	0.289
S_{a2*t} $f_{a2*t+s(A)+col}$	48	589.8	3.09	0.095
S_{a2*t} $f^{\wedge}_{a2*m(A)o(A)+s(A)*col}$	42	606.6	3.70	0.070
S_{a2*t} $f^{\wedge}_{a2*m(A)o(A)*s(A)+col}$	42	607.9	4.69	0.042
$S_{a2*t+s(A)}$ $f_{a2*t+s(A)+col}$	49	589.8	5.10	0.035
S_{a2*t} $f^{\wedge}_{a2*m(A)o(A)*s(A)*col}$	44	604.5	6.11	0.021

S: survival rate

f: recovery rate

a2: age effect (juveniles <1yr and adults)

t: time effect (annual)

s: sex effect

col: neck-collar effect

^: direct recovery effect

m: conservation measures effect (since 1998)

o: band solicitation effect (1990-93)
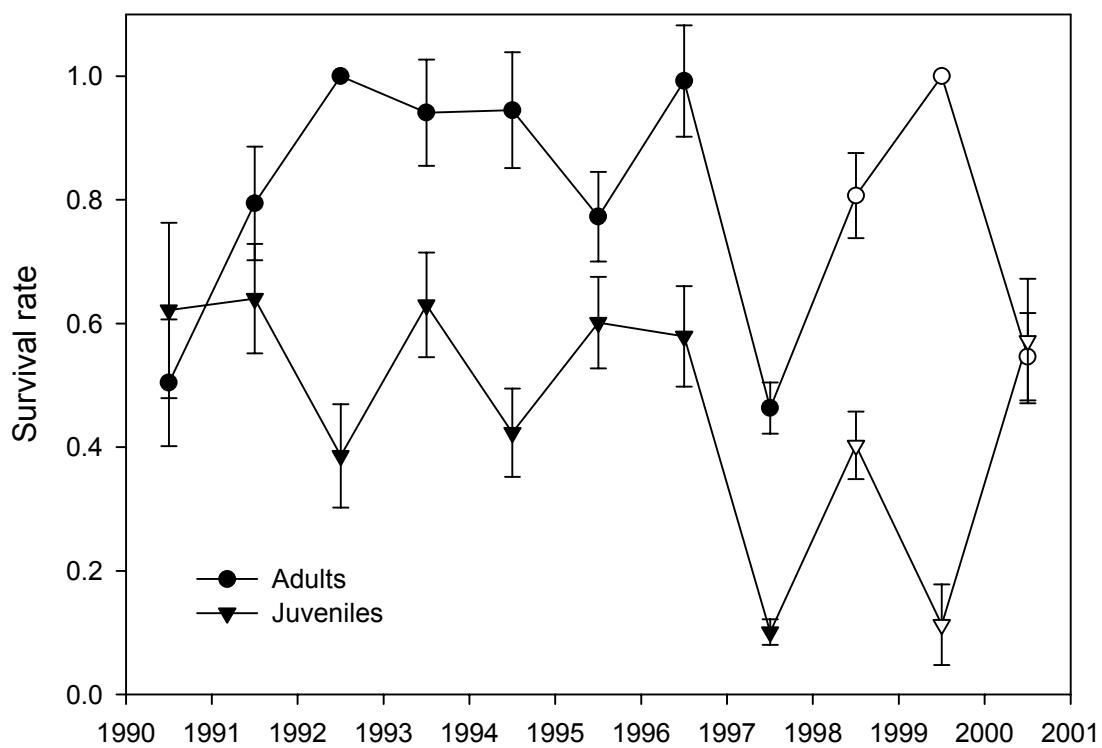
Figure 3. Annual survival rate estimates (mean ± SE) for adult (≥1 yr) and juvenile greater snow geese from 1990-2001, derived from the model $S_{a2*t} \ f_{a2*t+s(A)+col}$ (see Table 1) in program MARK. Empty dots refer to years/seasons after the implementation of conservation measures.

Models attempting to reduce temporal variations in survival rate to the periods before vs. after the introduction of conservation measures were not among the top-ranking ones (best model with this effect, $S_{a2*m(A)}$ $f_{a2*t+s(A)+col}$, $\Delta QAIC_c$ = 71.1). This could indicate either that conservation measures had no effect on survival rate, or that temporal variation in survival rate due to other factors was too large to allow a reduction of survival variation to this single effect. However, the lack of overlap in confidence intervals between mean adult survival rates before and after the initiation of conservation measures estimated from this model [0.835 (95% CI: 0.811-0.856) vs. 0.719 (0.666-0.766), respectively] suggests a reduction in survival with the regulation changes, supporting our second prediction for adults. A model also reducing variation in juvenile survival to the same two time periods (S_{a2*m} $f_{a2*t+s(A)+col}$) was ranked much lower ($\Delta QAIC_c$ = 152.58). The overlap in confidence intervals between juvenile survival estimates for 1990-97 and 1998-2001 [0.466 (0.412-0.521) vs. 0.508 (0.406-0.609) respectively] further suggests no effect of these measures on juveniles.

Reporting rates

Over the course of our study, reporting rate varied likely because of band solicitation from 1990-93 and to toll-free-number bands from 1996-2001. We therefore determined slope parameters of the f vs. H relationship in Fig. 2 separately for these 2 periods (we used only adult males to avoid heterogeneity due to the presence of neck-collar in females, and a high and variable migration mortality in juveniles). The slope (i.e. λ) was estimated at 0.48 for 1990-93 and 0.38 for 1996-2001. No slope could be estimated for the time period with no external effects on reporting rate because it consisted of only 2 years (1994-95). A value of 0.25 was chosen as we expected the reporting rate for that period to be lower than in other years, and this value fell within the range of literature values (Conroy 1985, Nichols et al. 1991, 1995, Reinecke et al. 1992). We considered that collared birds would have a reporting rate of approximately double that of non-collared birds, based on ratios of collared to non-collared total recoveries (assuming that both have equal survival and harvest rates; Menu et al. 2000, Reed 2003). We further assumed that 1) reporting rates were equal among regions and seasons within any given year as Nichols et al. (1995) found no difference in mallard reporting rates between Canada and the AF states, and 2) neither sex nor age would affect reporting rate. Consequently, we used reporting rate values of 48% (1990-93), 25% (1994-95) and 38% (1996-2001) for non-collared geese, and 96%, 50% and 76% respectively for collared geese, in the seasonal modelling of recovery rates in program SURVIV, as well as in subsequent kill rate calculations.

Seasonal recovery rate estimates

The goodness-of-fit test of SURVIV (χ^2 = 957.6, df = 832, P <0.001) gave a ĉ = 1.151. The unconstrained model was ranked highest among the 21 candidate models, indicating that recovery rates differed among seasons and age-sex groups (Table 3). Models with recovery rates equal between adult males and females (without collars) during the autumn and/or spring hunting seasons did not differ greatly from the unconstrained one. In contrast, a model allowing juveniles to take on adult recovery rates in the last season (spring) of their first year was rejected ($\Delta QAIC_c$ = 13.4), and even more strongly when the constraint was applied in winter ($\Delta QAIC_c$ > 120). Models constraining recovery rates to be equal among seasons within each year, or equal among years for each season all provided a poor fit ($\Delta QAIC_c$ > 45). Seasonal estimates derived from the best-fit model (Fig. 1) indicated that autumn and winter recoveries generally showed the same temporal trends as those of the annual estimates found with MARK. The increase in recovery rates in all seasons since the implementation of conservation measures thus supports our third prediction. The seasonal analyses nonetheless revealed that adult recovery rates, which were higher in autumn than in winter in the early 1990s, switched toward higher winter recovery rates in recent years. For juveniles, autumn recovery rates were always higher than winter rates. We found also that the sharp increase in annual recovery rates that started in 1998 was not due solely to the implementation of the hunt in spring 1999 (i.e. at the end of the 1998 "year"), as autumn and winter recoveries also increased. Curiously, this increase preceded the liberalisation of fall hunting regulations in these seasons which only started in 1999, although it did coincide with the start of more liberal winter regulations in 1998-99. Survival estimates from these analyses closely resembled those from MARK analyses.

Kill rate estimates

Because we had evidence that reporting rates changed over time (due to band-solicitation and toll-free-number bands), we accounted for this confounding factor by transforming our recovery rates into kill rates. Using the recovery rate (f) estimates obtained from the MARK and SURVIV models (Fig. 1), we calculated annual and seasonal kill rates as $K = f/\lambda c$ using our reporting rates (λ) and a retrieval rate (c) of 80% (Anderson and Burnham 1976). We estimated annual kill rates for each group and compared mean values between pre- and post-conservation measure time periods (Fig. 4). For all groups of adults and juveniles, the annual kill rate increased, further supporting our first prediction. Although some juveniles were killed during the spring hunt, kill rates of juveniles showed little change during the

regular seasons (both autumn and winter) with the conservation measures. In contrast, adults demonstrated increased kill rates during the spring and the winter following implementation of the conservation measures, but apparently not during the autumn. These results therefore partially supported our third prediction of seasonal conservation measure impacts, implying that only the winter regulation changes and spring hunt affected annual kill rates.

Table 3. The five best-fit models representing seasonal variation in recovery rates for greater snow geese from 1990-2001 (all other models had a $\Delta QAIC_c$ value >40), based on reporting rates ranging from 25-96% (see text for details), and with an overdispersion correction factor of $\hat{c}$ = 1.151. Each model is shown with its number of parameters, its log-likelihood (-2log(L)), the difference in $QAIC_c$ between the current and the best model ($\Delta QAIC_c$), and its $QAIC_c$ weight ($\omega QAIC_c$). The unconstrained model included year- and age-dependent survival rates, and recovery rates dependent on year, age, sex (adults only) and collar. Survival rates were dependent on age in all models, but not on sex or season in any models. Model notation refers to constraints imposed on recovery rates (f) with *J*, *F* and *M* referring to juveniles (both sexes), adult females (without collar) and adult males, respectively (collared females were always left separate), and f^a, f^w and f^p referring to autumn, winter and spring recovery rates (e.g. f^w *[M=F]* indicates that winter recovery rates were constrained to be equal between sexes each year).

Model Name	# Parameters	-2log(L)	$\Delta QAIC_c$	$\omega QAIC_c$
Unconstrained	134	31768.7	0.0	0.816
f^a *[M=F]*	122	31800.2	3.2	0.165
f^p *[M=F]*	130	31788.1	8.7	0.010
f^a *[M=F] and* f^p *[M=F]*	118	31816.7	9.4	0.007
f^p *[J=M]*	130	31808.0	13.4	0.001

.
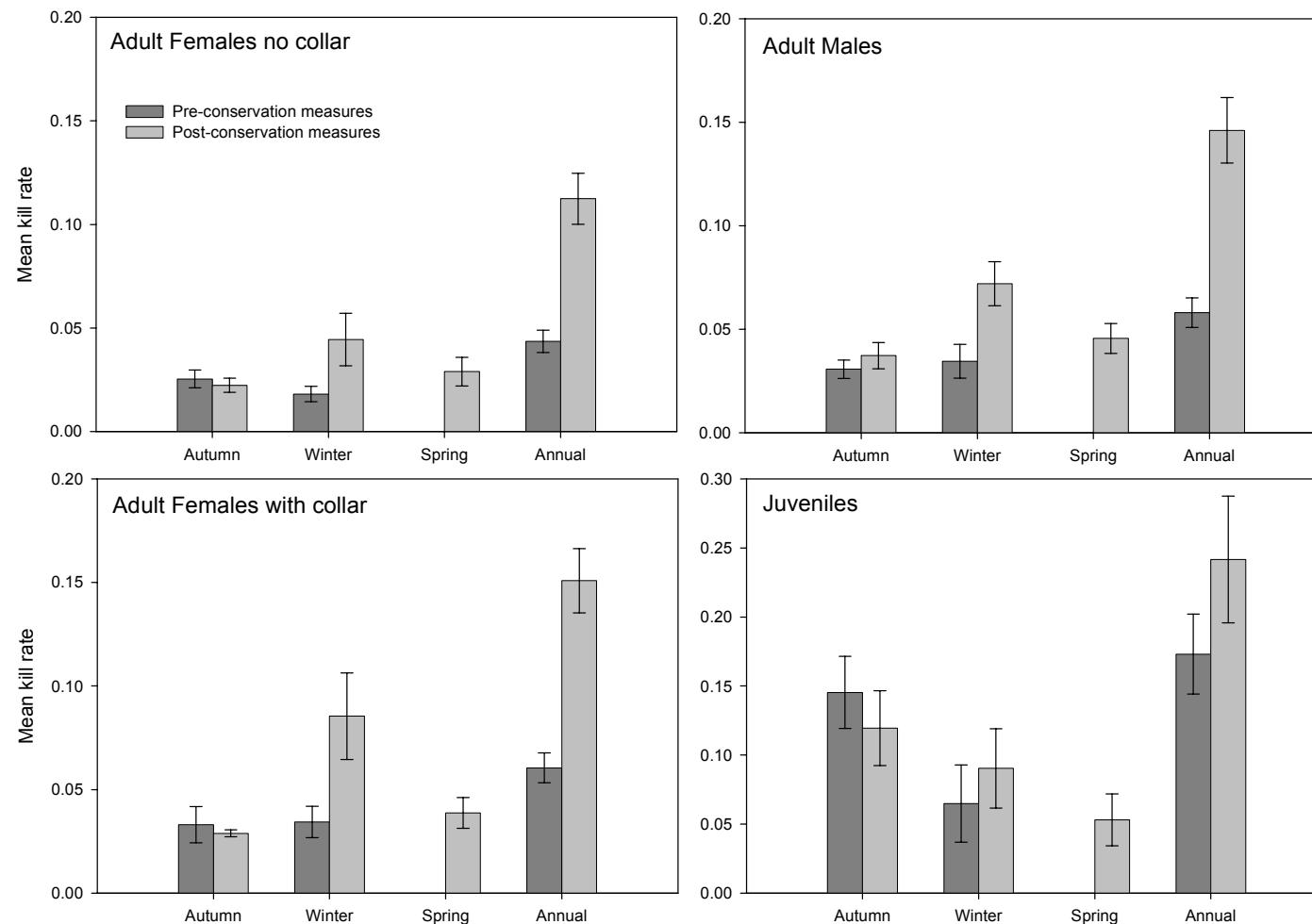
Figure 4. Kill rate estimates (mean ± SE) before and after the implementation of conservation measures for greater snow geese from 1990-2001. Kill rates were calculated by combining annual recovery rates (from Fig. 2), reporting rates (annual values ranging 25-96%, see text for details), and a retrieval rate of 80%. Autumn recoveries come from harvest in Québec, winter recoveries from harvest in Atlantic Flyway states, and spring recoveries from the spring conservation hunt implemented in Québec from 1999-2001. Because the conservation measures were implemented in the spring of 1999, they take effect during the 1998 season for spring and annual rates, but in the 1999 season for autumn and winter rates. Note the difference in scale between adult and juvenile graphs.

DISCUSSION

Effects of conservation measures on recovery and kill rates

Our *a posteriori* model provided good evidence that temporal variations in recovery rates could be divided into three main periods, and supported our first prediction of increased recovery rates since implementation of conservation measures in adults. Consistently high recovery rates after 1997 strongly suggest an increase in hunting mortality with the amendment of regulations. Juveniles, in contrast, showed highly variable recovery rates throughout the entire time period, with apparently little change since the conservation measures were begun.

Although no effect of toll-free-number bands was retained in our models, the increase in recovery rate after 1997 could still be partly due to an increase in reporting rate since 1996 resulting from the toll-free number bands. This is why we attempted to convert our recovery rate in kill rate using our best estimate of reporting rate for various periods. However, once recovery rates were adjusted for variable reporting rate, annual kill rates still showed a clear increase in 1998-2001 relative to 1990-97 in adults, and a similar trend in juveniles. Therefore, this analysis supports also our first prediction of an increase in hunting mortality with the initiation of the conservation measures. These measures were thus successful in affecting primarily adults, an original management goal (Giroux et al. 1998a).

Given that the spring hunt added a new hunting season during which no legal shooting had taken place for almost a century, we expected that this regulation change should have had the strongest impact. However, spring recovery and kill rates were generally intermediate to autumn and winter rates for adults, and were lower than other seasonal rates for juveniles. Seasonal recovery and kill rates indicated that regulation changes during the regular season in winter also contributed considerably to an increase in hunting mortality.

All groups showed an increase in autumn and winter recovery rates beginning in 1998, despite that the implementation of autumn regulation changes did not occur until the 1999 season. Although this increase could be the result of random variation in hunting success, it may have occurred also because of publicity surrounding overabundant goose populations and the need to increase sport harvest to control them, which preceded changes in regulations. Since 1999, adult recovery and kill rates showed a large increase in winter but not in autumn, suggesting that the regulation changes had a greater impact on harvest in the

Atlantic Flyway states than in Québec. The closing of the Canada Goose (*Branta canadensis*) hunt in Atlantic Flyway states from 1995-2000 (J. Kelley, USFWS, personal communication) combined with publicity surrounding overabundant snow goose populations could also have encouraged a switch by goose hunters from Canadas to snows during winter, although this is inconsistent with results from Chapter 1. In contrast, the lack of an effect of measures during autumn in Québec is surprising given that bag limits were increased there as well, and additional measures (e.g. electronic calls) were introduced in Québec only. Furthermore, calculations of harvest rates from hunter surveys in Québec suggested on the contrary an increase following regulation changes in autumn (G. Gauthier, unpublished data). Although we have no explanation for the apparent discrepancy between this dataset and our kill rate data, we note that the latter is quite sensitive to reporting rate values (see below), which may have some biases.

Other factors affecting recovery rates

Adult females marked with collars demonstrated much higher recovery rates than adults without collars throughout all time periods. However, this is likely due to elevated reporting rates (Samuel et al. 1990, Schmutz and Morse 2000, Menu et al. 2002) because the presence of a collar has no effect on survival in this population (Menu et al. 2000, Reed 2003). For non-collared adults, males experienced slightly higher recovery rates than females. Given that pairs remain together throughout the year and migrate through the same areas (Cooke et al. 1975, Robertson and Cooke 1999), both sexes should otherwise be exposed to equal hunting pressures. Low recovery rates of non-collared females may be an artefact due to small sample sizes: in most years, few females without collars were marked relative to those with collars and, given that survival rate was equal between the two groups in the models, this may have negatively affected recovery rate estimates of non-collared females.

Juvenile recovery rates resembled those for collared adults, being higher than for adults without collars, though with more inter-annual variation. High recovery rates of young reflects their higher vulnerability to hunting, as evidenced by their higher kill rate than adults. Juvenile recovery rate in autumn was equal to or higher than the winter rate in all years, and was generally lowest in spring, as expected if harvest vulnerability decreases over the course of their first year (Prevett and MacInnes 1980, Francis and Cooke 1992). Moreover, a model constraining juvenile recovery rates to be equal to adult rates in spring was preferred over

models eliminating age-effects in winter or autumn. This further suggests that juveniles' vulnerability to hunting diminishes over time, but that it remains higher than adults' throughout their first year. The high inter-annual variability in recovery rate of juveniles may be related to the proportion of young in the autumn flock. This proportion is highly variable in high arctic-nesting species like snow geese, and may have a strong influence on hunter's success in fall (Menu et al. 2002).

Effects of conservation measures on annual survival rates

Greater snow goose abundance has declined since the initiation of the regulation changes, from 938,000 in spring 1999 to 640,000 in 2002 (CWS, unpublished data). Although fecundity may have been reduced because of the spring hunt (Mainguy et al. 2002, Reed 2003), it seems more likely that this decline was mainly due to a reduction in survival, especially in adults, given the high sensitivity of population growth to change in adult survival (Gauthier and Brault 1998). Our analysis has indeed confirmed that kill rate has increased with the conservation measures, especially in adults. Evidence suggests that hunting mortality is additive to natural mortality in geese (Francis et al. 1992, Rexstad 1992, Hestbeck 1994), including this population (Gauthier et al. 2001), because low rates of natural mortality allow little room for compensation (Anderson and Burnham 1976). We therefore expected to observe an associated decline in survival rate for this time period, at least in adults.

We found that, on average, adult survival rate declined by 14% (from 0.835 to 0.719) since the amendment of hunting regulations in 1999. Moreover, the estimated survival rate pre-conservation measures corresponds exactly to that calculated by Gauthier et al. (2001) from resightings of collared females for the same period. Nevertheless, a reduction of the temporal variability in survival to simply pre- vs. post-measure values led to a model with a poor fit, suggesting high annual variability in adult survival. Some of this variability is likely explained by inter-annual fluctuations observed in harvest rate (Gauthier et al. 2001, Menu et al. 2002). Furthermore, because of problems of relatively small sample size caused by low recovery probability, band recovery analyses may not have the power or precision to detect relatively small survival changes over a short time period, and thus the effects of these measures may become clearer with more years of recoveries. Sample size problems might also partially explain the surprisingly low survival rates detected in some years. Juvenile survival was highly variable in the time period examined, but we found no evidence of a decline since the implementation of conservation measures, consistent with only a slight increase in kill rates,

although here again problems of sample size might reduce detection of effects. Nevertheless, these results are consistent with evidence of variable juveniles natural mortality due to fluctuating environmental conditions (Menu et al. in press) and harvest rates (Menu et al. 2002).

Methodological considerations

Our estimation of seasonal recovery rates provided new insight into within-year variation in hunting mortality. Greater snow geese have been historically managed separately from their sister subspecies, lesser snow geese, as is the case for species such as the mallard (*Anas platyrhynchos*) which exhibit several distinct migratory pathways (Nichols and Hines 1983, Royle and Dubovsky 2002). However, within-subspecies regional variations in the impact of hunting have not previously been considered for greater snow geese. The flexible model structure that we developed in program SURVIV allowed us a closer examination of small-scale hunting effects than would have been possible with a once-annual model structure. We had to make the simplifying assumption of no natural mortality during harvest seasons, but we felt this did not introduce severe biases given the low adult natural mortality for this population (Gauthier et al. 2001) and the relatively high juvenile survival during the hunting seasons (Menu et al. submitted).

A weak point in our analysis of seasonal recovery rate, and the subsequent calculations of kill rate, is the estimation of reporting rate (λ). Our estimation based on the relationship of recovery rate to harvest rate may not be very robust due, in part, to possible biases associated with the determination of harvest rate from hunter surveys. In addition, the introduction of toll-free-number bands during the course of our study and the presence of some band solicitation in Québec in early years complicated the estimation of λ and reduced the precision of the estimate when we divided the study period into shorter time intervals. For example, we expected that reporting rates would have been highest following the implementation of toll-free-number bands in 1996, but instead we found it to be highest during the period with some band solicitation. Furthermore, we could not estimate our reporting rate for the period 1994-95 and we had therefore to rely on a literature value, another potential bias. We had to assume also that reporting rate was constant within our three time periods and across hunting seasons (autumn and spring in Québec, winter in the AF states). Although most studies have not detected much time-variation in reporting rates (Conroy and Blandin 1984, Nichols et al. 1995), some variations may still be present. For example, if

reporting rate was lower in Québec than in the USA because of language differences, the impact of toll-free-number bands on reporting rates could thus have been more limited in Québec than the USA; there is some evidence for such regional differences in the 1970s and 1980s (Chapter 1). Such bias, if present, would lead to an underestimation of kill rate in Québec and an overestimation in the USA after 1996, and could thus explain the apparent lack of increase in kill rate following the conservation measures in Québec. The impact of such biases, however, would be reduced in our estimates of annual kill rate. Clearly, reward band studies could provide more reliable estimates of reporting rate for this population.

In our time-dependent model, survival rate estimates were surprisingly low in some years. The 1997 values, in particular, are extremely low relative to other estimates for this population in the same year (adult survival: 46.3% this study vs. 94.5% in Gauthier et al. 2001). Reduced juvenile survival that year may have been caused by unfavourable environmental conditions at fledging time (Menu et al. in press), but adult survival should be relatively independent of weather factors (Owen and Black 1991). These unusual estimates may also be a consequence of sampling biases, which are common in this type of data. Even though the total number of birds banded was large, division of the recoveries among 5 groups over many years led to relatively low recovery rates, especially for adults before the conservation measures. Our preferred models also had a large number of parameters, which may have contributed to the problem. These aberrant values for adults contributed to the high annual variation in survival rates that was thus not explained by a pre- vs. post-conservation measures model.

Implications for future management

Adaptive harvest management encourages frequent re-evaluation of the impacts of harvest strategies in order to maximise the likelihood of the desired outcome (Walters and Holling 1990, Williams and Johnson 1995). Our examination of the consequences of extreme conservation measures on greater snow goose survival and hunting mortality probabilities permits further insight into the effectiveness of these measures in stabilising abundance, and expands comprehension of the use of sport harvest to manipulate wildlife populations. Most importantly, our breakdown of the band recovery data by hunting region and season was innovative and allowed a finer evaluation of the impacts of the recent conservation measures.

The conservation measures were introduced with the intention of reducing adult survival and stabilising abundance but were not intended to be permanent (Giroux et al. 1998a). We showed that these actions were quite effective in reducing survival, at least in adults, and this was probably the main reason for the recent decline in the population. The spring hunting season, although considered a successful management initiative, was implemented as a transitory measure and will likely be discontinued at some point given the apparent effectiveness of these measures in stopping population growth. However, the agricultural food subsidy and refuges that have encouraged population growth in the past will still be available, and the fact that part of the population is continuing to migrate to areas with relatively low hunting pressure (Freemark and Cooch 1978, Olson 2001) may keep harvest rates low (Chapter 1). As a result, cessation of these measures may leave room for renewed growth in population size. While the decline in abundance observed since these changes has been attributed mostly to the spring hunting season, our results indicate that in fact the liberalisation of regulations on wintering grounds during the regular seasons was at least equally effective at increasing harvest mortality and consequently in decreasing adult survival. We suggest therefore that enhanced management actions during the regular hunting seasons may be sufficient in the future to maintain stability in this population. Our results demonstrate the value of analysing seasonal differences in sport harvest impacts in an experimental context, and may thus contribute to more efficient waterfowl management plans in the future.

LITERATURE CITED

Anderson, D. R. and K. P. Burnham. 1976. Population ecology of the mallard IV: The effect of exploitation on survival. US Department of the Interior, Fish and Wildlife Service Resource publication **128**:45 pp.

Anderson, D. R. and K. P. Burnham. 1978. Effect of restrictive and liberal hunting regulations on annual survival rates of the mallard in North America. Transactions of the North American Wildlife and Natural Resources Conference **43**:181-186.

Ankney, C. D. 1996. An embarrassment of riches: too many geese. Journal of Wildlife Management **60**:217-223.

Béchet, A., J.-F. Giroux, G. Gauthier, J. D. Nichols, and J. E. Hines. 2003. Spring hunting changes the regional movements of migrating greater snow geese. Journal of Applied Ecology **40**:553-564.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical Inference from Band-recovery Data: a Handbook. Second edition. U.S. Fish and Wildlife Service.

Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag New York Inc., New York, NY.

Conroy, M. J. 1985. Maximum likelihood methods for investigating reporting rates of rings on hunter-shot birds. Pages 215-241 *in* Statistics in Ornithology (B. T. J. Morgan and P. M. North, Eds.). Springer-Verlag, Berlin.

Conroy, M. J. and W. W. Blandin. 1984. Geographic and temporal differences in band reporting rates for American black ducks. Journal of Wildlife Management **48**:23-36.

Conroy, M. J. and D. G. Krementz. 1990. A review of the evidence for the effects of hunting on American black duck populations. Transactions of the North American Wildlife and Natural Resources Conference **55**:501-517.

Cooke, F. G., C. M. Francis, E. G. Cooch, and R. Alisauskas. 2000. Impact of hunting on population growth of mid-continent lesser snow geese. Pages 17-31 *in* Population

modelling and management of Snow Geese (H. Boyd, Ed.). Canadian Wildlife Service, Ottawa, ON.

Cooke, F. G., C. D. MacInnes, and J. P. Prevett. 1975. Gene flow between breeding populations of lesser snow geese. Auk **93**:493-510.

Canadian Wildlife Service (CWS) Waterfowl Committee. 2001. Migratory Game Bird Hunting Regulations in Canada: July 2001. CWS Migratory Birds Regulations Report No. 3.

Francis, C. M. and F. G. Cooke. 1992. Migration routes and recovery rates of lesser snow geese from southwestern Hudson Bay. Journal of Wildlife Management **56**:279-286.

Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology **73**:1346-1362.

Francis, C. M., J. R. Sauer, and J. R. Serie. 1998. Effect of restrictive harvest regulations on survival and recovery rates of American black ducks. Journal of Wildlife Management **62**:1544-1577.

Freemark, K. E. and F. G. Cooch. 1978. Geographic analysis of waterfowl kill in Canada. Pages 66-77 *in* Migratory game bird hunters and hunting in Canada (H. Boyd and G. H. Finney, Eds.). Canadian Wildlife Service, Ottawa, ON.

Gauthier, G. and S. Brault. 1998. Population model of the greater snow goose: projected impacts of reduction in survival on population growth rate. Pages 65-80 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Gauthier, G., R. Pradel, S. Menu, and J.-D. Lebreton. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology **82**:3105-3119.

Giroux, J.-F., B. Batt, S. Brault, G. Costanzo, B. Filion, G. Gauthier, D. Luszcz, and A. Reed. 1998a. Conclusions and management recommendations. Pages 81-88 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and

Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Giroux, J.-F., G. Gauthier, G. Costanzo, and A. Reed. 1998b. Impact of geese on natural habitats. Pages 32-57 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Giudice, J. H. 2003. Survival and recovery of mallards and gadwalls banded in eastern Washington, 1981-1998. Journal of Field Ornithology **74**:1-11.

Hestbeck, J. B. 1994. Survival of Canada geese banded in winter in the Atlantic flyway. Journal of Wildlife Management **58**:748-756.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management **66**:883-900.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature **406**:882-885.

Jensen, A. L. 1991. Simulation of fish population responses to exploitation. Ecological Modelling **55**:203-218.

Kirby, R. E., J. E. Hines, and J. D. Nichols. 1983. Afternoon closure of hunting and recovery rates of mallards banded in Minnesota. Journal of Wildlife Management **47**:209-213.

Krementz, D. G., J. E. Hines, and D. F. Caithamer. 1996. Survival and recovery rates of American eiders in eastern North America. Journal of Wildlife Management **60**:855-862.

Mainguy, J., J. Bêty, G. Gauthier, and J.-F. Giroux. 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? Condor **104**:156-161.

Menu, S., G. Gauthier, and A. Reed. 2002. Changes in survival rates and population dynamics of greater snow geese over a 30-year period: implications for hunting regulations. Journal of Applied Ecology **39**:91-102.

Menu, S., G. Gauthier, and A. Reed. In press. Survival of young greater snow geese during the fall migration. Auk.

Menu, S., J. B. Hestbeck, G. Gauthier, and A. Reed. 2000. Effects of neck bands on survival of greater snow geese. Journal of Wildlife Management **64**:544-552.

Myers, R. A. and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423**:280-283.

Nichols, J. D. 1991a. Responses of North American duck populations to exploitation. Pages 498-525 *in* Bird Population Studies: relevance to conservation and management (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, Eds.). Oxford University Press, Oxford.

Nichols, J. D. 1991b. Science, population ecology, and the management of the American black duck. Journal of Wildlife Management **55**:790-799.

Nichols, J. D., R. J. Blohm, R. E. Reynolds, R. E. Trost, J. E. Hines, and J. P. Bladen. 1991. Band reporting rates for mallards with reward bands of different dollar values. Journal of Wildlife Management **55**:119-126.

Nichols, J. D. and J. E. Hines. 1983. The relationship between harvest and survival rates of mallards: a straightforward approach with partitioned data sets. Journal of Wildlife Management **47**:334-348.

Nichols, J. D., R. E. Reynolds, R. J. Blohm, R. E. Trost, J. E. Hines, and J. P. Bladen. 1995. Geographic variation in band reporting rates for mallards based on reward banding. Journal of Wildlife Management **59**:697-708.

Olson, J. 2001. Comportement migratoire automnal de la Grande Oie des neiges dans le Québec méridional. MSc Thesis, Université de Québec à Montréal, Montréal, Québec.

Otis, D. L. and G. C. White. 2002. Re-analysis of a banding study to test the effects of an experimental increase in bag limits of mourning doves. Pages 479-495 *in* Statistical Analysis of Data from Marked Bird Populations (B. J. T. Morgan and D. L. Thomson, Eds.). Journal of Applied Statistics **29**.

Owen, M. and J. M. Black. 1991. The importance of migration mortality in non-passerine

birds. Pages 360-372 *in* Bird Population Studies: relevance to conservation and management (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, Eds.). Oxford University Press, Oxford.

Prevett, J. P. and C. D. MacInnes. 1980. Family and other social groups in snow geese. Wildlife Monographs No. 71, The Wildlife Society.

Reed, A., J.-F. Giroux, and G. Gauthier. 1998. Population size, productivity, harvest and distribution. Pages 5-31 *in* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Reed, E. T. 2003. Coûts des soins parentaux et effets des conditions environnementales sur la reproduction de la Grande Oie des neiges. PhD Dissertation, Université Laval, Ste-Foy, Québec.

Reinecke, K. J., C. W. Shaiffer, and D. Delnicki. 1992. Band reporting rates of mallards in the Mississippi Alluvial Valley. Journal of Wildlife Management **56**:526-531.

Rexstad, E. A. 1992. Effect of hunting on annual survival of Canada geese in Utah. Journal of Wildlife Management **56**:297-305.

Robertson, G. J. and F. Cooke. 1999. Winter philopatry in migratory waterfowl. Auk **116**:20-34.

Royle, J. A. and J. A. Dubovsky. 2001. Modeling spatial variation in waterfowl band-recovery data. Journal of Wildlife Management **65**:726-737.

Saether, B. E. and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81**:642-653.

Samuel, M. D., D. H. Rusch, and S. Craven. 1990. Influence of neck bands on recovery and survival rates of Canada geese. Journal of Wildlife Management **54**:45-54.

Schmutz, J. A. and J. A. Morse. 2000. Effects of neck collars and radiotransmitters on survival and reproduction on emperor geese. Journal of Wildlife Management **64**:231-237.

Sedinger, J. S. and E. A. Rexstad. 1994. Do restrictive harvest regulations result in higher survival rates in mallards? A comment. Journal of Wildlife Management **58**:571-577.

Smith, G. W. and R. E. Reynolds. 1992. Hunting and mallard survival, 1979-88. Journal of Wildlife Management **56**:306-316.

Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. Journal of Wildlife Management **47**:716-728.

White, G. C. 2002. Discussion comments on: the use of auxiliary variables in capture-recapture modelling. An overview. Journal of Applied Statistics **29**:103-106.

White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study **46**:S120-S138.

Williams, B. K. and F. A. Johnson. 1995. Adaptive management and the regulation of waterfowl harvests. Wildlife Society Bulletin **23**:430-436.

CONCLUSION GÉNÉRALE

L'IMPORTANCE DE L'ÉTUDE POUR LE DOMAINE DE LA GESTION

Dans mon mémoire, je me suis attaquée à la problématique de la gestion d'une population animale surabondante et aux conséquences de changements dans son régime d'exploitation. Je me suis servie de méthodes de modélisation récentes afin d'évaluer l'impact biologique de plusieurs changements à long terme survenus dans la chasse à la Grande Oie des neiges, et ultimement contribuer aux plans de gestion futurs de l'espèce. Dans le premier chapitre j'ai abordé la question de changements spatiaux et temporels dans la distribution de la récolte sportive pour essayer de comprendre les facteurs qui ont pu contribuer à la baisse du taux de récolte qui a encouragé la croissance de la population (Menu et al. 2002). Dans le deuxième chapitre, j'ai procédé à une analyse démographique de la chasse sportive et des effets annuels ainsi que saisonniers des changements récents au régime d'exploitation mis en place dans le but de stabiliser l'abondance (Gauthier et Brault 1998). Ce faisant, je désirais contribuer à l'amélioration de nos connaissances sur les impacts de la chasse sur la dynamique de populations exploitées, et aider au développement d'une gestion mieux informée et plus efficace de cette espèce.

Le concept de gestion adaptative nous encourage à mesurer constamment l'impact de nos actions afin d'améliorer nos connaissances sur la réponse du système, et à intégrer ces nouvelles connaissances dans la révision subséquente de nos plans de gestion (Walters 1986). De cette manière, la gestion serait basée non seulement sur les conditions initiales observées au début, mais aussi sur la situation actuelle telle que modifiée par nos actions passées afin de s'assurer que ces actions soient toujours pertinentes et appropriées (Williams et Johnson 1995). En plus, ce concept encourage la réduction de l'incertitude associée aux relations quantitatives intégrées à nos modèles de gestion, par exemple dans la relation entre la survie et la mortalité à la chasse des individus (Williams et al. 1996). Bien que Gauthier et al. (2001) ont mesuré cette relation chez les oies et ont démontré que la mortalité à la chasse est additive à la mortalité naturelle, l'incertitude dans la réponse de la population aux changements de règlements demeure. Donc, suivant les principes encouragés par ce concept, une évaluation des effets de la chasse sur la Grande Oie des neiges était nécessaire pour sa gestion future, et la détermination des effets des mesures de gestion spéciales était particulièrement importante.

L'instauration d'une saison de chasse printanière en 1999 était une initiative unique depuis la signature de l'accord de 1916 dans lequel le Canada et les États-Unis prohibaient toute

récolte d'oiseaux migrateurs pendant ou juste avant la saison reproductive. En conséquence, une évaluation des impacts de cette initiative unique est importante non seulement pour la gestion de cette population, mais aussi pour la gestion de nombreuses autres espèces de sauvagine exploitées. Néanmoins, il était aussi important de considérer les effets des autres mesures spéciales qui ont été prises pendant les saisons régulières car la chasse printanière n'était introduite que comme mesure temporaire, et les actions futures doivent prendre en considération l'ensemble des mesures actuelles mises en place. L'initiation de tous ces changements aux règlements de chasse nous a fourni une opportunité unique pour examiner à la fois les effets des mesures habituelles (tel que la libéralisation de règlements en saison régulière) et de mesures extrêmes (comme la nouvelle chasse printanière) sur une même population.

IMPLICATIONS DES RÉSULTATS

Les études à long terme sont essentielles dans le domaine de la dynamique de populations, car elles fournissent plusieurs informations utiles pour la gestion d'espèces exploitées (e.g. Smith et Reynolds 1992, Menu et al. 2002, Giudice 2003). Elles permettent de répondre à des questions qui ne sont pas abordables quand les données ne sont disponibles que pour quelques années seulement, comme par exemple des changements graduels dans les tendances ou des estimations précises de paramètres démographiques. Dans les deux parties de mon étude, j'ai utilisé des bases de données à long terme provenant d'enquêtes de chasse et de récupérations de bagues d'oiseaux marqués. Ces deux types de données sont rarement disponibles pour la même population, ce qui permet une comparaison entre ces deux sources d'information (e.g. Cooke et al. 2000). J'ai pu mettre en évidence des tendances similaires entre les informations provenant des enquêtes et celles des récupérations, ce qui suggère que ces deux sources de données sont fiables, mais ces deux types de données ont été utiles pour examiner différents aspects de la distribution de la récolte. En particulier, mes résultats ont mis en évidence un parallélisme entre les patrons temporels dans le taux de récolte par la chasse sportive et les changements dans la distribution géographique de la récolte en hiver, suggérant ainsi que la baisse du taux de récolte observée durant les années 1980 était probablement reliée à des changements dans la distribution des oies. Nos résultats indiquent un déplacement des oies vers le Nord en hiver qui coïncide avec une baisse soudaine dans le taux de récolte, probablement due à l'absence d'augmentation de la pression de chasse dans les régions nouvellement occupées.

Les données à long terme ont aussi contribué à l'analyse des effets des changements récents de mesures de gestion. L'estimation de paramètres démographiques tels que la survie et la mortalité à la chasse pour la période avant l'initiation des mesures spéciales m'a donné une base avec laquelle je pouvais comparer les tendances depuis ces changements. De plus, le taux de survie adulte moyen avant les mesures spéciales correspondait très bien avec la valeur estimée dans une autre étude avec un jeu de données différent (Gauthier et al. 2001), suggérant ainsi que mon approche fournissait des estimations valides pouvant être comparées avec les taux estimés après les mesures de gestion. J'ai pu ainsi mettre en évidence une augmentation de la mortalité à la chasse et une diminution du taux de survie chez les adultes depuis les mesures de conservation, en accord avec l'hypothèse de mortalité additive chez les oies (Francis et al. 1992a, Hestbeck et al. 1994, Gauthier et al. 2001). Mon étude confirme donc que les mesures spéciales ont permises d'atteindre les objectifs du plan de gestion du Arctic Goose Habitat Working Group, soit une diminution de survie adulte pour mener à une stabilisation de l'abondance (Giroux et al. 1998b).

Un aspect original de mon étude démographique fut la modélisation du taux de récupération saisonnière, qui m'a permis une analyse plus approfondie des variations temporelles intra-annuelles de la mortalité à la chasse. J'ai découvert une forte augmentation de la mortalité hivernale depuis l'instauration des mesures de gestion spéciales, mais apparemment aucun changement dans la mortalité d'automne. Ces résultats sont surprenants étant donné la libéralisation assez importante des règlements pendant les deux saisons de chasse régulières, mais ils soulignent l'importance d'examiner les effets de la chasse durant différentes périodes de l'année. Ici encore, une combinaison des résultats de différentes bases de données à long terme me fut utile. Par exemple, les estimations du taux de récupération hivernale dans mon deuxième chapitre indiquent une diminution au cours du début des années 1990, juste après la redistribution de la récolte hivernale observée au milieu des années 1980 dans mon premier chapitre. Ces deux informations combinées suggèrent que l'intérêt dans la chasse à l'Oie au milieu du Atlantic Flyway était probablement assez faible et n'a commencé à augmenter qu'avec les mesures spéciales. Il serait intéressant d'observer à quel niveau la pression de chasse retournerait si les règlements de chasse étaient ramenés à ceux d'avant 1999.

Globalement, les résultats des deux parties de mon étude suggèrent une importance pour cette population de la chasse hivernale. Dans mon premier chapitre, je souligne que les

changements dans l'aire d'hivernage démontrés par une grande partie de la population ont probablement directement contribué à la baisse du taux de récolte, ce qui a encouragé une croissance extraordinaire de la population. Sans cette redistribution des oies, la chasse aurait peut-être ralenti la croissance de la population, éliminant la nécessité de mesures extrêmes pour la contrôler actuellement. Dans mon deuxième chapitre, j'ai trouvé que les mesures prises en hiver semblent plus efficaces que celles prises à l'automne, et possiblement aussi efficaces que celles de la chasse printanière. Ceci suggère que le potentiel pour une augmentation de la récolte hivernale aux Etats-Unis était plus grand que pendant les autres saisons de chasse au Québec. Il serait donc souhaitable que les plans de gestion futurs se concentrent davantage sur cette partie du cycle annuel des oies. De plus, de nombreuses études ont démontré que les oiseaux migrateurs sont sensibles aux changements climatiques dans leurs aires d'hivernage (e.g. Marra et al. 1998, Saether et al. 2000, Cotton 2003) ce qui pourrait influencer la distribution des oies en hiver. En conséquence, il existe toujours la possibilité d'autres changements de récolte hivernale dans l'avenir.

CONSIDÉRATIONS MÉTHODOLOGIQUES ET DIRECTIONS FUTURES

Ma comparaison des taux de survie et de mortalité à la chasse avant versus après l'initiation des mesures spéciales a démontré l'utilité d'une telle situation quasi-expérimentale dans le cadre d'une expérience naturelle à grande échelle. Cependant, ce n'était qu'une expérience *a posteriori* facilitée par les circonstances, et donc il faut être prudent dans l'interprétation des résultats. Même si des effets associés aux changements des règlements de chasse ont été observés, on ne peut pas conclure avec certitude que les mesures spéciales en étaient la cause. Néanmoins, ces résultats suggèrent fortement que les mesures étaient la cause des changements observés dans la récolte sportive des oies et dans les autres paramètres démographiques, démontrant ainsi la pertinence de cette approche qui pourrait être suivie dans l'avenir. En particulier, l'établissement d'autres expériences comme celle-ci, mais planifiées *a priori* avec un plan expérimental, serait un outil très profitable dans l'évaluation des effets de l'exploitation sur les populations.

Dans mes analyses, j'ai utilisé l'approche analytique de la sélection de modèles basée sur le principe de la parcimonie, une approche qui est récemment devenue populaire à cause de sa pertinence dans le contexte d'études non expérimentales (Burnham et Anderson 1998). En remplacement d'un système de tests d'hypothèses où le seuil de signification est subjectif, cette approche permet une prise en compte plus nuancée de l'incertitude basée sur les poids

relatifs des modèles. Celle-ci m'a permis de déterminer quels facteurs jouaient un rôle important dans la variation spatio-temporelle de la distribution de la récolte sportive des oies, ainsi que dans les fluctuations interannuelles des taux de survie et de mortalité à la chasse. En plus, j'ai pu développer une structure de modèle flexible permettant une estimation des taux de mortalité à la chasse sur une base saisonnière, ce qui n'était pas possible avec des modèles traditionnels étant donné notre système d'étude (i.e. une seule période annuelle de baguage, ce qui représente la situation la plus commune). Cette flexibilité dans la modélisation a permise de mettre en évidence l'aspect saisonnier des mesures de gestion. En particulier, l'évidence d'une augmentation de mortalité plus forte en hiver qu'en automne a des implications importantes pour la planification des règlements de chasse dans l'avenir.

Il existe quand même des faiblesses non négligeables dans mes analyses, lesquelles ont pu affecter l'interprétation des résultats. On peut donc suggérer certaines avenues d'amélioration pour les prochaines études. Premièrement, l'absence de valeurs précises du taux de retour de bagues (λ), dont plusieurs calculs subséquents étaient dépendants, a peut-être biaisé mes comparaisons des taux de mortalité à la chasse. J'ai dû faire plusieurs suppositions concernant la similarité des taux entre régions et entre années, ce qui pourrait affecter les transformations de taux de récupération en taux de mortalité, ainsi que les estimations saisonnières, si ces supposition n'étaient pas valides. En particulier, l'absence d'augmentation du taux de mortalité à la chasse durant la saison d'automne malgré une forte augmentation en hiver pourrait s'expliquer si les taux de retour de bagues étaient peut-être plus élevés aux États-Unis qu'au Canada dans les dernières années. Des études avec des bagues à récompense ont été débutées en été 2003 sur l'Île Bylot, et devraient permettre l'estimation de taux de retour régionaux dans les années futures. Deuxièmement, les faibles tailles d'échantillons qui sont inévitables avec des données de récupération (sauf dans le cas de bagues à récompense, e.g. Nichols et al. 1995) apportent des estimations de faible précision pour certains paramètres. Les estimations de probabilités de survie, en particulier, avaient de grands intervalles de confiance, ce qui a possiblement contribué au choix de modèles dont la survie variait chaque année plutôt qu'uniquement en réponse aux mesures de gestion. Ici encore, l'utilisation de bagues à récompense pourrait être utile pour fournir des estimations plus précises de ces taux dans l'avenir.

En résumé, mon étude de maîtrise met en évidence des points importants pour l'étude d'esp-èces exploitées. Premièrement, j'ai démontré l'importance de tenir compte des aspects

géographiques de la récolte, car ceux-ci peuvent influencer la pression de chasse ressentie par la population. Considérées simultanément avec la démographie, les caractéristiques spatiales peuvent donc aider à une meilleure compréhension de l'interaction entre les mouvements migratoires et la mortalité à la chasse. Deuxièmement, j'ai mis en évidence un effet important des actions prises lors des saisons régulières, suggérant que l'augmentation de la mortalité à la chasse et la diminution de la survie n'étaient pas seulement dues à la nouvelle chasse printanière. Ces conclusions sont importantes car l'abondance de la Grande Oie des neiges semble avoir diminuée depuis l'initiation des mesures spéciales, et des décisions concernant sa gestion future sont imminentes. Étant donné l'importance de la chasse régulière d'hiver qui ressort de mes résultats, je suggère que celle-ci pourrait être un outil puissant pour la gestion future si la chasse printanière est arrêtée. J'espère que mon étude a contribué à améliorer notre compréhension de la dynamique entre la chasse et la démographie d'une population, et que mes résultats et ceux d'autres études similaires pourront aider à assurer une meilleure harmonie entre l'homme et l'animal dans l'avenir.

RÉFÉRENCES

Burnham, K. P. et D. R. Anderson. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag New York Inc., New York, NY.

Cooke, F., C. M. Francis, E. G. Cooch, et R. Alisauskas. 2000. Impact of hunting on population growth of mid-continent lesser snow geese. Pages 17-31 *dans* Population modelling and management of Snow Geese (H. Boyd, Ed.). Canadian Wildlife Service, Ottawa, ON.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences USA **100**:12219-12222.

Francis, C.M., M.H. Richards, F. Cooke, et R.F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology **73**:1346-1362.

Gauthier, G. et S. Brault. 1998. Population model of the greater snow goose: projected impacts of reduction in survival on population growth rate. Pages 65-80 *dans* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Gauthier, G., R. Pradel, S. Menu, et J.-D. Lebreton. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology **82**:3105-3119.

Giroux, J.-F., B. Batt, S. Brault, G. Costanzo, B. Filion, G. Gauthier, D. Luszcz, et A. Reed. 1998. Conclusions and management recommendations. Pages 81-88 *dans* The Greater Snow Goose: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, ON.

Giudice, J. H. 2003. Survival and recovery of mallards and gadwalls banded in eastern Washington, 1981-1998. Journal of Field Ornithology **74**:1-11.

Hestbeck, J. B. 1994. Survival of Canada geese banded in winter in the Atlantic flyway. Journal of Wildlife Management **58**:748-756.

Marra, P. P., K. A. Hobson, et R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science **282**:1884-1886.

Menu, S., G. Gauthier, et A. Reed. 2002. Changes in survival rates and population dynamics of greater snow geese over a 30-year period: implications for hunting regulations. Journal of Applied Ecology **39**:91-102.

Nichols, J. D., R. E. Reynolds, R. J. Blohm, R. E. Trost, J. E. Hines, et J. P. Bladen. 1995. Geographic variation in band reporting rates for mallards based on reward banding. Journal of Wildlife Management **59**:697-708.

Saether, B. E., J. Tufto, S. Engen, K. R. O. W. Jerstad, et J. E. Skatan. 2000. Population dynamical consequences of climate change for a small temperate songbirds. Science **287**:854-856.

Smith, G. W. et R. E. Reynolds. 1992. Hunting and mallard survival, 1979-88. Journal of Wildlife Management **56**:306-316.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan Publishing Co., New York, NY.

Williams, B. K. et F. A. Johnson. 1995. Adaptive management and the regulation of waterfowl harvests. Wildlife Society Bulletin **23**:430-436.

Williams, B. K., F. A. Johnson, et K. Wilkins. 1996. Uncertainty and the adaptive management of waterfowl harvests. Journal of Wildlife Management **60**:223-232.

ANNEXES

APPENDIX A. **Evaluation of plastic leg band effects on juvenile survival and recovery.**

Introduction

Analyses based on the re-encounter of marked individuals have been developed into powerful demographic tools, but nevertheless rely on a few simple assumptions (Brownie et al. 1985, Cooch and White 2001). One of the most important of these, and one which is not always tested before inferences are made, is that of the effect of the markers themselves: results will be biased if the method of marking impacts the parameters being estimated (Brownie et al. 1985). In waterfowl studies, it is assumed that standard metal leg bands have no effect, but often there are other auxiliary markers used simultaneously that may affect the individuals being monitored. Plastic neck collars, in particular, are frequently used as markers that can be read from a greater distance than leg bands, but these have been shown in some populations to affect survival (Castelli and Trost 1996, Schmutz and Morse 2000, Alisauskas and Lindberg 2002) or reproduction (Schmutz and Morse 2000, Reed 2003). In cases where juvenile birds are too small to affix with collars, plastic coloured leg bands may be used in addition to the metal bands, to facilitate identification from a distance, but we are aware of no previous analysis considering their effects. In our study of greater snow geese, a population in which neck collars do not affect survival (Menu et al. 2000, Reed 2003), we needed to establish whether plastic coloured leg bands should be included as a factor in our candidate model set. We therefore conducted a separate analysis with the objective of determining whether these auxiliary markers affected survival or recovery rates of juvenile greater snow geese.

Methods

Since 1998 on Bylot Island, a portion of captured juvenile geese have been marked with plastic coloured leg bands in addition to the standard metal bands; hereafter, these plastic coloured leg bands are referred to simply as "leg bands". More details of general banding and recovery methods are described in Chapter 2, Methods. We used banding and recovery data from seven groups: adult males, adult females with and without plastic neck collars, juvenile males with and without leg bands, and juveniles females with and without leg bands (total n = 13,674 banded, n = 1,557 recovered). We built Brownie et al. (1985) recovery models to test the potential effects of these leg bands on survival and recovery probabilities for the period 1998-2001 (each "year" began in August and ended the following July); this gave us four recovery periods and three survival intervals. Based on results from Chapter 2, a neck collar

effect was applied to recovery rate, but sex effects were not tested on survival or recovery for either age group. Leg band effects were tested on both survival and recovery rates for juveniles. Models were fitted in program MARK, and goodness-of-fit was tested with programs BROWNIE and ESTIMATE; the resulting ĉ value was used to adjust AIC_c values to $QAIC_c$. For more details on model selection methodology, see Chapter 2, Methods.

Results and Discussion

Pooled contingency test results from BROWNIE and ESTIMATE resulted in a ĉ estimate of 1.715 (χ^2 = 41.15, df = 24, P = 0.016), and that value was incorporated into the model selection in MARK. Of the 51 candidate models tested, the best model ($S_{a2*t}\ f_{a2*t+col}$) did not include any leg band effects on either survival or recovery (Table A1). The slope of the leg band effect on survival for the fifth model ($S_{a2*t+l}\ f_{a2*t*col}$, the highest-ranking model with a leg band effect) was estimated at 0.570 (95% CI: -0.123 – 1.263), an effect not differing from 0. Moreover, the cumulative $QAIC_c$ weight ($\Sigma\ \omega QAIC_c$) of all models including a leg band effect on survival was 0.085 ; for models including a leg band effect on recovery, $\Sigma\ \omega QAIC_c$ = 0.003. Such low cumulative model weights indicate a lack of support for a leg band effect on either parameter.

We therefore conclude that there is no evidence for any effect of plastic coloured leg bands on the survival or recovery probabilities of juvenile greater snow geese. Although auxiliary markers such as plastic neck collars have been shown to negatively affect survival in other populations, the marking of juvenile geese with additional leg bands does not appear to have such an effect in this population. Given that the reliable application of mark-recapture models is highly dependent on the assumption that markers have no effect on the parameters being estimated (Brownie et al. 1985), it was important to test these effects. The lack of evidence for any effect of these markers on juvenile geese allows us to proceed with long-term analyses while ignoring whether or not birds are marked with an extra leg band, and suggests that the parameter estimates obtained will therefore be robust.

Table A1. Model selection for an evaluation of the potential effects of plastic coloured leg bands on survival and recovery probabilities of juvenile greater snow geese from 1998-2001 with an overdispersion correction factor of ĉ = 1.715. The 5 best-fit models are shown below; parentheses with a capital letter after an effect refer to that effect being applied only to the groups mentioned (e.g. $t(J)$ indicates a time-effect on juveniles only). Each model is shown with its number of parameters, its deviance, the difference in QAIC$_c$ between the current and best model (ΔQAIC$_c$), and its QAIC$_c$ weight (ωQAIC$_c$).

Model Name	# Parameters	Deviance	ΔQAIC$_c$	ωQAIC$_c$
$S_{a2*t}\, f_{a2*t+col}$	15	80.60	0.00	0.368
$S_{a2*t}\, f_{a2+t+col}$	12	92.90	1.17	0.206
$S_{a2*t}\, f_{a2+t*col}$	14	87.82	2.21	0.122
$S_{a2*t(J)}\, f_{a2*t+col}$	13	93.62	3.59	0.061
$S_{a2*t+l}\, f_{a2*t*col}$	19	74.58	4.51	0.039

$S:$ survival rate

$f:$ recovery rate

$a2:$ age effect (juveniles <1yr and adults)

$t:$ time effect (annual)

$s:$ sex effect

$col:$ neck collar effect

$l:$ leg band effect

LITERATURE CITED

Alisauskas, R. T. and M. S. Lindberg. 2002. Effects of neckbands on survival and fidelity of white-fronted and Canada geese captured as non-breeding adults. Pages 521-537 *in* Statistical Analysis of Data from Marked Bird Populations (B. J. T. Morgan and D. L. Thomson, Eds.). Journal of Applied Statistics, **29**.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical Inference from Band-recovery Data: a Handbook. Second edition ed. U.S. Fish and Wildlife Service.

Castelli, P. M. and R. E. Trost. 1996. Neck bands reduce survival of Canada geese in New Jersey. Journal of Wildlife Management **60**:891-898.

Cooch, E. and G. White. 2001. Program MARK. A gentle introduction. Second edition.

Menu, S., J. B. Hestbeck, G. Gauthier, and A. Reed. 2000. Effects of neck bands on survival of greater snow geese. Journal of Wildlife Management **64**:544-552.

Reed, E. T. 2003. Coûts des soins parentaux et effets des conditions environnementales sur la reproduction de la Grande Oie des neiges. Thèse doctorale, Université Laval, Ste-Foy, Québec, Canada.

Schmutz, J. A. and J. A. Morse. 2000. Effects of neck collars and radiotransmitters on survival and reproduction on emperor geese. Journal of Wildlife Management **64**:231-237.

APPENDIX B. Full parameterisation of seasonal recovery models used in program SURVIV.

The following two tables represent the parameterisation of the expected number of band recoveries for each hunting season (autumn in Québec, winter in Atlantic Flyway states, spring in Québec since 1999) under an unconstrained model for greater snow geese, 1990-2001. The model includes year-specific adult (S_i) and juvenile (S'_i) survival rates, year-specific reporting rates (λ_i), and age-, season- and year-specific recovery rates (f_i^a, f_i^w, and f_i^p for adult autumn, winter and spring, and f'^a_i, f'^w_i, and f'^p_i for juvenile autumn, winter and spring, respectively). Banded samples are N_i for adults and M_i for juveniles. For simplicity, only one sex is shown, and collared adult females (whose reporting rates also differ, see text) are not shown. Also, parameterisation is only given for a reduced period of the time examined (1990-91, as an example of pre-spring hunt years, and 1998-99, as an example of spring-hunt years).

Table B1. Parameterisation of seasonal band recoveries for geese banded in 1990-91 (autumn and winter recovery seasons only).

		Seasonal recoveries			
		1990		1991	
Year	Banded	Autumn	Winter	Autumn	Winter
Adults					
1990	N_1	$N_1 f_1^a$	$N_1 f_1^w (1 - f_1^a / \lambda_1)$	$N_1 S_1 f_2^a$	$N_1 S_1 f_2^w (1 - f_2^a / \lambda_2)$
1991	N_2			$N_2 f_2^a$	$N_2 f_2^w (1 - f_2^a / \lambda_2)$
Juveniles					
1990	M_1	$M_1 f'^a_1$	$M_1 f'^w_1 (1 - f'^a_1 / \lambda_1)$	$M_1 S'_1 f_2^a$	$M_1 S'_1 f_2^w (1 - f_2^a / \lambda_2)$
1991	M_2			$M_2 f'^a_2$	$M_2 f'^w_2 (1 - f'^a_2 / \lambda_2)$

Table B2. Parameterisation of seasonal band recoveries for geese banded in 1998-99 (autumn, winter and spring recovery seasons); note that parameters are labelled as they would be for the 1990-2001 analysis (e.g. 1998 is the 9th year).

		Seasonal recoveries					
		1998			1999		
Year	Banded	Autumn	Winter	Spring	Autumn	Winter	Spring
Adults							
1998	N_9	$N_9\, f_9^a$	$N_9\, f_9^w (1- f_9^a /\lambda_9)$	$N_9\, f_9^p (1- f_9^w /\lambda_9)(1- f_9^a /\lambda_9)$	$N_9 S_9\, f_{10}^a$	$N_9 S_9\, f_{10}^w (1- f_{10}^a /\lambda_{10})$	$N_9 S_9\, f_{10}^p (1- f_{10}^w /\lambda_{10})(1- f_{10}^a /\lambda_{10})$
1999	N_{10}				$N_{10}\, f_{10}^a$	$N_{10}\, f_{10}^w (1- f_{10}^a /\lambda_{10})$	$N_{10}\, f_{10}^p (1- f_{10}^w /\lambda_{10})(1- f_{10}^a /\lambda_{10})$
Juveniles							
1998	M_9	$M_9\, f'^a_9$	$M_9\, f'^w_9 (1- f'^a_9 /\lambda_9)$	$M_9\, f'^p_9 (1- f'^w_9 /\lambda_9)(1- f'^a_9 /\lambda_9)$	$M_9 S'_9\, f_{10}^a$	$M_9 S'_9\, f_{10}^w (1- f_{10}^a /\lambda_{10})$	$M_9 S'_9\, f_{10}^p (1- f_{10}^w /\lambda_{10})(1- f_{10}^a /\lambda_{10})$
1999	M_{10}				$M_{10} f'^a_{10}$	$M_{10}\, f'^w_{10} (1- f'^a_{10} /\lambda_{10})$	$M_{10}\, f'^p_{10} (1- f'^w_{10} /\lambda_{10})(1- f'^a_{10} /\lambda_{10})$