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ÉLABORATION DE FACTEURS DE CORRECTION POUR LES INVENTAIRES AÉRIENS DE BÉLUGAS DU SAINT-LAURENT

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RÉSUMÉ

Des estimations d’abondance précises sont essentielles à la détection de tendances pour une population donnée. Toutefois, une partie d’une population inventoriée pourrait être cachée lors d’un relevé; c’est ce qu’on appelle le biais de disponibilité. Pour les cétacés, ceci a lieu lorsqu’ils se trouvent submergés sous l’eau, à une certaine profondeur. La population de bélugas du Saint-Laurent est en voie de disparition, et des relevés aériens photographiques et visuels sont effectués pour suivre l’évolution de sa taille. Les relevés actuels sont corrigés avec un facteur de correction unique et spécifique aux relevés photographiques, et comportent de grands intervalles de confiance. Nous avons émis l’hypothèse que l’inclusion de variables environnementales (profondeur et turbidité) et d’utilisation d’habitat (aires de haute résidence ou transit) aura un effet sur la disponibilité des animaux, et que tenir compte des différences du temps de détection entre les types de relevés rendra plus comparable les estimations d’abondance. Des données de plongée et de localisation, provenant de 30 bélugas équipés de balises enregistrant leur profondeur de plongée et leur position, ont été utilisées pour examiner l’effet de ces facteurs sur la disponibilité des bélugas aux deux types de relevés. En utilisant la proportion moyenne de temps à la surface, ainsi que des équations d’estimation généralisée (GEE) pour tenir compte de l’autocorrélation, nous avons déterminé que la disponibilité globale aux relevés photographiques est de 0,308, équivalant à multiplier par 3,25 les individus comptés, au lieu du 2,26 utilisé présentement. La turbidité diminue la disponibilité, mais la profondeur du milieu et le comportement ne sont pas de bons prédicteurs de disponibilité pour ce type de relevé. Lors des relevés visuels, un modèle GEE-GAM prédit que la durée des intervalles de surface et des plongées augmentent avec la profondeur du milieu, ou lorsque les bélugas sont dans une aire de haute résidence. Ces résultats montrent l’importance de tenir compte de l’hétérogénéité spatiale et du comportement pour corriger le biais de disponibilité pour cette population. Une fois appliqués aux relevés passés, ces facteurs de correction devraient permettre de réduire la variabilité entre les estimations d’abondance, et d’améliorer notre capacité à détecter des tendances.

Mots clés : biais de disponibilité, estimation d’abondance, relevés aériens, patrons de plongées, équations d’estimation généralisée, *Delphinapterus leucas*

ABSTRACT

Precise abundance estimates are essential to detect significant population trends. However, a proportion of a surveyed population may be unavailable to detection, resulting in availability bias. In cetaceans, this happens when animals are submerged under water, below a threshold depth. The St. Lawrence Estuary beluga population is endangered, and both photographic and visual aerial surveys are flown to keep track of population size. Currently, estimates from both types of surveys are corrected for availability bias using a unique correction factor developed for photographic surveys, and are associated with high confidence intervals. We hypothesized that the inclusion of environmental (depth and turbidity) and of habitat use (high residency areas or transit) variables will affect the availability of animals, and that accounting for differences in detection time between survey types will make point estimates obtained from photographic and visual surveys more comparable. We used diving and location data from 30 beluga equipped with time-depth recorders to examine the effect of these factors on beluga availability for both survey types. Based on the average proportion of time at the surface, and correcting for autocorrelation using generalized estimating equations (GEEs), we determined that overall availability to photographic surveys is 0.308, which means a 3.25 multiplier would be applied to counted animals, instead of the 2.26 multiplier currently used. Turbidity decreased availability, but depth and behaviour were not good predictors of availability to this type of survey. During visual surveys, a GEE-GAM model predicted that surface intervals and dives increased in length with bottom depth, or when beluga were in a high-use area. These results show the importance of taking into account spatial and behavioural heterogeneity in correcting availability bias for this beluga population. Once applied to past surveys, these correction factors should reduce the variability among survey estimates, and increase our capacity to detect trends.

Keywords: availability bias, abundance estimation, aerial survey, diving data, Generalized Estimating Equations, *Delphinapterus leucas*

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

INTRODUCTION GÉNÉRALE

1.1 TAILLE DES POPULATIONS ANIMALES

Les mesures démographiques les plus importantes d'une population sont sa taille et sa densité (Liebhold et Gurevitch, 2002). La taille représente le nombre total d'individus dans la population (leur abondance), tandis que la densité est le nombre d'individus par unité de surface (Eberhardt, Chapman et Gilbert, 1979; Smith et Smith, 2012). Ainsi, la densité est intrinsèquement liée à l'abondance. Ces mesures sont essentielles à des fins de conservation et de gestion; effectivement, elles servent à l'évaluation de l'état de populations, à effectuer des analyses de viabilité ainsi qu'à évaluer des procédures de gestion (Wade, 1998; Carretta *et al*, 2009). L'estimation de menaces potentielles dans le contexte de la mise en place de plans de gestion durable requiert aussi ces informations de base (Ribarič, 2017).

De nombreux facteurs biotiques et abiotiques, reliés à la survie et à la reproduction d'un organisme, peuvent influencer la taille d'une population. Plusieurs exemples de cela existent dans la littérature, que ce soit pour des facteurs internes (par ex., compétition intra-spécifique, Boström-Einarsson *et al.*, 2013) ou externes (par ex., disponibilité de ressources, Sileshi et Mafongoya, 2007; caractéristiques abiotiques de l'habitat et diversité de la communauté, Whitfeld *et al.*, 2013). De plus, la taille d'une population peut être autorégulée lorsque la capacité de soutien[1] du milieu est atteinte (Smith et Smith, 2012).

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[1] Capacité de soutien : la taille maximale d'une population que l'environnement peut soutenir à long terme, sans dégradation de l'environnement (Smith et Smith, 2012).

Des décomptes d’individus d’une population sont nécessaires afin d’obtenir sa taille. L’idéal, c’est de réaliser un recensement (par ex., baleine grise *Eschrichtius robustus*, Rice et Wolman, 1971), mais cela est rarement possible pour des populations non limitées dans le temps et dans l’espace. En effet, il n’y a habituellement pas de moyen de s’assurer que tous les individus seront visibles et pourront être comptés simultanément (Eberhardt, Chapman et Gilbert, 1979). Ainsi, le plus souvent, les relevés effectués permettent de dénombrer une portion d’une population, qui ne correspond pas nécessairement à sa taille réelle. Ils peuvent aussi permettre d’acquérir des informations sur la distribution et l’utilisation de l’habitat par la population, ainsi que sur les impacts anthropiques, le tout à de vastes échelles spatiales (Buckland *et al.*, 2001).

Dans le contexte de gestion de populations fauniques sauvages, une correction de la taille effective de la population, qui tient compte des individus manqués, n’est pas suffisante à l’obtention de sa taille réelle. Des paramètres supplémentaires sont nécessaires, entre autres les taux de mortalité et de natalité qui, comme mentionné précédemment, influencent l’abondance au fil du temps (Eberhardt, Chapman et Gilbert, 1979). Par contre, ces paramètres ne font pas toujours partie des informations pouvant être acquises lors de relevés.

1.2 RELEVÉS DE MAMMIFÈRES MARINS

Dans le cas des mammifères marins, trois types de relevés ont été identifiés et décrits par Eberhardt, Chapman et Gilbert (1979) : marquage-recapture, capture par unité d’effort et observations visuelles directes. Ces relevés doivent être effectués fréquemment et de façon standardisée pour permettre la détection de tendances dans l’abondance d’individus (Jewell *et al.*, 2012).

La méthode de marquage-recapture est utilisée avec des espèces pouvant être facilement recapturées, telles que les espèces chassées ou les pinnipèdes. Ces derniers mettent bas sur un substrat solide (glace ou terre), ce qui les rend plus accessibles (Bowen, Beck et Austin, 2009). Cette méthode consiste grossièrement à marquer un échantillon d'individus d'une population. Ensuite, des ré-échantillonnages sont effectués, où la proportion d'individus marqués est notée. Plusieurs postulats doivent être vérifiés afin de valider l'utilisation de cette technique : a) la capture et le marquage n'ont pas d'effet sur la survie des individus impliqués; b) les marques ne sont pas perdues et elles sont toutes notées lorsqu'elles sont observées; c) la présence d'une marque n'est pas liée à la probabilité de capture d'un animal; et d) la population est fermée, c'est-à-dire qu'aucun individu sans marque ne sera introduit entre les échantillonnages. L'avantage de la méthode de marquage-recapture, c'est qu'elle peut aussi permettre d'obtenir des données sur le taux de survie, le taux de croissance, et l'identification de routes migratoires. Un équivalent visuel a été développé pour des espèces qui ont des marques naturelles, telles que des patrons de coloration uniques ou des blessures (Hammond, Mizroch et Donovan, 1990). Les individus sont photographiés, et lors de relevés subséquents, la proportion d'individus déjà photographiés peut être déterminée. Par contre, une attention particulière doit être portée sur la sélection et la manipulation des images pour éviter des biais potentiels (Urian *et al.*, 2015).

Lorsqu'une population de mammifères marins est chassée, une estimation de sa taille peut être effectuée si l'on considère que le nombre d'individus attrapés équivaut au produit de l'effort et de la taille de la population; c'est ce qu'on appelle la capture par unité d'effort. Cette méthode est principalement utilisée pour des populations exploitées de cétacés, puisqu'il est plus difficile de l'appliquer s'il y a possibilité que tous les individus ne soient pas dans l'eau (i.e. pinnipèdes). L'effort peut être difficile à mesurer, puisque des facteurs tels que la vitesse du navire et les conditions météorologiques peuvent varier et influencer celui-ci. Toutefois, le postulat de population fermée nécessaire à l'utilisation de la méthode de marquage-recapture n'a pas besoin d'être respecté. Effectivement, des équations ont été développées pour les populations fermées ainsi qu'ouvertes.

Enfin, les observations visuelles directes consistent à compter le nombre d'individus observés, et à corriger le chiffre obtenu en fonction de la proportion d'animaux visibles lors du relevé. Les relevés visuels peuvent être réalisés de plusieurs façons. La prise de photos aériennes a l’avantage de produire une référence permanente, ce qui rend possible la vérification des décomptes par plusieurs observateurs, avec comme résultat un décompte final plus précis (Lowry, 1999). Les relevés photographiques sont aussi utiles pour le dénombrement de pinnipèdes dans une colonie (Buckland et York, 2009). Autrement, les observations visuelles peuvent être effectuées à partir de la terre ferme (par ex. Noad *et al.*, 2011), de navires (par ex. Williams et Thomas, 2009) ou d’avions (par ex. Pavanato *et al.*, 2017). Les relevés à partir de la terre ferme peuvent être pratiques pour les pinnipèdes ou pour des espèces dont la route migratoire passe près de la rive (Forney, 2009). En ce qui concerne les relevés à partir de navires, un grand inconvénient est que la réponse des espèces aux navires varie beaucoup. Ainsi, il est bien connu que les marsouins communs (*Phocoena phocoena*) évitent les bateaux, tandis que plusieurs espèces de dauphins aiment nager dans la vague de proue (Forney, 2009). L’avantage des navires, c’est qu’une grande gamme d’équipements peut être utilisée pour coupler les observations aux conditions océanographiques. Ensuite, les relevés aériens permettent de couvrir une grande superficie en relativement peu de temps, et pour un coût plus faible qu’un navire (Forney, 2009). De plus, il a récemment été démontré avec des rorquals à bosse (*Megaptera novaeangliae*) que les drones peuvent être un remplacement efficace aux méthodes traditionnelles (Hodgson, Peel et Kelly, 2017).

1.3 CORRECTION DES BIAIS LIÉS AUX RELEVÉS VISUELS

Il y a deux types de biais présents durant les relevés visuels, soit les biais de perception et de disponibilité. Le biais de perception consiste en la possibilité que des animaux visibles ne soient pas perçus par les observateurs, tandis que le biais de disponibilité s’explique par le fait que tous les animaux présents dans la zone inventoriée ne seront pas nécessairement visibles au moment où la plateforme d’observation les croise (Marsh et Sinclair, 1989). Dans le cas des cétacés, ils sont considérés disponibles lorsqu’ils sont assez près de la surface pour être visibles, et indisponibles lorsqu’ils sont submergés (Laake et Borchers, 2004).

De nombreuses études portent sur la correction du biais de perception, puisque les informations requises pour cette correction sont relativement faciles à obtenir. En effet, ce biais est corrigé en utilisant la méthode de double-plateforme (Borchers *et al.*, 1998), soit en ayant deux observateurs, ne pouvant pas communiquer entre eux, sur la même plateforme d'inventaire (Marsh et Sinclair, 1989). Les groupes d'animaux observés sont ensuite comparés pour déterminer s'ils ont été vus par seulement un observateur, ou les deux (Marsh et Sinclair, 1989).

Quant au biais de disponibilité, il est souvent ignoré puisqu'il requiert des données externes, c'est-à-dire obtenues hors des relevés effectués (Pollock *et al.,* 2006). Ceux qui étudient ce biais prennent différentes approches pour le corriger. Ces approches sont décrites par Hodgson, Peel et Kelly (2017), et incluent : a) des suivis focaux du comportement, à partir de la terre ferme ou d'un bateau; b) le déploiement de balises enregistrant des données de profondeur, où la profondeur à laquelle les animaux deviennent visibles est soit présumée, soit testée de façon empirique; et c) la comparaison entre des estimés d'abondance obtenus par relevés aériens et des estimés obtenus à partir de la terre ferme, ce qui produit un recensement de tous les individus ayant passé dans l'aire d'étude. Cependant, la majorité de ces études considèrent que la disponibilité de la population étudiée est identique à travers son aire de répartition. Ainsi, l'hétérogénéité de la disponibilité en fonction de l'environnement et de l'utilisation de l'espace n'est pas prise en compte (Pollock *et al.*, 2006).

1.4 LA POPULATION DE BÉLUGAS DE L'ESTUAIRE DU SAINT-LAURENT

Le béluga (*Delphinapterus leucas*) est une espèce à répartition arctique et subarctique, dont la population la plus au sud se retrouve dans l'estuaire du Saint-Laurent (ESL) (O'Corry-Crowe, 2009). La population de l'ESL est géographiquement isolée des autres (COSEWIC, 2014), et quelques études ont montré que la dispersion entre populations de bélugas est limitée, même lorsqu'il y a absence de barrières physiques (Brown Gladden, Ferguson et Clayton, 1997; O'Corry-Crowe *et al.*, 1997). De plus, parmi toutes les populations canadiennes, celles de l'ESL et de l'est de la Baie d'Hudson ont la plus faible diversité génétique d'ADN mitochondrial et d'allèles microsatellites (Brennin *et al.,* 1997), suggérant qu'il n'y a pas de recrutement externe pour les bélugas de l'ESL et qu'il y a potentiellement de la consanguinité (Patenaude *et al.*, 1994).

Les bélugas de l'ESL sont considérés en voie de disparition par le Comité sur la situation des espèces en péril au Canada et la Loi sur les espèces en péril (COSEWIC, 2014; Registre public des espèces en péril, 2011). Une chasse intensive a sévèrement réduit la taille de la population; Reeves et Mitchell (1984) ont estimé qu'environ 15 000 individus ont été extraits entre 1880 et 1950, avec seules quelques centaines d'individus encore vivants vers la fin des années 1970 (Pippard, 1985). Depuis 1979, la population est protégée (Lesage et Kingsley, 1998), mais elle ne semble pas se rétablir (Béland, Vézina et Martineau, 1988; DFO, 2005; Hammill *et al.*, 2007). Depuis le début des années 2000, cette population serait en déclin, perdant ses effectifs à raison d'environ 1% par an (Mosnier *et al.*, 2015). Plusieurs facteurs extrinsèques et intrinsèques peuvent limiter l'accroissement de la population, tels que sa petite taille (Gosselin *et al.*, 2017), son isolement géographique et génétique (Patenaude *et al.*, 1994), ses hauts taux de contaminants (Béland *et al.*, 1993; Hobbs *et al.*, 2003; Lebeuf, 2009) et l'exposition chronique au bruit et à l'activité associée au trafic maritime (Blane et Jaakson, 1994; Lesage *et al.*, 1999; Scheifele *et al*., 2005; Ménard *et al.*, 2014).

La répartition estivale des bélugas de l'ESL est centrée sur la rivière Saguenay, avec comme limites les Battures aux Loups marins à l'ouest et Forestville/Rimouski à l'est, et des observations occasionnelles en aval (Michaud, 1993; Mosnier *et al.,* 2010). Ils montent aussi la rivière Saguenay, allant jusqu'à Saint-Fulgence (Michaud, 1993). Durant l'hiver, ils se trouvent dans les secteurs libres de glace de l'estuaire inférieur et du nord-ouest du golfe (Mosnier *et al.,* 2010). Les bélugas sont grégaires et ont une distribution agrégée, ainsi qu'une ségrégation par âge et par sexe durant l'été (Michaud *et al.,* 1990; Michaud, 2005). Ils forment des groupes, soit des individus se déplaçant à quelques longueurs de corps les uns des autres, qui peuvent se rejoindre pour former des troupeaux. Ces troupeaux sont constitués soit a) majoritairement d’adultes (<10% juvéniles), probablement des mâles; b) d’adultes (probablement femelles) accompagnés de juvéniles, ces derniers constituant plus de 30% des individus; ou c) des troupeaux dits mixtes dont la composition est intermédiaire (Michaud, 1993). Dans la portion aval de leur aire de répartition, qui comprend les eaux profondes du chenal Laurentien, on retrouve surtout de grands troupeaux de mâles adultes (> 100 individus, > 5/groupe), tandis qu’en amont, dans les eaux plus chaudes et moins profondes, les troupeaux sont plus petits (< 30 individus, < 5/groupe) et composés de femelles adultes avec leurs jeunes. Quant aux troupeaux mixtes, ils se retrouvent fréquemment à la tête du chenal Laurentien (Michaud, 1993). Normalement, les individus d’un groupe sont relativement synchrones dans leurs patrons de plongée, plongeant en profondeur et refaisant surface pour ventiler environ au même moment.

Quelques études ont tenté de caractériser la distribution agrégée des bélugas en identifiant soit les aires les plus souvent fréquentées, soit les aires où l’on retrouve les plus fortes densités (Pippard et Malcolm, 1978; Michaud, 1993). Une étude plus récente a analysé les mouvements à fine échelle d’individus portant une balise avec émetteur VHF, et a ainsi identifié 28 aires de haute résidence (AHR), correspondant à des aires où les bélugas font de la recherche restreinte (*area restricted search*) (Lemieux Lefebvre *et al.*, 2012). Toutefois, seule une partie de l’aire de répartition était couverte par cette étude, et la fonction précise de ces AHR, ainsi que leur degré de connectivité, n’a pas encore été déterminée, quoique plusieurs idées aient été mises de l’avant (Mosnier *et al.*, 2010; Lemieux Lefebvre *et al.*, 2012). Une autre approche a défini des aires de haute densité (AHD; voir Figure 3 du Chapitre 1), en utilisant la méthode d’estimation par noyau (Mosnier *et al.,* 2016). Cette dernière approche couvre la totalité de l’aire de répartition des bélugas, tout en concordant généralement avec les AHR (Savenkoff *et al.*, 2017).

Des données de plongées, combinées à des informations sur le contenu stomacal, ont démontré que les bélugas ont un régime alimentaire assez varié, et peuvent se nourrir autant de proies benthiques que pélagiques (Vladykov, 1946; Martin, Smith et Cox, 1998; Richard *et al.*, 2001; Quakenbush *et al.*, 2015). Leurs plongées varient en durée et peuvent atteindre

25 minutes pour des plongées atteignant des profondeurs de 1000 mètres (Martin, Smith et Cox, 1998; Richard *et al.*, 2001). De fait, les plongées des bélugas du nord du Québec ont des caractéristiques qui suggèrent des plongées jusqu'au fond (Kingsley, Gosselin et Sleno, 2001). Pour les mammifères marins en général, il y a une relation entre le temps de plongée et la profondeur de plongée à cause de contraintes sur la vitesse de nage (Hooker et Fahlman, 2016). Ainsi, les plongées les plus profondes sont nécessairement plus longues, et vont généralement être associées à des séquences de ventilation à la surface d'une plus grande durée (Kooyman and Ponganis, 1998; Kramer, 1998). Pour la population de l'ouest de la baie d'Hudson, la fréquence des longues plongées augmente avec la profondeur du milieu (Martin, Hall et Richard, 2001); mais lorsqu'en transit, les bélugas de l'ouest du Groenland et du Canada font généralement moins de plongées (Heide-Jørgensen *et al.*, 2001). Une description détaillée des différents patrons de plongée effectués par les bélugas de l'ESL, ainsi que l'association de ces patrons à des activités de surface, se retrouve dans Lemieux Lefebvre *et al.* (2017).

Enfin, comme mentionné dans la section « Taille des populations animales », les taux de natalité et de mortalité sont des paramètres qui influenceront la taille d'une population (Eberhardt, Chapman et Gilbert, 1979). Dans le cas des bélugas de l'ESL, les données de mortalité proviennent principalement d'un programme de récupération des carcasses, tandis que le nombre de jeunes identifiés durant les relevés aériens ou lors de relevés par bateau peut informer sur les taux de natalité (Lesage *et al.*, 2014; Michaud, 2014; Mosnier *et al.*, 2015). Aussi, il est connu que les bélugas femelles ont un cycle reproducteur d'environ 3 ans (O'Corry-Crowe, 2009). Ces informations ont été modélisées afin de mieux comprendre la dynamique de la population de l'ESL, et les résultats suggèrent que la dynamique et la structure de la population étaient stables de 1984 jusqu'à 1998, et seraient maintenant instables (Mosnier *et al.*, 2015). Les distributions postérieures provenant du modèle permettent d'obtenir les médianes des paramètres démographiques. Lors de la période stable, la médiane du taux de mortalité des nouveau-nés variait de 14 à 27% avec des pics aux 3-4 ans; durant la période instable, les médianes variaient de 8 à 69%, avec des pics aux 2 ans à partir de 2008 (Mosnier *et al.*, 2015). Les bélugas de l'ESL seraient donc passés d'un cycle reproducteur de 3 ans, à un régime plus court de 2 ans. En ce qui a trait au taux de mortalité des adultes, la médiane annuelle se situe à 6,1%, mais varie de 4 à 8,7% (Mosnier *et al.*, 2015).

1.5 RELEVÉS DE BÉLUGAS DANS L'ESTUAIRE DU SAINT-LAURENT

Un nombre important de relevés estivaux ont été effectués depuis les années 1960 (Pippard et Malcolm, 1978; Pippard, 1985; Béland, Michaud et Martineau, 1987; Sergeant et Hoek, 1988; Kingsley et Hammill, 1991; Michaud, 1993; Kingsley, 1994, 1996, 1998, 1999, 2002; Gosselin, Lesage et Robillard, 2001; Gosselin, Hammill et Lesage, 2007; Gosselin, Hammill et Mosnier, 2014; Gosselin *et al.*, 2017). Toutefois, seuls les relevés effectués depuis 1988 sont standardisés; avant cela, la méthodologie différait entre relevés, rendant la comparaison impossible entre les estimations d'abondance (DFO et WWF, 1995). Entre 1988 et 2009, huit relevés aériens photographiques par bande (*strip-transect*) ont été réalisés, avec beaucoup de variabilité dans les estimations d'abondance obtenues. En 2001, 2003, 2005, 2007, 2008, 2009 et 2014, des relevés aériens visuels en ligne (*line-transect*) ont été réalisés (Gosselin *et al.*, 2017). Ce type de relevé est plus efficace afin d'estimer la taille d'une population à distribution clairsemée sur une grande aire géographique (Bukland *et al.*, 2001). De plus, il est moins coûteux, ce qui permet de faire plusieurs relevés par année et ainsi évaluer et atténuer la variabilité associée au comportement d'agrégation (Gosselin *et al.*, 2017).

Le biais de perception des relevés photographiques a été corrigé en ayant une lecture des photographies effectuée par deux observateurs indépendants (Gosselin *et al.*, 2017). Lorsqu'il y avait un désaccord, un troisième observateur aidait à atteindre un consensus (Gosselin *et al.*, 2017). Pour les relevés visuels, des études effectuées sur des populations de bélugas arctiques ont montré que le biais de perception requiert une correction relativement minime. Dans la polynie des eaux du Nord, la probabilité de détection variait entre 97 et 92% pour 2009 et 2010 respectivement (Heide-Jørgensen *et al.*, 2013). Dans le Golfe de Cook, le facteur de correction a été estimé à 1,5% pour la période 1994-1998, et à 2,1% pour la période 1999-2000 (Hobbs, Rugh et DeMaster, 2000). Jusqu'à maintenant, il n'existe pas d'information afin d'estimer ce biais de perception pour les bélugas du Saint-Laurent. Par conséquent, aucune correction de ce biais n'a à ce jour été appliquée aux relevés visuels (Gosselin *et al.*, 2017).

Quant au biais de disponibilité, Kingsley et Gauthier (2002) ont calculé un facteur de correction spécifique aux relevés photographiques de la population de l'ESL. Pour ce faire, ils ont pris des observations directes du comportement de plongée à partir d'un hélicoptère stationnaire et ont utilisé des disques de Secchi pour relier la visibilité des bélugas à la turbidité. Ils ont trouvé que les bélugas adultes sont visibles jusqu'à une profondeur correspondant à la profondeur de Secchi. Toutefois, ils n'ont pas trouvé d'effet significatif de la turbidité sur la visibilité, et ont ainsi obtenu un facteur de correction unique de 2,26. En corrigeant pour un chevauchement total (avant-arrière) de 30% entre photographies consécutives, ils ont obtenu un facteur de correction de 2,09. Cependant, cette correction ne devrait pas être appliquée aux relevés visuels. En effet, les relevés photographiques donnent un aperçu instantané du nombre de bélugas visibles, tandis que les relevés visuels permettent une certaine fenêtre de temps de détection. Ainsi, on peut supposer que les relevés visuels nécessiteraient un facteur de correction moins élevé que les relevés photographiques pour tenir compte des animaux non disponibles à la surface pour être inventoriés.

Plusieurs études concernant la correction du biais de disponibilité pour des inventaires aériens ont été réalisées avec des populations arctiques de bélugas et de narvals (*Monodon monoceros*) (Sergeant, 1973; Frost, Lowry et Nelson, 1985; Martin et Smith, 1992; Martin, Kingsley et Ramsay, 1994; Heide-Jørgensen et Dietz, 1995; Heide-Jørgensen, Richard et Rosing-Asvid, 1998; Hobbs, Waite et Rugh, 2000; Heide-Jørgensen et Acquarone, 2002; Richard, 2013; Doniol-Valcroze *et al.*, 2015; Watt *et al.*, 2015; Marcoux *et al.*, 2016). Les facteurs de correction obtenus varient entre 1,66 et 4,90. Puisque le facteur de Kingsley et Gauthier (2002) est inclus dans cette gamme, il a été appliqué aux relevés visuels de l'ESL, à défaut d'en avoir un spécifique aux relevés visuels de bélugas dans l'ESL (Gosselin *et al.*, 2017).

1.6 JUSTIFICATION DE L'ÉTUDE

Les estimations d'abondance de bélugas dans l'ESL sont très variables d'une année à l'autre, et entre les relevés effectués la même année (Gosselin, Mosnier et Hammill, 2014). Par exemple, des décomptes de 313 et de 729 individus ont été obtenus le 4 et 5 septembre 2009 respectivement, pour une même aire inventoriée (Gosselin, Mosnier et Hammill, 2014). Cette grande variabilité rend la détection de tendances difficile (Taylor *et al.*, 2007; Mosnier *et al.*, 2015; Gosselin *et al.*, 2017). Considérant le statut précaire de cette population, il est important d'avoir des estimations d'abondance précises, afin de pouvoir bien observer les tendances.

Récemment, plusieurs études ont démontré que l'hétérogénéité de l'environnement mène à une hétérogénéité des comportements de plongée d'animaux marins, ce qui affecte leur disponibilité (par ex. Pollock *et al.*, 2006; Thomson *et al.*, 2012; Hagihara *et al.*, 2013; Fuentes *et al.*, 2015; Nykänen *et al.*, 2018; Sucunza *et al.*, 2018). Par exemple, l'étude de Pollock *et al.* (2006) a montré que pour la population de dugongs (*Dugong dugon*) du détroit de Torrès, les estimations d'abondance diminuaient de 15,3% lorsque l'hétérogénéité environnementale était prise en compte. Considérant que les dugongs sont une espèce menacée et que cette population est exploitée par une pêcherie autochtone, cette correction est essentielle (Marsh *et al.*, 2004). Une autre étude menée par Thomson *et al.* (2012) sur deux espèces de tortues marines (*Chelonia mydas* et *Caretta caretta*) a montré que, si l'hétérogénéité du comportement de plongée n'était pas prise en compte, l'abondance serait sous-estimée par un facteur de 10,5 dans un habitat de 9 mètres de profondeur, et serait surestimée par un facteur de 3,5 dans un habitat de 3 mètres de profondeur.

Ainsi, on pourrait s'attendre à ce qu'une correction spatialement explicite du biais de disponibilité pour les bélugas de l'ESL puisse aider à augmenter la précision des estimations d'abondance.

1.7 OBJECTIFS

L'objectif de cette étude est d'élaborer des facteurs corrigeant le biais de disponibilité en tenant compte des variations spatiales de l'environnement et du comportement, afin d'augmenter la précision de l'estimation d'abondance de bélugas dans l'ESL. Les variables environnementales étudiées sont la turbidité et la profondeur du fond, tandis que l'utilisation de l'habitat par les bélugas (aires de haute résidence ou transit) sert d'indice quant à leur comportement. Les facteurs de correction élaborés seront aussi spécifiques au temps de détection associé au type de relevé aérien (photographique ou visuel), afin de rendre plus comparables les estimations d'abondance provenant de ces deux types de relevés. Pour atteindre ces objectifs, l'analyse de données de plongées couplées à des suivis visuels d'individus marqués, obtenues entre 2001 et 2005, sera effectuée.

CHAPITRE 1

ÉLABORATION DE FACTEURS DE CORRECTION POUR LES INVENTAIRES AÉRIENS DE BÉLUGAS DU SAINT-LAURENT

1.1 RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Des estimations d'abondance précises sont essentielles à la détection de tendances pour une population donnée. Toutefois, une partie d'une population inventoriée pourrait être cachée lors d'un relevé; c'est ce qu'on appelle le biais de disponibilité. Pour les cétacés, ceci a lieu lorsqu'ils se trouvent submergés sous l'eau, à une certaine profondeur. La population de bélugas du Saint-Laurent est en voie de disparition, et des relevés aériens photographiques et visuels sont effectués pour suivre l'évolution de sa taille. Les relevés actuels sont corrigés avec un facteur de correction unique et spécifique aux relevés photographiques, et comportent de grands intervalles de confiance. Nous avons émis l'hypothèse que l'inclusion de variables environnementales (profondeur et turbidité) et d'utilisation d'habitat (aires de haute résidence ou transit) aura un effet sur la disponibilité des animaux, et que tenir compte des différences du temps de détection entre les types de relevés rendra plus comparable les estimations d'abondance. Des données de plongée et de localisation, provenant de 30 bélugas équipés de balises enregistrant leur profondeur de plongée et leur position, ont été utilisées pour examiner l'effet de ces facteurs sur la disponibilité des bélugas aux deux types de relevés. En utilisant la proportion moyenne de temps à la surface, ainsi que des équations d'estimation généralisée (GEE) pour tenir compte de l'autocorrélation, nous avons déterminé que la disponibilité globale aux relevés photographiques est de 0,308, équivalant à multiplier par 3,25 les individus comptés, au lieu du 2,26 utilisé présentement. La turbidité diminue la disponibilité, mais la profondeur du milieu et le comportement ne sont pas de bons prédicteurs de disponibilité pour ce type de relevé. Lors des relevés visuels, un modèle GEE-GAM prédit que la durée des intervalles de surface et des plongées augmentent avec la profondeur du milieu, ou lorsque les bélugas sont dans une aire de haute résidence. Ces résultats montrent l'importance de tenir compte de l'hétérogénéité spatiale et du comportement pour corriger le biais de disponibilité pour cette population. Une fois appliqués aux relevés passés, ces facteurs de correction devraient permettre de réduire la variabilité entre les estimations d'abondance, et d'améliorer notre capacité à détecter des tendances.

Mots-clés : biais de disponibilité, estimation d'abondance, relevés aériens, plongées, équations d'estimation généralisée, *Delphinapterus leucas*

Cet article, intitulé « *Development of spatially and behaviourally explicit correction factors for St. Lawrence beluga counts during photographic and visual aerial surveys* », est destiné à être soumis pour publication en 2019 à la revue Methods in Ecology and Evolution. Les coauteurs (Véronique Lesage, Jean-François Gosselin, Robert Michaud et Dominique Berteaux) ont contribué à l'élaboration de l'étude, à la prise de données ou à la révision du manuscrit.

1.2 DEVELOPMENT OF SPATIALLY AND BEHAVIOURALLY EXPLICIT CORRECTION FACTORS FOR ST. LAWRENCE BELUGA COUNTS DURING PHOTOGRAPHIC AND VISUAL AERIAL SURVEYS

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ABSTRACT

Precise abundance estimates are essential to detect significant population trends. However, a proportion of a surveyed population may be unavailable to detection, resulting in availability bias. In cetaceans, this happens when animals are submerged under water, below a threshold depth. The St. Lawrence Estuary beluga population is endangered, and both photographic and visual aerial surveys are flown to keep track of population size. Currently, estimates from both types of surveys are corrected for availability bias using a unique correction factor developed for photographic surveys, and are associated with high confidence intervals. We hypothesized that the inclusion of environmental (depth and turbidity) and of habitat use (high residency areas or transit) variables will affect the availability of animals, and that accounting for differences in detection time between survey types will make point estimates obtained from photographic and visual surveys more comparable. We used diving and location data from 30 beluga equipped with time-depth recorders to examine the effect of these factors on beluga availability for both survey types. Based on the average proportion of time at the surface, and correcting for autocorrelation using generalized estimating equations (GEEs), we determined that overall availability to photographic surveys is 0.308, which means a 3.25 multiplier would be applied to counted animals, instead of the 2.26 multiplier currently used. Turbidity decreased availability, but depth and behaviour were not good predictors of availability to this type of survey. During visual surveys, a GEE-GAM model predicted that surface intervals and dives increased in length with bottom depth, or when beluga were in a high-use area. These results show the importance of taking into account spatial and behavioural heterogeneity in correcting availability bias for this beluga population. Once applied to past surveys, these correction factors should reduce the variability among survey estimates, and increase our capacity to detect trends.

Key words: abundance estimation, availability bias, aerial survey, diving data, Generalized Estimating Equations, *Delphinapterus leucas*

INTRODUCTION

Accuracy of abundance estimates is essential for determining the conservation status of populations, whereas precision around estimates can reduce the time required for detecting significant population trajectories (Taylor *et al.*, 2007). When conducting wildlife surveys, a proportion of animals may be missed either because they are available to be seen but go undetected, or because they are unavailable to detection. These biases, referred to as the perception and availability bias respectively, can both lead to an under-estimation of true population size (Marsh and Sinclair, 1989; Buckland *et al.*, 2004). In the case of marine mammals, availability bias occurs when animals are submerged and thus are unavailable to a passing survey platform; perception bias occurs when animals are at the surface but undetected by the survey platform (Eberhardt, Chapman and Gilbert, 1979; Marsh and Sinclair, 1989). Data to correct for perception bias can be acquired while conducting the survey using for example a double-count, i.e. two independent observers survey the same region and a two-sample mark-recapture estimator is applied (Graham and Bell, 1989; Buckland *et al.*, 2004). This is not the case for availability bias, which requires acquisition of external data (Marsh and Sinclair, 1989; Borchers *et al.*, 1998). As a result, availability bias is sometimes ignored, or when accounted for, it is assumed to be uniform across the surveyed region, even though availability is likely to vary spatially and temporally (Buckland *et al.*, 2004).

Abundance estimates are subject to several sources of uncertainty, and proper survey design is essential to obtain reliable estimates (Buckland *et al.*, 2004; Thomas *et al.*, 2010). For example, a larger number of survey replicates or higher survey coverage can increase estimate precision. The correction for availability bias represents an important source of uncertainty given this factor applies multiplicatively to abundance estimates. Applying a correction to each sighting according to animal behaviour and local environmental conditions might increase estimate accuracy; indirectly, this would also increase the precision of estimates issued from multiple replicates by reducing variance between surveys.

This would be helpful for marine mammals, and particularly cetaceans, since the precision around abundance estimates and the frequency of surveys are often so low that they do not allow detecting even precipitous population declines (Taylor *et al.*, 2007). Previous studies have shown that availability can vary according to different biological or environmental predictors for marine megafauna (e.g. Thomson *et al.*, 2012; Hagihara *et al.*, 2013; Fuentes *et al.*, 2015; Sucunza *et al.*, 2018). For cetaceans, various behavioural and environmental factors can influence availability to a passing survey platform. Environmental factors often include sea state, turbidity and bottom depth (e.g. Pollock *et al.*, 2006; Givens, Hoeting and Beri, 2010; Barlow, 2015). Sea state and turbidity influence the distance and depth at which animals are visible, whereas bottom depth can affect availability by affecting dive duration. Deep dives are generally longer than shallow dives and thus, reduce the relative proportion of time a cetacean spends at the surface over a predefined period (Hooker and Fahlman, 2016). However, the relative influence of bottom depth on availability may vary according to behaviour. In individuals feeding near the sea bed, the influence of bottom depth might be particularly strong (Martin and Smith, 1999; Doniol-Valcroze *et al.*, 2011). Conversely, availability may be higher and less influenced by bottom depth in animals travelling, resting or socializing at the surface (e.g. Whitehead and Weilgart, 1991).

Survey type can also impact availability. Marine mammals and several other species of wildlife are generally surveyed using visual or photographic surveys (Buckland *et al.*, 2004). Counts are expected to be higher during visual surveys given the longer period animals have to become available to a searching observer, compared to a photograph, which provides an instantaneous snapshot of animals available to the survey platform. Counts from visual and photographic surveys are therefore not directly comparable and need to be corrected for this difference in detection time.

The beluga (*Delphinapterus leucas*) is a particularly challenging species to survey given its highly social and gregarious nature (Michaud, 2005; Gosselin *et al*., 2017). As a result, abundance estimates are often associated with coefficients of variation in excess of 25-35% (e.g. Gosselin, Hammill and Lesage, 2007; Gosselin, Lesage and Hammill, 2009;

Gosselin, Hammill and Mosnier, 2014). Beluga counts may double even when surveys are conducted days apart (Gosselin, Hammill and Lesage, 2007; Gosselin *et al.*, 2017). Given the precarious conservation status of several beluga populations worldwide, obtaining accurate abundance estimates is particularly important to monitor trends for these populations, and assess the effectiveness of recovery actions. In this context, incorporating environmental and behavioural aspects should benefit the correction of availability bias.

The southernmost population of beluga is found in the St. Lawrence Estuary (SLE). This population is considered endangered (COSEWIC, 2014; Species at Risk Public Registry, 2011), and is declining at a rate of approximately 1% per year (Mosnier *et al.*, 2015). The SLE population has been monitored using systematic aerial surveys that cover their entire summer distribution since 1988 (Gosselin *et al.*, 2017). These surveys were exclusively photographic until 2001, when visual surveys started to be conducted on a regular basis to monitor population size and trends (Gosselin, Hammill and Lesage, 2007). Currently, a single correction for availability bias is applied uniformly to all survey counts (Kingsley and Gauthier, 2002; Gosselin *et al.*, 2017).

Areas where beluga aggregate consistently during summer, known as high-use areas, have been identified (Lemieux Lefebvre *et al.*, 2012; Mosnier *et al.*, 2016). Behaviour such as feeding likely occurs within high-use areas, while the rest of their distribution range is thought to be mainly used for transit. Therefore, availability is expected to differ according to location. As mentioned previously, bottom depth and turbidity at the location of sighted beluga are also of interest.

In this study, spatially and behaviourally explicit correction factors for availability bias are developed for photographic and visual aerial surveys using detailed dive profiles of SLE beluga obtained by deploying archival tags on individual whales. We hypothesized that accounting for environmental and behavioural features, and for differences in detection time between the two survey designs, will result in differing correction factors for availability bias, which are likely to improve the comparability of point estimates obtained from photographic and visual surveys.

METHODS

Survey methods and study area

Abundance estimates for SLE beluga are generally obtained during summer, when distribution is the most constrained (Mosnier *et al*., 2010; Gosselin *et al.*, 2017). While the SLE is flown using a line-transect survey design, the narrow Saguenay Fjord is flown up and down on a single track, and the observed maximum number of beluga seen during a pass is included as a total count (Gosselin *et al*., 2017). Line spacing for the photographic survey is 2 nautical miles; one line out of two is flown during visual surveys resulting in a 4 nm line spacing (Figure 1; Gosselin, Hammill and Mosnier, 2014).

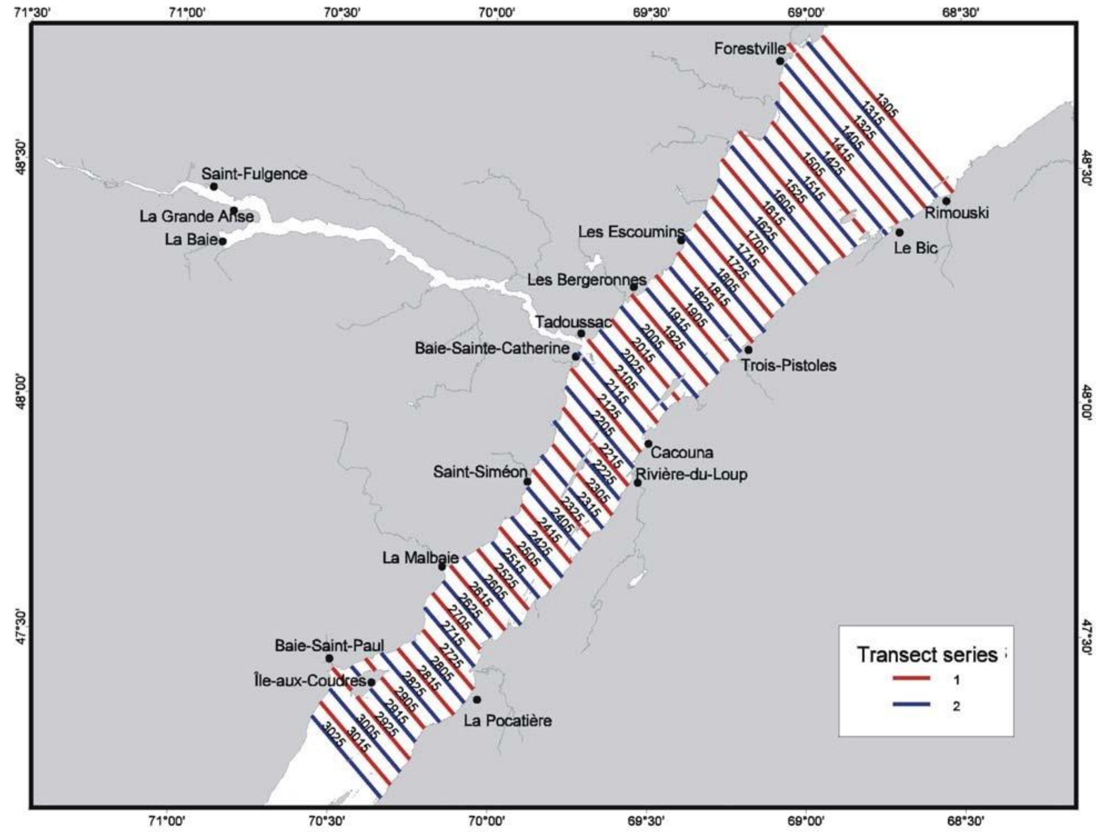

Figure 1 An example of transects flown during systematic photographic and visual surveys (the Saguenay track is not shown). Visual surveys followed one of the two transect series, while photographic surveys covered all transects (Gosselin, Hammill and Lesage, 2007).

The SLE beluga distribution range is heterogeneous in bottom topography and turbidity (Figure 2). For example, the mouth of the Saguenay Fjord is quite shallow, while 20 km north-east, the Laurentian Channel reaches more than 355 m (Figure 2a; Duchesne *et al.*, 2010). Water turbidity varies among sectors as a result of suspended particulate matter levels and salinity (Silverberg and Sundby, 1978; d'Anglejan, 1981; El Sabh and Silverberg, 1990). A Secchi-disk survey indicates a mean turbidity threshold of 4 m across the SLE beluga summer range during a year with no excessive rainwater runoff (Kingsley and Gauthier, 2002). However, during the two-year study, this threshold varied between 1.5 m and 11.6 m among sectors, and was higher (1.5-2.5 m) in the upstream portion of the SLE (Upper Estuary), intermediate (3.5-6.5 m) in the southern half of the downstream portion of the SLE (Lower Estuary), and lower (4.5-11.6 m) over the deep Laurentian Channel located in the northern half of the Lower Estuary (Figure 2b; Gauthier, 1999). The mid-range values for each of these turbidity zones were used as turbidity thresholds in subsequent analyses (i.e. 2, 5 and 8 m for zones 1 to 3 respectively), since average or median values for each zone were not available. Beluga will sometimes be detected below these thresholds, but they will also sometimes go undetected at depths shallower than the mid-range value.

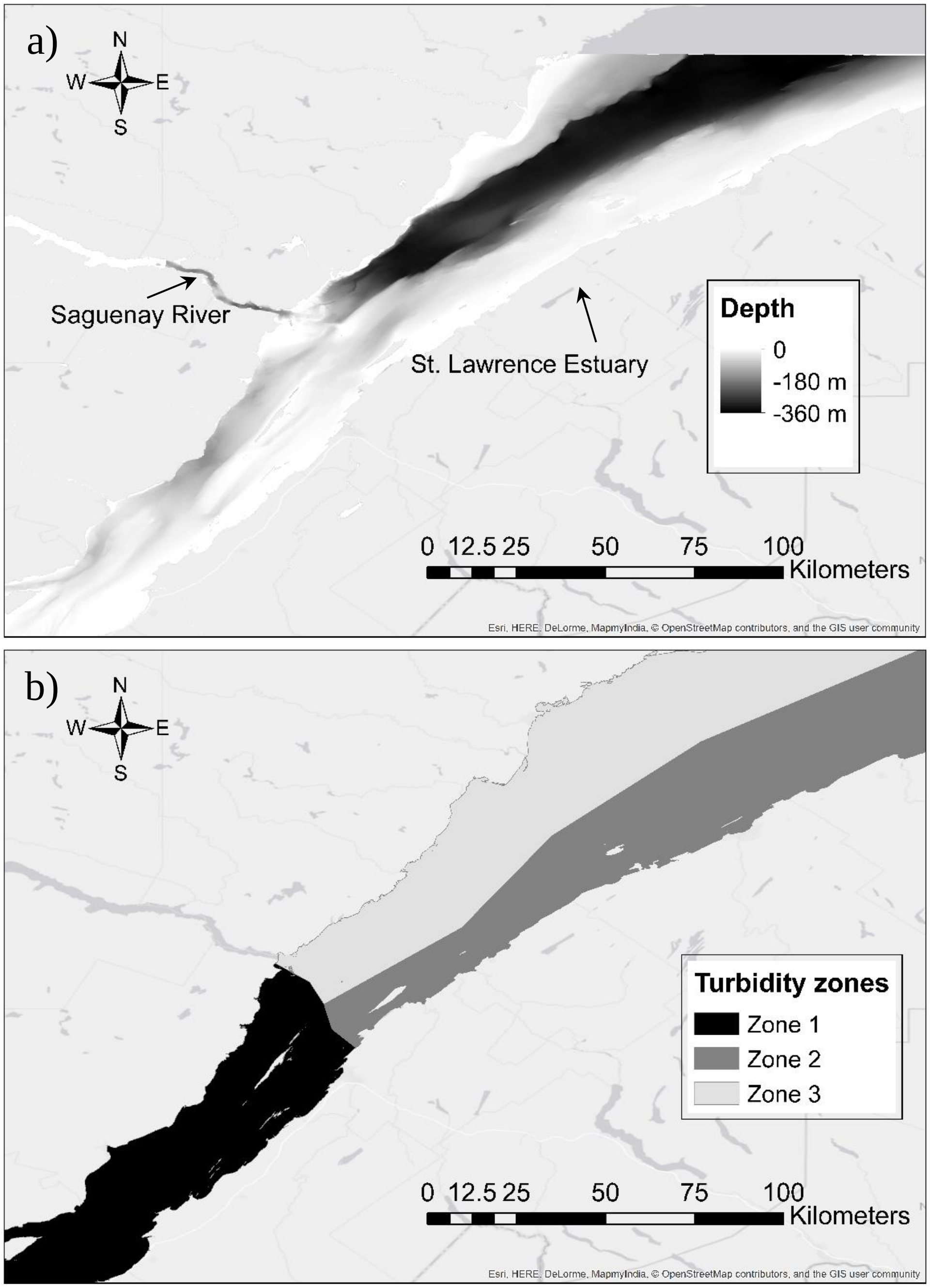

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Figure 2 In the SLE, both sea floor depth (a) and turbidity (b) are heterogeneous (modified from Canadian Hydrographic Service, and Gauthier, 1999). The north side of the SLE, downstream of the Saguenay is characterized by the deep Laurentian Channel, while the upstream portion is characterized by shallow water. Three turbidity zones have been described in Kingsley and Gauthier (2002): zone 1 is the most turbid, with a mid-range Secchi-disk depth of 2 m, while zone 2 is intermediate at 5 m and zone 3 is the clearest, at 8 m.

Data collection

Availability biases associated with photographic and visual aerial surveys, and the influence of behaviour and environmental features on availability to a passing airplane were examined using detailed diving behavioural information obtained from individually radio-tracked beluga. Between June and September of 2001 to 2005, archival tags were deployed from a small vessel on 44 belugas, using a cross-bow or a 3 m pole. Tags contained a time-depth-velocity recorder (TDR Mk8, Wildlife Computers, Redmond, WA) and a 300 g radio transmitter (VHF, Telonics, Mesa, AZ), housed in a floating remote-released package and attached to the animal with a suction cup. The release mechanism was a magnesium cap designed to release suction by corroding after 4 to 6 hours. Depth (± 0.25 m) was recorded every second. Beluga were tracked from a distance (400 to 600 m) to avoid affecting their behaviour. The GPS position of the vessel, along with the bearing and distance of the animal relative to the tracking vessel, were recorded after each surface interval to obtain its relative position. The follow ceased either at dusk, when the signal was lost, or when the tag was released. Some of the tags fell off the next day and on these occasions, data on nighttime activity were also recorded.

Positions of surface intervals with missing values were calculated from a linear interpolation of the preceding and following surface intervals. However, this procedure was only applied when the time elapsed between two known positions was less than 25 minutes, which is approximately the longest time period recorded between two successive surface intervals. The location of collected data throughout the SLE can be found in Figure 3.

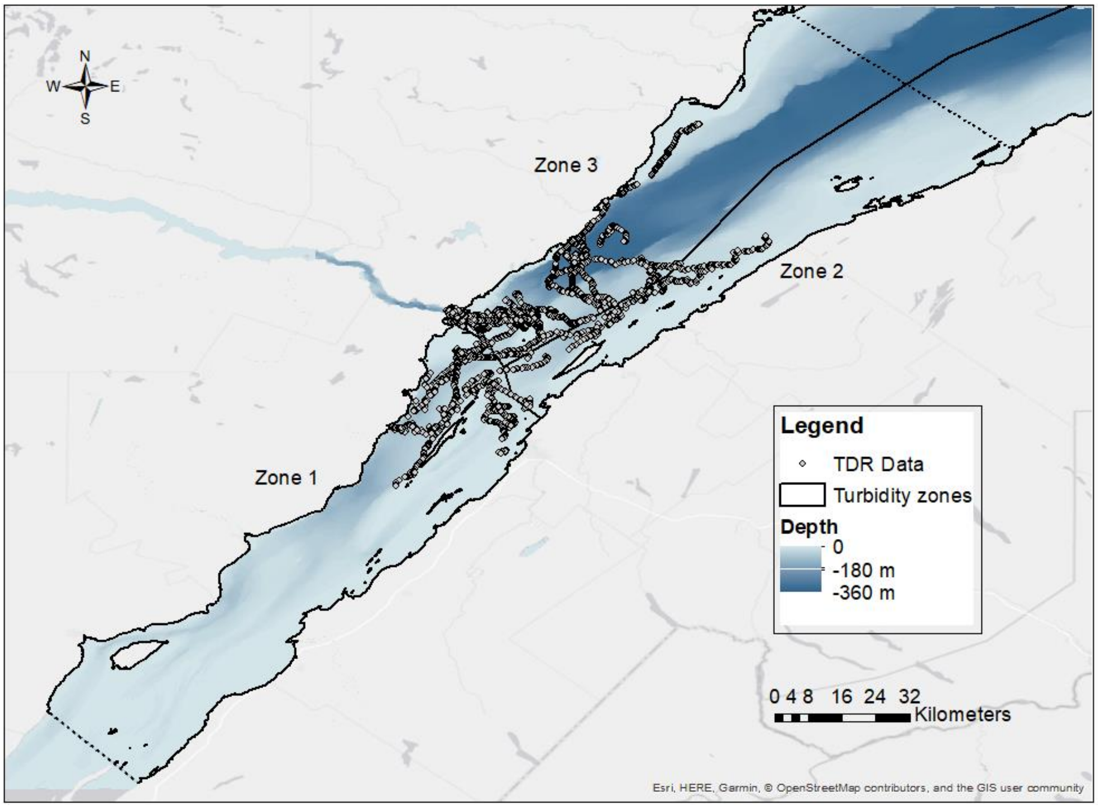

Figure 3 Spatial distribution of beluga dive data collected between June and September 2001 to 2005. Each dot corresponds to the position of a beluga at the start of a dive. The blue gradient represents depth, and the three turbidity zones are represented by the black contours. The dotted lines represent the limits of the beluga summer range (Michaud, 1993). See Figure 2 for more details on bottom depth and turbidity zones.

Dive data analysis

Zero-offset correction was performed manually using Instrument Helper (Wildlife Computers Inc., Redmond, WA). A custom-made program was used to obtain dive profiles and various statistics, including dive duration, time spent at the surface and maximum depth. The first and last intervals were removed since they might not have been complete. Dive data were excluded when location data were missing due to loss of contact for over 25 minutes, or when they were associated with periods outside of survey hours (i.e., between dusk and dawn, which varies throughout the summer), or when the animal was in the Saguenay Fjord where counts are uncorrected for availability bias (Gosselin *et al.*, 2017).

At first, a dive was defined as any excursion below 0.5 m. A surface interval consisted in a series of short and shallow dives, whereas an individual dive's duration corresponded to the time elapsed between two successive surface intervals. A bout-ending criterion with the maximum likelihood estimation method (MLM) was used to discriminate between these dive phases (Langton, Collett and Sibly, 1995; Luque and Guinet, 2007). An optimization algorithm (an extension of limited memory Broyden-Fletcher-Goldfarb-Shanno, or L-BFGS-B) was used as part of the function to identify bouts. The upper and lower bound values were specified following Luque (2007). Then, dive profiles were recomputed by defining a dive as any excursion below the global turbidity threshold and that of the three zones (i.e. 4, 2, 5 and 8 m respectively). The time stamps of surface intervals established previously with the bout-ending criterion method were used to identify any short dives below these turbidity thresholds that should in fact belong to surface intervals. Therefore, final surface intervals sometimes include very short periods of time during which beluga were below the turbidity threshold. The effect of this decision on surface interval length was measured by also measuring the length of surface intervals while excluding these short dives below the threshold.

Correcting for Availability Bias

The basis for the availability correction factor $a(S,x)$ for visual surveys comes from the model developed by McLaren (1961). This model was later improved to describe surface interval and individual dive durations ($E(s)$ and $E(d)$, respectively) as a two-state continuous-time Markov process (Eq. 1; Laake *et al.*, 1997). $E(s)$ and $E(d)$ were obtained from the tag data, and correspond to the mean duration of surface intervals and dives of individual beluga, averaged across the sample.

Eq. 1

$$a(S,x) = \frac{E(s)}{E(s)+E(d)} + \frac{E(d)\left[1-e^{-w(x)/E(d)}\right]}{E(s)+E(d)}$$

The first term of Eq. 1 corresponds to the relative duration of surface intervals. The second term estimates the probability *w(x)* of a group breaking the surface during the plane overpass. In the case of visual surveys, *w(x)* is estimated through Eq.2, given the observer's field of view (forward and backward angles $Ø_1$ and $Ø_2$, respectively), plane speed v and perpendicular distance x of the sighting relative to the transect line (Forcada *et al.*, 2004; Gómez de Segura *et al.*, 2006).

For comparison purposes with photographic survey results, *a(S,x)* for visual surveys was calculated for sightings at perpendicular distances varying from 172 m (i.e. the mean left truncation) to 3 000 m (i.e. the maximum distance recorded), while assuming typical visual survey conditions for forward and backward angles (30 and 20 degrees respectively) and plane speed (100 knots or 51.39 m/s).

Eq. 2

$$w(x) = \frac{x}{v}[\cot(\emptyset_1) + cot(\emptyset_2)]$$

In the case of photographic surveys, animals considered available to the passing plane are those located above a turbidity threshold. Availability is therefore calculated as the average proportion of time individually-tracked beluga spent above a turbidity threshold, regardless of surface interval or dive durations (Eq. 3).

Eq. 3

$$a = \frac{s}{s + d}$$

where *s* represents the time spent above a given turbidity threshold, and *d* corresponds to the time spent below the threshold.

Photographic correction factors need to take into account the overlap between adjacent photographs. The overall probability that a beluga would be visible in at least one image if it is present in the survey strip depends on the percent overlap *V*, the probability P_D of a beluga being in at least one of two photographs, and the availability a (Eq. 4; Kingsley and Gauthier, 2002).

Eq. 4

$$\bar{P} = \frac{(1-2V)a + VP_D}{1-V}$$

The achieved overlap between adjacent photographs used by Kingsley and Gauthier (2002) to develop their correction factor was 30%. For comparison purposes, results will be presented for this amount of overlap. As for P_D, it was estimated to be 51.7% with a standard error of 3.0% (Kingsley and Gauthier, 2002).

Data analysis

Availability bias for photographic and visual surveys and associated uncertainty were examined using three different approaches. First, they were calculated globally for the summer range of SLE beluga, without consideration for environmental heterogeneity or potential variability in behaviour. For the photographic survey, availability to the plane (s in Eq. 3) was set as the time spent above a 4 m turbidity threshold, which corresponded to the mean Secchi-disk value for the beluga summer habitat, that is the depth beyond which white beluga can no longer be seen from the surface (Kingsley and Gauthier, 2002). For visual surveys, the mean $E(s)$ and $E(d)$ were calculated, using the profiles where dives were defined as going below 4 m, as discussed earlier in ‘Dive data analysis’.

Second, availability biases for the two types of surveys were examined while accounting for local turbidity, by attributing each geo-referenced surface interval/dive duration to one of three turbidity zones identified by Kingsley and Gauthier (2002). Mean s, d, $E(s)$ and $E(d)$ were then recalculated for each zone, using for photographic surveys turbidity values of 2 m for zone 1, 5 m for zone 2 and 8 m for zone 3 (Figure 2b; Gauthier, 1999).

Third, availability biases were calculated while accounting for potential variability in behaviour, as reflected by beluga location in high-use versus transit areas, and in bottom depth. High-use areas have been identified in two long-term studies using different approaches and data sets (Lemieux Lefebvre *et al*., 2012; Mosnier *et al*., 2016). The two approaches converged in the areas identified (Savenkoff *et al.*, 2017). Mosnier *et al*. (2016) offered a full coverage of the SLE beluga summer range, and Lemieux-Lefebvre *et al.* (2012) only a partial coverage. Therefore, Mosnier's areas of high density (AHD; 50% kernel density) were used as a proxy for high-use areas (Figure 4). As we assume that feeding occurs mainly in high-use areas, and transit outside of these areas, availability to a passing plane might be less in high-use areas if belugas feed at depth, and might be higher outside of high-use areas when belugas are transiting and staying possibly closer to the surface. Availability is also likely to decrease with increasing depth. Information on seafloor depth, and whether the individual was within or outside of a high-use area, were extracted for each geo-referenced surface interval/dive duration. Bathymetric data (horizontal resolution of 50 m) were obtained from the Canadian Hydrographic Service.

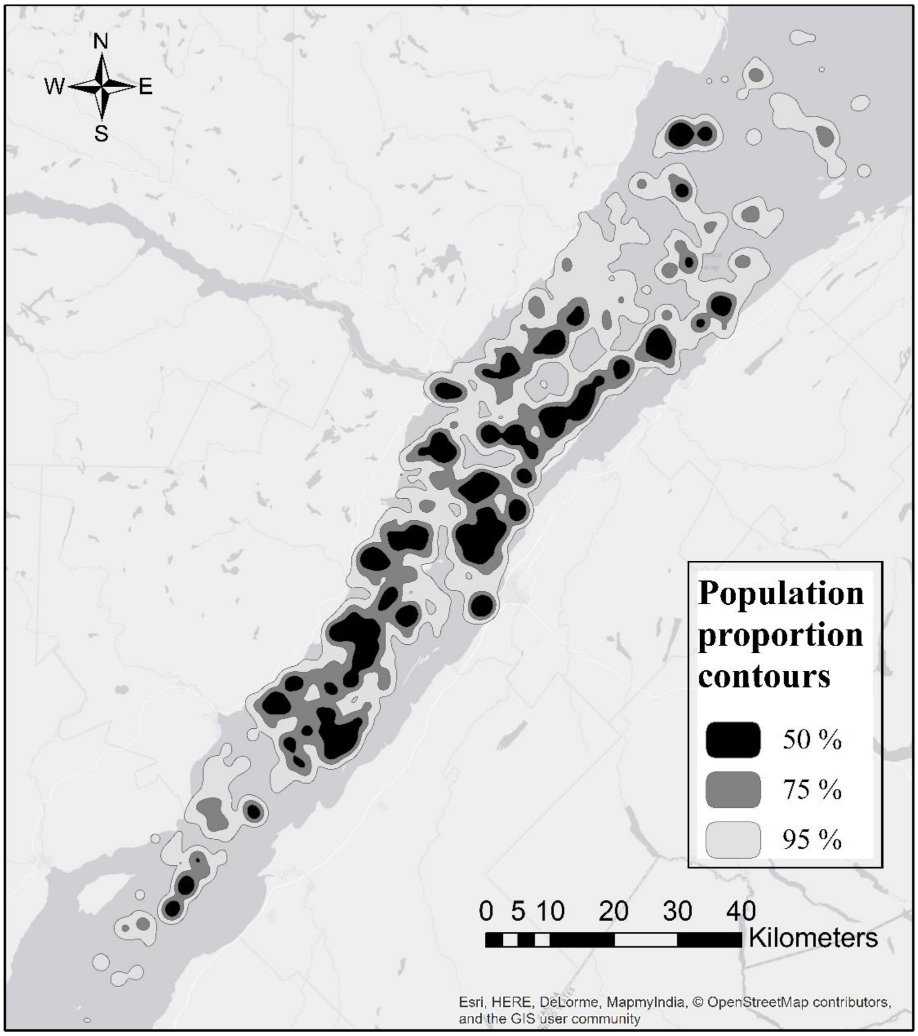

Figure 4 Areas of high density (AHD) cumulating 50, 75 and 95% of the beluga population, as defined by the kernel method, applied to data from 35 systematic aerial surveys led from 1990 to 2009 (modified from Mosnier *et al.*, 2016). The 50% contour was used as a proxy for high-use areas.

The proportion of time spent at the surface (photographic surveys) and surface interval/dive duration (visual surveys), as a function of depth and location relative to high-use areas (within or outside), were modeled using Generalized Linear Models (GLMs). To avoid sub-setting our data to reduce autocorrelation between successive dives, a Generalized Estimating Equation (GEE) approach specifying the correlation structure among residuals was applied to the data, bypassing the independence assumption (Liang and Zeger, 1986). This approach uses robust sandwich estimators to produce realistic standard errors, although these tend to be underestimated unless the sample size is very large (Liang and Zeger, 1986). It is an ideal approach when interest is in the mean effect of co-variates on the population response (Gardiner, Luo and Roman, 2009; Hubbard *et al.*, 2010), and is also robust to correlation structure misspecification (Liang and Zeger, 1986; Pan and Connett, 2002).

Normally distributed GEE-GLMs with identity link functions were carried out using the geepack library (Højsgaard, Halekoh and Yan, 2006) and individual beluga as a blocking factor. The terms of the model were: dive phase, which is binary (surface interval or dive); bottom depth; and location in or outside of an AHD, which is also binary. Depth, which is the only continuous independent variable, was modelled both as a linear and as a smooth term (cubic *B*-spline), thus leading to a GEE-GAM. Different correlation structures were tested: autoregressive, exchangeable and independent. Model selection was performed using an extension of the Akaike Information Criterion (AIC), the quasi-likelihood independence model criterion (QIC; Pan, 2001), which allows comparing covariance matrices under GEE models to the covariance matrix of models that assume no correlation within blocks. The approximation of this criterion is known as the QICu (Hardin and Hilbe, 2003), and is provided by the QICpack library in R (Hocking, 2014). The QICu score was used to confirm that the full model performed better than the null model, to select the best form (linear or smooth) for the depth variable, and to determine the order of variables. The model with the lowest QICu was considered as the model with the most appropriate correlation structure to fit the data.

Model adequacy was assessed based on a Wald-Wolfowitz run test for randomness of residuals and a scale parameter for dispersion. The significance of covariates was assessed using repeated Wald's tests on the final model (Hardin and Hilbe, 2003). As an indication of model performance, the root mean square error (RMSE) was computed with the hydroGOF library (Zambrano-Bigiarini, 2017). RMSE are in the same units as the response variable, and lower values relative to the response variable indicate a better accuracy.

Differences in the proportion of time spent at the surface (s or $E(s)$) or diving (d or $E(d)$) between the three turbidity zones were examined for statistical significance ($\alpha = 0.05$)

using ANOVAs. Linear regressions and ANOVAs were also employed to test the relationships between the response variables and AHD or depth before conducting GEE-GAMs. Transformations of the duration of surface intervals and dives (logarithmic base 10 and square root, respectively) were required for the ANOVAs and linear regressions. Regarding proportion of time spent at the surface, a logarithmic (base 10) transformation was required for the ANOVA comparing availability between turbidity zones; no transformation was required for the other ANOVA or linear regressions. All statistical analysis were conducted with R version 3.4.3 (R Core Team, 2017).

RESULTS

Fourteen of the 44 tags deployed could not be used: One was lost, three did not record data, three provided data solely in the Saguenay Fjord, and seven were deployed on beluga we lost sight of after tagging. Deployment duration varied among the thirty remaining tags, with the shortest deployment lasting 34 min, and the longest lasting 10 h 31 min. Total deployment length for these thirty tags was 293 h 38 min. Once nighttime activity and segments during which tagged individuals were lost from sight were removed, there remained a total of 134 h 05 min and an average of 4 h 28 min of usable data per beluga for analysis.

Global availability

The average proportion of time that beluga spent above the 4 m turbidity threshold was 0.308 (s.e. = 0.023), which would correspond to applying a multiplication factor of 3.25 (i.e. the reciprocal of 0.308) to photographic survey abundance estimates. When adjusted for a 30% photographic overlap, this proportion was 0.398 (s.e. = 0.013), equivalent to a multiplication factor of 2.51.

For visual surveys, availability estimated as the average surface interval length was 73.2 s (s.e. = 5.7), while the average dive duration was 153.4 s (s.e. = 14.1). Applying values for plane speed and observer field of view that are typical of SLE beluga visual surveys (see Methods), $w(x)$ varies from 0.97 at a perpendicular distance of 172 m, to 16.98 at the maximum distance of 3 000 m. The average proportion of time that a beluga group would be available to an observer varies from 0.327 to 0.394 within this perpendicular distance range (Figure 7).

Availability by turbidity zone

The proportion of time spent above a specified turbidity threshold and thus, available to a passing plane during a photographic survey, varied significantly between turbidity zones ($F_{2, 42} = 27.98$; $p < 0.001$). As expected, availability decreased with an increase in turbidity, and was the highest in zone 3 over the Laurentian Channel, and the lowest in zone 1, the Upper Estuary (Figure 5).

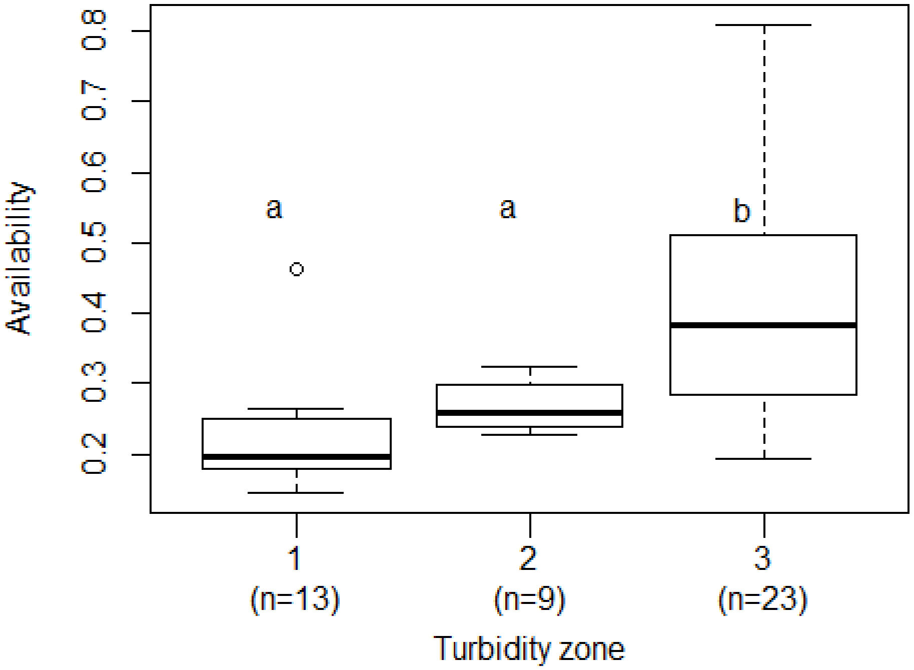

Figure 5 Availability to photographic survey planes for three turbidity zones in the St. Lawrence Estuary. Zone numbers correspond to the Upper Estuary (1, high turbidity), the southern Lower Estuary (2, intermediate turbidity) and the northern Lower Estuary (3, low turbidity). Sample size (n) corresponds to the number of beluga using each zone. Zones identified by different letters indicate a statistically significant difference (ANOVA, $p < 0.05$). See Appendix I for means and standard errors of availability for each turbidity zone.

For visual surveys, availability to a passing plane, measured by the duration of surface intervals, also increased significantly with a decrease in turbidity, with surface intervals over the Laurentian Channel (zone 3) being significantly longer than in the Upper Estuary (zone 1) (Figure 6a; $F_{2,\ 2130} = 10.62$, $p < 0.001$). While dive durations varied significantly among turbidity zones ($F_{2,\ 2151} = 43.56$; $p < 0.001$), they did not follow the gradation in turbidity (Figure 6b). Dive durations over the southern portion of the Lower Estuary and the Upper Estuary were similar and relatively long compared to dive durations from beluga above the Laurentian Channel (zone 3).

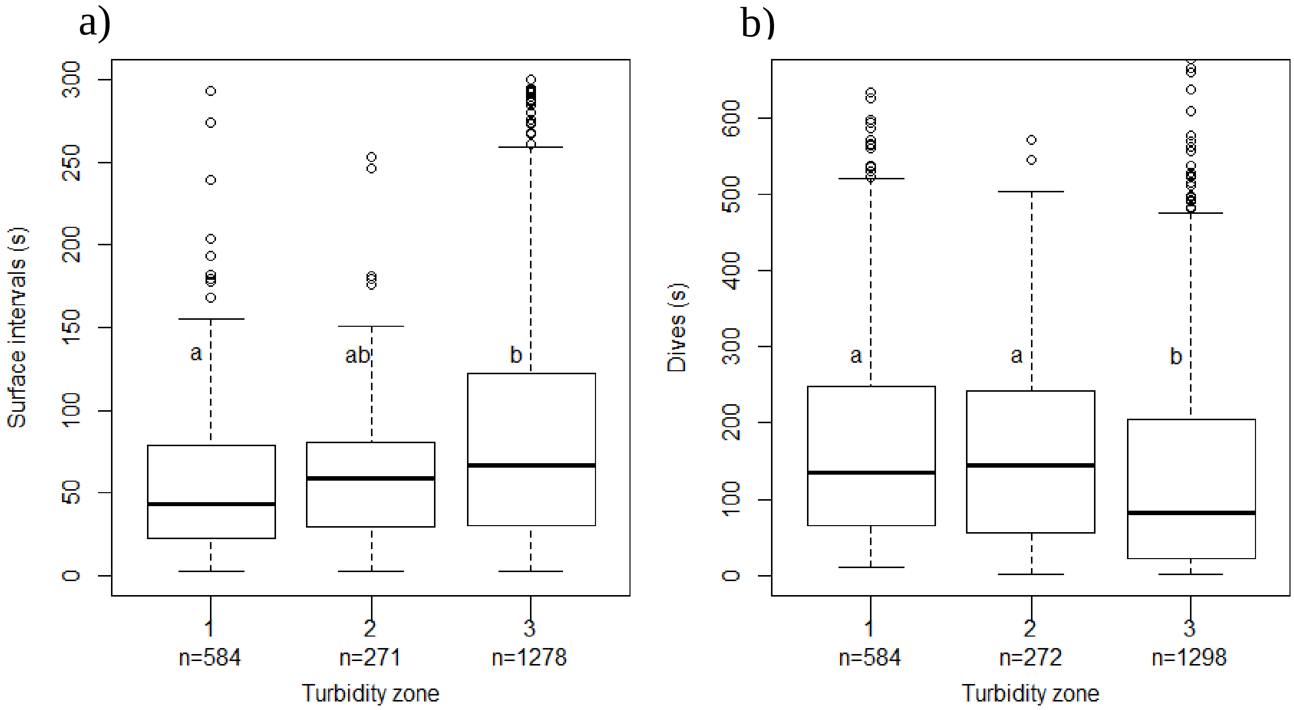

Figure 6 Surface interval durations (a) and dive durations (b) (*E(s)* and *E(d)* respectively), in seconds, for all three turbidity zones in the St. Lawrence Estuary. Zone numbers correspond to the Upper Estuary (1, high turbidity), the southern Lower Estuary (2, intermediate turbidity) and the northern Lower Estuary (3, low turbidity). Sample size (n) corresponds to the number of surface intervals or dive durations in each zone, using individual beluga as a blocking factor. Zones identified by different letters indicate a statistically significant difference (ANOVA, $p < 0.05$). Some outliers, but real data points, have been removed from the figure for clarity. See Appendix II for means and standard errors of surface intervals and dive durations in each turbidity zone.

The availability to visual surveys, when applied to perpendicular distances of 172 to 3 000 m from the trackline, was highest for zone 3 (0.456-0.519), which is the least turbid (Figure 7). Availability decreased with increasing turbidity, reaching 0.276-0.345 for zone 2, and 0.242-0.309 for zone 1, which is the most turbid.

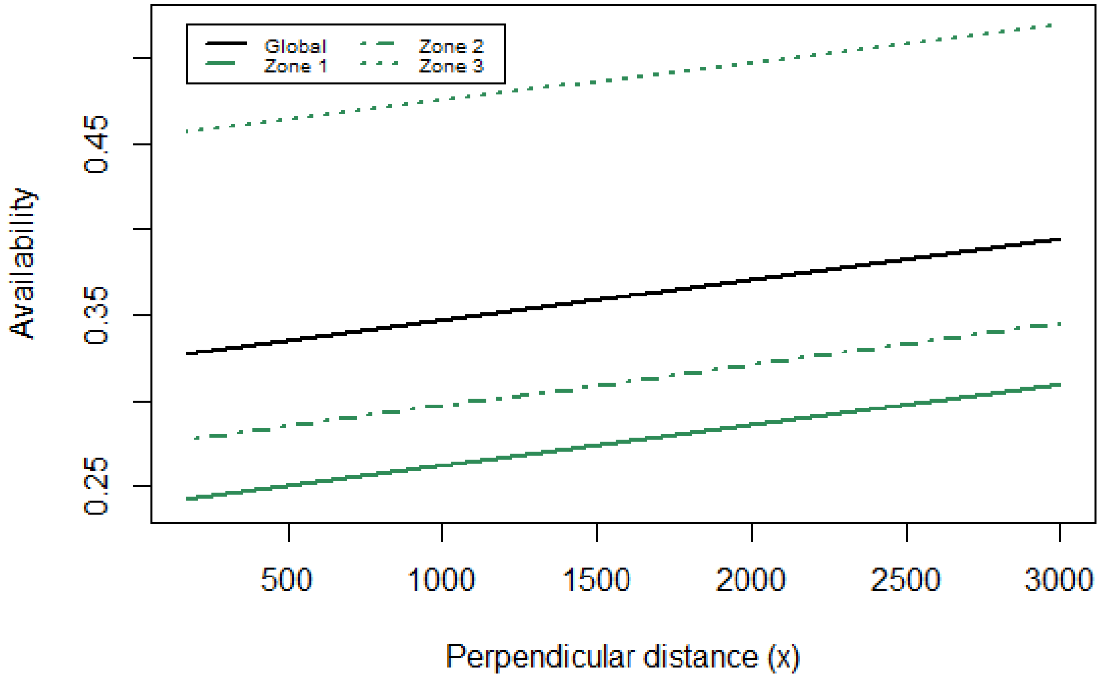

Figure 7 Availability to visual surveys for all data (solid black line), and separated according to the three turbidity zones (green lines). Typical survey values for plane speed and observer field of view were applied, for perpendicular distances from the trackline ranging from 172 to 3 000 m.

Availability while accounting for behaviour

Before running the GEE-GAM models, links between the independent variable and the covariates were explored. For photographic surveys, linear regressions using a global turbidity threshold of 4 m showed a marginally statistically significant relationship between bottom depth and the proportion of time an animal spent above 4 m (t = 1.83, p = 0.067). This effect became significant when separating data according to whether animals were in an AHD (t = 2.28, p = 0.023) or in transit (t = 2.05, p = 0.040). However, bottom depth only had an effect when using the global turbidity threshold of 4 m. When 2, 5 or 8 m thresholds were used, no significant relationships were found (all $p > 0.216$). Therefore, depth could be used to predict availability to photographic surveys when using the 4 m turbidity threshold, although fit is poor in all cases (all $r^2 < 0.004$).

An ANOVA using turbidity as a blocking factor (all three zones and the global 4 m threshold) was conducted to test the effect of being inside or outside of an AHD on the proportion of time spent at the surface. As expected from Figure 5, time spent at the surface varied significantly among turbidity zones ($F_{3, 121} = 7.498$, $p < 0.001$), and was also significantly different when animals were inside AHD compared to when they were outside these areas (in transit) ($F_{1, 121} = 5.439$, $p = 0.021$). However, this difference was not seen when global data (4 m threshold) were excluded ($F_{1, 70} = 0.957$, $p = 0.331$). These potential differences in availability at the surface depending on bottom depth and behaviour (inside or outside AHD) were further examined for the 4 m threshold, using GEE-GAM to account for autocorrelation in the data. The model with the best fit only had bottom depth as a predictor variable, modelled as a cubic *B*-spline with one knot at the median value, but its RMSE (1.47), which was many times higher than the range of values for the response variable (all below 1), indicated that the model performed poorly. When included in the model, location inside or outside an AHD was deemed non-significant ($p = 0.761$). In light of these results, additional analysis were not conducted and prediction maps for the proportion of time spent at the surface with beluga location relative to AHD were not created.

For visual surveys, global exploratory analysis (without taking into account turbidity) revealed that both surface interval and dive duration increased with bottom depth (surface interval slope: $t = -3.304$, $p < 0.001$; dive slope: $t = -6.677$, $p < 0.001$), although fit was poor ($r^2 = 0.005$ and 0.012, respectively). Surface interval and dive duration were also longer when beluga were inside as opposed to outside of an AHD (ANOVA with turbidity as a blocking factor, for surface intervals $F_{1, 4300} = 3.17$; $p = 0.075$ and dives $F_{1, 4345} = 11.82$; $p < 0.001$), and also varied per turbidity zone, as shown in Figure 6 (surface intervals: $F_{1, 4300} = 21.24$, $p = 0.006$, dives: $F_{1, 4345} = 6.98$; $p = 0.008$). Exploration of these relationships using GEE-GAMs and duration of a dive phase (either surface or dive) as the response variable revealed that bottom depth modelled as a cubic *B*-spline, with one knot placed at the median value and thus with four regression parameters, was the model best fitting the data without over-fitting. As expected, surface intervals and dives differed in duration and thus needed to be accounted for in the model (dive phase term was retained in the final model). Models not accounting for whether beluga were inside or outside an AHD performed better than those not accounting for bottom depth. This indicated that bottom depth explained a larger part of the variance than location relative to AHD, although this last variable also explained a significant part of the variance and was included in the final model. A Wald's test confirmed that this factor was not as important as the other two in explaining variability in dive or surface durations (Table 1).

Table 1 Predictor coefficients of the best model, which includes dive phase (surface interval or dive) as the first term, followed by the four regression parameters of depth as a cubic *B*-spline, and location within or outside of an AHD. Wald's test results (χ^2 and p) are also shown.

Variable	**Coefficient**	**S.E.**	**df**	**χ^2**	**p**
Intercept	9.432e-03	2.270e-03	/	/	/
Dive phase	-6.963e-03	1.066e-03	1	44.097	< 0.001
Depth 1	7.670e-03	3.593e-03	4	23.096	< 0.001
Depth 2	-3.155e-03	1.681e-03			
Depth 3	3.854e-03	1.590e-03			
Depth 4	8.903e-03	2.644e-03			
AHD	1.615e-05	1.247e-05	1	1.678	0.195

These results indicate that the duration of dives and surface intervals increased with bottom depth (positive coefficients for 3 out of the 4 depth parameters), and were higher when beluga were inside an AHD rather than outside these areas, i.e., in transit zones (Table 1). The independence correlation structure better described the data than autoregressive and exchangeable structures according to QICu scores (Table 2). The RMSE value was low compared to the range of values for the response variable (0.011 vs range of 50 to 670 s, depending on dive phase), indicating high model accuracy.

Table 2 QICu scores for the three tested correlation structures (independence, exchangeable and autoregressive). The correlation structure with the lowest score is the most appropriate one to fit the data. The scores shown here were obtained from best-fit models, in which depth was represented as a smooth term with one median knot. Dive phase was the first term in the model, followed by depth and AHD.

Correlation structure	**QICu**	**ΔQICu**
Independence	49318.12	0.00
Autoregressive	49328.18	10.06
Exchangeable	49373.62	55.50

Predicted surface intervals and dive durations varied in a very similar way over the beluga summer distribution (Figure 8). Dive durations and surface intervals were the longest in the deep Laurentian Channel, and when beluga were inside AHD. Standard errors of these predictions varied between 0.02 and 0.18 for surface intervals, and between 0.04 and 5.70 for dive durations (Figure 9). The higher range of standard errors for dive duration results from a few particularly long dives performed by one beluga while in the Laurentian Channel, and the smaller sample size for this specific zone.

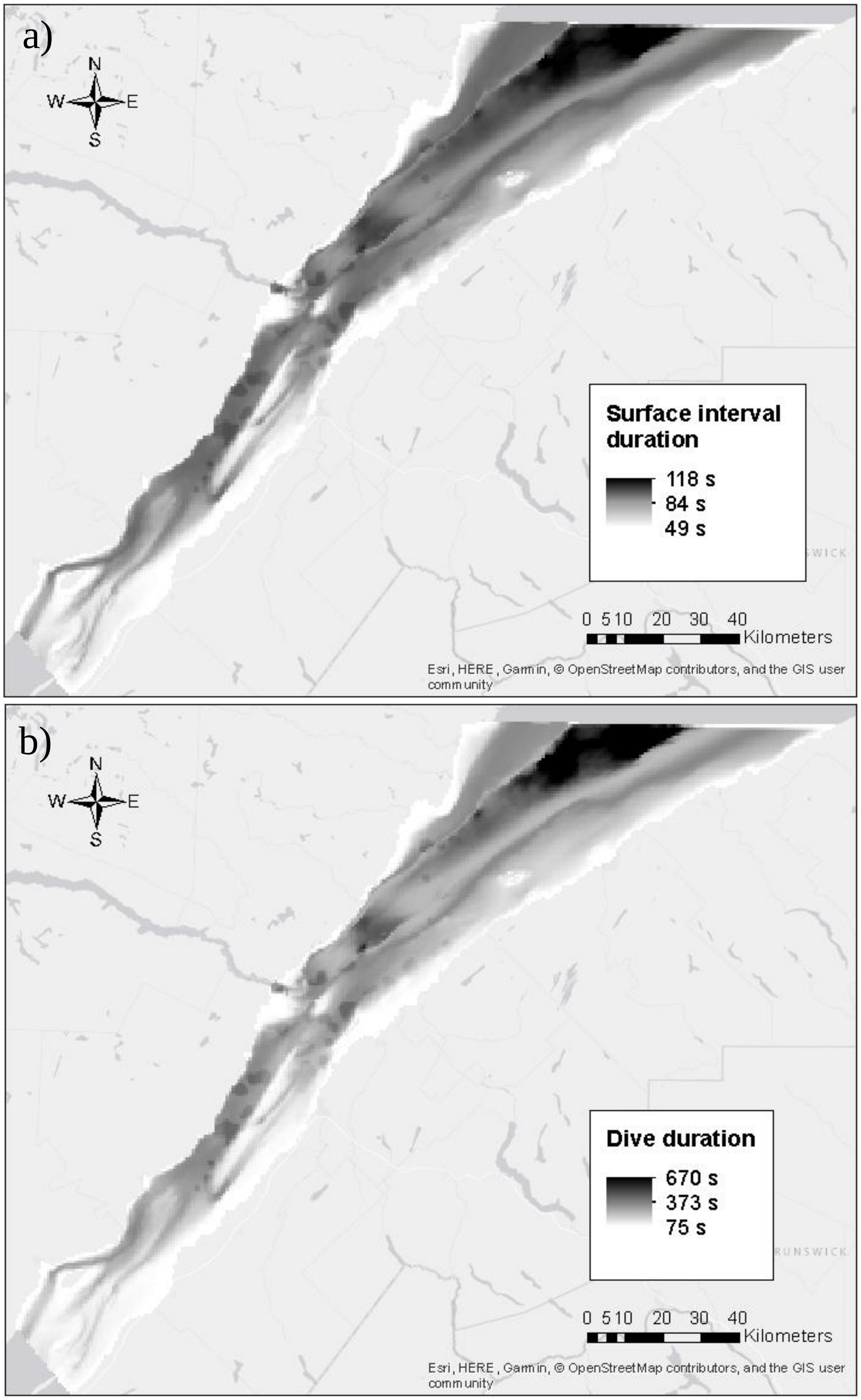

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Figure 8 Predicted surface interval durations (a) and dive durations (b) as a function of depth and location relative to areas of high density.

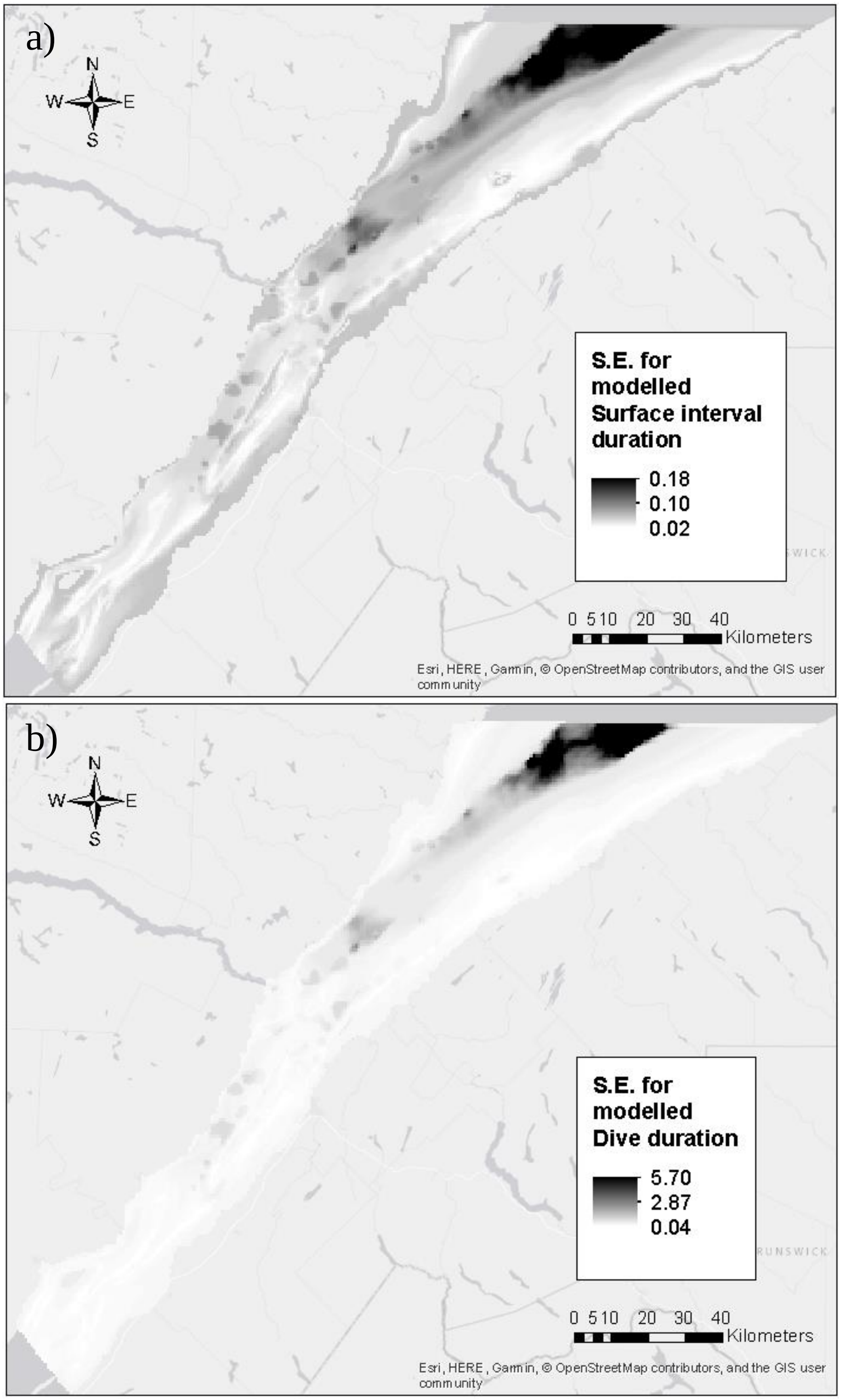

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Figure 9 Standard errors for modelled surface interval durations (a) and dive durations (b) as a function of depth and location relative to areas of high density.

Impact of inclusion of short dives on surface interval length

Surface interval lengths (*E(s)*) excluding any short excursion below a given turbidity threshold were calculated to quantify the bias introduced by the definition of surface interval used in this study. For thresholds of 4, 5 and 8 m, these surface intervals were only 4.4, 2.2 and 0.3 % shorter than the surface intervals that did include short dives. At a threshold of 2 m, the difference was much bigger with surface intervals 18.3 % briefer when short dives were excluded, due to beluga often diving deeper than 2 m during their surface intervals.

DISCUSSION

Correcting for availability bias is a recognized necessity for obtaining accurate abundance estimates. This study provides the first correction for availability bias that is specific to SLE beluga visual surveys, and a new correction factor for photographic surveys. For beluga, availability bias corrections have been developed for different populations, using a variety of methods, including archival tags logging information on time spent at depth, as well as visual observations of their diving patterns (Table 3). With one exception, correction factors for these populations were developed as global corrections, i.e., without accounting for environment heterogeneity or behaviour, and range from 0.224 to 0.555 (Sergeant, 1973; Frost, Lowry and Nelson, 1985; Martin and Smith, 1992; Heide-Jørgensen, Richard and Rosing-Asvid, 1998; Hobbs, Rugh and DeMaster, 2000; Hobbs, Waite and Rugh, 2000; Heide-Jørgensen and Acquarone, 2002; Richard, 2013; Marcoux *et al.*, 2016). These studies were mostly designed for a specific study area, although correction factors from areas with similar turbidity or depth were sometimes applied to areas with no data to correct for beluga availability bias (e.g. Richard, 2005). When available, durations of dives and of surface intervals were used to correct availability bias during visual aerial surveys. However, in some cases the sampling methodology could only allow calculating the proportion of time spent at the surface. In these cases, surface was defined as depths above an approximate turbidity threshold. Some studies accounted for detection time during visual surveys by using variations of McLaren's equation (1961) (Frost, Lowry and Nelson, 1985; Hobbs, Waite and Rugh, 2000), while others did not account for the differential availability during photographic versus visual aerial surveys (Heide-Jørgensen, Richard and Rosing-Asvid, 1998). In this context, our results bring a new perspective on the variability of availability bias, by considering the effect of survey design (photographic vs visual) as well as environmental and behavioural heterogeneity. Studies addressing similar effects have been led with various marine taxa (e.g. sea turtles, Thomson *et al.*, 2012 and Fuentes *et al.*, 2015; sharks, Nykänen *et al.*, 2018; dugongs, Pollock *et al.*, 2006 and Hagihara *et al.*, 2013; and dolphins, Sucunza *et al.*, 2018).

Table 3 Correction factors for availability bias that were developed in previous studies and applications.

Method	Data acquired	Best suited for	Study location	Correction factor	Applied to	Population	Reference
Visual observations (fixed-wing aircraft)	% time visible at surface	Photographic	Mouth of Churchill River	≈ 0.330	Visual, aerial	Western Hudson Bay	Sergeant, 1973
Radio-telemetry	Surface and dive data	Visual	Kvichak Bay	0.364	Visual, aerial	Bristol Bay	Frost, Lowry and Nelson, 1985
Archival tag	% time visible at surface	Photographic	Cunningham Inlet	0.400-0.555	Visual, aboard ship or aircraft	Eastern High Arctic	Martin and Smith, 1992
Archival tag	Surface and dive data	Visual	Eastern Devon Island	0.390	Visual and photographic, aerial	Eastern High Arctic	Heide-Jørgensen, Richard and Rosing-Asvid, 1998
Video recording	Surface and dive data	Visual	Cook Inlet	0.493	Visual, aerial	Cook Inlet	Hobbs, Waite and Rugh, 2000
Archival tag	% time visible at surface	Photographic	Eastern Devon Island	0.350	Visual, aerial	Eastern High Arctic	Heide-Jørgensen and Acquarone, 2002
Visual observations (helicopter)	% time visible at surface	Photographic	St. Lawrence Estuary	0.443	Visual and photographic, aerial	St. Lawrence	Kingsley and Gauthier, 2002
Archival tag	% time visible at surface	Photographic	Cumberland Sound	0.423-0.424	Visual and photographic, aerial	Cumberland Sound	Richard, 2013
Archival tag	% time visible at surface	Photographic	Cumberland Sound	0.224-0.485[1]	Visual and photographic, aerial	Cumberland Sound	Marcoux *et al.*, 2016

[1] Accounts for variability in turbidity by using 5 different depth bins to characterize time spent at the surface.

Our results indicate that SLE beluga counts would need to be multiplied by a factor of 2.51 to account for their availability at the surface during photographic surveys with a 30% photographic overlap. This value is higher than the 2.09 value developed specifically for this population using a different methodology (Kingsley and Gauthier, 2002). The correction factor in this other study was based on direct observations of beluga diving behaviour from a helicopter hovering over a group for an average of 10 minutes. Over 75% of the 72 groups sampled, of which about a third were composed of a single individual, were located off Rivière-du-Loup in the central portion of the beluga distribution area, in the shallow waters (< 50 m) of the south shore (Figure 12 in Gauthier, 1999). The first group encountered was sampled, and the proportion of time that beluga were available versus unavailable was determined by noting the number of beluga visible as often as it changed. The maximum number of beluga seen simultaneously was used as group size. The availability might have been overestimated in this study by selecting the first group encountered and thus possibly the most available individuals in the area, and by conducting the study mainly in shallow waters where, according to our results, availability may be enhanced, at least for animals located in AHD. The sector where most of the observations were made is one that appears to be used little by adult males during summer (Michaud, 1993), probably leading to an under-representation of this segment of the population in the sample.

As expected, availability to photographic survey platforms decreased with increasing turbidity, making beluga in the Upper Estuary, where waters are more turbid, less likely to be detected by a passing airplane than those using the clearer waters of the Laurentian Channel. Bottom depth did impact beluga availability to photographic surveys. However, this was only observed when using the global turbidity threshold of 4 m; no effect was seen when turbidity was added as a factor. This might result from both time at depth and time at the surface increasing with the increase in bottom depth, leading to a relatively unchanging proportion of time spent at the surface, as has been observed in other species such as blue whales when diving below 50 m (*Balaenoptera musculus*; Doniol-Valcroze *et al.*, 2011). Although availability during photographic surveys was less when beluga were in AHD as opposed to transit areas, the lack of a significant effect when turbidity was also taken into account probably has a similar explanation.

The raw number of beluga counted during visual surveys are higher than for photographic surveys, given the longer detection time associated with visual surveys (Gosselin *et al.*, 2017). This longer detection time during visual surveys is acknowledged when calculating availability by the addition of a second term to the relative duration of surface intervals (Eq. 1), and which allows for detection time to vary as a function of perpendicular distance from the trackline. While detection time during visual surveys approximates the instantaneous nature of photographic surveys for groups located directly on the trackline, it steadily increases for groups that are located further away, leading to a 20 % increase in availability over 3 000 m (Figure 7). The global estimates of availability bias for both visual and photographic surveys are within the upper range of those obtained for Arctic populations, suggesting that SLE beluga are more available to a passing aircraft than their Arctic counterparts. However, several studies of Arctic beluga were conducted in areas where availability was less as a result of turbid waters, with Secchi-disk depths sometimes as little as 1 cm (Sergeant, 1973; Frost, Lowry and Nelson, 1985; Hobbs, Waite and Rugh, 2000), or of much deeper environments such as in West Greenland (Heide-Jørgensen, Richard and Rosing-Asvid, 1998). This is consistent with our results, indicating a decrease in availability with turbidity, and with bottom depth.

Estimated mean surface intervals increased with decreasing turbidity, as expected, but the opposite was observed for estimated mean dive duration, with the longest occurring in the most turbid zone (the Upper Estuary), and the shortest occurring in the least turbid zone (over the Laurentian Channel; Figure 6). This zone was delineated based on Kingsley and Gauthier (2002), and includes both the deep waters of the Laurentian Channel and much shallower waters located at the head of the Channel, where several of our tagged beluga spent time (Figure 3). Tagging a larger number of beluga in the deeper waters of the Laurentian Channel might increase the average dive duration and surface intervals associated with this zone. Accounting for both turbidity and bottom depth could be required to adequately represent beluga availability to an aircraft. This might be especially recommended for visual surveys, where these factors were found to be more important in explaining variability in surface interval and dive duration, and even more so if animals are located within AHD as opposed to outside of these areas.

In our study, dive duration and surface intervals increased with bottom depth, and even more so when beluga were located within AHD as opposed to areas of transit. There is a vast literature documenting a relationship between surface time and dive time in marine mammals (Kooyman and Ponganis, 1998; Kramer, 1998; Doniol-Valcroze *et al*., 2011). Predators are also expected to maximize the time spent in a food patch when located at deeper depths to compensate travel costs (Houston and Carbone, 1992; Martin and Smith, 1999). Beluga can reach depths of up to 1 000 m in other areas (Citta *et al.*, 2013) and thus are not limited by bottom depth in the SLE. Beluga include benthic prey in their diet in the SLE (Valdykov, 1946; Lesage, 2014), and are expected to feed on the bottom at least in some of the AHD identified (Mosnier *et al.*, 2016).

Regarding the impact of including short excursions below the turbidity threshold within the length of surface intervals, we consider that the difference in mean surface interval length is reasonably small. It is very likely that the detectability of beluga by observers will not be affected by these short periods of unavailability, as they will mostly be shorter than the time during which a beluga will be within the field of view.

The availability thresholds relied on the only turbidity data available for our study area (i.e., Kingsley and Gauthier 2002). Turbidity values varied for a given zone by up to 7 meters (zone 1: 1.5-2.5 m; zone 2: 3.5-6.5 m; zone 3: 4.5-11.6 m), and were affected by freshwater runoff (Kingsley and Gauthier 2002). Conducting a fine-scale and multi-year Secchi-disk survey over the entire beluga summer distribution would help improve the estimate of availability as a function of turbidity. This might also help redefine the turbidity zones to better account for bottom depth heterogeneity and effects of these factors on surface interval and dive durations. For example, we might consider excluding the shallow area at the head of the Laurentian Channel from zone 3, and fully account for the characteristics of this shallow but less turbid area by making it a separate zone.

The turbidity thresholds were set to reflect the mid-range detection depths for white individuals. Beluga calves are dark grey or brown; they progressively lighten in color with age to become uniformly white at 10-20 years of age depending on sex (COSEWIC, 2014). Kingsley and Gauthier (2002) determined that darker individuals were only visible at 50% of Secchi depth, which suggests that population abundance will be under-estimated.

Beluga tagging effort covered a large portion of the summer distribution of SLE beluga, but did not reach the two extremities of the SLE (Figure 3). Depth ranges in the western portion of zone 1 were comparable to those in zone 1 where beluga were tagged; thus the behaviour of beluga in the uncovered area was probably well captured by the belugas tagged in the eastern portion of this zone. However, few of the beluga tagged in zone 3 spent time in the Laurentian Channel or were tagged specifically in these waters. Given they are much deeper but also much clearer than the other beluga habitats, and that 13 to 35% of the beluga may use this sector at any one time (Michaud, 1993), increasing sample size for this region would improve model accuracy.

Beluga tagging efforts also took place throughout the summer whereas surveys were generally conducted from mid-August to early September. There is a possibility that AHD may change over the summer due to prey availability; for instance, beluga might use specific areas to take advantage of spawning capelin or herring in early summer (Lesage and Kingsley, 1995). However, the similarity between the high residency areas identified using herd follows from June to September (Lemieux Lefebvre *et al.*, 2012) and the AHD identified from late summer aerial surveys (Mosnier *et al.*, 2016) suggests that AHD capture areas used intensively during late summer.

During summer, beluga in the SLE as well as in different parts of the Arctic tend to segregate by age and sex (Michaud *et al.*, 1990; Michaud, 1993; Smith and Martin, 1994; Smith, Hammill and Martin, 1994; Heide-Jørgensen and Lockyer, 2001; Michaud, 2005;

Loseto *et al.*, 2006). In the SLE, herds of sometimes large numbers (>100 individuals) of white individuals (most likely males) are commonly found in the Lower Estuary, both along the south shore and the deeper waters of the Laurentian Channel, as well as in the Saguenay River. Smaller herds (<30 individuals) of white individuals (most likely females) with calves and juveniles are mostly found in the Saguenay Fjord and the warmer and shallower waters of the Upper Estuary, as well as in the shallower waters of the Lower Estuary along the south shore (Michaud, 1993). The environment, sexual dimorphism and need to care for young shape habitat use and diving patterns. In the Arctic, females with calves tend to spend more time at the surface (Heide-Jørgensen *et al.*, 2001). While adult males, which are larger than females in beluga, are generally found offshore and favour deep diving, smaller whales are found in more inshore waters, spend more time at the surface, and dive more frequently, although not as deep as the bigger individuals (Heide-Jørgensen, Richard and Rosing-Asvid, 1998; Heide-Jørgensen *et al.*, 2001; Citta *et al.*, 2013). Given that our tagging effort covered a large portion of the summer distribution and the variety of habitats used by beluga in the SLE, it is likely that all herd types were sampled, and that our estimations of average availability are accurate. Although accounting for sex and age class might improve our estimations of availability, in practice, it is impossible to determine beluga sex or age composition of beluga groups encountered during line-transect aerial surveys.

For other species, such as the franciscana (*Pontoporia blainvillei*), group size is the main factor affecting time spent at the surface, and therefore availability (Sucunza *et al.*, 2018). Given that beluga within a group usually have synchronized diving patterns, this factor probably does not have as big an effect on availability. However, group size is likely to be systematically underestimated during visual aerial surveys, given the difficulty of accurately counting large groups during a short window of time, as opposed to studying a photograph. This potential bias does not apply to photographic surveys, given that counts are based on individuals instead of groups, with missed individuals being included in the correction for availability bias. Group size is more likely to have an impact on perception bias during visual surveys, with bigger groups having a greater chance of being noticed by an observer.

Conclusion

In the past, SLE beluga abundance from visual surveys were corrected for availability bias using factors developed for photographic surveys. Not accounting for the longer detection time during visual surveys overestimated abundance compared to those obtained from photographic surveys. In this study, we used archival tag data on diving behaviour and movement patterns to develop a correction for availability bias specific to visual surveys to make them more comparable to photographic surveys. We also provided a new and likely more realistic correction factor for photographic surveys that captured the behaviour of beluga of different age and sex and in more diverse habitat than the previous study (Kingsley and Gauthier, 2002). This study also demonstrates the impact of taking into account spatial heterogeneity and behaviour on availability bias correction factors.

In order to make photographic and visual surveys fully comparable, estimates from both types of surveys will need to be corrected for perception bias. Perception bias for photographic surveys can be reduced to very low levels by multiple counts of the permanent images (Stenson *et al.*, 2000; Gosselin, Hammill and Mosnier, 2014), and has been incorporated in past SLE beluga abundance estimates. For visual surveys, perception bias is usually estimated using a double-platform and mark recapture procedure, where the proportion of the animals at the surface that are detected by the observers is compared (Laake and Borchers, 2004). Without this correction, SLE beluga abundance estimated from visual surveys should be systematically lower than when estimated from photographic surveys. Although studies of beluga in various areas in the Arctic indicate that perception bias for beluga visual surveys is small (2-8%; Hobbs, Rugh, and DeMaster, 2000; Heide-Jørgensen *et al.*, 2013), a correction for this bias via a double platform survey design will be needed to make the photographic and visual abundance estimates for SLE beluga fully comparable. Once this is done, the two times series could be joined as a single time series to update models of population dynamics (e.g. Mosnier *et al.*, 2015).

Future research should examine the effect of applying spatially and behaviourally explicit correction factors on beluga counts from individual surveys, and on the confidence interval around mean abundance estimates from repeated surveys. It will be interesting to see how these new correction factors contribute to reducing the variability in abundance estimates that is currently observed between years, and how they can improve our ability to detect trends in SLE beluga abundance. Given the effect of turbidity and bottom depth that were documented in our study, comparisons of relationships between availability and spatial predictors across Arctic beluga populations would be valuable. This comparison could be extended in the St. Lawrence Estuary to predict seasonal changes in availability of SLE beluga as a result of changes in their seasonal distribution (Harvey *et al*., 2018).

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CONCLUSION GÉNÉRALE

Nos résultats montrent que différentes variables spatiales, soit la turbidité, la profondeur du milieu et la présence dans des aires de haute densité ou en transit, ont des effets importants sur la disponibilité des bélugas. La turbidité a un effet significatif sur la disponibilité pour les relevés photographiques; une augmentation de la turbidité mène à une diminution de la disponibilité. L'effet sur la disponibilité aux relevés visuels est moins clair, et nécessiterait une nouvelle délimitation des zones de turbidité tenant compte de la profondeur du milieu, afin de séparer ces effets confondants. La durée des intervalles de surface et des plongées augmente selon la profondeur du milieu, ainsi qu'avec la présence des bélugas lorsque ces derniers se situent dans les aires de haute densité par opposition aux zones entre celles-ci et dites de transit. Toutefois, ces deux variables spatiales n'ont pas un aussi grand effet sur la proportion de temps à la surface, indiquant l'importance de considérer les différences entre chaque type de relevé dans la correction du biais de disponibilité. Ceci devrait permettre de réduire jusqu'à un certain point la disparité actuelle entre les estimations d'abondance provenant des relevés visuels versus photographiques.

Les facteurs de correction développés ici sont spécifiques à la localisation de chaque groupe de bélugas observé durant un relevé aérien et devraient ainsi permettre de diminuer la variabilité entre les estimations d'abondances obtenues jusqu'à présent, mais de futures recherches sont requises pour le confirmer. Puisque les facteurs de correction obtenus sont plus élevés que ceux de Kingsley et Gauthier (2002), leur application systématique aux relevés de bélugas effectués depuis 1988 mènerait à des estimations d'abondance plus élevées, tout en réduisant possiblement la variabilité entre les estimations, permettant une détection plus rapide des tendances, et une réaction plus rapide afin d'améliorer les mesures de gestion et d'atténuation.

Les résultats obtenus amènent de nouveaux questionnements. Des relevés aériens visuels ont commencé à être effectués à l'extérieur de la période estivale, et couvrent une plus grande aire que durant l'été puisqu'une partie de la population est susceptible de se déplacer vers l'aval de l'estuaire et vers le golfe du Saint-Laurent durant l'hiver. Les facteurs de correction obtenus étant spécifiques à l'estuaire du Saint-Laurent en été, ils ne seraient pas applicables à ces nouveaux relevés. Il nous faudrait donc plus d'information sur les changements du comportement de plongée des bélugas d'une saison à l'autre, ainsi que des données sur les caractéristiques spatiales des nouveaux habitats couverts par les relevés non-estivaux. Entre autres, on ne connaît pas les aires de haute résidence à l'extérieur de la saison estivale, quoique certaines puissent commencer à être identifiées à partir des données recueillies durant ces nouveaux relevés aériens. Comme mentionné dans le Chapitre 1, il est probable que les tendances observées de la disponibilité en fonction de la turbidité et de la profondeur du milieu restent similaires durant l'année; toutefois, les données concernant les variations saisonnières de la turbidité sont actuellement fragmentaires et doivent être bonifiées.

Bref, étant une population fermée avec une distribution estivale bien connue et des études antérieures ayant identifié les aires de haute résidence, les bélugas de l'estuaire du Saint-Laurent constituent un modèle idéal pour déterminer l'impact de l'hétérogénéité environnementale et comportementale sur la disponibilité. Cette étude appuie l'utilisation de facteurs de correction spatialement hétérogènes pour corriger le biais de disponibilité chez cette population de bélugas. Il serait maintenant intéressant d'investir dans l'obtention de données environnementales et de patrons de plongées pour des bélugas appartenant à d'autres populations. En effet, ces nouvelles données permettraient de voir si des relations similaires entre la disponibilité et les variables spatiales sont observées; et ce, surtout pour les populations en déclin ou en péril, pour lesquelles de bonnes estimations d'abondance seraient requises pour effectuer un suivi de leur statut.

ANNEXES

Appendix I The average availability to photographic surveys, by their standard errors, for all three turbidity zones identified in the St. Lawrence Estuary. Zone 1 corresponds to the Upper Estuary, while zone 2 is the southern portion of the Lower Estuary, and zone 3 is the northern portion.

Turbidity zone	**Mean**	**S.E.**
Zone 1	0.222	0.023
Zone 2	0.271	0.013
Zone 3	0.409	0.033

Appendix II The average length of surface intervals and dive durations (*E(s)* and *E(d)* respectively), in seconds, accompanied by their standard errors, for all three turbidity zones identified in the St. Lawrence Estuary. Zone 1 corresponds to the Upper Estuary, while zone 2 is the southern portion of the Lower Estuary, and zone 3 is the northern portion.

Turbidity zone	**Dive phase**	**Mean**	**S.E.**
Zone 1	E(s)	54.1	8.9
	E(d)	173.7	27.3
Zone 2	E(s)	59.9	3.5
	E(d)	160.6	6.5
Zone 3	E(s)	107.3	9.2
	E(d)	129.9	15.8

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