UNIVERSITÉ DU QUÉBEC À RIMOUSKI

DÉPLACEMENTS ET PATRONS DE RÉSIDENCE
CHEZ LA POPULATION DE BÉLUGAS (*DELPHINAPTERUS LEUCAS*)
DE L'ESTUAIRE DU ST-LAURENT

MÉMOIRE PRÉSENTÉ À
L'UNIVERSITÉ DU QUÉBEC À RIMOUSKI

Comme exigence partielle du programme de
Gestion de la faune et de ses habitats

PAR

SÉBASTIEN LEMIEUX LEFEBVRE

Mars, 2009

UNIVERSITÉ DU QUÉBEC À RIMOUSKI
Service de la bibliothèque

Avertissement

REMERCIEMENTS

J'aimerais tout d'abord remercier mon trio de directeurs pour leurs rôles importants dans ce long processus qu'aura été mon projet de maîtrise. Un premier grand merci au grand Manitou Robert qui m'a lancé dans cette aventure. Je me rappelle encore de ce téléphone où Robert m'offrait une maîtrise alors que je faisais de la rénovation dans un sous-sol : un beau changement de perspective et la chance de réaliser mon rêve de petit gars, étudier les baleines...! Merci de m'avoir donné la chance de « jouer » avec ces données si longuement et chèrement acquises et merci pour tes conseils et « ré-enlignements » judicieux. Un grand merci aussi à Véronique pour ta présence constante tout au long du projet (et ce malgré deux grossesses !!!). Véronique avec qui j'ai appris qu'un bon travail peut malgré tout être couvert de rouge de bout en bout! Tes corrections minutieuses m'ont appris beaucoup sur les difficultés du travail de chercheur mais aussi sur les satisfactions qu'il peut nous apporter. Merci aussi pour les opportunités que tu m'as offertes d'enrichir mon parcours de belles expériences : Tadoussac, l'Afrique, le Nord... fantastique! Un grand merci aussi à Dominique d'avoir accepté de diriger un autre étudiant orphelin des baleines! Merci pour ton support tout au long de mon parcours académique et pour m'avoir permis de faire partie du lab le plus dynamique et gourmand qui soit !

Je veux aussi dire un immense merci à tous ceux qui, au fil des ans, ont participé aux efforts de terrain ayant permis de ramasser les précieuses données dont je me suis servies pour ce projet : ces données, c'est de l'or ! Un merci spécial à ceux que j'ai côtoyés sur l'eau : Michel, Renaud, Yves, Samuel et Geneviève. Merci aussi à Arnaud Mosnier,

mon « cousin » de travail, avec qui les pauses café dérivaient souvent vers les dimensions profondes et incongrues de l'analyse spatiale. Merci pour ton aide, tes conseils et ta patience face à mes mille questions ! Un merci spécial à Tadoussac, mon village d'adoption l'été, et à toutes les belles rencontres que j'y ai faites : tous ces amis mordus de baleines, de plongée, de pêche et de mimes !

Finalement, je tiens à remercier infiniment tous ceux et celles (surtout celles !) qui m'ont supporté durant ce long périple, pour le meilleur et pour le pire…!

AVANT-PROPOS

Ce mémoire est présenté sous la forme d'un article à être soumis à une revue scientifique.

Contribution des auteurs

Bien que Véronique Lesage, Robert Michaud et Dominique Berteaux soient co-auteurs de l'article, le manuscrit doit être considéré comme le mémoire de l'étudiant.

V. Lesage, R. Michaud et D. Berteaux ont guidé l'étudiant lors de la rédaction du mémoire. R. Michaud a fourni la majorité de la base de données à long-terme sur les mouvements des troupeaux de bélugas (1989-2005), complétée par les données de V. Lesage (2003-2005). R. Michaud et V. Lesage ont aussi collaboré à la réalisation des suivis télémétriques et fourni conjointement les données sur les mouvements individuels des bélugas. Sébastien Lemieux Lefebvre a participé à l'effort de terrain à l'été 2005, planifié et récolté les données pour l'échantillonnage particulier de 2006, fait les analyses statistiques et rédigé le mémoire.

RÉSUMÉ

La population des bélugas du St-Laurent est classée comme *menacée* selon la Loi sur les espèces en Péril du Canada. Malgré qu'elle soit protégée depuis plus de 25 ans, aucun rétablissement de cette population n'a été observé à ce jour. Plusieurs facteurs limitant tels que la contamination, le dérangement, la dégradation de l'habitat, la compétition pour les ressources alimentaires, les prises accidentelles et la faible diversité génétique de la population, ont été avancés pour expliquer cette absence de rétablissement. Cependant, bien que des informations semi-quantitatives sur des aires de forte utilisation existent pour cette population, il demeure nécessaire, pour mieux comprendre l'impact potentiel de différents facteurs, de déterminer plus précisément les habitats utilisés intensément par cette population ainsi que leurs fonctions. Dans cette perspective, l'objectif principal de la présente étude était d'analyser, à fine échelle, les déplacements journaliers des individus et des troupeaux pour permettre l'identification des aires de forte résidence utilisées par la population au sein de son aire de répartition estivale.

Le premier objectif spécifique de cette étude consistait à identifier les variations dans les patrons de déplacement de 30 individus suivis à l'aide d'émetteurs radio à partir de l'analyse du premier temps de passage (*first-passage time*, FPT). L'analyse du FPT procure de l'information sur les échelles auxquelles les animaux effectuent de la recherche restreinte (c'est-à-dire à quelles échelles ils investissent plus de temps le long de leur trajet) et sur la localisation et la taille des aires de recherche restreintes (ARR). Nos résultats ont permis d'identifier 33 ARR distribuées à deux échelles distinctes soit : une première échelle d'environ 500m et une seconde échelle d'environ 1500m. Les échelles auxquelles sont effectués ces déplacements constitueraient une réponse des bélugas à l'hétérogénéité de leur environnement et aux différents facteurs gouvernant cette hétérogénéité tels que la répartition des proies, les structures topographiques ou l'occurrence de processus océanographiques à méso-échelle. Cependant, malgré que les patrons de déplacements correspondant à la recherche restreinte soient généralement reliés à des comportements d'alimentation, ceux observés chez les bélugas pourraient aussi être reliés à d'autres comportements tels que la socialisation.

Le second objectif spécifique de cette étude visait à établir l'utilisation d'aires de forte résidence par les bélugas du St-Laurent au sein de leur aire de répartition estivale par l'analyse des déplacements de 645 troupeaux de bélugas suivis visuellement entre 1989 et 2005. Les résultats obtenus lors de l'analyse des suivis individuels ont servi à établir un seuil pour identifier les vitesses de déplacement des troupeaux associées à de la forte résidence. Les échelles associées à la recherche restreinte ont de plus servi à déterminer les tailles de cellules de deux grilles spatiales utilisées pour analyser l'association entre les déplacements des troupeaux et l'utilisation de l'habitat. Les résultats de ces analyses nous ont permis d'identifier 26 aires de forte résidence à l'intérieur de l'aire de répartition estivale de la population dont la répartition coïncide avec celle de plusieurs aires de fortes utilisations identifiées précédemment. Cette constatation suggère que certaines d'entre elles doivent correspondre à des habitats d'importance particulière pour la population.

Cependant, les fonctions spécifiques de ces aires de forte résidence pour les bélugas du St-Laurent restent à déterminer. Ceci pourrait être réalisé ultérieurement par l'étude des liens entre les comportements de plongée et les activités de surface des animaux suivis individuellement. Ces liens pourraient être transposés aux troupeaux suivis visuellement depuis 1989 afin de déduire les comportements à partir des activités de surface. Leurs corrélations spatiales et avec des variables environnementales permettraient alors l'assignation de comportements spécifiques aux diverses aires de forte résidence et de là, la détermination de leur caractère essentiel ou non.

TABLE DES MATIÈRES

CHAPITRE 1

INTRODUCTION GÉNÉRALE

L'analyse des déplacements dans l'étude de l'utilisation de l'habitat

La plupart des animaux doivent se déplacer pour remplir les différents besoins reliés à leur cycle de vie, soit se nourrir, se reproduire, socialiser, etc. (Mysterud et al. 1999; Rettie et Messier 2001; Austin et al. 2004). Les choix gouvernant ces déplacements sont fonction de l'hétérogénéité de l'environnement, c'est-à-dire qu'ils dépendent de l'abondance, la qualité et la disponibilité des ressources, et visent à maximiser leur acquisition (Pyke 1978). Les bénéfices de la quête de ces ressources sont contrebalancés par les coûts encourus pour les acquérir, et dépendent de l'efficacité des tactiques employées pour y parvenir (Zollner et Lima 1999). On peut donc s'attendre à ce que les stratégies de déplacement varient selon les activités des individus et les habitats utilisés (Nams 1989; Mårell et al. 2002). La répartition d'une population étant la résultante de la distribution de ses individus, les stratégies de déplacement utilisées par les individus sont donc déterminants pour la compréhension de l'utilisation globale des habitats au niveau de la population (Turchin 1998; Harrison et al. 2006; Martins et al. 2006).

L'interaction entre l'hétérogénéité de l'environnement et les déplacements des individus représente ainsi un aspect important de l'étude de l'écologie des espèces animales (Turchin 1998). Pour étudier et comprendre cette interaction, deux grandes approches ont été préconisées : l'approche Eulérienne et l'approche Lagrangienne (Turchin 1998). Dans l'approche Eulérienne, l'attention porte sur des points précis de l'espace caractérisés par les densités et fluctuations de présence des individus à chacun d'eux. Dans l'approche Lagrangienne, l'attention porte sur les patrons de déplacement des individus ou autre unité définie (troupeaux, groupe, etc.) et sur les caractéristiques spatio-temporelles de ces déplacements, telles que la tortuosité, l'angularité, la vitesse, le déplacement net et/ou l'échelle. Ces deux approches permettent donc l'analyse de la distribution des individus et des populations mais sous des angles différents, l'approche Eulérienne étant centrée sur les variations dans la distribution d'une population ou d'un échantillon dans son ensemble à des points précis de l'espace, alors que l'approche Lagrangienne est centrée sur les déplacements des individus ou autre unité définie et sur leur influence sur la distribution de la population (Turchin 1998).

Au cours des dernières décennies, l'accroissement rapide de la puissance d'analyse et la disponibilité grandissante de données sur les déplacements individuels suivant le développement des technologies de télémétrie a mené à une utilisation croissante de l'approche Lagrangienne (ex : Barber et al. 2001; Mouillot et Viale 2001; Bradshaw et al. 2002; Jonhson et al. 2002; Franke et al. 2004; Frair et al. 2005; Elwen et al. 2006; Jonsen et al. 2007; Lydersen 2007). Cette approche a entre autre permis l'étude d'espèces pour lesquelles l'observation directe des individus et de leur comportement représentait des défis

logistiques importants (ex : Bergman et al. 2000; Pinaud et Weimerskirch 2005; Jonsen et al. 2006; Austin et al. 2006; Suryan et al. 2006; Jonsen et al. 2007; Pinaud et Weimerskirch 2007; Bailleul et al 2008). Pour analyser cette quantité grandissante de données, plusieurs outils d'analyse ont aussi été parallèlement développés parmi lesquels on retrouve principalement les modèles de marches aléatoires corrélées (*correlated random walk*) (Karieva et Shigesada 1983 ; Zollner et Lima 1999; Bergman et al. 2000; Morales et al. 2004; Bartumeus et al. 2005; Fortin et al. 2005), les analyses fractales (Mouillot et Viale 2001; Mårell et al. 2002; Laidre et al. 2004a; Nams et Bourgeois 2004; Nams 2005), les modèles « *state-space* » (Jonsen et al. 2006; Forester et al. 2007; Jonsen et al. 2007) ainsi que les analyses du premier temps de passage (*first-passage time*) (Fauchald et Tveraa 2003; Frair et al. 2005; Pinaud et Weimerskirch 2005; Bailey et Thompson 2006; Fauchald et Tveraa 2006; Pinaud et Weimerskirch 2007; Freitas et al. 2008). Le développement de ces différents outils a permis d'utiliser les analyses des déplacements pour une grande diversité d'applications et d'approfondir considérablement les connaissances sur les déplacements, les comportements et l'utilisation de l'habitat chez plusieurs espèces animales.

Parmi les applications des analyses de déplacements, on retrouve, tout d'abord, l'identification des patrons de déplacements utilisés par les individus. Ces patrons peuvent être reconnus à partir de l'analyse des caractéristiques spatiaux-temporelles des déplacements et de leur variations (Turchin 1998). Par exemple, un patron de déplacement caractérisé par une forte composante linéaire et des vitesses élevées peut être séparé d'un patron de déplacement caractérisé par des changements de direction fréquents et des

vitesses de déplacement moindres (Karieva et Shigesada 1983; Turchin 1991; Zollner et Lima 1999; Mårell et al. 2002; Fauchald et Tveraa 2003; Morales et al. 2004). Compte tenu que différentes stratégies de déplacement caractérisent généralement des activités distinctes, celles-ci peuvent souvent être reliées à des comportements particuliers (Jonhson et al. 2002; Mårell et al. 2002; Fortin et al. 2005; Bailey et Thompson 2006; Jonsen et al. 2007). Cependant, l'observation directe des comportements associés aux déplacements n'étant que rarement possible durant les suivis des individus, la nature des comportements utilisés sera souvent inférée à partir des caractéristiques des déplacements et/ou des connaissances disponibles *a priori* sur les déplacements et comportements de l'espèce à l'étude (Jonhson et al. 2002).

Une autre utilité des analyses de déplacement est l'identification des différentes échelles auxquelles les animaux interagissent avec leur environnement. La distribution hétérogène des ressources dans l'environnement est structurée par des processus agissant à diverses échelles (Nams 2005). En exploitant ces ressources, les animaux perçoivent et réagissent à l'hétérogénéité de l'environnement à des échelles spécifiques (Bradshaw et al. 2002; Fauchald et Tveraa 2003; Nams et Bourgeois 2004; Suryan et al. 2006). Cet ajustement peut ainsi être reconnu par la présence de variations dans les patrons de déplacement à ces échelles (Frair et al. 2005; Fauchald et Tveraa 2006; Bailleul et al. 2008; Pinaud 2008). Par exemple, un individu se déplaçant à la recherche de proies distribuées de façon agrégée devrait concentrer ses déplacements à l'intérieur des agrégats de façon à maximiser son taux de rencontre et d'acquisition des proies. Pour être en mesure d'établir la relation existant entre les déplacements des individus et leur utilisation de l'habitat, il est

donc important de reconnaître les échelles auxquelles les individus interagissent avec leur environnement (Fauchald et Tveraa 2003; Nams 2005; Pinaud et Weimerskirch 2005). Cependant, l'analyse des échelles auxquelles sont associés différents patrons de déplacement est aussi dépendante de l'échelle de résolution des données (Bradshaw et al. 2002) : des données à faible résolution spatiale et temporelle permettront d'identifier essentiellement des patrons de déplacements à l'échelle de grandes échelles tels que les migrations (Bergman et al. 2000; Jonsen et al. 2006) alors que des données à haute résolution spatiale et temporelle permettront de reconnaître des patrons de déplacement beaucoup plus fins comme les déplacements journaliers des individus à l'échelle locale de leurs domaines vitaux (Nams et Bourgeois 2004; Fortin et al. 2005).

Finalement, une application importante de l'analyse des déplacements est l'étude même de l'utilisation des habitats par les individus suivis. Plusieurs études ont en effet établi des relations entre les patrons de déplacement des individus et différents facteurs reliés à l'utilisation de l'habitat. Il a ainsi été démontré que les patrons de déplacement et d'utilisation de l'habitat peuvent varier en fonction du temps (Bergman et al. 2000; Jonsen 2006), des individus (Rettie et Messier 2001; Austin et al. 2004; Freitas et al. 2008), de la distribution des ressources (Banks et Yasenak 2003; Garcia et al. 2005; Frair et al. 2005) et des caractéristiques environnementales (Fortin 2005 et al. 2005; Pinaud et Weimerskirch 2005, Suryan et al. 2006; Weimerskirch et al. 2007). La distribution des patrons de déplacements et des comportements leurs étant associés peut aussi être employée pour caractériser les zones visitées par les individus (ex : LeBoeuf et al. 2000; Fauchald et Tveraa 2006; Suryan et al. 2006; Pinaud et Weimerskirch 2007). Ainsi, une zone où la

majorité des déplacements sont rectilignes et rapides pourra être catégorisée comme zone ou habitat de transit alors qu'une zone où les déplacements sont sinueux et lents, comme c'est souvent le cas lors de la quête alimentaire, pourra être caractérisée comme une zone ou habitat d'alimentation (LeBoeuf et al. 2000; Pinaud et Weimerskirch 2007). Considérant que les animaux visent à maximiser le temps passé dans les habitats les plus profitables, celui-ci ou en d'autres mots leur patron de résidence pourra servir d'indice de la profitabilité d'une zone. Les animaux ayant tendance à s'agglomérer là où leur résidence est forte, les patrons de résidence des individus auront une influence sur la distribution des troupeaux et de la population (Turchin 1998), et pourront servir à établir l'importance relative de ces habitats pour celle-ci.

Déplacements et utilisation de l'habitat chez les cétacés

Les cétacés évoluent dans un milieu complexe influencé par des composantes physiques hautement dynamiques (Bräger et al. 2003). De plus, ces animaux passent généralement très peu de temps à la surface et leur observation directe sous l'eau n'est que rarement possible. Aussi, plusieurs espèces de cétacés possèdent des aires de répartition étendues et certaines peuvent entreprendre des migrations de plusieurs milliers de kilomètres (Laidre et al. 2004a). Ces différents facteurs font de l'étude de l'utilisation de l'habitat chez les cétacés un défi de taille pour la recherche.

Une partie importante des analyses de l'utilisation de l'habitat chez les cétacés a été réalisée suivant l'approche Eulérienne, c'est-à-dire en quantifiant l'utilisation de l'habitat

selon les densités et fréquences d'observations des individus à des points précis dans l'espace. Ces études ont permis de reconnaître des caractéristiques importantes de l'utilisation de l'habitat chez les cétacés tel que des préférences pour certains paramètres physiques (ex : Ingram et Rogan 2002; Hastie et al. 2003; Naud et al. 2003; Laidre et al. 2004b; Panigada et al. 2005; Doniol-Valcroze et al. 2007; Skov et al. 2008), la présence d'aires de forte utilisation (ex : Ingram et Rogan 2002; Lusseau et Higham 2004; Parra 2006; Garaffo et al. 2007; Nichols et al. 2007), une variabilité spatiale des comportements (ex : Hastie et al. 2003; Garaffo et al. 2007; Cañadas et Hammond 2008) et de l'utilisation de l'habitats selon les groupes (ex : Martins et al. 2001; Ersts et Rosenbaum 2003; Wimmer et Whitehead 2004; Garaffo et al. 2007; Cañadas et Hammond 2008).

L'analyse des déplacements de surface, i.e., l'approche Lagrangienne, offre une approche privilégiée afin d'examiner l'utilisation de l'habitat et de mettre en lumière divers patrons de déplacement chez les cétacés. Par exemple, Laidre et al. (2004a) ont pu différencier deux patrons de déplacements chez les narvals (*Monodon monoceros),* l'un caractérisé par des composantes linéaires importantes reliés aux migrations et l'autre, par une forte tortuosité relié aux sites d'alimentation et vraisemblablement à la quête alimentaire. Dalla Rosa et al. (2008) ont quant à eux observé que les rorquals à bosse (*Megaptera novaengliae*) utilisaient aussi des déplacements de courtes et longues distances résultant en des faibles résidences entre les habitats présumés d'alimentation et des déplacements plus « erratiques » dans ces derniers. Cette diversité des patrons de déplacement seraient reliée à celle des comportements utilisés par les cétacés (Jacquet et al.

2003; Laidre et al. 2004a; Whitehead et Rendell 2004, Bailey et Thompson 2006; Elwen et al. 2006; Dalla Rosa et al. 2008).

Ces études se sont basées majoritairement sur des données de faible résolution et ont permis d'étudier les patrons de déplacement à de grandes échelles spatiales et temporelles. Les analyses à fines échelles ont plus rarement été utilisées mais demeurent un outil privilégié pour ce genre d'étude, mais sur une base journalière. Parmi les rares études portant sur les déplacements à fines échelles, mentionnons celle de Flores et Bazzalo (2004) qui ont pu établir les tailles de domaines vitaux, aires de fréquentation intensive, distances journalières parcourues, taux de déplacement en lien avec la bathymétrie grâce à des suivis visuels de dauphins Tucuxi (*Sotalia fluviatilis*). Les résultats de leur étude ont aussi permis d'émettre des recommandations pour la conservation de cette population en soulignant la nécessité d'établir des règles de contrôle du trafic maritime dans les aires de fréquentation intensive et l'importance de réglementer cette activité et l'aquaculture dans les zones non protégées utilisées par les dauphins (Flores et Bazzalo 2004).

Les études Lagrangiennes ont aussi pu relier les déplacements et l'utilisation de régions spécifiques par des individus à des comportements spécifiques (migrations, alimentation, socialisation, repos) (Real et Westgate 1997; Heide-Jørgensen et al. 2002; Elwen et al. 2006), à des facteurs physiques particuliers (bathymétrie, distribution des glaces, distance de la côte) (Heide-Jørgensen et al. 2002; Laidre et al. 2004a; Flores et Bazzalo 2004) et à la disponibilité des proies et au succès d'alimentation (Jacquet et al. 2003; Whitehead et Rendell 2004). Ces études démontrent comment l'analyse des déplacements et des comportements des individus, par opposition aux études fondées

essentiellement sur la distribution ponctuelle des individus, peut contribuer à la compréhension de l'utilisation de l'habitat chez les cétacés. Une étude de Bailey et Thompson (2006) en constitue un bon exemple. Ces auteurs ont pu établir chez les grands dauphins (*Tursiops truncatus*) la présence de trois patrons de déplacements caractérisés par des taux de déplacement net plus ou moins élevés. Certains de ces déplacements ont été associés à des comportements de recherche restreinte durant lesquels les individus concentraient leurs déplacements à une échelle précise, soit à l'intérieur de cercles de 200 m de rayon. Cette étude est d'ailleurs l'une des rares ayant pris en compte les échelles d'interaction entre les déplacements des cétacés et leur environnement. À l'aide d'observations directes des individus, Bailey et Thompson (2006) ont relié ces déplacements à des comportements d'alimentation et établi, à l'échelle à laquelle la recherche restreinte était effectuée, la répartition des aires d'alimentation existant dans leur aire d'étude.

Le cas du béluga du St-Laurent

Le béluga *Delphinapterus leucas* est un odontocète adapté au milieu arctique que l'on retrouve dans les eaux côtières du Canada, de l'Alaska, de la Russie et du Groenland. La population la plus méridionale de cette espèce se situe dans l'estuaire du Saint-Laurent (Brodie 1989). La présence de bélugas à cet endroit résulterait du réchauffement climatique de la fin de la dernière glaciation qui aurait entraîné une inondation des côtes et la formation de la mer de Champlain. Certains mammifères marins, dont les bélugas, se

seraient aventurés dans cette mer intérieure. Suite à l'abaissement du niveau de la mer de Champlain, une population de béluga serait restée dans ce qui constitue le St-Laurent d'aujourd'hui et serait à la source de la population actuelle (Lesage et Kingsley 1995).

La répartition estivale actuelle du béluga s'étend dans l'estuaire de l'Île aux Coudres à l'ouest jusqu'à Les Escoumins / Rimouski à l'est, et jusqu'à St-Fulgence dans la rivière Saguenay (Michaud et al. 1993). Dans cette région, trois types de troupeaux ayant des compositions différentes selon la proportion d'adultes et de jeunes occupent des secteurs distincts soit : les troupeaux composés d'individus adultes et de jeunes dans le secteur en amont, les troupeaux composés d'adultes de grande taille dans le secteur en aval, et finalement les troupeaux dits « mixtes » dans le secteur centre (Michaud et al. 1990). Au printemps, la répartition est similaire à celle de l'été avec, cependant, une plus forte concentration d'animaux dans le secteur en amont et une absence des troupeaux d'adultes généralement présents dans le secteur plus en aval. Vers l'automne, le centre de la répartition de la population se déplace vers l'aval et durant l'hiver, une partie des animaux quitte l'estuaire pour se diriger vers le golfe (Michaud et al. 1990). Les déplacements saisonniers de la population du St-Laurent entre l'estuaire et le golfe (quelques centaines de kilomètres) sont faibles en comparaison avec ceux de plusieurs milliers de kilomètres observés chez certaines populations de l'arctique canadien (Richard et al. 1990).

La population de béluga du St-Laurent a été longtemps exploitée par l'homme pour la chair, le gras et le cuir. Cependant, une diminution évidente de la taille de la population à environ 350 individus a entraîné l'arrêt complet de la chasse en 1979 et mené à la

désignation de cette population comme population en voie de disparition par le COSEPAC (Pippard 1985). Suite à cette désignation, plusieurs inventaires ont été menés à l'aide de diverses méthodes, incluant une série d'inventaires aériens systématiques suivant une méthodologie similaire. Ces estimations variaient de 431 à 607 bélugas (Kingsley 1998), et dénotaient toutes la petite taille de la population. L'application de nouveaux facteurs de correction pour tenir compte des individus submergés a permis de réviser ces premières estimations et d'établir que la population devait se composer d'environ 1000 à 1200 individus (Kingsley 1999; Kingsley et Gauthier 2002; Gosselin et al. 2001). Une harmonisation des critères d'évaluation du COSEPAC avec ceux de l'Union Internationale pour la Conservation de la Nature mena à la révision du statut de cette population qui est dorénavant désignée menacée d'extinction au Canada. La série temporelle d'inventaires suivant l'évolution de cette population depuis 1988 ne décèle aucun accroissement significatif de la taille de celle-ci (Kingsley 1998; Michaud et Béland 1999; Gosselin et al. 2001).

Pour expliquer ce faible taux de croissance malgré l'arrêt de la chasse, d'autres facteurs pouvant poser un frein à la capacité de récupération de cette population et un risque pour sa survie à long terme ont été suggérés. Ils comprennent entre autre la contamination, le dérangement, la dégradation de l'habitat, la compétition pour les ressources alimentaires, les prises accidentelles et la faible diversité génétique de la population (revue COSEPAC 2004). Cependant, l'impact de ces facteurs sur la population reste à établir (Hammill et al. 2007). Ainsi, pour répondre aux inquiétudes concernant la survie et le rétablissement de cette population, certains aspects de son écologie doivent être

mieux compris. Un de ces aspects est l'identification des habitats essentiels du béluga du St-Laurent dans son aire de répartition estivale, ce qui permettrait d'orienter prioritairement les efforts de conservation.

Quelques études se sont déjà penchées sur l'utilisation de l'habitat chez cette population et sur l'identification des habitats d'importance relative pour celle-ci. Pippard et Malcolm (1978) ont établi des aires de concentration correspondant aux zones «... *used regularly by white whales for one or more purposes of social congregating, feeding, calving, resting and travelling...* ». Cependant, cette étude était basée sur une courte couverture temporelle et spatiale de la répartition de la population ainsi que sur peu de données quantitatives. Par la suite, deux études plus détaillées de l'utilisation de l'habitat chez les bélugas du St-Laurent ont été réalisées par Michaud et al. (1990) et Michaud (1993). Michaud et al. (1990) fournissent une caractérisation biologique et physico-chimique de 17 habitats présumés du béluga dans son aire de répartition estivale. Les paramètres retenus lors de cette caractérisation comprennent : la profondeur, le type de substrat, la température et la salinité de l'eau, les courants et la présence de barre de courant, les zones de remontées d'eau profonde et la présence et le stade de proies présumées du béluga. Cependant, les données disponibles pour cette étude n'ont pu permettre une analyse quantitative de la relation existant entre ces différents paramètres biologiques et physico-chimiques et l'utilisation de l'habitat par les bélugas. La seconde étude fournit une première analyse semi-quantitative de l'utilisation de l'habitat des bélugas en définissant 18 aires de fréquentation intensive. Cette étude est basée sur la combinaison de données provenant de transects systématiques maritimes et aériens (Michaud et al.

1993). Elle a ainsi permis d'établir les aires caractérisées par la plus grande fréquence d'observation des bélugas et le plus grand nombre de bélugas présents. Cependant, les fonctions de ces aires de fréquentation intensive et leur importance dans le cycle vital des bélugas restent à établir.

Objectifs du projet de recherche

À partir de 1986, le Groupe de Recherche et d'Éducation sur les Mammifères Marins (GREMM) a entrepris un projet de recherche à long terme sur l'écologie des bélugas du St-Laurent. À travers ces recherches, des données ont été compilées sur les comportements et les déplacements des troupeaux de bélugas lors d'efforts de photo-identification. Ces efforts de recherche ont résulté en une banque de données comprenant plusieurs centaines de suivis visuels des troupeaux. Entre 2001 et 2005, les équipes de recherche de Pêches et Océans Canada et du GREMM ont de plus réalisé 44 suivis télémétriques individuels à l'aide de balises radio et d'instruments archives déployés directement sur les bélugas. L'objectif premier de ces suivis était de fournir de l'information sur les comportements de plongée des bélugas en présence et en absence de l'industrie d'observation des mammifères marins. Durant ces suivis, la position des individus était enregistrée à la fin de chaque séquence de ventilations, fournissant les détails sur les déplacements de chaque individu à fine échelle.

À l'aide de l'information sur les déplacements contenue dans les deux bases de données de suivis de troupeaux et de suivis individuels, le présent projet de maîtrise a

comme objectif général l'étude des déplacements à fine échelle des déplacements journaliers des bélugas et l'identification des aires de forte résidence de cette population durant la saison estivale. Plus spécifiquement, l'étude des déplacements individuels vise à identifier les patrons de déplacement durant lesquels les individus investissent plus de temps dans certains secteurs et l'échelle à laquelle ces déplacements sont déployés. Les résultats de ces analyses serviront ensuite à développer un critère pour reconnaître les déplacements associés à de la forte résidence chez les troupeaux et à établir l'échelle à laquelle analyser les déplacements des troupeaux dans leur aire estivale de répartition. Ceci permettra d'analyser les patrons de résidence au niveau de la population à partir des suivis visuels des troupeaux et d'établir la distribution des aires de forte résidence de cette population à l'intérieur de son aire de répartition estivale.

Bibliographie

Austin, D., W.D. Bowen, et J. I. McMillan. 2004. « Intraspecific variation in movement patterns: modelling individual behaviour in a large marine predator ». **Oikos** 105:15-30.

Austin, D., W.D. Bowen, J.I. McMillan, et S.J. Iverson. 2006. « Linking movement, diving, and habitat to foraging success in a large marine predator ». **Ecology** 87: 3095-3108.

Bailey, H., et P. Thompson. 2006. « Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging ». **Journal of Animal Ecology** 75:456-465.

Bailleul, F., D. Pinaud, M. Hindell, J.B. Charrassin, et C. Guinet. 2008. « Assessment of scale-dependent foraging behaviour in southern elephant seals incorporating the vertical dimension : a development of the First Passage Time method ». **Journal of Animal Ecology** 77:948-957.

Banks, J.E., et C.L Yasenak. 2003. « Effects of plot vegetation diversity and spatial scale on *Coccinelle septempuntata* movement in the absence of prey ». **Entomologia Experimentalis et Applicata** 108:197-204.

Barber, D. G., E. Saczuk, and P. R. Richard. 2001. « Examination of beluga habitat relationships through use of telemetry and a geographic information system ». **Arctic** 54:305-316.

Bartumeus, F., M.G.E. Da Luz, G.W. Viswanathan, et J. Catalan. 2005. « Animal search strategies : a quantitative random-walk analysis ». **Ecology** 86:3078-3087.

Béland, P., S. DeGuise, C. Girard, A. Lagacé, D. Martineau, R. Michaud, D.C.G. Muir, R.J. Norstrom, E. Pelletier, S. Ray, et L.R. Shugart. 1993. « Toxic compounds and health and reproductive effects in the St. Lawrence beluga whales ». **Journal of Great Lakes Research** 19:766-775.

Bergman, M.C., A.S. James, et S.N. Luttich. 2000. « Caribou movement as a correlated random walk ». **Oecologia** 123:364-374.

Bradshaw, C.J.A., M.A. Hindell, K.J. Michael, et M.D. Sumner. 2002. « The optimal spatial scale for the analysis of elephant seal foraging as determined by geo-location in relation to sea surface temperatures ». **Journal of Marine Science** 59:770-781.

Bräger, S., B.F. Harraway, et B.F.J. Manly. 2003. « Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*) ». **Marine Biology** 143:233-244.

Brodie, P.F. 1989. The white whale *Delphinapterus leucas* (Pallas, 1776), Pages 119-144. *in* Rigway, S.H. et R.J. Harrison, eds. **Handbook of marine mammals, vol.4.** Academic Press, London.

Cañadas, A., et P.S. Hammond. 2008. « Abundance and habitat preferences of the short-beaked common dolphin *Delphinus delphis* in the southwestern Mediterranean : implications for conservation ». **Endangered Species Research** 4:309-331.

COSEPAC. 2004. «Évaluation et Rapport de situation du COSEPAC sur le béluga (Delphinapterus leucas) au Canada – Mise à jour. » **Comité sur la situation des espèces en péril au Canada.** Ottawa. x + 77 pages.

Dalla Rosa, L., E.R. Secchi, Y.G. Maia, A.N. Zerbini, et M.P. Heide-Jørgensen. 2008. « Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula ». **Polar Biology** 31:771-781.

Doniol-Valcroze, T., D. Berteaux, P. Larouche, et R. Sears. 2007. « Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence ». **Marine Ecology Progress Series** 335:207-216.

Elwen, S., M.A. Meÿer, P.B. Best, P.G.H. Kotze, M. Thornton, et S. Swanson. 2006. « Range and movements of female heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-linked telemetry ». **Journal of Mammalogy** 87:866-877.

Ersts, P.J. et H.C. Rosenbaum. 2003. « Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. ». **Journal of Zoology** 260:337-345.

Fauchald, P., et T. Tveraa. 2003. « Using first-passage time in the analysis of area-restricted search and habitat selection ». **Ecology** 84:282-288.

Fauchald, P., et T. Tveraa. 2006. « Hierarchical patch dynamics and animal movement pattern ». **Oecologia** 149:383-395.

Flores, P.A.C., et M. Bazzalo. 2004. « Home ranges and movement patterns of the marine Tucuxi dolphin, *Sotalia Fluviatilis*, in Baía Norte, Southern Brazil ». **Latin American Journal of Aquatic Mammals** 3:37-52.

Forester, J.D., A.R. Ives, M.G. Turner, D.P. Anderson, D. Fortin, H.L. Beyer, D.W. Smith, et M.S. Boyce. 2007. « State-space models link elk movement patterns to landscape characteristics in yellowstone national park ». **Ecological Monographs** 77:285-299.

Fortin, D., H.L. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, et J.S. Mao. 2005. « Wolves influence elk movements : behavior shapes a trophic cascade in yellowstone national park ». **Ecology** 86:1320-1330.

Frair, J.L., E.H. Merrill, D.R. Visscher, D. Fortin, H.L. Beyer, et J.M. Morales. 2005. « Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk ». **Landscape Ecology** 20:273-287.

Franke, A., T. Caelli, et R.J. Hudson. 2004. « Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models ». **Ecological Modelling** 173:259-270.

Freitas, C., K.M. Kovacs, R.A. Ims, M.A. Fedak, et C. Lydersen. 2008. « Ringed seal post-moulting movement tactics and habitat selection ». **Oecologia** 155:193-204.

Garcia, F., P. Carrère, J.F. Soussana, et R. Baumont. 2005. « Characterisation by fractal analysis of foraging paths of ewes grazing heterogeneous swards ». **Applied Behaviour Animal Science** 93:19-37.

Garaffo, G.V., S.L. Dans, S.N. Pedraza, E.A. Crespo, et M. Degrati. 2007. « Habitat use by dusky dolphin in patagonia : how predictable is their location? » **Marine Biology** 152:165-177.

Gosselin, J.-F., V. Lesage, et A. Robillard. 2001. « Population index estimate for the beluga of the St Lawrence River Estuary in 2000 ». **Canadian Science Advisory Secretariat**, Research Document 2001:049.

Harrison, P.J., S.T. Buckland, L. Thomas, R. Harris, P.P. Pomeroy, et J. Harwood. 2006. « Incorporating movement into models of grey seal population dynamics ». **Journal of Animal Ecology** 75:634-645.

Hastie, G., B. Wilson, et P.M. Thompson. 2003. « Fine-scale habitat selection by coastal bottlenose dolphins : application of a new land based video-montage technique ». **Canadian Journal of Zoology** 81:469-478.

Hammill, M.O., L.N. Measures, J.-F. Gosselin, et V. Lesage. 2007. « Lack of recovery in St. Lawrence Estuary beluga ». **Canadian Science Advisory Secretariat**, Research Document 2007:026.

Heide-Jørgensen, M.P., R. Dietz, K.L. Laidre, et P. Richard. 2002. « Autumn movements, home ranges and winter density of narwhals (*Monodon monoceros*) tagged in Tremblay Sound, Baffin Island ». **Polar Biology** 25:332-341.

Ingram, S.N., et E. Rogan. 2002. « Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus* ». **Marine Ecology Progress Series** 244:247-255.

Jacquet, N., D. Gendron, et A. Coakes. 2003. « Sperm whales in the gulf of California : residency, movements, behaviour and the possible influence of variation in food supply ». **Marine Mammal Science** 19:545-562.

Johnson, C.J., K. Parker, D. Heard, et M.P. Gilligham. 2002. « Movement parameters of ungulates and scale-specific responses to the environment ». **Journal of Animal Ecology** 71:225-235

Jonsen. I.D., R.A. Myers, et M.C. James. 2006. « Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles ». **Journal of Animal Ecology** 75:1046-1057.

Jonsen, I.D., A.M. Random, et M.C. James. 2007. « Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model ». **Marine Ecology Progress Series** 337:255-264.

Karieva, P.M., et N. Shigesada. 1983. « Analysing insect movement as a correlated random walk ». **Oecologia** 56:234-238.

Kingsley, M.C.S. 1999. « Indices d'abondance et estimations de la population de bélugas de l'estuaire du St-Laurent ». **Rapport technique canadien des sciences halieutiques et aquatiques** 2266 : vii + 27 pages.

Klaassen, R.H.G., B.A. Nolet, J.A. van Gils, et S. Bauer. 2006. « Optimal movement between patches under incomplete information about the spatial distribution of food items ». **Theoretical Population Biology** 70:452-463.

Laidre, K.L., M.P. Heide-Jørgensen, M.L. Logdson, R.C. Hobbs, R. Dietz, et G.R. VanBlaricom. 2004a. « Fractal analysis of narwhal space use patterns ». **Zoology** 107:3-11.

Laidre, K.L., M.P. Heide-Jørgensen, M.L. Logdson, R.C. Hobbs, P. Heagerty, R. Dietz, O.A. Jørgensen, et M.A. Treble. 2004b. « Seasonal narwhal habitat associations in the High Arctic ». **Marine Biology** 145:821-831.

LeBoeuf, B.J., D.E. Crocker, D.P. Costa, S.B. Blackwell, P.M. Webb, et D.S. Houser. 2000. « Foraging ecology of the northern elephant seals ». **Ecological Monographs** 70:353-382.

Lesage, V., et M. C. S. Kingsley. 1995. « Bilan des connaissances de la population de bélugas (*Delphinapterus leucas*) du Saint-Laurent ». **Rapport technique canadien des sciences halieutiques et aquatiques** 2041 : 44pages.

Lesage, V., C. Barette, M.C.S. Kingsley, et B. Sjare. 1999. « The effect of vessel noise on the vocal behavior of Belugas in the St. Lawrence River estuary, Canada ». **Marine Mammal Science** 15:65-84.

Lusseau D., et J.E.S. Higham. 2003. « Managing the impacts of dolphin-based tourism through the definition of critical habitats: the case of Doubtful Sound, New Zealand ». **Tourism Management** 25:657-667.

Lydersen, C., A.R. Martin, I. Gjertz, et K.M. Kovacs. 2007. « Satellite tracking and diving behaviour of sub-adult narwhals (*Monodon monoceros*) in Svalbard, Norway ». **Polar Biology** 30:437-442.

Mårell, A., J.P. Ball, et A. Hofgaard. 2002. « Foraging and movement paths of female reindeer : insights from fractal analysis, correlated random walks, and Lévy flights ». **Canadian Journal of Zoology** 80:854-865.

Martins, C.C.A., M.E. Morete, M.H. Engels, A.C. Freitas, E.R. Secchi, et P.G. Kinas. 2001. « Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground ». **Memoirs of the Queensland Museum** 47:83-90.

Michaud, R., A. Vézina, N. Rondeau, et Y. Vigneault. 1990. « Annual distribution and preliminary characterization of beluga (*Delphinapterus leucas*) habitats in the St. Lawrence ». **Canadian technical report of fisheries and aquatic sciences** 1757 : 37pages.

Michaud, R. 1993. « Distribution estivale du béluga du Saint-Laurent; synthèse 1986 à 1992 ». **Rapport Technique Canadien des Sciences Halieutiques et Aquatiques** 1906 : 28pages.

Michaud, R., et P. Béland. 1999. « Looking for trends in the endangered St. Lawrence beluga population. A critique of Kingsley, M.C.S., 1998. Population index estimates for the St. Lawrence belugas, 1973-1995 ». **Marine Mammal Science** 17:206-212.

Morales, J.M., et S.P. Ellner. 2002. « Scaling up animal movements in heterogeneous landscapes : the importance of behavior. » **Ecology** 83:2240-2247.

Mouillot, D., et D. Viale. 2001. « Satellite tracking of a fin whale (*Balaenoptera physalus*) in the north-western Mediterranean Sea and fractal analysis of its trajectory ». **Hydrobiologia** 452:163-171.

Myterud, A., P.K. Larsen, R. A. Ims, et E. Ostbye. 1999. « Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? ». **Canadian Journal of Zoology** 77:776-783.

Nams, V.O. 1989. « A technique to determine the behavior of radio-tagged animal. » **Canadian Journal of Zoology** 67:254-258.

Nams, V.O. 2005. « Using animal movement paths to measure response to spatial scale ». **Oecologia** 143:179-188.

Nams, V.O., et M. Bourgeois. 2004. « Fractal analysis measures habitat use at different spatial scales: an example with American marten ». **Canadian Journal of Zoology** 82:1738-1747.

Naud, M.J., B. Long, J.-C. Brêthes, et R. Sears. 2003. « Influences of underwater bottom topography and geomorphology on Minke whale (*Balaenoptera acutorostrata*) distribution in the Mingan Islands (Canada) ». **Journal of Marine Biology** 83:889-896.

Nichols, O.C., R.D. Kenney, et M.W. Brown. 2008. « Spatial and temporal distribution of North Atlantic right whales (*Eubalaena glacialis*) in Cape Cod Bay, and implications for management. » **Fisheries Bulletin** 108:270-280.

Panigada, S., G.N. DiSciara, M.Z. Panigada, S. Airoldi, J.F Borsani, et M. Jahoda. 2005. « Fin whales (Balenoptera physalus) summering in the Ligurian Sea : distribution, encounter rate, mean group size and relation to physiographic variables ». **Journal of Cetacean Research and Management** 7:137-145.

Parra, G.J. 2006. « Resource partitioning in sympatric delphinids : space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. » **Journal of Animal Ecology** 75:862-874.

Patenaude, N.J., J.S. Quinn, P. Béland, M. Kingsley, et B.N. White. 1994. « Genetic variation of the St. Lawrence beluga whale population assessed by DNA fingerprinting ». **Molecular Ecology** 3:375-381.

Pinaud, D., et H. Weimerskirch. 2005. « Scale-dependent habitat use in a long-ranging central place predator ». **Journal of Animal Ecology** 74:852-863.

Pinaud, D., et H. Weimerskirch. 2007. « At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study ». **Journal of Animal Ecology** 76:9-19.

Pinaud, D. 2008. « Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems ». **Journal of Applied Ecology** 45:91-99.

Pippard, L. 1985. « Status of the St Lawrence River population of Beluga, *Delphinapterus leucas* ». **Canadian Field-Naturalist** 9:438-450.

Pippard, L., et H. Malcolm. 1978. « White whales (*Delphinapterus leucas*). Observations on their distribution, population and critical habitats in the St. Lawrence and Saguenay rivers ». Unpublished report prepared for Department of Indian And Northern Affairs, Parks Canada, Ottawa, 161 pages.

Pyke, G.H. 1978. « Optimal foraging: movement patterns of bumblebees between inflorescences ». **Theoretical Population Biology** 13:72-98.

Real, A.J. et A.J. Westgate. 1997. « Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. » **Marine Biology** 130:315-322.

Rettie, J. W., et F. Messier. 2001. « Range use and movement rates of woodland caribou in Saskatchewan ». **Canadian Journal of Zoology** 79:1933-1940.

Richard, P.R., Orr, J.R., and Barber, D.G. 1990. «The distribution and abundance of belugas, *Delphinapterus leucas* , in eastern Canadian subarctic waters: a review and update. » p. 23-38. Dans: Smith, T.G. D.J. St.Aubin, and J.R. Geraci Advances in research on the beluga whale, *Delphinapterus leucas*. **Canadian Bulletin of Aquatic Science** 224 pages.

Skov, H., T. Gunnlaugsson, W.P. Budgell, J. Horne, L. Nøttestad, E. Olsen, H. Søiland, G. Vikingsson, et G. Waring. 2008. « Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge ». **Deep-Sea Research II** 55:254-268.

Suryan, R.M., F. Sato, G.R. Balogh, K.D. Hyrenbach, P.R. Sievert, et K. Ozaki. 2006. « Foraging destinations and marine habitat use of short-tailed albatrosses: A multi-scale approach using first-passage time analysis ». **Deep-Sea Research II** 53:370-386.

Turchin, P. 1991. « Translating foraging movement in heterogeneous environments into spatial distribution of foragers ». **Ecology** 72:65-83.

Turchin, P. 1998. **Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants**. Sinauer Associates, Sunderland.

Weimerskirch, H., D. Pinaud, F. Pawlowski, et C.-A. Bost. 2007. « Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the Wandering albatross ». **The American Naturalist** 170:734-743.

Whitehead, H., et L. Rendell. 2004. « Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales ». **Journal of Animal Ecology** 73:190-196.

Wimmer, T., et H. Whitehead. 2004. « Movement and distribution of northern bottlenose whales, *Hyperoodon ampullatus*, on the Scotian Slope and in adjacent waters ». **Canadian Journal of Zoology** 82:1782-1794.

Zollner P.A., et S.L. Lima. 1999. « Search strategies for landscape-level interpatch movements ». **Ecology** 80:1019-1030.

CHAPITRE 2

MOVEMENT AND RESIDENCY PATTERNS OF THE ST LAWRENCE

BELUGA WHALES

Lemieux Lefebvre, Sébastien[1,3], Michaud, Robert[2], Lesage, Véronique[3], Berteaux, Dominique[1].

(1)   *Département de Biologie, de Chimie et de Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec, G5L 3A1, Canada*

(2)   *Groupe de Recherche et d'Éducation sur les Mammifères Marins, 295 chemin Ste-Foy, Québec, Québec, G1R 1T5, Canada*

(3)   *Ministère des Pêches et des Océans, Institut Maurice Lamontagne, 850 Route de la Mer, P.O. Box 1000, Mont-Joli, Québec, G5H 3Z4, Canada*

Abstract

The St Lawrence beluga whale population is *threatened* under the Canadian Species At Risk Act and not recovering despite 25 years of protection. Many potentially limiting factors have been proposed to explain this lack of recovery. However there is a need to define intensively used habitats and their functions for the population in order to better understand their contribution to the current status of the population. In this perspective, we used fine-scale analyses of individual and herd movements to describe residency patterns of this population during summer. We used radio-telemetry to study the fine-scale daily movements of 30 belugas using a first-passage time (FPT) approach. The FPT corresponds to the time required by an animal to cross a circle of a given size. When measured regularly along an animal's path, FPT provides information on variation of search effort during displacements, the scale at which area restricted search (ARS) occur, and the location and size of the ARS zones. We then used the scales and swimming speed associated with individual ARS to adapt a spatial grid and define a criterion of high residency for the quantitative analysis of 645 herd visual follows and the identification of areas of high residency (AHR).

Thirty-three ARS zones were identified at two different spatial scales: a small-scale (~500 m) and a larger-scale (~1500 m). Using these scales to grid the study area resulted in the identification of 26 AHR used by beluga herds within their summer distribution area. The functions associated with these habitats and their relative importance for the beluga population remain to be established. This could be accomplished through future studies, by examining the links between diving behaviour and surface activities of individually-tagged

beluga, and using this coupling of information to examine herd surface activities and deduce their behaviour in the different areas of high residency.

Introduction

Most animals live in complex heterogeneous environments where resources, i.e., prey, breeding areas, calving areas, etc., vary in quality and are distributed unevenly. In such environments, animals are expected to move among habitats associated with these resources and to maximize the use of the most profitable ones (Pyke 1978; Turchin 1991). Movement patterns are also expected to change depending on whether animals are in transit between, or are exploiting a profitable habitat. Although habitat profitability is difficult to assess directly from animal tracking, individual movement patterns can be quantified through changes in orientation and speed, resulting in unevenly distributed time investments or residency through visited habitats. In particular, animal tracking can be used for the identification of areas where animals show relatively high turning rates and small net horizontal displacements, a behaviour called Area-Restricted Search or ARS (Fauchald 1999). It is assumed that ARS is a behavioural sequence used by the animal to increase its encounter rate with a resource of quality, whether it is prey or something else, within limited boundaries. Under this assumption, boundaries of ARS zones might be used as a proxy for areas of higher resource densities or profitability. Because herd movements result from the combined movements of individuals, net horizontal displacements of herds might also represent, under the same assumption, a good proxy for habitat profitability. Residency

of herds would be expected to be high where individuals undertake restricted search, i.e. in the most profitable habitats.

Across the landscape, resources and associated habitats are distributed according to various scales to which organisms are expected to respond (Bradshaw *et al.* 2002; Fauchald and Tveraa 2003; Nams and Bourgeois 2004; Morin et al. 2005; Suryan *et al.* 2006). This scaled heterogeneity in resource distribution may be hierarchical, where small patches are nested within larger patches, creating a mosaic of hierarchies that individuals have to monitor and to which they have to respond by adjusting their movement patterns (Fauchald and Tveraa 2006). This assemblage may also be time-specific since habitat characteristics and quality may vary over time. Consequently, analyses employed to describe habitat use should take into account the specific scale at which a species perceives and responds to its environment and be based on data acquired at a temporal scale relevant to this response and that of environmental changes (Johnson *et al.* 2002). The notion of scale of habitat use is also important for conservation purposes, when there is a need for accurate identification of management units (Nams *et al.* 2006).

Quantitative analyses of movements have been attempted with a large spectrum of organisms and scales, ranging from the very precise tracks of insects (e.g. Karieva and Shigesada 1983; Morales and Ellner 2002; Banks and Yasenak 2003) to the coarser paths of species migrating over thousands of kilometres (e.g. Bergman *et al.* 2000; Jonhson *et al.* 2002; Laidre *et al.* 2004a, b; Jonsen *et al.* 2007). In recent years, the development of high-performance tracking instruments has facilitated the study of movements, especially for far-ranging species (e.g. Jonhson *et al.* 2002; Austin *et al.* 2004; Laidre *et al.* 2004a; Jonsen *et*

al. 2006; Pinaud and Weimerskirch 2007). Simultaneously, new tools have been developed for the analysis of the large volume of precise telemetry data. One of these tools, the analysis of first-passage time, FPT (Fauchald and Tveraa 2003), has recently been developed to study the scaling response of individuals to spatial heterogeneity and detect behaviours such as area-restricted search. This approach also provides information on the spatial distribution of these behaviours, and scale(s) at which they occur. To date, this approach has been used almost exclusively in the context of central place foraging, where predators use area-restricted search patterns in response to the patchy distribution of prey (Fauchald and Tveraa 2003; Pinaud and Weimerskirch 2005; Fauchald and Tveraa 2006; Pinaud and Weimerskirch 2007; Bailleul *et al.* 2008). Nevertheless, this method could be used in other contexts, as the FPT analysis can identify scaled responses of any behaviour leading to a quantitative variation in residency of an individual along its path.

Quantitative analyses of movement patterns have been the focus of several recent studies of marine mammals (e.g. Barber *et al.* 2001; Jacquet *et al.* 2003; Laidre *et al.* 2004a,b; Austin *et al.* 2004, Martin and da Silva 2004, Whitehead and Rendell 2004; Ream *et al.* 2005, Austin *et al.* 2006; Campagna *et al.* 2006). These studies have demonstrated that movement patterns of marine mammals, as those of terrestrial mammals, are highly diverse and depend on multiple physical and biological factors such as ice cover, bathymetry, currents, prey distribution, foraging success and individual age and gender. Many of these analyses have examined movements over relatively large scales, i.e., several tens or hundreds of kilometres, using data with low temporal and spatial resolution, i.e., several hours and kilometres apart. Fine-scale analyses have more rarely been used to

describe movement patterns of marine mammals (Hindell *et al.* 2002, but see Hastie *et al.* 2003; Flores and Bazzalo 2004; Bailey and Thompson 2006). Analyses of movements over this scale can provide valuable information on short-term habitat use of relatively sedentary species distributed over relatively small areas.

St Lawrence beluga whales, *Delphinapterus leucas,* have a limited summer distribution as they occupy a 200-km stretch of an Estuary only a few tens of kilometres wide (Michaud 1993). This population is *threatened* under the Canadian Species At Risk Act (SARA) and non-recovering despite 25 years of protection (COSEWIC 2004). Reasons for this situation are unclear, but may include factors related to the quality of the available habitat. In this perspective, there is a need to determine more precisely intensively used habitats and their functions.

In 1989, a long-term research program investigating the biology, ecology and behaviour of the St Lawrence beluga whales was initiated by the Group of Research and Education on Marine Mammals (GREMM). As part of this program, several hundreds of hours were spent each year, predominantly during summer and early autumn, in search of opportunistic encounters of beluga herds for photo-identification purposes. Data on herd movement and behaviour were also collected at regular intervals throughout these encounters. These sustained efforts resulted in a large database composed of several hundreds of herd encounters. In combination to these surveys, several individuals were equipped with time-depth recorders and radio transmitters between 2001 and 2005 to examine individual movement, diving and surface activity patterns through continuous visual tracking of the tagged individuals.

As a first step toward the objective of identifying critical habitats of St Lawrence belugas, this study aimed at examining residency patterns of St Lawrence beluga whales using a combination of two approaches. First, the precise movement patterns of beluga individually tracked using radio-telemetry were analysed using a FPT approach to identify areas, times and scale(s) at which ARS occurs in this population. Based on the premise that movement characteristics related to individual ARS can be transposed to herd behaviours, scale(s) and swimming speed associated with individual ARS were then used to define a criterion for high residency, and to grid the study area so to perform over these cells a quantitative analysis of 16 years of beluga herd visual tracking data and identify areas of high residency (AHR) within the summer distribution of the population.

Methods

DATA COLLECTION

Radiotracking of individuals

Search of beluga herds for individual tag deployment covered the central portion of the summer distribution area of St Lawrence beluga (Fig.1) where all gender and age classes were expected to be regularly encountered (Fig.A1.1). This area was chosen primarily to maximise the number of tracking in areas where interactions or overlap of belugas with human activities are presumed to be the most important. The logistic constraints of tagging individuals far from the research station and anticipated small number of successful tagging also precluded attempts at the limits of the population

distribution. This area was divided into smaller sectors, which were searched alternately for the occurrence of beluga. Once a herd (i.e., one individual or more) was encountered, a herd follow was initiated and location and observational data were collected following sampling protocols described in the next section.

Only individuals close and parallel to the vessel and displaying a predictable behaviour were targeted for tagging. Females with calves of the year, calves and small grey-coloured individuals were not subject to tagging. Once a tag was successfully deployed, the tagged individual was tracked from a distance (usually 400—600 m) and its behaviour and position relative to the tracking vessel and other belugas in the herd were described following each surface sequence. Other information included the individual movement patterns and general direction, group size and composition, dynamism, synchronicity relative to other belugas in the herd, occurrence of aerial vocalizations or unusual surface activities (splashes, spy-hopping, side-swimming, tail lobbing, etc.), a description of closest group and vessel traffic (type, distance, number). Herd characteristics were also described in details following the basic protocol (see below). Simultaneous recording of the vessel GPS location and information on the individual's distance from the tracking vessel and angle relative to the magnetic North allowed the precise positioning of animals through triangulation calculation:

$$\text{LAT}_{animal} = \text{LAT}_{boat} + \text{Distance Cos } (\pi \text{ Angle}/180) * 9 \ 10^{-6}$$

$$\text{LONG}_{animal} = \text{LONG}_{boat} + \text{Distance Sin } (\pi \text{ Angle}/180) * 13.4 \ 10^{-6}$$

Tags comprised a time-depth-velocity recorder (TDR Mk-08, Wildlife Computers Inc., Redmond, USA) and a 304 g radio transmitter (VHF, Telonics, 932 E. Impala Avenue Mesa, USA). The TDR and VHF were housed in a remote-released package made of floatation material and were attached to beluga using a suction cup following a design developed by Robin Baird (Hooker and Baird 1999). Tag deployments and beluga tracking were made from a 28- or 32-feet vessel equipped with a Geographic Positioning System (GPS) and a six-element Yagi antenna. Tags were projected from a distance of approx. 10 m using a cross-bow, or were attached directly to animals using a 3-m wooden pole. A minimum control over tag release time was achieved by the use of a magnesium cap that was intended to corrode and release suction after 4-6 h depending on cap thickness. Tagged individuals were followed until dusk, release of the tag or loss of the signal.

Visual survey of herds

Between 1989 and 2005, more than 1700 herds were encountered and tracked under different research protocols including mostly photo-identification but also biopsy sampling and radio-tagging. The vast majority of the data was acquired by one research team (GREMM), except in 2003-2005 when a second team was added during beluga VHF-TDR tagging efforts. Areas surveyed were selected daily based on previous knowledge of the population distribution (Michaud 1993), weather conditions and according to areas covered the previous days to avoid repeated sampling of the same area over short periods of time. Surveys were neither random nor systematic but covered a large portion of the population

summer distribution and a broad range of habitats on a regular basis. From 1989 to 1995 the study area encompassed the full extent of the known population summer distribution. However, beginning in 1996, the study area was restricted to the central portion of the summer distribution of the population, in an effort to investigate social networking of specific segments of the population present in this portion of the Estuary (Michaud 1993). All surveys were conducted from a 28 or 32 feet vessel equipped with a 4-m observation platform using one or two observers.

A herd was defined as an assemblage of groups of beluga in which inter-group distances were small compared with the extent of the herd. Groups were composed of animals swimming within one body length from one another, generally in a coordinated fashion. Once a herd was encountered, a distance from the herd of approximately 300-500 m was maintained for 15 min during which time, preliminary information were acquired on herd composition, size and other characteristics. The research vessel then proceeded within the herd to approach groups according to specific protocols (e.g., photo-identification, biopsy sampling and radio-tagging). A detailed description of herd characteristics (hereafter called *summary survey*) was made every 30 min during these approaches. Summary surveys included information on herd size and composition (adult, grey-coloured individuals, calves of the year), percent contribution by grey animals including calves, herd radius, geometrical structure, predominant movement patterns, swimming direction and dynamism, presence of surface activity or vocalisation, and number, distance and types of other vessels. Position of the research vessel and prevailing weather conditions were also

noted as part of summary surveys. Surveys stopped with the end of sampling protocols or after an arbitrary limit of 3 h.

DATA ANALYSIS

First passage time analysis

The first passage time (FPT) corresponds to the time required by an animal to cross a circle of a given radius r (Johnson *et al.* 1992). When measured regularly along the path of a central place forager, FPT provides information on search effort variation during displacements (Fauchald and Tveraa 2003). A peak in relative variance among FPT values calculated at multiple scales (i.e. different r values) indicates the scale at which restricted search patterns occurred (Fauchald and Tveraa 2003). In other types of foragers, information provided by FPT is not necessarily related to search effort but does measure variations in degree of residency of animals along their track. Paths were generated from position data of individually tracked beluga using ArcGIS 9.1 (ESRI inc. 12 Concorde Place, Suite 900 Toronto, Canada). Step lengths, turning angles and net displacements were calculated using the Hawth's analysis tool extension for ArcGIS (Beyer 2004). Because the quality of FPT analyses depends on tracking duration and number and accuracy of positions of successive moves (Pinaud 2008), short tracking records (arbitrarily defined as < 15 positions) were dropped from the analysis. In addition, original tracks were segmented whenever the interval between two consecutive positions was longer than one hour to minimize errors associated with linear approximation. Segments were interpolated to obtain

a position every 50 m. The relative variance in FPT was calculated for circles with radius (r) increments of 100 m, from 200 m to 3000 m. Variance values were log-transformed to insure independency from the magnitude of r (Fauchald and Tveraa 2003). Circle radii associated with peaks in FPT variances were identified as corresponding to the scale of restricted search behaviour (hereafter referred to as Var-max).

Intensively searched areas were identified from segments with an observed peak in FPT variance following Bailey and Thompson (2006). This method identified the interpolated point with the highest FPT (at Var-max) as the centre of a circle (of radius r_{max}) delimiting intensively searched primary areas, hereafter called *ARS zones* (using the terminology of Pinaud and Weimerskirch 2007). However, since it is reasonable to assume that an individual could display restricted search many times during a single tracking, a method was developed to identify multiple ARS zones within a given segment. Some authors have used a threshold value of FPT associated with restricted search based on multimodal distribution of FPT values at Var-max to identify multiple ARS zones (Pinaud and Weimerskirch 2007; Weimerskirch *et al.* 2007). This approach is convenient for movements where rapid changes in speed and searching behaviour result in step variation of FPT values and clear visual thresholds (e.g., Fig. S1 in Pinaud and Weimerskirch 2007). However, for movement paths with more gradual transitions in FPT values, the visual examination of FPT series is not sufficient to identify transitions toward ARS. Here, we used piecewise-regressions to detect breakpoints in FPT values at a given scale corresponding to transitions between restricted search and other behaviours. To define these breakpoints, FPT values (at Var-max) were classified in ascending order for each segment.

A two and three processes (one and two breakpoints) piecewise-regression model was then applied to the data series using the MODEL procedure in SAS (SAS Institute Inc. 2003). The continuous function for the one-breakpoint model took the following form:

$$y = a_1 + b_1x \qquad\qquad \text{for } c_1 \leq x$$

$$y = \{a_1 + c(b_1 - b_2)\} + b_2x \qquad\qquad \text{for } c_1 > x$$

whereas the continuous function for the two-breakpoints model took the following form:

$$y = a_1 + b_1x \qquad\qquad \text{for } c_1 \leq x$$

$$y = \{a_1 + c_1(b_1 - b_2)\} + b_2x \qquad\qquad \text{for } c_1 < x \leq c_2$$

$$y = \{a_1 + c_1(b_1 - b_2)\} + c_2(b_2 - b_3)\} + b_3x \qquad\qquad \text{for } x > c_2$$

Where y and x were the coordinates of slopes described by the ordinate at origin a_i, the slope b_i and separated at the breakpoint c_i.

Piecewise-regression models assumed variances homogeneity, and independency and normality of residuals, assumptions that were not met in this study. To correct for residual autocorrelation, autoregressive moving average error processes (FIT statement of the MODEL procedure in SAS) were applied to the data. The autoregressive order was determined with a Durbin-Watson test. Violation of the heteroscedasticity assumption was minimized by applying the FIT statement *hccme3* of the same SAS procedure. Once corrected for heteroscedasticity and autocorrelation, differences between slopes were tested using two-sample paired *t*-tests. A significant difference between slopes indicated the

potential occurrence of other ARS zones. To determine whether multiple spatially distinct ARS zones occurred in a segment, the value corresponding to the 95% confidence interval of the calculated breakpoint was selected as a threshold. Interpolated points with FPT values falling above this threshold were extracted and mapped in ArcGIS with their associated circle of radius equal to Var-max. Then, starting with the highest FPT value, points were screened one by one. A point was considered the centre of a new ARS zone when the circle associated with this point did not overlap with points associated with other ARS zones on the same segment. This step was repeated until no more point above the threshold could be considered as a new ARS zone centre, based on the aforementioned criteria.

Visual survey of herds

Herd follows were classified based on the number of summary surveys with available GPS locations, consistency of time intervals between locations and completeness of summary surveys. Follows that were retained for the analysis were composed of at least three positions separated by a constant 30 min time intervals, had an estimate of herd radius and highly detailed summary surveys (i.e., missing less than an arbitrary limit of four herd descriptor values every three summary surveys). Paths and associated movement parameters were calculated from position data using the same procedure as for telemetry data. Paths were divided into segments of two successive positions representing the interval (30 min) between two summary surveys. A buffer of a size equivalent to the estimated

radius of the herd for this segment was created around each segment (Fig. 2) to represent the spread of the herd during displacement. Herd speed and radius associated with the second position were attributed to the entire buffered segment as they corresponded to the movement and spread of the herd over the 30 min constituting the segment. Any part of the buffer overlapping with land features was removed from the analysis.

The research vessel did not maintain the same position relative to the herd during a herd follow. However, it was assumed that its position represented a good estimator of the position of the herd, and that using this metric had no significant effects on estimates of segments buffer size and beluga moving speed associated with these segments when compiled across numerous surveys. Distance and orientation of the research vessel relative to the estimated centre of the herd, i.e. the two metrics used in our analysis, were noted during 40 summary surveys in 2006 to test this assumption. Vessel orientation and distance relative to the estimated herd centre were estimated visually by an observer independent from the one completing summary surveys. Corrected herd centre was calculated using the same equation as for VHF positioning of individual beluga (see above), but using distance (D) and orientation (A) of the research vessel relative to the herd centre. A buffer was added to the research vessel and herd tracks using the method described above. Segments buffered area and associated average speeds were compared using paired samples t-tests. A second test was performed to verify the presence of a systematic bias in positions of the research vessel relative to the herd centre, which could have influenced the overall positioning of the buffered segments. Distributions of the x and y parameters of vectors describing the distance and orientation of the vessel relative to the herd centre were tested

for normality using a Shapiro-Wilk test. Given that both distributions deviated significantly from normality, a Hodges' bivariate sign test and Wilcoxon's signed-rank test were used to test if the resultant vector differed significantly from the centre (Batchelet, 1981). The Wilcoxon's signe-rank test was calculated using the program VassarStats (available at http://faculty.vassar.edu/lowry/wilcoxon.html). Other statistical analyses were completed using Systat 9.1 (Systat Software Inc., 225 W Washington St., Chicago, USA).

Scales of ARS that were defined using telemetry data were used as a basis to grid the study area and study movements of herds visually-tracked since 1989. Cell size was defined as corresponding to the average diameter of zones where ARS was documented in radio-tracked individuals (i.e. twice the mean Var-max radius, or 1000 and 3000 m) (Bailey and Thompson 2006). This procedure allowed for using non-arbitrary cell size corresponding to a scale likely relevant to the belugas' perception of their environment (as defined through FPT analyses). The ArcGIS spatial-join tool was used to associate each segment of herd follows with grid cells. When a cell was covered by two or more segments issued from a same follow (sampling unit), segment parameters with numerical values were averaged, whereas those with categorical but qualitatively incrementing values were scored with a value of one per represented category. Only cells visited by a minimum of three herds over the 16-year sampling period were retained for the analyses (Fig. 3).

A matrix constituted of herd net displacement per 30 min interval was used to identify areas of high residency (AHR). In order to calculate net displacements of individually-tracked beluga over temporal scales comparable to herd movement data, i.e. 30 min, positions of individually-tracked beluga, which were taken after each sequence of

respirations, were re-sampled using a moving average. Tracking segments of 30 min, and including at least some time (> 0%) spent within an ARS zone were used in the moving average calculation to account for the fact that herd net displacements over 30 min periods likely included some activities located outside ARS zones. Taking into account these transitions was important since, as opposed to individual tracking data, there was no precise indication as to when herds entered in ARS. Using only net displacement speeds of individuals that were comprised fully within the boundaries of an ARS zone would have resulted in a conservative threshold (i.e., low net displacement speed) for selecting herd movements that were characteristic of ARS; it would have eliminated any herd 30 min segments where a herd was in transition toward or from an ARS zone. It should be noted that the variability in the intervals between ventilation sequences resulted in a variable number of positions being used to calculate the moving averages, and in a window length of slightly longer than 30 min. However, this variability had little effects on the results as the computed value was a net displacement speed and not a net displacement. The percentage of time spent within the ARS zone was calculated for each moving average and plotted against net displacement speeds to determine whether a threshold for herd net displacement speeds could be identified visually from this plot. However, this approach was unsuccessful as no threshold could be identified in this manner (see results).

An alternate way of defining the net displacement criterion to identify ARS in herds was to consider only segment windows where individually-tracked beluga spent at least 50% of their time within an ARS zone. The rationale for selecting 50% as a threshold was based on the methodology of herd sampling during summary surveys, i.e., a characteristic

had to be displayed *predominantly* (more than 50% of the time) during the 30 min preceding the summary to be logged as a descriptor of the herd. An average net displacement speed was calculated for each ARS zone. However, given that more than one ARS zone were identified for some belugas, the effect of using net displacement speed calculated from one ARS zone vs another was tested by calculating net displacement speeds per ARS zone while using only one randomly selected ARS per individual, and by repeating this random selection ten times. The 90th percentile (Method 5, SAS Institute Inc. 2003) of each of the ten sets of moving averages was determined across all ARS zones, and the ten values were averaged to constitute the threshold net displacement speed for herd to be considered in high residency mode. The 90th percentile was preferred to the more commonly used 95th percentile to minimize the potentially strong impact of extreme values on percentiles calculated over datasets with relatively small sample sizes (N = 15). AHR were defined as cells where 50% of the herds travelled at a speed equal to or lower than the identified threshold speed associated with high residency. Boundaries of AHR were defined by grouping cells that were adjacent on at least one side. To limit the analysis to the most important sectors, only areas composed of a least two adjacent cells were retained as high residency areas in the *fine scale* grid.

The sensitivity of the delimited AHR to the criteria used to define them was tested in two different ways. First, the criteria using the net displacement speed associated with high residency of herds was changed by using the lower and upper extremes of the 90th percentile from the ten values obtained through the moving average analysis. A second

approach consisted in changing the percentage of herds travelling below this threshold value by an arbitrary factor, 5% in this case.

Results

RADIOTRACKING OF INDIVIDUALS AND FIRST-PASSAGE TIME ANALYSIS

Between June and October 2001-2005, 44 belugas were successfully tagged and followed, with an average tag deployment duration of 7h08 (range: 0h30-29h09). Thirty of the 44 radio–tracked belugas provided 38 segments of sufficient duration ($\geq$ 15 positions) for the analysis of fine-scale daily movements using the first-passage time approach. These segments were composed of an average of 43 positions (range: 15-110 positions) acquired over an average total non-linear distance of 23.4 km (range: 5.3-60.7 km) and a period of 4h27 (range: 0h41—9h36) (Table 1). The average interval between positions was of 6m41s $\pm$ 5m19s and of 0.57km $\pm$0.31km. The average swimming speed of individuals during follows was 5.8 km h^{-1} $\pm$ 1.7 km h^{-1} (range: 0.15 km h-1 - 22.35 km h^{-1}).

A total of 17 peaks in relative variance of FPT (Var-max values), indicative of ARS, were observed in 39.5% of the segments (15/38) (see example in Fig. 4). Var-max values were not continuously distributed and formed two groups (Fig. 5), corresponding to the two scales where ARS arose: a *small scale* of 300-700 m (n = 8, mean = 512 m) and a *larger scale* of 1100-1700 m (n = 9, mean = 1467 m). Peaks were identified at both scales in two of the segments (Fig. 4). The piecewise regression revealed multiple peaks in relative variance of FPT, indicative of multiple ARS zones, in 14 of the 17 segments: 10 segments

fitted the one breakpoint model (Fig. 5a and b), whereas 4 others fitted the two breakpoints model (Fig. 5c and d). Screening the points above the 95% confidence limit of the first breakpoint for each FPT value series resulted in the identification of 33 ARS zones: 18 at the *small scale* and 15 at the *larger scale* (Table 2). A maximum of four ARS zones were identified for a single segment at a specific scale.

The distribution of ARS zones in the Estuary overlapped among individually-tracked beluga (Fig. 6), where 15 of the 33 identified ARS overlapped at least partially with another ARS. In two individuals, *small scale* ARS zones were also embedded within *larger scale* ARS zones (Fig. 4). ARS occurred in several sectors of the Estuary, including the Saguenay river mouth, southwest of the Batture aux Alouettes, east of Île Blanche, off Cap-de-la-Tête-au-Chien, Cacouna and Île aux Basques and along the southern slope of the Laurentian Channel (Fig. 6).

The re-sampling of individual tracking data to calculate net displacement speeds over intervals comparable to herd movement data, i.e., 30 min, resulted in no clear breakpoints in the proportion of the 30 min interval comprised within ARS zones (Fig. 7). Consequently, no clear threshold to identify high residency behaviors in beluga herds was obtained using this approach. Using the moving average and 90th percentile approach resulted in a net displacement speed threshold of 3.53 km h^{-1} ± 0.17 km h^{-1}, ranging between 3.42 km h^{-1} and 3.78 km h^{-1}, when re-sampling individuals contributing to more than one ARS zone.

VISUAL SURVEY OF HERDS

A total of 645 of the 1700 herd follows performed between 1989 and 2005 were retained for analysis. Selected herd follows were composed on average of 4.4 positions and were characterized by herd net displacement speeds varying from 0.04 to 17.84 km h^{-1}, with an average speed of 3.53 km h^{-1} ± 2.53 km h^{-1}. The total area covered by the buffered segments was 1.3% larger when using the boat as a proxy for the centre of herds instead of the true herd centres (53.28 km^2 vs 52.59 km^2), but this difference was non-significant (paired sample t-test: $t = -0.508$, df $= 26$; $P = 0.616$). Herd average speeds calculated by segment using either herd or vessel positions were also non-significantly different (paired sample t-test: $t = 0.709$, df $= 26$; $P = 0.484$). These results indicate that no significant bias was introduced in total coverage of buffered segments or beluga average swimming speeds in those segments. Both the Hodge's bivariate sign test (N $= 40$, K $= 12$, p $= 0.163$ from table J in Bachelet 1981) and the Wilcoxon's signed-rank test ($N_{s/r} = 40$, W $= 123$, p $= 0.4122$) indicated no systematic bias in the position of the boat relative to the herd centre, and thus, no significant effect of using a substitute metric (research vessel position) on the overall positioning of the buffered segments.

The detection of restricted search behaviour in the FPT analysis at scales of 500 m and 1500 m led to the creation of two grids: a fine-scale grid with a cell size of 1000 m * 1000 m and a large-scale grid with a cell size of 3000 m * 3000 m, i.e., each cell size corresponding to two times the average radius of the *small scale* ARS zone (~ 500 m) and *larger scale* ARS zone (~1500 m). The 645 herd follows retained for the analysis resulted in 1810 and 286 cells that were visited by at least one herd for the *fine scale* (1000 m*1000

m) and *coarser scale* (3000 m * 3000 m), respectively (Fig. 3). These non-zero cells covered 62.2% (1736 km^2) and 81.5% (2273 km^2) of the population summer distribution area, respectively. However, when considering only cells visited by at least three herds, this total was reduced to 1056 cells at the *fine scale* and 190 cells at the *coarser scale* (Fig. 8). These cells covered 1009 km^2 or 36.2% of the population summer distribution at the *fine scale*, and 1524 km^2 or 54.6% of this area at the coarser scale.

Using a value of 3.53 km h^{-1} as a threshold to identify high residency with herd data resulted in 343 (*fine scale*) and 72 (*coarser scale*) cells with at least 50% of the herds travelling at a speed slower than this threshold. Based on this criterion and depending on the scale, high residency behaviours occurred in 32.5% (*fine scale*) and 37.9% (*coarser scale*) of the cells that qualified for the analyses, i.e., cells visited by at least three herds (Fig. 8). Joining adjacent cells at the *fine* and *coarser* scales resulted in the identification of 26 and 14 areas of high residency, respectively (Fig. 9). The AHR identified at the *fine scale* showed an 85 % overlap with those identified at the *larger* scale. Considering this substantial overlap, and considering that cells created at the finer scale allowed subdivision and more precise delimitation of AHR and the identification of areas not detected at the *coarser scale*, only AHR identified at the *fine scale* were presented in more details (Fig. 9). These areas of high residency covered 320 km^2 or 11.5% of the summer distribution area of St Lawrence beluga whales.

The sensitivity analysis using the lower and upper extremes of the mean net displacement speeds, i.e., 3.42 km h^{-1} and 3.78 km h^{-1}, for the definition of AHR resulted in areas identified as AHR of 308 km^2 and 362 km^2, respectively. These values represented

respectively -3.75% and +13.1% of the extent of the AHR obtained when using the average threshold value (3.53 km h^{-1}). No AHR were lost when using the most severe criterion (i.e., 3.42 km h^{-1}), although one AHR was subdivided into two smaller areas. Using the more permissive criterion resulted in the identification of three previously unidentified AHR - one at the Batture aux Alouettes, one off Baie des Rochers and one west of Kamouraska (Fig. 12).

The sensitivity analysis using values of 55% and 45% as the triggers for defining AHR based on proportions of herds travelling below the speed threshold resulted in variations of -12.6% and +18.1% in the extent of AHR (i.e., 283 km^2 and 378 km^2, respectively) (Fig.13). The use of the most severe criterion (55%) resulted in the subdivision of two AHR into five smaller areas and in the disappearance of two AHR, the ones located off Île Rouge and off Île verte. The use of the less restrictive criterion (45%) resulted in the appearance of four AHR – three in the same sectors as those identified in the previous sensitivity analysis and one to the southeast of Batture aux Alouettes.

The AHRs were widely distributed across the St Lawrence Estuary and Saguenay River (Fig. 9) and included the head of the Laurentian channel, South channel, south-east of Île Rouge, Saguenay river mouth and Saguenay River (with an AHR in Baie-St-Marguerite), the sector between the north tip of Île-aux-Lièvres and the Saguenay River mouth, the western tips of Île Verte and Île-aux-Lièvres, and areas off Saint-George-de-Cacouna, Rivière-du-Loup, Île-du-Pot-à-l'Eau-de-Vie, the east and west coasts of Saint-Siméon, Îles-de-Kamouraska, and eastern Île-aux-Coudres. The overlap between the ARS zones identified using individually-tracked beluga, and the AHR identified using herd

tracking data was 33.80 km^2 or 33.9%. The main overlapping areas were located at the Saguenay river mouth, head of Laurentian channel, off Saint-George-de-Cacouna and Rivière-du-Loup and east of St-Siméon (Fig. 10).

Discussion

Identifying when, where and why animals change from one movement pattern to another constitutes an important step toward an understanding of habitat use (Johnson *et al.* 2002; Frair *et al.* 2005; Nams 2005). This study proposed an innovative way of analysing herd movement data acquired through visual tracking methods by using fine-scale movement data from radio-tracked individuals. A first-passage time approach was successfully applied to radio-tracking data acquired from a subset of beluga whales and resulted in the identification of two scales (i.e., 500 m and 1500 m) over which beluga likely perceived and reacted to environment heterogeneity in the St Lawrence Estuary. Information on scales of occurrence of these episodes and associated net displacement speeds was used to develop an objective criterion to detect high residency movement patterns in visually-tracked beluga herds. Using this approach, a total of 26 areas of relatively high residency were identified within the St Lawrence beluga summer distribution area.

RADIOTRACKING OF INDIVIDUALS AND FIRST-PASSAGE TIME ANALYSIS

The number of belugas that were successfully tagged (N = 44) in this study is high compared to existing studies of cetaceans (Hooker and Baird 1999; Laidre *et al.* 2002; Johnson and Tyack 2003; Baird *et al.* 2005; Baird *et al.* 2006). However, analytical requirements of the FPT analysis reduced the number of usable records: some records were dropped due to short instrument retention times; other records were truncated or also dropped due to short, but significant contact losses with the tracked individual. These considerations and the geographically-restricted tagging effort limited the usefulness of tracking data of individual beluga for inferring locations of high residency areas over the summer range of the population as a whole. However, sample size and the spatial distribution of tagging efforts were adequate to identify scales over which these events occur in this population.

Episodes of slow net displacement speeds were referred to as ARS in this study. ARS is usually assumed to represent foraging activities (Fauchald and Tveraa 2003; but see Pinaud and Weimerskirch 2007). This approach may be adequate when behaviours other than foraging are not expected to occur, as this might be the case for some central-place foragers involved in short foraging trips. However, given that the FPT analyses aims at quantifying variation in search effort along an animal's path, any behaviour resulting in an animal investing more time within a particular area could lead to the detection of peaks in variance of FPT from which ARS are deduced. In other words, episodes of so-called area-restricted search may well represent behaviours other than foraging. In studies such as ours, various activities including foraging were expected to be sampled, and any behaviour

leading to larger time investments within particular zones, regardless of the reasons leading to changes in movement patterns, were of interest.

The FPT analysis of radio-tracking records indicated that belugas, like many other marine predators, exhibited scale-specific adjustments of their movement patterns resulting in slow net displacement speeds. Multiple scales of ARS and nested ARS were documented in this study. Area-restricted search occurred at scales of approximately 500 m and 1500 m, suggesting that factors affecting movement decisions occurred at these scales. These ARS radii were small compared to ARS scales of several tens to hundreds of kilometers that have been documented in petrels and albatrosses, and in other marine species (e.g. Fauchald and Tveraa 2003; Suryan *et al.* 2006; Pinaud and Weimerskirch 2007; Freitas *et al.* 2008), but were comparable to scales identified for bottlenose dolphins (Bailey and Thompson 2006). Scales over which ARS occur most certainly depend on the general landscape and distance traveled by individuals. The detection of ARS over radii greater than a few kilometres was unexpected in the St Lawrence Estuary considering its small size and small distances traveled by belugas.

Scales of ARS likely depend also on the behaviours resulting in these slow net displacement speeds, as the space over which feeding occurs may differ from that needed for calving a young. The corollary of this is that ARS may be observed over various scales in a given sector if different behaviours occur there. In the Arctic, for example, belugas congregate in river mouths where they spend extensive periods of time, as a result of various possible activities including calving, feeding, breeding, moulting and social interactions (Kleinenberg *et al.* 1964; Tomilin 1967; Brodie 1971; Sergeant 1973; Finley

1982; Finley *et al.* 1982; Reeves and Mitchell 1989; St. Aubin and Geraci 1988; St. Aubin *et al.* 1990; Boily 1995). In the Estuary, beluga historically formed large concentrations in river mouths (e.g., near Manicouagan and Rivière-Ouelle) (Vladykov 1944). They still congregate in areas of shallow water today (e.g., Baie Ste-Marguerite in the Saguenay River), possibly for the same reasons as in the Arctic or for a combination of activities (Pippard 1985a; Michaud 1992; Chadenet 1997). Accumulation of beluga in those areas would likely result in ARS, the scale of which could vary according to the activity taking place. Although ARS over various scales were observed in some areas of the Estuary during this study, identification of individual activities related to ARS behaviour was beyond the scope of this study. One way to infer specific activities related to ARS behaviour would be through the analysis of the underwater behaviour of individually-tracked beluga by relating diving patterns, surface activities and environmental characteristics.

Scales of ARS may also vary for a same behaviour among individuals, as a result of individually-specific factors such as social learning, allometry or energy requirements (e.g., Hindell *et al.* 1991; LeBoeuf *et al.* 1992; Beck *et al.* 2003; Austin *et al.* 2004; Sargeant *et al.* 2007). In St Lawrence beluga whales, males and females occupy different trophic levels and differ in the fatty acid composition of their blubber, a difference probably related partly to sexual dimorphism, but also to the spatial segregation of males and females during summer (Michaud 1993, Lesage *et al.* 2001; Nozères 2006). Differences in diet and habitat use among gender classes in beluga may involve different feeding tactics between males and females. However, sample size in this study was too small to compare ARS behaviours

among gender classes. Despite this limitation, small and larger scale ARS were observed in sectors preferentially used either by herds of females or males suggesting that the two scales at which ARS was displayed were not gender-related.

Area-restricted search was performed by 38.5% of the radio-tracked individuals, an occurrence that is low compared to other studies that have used FPT analyses (Pinaud and Weimerskirch 2005; Bailey and Thompson 2006; Fauchald and Tveraa 2006; Pinaud and Weimerskirch 2007). Although functions or individually-specific factors associated with ARS may have played a role in the frequency of detection of these events, the short duration of beluga radio-tracking records relative to the several-days records in other studies likely constituted a limitation to the probability of capturing these events in this study. Only one study where bottlenose dolphins were tracked over periods comparable to those analysed in the present study showed higher occurrences of ARS, but this study was conducted in a foraging area and thus, where ARS is likely to occur regularly (Bailey and Thompson 2006). Tagging in this study was attempted regardless to where encounters took place, which might have reduced the likeliness of capturing those events. Other factors that might regulate the occurrence of ARS include the degree of sociability of the species studied and period of the year. Belugas are highly social marine mammals, which give birth during summer (Pippard and Malcolm 1978). Although stomach contents indicate that beluga feed during summer in the Estuary (Vladykov 1946; V. Lesage, DFO, unpubl. data), the overall occurrence of ARS behaviours related to foraging may be less frequent in beluga during summer than in other species or at other times of the year (Martin and Smith

1992). This may or may not be counterbalanced by ARS related to other behaviours such as calving or social interactions.

Area-restricted search has been correlated with foraging in many species, including albatrosses and petrels (Pinaud and Weimerskirch 2005; Pinaud and Weimerskirch 2007), bottlenose dolphins (Bailey and Thompson 2006), and ringed seals (Freitas *et al.* 2008). When foraging, a predator should minimize the time spent travelling between patches of prey and maximize the time spent within high density patches (Pyke 1978). Movement strategies used by predators searching for patchily distributed prey depend on its perceptual range, on patch distribution and degree of predictability in space and time, and previous knowledge of this distribution (Zollner and Lima 1999; Austin *et al.* 2004; Klaassen *et al.* 2006). When encountering a profitable patch, predators are expected to increase the tortuosity of their displacement and decrease their speed, resulting in small net displacements and increased residency times within patches (Benhamou 1992). A predator should also respond to patch boundaries so to remain in contact with high density resources, leading to an ARS pattern in movements. The time invested in ARS and scale of occurrence will depend on patch extent and density (Karieva and Odell 1987; Fauchald 1999; Fauchald and Tveraa 2006).

ARS can be triggered by various environmental cues, including prey encounter rates, aggregation densities and oceanographic features such as fronts and eddies (Frair *et al.* 2005; Pinaud and Weimerskirch 2005). These cues can lead the animal to move non-randomly toward sectors of predictable oceanographic features or prey densities, and to explore these environments using ARS in search of prey aggregations. Once prey are

detected, the predator could limit further its ARS to remain within higher quality and more profitable smaller and denser aggregations, such as prey schools or swarms (Fauchald and Tveraa 2006; Pinaud and Weimerskirch 2007). A search strategy of this type could lead to multiple scales of ARS (Fauchald and Tveraa 2006; Pinaud and Weimerskirch 2007) and to nested patterns of ARS, i.e., small scale ARS within larger-scale ARS zones (Fauchald 1999; Fauchald and Tveraa 2006). Adjacent or overlapping ARS zones of both scales forming zones of a few kilometers in diameter were observed in sectors near Cacouna, Cap-de-la-Tête-au-Chien and the Saguenay river mouth (Fig. 6). Although behaviours associated with these ARS could not be confirmed in the context of this study, their spatial organization suggested the existence of a meta-structure of environmental features attracting beluga in these environments.

Meso-scale features, such as fronts and eddies, have often been correlated with the distribution of foraging whales profiting from their herding effects on pelagic prey (e.g. Ream et al. 2005; Campagna et al. 2006; Doniol-Valcroze et al. 2007; Skov et al. 2008). Many predictable meso-scale oceanic processes occur in the Estuary, including two of the sectors mentioned above, but also the south channel downstream of Île-aux-Lièvres, and the head of the Laurentian channel. Some of the meso-scale features operate at scales of 50 to 500 m, i.e., at scales comparable to those of the small scale of ARS observed in St Lawrence beluga (Ingram and El-Sabh 1990). These meso-scale features can act as environmental cues to which beluga respond, and may serve at aggregating prey (Marchand et al. 1999).

In the St Lawrence Estuary and elsewhere, beluga whales feed on a wide variety of prey that range from small polychaete worms to large fishes such as salmon (Vladykov 1946; Kleinenberg 1964, Sergeant 1973). Many of these preys, including capelin, herring and smelt, show a patchy distribution to which belugas can respond by using ARS. Feeding on patchy aggregations of these species could concur with observations of Martin and Smith (1992) of belugas in the High Arctic moving *"very little distance horizontally"* in areas of deep waters where they are suspected to forage on patchily distributed Greenland halibut. Pippard and Malcolm (1978) also described foraging in belugas as characterized by individuals going back and forth within limited areas where they executed tight circles, half circles and reversals of direction. Similar movement patterns were also described by Watts and Draper (1986) when observing Hudson Bay beluga foraging on capelin aggregations. These descriptions of movement patterns of foraging belugas present a good correspondence with the definition of ARS patterns of movements. It remains however hazardous to relate findings on ARS scales to those of aggregations of potential prey since actual patch sizes are unknown and can vary extensively over short periods of time for species such as capelin (Simard *et al.* 2002).

There was a relatively good spatial correspondence between ARS and AHR defined at the finer scale through herd survey analysis (Fig. 10), as 52% of the areas overlapped at least partially, for a total overlap between ARS and AHR of 34%. The main sectors of overlap were located at the mouth of the Saguenay river, at the head of the Laurentian channel and off St-George-de-Cacouna and Rivière-du-Loup (Fig. 10). These results

indicate that individuals followed through VHF tracking used these areas with behaviours leading to high residency, as did the majority of the herds tracked in the same areas.

However, individuals also used ARS in sectors not recognized as AHR through herd follows. This observation is not surprising considering the dynamic nature of marine environments and the difference between the number and period covered by individual and herd follows. Marine environments are influenced by physical processes acting over multiple temporal scales (tidal and lunar cycles, seasons, years, etc.) (Trujillo 2008). Accordingly, habitats preferentially used by marine organisms are expected to change across these multiple temporal scales (Austin *et al.* 2006). For example, foraging habitats of marine predators can vary in quality and location on a daily basis according to tidal currents as they likely influence the distribution of water masses and their associated resources such as zooplankton or small pelagic fishes (Michaud and Giard 1997; Simard and Lavoie 1999; Simard *et al.* 2002). High quality habitats may be highly ephemeral in dynamic systems such as the Estuary, but may be recurrent over predictable time scales. Quality and location of resources can also vary over seasonal or annual scales and influence habitat selection by marine predators over these scales (Sourisseau *et al.* 2006). Given that individual tracking was conducted only over the last five years of this 17-year project, inter-annual or longer term variability in the Estuary ecosystem and habitat quality might explain some of the discrepancy observed in the distribution of the ARS vs AHR.

The number of belugas that were tracked individually in this study was small and covered a short period compared with the study period over which herds were followed. Consequently, the tagging study provided an incomplete image of where individual

movements may lead to high residency — the 33 ARS zones. The limitations in this study of habitat preferences, arising from the small number of tracked individuals and from the coarse resolution of herd movement patterns, were overcome by combining the two approaches, as individual movement patterns provided the basis to analyze herd movements. The FPT analysis identified movement patterns leading to high residency, and provided net displacement speeds necessary to relate individual to herd movements. The identification of scales to which individuals responded to their environment also provided a second basis for the analysis of herd movement patterns. Scales to analyse habitat use are often chosen arbitrarily or are selected to fit the scale of environmental variables with the lowest resolution. In this study, such an adjustment was not required given that no environmental variables were included in the analysis, and information on scales was used as a non-arbitrary value to analyse habitat use and to grid the summer distribution area of beluga at a scale susceptible to encompass meaningful biotic or abiotic features to which belugas responded. The proposed approach also defined areas of high residency according to scales and cell sizes that were likely more meaningful in the context of conservation or definition of management units.

VISUAL SURVEY OF HERDS

The database used in this study to assess patterns of residency of St Lawrence beluga was of a high standard considering the consistency of visual survey methodologies over the years, their total span (16 years) and spatial distribution, which covered in some

years the entire summer distribution. Nevertheless, and as indicated earlier, survey effort was non-uniformly distributed across the study area, the central portion of the beluga summer distribution being surveyed more frequently (Fig. 3). The criteria for selecting herd follows (see methods) greatly reduced sample size. Although AHR were identified in the least visited sectors of the Estuary (i.e., west of Île-aux-Fraises and east of Île-aux-Basques), some AHR may have gone undetected in those sectors as a result of lower sampling effort (Fig. 3). Sampling effort was, however, adequate to study residency patterns in the central portion of the beluga summer distribution, i.e., in sectors comprised between Kamouraska/St-Siméon to the south-west, Les Escoumins/Trois-Pistoles to the north-east, and north of Baie Ste-Marguerite in the Saguenay River. All segments of the population were expected to be regularly encountered in this area (Michaud 1993). The effect of sample size on the probability of identification of AHR cells was not examined. However, cells characterized by a smaller sample size and identified as part of AHR were regularly found adjacent to AHR cells with higher sample size (Fig.3a, Fig. 9a and Fig. 10a), suggesting that an increase in sample size would not have substantially influenced the distribution of the AHR in these regions.

The criterion used to define high residency of herds was based on the rationale that the net displacement speed of herds composed of individuals performing restricted search should be slower and should result in higher residency times than when herds are composed of individuals in a travelling mode between high residency areas. Defining a criterion to discriminate among herd movement types using individual movement patterns constituted the most logical and scientifically defendable criterion for high residency with data

collected using different temporal and spatial resolutions. To accommodate differences in sampling and data resolution, a transition period was incorporated in the calculation of the net displacement speed associated with ARS (see methods). This transition also permitted to consider segments of herd tracking records associated with progressive changes in behaviour when approaching or leaving high residency areas. Not including this transition in the calculation of the net speed criterion, i.e., using only 30-min segments comprised entirely within an ARS zone, would have resulted in a lower net displacement speed criterion to classify herd movements and hence, in a smaller number of cells associated with herd speeds slower than this criterion.

The sensitivity analyses indicated a certain robustness of the AHR areas to changes in the definition criteria, although they cautioned about the exact locations of their boundaries. A small number of AHRs appeared or disappeared when changing the value of the criteria. Three of the four new AHRs identified in the sensitivity analysis based of speeds overlapped partially with those identified in the analysis based on herd proportions (Fig. 12 and 13). Two of these areas - west of Kamouraska and at the Battures aux Alouettes - have been recognized previously as areas of importance for belugas in the Estuary (Pippard and Malcolm 1978; Michaud 1993). The slightly lower percentage of herds travelling below the threshold speed or lower mean speed of herds in these cells may not necessarily suggest that the habitat is of lower quality. A given sector might have various functions over time and may be used as an AHR only during relatively short periods over various temporal scales (e.g., dial, seasonal, annual). A more restricted usage of a sector might then translate into a lower probability of detecting herds involved in behaviours leading to AHR, and

thereof, in a lower percentage of herds with travelling speeds below the threshold. Further investigations qualifying environmental factors and their variation over time are needed in order to better understand the usage and relative quality of the various AHR.

Many cells with large sample sizes were not identified as being part of an AHR due to a majority of herds having net displacement speeds above the selected threshold. These results suggested that beluga consistently moved more directionally in those cells. This was the case for example, in the sectors located in the Saguenay River, north-west of Île Verte and south-east of Île-aux-Lièvres (Fig. 8). Pippard (1985b) identified different travelling corridors for belugas, especially within the Saguenay River. Some of the cells characterized by high numbers of tracks and high net herd displacement speeds probably served this purpose. However, the focus of the present study being the delimitation of high residency areas, the definition of travelling corridors will be explored more fully in a subsequent study.

Conversely, some cells adjacent to cells where many herds were followed were characterized by a small sample size or absence of herd follows. This was the case for an area in the middle of the Estuary between Trois-Pistoles and Grandes-Bergeronnes, for an area north of Île Rouge, for two areas located approximately 10 km west of Île Verte, one extending from the west side of Île-aux-Lièvres to St-Siméon and one located between the south-west tip of Îles-aux-Fraises and Kamouraska (Fig. 3). The proximity of these areas with highly sampled areas indicates that, over the years, the research vessel spent considerable time in the vicinity of these areas that were within visual range of onboard observers, but that no beluga herds were detected there. These results may indicate that

these areas were systematically avoided by belugas. However, information on search effort is lacking in most years, preventing the analysis of beluga sightings in relation to effort.

Two earlier studies have defined areas of *relative importance* for St Lawrence beluga during summer. One study proposed *"concentration areas"* (Pippard and Malcolm 1978) for the population based on two years of field observations and interviews with scientific experts, fishermen and local residents (Pippard and Malcolm 1978). These areas were located in a sector comprised between the west tip of Île-aux-Lièvres and Les Escoumins (Fig. A1.2) and were *"...used regularly by white whales for one or more purposes of social congregating, feeding, calving, resting and travelling..."*. The distribution of these habitats coincided with some of the AHR identified in the present study, specifically those located at the mouth and in the Saguenay River and around Île-aux-Lièvres. However, results from the latter study should be interpreted with caution considering the limited duration, spatial extent and amount of quantitative data on which these analyses were based.

A second study used systematic vessel and aerial transects conducted between 1986 and 1992, and resulted in the identification of 18 areas of *"intensive use"* by St Lawrence beluga (Michaud 1993; Fig. A1.1). Intensity of use was defined using number of belugas and frequency of occurrence in a given area during repeated surveys. The Michaud study used an Eulerian approach, i.e., with points in space being defined by individual densities and frequency of occurrences, whereas the present study used a Lagrangian approach based on the analysis of movement patterns (Turchin 1998). In the former study, conclusions were based on repeated snapshots of distribution patterns, where repeated sightings of large

numbers of beluga were interpreted as an index of high usage. This approach inherently assumed that herds were more likely to be detected in sectors where they spent more time. This rationale is defendable given that individuals tend to accumulate in areas where their motility is low (Turchin 1998). In the current study, conclusions were based on repeated longitudinal tracking of herd movements, where a slow net displacement speed of a majority of herds was interpreted as an index of high residency. Although this approach provided direct information on the time spent in each sector when these sectors were used, it provided only a rough estimate of the frequency of use of each sector. These two approaches thus provided different information on habitat use and population distribution. The two studies also covered a different period, the present study covering more than twice as many years as the Michaud study. However, the latter study covered the entire summer distribution of the population, whereas this study covered more thoroughly only its central portion.

These differences in methodology and study area might explain some of the differences in habitat use observed between the two studies. For example, five of the six western-most areas of intensive use identified by Michaud (1993) were located outside of the area covered by the present study, and only the area near the Kamouraska islands coincided with one of the AHR. However, we cannot rule out the possibility of these differences being related to changes in habitat use and/or ecosystem structure over the last few decades in the Estuary. Although no detailed information on ecosystem changes of the Estuary is available at present, the major changes that occurred over the last few decades in the nearby ecosystem of the Gulf of St Lawrence following the collapse of the groundfish

stocks (Savenkoff *et al.* 2004; Savenkoff et *al.* 2007a, b) could also have influenced the food web structure in the Estuary.

Despite these differences, many areas of intensive use identified by Michaud overlapped with AHR identified in the present study (Figures 9 and A1.1). A particularly good correspondence between the two studies was found in the area of Baie Ste-Marguerite, at the mouth of the Saguenay River, at the head of the Laurentian channel, around Île-aux-Lièvres, off Saint-George-de-Cacouna and Rivière-du-Loup and in the sector of Kamouraska. These areas might be relatively stable in their characteristics over time, and may result in belugas visiting them on a regular basis with movement patterns leading to high residency. Many of these areas also overlapped with individual ARS, providing further evidences of their special significance for belugas (Fig. 10).

The specific biological functions associated with the AHR identified in this study could not be established with the present analysis. Various studies have proposed possible functions for areas overlapping with the AHR identified here, but these were based largely on circumstantial evidences or anecdotal observations. Areas such as those located north of Île-aux-Fraises, west and south of Île-aux-Lièvres, east of Île Blanche, north of Rivière-du-Loup and Gros-Cacouna, east of Île Rouge, north of Île-aux-Basques, at the mouth of the Saguenay River and head of the Laurential Channel, in Baie Ste-Catherine and Baie Ste-Marguerite were all proposed as potential feeding areas (Fig. A1.3; Michaud 1990 *et al.*; Lesage and Kingsley 1995). On similar bases, the south of Île-aux-Lièvres, north of Rivière-du-Loup and Gros-Cacouna, the Baie Ste-Catherine and Baie Ste-Marguerite have been proposed as potential calving areas (Fig. A1.4; Michaud *et al.* 1990). However, a

thorough understanding of functions associated with these habitats and their relative importance for the beluga population remains a challenge. Future studies to quantitatively estimate the importance of the different AHR for critical functions could be achieved through the study of individual diving behaviour in relation to individual and herd surface behaviours, and activity budgets within the different areas of high residency.

The technique developed in the present study to examine fine-scale herd movement patterns allowed the quantitative analysis of non-systematic opportunistic herd follow data. In the literature, the rare accounts of residency patterns usually refer to the amount of time an individual, a group or a species were continuously observed within a specific area (e.g., Jacquet *et al.* 2003; Martin and da Silva 2004; Lusseau 2005; Parra *et al.* 2005; Bearzi *et al.* 2008). In the present study, the approach was based on herd tracking rather than site tracking, which constitute a more powerful means of studying habitat preferences. Data of this nature (i.e., opportunistic herd tracking data) exist for several marine mammal species and could be explored using methods similar to those presented here.

Interdepartmental Research Fund of Environment Canada, the Saguenay-St. Lawrence

Marine Park, la Fondation de la Faune du Québec, and Parks Foundation.

References

Austin, D., Bowen, W.D. & McMillan, J.I. (2004) Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos*, **105**, 15-30.

Austin, D., Bowen, W.D., McMillan, J.I. & Iverson, S.J. (2006) Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology*, **87**(12), 3095-3108.

Bailey, H. & Thompson, P. (2006) Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *Journal of Animal Ecology*, **75**, 456-465.

Baird, R.W., Hanson, M.B. & Dill, L.M. (2005) Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. *Canadian Journal of Zoology*, **83** (2), 257-267.

Baird, R.W., Webster, D.L., McSweeney, D.J., Ligon, A.D., Schorr, G.S. & Barlow, J. (2006) Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawaii. *Canadian Journal of Zoology*, **84** (8), 1120-1128.

Banks, J.E. & Yasenak, C.L. (2003) Effects of plot vegetation diversity and spatial scale on *Coccinelle septempuntata* movement in the absence of prey. *Entomologia Experimentalis et Applicata*, **108**, 197-204.

Barber, D.G., Saczuki, E. & Richard, P.R. (2001) Examination of beluga-habitat relationships through the use of telemetry and a geographic information system. *Arctic*, **54**(3), 305-316.

Batchelet, E. (1981) *Circular statistics in biology*. Academic Press, New York.

Bearzi, G., Agazzi, S., Bonizzoni, S., Costa, M. & Azzellino, A. (2008) Dolphins in a bottle: abundance, residency patterns and conservation of bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **18**, 130-146.

Beck, C.A., Bowen, W.D., McMillan, J.L. & Iverson, S.J. (2003) Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Animal Behaviour*, **66**, 777-789.

Benhamou, S. (1992) Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology*, **159**, 67-81.

Bergman, M.C., James, A..S. & Luttich, S.N. (2000) Caribou movement as a correlated random walk. *Oecologia*, **123**, 364-374.

Beyer, H. L. (2004) Hawth's analysis tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Boily, P. (1995) Theoretical heat-flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *Journal of Theoretical Biology*, **172** (3), 235-244.

Bradshaw, C.J.A., Hindell, M.A., Michael, K.J. & Sumner M.D. (2002) The optimal spatial scale for the analysis of elephant seal foraging as determined by geo-location in relation to sea surface temperatures. *ICES Journal of Marine Science*, **59**, 770-781.

Brodie, P.F. (1971) A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. *Journal of Fisheries Research*, **28**, 1309-1318.

Campagna, C., Piola, A.R., Marin, M.R., Lewis, M. & Fernández, T. (2006) Southern elephant seal trajectories, fronts and eddies in the Brazil/Malvinas Confluence. *Deep-Sea Research I*, **53**, 1907-1924.

Chadenet, V. (1997) *Fréquentation et bilan d'activité du béluga* (Delphinapterus leucas) *du Saint-Laurent dans la Baie Sainte-Marguerite.* MSc thesis, Université Laval, Quebec.

COSEWIC (2004) Assessment and update status report on the beluga whales *Delphinapterus leucas* in Canada. Ottawa, 70 p.

Doniol-Valcroze, T., Berteaux, D., Larouche, P. & Sears, R. (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Series*, **335**, 207-216.

Fauchald, P. (1999) Foraging in a hierarchical patch system. *American Naturalist*, **153**, 603-613.

Fauchald, P. & Tveraa, T. (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, **84**(2), 282-288.

Fauchald, P. & Tveraa, T. (2006) Hierarchical patch dynamics and animal movement pattern. *Oecologia*, **149**, 383-395.

Finley, K. J. (1982) The estuarine habit of the beluga or white whale *Delphinapterus leucas*. *Cetus*, **4,** 4-5.

Finley, K. J., Miller, M. A., Allard, M., Dans, R. A. & Evans, C. R. (1982) The belugas (*Delphinapterus leucas*) of northern Quebec: distribution, abundance, stock identity, catch

history and management. *Canadian Technical Report of Fisheries and Aquatic Sciences*, **1123** (v), 57p.

Flores, P.A.C. & Bazzalo, M. (2004) Home ranges and movement patterns of the marine Tucuxi dolphin, *Sotalia Fluviatilis*, in Baía Norte, Southern Brazil. *Latin American Journal of Aquatic Mammals*, **3**(1), 37-52.

Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L. & Morales, J.M. (2005) Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, **20**, 273-287.

Freitas, C., Kovacs, K.M., Ims, R.A., Fedak, M.A. & Lydersen, C. (2008) Ringed seal post-moulting movement tactics and habitat selection. *Oecologia,* **155**, 193-204.

Hastie, G.D., Wilson, B. & Thompson, P.M. (2003) Fine-scale habitat selection by coastal bottlenose dolphins: application of new land-based video-montage technique. *Canadian Journal of Zoology*, **81**, 469-478.

Hindell, M.A., Slip D.J. & Burton, H.R. (1991) The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia, Phocidae). *Australian Journal of Zoology*, **39** (5), 595-619.

Hindell, M.A., Harcourt, R., Waas, J.R. & Thompson, D. (2002) Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii. Marine Ecology Progress Series,* **242**, 275-284.

Hooker, S.K. & Baird, R.W. (1999) Deep-diving behaviour of northern bottlenose whales, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proceedings of the Royal Society, London* B., **266**, 671-676.

Ingram, R.G. & El-Sabh, M.I. (1990) Fronts and meso-scale features in the St. Lawrence Estuary. *Oceanography of a large-scale estuarine system : the St. Lawrence* (eds. El-Sabh, M.I., & Silverberg, N.), pp. 71-93. Springer-Verlag, Berlin. *Coastal and estuarine studies,* **39**.

Jacquet, N., Gendron, D. & Coakes, A. (2003) Sperm whales in the gulf of California: residency, movements, behaviour, and the possible influence of variation in food supply. *Marine Mammal Science,* **19**(3), 545-562.

Johnson, A. R., Wiens, J. A., Milne, B. T. & Crist, T. O. (1992) Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology,* **7**, 63–75.

Johnson, D.H., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002) Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, **71**, 225-235.

Johnson, M. P. & Tyack, P. L. (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, **28**(1), 3-12.

Jonsen. I.D., Myers, R.A. & James, M.C. (2006) Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *Journal of Animal Ecology*, **75**, 1046-1057.

Jonsen, I.D., Random, A.M. & James, M.C. (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series*, **337**, 255-264.

Karieva, P.M. & Shigesada, N. (1983) Analysing insect movement as a correlated random walk. *Oecologia*, **56**, 234-238.

Karieva, P. & Odell, G. (1987) Swarms of predators exhibit "prey-taxis" if individual predators use areas-restricted search. *American Naturalist*, **130**, 233-270.

Klaassen, R.H.G., Nolet, B.A., Gils, J.A. & Bauer, S. (2006) Optimal movement between patches under incomplete information about the spatial distribution of food items. *Theoretical Population Biology*, **70**, 452-463.

Kleinenberg, S.E., Yablokov, A.V., Bel'kovich, B.M. & Tarasevich, M.N. (1964) Beluga (*Delphinapterus leucas*): investigation of the species. Akad. Nauk SSSR, Moscow. Translated from Russian. Israel Program for Science Translation, Jerusalem, 1969, 376 p.

Laidre, K. L., Heide-Jørgensen M. P. & Dietz, R. (2002) Diving behavior of narwhals (*Monodon monoceros*) at two coastal localities in the Canadian High Arctic. *Canadian Journal of Zoology*, **80**, 624-635.

Laidre, K.L., Heide-Jørgensen, M.P., Logdson, M.L., Hobbs, R.C., Dietz, R. & VanBlaricom, G.R. (2004a) Fractal analysis of narwhal space use patterns. *Zoology*, **107**, 3-11.

Laidre, K.L., Heide-Jørgensen, M.P., Logdson, M.L., Hobbs, R.C., Heagerty, P., Dietz, R., Jørgensen, O.A. & Treble, M.A. (2004b) Seasonal narwhal habitat associations in the High Arctic. *Marine Biology*, **145**, 821-831.

LeBoeuf, B.J., Naito, Y., Asaga, T., Crocker, D. & Costa, D.P. (1992) Swim speed in female northern elephant seal: metabolic and foraging implications. *Canadian Journal of Zoology*, **70** (4), 786-795.

Lesage, V., Hammill, M.O., & Kovacs, K.M. (2001) Marine mammals and the community structure of the Estuary and Gulf of St. Lawrence, Canada: evidence from stable isotope analysis. *Marine Ecology Progress Series*, **210**, 203-221.

Lesage, V. & Kingsley, M.C.S. (1995) Bilan des connaissances de la population de bélugas (*Delphinapterus leucas*) du Saint-Laurent. *Rapport technique canadien des sciences halieutique et aquatique*, **2041**, 51 p.

Lusseau, D. (2005) Residency pattern of bottlenose dolphins *Tursiops spp.* in Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series*, **295**, 265-272.

Marchand, C. Simard, Y. & Gratton, Y. (1999) Concentration of capelin (*Mallotus villosus*) in tidal upwelling fronts at the head of the Laurentian Channel in the St. Lawrence estuary. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1832-1848.

Martin, A.R. & da Silva, V.M.F. (2004) Number, seasonal movements, and residency characteristics of river dolphins in an Amazonian floodplain lake system. *Canadian Journal of Zoology*, **82**, 1307-1315.

Martin, A.R. & Smith, T.G. (1992) Deep diving in wild, free ranging beluga whales, *Delphinapterus leucas. Canadian Journal of Fisheries and Aquatic Science*, **49**, 462-466.

Michaud, R., Vézina, A., Rondeau, N. & Vigneault, Y. (1990) Annual distribution and preliminary characterization of beluga (*Delphinapterus leucas*) habitats in the St. Lawrence. *Canadian technical report of fisheries and aquatic sciences*, **1757**, 37p.

Michaud, R. (1992) Fréquentation de la Baie Sainte-Marguerite par le beluga du Saint-Laurent (*Delphinapterus leucas*). *Prepared for the Department of Fisheries and Oceans*, 34p.

Michaud, R. (1993) Distribution estivale du béluga du Saint-Laurent; synthèse 1986 à 1992. *Rapport Technique Canadien des Sciences Halieutiques et Aquatiques*, **1906**, 28p.

Michaud, R. & Giard, J. (1997) Les rorquals communs et les activités d'observations en mer dans l'estuaire du St-Laurent entre 1994 et 1996. 1. Étude de l'utilisation du territoire et évaluation à l'aide de la télémétrie VHF. *Final report presented to Park Canada*, GREMM, Quebec, 45p.

Morales, J.M. & Ellner, S.P. (2002) Scaling up animal movements in heterogeneous landscapes: the importance of behaviour. *Ecology*, **83** (3), 2240-2247.

Morin, P., Berteaux, D. & Klvana, I. (2005) Hierarchical habitat selection by North American porcupines in southern boreal forest. *Canadian Journal of Zoology*, **83** (10), 1333-1342.

Nams, V.O. & Bourgeois, M. (2004) Fractal analysis measures habitat use at different spatial scales: an example with American marten. *Canadian Journal of Zoology*, **82**, 1738-1747.

Nams, V.O. (2005) Using animal movement paths to measure response to spatial scale. *Oecologia*, **143**, 179-188.

Nams, V.O., Mowat, G. & Panian, M.A. (2006) Determining the spatial scale for conservation purposes – an example with grizzly bears. *Biological Conservation*, **128**, 109-119.

Nozères, C. (2006) *Régime alimentaire du beluga,* Delphinapterus leucas, *de l'estuaire du St-Laurent, Canada, tel que révélé par l'analyse des acides gras du lard.* MSc thesis, Université Laval, Quebec.

Parra, G.J., Corkeron, P.J. & Marsh, H. (2006) Population sizes, site fidelity and residence patterns of australian snubfin and Indo-Pacific humpback dolphins: Implications for conservation. *Biological Conservation*, **129** (2), 167-180.

Pinaud, D. (2008) Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems. *Journal of Applied Ecology*, **45**, 91-99.

Pinaud, D. & Weimerskirch, H. (2005) Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology*, **74**, 852-863.

Pinaud, D. & Weimerskirch, H. (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *Journal of Animal Ecology*, **76**, 9-19.

Pippard, L. (1985a) Status of the St. Lawrence River population of beluga, *Delphinapterus leucas*. *The Canadian Field-Naturalist*, **99**, 438-450.

Pippard, L. (1985b) Patterns of Movement of The St. Lawrence White Whales (*Delphinapterus leucas*). *Canadian Wildlife Service and Parks Canada*, Technical Report, 500p.

Pippard, L. & Malcolm, H. (1978) White whales (*Delphinapterus leucas*). Observations on their distribution, population and critical habitats in the St. Lawrence and Saguenay rivers. Unpublished report prepared for Department of Indian And Northern Affairs, Parks Canada, Ottawa, 161 p.

Pyke, G.H. (1978) Optimal foraging: movement patterns of bumblebees between inflorescences. *Theoretical Population Biology*, **13**, 72-98.

Ream, R.R., Jeremy, T.S. & Loughlin, T.R. (2005) Oceanographic features related to northern fur seal migratory movements. *Deep-Sea Research II*, **52**, 823-843.

Reeves, R.R. & Mitchell, E. (1989) Status of white whales, *Delphinapterus leucas*, in Ungava Bay and eastern Hudson Bay. *Canadian Field Naturalist*, **103**, 220-239.

Sargeant, B.L, Wirsing, A.J., Heithaus, M.R. & Mann, J. (2007) Can environmental heterogeneity explain individual foraging variation in the wild bottlenose dolphins (*Tursiops sp.*)? *Behavioral Ecology and Sociobiology*, **61** (5), 679-688.

SAS manual. SAS Institute Inc., SAS Circle, Box 8000, Cary, NC 27512-8000.

Savenkoff, C., Castonguay, M., Vézina, A.F., Despatie, S.-P., Chabot, D., Morissette, L. & Hammill, M.O. (2004) Inverse modelling of trophic flows through an entire ecosystem: the

northern Gulf of St. Lawrence in the mid-1980s. *Canadian Journal of Fisheries and Aquatic Science*, **61**, 2194-2214.

Savenkoff, C., Swain, C. D.P., Hanson, J.M., Castonguay, M., Hammill, M.O., Bourdages, H., Morissette L. & Chabot D. (2007a) Effects of fishing and predation in a heavily exploited ecosystem: Comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). *Ecological Modelling*, **204**, 115-128.

Savenkoff, C., Castonguay, M., Chabot, D., Hammill, M.O., Bourdages, H. & Morissette L. (2007b) Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? *Estuarine, Coastal and Shelf Science*, **73**, 711-724.

Sergeant, D.E. (1973) Biology of white whales (*Delphinapterus leucas*) in Western Hudson Bay. *Journal of Fisheries Research Board of Canada*, **30**, 1065-1090.

Simard,Y. & Lavoie, D. (1999) The rich krill aggregation of the Saguenay—St. Lawrence Marine Park: hydroacoustic and geostatistical biomass estimates, structure, variability and significance for whales. *Canadian Journal of Fisheries and Aquatic Science*, **56**, 1182–1197.

Simard, Y., Lavoie, D. & Saucier, F.J. (2002) Channel head dynamics: capelin (*Mallotus villosus*) aggregation in the tidally driven upwelling system of the Saguenay-St. Lawrence Marine Park's whale feeding ground. *Canadian Journal of Fisheries and Aquatic Science*, **59**, 197-210.

Skov, H., Gunnlaugsson, T., Budgell, W.P., Horne, J., Nøttestad, L., Olsen, E., Søiland, H., Vikingsson, G. & Waring, G. (2008) Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. *Deep-Sea Research II*, **55**, 254-268.

Sourisseau, M., Simard, Y. & Saucier, F.J. (2006) Krill aggregation in the St. Lawrence system, and supply of krill to the whale feeding grounds in the estuary from the gulf. *Marine Ecology Progress Series*, **314**, 257-270.

St. Aubin, D.J. & Geraci, J.R. (1988) Capture and handling stress suppresses circulating levels of thyroxine (T4) and triiodothyronine (T3) in beluga whales *Delphinapterus leucas*. *Physiological Zoolology*, **61**, 170-175.

St. Aubin, D.J., Smith, T.G. & Geraci, J.R. (1990) Seasonal epidermal molt in beluga whales, *Delphinpaterus leucas*. *Canadian Journal of Zoology*, **68**, 359-367.

Suryan, R.M., Sato, F., Balogh, G.R., Hyrenbach, K.D., Sievert, P.R. & Ozaki, K. (2006) Foraging destinations and marine habitat use of short-tailed albatrosses: A multi-scale approach using first-passage time analysis. *Deep-Sea Research II*, **53**, 370-386.

Tomolin, A.G. (1967) Mammals of the U.S.S.R. and adjacent countries. Vol. 9, Cetacea. Translated by Israel Program for Scientific Translations, Jerusalem.

Trujillo, A.P. (2008) *Essential of oceanography*. Pearson Prentice Hall, New Jersey.

Turchin, P. (1991) Translating foraging movement in heterogeneous environments into spatial distribution of foragers. *Ecology*, **72**, 65-83.

Turchin, P. (1998) *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants.* Sinauer Associates, Sunderland.

Vladykov, V.D. (1944) Étude sur les mammifères aquatiques. III. Chasse, biologie, et valeur économique du marsouin blanc ou béluga (*Delphinapterus leucas*) du fleuve et du golfe Saint-Laurent. *Département des pêcheries*, Québec, 194 p.

Vladykov, V.D. (1946) Études sur les mammifères aquatiques. IV. Nourriture du marsouin blanc (*Delphinapterus leucas*) du fleuve Saint-Laurent. *Département des pêcheries*, Québec, 129p.

Watts, P.D. & Draper, B.A. (1986) Note on the behaviour of beluga whales feeding on capelin. *Arctic and Alpine Research*, **18** (4), 439.

Weimerskirch, H., Pinaud, D., Pawlowski, F. & Bost, C.-A. (2007) Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the Wandering albatross. *The American Naturalist*, **170** (5), 734-743.

Whitehead, H. & Rendell, L. (2004) Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *Journal of Animal Ecology*, **73**, 190-196.

Zollner P.A. & Lima S.L. (1999) Search strategies for landscape-level interpatch movements. *Ecology*, **80** (3), 1019-1030.

Tables and figures

Fig. 1 The St Lawrence Estuary and Saguenay River in Québec, Canada, including the summer distribution area of the beluga population (crosshatched).

Fig. 2 Example of a herd displacement pattern divided into 30 min segments (grey scale) with their associated buffers. Buffer size corresponds to the herd radius.

Fig. 3 Number of herd visual follows per cell a) at the finer scale (1000 m * 1000 m) and b) at the coarser scale (3000 m * 3000 m).

Fig. 4 Example of variance in first-passage time as a function of the radius r (left) with the associated segment and resulting ARS zones (right). (a) Example of FPT curve with one peak at 700 m (segment 14). (b) Example of FPT curve with two peaks, one at 500 m and one at 1700 m (segment 11).

Fig. 5 Number of Var-max values and their corresponding spatial scales.

Fig. 6 Piecewise regression analysis examples corresponding to the one break-point model (a and b) and to the two-break-point model (c and d). a) FPT values series in ascending order for segment 11 at the 500-m scale (dash line indicating the first break-point, c_i). b) FPT values series in temporal order with identified threshold and ARS zones for segment

11. c) FPT values series in ascending order for segment 9 at the 300 m scale. d) FPT values series in temporal order with identified threshold and ARS zone for segment 9.

Fig. 7 Distribution of Area-Restricted Search zones and associated displacements of radio-tracked belugas.

Fig. 8 Speed associated with lag of moving average as a function of percentage of the lag outside the ARS zone.

Fig. 9 Mean net displacement speed for cells visited by a least three herd evaluated at a) the *finer scale* (1000 m * 1000 m) and b) the *coarser scale* (3000 m * 3000 m). White cells indicate non-zero but less than three herd follows.

Fig. 10 Distribution of Areas of High Residency (AHR) at a) the finer scale (1000 m * 1000 m) and b) the coarser scale (3000 m * 3000 m).

Fig. 11. Regions of overlap (in dark) between areas of restricted search (ARS) and fine-scale Areas of high residency (AHR).

Fig. 12. Effect of changing the threshold speed selected to define AHR on the boundaries of these AHRs. Colour scale indicates the severity of the criterion.

Fig. 13. Effect of changing the percentage of herds (travelling below the threshold for speed) selected to define the AHR on the boundaries of these AHRs. Colour scale indicates the severity of the criterion.

Table 1. Summary of the 38 segments retained for the first-passage time analysis.

Segment	VHF Track	N of position	Deployment time (hh:mm:ss)	Displacement (km)	ARS scale (m)
1	DLT0103	49	6:12:06	30.23	-
2	DLT0104	28	2:34:12	22.55	1600
3	DLT0205	21	1:19:29	11.23	-
4	DLT0302	55	4:47:08	18.78	1200
5	DLT0302	20	2:59:13	6.31	-
6	DLT0303	62	7:48:40	60.69	-
7	DLT0305	18	2:01:14	12.66	-
8	DLT0308	73	8:14:20	48.42	1100
9	DLT0309	88	5:39:02	41.89	1 700
10	DLT0309	19	0:57:03	6.91	-
11	DLT0401	72	8:07:21	32.68	500 ; 1700
12	DLT0403	20	1:05:13	8.94	-
13	DLT0403	26	2:07:36	11.71	-
14	DLT0404	15	0:41:21	5.32	-
15	DLT0405	39	3:11:49	25.84	
16	DLT0405	29	4:06:55	9.53	300
17	DLT0407	94	8:25:00	49.89	-
18	DLT0410	29	3:36:43	10.44	-
19	DLT0411	21	3:06:20	7.01	-
20	DLT0411	25	1:55:02	13.46	-
21	DLT0412	60	3:59:10	12.63	600 ; 1600
22	DLT0412	36	3:45:31	13.79	-
23	DLT0413	31	2:53:50	13.69	-
24	DLT0415	25	2:24:40	11.98	-
25	DLT0501	21	3:22:27	18.96	300
26	DLT0502	67	7:04:50	44.05	-
27	DLT0502	34	4:12:03	11.15	500
28	DLT0503	99	9:36:47	51.03	-
29	DLT0504	53	5:30:50	30.41	-
30	DLT0505	20	3:08:00	8.60	-
31	DLT0505	15	1:32:28	8.56	-
32	DLT0508	21	2:47:38	12.51	700
33	DLT0509	52	6:42:35	37.01	700
34	DLT0510	110	9:07:32	51.19	1200
35	DLT0307	26	4:40:00	35.43	-
36	DLT0402	63	7:54:00	35.21	1400
37	DLT0406	29	2:54:43	14.75	400
38	DLT0507	78	8:34:45	44.14	1700

Table 2. Areas of restricted search (ARS) detected in each segment at the scale of maximum variance, and associated first passage time (FPT) in minutes.

Segment	VHF track	ARS Scale (m)	Spatial scale	FPT (min)
2	DLT0104	1600	Large	49.3
4	DLT0302	1200	Large	47.0
8	DLT0308	1100	Large	81.0
8	DLT0308	1100	Large	68.2
8	DLT0308	1100	Large	62.9
8	DLT0308	1100	Large	43.7
9	DLT0309	1200	Large	76.3
11	DLT0401	500	Small	78.9
11	DLT0401	500	Small	61.4
11	DLT0401	500	Small	29.9
11	DLT0401	500	Small	29.5
11	DLT0401	1700	Large	242.8
11	DLT0401	1700	Large	109.5
16	DLT0405	300	Small	66.7
22	DLT0412	600	Small	81.2
22	DLT0412	1600	Large	203.0
25	DLT0501	300	Small	37.6
25	DLT0501	300	Small	17.3
25	DLT0501	300	Small	14.2
27	DLT0502	500	Small	190.6
32	DLT0508	700	Small	53.8
32	DLT0508	700	Small	24.3
32	DLT0508	700	Small	24.3
33	DLT0509	700	Small	56.4
33	DLT0509	700	Small	38.0
33	DLT0509	700	Small	30.8
34	DLT0510	1200	Large	112.7
34	DLT0510	1200	Large	70.1
36	DLT0402	1400	Large	222.2
37	DLT0406	400	Small	59.4
37	DLT0406	400	Small	35.7
38	DLT0507	1700	Large	103.2
38	DLT0507	1700	Large	81.9
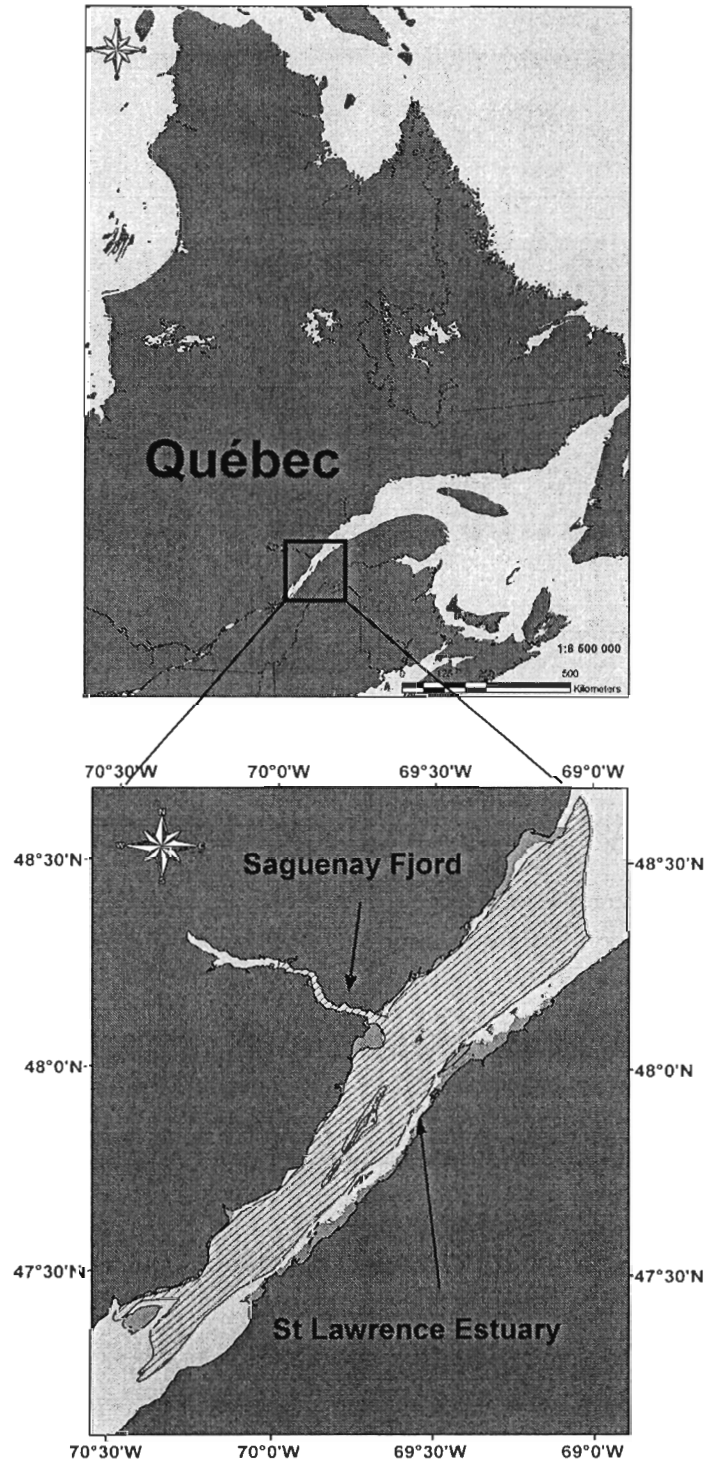
Lemieux Lefebvre *et al.* Fig. 1.
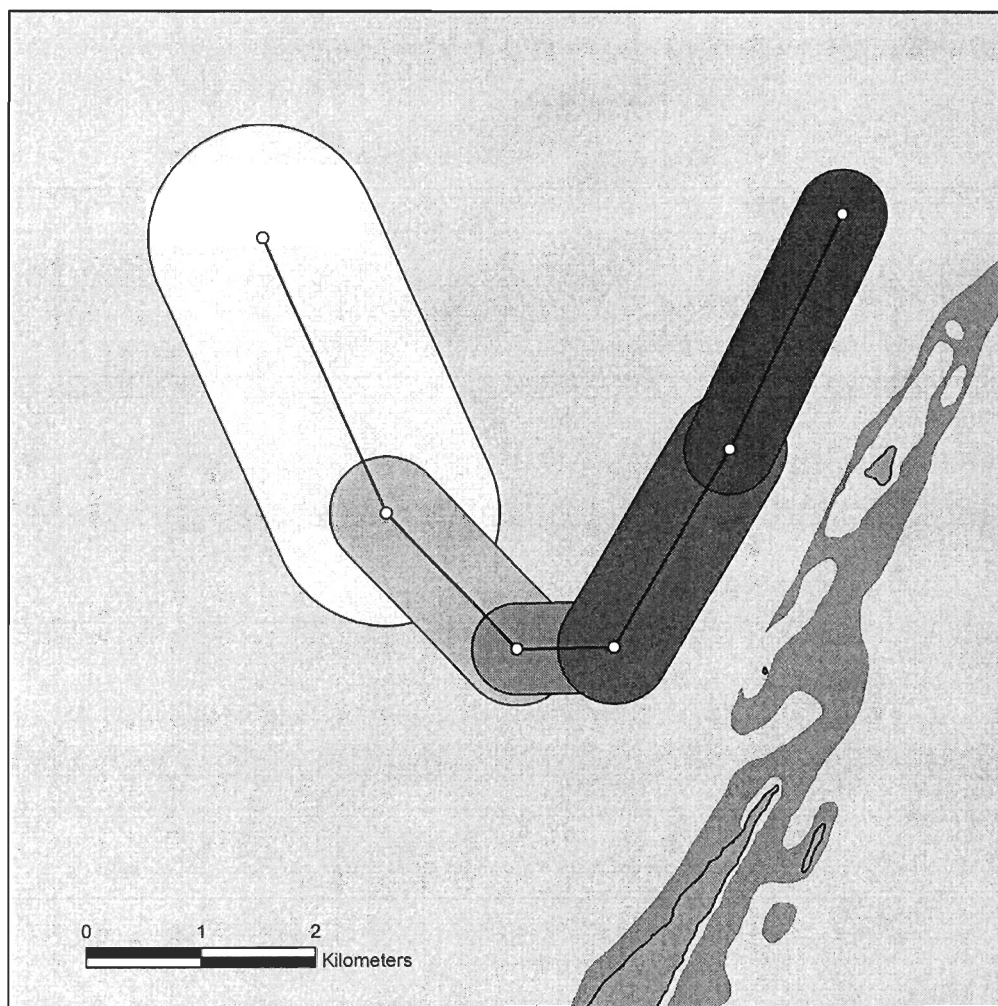
Lemieux Lefebvre *et al.* Fig. 2.
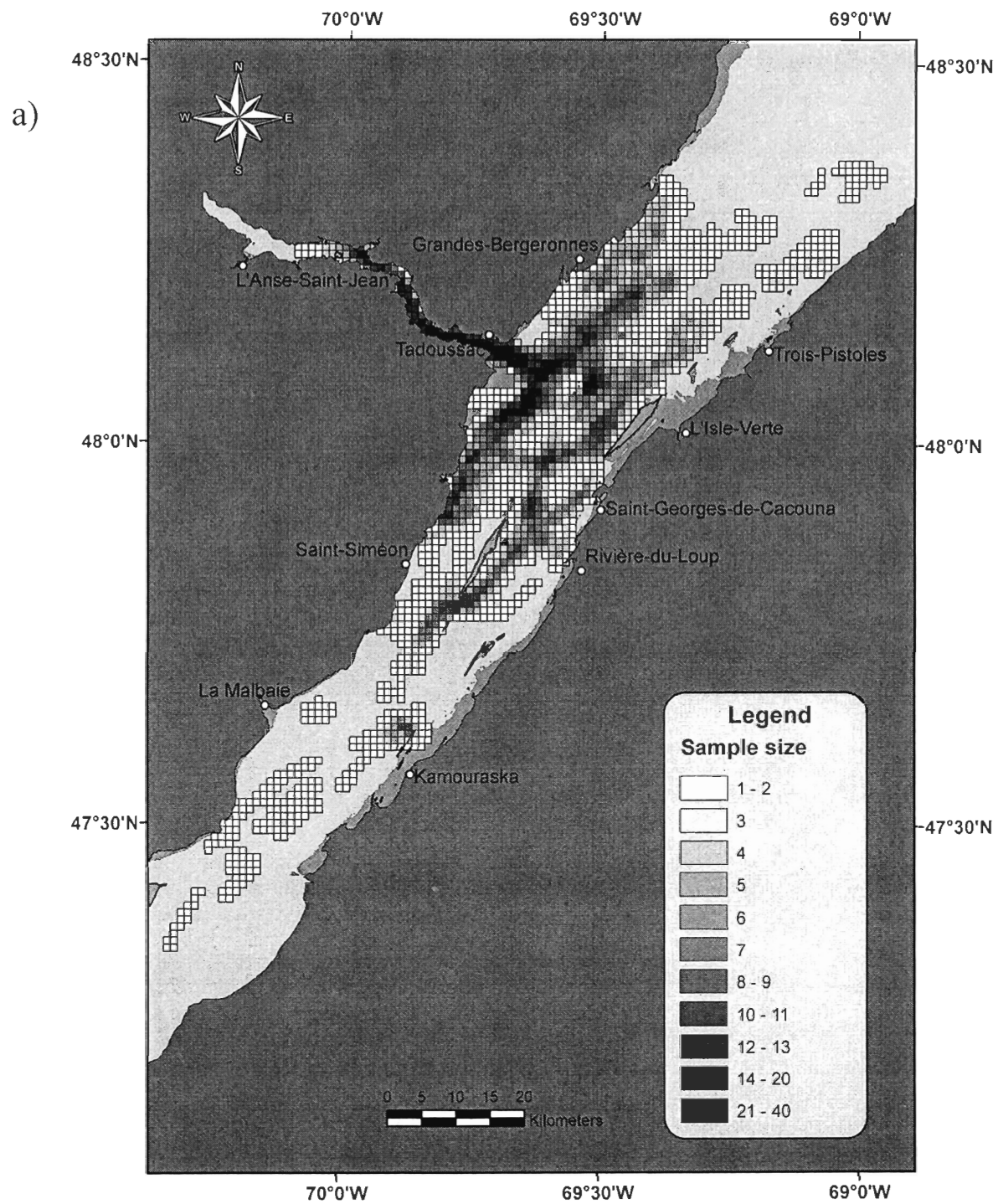
Lemieux Lefebvre. *et al.* Fig. 3. a.
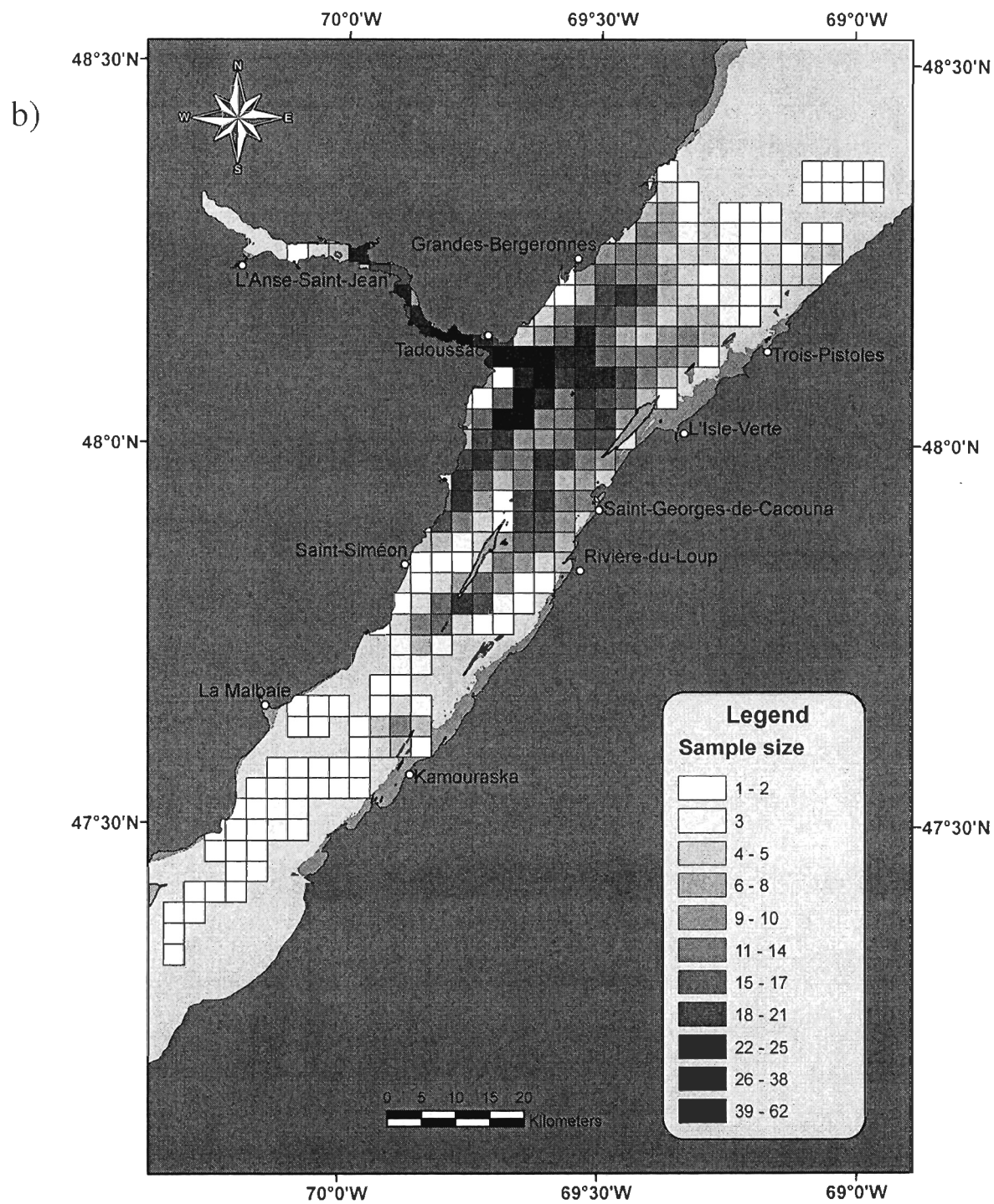
Lemieux Lefebvre. *et al.* Fig. 3. b.
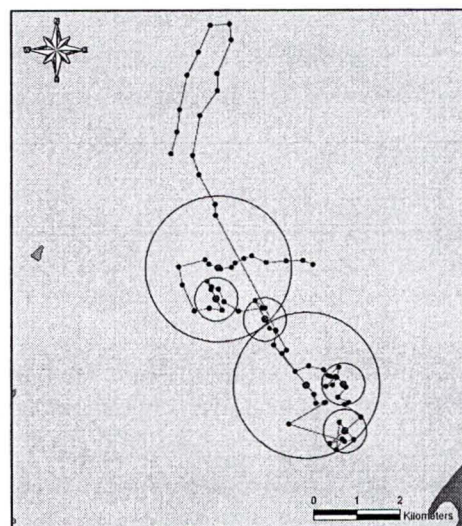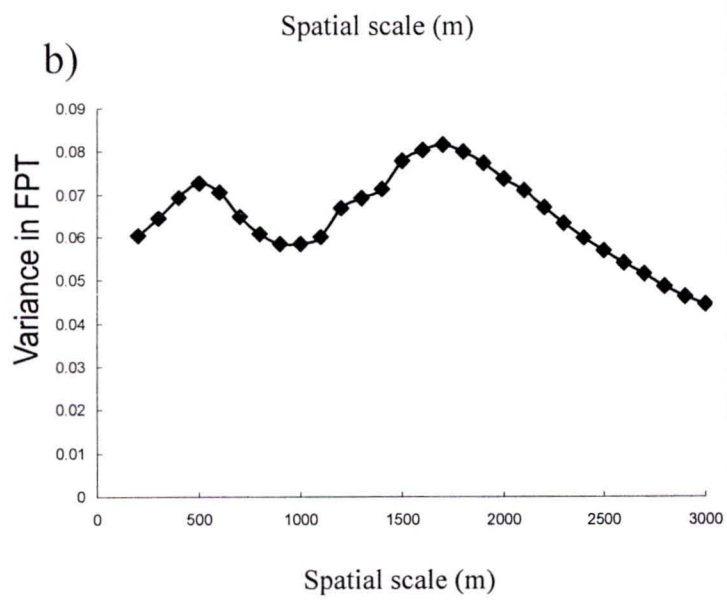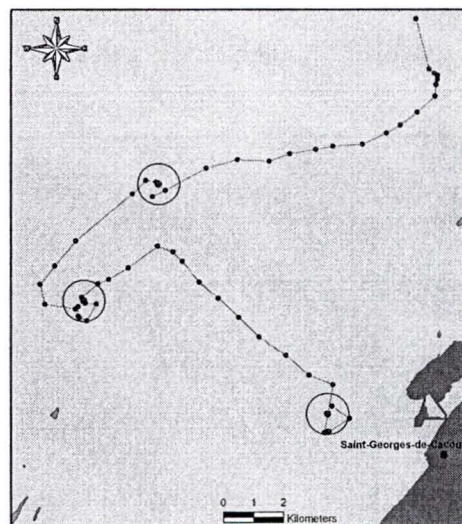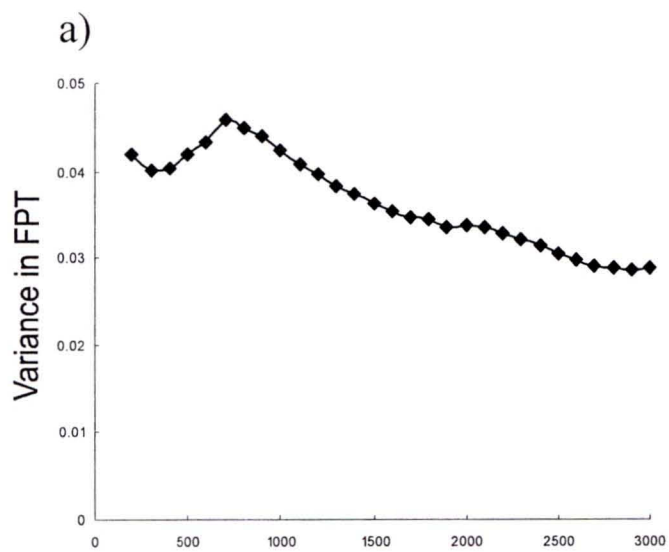
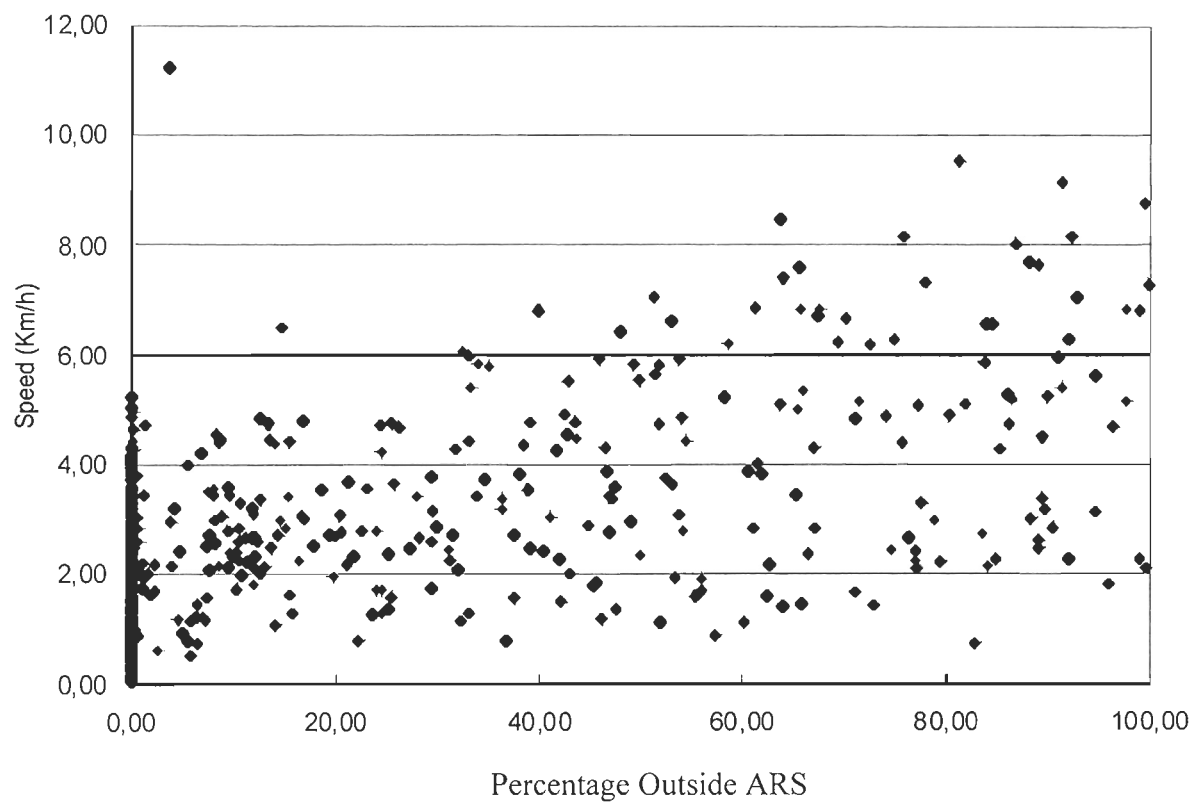Lemieux Lefebvre *et al.* Fig. 4. a, b.
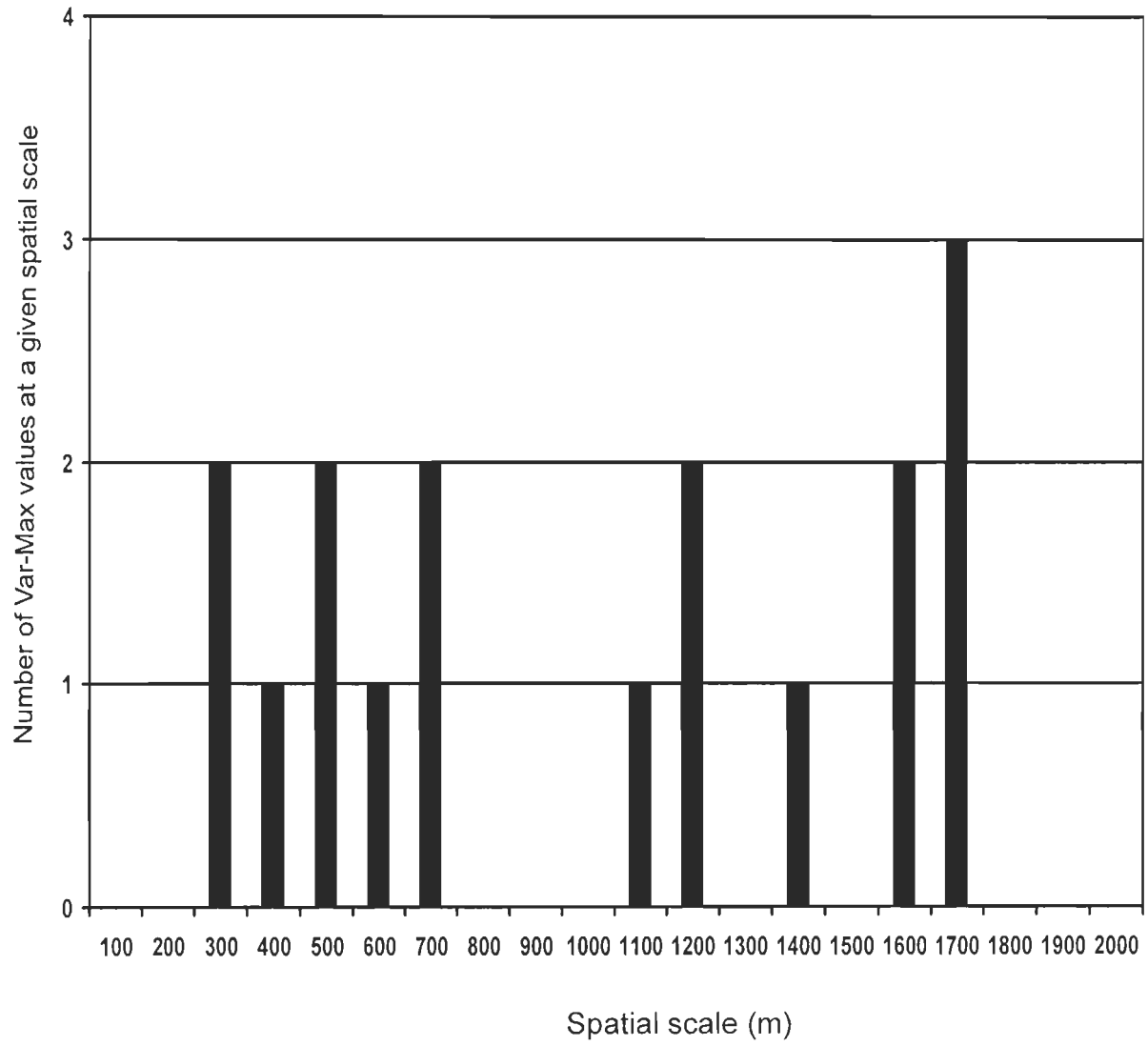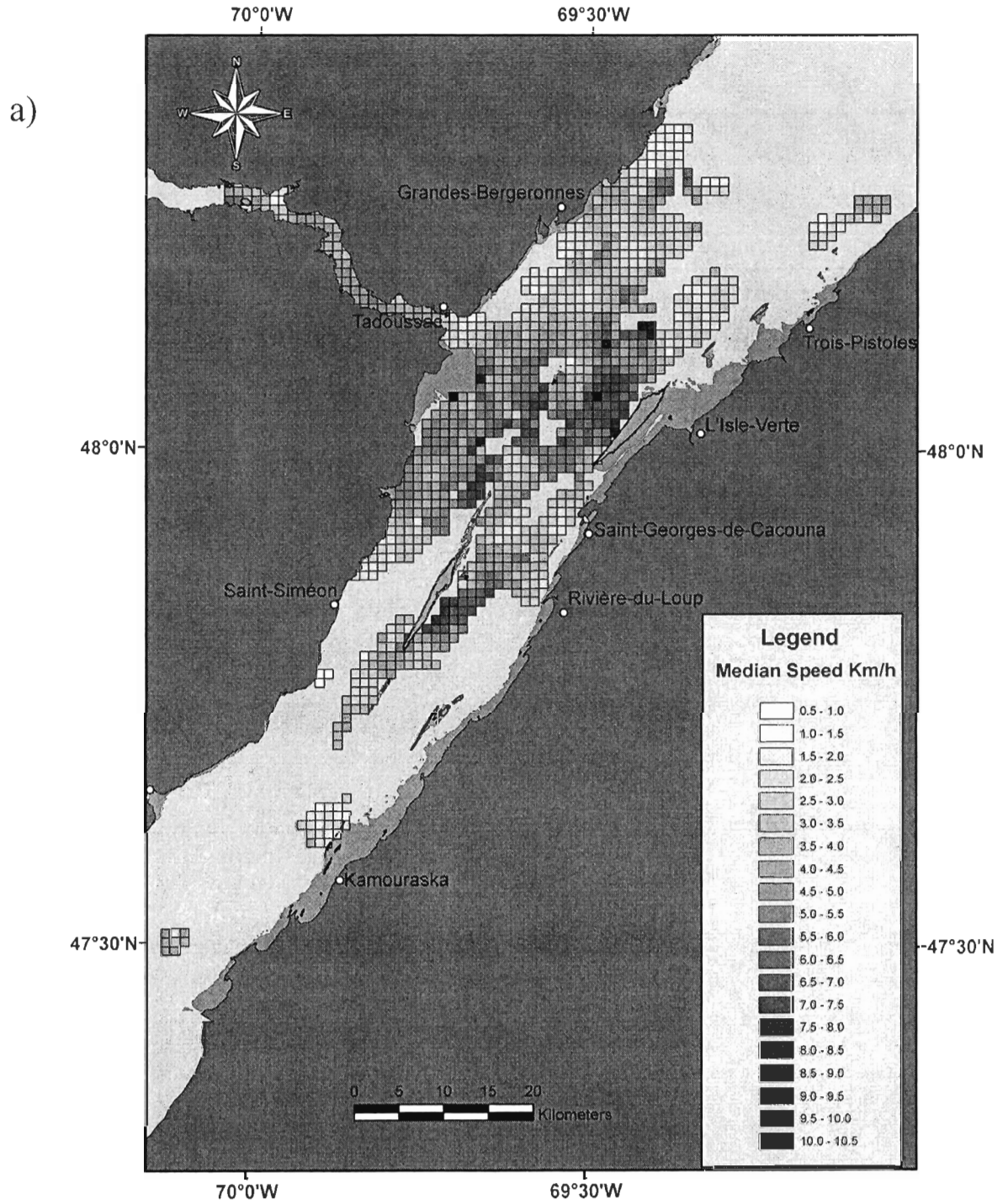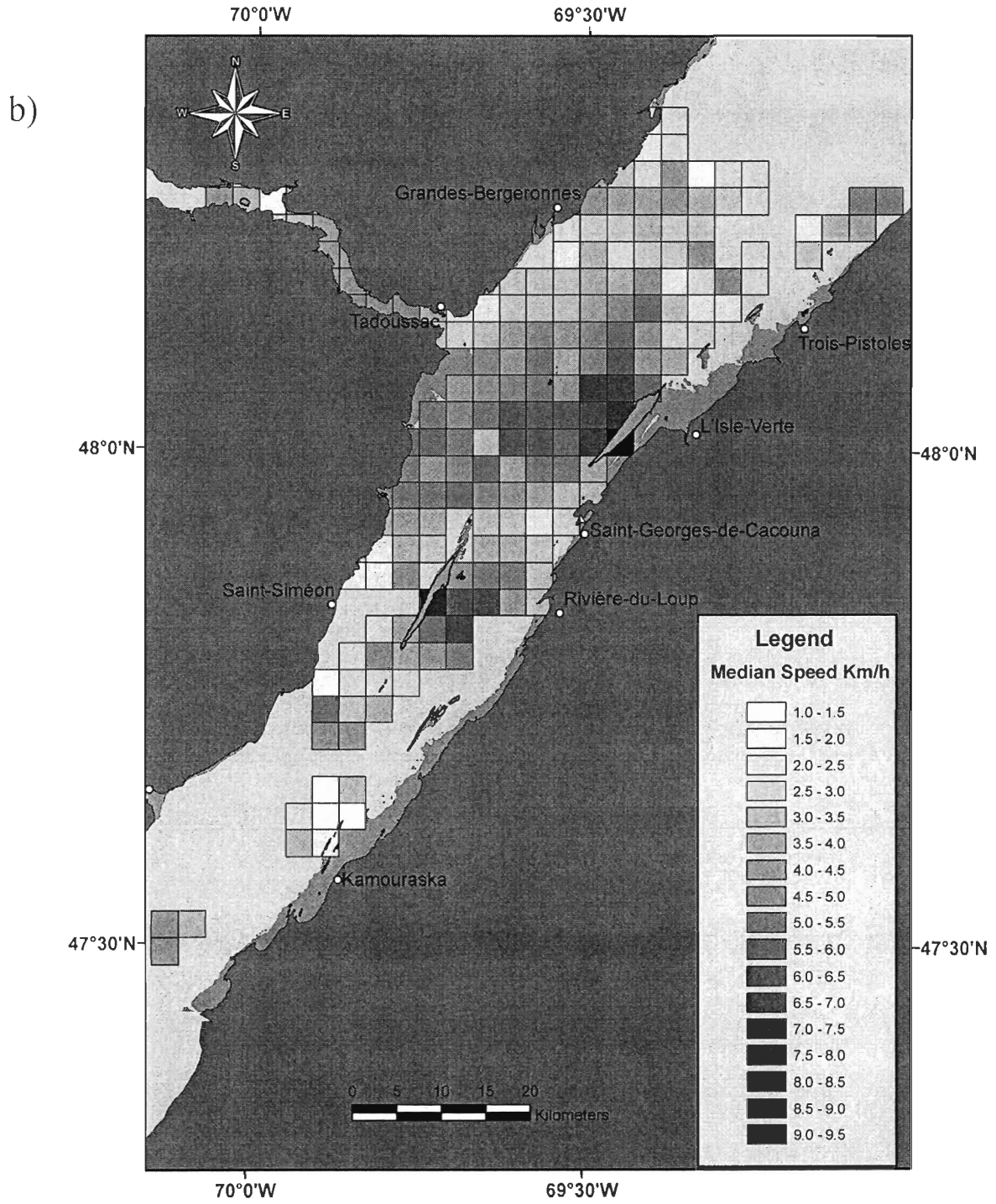
Lemieux Lefebvre *et al.* Fig. 5.
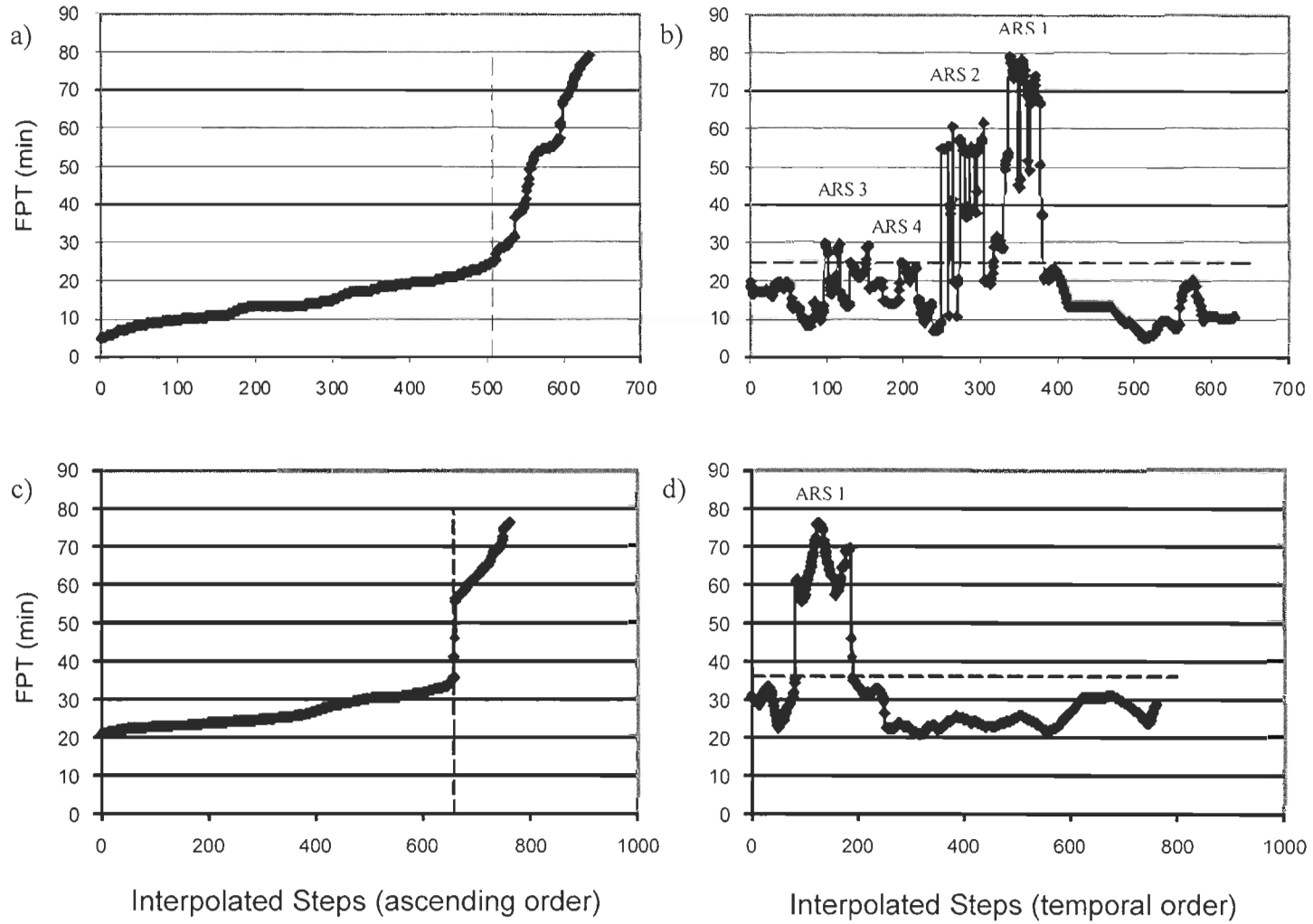
Lemieux Lefebvre *et al.* Fig. 6. a, b, c and d.
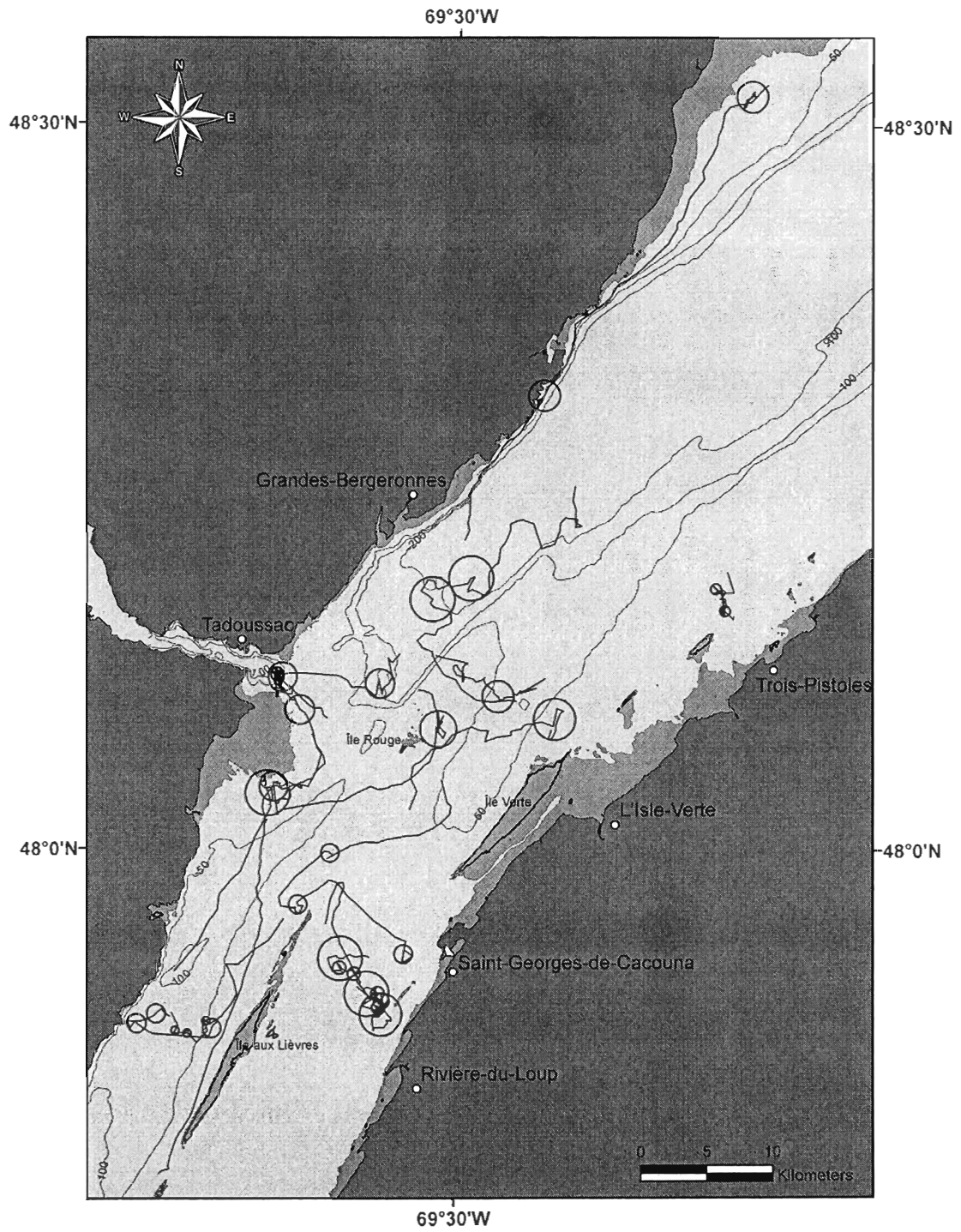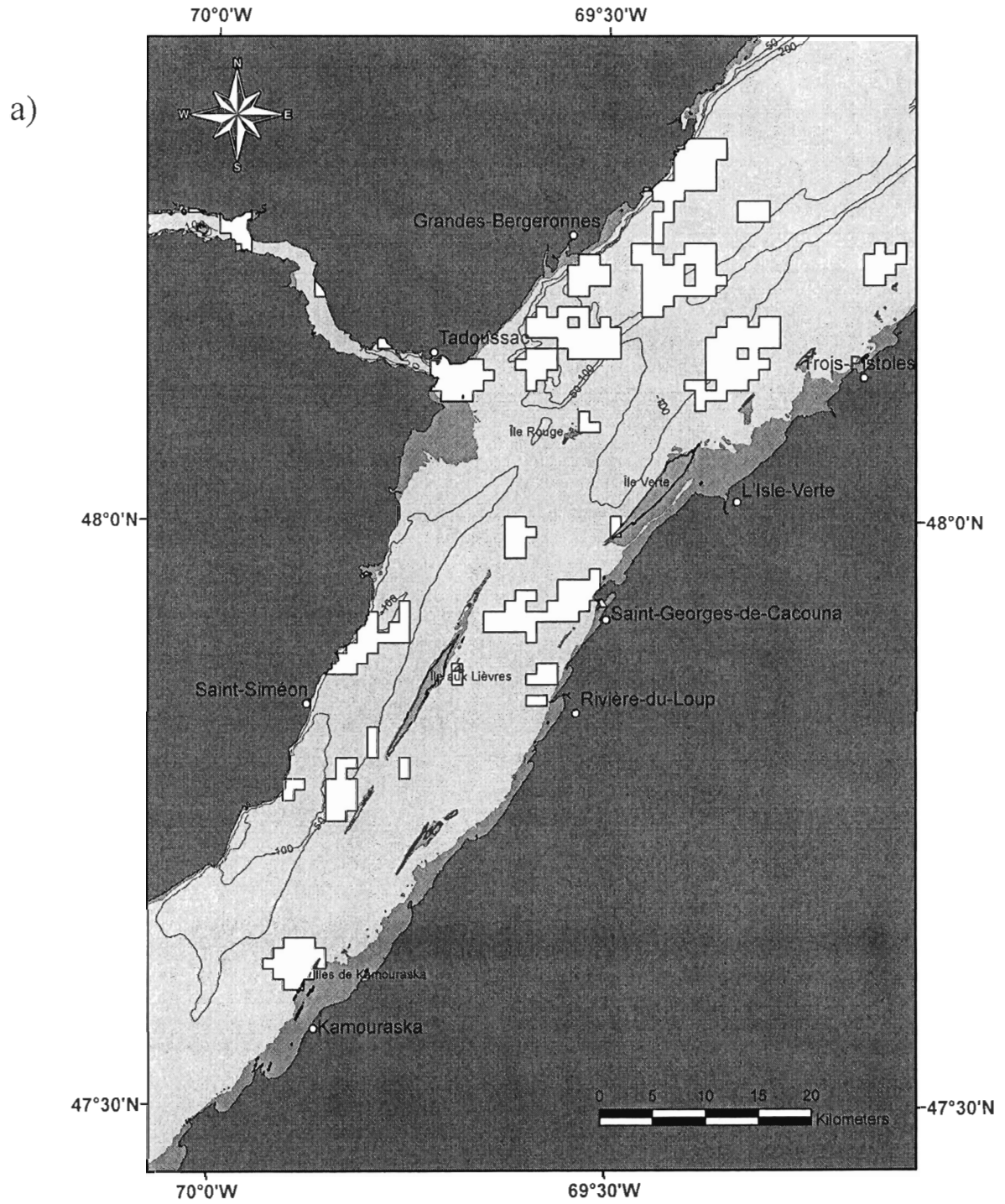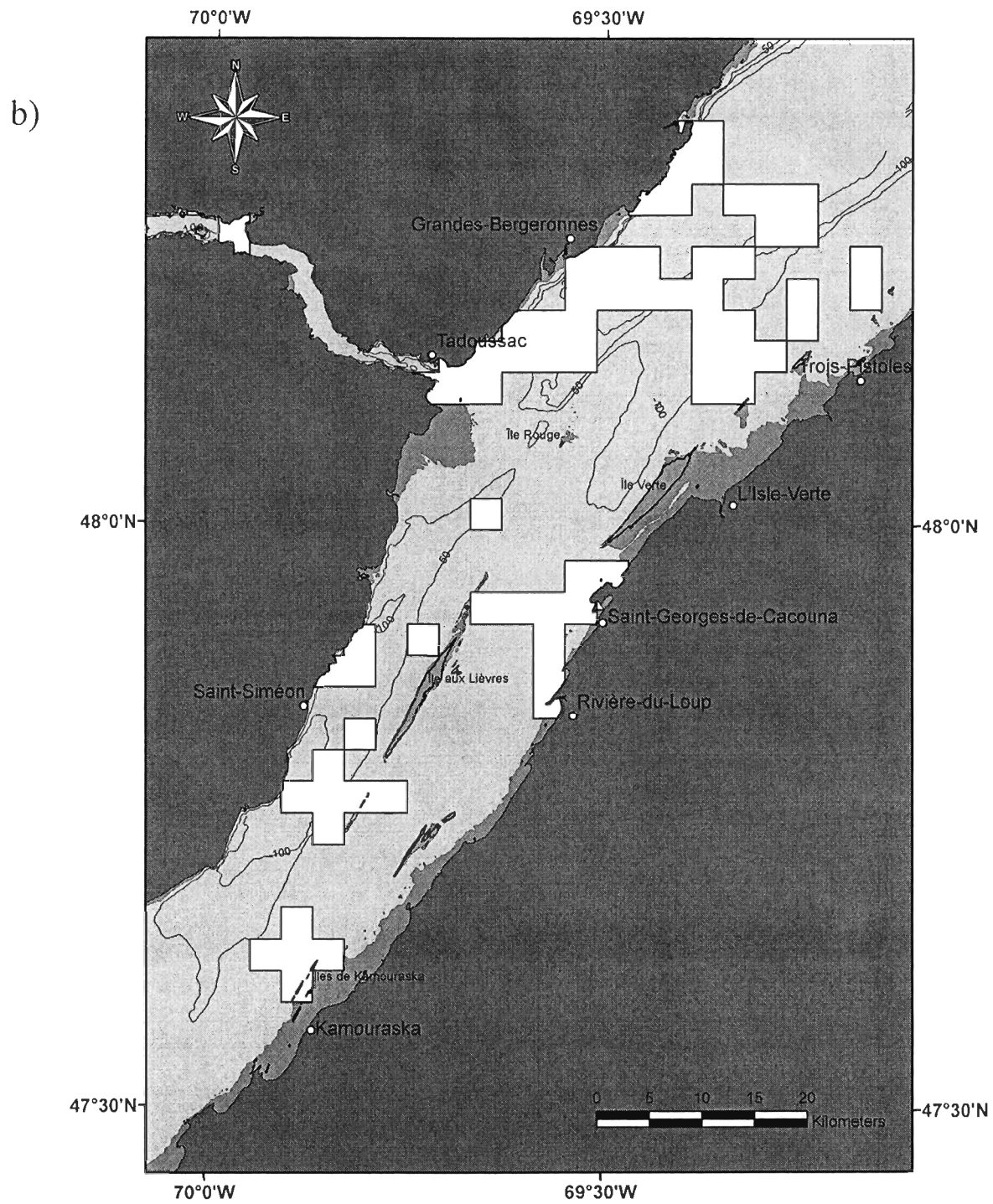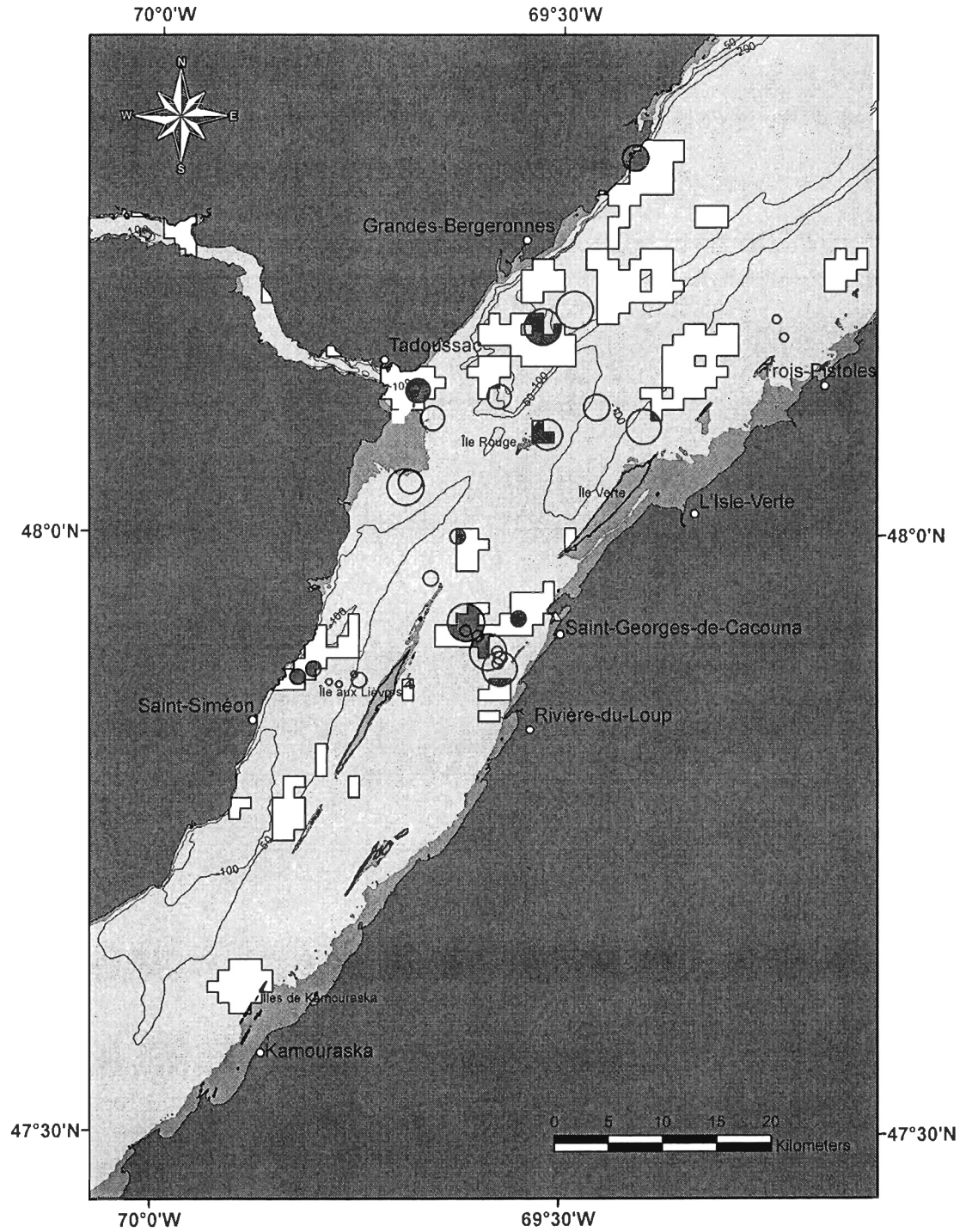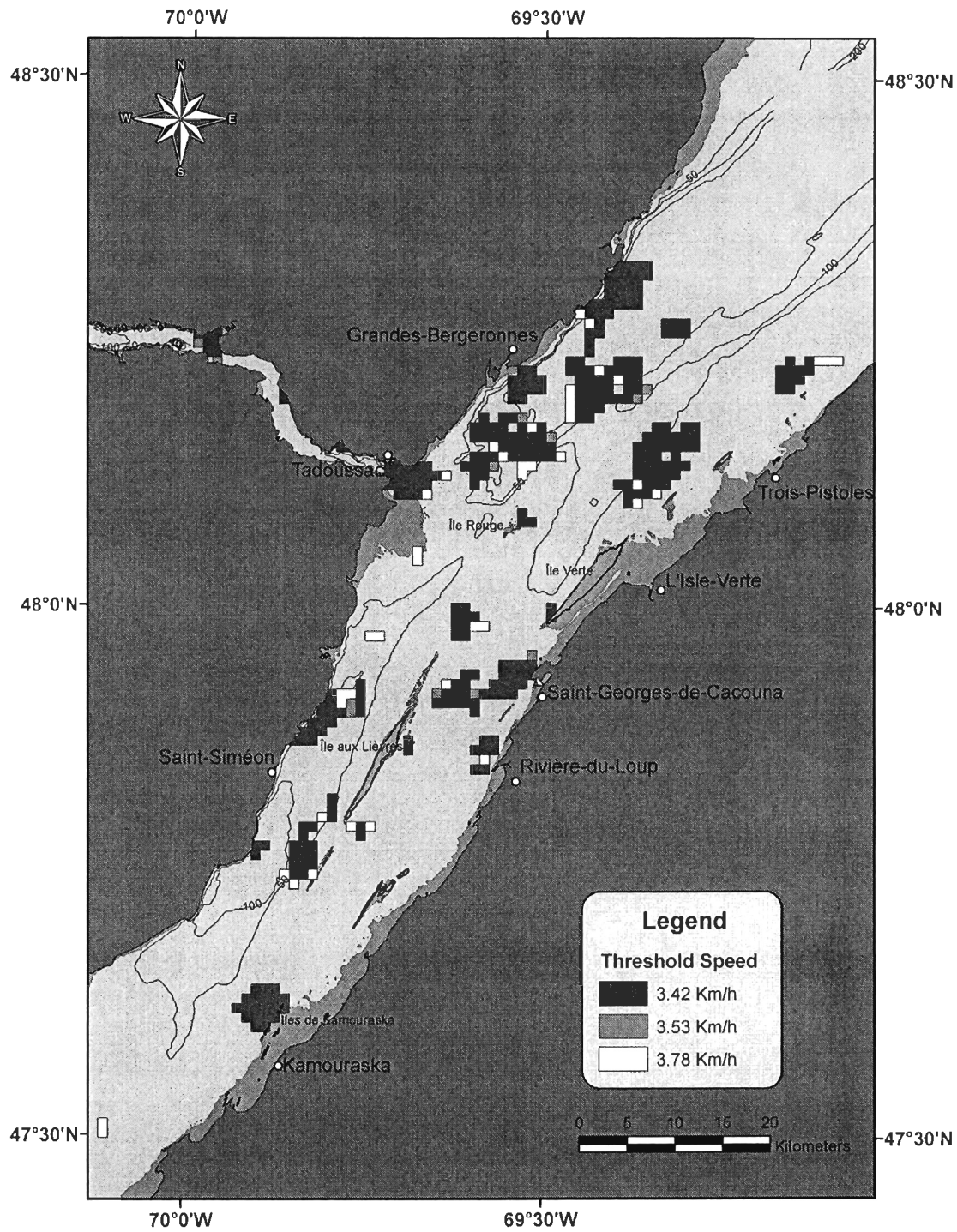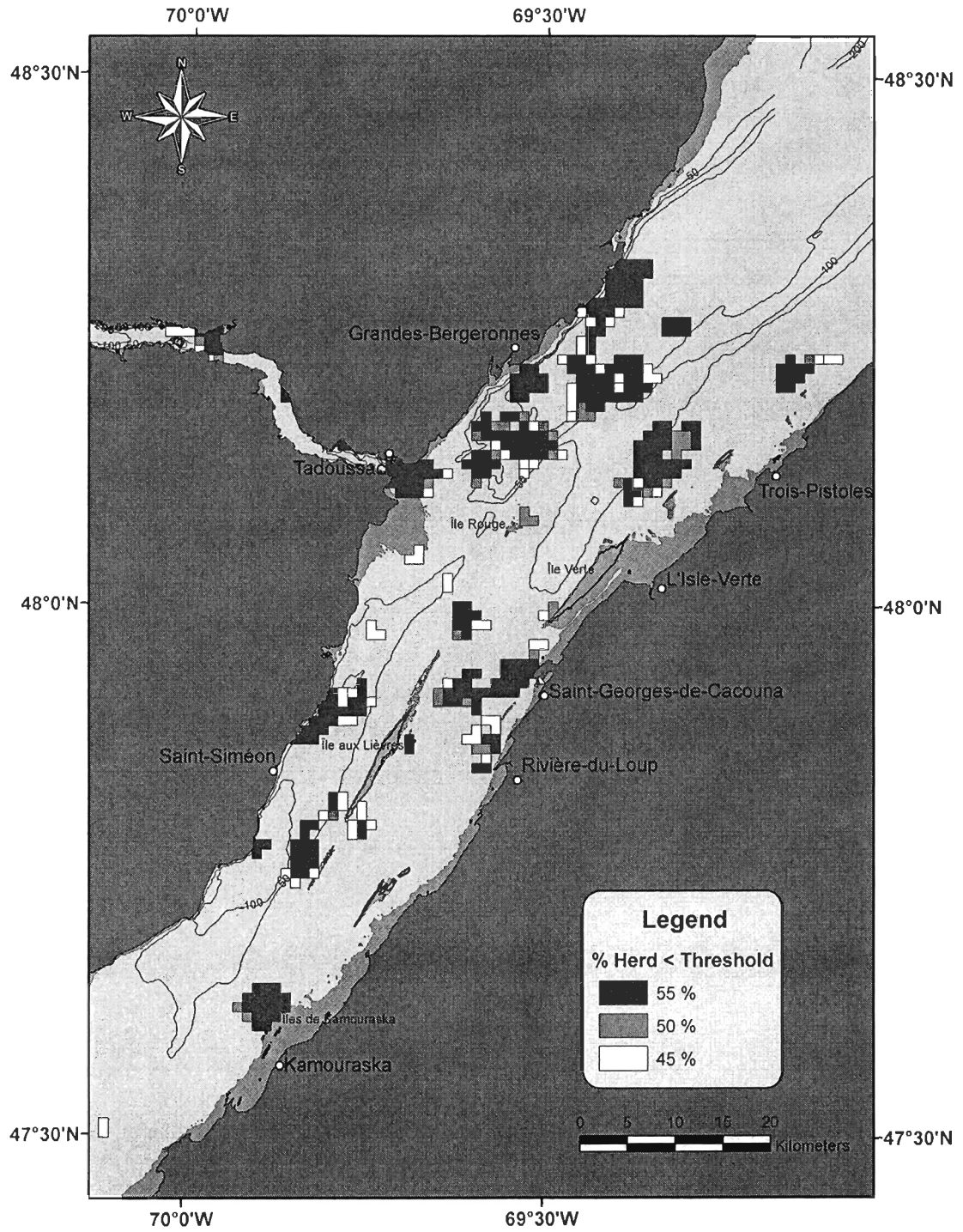
Lemieux Lefebvre *et al.* Fig. 7.

Lemieux Lefebvre *et al.* Fig. 8.

Lemieux Lefebvre *et al.* Fig. 9. a.

Lemieux Lefebvre *et al.* Fig. 9. b.

Lemieux Lefebvre *et al.* Fig. 10. a.

Lemieux Lefebvre *et al.* Fig. 10. b.

Lemieux Lefebvre *et al.* Fig. 11.

Lemieux Lefebvre *et al.* Fig. 12.
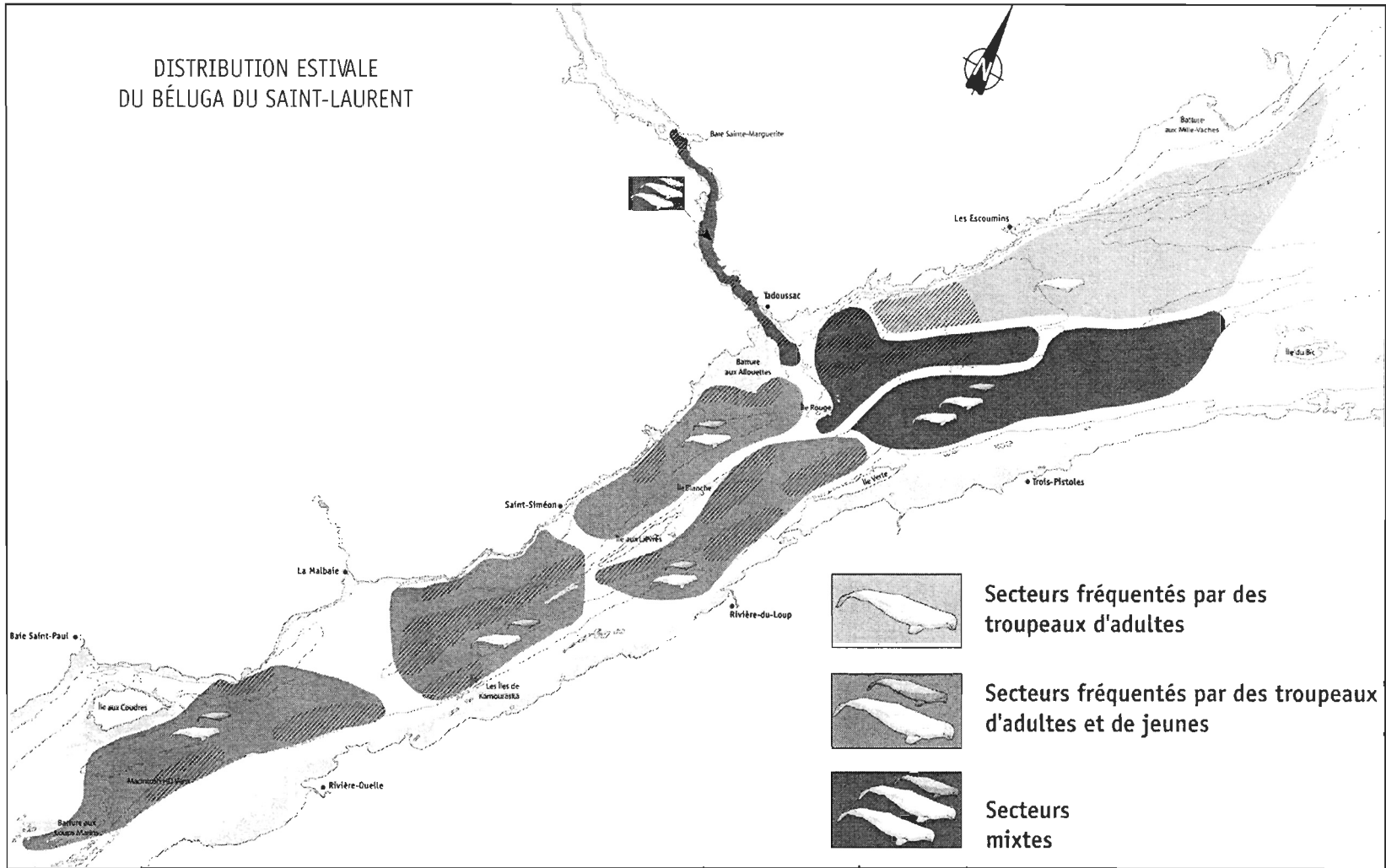
Lemieux Lefebvre *et al.* Fig. 13.

Appendix

APPENDIX 1.

Fig. A1.1 Figure 7 in Michaud (1993). Summer distribution and areas of intensives use of the St Lawrence Estuary beluga whale.
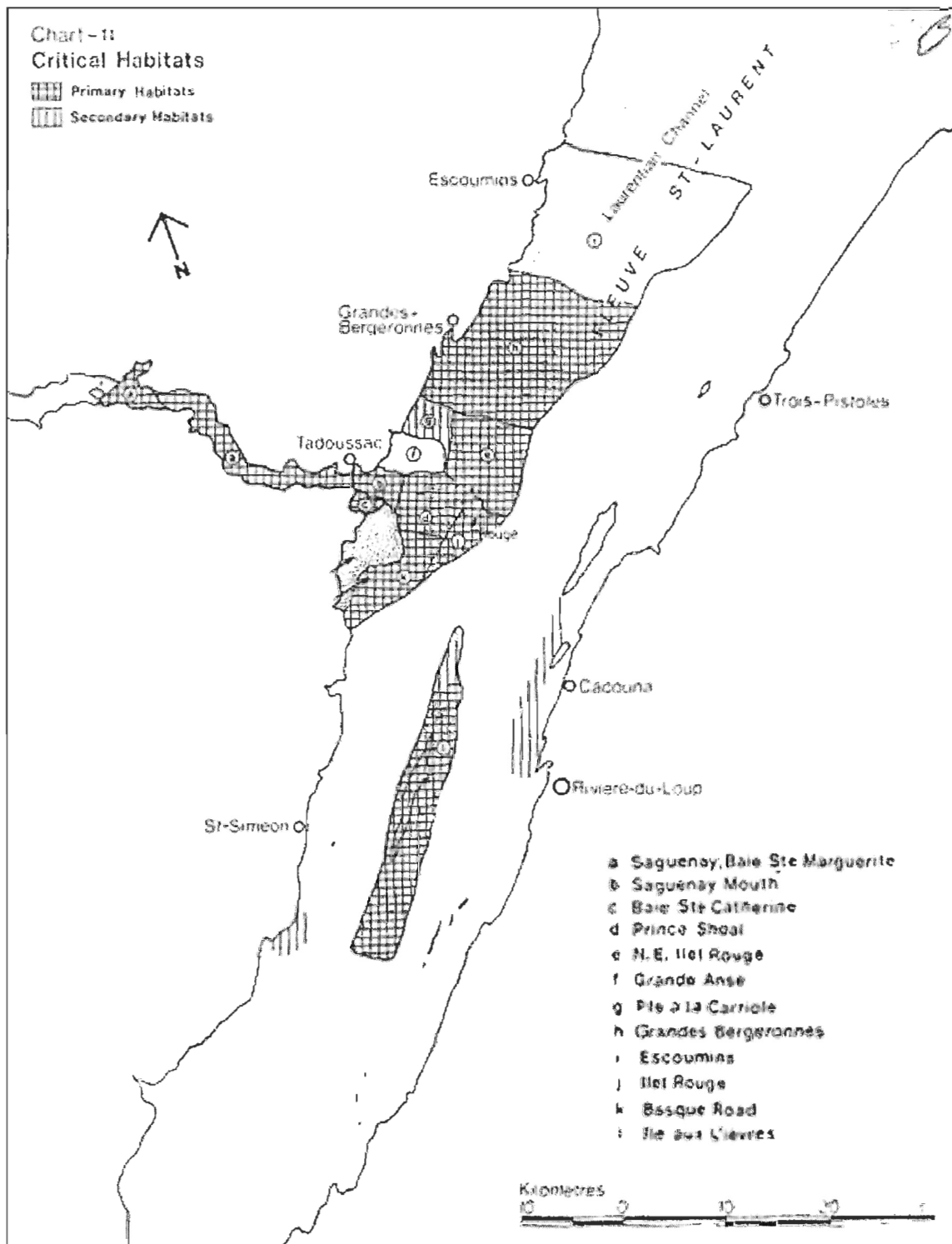
Fig. A1.2 Chart 11 in Pippard and Malcolm (1978). Critical habitats of the St Lawrence Estuary beluga whale.
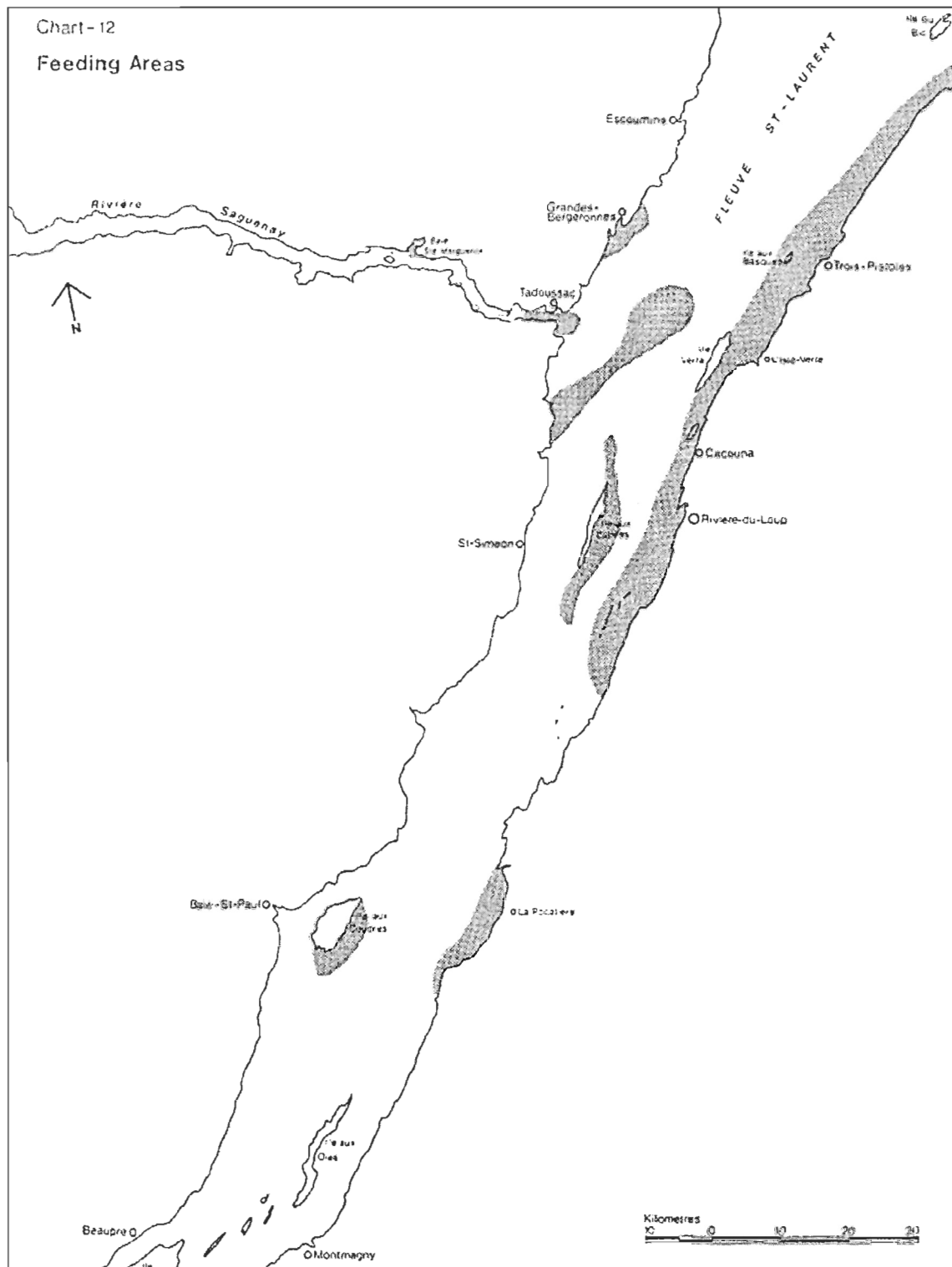
Fig. A1.3 Chart 12 in Pippard and Malcolm (1978). Feeding areas of the St Lawrence Estuary beluga whale.

Fig. A1.4 Chart 13 in Pippard and Malcolm (1978). Possible calving areas of the St Lawrence Estuary beluga whale.
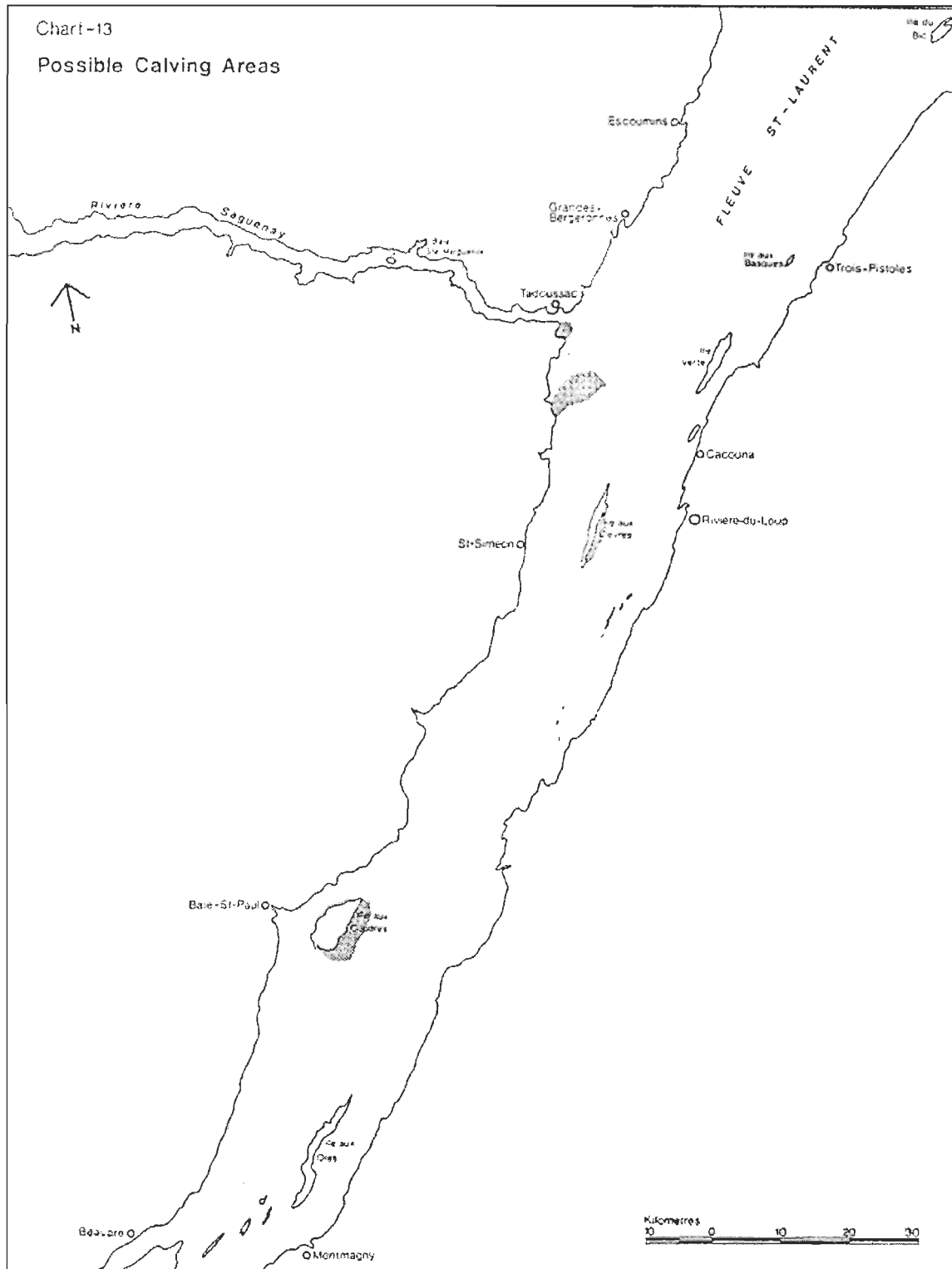

Lemieux Lefebvre *et al.* Fig.A1.1.

Lemieux Lefebvre *et al.* Fig. A1.2.

Lemieux Lefebvre *et al.* Fig. A1.3.

Chart-13

Possible Calving Areas

Lemieux Lefebvre *et al.* Fig. A1.4.

CONCLUSION DU MÉMOIRE

Comme plusieurs prédateurs marins, les bélugas du St-Laurent démontrent un ajustement de leurs patrons de déplacement à des échelles spécifiques en les circonscrivant dans des aires restreintes. Malgré que ces patrons de déplacement soient généralement reliés à des comportements d'alimentation, ceux observés chez les bélugas pourraient aussi être reliés à d'autres comportements tels que la socialisation. Les échelles auxquelles sont déployés ces déplacements constitueraient une réponse des bélugas à l'hétérogénéité de leur environnement et aux différents facteurs provoquant cette hétérogénéité tels que la distribution des proies, les structures topographiques ou l'occurrence de processus océanographiques à méso-échelle. L'identification de ces patrons de déplacement individuels a servi de base pour l'analyse des déplacements des troupeaux et nous a permis d'étudier les patrons de résidence de la population. Ainsi, nous avons pu observer que les troupeaux de bélugas modifient leurs vitesses de déplacement selon les habitats qu'ils visitent à l'intérieur de leur aire de répartition estivale où nous avons pu identifier la présence de 26 aires de forte résidence.

Cette étude avait comme objectif principal une première caractérisation quantitative de l'utilisation de l'habitat chez les bélugas du St-Laurent par l'analyse de leurs patrons de résidence. Pour ce faire, une importante base de données de suivis de troupeaux, réalisés lors des efforts de photo-identification, a été utilisée. Cependant, les

protocoles de récoltes de données lors de ces suivis n'ayant pas été élaborés directement en fonction de l'objectif principal de la présente étude, le développement de stratégies d'analyse originales a été nécessaire pour l'atteinte de cet objectif. Les stratégies développées ont permis l'utilisation des données à haute résolution spatio-temporelle provenant des suivis télémétriques individuels comme base pour l'analyse des données à plus faible résolution des suivis de troupeaux. Cela a ainsi permis d'augmenter de manière importante la taille d'échantillonnage et l'étendue spatiale et temporelle de l'étude. Des données telles que celles utilisées dans la présente étude existent pour plusieurs espèces de mammifères marins et pourraient être explorées à l'aide de méthodes similaires à celles présentées dans ce mémoire. Ceci pourrait être particulièrement souhaitable dans le cas d'espèces menacées, pour lesquelles l'identification de l'utilisation préférentielle de certains habitats contribue à orienter les actions visant le maintien et le rétablissement de leurs populations.

La présente étude a été rendue possible grâce à la récolte de données entreprise dans le cadre du projet de recherche à long terme sur l'écologie des bélugas du St-Laurent initié par le GREMM en 1986. De tels programmes à long terme sont d'une grande valeur pour l'acquisition de données pouvant permettre une compréhension plus approfondie de l'écologie des espèces. Les données à long terme peuvent entre autre permettre de mieux comprendre les relations existant entre l'utilisation de l'habitat d'une population et les changements prenant place dans son environnement. Or, plusieurs changements environnementaux sont susceptibles d'avoir influencés les caractéristiques et qualités des habitats de l'estuaire du St-Laurent au cours des dernières décennies (Dufour et Ouellet 2007). Cet aspect n'a cependant pas été étudié dans ce mémoire, mais

pourrait l'être lors de projets ultérieurs portant sur l'étude des variations annuelles dans les patrons de résidence de la population. Ceci permettrait d'examiner si les changements ayant eu lieu dans l'estuaire au cours des dernières décennies sont corrélés à des changements dans l'utilisation de l'habitat chez les bélugas du St-Laurent.

Malgré la nécessité d'étudier leur variation temporelle, la délimitation présentée des aires de forte résidence pourrait servir à la conservation de cette population menacée. Plusieurs facteurs limitant reliés à l'activité humaine ont été proposés comme cause potentielle de l'absence de rétablissement de la population, dont l'effet de la contamination sur la survie et la reproduction, la pollution sonore et le dérangement, la perte d'habitats, les collisions avec les bateaux et la compétition avec les pêcheries commerciales et d'autres mammifères marins (Hammill *et al.* 2007). L'intensité des effets négatifs reliés à certains de ces facteurs peut être directement reliée au niveau d'exposition auxquels les bélugas sont sujets et donc influencée par leurs patrons de résidence. Un de ces facteurs est la pollution sonore de source anthropogénique dont les effets négatifs sur les bélugas, tels que la perte temporaire ou permanente de l'ouïe, le masquage des sons naturels, les changements dans le comportement vocal, la réduction de l'efficacité de la communication et l'augmentation du niveau de stress, sont tous reliés à la durée d'exposition, l'intensité et la proximité de la source sonore (Lesage et al 1999). Les impacts négatifs d'autre facteurs tels que la contamination et les risques de collisions avec les bateaux, seront aussi influencés par leur niveau d'exposition à ceux-ci et donc par leurs patrons de résidence. La relation entre ces différents facteurs et les patrons de résidence des bélugas du St-Laurent devrait ainsi être tenue en compte dans la gestion et la protection de cette population menacée.

Cependant, pour mieux protéger cette population, il est nécessaire d'être à même d'établir quels sont les habitats essentiels qu'elle utilise. Selon la *Loi sur les Espèces en Péril* du Canada (L.R. 2002. ch.29. S-15.3), un habitat essentiel se définit comme « *un habitat nécessaire à la survie et au rétablissement des espèces sauvages* ». Ainsi, pour établir le caractère essentiel ou non des aires de fortes résidences, les fonctions spécifiques associées à celles-ci devront être définies, ce qui nécessitera d'identifier les comportements et les caractéristiques environnementales reliées à l'utilisation de ces aires par les bélugas du St-Laurent. Ceci pourra être réalisé par l'étude des comportements individuels de plongée mis en relation avec les comportements de surface des individus et des troupeaux, avec les budgets d'activités et avec les variables environnementales caractérisant les différentes aires de forte résidence.

Bibliographie

Dufour R. et Ouellet P. 2007 « Rapport d'aperçu et d'évaluation de l'écosystème marin de l'estuaire et du golfe du Saint-Laurent.». **Rapport technique canadien des sciences halieutiques et aquatiques** 2744F : vii + 123 pages.

Hammill, M.O., L.N. Measures, J.-F. Gosselin, et V. Lesage. 2007. « Lack of recovery in St. Lawrence Estuary beluga ». **Canadian Science Advisory Secretariat**, Research Document 2007:026.

Lesage, V., C. Barette, M.C.S. Kingsley, et B. Sjare. 1999. « The effect of vessel noise on the vocal behavior of Belugas in the St. Lawrence River estuary, Canada ». **Marine Mammal Science** 15:65-84.