UNIVERSITÉ DU QUÉBEC EN OUTAOUAIS

Dynamique spatiale des bélugas de l'estuaire du Saint-Laurent : utilisation de l'habitat, patrons de de déplacement et dynamique de fission–fusion

Spatial dynamics of St. Lawrence Estuary belugas: habitat use, movement patterns and fission–fusion dynamic.

Thèse présentée

dans le cadre du programme de doctorat sur mesure en écologie comportementale des mammifères marins

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par

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RECONNAISSANCE TERRITORIALE

Au cours de cette thèse doctorale, j'ai principalement travaillé depuis le campus de Ripon de l'Université du Québec en Outaouais (UQO), et j'ai également mené des travaux de terrain depuis Tadoussac. Je reconnais que l'UQO se situe au sein d'un territoire autochtone non cédé de la nation Anishinabeg Omàmiwininiwak. Les données utilisées dans cette thèse ont été récoltées dans les territoires ancestraux non cédés des peuples Wolastoqiyik et Innu.

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AVANT-PROPOS

A translated version of the preface in English is available in Appendix A.

Cette thèse s'inscrit dans un programme de recherche multidisciplinaire initié en 2018 par le Dr. Clément Chion qui vise à modéliser le trafic maritime et son impact sur le comportement spatial des mammifères marins de l'estuaire du Saint-Laurent et le Fjord du Saguenay. La thèse s'intègre particulièrement dans le volet 1 et fournit des informations inédites pour la paramétrisation des modèles de déplacements des bélugas, afin de quantifier les impacts du bruit.

Ma thèse, débutée en septembre 2019, porte sur la dynamique sociale et spatiale d'un cétacé, le beluga du Saint-Laurent. Elle s'appuie sur des séries de données exceptionnelles, intégrant plus de trente ans de suivi de troupeaux et dix ans de suivis télémétriques pour plus de cinquante individus. Ces données ont été collectées par les équipes du GREMM (Groupe de Recherche et d'Education sur les Mammifères Marins) et celles du MPO (Pêche et Océans Canada). J'ai participé à la collecte des données à l'été 2021. La thèse comporte cinq sections : l'introduction générale décrit les principaux concepts écologiques abordés dans les axes de recherche et les objectifs de recherche, suivie de trois chapitres, correspondant à des articles scientifiques originaux menés pendant la thèse. Ces chapitres sont écrits en anglais, l'un est publié et les deux autres seront soumis prochainement dans différentes revues internationales soumises à l'évaluation par les pairs. Les résultats ont également été diffusés en congrès nationaux et

internationaux. J'ai également été invitée à présenter mes travaux lors de séminaires et ateliers. La thèse se conclut par une discussion générale reprenant les principaux résultats obtenus dans les trois chapitres et le fil conducteur qui les relie, les limites de l'étude, les implications pour la conservation et met en perspective l'apport des connaissances auxquelles ce travail aura contribué.

Conférences (présentations orales : 10; affiches : 2)

Barreau E., Lesage L., Michaud R.,Bonnell T., Chion C., Dupuch A. – Scale matters: quantifying fusion-fission dynamic events of beluga herds in the St. Lawrence Estuary. 17th Ecology and behavior conference; August 2025; Montpellier, FRANCE.

Barreau E., Lesage L., Bonnell T., Michaud R., Senecal J-F., Chion C., Dupuch A. – Decoding beluga movements: a telemetry study in the St. Lawrence Estuary. 54ème Colloque de la Société Française pour l'Etude du Comportement Animal; Juin 2025; Nanterre, FRANCE.

Barreau E., Lesage L., Bonnell T., Michaud R., Senecal J-F., Chion C., Dupuch A. – Uncovering movement patterns of belugas in the St. Lawrence Estuary from telemetry data. 16th Ecology and behavior conference; August 2024; Chizé, FRANCE.

Barreau E., Lesage L., Michaud R.,Bonnell T., Chion C., Dupuch A. – Uncovering movement patterns of belugas in the St. Lawrence Estuary from telemetry data. 19th International Society for Behavioral Ecology; September-October 2024; Melbourne, AUSTRALIE.

Barreau E., Lesage L., Michaud R.,Bonnell T., Chion C., Dupuch A. – Uncovering movement patterns of belugas in the St. Lawrence Estuary from telemetry data. 16th Ecology and behavior conference; August 2024; Chizé, FRANCE.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Dupuch A. – Behavior-specific habitat use in beluga from the St. Lawrence Estuary, Canada. 48ème congrès de la Société Québécoise pour l'étude biologique du comportement Novembre 2023; Montréal, Canada. *Prix Julie Morand-Ferron*.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Dupuch A. – Fonction des habitats identifiés comme importants pour les bélugas de l'estuaire du St. Laurent : implications pour la conservation de la population. Symposium sur le béluga Mai 2023; Montréal, Canada.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Lemieux Lefebvre S., Dupuch A. – Behavior-specific habitat use in beluga from the St. Lawrence

Estuary, Canada. Réunion Scientifique Annuelle de Québec-Océan février 2023; Rivière du Loup, Canada.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Lemieux Lefebvre S., Dupuch A. – Behavior-specific habitat use in beluga from the St. Lawrence Estuary, Canada. 24th Biennial Conference on the Biology of Marine Mammals; August 2022; Florida, USA.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Lemieux Lefebvre S., Dupuch A. – Behavior-specific habitat use of belugas in the St. Lawrence Estuary. 6ème Colloque de l'ISFORT, avril 2022.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Dupuch A. – Etude de la dynamique spatiale du béluga de estuaire du Saint-Laurent dans un contexte de conservation de la population. 6ème Colloque de l'ISFORT, mars 2021. *Prix (1ère place) de la meilleure présentation éclair*

Barreau E., Lesage V., Michaud R., Chion C., Dupuch A. - Investigating movement dynamics of the St. Lawrence Estuary beluga: implications for conservation. Virtual summit of research of Canadian Parks Collective for Innovation and Leadership (CPCIL); March 2021, online

Séminaires & comités (3 présentations en tant qu'invitée)

Barreau E. Spatial dynamic of St. Lawrence Esturay beluga. Présentation à la réunion annuelle Prédateurs marins. 30 mai 2022, Chizé (France)

Barreau E. Functions of habitat highly used by St. Lawrence Esturay beluga. Comité national d'examen par les pairs sur les mammifères marins. 20 octobre 2023, Halifax (Canada)

Barreau E. Détermination des fonctions des habitats utilisés par les troupeaux de béluga de l'Estuaire du St. Laurent. Présentation au Groupe de travail sur le trafic maritime (G2T3M). 5 mai 2022, en ligne.

LISTE DES ABREVIATIONS, SIGLES ET ACRONYMES

AHR : Area of High Residency

AIC : Akaike Information Criteria

AICc : Akaike Information Criteria corrected

ARS : Area Restricted Search

BFD : Benthic Foraging Dominant

COSEWIC : Committee on the Status of Endangered Wildlife in Canada

CTCRW : Continuous-Time Correlated Random Walk Model

ESL : Estuaire du Saint-Laurent

DFO : Fisheries and Ocean Canada

FF : Fission-fusion

FPT : First Passage Time

Gi* : Getis-Ord statistic

GPS : Global Positioning System

GREMM : Group of Research and Education on Marine Mammals

GVIF : Generalized Variance Inflation Factor

HMM : Hidden Markov model

LEP: Loi sur les Espèces en Péril

MLR : Multinomial Logistic Regression

OR : Odd ratio

PFD : Pelagic Foraging Dominant

SLE : St. Lawrence Estuary

TD : Travel Dominant

TPF : Travel and Pelagic Foraging

VHF : Very High Frequency

RÉSUMÉ

Comprendre les déterminants de la distribution et des déplacements des espèces est essentiel à leur conservation. Chez les espèces grégaires, les décisions spatiales ne peuvent être dissociées du comportement social. La considération de l'environnement social est donc cruciale pour une pleine compréhension de leur comportement spatial. La population de bélugas de l'Estuaire du Saint-Laurent (ESL), considérée en voie de disparition en vertu de la *Loi sur les Espèces en Péril* au Canada, est exposée à de nombreuses menaces dans son habitat essentiel estival. Afin de gérer plus efficacement sa conservation, il est essentiel de comprendre les facteurs qui sous-tendent la dynamique spatiale des bélugas de l'ESL. L'hypothèse centrale de la présente thèse est que leur comportement spatial résulte de l'interaction entre les caractéristiques de l'habitat et l'environnement social. Les trois objectifs spécifiques consistaient à : 1) identifier les fonctions des habitats jugés importants pour la population et examiner leur discrimination sur la base des caractéristiques de l'habitat et de la composition sociale des troupeaux ; 2) déterminer quelles caractéristiques de l'habitat et de leur environnement social influencent les comportements de déplacement individuel ; 3) quantifier la dynamique de fission-fusion au sein des troupeaux de bélugas et déterminer dans quels contextes environnementaux, sociaux, comportementaux et anthropogéniques se produisent les événements de fission et de fusion. Cette thèse s'appuie sur une longue série temporelle de suivis focaux de troupeaux (utilisée dans les trois chapitres) ainsi que de nombreux suivis télémétriques

individuels (Chapitre 2) collectés durant la saison estivale dans l'ESL et le Fjord du Saguenay.

L'étude a permis d'identifier les fonctions des aires de haute résidence, utilisées principalement pour des activités liées à l'alimentation et/ou à la socialisation, ainsi que de valider que les corridors sont majoritairement utilisés pour le déplacement. Malgré la prise en compte de l'organisation sociale des troupeaux, les associations entre les fonctions et les caractéristiques environnementales ne permettent pas de discriminer les habitats entre eux. Néanmoins, jusqu'à trois modes comportementaux ont pu être identifiés à partir des trajectoires. Les transitions entre ces modes varient avec les courants, ce qui est cohérent avec les stratégies d'optimisation énergétique. En outre, l'influence de la composition sociale du troupeau sur les probabilités de transition entre les modes de déplacement est fonction de leur interaction avec les variables environnementales. Enfin, l'étude décrit un degré de fission-fusion intermédiaire au sein des troupeaux avec des changements plus fréquents au niveau de la taille et de la cohésion spatiale que de la composition. Les événements de fission-fusion sont principalement influencés par des facteurs sociaux, environnementaux et comportementaux.

En conclusion, la présente thèse a contribué à enrichir les connaissances sur le comportement spatial et social des bélugas de l'ESL. Les résultats ont mis en évidence l'importance d'intégrer conjointement des variables environnementales et sociales pour une pleine compréhension du

phénotype spatial. La thèse fournit également des informations inédites sur les fonctions vitales soutenues par les habitats importants pour la population, essentielles pour orienter la planification et la hiérarchisation des mesures de conservation et suivre l'évolution des habitats. Les futures recherches devraient viser à améliorer la compréhension mécanistique des facteurs qui influencent leur comportement spatial et social.

Mots clés : Béluga (*Delphinapterus leucas)*, Estuaire du Saint-Laurent (Canada), Phénotype spatial, Phénotype social, Utilisation de l'habitat, Patrons de déplacement, Dynamique de fission-fusion, Suivis focaux de troupeaux, télémétrie, conservation

ABSTRACT

Understanding the drivers underlying a specie distribution and movements is essential for their conservation. In gregarious species, spatial decisions are tied to social behaviour, making integration of the social environment crucial to fully understanding their spatial behaviour. The St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas*) population, listed as endangered under Canada's Species at Risk Act, is exposed to multiple threats within its critical summer habitat. To implement efficient conservation measures, it is essential to understand the factors underlying the spatial dynamics of SLE belugas. The central hypothesis of this thesis is that beluga spatial behaviour arises from the interaction between habitat characteristics and the social environment. The three specific objectives were to: (1) identify the functions of habitats considered important for the population and assess how well they can be discriminated based on habitat characteristics and herd social composition; (2) determine which habitat features and aspects of the social environment influence individual movement patterns; and (3) quantify fission-fusion dynamics within beluga herds and determine under which environmental, social, behavioural, and anthropogenic contexts fission and fusion events occur. This thesis used a long-term time series of focal herd follows (used in all three chapters), as well as individual telemetry tracks (Chapter 2), collected in summer in the SLE and the Saguenay Fjord.

The study identified the functions of high residency areas, which are used primarily for foraging and/or social activities, and validated that corridors are predominantly used for travelling. Despite accounting for herd social organization, associations between habitat functions and environmental characteristics did not allow a clear discrimination among habitats. The study further identified up to three behavioural states from tracks, with transitions among states varying with tidal currents, consistent with energy-optimization strategies. Moreover, herd social composition influenced transition probabilities between movement states when in interaction with environmental variables. Finally, the study documented an intermediate degree of fission-fusion dynamics within herds, with more frequent changes in herd size and spatial cohesion than in composition, and showed that fission–fusion events are mainly driven by social, environmental, and behavioural factors.

This thesis advances our understanding of the spatial and social behaviour of SLE belugas and highlights the importance of integrating both environmental and social variables to gain in-depth understanding of their spatial behaviours. It also provides information on the critical functions supported by key habitats for this population, which is essential for guiding conservation planning, prioritizing management measures, and monitoring habitat change. Future research should aim to improve the mechanistic understanding of the factors that shape beluga spatial and social behaviour.

Keywords: Beluga whale (*Delphinapterus leucas*); St. Lawrence Estuary (Canada); spatial phenotype; social phenotype; habitat use; movement patterns; fission–fusion dynamics; herd focal follows; telemetry; conservation

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median indicated by an horizontal line inside the box. Asterisks mark significant differences between groups: **p < 0.01, ***p < 0.001.

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Figure 3.3 : State stationary probabilities for the A) 2-state (ARS and transit) and B) 3-state (ARS, Slow and Fast transit) candidate models as a function of probability of sand lance occurrence, swim direction relative to current, and bathymetry. Solid lines show model-predicted probabilities around the median, with shaded areas indicating the 95% confidence interval. Beluga are considered to swim with the current when angles are <60°, to move

perpendicularly to current when between 60° and 120°, and to swim against the current when >120°.

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“The more clearly we can focus our attention on the wonders and realities of the universe about us, the less taste we shall have for destruction”

Rachel Carson

INTRODUCTION GÉNÉRALE

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A translated version of the GENERAL INTRODUCTION in English is available in Appendix B.

Le phénotype spatial

L'organisation spatiale des individus

Comprendre la relation entre la distribution des animaux et les conditions environnementales dans lesquelles ils évoluent constitue une question centrale en écologie. Le déplacement, défini par un changement de position dans le temps et l'espace, est omniprésent dans la vie animale (Nathan et al. 2008 ; Webber et al. 2023). Il permet aux individus d'utiliser l'espace pour divers évènements ou comportements liés à leur cycle de vie (Mayor et al. 2009 ; Burt 1943). Les animaux sélectionnent des habitats spécifiques parmi un ensemble d'habitats disponibles au sein de leur domaine vital (i.e., aire fréquentée régulièrement par un individu au cours de activités) afin de remplir des besoins indispensables à leur survie ou à leur reproduction (Burt, 1943; Hooten et al. 2017 ; Morris 2003 ; Nathan et al. 2008 ; Péron 2019). Plusieurs habitats peuvent être nécessaires pour satisfaire des fonctions vitales, et certains habitats peuvent satisfaire plusieurs besoins. La qualité d'un habitat est influencée par de multiples facteurs, tels que la motivation de l'individu (e.g., acquisition d'énergie, interaction sociale, protection), son accessibilité, et sa valeur intrinsèque définie par les conditions environnementales biotiques et abiotiques (i.e., distribution des ressources et des risques ; Nathan et al. 2008 ; Morales et al. 2010 ; Hooten et al. 2017).

La distribution des individus est étroitement liée aux caractéristiques de l'habitat, mais l'identification de leur fonction sous-jacente est conditionnée par

notre compréhension des processus comportementaux (Bastille-Rousseau & Wittemeyer 2021 ; Alston et al. 2022; Noren & Hauser 2016). Le comportement constitue en effet le lien entre les besoins vitaux et l'utilisation de l'habitat, et est donc central pour comprendre pourquoi les animaux sélectionnent et utilisent des habitats distincts (Morris 2003, Nathan et al. 2008 ; Péron 2019 ; Bastille-Rousseau & Wittemeyer 2021 ; Alston et al. 2022). Par exemple, le couplage des comportement avec l'utilisation des habitats a ainsi permis d'identifier les aires dédiées au repos pour les dauphins long bec (*Stenella longirostris* ; Tyne et al. 2015), et à l'alimentation chez les grands dauphins (*Tursiops truncatus* ; Hastie et al. 2004).

Les comportements à la base de l'utilisation de l'espace

Les ressources biologiques et les conditions abiotiques étant hétérogènes dans le temps et l'espace, les animaux doivent adapter leurs déplacements et l'organisation de leurs activités comportementales pour maximiser leur valeur sélective (Stephen & Krebs 1986; Sheppard et al. 2013). La compréhension des liens entre les conditions environnementales et les patrons de déplacement est donc essentielle pour élucider comment les animaux font face aux contraintes écologiques.

Le paradigme du déplacement décrit le déplacement individuel comme la résultante de quatre composantes majeures interconnectées : son état physiologique qui détermine la motivation à se déplacer (e.g., état de faim) ; sa capacité à naviguer (i.e., l'aptitude à s'orienter via ses capacité

sensorielles) ; sa capacité motrice (i.e., aptitude à exécuter le déplacement) ; et les conditions environnementales rencontrées (Nathan et al. 2008). En assumant qu'une trajectoire individuelle reflète l'alternance de modes de déplacement distincts, diverses approches, telles que les modèles de Markov cachés, peuvent décomposer ces modes pour en inférer les comportements sous-jacents (Morales et al. 2010; Patterson et al. 2008 ; Hooten et al. 2017 ; Gurarie et al. 2016 ; McClintock et al. 2020). L'interprétation de ces modes dépend de l'échelle spatio-temporelle considérée. A large échelle, ils peuvent refléter des migrations saisonnières, des aires de résidences, ou bien des mouvements nomadiques (Pedersen et al. 2011 ; Bunnefeld et al. 2011 ; Hooten et al. 2017 ; Teitelbaum & Mueller 2019; Vogel et al. 2025). A fine échelle, ils peuvent révéler des comportements de recherche alimentaire (Hooten et al. 2017 ; Dorfman et al. 2022). Le passage de l'échelle individuelle à celle de la population, bien qu'il pose certains défis, offre une compréhension plus mécanistique de la dynamique et la répartition des populations, en les considérant comme la résultante du comportement individuel, des contraintes physiologiques et des conditions environnementales (Nathan et al. 2008).

ENCADRE 1: Définitions clés

Unité sociale: Individus qui partage un espace commun et interagissent plus fréquemment entre eux qu'avec d'autre congénères (e.g., groupe; Kappeler & van Schaik 2002 ; Whitehead 2008).

Dynamique de fission-fusion: Variation spatio-temporelle de la cohésion spatiale (i.e., distance interindividuelles), de la taille (i.e., nombre d'individus), et de la composition (i.e., identité des individus) dans l'unité sociale considérée (Aureli et al. 2008).

Environnement social: Taille, composition, type d'interactions entre les individus au sein d'une unité sociale ou d'une population (Webber et al. 2023).

Phénotype social: Position sociale d'un individu au sein d'une société, résultant de ces interactions sociales avec d'autres individus (e.g., familiarité sociale). L'interaction de ces phénotypes individuels génère la dynamique de fission-fusion au niveau collectif (e.g., groupe) (Webber et al. 2023).

Organisation sociale: Taille, composition, cohésion spatiale d'une unité sociale, et degré de variation temporel de ces trois dimensions (Kappeler & van Schaik 2002; Whitehead 2008 ; Aureli et al. 2008).

Structure sociale: Propriété émergente des types d'interactions et des relations sociales résultantes entre les individus d'une unité sociale (Kappeler & van Schaik 2002 ; Whitehead 2008).

Société multi-niveau: Type d'organisation sociale caractérisé par l'imbrication hiérarchique d'au moins deux niveaux d'unité sociale (e.g., paire, groupe) (Cantor et al. 2015). Le premier niveau présente une composition généralement stable dans le temps (e.g., paire), et fusionne périodiquement pour former des groupes plus larges, qui à leur tour peuvent former des groupes encore plus grands, résultant d'une dynamique de fission-fusion (Grueter et al. 2020).

Les déterminants du phénotype spatial chez les espèces grégaires

La compréhension du comportement spatial chez les espèces grégaires doit prendre en compte la dynamique sociale entre les individus. L'organisation sociale (Encadré 1) influence en effet le compromis coûts-bénéfices lié à la sélection d'un habitat, conduisant à des schémas d'utilisation de l'habitat qui varient selon la taille et/ou la composition des groupes (Whitehead & Rendall 2004; Fortin et al. 2009 ; Cañadas & Hammond 2008 ; Fury et al. 2013 ; Pirotta et al. 2020). Par exemple, la présence de jeunes au sein du groupe influence la sélection d'habitats ayant des caractéristiques adaptées simultanément aux besoins de l'ensemble des membres du groupe et propices au soins maternels (Cañadas et Hammond, 2008; Weir et al. 2008; Fury et al. 2013). De plus, à l'échelle de la population, l'apprentissage social peut en outre conduire à des utilisations d'habitat et/ou des ressources (e.g., proies) différentes entre les individus (Brakes et al. 2021), comme les clans de cachalots qui n'exploitent pas les mêmes habitats selon leur appartenance sociale (Whitehead & Rendall 2004; Pirotta et al. 2020). Les comportements spatiaux et sociaux sont donc étroitement liés, soulignant la nécessité de les étudier conjointement pour élucider la dynamique spatiale des espèces grégaires (Webber et al. 2020, 2023).

L'environnement correspond à l'ensemble des éléments spatiaux et sociaux qu'un animal rencontre (Encadré 1 ; Webber et al. 2023). Bien que le rôle de l'environnement social soit implicite dans le paradigme du

déplacement, les espèces grégaires se distinguent par l'ajustement de leur comportement spatial en se déplaçant avec ou vers les autres pour interagir avec leur congénères. L'environnement spatial (e.g., la distribution des ressources) et social (e.g., taille et composition d'un groupe, type d'interactions entre les individus) influencent conjointement le déplacement individuel (Webber et al. 2023). Le cadre conceptuel de l'interface socio-spatiale étend le paradigme de l'écologie du déplacement en clarifiant le lien inhérent entre l'écologie sociale et l'écologie du déplacement à travers les échelles (Webber et al. 2023 ; Picardi et al. 2024). Selon ce cadre, le déplacement individuel constitue un lien mécanistique entre les traits intrinsèques individuels (e.g., l'âge, le sexe), les conditions environnementales sociales et spatiales rencontrées (e.g., configuration de l'habitat, appartenance à un groupe), dont émergent les phénotypes spatiaux et sociaux (e.g., utilisation de l'habitat, structure sociale dans la population). Les environnements spatiaux et sociaux précèdent le processus de déplacement en influençant les motivations et les coûts-bénéfices du déplacement, alors que les phénotypes spatiaux et sociaux résultent des ajustements comportementaux individuel (Figure 1.1 ; Webber et al. 2023).

Le déplacement individuel varie selon la composition du groupe en réponse aux contraintes liées aux capacités locomotrices ou les besoins physiologiques des autres individus (Sueur et al. 2011 ; Webber et al. 2023). Par exemple, les capacités de locomotion réduites des jeunes individus influencent la manière dont les adultes du groupe se déplacent, telles que les

distances parcourues (Papageorgiou & Farine 2015) ou la vitesse maximale de déplacement (Noren et al. 2023). Néanmoins, peu d'études intègrent les facteurs spatiaux et sociaux dans un cadre analytique unifié (Fortin et al. 2009 ; McKellar et al. 2015 ; Strandburg-Peshkin et al. 2017 ; Webber et al. 2024), en particulier chez les espèces marines (Hays et al. 2016). La prise en compte des interactions entre l'habitat et l'environnement social améliore les prédictions des modes de déplacements et approfondit la compréhension des décisions individuelles (Strandburg-Peshkin et al. 2017), soulignant la nécessité d'inclure ces deux dimensions dans les études sur le déplacement animal. En effet, l'effet des environnements spatial et social est généralement examiné séparément, limitant notre appréhension des processus sous-jacents.

Le phénotype social

La socialité, définie par la tendance des individus à vivre en groupe, est courante dans le règne animal (Alexander, 1974 ; Ward & Webster 2016). La vie de groupe apporte des avantages pour les individus tels que la coopération dans la recherche alimentaire ou le soin aux jeunes, ou la réduction du risque de prédation, mais elle implique aussi des coûts comme la compétition alimentaire ou la transmission de pathogènes (Ward & Webster 2016). Au-delà de ces compromis, les groupes peuvent se distinguer par leur aptitudes comportementales (e.g., préférences alimentaires, techniques de chasses, utilisation d'outils), et par les connaissances écologiques partagée entre les

membres de ce groupe (Ward & Webster 2016 ; Brakes et al. 2021). L'appartenance à un groupe confère des avantages pouvant affecter, *in fine*, la survie individuelle, et par conséquent la valeur sélective (Busson et al. 2019).

Inspirée des principes généraux des compromis coûts-bénéfices (MacArthur & Pianka, 1966), la théorie socio-écologique vise à comprendre quelles pressions évolutives façonnent les systèmes sociaux des animaux. Elle relie l'organisation et/ou la structure sociale d'une population aux contraintes écologiques des différents habitats qu'elle utilise (Crook 1964 ; Crook & Gartla, 1966 ; Wittemyer et al. 2005 ; Sueur et al. 2011). Initialement centrée sur l'environnement spatial (e.g., distribution des ressources et des risques), cette théorie intègre désormais explicitement l'environnement social pour une compréhension plus complète des systèmes sociaux (Webber et al. 2020, 2023). L'étude des espèces ayant une flexibilité comportementale marquée, telle que la dynamique de fission-fusion (Encadré 1), permet d'examiner les variations de l'organisation sociale en réponse aux facteurs écologiques (Figure 1.1 ; Aureli et al. 2008 ; Sueur et al. 2011 ; Webber et al. 2023).

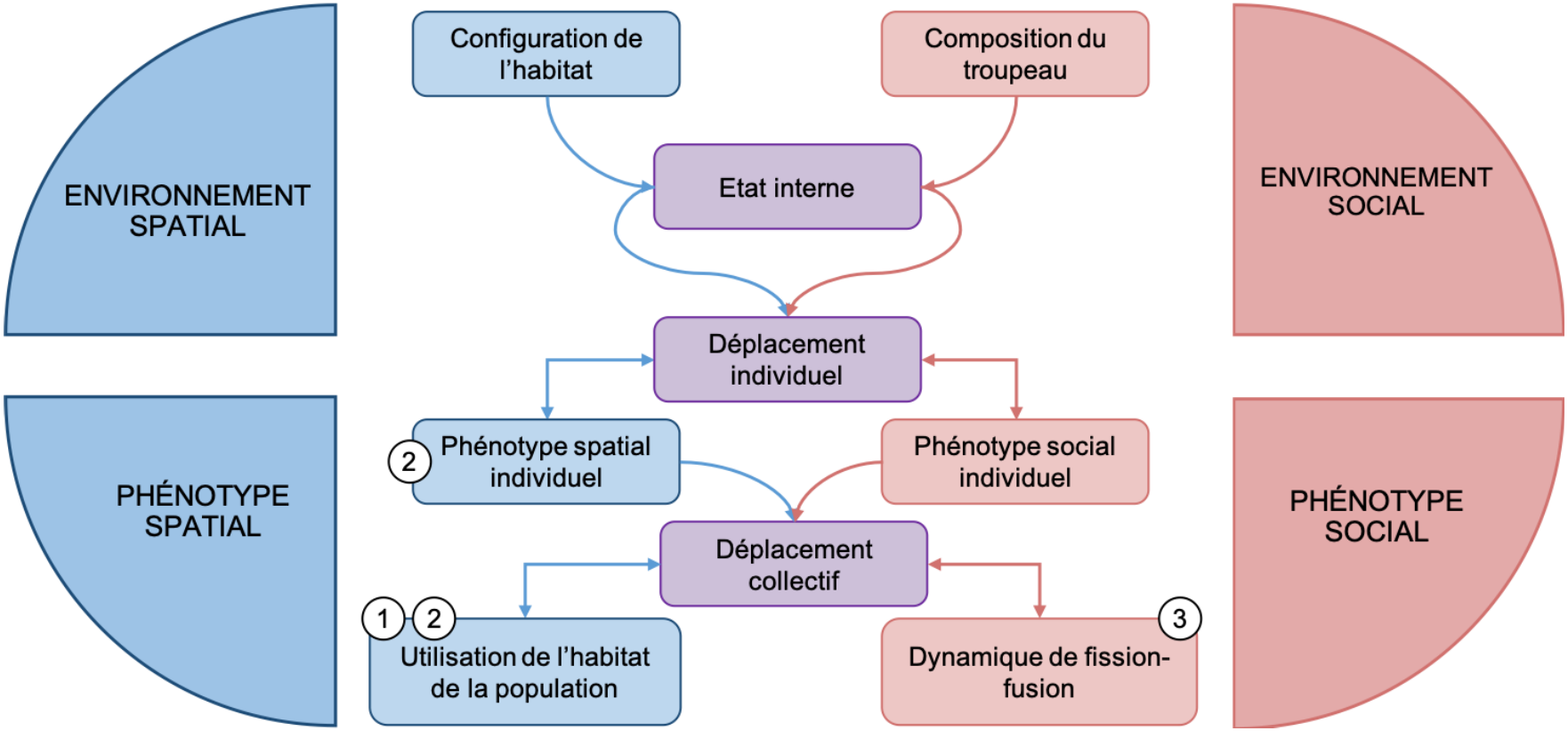

Figure 1.1 : Schéma conceptuel adapté de Webber et al. (2023) représentant le lien central du déplacement individuel à l'interface entre l'environnement spatial, l'environnement social, le phénotype spatial et le phénotype social. Chaque numéro indique l'un des chapitres de cette thèse.

La dynamique de fission-fusion

L'organisation sociale d'une unité sociale n'est pas figée et peut varier dans l'espace et le temps. Chez les primates non humains, Kummer (1971) qualifiait de « fission-fusion » les sociétés formées d'unités sociales à taille et composition variables, se divisant et fusionnant fréquemment selon l'activité comportementale et la disponibilité des ressources. Toutefois, cette définition donnait une perspective dichotomique restrictive (i.e., organisation flexible versus cohésive), excluant que la dynamique de fission-fusion se produise dans une certaine mesure chez la plupart des espèces.

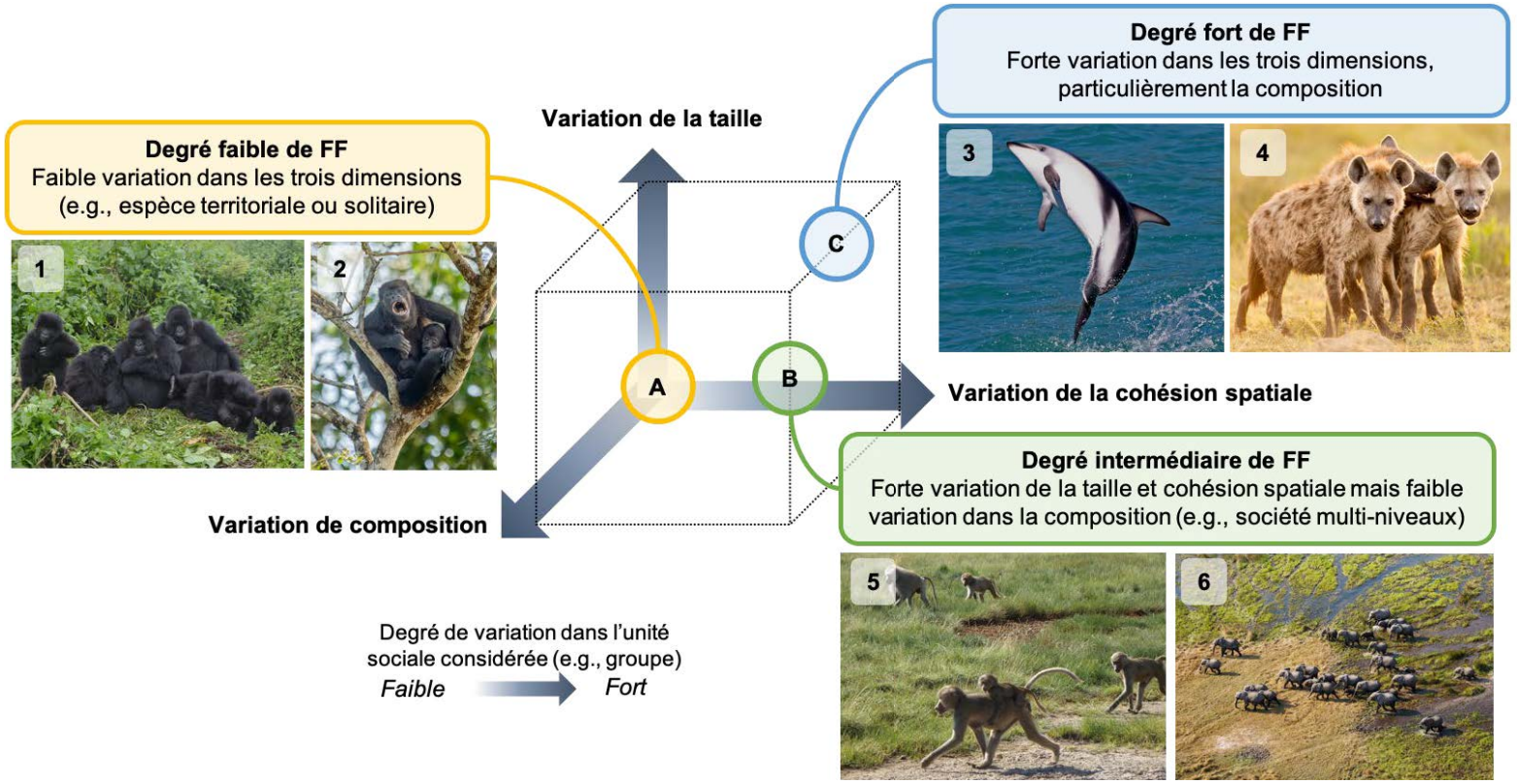

Figure 1.2 : Schéma conceptuel adapté d'Aureli et al. (2008) représentant les trois dimensions de la dynamique de fission-fusion : cohésion spatiale (axe x), la taille (axe y) et la composition (axe z). 1 : Gorille (*Gorilla beringei beringei*, © D. Fossey); 2 : Singe hurleur (*Alouatta pigra*, © Rhododendrites); 3 : Dauphin obscur (*Lagenorhynchus obscurus*, © S. Meriotte); 4 : Hyène tachetée (*Crocuta crocuta*, © F. Lanting); 5 : Babouin hamadryas (*Papio hamadryas*, © jeanjacquesgodon; 6 : Elephant d'Afrique (*Loxodonta africana*; © T. Dressler)

Le cadre conceptuel d'Aureli et al. (2008) définit la dynamique de fission-fusion comme le degré de la variation temporelle selon trois dimensions fondamentales : la cohésion spatiale, la taille, et la composition au sein d'une unité sociale. De nombreux taxons se positionnent ainsi le long d'un gradient (Figure 1.2), incluant les mammifères (e.g., *ongulés* : Wittemyer et al. 2005; Wielgus 2023 ; *primates* : Lehmann et Boesch 2004; Ramos-Fernández et Morales 2014 ; *carnivores* : Smith et al. 2008 ; Mbizah et al. 2019 ; *chiroptères* : Kerth et al. 2011 ; *cétacés* : Parra et al. 2011; Castro et al. 2022), les oiseaux (Silk et al. 2014), et les poissons (Wilson et al. 2014 ; Papastamatiou et al. 2020). Certaines unités sociales maintiennent une composition relativement stable mais varient en taille et cohésion spatiale (i.e., zone B : degré intermédiaire de fission-fusion, Figure 1.2 ; Wittemyer et al. 2005 ; Aureli et al. 2008). D'autres présentent une forte variabilité dans les trois dimensions (i.e., zone C : degré fort de fission-fusion, Figure 1.2 ; Pearson 2008 ; Smith et al. 2008). Cette diversité reflète les réponses adaptatives aux compromis coûts-bénéfices de la vie grégaire face aux conditions socio-écologiques (Sueur et al. 2011 ; Aureli et al. 2008 ; Webber et al. 2020 ; 2023). La compréhension des différents facteurs sous-jacents à la dynamique de fission-fusion est primordiale car les événements de fission-fusion influencent les processus clés d'une population (Figure 1.2), tels que la sélection et l'utilisation de leur habitat (Heithaus et Dill., 2002; Fortin et al. 2009), les déplacements (Haulsee et al. 2016), leur forme physique (Foster et al. 2012; Silk et al. 2014), le flux de gènes (Reisinger et al. 2017) et la façon

dont les informations, la culture (Mann et al. 2012; Allen et al. 2013) et les maladies (Altizer et al. 2003) sont transmises entre les individus.

De nombreux facteurs influencent les évènements de fission et fusion, mais leur importance relative varie entre espèces et au sein d'une même espèce. La disponibilité des ressources alimentaires est un facteur assez commun entre les espèces (Aureli et al. 2008 ; Sueur et al. 2011). Les animaux peuvent ajuster leur dynamique de groupe en fusionnant lorsque les ressources sont abondantes, ou fissionnant lorsqu'elles deviennent limitées afin de réduire la compétition intraspécifique et optimiser leur apport énergétique (Sueur et al. 2011). D'autres facteurs interviennent dans ces décisions comportementales, tels que l'état intrinsèque des individus (e.g., la fission peut se produire si les besoins entre les membres d'un groupe divergent ; Conradt & Ropert 2000 ; Sueur et al. 2011 ; Webber et al. 2023), l'accès à l'information sur la localisation et la qualité des ressources alimentaire ou des sites de repos ; Ramos-Fernandez & morales 2014 ; Sueur et al. 2011), ainsi que les risques de prédation (Heithaus & Dill 2002 ; Fortin et al. 2009).

Parmi les facteurs sociaux, la nature des relations entre les individus (e.g., familiarité et préférence d'association ; Wittemeyer 2005 ; Ramos-Fernandez et al. 2014 ; Le Goff et al. 2024), ainsi que la présence de jeunes individus dépendants (Lunardi et al. 2014 ; Castro et al. 2022) tendent à promouvoir la stabilité des groupes (i.e., peu de fission ou fusion). Cette

cohésion peut permettre la coopération pour le soin aux jeunes (Couzin 2006 ; Wittemeyer 2005 ; Gowans 2019), la protection contre les prédateurs (Bond et al. 2010), les agressions sexuelles (Cassini 2021), et les infanticides (Smith et al. 2008 ; Packer et al. 1990).

Les populations animales à l'ère de l'anthropocène

L'empreinte incontestable des activités humaines sur l'ensemble des composantes de notre planète (i.e., atmosphère, hydrosphère, cryosphère, biosphère et lithosphère) définit l'ère géologique actuelle : l'Anthropocène (Zalasiewicz et al. 2019). Ces activités, menées à un rythme effréné, exercent des pressions écologiques et évolutives sur les organismes (Hendry et al. 2017; Pelletier & Coltman 2018). La surexploitation des ressources, la dégradation et la perte des habitats, et les effets des changements climatiques constituent des modifications environnementales majeures et complexes pouvant entraîner le déclin et/ou l'extinction des populations animales (Monasterky 2014; Pachauri et al. 2014; Calvin et al. 2023). Par conséquent, de plus en plus d'études soutiennent qu'une sixième extinction de masse est en cours (Barnosky et al. 2011 ; Kolbert, 2014 ; Ceballos et al. 2015 ; McCallum, 2015 ; Cowie, Bouchet & Fontaine, 2022; Richardson et al. 2023), même si les réponses et l'ampleur des organismes touchés varient selon les taxons et les écosystèmes (Finn et al. 2023).

Zoom sur les mammifères marins

Dans les océans, peu d'espèces échappent à l'influence humaine (Halpern et al. 2015, 2019; Duarte et al. 2021). Parmi les 136 espèces de mammifères marins recensées (Comité taxonomique 2025), beaucoup sont menacées par de multiples activités anthropiques : trafic maritime, pêcherie, chasse, épuisement des ressources, pollution, introduction de pathogènes et espèces, et altération physico-chimique des océans (Avila et al. 2018; Erbe et al. 2019; Nelms et al. 2021; Plön et al. 2024). Les voies maritimes se sont intensifiées ces dernières décennies, générant des zones de passage très denses (Pirotta et al. 2019). Elles fragmentent, dégradent, et polluent les habitats, induisant des stress physiologiques et comportementaux chez les mammifères marins (Pirotta et al. 2019; Duarte et al. 2021; Erbe et al. 2019). Les collisions, documentées chez au moins 75 espèces de la mégafaune marine (Schoeman et al. 2020), provoquent des mortalités importantes. Par exemple, chez la baleine noire de l'Atlantique Nord (*Eubalaena glacialis*), plus de 52% des individus nécropsiés portaient des blessures (Campbell-Malone et al. 2008).

Les océans sont également devenus très bruyants depuis la révolution industrielle (Duarte et al. 2021). Le son joue un rôle central dans les activités comportementales vitales des mammifères marins (Southall 2017). De nombreuses études soutiennent que l'exposition chronique au bruit sous-marin constitue une forme majeure de dégradation de l'environnement

acoustique, en masquant des sons biologiquement importants (e.g., prédateurs, congénères ou proies), perturbant les activités comportementales essentielles, ou bien encore en causant des lésions physiques et un stress chronique (Ellison et al. 2012; Clark et al. 2009 ; Erbe et al. 2019 ; Williams et al. 2015; Gomez et al. 2016 ; Nowacek et al. 2007). Les réactions comportementales au bruit dépendent du contexte (Ellison et al. 2012; Gomez et al. 2016) et peuvent modifier la fidélité au site, voire entraîner l'abandon d'habitats importants tant que la perturbation sonore persiste (Allen et Read, 2000 ; Morton & Symonds 2002; Lusseau, 2005 ; Bejder et al. 2006 ; Pirotta et al. 2013; Forney et al. 2017 ; Stern et al. 2017). Le trafic maritime et les ports représentent également une source majeure de pollution via la dispersion des rejets chimiques et des déchets (Halpern et al. 2015).

Les pêcheries dégradent les habitats et les chaines trophiques, provoquant une défaunation marine globale (McCauley et al. 2015). La réduction des proies disponibles par surpêche entraîne des déclins de populations de mammifères marins (Avila et al. 2018; Nelms et al. 2021). En mer Méditerranée, le déclin de la population de dauphins communs à bec court (*Delphinus delphis*) est principalement attribué au déclin de leur proies pélagiques (Piroddi et al. 2011). Dans les eaux côtières du Nord-Ouest Pacifique, les taux de reproduction et de survie des épaulards résidents du sud (*Orcinus orca*) ont également diminué en raison du déclin de leur proie (Ford et al. 2010). De plus, les prises accessoires de la pêche (i.e., capture ou enchevêtrement accidentel dans les engins de pêche) constituent une menace

d'extinction pour certaines espèces, dont le phoque moine (*Monachus monachus*) en mer Méditerranée (Karamanlidis et al. 2008), et le vaquita (*Phocoena sinus*) dans le Golfe de Californie au Mexique (Jaramillo-Legorreta et al. 2019).

Les mammifères marins accumulent également des polluants persistants en ingérant des proies contaminées. Ces contaminants bioaccumulent dans la chaine alimentaire (de Lima Silva et al. 2024), et augmentent les risques de troubles de la reproduction et de susceptibilité aux maladies (Reijnders et al. 2017). Le faible rétablissement de certaines populations est attribué à l'exposition chronique de contaminants. Les polluants organiques persistants seraient liés à de nombreux cas de cancer chez les bélugas (*Delphinapterus leucas;* Poirier et al. 2019), et les fortes concentrations d'hydrocarbures consécutives à une marée noire auraient causé d'importantes mortalités chez les orques (Matkin et al. 2008). Par ailleurs, l'ingestion de grandes quantités de déchets plastiques peut mener à des mortalités comme observé chez un cachalot (*Physeter macrocephalus;* De Stephanis et al. 2014).

Stratégies de conservation

Les mesures de gestions concernant les effets des activités humaines sur la faune sauvage devraient idéalement être décidées avant que les populations ciblées ne commencent à décliner. Pour les mammifères marins, Evans (2018) distingue deux grandes approches de conservation : la

conservation par les aires, qui vise à gérer des espaces géographiques délimités (e.g., aires marine protégée), et la conservation par les pressions, qui cible directement la réduction des facteurs de stress anthropiques (e.g., redéfinition du trafic maritime). Considérant que les cétacés sont des espèces très mobiles, des mesures axées sur les pressions pourraient s'avérer plus efficaces (Evans 2018). La mise en place de mesures de conservation pour ces espèces repose sur une compréhension approfondie de la façon dont les organismes interagissent avec leur environnement (Redfern et al. 2006; Ross et al. 2011; Brakes & Dall 2016). Le comportement est un mécanisme clé par lequel les individus répondent à leur environnement, conditionnant la survie et la reproduction, et, *in fine*, la dynamique de population (Webber et al. 2020, 2023). L'écologie comportementale est ainsi une composante essentielle de la biologie de la conservation (Berger-Tal et al. 2011, 2016). Pour les espèces grégaires, les différences entre groupes sociaux peuvent entraîner des expositions inégales aux menaces anthropiques et des besoins de conservation variables selon les segments de la population (Brakes et al. 2021 ; Maldonado-Chaparro et al. 2021). Néanmoins, la considération du comportement social dans les stratégies de conservation demeure encore limitée (Berger-Tal et al. 2016 ; Brakes et al. 2021; Maldonado-Chaparro et al. 2021).

L'étude des schémas de déplacement permet d'élucider la distribution spatio-temporelle des individus au sein d'une population et de caractériser leur utilisation de l'espace. Au sein du domaine vital, l'identification des habitats

clés et des comportements qu'y s'y concentrent constitue un prérequis pour comprendre les fonctions écologiques de ces habitats et les déterminants de leur fréquentation (Mayor et al. 2009 ; Hooten et al. 2017 ; Bastille-Rousseau & Wittemeyer 2021). Ces connaissances permettent en outre de localiser les zones de chevauchement entre les habitats importants pour les individus et les menaces anthropiques, permettant une évaluation des risques d'exposition.

Chez les espèces longévives, les longues séries temporelles de données (e.g., observation, télémétrie, capture-recapture, isotopie stable, suivis acoustique, génétique) sont inestimables. Elles permettent de modéliser les patrons d'utilisation de l'habitat, les tendances démographiques et leur résilience face aux menaces anthropiques sur des échelles temporelles compatibles avec leur cycle de vie (e.g., baleine franche de l'Atlantique Nord : Pirotta et al. 2023). Ces données peuvent également fournir des informations de références, par exemple sur l'utilisation de l'habitat, et déterminer l'efficacité de la mise en place de mesure de conservation (Magurran et al. 2010).

Modèle biologique : le béluga de l'Estuaire du Saint-Laurent

Traits d'histoire de vie

Le béluga (*Delphinapterus leucas)* est un cétacé odontocète de taille moyenne (i.e., 3.5 – 5.5 mètres) appartenant à la famille des *Monodontidae*

(O'Corry-Crowe, 2018). En milieu naturel, son espérance de vie peut dépasser 90 ans (Ferguson et al. 2020). La couleur du corps varie au cours du développement : les veaux présentent une teinte brune à brun-bleuâtre foncée, qui s'éclaircit progressivement pour devenir grise durant les premières années de vie, puis uniformément blanche à l'âge adulte. La maturité sexuelle est atteinte entre 8 et 13 ans chez les femelles, et 8 à 11 ans chez les mâles (Finley et al. 1982; Ferguson et al. 2020; Inyakina et al. 2022; Hill et al. 2024). L'espèce présente un système de reproduction polygynandrique (i.e., mâles et femelles ont plus d'un partenaire au cours d'une même saison de reproduction ou au cours de plusieurs saisons; O'Corry-Crowe et al. 2026). La reproduction, vraisemblablement saisonnière, se produirait à la fin de l'hiver ou au début du printemps selon les populations (Brodie, 1971; Inyakina et al. 2022; O'Corry-Crowe, 2018). La gestation dure environ 14 mois et la lactation environ deux ans (Matthews and Ferguson 2015). Les femelles donnent naissance à un seul veau, et présentent de longs intervalles inter-naissances de 2 à 4 ans (Sergeant, 1973; O'Corry-Crowe, 2018; Fergusson et al. 2020 ; Hill et al. 2024). Enfin, les bélugas comptent parmi les rares espèces chez lesquelles une période post-reproductive est documentée (i.e., ménopause ; Ellis et al. 2018).

Comportement spatial

Le béluga occupe les régions Arctique et subarctique, au sein desquelles il effectue des migrations saisonnières dont l'ampleur varie entre

les populations (O'Corry-Crowe, 2018). La population de l'estuaire du Saint-Laurent, étudiée dans cette thèse, correspond à la plus méridionale de l'aire de répartition de l'espèce (Figure 1.3a; COSEWIC, 2016; Lesage 2021). Elle représente une relique de la glaciation du Wisconsin (Harington 2008). Cette population est désormais isolée à la fois géographiquement et génétiquement des autres populations de l'arctique (De March et al. 2002; COSEWIC, 2016; Postma 2017; Lesage 2021; Montana et al. 2024).

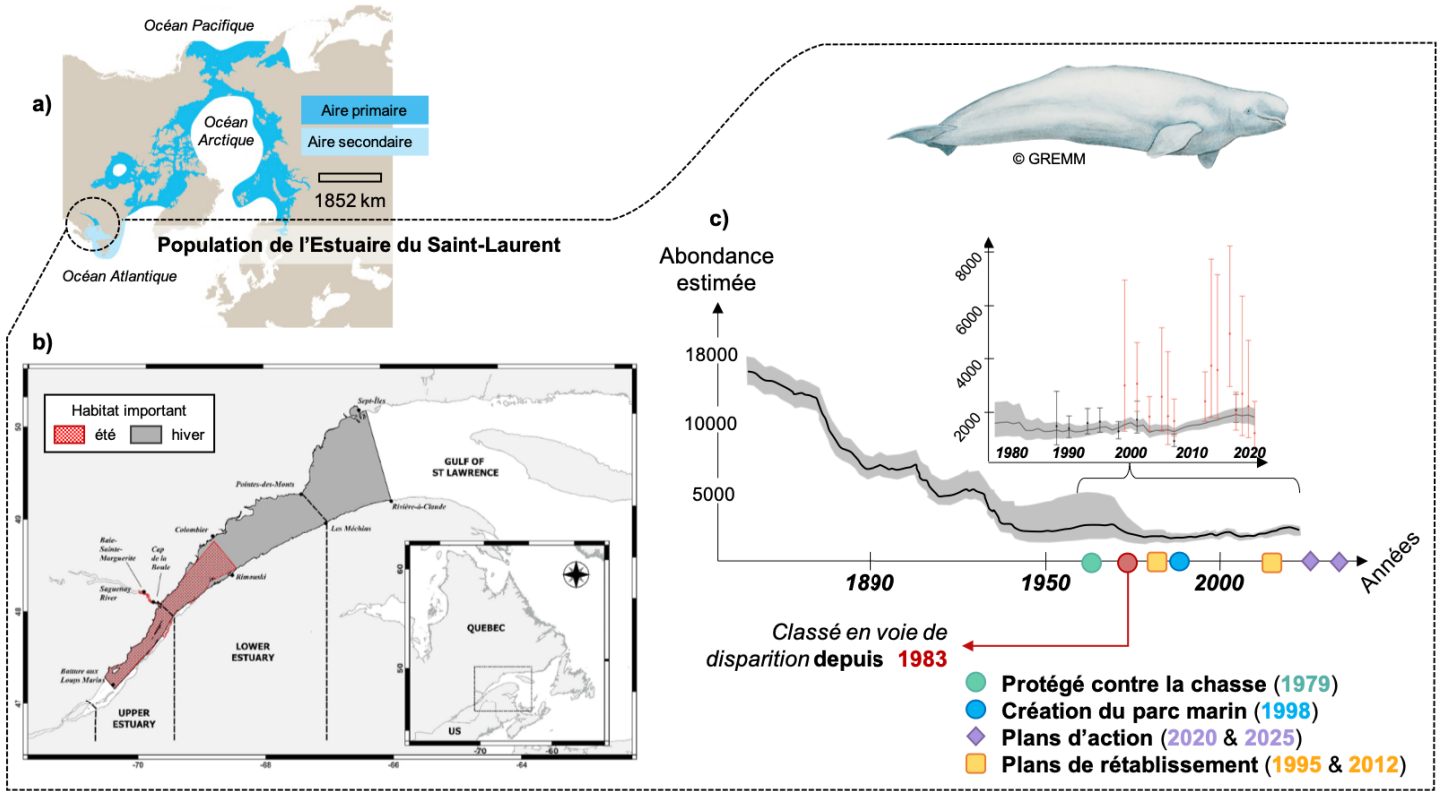

Figure 1.3 : Contexte biogéographique et démographique de la population de bélugas de l'estuaire du Saint-Laurent (ESL). a) Distribution mondiale de l'espèce (d'après O'Corry-Crowe 2018) ; c) Distribution de l'habitat important pour la population de l'ESL (voir détails dans Lesage et al. 2024) ; c) Tendances démographiques de la population estimées à partir de relevés aériens photographiques. La ligne pleine représente l'abondance moyenne estimée par le modèle pour chaque année, tandis que la bande ombrée illustre l'incertitude (intervalle de crédibilité à 95%) autour de cette estimation (voir détails dans Tinker et al. 2024). Les symboles montrent les dates clés de mises en place de mesures de protection et d'efforts de conservation.

L’aire de répartition, varie saisonnièrement et s’étend dans le nord-ouest du golfe du Saint-Laurent, bien qu’une portion de la population demeure dans l’estuaire du Saint-Laurent (ESL) à l’année (Lesage et al. 2024). L'habitat essentiel du béluga de l’ESL est défini comme l'aire estivale utilisée par les femelles, les juvéniles et les veaux entre juin et octobre, incluant les habitats et les caractéristiques considérées nécessaires aux activités vitales et à la survie de la population (zone grise hachurée sur la Figure 1.3c; DFO 2012). Durant l’été (i.e., période de juin à octobre), la population se concentre autour du Fjord du Saguenay jusqu’à St. Fulgence et s’étend en amont et en aval de l’ESL entre Battures aux Loups Marins et Rivière-Portneuf/Rimouski (Figure 1.3c). Les bélugas se déplacent entre l’estuaire et les eaux du Golfe du Saint-Laurent, généralement vers l’est à l'automne et vers l'ouest au printemps, ce qui représente des déplacements de distance de dizaines à centaines de kilomètres (Vladykov 1944; Mosnier et al. 2010; Gosselin et al. 2014 ; Simard et al. 2023 ; Harvey et al. 2024). Les bélugas utilisent le Fjord du Saguenay toute au long de l’année, avec une fréquentation plus intense entre juin et octobre (Conversano et al. 2017; Simard et al. 2023 ; Harvey et al. 2025).

Durant l’été, les bélugas de l’ESL n’utilisent pas les habitats disponibles de manière homogène. Les zones fortement utilisées telles que les aires de recherches restreintes, les aires de haute résidence, et les aires de haute densités ont été identifiées et sont connectées par un réseau de corridors (Michaud, 1993; Lefebvre et al. 2012; Mosnier et al. 2016; Ouellet et al. 2021;

Harvey et al. 2025). Bien que ces zones importantes soient identifiées, leurs fonctions restent présumées (e.g., corridors) ou inconnues (e.g., aires de haute résidence). Les bélugas s'y adonnent à de multiples activités jugées essentielles à leur cycle annuel telles que l'alimentation, la socialisation, le repos, la mise bas, ainsi que l'allaitement des nouveau-nés et les soins aux jeunes (Mosnier et al. 2010; Lefebvre et al. 2018). Les caractéristiques environnementales associées aux habitats dans lesquels ces activités ont lieu semblent également varier (Mosnier et al. 2016). Par exemple, le régime alimentaire des bélugas de l'ESL est diversifié, comprenant des espèces de proies à la fois benthiques et pélagiques (Vladykov 1944 ; Lesage et al. 2014 , 2020 ; Cabrol et al. 2025), suggérant que les habitats dédiés à l'alimentation diffèreraient selon l'écologie des proies.

La fidélité au site et la ségrégation par sexe et âge, typique de l'espèce, est également documentée durant l'été. Les troupeaux de femelles accompagnées de jeunes et de veaux tendent à utiliser plus souvent l'amont comparativement aux adultes seuls (e.g., les mâles) qui passent plus de temps à l'aval de l'estuaire (Michaud, 1993; Mosnier et al. 2016 ; Ouellet et al. 2021 ; Bonnell et al. 2022, 2024), résultant en une composition différente de la diète entre les mâles et les femelles (Lesage et al. 2014 ; Lesage et al. 2020).

Comportement social

Surnommé le « canaries des mers », le béluga possède un répertoire vocal particulièrement diversifié, considéré comme le reflet de la complexité de son système social (Sjare & Smith 1986 ; Michaud 2005 ; Alekseeva et al. 2013 ; Vergara et al. 2019 ; Garland et al. 2015 ; Panova et al. 2023). De nature grégaire, leur organisation sociale est très variable dans le temps et dans l'espace selon les contextes écologique et social. Leur structure sociale semble être hiérarchisée en plusieurs niveaux (Aubin et al. 2026), les individus pouvant être observés seuls, en dyades, en petits groupes ou en troupeaux pouvant atteindre plusieurs centaines d'individus, sans structuration sociale exclusive autour d'individus apparentés (Alekseeva et al. 2014 ; Mayette et al. 2022 ; Michaud 1993 ; O'Corry-Crowe et al. 2020 ; Stewart et al. 2025 ; Panova et al. 2025). Cette flexibilité sociale témoigne d'une dynamique de fission-fusion (Aureli et al. 2008), dont le degré et les facteurs sous-jacents sont actuellement inconnus. La socialité des femelles, probablement matrifocale (i.e., structure sociale centrée sur la maternité entre apparentés et non apparentés; O'Corry-Crowe et al. 2020 ; Aubin et al. 2026), semblerait permettre l'apprentissage culturel des routes migratoires et des aires estivales (Colbeck et al. 2023), ainsi que l'existence de comportements coopératifs tels que l'allocare (i.e., collaboration pour le soin des jeunes ; Aubin et al. 2021 ; 2023). La longue période de dépendance chez les veaux jusqu'à leur sevrage (association avec les mères jusqu'à 5 ans ; McGuire et al. 2020) permettrait l'apprentissage de comportements critiques liés à la communication, au

déplacement ou encore à la recherche de nourriture (Brodie 1969, Tyack 1986, Colbeck et al. 2013, Krasnova et al. 2014).

Rétablissement et conservation

Des siècles d'exploitation intensive ont sévèrement décimé la population lorsqu'elle a été protégée contre la chasse (Figure 1.3b; Pippard et Malcolm 1978, Sergeant et Hoek 1988, Kingsley 1998). Dès lors, cette population est demeurée fluctuante mais généralement stable. Mais depuis 2010, les taux de survie varient de plus en plus, avec une hausse soudaine des mortalités des femelles en gestation (Figure 1.3b). En 2022, un modèle a estimé l'abondance des bélugas à environ 1 850 individus (intervalle de crédibilité à 95 % : 1500-2200 individus; Tinker et al. 2024). La population est considérée comme « en voie de disparition » (Pippard 1985; COSEWIC 2014), un statut qui a trouvé un écho également dans le cadre de la Loi sur les Espèces en Péril (LEP) du Canada ainsi que la loi relative aux espèces menacées et vulnérables du Québec (RLRQ, c. E-12.01; Canada Gazette 2017).

Au Canada, lorsque le comité sur la situation des espèces en péril (référencé COSEWIC dans la thèse) évalue une espèce comme étant menacée, en voie de disparition, ou disparue, et que celle-ci est ensuite listée en vertu de la LEP, le ministère fédéral compétent est responsable de l'élaboration de plans de rétablissement et d'actions. Ces plans requièrent des informations scientifiques sur l'état de la population, les menaces pesant sur

sa survie et son rétablissement, ainsi que la faisabilité de son rétablissement. La conservation des habitats constitue un élément central à toute initiative de protection et de rétablissement des espèces pour mitiger les effets des activités anthropiques.

Malgré des efforts de protection considérables au cours des 40 dernières années (DFO 2012, 2020, 2025; Ménard et al. 2018), de multiples menaces pèsent sur le rétablissement de la population et sont d'origine variées. En vivant dans l'une des principales voies navigables de l'Amérique du Nord, les bélugas de l'ESL sont exposés à des niveaux de bruit élevés provenant du trafic maritime et des projets de développement marins (McQuinn et al. 2011; Gervaise et al. 2012; Ménard et al. 2018). Ils sont également exposés chroniquement à des niveaux élevés de contaminants en raison de la nature fortement industrialisée du bassin versant du Saint-Laurent (DFO 2012). D'autre part, la dégradation à long terme de son habitat par la pêche, les perturbations environnementales (e.g. prolifération d'algues toxiques) et anthropiques (e.g., opérations de dragage), les effets liés aux changements climatiques, et l'introduction d'espèces exotiques causent une réduction de l'abondance, de la qualité et de la disponibilité des ressources alimentaires (Plourde et al. 2014; Galbraith et al. 2023 ; Williams et al. 2021 ; Lesage et al. 2021 ; Lesage et al. 2024). La nature cumulative de ces facteurs de stress complique la prédiction de leurs conséquences à long terme sur la dynamique de la population, d'autant plus que les impacts varient

probablement selon le contexte d’exposition des différents segments de la population (Chion et al. 2021 ; Lesage et al. 2024).

Les inquiétudes concernant le déclin de la population ont déclenché la mise en œuvre d'une série de programmes qui ont été rigoureusement maintenus au fil du temps pour surveiller la santé, la démographie et la dynamique de la population (Figure 1.3b; Lesage et al. 2014 ; Lair et al. 2015, 2016 ; Mosnier et al. 2015 ; St-Pierre et al. 2024 ; Tinker et al. 2024). Cet ensemble de données est l'une des séries temporelles les plus longues pour un cétacé, faisant du béluga de l'ESL la population de béluga la mieux surveillée (Norman et al. 2022), et l'une des populations de cétacés les mieux surveillées au monde. Cette thèse s’appuie sur ces séries temporelles exceptionnelles pour approfondir notre compréhension de la dynamique spatiale et sociale des bélugas de l’ESL, et informer les stratégies de conservation.

Objectifs de la thèse

Cette thèse vise à identifier les facteurs qui sous-tendent la dynamique spatiale des bélugas de l’ESL dans l’optique d’informer les politiques de conservations de cette population. L’hypothèse centrale de cette thèse est que leur comportement spatial résulte de l’interaction entre les caractéristiques de l’habitat et l’environnement social (Webber et al. 2023). La thèse s’articule en trois chapitres. Elle explore d’abord les schémas d’utilisation de l’habitat par

les troupeaux et les patrons de déplacement individuel; puis, elle examine la dynamique de fission-fusion (Figure 1.1).

Questions de recherche

Quelles sont les fonctions des habitats identifiés comme importants pour la population? En tenant compte de la composition générale des troupeaux, dans quelle mesure l'association entre ces fonctions et les caractéristiques biotiques et abiotiques de l'habitat diffère-t-elle selon les variables explicatives considérées?

Le **chapitre 1** identifie les fonctions des habitats importants utilisés par les troupeaux de béluga de l'ESL. Ce chapitre s'appuie sur une classification comportementale, reliant l'activité et la configuration en surface des troupeaux et leur comportement de plongée (Lemieux Lefebvre et al. 2018). Il intègre ces comportements dans un cadre spatialement explicite combinant deux types d'habitats : les aires de haute résidence (Lemieux Lefebvre et al. 2012) et les routes de corridor (Ouellet et al. 2021). Les proportions relatives de ces comportements, calculées dans chaque habitat, ont servi de base pour regrouper statistiquement les zones selon leur fonction prédominante. Ces groupes ont ensuite été examinés en fonction des variables biophysiques de l'habitat, en distinguant les différents types de troupeaux pour tenir compte de leur comportement grégaire. Ce chapitre fournit une première quantification empirique des activités comportementales associées aux habitats jugés importants, dont les fonctions étaient jusqu'alors seulement supposées. Cette étude a été publiée en décembre 2025 dans la revue *Endangered Species Research.*

Quels sont les déterminants environnementaux des déplacements individuels? Est-ce que les comportements de déplacement se concentrent dans des zones spécifiques ?

Le **chapitre 2** détermine comment les facteurs environnementaux (caractéristiques de l'habitat et facteurs sociaux) influencent les comportements de déplacement individuels. L'utilisation de modèles de Markov cachés (HMM) a d'abord aidé à déterminer le nombre de comportement distincts à partir de données bidimensionnelles (i.e., angle de braquage et longueur de pas en surface), et l'échelle temporelle pertinente. L'intégration de covariables environnementales dans les HMM a ensuite permis d'examiner leur effet sur les probabilités de rester dans un même comportement ou de transiter d'un comportement à l'autre. Complémentaire avec le chapitre 1, cette approche fournit également une compréhension à fine échelle de l'utilisation de l'habitat à partir de la distribution des comportements. Cette étude est actuellement soumise pour révision dans la revue *Movement Ecology*.

Quel degré caractérise la dynamique de fission-fusion chez les troupeaux de béluga de l'ESL? Quels contextes sociaux, comportementaux, environnementaux, et anthropiques influencent les évènements de fission et fusion dans ces troupeaux ?

Le **chapitre 3** caractérise la dynamique de fission-fusion des troupeaux. En s'appuyant sur le cadre conceptuel d'Aureli et al. (2008), les événements de fission et de fusion ont été quantifiés à partir des variations de taille, de composition et de dispersion spatiale. Ces évènements ont ensuite été

modélisés en fonction des facteurs sociaux, comportementaux, environnementaux (i.e., caractéristiques de l'habitat), et anthropiques. Ce chapitre quantifie le degré de fission-fusion chez cette espèce, et identifie les contextes dans lesquels les évènements de fission et fusion se produisent. Les résultats de cette étude feront l'objet d'une soumission prochaine dans une revue révisée par les pairs.

Données disponibles dans le cadre de la thèse

Pour répondre à ces questions, cette recherche s'appuie sur deux sources de données complémentaires collectées durant la saison estivale (Figure 1.4). Depuis 1989, le Groupe de Recherche et d'Éducation sur les Mammifères Marins (GREMM) mène un programme de suivis focaux ayant permis de constituer une base de données comprenant plusieurs milliers de suivis de troupeau (~ 3961 entre 1989 et 2023), et couvrant une vaste gamme d'habitats à l'échelle de la répartition estivale de la population (Michaud, 1993 ; Lemieux Lefebvre et al. 2012 ; Ouellet et al. 2021). Ces suivis documentent, à intervalles réguliers sur des périodes d'environ 3 heures, l'organisation sociale et le comportement des troupeaux. L'étendue spatio-temporelle de la série et la taille de l'échantillon confèrent une puissance statistique robuste pour faire des inférences à l'échelle de la population. Ces suivis focaux intègrent ponctuellement des protocoles complémentaires comme par exemple de la photo-identification, des biopsies, des survols par drone, ou de la télémétrie. Cette longue série temporelle a été utilisée dans chacun des

trois chapitres de la thèse. En complément, des suivis télémétriques réalisés entre 2001 et 2020 par le GREMM et Pêches et Océans Canada ont fourni des trajectoires individuelles à fine résolution journalière, à partir de deux types de balises équipées d'un transmetteur radio : des balises TDR (44 individus, 2001-2005) et des Dtag (30 individus, 2018-2020). Ces données, utilisées dans le **Chapitre 2**, apportent une échelle individuelle plus fine, difficile à obtenir par l'observation seule, et le nombre total de trajectoires offre une puissance statistique suffisante pour des inférences à l'échelle de la population (Sequeira et al. 2018).

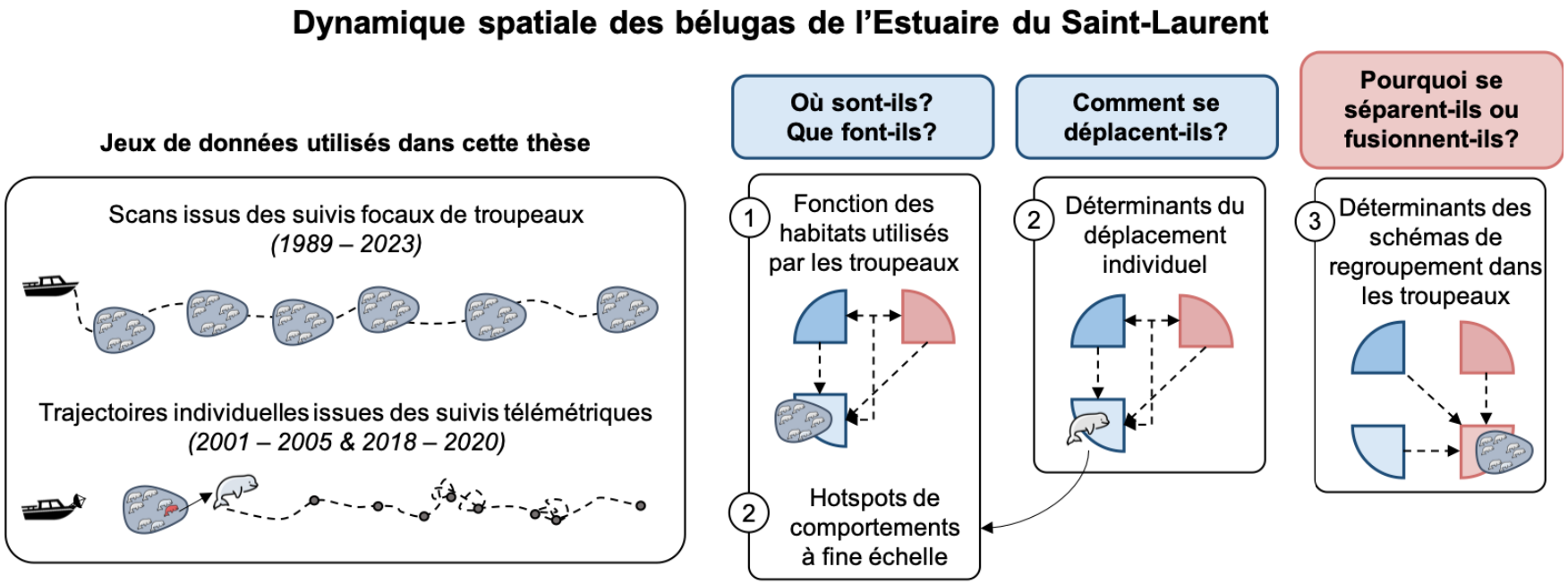

Figure 1.4 : Illustration des jeux de données utilisés et des questions de recherche adressées dans chaque chapitre de la thèse. Les flèches en pointillés indiquent les relations entre les composantes de l'interface socio-spatiale (Webber et al. 2023) testées dans chaque chapitre.

CHAPITRE 1 : 30 YEARS OF HERD FOCAL FOLLOWS REVEAL THE FUNCTIONS OF IMPORTANT HABITATS IDENTIFIED FOR THE ENDANGERED ST. LAWRENCE ESTUARY BELUGA

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Abstract

Identifying habitat functions is crucial for understanding how endangered populations such as the St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas*) use their environment, and for guiding effective conservation measures. Often, the only way to infer the behaviour of cetacean herds is by observing their surface activity and configuration. A previous study developed a classification connecting SLE beluga herd surface characteristics to their underwater diving behaviour, enabling the inference of behaviour from surface cues alone. Using this method, this research analyzed surface activity descriptors collected every 30 min during multi-hour focal follows of 1496 beluga herds tracked in 1991 – 2020 to classify their behaviour into six categories : 1) benthic feeding/resting/care of young, 2) pelagic feeding, 3) pelagic exploration, 4) socialization/benthic feeding, 5) transit, and 6) mixed activities. The relative frequency of these behaviours within each of twenty-seven previously-identified key beluga areas formed the basis for statistically grouping areas by their dominant function. Two groups characterized by high directional movement closely matched (≥ 90%) previously-hypothesized transit corridors. The other two groups predominantly exhibited foraging and social behaviours, and matched mainly (≥ 70%) areas with high beluga residency whose specific function was previously unclear. Although habitat groups varied in environmental characteristics, no clear separation was observed, suggesting other factors may shape habitat use at multiple scales. This study highlighted that beluga have limited alternative habitats to support vital

functions should local stressors compromise habitat quality or accessibility. These findings are critical because segments of the population show strong fidelity to specific summer sites.

Keywords : Beluga, St. Lawrence Estuary, Behavioural classification, Habitat use, Habitat functions, Herd focal-follow, Spatial management

Introduction

Animals navigate heterogeneous environments, where they select habitats that meet their requirements, and optimize their fitness (Morris 2003; Péron 2019). Several habitats may be required to satisfy important life functions, with some habitats supporting multiple needs. Habitat suitability is influenced by various factors, including individual motivations (e.g., energy provision, safety, social interaction), habitat accessibility, and habitat value which is defined by biotic and abiotic environmental conditions (Nathan et al. 2008). Behaviour, which provides the fundamental link between life-history requirements and habitat use, is therefore key to understanding why animals use specific habitats (Morris 2003, Nathan et al. 2008, Péron 2019).

Habitat degradation, through contamination or chronic high noise levels or human activity, may pose a significant threat to the survival of wildlife species (Williams et al. 2022), including cetaceans (Reeves 2018). Small populations showing high site fidelity and small home ranges may be especially vulnerable to habitat degradation as they may have few alternative habitats to support their biological needs (Forney et al. 2017; Merkle et al. 2022). For mitigation measures to be effective, there is a need to understanding habitat use patterns and habitat functions (Redfern et al. 2006; Ross et al. 2011; Brakes & Dall 2016). Boat-based surveys, aerial surveys, and short-term visual tracking (hereafter ‘focal follows’) of herds or groups often constitute the most comprehensive long-term data sets for cetaceans;

when analyzed alongside environmental characteristics and herd behaviours, they can reveal the life functions supported by specific habitats (Redfern et al. 2006, Ross et al. 2011, Brakes & Dall 2016).

The St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas*) resides at the southern edge of the species range (COSEWIC 2016; Lesage 2021). The habitat of this endangered population (COSEWIC 2014) is located downstream of a densely industrialized and urban region, that is chronically exposed to toxic chemical substances and high ambient noise levels (Lesage 2021; Lesage et al. 2024). While part of the SLE beluga population move seasonally into the northwestern Gulf of St. Lawrence, some individuals remain within the limits of the SLE year-round (Lesage et al. 2024; Harvey et al. 2025).

This population is among the most extensively studied within the species, and has the longest time series of observation data from aerial surveys and herd follows (Norman et al. 2022; Lesage et al. 2024; St-Pierre et al. 2024). The use of these datasets formed the basis for the designation of the critical habitat of this population (Mosnier et al. 2010; Lesage et al. 2024), and has allowed the detection of site fidelity (Bonnell et al. 2024) and differential exposure of the various segments of this population to local stressors (Chion et al. 2021; Bonnell et al. 2022). Specifically, herd focal follows were analyzed with a focus on movement directionality relative to environmental characteristics to identify corridor routes (those with high travel

speeds and strong directional movements) and highlight summer habitat connectivity (Ouellet et al. 2021). Herd movements and displacement speeds were further analyzed to identify areas where beluga showed area-restricted search and a higher degree of residency (areas of high residency, AHRs; Lemieux Lefebvre et al. 2012). Similarly, aerial survey data were analysed using a kernel approach to identify areas of high beluga densities (Mosnier et al. 2016; Harvey et al. 2025). While these three studies spatially-located key areas for beluga, their functions were either presumed as based on indirect evidence (corridor routes) or unknown (high-use area).

During summer (defined here as June to October), SLE beluga are expected to engage in multiple activities including feeding, socializing, resting, and calving (Lesage et al. 2024). During this period, the occurrence of area-restricted search in high-use areas may suggest the occurrence of foraging behaviour (Dorfman et al. 2022). Given SLE beluga feed both on pelagic and benthic prey (Lesage et al. 2020), whales may adopt multiple foraging strategies depending on expected prey encounter rate. For instance, beluga may conduct active patrols when prey are relatively stationary, and use sit-and-wait techniques when prey are more mobile (Bowen et al. 2002). As a result, high-use areas with a foraging function may not all present the same environmental characteristics.

Beluga are highly gregarious and exhibit a fission-fusion grouping pattern (Michaud, 2005; O'Corry-Crowe et al. 2020), and are spatially

segregated by sex and age in the SLE and other ecosystems (Michaud, 1993; Ouellet et al. 2021). Furthermore, a recent study indicates that specific segments of the population exhibit site fidelity to different sectors within their summer habitat (Bonnell et al. 2022, 2024). On top of these social factors, there is a number of environmental features that can affect beluga distribution and habitat use over time and space. Bathymetric features and oceanographic processes (e.g., water mass movement, up- and downwelling zones) may promote pelagic prey concentration and enhance foraging opportunities (Michaud 1990; Mosnier et al. 2016; Scharffenberg et al. 2019; Ouellet et al. 2021). Areas near large river mouths (resulting in larger catchment and greater discharge i.e., of higher Strahler stream order) can generate environmental gradients (e.g., salinity, temperature) and increase prey availability (Goetz et al. 2012; Hauser et al. 2017; McGuire et al. 2020; Ausen et al. 2023). Beluga may profit from tidal and surface currents when travelling (Ouellet et al. 2021) to minimize energetic costs (Goetz et al. 2012, McGuire et al. 2020).

In this study, 30 years of focal follow data documenting SLE beluga herd surface activity and configuration in relation to habitat types were used to attribute functions to the high-use areas previously-identified by Mosnier et al. (2016) and Lemieux Lefebvre et al. (2012), and to validate the hypothetic function of corridor routes for areas where high speed and directionality of movement were observed from beluga herds. High-use areas and presumed corridor routes were then examined for potential differences in environmental characteristics and usage according to beluga herd composition.

Materials & methods

Figure 1 summarizes the data sources, along with both the analyses from prior work utilized in this study and the analyses newly conducted as part of our research. Briefly, the foundation for the current study is a previously-developed classification method, which connected SLE beluga herd surface activity and configuration to their underwater diving behaviour, and which enabled herd behaviour to be inferred from surface cues alone (Lemieux Lefebvre et al. 2018). Using this method, the current study analyzed surface activity descriptors collected every 30 min during multi-hour focal follows of 1496 beluga herds tracked in 1991 – 2020 to classify herd behaviours into one of the six potential categories defined by Lemieux Lefebvre et al. (2018). For each of the 26 previously-identified high-use areas or presumed corridor routes, the relative frequency of these six behavioural categories was then used to statistically group areas based on similarity in main functions. Groups of habitats were then examined for potential differences in environmental characteristics and usage according to beluga herd composition.

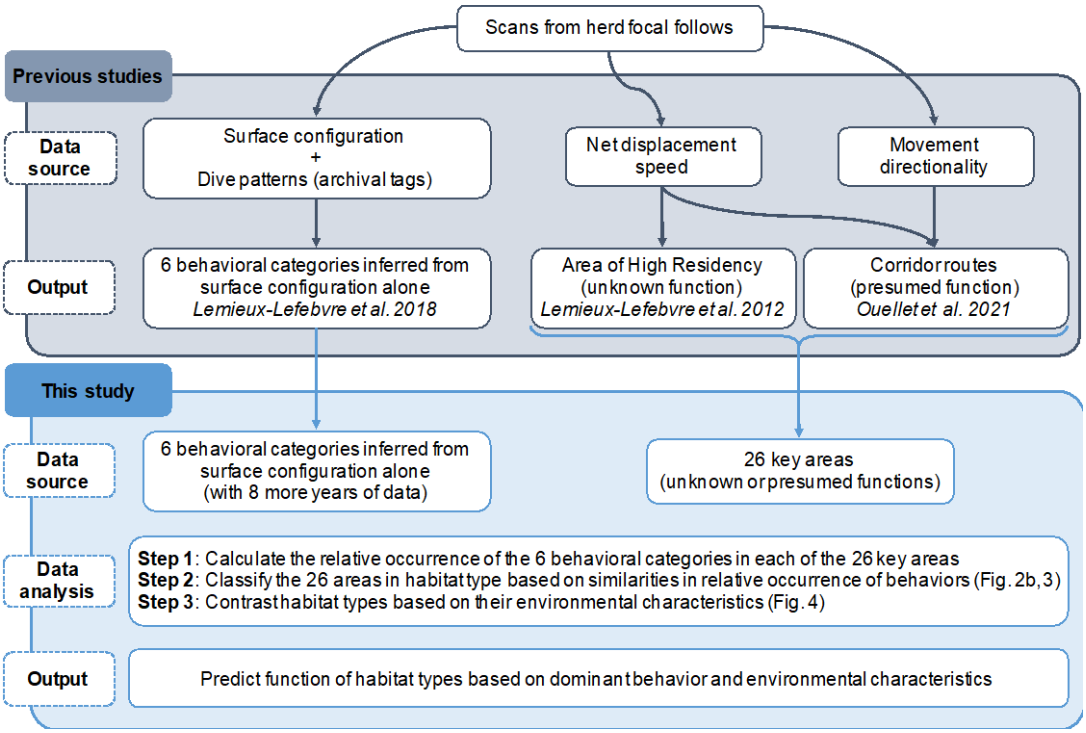


Figure 2.1 : Summary showing the specific data sources, analytical procedures, and outputs from studies that have used scans of beluga herd focal follows, with previous studies indicated by grey arrows and boxes, and the current study by blue arrows and boxes). Scans refer to the collection of herd surface configuration and activity characteristics (hereafter 'surface configuration') that were recorded at 30-min intervals during focal follows.

Data collection

Vessel-borne focal follows of beluga herds were conducted in the St. Lawrence Estuary and Saguenay Fjord between June and October of 1989 – 2020, as part of a long-term research program on the SLE beluga. This study covered a large portion of the SLE beluga summer distribution, and included a broad range of habitats used by all types of herds (Michaud 1993; Lemieux Lefebvre et al. 2012; Ouellet et al. 2021; Lesage et al. 2024). The search area was chosen daily according to weather conditions in a way to avoid resampling the areas covered in the previous days, and to maximize spatial coverage.

Upon opportunistic encounter with a beluga herd, the research vessel was maintained away (~300 m) from the herd for approximately 15 min. A herd was defined as an assemblage of groups, each composed of animals swimming within one body length of each other, generally in a relatively coordinated fashion. Following this 15-min observation period, the research vessel proceeded into the herd at a slow cruising speed (<5 knots) to approach groups in turn for photo-identification or other research protocols. A detailed description (hereafter called scan) of the herd surface configuration and activity was made every 30 minutes, using 10 specific herd metrics : 1) herd size, 2) herd type based on age composition, 3) radius, 4) geometrical structure, 5) form, 6) dispersion, 7) predominant movement patterns, 8) swimming dynamism, and presence or not of 9) acrobatic surface events and 10) surface vocalizations. Categories for each of these descriptors are presented in Suppl. Mat. 2.1. Age composition was based on skin color for juveniles (shades of grey) and adults (white). Young of the year (calves) were identified by a combination of length (half the body length of adults), color (dark grey or brown), and for neonates, also by fetal folds, consistent chin ups when breaking the surface, close proximity to an adult, and dark circle around the eye (Michaud 2014). Herd composition was derived from these age classes (see Suppl. Mat. 2.1). A herd follow was usually limited to 3 hours, and produced up to 5-6 scans per herd, though occasionally fewer due to factors like changing weather. Location of the research vessel was used as a proxy for the centroid of the herd; previous work has indicated that there was no

systematic bias in the research vessel positioning relative to the herd centre (Lemieux Lefebvre 2009).

Herd surface activities and inference of behaviour

In a previous study, Lemieux Lefebvre et al. (2018) developed a methodology to infer the behaviour of SLE beluga herds based on surface cues alone. Specifically, using the 10 descriptors of herd configuration and surface activity (see previous section) in a cluster analysis, these authors assigned beluga surface activities to one of six potential categories. By using dive characteristics from 45 belugas equipped with archival tags while conducting focal follows and scan surveys of their respective herds, Lemieux Lefebvre et al. (2018) were able to infer from 16 descriptors of dive characteristics, the most likely behaviours associated with each of these six surface activity categories. The inferred behaviour for each of these categories were : 1) benthic foraging/resting/care of young, 2) socialization/benthic foraging, 3) pelagic foraging, 4) pelagic exploration, 5) travelling and 6) mixed activity (definitions in Table 1). Note that some categories may include multiple potential behaviours; limits on the type of sensors for archival tags, and the availability of other contextual information precluded further refinements of these classes (see Lemieux Lefebvre et al. 2018).

Lemieux Lefebvre et al. (2018) developed their classification scheme using SLE beluga focal follows conducted from 1991 to 2012. In our study, their classification was applied to an additional 497 herds followed between

2013 and 2020; each scan during these focal follows were assigned to one of the six pre-defined behavioural categories. Combining assignments from the most recent period with the assignments made by Lemieux Lefebvre et al. (2018) for previous years provided 30 years of focal follows (1991-2020) and herd inferred behaviours to assess the spatial occurrence of these behavioural categories and habitat functions and characteristics. As in Lemieux Lefebvre et al. (2018), only scans with a complete set of surface configuration variables (Suppl. Mat. 2.1) were retained for this classification. The cluster analysis was carried out in SAS ® (PROC *fastclust* function, *version 9.2,* SAS 2008).

Table 2.1 : Definitions of the six inferred behavioural categories that were identified by Lemieux Lefebvre et al. (2018) from the combined analysis of herd surface activity and configuration (hereafter 'surface activity'), and corresponding dive characteristics (hereafter 'dive type') from beluga equipped with archival tags and tracked within herds with these surface activity characteristics.

	Behavioral category	Main characteristics	
		Surface activity	Dive type
1	Benthic foraging or resting or caring for young	Milling movements with reduced (low to moderate) dynamism	Near-surface and benthic diving bouts (v-shaped, slow speed dive)
2	Socializing or benthic foraging	Milling movements with occurrence of surface events and vocalizations	Benthic diving bout (v-shaped, fast speed dive)
3	Pelagic foraging	Multidirectional movements with reduced (low to moderate) dynamism	Pelagic diving bouts with wiggles
4	Pelagic exploration	Directional movements by dispersed herds	Pelagic diving bouts
5	Traveling	Directional movements	Near-surface and pelagic diving bouts
6	Mixed	Milling and directional movements	Pelagic and benthic diving bouts

Spatial occurrence of behavioural categories

The assessment of the spatial occurrence of the six behavioural categories required that corridor routes identified by Ouellet et al. (2021) and AHR defined by Lemieux Lefebvre et al. (2012) be merged (Figure 2A). Areas of high residency were defined on a per-cell basis (1 km^2) using displacement

speeds of beluga herds, resulting in polygons with irregular boundaries (see Figure 2A). While corridors were also identified using quantitative movement metrics (i.e., correlated movement directions in adjacent cells), and same cell size as in Lemieux Lefebvre et al. (2012), polygon boundaries were guided but not fully based on geomatic methods. To ensure connectivity of AHR with the transit corridors, scans classified as foraging behaviour or other non-transit activities, and falling outside AHR zones but within corridor routes, were used to adjust AHR zone boundaries (see Figure 2A). No expansions were done beyond the predicted contours of corridors identified by Ouellet et al. (2021).

Polygons with fewer than 15 scans available to characterize the occurrence of the six categories of behaviour were discarded. The minimum number of scans per polygon was determined through a sensitivity analysis examining the stability of the clustering results for minimum sample sizes per polygon of 10, 15, 20 and 30 scans (not shown). AHR polygons with at least 15 scans that were located within 2 km (i.e., 2 cells) from another AHR polygon with 15 or more scans were merged, leading to 27 habitat polygons composing the spatially-explicit mosaic of beluga habitat (Figure 2A; Suppl. Mat. 2.2).

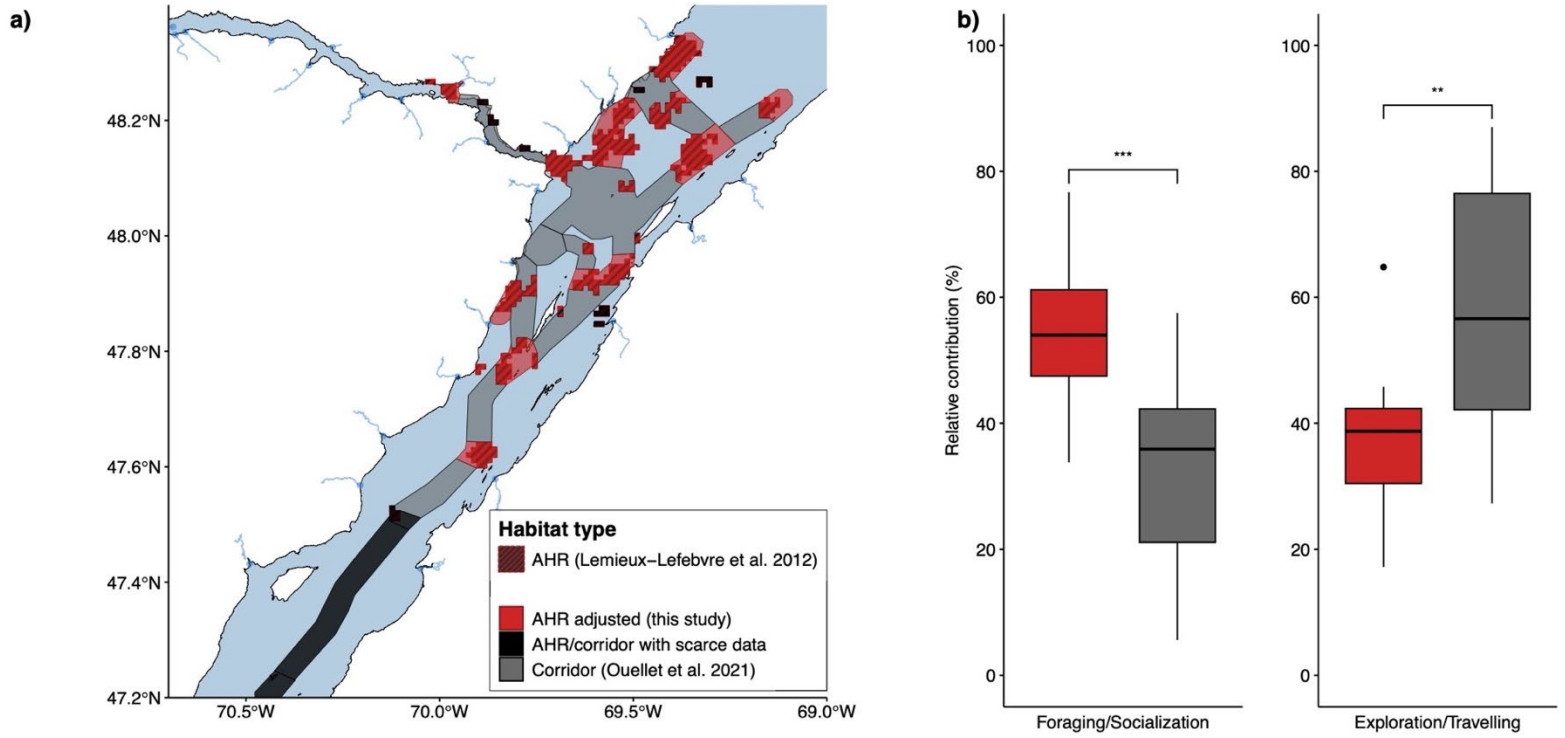


Figure 2.2 : (a) Existing information on the location of areas of high residency (AHR, in red) and corridor routes (in grey) for St. Lawrence Estuary beluga, based on Lemieux Lefebvre et al. (2012) and Ouellet et al. (2021). Original limits for AHR (red with black stripes) and those adjusted to fit corridor routes (limits in red solid) are both presented. AHR/corridor with scarce data (in black) corresponds to polygons with less than 15 scans. The blue lines correspond to locations of river mouths with a Strahler stream of order 4. (b) Our own analysis of descriptors for surface activity of beluga herds that were collected every 30 min from herds followed between 1991 and 2020, and which contrasts the relative occurrence of predicted categories of behaviour between AHR and corridor routes. Each box represents the interquartile range, with the median indicated by a horizontal line inside the box. Asterisks mark significant differences between groups : **p < 0.01, ***p < 0.001.

Identification of habitat types

The relative occurrence of the six previously-defined behaviour categories was calculated for each of the 27 habitat polygons. As an initial step to evaluate whether AHR truly represented behaviours involving greater residency and corridor routes being use for transit behaviour, the six categories were consolidated into three. Foraging (both benthic and pelagic) and socializing activities (categories 1 to 3 in Table 1) were combined as these behaviours likely involved frequent changes in movement direction. Pelagic exploration and traveling categories were also combined (categories 4 and 5 in Table 1) as they likely implied more directional movements. Mixed behaviour (Category 6 in Table 1) was not considered in this first analysis. The frequency of these two behavioural classes was compared across the 27 corridor and AHR polygons using Welch's two sample t-tests (with independent observations), hypothesizing that foraging/socializing behaviour should prevail in AHR polygons, and pelagic exploration/travelling should dominate in corridor polygons. Frequency distributions were checked for normality and heteroscedasticity (Levene's test). Bonferroni-adjusted p-values were applied to two-sample t-tests to reduce Type I error from multiple comparisons.

In a second step, habitat polygons were grouped according to similarities in the relative frequency of occurrence of the six behaviour categories using an agglomerative hierarchical cluster analysis based on Euclidean distance among groups and Ward D2 minimum variance method (Murtagh & Legendre, 2014) (R packages "*FactoMineR" version 2.7* and

"*Factoextra" version 1.0.7*). The optimal number of habitat types was determined using the most popular solution provided by 30 different indices (R package "*NBclust" version 3.0*). Following this analysis, each scan during a focal follow was assigned a behaviour among the six potential category, and a habitat type.

Environmental characteristics of habitat types

To improve the characterization of the identified habitat types and underlying functions, each scan was assigned eight environmental characteristics likely relevant to SLE beluga ecology (Table 2), based on the closest matching location and time. Bathymetry data (10 m horizontal and < 1 m vertical resolutions) were obtained from the Canadian Hydrographic Service (https://open.canada.ca/data/en/dataset/d3881c4c-650d-4070-bf9b-1e00aabf0a1d). Following Mosnier et al. (2016), the slope was determined using a reference grid of 50 by 50 m, and by comparing slope and seafloor depth at the center of each grid cell with the bathymetric variation observed within a 15-km radius around that cell (Suppl. Mat. 2.3, Jenness 2006). Slopes close to the coast could not be a ridge and were classified as mid-slopes. Distance to the nearest coastline and to river mouths were calculated as the shortest distance between these features; interfering islands were accounted for by calculating the shortest distance that bypassed the obstacle. Location of river mouths with a Strahler stream of order 4 (i.e., mid-sized tributaries formed by the confluence of multiple smaller streams including at least three of order

3, and having large catchment area and discharge; see blue lines in Figure 2A) were obtained from the Geobase of the Quebec hydrographic network (https://mrnf.gouv.qc.ca/repertoire-geographique/reseau-hydrographique-grhq/). Surface current speeds were obtained from a well-established and -validated three-dimensional oceanographic model developed for the study area, using a 400 m spatial and 1 h temporal resolution (Saucier et al. 1999; Saucier & Chasse, 2000). Tidal phase was calculated from the time since the last low tide, using forecasts for Tadoussac, Quebec, as a reference. Following Ouellet et al. (2021), tide was classified in 3 h bins (low, rising, high, ebb times), where high tide occurred 5 to 7 h after low tide. Scans were attributed to one of these tidal phases using forecasted tide phase at the time nearest to the herd scan. The probability of sandlance (*Ammodytes americanus*) occurrence, a potential prey of SLE beluga (Vladykov 1946, Lesage, 2014, Lesage et al. 2020), and sediment classification (see Table 2 for definitions) were obtained from benthic imagery during inventories of 137 sites between 2008 and 2010 (detailed methodology and Figure 8 in Mosnier et al. 2016). Geoprocessing of environmental variables was performed in QGIS (*version* 3.18.2, QGIS, Development Team 2021) and SAGA (*version 7.2.0,* SAGA, 2015).

Environmental characteristics were used as explanatory variables in multinomial logistic regressions (MLR) to assess their capacity to discriminate among the four habitat types (the response variable), and determine if environmental characteristics selected to explain habitat use were the same for all types of herds. Conceptually, MLR generalizes a model with a response

variable following a binomial distribution, by allowing multiple (i.e., more than two) categorical response variables. Covariates having a significant influence on the response variable are determined by comparing each categorical response variable (here, each habitat type, coded 1) with a predefined habitat type baseline (coded 0) (Agresti 2012). For instance, in the case where four habitat types were identified, three logistic regressions would be estimated simultaneously, with each of three habitat types being compared to the fourth habitat type serving as a baseline. The habitat type with the most uniform behaviour composition (i.e., at least 50% in one behavioural category) was chosen as the baseline.

Table 2.2 : Environmental characteristics used to discriminate among habitat types.

	Environmental variable	Description
1	Bathymetry	Seafloor depth at 10 m horizontal and <1 m vertical resolutions
2	Slope	Seafloor slope based on bathymetry data with horizontal resolution of 50 m
	Flat	Region where seafloor bathymetry changes by ≤5°
	Valley	Region with slope lower than the surrounding seafloor (e.g. bottom between steep slope ≥6)
	Mid-slope	Region with a change in bathymetry >5°
	Ridge	Region with slope greater than the surrounding seafloor (e.g. summit between steep slope slopes >5° or near the top)
3	Distance to coastline	Closest distance (in km) between coastline (mainland or islands) and herd location
4	Distance to river mouth	Closest distance (in km) between a herd and the mouth of a river with a Strahler stream of order 4 (i.e. a river with more than 2 tributaries)
5	Surface current speed	Modeled surface current velocity and direction at a resolution of 400 m and 1 h
6	Tidal phase	Four tidal phases at 3 regular intervals assigned based on the nearest hour at the time of herd observation
7	Sediment size	Classification based on benthic imagery
	Small	Exclusively or predominantly small-sized sediments (e.g. sand)
	Medium	Exclusively or predominantly medium-sized sediments (e.g. gravel)
	Large	Exclusively or predominantly large-sized sediments (e.g. rock)
	Mixed	Mix of medium and large sediments
8	Sand lance	Predicted probability of sand lance occurrence based on benthic imagery

MLR were implemented using the "*mclogit*" R package (*version 0.9.6*), while first considering all herd types together, then each of the three herd types separately (i.e. adults only, adult-grey, adult-grey-calf), for a total of four

models. Environmental variables were first examined for their distribution and presence of outliers (continuous variables) or balance among categories (categorical variables). Due to convergence issues, it was not possible to use mixed-effects models; thus, only fixed-effects MLR were implemented, with several scans contributed by each herd. The potential for residual temporal autocorrelation was assessed graphically (*acf* function in R package "*car" version 3.1-2)*; residual spatial autocorrelation was assessed using Moran's test (R package *"SPDEP" version 1.3-11).* All possible combinations of the eight environmental variables were considered (R package "*Mumin"* version 1.47.1). For categorical variables, the intercepts were set to "Low" (tidal phase), "Mid-slope" (slope) and "Mix" (sediment size). Generalized Variance Inflation Factors (GVIFs) corrected for degrees of freedom were used to quantify multicollinearity among explanatory variables. Model selection for the MLR on adults only was constrained to a maximum of three explanatory variables due to the smaller sample size for this herd type (Suppl. Mat. 2.4, Agresti 2012). Model selection was based on the lowest Akaike Information Criteria corrected for small sample size (AICc) (Anderson & Burnham, 2002). Model fit and potential within-herd correlation were assessed from the distribution of median Pearson residuals per herd and behavioural class.

The efficiency of MLR models in classifying habitat types from environmental variables was assessed using misclassification rates (R package "*caret" v6.03.95*). Model accuracy represented the proportion of correctly classified scans, whereas sensitivity and specificity measured true

positives and true negatives per habitat type, respectively. Sensitivity and specificity were averaged over habitat types to assess the overall performance of models. Balanced accuracy - the mean of sensitivity and specificity - accounted for potential imbalanced sample size between habitat types, and was used as an additional measure of model performance. These four metrics assessed model robustness to the chosen baseline. Nagelkerke pseudo R^2 evaluated model fit and predictive strength of environmental variables (Nagelkerke 1991). Predictive margins plots illustrated how the probability of falling into each habitat type (including the baseline) changed with each environmental variable (R package "*mpred"* version 0.2.4.1), revealing the direction and strength of associations. All statistical analyses were conducted in R (*version 4.2.2,* R Core Team, 2022).

Results

Data collection

Of the 3500 herds followed between June and October of 1989—2020, approximately half (n = 1496 herds) had one or more scans with complete information on herd surface configuration and activity. Overall, 3098 scans (all from 1991 – 2020) from these 1496 herds were assigned a behavioural category following the methodology developed by Lemieux Lefebvre et al. (2018). Nineteen of them were excluded from the MLR analysis due to missing values for sediment type.

Spatial occurrence of behavioural categories

Foraging and socializing behaviours (Categories 1 to 3 in Table 1) were significantly more frequent in polygons previously identified as AHRs ($t = 3.9$, $df = 24.5$, $p < 0.001$; Fig. 2b), whereas exploration and traveling behaviours (Categories 4 and 5 in Table 1) were significantly more frequent in polygons identified as presumed transit corridors ($t = 3.4$, $df = 22.6$, $p = 0.002$; Fig. 2b).

Identification of habitat types

The hierarchical cluster analysis grouped the 27 high-use areas and corridors into four habitat types, which differed in the relative occurrence of the various behaviours (Figure 3). Two habitat types - Travel Dominant (TD) and Travel and Pelagic Foraging (TPF) - included exclusively (100%) or almost exclusively (88%) polygons identified as corridor routes (Figure 3). Behaviours involving directional movements or exploratory dives dominated these two habitat types (80 and 60%, for TD and TPF, respectively), with infrequent occurrence of foraging behaviours. In contrast, Pelagic Foraging Dominant (PFD) and Benthic Foraging Dominant (BFD) habitat types were respectively composed at 73% and 100% of habitat polygons identified as AHRs. These habitat types showed a high prevalence (> 60%) of foraging or mixed behaviours, mainly pelagic foraging in PFD, and benthic foraging in BFD (Figure 3). Socialization and some rarely observed behaviours such as resting or caring for youngs (Category 1 in Table 1) occurred at low frequencies in all habitat types, but were overall more frequent in habitats classified as BFD.

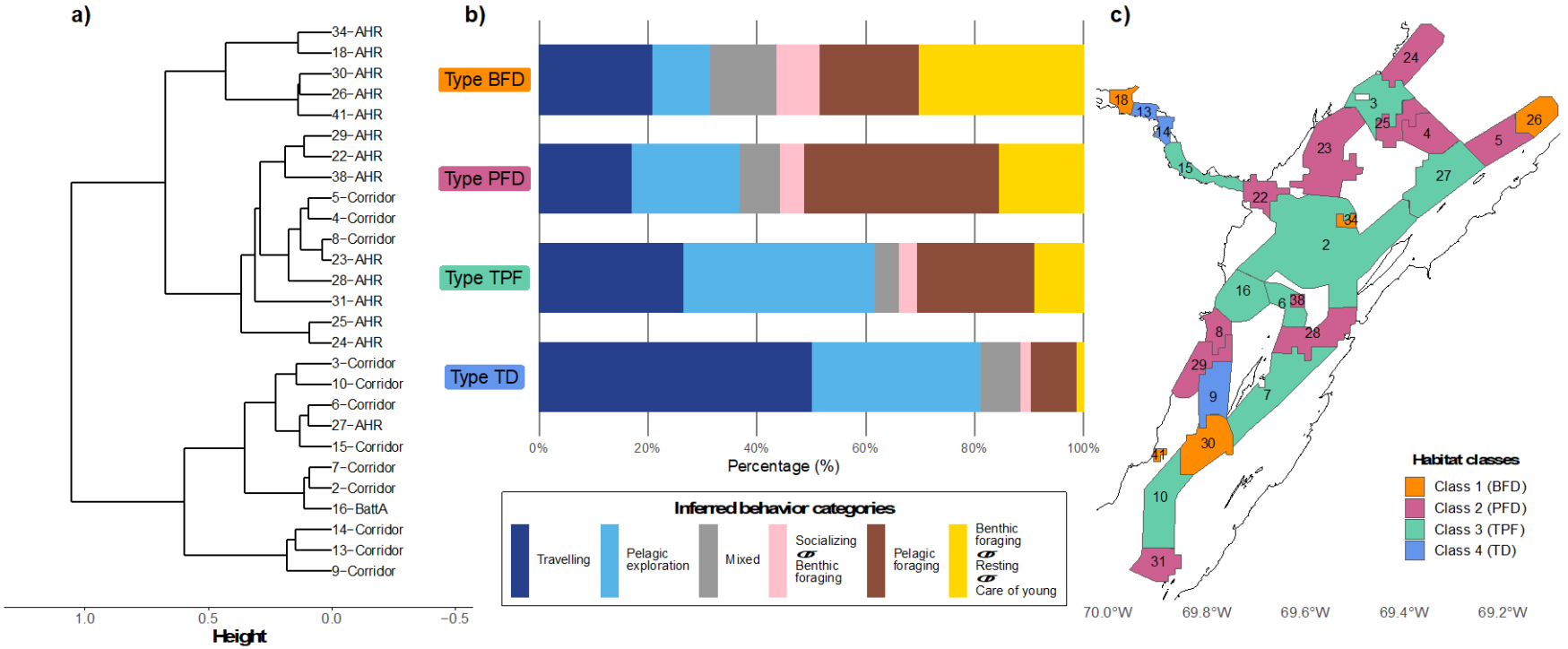


Figure 2.3 : a) Habitat types identified by hierarchical cluster analysis of habitat polygons (see panels a and c), using the relative occurrence of various inferred behaviours as input variables. The four habitat types identified (different colors in panels a and b) are described as : Benthic foraging dominant (Type BFD), Pelagic foraging dominant (Type PFD), Travel & pelagic foraging (Type TPF), Travel dominant (Type TD). b) Relative contribution of the six behavioural categories to each habitat type, and c) distribution of habitat polygons and associated types within the SLE beluga summer habitat are presented in panels b and c. Behaviour categories are as defined by Lemieux Lefebvre et al. (2018).

Environmental characteristics of habitat types

The TD habitat type was selected as the baseline, as it was the single type with a behaviour (travelling) accounting for at least 50% of all observed behaviours (Figure 3B). Despite imbalanced sample sizes among polygons (Suppl. Mat. 2.2), MLR performance indicators suggested a moderately good accuracy of the global and herd type-specific models in defining habitat types based on environmental characteristics (Table 3). Overall accuracy varied from 61 to 70% depending on models (i.e., equivalent to misclassification rates of 30 to 39%), and had generally slightly higher balanced accuracy indicators compared to overall accuracy indicators, suggesting model robustness to imbalanced sample sizes. In all cases, specificity surpassed sensitivity, indicating a higher efficiency at accurately recognizing scans as belonging to particular habitat types than at identifying scans that did not fit those habitat types. Model goodness of fit (Nagelkerke R^2) was of 0.70 or more for all models (Table 3). Performance metrics were similar regardless of the habitat type chosen as baseline. Generally, temporal autocorrelation did not exceed two consecutive scans (i.e., beyond 1 h) (Suppl. Mat. 2.5 to 2.8). Median residuals were centered around zero for habitat types TD and BFD but were more dispersed or skewed for TPF and PFD (Suppl. Mat. 2.9 to 2.12). However, spatial autocorrelation in residuals was detected for all models (Moran's I values ranging from 0.26 to 0.57, all with $p < 0.05$), indicating that some spatial patterns in habitat use were not fully accounted for by the environmental predictors. Together, these results suggest that models may have limited

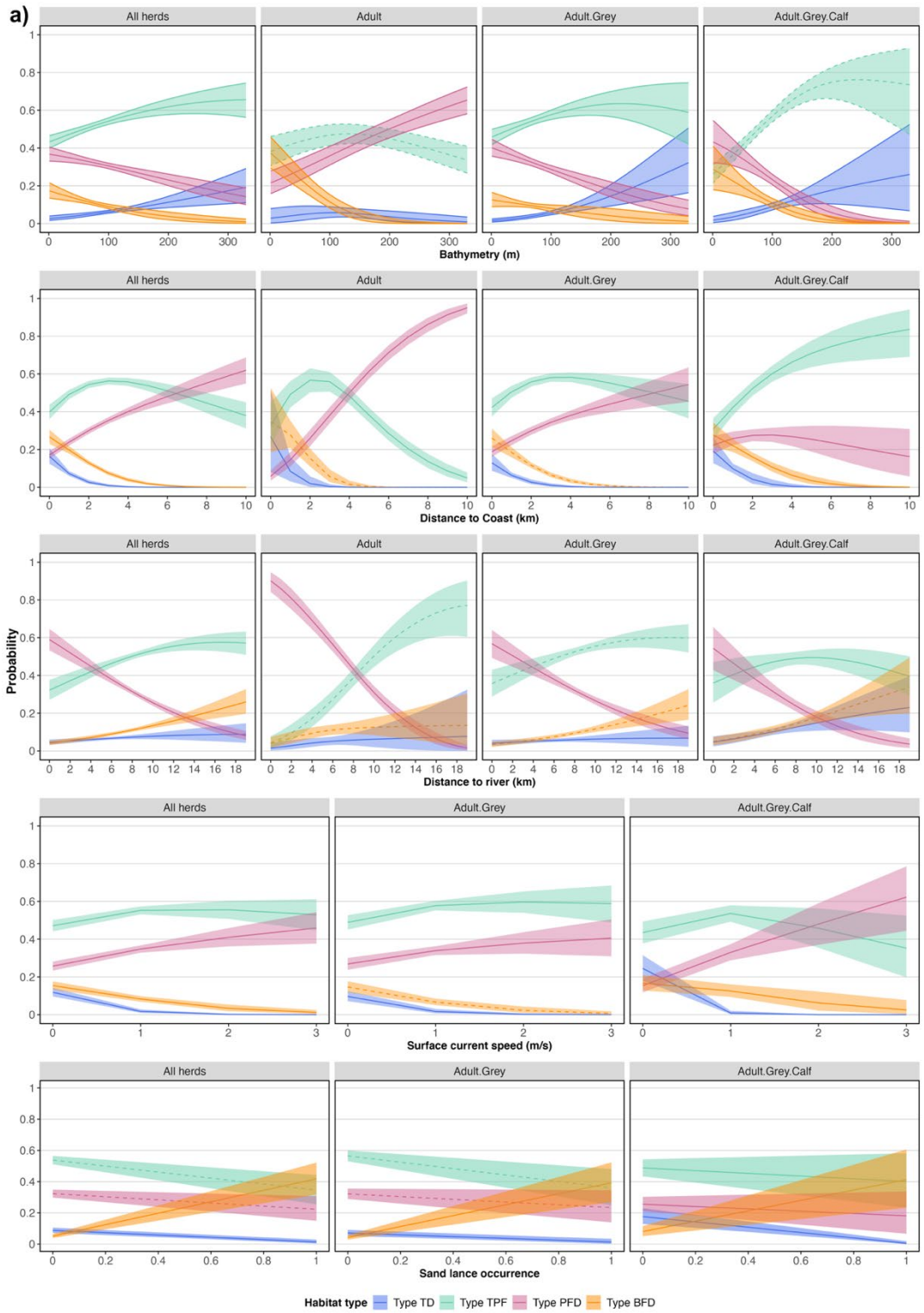
predictive power for identifying habitat functions based on environmental characteristics alone (see black areas in Figure 2a).

The top-ranked model for the various herd types included the same seven environmental variables (i.e., all but tidal phase), except adults-only herds, which were allowed only three variables (i.e., bathymetry, distances to coast and river mouth; Suppl. Mat. 2.13). GVIF indicated no significant correlation among environmental variables (Suppl. Mat. 2.14). Predicted probabilities for all models showed that habitats dominated by travel behaviours (TD) were most likely near the coastline, in deeper waters with mid-slope, medium sediments, low current, and fewer sand lance, though effects were weak (probabilities < 0.20). Predicted probabilities for habitats associated with travel and pelagic foraging (TPF) remained stable across environmental gradients, and increased only slightly with depth, suggesting environmental characteristics were not as specific for this habitat type. Habitats where pelagic foraging dominated (PFD) were more likely farther from the coast and closer to river mouths, predominantly in shallower waters with mid-slope or valley-shaped seafloor, higher currents, smaller and mixed sediments. Habitats suitable for benthic foraging (BFD) were generally the opposite - in shallow areas close to shore and away from river mouths, where current speed is low and probability of sand lance occurrence is high.

Table 2.3. Comparison of accuracy metrics for multiple logistic regressions (MLRs) predicting habitat types from environmental variables using all types of herds ('all types') or each herd type separately. Grey corresponds to juveniles identified based on their skin grey color

	Models by herd type			
	All types	Adult only	Adult–grey	Adult–grey–calf
Number of scans	3076	347	1958	771
Overall accuracy (% of classes correctly classified with 95% confidence interval)	65 (63–67)	70 (65–75)	66 (64–68)	61 (57–64)
Mean sensitivity (% of true positives)	61	53	46	54
Mean specificity (% of true negatives)	85	88	81	83
Balanced accuracy (%) (with 95% confidence interval)	73 (71–75)	70 (67–79)	64 (62–67)	69 (74–81)
Nagelkerke's pseudo-R^2	0.69	0.80	0.72	0.69

Results were generally similar when considering herd types separately, suggesting drivers of habitat use varied little with herd composition (Figure 4). However, habitats dominated by pelagic foraging (PFD) and used by adults-only tended to occur in deeper waters, farther from the coast and closer to river mouths compared to habitats used by herds composed of adults and greys, or of adults, greys and calves (Figure 4).


a)
All herds
Adult
Adult.Grey
Adult.Grey.Calf
Probability
Bathymetry (m)
Distance to Coast (km)
Distance to river (km)
Surface current speed (m/s)
Sand lance occurrence
Habitat type
Type TD
Type TPF
Type PFD
Type BFD

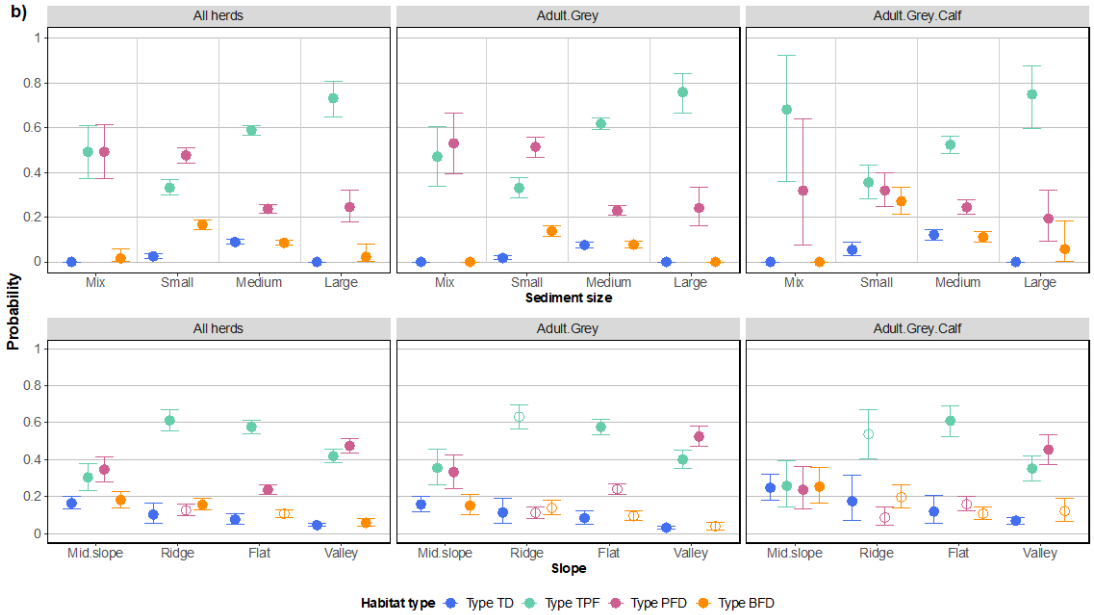


Figure 2.4 : Predictive margins plot assessing, from the fitted multiple logistic regressions (MLRs) for different herd compositions, the probability of falling into each habitat type (response) according to (a) continuous and (b) categorial environmental variables. The 4 habitat types are described as benthic foraging dominant (BFD), pelagic foraging dominant (PFD), travel and pelagic foraging (TPF), and travel dominant (TD). Note that only the first 3 continuous variables were included in the model for adult-only herds given the small sample size for this herd type. Effect sizes are shown by 95 % confidence intervals. Dashed lines in (a) and empty points in (b) indicate non-significant associations with environmental variables (see Suppl. Mat. 2.15)

Discussion

This study used long-term observational data to identify dominant behaviour and functions of habitats, which were deemed important for SLE beluga but for unknown reasons until our study. SLE beluga are an interesting case study because of the range of behaviours that are expected to occur in their summer habitat, in addition to foraging, their segregation by sex and age, and the heterogeneity in environmental characteristics of their summer habitat. Our findings indicate that beluga may use a given habitat for multiple functions,

and that environmental variables driving the connection between habitat use and function can vary with herd composition.

Habitat functions

Using an extensive dataset of beluga herd follows (1991 – 2020) and a spatially explicit framework of key habitats with so far unknown functions, this study identified biologically interpretable habitat types in the SLE, each characterized by distinct predominant functions. Habitats categorized as TD and TPF consisted mainly of corridors and were used primarily for travelling and exploration, supporting their function as transit routes (Ouellet et al. 2021). Surface current speeds were generally weaker in TD habitats compared to TPF habitats, which were associated with a wider range of current velocities. Tidal phases did not emerge as an important variable despite evidence that beluga modulate their movements according to tidal flow direction and phase (Ouellet et al. 2021). The SLE is characterized by a highly complex hydrology and a salt-wedge estuary with strong stratification of water masses. During rising tides, marine water flows upstream beneath a freshwater layer, creating lower surface current speeds compared to ebb tide conditions (Saucier & Charrier 2000). This estuarine circulation dynamics may explain the weaker surface currents in TD habitats, which likely reduces the detectability of tidal effects in models based on herd surface activity alone.

Habitats categorized as PFD and BFD in which belugas were mostly engaged in foraging, were mainly composed of AHRs, supporting predictions

of their role as foraging areas (Michaud 1993, Lemieux Lefebvre et al. 2012). The spatial variation in benthic and pelagic foraging behaviours across habitat types indicated that SLE beluga use distinct areas to target different prey type, reflecting both habitat-specific prey availability and the species' generalist diet (Vladykov 1946, Lemieux Lefebvre et al. 2018, Lesage et al. 2020; Cabrol et al. 2025). Benthic foraging was included in both BFD and PFD habitat types, but differed in associated movement and dive characteristics. In the BFD type, benthic foraging was generally linked to slower swim speeds and v-shaped dives (Lemieux Lefebvre et al. 2018), suggesting sit-and-wait or slow patrolling strategies (Bowen et al. 2002). Conversely, benthic foraging observed in the PFD type involved higher swim speeds and more dynamic dives, suggesting a more active search or pursuit strategy. Furthermore, the presence of sand lance, a benthic prey for beluga strongly associated with fine sediment (Mosnier et al. 2016), had a larger influence on the probability of habitat being assigned to BFD, where benthic foraging may involve stationary tactics (i.e., slow patrol or sit-and-wait) to a larger extent. However, due to the non-exclusive nature of behavioural categories (e.g., 'benthic foraging or resting or care of young'), and the limitations of movement data alone, some ambiguity remained. Future work incorporating information on pitch, roll, and yaw and on acoustic environment (click emission, or sounds associated with prey capture) could improve the discrimination of these behaviours and confirm prey capture events (e.g., Wright et al. 2021).

Beluga exhibit spatial segregation and sexual dimorphism that are manifested in dietary differences across age and sex classes both in the SLE and elsewhere (Loseto et al. 2006; Marcoux et al. 2012; Lesage et al. 2020; Louis et al. 2021; Michaud 1993; Ouellet et al. 2021; Cabrol et al. 2025). Generally, adult females accompanied by youngs tend to favor relatively warm and shallow waters, though their summer distribution in the SLE do overlap with adult males in some areas (Ouellet et al. 2021). In contrast, adult males tend to occur more regularly in deeper and colder waters (e.g., Laurentian Channel in the SLE) (Ouellet et al. 2021), a characteristic that may reduce intraspecific competition and limit aggressions of females with neonates during the calving period (Lesage et al. 2024). Consistent with these species traits, deeper habitats were more likely to be classified as PFD when used by herds of adults only, whereas the reversed trend emerged for adults accompanied by juveniles and/or calves. Males can devote more energy to prey on higher-quality fish in these deeper waters than females, which are constrained by reproductive and social needs. While mothers may require high-quality prey to compensate lactation (Lesage et al. 2020), accessing these resources may be facilitated through association with other females, where other individuals can help care for the calves during feeding (Krasnova et al. 2014; Aubin et al. 2023).

AHRs were also used for socializing and possibly for other behaviours that are suspected, though rarely observed, such as resting, nursing or giving birth (see Béland et al. 1990, Lemieux Lefebvre et al. 2018; Lesage et al.

2024). While socializing activities were detected in all habitat types, they occurred with the highest frequency in BFD habitats. These habitats, were generally located in the shallow and warm waters of the Saguenay Fjord and Upper Estuary, and along the south shore in the Lower Estuary, possibly providing shelter from wind and waves (Loseto 2006, Anderson et al. 2017, Sharffenberg et al. 2019).

Methodological considerations and futures directions

While the long-term dataset exploited in our work is extensive, this study was limited by the amount of data available and the broad and non-exclusive behavioural categories that could be derived from the match between herd surface configuration and activity and diving data (see Lemieux Lefebvre et al. 2018). Some important behaviours like nursing and parturition were not quantified as these cryptic behaviours were not observed during herd follows (Béland et al. 1990; Lesage et al. 2024). Moreover, the identified habitat functions represent averages over the summer period, and do not extend to other seasons due to temporal limitations in data collection. The purpose and importance of these habitats, including prey availability, are likely to change seasonally and possibly over the long term (Rioux et al. 2023; Cabrol et al. 2025). Whether the observation of multiple behaviours in a given habitat was related to uncaptured seasonal changes in habitat functions or to their true overlap in space due to the small summer range and residency of this population cannot be determined. The small sample size of the focal follow

dataset, once divided by cell and habitat polygon, precluded the examination of change in habitat functions over time, even at a decadal scale. However, the analysis of three decades of aerial survey data does not support a change in the location of key areas over time, though a greater use of key areas of the eastern portion of the summer habitat was noted in recent years (Lesage et al. 2024; Harvey et al. 2025).

This study could have benefited from the inclusion of additional predictors of habitat use, which might have accounted for the residual spatial dependency in our models. Density and biomass information for prey species other than sand lance could have increased our discriminating power for foraging tactics. However, data on invertebrate and fish distribution and abundance remain highly limited for the SLE, and the Upper Estuary in particular, where a large proportion of the females, juveniles and calves occur from spring to fall (Lesage et al. 2024). Other potentially useful predictors of habitat use and that may alter beluga distribution by creating avoidance include density of potential competitors for food resources (e.g., harp and grey seals, redfish, striped bass, Lesage 2021; Cabrol et al. 2025) and environmental stressors such as vessel traffic (Tervo et al. 2023).

This study highlighted the challenge of achieving clear discrimination among habitat type based on environmental characteristics alone, and suggests that other factors, possibly social factors, operating at other temporal or spatial resolutions, may be driving habitat use patterns. Beluga exhibit a

high degree of sociality, cultural learning, and fusion-fission dynamics (Michaud 2005, O'Corry-Crowe et al. 2020), as well as site fidelity and sexual and age segregation. All these social behaviours may interact with optimal environmental variables. In this study, comparisons among herd types were impaired by small the sample size for herds of adult-only, which likely stem from their more localized occurrence in the study area, larger herd sizes (Michaud et al. 1990) and thus, lesser chances of being sampled. The fusion-fission dynamics is not well understood in beluga but may result from balancing the benefits of joining and leaving herds to access food, care for youngs, reduce competition, avoid conflicting interactions between males and females with calves (R. Michaud, GREMM, Unpublished data), and participate in social learning and cultural tradition (Michaud, 2005, Whitehead 2008, Eguiguren et al. 2019). Further investigation of fusion-fission dynamics could enhance our understanding of how sociality may drive space usage and movement patterns in SLE beluga.

Implications of habitat use patterns for conservation

This study estimated the relative frequency of various behaviours in previously-identified key summer areas for SLE, and identified habitat type and their main functions by combining observed behaviours with environmental characteristics. Since the impact of anthropogenic threats varies with context, this information provides a basis for guiding planning and prioritization of

mitigation measures (Redfern et al. 2006, Ross et al. 2011, Brakes & Dall 2016).

This study emphasized the limited availability of habitats for beluga to fulfill critical needs in their summer range. Their site fidelity (Chion et al. 2021; Bonnell et al. 2024), the fact that portions of the population use different habitats within sex and age classes (Bonnell et al. 2022) on top of the age and sexual segregation (Michaud 1993; Ouellet et al. 2021) may increase their vulnerability to local stressor and limit access to alternative habitats (Brakes & Dall 2016, Forney et al. 2017, Merkle et al. 2022). Environmental stressors such as vessel noise can mask belugas calls and modify acoustic behaviour causing behavioural disruption (Constantine et al. 2004; Pirotta et al. 2015; Wisniewska et al. 2018). Scenarios of increased marine traffic in the Saguenay Fjord for instance, could expose females accompanied by calves disproportionally to noise given their fidelity to this sector (Chion et al. 2021).

Conclusion

Identifying areas of aggregation or regularly used is often the initial step for understanding habitat use in wildlife species. This study built on a previous study which identified key areas for SLE beluga. Using an existing method developed to identify herd behaviour from surface activity alone, we were able to determine the relative occurrence of various behaviours in each of these areas and identify their primary functions. This exercise has emphasized the limited number of alternative habitats available to SLE beluga in the event that

local stressors would degrade habitat quality or accessibility. This is of paramount importance for this endangered population, given their summer range is among the smallest for the species (COSEWIC 2014) and is fragmented by the species site fidelity and small home ranges within this habitat.

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Authors' contributions

EB, VL, AD, RM, and CC conceived the study; VL, CC, and RM obtained funding; VL, and RM conducted field research; EB and J.FS contributed to data preparation; EB conducted the analysis; EB, VL, and AD wrote the manuscript with contributions from RM, J.FS, and CC.

Supplementary Material

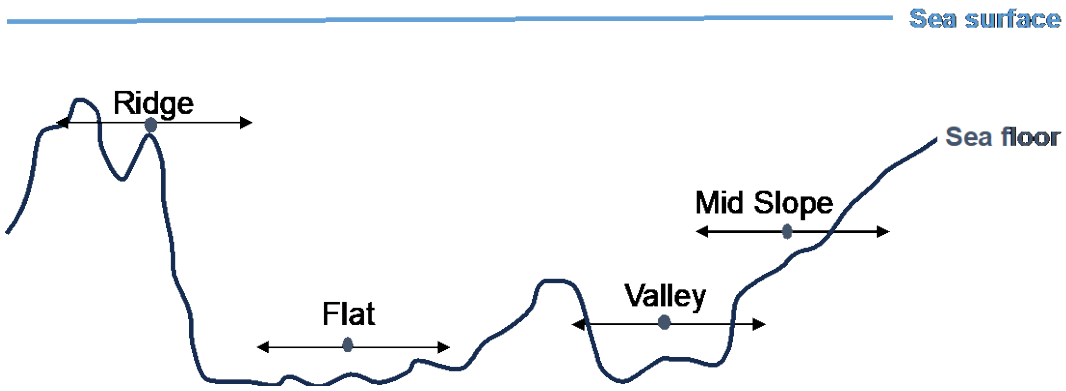
Suppl. Mat. 2.1 : Descriptors used to characterize herd configuration and surface activity used in our analysis and in the previous study by Lemieux Lefebvre et al. 2018. Ranges shown reflect the minimum and maximum values observed in the dataset; no a priori threshold was imposed on group size or radius.

Variable	Category	Description
Size	2-225	Number of individuals within herd
Radius	5-2000	Radius of the herd spatial extent (m)
Composition	Adult only Adult-grey Adult-grey-calf	Less than 10% of grey individuals White individuals and grey colored juveniles White individuals, grey colored juveniles, and young of the year
Form	Broken Front Line	Individuals or groups do not show a precise configuration Individuals or groups are abreast from one another forming a front Individuals or groups are following one another forming a line
Structure	Uniform Clustered	Individuals or groups are uniformly distributed within the herd Individuals or groups are distributed in a few distinct clusters
Dispersion	Tight Tight Dispersed	Distance between individuals or groups < 100 m Distance between individuals or groups = 100 – 300 m Distance between individuals or groups > 300 m
Predominent movement pattern	Directional Multi-Directional Milling	Continuous unidirectional movement Directional movement with frequent deviation from the main axis Circular movement at the surface resulting in low net displacement
Swimming dynamism	Low Low to Moderate Moderate Moderate to High High	Level of energy displayed by individuals at the surface
Surface event	Yes No	Spy hoping, tail or pectoral slash, breach, body contacts
Surface vocalizations	Yes No	Vocalizations can be heard from the research vessel

Suppl. Mat. 2.2 : Surface area (km²) and sample size for each of the 27 polygons used in the hierarchical cluster analysis. Polygon IDs correspond to those shown in Figure 3c.

ID_polygone	surface_km2	n_scans
41-AHR	0.87	15
26-AHR	14.33	16
9-Corridor	17.12	18
10-Corridor	43.07	33
5-Corridor	17.12	34
24-AHR	29.69	38
38-AHR	2.15	40
4-Corridor	25.61	40
6-Corridor	18.14	49
31-AHR	18.65	58
25-AHR	22.96	59
3-Corridor	41.26	62
8-Corridor	13.84	83
34-AHR	3.31	93
14-Corridor	4.94	115
30-AHR	36.70	121
13-Corridor	3.51	123
29-AHR	27.38	148
16-Corridor	37.41	156
7-Corridor	73.57	171
28-AHR	45.85	185
18-AHR	4.73	206
27-AHR	48.62	213
23-AHR	86.09	222
22-AHR	12.25	281
15-Corridor	29.10	431
2-Corridor	288.06	1 011

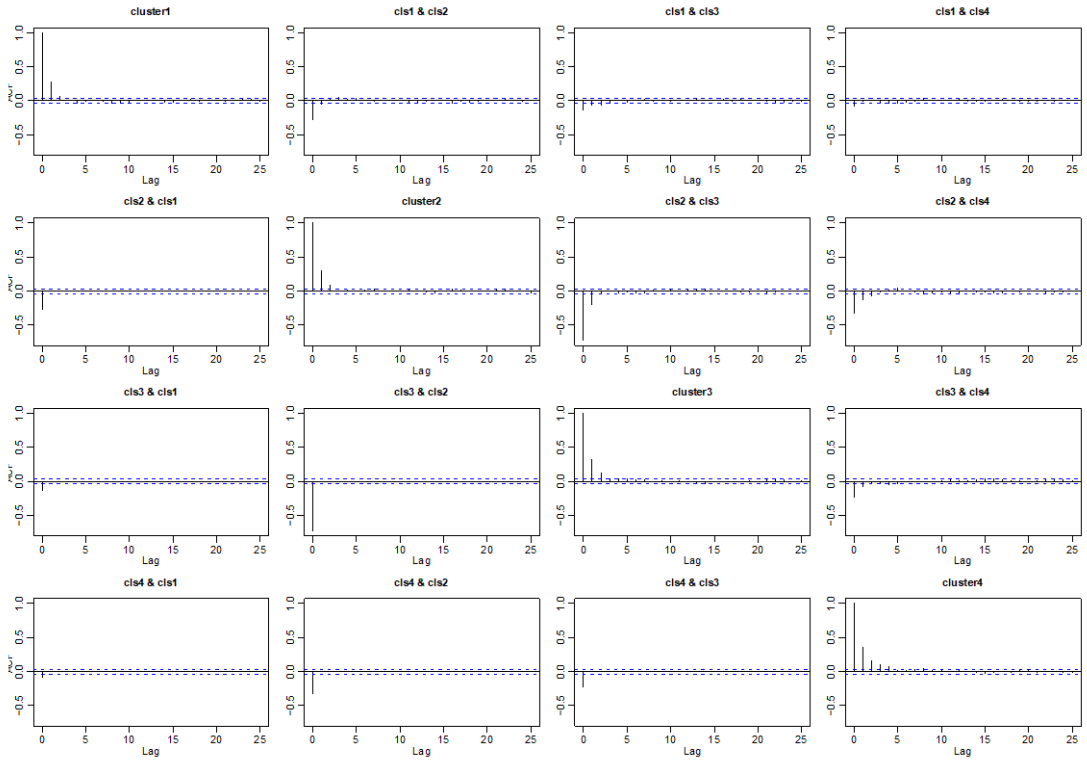
Suppl. Mat. 2.3 : Classification of the seafloor according to its position in relation to the general topography. Figure adapted from Jenness (2006).



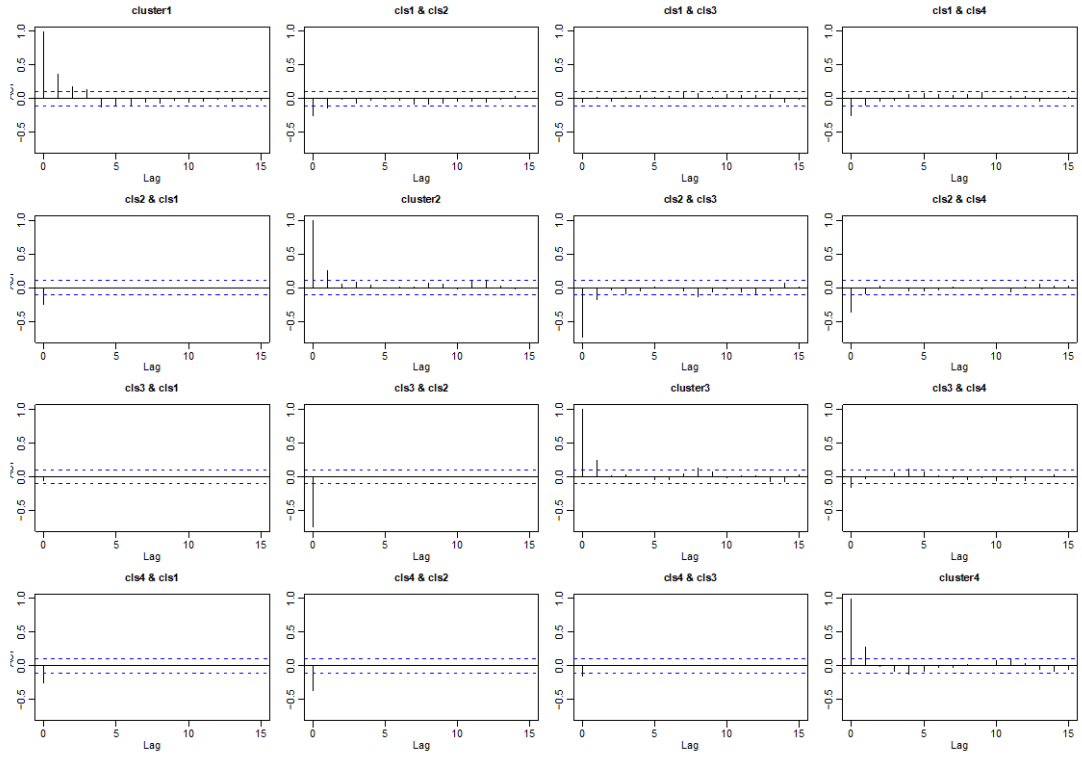
Suppl. Mat. 2.4 : Total number of 30-min scans assigned to each habitat type and presented per herd type.

Herd type	Habitat type	n of scans
all	TD	204
	TPF	1581
	PFD	950
	BFD	342
adult-only	TD	17
	TPF	143
	PFD	149
	BFD	38
adult-grey	TD	109
	TPF	1054
	PFD	606
	BFD	190
adult-grey-calf	TD	78
	TPF	384
	PFD	195
	BFD	114

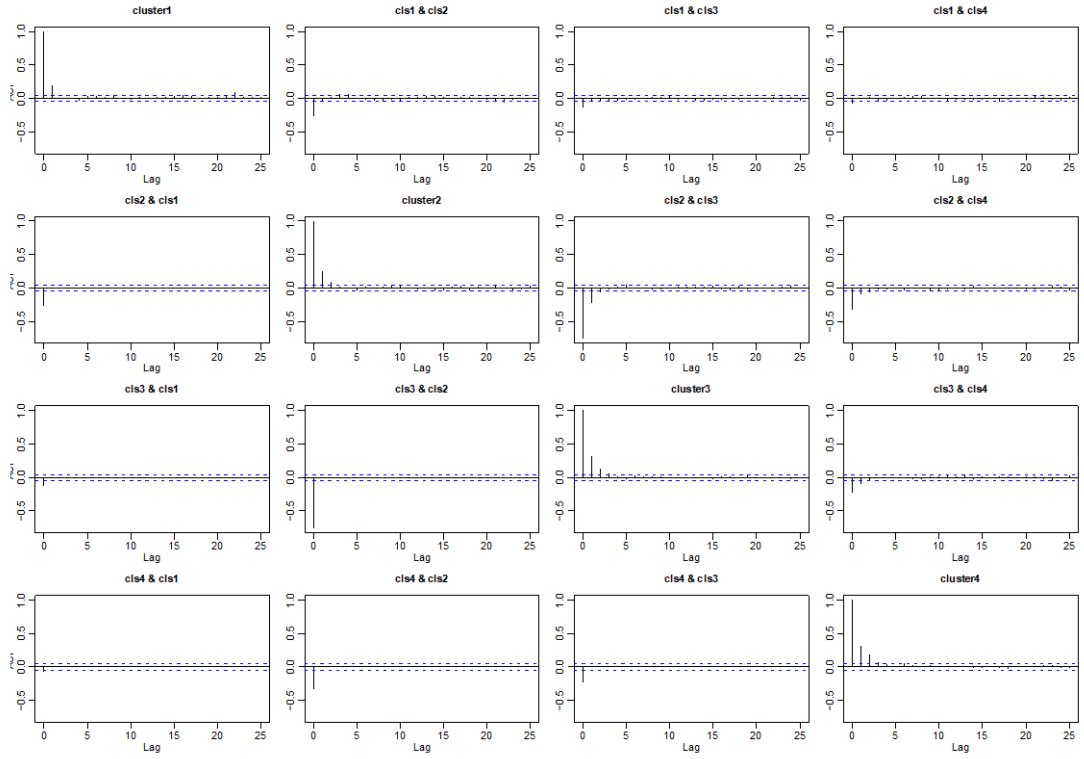
Suppl. Mat. 2.5 : Temporal autocorrelation (ACF) of residuals across scans by habitat type (indicated as cluster or cls) from a multinomial logistic regression considering all herd types. Bars extending beyond the 95% confidence interval (dotted blue lines) indicate statistically significant autocorrelation at the corresponding number of scans. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



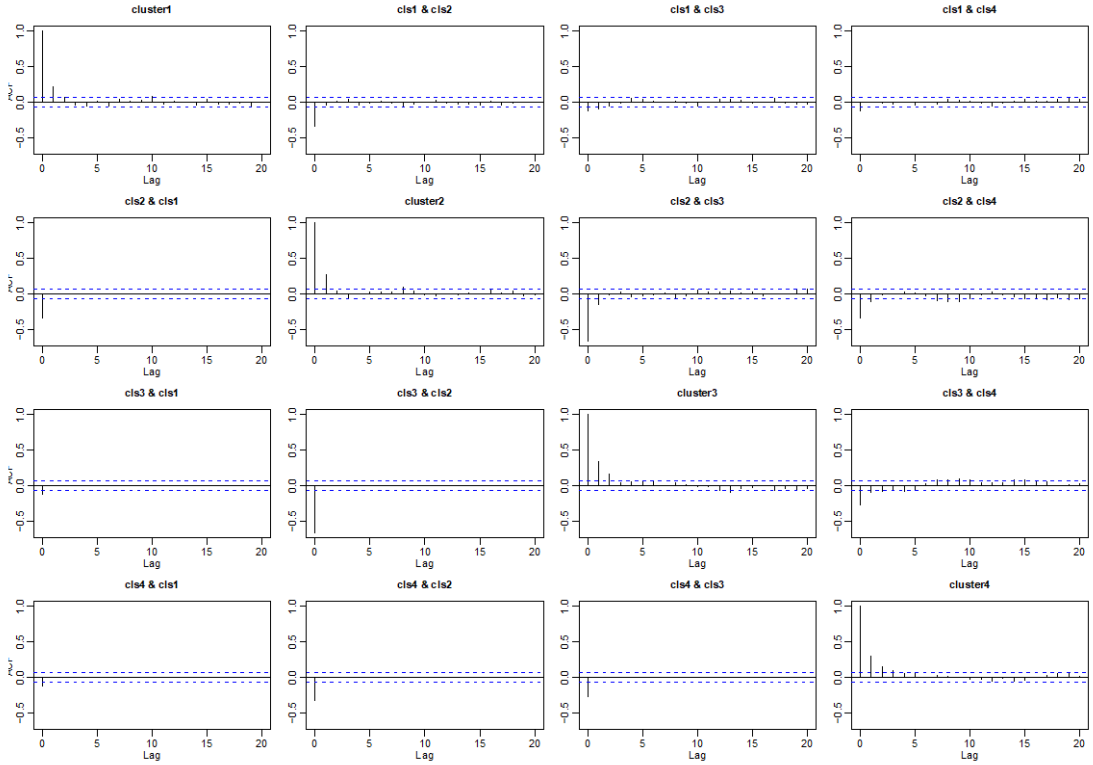
Suppl. Mat. 2.6 : Temporal autocorrelation (ACF) of residuals across scans by habitat type (indicated as cluster or cls) from a multinomial logistic regression considering adult-only herd types. Bars extending beyond the 95% confidence interval (dotted blue lines) indicate statistically significant autocorrelation at the corresponding number of scans. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



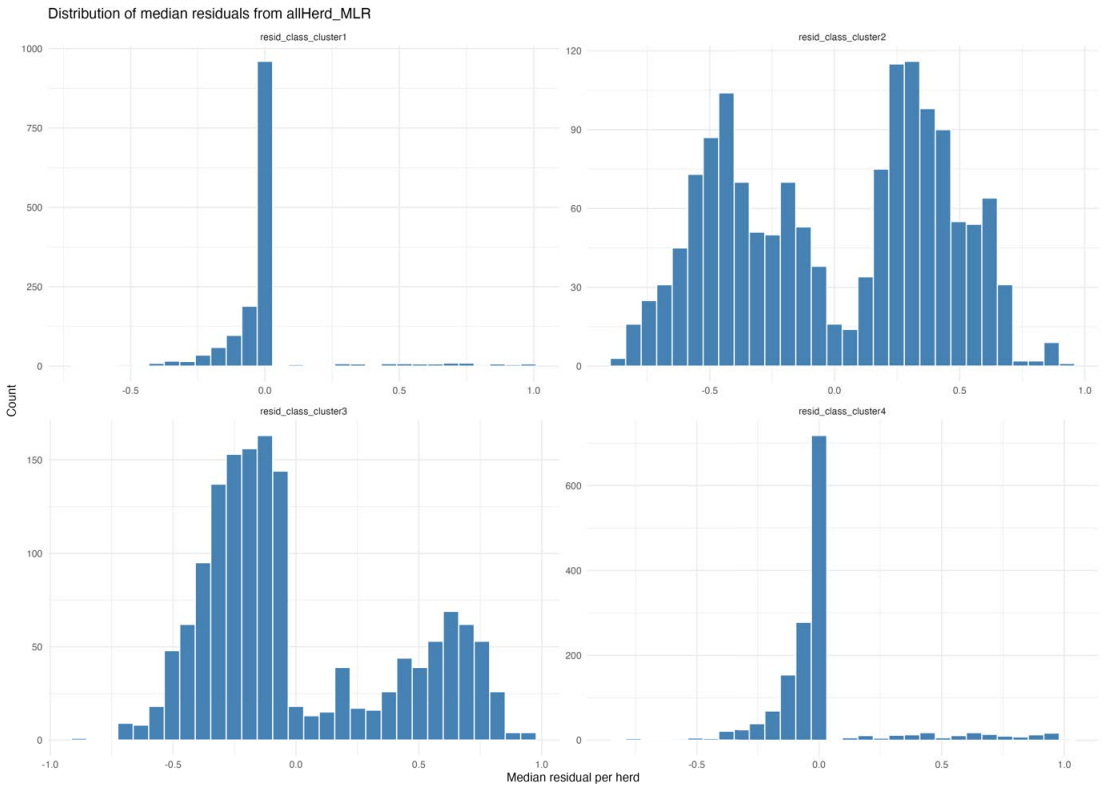
Suppl. Mat. 2.7 : Temporal autocorrelation (ACF) of residuals across scans by habitat type (indicated as cluster or cls) from a multinomial logistic regression considering adult-grey herd types. Bars extending beyond the 95% confidence interval (dotted blue lines) indicate statistically significant autocorrelation at the corresponding number of scans. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



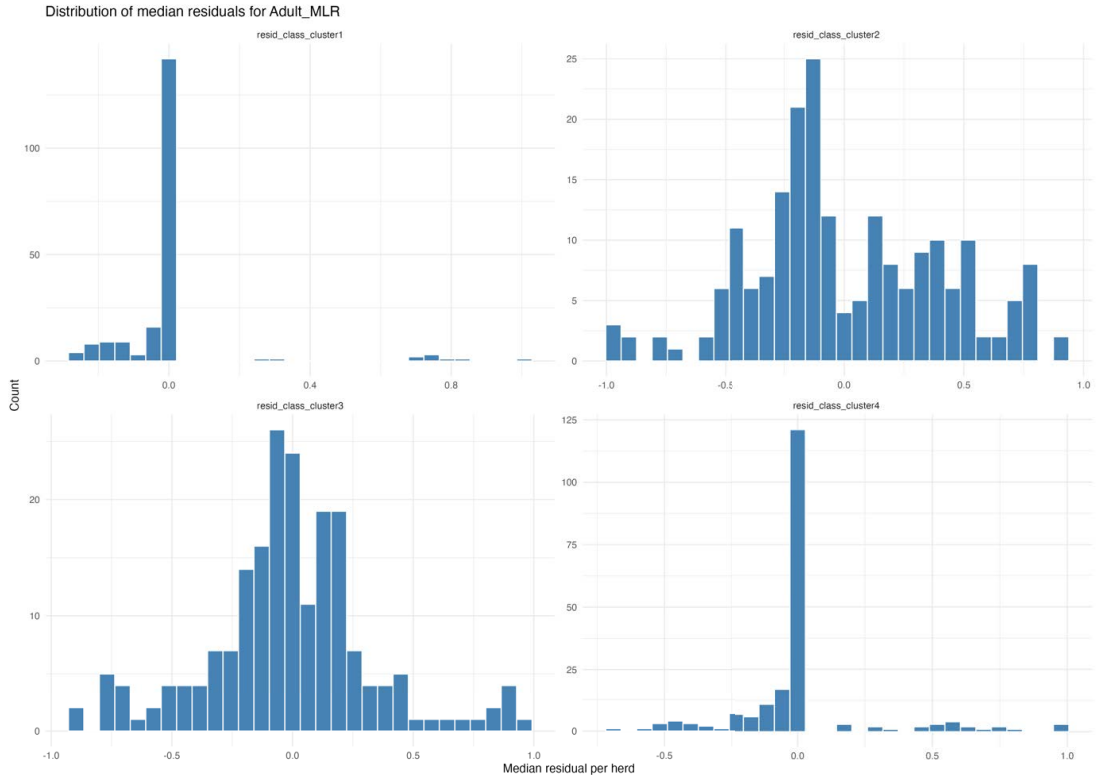
Suppl. Mat. 2.8 : Temporal autocorrelation (ACF) of residuals across scans by habitat type (indicated as cluster or cls) from a multinomial logistic regression considering adult-grey-calf herd types. Bars extending beyond the 95% confidence interval (dotted blue lines) indicate statistically significant autocorrelation at the corresponding number of scans. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



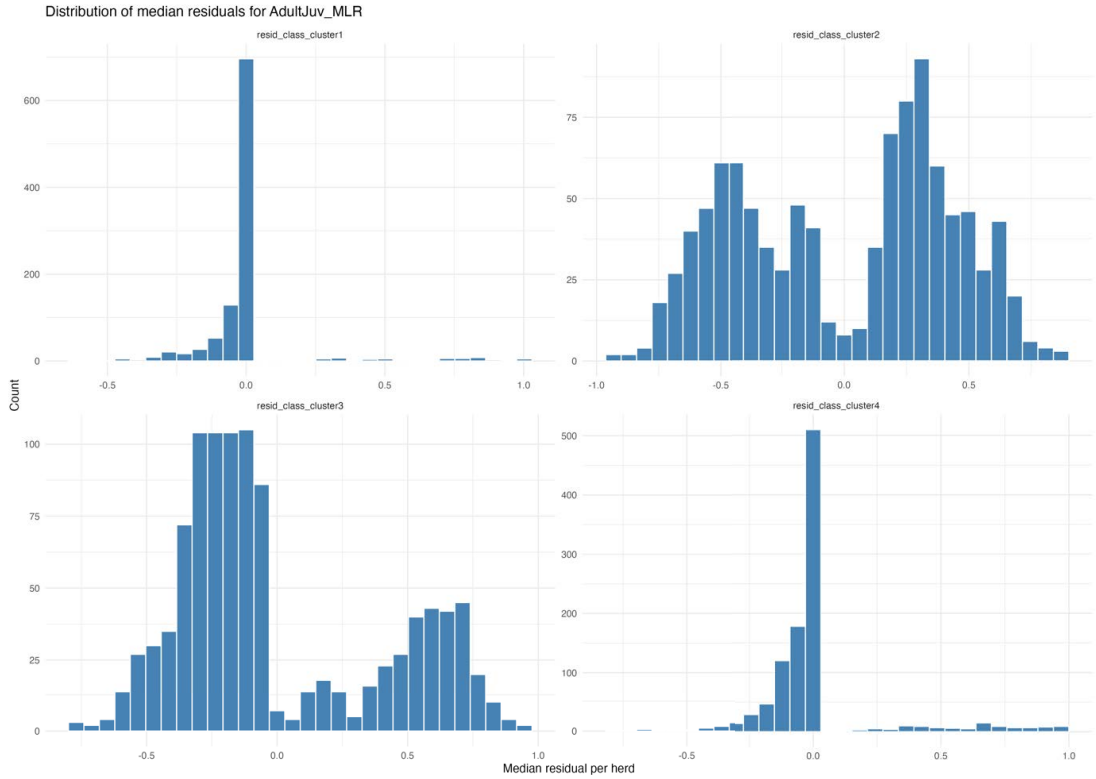
Suppl. Mat. 2.9 : Within-herd residuals across habitat type (indicated as cluster) from a multinomial logistic regression considering all herd types. Each panel represents a different habitat class, with the x-axis indicating the median residual value for a given herd and the y-axis showing the number of herds. This visualization summarizes the central tendency and dispersion of model residuals across all herds and habitat classes. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



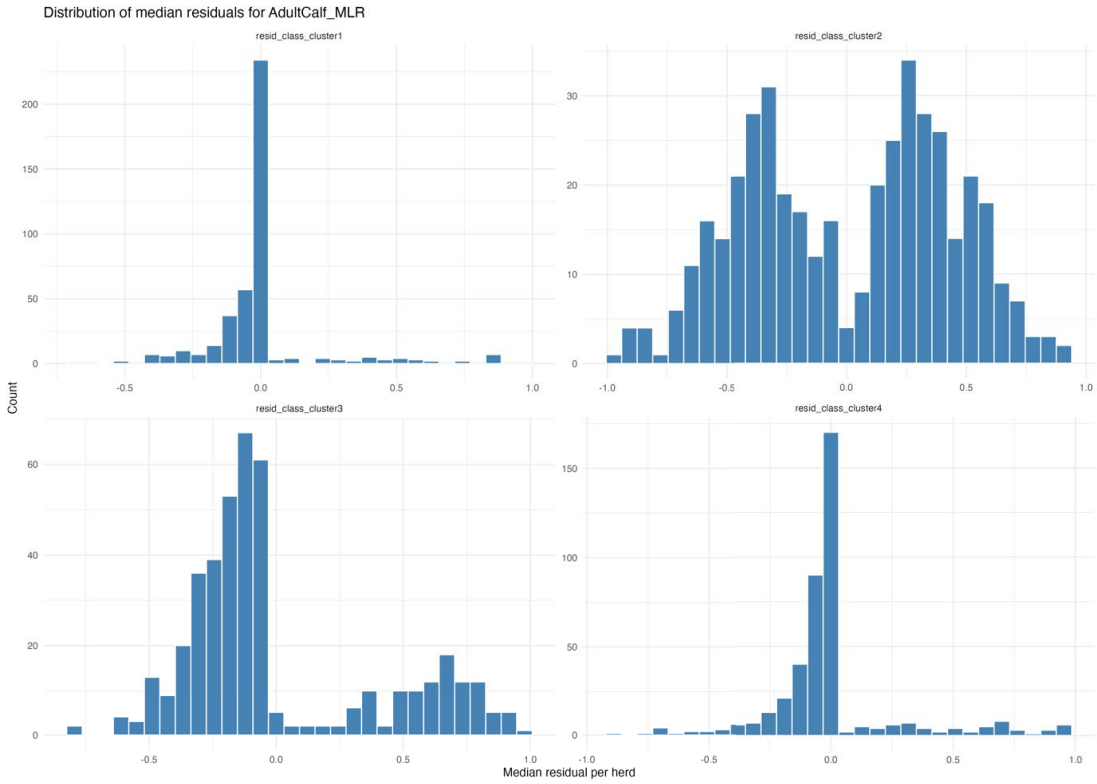
Suppl. Mat. 2.10 : Within-herd residuals across habitat type (indicated as cluster) from a multinomial logistic regression considering adult-only herd types. Each panel represents a different habitat class, with the x-axis indicating the median residual value for a given herd and the y-axis showing the number of herds. This visualization summarizes the central tendency and dispersion of model residuals across all herds and habitat classes. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



Suppl. Mat. 2.11 : Within-herd residuals across habitat type (indicated as cluster) from a multinomial logistic regression considering adult-grey herd types. Each panel represents a different habitat class, with the x-axis indicating the median residual value for a given herd and the y-axis showing the number of herds. This visualization summarizes the central tendency and dispersion of model residuals across all herds and habitat classes. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



Suppl. Mat. 2.12 : Within-herd residuals across habitat type (indicated as cluster) from a multinomial logistic regression considering adult-grey-calf herd types. Each panel represents a different habitat class, with the x-axis indicating the median residual value for a given herd and the y-axis showing the number of herds. This visualization summarizes the central tendency and dispersion of model residuals across all herds and habitat classes. Clusters are classified as follows : 1 = TD, 2 = TPF, 3 = PFD, and 4 = BFD.



Suppl. Mat. 2.13 : Results of model selection for fixed-effects multinomial logistic regressions (MLR) assessing the effect of environmental variables on the probability of belonging to various habitat classes, presented while considering all herd types (all herds), or herds composed of adults only (Adult), adult and grey animals(Adult.Grey), and adults, grey animals and calves (Adult.Grey.Calf) separately. Environmental variables include bathymetry (Bathy), distance to coastline (DistC), distance to river mouth (DistR), sand lance (SandL), sediment size (Sed), tidal phases (Tid), Slope (Slope) and surface current speed (Current)). Cell shading indicates variables included (white) and not include (grey) in the model.

Herd Type model	Model rank	(Intercept)	Bathy	DistC	DistR	SandL	Sed	Tide	Slope	Current	df	AICc	Δ AICc	AICc weight
all herds	**1**	**+**	**+**	**+**	**+**	**+**	**+**		**+**	**+**	**36**	**5332**	**0**	**1**
	2	+		+	+	+	+		+	+	33	5381.8	49.8	0
	3	+	+	+	+		+	+	+	+	33	5391.7	59.7	0
	4	+	+	+	+	+	+		+		33	5417.9	85.9	0
	5	+	+	+		+	+		+	+	33	5453.1	121.1	0
	6	+		+	+		+	+	+	+	30	5461.2	129.2	0
	7	+		+	+	+	+	+	+		30	5478.8	146.8	0
	8	+	+	+	+		+		+		30	5503.1	171.1	0
	9	+	+	+		+	+	+	+		30	5515.8	183.8	0
	10	+	+	+	+	+	+			+	27	5523.7	191.7	0
Adult	**1**	**+**	**+**	**+**	**+**						**12**	**504.4**	**0**	**1**
	2	+		+	+	+	+				12	536.0	31.6	0
	3	+	+	+		+					12	552.2	47.8	0
	4	+	+	+			+				18	557.4	53.0	0
	5	+		+	+						18	561.5	57.1	0
	6	+		+		+	+				18	571.2	66.8	0
	7	+		+	+						9	585.9	81.5	0
	8	+	+	+				+		+	12	588.5	84.1	0
	9	+	+	+							9	589.7	85.3	0

	10	+		+	+					+	12	590.8	86.4	0
Adult.Grey	**1**	**+**	**+**	**+**	**+**	**+**	**+**		**+**	**+**	**36**	**3312.6**	**0**	**1**
	2	+	+	+	+		+		+	+	33	3344.6	32.0	0
	3	+		+	+	+	+	+	+	+	33	3354	41.4	0
	4	+	+	+	+	+	+		+		33	3356.2	43.6	0
	5	+	+	+		+	+	+	+	+	33	3373.6	61.1	0
	6	+		+	+		+		+	+	30	3389.1	76.5	0
	7	+		+	+	+	+	+	+		30	3406.1	93.5	0
	8	+	+	+		+	+	+	+		30	3406.4	93.8	0
	9	+	+	+	+		+		+		30	3406.8	94.2	0
	10	+	+	+			+		+	+	30	3411.6	99.0	0
Adult.Grey.Calf	**1**	**+**	**+**	**+**	**+**	**+**	**+**		**+**	**+**	**36**	**1416.4**	**0**	**1**
	2	+	+	+	+		+	+	+	+	33	1434.5	18.1	0
	3	+	+	+	+	+	+		+	+	27	1448.2	31.8	0
	4	+	+	+		+	+		+	+	33	1462.1	45.8	0
	5	+	+	+	+	+	+		+		33	1471.2	54.8	0
	6	+		+	+	+	+		+	+	33	1473.5	57.2	0
	7	+	+	+	+	+	+	+		+	27	1476.7	60.3	0
	8	+	+		+	+	+	+	+	+	33	1482.8	66.4	0
	9	+	+	+			+	+	+	+	30	1483.3	66.9	0
	10	+	+	+	+		+	+	+		30	1486.6	70.3	0

Notes : The 10 best models were selected according to their Akaike's information criterion corrected for small sample size (AICc). Initially, mixed-effect MLR were attempted with the eight habitats characteristics as fixed explanatory variables and ID-herd as a random intercept effect to address potential residual autocorrelation among successive scans during a herd follow. However, due to convergence issues with mixed-effects MLR candidate models, fixed-effects MLR were implemented instead. All different possible subsets of candidate models were tested from each global model (i.e. all herds, adults-only, adult-grey, adults-grey-calf). Influence of possible autocorrelation was checked in fixed-effect MLR using the acf function from the car R package (version 3.1-2) and showed no clear indication of violation of independence (Figure S2, S3, S4, S5). Explanatory variables included in each candidate model are marked with +. The candidate model selected for each herd type is highlight in bold.

Suppl. Mat. 2.14 : Generalized Variance Inflation Factor (GVIF) values estimated between explanatory variables considered in models including all herd types, adults only, adult-grey, and adult-grey-calf herds. GVIF for categorial variables are corrected for degrees of freedom. GVIF values < 3 indicate an absence of collinearity among explanatory variables.

Explanatory variables	**Df**	**GVIF**			
		all herds	adult	adult-grey	adult-grey-calf
Slope	3	1.2	1.3	1.2	1.3
Bathymetry	1	1.7	2.1	1.7	1.9
Distance to coastline	1	1.3	1.5	1.3	1.4
Distance to river mouth	1	1.3	1.4	1.3	1.3
Surface current speed	1	1.3	1.4	1.2	1.3
Tidal phase	3	1	1.1	1	1
Sand lance	1	1.3	1.2	1.3	1.3
Sediment size	6	1.1	1.2	1.1	1.1

Suppl. Mat. 2.15 : Environmental variables for the different habitat types and herd compositions. Coefficients are given with confidence interval in parentheses. Statistically significant P values (alpha i.e., < 0.05), with 95% CI not overlapping 0, are highlighted in bold. Habitat type 1 is not presented as it was used as the baseline.

Variables	Type TPF	Type PFD	Type BFD
All herds			
Bathymetry	**-0.01(-0.01 — 0)**	**-0.01 (-0.02 — 0.01)**	**-0.02 (-0.02 — 0.01)**
CurrentVelocity	**2.55 (1.76 — 3.34)**	**2.74 (1.94 — 3.54)**	**1.44 (0.58 — 2.3)**
DistanceToCoast	**1.24 (0.89 — 1.58)**	**1.41 (1.06 — 1.75)**	**0.46 (0.09 — 0.83)**
DistanceToRiver	-0.05 (-0.12 — 0.02)	**-0.21 (-0.28 — -0.13)**	0.07 (0 — 0.15)
SandLance	1.2 (-0.02 — 2.42)	1.19 (-0.1 — 2.47)	**4.58 (3.18 — 5.99)**
Sed.Large	**8.72 (7.71 — 9.73)**	**7.49 (6.44 — 8.55)**	**8.76 (6.81 — 10.72)**
Sed.Medium	**-11.04 (-11.84 — -10.24)**	**-12.09 (-12.93 — 11.25)**	**-9.06 (-10.52 — -7.6)**
Sed.Small	**-10.2 (-11.07 — -9.33)**	**-9.87 (-10.78 — -8.97)**	**-6.9 (-8.4 — -5.4)**
Slope.Flat	**1.91 (1.23 — 2.58)**	**0.84 (0.16 — 1.52)**	0.36 (-0.36 — 1.08)
Slope.Ridge	**1.45 (0.53 — 2.37)**	-0.36 (-1.31 — 0.58)	0.39 (-0.53 — 1.31)
Slope.Valley	**2.33 (1.73 — 2.94)**	**2.41 (1.81 — 3.02)**	0.39 (-0.29 — 1.06)
Adult only			
Bathymetry	0.01 (0 — 0.02)	**0.02 (0.01 — 0.03)**	**-0.02 (-0.03 — 0)**
DistanceToCoast	**1.96 (0.73 — 3.2)**	**2.82 (1.57 — 4.07)**	0.57 (-0.71 — 1.85)
DistanceToRiver	-0.04 (-0.29 — 0.21)	**-0.64 (-0.92 — -0.35)**	-0.02 (-0.27 — 0.24)
Adult.Grey			
Bathymetry	**-0.01 (-0.02 — -0.01)**	**-0.02 (-0.03 — -0.01)**	**-0.02 (-0.03 — -0.01)**
CurrentVelocity	**2.39 (1.33 — 3.45)**	**2.49 (1.42 — 3.56)**	1.12 (-0.04 — 2.28)
DistanceToCoast	**1.1 (0.67 — 1.53)**	**1.23 (0.79 — 1.66)**	0.31 (-0.15 — 0.77)
DistanceToRiver	-0.04 (-0.13 — 0.05)	**-0.18 (-0.28 — -0.09)**	0.08 (-0.02 — 0.19)
SandLance	0.93 (-0.74 — 2.6)	1.03 (-0.71 — 2.76)	**4.43 (2.53 — 6.34)**
Sed.Large	**10.65 (10.24 — 11.05)**	**9.22 (8.81 — 9.62)**	**5.65 (5.65 — 5.65)**
Sed.Medium	**-10.69 (-11.19 — -10.18)**	**-11.97 (-12.47 — 11.47)**	**5.2 (4.73 — 5.68)**
Sed.Small	**-9.63 (-10.32 — -8.95)**	**-9.34 (-10.03 — -8.64)**	**7.47 (6.79 — 8.15)**
Slope.Flat	**1.66 (0.81 — 2.51)**	0.79 (-0.08 — 1.66)	0.36 (-0.57 — 1.29)
Slope.Ridge	1.17 (-0.02 — 2.35)	-0.64 (-1.86 — 0.58)	0.29 (-0.91 — 1.5)
Slope.Valley	**2.74 (1.9 — 3.59)**	**3.2 (2.33 — 4.06)**	0.81 (-0.16 — 1.78)
Adult.Grey.Calf			
Bathymetry	-0.01 (-0.02 — 0)	**-0.03 (-0.04 — -0.01)**	**-0.03 (-0.04 — -0.02)**
CurrentVelocity	**4.37 (2.75 — 5.99)**	**5 (3.36 — 6.64)**	**3.62 (1.9 — 5.35)**
DistanceToCoast	**1.28 (0.64 — 1.93)**	**1.15 (0.49 — 1.8)**	**0.48 (-0.2 — 1.16)**
DistanceToRiver	**-0.17 (-0.3 — -0.04)**	**-0.33 (-0.47 — -0.19)**	**0.01 (-0.14 — 0.16)**
SandLance	**3.82 (1.37 — 6.27)**	**3.71 (1.15 — 6.27)**	**6.43 (3.69 — 9.18)**
Sed.Large	**8.06 (7.04 — 9.08)**	**7.36 (6.3 — 8.41)**	**21.9 (20.85 — 22.95)**
Sed.Medium	**-13.66 (-14.65 — -12.68)**	**-13.72 (-14.7 — 12.74)**	**1.51 (0.76 — 2.26)**
Sed.Small	**-13.09 (-14.21 — -11.97)**	**-12.39 (-13.54 — 11.23)**	**3.83 (2.87 — 4.79)**
Slope.Flat	**2.2 (0.86 — 3.53)**	0.82 (-0.55 — 2.19)	-0.2 (-1.62 — 1.22)
Slope.Ridge	1.42 (-0.24 — 3.09)	-0.46 (-2.21 — 1.29)	0.07 (-1.58 — 1.72)
Slope.Valley	**2.56 (1.39 — 3.72)**	**3.1 (1.89 — 4.31)**	1.12 (-0.12 — 2.36)

CHAPITRE 2 : ENVIRONMENTAL AND SOCIAL DRIVERS OF MOVEMENT PATTERNS OF ST. LAWRENCE ESTUARY BELUGA

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Abstract

Estimating the impact of anthropogenic stressors on animal populations requires an in-depth understanding of movement patterns of individuals. In this study, 55 fine-scale daily trajectories of St. Lawrence Estuary belugas (*Delphinapterus leucas*), obtained by radio-tracking, were investigated using Hidden Markov Models (HMM) analytical framework. Specific aims were to 1) infer discrete behavioural states from two-dimensional movement metrics (step length and turning angle); 2) assess how physical (bathymetry, surface currents, and probability of prey occurrence) and social (herd size, composition and spatial dispersion) variables influenced state transition probabilities; and 3) map the spatial distribution of inferred behavioural states within the summer habitat. Models with two or three states best captured underlying behavioural patterns in the population. These states distinguished Area-Restricted Search (ARS) as slow and tortuous movements, and transit behaviour as more directional movements, which the 3-states HMM further refined as slow- and fast-directed movements. The probability of switching from transit to ARS increased significantly when both the probability of sand lance occurrence and the proportion of juveniles in the herd were higher. Furthermore, belugas exhibited behaviours consistent with energy optimization strategies, being more likely to be transiting with tidal currents, and being in ARS when swimming against the flow, likely to increase prey encounter rate. Spatially, zones of inferred ARS showed strong concordance with previous work, although additional ARS hotspots were also identified. These findings

emphasize the importance of integrating both physical and social contexts into movement analysis in gregarious species. This study also provides the basis for detecting potential shifts in habitat use and function, and for identifying and mitigating activities that could disrupt key behaviours of this endangered population.

Key words : Movement ecology, Hidden Markov model (HMM), Behavioural state, physical environment, social organization, St. Lawrence Estuary beluga

Introduction

Movement is ubiquitous in animal life (Nathan et al. 2008). Individual movement decisions directly determine an animal's capacity to acquire resources, locate mates, establish and defend territories, and mitigate risks such as predation, competition, and anthropogenic stressors (Nathan et al. 2008; Fortin et al. 2009; Doherty et al. 2021). These decisions shape ecological and evolutionary processes across scales from individual fitness to population-level dynamics (Picardi et al. 2024), such as distribution patterns, home range formation (Hooten et al. 2017), and demographic trends (Morales et al. 2010). Uncovering the drivers of animal movement is therefore essential for understanding these spatial patterns and predicting their implications for populations dynamics.

According to the movement ecology paradigm (Nathan et al. 2008), individual movement patterns result from the dynamic interplay between an animal's internal state (e.g., physiological condition, energetic requirements), its motion and navigation capacity (e.g., locomotor ability), and its response to external environmental factors. Extending this paradigm, the spatial-social interface framework (Webber et al. 2023) clarifies the inherent link between a species' social and movement ecology across scales (Webber et al. 2023; Picardi et al. 2024). Individual movement constitutes the mechanistic link between intrinsic traits (e.g., sex, age), the physical and social environmental conditions encountered (e.g., habitat configuration, group membership), and

the spatial and social phenotypes (e.g., population-level space use, social structure) emerging through reciprocal feedbacks (Webber et al. 2023).

Modern animal telemetry systems enabling high-resolution tracking data collection (Ropert-Coudert 2009), coupled with advanced analytical methods such as Hidden Markov models (McClintock & Michelot 2018), provide empirical insight into how animals perceive, respond to, and exploit their environment (Hooten et al. 2017; Florko et al. 2025). A central challenge is that behavioural states are not directly observable; inference relies on the assumption that each behavioural state produces distinctive movement geometry (e.g., step lengths and turning angles) that are detectable in tracking data. Many movement ecology studies rely on two contrasting movement modes, such as Area Restricted Seach (ARS) and directed transit behaviour (McClintock & Michelot, 2018; Hooten et al. 2017). ARS, marked by slow and tortuous movements, is typically suggestive of different behaviours such as foraging, socializing, or resting activities (Dorfman et al. 2022). However, behavioural inferences based on movement geometry are highly sensitive to the temporal sampling resolution, representing a limitation frequently underappreciated (Codling & Hill, 2005; Postlethwaite & Dennis 2013; Schlägel & Lewis, 2016; Schoombie et al. 2024). Careful consideration of sampling scale is thus essential to ensure robust behavioural inferences and meaningful biological interpretation (Pohle et al. 2017).

In group-living species, movement and social ecology are strongly interconnected (Webber et al. 2023). For instance, travelling patterns vary with

the proximal presence of vocalizing conspecifics in minke whales (*Balaenoptera acutorostrata*; Helble et al. 2023), distances travelled correlate with group size in vulturine guineafowl (*Acryllium vulturinum*) (Papageorgiou & Farine 2020), whereas habitat selection is group-size dependent in bison (*Bison bison*) (Fortin et al. 2009). Transitions between movement states may also vary with group size, composition, social preference (i.e., non-random associations with specific individuals), and inter-individual distances (Haydon et al. 2008; McKellar et al. 2015; Webber et al. 2024). Social influences arise from multiple mechanisms, including the need for cohesion while moving through heterogeneous environments (Sueur et al. 2011), similarities in energetic or nutritional requirements among individuals that favour synchronised activity patterns (activity budget hypothesis; Webber et al. 2023), and shared benefits of reducing predation risk (Fortin et al. 2009). Despite this growing body of work, animal movement studies still commonly investigate the effect of habitat configuration or social variables separately, and relatively few integrate both spatial and social drivers in a unified analytical framework (Fortin et al. 2009; McKellar et al. 2015; Webber et al. 2024), particularly in marine species (Hays et al. 2016). Accounting for interactions between habitat and social environments can substantially improve movement predictions and provide deeper insight into individual decision-making (e.g., Strandburg-Peshkin et al. 2017), highlighting the importance of including these factors in animal movement studies.

Beluga (*Delphinapterus leucas*) in the St. Lawrence Estuary (SLE), occupy the southernmost extent of the specie's range, with part of the population remaining in the SLE year-round (COSEWIC 2016; Simard et al. 2023; Harvey et al. 2025). They are considered endangered as the population remains small, and is chronically exposed to high ambient noise levels, a heavy burden of toxic substances, and changes in prey availability (Lesage et al. 2024). A First Passage Time analysis on fine-scale daily movements of individuals was used to identify area-restricted search (ARS), and subsequently identify areas where herds showed high residency (Lemieux Lefebvre et al. 2012). In these areas of high residency, herds exhibited milling (i.e., slow circular movement at the surface) and multidirectional movements (i.e., directional movement with frequent deviations from the main axis), which were deemed to be associated with foraging, socializing, and resting (Lemieux Lefebvre et al. 2018; Barreau et al. 2025). Further analysis on herd focal follows highlighted habitat connectivity based on high travel speed and strong directionality in herd movement, with herds generally moving between areas of high residency with surface and tidal currents (Ouellet et al. 2021). While these studies identified movement patterns at the individual and herd levels, factors influencing transitions between movement modes are unknown. Moreover, belugas are highly social and form herds of variable membership, and exhibit relatively frequent fission-fusion behaviours (Barreau et al. *in prep).* Yet, how this pronounced sociality interacts with the physical habitat to shape habitat individual movement patterns remains largely unknown.

In this study, two-dimensional individual movement data from SLE beluga were examined in a HMM framework to identify discrete behavioural states, assess their spatial distribution within the beluga summer habitat, and investigate how habitat characteristics and social context influence beluga movement patterns.

Methods

Data collection

Archival tags (Mk8 recorders, Wildlife computers, Redmond, WA; D-tags, Johnson & Tyack 2003) coupled with a VHF radio transmitter (VHF, Telonic, Mesa, AZ) were deployed opportunistically on 74 Individual beluga during herd follows conducted in the central portion of their summer distribution. Tagging efforts spanned from June to September of 2001 – 2005 and 2018 – 2020, and covered a variety of habitat used by all herd types and segments of the population (Figure 3.1; Lemieux Lefebvre et al. 2012; Ouellet et al. 2021; Barreau et al. 2025). Tags were housed in a floating package, and were attached to beluga with a suction cup, and deployed using a handheld pole or a crossbow. The radio transmitter allowed remote tracking (400-600 m) of each whale, with minimal effect on behaviour (Blane & Jaakson, 1994). Individuals were tracked and geolocated during each surface interval from an 8 meters boat equipped with a 6-element Yagi antenna. Locations were determined by measuring the animal's angle relative to magnetic North (using binocular with compass), estimating its distance from the boat (by eye or range

finder), and recording the research vessel's GPS positions every minute. Animals were generally tracked for a few hours each until release of tag, loss of signal or dusk.

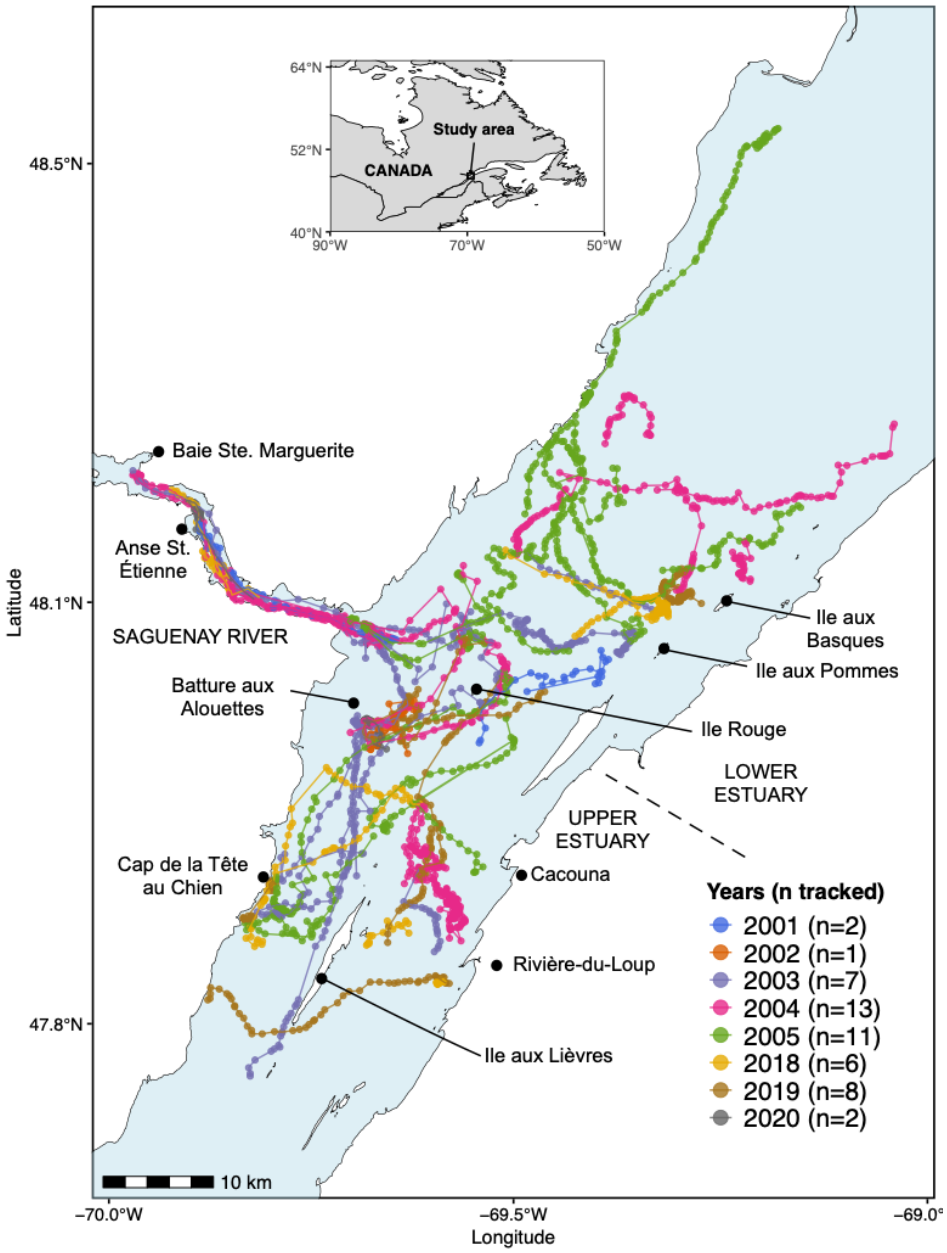

Figure 3.1 : Study area in the St. Lawrence Estuary, Canada, showing full tracks for the 50 belugas equipped with radio-transmitters (VHF) and archival tags, and that were included in the movement analysis. Dots represent locations identified via VHF signals when tracked individuals were observed surfacing.

Each individual was tracked concurrently with focal follows of their herds. A beluga herd was defined as an assemblage of groups, with inter-group distances smaller than the overall extent of the herd (i.e., herd radius of less than 2000 meters) and inter-individual distance within groups being generally less than one body length. Herd level characteristics were recorded every 30 minutes through scan sampling, and included information on herd size (i.e., total number of individuals), composition (i.e., proportion of juveniles identified by their greyish skin color; Michaud 2014), and dispersion (i.e., distance between groups within herd).

Modelling movement states

Movement patterns and transitions between behavioural state were examined using a Hidden Markov Model (hereafter HMM). HMMs examine animal movement as a time series, composed of observed measurements ($Z_1,\ldots,Z_T$) and underlying, unobserved behavioural states ($S_1,\ldots,S_T$) (Langrock et al. 2012; Hooten et al. 2017). The observed process are derived from regularly sampled locations ($x_1, \ldots x_T$), represented by N state-dependent probability distributions. The state process (S) follows an N-state Markov chain defined by a transition probability matrix that describes the dynamics of the hidden process (i.e., probability of switching between states), which can be modelled as a function of explanatory variables (Langrock et al. 2012; Hooten et al. 2017). Each observation (Z_T) consists of step length (l_t) and turning angle (φ_t). Step length corresponds to the Euclidean distance between two successive locations, indicating distance traveled per time unit. Turning angle

is the change in direction between successive locations, indicating directional persistence of movement.

Model structure

Following Lemieux Lefebvre et al. (2012), who also analyzed SLE beluga herd focal follow data, tracks spanning more than one day were subdivided (i.e., one per day). Tracks were further segmented when the interval between consecutive positions exceeded 1 h to minimize errors associated with linear approximation. Those constituted of <15 positions or requiring unrealistic travel speeds (i.e. >23 km h^{-1}, the maximum travel speeds observed by Lemieux Lefebvre et al. 2012) were discarded (Suppl. Mat. 3.1).

Track interpolation - The HMM requires interpolating tracks with equal time steps between sequential locations (McClintock & Michelot, 2018). As a first analytical step, a Continuous-Time Correlated Random Walk (CTCRW) model was fitted to each track using the crawl R package (Johnson & London 2008) and '*crawlWrap*' function in the *momentuHMM* R package (v. 1.5.5; McClintock & Michelot, 2018). Multiple time steps were evaluated because interpolation time step can strongly affect track accuracy and behavioural inferences. Overly fine steps may under- or overestimate sinuosity, while coarse steps may oversmooth paths, mask sinuosity, and artificially shorten tracks (Codling & Hill, 2005; Postlethwaite & Dennis 2013; Schlägel & Lewis, 2016; Schoombie et al. 2024). CTCRW models were fitted using the median (5 min) and mean (6 min) time step between valid successive positions, as well

as time steps of 3 min (half the mean), 12 min (twice the mean), 18 min (3 times the mean), and 30 min. The latter was, however, discarded due to substantial loss of trajectory resolution (Suppl. Mat. 3.2). Convergence of CTCRW models was assessed by verifying that the covariance matrices of movement parameters were successfully computed and found to be positive-definite, thereby confirming stability in velocity and directional persistence estimations. Interpolated tracks were visually inspected to ensure that predicted trajectories accurately reflected observed trajectories, i.e., that there were no substantial deviations from the observed track or interpolated locations caused by unrealistic speeds or abrupt directional changes between consecutive filtered locations.

Number of behavioural states – In a second step, the optimal number of behavioural states to describe the data was determined by fitting the HMM to interpolated locations, using the '*prepData*' function in *momentuHMM*, which calculated step lengths and turning angles between successive positions. Four n-state HMMs were fitted, with step length modelled via gamma distributions, and turning angles via Von Mise distributions to capture combination of ARS (slow, tortuous movements) and transit (fast, directed movement) states. Histograms of observed step lengths and turning angles were inspected to define a biologically realistic range for each parameter (see Suppl. Mat. 3.3) guided by Michelot & Langrock (2023). The four n-state HMMs included : a 2-state HMM, distinguishing ARS from transit; two 3-state HMMs, which included either two ARS and one transit states (3a-state) or one ARS and two transit

states (3t-state); and a 4-state HMM, which encompassed two ARS and two transit states. Running the four n-state HMMS for each temporal resolutions (3, 5, 6, 12, and 18 minutes) resulted in a total of 20 models. The Viterbi algorithm assigned the most likely behavioural state to each observed step. The analysis did not include a random effect for individual ID, as variation between belugas could not be examined due to short track durations; estimated model coefficients were therefore shared among individuals (McClintock, 2021).

Model structure selection

The interpolated time step and number of behavioural states adequate for our dataset were determined using multiple complementary criteria, given that standard metrics like AIC or BIC often favor HMMs with a higher number of states, which may not be biologically meaningful (Li & Bolker, 2017; Pohle et al. 2017). Following recommendations by Pohle et al. (2017), the number of states was chosen by balancing parsimony and biological interpretability across the following metrics : model convergence stability, model goodness-of-fit, AIC, visual inspection of movement parameter distributions, and uncertainty in state assignment probability. Convergence stability was evaluated following the optimization protocol of Michelot & Langrock (2023). Each of the 20 HMM models was fitted 25 times, using varying sets of initial step length and turning angle parameters, sampled randomly from the observed range for each parameter (see Suppl. Mat. 3.4), using the *runif R* function. Convergence stability was assessed using the highest likelihood

value achieved across the 25 fitting attempts, and consistency with which this value was reached. Goodness-of-fit was examined by visual inspection of pseudo-residuals plots to verify model assumptions, including homoscedasticity, residuals normality, and minimal residual autocorrelation (Langrock et al. 2012; Zucchini, MacDonald & Langrock 2016). Model performance was compared across models using AIC. Step length and turning angle distributions associated with each state identified by the Viterbi algorithm were visually inspected to confirm that each state corresponded to the expected behavioural state. Finally, uncertainty in state assignment probabilities was quantified using the '*statProbs*' function in *momentuHMM*. Among the 20 candidate HMMs, only the best-performing n-state and n-time step HMMs (hereafter referred to as the null model) were retained for the spatial analysis and for identifying drivers of behavioural states.

Environmental and social correlates

State transition probabilities (i.e., the response variable corresponding to the likelihood of switching from one state to another) were modelled against four habitat covariates (bathymetry, current speed, animal motion relative to current direction, and probability of sand lance occurrence; see Suppl. Mat. 3.5), and three social covariates (i.e., herd size, composition, and dispersion). A relative swim direction of zero indicated motion with the current's direction. Covariates were selected based on earlier modelling efforts with SLE beluga (Mosnier et al. 2016; Ouellet et al. 2021) whereas social covariates were selected based on the expectation that they may affect state transitions in

species with a fusion-fission dynamics (Aureli et al. 2008). Habitat covariates were available for each location, and assigned using the *crawlMerge* function in *momentuHMM*. Social covariates, however, were available from the 30 min-scan samples of the herd and thus, did not exactly match interpolated locations. Herd-level covariates from the nearest herd survey were assigned to an interpolated location if it occurred within ± 15 min; unmatched positions were assigned missing values. All covariates were checked for collinearity using Pearson correlation matrix (*rcorr* function in *Hmisc* R package) prior to modelling.

The selected n-state HMMs (i.e., null model) first used only environmental variables for state-transition probabilities, as including social covariates simultaneously would have halved sample size due to missing data (herd size, composition and dispersion unavailable for 50%, 62%, and 66% of interpolated observations, respectively). HMMs were then rerun using social covariates alone or in combination with habitat covariates, but were restricted to data subsets complete for each specific social covariate – yielding ~50%, ~38%, and ~34% of observations, respectively (Suppl. Mat. 3.12). This approach prevented AIC comparisons across covariates and caused convergence failures in some cases. All combinations of covariates were tested, resulting in 15 candidate HMMs for habitat models, and six candidate HMMs for habitat and social models including either a single social covariate or one social-habitat interaction term. Temporal autocorrelation in step length and turning angle parameters was assessed graphically using *plotPR* function

in *momentuHMM*, and accounted for by adding an autocorrelation term (e.g., StepLag corresponding to the previous step length) in all HMMs (Lawler et al. 2019).

Model selection within categories (habitat only, social only, or both) was based on AIC, with candidate HMMs considered equivalent if ΔAIC < 2 (Anderson & Burnham 2002). Goodness-of-fit of the final HMMs was assessed by visual inspection of pseudo-residuals plots. Stationary state probabilities, representing the equilibrium probabilities of being in each state given covariates fixed at their median values (i.e., equilibrium of the Markov process), were derived from the transition matrix using the '*plotStationary'* function in *momentuHMM*. State transition probabilities between behavioural states and their 95% confidence intervals were estimated to quantify the magnitude and significance of covariate effects (McClintock & Michelot, 2018). Interactions between habitat and social covariates were illustrated by plotting transition probabilities while fixing all social covariates at their 25th, 50th, and 75th percentiles.

Spatial distribution of behavioural states

A Getis-Ord analysis (hereafter Gi*; Getis & Ord 1992) was used to identify spatial clustering of HMM-estimated behavioural states. To ensure a reliable characterization of behaviour spatial clustering, only inferred behavioural states with assignment probabilities exceeding 0.7 were retained for analysis. A regular grid with a 1 km x 1 km cell size was superimposed on

the interpolated tracks, with cell size being informed by a First Passage Time analysis reflecting a spatial scale ecologically relevant to SLE beluga (Lemieux Lefebvre et al. 2012). The behavioural state estimated for each interpolated location was assigned to the corresponding cell. Only cells containing at least one location were retained, producing an irregular grid where the number of neighbouring cells varied among cells from the maximum of eight to none. Number of locations per behavioural state was calculated for each cell.

The degree to which the spatial distribution of a given behavioural state deviated significantly from randomness was assessed using the local Gi* statistic. Neighbouring cells were defined by first-order contiguity (each cell adjacent to its eight bordering cells), using the '*poly2nb*' function in R package *spdep* (Bivand et al. 2005; Ord & Getis, 1995). For each cell, the Gi* statistic produced a z-score comparing the local sum of the behavioural state (target cell plus neighbours) to the global sum across the entire grid. Adjusted p-values associated with the z-score indicated whether observed clustering departed from random spatial distribution at a confidence level of 95%. Cells with high positive z-score (i.e., z-score ≥ 1.96, p-value ≤ 0.05) were identified as hotspots for a given state, whereas cells with high negative z-score (i.e., ≤ -1.96, p ≤ 0.05) were identified as cold spots, where a given state was unlikely to aggregate. Cells with non-significant positive or negative z-scores (z-score ≤ 1.96, p-value >0.05) were classified as "uncertain hotspots or cold spots", respectively. Cells with incomplete neighbours (i.e., < 8), which yielded indeterminate (e.g., NA) Gi* values, were categorized as "Areas of

undetermined function". All data processing and analysis were performed in R v. 4.2.2 (R Core team, 2022).

Results

Data collection

Fifty of the 74 radio-tracked belugas provided 55 tracks that met quality standards for movement analyses (Figure 3.1; Suppl. Mat. 3.1). The number of location and duration varied substantially among tracks (range : 15 – 110 locations; range : 0 h 41 min to 9 h 46 min).

Model structure

The CTCRW applied to beluga tracks converged in all cases (not shown). Examples of CTCRW interpolations at multiple time steps are presented in the supplement (Suppl. Mat. 3.2). These and other beluga tracks (not shown) indicated that a 30-min interpolation time step resulted in a substantial loss of trajectory resolution. This time step was dropped from the analyses.

AIC consistently favored the most complex, 4-state HMM across all temporal scales (Suppl. Mat. 3.6). However, the 4-state HMM exhibited poor convergence stability (Suppl. Mat. 3.7), lower confidence level in state assignments (Figure 3.2A, Suppl. Mat. 3.8), and lower effective sample size (Figure 3.2B), indicating overparameterization and a less reliable classification scheme. This indicated that beluga movement was better captured by simpler

models with two or three states. Step length and turning angle distributions remained largely consistent across time steps and n-state HMMs (Suppl. Mat. 3.9 – 3.11). However, the 3a-state HMM with two ARS behaviours mischaracterized moderate ARS at multiple time steps (3, 6 and 18 min), assigning highly directional turning angles (peaked at zero) instead of the expected tortuous movement observed in the other structures (Suppl. Mat. 3.10). Both the 2-state and 3t-state HMMs were thus retained as the most robust candidates, thereby allowing comparison of model complexity and assessment of the ecological value of adding a third behavioural state (Suppl. Mat. 3.9 – 3.11).

In both the 2- and 3t- state HMMs, the step length associated with each behavioural state increased with the interpolation time step (Suppl. Mat. 3.9). The frequency of transiting behaviour was high at both the shortest (3 min) and longest (18 min) time steps (Figure 3.2). This pattern likely reflected a greater directional persistence among positions collected only minutes apart, and the smoothing of tortuous movement at coarser temporal scales (Figure 3.2B). The 5-min time step (corresponding to the median of data collection) provided the best trade-off between convergence stability (Suppl. Mat. 3.7), goodness-of-fit, reliable state classification, and allowed all 55 tracks to be retained (Figure 3.2). Therefore, all following inferences will be interpreted at the 5-min time step.

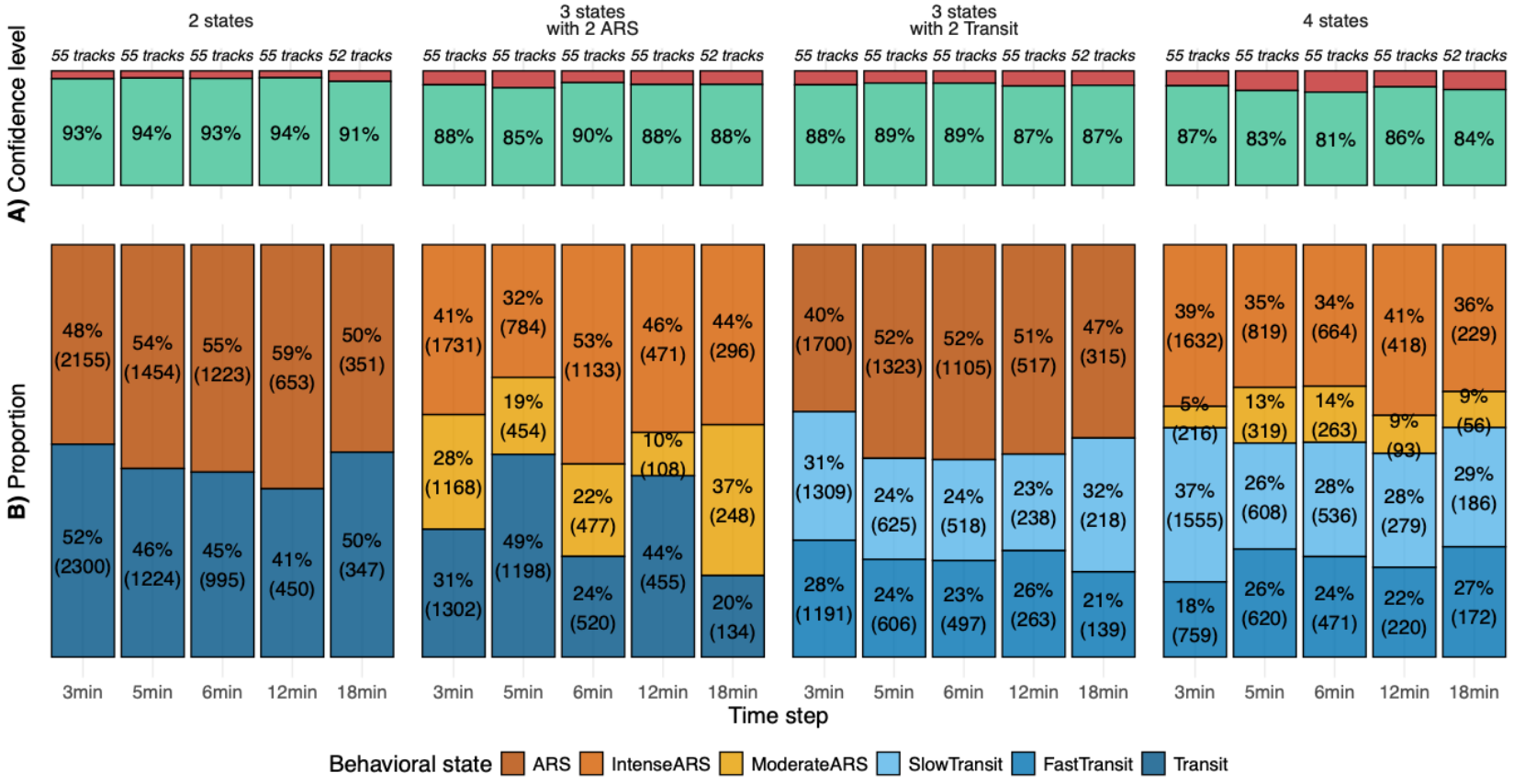

Figure 3.2 : A) Confidence level in state assignments, with proportions (in %) of low (< 0.7) and high (≥ 0.7) confidence levels being shown in red and green, respectively. B) Proportion of interpolated locations (in %, with sample size in parentheses) with confidence level in assignment ≥ 0.7 that were attributed to each behavioural state. Results are presented according to the number of possible states identified by the HMM, and timescale for interpolation. Note that for 18 minutes, 3 of the 55 interpolated tracks were excluded due to insufficient data (<5 locations per track).

Environmental and social correlates

Including a one-step lag in step length as an autocorrelation term when estimating state transition probabilities in habitat-covariate HMMs consistently lowered AIC values for both 2-state and 3-state models (Suppl. Mat. 3.12 & 3.13). This term reduced, but did not eliminate, significant positive autocorrelation in environmental variables, particularly in the 2-state HMM, indicating residual temporal structure. Covariate effects, especially in the 2-state HMM, should thus be interpreted with cautiously.

Pearson correlation analyses indicated low (i.e., sand lance probability of occurrence vs. current speed and bathymetry) to no association among the four habitat covariates tested (Pearson r range : -0.15 – 0.12; Suppl. Mat. 3.14). For both HMMs structures, a set of competing models was identified, with those including swim direction relative to current direction, and probability of sand lance occurrence yielding the best fit (Suppl. Mat. 3.12). Bathymetry was also included as a covariate among the best-performing models for the 2-state but not the 3-state HMM (Suppl. Mat. 3.12). In general, belugas were more likely to be in ARS when swimming against the current and in areas with higher probability of sand lance occurrence, and more likely to be in transit when moving with the current and in areas of low probability of sand lance occurrence (Figure 3.3). These patterns were broadly consistent between the 2-state and 3-state HMMs and in the latter case, the probability of slow transit, like for ARS, was associated with high sand lance probability of occurrence and movement against the current (Figure 3.3). Stationary state probabilities

for ARS and transit (2-state HMM) remained constant near 0.5 across all depths, indicating equal likelihood of both states regardless of bathymetry (Figure 3.3). Effects of the two significant habitat covariates (swim direction relative to current; sand lance occurrence probability) on state transitions were limited to transitions from transit to ARS in the 2-state HMM, increasing with sand lance probability and when beluga swam against the current (Suppl. Mat. 3.15 ; Figure 3.4A). In the 3-state HMM, similar effects occurred for transitions from ARS to fast transit (to accommodate the new 'slow transit' state; Suppl. Mat. 3.15; Figure 3.4B). Swimming against the current also promoted transitions from fast to slow transit while reducing transitions from ARS to fast transit (Figure 3.4B), with stronger covariate effects on fast-to-slow transit than ARS-to-fast transit (Suppl. Mat. 3.16). Models including only social covariates performed similarly to the null models, with all competing models withing 2 AIC units under both a 2- and 3-state structures(Suppl. Mat. 3.12).

When testing interactions between habitat and social covariates, only herd size and composition showed significant effects on state transition probabilities (Figure 3.5; Suppl. Mat. 3.12). No interactions involving herd dispersion altered habitat effects on state transition in either the 2- or 3-state HMMs. Bathymetry effects on transition probabilities varied by herd size in both HMMs (despite lowest AIC for the habitat-only null in the 2-state HMM). Sand lance occurrence probability influenced transitions differently depending on herd composition in the 2-state HMM only (Suppl. Mat. 3.12) : transit-to-ARS probability increased with sand lance probability of occurrence and proportion

of young in the herd (Figure 3.5A; Suppl. Mat. 3.17), but remained stable for herds with low proportions of young (i.e., 25th percentile, 13% of young individuals; Figure 3.5A). In the 3-state HMM, transition probabilities between these two states (Fast transit and ARS), in both directions, were influenced only by the interaction between bathymetry and herd size (Figure 3.5B). These transitions were generally rare (Suppl. Mat. 3.16), and the interaction indicated only weak decreases in transition probability with increasing bathymetry. The only clear exception occurred for larger herds (75th percentile, ~45 individuals or more), for which the probability of transitioning from ARS to fast transit increased in shallow waters, and the probability of transitioning from fast transit to ARS decreased.

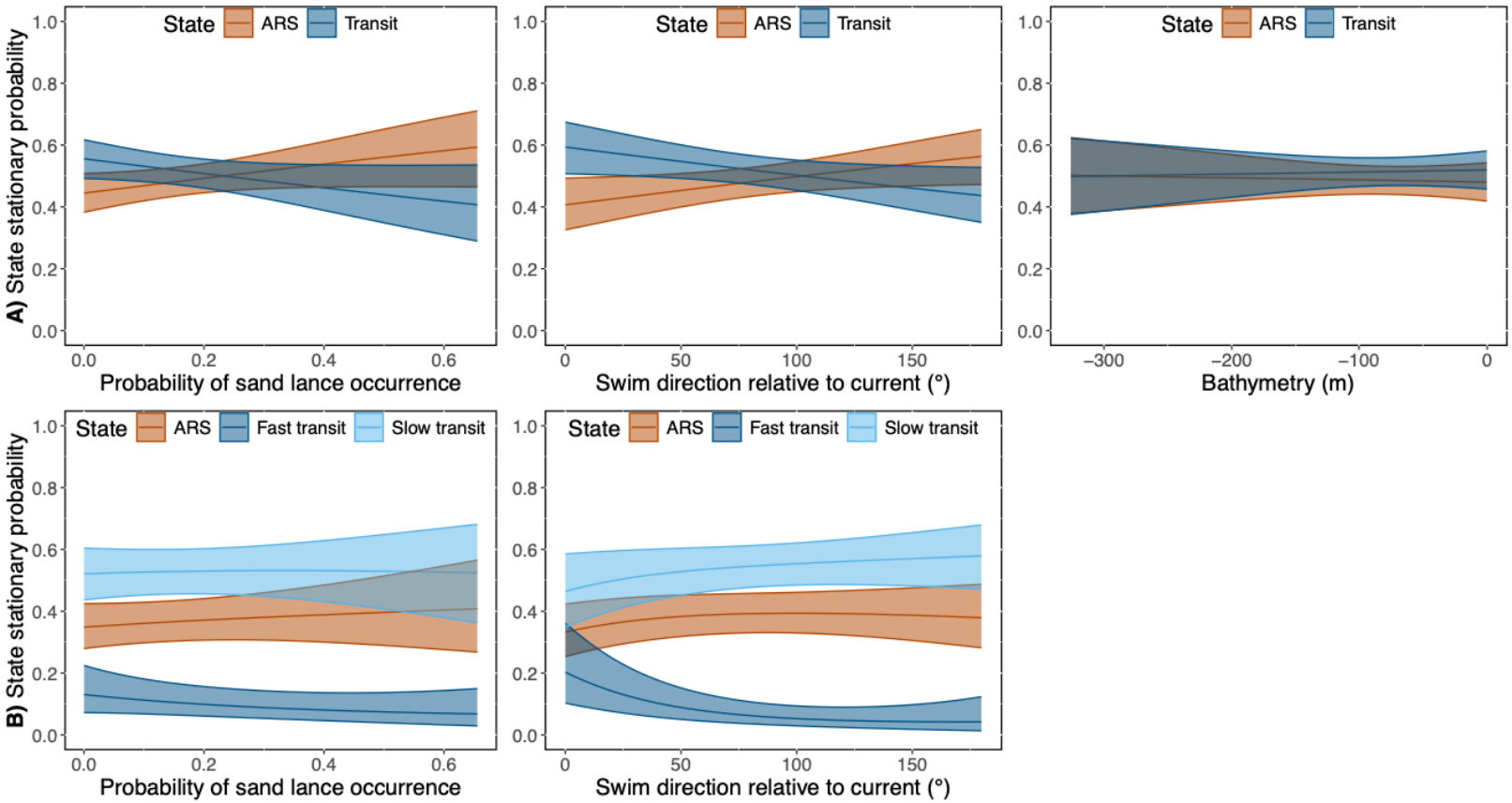

Figure 3.3 : State stationary probabilities for the A) 2-state (ARS and transit) and B) 3-state (ARS, Slow and Fast transit) candidate models as a function of probability of sand lance occurrence, swim direction relative to current, and bathymetry. Solid lines show model-predicted probabilities around the median, with shaded areas indicating the 95% confidence interval. Beluga are considered to swim with the current when angles are <60°, to move perpendicularly to current when between 60° and 120°, and to swim against the current when >120°.

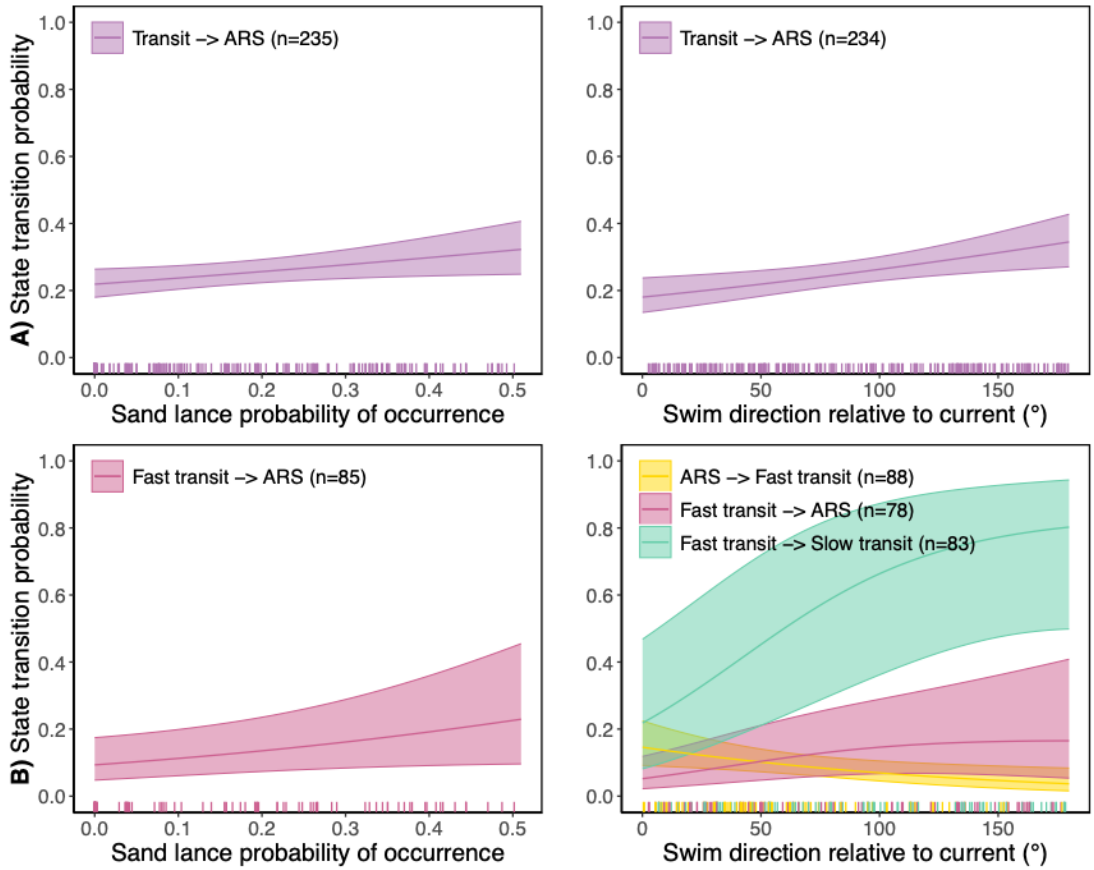

Figure 3.4 : State transition probabilities for the 3-state model as a function of A) probability of sand lance occurrence and B) swim direction relative to current direction. Only transitions with statistically significant covariate effects are shown. Solid lines represent model-predicted median transition probabilities, with shaded areas indicating their 95% confidence interval. For each transition, “n” denotes observed transitions. In panel B, belugas swim with the current at angles <60°, perpendicularly at 60° - 120°, and against at >120°.

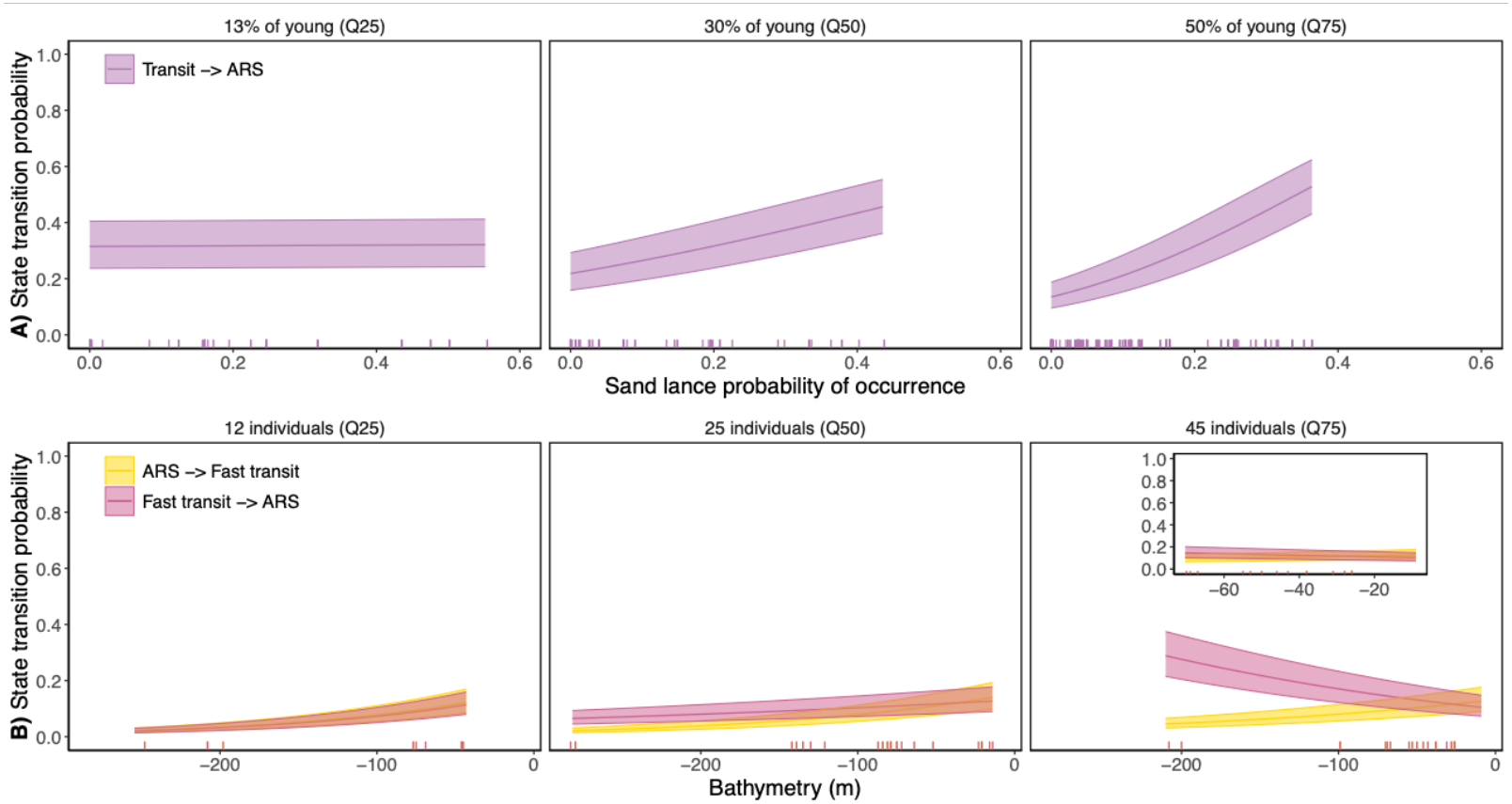

Figure 3.5 : Transition probabilities as a function of A) the interaction between probability of sand lance occurrence and proportion of young (2-state model) and B) the interaction between bathymetry and herd size (3-state model). Solid lines show model-predicted probabilities, with shading areas indicating 95 % confidence intervals. Facets illustrate interactions effects, showing transitions probabilities estimated by fixing all social covariates at their 25th, 50th, and 75th percentiles. Only transitions showing statistically significant effects of the covariate are displayed.

Spatial distribution of behavioural states

The distribution of ARS hotspots was consistent between the 2-state and 3-state HMMs, being largely concentrated in three areas of the Upper Estuary (Batture aux Alouettes, Rivière-du-Loup/Cacouna, and Cap de la Tête au Chien), at the mouth and in the upper Saguenay Fjord (Anse St-Étienne), at Ile Rouge, and along the south shore of the Lower Estuary in the Ile aux Pommes/Ile aux Basques area (Figure 3.6). In the northern portion of the Lower Estuary, an ARS hotspot was detected at the sill of the Laurentian Channel, though there notably few ARS hotspots identified over the deeper waters of the Channel. Corridor hotspots were also similarly distributed using the 2-state and 3-state HMMs, with the highest concentration area occurring throughout the , between Batture aux Alouettes and Ile Rouge, and between Ile aux Pommes/Ile aux Basques and the Laurentian Channel. In the 3-state HMM, slow transit states generally coincided with ARS hotspots and their periphery more than with fast transit hotspots from the 2-state HMM.

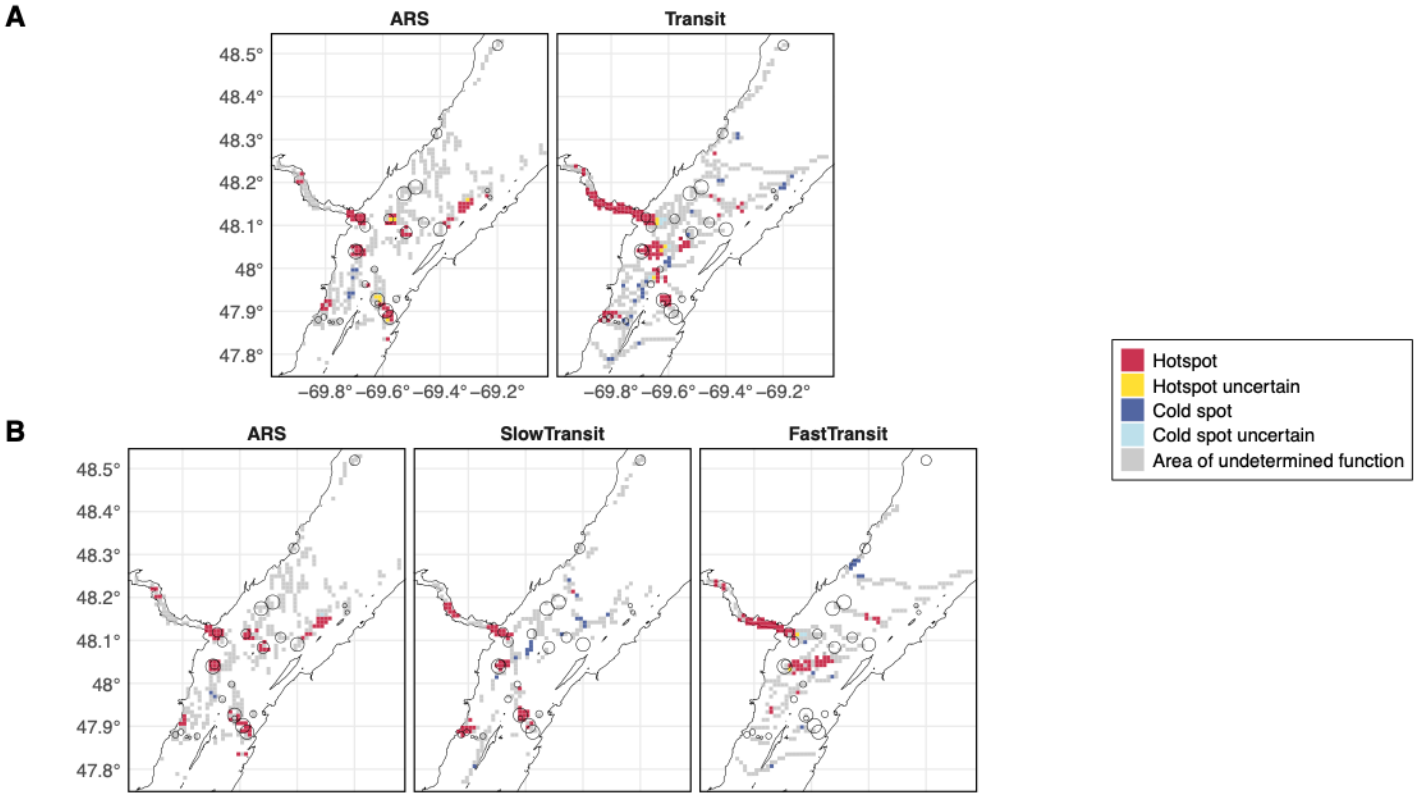

Figure 3.6 : Areas of behavioural activity (i.e., number of data per behaviour) from models including A) two states and B) three states. Red cells represent significant hotspots (area of high use), while blue cells represent significant coldspots (areas of low use). Yellow and light blue indicate uncertain hotspots and coldspots, respectively. Gray cells represent areas of undetermined function. Empty circles correspond to the area restricted search (ARS) contours delineated using a first-passage time (FPT) analytical approach and based on a subset of the same tracking dataset (thirty belugas radio-tracked between 2001 and 2005; Lemieux, 2009, Lemieux et al. 2012). These contours are shown for visual comparison of their correspondence with the ARS areas identified using HMMs in our study.

Discussion

Model complexity

Most HMM applications to track geometry (e.g., step lengths, turning angles) focus on binary states at the two ends of the behavioural spectrum, ARS and travel (McClintock & Michelot, 2018; Hooten et al. 2017). Quantification of intermediate behavioural states and their ecological interpretation across multiple scales from such data has received limited attention (Carter et al. 2025). Our results demonstrated that 2- and 3-state models best captured underlying behavioural patterns in SLE belugas. Adding a third state enabled more nuanced differentiation of directed movement into slow and fast transit modes. This aligns with predominant herd movement patterns, where directional movements at the surface are typically categorized into two types based on associated dive profiles (e.g., pelagic exploration and travelling; Lemieux Lefebvre et al. 2018). The near-zero switching probabilities between slow and fast transit, combined with the spatial occurrence of slow transit around and within ARS hotspots, suggest that slow-directional movements represent a distinct behaviour from travelling (i.e., fast transit). Thus, the addition of a third state was warranted.

Marine predators may search for prey over multiple spatial scales, adapting their movements to enhance prey encounter rate in heterogeneous landscapes (Dorfman et al. 2022). Search-type movements are intermediate in speed and tortuosity – slower than transit but faster and more directed than

ARS (Dorfman et al. 2022). Therefore, slow transit may align with pelagic exploration, a herd directional movement pattern reflecting mixed behavioural use, including exploration and prey searching (Lemieux Lefebvre et al. 2018). This interpretation finds support in comparative evidence and the observed proximity of slow transit to ARS hotspots in SLE belugas. For instance, ARS-like behaviours interspersed with slow-directed movement were interpreted in little penguins (*Eudyptula minor)* as representing within- and between-patch movements (Caroll et al. 2017; Phillip et al. 2019). Southern elephant seals (*Mirounga leonina*) in foraging areas alternated between searching (slow and directed movements) and foraging (slow and tortuous movements) (McClintock & Michelot, 2018), whereas killer whales (*Orcacinus orca)* around Norway exhibited slow-speed movements with intermediate directional persistence (i.e., intermediate tortuosity), which were interpreted as exploratory movements within and around foraging areas (Vogel et al. 2025). Overall, these patterns highlight how animals organize their movements gradually from directional exploration (global, extensive search) to focused exploitation (local, intensive search), in response to landscape heterogeneity and ecological processes such as prey patches depletion or competition (Dorfman et al. 2022).

Including multiple ARS types greatly enhanced classification accuracy and foraging-like activity estimates at the population level. Using grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seal locations, Carter et al. (2025) found that focussed (fine-scale) ARS bouts were intersperced with

broad (coarse-scale) ARS, with regional variation, whereas single-ARS models substantially underestimated foraging-like activity (e.g., by up to 46% in harbour seals). In our study, refining ARS classification into two ARS types resulted in frequent misclassification, lower assignment confidence, and directional movements resembling transit rather than the tortuous movements typically expected with ARS-like behaviour (Dorfman et al. 2022). This suggests that location data alone may not fully capture the behavioural complexity underlying ARS-like movements in belugas. Moreover, population-level HMM may also risk misspecification when the number of plausible states does not accommodate individual variation, a particular concern given the documented sexual segregation and dietary differences in SLE belugas (Michaud 1993; Ouellet et al. 2021; Cabrol et al. 2025). However, our sample size limited detection of such effects (e.g. fitting independent models for each herd type).

ARS hotspots identified in this study overlapped with areas previously linked to foraging in SLE beluga, where herd configuration and diving behaviour were used to infer habitat function, suggesting that at least part of our inferred ARS-like behaviours also corresponds to foraging activity (Lemieux Lefebvre et al. 2012; 2018; Barreau et al. 2025). Nevertheless, ARS-like behaviour may also reflect other behaviours such as resting or socializing (Dorfman et al. 2022). Achieving finer behavioural resolution will require complementary data streams beyond two-dimensional tracks, such as multiple sensor archival biologgers that resolve three-dimensional movements and

acoustic behaviour of the tracked individual and neighbouring whales with a high temporal resolution (Langrock et al. 2012; McClintock & Michelot 2018; Pohle et al. 2016). For instance, dive depth, stereotyped pulsed calls and whistles, and acceleration variables (i.e., pitch, roll and heading) distinguished search from capture phases in fish-eating killer whales (Tennessen et al. 2019).

Environmental and social drivers of movement patterns

Our analytical approach explicitly accounted for temporal autocorrelation in step lengths (Lawler et al. 2019), yet residual correlation persisted, particularly in the 2-state model, reflecting expected within-state dependence characteristic of fine-scale movement data (Johnson & London 2008; Hooten et al. 2017). This may have reduced state decoding precision. While simultaneous multi-lag modelling could reduce this autocorrelation, we avoided it to prevent overfitting, particularly given that models' goodness-of-fit were satisfactory. Crucially, as we modelled covariates on state transitions rather than on each single step, state-habitat associations remained interpretable. Both the 2- and 3-state models revealed consistent behavioural state-habitat associations.

Optimal foraging theory predicts that individuals should tune their movement patterns to prey availability and accessibility in order to maximize their energy intake through cost-benefit decisions (Stephens & Krebs, 1986; Dorfman et al. 2022). In tidally-dominated systems, oceanographic conditions

simultaneously constrain predator locomotion and prey distribution and densities (Benjamin et al. 2015). In our study, tidal current emerged as a significant driver of beluga movement patterns in both models, while bathymetry did not. Individuals exhibited a marked preference relative to current flow : they were more likely to be in, or switch into, fast transit when swimming with surface currents, and to engage in, or switch into, ARS or slow transit when swimming against currents. This pattern aligns with the energy landscape theory, predicting that animals reduce locomotory costs by exploiting currents during movements between habitat patches (Shepard et al. 2013). This finding is further supported by an independent study, showing that SLE beluga herds tended to transit with surface currents, particularly during the ebb tide phase, with no evidence of bathymetry driving transit corridor routes selection (Ouellet et al. 2021).

Counter-current swimming, by contrast, constitutes an energetically costly movement pattern (Shepard et al. 2013), which marine predators may adopt as active or passive foraging tactics depending on prey behaviour, local hydrodynamic conditions, and their own navigational capacity relative to current velocity (Benjamin et al. 2015). Previous observations of beluga swimming against the current in the SLE and elsewhere were interpreted as foraging behaviour (Lesage & Kingsley 1995; Finley et al. 1982; Conversano 2017). SLE belugas consume diverse schooling pelagic fish and invertebrates (Vladykov 1946; Lesage et al. 2020; Cabrol et al. 2025), whose aggregations respond to oceanographic features (e.g., tidal currents, up- and downwelling,

and fronts) and local topography. For instance, capelin move predictably with tidal currents and aggregate in near-bottom water layer along shelf breaks and steep slopes, including in the SLE (Simard et al. 2002; Benjamin et al. 2015). By swimming against the current, belugas may remain stationary within a specific location (i.e., a foraging patch), and increase their prey encounter rate through ambush behaviour, using the current to bring pelagic prey towards them (Benjamin et al. 2015). Alternatively, stalking behaviour may allow them to conceal their presence by approaching their prey closely before attacking (Chevallay et al. 2024).

Prey availability also emerged as a significant driver, with belugas being more likely to exhibit and switch into ARS and slow transit as sand lance probability of occurrence increased, supporting the interpretation of both states as foraging-related behavioural states. However, sand lance appears to be consumed only seasonally, and represents one of many preys in the highly diverse diet of SLE beluga (Vladykov 1946; Cabrol et al. 2025; Lesage et al. 2020), limiting its explanatory scope. Moreover, belugas engaged in ARS in habitats with highly variable bathymetry. This variability in habitat characteristics likely reflected the characteristics of their highly diverse diet, which is comprised of both benthic and pelagic preys.

Social covariates failed to explain behavioural state transitions when examined in isolation. They became meaningful only when combined with environmental context, although inconsistencies arose between 2- and 3-state models. Body size and age generate distinct energetic requirements that may

necessitate different diets and habitats, while social factors – such as females with calves seeking shelter from predators or aggressors – can drive divergent habitat use by age and sex classes (Webber et al. 2023; Lesage et al. 2024). Notably, the concurrent increase in sand lance probability of occurrence and juvenile proportion in herds during switches into ARS aligns with isotopic evidence of slightly higher intake of sand lance by adult females and juveniles – which often occur together – compared to adult males (Cabrol et al. 2025). These patterns match the distribution of areas of high sand lance probability of occurrence, which are abundant in sectors used by females and juveniles or shared with adult males, but few in male-exclusive zones (Mosnier et al. 2016), areas deemed important for benthic foraging (Barreau et al. 2025). However, juvenile proportion captures only a subset of known SLE beluga herd compositions (Michaud 1993), limiting our ability to fully resolve individual movement patterns within social contexts.

The effect of bathymetry on switching probabilities between fast transit and ARS varied significantly with herd size. Although the magnitude of these effects remained weak and constrained by small sample size, they may highlight social modulation of environmental responses in SLE belugas. Movement patterns in gregarious species emerges from the interplay between environmental and social contexts (Aureli et al. 2008; Sueur et al. 2011). For instance, larger groups may enhance selection of profitable resource detection through social information sharing and cooperation, thereby reducing individual search costs. Conversely, smaller groups may minimize intraspecific

competition and slower resource depletion (Fortin et al. 2008; McKellar et al. 2015; Gowan 2019; Webber et al. 2024). Future research integrating acoustic telemetry could help address this gap by linking social communication directly to behaviour, and clarifying how social context drives behavioural state switches.

Spatial distribution of behavioural states

This study generated population-level inference of important behaviours that contribute to the assessment of habitat use and function. Spatial mapping of the inferred ARS state estimated from the 2- and 3-state HMMs revealed strong concordance with ARS contours estimated using First Passage Time analysis using a subset of the tag data (see Figure 11 in Lemieux Lefebvre, 2009), confirming cross-method consistency and validating the HMM-based inference of ARS-like behaviour. Both the 2- and 3-state models – using a larger dataset – uncovered additional ARS zones in the Upper and Lower SLE, notably north-west of Ile aux Lièvres and south-west of Ile aux Basques. These newly-identified ARS hotspots overlapped with areas of high residency identified using herd movement data, and that were deemed to be used for pelagic foraging or a mix of travel and pelagic foraging, respectively (Barreau et al. 2025), suggesting these ARS hotspots support foraging.

The Saguenay Fjord is often cited as important habitat that SLE beluga primarily traverse to reach Baie-Sainte-Marguerite – a river estuary used by all population segments where social activity appears particularly intense

(Chadenet 1997; Conversano 2017; Ouellet et al. 2021; Barreau et al. 2025). Our analysis revealed that both ARS and slow transit hotspots occur near Anse St-Étienne. These locations are consistent with areas of high residency (herd data) or of higher density (aerial survey data) that have been identified in the Saguenay Fjord, including Anse St-Étienne sector (Lemieux Lefebvre et al. 2012; Harvey et al. 2025). Together, these results provide further evidence that the Saguenay Fjord also serves a foraging function for SLE beluga.

The spatial definition of transit was sharper in the 3-state than the 2-state model, revealing distinct hotspots associated with fast and slow transit. Comparison with the 2-state model indicated that areas classified as slow transit in the 3-state model often corresponded to ARS hotspots in the 2-state model, although in some cases they aligned with fast transit hotspots instead. The fact that slow-transit behaviour was generally influenced by the same habitat features as ARS suggest that these hotspots may also support foraging-like behaviours, though they may facilitate connectivity among habitats (Bastille-Rousseau & Wittemeyer 2021). In contrast, fast transit hotspots substantially overlapped three main corridor routes connecting high-use habitats identified using SLE beluga herd data : a large portion of the Saguenay Fjord, the Upper SLE between Batture aux Alouette and Ile Rouge, and the Lower Estuary between Ile aux Pommes/Ile aux Basques and the Laurentian Channel (Ouellet et al. 2021). These fast-transit hotspots are likely shaped by responses to local environmental features and spatial memory (Nathan et al. 2008; Alavi et al. 2022). Belugas exhibit vertical transmission of

migratory routes and summering areas (reviewed in Aubin et al. 2026), reflecting social learning processes through which individuals acquire spatial knowledge that promote efficient movements toward suitable foraging and socializing habitats (Alavi et al. 2022; Barreau et al. 2025).

Although our dataset was, in principle, large enough to capture population-level spatial patterns of behaviour (55 tracks; Sequeira et al. 2019), the absence of ARS or transit hotspots in areas previously identified as high residency or corridor zone suggests that the spatial distribution of tracks and sample size within sectors may have been insufficient to detect all areas supporting these functions. For example, Baie Sainte-Marguerite in the Saguenay Fjord – a key area for foraging, socializing and resting across all herd types – and the Laurentian Channel, important for pelagic foraging by adult herds (Barreau et al. 2025), lacked corresponding hotspots in our analysis. Similarly, the absence of fast-transit hotspots along certain previously identified corridor routes does not preclude that these corridors exist biologically. Their limited occurrence is consistent with patterns observed in other species, such as elephants, where fast-transit corridors represent only small portions of the home range (Bastille-Rousseau & Wittemeyer 2021). These gaps likely stem from the trackin dataset's incomplete, irregular, and overall low spatial coverage across the summer range.

Consequently, our behavioural state maps offer conservative yet actionable valuable guidance for conservation planning, with some behaviourally important areas remaining undetected. Because the energetic

cost of locomotion scales with movement speed, beluga likely exhibit fast transit preferentially in areas where environmental features, such as favorable currents, minimize energy expenditure (Sheppard et al. 2013). Future integration of habitat availability into HMMs (e.g., Resource Selection Function; Florko et al. 2025) would provide deeper insights into behaviour-specific habitat selection. This approach could empirically test whether fast transit is actively selected under energy-minimizing hydrodynamic conditions, particularly in areas like the southern shore of Île aux Lièvres where counter-current swimming is very unlikely (Ouellet et al. 2021).

Conclusion

Understanding movement patterns of free-ranging animals remains fundamental to linking habitat use with population dynamics and effective conservation. Our HMM analysis revealed a nuanced 3-state framework (ARS, slow transit, fast transit) for SLE beluga movements, extending beyond traditional binary models by capturing responses to tidal currents, bathymetry-herd interactions, and social modulation. These findings validated key corridor routes and foraging hotspots while exposing data gaps in other habitats like Baie-Sainte-Marguerite, likely due to limited tracking coverage. Nevertheless, our spatially explicit behavioural maps add to the available information for detecting potential shifts in habitat use and function, and for anticipating or mitigating activities that could disrupt critical behaviours in this endangered population.

Acknowledgments

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Authors' contributions

EB, VL, AD, RM, TB, and CC conceived the study; VL, CC, and RM obtained funding; VL, and RM conducted field research; EB and J.FS contributed to data preparation; EB and TB conducted the analysis; EB, VL, and AD wrote the manuscript with contributions from TB, RM, J.FS, and CC.

Supplementary Material

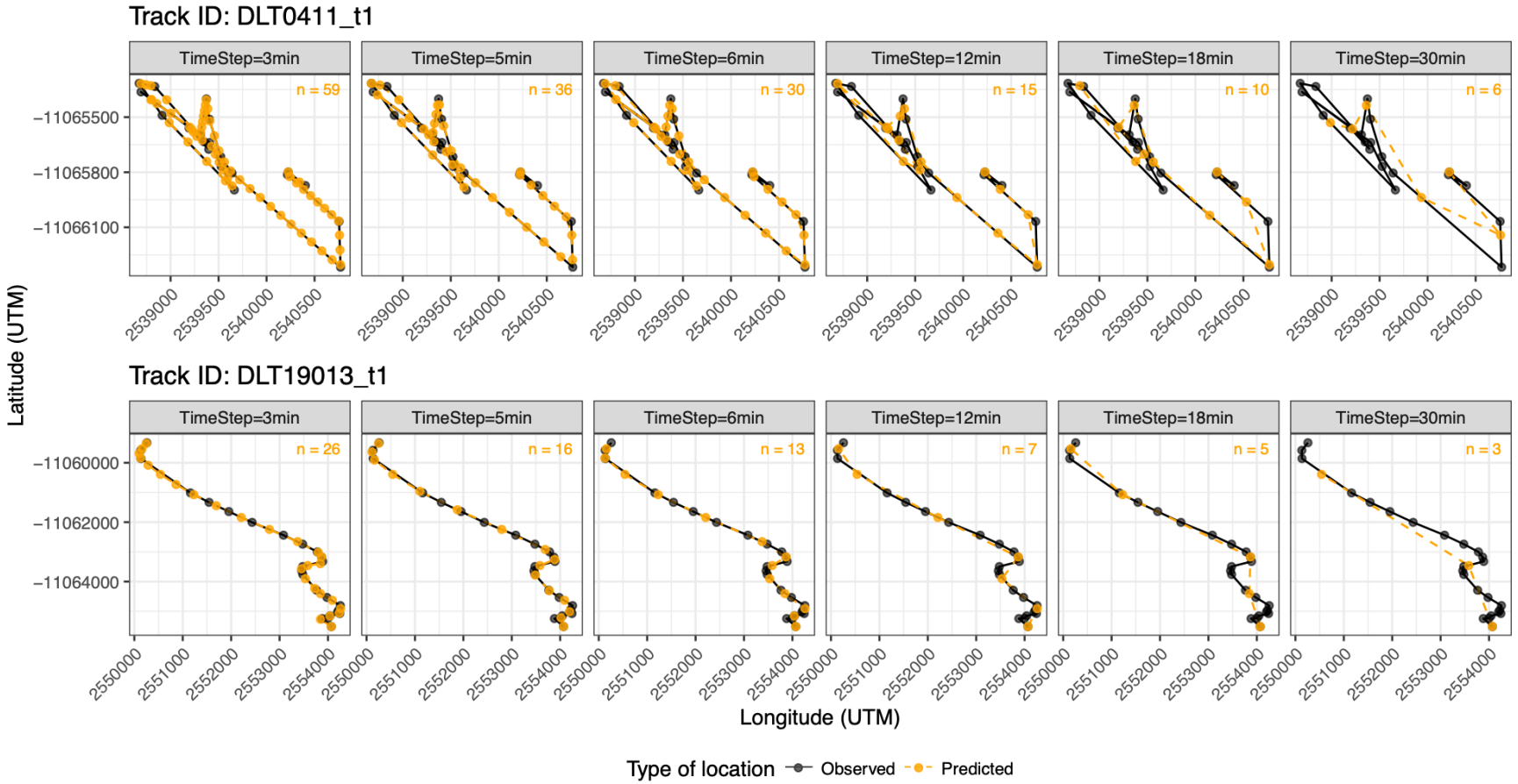
Suppl. Mat. 3.1 : Overview of tracking duration and number of locations of the 55 trajectories (obtained from fifty beluga tracked in SLE) used in this study. ID combines beluga and track segment ID, respectively.

Track ID	Deploy date	Started at	Ended at	Tracking Duration	Number location
DLT0103_t1	2001-08-15	13:42:00	19:54:06	06:12:06	49
DLT0104_t1	2001-08-17	08:48:00	12:11:31	03:23:31	30
DLT0205_t1	2002-09-06	14:20:35	16:34:48	02:14:13	25
DLT0302_t1	2003-07-01	15:42:42	18:41:55	05:28:48	56
DLT0302_t2	2003-07-01	15:42:42	18:41:55	02:59:13	22
DLT0303_t1	2003-07-30	10:58:00	19:27:04	08:29:03	65
DLT0305_t1	2003-08-29	09:25:00	11:26:14	02:01:14	18
DLT0307_t1	2003-09-05	11:49:00	17:04:59	05:15:59	31
DLT0308_t1	2003-09-09	08:40:00	17:33:12	08:53:12	77
DLT0309_D1_t1	2003-09-22	07:34:00	14:59:59	07:25:59	97
DLT0309_D2_t1	2003-09-23	08:35:51	10:04:07	01:28:15	21
DLT0401_t1	2004-06-16	11:53:00	20:00:21	08:07:21	73
DLT0402_t1	2004-06-17	08:07:00	16:07:59	08:00:59	66
DLT0403_t1	2004-06-22	13:01:47	15:09:23	03:11:22	25
DLT0403_t2	2004-06-22	13:01:47	15:09:23	02:07:35	26
DLT0404_t1	2004-06-30	10:56:00	11:37:21	00:41:21	15
DLT0405_t1	2004-07-22	11:09:00	20:55:39	09:46:38	84
DLT0406_t2	2004-07-28	15:51:37	18:46:20	02:54:43	29
DLT0407_t1	2004-08-04	08:56:00	17:50:11	08:54:10	97
DLT0408_t2	2004-08-05	15:08:44	18:55:09	03:46:24	17
DLT0410_t1	2004-08-16	09:25:00	13:11:11	03:46:11	30
DLT0411_t1	2004-08-17	15:24:21	17:19:24	03:06:20	21
DLT0411_t3	2004-08-17	15:24:21	17:19:24	01:55:02	26
DLT0412_t1	2004-08-24	14:41:30	18:27:01	03:59:09	62
DLT0412_t2	2004-08-24	14:41:30	18:27:01	03:45:31	36
DLT0413_t1	2004-09-20	12:34:00	15:37:27	03:03:26	31
DLT0415_t1	2004-09-27	09:47:00	12:50:22	03:03:22	30
DLT0501_t2	2005-06-08	16:15:28	19:37:55	03:22:26	21
DLT0502_D1_t1	2005-06-09	12:28:00	19:32:49	07:04:48	67
DLT0502_D2_t1	2005-06-10	15:03:07	19:15:09	04:12:01	34
DLT0503_t1	2005-06-29	09:33:00	19:09:47	09:36:46	99
DLT0504_t1	2005-07-11	14:07:00	19:37:50	05:30:49	53
DLT0505_t1	2005-07-26	15:36:17	17:08:45	03:08:00	20
DLT0505_t2	2005-07-26	15:36:17	17:08:45	01:32:28	15
DLT0507_t1	2005-08-15	10:20:53	19:00:25	08:39:31	79
DLT0508_t1	2005-08-15	12:10:00	14:57:38	02:47:37	21

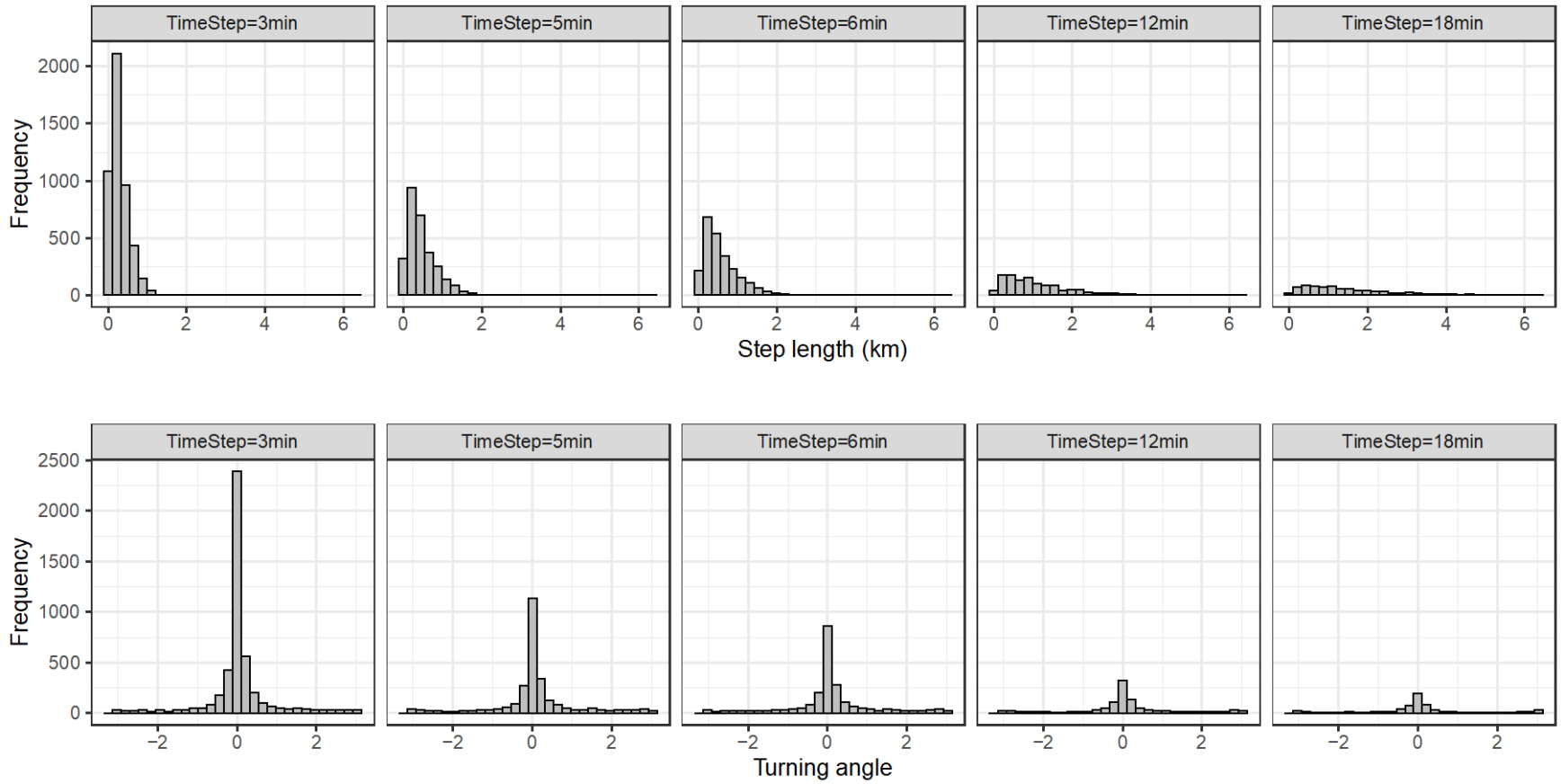
DLT0509_t1	2005-08-18	11:38:00	18:20:35	06:42:34	52
DLT0510_t1	2005-08-26	08:52:00	17:59:32	09:07:31	110
DLT0511_t1	2005-09-08	08:26:59	11:39:44	03:12:45	17
DLT18001_t1	2018-06-21	10:52:00	13:09:59	02:17:58	15
DLT18002_t1	2018-07-03	10:26:00	14:38:16	04:12:16	50
DLT18003_t1	2018-07-04	12:13:00	19:59:19	07:46:18	66
DLT18005_t1	2018-08-01	14:12:00	15:05:50	00:53:50	17
DLT18009_t1	2018-08-17	13:56:06	19:58:03	06:01:56	85
DLT18011_t2	2018-08-31	11:53:20	14:39:49	02:46:28	22
DLT19006_t1	2019-07-10	11:38:38	16:22:05	04:43:26	41
DLT19007_t1	2019-07-22	09:24:00	12:24:08	03:00:07	26
DLT19008_t1	2019-07-24	12:31:00	17:57:10	05:26:10	81
DLT19009_t2	2019-07-25	11:01:09	15:23:30	04:22:21	34
DLT19010_t1	2019-07-26	09:20:32	12:37:13	03:16:41	26
DLT19011_t1	2019-09-09	10:25:56	14:56:00	04:30:03	50
DLT19013_t1	2019-09-12	13:40:52	15:05:12	01:24:19	26
DLT19014_t1	2019-10-09	09:46:43	14:22:31	04:35:48	34
DLT20001_t1	2020-07-15	10:33:29	14:28:05	03:54:35	73
DLT20002_t1	2020-07-31	10:45:50	15:03:44	04:17:53	33

Note : the data presented in the table are those obtained after several filtration steps (at least 15 GPS, GPS time interval <1h (sub-tracks segmentation), and complete spatial–temporal records (latitude, longitude, timestamps).

Suppl. Mat. 3.2 : Comparison of observed and predicted locations for two individual tracks across different temporal resolutions. Observed positions correspond to raw GPS fixes, while predicted positions were estimated using a CTCRW model fitted to each track and using 6 timestep (3, 5, 6, 12, 18 and 30 minutes). The number of predicted locations is indicated in the top-right corner of each facet.



Suppl. Mat. 3.3 : Step length and turning angle distributions at multiple interpolation time steps, illustrating the empirical basis for selecting state-dependent initial parameter ranges in n-state HMMs (see Table S1).



Suppl. Mat. 3.4 : Range of initial values for step length means (km) and turning angle concentration (i.e., around the mean direction) parameters in n-state HMMs, as applied across five interpolation time steps (3, 5, 6, 12, 18 min). Following Michelot & Langrock (2023), state-specific ranges were set by visual inspection of histograms (Figure S1). Initial means were chosen near the minimum (area-restricted search, ARS) and maximum (transit) observed step length, and the corresponding standard deviations were set equal to these mean values. Angle concentration was assigned low for ARS (reflecting high sinuosity) and high for transit (reflecting high directional persistence). To specify 3- or 4-state HMMs, the 2-state ranges were subdivided to assign intermediate values, ensuring parameters for each state remained within the overall observed range and reflected a gradation of movement patterns. Standard deviation was made equal to the mean for step length.

Parameters	**n-state HMM**	**State**	**Range of initial starting values**				
			3 min	**5 min**	**6 min**	**12 min**	**18 min**
Step length mean (km)	**2-state**	ARS	0.01–0.4	0.01–0.6	0.01–1.2	0.01–1	0.001–1.5
		Transit	0.3–2.5	0.5–2.5	1–4	0.8–4.5	1.4–6.5
	3-state *(2 transit)*	ARS	0.01–0.4	0.01–0.5	0.01–1.2	0.01–1	0.001–1.5
		Slow transit	0.35–0.8	0.5–1	1–2	0.8–2	1.4–2.5
		Fast transit	0.7–2.5	0.8–2.5	1.8–4	1.9–4.5	2.4–6.5
	3-state *(2 ARS)*	Intense ARS	0.01–0.1	0.01–0.2	0.01–0.3	0.01–0.4	0.001–0.5
		Moderate ARS	0.2–0.4	0.25–0.5	0.2–1	0.5–1	0.6–1.5
		Transit	0.5–2.5	0.5–2.5	1–4	0.8–4.5	1.4–6.5
	4-state	Intense ARS	0.01–0.1	0.01–0.2	0.01–0.5	0.01–0.4	0.001–0.5
		Moderate ARS	0.1–0.4	0.25–0.5	0.5–1.2	0.5–1	0.6–1.5
		Slow transit	0.35–0.8	0.5–1	1–2	0.8–2	1.4–2.5
		Fast transit	0.7–2.5	0.8–2.5	1.8–4	1.9–4.5	2.4–6.5
Turning angle concentration	**2-state**	ARS	0.5–1	0.5–1	0.5–1	0.5–1	0.5–1
		Transit	5–20	5–20	5–20	5–20	5–20
		ARS	0.5–1	0.5–1	0.5–1	0.5–1	0.5–1

	3-state *(2 transit)*	Slow transit	5–10	5–10	5–10	5–10	5–10
		Fast transit	5–20	5–20	5–20	5–20	5–20
	3-state *(2 ARS)*	Intense ARS	0.5–1	0.5–1	0.5–1	0.5–1	0.5–1
		Moderate ARS	0.6–2	0.6–2	0.6–2	0.6–2	0.6–2
		Transit	5–20	5–20	5–20	5–20	5–20
	4-state	Intense ARS	0.5–1	0.5–1	0.5–1	0.5–1	0.5–1
		Moderate ARS	0.6–2	0.6–2	0.6–2	0.6–2	0.6–2
		Slow transit	5–10	5–10	5–10	5–10	5–10
		Fast transit	5–20	5–20	5–20	5–20	5–20

Suppl. Mat. 3.5 : Environmental covariate data descriptions and sources

Environmental covariate	Description	Source
Bathymetry	Seafloor depth at a 10 m horizontal and < 1 m vertical resolutions.	Canadian Hydrographic Service
Surface current speed	Modelled surface current velocity and direction at a 400 m and 1 h resolution. Following Ouellet et al. (2021), the absolute difference between animal step direction and current direction was calculated, with 0 indicating motion aligned with the current.	Oceanographic model from Saucier & Chassé (2000)
Animal motion relative to current direction		
Probability of sand lance occurrence	Predicted probability of sand lance (*Ammodytes americanus*) occurrence obtained from benthic imagery.	Inventories of 137 sites between 2008 and 2010 (Larocque et al. unpublished data)

Suppl. Mat. 3.6 : Comparison of model performance (AIC) for each time step and number/state structure. For each time step, the model with the lowest AIC is in bold.

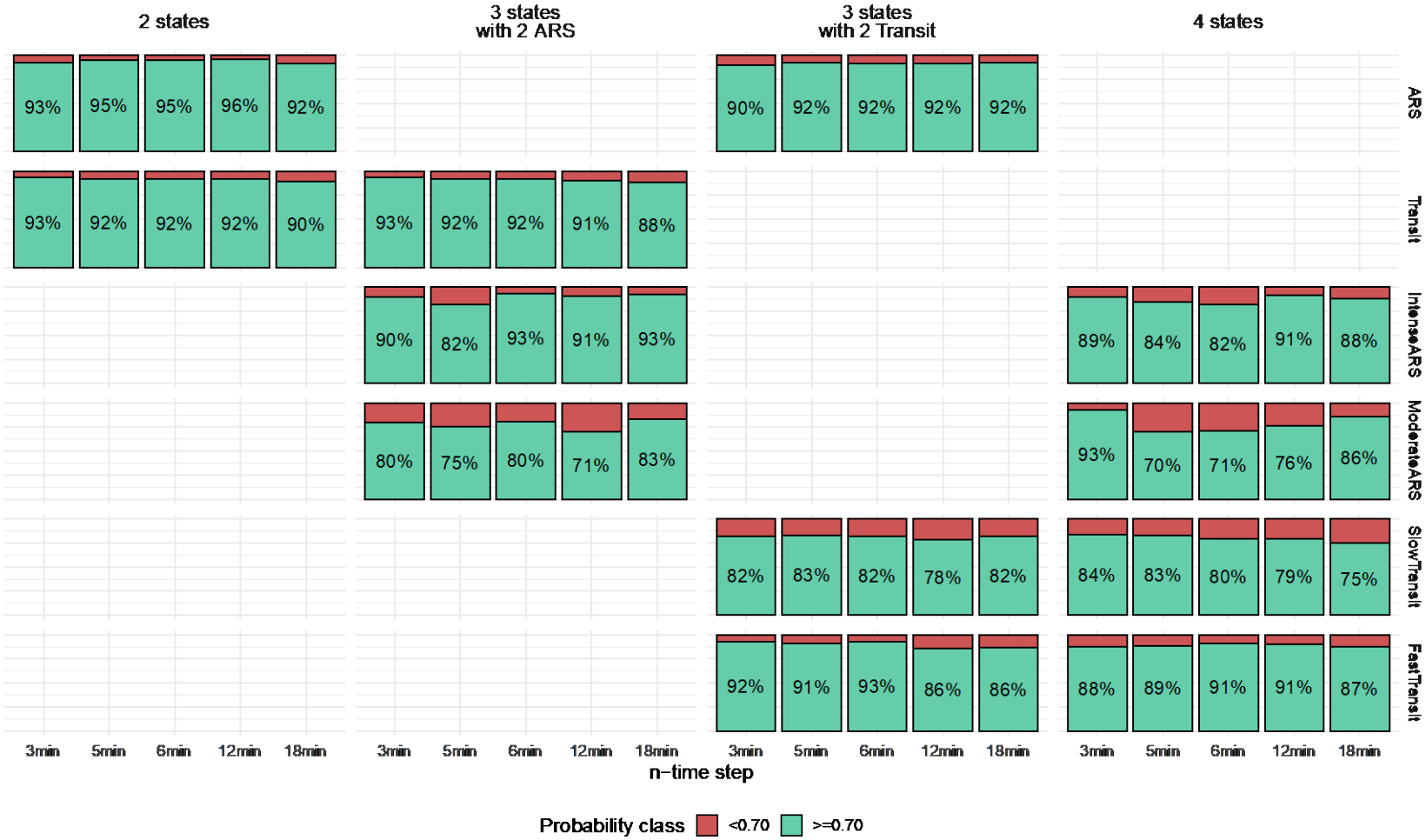
Time step (min)	n-state models	AIC
3	**4 states**	**-3463.2**
	3 states with 2 transit	-2395.8
	3 states with 2 ARS	-2329.4
	2 states	-927.1
5	**4 states**	**3334.7**
	3 states with 2 transit	3763.8
	3 states with 2 ARS	4007.9
	2 states	4385.8
6	**4 states**	**4174**
	3 states with 2 transit	4469.3
	3 states with 2 ARS	4489.6
	2 states	4976.6
12	**4 states**	**4162.3**
	3 states with 2 transit	4332.4
	3 states with 2 ARS	4378.9
	2 states	4521.7
18	**4 states**	**3324.7**
	3 states with 2 transit	3445.5
	3 states with 2 ARS	3455.3
	2 states	3580.9

Suppl. Mat. 3.7 : Likelihood convergence summary from 25 fitting attempts of the n-state HMM, each initialized with different sets of starting values (mean and sd) of step length and turning angle, across different time steps. The most frequent likelihood value across runs was selected as the best estimate. The number of model runs indicates how many, from the 25 fitting attempts, converged to the same likelihood value as the selected model, with higher counts suggesting numerical stability and robustness. The likelihood range represents variability in convergence results, with narrow range denoting stable optimization, whereas wider range indicate potential instability.

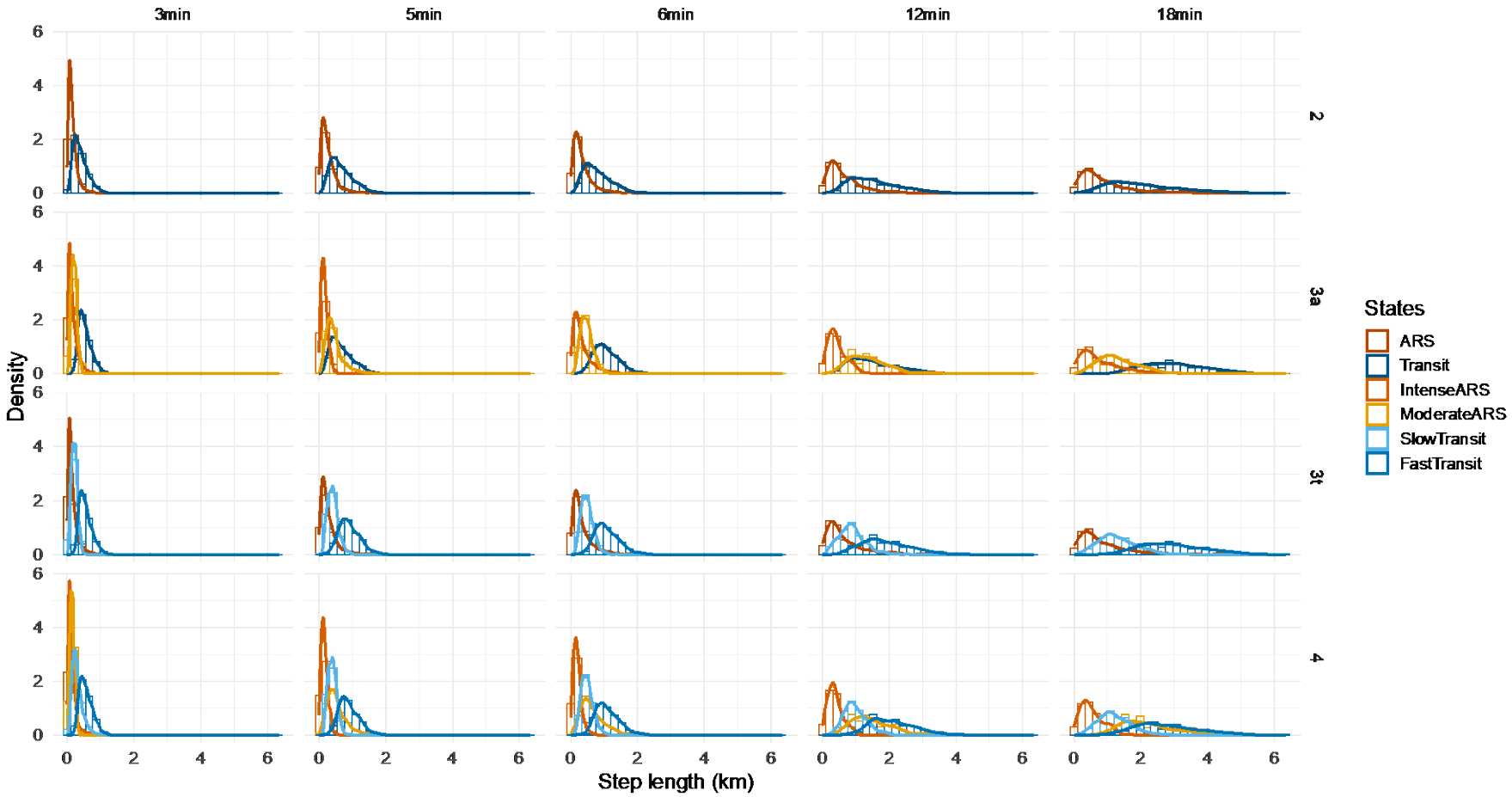
n-state models	Time step used in CTCRW (min)	Most frequent likelihood value	No of runs converging to this value
2 states	3	-474.6	19
	5	2181.9	23
	6	2477.3	21
	12	2249.9	24
	18	1779.5	23
3 states with 2 ARS	3	-1066.7	5
	5	2051.9	12
	6	2346.6	8
	12	2169.4	13
	18	1712.4	19
3 states with 2 transit	3	1861.9	14
	5	2218.1	19
	6	2156.4	15
	12	1707.7	8
	18	-1625.9	22
4 states	3	1642.1	4
	5	2056	7
	6	2050.1	4
	12	1634.9	3
	18	-474.6	7

Note : A low (i.e., negative) likelihood value indicates that the model provides a poor fit to the data.

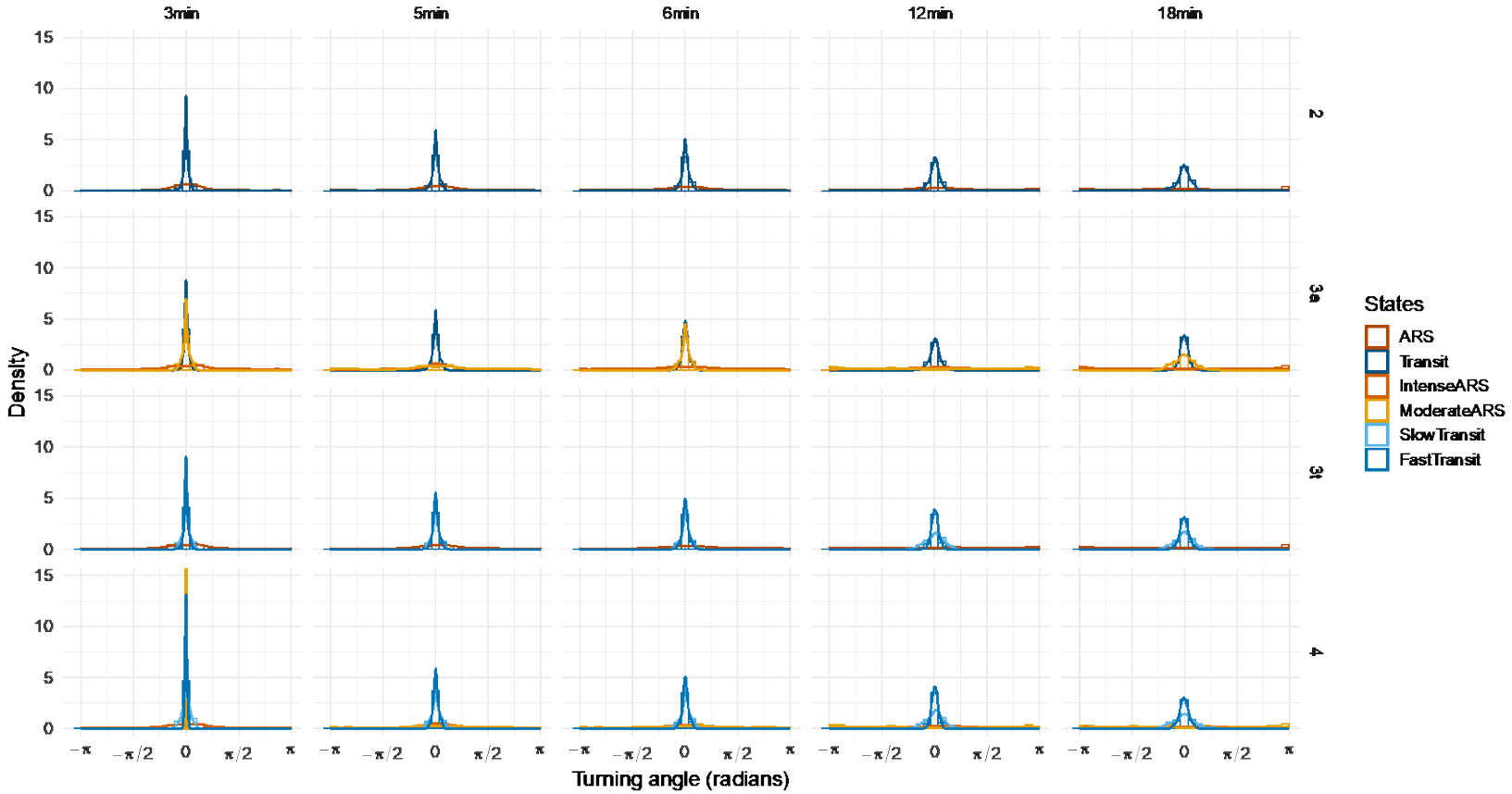
Suppl. Mat. 3.8 : Confidence level in state assignments presented for each behavioural state (rows) and model type (columns) at various time steps. The proportion (in %) of assignments that were made with a low (< 0.7) and high (≥ 0.7) confidence level are shown in red and green, respectively.



Suppl. Mat. 3.9 : Step length distribution by behavioural state (color), presented for various interpolation time steps (columns), and models (rows). Histograms and density curves are overlaid for each state using the corresponding state color coding.



Suppl. Mat. 3.10 : Turning angle distributions by behavioural state (color), presented for various interpolation time step *(*columns*),* and model type (rows). Histograms and density curves are overlaid for each state using the corresponding state color coding.



Suppl. Mat. 3.11 : Summary of mean (± SD) step length and mean turning angle for behavioural states identified by the 2-state and 3-state Hidden Markov Models (HMMs). ARS = Area-Restricted Search.

n-state HMM	Behavioural State	Step length (km, mean ± SD)	Turning angle (radians, mean)
2 state	State 1 (ARS)	0.29 ± 0.22	0.17
	State 2 (transit)	0.68 ± 0.34	0.01
3 states with 2 transit	State 1 (ARS)	0.29 ± 0.23	0.20
	State 2 (slow transit)	0.41 ± 0.16	0.01
	State 3 (fast transit)	0.91 ± 0.32	0.01

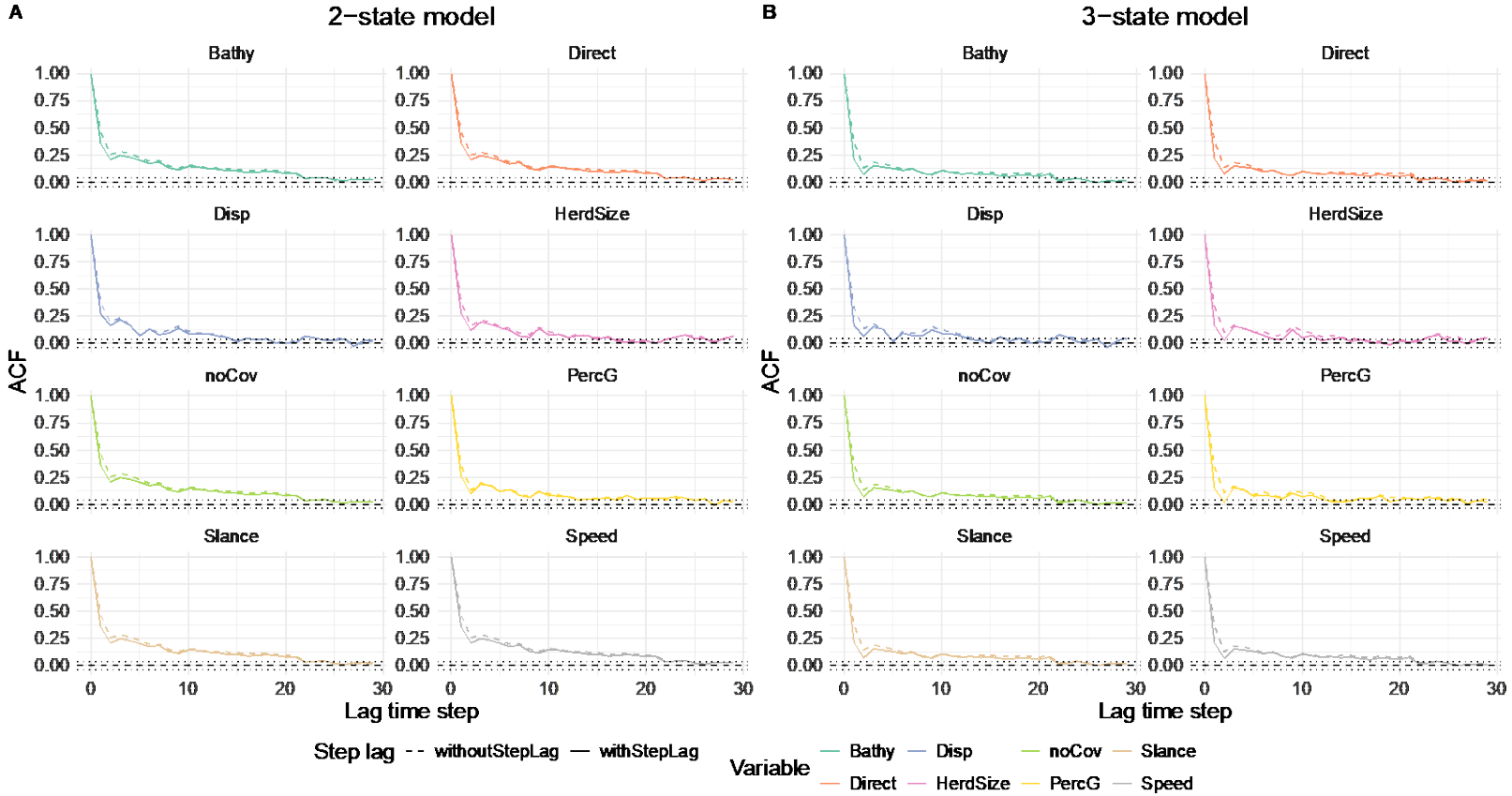
Suppl. Mat. 3.12 : Summary of the Akaike information criterion (AIC) for the null (i.e., no covariates included), univariate and multivariate HMMs. Covariates included bathymetry (Bathy), swim direction relative to current direction (DiffC), sand lance probability of occurrence (SLance), current speed (SpeedC), herd size (HerdSize), herd composition (proportion of juvenile individuals : PercG), and dispersion of groups within herds (Disp). For each social covariate, the subset of observations where that specific social and all non-missing habitat covariates were non-missing were used to estimate a new null model and models including potential covariates. The n indicate the number of observations used in each models. The Autocorrelation term column indicates whether a one-step lag term was included ("yes") or not ("no") to account for temporal autocorrelation. For each HMM (2 or 3 states), the model with the lowest AIC is highlighted in bold. Models with ΔAIC < 2, also in bold, are considered candidate models with similar support. Grey cells with NA values indicate models were excluded due to convergence failure.

Model	**Autocorrelation term**	**2-state HMM**		**3-state HMM**	
		AIC	**Δ AIC**	**AIC**	**Δ AIC**
Habitats covariates (n=2693)					
ModelNull	no	4448.5	217.8	3839.5	337.2
ModelNull	yes	4236.5	5.8	3552.4	50.2
Bathy	no	4447.8	217	3845.9	343.7
Bathy	yes	4237.9	7.2	3555.4	53.2
DiffC	no	4430.6	199.8	3793.6	291.3
DiffC	**yes**	**4232.1**	**1.4**	**3502.2**	**0**
SpeedC	no	4451.9	221.1	3836.8	334.5
SpeedC	yes	4240.1	9.3	3553.9	51.7
SLance	no	4445	214.2	3836.9	334.6
SLance	yes	4235.3	4.6	3551.6	49.4
Bathy+DiffC	no	4430.4	199.6	3798.3	296.1
Bathy+DiffC	yes	4233.4	2.7	3507.9	5.6
Bathy+SLance	no	4444.8	214	3841.7	339.5
Bathy+SLance	yes	4236.9	6.2	3552.4	50.2
Bathy+SpeedC	no	4451.1	220.4	3843.3	341.1
Bathy+SpeedC	yes	4241.5	10.7	3557.2	55
DiffC+SLance	no	4427.7	197	3793.1	290.9
DiffC+SLance	**yes**	**4230.8**	**0**	**3502.3**	**0.1**
DiffC+SpeedC	no	4434.5	203.7	3794.2	292
DiffC+SpeedC	yes	4235.1	4.4	3505.7	3.4
SpeedC+SLance	yes	4448.8	218	3835.4	333.2
SpeedC+SLance	no	4238.8	8.1	3555.1	52.9
Bathy+DiffC+SLance	no	4428.1	197.3	3797.5	295.3
Bathy+DiffC+SLance	**yes**	**4232.3**	**1.5**	3505.5	3.3

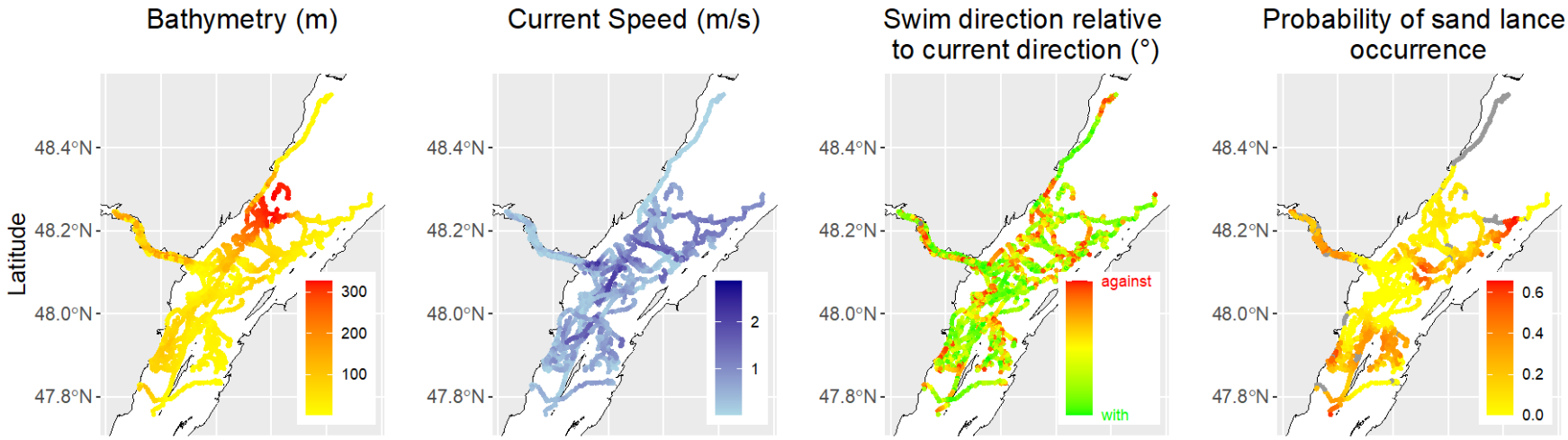
Bathy+SpeedC+SLance	no	4448.6	217.8	3841.1	338.8
Bathy+SpeedC+SLance	yes	4240.4	9.6	3556	53.8
DiffC+SpeedC+SLance	no	4431.5	200.7	3794.1	291.8
DiffC+SpeedC+SLance	yes	4233.5	2.7	3506.2	3.9
Bathy+SpeedC+DiffC+SLance	no	4431.8	201	3798.3	296.1
Bathy+SpeedC+DiffC+SLance	yes	4235	4.2	3509.2	7
Social covariates and habitat interactions					
Herd size (n=1306)					
ModelNull	no	2104	142	1865.7	205.4
ModelNull	**yes**	**1962**	**0**	1664.4	4.1
HerdSize	no	2107.4	145.4	1877	216.8
HerdSize	yes	1965.9	3.9	1674.1	13.8
HerdSize*Bathy	no	2107.4	145.4	1865.3	205
HerdSize*Bathy	**yes**	**1963.3**	**1.3**	**1660.3**	**0**
HerdSize*DiffC	no	2109.6	147.6	1877	216.8
HerdSize*DiffC	yes	1973.1	11.1	1684.8	24.5
HerdSize*SLance	no	2109.9	147.9	1873.1	212.9
HerdSize*SLance	yes	1971.2	9.2	1669.1	8.8
HerdSize*SpeedC	no	2113.6	151.6	1882.6	222.4
HerdSize*SpeedC	yes	1972.6	10.6	1686.1	25.8
Composition (n=1029)					
ModelNull	no	1749.3	124.1	1577.7	169.8
ModelNull	**yes**	1633.5	8.3	**1408**	**0**
PercG	no	1740.7	115.5	1573.5	165.5
PercG	yes	1633.5	8.3	1413	5
PercG*Bathy	no	1742.6	117.4	1587.7	179.7
PercG*Bathy	yes	1630.2	5	1450.9	42.9
PercG*DiffC	no	1744.1	118.8	1600.8	192.8
PercG*DiffC	yes	1640	14.8	1423.2	15.3
PercG*SLance	no	1732	106.8	1578.2	170.3
PercG*SLance	**yes**	**1625.2**	**0**	NA	NA
PercG*SpeedC	no	1740.2	115	1581.8	173.8
PercG*SpeedC	yes	1632.5	7.3	1459.4	51.4
Dispersion (n=863)					
ModelNull	no	1506.9	90.8	1340.4	128.3
ModelNull	**yes**	**1416.5**	**0.5**	**1212**	**0**
Disp	no	1510.8	94.7	1352.4	140.4
Disp	**yes**	**1416.1**	**0**	1219.8	7.7
Disp*Bathy	no	1515.3	99.2	1366.4	154.3
Disp*Bathy	yes	1422.9	6.8	1244.3	32.3

Disp*DiffC	no	1512.7	96.6	1352.2	140.2
Disp*DiffC	yes	1423.6	7.5	1236.7	24.7
Disp*SLance	no	1515.2	99.1	1348.7	136.6
Disp*SLance	yes	1420.6	4.5	NA	NA
Disp*SpeedC	no	1517.9	101.8	NA	NA
Disp*SpeedC	yes	1427	11	1242	29.9

Suppl. Mat. 3.13 : Comparison temporal autocorrelation (ACF) of step residuals for each covariate between models including (solid line) and not including (dashed line) an autocorrelation term. Panels A and B correspond to 2-state and 3-state models, respectively. Lines above the 95% confidence interval (dotted black lines around zero) indicate statistically autocorrelation at the corresponding lag time step. Variables include bathymetry (Bathy), swim direction relative to current direction (Direct), sand lance probability occurrence (Lance), current speed (Speed), herd size (HerdSize), herd composition (proportion of juvenile individuals : percG), and herd dispersion (Disp), while . The null model correspond to noCov.



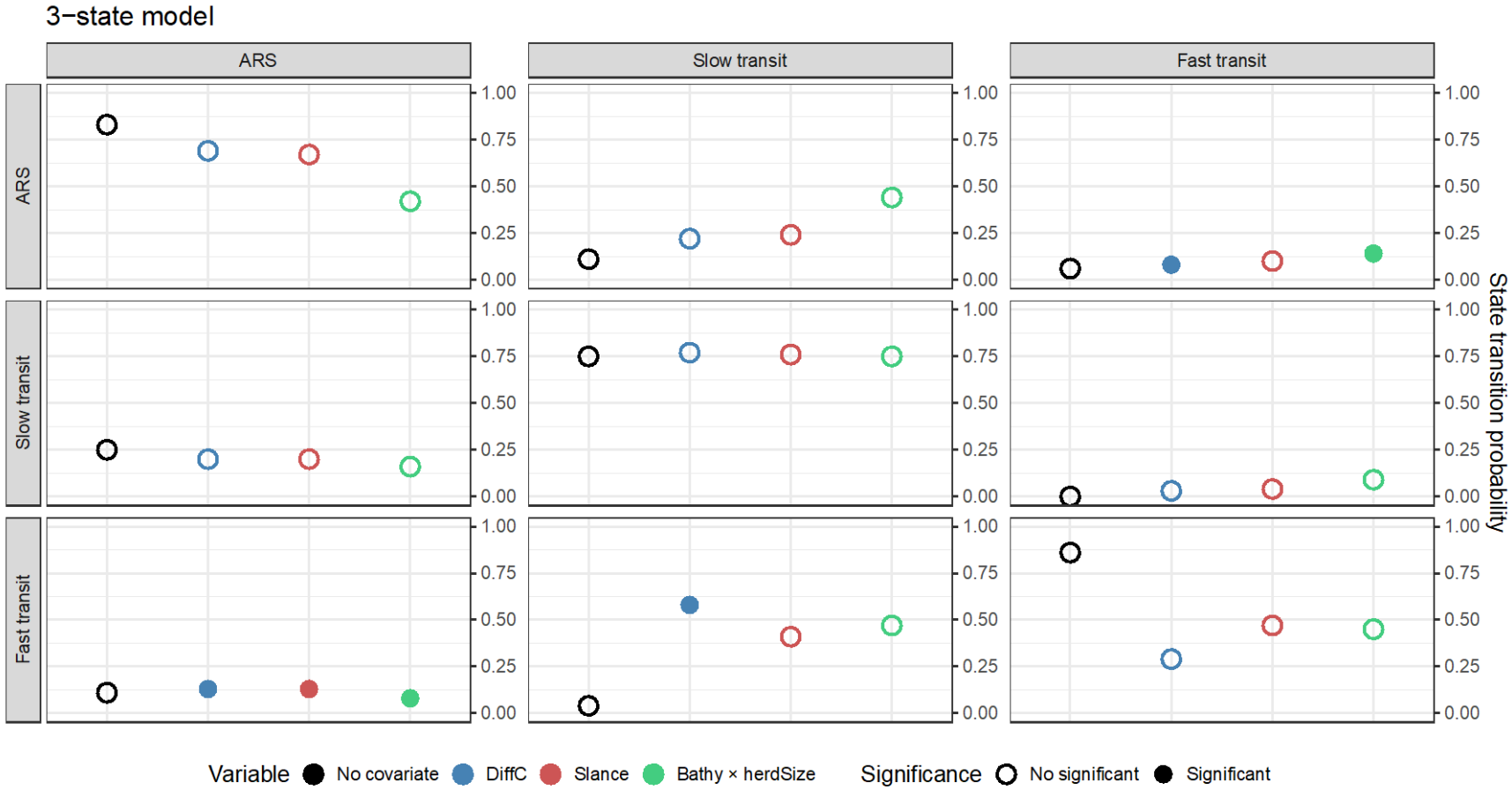
Suppl. Mat. 3.14 : Spatial distribution of habitat and social covariates once assigned to individual tracking locations. The upper row displays distributions of four habitat variables : bathymetry (m), current speed (m/s), swim direction relative to current direction (degrees), and probability of sand lance occurrence (proportion from 0 to 1).



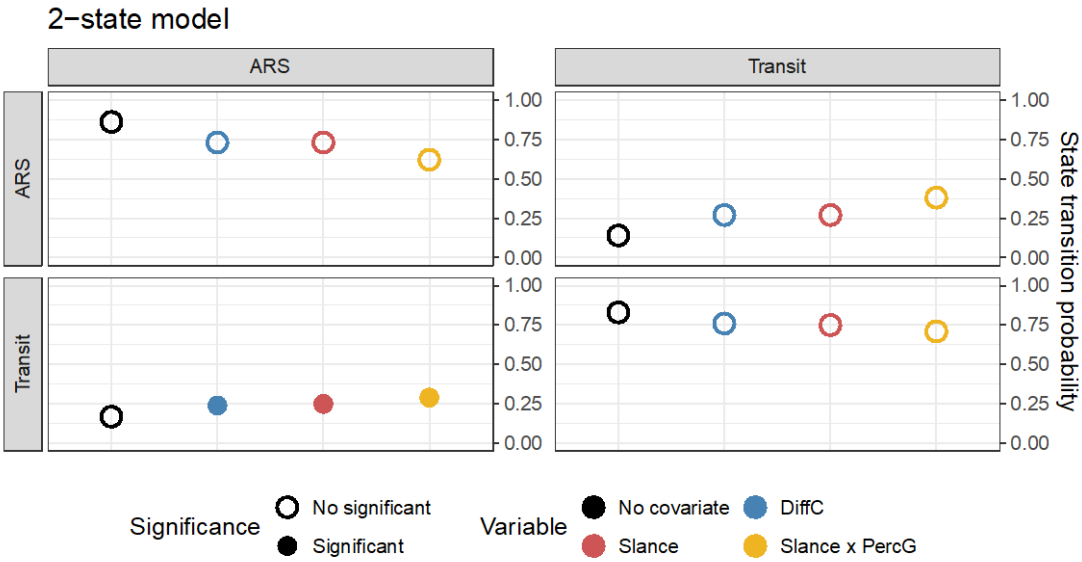
Suppl. Mat. 3.15 : Regression coefficients for the transition probabilities between behavioural states. Covariates are those retained following model selection and include bathymetry (Bathy), swim direction relative to current direction (DiffC), and sand lance probability of occurrence (SLance). For models with social variables, they included herd size (HerdSize), and herd composition (proportion of juvenile individuals : percG). Within models with the same n-state levels, significant covariate effects are shown in bold, while non-significant effects are shaded in grey. States are ARS (1) and transit (2) for the 2-state model, and ARS (1), slow transit (2) and fast transit (3) for the 3-state model.

n-state model	Covariate	Transition	Estimate	SE	CI
Habitats covariates					
2 state	DiffC	1 → 2	0	0.1	[-0.2; 0.2]
	DiffC	**2 → 1**	**0.3**	**0.1**	**[0.1; 0.4]**
	SLance	1 → 2	0	0.1	[-0.2; 0.2]
	SLance	**2 → 1**	**0.2**	**0.1**	**[0; 0.3]**
	Bathy	1 → 2	0.1	0.1	[-0.1; 0.3]
	Bathy	2 → 1	0.1	0.1	[-0; 0.3]
3 states	DiffC	1 → 2	0.1	0.1	[-0.1; 0.3]
	DiffC	**1 → 3**	**-0.4**	**0.2**	**[-0.8; -0.1]**
	DiffC	2 → 1	0	0.1	[-0.2; 0.2]
	DiffC	2 → 3	0.3	0.4	[-0.4; 1.1]
	DiffC	**3 → 1**	**1.3**	**0.3**	**[0.7; 1.8]**
	DiffC	**3 → 2**	**1.3**	**0.4**	**[0.6; 2.1]**
	SLance	1 → 2	-0.1	0.1	[-0.3; 0.1]
	SLance	1 → 3	0	0.2	[-0.3; 0.3]
	SLance	2 → 1	-0.1	0.1	[-0.3; 0.1]
	SLance	2 → 3	-0.5	0.5	[-1.5; 0.5]
	SLance	**3 → 1**	**0.4**	**0.1**	**[0.1; 0.6]**
	SLance	3 → 2	0.1	0.3	[-0.5; 0.6]
Social covariates and habitat interactions					
2 states	PercG	1 → 2	-0.2	0.2	[-0.5; 0.1]
	PercG	2 → 1	-0.1	0.1	[-0.4; 0.1]
	SLance:PercG	1 → 2	-0.1	0.2	[-0.4; 0.3]
	SLance:PercG	**2 → 1**	**0.5**	**0.2**	**[0.2; 0.8]**
3 states	Bathy:HerdSize	1 -> 2	-0.1	0.2	[-0.5; 0.3]
	Bathy:HerdSize	**1 -> 3**	**-0.7**	**0.3**	**[-1.2; -0.1]**
	Bathy:HerdSize	2 -> 1	0	0.3	[-0.6; 0.5]
	Bathy:HerdSize	2 -> 3	0.3	0.3	[-0.3; 0.9]
	Bathy:HerdSize	**3 -> 1**	**1.5**	**0.5**	**[0.5; 2.4]**
	Bathy:HerdSize	3 -> 2	0.4	0.4	[-0.3; 1.1]

Suppl. Mat. 3.16 : Transition probability (based on mean covariate values) resulting from the 3-state HMM without covariates, and including swim direction relative to current direction (DiffC), sand lance probability of occurrence (SLance), and interaction between bathymetry (Bathy) and herd size (HerdSize). Full colored points indicate significant covariates effect on state transition.



Suppl. Mat. 3.17 : Transition probability between behavioural states (based on mean covariate values) resulting from the 2-state HMM without covariates and including swim direction relative to current direction (DiffC), sand lance probability of occurrence (SLance), and its interaction with herd composition (proportion of juvenile individuals : percG). Covariate with significant effect on state transition are shown in bold and colored according to figures 4 and 5a.



CHAPITRE 3 : BELUGA FISSION-FUSION DYNAMICS IN THE ST. LAWRENCE ESTUARY, CANADA

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An original research paper that will be submitted for peer-review

Abstract

Fission-fusion (FF) dynamics represents an important feature of social systems, allowing individuals to adjust their group size, composition and spatial cohesion in response to changing environmental and social conditions. Although these three dimensions are rarely examined together, their integration is essential for characterizing the degree and drivers of FF dynamics across species. This study aimed to explore the FF dynamics of a highly social cetacean, the beluga (*Delphinapterus leucas*). By using an extensive 34-year dataset comprising observations from over 2500 beluga herds from the St. Lawrence Estuary, Canada, fission and fusion events were quantified based on changes in herd size, composition and spatial dispersion detected from paired scans collected during multi-hour focal follows of herd movements and surface configurations. Herd size and spatial cohesion changed more frequently – approximately once per hour for both measures – than herd composition, placing beluga in an intermediate category along the FF continuum defined by Aureli et al. (2008), similar to other multilevel species. Social, behavioural, and environmental factors influenced FF event probabilities overall, though effect direction and magnitude varied by indicator (herd size, composition or dispersion) and event type (fission or fusion). The presence of calves consistently led to greater herd stability (i.e., a lower likelihood of fission or fusion events) across all three dimensions. Clustered herds structure was the only predictor affecting fission probabilities while herd movement patterns, habitat type, and tidal phase influenced fusion

probabilities. Anthropogenic variable showed no significant association with FF events, but the observed trend toward increased of both fission and fusion event when boat are present may suggest that boat occurrence is insufficient to detect potential effect. The marked variability in FF dynamics among herds suggest that FF events result from complex interactions among ecological, social and anthropogenic factors. Future work should aim at refining our understanding of these interactions so enhance our ability to predict how variations in social dynamics may influence key biological processes such as reproductive success and survival.

Keywords : Fission-fusion, herd size, herd composition, spatial cohesion, Cetacean

Introduction

Sociality, or group living, shapes the behaviour and ecology of many animal species (Alexander 1974). By forming groups, individuals can benefit from enhanced foraging efficiency, information sharing, cooperative offspring care, and collective vigilance and defense against predators (Krause & Ruxton 2002; Ward & Webster 2016). Yet, group living also entails costs, including intensified competition for resources or mates, greater pathogen transmission risk, and increased social stress (Krause & Ruxton 2002; Ward & Webster 2016). Each individual is therefore confronted with trade-offs between physiological demands and social needs to maximize fitness, influencing decisions to leave or remain in the group (Conradt & Ropert 2000, Sueur et al. 2011; Ward & Webster 2016). Consequently, grouping patterns in many species are inherently flexible and can be characterized by varying degree of fission-fusion dynamics (Aureli et al. 2008).

Fission-fusion (FF) dynamics has evolved across diverse taxa. According to the three dimensional framework proposed by Aureli et al. (2008), FF dynamics describes temporal variability in group membership (i.e., size and composition) and spatial cohesion (i.e., interindividual distance) within any social system along a continuum. Species exhibit striking variation in their degree of FF dynamics : some maintain relatively stable group composition while varying size and spatial cohesion (e.g., African elephant*, Loxodonta africana* : Wittemyer et al. 2005; Masai giraffe, *Giraffa camelopardalis tippelskirchii* : Bond et al. 2019; Killer whale, *Orcacinus orca* : Tavares et al.

2017). Others exhibit high variability in both membership and spatial cohesion (e.g., Black-and-White Ruffed Lemurs, *Varecia variegata* : Baden et al. 2016; Spotted hyena, *Crocuta crocuta* : Smith et al. 2008; Common dolphin, *Delphinus delphis* : Castro 2022).

Quantifying FF dynamics in a meaningful way poses both conceptual and methodological challenges (Whitehead 2008). Because FF dynamics operate simultaneously across spatial, temporal and social scales, consideration of these scales is critical to estimate a meaningful degree (Aureli et al. 2008; Robitaille et al. 2021; Madsen et al. 2024). The temporal scale, in particular, deserves careful consideration as social interactions within a social unit integrate multiple timescales, from brief proximity changes to longer-term shifts in group membership and association patterns (e.g., second to year; Robitaille et al. 2021; Madsen et al. 2024). When the biologically relevant social timescale is unknown, examining a range of observation intervals is therefore warranted to assess the sensitivity of FF metrics to temporal resolution and to verify the robustness of resulting patterns (Whitehead 2008; Picardi et al. 2024).

The diversity in FF dynamics among species reflects adaptive responses to socio-ecological conditions that vary across space and time (Sueur et al. 2011; Aureli et al. 2008; Webber et al. 2023). FF dynamics is often behaviour-specific, with spatio-temporal variability in resource availability commonly representing a primary ecological driver of fission or fusion events across diverse taxa (Aureli et al. 2008; Sueur et al. 2011). For instance,

animals may adjust their grouping patterns by merging when food is abundant or splitting when food becomes scarce to reduce intraspecific competition and optimize their energy intake (Sueur et al. 2011). These decisions are further influenced by intrinsic state of individual (e.g., mismatches between group member's requirements; Conradt & Ropert 2000; Webber et al. 2023), access to social information (e.g., knowledge sharing about the location of food sources or nesting sites; Ramos-Fernandez & Morales 2014), and predation risk (Heithaus & Dill 2002; Fortin et al. 2009).

Social factors also strongly shape FF dynamics (Webber et al. 2023). The strength of social relationships (e.g., familiarity or preference among group members; Wittemyer 2005; Ramos-Fernandes et al. 2014; Le Goff et al. 2024), and the presence of mothers with dependent calves promote stable dyadic units that can merge into longer-term groups with relatively high stability (i.e., less likely to exhibit fission or fusion; Lunardi et al. 2014; Castro et al. 2022). Such cohesion provides benefits including cooperation in offspring care (Couzin 2006; Wittemyer 2005; Gowans 2019), protection against predators (Bond et al. 2019), male aggression (Cassini 2021), and infanticide (Smith et al. 2008). This stability can also enhance maternal foraging efficiency during lactation (Gowans et al. 2019).

Extrinsic factors such as anthropogenic activities can also influence FF dynamics in various ways. In some cetaceans, boat presence (e.g., density, distance, generated noise) and long-term harvest have led to smaller group sizes and more solitary individuals or pairs (Steward et al. 2025; La Manna et

al. 2023). In killer whales, rapid losses of individuals from stable groups due to illegal fisheries appear to have triggered regrouping – likely to maintain functional group sizes – though this may have weakened social relationships reduced survival in subsequent years (Busson et al. 2019). While integration of social, behavioural, ecological and anthropogenic factors is critical to gain insights into the drivers of FF dynamics, few studies have examined these factors within a unified analytical framework (Bond et al. 2019; La Manna et al. 2023).

Cetaceans constitute a particularly relevant system for studying FF dynamics given the high sociality observed in some species (Gowans et al. 2019). Belugas (*Delphinapterus leucas)* for example have a highly diverse vocal repertoire thought to reflect the complexity of their social system (Sjare & Smith 1986; Michaud 2005; Alekseeva et al. 2013; Vergara et al. 2019; Garland et al. 2015; Panova et al. 2019, 2023). Beluga form a wide variety of social groupings ranging from solitary to pairs, small groups or large herds that can reach hundreds of individuals, that may vary according to immediate social, behavioural, ecological, and anthropogenic contexts (Michaud 1993; Alekseeva et al. 2014; Lemieux Lefebvre et al. 2018; O'Corry-Crowe et al. 2020; Mayette et al. 2022; Stewart et al. 2025; Panova et al. 2025; Aubin et al. 2026). This apparent social flexibility share commonalities with what defines FF societies (Aureli et al. 2008), leading to their consistent classification as a FF species across studies (Michaud et al. 2005; Mayette et al. 2022; O'Corry-Crowe et al. 2020; Stewart et al. 2025; Aubin et al. 2026). However, our

understanding of beluga FF dynamics remains fragmentary. Most prior research has focused on group-level metrics, description of only size and composition dimensions from the FF dynamics conceptual framework (O'Corry-Crowe et al. 2020), with only limited attention to spatial cohesion FF dimensions (Stewart et al. 2025) or the temporal dynamics of FF events themselves. Understanding FF drivers is critical, as social structure likely influences fitness, survival and genetic structure (Archie et al. 2008; La Manna et al. 2023), which are key factors for beluga conservation.

This study aimed to explore the FF dynamics of a highly social cetacean, the beluga, using a 34-year dataset of multi-hour herd focal follows conducted during summer in the St. Lawrence Estuary, Canada. Like in other regions, beluga in the SLE segregate by sex and age-class during summer, although some sectors are shared by all segments of the population (Ouellet et al. 2021). Their distribution between June and October has been well studied, with areas used predictably for transit and for other functions such as foraging having been identified (Lemieux Lefebvre et al. 2012; Barreau et al. 2025). During this period, SLE beluga are expected to engage in multiple behaviours including feeding, socializing, resting, calving and transiting (Lemieux Lefebvre et al. 2018; Ouellet et al. 2021; Barreau et al. 2025).

Our aims were to (1) characterize variability in herd fission and fusion across herd size, composition, and spatial dispersion, and (2) identify drivers among social, ecological and anthropogenic factors. Building on the conceptual FF framework of Aureli et al (2008), we posited high degree of FF

dynamics if all three dimensions varied frequently, or intermediate dynamics if size and spatial cohesion changed more than herd composition (Aureli et al. 2008). We tested specific hypotheses : (a) FF events should be less frequent in herds with calves due to allocaring in beluga (Wittemyer 2005; Lunardi & Ferreira 2014; Castro et al. 2022; Aubin….); (b) FF events are likely to vary by movement type (e.g, foraging, socializing, resting, travelling) reflecting behavioural context (Lunardi & Ferreira 2014; Lemieux Lefebvre et al. 2018; Castro et al. 2022); (c) FF events should occur more often in foraging areas (Barreau et al. 2025), reflecting spatial predictability of resource distribution and resource competition (Aureli et al. 2008; Sueur et al. 2011); (d) FF events should be influenced by tidal phase which affects food availability (Sueur et al. 2011); (e) dispersion should increase in presence of vessels (Kowalski et al. *2026)*.

Methods

Focal follow observations

Vessel-borne focal follows of beluga herds were conducted in the St. Lawrence Estuary and during summer and early fall between 1989 and 2023. Each focal follow typically lasted three hours, and consisted of scans made approximately every 30 min to describe herd surface configuration and movement patterns. Focal follows lasting up to 10-12 h were conducted in some years when tracking tagged individuals (see Barreau et al. in prep.). The daily search area was selected to maximize spatial coverage, avoid

resampling areas covered in previous days, and to account for weather conditions. Focal follows covered a large portion of the SLE beluga summer distribution, and includedd a broad range of habitats used for various purposes by all types of herds (Lemieux Lefebvre et al. 2012, Ouellet et al. 2021; Barreau et al. 2025).

A chain rule incorporating a behavioural criterion was used to define beluga herds and groups (Whitehead et al. 2008; Aubin et al. 2026). A beluga herd was defined as an assemblage of distinct groups, where inter-group distances were smaller than the overall extent of the herd (i.e., herd radius < 2000 m) and inter-individual distance within groups were less than 2-3 body lengths. Herd focal follows started upon encountering a beluga herd. An initial scan recorded a brief description of the herd size, surface configuration and movement patterns, with the research vessel positioned 300 – 500 m away to minimize disturbance. After 15 min, the research vessel then approached the herd at slow speed (<5 knots) to conduct detailed scans every 30 min (average ± SD : 32 ± 10 min). These scan documented herd size, age composition, geometrical configuration (herd structure and dispersion), and predominant movement patterns (see categories in Table 4.1). Herd age composition was informed mainly by skin coloration and body size. Juveniles were identified by greyish skin; calves (young of the year) by their smaller size (~ half adult size), darker tones (dark grey/brown), and, for neonates, by additional features such as fetal folds, close adult proximity, frequent chin-up behaviour, and a dark eye

ring (Michaud 2014). Vessel traffic was also characterized, including boat types and their numbers within a 0–2000 m radius of the herd (Table 4.1).

Estimation of FF events

Following the conceptual FF framework proposed by Aureli et al. (2008), three dimensions were used to characterize FF events within herds. The two membership dimensions were defined by herd size (i.e., number of individuals) and herd composition (i.e., proportion of juveniles), while the spatial cohesion dimension was defined by herd dispersion (i.e., spatial distance between groups) (Table 4.1). When values were uncertain, herd size and composition were recorded as ranges. For data analysis, the midpoint of each range was used and rounded up to the next integer. Only detailed scans with data available for at least one dimension were retained.

Table 4.1 : Predictors variables included in the multinomial analysis to characterize fusion-fission dynamics.

Variable type		Description
Response variables		
Herd size		Number of individuals surfacing at any given time
Herd composition		Proportion of juvenile grey-colored individuals surfacing during the same period
Herd dispersion	Tight (<100m)	Average distance between individuals or group within herd
	Loose (100-300m)	
	Disperse (>300m)	
Explanatory variables		
Social		
Herd structure	Uniform	Individuals or groups distributed uniformly within the herd
	Clustered	Individuals or groups distributed in a few distinct clusters
Presence of calf (Yes/No)		Presence of at least one calf within herd
Behaviour		
Herd predominant movement pattern	Directional	Continuous unidirectional movement
	Multidirectional	Directional movement with frequent deviation of the principal axes
	Milling	Circular movement at the surface resulting in low net displacement
Environmental		
Tidal phase	Low	Tide was classified in 3-h bins
	Rising	
	High	
	Ebb	
Type of habitat	AHR	Areas of High Residency (identified by Lemieux Lefebvre et al. 2012) primarily used for foraging and socializing (Barreau et al. accepted)
	Corridor	Areas (identified by Ouellet et al. 2021) primarily used for exploration and travelling (Barreau et al. accepted)
	Undefined	Areas where habitat use is uncertain or does not fit established categories of residency or travel
Anthropogenic		
Presence of boat (Yes/No)		Presence of at least one boat (e.g., pleasure boats, whale-watching boat, ferry and merchant ships) within a 0–2000 m radius of the herd

Fission and fusion events were identified based on changes in herd size, composition and dispersion between successive scans, excluding the initial scan of each focal follow. Each dimension was analyses independently : for each herd, all pairs of scans with available data for a given dimension were included, resulting in a variable number of scan pairs per herd and per metric (Table S1). Changes in herd size and composition for paired scans were expressed as percent change relative to the value from the first scan. Following the methodology of Pearson (2009) and Castro et al. (2021), a minimum 25% and 33.33% change were applied to herd size and composition, respectively, to account for uncertainty in estimates and minimize misidentification of FF events. These thresholds were based on the median percent change calculated from scan pairs where herd size or composition were recorded as a range. Paired scans showing changes smaller than these thresholds were classified as stable in herd size or composition (no FF event). FF events based on change in dispersion were determined by comparing distance categories between consecutive scans. A fusion event was defined as a shift toward a tighter spatial configuration (i.e., from dispersed to loose, loose to tight or dispersed to tight), whereas a fission event was defined as a shift toward a more dispersed configuration (i.e., from tight to loose, tight to dispersed or loose to dispersed).

Timescale of FF events

To determine the scale at which FF events typically occur in SLE beluga, the occurrence of FF events was assessed for each of the three

dimension at 30-min incremental timescales ranging from 0.5 to 3 h. Specifically, FF occurrence at the 30-min scale was calculated using consecutive scans (scan 1 *vs.* 2, 2 *vs.* 3, etc.), while FF occurrence at 1-h and 1.5-h intervals scales used every third scan (1 *vs.* 3, 2 *vs.* 4, etc) or every fourth scan (1 *vs*. 4, 2 *vs* 5, etc.), respectively. Pairs of scans deviating by no more than 10 min from the expected interval were retained (i.e., 20 – 40 min apart for the 30-min scale, 50 – 70 min for the 1-h scale, etc.). This filtering ensured consistent scan intervals and reliable FF event detection (Suppl. Mat. 4.1).

Three complementary approaches were used to characterize the occurrence of FF events using paired scans at each timescale. A cross-sectional approach calculated *prevalence* as the proportion of FF events, pooled across herds. A longitudinal approach calculated *frequency* as the number of FF event rate (events per scan pairs per focal follow), averaged across herds. Finally, *magnitude* was calculated as the absolute number of FF events detected at each timescale, averaged across herds (accounting for both all herd or those herds that experienced at least one FF).

These three approaches did not presupose any timescale as the most representative; instead, they assessed whether re-aggregating pairs of scans to coarser temporal resolutions (i.e., over 30 minutes) would yield different *prevalence*, *frequency,* or *magnitude* of FF events, thereby guiding the timescale retained for subsequent analysis.

Predictors of FF events

To assess whether social, behavioural, environmental or anthropogenic context affects the likelihood of FF events, mixed multinomial logit regressions (Mixed-effects MLR) were used to model the probabilities of FF events as a function of six predictor variables. The probability of FF events (the response variable) was evaluated separately for each of the three dimensions (herd size, composition and dispersion) given they were not correlated (Pearson r : -0.04 – 0.05). Explanatory variables included four variables acquired during the 30-min scans (herd structure, the presence of calves or vessels, and predominant movement patterns), as well as tidal phase and habitat type (Table 1). Habitat type was defined as either an area of high residency (AHR) or a corridor route (Lemieux Lefebvre et al. 2012; Ouellet et al. 2021), and assigned to scans using a spatial join based on herd location (function *st_join* from *sf* R package, *version 1.0-19*). Scans located outside defined habitat types were considered to occur in an 'undefined habitat'. Each scan was assigned a tidal phase using forecasts for Tadoussac –the centre of the study area – by dividing the tidal cycle into 3-h bins (low, rising, high, ebb), with high tide occurring 5 – 7 h after low tide (Table 1; Ouellet et al. 2021), and by matching the tidal phase closest to the time of the herd scan. Because the response variable described the change between two consecutive scans, each row in the dataset for a given timescale represents a pair of scans plus a categorical outcome (fission, fusion, or stable). Each explanatory variable was assigned the value recorded

during the first scan of the pair, based on the asumption that these initial conditions influenced the subsequent response.

Conceptually, MLRs extend binomial models by allowing response variables with more than two categorical outcomes. In this analysis, the stable event was defined as the baseline category of the response variable. The effects of predictors on the response variable were assessed by comparing each non-baseline category (fission or fusion, coded 1) against the baseline (stable, coded 0) (Agresti et al. 2012). Estimated effects are expressed as odd ratios (OR), which quantify how each predictor influences the likelihood of fission or fusion relative to stability. OR values indicate both the direction and the strength of the association; an OR of 1 denotes no effect, whereas ORs > 1 or < 1 indicate, respectively, a higher or lower probability of a fission or fusion event relatively to stability.

Mixed-effects MLR were fitted using the *mblogit* function from the *mclogit* R package (version 0.9-6), using herd as a random factor to account for potential residual autocorrelation among successive scans within a herd follow. Residual temporal autocorrelation was assessed graphically using autocorrelation plots (*acf* function from the *car* R package, version 3.1-2). Across all three response variables (herd size, composition, dispersion), predictor–outcome combinations contained 17 – 1237 events, exceeding the recommended minimum of 10 – 20 events per predictor parameter in the rarest outcome category (Suppl. Mat. 4.2). All combinations of the six predictors were considered in model selection (*dredge* function from the *Mumin* R package,

version 1.47.1). Categorial predictors with more than two levels were coded using sum contrasts (*contr.sum* R function), so that each level's effect was estimated relative to the overall mean of all levels combined. Multicollinearity among predictors was assessed using generalized variance inflation factors (GVIFs) adjusted for degrees of freedom (*car* R package *version 3.1-2*). Model selection was based on the Akaike Information Criterion corrected for small sample size (AICc), with candidate models having ΔAICc < 2 considered to have comparable support (Anderson & Burnham, 2002). Significance of predictors and effect size were assessed from their ORs and 95% confidence intervals (CIs); significance was determined when the 95% CI did not overlap OR = 1. Nagelkerke pseudo R^2 was used to evaluate model fit and explanatory power (Nagelkerke 1991). All statistical analyses were conducted in R (version 4.2.2, R Core Team, 2022). Values are mean ± standard deviation unless otherwise stated.

Results

Of the 3961 herd focal follows conducted between June and October 1989 – 2023, 2542 herds met quality criteria for quantifying FF events and analyzing their frequency and environmental, social and behavioural context (Figure 4.1; Suppl. Mat. 4.3). Herds varied widely in size from 1 to 225 individuals, with a mean herd size of 25 ± 23 individuals (median = 20; n = 14020 scans). While herds entirely composed of grey or white individuals were encounted, they had an average of 33% ± 21% grey individuals (median = 35%; n = 9245 scans). Although herds in tight configuration were slightly more

frequently observed (42%), loose (31%) and dispersed (27%) herds were also regularly observed (n = 8503 scans) (Figure 4.2).

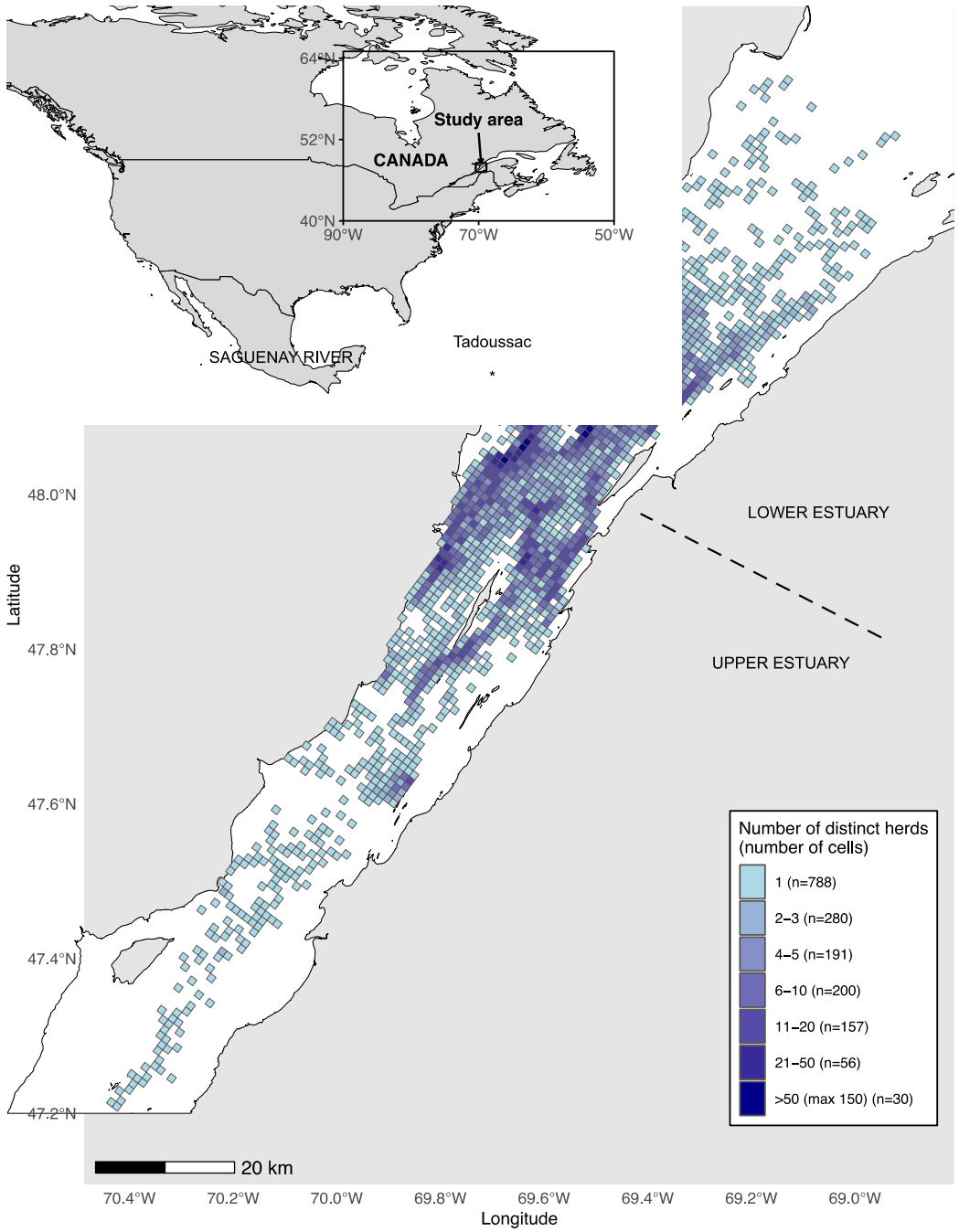

Figure 4.1 : Herd focal follow densities in the St. Lawrence Estuary (Canada) from 1989 to 2023 (from June to September). The number of distinct herds crossing each 1 km^2 cell are color-coded according to density (darker tones indicating higher numbers). Number of cells in each category is presented in the figure legend.

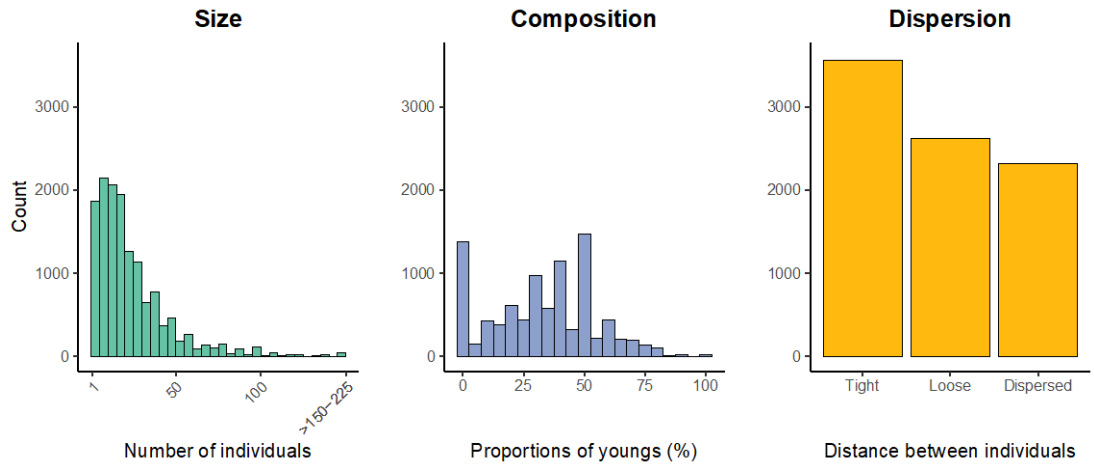

Figure 4.2 : Frequency distribution of 30-min scans recorded for each fission-fusion dimension. Each panel displays the count of scans per bin (with bin width set to five for both size and composition) or category.

Occurrence of FF events

The prevalence, frequency and magnitude of FF events increased as timescale increased from 30 min to 1 h regardless of the dimension used to characterize the occurrence of FF events (Figure 4.3). Passed 1 h and up to 2 h, FF occurrence continued to increase slowly using all three dimensions for prevalence and frequency, but not magnitude. Overall, herd size showed higher detections of FF events than the other two dimensions. High standard deviations around the means for all three metrics indicate substantial variation in FF dynamics across herds and timescales.

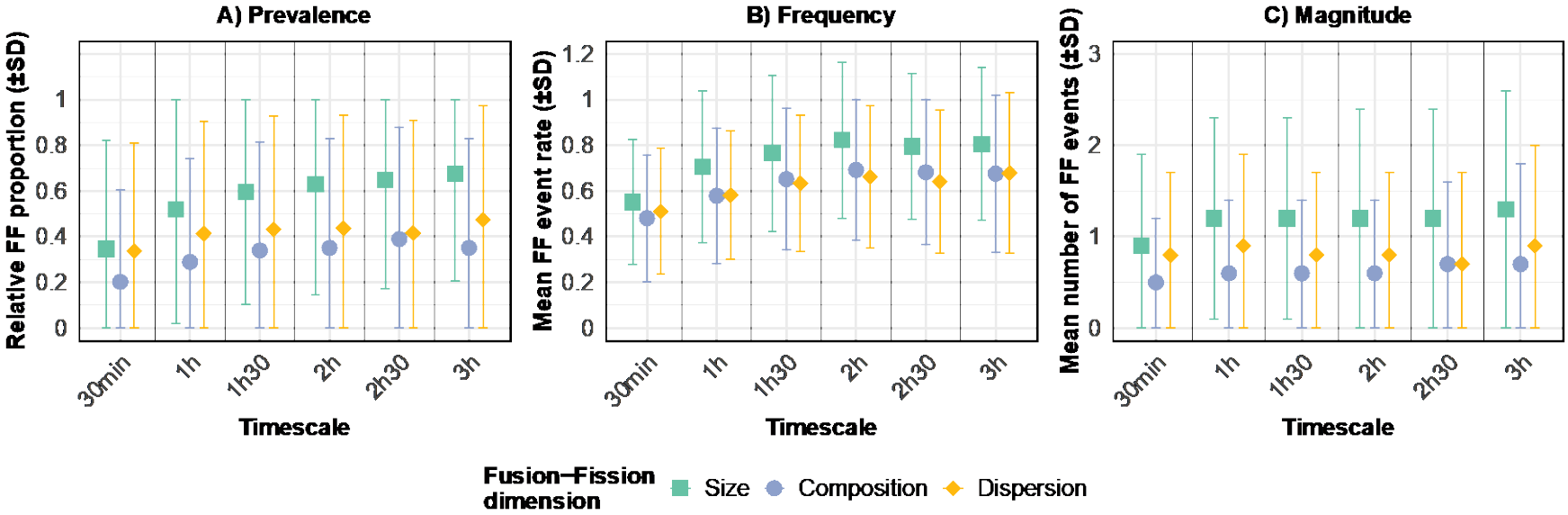

Figure 4.3 : Fission-fusion (FF) patterns across each timescale-dimension combinations. A) Prevalence of FF events expressed as the relative proportions of paired scans classified as FF events, pooled across herds; B) Frequency of FF events expressed as the FF event rate, averaged across herds; C) Magnitude of FF events expressed as the absolute number of FF events, averaged across all herds. Error bars represent standards deviations in all panels. Shapes and colors denote the three dimensions used to detect FF events, i.e., Size (green squares), Composition (blue circles), Dispersion (yellow triangles).

With over 2,000 scans pairs classified as FF events across all dimensions (Suppl. Mat. 4.3), the 1-h timescale captured most events with robust statistical power. Longer timescales suffered from a ≥ 50% drop in sample size for scan pairs and herd focal follows, potentially compromising reliability. Thus, the 1-h timescale was retained in the following analysis as it provided an optimal balance between accurate event detection and sample size. At this time scale, we would conclude that FF events occurred on average approximately once per hour (herd size : 1.2 ± 1.1; herd composition : 0.6 ± 0.8; dispersion : 0.9 ± 1; Figure 4.3C).

Predictors of FF events

Model selection identified a single top-ranked model for herd size, whereas four and two models had similar support for herd composition and dispersion, respectively (ΔAICc < 2, Suppl. Mat. 4.5). Given that effect size and direction of predictors were consistent across competitive models (Suppl. Mat. 4.6), models retaining only significant predictors were chosen to illustrate results. Therefore, the most parsimonious model was selected for herd composition and dispersion (Suppl. Mat. 4.5). Model diagnostics indicated no multicollinearity among predictors (all GVIF ≤ 3; Suppl. Mat. 4.7), and little residual autocorrelation beyond 30 min (Suppl. Mat. 4.8). Variance explained by fixed effects varied depending on whether herd size (18%), composition (56%), or dispersion (27%) was used as indicators of FF events (Suppl. Mat. 4.7). A substantial proportion of variance in fission-fusion probabilities was

attributable to between-herd differences (i.e. random effects) for herd size and composition (40 – 50%), but much less for herd dispersion (Suppl. Mat. 4.7).

Social, behavioural, and environmental factors influenced FF event probabilities overall, though effect direction and magnitude varied by indicator (herd size, composition or dispersion) and event type (fission or fusion; Figure 4.4). Boat presence was identified as a factor influencing FF event probabilities in two top candidates models, increasing both fission and fusion events, although these effects were not significant and associated confidence interval were wide (Suppl. Mat. 4.6). Herd structure was the only predictor affecting fission probabilities, herd movement patterns, habitat type and tidal phase influenced fusion probability. Calf presence consistently reducted fusion probabilities across all three dimensions (size, composition, dispersion), suggesting greater stability in herds with calves. Other predictors showed dimension-specific effects. Fission probability increased in clustered herds but decreased in uniformly structured herds when using herd size as an indicator. Milling behaviour consistently reduced the probability of fusion when using herd composition and dispersion as indicators, suggesting greater stability. Fusion probability increased with directional movement (composition indicator), and with multidirectional movements, corridor habitat, and rising tides (dispersion indicator), but fusion probability decreased at high tide (dispersion indicator).

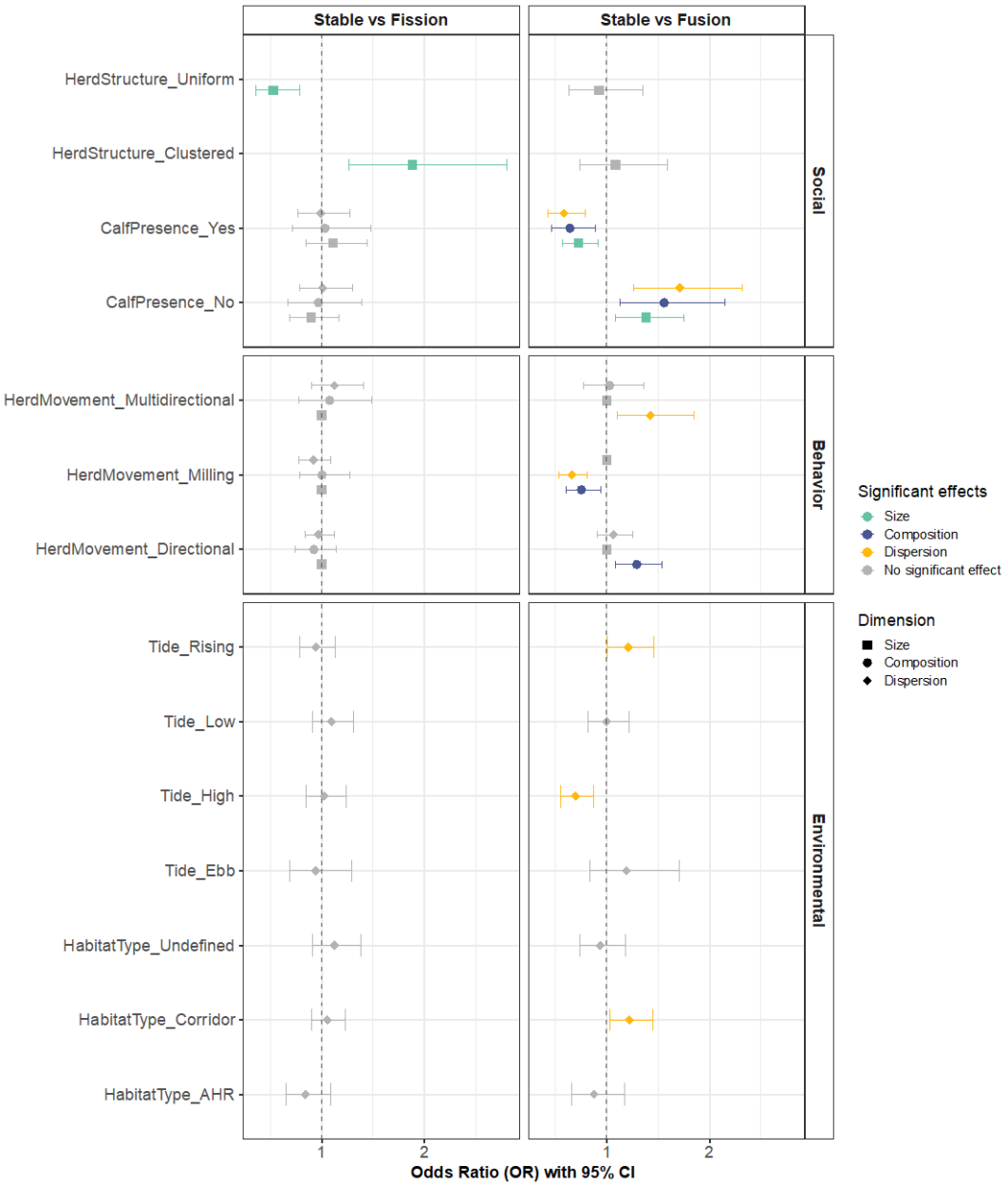

Figure 4.4 : Odds ratios (OR) and 95% confidence intervals (CI) from final multinomial logit regression models (MLR) estimating the probabilities of fission (left panel) and fusion (right panel) events as a function of social, behavioural, and environmental predictors. Separate MLR were fitted for each indicator of fission-fusion event, i.e., herd size (squares), composition (circles) and dispersion (triangles). Significant predictors (not including 1 in their CI) are in color (herd size = green, composition = blue, dispersion = yellow), with non-significant results in grey. The dashed vertical line denotes the null effect (OR = 1).

Discussion

Using the three dimensions of the FF framework proposed by Aureli et al. (2008), this study quantified the fission-fusion dynamics of a highly social cetacean species and identified some drivers of these events. Our findings show that such events are frequent in beluga, often occurring within 30 min or 1 h, and can be detected based on herd size, composition and dispersion. Among these metrics, changes in herd size appear to be a particularly good indicator for monitoring the occurrence of FF events.

Degree of FF

The temporal scale of observations critically limits the timeframe within which social organization changes can be detected in a distinct social unit (e.g., group, herd) (Whitehead 2008). The marked increased in FF prevalence, frequency and magnitude between the 30 min and 1 h timescales, followed by only slight increase of prevalence and frequency and none for magnitude, supported the selection of an hourly timescale for beluga herd. It also indicated that selecting a higher timescale would be unlikely to alter the qualitative characterization of the FF degree in our study. These results suggested that most short-term interactions among individuals and/or groups shaping herd-level general patterns of FF are captured at the hourly scale.

Cross-system comparisons of fission–fusion rates are inherently constrained by variation in the choice and definition of social units (i.e., dyad, group, herd, or clan) (Aureli et al. 2008). The rates reported in this study reflect

patterns of FF at the herd scale. Given the criteria we used for identifying a fission or fusion events (e.g., herd size and composition must change by > 25% and 33%, respectively), herds may have been considered as being more stable than they actually were. Furthermore, because FF events were not quantified at the level of the individual and group, both fission and fusion may have occurred within a given sampling interval at the scale of these two social units. When herd size remained stable, such individual- and group-level events, and any associated change in herd composition, would have remained undetected (Pearson 2009; Castro 2022). Beluga herd changed approximately once per hour, with magnitude of change being more pronounced in size and spatial cohesion than in composition. This rate falls within the same order of magnitude as group-unit change in size and/or composition reported for bottlenose dolphins (mean rate ± sd : 54 ± 23 min, Lewis et al. 2011), spotted hyenas (mean rate ± sd : 56.3 ± 5.9 min, Smith et al. 2008), and chimpanzees (mean rate ± sd : 41.6 ± 63.4 min, Lehmann & Boesch 2004). Conversely, beluga herd FF rates contrasted with species exhibiting either markedly higher group-unit FF rates, such as common dolphin, guinea dolphin and dusky dolphin (group change every 6 to 12 min, Castro et al. 2022, Pearson 2009, Lunardi & Ferreira 2014), or lower rates, such as black and white ruffed lemurs (group-unit change every 90 min, Baden et al. 2016), caribou (dyad-unit change every six hours, Le Goff et al. 2023), Cape buffalo (dyad-unit change once per day, Wielgus et al. 2023), and killer whales (group-unit change every 21 days, Tavares et al. 2017). However, these rates generally capture temporal snapshot within a single social unit, which may complicate

interpretation of FF dynamics in species characterized by multilevel social systems, where FF events span multiple social scales (Grueter et al. 2020; Robitaille et al. 2021; Madsen et al. 2024).

Many species are characterized by pronounced social stratification, in which at least one stable core unit is embedded within higher-level groupings that undergo FF dynamics (Grueter et al. 2020). Referred to as multilevel species, they occupy an intermediate position along the FF continuum, as they generally show greater variation in spatial cohesion and group size than in composition (Aureli et al. 2008). Beluga are long-lived and likely live in multilevel societies (O'Corry-Crowe et al. 2020), with the herd social unit representing a third level (Aubin et al. 2026). This social stratification may promote interactions among individuals and development of long-term relationships (O'Corry-Crowe et al. 2020; Aubin et al. 2026). Herd-level observations revealed that size and spatial dispersion varied more frequently than composition, a pattern consistent with the intermediate FF degree described for multilevel species (Aureli et al. 2008). However, juvenile proportions do not fully capture herd composition, suggesting that change in composition may be more subtle. Genetic evidence from Arctic beluga populations, showed that individuals associate with kin and non-kin of different ages and se4. Female-calf dyads are almost always parent-offspring pairs, males maintain long-lasting associations, and groups or herds comprising multiple mother-calf dyads showed intermediate relatedness. Similar to adults, juveniles occupy either central or peripherical positions within their social

network suggesting that they develop and maintain social relationships (O'Corry-Crowe 2020). Future work should combine monitoring approaches to integrate information on individual relationships, group composition and kinship to refine the characterization of the FF degree of SLE beluga. Aerial drone surveys will be essential to validate the hourly timescale for characterizing the herd-level FF dynamics, and determine whether finer temporal resolutions (i.e., < 30min) could also provide an accurate representation of herd-level FF dynamic. They would also enable more detailed description of group composition within herd and provide a finer resolution to quantify FF events at the group-unit scale. Moreover, long-term photo-identification would identify stable relationships among individuals within the population (e.g., Tavares et al. 2017), and genetic sampling would clarify the role of kinship in FF patterns (Archie et al. 2008).

Predictors of Fission–Fusion Dynamics

FF events are influenced by the social context (Webber et al. 2023). As predicted, herds including calves exhibited greater stability (i.e., less likely to exhibit fission or fusion) across the three dimensions. This pattern is consistent with findings in other cetaceans, in which group comprising calves were more stable (Lunardi et al. 2014; Castro et al. 2022). Beluga offspring depend on the care from alloparents (i.e., care of offspring from nonparents; Aubin et al. 2023). A stable social environment may enhance a number of aspects critical to calf survival, including cognitive development, social bonds, and social learning (e.g., cultural learning of migration routes and vocal traits) (Colbeck

et al. 2013; Gowens 2019; Vergara et al. 2019). Stability may also relate to maternal protection strategies from male harassment and infanticide (Michaud 2005; Smith et al. 2008). Conversely, herd geometry influenced size variation, with fission events more likely to occur in clustered herds. This finding is consistent with Kowalski et al. (*2026*) showing, in the SLE beluga, that clustered herd were more prone to undergo changes in their spatial dispersion than uniform herds. Herds exhibiting mixed surface behaviour (i.e., milling and directional movements, pelagic and enthic diving bouts) displayed exclusively clustered structures and were rarely seen with calves (Lemieux Lefebvre et al. 2018). This spatial configuration may predisposes groups to fragment more readily than dispersed ones when behavioural context shifts, as evidenced by more frequent FF events in cohesive than dispersed group in spider monkeys (Ramos-Fernández & Morales 2014).

Furthermore, FF events were influenced by behavioural context. Herd engaged in milling movement, which encompasses a range of behavioural activities such as benthic foraging, socializing, resting and care of young (Lemieux Lefebvre et al. 2018), exhibited greater stability (i.e., less likely to fusion) in their dispersion and composition dimensions. Stability during socializing may reflect the importance of within-herd interactions for social bond formation, relationship development, and/or cooperative behaviours (Gowans 2019; Couzin et al. 2006). Stability during foraging could also promote long-term bond if individuals cooperatively locate and pursue preys (Gowans 2007). Although competition over resources may drive group fissions

(Sueur et al. 2011), cooperative foraging strategies can increase foraging efficiency (Gowans 2007). Alternatively, this stability may correspond to periods when mothers dive to forage while calves remain at the surface, often engaged in playful interactions, which may enhance the development of motor and social skills (Krasnova et al. 2014). Conversely, herds exhibited fusion during directional (composition indicator) and multidirectional movements (dispersion indicator). Directional movements indicate transit occuring predominantly in corridors areas (Lemieux Lefebvre et al. 2018; Barreau et al. 2025). Increased juvenile proportions during travel may suggest that dependent young individuals maintain proximity with adults, who may be important repositories of social and ecological knowledge (O'Corry-Crowe et al. 2020). Multidirectional movements indicate pelagic foraging occuring predominantly in AHR (Lemieux Lefebvre et al. 2018; Barreau et al. 2025). Fusion events, defined by reduced interindividual distance during these movements, could indicate foraging behaviour with group spatial cohesion, as observed in pelagic cetaceans like spinner dolphin where individuals form tight groups exhibiting coordinated movement to forage on prey herding (Gowans 2007; Benoit-Bird & Au 2009). However, cooperative behaviours beyond allocare contexts remain unclear and warrant further investigation in beluga.

Environmental variables demonstrated limited with FF dynamics. Indeed, we found only that interindividual distances likely decreased (i.e., fusion event) when herd were in corridor habitat-type and during rising tide, a pattern that may reflect the documented herd movement synchronization with

tidal cycles (Ouellet et al. 2021). Regarding anthropogenic factor, boat presence increased the probability of fusion and fission event (composition indicator), though this result was not significant. Behavioural responses of belugas to marine traffic are highly variable, ranging from acoustic behaviour changes, reduced communication range, and altered group characteristics, to no detectable response, depending on exposure history and local conditions (Lesage et al. 1999; Stewart et al. 2025; Ausen et al. 2022; Kowalski et al. *2026*). Our result contrasts with recent work showing increased changes in spatial dispersion with recreational boats density (Kowalski et al. *2026),* a discrepancy likely reflecting differences in spatial scales that have been considered. Kowalski et al. examined a small, narrow section of the Saguenay Fjord, whereas the present analyses encompassed a broader area within the summer habitat, where exposure to marine traffic is more heterogeneous (i.e., diluted in time and space). Grouping all vessel types and without accounting for their relative distance from the herd may not fully capture how individuals experience marine traffic. The wide confidence intervals around boat presence effect may suggest that grouping responses vary among herds to marine traffic, and may depend on vessel type, number and proximity. For instance, beluga acoustic responses are known to differ between large ferry and small motorboat (Lesage et al. 1999).

Beyond the factor explored in this study, quantification of fission–fusion events was based on visual observation of at-surface grouping characteristics, which likely underestimate beluga social experience. Beluga are highly vocal,

with distinctive vocal signatures in their contact calls that contribute to their social cohesion, and thus likely possess a communication system well-adapted to FF dynamics enabling individuals to keep track of each other (Vergara et al. 2019; Panova & Agafonov 2023; Aubin et al. 2026). Given the importance of communication for group cohesion (Sueur et al. 2011), acoustic features may be essential to gain a deeper understanding of beluga FF dynamics. Future work integrating acoustic monitoring during at-surface fission–fusion events would not only enable prediction of FF events based on distinct acoustic signatures, but also elucidate whether vessel noise influence grouping patterns through acoustic communication interference.

Conclusion

This study quantified the FF dynamics of a highly social cetacean species and identified some social, behavioural and environmental drivers of these FF events. Our findings show that FF events are frequent in beluga, often occurring within 30 min or 1 h, and can be detected based on herd size, composition and dispersion. Among these metrics, changes in herd size appear to be a particularly good indicator for monitoring the occurrence of FF events. Results further emphasized marked variability in FF dynamics among herds, underscoring that further investigations are required to understand the interplay among ecological, social, behavioural and anthropogenic factors. Future work combining monitoring approaches (e.g., drone-based observations, photo-ID) to integrate information on individual relationships and group composition would refine the characterization of the FF degree across

other social units of beluga's multilevel social structure (Aubin et al. 2026). Beluga rely heavily on social relationships for cultural learning (e.g., vertical transmission of migratory routes and summering areas, Colbeck et al. 2013) and cooperative behaviours (e.g., allocare, Aubin et al. 2023). Such investigations would therefore not only refine our understanding of the drivers shaping FF dynamics, but also enhance our ability to understand and predict the consequences of sociality on other biological processes such as reproductive success and survival.

Acknowledgments

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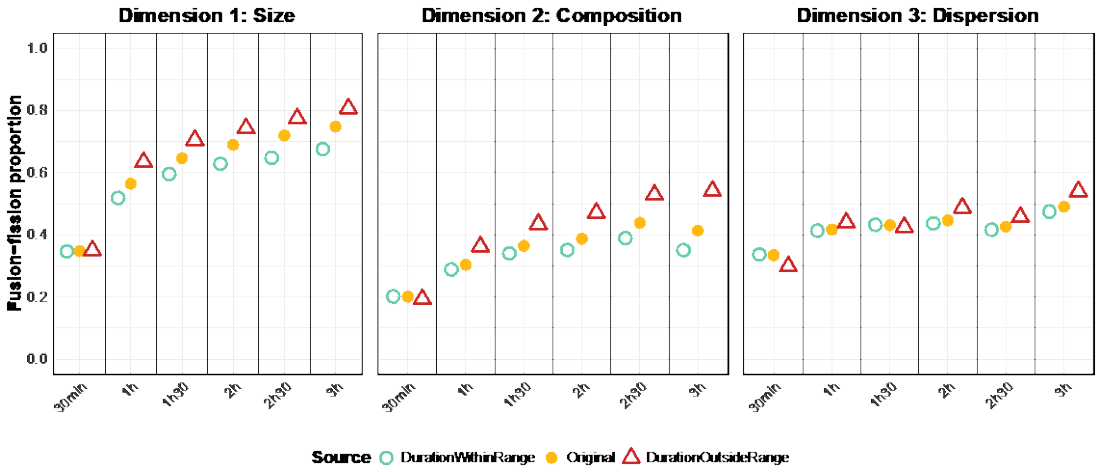
Authors' contributions

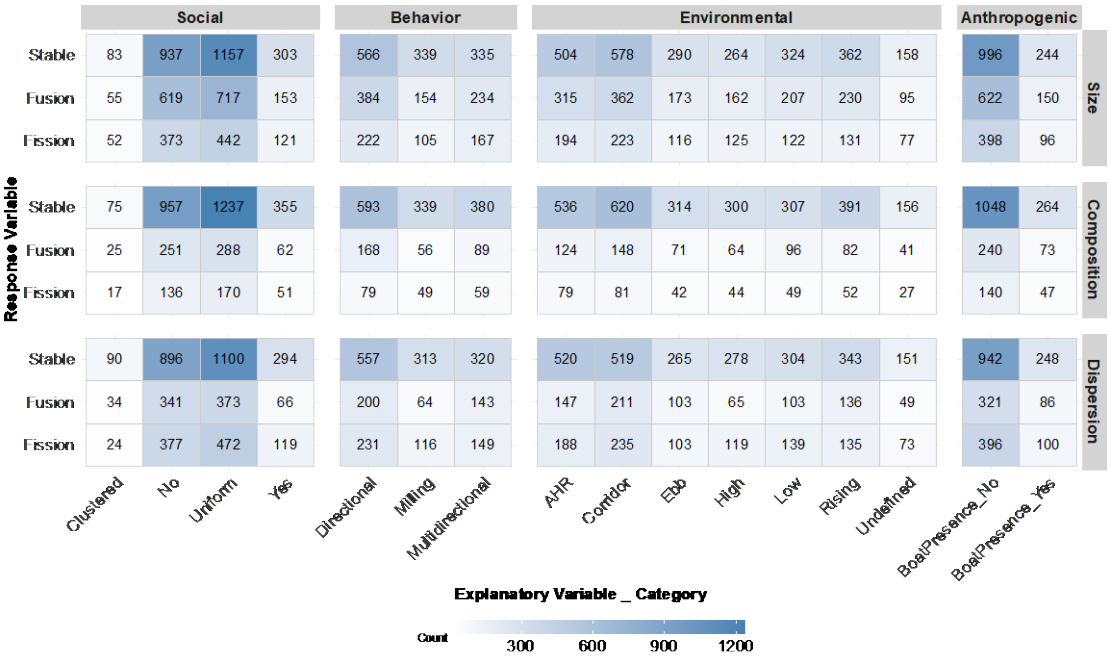
EB, VL, AD, RM conceived the study; VL, CC, and RM obtained funding; VL, and RM conducted field research; EB and J.FS contributed to data preparation; EB conducted the analysis; EB, VL, and AD wrote the manuscript with contributions from TB, RM, J.FS, and CC.

Supplementary Material

Suppl. Mat. 4.1 : Relative proportions of scan pairs classified as fusion-fission events (pooled across all herds) across each timescale-dimension combinations. Shapes and colors distinguish temporal filtering methods : green open circles represent scan pairs within a ±10-minute interval of the expected timescale (DurationWithinRange), yellow filled points indicate unfiltered scan pairs (Original), and red open triangles display scan pairs occurring outside the expected interval of the expected timescale (DurationOutsideRange).



Suppl. Mat. 4.2 : Cross-tabulation showing counts of fusion-fission event categories (fusion, fission, stable) per dimension (herd size, composition and dispersion) across the six explanatory variables grouped into Social, Behavioural, Spatial, Temporal, and Anthropogenic at the hourly timescale. Color intensity indicates the number of observed scans within each category-variable-dimension combination.



Suppl. Mat. 4.3 : Sample size and per-herd statistics for fission-fusion (FF) quantification across timescale-dimension combinations. Metrics are reported separately for all scan pairs (i.e., classified stable, fission, or fusion) and FF scans pairs only (i.e., excluding those classified as stable, herd experiencing at least one FF event). Columns show the number of distinct herds (n_{herd}), total scan pairs (N_{pairs}), relative proportion of FF with standard deviation (PropFF ± SD, FF events rate with standard deviation (Rate ± SD), mean number of FF events with standard deviation (MeanFF ± SD), and range of numbers of scan pairs (i.e., min-max; Range).

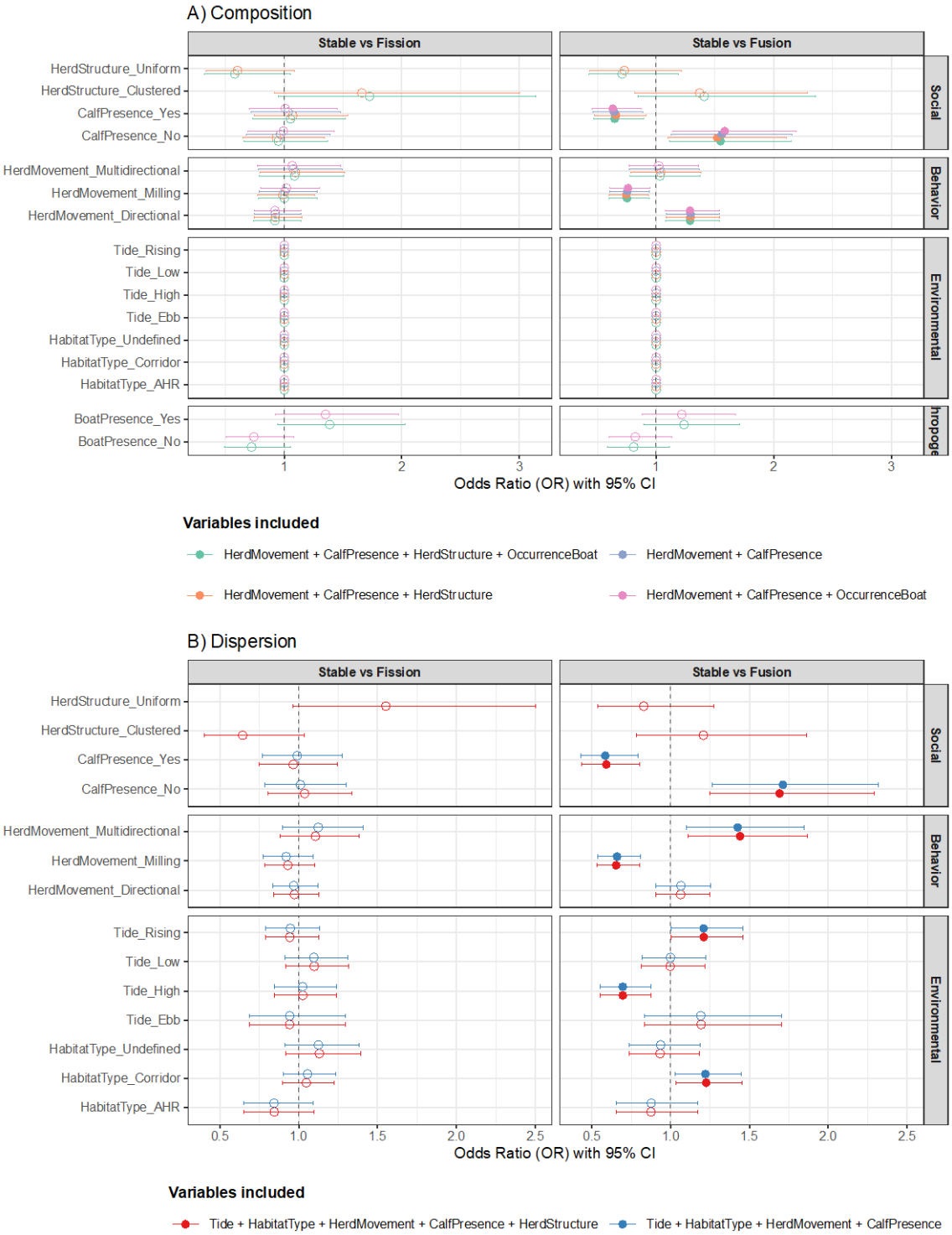
Dimension	**Timescale**	**All scan pairs**						**FF scan pairs**			
		n_{herd}	*N_{pairs}*	*PropFF ± sd*	*RateFF ± sd*	*MeanFF ± sd*	*Range*	*n_{herd}*	*N_{pairs}*	*MeanFF ± sd*	*Range*
Size	30min	2518	6524	0.3 ± 0.5	0.6 ± 0.3	0.9 ± 1	1-15	1496	2265	1.5 ± 0.8	1-8
Size	1h	1784	3991	0.5 ± 0.5	0.7 ± 0.3	1.2 ± 1.1	1-14	1248	2070	1.7 ± 1	1-8
Size	1h30	1092	2202	0.6 ± 0.5	0.8 ± 0.3	1.2 ± 1.1	1-13	799	1312	1.6 ± 1	1-9
Size	2h	603	1142	0.6 ± 0.5	0.8 ± 0.3	1.2 ± 1.2	1-12	444	718	1.6 ± 1.1	1-9
Size	2h30	298	557	0.6 ± 0.5	0.8 ± 0.3	1.2 ± 1.2	1-11	223	361	1.6 ± 1.2	1-9
Size	3h	156	290	0.7 ± 0.5	0.8 ± 0.3	1.3 ± 1.3	1-10	121	196	1.6 ± 1.3	1-8
Composition	30min	1846	4393	0.2 ± 0.4	0.5 ± 0.3	0.5 ± 0.7	1-15	681	889	1.3 ± 0.6	1-5
Composition	1h	1270	2573	0.3 ± 0.5	0.6 ± 0.3	0.6 ± 0.8	1-14	542	744	1.4 ± 0.7	1-5
Composition	1h30	761	1383	0.3 ± 0.5	0.7 ± 0.3	0.6 ± 0.8	1-13	345	471	1.4 ± 0.7	1-6
Composition	2h	398	677	0.4 ± 0.5	0.7 ± 0.3	0.6 ± 0.8	1-12	177	238	1.3 ± 0.7	1-5
Composition	2h30	179	313	0.4 ± 0.5	0.7 ± 0.3	0.7 ± 0.9	1-11	89	122	1.4 ± 0.9	1-5
Composition	3h	80	148	0.4 ± 0.5	0.7 ± 0.3	0.7 ± 1.1	1-10	31	52	1.7 ± 1.2	1-5
Dispersion	30min	1919	4577	0.3 ± 0.5	0.5 ± 0.3	0.8 ± 0.9	1-15	1057	1544	1.5 ± 0.8	1-6
Dispersion	1h	1192	2483	0.4 ± 0.5	0.6 ± 0.3	0.9 ± 1	1-14	682	1027	1.5 ± 0.8	1-6
Dispersion	1h30	654	1265	0.4 ± 0.5	0.6 ± 0.3	0.8 ± 0.9	1-13	375	547	1.5 ± 0.8	1-6
Dispersion	2h	334	611	0.4 ± 0.5	0.7 ± 0.3	0.8 ± 0.9	1-12	190	267	1.4 ± 0.8	1-5
Dispersion	2h30	157	276	0.4 ± 0.5	0.6 ± 0.3	0.7 ± 1	1-11	83	115	1.4 ± 0.9	1-6
Dispersion	3h	61	120	0.5 ± 0.5	0.7 ± 0.4	0.9 ± 1.1	1-10	37	57	1.5 ± 1	1-5

Suppl. Mat. 4.5 : Model selection for mixed-effects multinomial logistic regressions assessing the effect of various predictors on the probability of fission-fusion events, presented for each FF detection metric (i.e., size, composition, and dispersion). Explanatory variables included social (presence of calves, herd structure), behavioural (herd predominant movement pattern, PMP), environmental (tidal phases, habitat type), and anthropogenic (boat presence) predictors. Those included (+) and not included (grey shading) in the model formulation are indicated. The top 10 models are presented, with those within AICc < 2 of the top model (asterisk) indicated in boldface.

Dimension model	(Intercept)	*Social*		*Behaviour*	*Environmental*		*Anthropogenic*	df	AICc	Δ AICc	AICc weight
		Calf presence	Herd Structure	Herd PMP	Tidal phase	Habitat type	Boat presence				
Size	+	+	+	+				10	**5150.2***	0	0.6
	+		+	+				8	5153.2	3.0	0.1
	+	+	+	+			+	12	5154.2	4.0	0.1
	+	+	+	+		+		14	5154.4	4.2	0.1
	+	+		+				8	5156.3	6.1	0
	+		+	+			+	10	5157.1	6.9	0
	+	+	+	+	+			16	5157.6	7.4	0
	+		+	+		+		12	5158.2	8.1	0
	+	+	+	+		+	+	16	5158.4	8.2	0
	+			+				6	5158.7	8.5	0
Composition	+	+	+	+			+	12	**2792.2**	0	0.2
	+	+	+	+				10	**2792.3**	0.1	0.2
	+	+		+				8	**2792.5***	0.3	0.2
	+	+		+			+	10	**2793.0**	0.8	0.1
	+		+	+				8	2794.8	2.5	0.1

Dispersion	+		+	+			+	10	2795.0	2.8	0.1
	+			+				6	2795.6	3.4	0
	+	+	+				+	8	2796.1	3.8	0
	+	+						4	2796.4	4.2	0
	+	+					+	6	2796.4	4.2	0
	+	+	+	+	+	+		20	**4076.7**	0	0.4
	+	+		+	+	+		18	**4078.4***	1.6	0.2
	+	+	+	+	+			16	4079.4	2.7	0.1
	+	+	+	+	+	+	+	22	4080.3	3.5	0.1
	+	+		+	+			14	4080.9	4.2	0.1
	+	+	+	+		+		14	4081.1	4.3	0.1
	+	+		+	+	+	+	20	4082.1	5.4	0
	+	+		+		+		12	4082.6	5.8	0
	+	+	+	+	+		+	18	4082.9	6.2	0
	+	+	+	+				10	4083.4	6.7	0

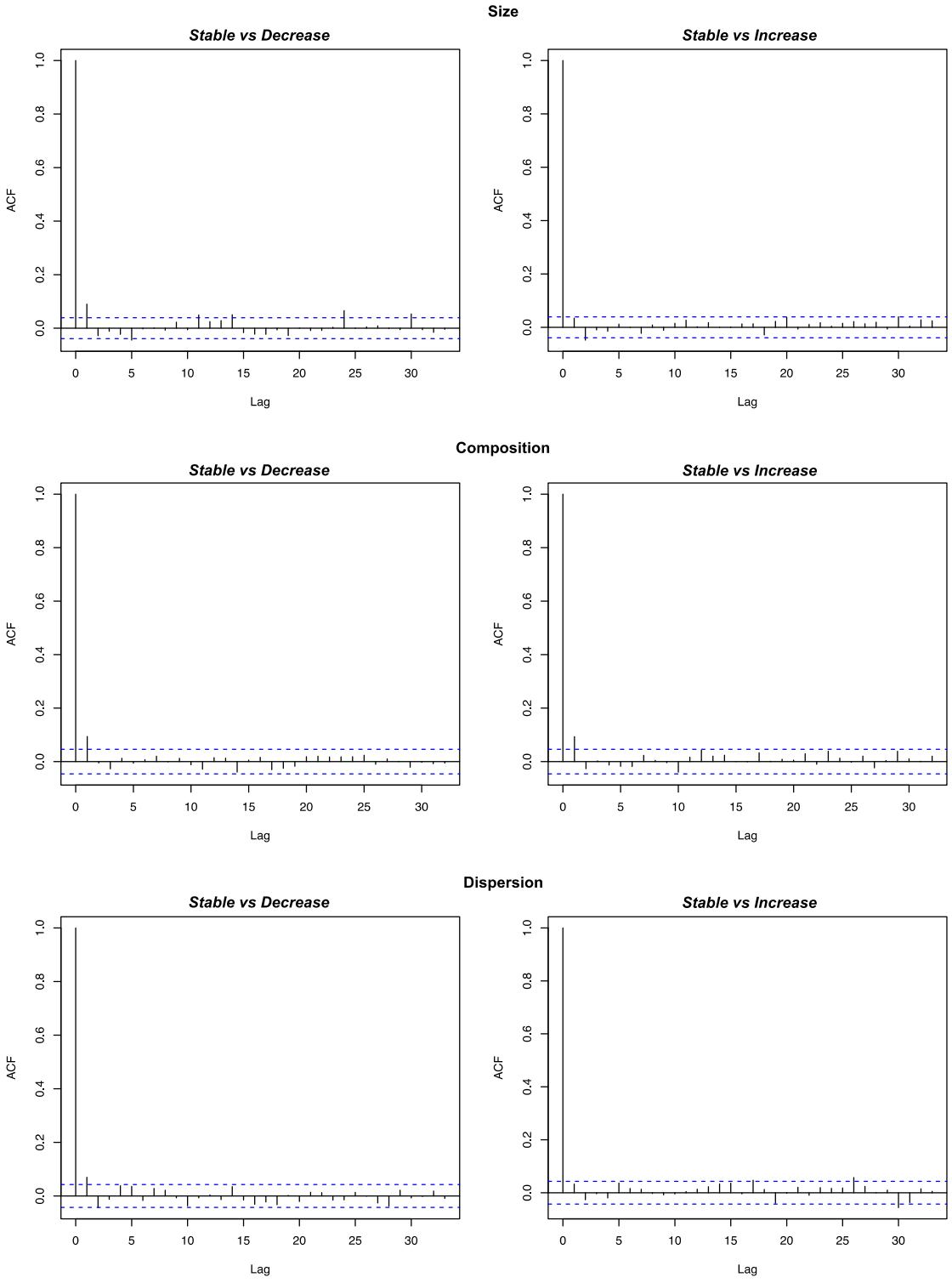
Suppl. Mat. 4.6 : Estimated odds ratios (OR) and 95% confidence intervals for predictors identified as significant in the best multinomial logit regressions models (ΔAICc < 2) estimating the probabilities of fission (left panels) and fusion (right panels) events as a function of selected predictors, using A) herd dispersion and B) composition to detect these events. The dashed vertical line indicates the null effect (OR = 1).



Suppl. Mat. 4.7 : Summary of multinomial model diagnostics of the best model for each indicator of fission-fusion (FF) events. Multicollinearity among explanatory variables was evaluated using the Generalized Variance Inflation Factor (GVIF). GVIF values < 3 indicate no evidence of problematic collinearity among explanatory variables. Model fit was assessed using Nagelkerke pseudo-R^2. Herd level heterogeneity (i.e., random effects) represents the variance attributable to between-herd differences.

FF event indicator	**Multicollinearity**			**Nagelkerke pseudo-R^2**	**Herd level heterogeneity**
	Predictor	***df***	***GVIF***		
Herd size	Herd movement	2	2.21	0.18	Stable *vs* Fission : 50% Stable *vs* Fusion : 42%
	Calf presence	1	1.24		
	Herd structure	1	1.37		
Herd composition	Herd movement	2	1.37	0.56	Stable *vs* Fission : 51% Stable *vs* Fusion : 53%
	Calf presence	1	1.18		
Herd dispersion	Tidal phase	3	1.78	0.27	Stable *vs* Fission : 13% Stable *vs* Fusion : 12%
	Habitat type	2	1.33		
	Herd movement	2	1.37		
	Calf presence	1	2.19		

Suppl. Mat. 4.8 : Temporal autocorrelation (ACF) of residuals across pairwise scans by fission or fusion (Stable vs decrease, Stable vs increase), from the final multinomial logistic regression (shown in Figure 4) considering herd size (top), composition (middle) and dispersion (bottom). Bars extending beyond the 95% confidence interval (dotted blue lines) indicate statistically significant autocorrelation at the indicated lag.



DISCUSSION GÉNÉRALE

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A translated version of the GENERAL DISCUSSION in English is available in Appendix C.

Contribution de la thèse

Comprendre où les animaux se trouvent, ce qu'ils y font, et pourquoi, constituent des questions centrales en écologie spatiale (Nathan et al. 2008 ; Hooten et al. 2017). Chez les espèces grégaires, ces questions nécessitent de considérer les décisions spatiales en lien avec le comportement social de l'espèce, et par conséquent de considérer l'ensemble des composantes de l'interface socio-spatiale (Webber et al. 2020 ; 2023). Néanmoins, les études empiriques intégrant conjointement les environnements spatiaux et sociaux pour comprendre les phénotypes (Fortin et al. 2008 ; McKellar et al. 2015 ; Strandburg-Peshkin et al. 2017 ; Webber et al. 2024), ainsi que celles liant les phénotypes spatial et social (Kratofil et al. 2026), demeurent encore rares, limitant notre capacité à élucider les comportements dans toute leur complexité (Webber et al. 2023).

La thèse fournit des connaissances inédites contribuant à améliorer notre compréhension du comportement spatial et social du béluga de l'ESL durant l'été. Bien que plusieurs décennies de recherches aient permis d'identifier et de cartographier les habitats importants dans son aire estivale (Lemieux Lefebvre et al. 2012 ; Mosnier et al. 2016 ; Ouellet et al. 2021 ; Harvey et al. 2025), les activités vitales associées à ces habitats étaient soit présumées sur la base d'indices indirects soit inconnues. En reliant explicitement les différents comportements exprimés par les troupeaux à leur localisation, le **Chapitre 1** identifie les fonctions des aires de haute résidence et des corridors. De plus, la détermination des états comportementaux à partir

des données de trajectoires individuelles raffine notre compréhension des patrons d'utilisation de l'habitat. La distribution spatiale de ces comportements et leur prévalence permet d'établir les fonctions des habitats préalablement identifiés et la disponibilité des habitats nécessaires pour certaines fonctions vitales (**Chapitre 1)**, tout en révélant de nouvelles aires de recherche restreinte vraisemblablement également importante pour cette population (**Chapitre 2**). Ensemble, ces résultats contribuent à identifier la valeur fonctionnelle des habitats utilisés par les bélugas, fournissant une meilleure compréhension de pourquoi les bélugas sélectionnent et utilisent ces habitats dans l'ESL.

La thèse contribue également à fournir une première caractérisation explicite de la dynamique de fission-fusion chez l'espèce, à l'échelle du troupeau (**Chapitre 3**), correspondant au troisième niveau social chez cette espèce récemment décrite comme organisée en multiples niveaux (Aubin et al. 2026). L'étude intègre les trois dimensions du cadre conceptuel d'Aureli et al. (2008), ce qui est généralement rare, particulièrement chez les cétacés (Lunardi et al. 2014).

Enfin, la thèse clarifie empiriquement certaines relations entre les composantes de l'interface socio-spatiale chez cette espèce grégaire. Pris ensemble, les trois chapitres montrent que les caractéristiques de l'environnement dans lequel évolue le béluga ainsi que le contexte social influencent les phénotypes spatiaux (**Chapitre 1 & 2**) et sociaux (**Chapitre 3**),

mais que les relations entre ces composantes sont modulées en fonction de l'échelle considérée et des comportements exprimés.

A l'échelle de la population, les conditions environnementales, seules ou en considérant l'organisation sociale des troupeaux, peuvent expliquer dans une certaine mesure les patrons d'utilisation de l'habitat à l'échelle de la population, en particulier dans les habitats où l'alimentation pélagique prédomine (**Chapitre 1**). A l'échelle individuelle, les transitions entre les modes de déplacement sont liés aux contraintes environnementales ou la disponibilité de proies, tandis que l'organisation sociale du troupeau influence ces transitions seulement lorsqu'elles sont en interaction avec le contexte spatial (**Chapitre 2**). Ces résultats pourraient suggérer un potentiel effet descendant (Picardi et al. 2024), selon lequel la composition ou la taille du troupeau, en tant qu'environnement social à grande échelle, influencerait les schémas de déplacement individuel à petite échelle lorsque celui-ci est confronté à certaines conditions environnementales. Le déplacement individuel détermine les secteurs fréquentés, la durée d'utilisation et les types de comportements exprimés, liant par conséquent la sélection d'habitat et l'utilisation de l'espace à l'échelle de la population (Nathan et al. 2008 ; Morales et al. 2010 ; Webber et al. 2023). Les résultats du **Chapitre 2** pourraient contribuer à expliquer l'organisation spatiale estivale à l'échelle de la population, telle que la ségrégation sexuelle (Michaud 1993 ; Ouellet et al. 2021) ou la fidélité à certains secteurs (Bonnell et al. 2021).

Une grande diversité d'interactions s'opère également entre les phénotypes spatiaux et sociaux (Webber et al. 2024). Les probabilités de changements d'organisation sociale au sein des troupeaux résultent non seulement des variations dans les environnementaux spatial et social, mais également des patrons de déplacement collectifs définis en tant que phénotype spatial (**Chapitre 3**).

Limites de la thèse

Étudier les cétacés en milieu naturel impose des contraintes logistiques importantes : ce sont des espèces très mobiles, occupant des habitats dynamiques, et ne faisant surface que brièvement. La collecte de données exhaustive sur l'environnement social est particulièrement difficile, comme l'illustrent les disparités de résolution temporelle et les données manquantes imputable à la visibilité en surface lors des suivis simultanés de troupeau et de déplacement individuel (**Chapitre 2**). Ainsi, plusieurs limites sont à garder à l'esprit pour l'interprétation des résultats, d'autant plus que les conclusions de cette thèse ont des implications directes pour la conservation de cette population classée en voie de disparition.

Couverture temporelle

Dans cette thèse, la période d'étude est limitée à la saison estivale. Les fonctions des habitats identifiées représentent des moyennes sur cette période (**Chapitres 1 & 2**), et ne peuvent donc pas être extrapolées à l'ensemble du cycle annuel. L'utilisation et l'importance de ces habitats (e.g.,

disponibilité des ressources) sont pourtant susceptibles de varier saisonnièrement, voire à long terme (Rioux et al. 2023; Cabrol et al. 2025). La taille de l'échantillon disponible dans le **Chapitre 1** ne permettait pas d'examiner une éventuelle variabilité interannuelle de ces fonctions à l'été, même en les regroupant à une échelle décennale. Les résultats de cette thèse constituent une référence spatiale statique. L'ajout de nouvelles données issues des suivis des troupeaux à long terme à la classification comportementale utilisée pour classer les fonctions sera nécessaire pour détecter d'éventuels changements dans les fonctions des habitats au fil des années. L'analyse récente de trois décennies de survols aériens (1990 à 2023) ne suggère pas de déplacements des zones de forte densité utilisées durant l'été, mais révèle une utilisation plus importante de ces zones dans la portion Est au fil des années (Harvey et al. 2025).

Classification comportementale

Les conclusions du **chapitre 2** reposent en grande partie sur la classification correcte des états comportementaux. Cependant, il est important de garder à l'esprit que les états dérivés des modèles de Markov cachés constituent une estimation des comportements réels des animaux (Hooten et al. 2017; McClintock & Michelot 2021). Cette limite est particulièrement marquée dans les approches non supervisées, comme celle employée dans le **chapitre 2**. Afin de préserver une interprétation biologique claire, une analyse approfondie a été réalisée pour déterminer le nombre d'état et l'échelle temporelle appropriée. Les trois états comportements retenus

présentent des distributions distinctes de longueurs de pas et d'angles de braquage (Pohle et al. 2017; Michelot 2020), et sont consistants avec la description des mouvements prédominants en surface des troupeaux dans cette population (Lemieux Lefebvre et al. 2018). Cela renforce la fiabilité de la classification pour capturer une large part de la variabilité comportementale chez les bélugas. Toutefois, les données horizontales limitent la confiance dans la distinction des comportements attribués à l'état de recherche en aire restreinte. L'intégration de données tridimensionnelles (e.g., accélération, profils de plongées) dans les modèles de Markov cachés hiérarchiques permettrait d'affiner la classification comportementale en modélisant simultanément les comportements à fine et large échelle (Adam et al. 2019).

Variables explicatives

Certains facteurs n'ont pas pu être pris en compte en raison de des données disponibles. Les informations sur la densité et la biomasse des espèces de proies, autres que le lançon, auraient amélioré la distinction des habitats associés aux différentes stratégies de recherches alimentaire (**Chapitres 1 & 2**), mais ces données demeurent limitées dans l'ESL (Lesage et al. 2024). Elles auraient également permis de déterminer si les évènements de fission observés dans les aires de hautes résidence sont attribuables, dans une certaine mesure, à la compétition intraspécifique pour les ressources (**Chapitre 3**). Par ailleurs, la compétition interspécifique pour les ressources alimentaires est susceptible d'influencer la distribution des bélugas. Cependant, la densité de compétiteurs potentiels sur les proies consommées

par les bélugas tels que le phoque du Groenland (*Pagophilus groenlandicus*), le phoque gris (*Halichoerus grypus*), le sébaste (*Sebastes spp.*) et le bar rayé (*Morone saxatilis*) (Lesage 2021, Cabrol et al. 2025) n'a pas été considérée dans les analyses. Concernant les variables sociales, des descriptions plus fines de la composition détaillée du troupeau (i.e., proportion d'individus pour chaque classe d'âge), le nombre et la composition des groupes, et les types d'associations interindividuelles permettraient d'affiner notre compréhension du rôle de l'environnement social sur les comportements spatiaux (**Chapitres 1 & 2**) et la dynamique de fission-fusion (**Chapitre 3**). L'intégration de la structure sociale est notamment développée dans la section perspective. Enfin, les interactions entre les variables explicatives dans le **Chapitre 3** n'ont pas pu être testées en raison du nombre d'observations insuffisant pour chaque combinaison de catégories entre les variables réponses et explicatives. La dynamique de fission-fusion pourrait également résulter de l'effet combiné entre chaque facteurs, comme le suggère certains résultats du **Chapitre 2**. Ces contraintes définissent des pistes pour les futures recherches, mais ne remettent pas en cause la valeur des résultats obtenus. En effet, les relations environnement-phénotype identifiées dans chaque chapitre sont biologiquement cohérentes avec ce que l'on connaît de l'espèce et concordent avec les prédictions théoriques (Webber et al. 2023).

Impact du bateau de recherche

Cette thèse repose sur des données récoltées depuis un bateau de recherche (**Chapitres 1 – 3**). Afin de limiter le dérangement des bélugas, le protocole de

suivis focaux prévoyait une période de latence d'environ 15 minutes entre la première approche à distance du troupeau (~ 300-500 mètres), permettant d'effectuer un relevé sommaire avant que le bateau de recherche ne se rapproche du troupeau pour effectuer les relevés détaillés. Les relevés sommaires n'ont été utilisés dans aucune des analyses présentées dans les trois chapitres. De plus, les scans réalisés durant des protocoles de biopsies ont été exclus des analyses car une analyse exploratoire révélait des proportions plus élevées d'évènements de fission et fusion pouvant refléter une réaction à ce protocole invasif (**Chapitre 3**). Malgré ces précautions, la présence d'un bateau de recherche et le bruit qu'il génère peuvent affecter le comportement acoustique et les patrons de déplacement (Guerra et al. 2014), pouvant influencer les résultats (Erbe et al. 2019). De plus, certains individus peuvent être plus sensibles que d'autres (Ellison et al. 2012), comme les groupes comprenant des veaux qui sont particulièrement sensibles à la présence et au bruit du bateau (Guerra et al. 2014 ; Williamson et al. 2016). L'impact potentiel du bateau de recherche n'est pas testé explicitement dans cette thèse, car cela nécessiterait des situations de « contrôle » sans aucun bateau présent, y compris celui de recherche, ce qui est difficile à obtenir dans l'ESL qui est fortement achalandé durant l'été. Les données permettent d'identifier des situations où la présence de bateaux supplémentaires, en plus du bateau de recherche (opéré avec précaution), influencerait le comportement des bélugas (**Chapitre 3**). Cela ne démontre pas l'absence d'impact du bateau de recherche, mais suggérerait que les effets mesurés se produisent au-delà de son propre effet.

Implication pour la conservation

Fonctions des habitats importants

L'ESL représentent une zone importante pour plusieurs espèces de cétacés autre que le béluga (Mosnier et al. 2022). Pendant la saison estivale, le cœur de la distribution des bélugas correspond à une aire d'approximativement 2800km2 (Mosnier et al. 2010, DFO 2012), au sein de laquelle environ un tiers (966.33 km2) a pu être attribuée avec des fonctions écologiques (**Chapitre 1**). En fournissant des informations inédites sur les fonctions vitales soutenues par les habitats importants pour la population de bélugas de l'ESL (**Chapitres 1 & 2**), cette thèse est essentielle pour orienter la planification et la hiérarchisation des mesures d'atténuation selon la vulnérabilité de certaines activités vitales aux perturbations anthropiques (Redfern et al. 2006 ; Ross et al. 2011 ; Brakes & Dall 2016). Ces résultats s'intègrent directement dans la stratégie d'acquisition de connaissances sur les habitats, leurs fonctions et leur utilisation (e.g., mesure 9, DFO 2020 ; mesures 2 & 18, DFO 2025), et permet d'identifier les secteurs clés à protéger (e.g., mesures 21 & 22, DFO 2020 ; mesures 30, 31 & 34, DFO 2025).

La délimitation spatiale de ces habitats et leur fonction permet d'évaluer le chevauchement avec les activités anthropiques, notamment le trafic maritime lié au tourisme, à la plaisance, et à la marine marchande, particulièrement intense dans l'habitat estival (DFO 2020 ; Lesage et al. 2024). Les segments de la population qui utilisent des habitats qui chevauchent des

zones à fort trafic maritime peuvent être davantage exposés aux perturbations que ceux empruntant des voies plus calmes (Chion et al. 2021). Il est essentiel que les mesures de mitigation garantissent que les pressions anthropiques restent dans les limites compatibles avec l'intégrité fonctionnelle des habitats, en tenant compte des besoins spécifiques des différents segments de la population. Les mesures visant à réduire le bruit et les dérangements dans les habitats importants, telles que les réductions de vitesse, les déviation de routes, ou les zones d'exclusion, pourraient contribuer à améliorer le potentiel de rétablissement de la population en réduisant le masquage de la communication (e.g., appels de contacts) ou en limitant les perturbations de comportement important chez cette espèce très sociale (Lesage et al. 2024 ; DFO 2020, 2025). Par ailleurs, le projet d'agrandissement du parc marin du Saguenay-Saint-Laurent permettrait d'étendre l'application de ces mesures de réduction du dérangement physique et acoustique à un plus grand nombre d'habitats importants pour le béluga (Ménard et al. 2022 ; DFO 2020, 2025), notamment pour l'alimentation et la socialisation (**Chapitres 1 & 2**).

Suivre l'évolution des habitats

Depuis 2010, un changement significatif a été observé dans les mortalités de veaux et la survie des femelles adultes, entrainant un ralentissement de la croissance de la population et un déclin possible depuis 2018 (Tinker et al. 2024). Ces changements dans la dynamique de population coïncident avec une hausse des températures de l'eau, une réduction de la glace de mer, et des changements à long terme de la structure trophique de

l'écosystème du Saint-Laurent (Plourde et al. 2014; Rioux et al. 2023; Galbraith et al. 2025).

Les résultats du **Chapitre** 1 mettent en évidence une disponibilité limitée d'habitats dans l'aire estivale lorsqu'on tient compte de la fidélité au site (Bonnell et al. 2022) et de la ségrégation par âge et par sexe (Michaud 1993, Ouellet et al. 2021). Ces particularités peuvent accroître la vulnérabilité des différents segments de la population aux facteurs de stress locaux. Lorsque la qualité ou l'accès à ces habitats est compromise, les animaux doivent évaluer les coûts et les bénéfices d'un déplacement vers des habitats moins perturbés (Brakes & Dall 2016 ; Forney et al. 2017 ; Hastie et al. 2021 ; Merkle et al. 2022). Ce déplacement peut survenir lorsque la tolérance individuelle atteint un seuil où les coûts de rester dans l'habitat perturbé dépassent les avantages qu'il procure (Bejder et al. 2006 ; Forney et al. 2017). Cependant, les habitats de remplacement susceptibles de soutenir les mêmes fonctions écologiques peuvent être rares. De plus, ce déplacement peut réduire le temps et l'énergie que les individus consacrent aux fonctions vitales (Constantine et al. 2004 ; Pirotta et al. 2015, 2013 ; Wisniewska et al. 2018), les exposer à des menaces supplémentaires (Forney et al. 2017), et affecter leurs taux vitaux (Bejder et al. 2006 ; Tenan et al. 2020), avec des conséquences potentiellement négatives à l'échelle de la population. Dans ce contexte, les fonctions des habitats identifiées dans les **Chapitres 1 & 2** fournissent un cadre de référence pour détecter d'éventuels changements dans l'utilisation des habitats dans le futur.

Conservation des comportements sociaux

Le manque de résilience des cétacés face aux menaces anthropiques est généralement attribué à leurs traits d'histoire de vie (i.e., longévité, maturité sexuelle tardive, long intervalle entre les naissances ; Chivers 2017). Cependant, la survie et le succès reproducteur de nombreuses espèces reposent également sur des traits sociaux, tels que la cohésion sociale, la coopération alloparentale, le transfert intergénérationnel de connaissances, et le rôle d'individus expérimentés (Wade et al. 2012). Lorsque ces comportements sont acquis et partagés au sein d'une communauté par l'apprentissage social, ils définissent la culture animale (Whitehead et al. 2004 ; Brakes et al. 2021). La biologie de la conservation s'intéresse désormais à la valeur intrinsèque de ces comportements sociaux et culturels pour les espèces dont les phénotypes spatiaux sont socialement transmis (Berger-Tal et al. 2011, 2016 ; Brakes & Dall 201 ; Oestreich et al. 2025).

Le béluga est une espèce longévive et grégaire dont la structure sociale repose sur de longue période de soins parentaux, la coopération alloparentale (Aubin et al ; 2023) et la présence de femelles post-reproductives au sein des groupes (Ellis et al. 2018 ; O'Corry-Crowe et al. 2020). Ces caractéristiques, combinées à leur dynamique de fission-fusion dans laquelle l'organisation sociale des troupeaux varie en fonction du contexte (**Chapitre 3**), créent des conditions sociales particulièrement favorables à l'apprentissage social (O'Corry-Crowe et al. 2020). La longue période de dépendance des veaux est considérée comme une phase critique de l'acquisition de comportement vitaux

(Krasnova et al. 2009, 2014), et des preuves de transmission culturelle verticale ont été établies pour les routes migratoires et les répertoires vocaux (synthèse dans Aubin et al. 2026). Il est plausible que d'autres formes de cultures existent (Aubin et al. 2026).

Certains résultats de la thèse montrent que les comportements spatiaux sont liés à l'organisation sociale des troupeaux. Les troupeaux comprenant des jeunes (juvéniles et/ou veaux) utilisent des habitats d'alimentation moins profond que ceux utilisés par les troupeaux de mâles (**Chapitre 1)**, et la relation entre les comportements présumés de quête alimentaire et la disponibilité probable du lançon est modulée par la proportion de juvéniles dans le troupeau (**Chapitre 2**). Ces différences d'utilisation de l'habitat concordent avec la ségrégation spatiale par âge et par sexe documentée dans l'ESL (Michaud 1993 ; Mosnier 2016 ; Ouellet et al. 2021), et peuvent en partie s'expliquer par le dimorphisme sexuel et les besoins énergétiques contrastés entre les mâles, les femelles et les juvéniles (Loseto et al. 2006 ; O'Corry Crowe 2018 ; Mayette et al. 2022) ainsi que les capacités de locomotion limitées des veaux (Papageorgiou & Farine 2015 ; Noren et al. 2023). Cependant, si ces différences ne reflétaient pas uniquement des facteurs physiologiques, on pourrait s'attendre à ce qu'elles fluctuent avec la disponibilité des proies. Les différences entre leurs régimes alimentaires persistent sur plusieurs décennies (*analyse des contenus stomacaux (1938-1939, n=107) :* Vladykov 1946 ; *(1989-2019, n=89) :* Lesage et al. 2020 ; *analyse isotopique (1997-2003 & 2015-2020, n= 52 et 44) :* Cabrol et al. 2025).

La comparaison entre ces périodes doit être interprétée avec prudence en raison des limites propres aux méthodes et nature des échantillons utilisés (e.g., meilleure persistance des otolithes de grandes espèces dans les carcasses). Les différences trophiques entre les sexes persistent malgré les changements survenus dans la structure trophique de l'écosystème du Saint-Laurent (Rioux et al. 2023), suggérant que des facteurs comportementaux, comme par exemple l'apprentissage social, pourraient y contribuer. Cette hypothèse reste à examiner.

Si l'utilisation différentielle de l'habitat selon la composition des troupeaux reflète effectivement une composante d'apprentissage social, cela a des implications directes pour la conservation. La perte d'individus jouant un rôle de transmission de l'information pourrait compromettre la capacité de rétablissement de la population (Ward et al. 2011 ; Wade et al. 2012 ; Wade 2018 Brakes et al. 2021). Les espèces sociales avec des populations de petites taille sont particulièrement vulnérables aux effets Allee (i.e., fitness individuelle ou taux de croissance de la population qui décroît à mesure que la taille de la population diminue ; Stephen et al. 1999), puisque les activités critiques sont influencées par l'organisation sociale du groupe (Angulo et al. 2018). Par exemple, leur succès de reproduction peut réduire si le nombre d'adultes est insuffisant pour la coopération au soin des jeunes (Angulo et al. 2018). La population de l'ESL est de petite taille, a une faible variation génétique, et très peu d'immigration (Postma 2017), ce qui ne permet pas d'exclure de potentiels effets Allee à l'échelle des individus (Montana et al.

2024). Ces incertitudes soulignent la nécessité de poursuivre les suivis à long terme et d'approfondir la compréhension de la structure sociale de la population (développé dans les perspectives) afin d'évaluer dans quelle mesure les phénotypes spatiaux sont façonnés par des mécanismes d'apprentissage social.

Perspectives de recherche

La sélection d'habitat

Dans les **chapitres 1 & 2**, les comportements et les habitats utilisés ont été caractérisés, mais la sélection a déjà opéré dans ces analyses : aucune comparaison entre les habitats utilisés *versus* les habitats disponibles n'a été réalisée. Une question centrale reste donc ouverte : pourquoi les bélugas sélectionnent ces zones particulières ? La sélection de l'habitat constitue un phénotype spatial influencé par l'environnement social et spatial (Webber et al. 2023). Les animaux se déplacent dans un environnement généralement hétérogène dans l'espace et le temps. Les théories d'optimisation prédisent que les animaux sélectionnent préférentiellement certains habitats en fonction de la balance coût-bénéfices associée à leur utilisation (i.e., théorie de recherche optimale : Stephens & Krebs 1986 ; théorie du paysage énergétique : Shepard et al. 2013). Puisque les coûts énergétiques de la locomotion augmentent avec la vitesse de déplacement (Sheppard et al. 2013), les bélugas pourraient par exemple privilégier le transit rapide dans les zones où les courants favorables minimisent la dépense énergétique. Les

données de déplacement individuel du **Chapitre 2** offrent l'opportunité de tester cette hypothèse. L'intégration de fonctions de sélection des ressources dans les modèles de Markov cachés permettrait de quantifier dans quelle mesure chaque état comportemental est associé à une sélection active des conditions environnementales, liant ainsi les mécanismes de sélection d'habitat aux comportements identifiés dans cette thèse (Florko et al. 2025).

La structure sociale

Dans le **Chapitre 3,** les résultats des modèles ont mis en évidence une variabilité marquée de la dynamique de FF entre les troupeaux, en particulier pour les dimensions de taille et de composition. L'exploration des intercepts (ID des troupeaux) n'a pas suffi à expliquer la variabilité inter-troupeaux, même en distinguant la composition des troupeaux par classe d'âge (i.e., adultes, adultes-juvéniles, adultes-juvéniles-veaux), suggérant que d'autres aspects de la structure sociale sont à considérer. Le troupeau est en effet un assemblage de groupe au sein desquels les individus peuvent former des associations durables sur plusieurs semaines (Panova et al. 2025) ou années (e.g., dyades mère-veau : McGuire et al. 2020 ; adultes : Aubin et al. 2026). La force des relations interindividuelles pourrait influencer la dynamique de fusion-fission (i.e., hypothèse de la cohésion sociale) : des individus ayant des liens forts seraient moins enclins à se séparer, réduisant ainsi la probabilité de fission au sein du troupeau (Aureli et al. 2008 ; Sueur et al. 2011 ; Le Goff et al. 2024). Les données photographiques collectées durant les suivis focaux des troupeaux permettraient de quantifier les relations

dyadiques entre les individus de la population de l'ESL sur plusieurs décennies. L'indice d'association dyadique (i.e., HWI) mesure la force du lien entre chaque paires d'individus (Whitehead 2008). Agrégé à l'échelle du troupeau, cet indice permettrait de dériver trois variables : le HWI moyen caractérisant la cohésion sociale globale du troupeau, la différentiation sociale indiquant l'hétérogénéité des liens (i.e., coefficient de variation des HWI), et la proportion de dyades à liens fort (i.e., densité des liens préférentiels) (Whitehead 2008). Intégrées comme variables explicatives dans les modèles multinomiaux du **Chapitre 3**, ces métriques permettraient de tester si la qualité des associations au sein du troupeau prédit dans une certaine mesure les évènements de fission et fusion, et si leur inclusion réduit la variance résiduelle de l'effet aléatoire ID troupeau.

Comportement acoustique

Cette thèse ne tient pas compte du comportement acoustique, dont l'intégration permettrait d'approfondir les résultats des **Chapitres 2** & **3**. Les cétacés dépendent largement des signaux acoustiques pour naviguer dans leur environnement, localiser des proies, et communiquer avec leurs congénères (Tyack & Clark 2000). Le béluga possède l'un des répertoires vocaux les plus diversifié parmi les odontocètes (i.e., cétacés à dents ; O'Corry Crowe 2018). Les clics d'écholocation sont notamment associés à la détection active de proies (Castellote et al. 2021), tandis que les appels de contact permettent de maintenir la cohésion sociale des groupes (Vergara et al. 2019 ; Panova & Agafono 2023 ; Aubin et al 2026).

Dans le cadre du **Chapitre 2**, l'intégration de données acoustiques aux suivis télémétriques permettrait de renforcer et raffiner la classification états comportementaux inférés par le modèle. En particulier, la détection de clics d'écholocation pourrait confirmer que les épisodes de recherche en aire restreinte correspondent effectivement à des comportements de quête alimentaire, et non à d'autres formes de déplacement lent (e.g., repos, socialisation). Par ailleurs, la portée des appels de contacts est estimée à 6.7km dans un environnement calme et à 2.9km dans un environnement bruyant (Vergara et al. 2021), ce qui implique que des interactions sociales sont possibles à des distances supérieures que celles observées en surface (Aubin et al. 2026). Considérant que la communication est importante pour la cohésion du groupe durant les décisions de fission et de fusion (Sueur et al. 2011), les caractéristiques acoustiques pourraient s'avérer essentielles pour mieux comprendre la dynamique de fission-fusion (**Chapitre 3**). Ce type d'étude est envisageable à partir de données existantes : dans le cadre de sa thèse, Aubin (2025) a collecté des enregistrements acoustiques en simultané avec les suivis focaux de troupeaux. Il serait ainsi possible d'explorer si le nombre moyen d'appels de contacts émis entre deux observations prédit les évènements de fission-fusion, permettant d'évaluer dans quelle mesure la communication vocal influencent la dynamique sociale des troupeaux.

Conclusions

Les suivis à long terme menés sur la population de bélugas de l'estuaire du Saint-Laurent permettent d'aborder des questions fondamentales sur le

comportement et l'écologie de l'espèce. Cette thèse contribue à la compréhension de l'utilisation de l'habitat, les déplacements et la dynamique de fission-fusion des bélugas de l'estuaire du Saint-Laurent. Ces résultats constituent une base de connaissances solides et pourront orienter les mesures de conservation nécessaires au rétablissement de cette population classée en voie de disparition. Les futures recherches devraient viser à améliorer la compréhension mécanistique des facteurs qui influencent leur phénotype spatial et social.

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APPENDIX A

This thesis is part of a multidisciplinary research program initiated in 2018 by Dr. Clément Chion, that aimed at modelling maritime traffic and its impact on the spatial behaviour of marine mammals in the St. Lawrence Estuary and the Saguenay Fjord. The thesis contributes specifically to the first axis of this program and provides novel information for the parameterization of beluga movement models used to quantify the impacts of underwater noise.

My thesis, begun in September 2019, and focuses on the spatial and social behaviour of a cetacean, the St. Lawrence beluga whale. It uses exceptional long-term datasets, integrating more than thirty years of herd follows and ten years of telemetry tracking including more than fifty individuals. These data were collected by the GREMM and DFO teams. I participated in field data collection during the summer of 2021. The thesis comprises five sections : the general introduction describes the main ecological concepts addressed in the research axes and outlines the research objectives, followed by three chapters, each corresponding to an original scientific article produced during the thesis. The chapters are written in English; one has been published and the other two will be submitted shortly to different international peer-reviewed journals. Results have also been presented at national and international conferences, seminars and committee meetings. The thesis concludes with a general discussion summarizing the main results obtained across the three chapters and the common thread linking them, addressing

contribution of this work to current knowledge, the limitations of the study, implications for conservation, and perspectives.

Conferences (oral presentations : 10; posters : 2)

Barreau E., Lesage L., Michaud R.,Bonnell T., Chion C., Dupuch A. – Scale matters : quantifying fusion-fission dynamic events of beluga herds in the St. Lawrence Estuary. 17th Ecology and behavior conference; August 2025; Montpellier, FRANCE.

Barreau E., Lesage L., Bonnell T., Michaud R., Senecal J-F., Chion C., Dupuch A. – Decoding beluga movements : a telemetry study in the St. Lawrence Estuary. 54ème Colloque de la Société Française pour l'Etude du Comportement Animal; Juin 2025; Nanterre, FRANCE.

Barreau E., Lesage L., Bonnell T., Michaud R., Senecal J-F., Chion C., Dupuch A. – Uncovering movement patterns of belugas in the St. Lawrence Estuary from telemetry data. 16th Ecology and behavior conference; August 2024; Chizé, FRANCE.

Barreau E., Lesage L., Michaud R.,Bonnell T., Chion C., Dupuch A. – Uncovering movement patterns of belugas in the St. Lawrence Estuary from telemetry data. 19th International Society for Behavioral Ecology; September-October 2024; Melbourne, AUSTRALIE.

Barreau E., Lesage L., Michaud R.,Bonnell T., Chion C., Dupuch A. – Uncovering movement patterns of belugas in the St. Lawrence Estuary from telemetry data. 16th Ecology and behavior conference; August 2024; Chizé, FRANCE.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Dupuch A. – Behavior-specific habitat use in beluga from the St. Lawrence Estuary, Canada. 48ème congrès de la Société Québécoise pour l'étude du comportement Novembre 2023; Montréal, Canada. *Price Julie Morand-Ferron*.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Dupuch A. – Fonction des habitats identifiés comme importants pour les bélugas de l'estuaire du St. Laurent : implications pour la conservation de la population. Symposium sur le béluga Mai 2023; Montréal, Canada.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Lemieux Lefebvre S., Dupuch A. – Behavior-specific habitat use in beluga from the St. Lawrence Estuary, Canada. Reunion Scientifique Annuelle de Québec-Océan février 2023; Rivière du Loup, Canada.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Lemieux Lefebvre S., Dupuch A. – Behavior-specific habitat use in beluga from the St. Lawrence Estuary, Canada. 24th Biennial Conference on the Biology of Marine Mammals; August 2022; Florida, USA.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Lemieux Lefebvre S., Dupuch A. – Behavior-specific habitat use of belugas in the St. Lawrence Estuary. 6ème Colloque de l'ISFORT, avril 2022.

Barreau E., Lesage L., Michaud R., Chion C., Bonnell T., Dupuch A. – Etude de la dynamique spatiale du béluga de estuaire du Saint-Laurent dans un contexte de conservation de la population. 6ème Colloque de l'ISFORT, mars 2021. *Price (1ère place) for the best presentation*

Barreau E., Lesage V., Michaud R., Chion C., Dupuch A. - Investigating movement dynamics of the St. Lawrence Estuary beluga : implications for conservation. Virtual summit of research of Canadian Parks Collective for Innovation and Leadership (CPCIL); March 2021, online

Séminars & committees (3 guest presentations)

Barreau E. Spatial dynamic of St. Lawrence Esturay beluga. Présentation à la réunion annuelle Prédateurs marins. 30 mai 2022, Chizé (France)

Barreau E. Functions of habitat highly used by St. Lawrence Esturay beluga. Comité national d'examen par les pairs sur les mammifères marins. 20 octobre 2023, Halifax (Canada)

Barreau E. Détermination des fonctions des habitats utilisés par les troupeaux de béluga de l'Estuaire du St. Laurent. Présentation au Groupe de travail sur le trafic maritime (G2T3M). 5 mai 2022, en ligne.

APPENDIX B

The translation was checked using an IA (DeepL.com, free version online)

The Spatial Phenotype

Spatial organization of individuals

Understanding the relationship between animal distribution and the environmental conditions in which individuals live is a central question in ecology. Movement, defined as a change in position through time and space, is ubiquitous in animal life (Nathan et al. 2008; Webber et al. 2023). It allows individuals to use space for various activities and behaviours tied to their life cycle (Mayor et al. 2009; Burt 1943). Animals select specific habitats from a set of available options within their home range (i.e., the area regularly used by an individual during its activities) to meet needs essential for survival and/or reproduction (Burt 1943; Morris 2003; Nathan et al. 2008; Hooten et al. 2017; Péron 2019). Multiple habitats may be required to satisfy vital functions, and some habitats can fulfil several needs simultaneously. Habitat quality is shaped by multiple factors, including the individual's motivation (e.g., energy acquisition, social interaction, protection), accessibility, and intrinsic value defined by biotic and abiotic environmental conditions (i.e., distribution of resources and risks; Nathan et al. 2008; Morales 2010; Hooten et al. 2017).

Individual distribution is closely linked to habitat characteristics, but identifying underlying habitat functions depends on an understanding of behavioural processes (Bastille-Rousseau & Wittemyer 2021; Alston et al.

2022; Noren & Hauser 2016). Behaviour is the link between vital needs and habitat use, and is therefore central to understanding why animals select and use distinct habitats (Morris 2003; Nathan et al. 2008; Péron 2019; Bastille-Rousseau & Wittemyer 2021; Alston et al. 2022). Coupling behaviours and space use allowed the identification of resting areas in spinner dolphins (*Stenella longirostris*; Tyne et al. 2015) and foraging areas in common bottlenose dolphins (*Tursiops truncatus*; Hastie et al. 2004).

Behaviours underlying space use

Because resources and abiotic conditions are heterogeneous in time and space, animals must adapt their movement and organize their behavioural activities to optimally exploit these fluctuating resources and maximize fitness (Stephens & Krebs 1986; Shepard et al. 2013). Understanding the links between environmental conditions and movement patterns is therefore essential for elucidating how animals cope with ecological constraints.

The movement paradigm describes individual movement as the outcome of four major interconnected components : physiological state, which determines the motivation to move (e.g., hunger); navigation capacity (i.e., ability to orient using sensory cues); locomotor capacity (i.e., ability to execute movement); and the environmental conditions encountered (Nathan et al. 2008). Assuming that an individual trajectory reflects the alternation of distinct movement states, various analytical approaches, such as hidden Markov models, decompose these states to infer underlying behaviours (Morales;

Patterson et al. 2008; Hooten et al. 2017; Gurarie et al. 2016; McClintock et al. 2020). The interpretation of these states depends on the spatio-temporal scale considered. At broad scales, they may reflect seasonal migrations, residency areas, or nomadic movements (Pedersen et al. 2011; Bunnefeld et al. 2011; Hooten et al. 2017; Teitelbaum & Mueller 2019; Vogel et al. 2025). At fine scales, they may reveal foraging behaviours (Hooten et al. 2017; Dorfman et al. 2022). While challenging, scaling from the individual to the population level offers a mechanistic understanding of population dynamics and distribution as a result of individual behaviour, physiological constraints, and environmental conditions (Nathan et al. 2008).

Drivers of the spatial phenotype in gregarious species

Understanding spatial behaviour in gregarious species requires accounting for social dynamics among individuals. Social organization (Box 1) influences the cost–benefit trade-offs associated with habitat selection, leading to patterns of habitat use that vary with group size and/or composition (Whitehead & Rendall 2004; Fortin et al. 2009; Cañadas & Hammond 2008; Fury et al. 2013; Pirotta et al. 2020). For example, the presence of young individuals within a group influences selection of habitats simultaneously meeting the needs of all group members and favorable for maternal care (Cañadas & Hammond 2008; Weir et al. 2008; Fury et al. 2013). At the population scale, social learning can further lead to different habitat and resource use (e.g., prey) among individuals (Brakes et al. 2021), as illustrated by sperm whale clans using distinct habitats according to their social affiliation

(Whitehead & Rendall 2004; Pirotta et al. 2020). Spatial and social behaviours are thus tightly linked, underscoring the need to study them together to understand the spatial dynamics of gregarious species (Webber et al. 2020, 2023).

BOX 1: Key definitions

Social unit: Individuals that share a common space and interact more frequently with one another than with other conspecifics (e.g., group; Kappeler & van Schaik 2002; Whitehead 2008).

Fission-fusion dynamics: Spatio-temporal variation in spatial cohesion (i.e., interindividual distance), size (i.e., number of individuals), and composition (i.e., identity of individuals) within a given social unit (Aureli et al. 2008).

Social environment: Size, composition, and type of interactions among individuals within a social unit or population (Webber et al. 2023).

Social phenotype: An individual's social position within a society, resulting from their social interactions with other individuals (e.g., social familiarity). The interplay among individual phenotypes generates fission-fusion dynamics at the collective level (e.g., group) (Webber et al. 2023).

Social organization: Size, composition, and spatial cohesion of a social unit, and the degree of temporal variation across these three dimensions (Kappeler & van Schaik 2002; Whitehead 2008; Aureli et al. 2008).

Social structure: An emergent property of the types of interactions and resulting social relationships among individuals within a social unit (Kappeler & van Schaik 2002; Whitehead 2008).

Multi-level society: A type of social organization characterized by the hierarchical interweaving of at least two levels of social units (e.g., pair, group) (Cantor et al. 2015). The first level generally has a composition that remains stable over time (e.g., pair) and periodically fuses to form larger groups, which in turn can form even larger groups, resulting in a fission-fusion dynamic (Grueter et al. 2020).

The environment encompasses both the spatial and social elements an animal encounters (Box 1; Webber et al. 2023). Although the role of the social environment is implicit in the movement paradigm, gregarious species are distinguished by their adjustment of spatial behaviour through moving with or toward conspecifics. The spatial environment (e.g., resource distribution) and the social environment (e.g., group size and composition, type of interactions) both influence individual movement (Webber et al. 2023). The socio-spatial interface framework extends the movement ecology paradigm by clarifying the inherent link between social ecology and movement ecology across scales (Webber et al. 2023; Picardi et al. 2024). Under this framework, individual movement is a mechanistic link between intrinsic individual traits (e.g., age, sex), the spatial and social environmental conditions encountered (e.g., habitat configuration, group membership), from which spatial and social phenotypes emerge (e.g., habitat use, social structure). Spatial and social environments precede the movement process by influencing motivations and movement cost–benefit trade-offs, while spatial and social phenotypes result from individual behavioural adjustments (Figure 1.1; Webber et al. 2023).

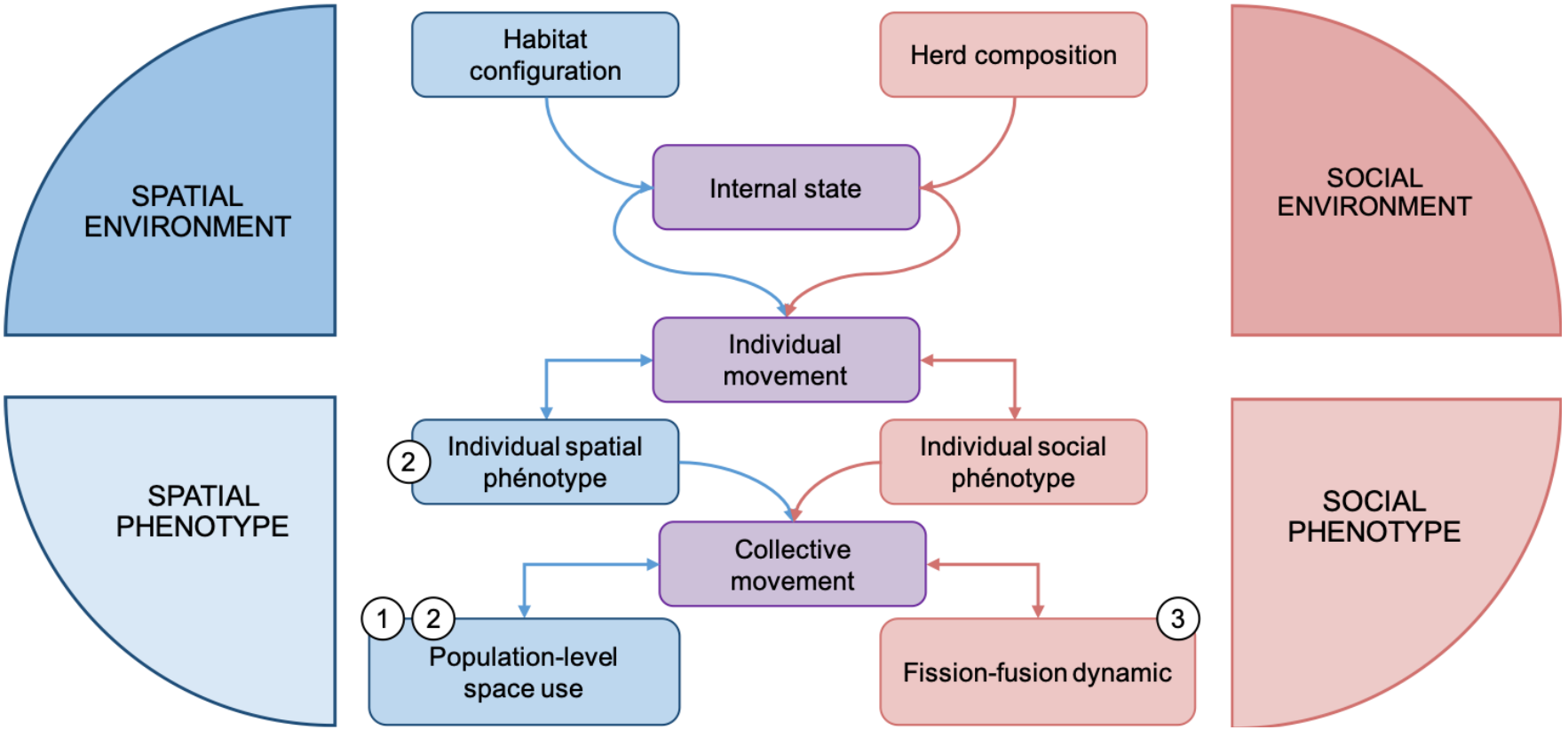

Figure 1.1 : Conceptual framework adapted from Webber et al. (2023) illustrating the central role of individual movement at the interface between the spatial environment, the social environment, the spatial phenotype, and the social phenotype. Each number refers to one of the chapters of this thesis.

Individual movement varies with group composition in response to constraints related to the locomotor capacities or physiological needs of other group members (Sueur et al. 2011; Webber et al. 2023). For example, the reduced locomotor capacities of young individuals influence how adults within the group move, including distances travelled (Papageorgiou & Farine 2015) or maximum swimming speed (Noren et al. 2023). However, few studies integrate spatial and social factors within a unified analytical framework (Fortin et al. 2009; McKellar et al. 2015; Strandburg-Peshkin et al. 2017; Webber et al. 2024), particularly in marine megafauna (Hays et al. 2016). Accounting for interactions between habitat and the social environment improves predictions of movement states and understanding of individual decisions (Strandburg-Peshkin et al. 2017), highlighting the need to include both environment in animal movement studies. The effects of spatial and social environments are typically examined separately, limiting insight into the underlying processes.

The social phenotype

Sociality, defined as the tendency of individuals to live in groups, is widespread across the animal kingdom (Alexander 1974; Ward & Webster 2016). Group living confers advantages such as cooperative foraging or care of young and reduced predation risk, but also involves costs such as food competition and pathogen transmission (Ward & Webster 2016). Beyond these trade-offs, groups may differ in their behavioural repertoires (e.g., dietary preferences, hunting techniques, tool use) and ecological knowledge shared among members (Ward & Webster 2016; Brakes et al. 2021). Group

membership can confer advantages that ultimately affect individual survival and, consequently, fitness (Busson et al. 2019).

Inspired by the general principles of cost–benefit trade-offs (MacArthur & Pianka 1966), socio-ecological theory aims to understand the evolutionary pressures shaping animal social systems. It links the social organisation and/or structure of a population to the ecological constraints of the different habitats it uses (Crook 1964; Crook & Gartlan 1966; Wittemyer et al. 2005; Sueur et al. 2011). Initially centred on the spatial environment (e.g., distribution of resources and risks), this theory now explicitly incorporates the social environment for a more complete understanding of social systems (Webber et al. 2020, 2023). Studying species with marked behavioural flexibility, such as fission–fusion dynamics (Box 1), allows examination of variation in social organisation in response to ecological factors (Aureli et al. 2008; Sueur et al. 2011; Webber et al. 2023).

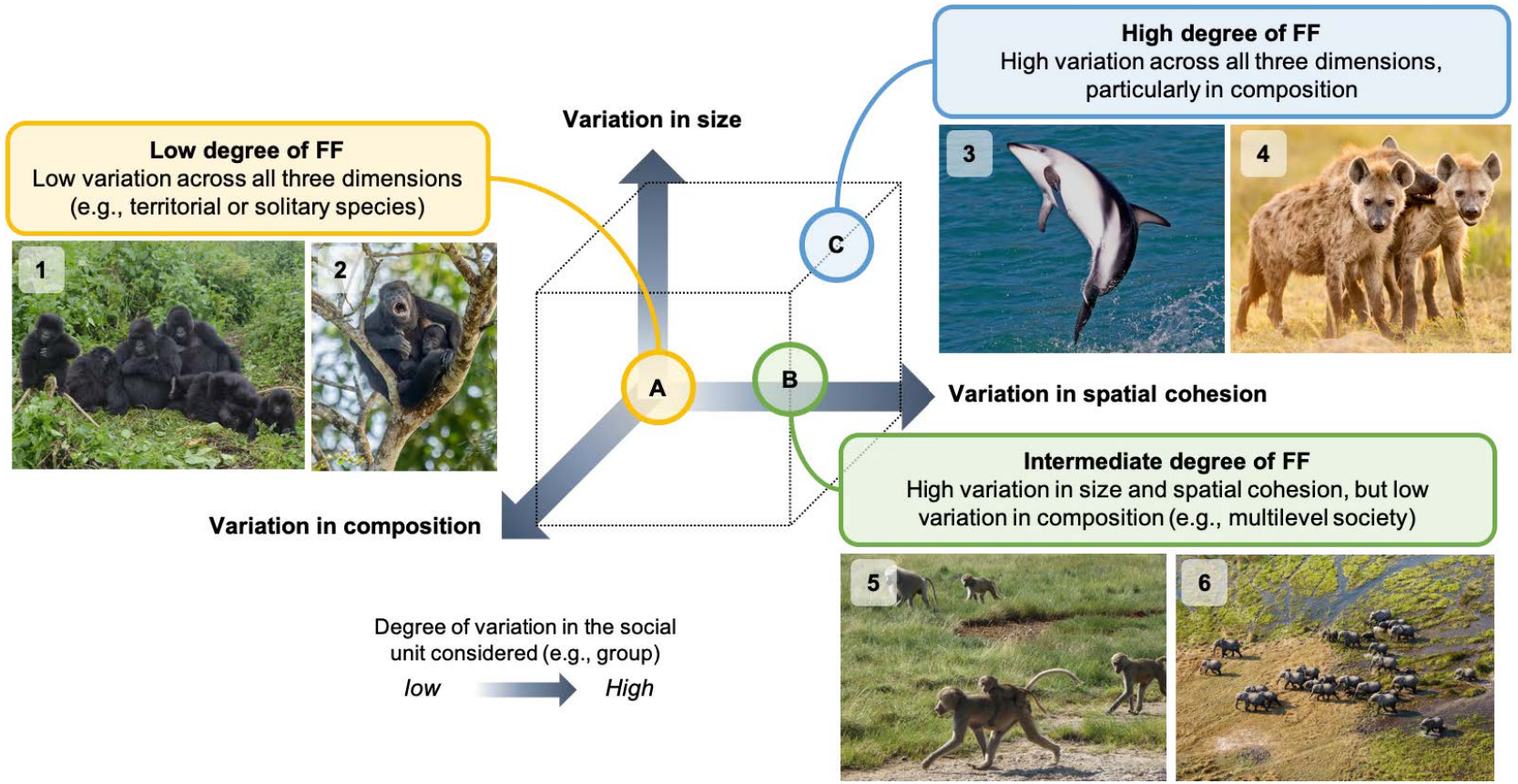

Figure 1.2 : Conceptual diagram adapted from Aureli et al. (2008) illustrating the three dimensions of fission-fusion dynamics: spatial cohesion (x-axis), group size (y-axis), and composition (z-axis). 1 : Mountain gorilla (*Gorilla beringei beringei*, © D. Fossey); 2 : Black howler monkey (*Alouatta pigra*, © Rhododendrites); 3 : Dusky dolphin (*Lagenorhynchus obscurus*, © S. Meriotte); 4 : Spotted hyena (*Crocuta crocuta*, © F. Lanting); 5 : Hamadryas baboon (*Papio hamadryas*, © jeanjacquesgodon); 6 : African elephant (*Loxodonta africana*, © T. Dressler).

Fission–fusion dynamics

The social organization of a social unit is not fixed and can vary in space and time. In non-human primates, Kummer (1971) described as "fission-fusion" those societies formed by social units of variable size and composition, frequently splitting and merging according to behavioural activity and resource availability. However, this definition provided a restrictive dichotomous perspective (i.e., flexible versus cohesive organisation), excluding the possibility that fission–fusion dynamics occur to some degree in most species.

The conceptual framework of Aureli et al. (2008) defines fission-fusion dynamics as the degree of temporal variation across three dimensions : spatial cohesion, size, and composition within a social unit. Numerous taxa are positioned along a gradient (Figure 1.2), including mammals (e.g., ungulates : Wittemyer et al. 2005; Wielgus 2023; primates : Lehmann & Boesch 2004; Ramos-Fernández & Morales 2014; carnivores : Smith et al. 2008; Mbizah et al. 2019; bats : Kerth et al. 2011; cetaceans : Parra et al. 2011; Castro et al. 2022), birds (Silk et al. 2014), and fish (Wilson et al. 2014; Papastamatiou et al. 2020). Some social units maintain relatively stable composition but vary in size and spatial cohesion (Zone B : intermediate degree of fission–fusion, Figure 1.2; Wittemyer et al. 2005; Aureli et al. 2008). Others exhibit high variability across all three dimensions (Zone C : high degree of fission–fusion, Figure 1.2; Pearson 2008; Smith et al. 2008). This diversity reflects adaptive responses to cost–benefit trade-offs of gregarious life under socio-ecological conditions (Sueur et al. 2011; Aureli et al. 2008; Webber et al. 2020, 2023).

Understanding the factors underlying fission–fusion dynamics is critical, as fission–fusion events influence key population processes (Figure 1.2), including habitat selection and use (Heithaus & Dill 2002; Fortin et al. 2009), movement (Haulsee et al. 2016), fitness (Foster et al. 2012; Silk et al. 2014), gene flow (Reisinger et al. 2017), and the transmission of information, culture (Mann et al. 2012; Allen et al. 2013), and disease (Altizer et al. 2003).

Many factors influence fission and fusion events, but their relative importance varies across and within species. Food resource availability is a common driver across species (Aureli et al. 2008; Sueur et al. 2011). Animals may adjust group dynamics by merging when resources are abundant or splitting when they become limited, reducing intraspecific competition and optimizing energy intake (Sueur et al. 2011). Other factors influence these behavioural decisions, including individual intrinsic state (e.g., fission may occur when the needs of group members diverge; Conradt & Roper 2000; Sueur et al. 2011; Webber et al. 2023), access to information on the location and quality of food resources or resting sites (Ramos-Fernández & Morales 2014; Sueur et al. 2011), and predation risk (Heithaus & Dill 2002; Fortin et al. 2009).

Among social factors, the nature of relationships among individuals (e.g., familiarity and association preferences; Wittemyer 2005; Ramos-Fernández et al. 2014; Le Goff et al. 2024) and the presence of dependent young tend to promote group stability (i.e., few fission or fusion events; Lunardi et al. 2014; Castro et al. 2022). This cohesion may facilitate cooperative care

of young (Couzin 2006; Wittemyer 2005; Gowans 2019), protection from predators (Bond et al. 2010), sexual aggression (Cassini 2021), and infanticide (Smith et al. 2008; Packer et al. 1990).

Animal populations in the anthropocene

The influence of human activities on all components of the planet, atmosphere, hydrosphere, cryosphere, biosphere, and lithosphere, defines the current geological era : the Anthropocene (Zalasiewicz et al. 2019). These activities, pursued at an unprecedented pace, exert ecological and evolutionary pressures on organisms (Hendry et al. 2017; Pelletier & Coltman 2018). Overexploitation of resources, habitat degradation and loss, and the effects of climate change constitute major and complex environmental modifications that can drive the decline and/or extinction of animal populations (Monasterky 2014; Pachauri et al. 2014; Calvin et al. 2023). A growing body of evidence supports that a sixth mass extinction is underway (Barnosky et al. 2011; Kolbert 2014; Ceballos et al. 2015; McCallum 2015; Cowie, Bouchet & Fontaine 2022; Richardson et al. 2023), although the responses and magnitude of impacts vary across taxa and ecosystems (Finn et al. 2023).

Marine Mammals

In the oceans, many species are exposed to human activities (Halpern et al. 2015, 2019; Duarte et al. 2021). Among the 136 recognised marine mammal species (Taxonomy Committee 2025), many are threatened by multiple anthropogenic activities : vessel traffic, fisheries, hunting, resource

depletion, pollution, introduction of pathogens and invasive species, and physicochemical alteration of the oceans (Avila et al. 2018; Erbe et al. 2019; Nelms et al. 2021; Plön et al. 2024). Maritime routes have intensified over recent decades, generating zones of dense traffic (Pirotta et al. 2019). They fragment, degrade, and pollute habitats, inducing physiological and behavioural stress in marine mammals (Pirotta et al. 2019; Duarte et al. 2021; Erbe et al. 2019). Vessel strikes, documented in at least 75 species of marine megafauna (Schoeman et al. 2020), cause substantial mortality. In the North Atlantic right whale (*Eubalaena glacialis*), for instance, more than 52% of necropsied individuals bore strike-related injuries (Campbell-Malone et al. 2008).

The oceans have also become considerably noisier since the industrial revolution (Duarte et al. 2021). Sound plays a central role in the vital behavioural activities of marine mammals (Southall 2017). Chronic exposure to underwater noise constitutes a major form of acoustic habitat degradation, masking biologically important sounds (e.g., predators, conspecifics, or prey), disrupting essential behavioural activities, and causing physical injury and chronic stress (Ellison et al. 2012; Clark et al. 2009; Erbe et al. 2019; Williams et al. 2015; Gomez et al. 2016; Nowacek et al. 2007). Behavioural responses to noise are context-dependent (Ellison et al. 2012; Gomez et al. 2016) and can modify site fidelity or lead to the abandonment of important habitats as long as acoustic disturbance persists (Allen & Read 2000; Bejder et al. 2006; Forney et al. 2017; Lusseau 2005; Pirotta et al. 2013; Morton & Symonds

2002; Stern et al. 2017). Maritime traffic and harbours also represent a major source of pollution through the dispersal of chemical waste and debris (Halpern et al. 2015).

Fisheries degrade habitats and food webs, driving global marine defaunation (McCauley et al. 2015). The reduction of available prey through overfishing contributes to marine mammal population declines (Avila et al. 2018; Nelms et al. 2021). In the Mediterranean Sea, the decline of the short-beaked common dolphin (*Delphinus delphis*) population is primarily attributed to the collapse of their pelagic prey (Piroddi et al. 2011). In the coastal waters of the Pacific Northwest, survival and reproductive rates of resident killer whales (*Orcinus orca*) have declined following a reduction in their primary prey (Ford et al. 2010). In addition, bycatch (i.e., accidental capture or entanglement in fishing gear) poses an extinction threat to certain species, including the Mediterranean monk seal (*Monachus monachus*) and the vaquita (*Phocoena sinus*) in the Gulf of California, Mexico (Jaramillo-Legorreta et al. 2019).

Marine mammals also accumulate persistent pollutants by ingesting contaminated prey. These contaminants biomagnify through the food chain (de Lima Silva et al. 2024) and increase the risk of reproductive disorders and disease sensibility (Reijnders et al. 2017). The absence of recovery of certain populations has been linked to chronic contaminant exposure. Persistent organic pollutants have been associated with high cancer rates in beluga whales (*Delphinapterus leucas*; Poirier et al. 2019), and high hydrocarbon concentrations following an oil spill caused significant mortality in killer whales

(Matkin et al. 2008). Ingestion of large quantities of plastic waste has also led to mortality, as documented in sperm whales (*Physeter macrocephalus*; De Stephanis et al. 2014).

Conservation strategies

Management measures addressing the effects of human activities on wildlife should ideally be implemented before target populations begin to decline. For marine mammals, Evans (2018) distinguishes two broad conservation approaches : area-based conservation, which manages delineated geographic spaces (e.g., marine protected areas), and pressure-based conservation, which targets the direct reduction of anthropogenic stressors (e.g., rerouting vessel traffic). Given that cetaceans are highly mobile species, pressure-based measures may be more effective (Evans 2018).

Conserving these species depends on a thorough understanding of how organisms interact with their environment (Redfern et al. 2006; Ross et al. 2011; Brakes & Dall 2016). Behaviour is a key mechanism through which individuals respond to their environment, driving their survival and reproduction and, ultimately, population dynamics (Webber et al. 2020, 2023). Behavioural ecology is therefore an essential component of conservation biology (Berger-Tal et al. 2011, 2016). For gregarious species, differences between social groups can lead to unequal exposure to anthropogenic threats and variable conservation needs across population segments (Brakes et al. 2021; Maldonado-Chaparro et al. 2021). However, the consideration of social

behaviour in conservation strategies remains limited (Berger-Tal et al. 2016; Brakes et al. 2021; Maldonado-Chaparro et al. 2021).

Studying movement patterns allows for the characterization of the spatio-temporal distribution of individuals within a population and for describing their use of space. Within the home range, identifying key habitats and the behaviours concentrated within them is a prerequisite for understanding the ecological functions of these habitats and the determinants of their use (Mayor et al. 2009; Hooten et al. 2017; Bastille-Rousseau & Wittemyer 2021). This knowledge also enables the identification of overlap zones between important habitats and anthropogenic threats, facilitating exposure risk assessments.

For long-lived species, long-term data series (e.g., observation, telemetry, mark-recapture, stable isotopes, acoustic monitoring, genetics) are invaluable. They allow modelling of habitat use patterns, demographic trends, and resilience to anthropogenic threats on timescales compatible with the species' life cycle (e.g., North Atlantic right whale : Pirotta et al. 2023). These data can also provide baseline information — for example, on habitat use — enabling a better understanding of a species over time and assessment of the effectiveness of management measures (Magurran et al. 2010).

Biological Model : the St. Lawrence Estuary Beluga Whale

Life history traits

The beluga whale (*Delphinapterus leucas*) is a medium-sized odontocete cetacean (3.5–5.5 m) belonging to the family *Monodontidae* (O'Corry-Crowe 2018). In the wild, lifespan can exceed 90 years (Ferguson et al. 2020). Body coloration changes during development : calves are born brown to dark blue-brown, gradually lightening to grey in early life, then becoming uniformly white in adulthood. Sexual maturity is reached between 8 and 13 years in females and between 8 and 11 years in males (Finley et al. 1982; Fergusson et al. 2020; Inyakina et al. 2022; Hill et al. 2024). The species exhibits a polygynandrious mating system (i.e., both males and females have multiple partners within or across breeding seasons; O'Corry-Crowe et al. 2026). Reproduction, likely seasonal, is thought to occur in late winter or early spring depending on the population (Brodie 1971; Inyakina et al. 2022; O'Corry-Crowe 2018). Gestation lasts approximately 14 months and lactation nearly two years (Matthews and Ferguson 2015). Females give birth to a single calf and have long inter-birth intervals of 2 to 4 years (Sergeant 1973; O'Corry-Crowe 2018; Hill et al. 2024; Ferguson et al. 2020). Belugas are among the rare species in which a post-reproductive period is documented (i.e., menopause; Ellis et al. 2018).

Spatial behaviour

Beluga whales occupy Arctic and subarctic regions, within which they undertake seasonal migrations of varying extent across populations (O'Corry-Crowe 2018). The St. Lawrence Estuary (SLE) population studied in this thesis represents the southernmost population in the species' range (Figure 1.3a; COSEWIC 2016; Lesage 2021). It constitutes a relic of the Wisconsin glaciation (Harington 2008) and is now both geographically and genetically isolated from other Arctic populations (De March et al. 2002; COSEWIC 2016; Postma 2017; Lesage 2021; Montana et al. 2024).

The range varies seasonally and extends into the northwestern Gulf of St. Lawrence, although a portion of the population remains in the SLE year-round. The critical habitat of SLE beluga is defined as the summer area used by females, juveniles, and calves between June and October, including the habitats and features considered necessary for critical activities and the survival of the population (grey hatched area in Figure 1.3c; DFO 2012). During summer (June to October), the population concentrates around the Saguenay Fjord up to St-Fulgence and extends upstream and downstream between Battures aux Loups Marins and Rivière-Portneuf/Rimouski (Figure 1.3c). Belugas move between the estuary and the Gulf of St. Lawrence, generally eastward in autumn and westward in spring, covering distances of tens to hundreds of kilometres (Vladykov 1944; Mosnier et al. 2010; Gosselin et al. 2014; Simard et al. 2023; Harvey et al. 2024). Beluga whales use the

Saguenay Fjord year-round, with more intensive use between June and October (Conversano et al. 2017; Simard et al. 2023; Harvey et al. 2025).

During summer, SLE belugas do not use available habitats uniformly. High used areas, including restricted-area search zones, high-residency areas, and high-density areas, have been identified and are connected by a network of corridor routes (Michaud 1993; Lemieux Lefebvre et al. 2012; Mosnier et al. 2016; Harvey et al. 2025; Ouellet et al. 2021). While these important areas have been identified, their functions remain either presumed (e.g., corridors) or unknown (e.g., high-residency areas). Belugas engage in multiple activities considered essential to their annual cycle, including foraging, socialization, resting, calving, and nursing of newborns and care of young (Mosnier et al. 2010; Lemieux Lefebvre et al. 2018). The environmental characteristics associated with habitats where these activities occur also appear to vary (Mosnier et al. 2016). For instance, the diet of SLE belugas is varied, comprising both benthic and pelagic prey species (Vladykov 1944; Lesage et al. 2014, 2020; Cabrol et al. 2025), suggesting that foraging habitats differ according to prey ecology.

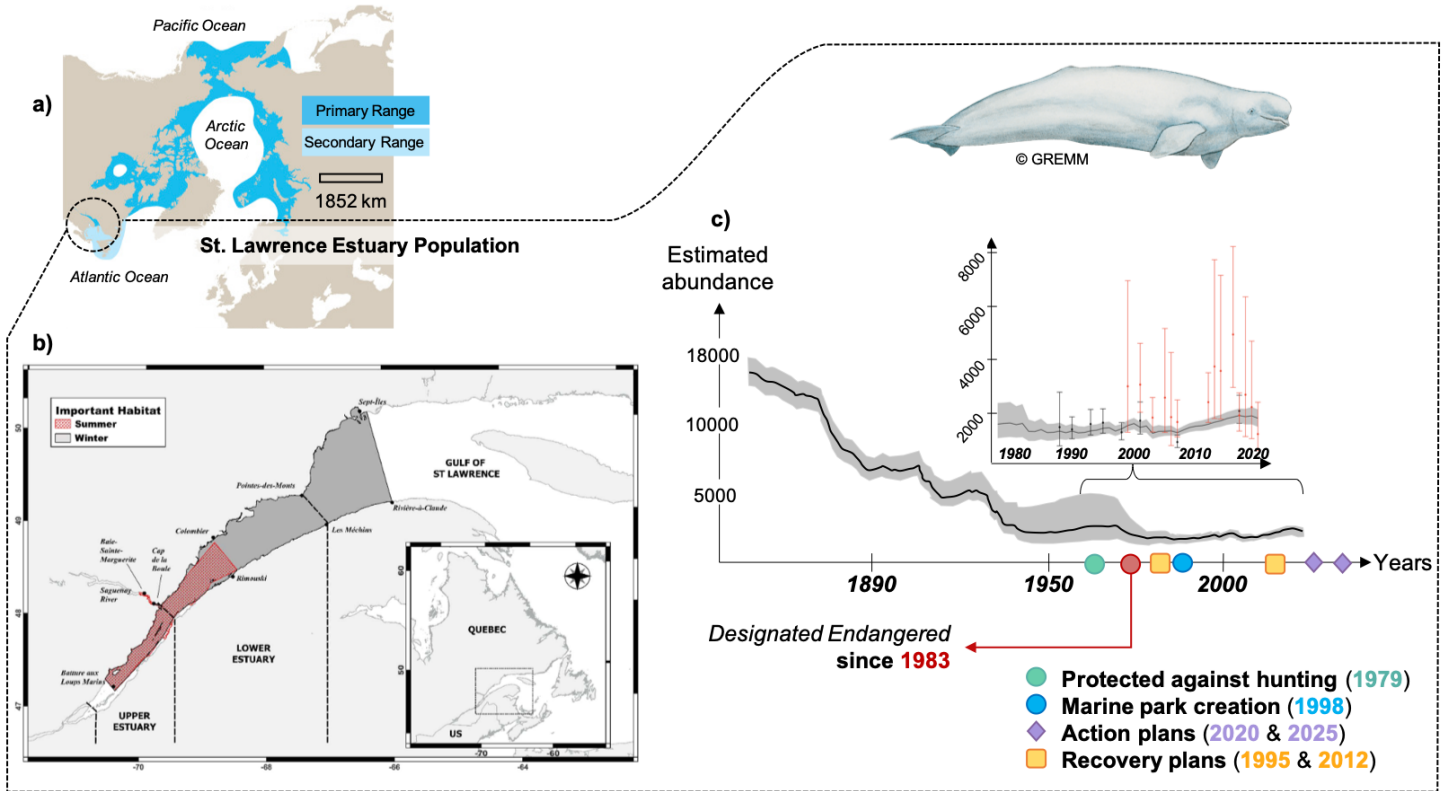

Figure 1.3 : Biogeographic and demographic context of the St. Lawrence Estuary beluga whale population. a) Global specie distribution (from O'Corry-Crowe 2018); Distribution of important habitat for the SLE population (see details in Harvey et al. 2025); c) Population demographic trends estimated from aerial photo-based survey. The solid line shows the mean abundance estimated by the model for each year, while the shaded band shows the uncertainty (95% CI) around that estimate. (see details in Tinker et al. 2024). Symbols indicate key dates in the implementation of legal protection and conservation efforts.

Site fidelity and sex- and age-segregation, typical of the species, are also documented during summer. Herds of females accompanied by young and calves tend to use the upstream portion of the estuary more frequently than adults without young (e.g., males), which spend more time downstream (Michaud 1993; Mosnier et al. 2016; Ouellet et al. 2021; Bonnell et al. 2022, 2024), resulting in dietary differences between males and females (Lesage et al. 2014, 2020).

Social behaviour

Known as the "canary of the sea", the beluga possesses a particularly diverse vocal repertoire, considered a reflection of its complex social system (Sjare & Smith 1986; Michaud 2005; Alekseeva et al. 2013; Vergara et al. 2019; Garland et al. 2015; Panova et al. 2023). Belugas are gregarious and their social organization is highly variable in time and space according to ecological and social context. Social structure appears to be hierarchically organized at multiple levels (Aubin et al. 2026) : individuals can be observed alone, in dyads, in small groups, or in herds of up to several hundred individuals, without exclusive organization around related individuals (Alekseeva et al. 2014; Mayette et al. 2022; Michaud 1993; O'Corry-Crowe et al. 2020; Stewart et al. 2025; Panova et al. 2025). This social flexibility is indicative of fission–fusion dynamics (Aureli et al. 2008), whose degree and underlying drivers are currently unknown. Female sociality, likely matrifocal (i.e., social structure centered on maternal bonds among related and unrelated individuals; O'Corry-Crowe et al. 2020; Aubin et al. 2026), appears to facilitate

cultural transmission of migratory routes and summer areas (Colbeck et al. 2013), as well as cooperative behaviours such as alloparental care (Aubin et al. 2021, 2023). The long dependency period of calves until weaning (association with mothers up to 5 years; McGuire et al. 2020) may allow acquisition of critical behaviours related to communication, movement, and foraging (Brodie 1969; Tyack 1986; Colbeck et al. 2013; Krasnova et al. 2014).

Recovery and conservation

Centuries of intensive hunting severely decimated the population when protection from hunting was enacted (Figure 1.3b; Pippard & Malcolm 1978; Sergeant & Hoek 1988; Kingsley 1998). Since then, the population has remained fluctuating but generally stable. However, since 2010, survival rates have become increasingly variable, with a sudden rise in mortalities among pregnant and parturient females (Figure 1.3b). In 2022, a model estimated beluga abundance at approximately 1,850 individuals (95% confidence interval : 1,500–2,200; Tinker et al. 2024). The population has been designated as "endangered" since 1983 (Pippard 1985; COSEWIC 2014), a status reflected in Canada's Species at Risk Act and Quebec's Act Respecting Threatened or Vulnerable Species (RLRQ, c. E-12.01; Canada Gazette 2017).

In Canada, when the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assesses a species as threatened, endangered, or extinct, the relevant federal ministry is responsible for developing action plans. These plans require scientific information on population status, threats to survival and recovery, and the feasibility of recovery. Habitat conservation is a

central element of any species protection and recovery initiative to mitigate the effects of anthropogenic activities.

Despite considerable protection efforts over the past 40 years (DFO 2012, 2020; Ménard et al. 2018), multiple threats, that originate from diverse sources, continue to impede population recovery. Living in one of North America's main shipping lanes, SLE belugas are exposed to high noise levels from vessel traffic and marine development projects (McQuinn et al. 2011; Gervaise et al. 2012; Ménard et al. 2018). They are also chronically exposed to elevated contaminant levels, owing to the highly industrialized nature of the St. Lawrence watershed (DFO 2012). Long-term habitat degradation through fishing, environmental disturbances (e.g., toxic algal blooms), and anthropogenic activities (e.g., dredging operations), combined with climate change effects and the introduction of exotic species, is reducing the abundance, quality, and availability of food resources (Plourde et al. 2014; Galbraith et al. 2023; Williams et al. 2021; Lesage et al. 2021; Lesage et al. 2024). The cumulative nature of these stressors complicates prediction of long-term consequences for population dynamics, particularly given that impacts likely vary according to the exposure context of different population segments (Chion et al. 2021; Lesage et al. 2024).

Concerns about population decline have triggered the implementation of a series of monitoring programs, rigorously maintained over time, to track population health, demography, and dynamics (Figure 1.3; Lesage et al. 2014; Lair et al. 2015, 2016; Mosnier et al. 2015; St-Pierre et al. 2024; Tinker et al.

2024). This dataset constitutes one of the longest time series for any cetacean, making the SLE population the most closely monitored in beluga specie (Norman et al. 2022) and one of the most thoroughly monitored cetacean populations worldwide. This thesis draws on these exceptional long-term datasets to advance understanding of the spatial and social dynamics of SLE belugas and to inform conservation strategies.

Thesis objectives

This thesis aims to identify the factors underlying the spatial dynamics of SLE belugas, with the goal of informing conservation policies for this population. The central hypothesis is that spatial behaviour results from the interaction between habitat characteristics and the social environment (Webber et al. 2023). The thesis is structured around three chapters : it first explores patterns of habitat use by herds and individual movement patterns, then examines fission–fusion dynamics (Figure 1.2).

Research questions

What are the functions of habitats identified as important for the population? Accounting for herd composition, how associations between these functions and the biotic and abiotic characteristics of the habitat differ according to the explanatory variables considered?

Chapter 1 identifies the functions of important habitats used by SLE beluga herds. This chapter builds on a behavioural classification linking surface activity and herd configuration to diving behaviour (Lemieux Lefebvre

et al. 2018). It integrates these behaviours into a spatially explicit framework combining two types of habitats : high-residency areas (Lemieux Lefebvre et al. 2012) and corridor routes (Ouellet et al. 2021). The relative proportions of behaviours, calculated for each habitat, formed the basis for statistically grouping zones according to their predominant function. These groups were then examined in relation to biophysical habitat variables, distinguishing different herd types to account for their gregarious behaviour. This chapter provides the first empirical quantification of behavioural activities associated with habitats considered important, whose functions were previously only assumed. This study was published in December 2025 in the journal Endangered Species Research.

What are the environmental drivers of individual movement? Do movement patterns concentrate in specific areas?

Chapter 2 determines how environmental factors (habitat characteristics and social factors) influence individual movement patterns. Hidden Markov models (HMMs) were first used to determine the number of distinct behavioural states from two-dimensional data (i.e., turning angle and step length) and the relevant temporal scale. Integration of environmental covariates into the HMMs then allowed examination of their effects on probabilities of remaining in the same behavioural state or transitioning between states. Complementary to **Chapter 1**, this approach also provides a fine-scale understanding of habitat use based on the distribution of behaviours. This study is currently submitted for review in the journal M*ovement Ecology*.

What degree characterizes fission–fusion dynamics in SLE beluga herds? What social, behavioural, environmental, and anthropogenic drivers influence fission and fusion events in these herds?

Chapter 3 characterizes the fission–fusion dynamics of herds. Drawing on the conceptual framework of Aureli et al. (2008), fission and fusion events were quantified from variations in size, composition, and spatial dispersion. These events were then modelled as a function of social, behavioural, environmental (i.e., habitat characteristics), and anthropogenic factors. This chapter quantifies the degree of fission–fusion dynamics in this species and identifies the contexts in which fission and fusion events occur. The results of this study will be submitted to a peer-reviewed journal.

Data sources

To address these questions, this research draws on two complementary data sources collected during the summer season (Figure 1.4). Since 1989, the Groupe de Recherche et d'Éducation sur les Mammifères Marins (GREMM) has conducted a focal follow program, building a database comprising several thousand herd follows (~3,961 between 1989 and 2023) and covering a wide range of habitats across the summer distribution area of the population (Michaud 1993; Lemieux Lefebvre et al. 2012; Ouellet et al. 2021). These herd focal follows describe, at regular intervals over periods of approximately three hours, the social organization and behaviour of herds. The spatio-temporal extent of the series and sample size provide robust statistical

power for population-level inferences. These focal follows occasionally incorporate complementary protocols such as photo-identification, biopsies, drone surveys, or telemetry. This long-term series was used in **all three chapters** of the thesis. In addition, telemetry data collected between 2001 and 2020 by GREMM and teams from Fisheries and Oceans Canada provided high-resolution daily individual trajectories from two types of radio-transmitter tags : TDR tags (44 individuals, 2001–2005) and DTags (30 individuals, 2018–2020). These data, used in **Chapter 2**, provide a finer individual-level scale than observation alone can yield, and the total number of trajectories offers sufficient statistical power for population-level inferences (Sequeira et al. 2018).

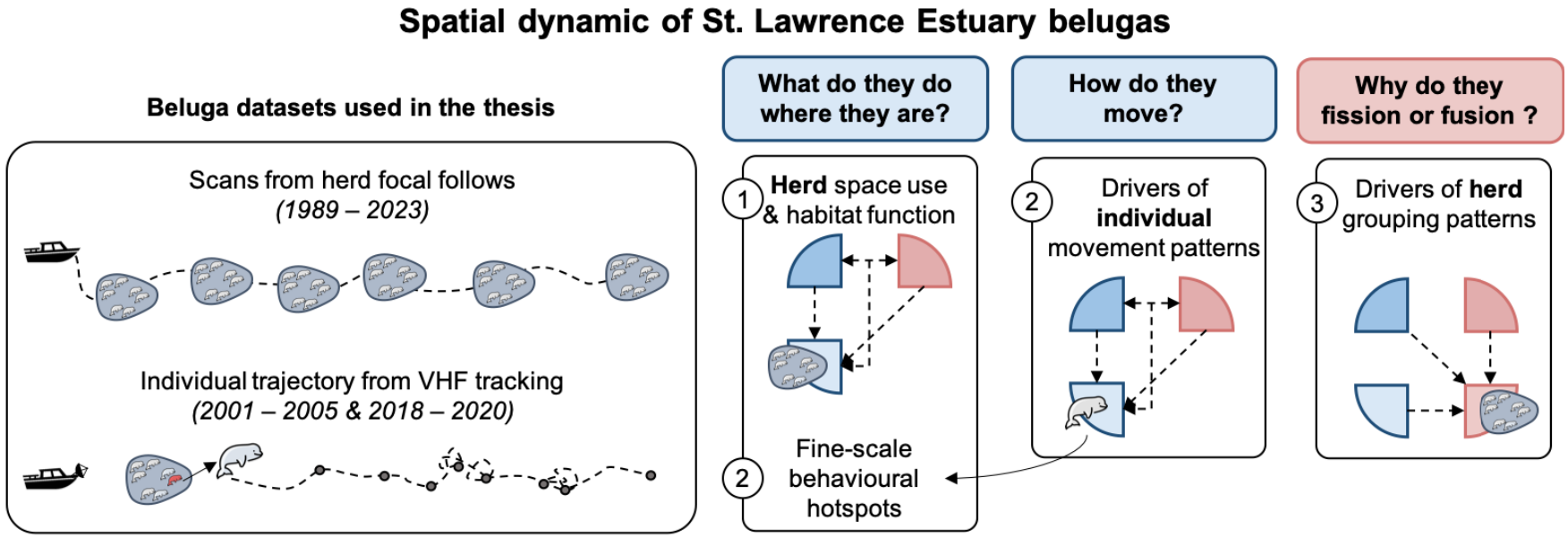

Figure 1.4 : Illustration of the datasets used and research questions addressed in each chapter of the thesis. The dashed arrows indicate the relationships between the components of the socio-spatial interface (Webber et al. 2023) tested in each chapter.

APPENDIX C

The translation was checked using an IA (DeepL.com, free version online)

Thesis contribution

Understanding where animals are, what they do there, and why, constitutes a central question in spatial ecology (Nathan et al. 2008; Hooten et al. 2017). For gregarious species, these questions require considering spatial decisions in relation to social behaviour and, thus, taking into account all components of the socio-spatial interface (Webber et al. 2020, 2023). However, empirical studies integrating both the spatial and social environments to understand phenotypes (Fortin et al. 2008; McKellar et al. 2015; Strandburg-Peshkin et al. 2017; Webber et al. 2024), and those that link spatial and social phenotypes (Kratofil et al. 2026) remain rare, limiting our ability to elucidate behaviours in all their complexity (Webber et al. 2023).

This PhD provides new insights that contribute to a better understanding of the spatial and social behaviour of beluga in the SLE during the summer. Although several decades of research have identified and mapped key habitats within their summer range (Lemieux-Lefebvre et al. 2012; Mosnier et al. 2016; Ouellet et al. 2021; Harvey et al. 2025), the behavioural activities occurring in these habitats have either been inferred from indirect evidence or remain unknown. By explicitly linking the various behaviours exhibited by herds to their locations, **Chapter 1** identifies the functions of high-residence areas and corridors. Furthermore, determining behavioural states from

individual tracking data refines our understanding of habitat use patterns. The spatial distribution and prevalence of these behaviours help to establish the functions of previously identified habitats and those necessary for certain vital functions (**Chapter 1**), while also revealing new restricted-search areas that are likely important for this population (**Chapter 2**). Together, these results help to identify the functional value of the habitats used by belugas and provide a better understanding of why they select and use these habitats in the SLE.

The PhD also provides the first explicit characterization of fission-fusion dynamics at the herd level in this species (**Chapter 3**), corresponding to the third social level in the species recently described as organized with a multilevel social structure (Aubin et al. 2026). The study incorporates all three dimensions of the conceptual framework proposed by Aureli et al. (2008), that is generally rare in studies, particularly among cetaceans (Lunardi et al. 2014).

Finally, this PhD provides empirical clarification of certain relationships among the components of the socio-spatial interface in this gregarious species. Together, the three chapters demonstrate that the characteristics of the beluga's environment and the social context influence spatial (**Chapters 1 and 2**) and social (**Chapter 3**) phenotypes. However, the relationships between these components depend on the scale considered and the behaviours exhibited.

At the population level, environmental conditions, either alone or in interaction with the social organisation of herds, can explain habitat-use

patterns to a certain extent, particularly in habitats where pelagic feeding predominates (see **Chapter 1**). At the individual level, transitions between movement modes are linked to environmental constraints or prey availability. However, the social organisation of the herd only influences these transitions when they interact with the spatial context (**Chapter 2**). These results may suggest a potential top-down effect (Picardi et al. 2024), whereby herd composition or size influences small-scale individual movement patterns when the individual face certain environmental conditions. Individual movement determines the areas frequented, how long they are used for, and the behaviours exhibited, thereby linking habitat selection and space use at the population level (Nathan et al. 2008; Morales et al. 2010; Webber et al. 2023). The results from **Chapter 2** may help to explain the spatial organisation of populations in summer, such as sex segregation (Michaud 1993 ; Ouellet et al. 2021) or site fidelity (Bonnell et al. 2021).

There is also a wide variety of interactions between spatial and social phenotypes (Webber et al. 2024). Changes in social organisation within herds do not only result from variations in spatial and social environments, but also of collective movement patterns, which are defined as a spatial phenotype (see **Chapter 3**).

Thesis limitations

Studying cetaceans in the wild poses substantial logistical constraints : these are highly mobile species occupying dynamic habitats and surfacing only briefly. Comprehensive collection of data on the social environment is

particularly challenging, as illustrated by disparities in temporal resolution and missing data attributable to surface visibility during simultaneous herd and individual movement follows (**Chapter 2**). Several limitations must therefore be kept in mind when interpreting the results, especially given that the conclusions of this thesis have direct implications for the conservation of this population classified as endangered.

Temporal coverage

The study period is restricted to the summer season. The habitat functions identified represent averages across this period (**Chapters 1 & 2**) and cannot be extrapolated to the entire annual cycle. However, the use and importance of these habitats (e.g., resource availability) are likely to vary seasonally and over the long term (Rioux et al. 2023; Cabrol et al. 2025). Sample size in **Chapter 1** did not allow examination of potential inter-annual variability in summer habitat functions, even when grouped at a decadal scale. The results of this thesis therefore constitute a static spatial baseline. Additional data from long-term follows will be necessary to detect any changes in habitat functions over time. A recent analysis of three decades of aerial surveys (1990–2023) did not reveal a shift in the high-density areas used during summer, but showed increased use of the eastern portion of these zones over the years (Harvey et al. 2025).

Behavioural classification

The conclusions of **Chapter 2** rely largely on the correct classification of behavioural states. It is important to note that states derived from hidden Markov models represent estimates of animals' actual behaviours (Hooten et al. 2017; McClintock & Michelot 2021). This limitation is particularly pronounced in unsupervised approaches, such as that employed in **Chapter 2**. To preserve clear biological interpretation, a thorough analysis was conducted to determine the appropriate number of states and temporal scale. The three retained behavioural states show distinct distributions of step lengths and turning angles (Pohle et al. 2017; Michelot 2020) and are consistent with descriptions of predominant surface movement patterns in this population (Lemieux Lefebvre et al. 2018), reinforcing the reliability of the classification for capturing a large portion of beluga behavioural variability. Nonetheless, horizontal movement data limit confidence in distinguishing behaviours assigned to the area-restricted search state. Integrating three-dimensional data (e.g., acceleration, dive profiles) in hierarchical hidden Markov models would refine behavioural classification by simultaneously modelling behaviours across scales (Adam et al. 2019).

Explanatory variables

Certain factors could not be accounted due to data constraints. Information on the density and biomass of prey species other than sand lance would have improved discrimination of habitats associated with different

foraging strategies (**Chapters 1 & 2**), but these data remain limited and fragmented in the SLE (Lesage et al. 2024). They would also have helped determine whether fission events observed in high-residency areas are partly attributable to intraspecific resource competition (**Chapter 3**). Interspecific competition for food resources also likely influences beluga distribution; however, the density of potential prey competitors, such as harp seals (*Pagophilus groenlandicus*), grey seals (*Halichoerus grypus*), redfish (*Sebastes* spp.), and striped bass (*Morone saxatilis*) (Lesage 2021; Cabrol et al. 2025), was not included in the analyses. Regarding social variables, more detailed herd composition data (i.e., proportions of individuals per age class), the number and composition of groups, and the types of inter-individual associations would refine understanding of the role of the social environment in spatial behaviour (**Chapters 1 & 2**) and fission-fusion dynamics (**Chapter 3**). Integration of social structure is developed further in the research perspectives section. Finally, interactions among explanatory variables in **Chapter 3** could not be tested due to insufficient observations for each combination of response and explanatory variable categories. Fission-fusion dynamics could also reflect the combined effect of multiple factors, as some results of **Chapter 2** suggest. These constraints define avenues for future research but do not undermine the value of the results obtained, as the environment–phenotype relationships identified in each chapter are biologically consistent with what is known about the species and accord with theoretical predictions (Webber et al. 2023).

Research boat impact

This PhD rely on data collected from a research vessel (see **Chapters 1–3**). To minimize disturbance to belugas, the herd focal follow protocol included a period of approximately 15 minutes between the initial approach to the herd at a distance (~300–500 m), during which a preliminary survey was conducted, before the research vessel approached the herd to carry out detailed surveys. These preliminary surveys were not used in any of the analyses presented in **Chapters 1–3**. Furthermore, scans conducted during biopsy protocols were excluded from the analyses because an exploratory analysis revealed higher proportions of fission and fusion events, which may reflect a reaction to this invasive procedure (see **Chapter 3**). Despite these precautions, the presence of a research vessel and the noise it generates can affect acoustic behaviour and movement patterns (Guerra et al. 2014), which may influence the results (Erbe et al. 2019). Furthermore, some individuals may be more sensitive than others (Ellison et al. 2012), particularly groups containing calves (Guerra et al. 2014; Williamson et al. 2016). This thesis does not explicitly test the potential impact of the research vessel, as this would require 'control' conditions with no vessels present, including the research vessel, which is difficult to achieve in the heavily trafficked SLE during the summer. However, the data allow us to identify situations in which the presence of additional boats, in addition to the research vessel (which was operated with caution), would influence the belugas' behaviour (see **Chapter**

3). While this does not prove that the research vessel has no impact, it suggests that the measured effects occur beyond the vessel's own influence.

Conservation implications

Functions of important habitats

The SLE represent an important area for several cetacean species other than the beluga Mosnier et al. 2022. During summer, the core of beluga distribution corresponds to an area of approximately 2,800 km² (Mosnier et al. 2010; DFO 2012), within which approximately one third (966.33 km²) has been assigned ecological functions (**Chapter 1**). By providing novel information on the vital functions supported by important habitats for the SLE beluga population (**Chapters 1 & 2**), this thesis is essential for guiding the planning and prioritization of mitigation measures according to the vulnerability of certain vital activities to anthropogenic disturbance (Redfern et al. 2006; Ross et al. 2011; Brakes & Dall 2016). These results integrate directly into the habitat knowledge strategy in actions plans regarding habitat functions and use (e.g., measure 9, DFO 2020; measures 2 & 18, DFO 2025) and also allow to identify key areas requiring protection (e.g., measures 21 & 22, DFO 2020; measures 30, 31 & 34, DFO 2025).

The spatial delineation of these habitats and their functions enables assessment of overlap with anthropogenic activities, notably maritime traffic linked to tourism, recreational boating, and commercial shipping, which is particularly intense in the summer habitat (DFO 2020; Lesage et al. 2024).

Population segments using habitats that overlap with high-traffic areas may be more exposed to disturbance than those using quieter routes (Chion et al. 2021). Mitigation measures must ensure that anthropogenic pressures remain within limits compatible with the functional integrity of these habitats, accounting for the specific needs of different population segments. Measures aimed at reducing noise and disturbance in important habitats, such as speed reductions, route deviations, or exclusion zones, could contribute to improving the population's recovery potential by reducing acoustic masking of communication (e.g., contact calls) or limiting disruption of important behaviours in this highly social species (Lesage et al. 2024; DFO 2020, 2025). Furthermore, the planned expansion of the Saguenay–St. Lawrence Marine Park would extend the application of these disturbance reduction measures to a larger range of important habitats for beluga (Ménard et al. 2022; DFO 2020, 2025), including those for foraging and socialising (**Chapters 1 & 2**).

Monitoring Habitat Change

Since 2010, the range has reduced considerably relative to its historically documented extent, being approximately 65% smaller (Mosnier et al. 2010; COSEWIC 2014). From the same period, a significant change has been observed in calf mortality and adult female survival, slowing population growth and suggesting a possible decline since 2018 (Tinker et al. 2024). These demographic changes coincide with rising water temperatures, reduced sea ice, and long-term changes in the trophic structure of the St. Lawrence ecosystem (Plourde et al. 2014; Rioux et al. 2023; Galbraith et al. 2025).

The results of **Chapter 1** highlight limited habitat availability in the summer range when accounting for site fidelity (Bonnell et al. 2022) and age- and sex-segregation (Michaud 1993; Ouellet et al. 2021). These characteristics may increase the vulnerability of different population segments to local stressors, especially given that the summer range is already substantially reduced relative to its historical extent (Mosnier et al. 2010; COSEWIC 2014). When the quality or accessibility of these habitats is compromised, animals must weigh the costs and benefits of moving to less disturbed habitats (Brakes & Dall 2016; Forney et al. 2017; Hastie et al. 2021; Merkle et al. 2022). Such displacement may occur when individual tolerance reaches a threshold at which the costs of remaining in the disturbed habitat outweigh its benefits (Bejder et al. 2006; Forney et al. 2017). However, alternative habitats suitable to support the same ecological functions may be scarce. Moreover, displacement may reduce the time and energy individuals devote to vital functions (Constantine et al. 2004; Pirotta et al. 2015, 2013; Wisniewska et al. 2018), expose them to additional threats (Forney et al. 2017), and affect vital rates (Bejder et al. 2006; Tenan et al. 2020), with potentially negative consequences at the population scale. In this context, the habitat functions identified in **Chapters 1 & 2** provide a reference framework for detecting possible future changes in habitat use.

Conservation of social behaviours

The limited resilience of cetaceans in the face of anthropogenic threats is generally attributed to their life history traits (i.e., longevity, late sexual

maturity, long inter-birth intervals; Chivers 2017). However, the survival and reproductive success of many species also depend on social and behavioural traits, such as social cohesion, alloparental cooperation, intergenerational knowledge transfer, and the role of experienced individuals (Wade et al. 2012). When these behaviours are acquired and shared within a community through social learning, they define animal culture (Whitehead et al. 2004; Brakes et al. 2021). Conservation biology now recognizes the intrinsic value of these social and cultural behaviours for species whose spatial phenotypes are socially transmitted (Berger-Tal et al. 2011, 2016; Brakes & Dall 2016; Oestreich et al. 2025).

The beluga is a long-lived, gregarious species whose social structure relies on long periods of parental care, alloparental cooperation (Aubin et al. 2023), and the presence of post-reproductive females within groups (Ellis et al. 2018; O'Corry-Crowe et al. 2020). These characteristics, combined with fission-fusion dynamics in which herd social organization varies according to context (Chapter 3), create social conditions particularly favorable to social learning (O'Corry-Crowe et al. 2020). The long dependency period of calves is considered a critical phase for the acquisition of vital behaviours (Krasnova et al. 2009, 2014), and evidence of vertical cultural transmission has been established for migratory routes and vocal repertoires (reviewed in Aubin et al. 2026). Other forms of culture could exist (Aubin et al. 2026).

Several results of this thesis show that spatial behaviours are linked to herd social composition. Herds containing young individuals (juveniles and/or

calves) use shallower foraging habitats than those used by adult male herds (**Chapter 1**), and the relationship between presumed foraging behaviour and the likely availability of sand lance is modulated by the proportion of juveniles in the herd (**Chapter 2**). These differences in habitat use are consistent with the age- and sex-based spatial segregation documented in the SLE (Michaud 1993; Mosnier 2016; Ouellet et al. 2021) and may in part be explained by sexual dimorphism and contrasting energetic requirements between males, females, and juveniles (Loseto et al. 2006; O'Corry-Crowe 2018; Mayette et al. 2022), as well as the limited locomotor capacities of calves (Papageorgiou & Farine 2015; Noren et al. 2023). However, if these differences did not solely reflect physiological factors, they might be expected to fluctuate with prey availability. Yet dietary differences between these groups have persisted across several decades (stomach content analyses, 1938–1939, n = 107 : Vladykov 1946; 1989–2019, n = 89 : Lesage et al. 2020; isotopic analyses, 1997–2003 & 2015–2020, n = 52 and 44 : Cabrol et al. 2025), despite changes in the trophic structure of the St. Lawrence ecosystem (Rioux et al. 2023). While comparisons between these periods should be interpreted with caution due to limitations inherent in the methods and nature of the samples used (e.g., otoliths from larger species are better preserved in carcasses), this persistence may suggest that behavioural factors, such as social learning, may contribute to these differences. This hypothesis remains to be examined.

If differential habitat use according to herd composition does reflect a component of social learning, this would have direct conservation implications.

The loss of individuals acting as information transmitters could compromise the population's recovery capacity (Ward et al. 2011; Wade et al. 2012; Wade 2018; Brakes et al. 2021). Socially complex species with small populations are particularly vulnerable to Allee effects (i.e., a decrease in individual fitness or population growth rate as population size declines; Stephens et al. 1999), since critical activities are influenced by group social organization (Angulo et al. 2018). For example, reproductive success may decline if the number of adults is insufficient for cooperative care of young (Angulo et al. 2018). The SLE population is small, has low genetic diversity, and experiences very little immigration (Postma 2017), meaning potential Allee effects at the individual scale cannot be excluded (Montana et al. 2024). These uncertainties underscore the need to continue long-term monitoring and understand the population social structure (developed in the perspectives section) to assess the extent to which spatial phenotypes are shaped by social learning mechanisms.

Research perspectives

Habitat selection

In **Chapters 1 & 2**, behaviours and habitats used were characterized, but selection had already operated within these analyses : no comparison was made between used versus available habitats. A central question therefore remains open : why do belugas select these particular areas? Habitat selection constitutes a spatial phenotype influenced by both the spatial and social environments (Webber et al. 2023). Animals move through environments that

are generally heterogeneous in space and time. Optimization theories predict that animals preferentially select habitats based on the cost–benefit balance associated with their use (i.e., optimal foraging theory : Stephens & Krebs 1986; energy landscape theory : Shepard et al. 2013). Since energetic costs of locomotion increase with movement speed (Shepard et al. 2013), belugas may exhibit fast transit in areas where favorable currents minimize energy expenditure. The individual movement data from **Chapter 2** offer an opportunity to test this hypothesis. Integrating resource selection functions into hidden Markov models would quantify the extent to which each behavioural state is associated with active selection of environmental conditions, linking habitat selection mechanisms to the behaviours identified in this thesis (Florko et al. 2025).

Social structure

In **Chapter 3**, model results revealed marked variability in fission–fusion dynamics among herds, particularly for the size and composition dimensions. Exploration of random effects (herd IDs) could not explain inter-herd variability, even when distinguishing herd composition by age class (i.e., adults; adults-juveniles; adults-juveniles-calves), suggesting that other aspects of social structure warrant consideration. A herd is an assemblage of groups within which individuals can form lasting associations over several weeks (Panova et al. 2025) or years (e.g., mother–calf dyads : McGuire et al. 2020; adults : Aubin et al. 2026). The strength of inter-individual relationships could influence fission–fusion dynamics (i.e., the social cohesion hypothesis) : individuals with

strong bonds may be less likely to separate, thereby reducing fission probability within the herd (Aureli et al. 2008; Sueur et al. 2011; Le Goff et al. 2024). Photographic data collected during focal herd follows would allow quantification of dyadic relationships among individuals in the SLE population across several decades. The dyadic association index (i.e., half-weight index, HWI) measures the strength of bonds between pairs of individuals (Whitehead 2008). Aggregated at the herd level, three variables could be derived from this index : the mean HWI characterizing overall social cohesion of the herd; social differentiation indicating the heterogeneity of bonds (i.e., coefficient of variation of HWI values); and the proportion of strongly bonded dyads (i.e., density of preferential bonds; Whitehead 2008). Integrated as explanatory variables in the multinomial models of **Chapter 3**, these metrics would test whether the quality of within-herd associations predicts fission and fusion events, and whether their inclusion reduces residual variance in the herd ID random effect.

Acoustic behaviour

This thesis does not address acoustic behaviour, whose integration would deepen results from **Chapters 2 & 3**. Cetaceans rely heavily on acoustic signals to navigate their environment, locate prey, and communicate with conspecifics (Tyack & Clark 2000). Beluga whales possess one of the most diverse vocal repertoires among odontocetes (O'Corry-Crowe 2018). Echolocation clicks are associated with active prey detection (Castellote et al. 2021), while contact calls maintain group social cohesion (Vergara et al. 2019; Panova & Agafonov 2023; Aubin et al. 2026). In **Chapter 2**, integrating

acoustic data with telemetry follows would strengthen and refine classification of the behavioural states inferred by the model. In particular, detection of echolocation clicks could confirm that area-restricted search episodes do indeed correspond to foraging behaviour, rather than other forms of slow movement (e.g., resting, socialisation). The transmission range of contact calls is estimated at 6.7 km in a quiet environment and 2.9 km in a noisy one (Vergara et al. 2021), implying that social interactions may occur at distances greater than those observed at the surface (Aubin et al. 2026). Given that communication is important for group cohesion during fission and fusion decisions (Sueur et al. 2011), acoustic characteristics could prove essential for a better understanding of fission–fusion dynamics (**Chapter 3**). This type of study is feasible using existing data : as part of her thesis, Aubin (2025) collected acoustic recordings simultaneously with focal herd follows. It would therefore be possible to explore whether the mean number of contact calls emitted between two observations predicts fission–fusion events, enabling assessment of the extent to which vocal communication influences herd social dynamics.

Conclusion

Long-term monitoring of the SLE beluga population enables investigation of fundamental questions about the species' behaviour and ecology. This thesis contributes to understanding habitat use, movement, and fission–fusion dynamics in SLE beluga whales. The results provide a robust knowledge basis and can guide conservation measures necessary for the

recovery of this endangered population. Future research should aim to improve the mechanistic understanding of the factors influencing their spatial and social phenotypes.