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à Rimouski

Analyse spatiale des assemblages de mammifères marins de l'estuaire du Saint-Laurent

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PAR

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Je dédie ce mémoire à ma
famille qui a toujours cru en moi.

Rome ne s'est pas construite en
criant : « Lapin, je ne boirai pas de ton
eau ! » *Capitaine Charles Patenaude*

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RÉSUMÉ

Une des conditions essentielles de la préservation de la biodiversité des espèces est de comprendre les facteurs qui influencent leur distribution. L'importance de l'estuaire du Saint-Laurent (ESL) pour plusieurs espèces de mammifères marins de l'Atlantique Nord-Ouest est reconnue depuis longtemps, mais il existe très peu de données spatiales et temporelles sur leur abondance et leur distribution dans cette région. La modélisation prédictive peut aider à combler le manque d'information et à interpoler les prédictions de distribution sur l'aire potentielle d'utilisation par les mammifères marins. Un total de 4012 observations, portant sur neuf espèces de mammifères marins, recueillies lors de 100 relevés hebdomadaires effectués entre 2009 et 2014 dans l'estuaire maritime du Saint-Laurent, a servi à générer des cartes de probabilité de distribution des assemblages de mammifères marins sur l'ensemble de l'ESL. Une classification hiérarchique a été utilisée afin de définir les assemblages en regroupant les observations de mammifères marins en fonction de la similitude des relations entre les mammifères marins observés et quatre variables océanographiques, à savoir la température et la salinité de surface moyennes, la profondeur et la pente du fond. Les assemblages ont été caractérisés et leur biodiversité a été évaluée à l'aide d'indices écologiques. Le regroupement a révélé quatre assemblages utilisant trois types d'habitats : les eaux profondes du secteur du chenal Laurentien, les eaux peu profondes côtières et à la tête du chenal, et la pente du chenal. Les indices de diversité ont indiqué que les assemblages retrouvés dans les eaux peu profondes et la pente du chenal sont les plus diversifiés. Un modèle de régression logistique multinomiale a par la suite été utilisé afin de produire des cartes de distribution montrant la probabilité d'occurrence des assemblages en fonction des quatre variables océanographiques énumérées ci-dessus. Cet exercice a permis de qualifier l'importance des zones habituellement difficiles à qualifier en raison d'un manque de données. Ces nouvelles connaissances sur la biodiversité des mammifères marins de l'ESL pourraient aider à comprendre et prévoir les changements potentiels de la distribution des assemblages et de l'occurrence des espèces en réponse aux effets à long-terme des changements environnementaux, et ainsi contribuer à l'élaboration de mesures de conservation visant à protéger ces animaux.

Mots clés : mammifères marins, assemblages, estuaire du Saint-Laurent, modélisation prédictive, biodiversité

ABSTRACT

Understanding the distribution of species is a key prerequisite for the preservation of biodiversity. The St. Lawrence Estuary (SLE) has long been recognized as an important ecosystem for marine mammals of the western North Atlantic, but little data are available to assess the abundance and distribution of these species at different temporal and spatial scales. Predictive modeling can be used to fill these gaps and interpolate distribution predictions over the potential range of species. A total of 4,012 sightings of nine species detected during 100 weekly surveys carried out between 2009 and 2014 in the Lower SLE were used to generate probability distribution maps of marine mammal assemblages for the SLE as a whole. Hierarchical clustering was used to define assemblages by grouping marine mammal sightings according to the similarity of their relationships with mean sea surface temperature and salinity, depth and slope. The resulting assemblages were characterized, and their diversity was measured using diversity indices. Hierarchical clustering revealed four assemblages found in three types of habitats: deeper waters of the Laurentian Channel, shallower waters near the coast and at the head of the Channel, and slope of the Channel. Diversity indices indicated that assemblages found in shallower waters and on the slope of the Channel were more diverse. A multinomial logistic regression model was then used to generate distribution maps showing the probability of assemblage occurrence based on the four environmental variables. This exercise allowed us to qualify the importance of areas usually difficult to qualify due to the lack of data. This increased knowledge of marine mammal biodiversity in the SLE could help us understand and predict the potential changes in assemblage distribution and species occurrence in response to long-term climate change effects, and therefore has the potential to guide the development of efficient management actions for the conservation of these animals.

Keywords: marine mammals, assemblages, St. Lawrence Estuary, predictive modeling, biodiversity

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INTRODUCTION GÉNÉRALE

La biodiversité à la base des services écosystémiques

La dégradation des écosystèmes naturels par l'homme menace de plus en plus la biodiversité des milieux terrestres et marins et met en péril leur équilibre fragile. À l'aube de 2020, pratiquement tous les écosystèmes de la planète ont été touchés par une ou plusieurs activités d'origine anthropique, et le déclin de centaines d'espèces a été enregistré dans la majorité des biomes (Butchart et al., 2010). L'utilisation excessive et la dégradation du territoire, les changements globaux, les espèces invasives, la surexploitation et la pollution sont les principales causes connues de ce déclin. L'importance de l'impact de ces vecteurs varie selon le type de vecteur, mais aussi en fonction des écosystèmes. Par exemple, la dégradation du territoire liée à la déforestation est le vecteur ayant le plus affecté les écosystèmes terrestres dans les dernières décennies, alors que la surexploitation liée aux pratiques de pêche mal ou non gérées a eu le plus grand impact sur les écosystèmes marins (Millennium Ecosystem Assessment, 2005). Confronté à l'une des plus grandes crises de la biodiversité qu'il ait connue, l'Homme n'a d'autre choix que de trouver des solutions, adaptées aux différents types d'écosystèmes, afin de préserver les richesses naturelles qui lui sont essentielles.

La biodiversité est à la base des services écosystémiques dont la race humaine dépend. Ces services relèvent de plusieurs catégories, allant de la production primaire à l'offre d'habitat, de l'approvisionnement en nourriture à la régulation du climat, etc. Une biodiversité élevée renforce la stabilité des écosystèmes. Les communautés biologiques présentant une biodiversité supérieure contiennent entre autres plus d'espèces clés ayant une influence positive sur la productivité des écosystèmes. À l'inverse, une perte de biodiversité peut réduire l'efficacité des communautés écologiques à capturer les ressources

biologiques essentielles, à produire de la biomasse et à décomposer et recycler les nutriments essentiels (Cardinale et al., 2012). La perte d'espèces diminue donc concrètement l'efficacité de fonctionnement d'un écosystème (Isbell et al., 2018).

Le milieu océanique et les préoccupations en matière de préservation de la biodiversité

Les écologistes terrestres reconnaissent depuis longtemps l'importance de la biodiversité comme indicateur de la santé et du bon fonctionnement des écosystèmes. La conservation des *hotspots* de biodiversité dans les écosystèmes terrestres est effectivement connue depuis longtemps comme un outil efficace de protection visant plusieurs espèces simultanément (Worm et al., 2003). Toutefois, à cause du peu d'attention accordée aux écosystèmes océaniques par rapport au milieu terrestre – ce dernier étant souvent plus accessible que son homologue marin, les connaissances sur la biodiversité marine sont largement incomplètes, ce qui fait que le lien entre la biodiversité et son incidence sur les écosystèmes marins est encore bien mal compris. Ceci empêche le développement de mesures de protection et de conservation crédibles et réellement efficaces. La nécessité de documenter davantage la diversité des espèces aquatiques devient urgente, surtout compte tenu des préoccupations liées au réchauffement climatique, à la dégradation des habitats et aux menaces anthropiques qui se révèlent de plus en plus complexes (Archambault et al., 2010).

L'importance des prédateurs apicaux en tant qu'outils de conservation

La biodiversité est une notion aussi vaste que complexe, et il est difficile de savoir comment s'y prendre pour la protéger. Mais, étant donné que les effets du déclin de la biodiversité sont au cœur d'un grand nombre de recherches depuis les 30 dernières années, plusieurs approches existent aujourd'hui afin de protéger la diversité biologique des écosystèmes (Cardinale et al., 2012). Certaines approches plus traditionnelles, par exemple,

sont centrées sur la protection d'espèces frôlant l'extinction et qui, de par leur profil dit plus « *glamour* », captent l'attention d'un plus grand nombre de gens (Scott et al., 1993). Mais en cette ère de défis de conservation grandissants, plusieurs s'entendent sur la nécessité d'adopter une vision plus globale afin de préserver la biodiversité sur une plus grande échelle. Une des alternatives possibles consiste à considérer plusieurs espèces à la fois, notamment les espèces dites représentatives. Celles-ci se retrouvent dans trois grandes catégories : les espèces fondamentales, indicatrices et parapluie. Les espèces fondamentales jouent un rôle essentiel dans la structure, le fonctionnement et la productivité d'un habitat. Leur rôle est souvent disproportionné par rapport à leur abondance. Les espèces indicatrices, elles, informent sur la santé ou la qualité d'un écosystème. Elles reflètent la présence d'autres espèces dans la communauté, mais reflètent également les changements dans l'environnement. Les espèces parapluie sont celles dont la protection entraîne aussi celle d'autres espèces qui fréquentent le même milieu (Simberloff, 1998). Le fait de concentrer les efforts sur ces espèces clés peut être bénéfique à la protection de la biodiversité, surtout si leur protection résulte par le fait même en la conservation d'un plus grand nombre de taxons (Walpole & Leader-Williams, 2002).

Les grands prédateurs apicaux – ces espèces situées aux plus hauts rangs du réseau trophique et qui, en général, se nourrissent principalement de vertébrés – ont toujours fasciné les humains. L'ours, le lion, le grand requin blanc et l'orque ne sont que quelques exemples d'animaux qui fascinent et inspirent le respect. Les scientifiques ont su exploiter la popularité de ces espèces comme levier d'action afin d'obtenir un support financier et accroître la sensibilisation du public. Mais le charisme de ces animaux n'est pas le seul facteur venant justifier leur protection : ces prédateurs peuvent réellement être considérés comme des espèces représentatives constituant des outils de conservation concrets et efficaces (Sergio et al., 2005). Sergio et al. (2008) ont publié une étude sur les liens entre les grands prédateurs et la biodiversité, et sur l'efficacité de leur protection en termes de bénéfices apportés aux écosystèmes. Selon eux, la présence de prédateurs dans un écosystème serait hautement susceptible d'entraîner une hausse de biodiversité en facilitant le flux de ressources et en déclenchant des réactions en chaîne causant une restructuration

des communautés. Et si la présence de prédateurs n'est pas toujours directement associée à une biodiversité accrue, elle semblerait au moins y être liée dans l'espace et dans le temps. Par exemple, la densité de carnivores terrestres (Carroll et al., 2001), de rapaces (Seoane et al., 2003; Sergio et al., 2003) et de prédateurs marins (Worm et al., 2003) a déjà été corrélée avec plusieurs paramètres de productivité écosystémique, qui eux, constituent des indicateurs de valeur de la diversité. De plus, les grands prédateurs sélectionnent généralement des habitats très complexes, où une forte biodiversité est favorisée par une combinaison de caractéristiques spécifiques. Les prédateurs apicaux sont également très sensibles aux perturbations de leur milieu (p. ex., pollution chimique, altération et fragmentation de l'habitat). Celles-ci sont susceptibles d'avoir un impact sur toute la communauté et donc sur la biodiversité de l'écosystème. Les prédateurs apicaux possèdent donc des qualités d'espèces fondamentales et indicatrices qui justifient leur protection, en raison, d'une part, de leur important rôle écosystémique, et d'autre part, de leur valeur en tant qu'espèces bioindicatrices. De plus, vu les exigences en termes de taille et d'interconnectivité de leurs aires d'alimentation et de reproduction, les grands prédateurs constituent d'excellentes espèces parapluie dont les besoins englobent ceux de plusieurs autres espèces (Roberge & Angelstam, 2004).

Le rôle des mammifères marins dans les écosystèmes océaniques

Les mammifères marins, groupe d'espèces englobant cétacés, pinnipèdes et siréniens, sont des organismes de grande taille hautement mobiles et vivant dans des environnements extrêmement dynamiques. Ils fréquentent tous les océans entre les deux pôles, et tous les types d'environnement, de côtiers à océaniques. Certains même se retrouvent dans les milieux d'eau douce. Ils occupent une large gamme de niches écologiques, ce qui leur confère une haute tolérance à un large éventail de conditions environnementales. Leur capacité de déplacement sur de longues distances, leur grande taille, leur abondance et leur taux métabolique élevé sont des facteurs qui contribuent à l'influence qu'ils exercent sur la

structure et le fonctionnement des écosystèmes marins (Harwood, 2001; Kiszka et al., 2015).

En raison de leur capacité à extraire d'énormes quantités de proies, ils ont une forte incidence sur la structure des communautés et la dynamique des populations qui se propage sur tout le réseau trophique (Bowen, 1997). À l'inverse, la grande taille des mammifères marins, en particulier de plusieurs espèces de cétacés, fait aussi d'eux des proies de choix pour plusieurs grands prédateurs, comme les épaulards ou les requins blancs par exemple, un détail important sachant que les ressources alimentaires en milieu océanique sont généralement dispersées et limitées (Roman et al., 2014). Les mammifères marins jouent également un rôle significatif dans le recyclage et le transfert horizontal et vertical de nutriments, et aident ainsi à maintenir la stabilité et la santé des océans. Lorsqu'ils plongent en profondeur pour s'alimenter et remontent à la surface pour respirer, ils peuvent relâcher d'énormes panaches fécales qui injectent dans les eaux de surface une quantité considérable de nutriments essentiels et limitants provenant des profondeurs. Cette facilitation de nutriments stimule la croissance du phytoplancton qui constitue la base du réseau trophique océanique (Roman & McCarthy, 2010).

Un grand nombre de mammifères marins, en particulier les cétacés, sont reconnus pour leurs longues migrations. Plusieurs espèces parcourent des milliers de kilomètres chaque année pour se déplacer entre les aires d'alimentation et les aires de mise bas, transportant ainsi de l'engrais, sous forme de fèces, d'endroits très productifs vers des endroits peu productifs. Le rôle de ces géants est également important après leur mort (Branch & Williams, 2006). Les carcasses de baleines, par exemple, constituent une source significative de débris océaniques. Lorsqu'elles coulent au fond de l'océan, ces carcasses offrent une source de nourriture concentrée pouvant supporter une succession de communautés biologiques pendant plusieurs années voire décennies (Smith et al., 2015). Les ressources alimentaires étant très rares en haute mer, cet apport ponctuel fournit une partie importante de l'énergie nécessaire aux micro-organismes qui la réintroduisent ensuite dans le réseau trophique. Plus de 400 espèces, incluant charognards, détritivores et

bactéries, seraient associées à ces carcasses, et une trentaine de celles-ci seraient endémiques (Dahlgren et al., 2006; Smith & Baco, 2003). Pour toutes ces raisons, les mammifères marins contribuent à la bonne santé de leur environnement et constituent une composante essentielle des écosystèmes marins. La protection de ces grands prédateurs est fondamentale et essentielle à toute action visant à mieux préserver et favoriser la biodiversité de leur milieu.

Les mammifères marins et le Saint-Laurent

Le système hydrographique du Saint-Laurent représente une aire d'alimentation importante pour plusieurs espèces de mammifères marins du nord-ouest de l'océan Atlantique. La présence de nourriture abondante, stimulée par l'interaction favorable des conditions océaniques de l'estuaire du Saint-Laurent et de sa topographie accidentée, attire chaque année, de nombreuses espèces de poissons, d'oiseaux marins, et bien sûr, de pinnipèdes et de cétacés. La plupart de ces derniers effectuent d'importantes migrations annuelles, parcourant ainsi les dizaines de milliers de kilomètres qui séparent leurs aires de reproduction de leurs zones d'alimentation. Pour plusieurs, le Saint-Laurent représente une opportunité incontournable de s'approvisionner en nourriture et de reconstituer leur réserve de gras, indispensable pour le bon déroulement de leur cycle vital. Une vingtaine d'espèces de mammifères marins, incluant phoques, marsouins, baleines, rorquals et dauphins, sont recensées chaque année dans les eaux du Saint-Laurent, et près de la moitié sont fréquemment observées dans l'estuaire du Saint-Laurent, qui se trouve à plusieurs centaines de kilomètres de l'océan Atlantique.

Malgré cette impressionnante diversité d'espèces, les données quantitatives sur l'abondance et la distribution d'un grand nombre d'entre elles demeurent incomplètes, voire inexistantes. De plus, les sources d'information sont sporadiques, regorgent d'incertitudes et ne couvrent souvent qu'un secteur de l'estuaire ou du golfe du Saint-Laurent, ou une période restreinte de l'année (Gagné et al., 2013). Ce manque de

connaissances est entre autres lié aux divers défis posés par l'étude des espèces en milieu marin. En effet, les relevés visant la récolte de données sur les espèces marines sont souvent complexes et coûteux à organiser, en plus d'être grandement dépendants des conditions météorologiques. De plus, la grande variabilité dans les méthodologies utilisées entrave l'évaluation des tendances démographiques des espèces (Magera et al., 2013). Plus spécifiquement, les mammifères marins sont un des taxons de vertébrés les plus difficiles à étudier. Ils sont hautement mobiles et passent la majorité de leur temps sous la surface de l'eau. Certaines espèces sont solitaires, ce qui diminue grandement la probabilité de les détecter. De plus, l'environnement dans lequel elles vivent est vaste, et la plupart des espèces présentent des distributions qui s'étendent sur des milliers de kilomètres (Hunt et al., 2013).

L'insuffisance de données et de résultats interprétables représente un obstacle majeur aux prises de décision concernant la protection des mammifères marins de l'estuaire du Saint-Laurent, dont plusieurs espèces, notamment le béluga (COSEWIC, 2014) et le rorqual bleu (COSEWIC, 2012), qui ont un statut précaire. L'estuaire du Saint-Laurent est influencé par diverses pressions environnementales ou anthropiques; toutes les espèces de mammifères marins y passant une partie ou la totalité de leur cycle vital sont donc exposées à de multiples facteurs de stress (Williams et al., 2017). Ceux-ci incluent une importante navigation commerciale et récréotouristique, l'accumulation de contaminants industriels, la pêche commerciale, les changements climatiques et l'eutrophisation côtière (Dufour & Ouellet, 2007). Devant l'augmentation des activités humaines et leurs conséquences de plus en plus complexes sur les écosystèmes aquatiques, il devient urgent pour les organismes décisionnels de s'appuyer sur des connaissances et des avis scientifiques solides afin de limiter les dommages liés à ces activités (Savenkoff et al., 2017; Schloss et al., 2017).

Contexte, objectifs et hypothèses de l'étude

L'importance des mammifères marins pour le bon fonctionnement écosystémique de l'estuaire du Saint-Laurent est indéniable, mais mal comprise. Leur position dans le réseau trophique, leur rôle structurant ainsi que l'incidence positive qu'ils peuvent avoir sur la biodiversité de cet écosystème ne sont que quelques exemples qui poussent les scientifiques à recueillir un maximum d'informations sur ces espèces fondamentales afin de mieux les protéger, et par le fait même, de mieux protéger leur environnement. Ce projet de recherche constitue une pièce du casse-tête qu'est le concept de l'approche écosystémique, qui représente une solution possible aux problématiques de gestion liées à la détérioration des écosystèmes marins.

L'objectif principal de cette étude est de réaliser une analyse spatiale des assemblages de mammifères marins dans l'estuaire du Saint-Laurent. Plus précisément, il s'agit (1) d'approfondir nos connaissances sur la composition et la biodiversité des assemblages et (2) d'établir une corrélation entre leur distribution spatiale et les caractéristiques océanographiques de la zone d'étude, pour ensuite (3) générer un modèle prédictif et (4) produire des cartes de distribution des assemblages. Les analyses permettant d'exécuter ces étapes seront effectuées à partir d'une quantité considérable de données d'observations de mammifères marins recueillies lors d'une centaine de relevés systématiques effectués par bateau, et répétés dans une même zone d'étude et lors d'une même période de l'année et ce, pendant six saisons consécutives. Les cartes générées aideront à combler les lacunes causées par un manque de données important dans la région concernée. En effet, très peu de relevés, voire aucun, couvrent la totalité de l'estuaire, en particulier l'estuaire moyen, qui représente un habitat fréquenté par plusieurs espèces de mammifères marins, dont deux sont résidentes. Ceci limite notre compréhension de la distribution et de l'abondance de plusieurs espèces et freine le processus décisionnel en matière de gestion écosystémique.

L'hypothèse est que la distribution des assemblages de mammifères marins dans l'estuaire du Saint-Laurent est hétérogène et qu'elle est régie par certains paramètres environnementaux qui agissent étroitement sur la distribution et l'abondance des proies : la

température et la salinité de l'eau, la profondeur de l'eau et la topographie sous-marine. L'influence de l'environnement sur les espèces constituant les assemblages devrait être notée en examinant leur distribution, mais aussi en étudiant leur composition. Un faible chevauchement spatial entre les espèces est attendu, chevauchement qui devrait dépendre principalement d'espèces pélagiques peu motiles comme le zooplancton, d'espèces se nourrissant surtout de poissons pélagiques, et d'espèces se nourrissant essentiellement d'organismes démersaux. Les relations entre la composition des assemblages, la diète principale des espèces et les propriétés environnementales ayant une influence sur la distribution et l'abondance des proies des mammifères marins fréquentant l'aire d'étude devraient être suffisamment fortes pour prédire avec un degré de certitude relativement élevé la distribution spatiale des zones favorisant chaque type d'agrégation.

CHAPITRE 1:
SPATIAL ANALYSIS OF MARINE MAMMAL ASSEMBLAGES IN THE
ST. LAWRENCE ESTUARY (CANADA)

1.1 INTRODUCTION

There is a well-documented loss of marine biodiversity worldwide, which is mainly due to human activities and their resulting pressures (Butchart et al., 2010; Jenkins & Van Houtan, 2016; Jones et al., 2007; McCauley et al., 2015; Tittensor et al., 2010; Worm et al., 2006). Human existence relies permanently on the oceans, and its impacts have increased over the past decades, mainly as a result of population growth, major developments in technology and numerous changes in land use (Halpern et al., 2008). Pressures on the oceanic environment are persistent and result from multiple usages and stressors, with the most notable ones including habitat degradation, overfishing and bycatch, toxic spills and climate change (Halpern et al., 2015). Marine mammals are threatened by all of them, directly or indirectly (Heithaus et al., 2008). Although accidental mortality through fisheries bycatch and vessel strikes are the two dominant threats, especially for species found in coastal areas, chemical pollution, noise, climate change and disease affect a great percentage of marine mammal populations (Schipper et al., 2008).

Marine populations and species are disappearing from ecosystems at a rapid pace as a result of pressures on the marine environment; in the case of marine mammals, at least 20% of species are currently considered at risk of extinction (IUCN, 2017). Marine mammals play a key role in ecosystems, shaping communities through predation and nutrient recycling (Bowen, 1997; Schipper et al., 2008; Smetacek & Nicol, 2005). Both cetaceans and pinnipeds are indeed important consumers occupying a variety of trophic niches. Their ecological significance is determined by their abundance and large body size, and is directly related to their potential to consume large quantities of prey (Kiszka et al., 2015). Marine mammals also contribute to nutrient cycling and enhance the productivity of ecosystems by feeding at depths and then defecating in the euphotic zone, and by

transferring nutrients downward to benthic communities through sinking of their carcasses after death (Lavery et al., 2014; Roman & McCarthy, 2010). Because of their generally important ecological role, the depletion of marine mammal populations can cascade into a series of effects on the ecosystem dynamics and structure (Harwood, 2001).

Less is known about marine ecosystem functioning when compared to terrestrial ecosystems, mainly as a result of logistical and financial constraints associated with research in this environment, where opportunities to conduct controlled experiments like those offered on land remain relatively rare (Archambault et al., 2010; Bowen, 1997). This has contributed to limiting our understanding of global patterns in species richness and their predictors (Tittensor et al., 2010). These data gaps, along with the challenges of implementing and enforcing conservation policies in the marine environment, likely contributed to the observed difference in protection levels between the two environments: oceans cover more than two thirds of the planet, yet less than 4% of the marine environment has received formal protection whereas 12% of the land is protected through national parks and reserves (Jenkins & Van Houtan, 2016). Data paucity is exacerbated in the case of marine mammals by their often wide-ranging movements, their vast distribution range, and the substantial amount of time they spend beneath the surface (Kaschner et al., 2011). In addition, some species are highly pelagic, spending their lives in offshore waters, away from the continents. As a result of these ecological factors, surveys dedicated to collecting data on marine mammal habitat use and distribution often cover only a fraction of their distribution range (Kaschner et al., 2006).

To effectively assess impacts of environmental pressures on marine mammals and aim for meaningful conservation efforts, the distribution of species in relation to their environment must be understood (MacLeod et al., 2008). With the development of high-speed computers and geographic mapping technology of the past decades, predictive ecological modeling became an inescapable research tool for quantifying species-environment relationships (Ovaskainen et al., 2017). Predictive distribution modeling is an associative method that relates occurrence or density data at known locations for a given

species (distribution data) to environmental characteristics of those locations (Gomez & Cassini, 2015). This geostatistical approach allows the interpolation or extrapolation of a few field observations to the entire potential range of a species and can be used for predicting the probability of species occurrence-based habitat suitability. It represents an attractive solution for getting around challenges related to data paucity (Rodriguez et al., 2007). Predictive modeling of species distribution exploits various methods and statistical techniques depending on the type of input data. Presence-absence data offer the greatest potential for robust model predictions. However, the widespread availability of presence-only data with no reliable information about absence locations has stimulated the development of methods exploiting this type of data (Pearce & Boyce, 2006). Predictive modeling serves two main purposes: identifying environmental drivers of species distributions and predicting distributions in hypothetical scenarios, assuming that the variables included in the model are relevant to species distribution and habitat use (Gomez & Cassini, 2015). Predictive modeling of distribution has a plethora of applications in conservation biology. In the absence of data, or in support of partial information on species habitat use and distribution, this approach has become an important research tool to assess the impact of environmental change on the distribution of species and to implement and prioritize conservation actions (Guisan & Thuiller, 2005). Maps generated by predictive modeling also help in forecasting where risk of interactions between human activities and species are likely to occur (Rodriguez et al., 2007). Modeling species responses to environmental predictors using presence-only data represents an appealing solution to the data paucity that is recurrently associated with wide-ranging or cryptic species such as marine mammals (Ready et al., 2010).

In general, species distribution modeling operates on a single-species basis, i.e., it assumes that species respond individualistically to changes in their environment (Bonthoux et al., 2013). However, the distribution of species is likely to be influenced by the distribution of other taxa, either through competition, predation or interspecific associations and relationships. These negative and positive associations between species can be captured by using community-level predictive modeling and may help better forecast community-

level responses and potential changes in biodiversity spatial patterns, especially at a finer scale (Elith & Leathwick, 2007). Species assemblages represent important features of an ecosystem that contribute to its structure, diversity and stability (Francis et al., 2002). They are also an important parameter in describing habitat diversity and richness that can help identify biologically and ecologically significant areas and inform management decisions (Chouinard & Dutil, 2011; Kenchington et al., 2011). Community-level predictive distribution modeling can be done using three broad strategies. The first one consists in grouping species into assemblages first, and then modeling the distribution of these assemblages. A second strategy consists in predicting the distribution of individual species first, and then grouping these species into assemblages. The third strategy involves joint modeling of individual species and species assemblages (Chapman & Purse, 2011). The first approach was used in this study since it allowed using all the sightings, including those of species rarely observed, and explicitly accounted for species co-occurrence or co-exclusion (Ferrier & Guisan, 2006).

Modeling of community or assemblage responses to environmental factors has been conducted for a variety of species including benthic organisms (e.g., Degraer et al., 2008; Moritz et al., 2013), birds (e.g., Hyrenbach et al., 2007; Woehler et al., 2003), fish (e.g., Chouinard & Dutil, 2011; Tamdrari et al., 2015), insects (e.g., Dufrêne & Legendre, 1997; Kremen, 1992), mammals (e.g., Ahumada et al., 2011; Hortal et al., 2008) and plants (e.g., Ackerly & Cornwell, 2007; Lortie et al., 2004). Many have explored the usefulness of species assemblages as indicators of biological diversity and integrity, but despite this increasing interest for community-based research, little has been done to study the distribution of marine mammal assemblages due to the difficulty of gathering sufficient data. Examples of studies about the structure of marine mammal communities include work from (Baumgartner et al., 2001) who examined the distribution of five cetacean species groups in the Gulf of Mexico, from (Hamazaki, 2002), who constructed a cetacean habitat model in the mid-west North Atlantic using sightings from 13 cetacean species, and from (Schick et al., 2011), who used community ecology analyses to uncover the structure of pelagic marine mammal communities in three different areas of the western North Atlantic.

The St. Lawrence Estuary (SLE) is a productive area in Eastern Canada, where several species of marine mammals are known to occur either year-round or on a seasonal basis (Savenkoff et al., 2017). It is located downstream of industrialized areas and represents the main waterway to central North America in addition to supporting a multimillion-dollar whale-watching industry. Human pressures are numerous in this environment, and could be cumulative (Schloss et al., 2017), leading to habitat degradation through noise and disturbance, chemical contamination, and for some species, reduced availability of food resources as a result of fishing or climate variability (DFO, 2014; Lesage et al., 2017; Simard et al., 2010; Williams et al., 2017). Habitat use by the various species of marine mammals occurring in the SLE is currently poorly described (Lesage et al., 2007).

The objectives of this study were to use marine mammal presence-only data obtained during systematic line transect surveys in the SLE in order to: (1) explore, using multivariate analyses, the composition and distribution of marine mammal assemblages in the SLE, (2) describe the relationship between the probability of occurrence of each assemblage using environmental factors and community-level predictive modeling, and (3) predict the probable distribution of assemblages over a larger area of the SLE using multinomial logistic regression and changes in distribution according to scenarios of varying temperature and salinity.

1.2 METHODOLOGY

1.2.1 Study area

This study was conducted in the St. Lawrence Estuary, Canada, more specifically in the Lower SLE (LSLE), a 200 km long, 40 km wide body of water that extends from the mouth of the Saguenay Fjord, near Tadoussac, downstream to Pointe-des-Monts/Sainte-Anne-des-Monts, the western limit of the Gulf of St. Lawrence (GSL) (Figure 1). Due to its dimensions and major connections to oceanic waters, the LSLE is considered as a marine environment (El-Sabh & Silverberg, 1990). The Laurentian Channel (LC), a 350 to 450 m deep canyon that runs from the Atlantic Ocean off the continental shelf all the way through the LSLE, establishes a major link between the two environments, influencing the circulation, mixing and characteristics of water masses (Lavoie et al., 2000). The LC ends abruptly at the confluence of the Saguenay Fjord and the SLE, resulting in an upwelling of cold mineral-rich waters and enhanced productivity that attracts several marine species, including at least twelve species of marine mammals (Savenkoff et al., 2017). The beluga (*Delphinapterus leucas*) and the harbour seal (*Phoca vitulina*) are known residents of the SLE, although a portion of these populations seasonally migrate east into the GSL (Lesage et al., 2004; Mosnier et al., 2010).

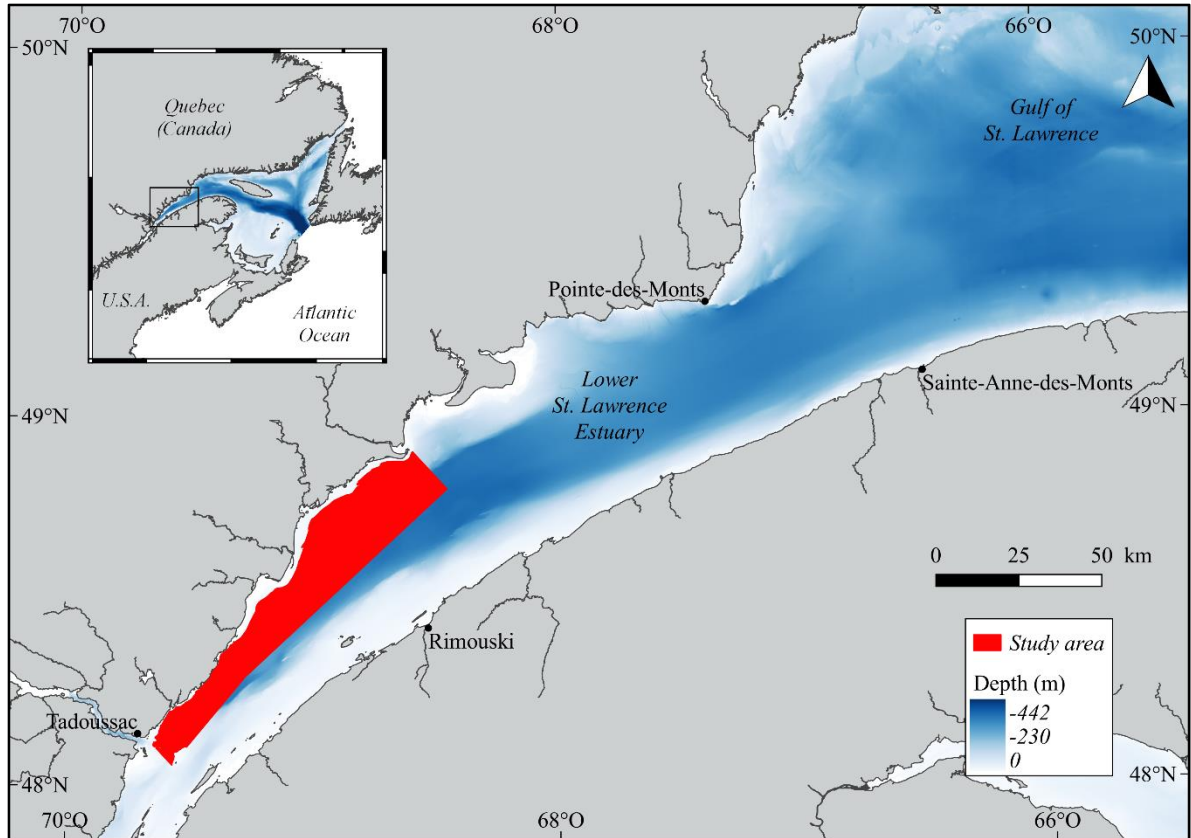


Figure 1. The Estuary and Gulf of St. Lawrence, Eastern Canada. The area where this study took place (in red) is located in the Lower St. Lawrence Estuary (LSLE).

1.2.2 Surveys and marine mammal sightings

Vessel-based surveys of the northern portion of the LSLE, including the LC (Figure 2), were conducted weekly (weather permitting) between April and November of 2009 through 2014. Start and end dates of surveys in the spring and fall varied between years according to ice conditions. The survey platform was a 32 feet long rigid hull zodiac (the Cetus) equipped with a cabin and a flying bridge where two observers were posted. Surveys covered an area of approximately 980 km² on average, and followed a systematic line transect design with a random start point for each survey. Transects were limited to waters 10 m deep or more. They were oriented across bathymetry gradients, were spaced by 7 km,

and were 13 km long on average. This sampling design afforded all points in the study area an equal probability of being sampled (Buckland et al., 2001).

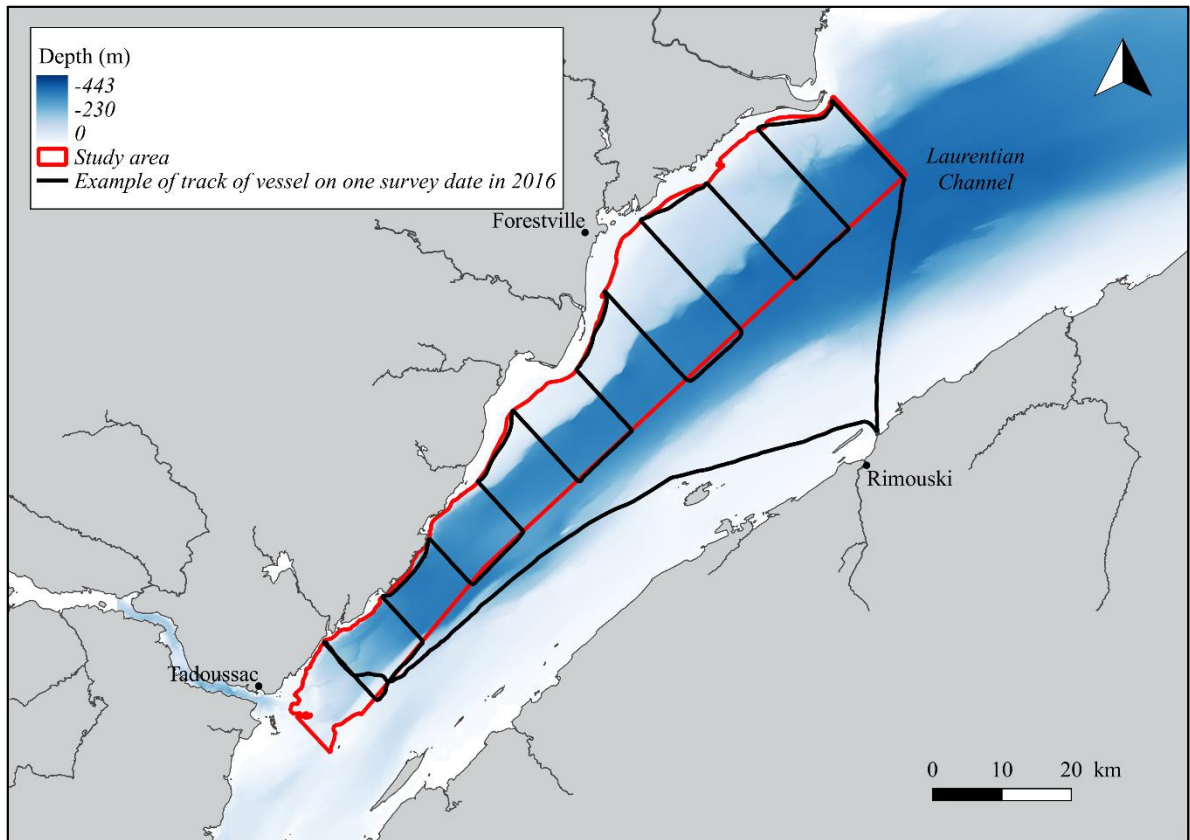


Figure 2. Typical sampling design on a survey day in the Lower St. Lawrence Estuary (LSLE). The red line delineates the area in which surveys were done. The black line is an example of a track followed by the research vessel. Observers were on effort when surveying perpendicular to the coast; only opportunistic sightings were collected during transits between transects (parallel to the coast) and these were not included in the analysis. Depth data were obtained from a 50 m resolution raster created by interpolating data from the Canadian Hydrographic Service.

Observers varied between survey days and years, given the time span of this study. However, they were trained by experienced observers over multiple surveys before being considered as primary observers. All aquatic megafauna species encountered were recorded; sightings of sea turtles, sharks or tunas were highly infrequent and were not

considered here. Observers recorded information on audio tape recorders and searched for megafauna primarily with the naked eye, and periodically using binoculars. They noted the species, number of individuals (young and adults combined), time, relative angle of the sighting with respect to the heading of the vessel, and relative distance using primarily reticules in the binoculars, or naked eye when the sighting was within 50 m from the survey platform. Weather conditions (sea state, sun glare intensity, cloud cover and visibility) were also recorded at the beginning and at the end of each transect, or as they changed during transects. Information on relative distance and angle from the vessel were used to position each sighting. Only sightings of positively identified species were retained for the analyses.

1.2.3 Environmental data

When predicting the spatial or temporal distribution of wildlife, it is always best to rely on ecological parameters believed to be the driving forces of their distribution (Guisan & Zimmermann, 2000). Prey availability is the variable most likely to affect marine mammal distribution during the foraging season (Baumgartner et al., 2001). In the LSLE however, the near-absence of fishing activities has resulted in little scientific effort being steered toward monitoring invertebrate and fish abundance and distribution (Mosnier et al., 2016). While data exist for some species, there was a mismatch in the temporal and spatial resolutions of the available data on prey species distribution and abundance and the data on marine mammal occurrence collected during the systematic surveys. Because the aggregation and distribution of zooplankton and fish are often driven by physical environment properties, abiotic variables can be used as a proxy for prey distribution (Torres et al., 2008). For the subsequent analyses, such variables were selected considering their likely ecological significance for marine mammal occurrence as well as data availability (Correia et al., 2015).

Four environmental variables were gathered from different sources. Depth was obtained from a 50 m resolution raster created by interpolating data from the Canadian

Hydrographic Service (Figure 2). Bottom changes in topography (slope) were derived from the same raster by calculating the maximum rate of change (in degrees) in depth between neighbouring cells (Figure 3). Data for these two variables were extracted and compiled for each georeferenced sighting recorded during the 2009 to 2014 observation period.

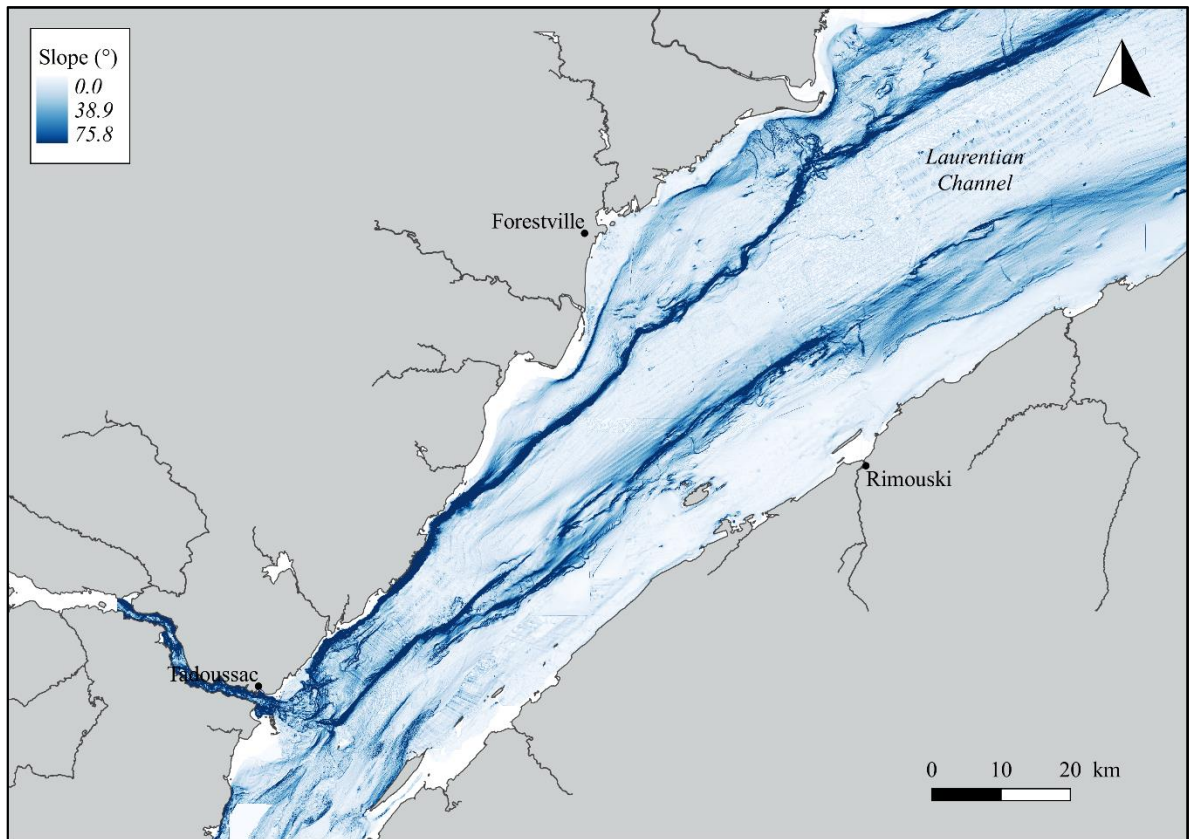


Figure 3. Bottom slope (in degrees) of the Lower St. Lawrence Estuary (LSLE) computed from depth data obtained from a 50 m resolution raster created by interpolating data from the Canadian Hydrographic Service.

Predictive models combining static (e.g., depth and slope) and dynamic variables (variables that change over the timeframe being modeled) tend to perform better than models based on static variables alone (Ballance et al., 2006). Therefore, sea surface temperature (SST) and salinity (SSS) were added because they may represent good proxies for species distribution in marine habitats (Correia et al., 2015; Redfern et al., 2006). These

parameters were not collected during the surveys, so other available sources, including remotely sensed data and models of oceanographic processes, were exploited. Data on SST were extracted from NOAA's Advanced Very High Resolution Radiometer satellite images (~ 1.1 km resolution; available at ogsl.ca). Eleven different values of SST were considered: mean SST over the 1, 3, 5, 7 and 15 d previous to the sighting including survey date, 3 and 5 d means centered on the survey date, and 3 d means with a 3, 5, 7 and 15 d lag from the survey date. Collinearity among these variables was examined using Pearson's correlation coefficients (r). SSTs with $r > 0.5$ were considered correlated and the SST value with the least amount of missing data was kept while the others were removed from the dataset. SSS at the sighting location was estimated (~ 6 km resolution) from an oceanographic model for each survey date (Saucier et al., 2009; Saucier & Chassé, 2000). Sightings with missing data on one or more environmental variables, which represented < 1% of the initial data, were eliminated from the dataset. Environmental variables (depth, slope, SST and SSS) were standardized (mean of 0, variance of 1) to avoid biases associated with discordant scales.

Other variables potentially useful for describing marine mammal habitats were not included in the analysis as they were limited in their spatial resolution and distribution, and would have resulted in the loss of a high number of sightings. These variables included surface and subsurface water properties (i.e., depth of thermocline, mixed layer and euphotic zone, sea surface dynamic height, frontal regions), water conditions or index of productivity (i.e., fluorescence, chlorophyll a, dissolved oxygen content, water color), bathymetry (i.e., distance to shelf edge, distance to shore) and prey availability (Dransfield et al., 2014; Redfern et al., 2006, 2017). Other variables, like depth of the cold intermediate layer and euphotic zone, sea level anomalies, oceanic fronts and sediment grain size were explored for inclusion in a previous study specifically examining beluga habitat but were discarded for various reasons (see Mosnier et al., 2016).

1.2.4 Statistical analysis and modeling framework

Species presence-only data were used to model assemblage distribution as opposed to species abundance. The presence of certain constraints regarding the size of the study area, the resolution of environmental layers used as background data, and the number of marine mammal sightings made presence-only data the optimal data to use in order to reach our research objectives. Results of occurrence models are still considered as good indicators of variations of species abundance, and these models do reflect environmental suitability, where more taxa should inhabit most suitable areas (Estrada & Arroyo, 2012).

Marine mammal assemblages in the LSLE were identified using a hierarchical cluster analysis performed on the environmental data and based on a dissimilarity matrix. Ward's minimum variance agglomeration method (Ward, 1963) was preferred over other common linkage methods as it is less susceptible to be distorted by outliers (Blashfield, 1976; Hands & Everitt, 1987; Kuiper & Fisher, 1975). The Euclidean distance was chosen over non-Euclidean distances or dissimilarity measures such as the Bray-Curtis dissimilarity index, the Manhattan distance or the Jaccard index because the analysis was performed on the similarity of sightings (presence data) in relation to environmental variables that described them, and not on species abundances.

Three methods were used to identify the appropriate number of clusters for describing our dataset on marine mammal sightings. First, a static tree cut method was applied to define separate clusters as contiguous branches below a fixed height cut-off (Langfelder et al., 2008). Second, total within-cluster sum of squares was calculated for the k possible clusters, and k with the smallest sum of squares was selected as the appropriate number of clusters. Finally, the choice of the appropriate number of clusters was validated using Hubert's statistic, a graphical method in which one searches for a significant peak of second differences, which corresponds to the relevant number of clusters in a dataset (Charrad et al., 2014; Hubert & Arabie, 1985).

An analysis of group similarities (ANOSIM) with 4,999 permutations was performed to verify that observations in the various clusters differed in their environmental characteristics, i.e., to determine whether the assemblages displayed different environmental characteristics. Between-cluster differences for each of the environmental variables were examined using univariate Kruskal-Wallis rank sum tests, and specific clusters differing in characteristics were identified using pairwise comparisons and Bonferroni-corrected *post hoc* Wilcoxon rank sum tests.

Clusters of observations, hereafter referred to as assemblages, were then described in terms of species composition, dominant species and biodiversity. The proportions and relative abundances of sightings (percentages of sightings of one species in each assemblage and percentages of sightings of the various species in a given assemblage, respectively) were considered. Variations in the proportion of sightings of each species within each assemblage were also tested with Pearson's Chi-squared tests. Dominant species were assessed by comparing their relative abundances of sightings in each assemblage. Assemblage biodiversity was considered in three ways: species richness, diversity and evenness. Species richness (S) is the total number of species. Species diversity was measured using Shannon's diversity index (H'), which considers the relative frequency of each species, as well as the number of individuals for each species. Species evenness, referring to how evenly the individuals are distributed across species, was measured using Pielou's evenness index (J) to analyze the uniformity of assemblages (Magurran, 2004).

Multinomial logistic regression (MLR) was used to predict the probability of a sighting falling into a given assemblage given its characteristics in terms of the following four independent continuous variables (X): mean SST over the 15 days previous to the sighting including survey date (SST15), mean SSS on survey date (SSS1), depth and slope. MLR is an extension of a logistic regression, where the response variable (Y) is nominal, i.e., it has multiple categories ($k > 2$) that cannot be ordered in any meaningful way. When $k > 2$, there are $k * (k - 1) / 2$ logit functions that can be formed, of which only $(k - 1)$ are non-redundant. The $k - 1$ logit functions are regressed against a "pivot" category of the

response variable, where coefficients are estimated using maximum likelihood, as opposed to an ordinary least square estimator. The choice of the pivot category does not affect the estimated coefficients, calculated probabilities or significance of variables (Menard, 1995).

In our study, the outcome variable had four categories; therefore, there were three equations following the same generic structure, in which the log of the odds ratios were calculated for all other categories (assemblage 2, 3 or 4) relative to the pivot category (assemblage 1), resulting in a linear function of the predictors:

$$\ln\left(\frac{\text{Prob. } Y}{\text{Prob. } 1}\right) = \beta_0 + \beta_1(SST15) + \beta_2(SSS1) + \beta_3(\text{Depth}) + \beta_4(\text{Slope})$$

All models with a combination of one to all variables were tested. The *multinom* function from the *nnet* R package (Venables & Ripley, 2002) was used for MLR estimations. Selection of the model best predicting observations was based on the Akaike Information Criterion (AIC) where the best model was the one with the lowest AIC (Akaike, 1974). The relevance of each environmental variable was examined by leaving one variable out at a time and by comparing residual deviances of resulting models with the optimal model. The predictive performance of the selected model was tested by running the MLR on a “training” dataset composed of 3,212 randomly selected sightings from the main dataset, representing 80% of the sightings. The accuracy of predictions about assemblage membership was tested using the remaining 800 observations by comparing model predictions with the observed assemblage assignments and estimating classification error rates.

MLR makes no assumption about the relationship between the dependent and independent variables, the distribution of data, the errors or the variance. However, MLR makes the assumption of observation independency and may be sensitive to multicollinearity and to small sample size given that MLR uses maximum likelihood to estimate regression parameters (Quinn & Keough, 2002). Given that all assumptions can rarely be met in empirical data, validation of model predictions is often performed using an independent source of data.

Model predictions, i.e., probability of a sighting being assigned to a given assemblage considering the selected environmental characteristics, were plotted on a 1 km grid cell covering the SLE from the area north of Seal Islands in the Upper SLE and Forestville in the LSLE (Figure 4). This was done for five scenarios, in which values of SST and SSS changed, to assess the effect of the variability in dynamic variables on model predictions. SST (15 d means) was extracted for five time periods in 2014 (Table 1). SSS (1 d means) of the last day of each time period was estimated using an oceanographic model (refer to section 1.2.3 for methodology on the extraction of SST and estimation of SSS). In each scenario, cells of the prediction grid were attributed the value of each predictor variable at the cell centroid. Cells with a centroid located on land were deleted from the prediction grid. Data were analyzed using R version 3.4.1 (R Core Team, 2017). Geographical distribution of marine mammal assemblages was mapped using ArcGIS software (version 10.2, ESRI Inc.).

Table 1. Names, time periods and days used for the extraction of mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15) and estimation of mean sea surface salinity on survey date (SSS1) for the five scenarios used to model assemblage membership for each 1 km cell of the prediction grid.

Scenario	Name used	Time period for SST15 extraction	Day used for SSS1 estimation
1	April	March 24 - April 7	April 7
2	June	June 2 - 16	June 16
3	July	July 8 - 22	July 22
4	August	August 14 - 28	August 28
5	September	September 16 - 30	September 30

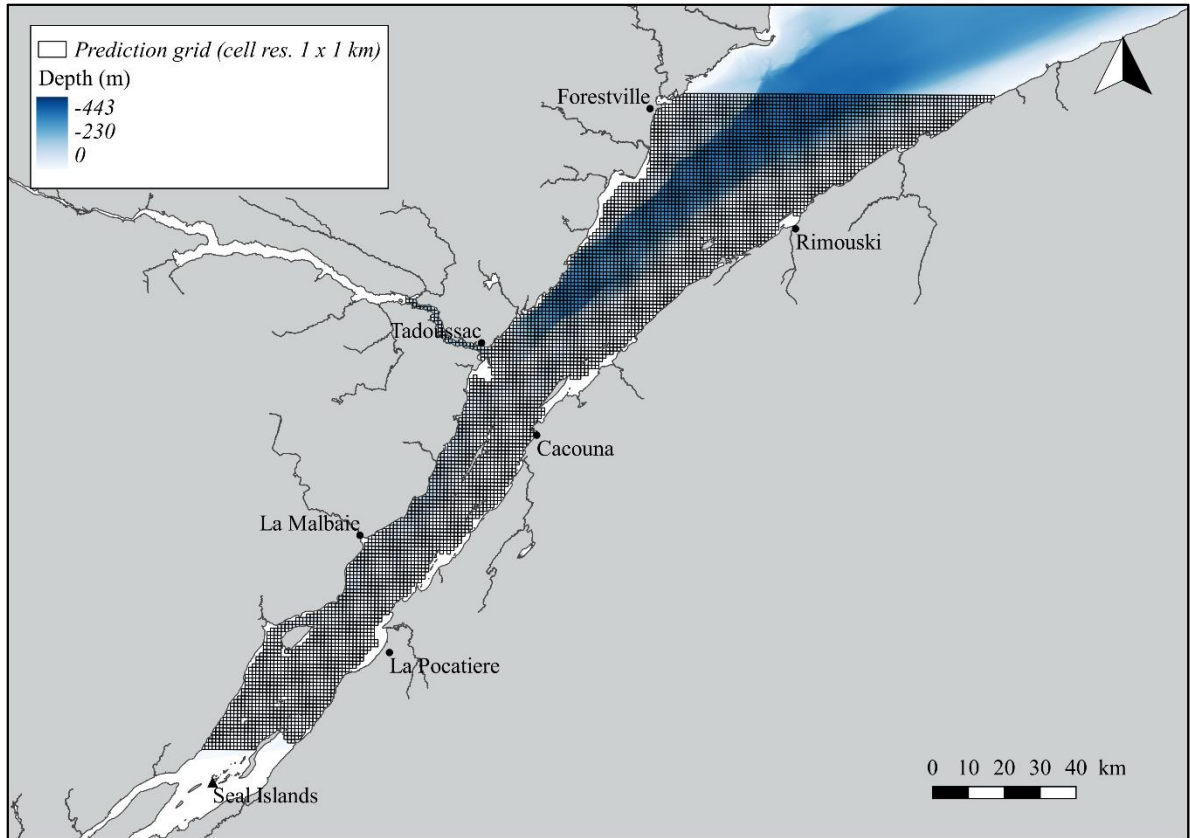
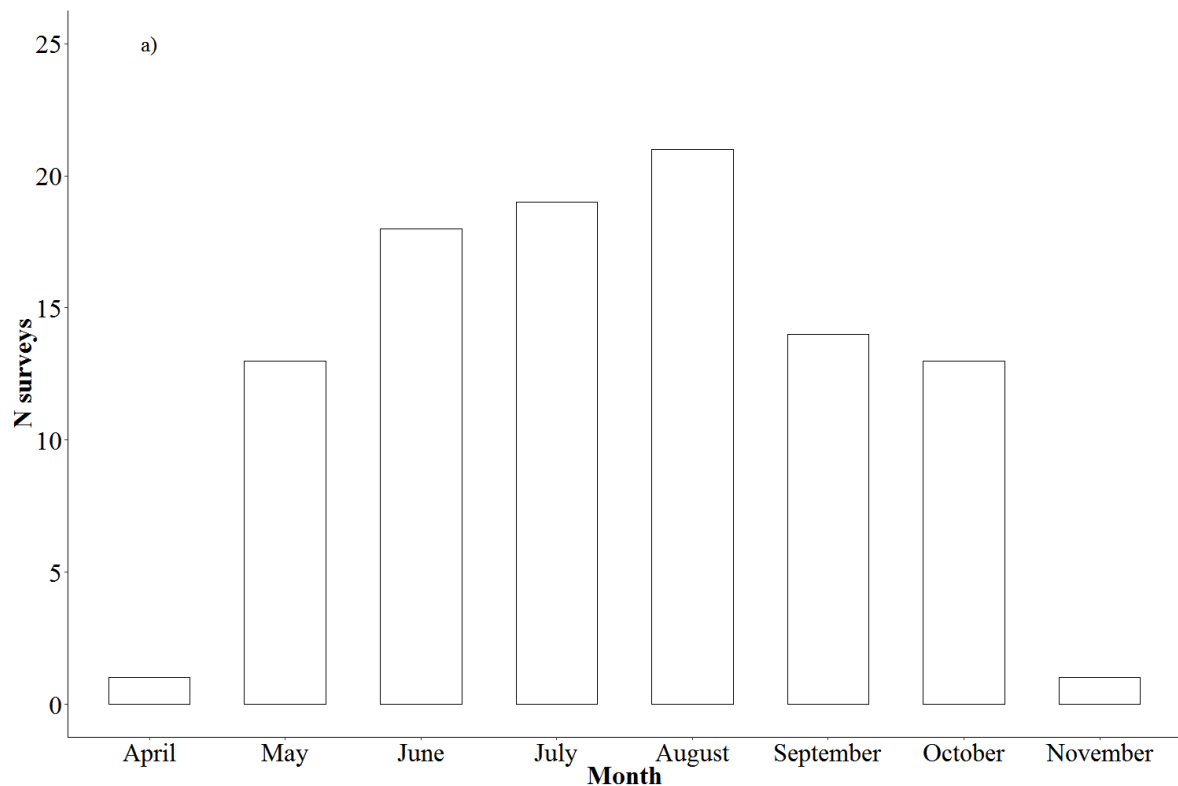


Figure 4. Grid used for predicting probable assemblage distribution (1 km grid cell).

1.3 RESULTS

1.3.1 Marine mammal sightings

Between 11 and 25 weekly surveys were completed each year between April and November, mainly between May and October, resulting in 100 surveys for the period of 2009 to 2014, and 4,029 sightings of nine marine mammal species (Figure 5a). Species included baleen whales [minke whales (*Balaenoptera acutorostrata*), blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*)], odontocetes [belugas (*Delphinapterus leucas*) and harbour porpoises (*Phocoena phocoena*)], and pinnipeds [grey seals (*Halichoerus grypus*), harp seals (*Pagophylus groenlandicus*) and harbour seals (*Phoca vitulina*)] (Figure 6).



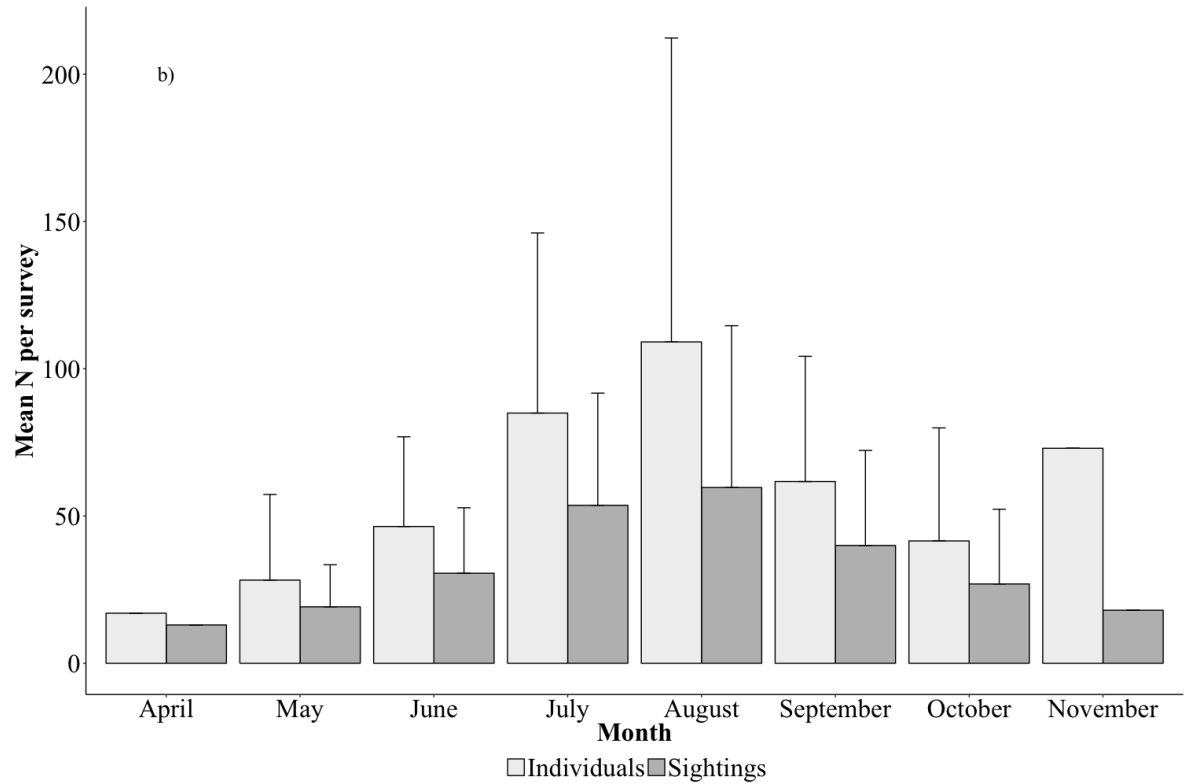
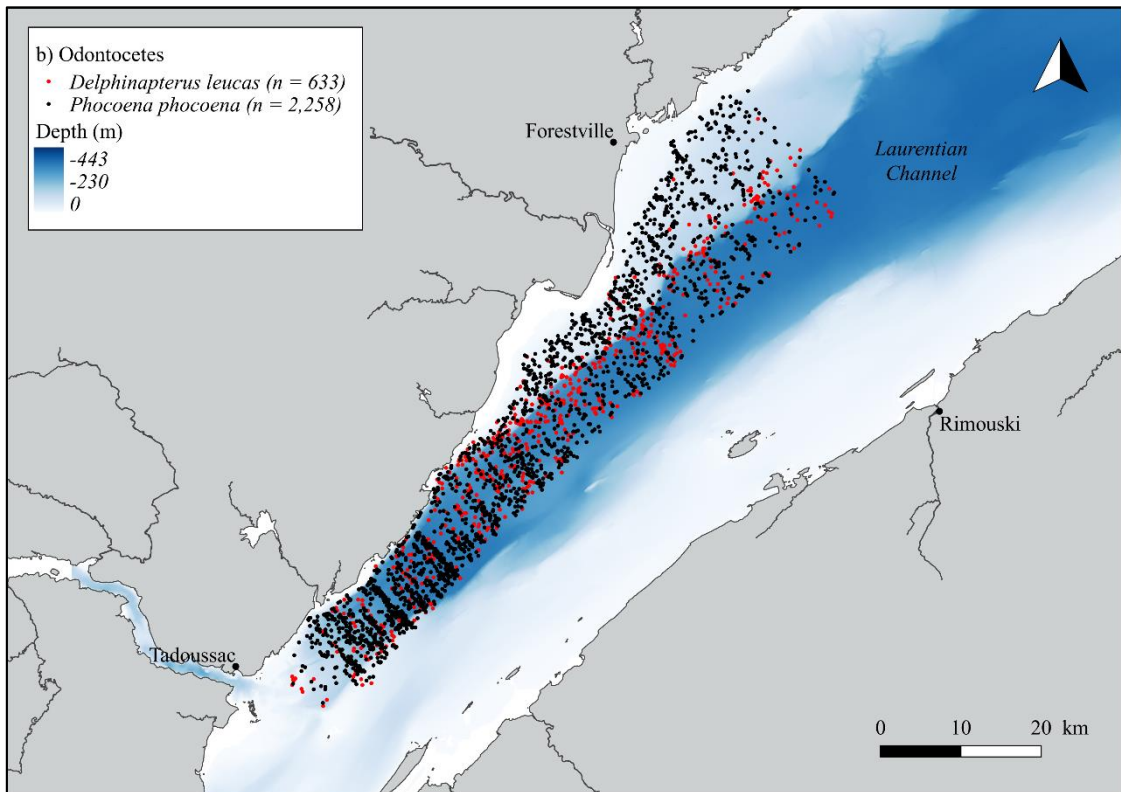
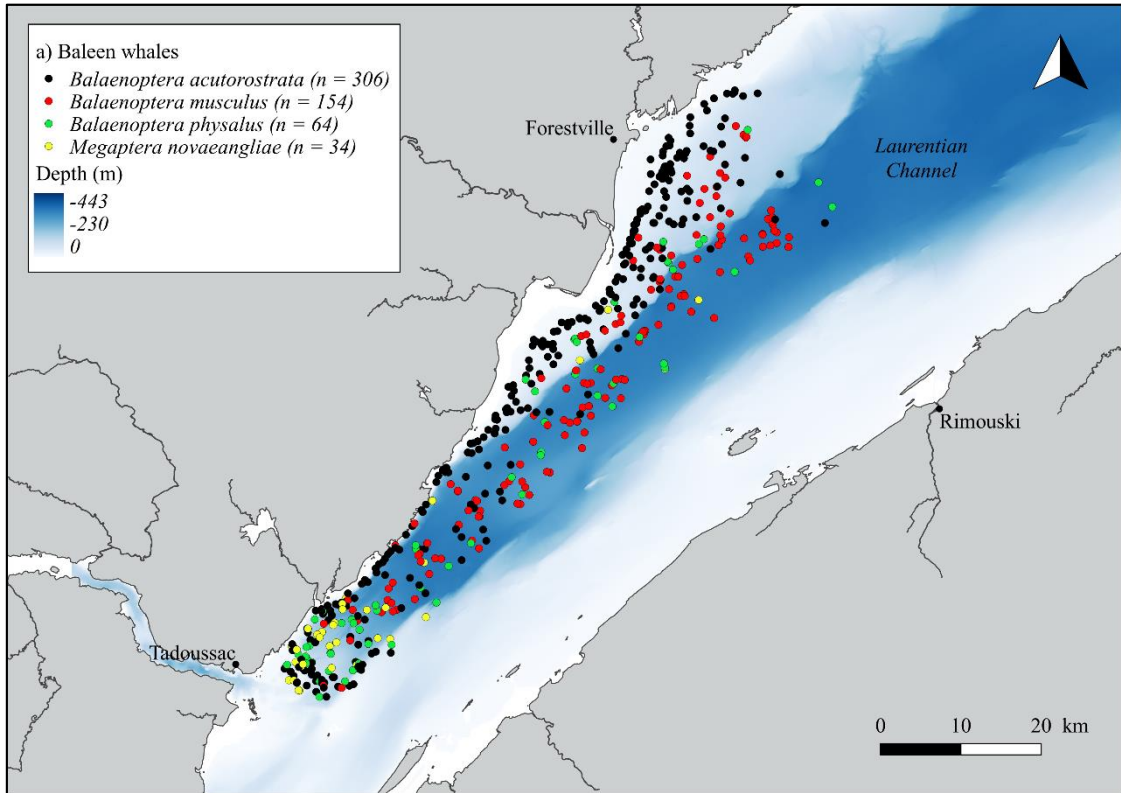


Figure 5. a) Number of surveys per month, and b) effort-corrected seasonal change in the number of sighted individuals (light grey bars) and sightings (dark grey bars) (\pm SD).



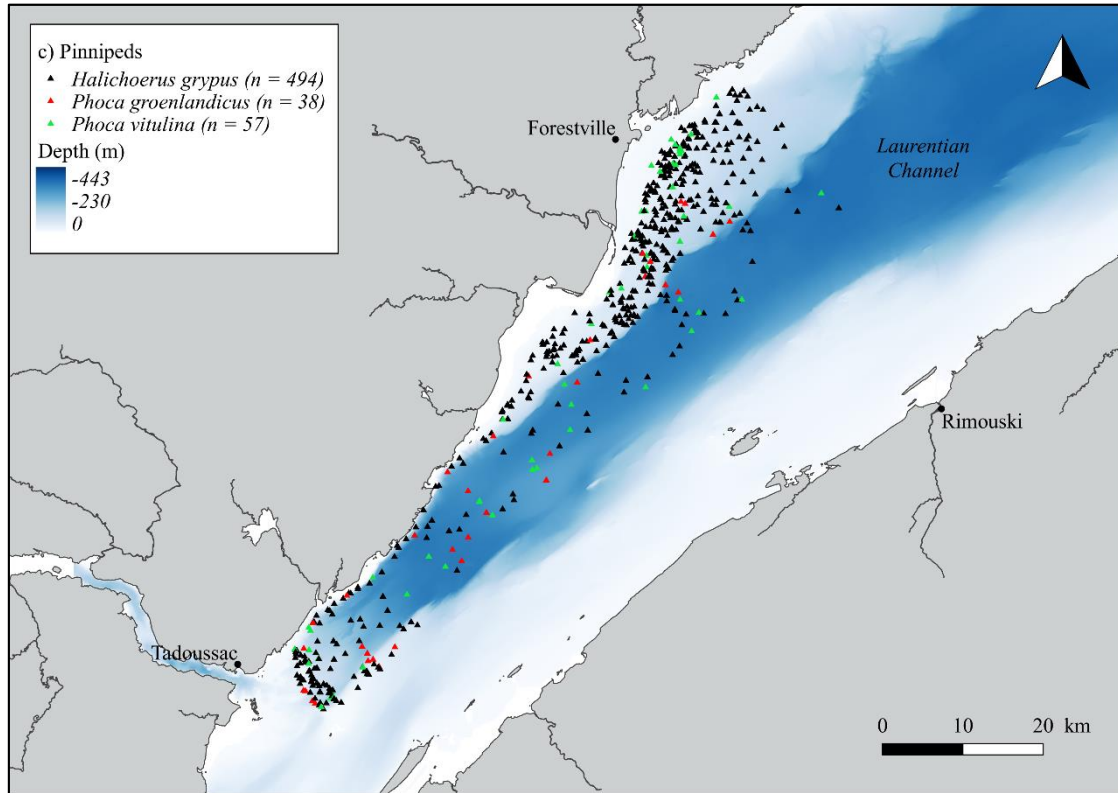


Figure 6. Spatial distribution of sightings of a) baleen whales (n = 549), b) odontocetes (n = 2,891) and c) pinnipeds (n = 589).

The number of sightings and individuals per survey shows a progressive increase in marine mammal occurrence in the LSLE from April through July and August, followed by a progressive decline from September through November (Figure 5b). This trend was mainly driven by odontocetes, which comprised the most abundant species group (see below), but also by pinnipeds (Figure 7). Baleen whales increased in mean occurrence per survey from April through June and remained present at constant levels until October after which their occurrence declined.

Based either on the number of sightings or sighted individuals, harbour porpoises were by far the most commonly observed species in the LSLE, followed by belugas and grey seals (Table 2). Humpback whales and harp seals were the least frequently observed

species. Mean group size differed among species, with harp seals and belugas being observed mostly in groups. Occasionally, groups of several tens of grey seals were encountered at sea, contributing to increase the variance in group size for this species. Harbour seals and minke whales were generally observed on their own.

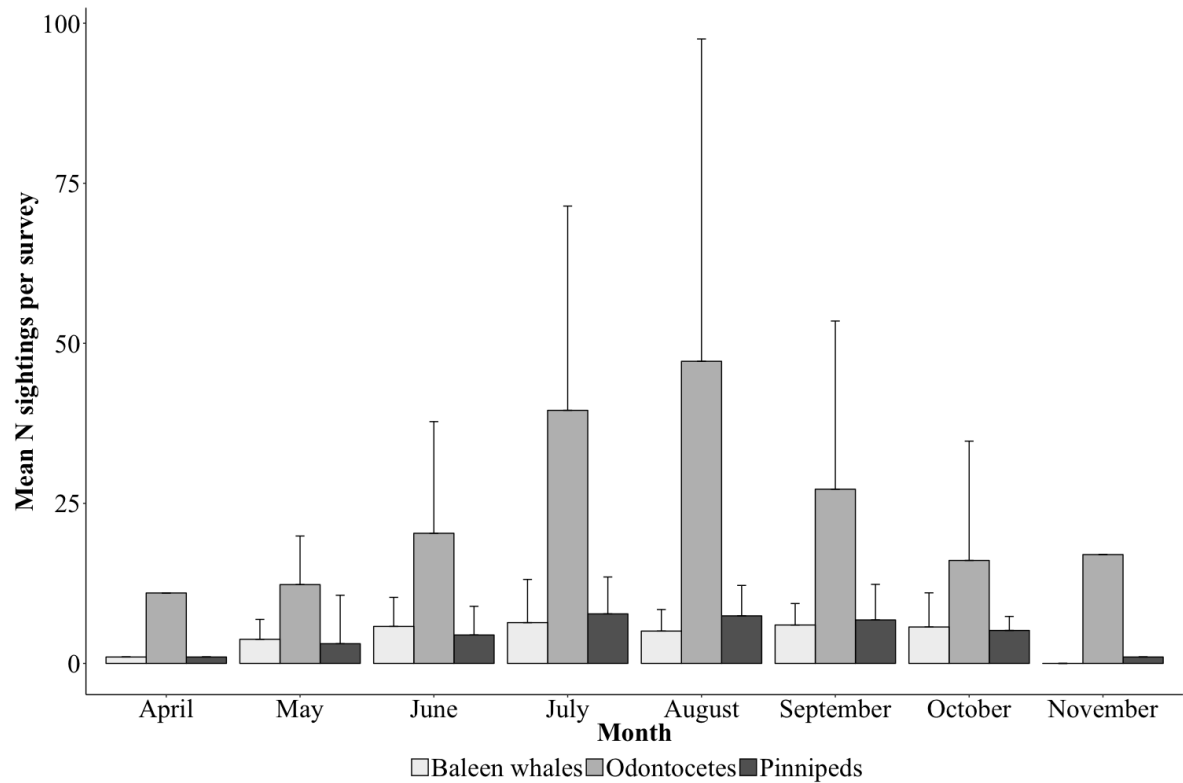


Figure 7. Seasonal change in the mean number of sightings per survey presented by species group (\pm SD).

Table 2. Number of sightings and proportions (%) of sightings and individuals, mean group size and standard deviation (\pm SD) of encountered marine mammal species in the Lower St. Lawrence Estuary (LSLE).

Common name	Species group	<i>n</i> sightings	% sightings	<i>n</i> individuals	% individuals	Mean group size (\pm SD)
Minke whale	Baleen whales	306	7.6	311	4.7	1.0 \pm 0.1
Blue whale	Baleen whales	145	3.6	157	2.4	1.1 \pm 0.3
Fin whale	Baleen whales	64	1.6	82	1.2	1.3 \pm 0.6
Humpback whale	Baleen whales	34	0.8	40	0.6	1.2 \pm 0.5
Beluga	Odontocetes	633	15.7	1,335	20.1	2.1 \pm 2.3
Harbour porpoise	Odontocetes	2,258	56.0	3,716	56.0	1.6 \pm 1.0
Grey seal	Pinnipeds	494	12.3	817	12.3	1.7 \pm 5.2
Harp seal	Pinnipeds	38	0.9	115	1.7	3.0 \pm 6.1
Harbour seal	Pinnipeds	57	1.4	59	0.9	1.0 \pm 0.2
All species		4,029		6,632		

1.3.2 Environmental correlates and marine mammal assemblages

Among the 14 oceanographic or topographic variables associated with the sightings, depth, slope and SSS showed weak correlations with other variables ($r < 0.2$) (Table 3) and were included in the MLR (Table 4). All SST variables were moderately to highly correlated with each other ($r \geq 0.3$); as a result, only mean SST over the 15 days previous to the sighting including survey date (SST15) was added to the model as it showed a strong correlation ($r \geq 0.6$) with every other SST variable, and had also the smallest proportion of missing data, reducing effects on the size of our dataset.

Depth													0.15
SSS1												-0.03	-0.03
SSTlag15											-0.11	0.10	-0.02
SSTlag7										0.54	-0.10	0.04	-0.02
SSTlag5									0.87	0.58	-0.18	0.03	-0.03
SSTlag3								0.82	0.71	0.48	-0.20	0.03	-0.03
SSTc5						0.85	0.65	0.63	0.33	-0.18	0.00	-0.03	
SSTc3					0.98	0.83	0.65	0.63	0.31	-0.18	-0.01	-0.05	
SST15				0.94	0.86	0.89	0.86	0.84	0.60	-0.23	0.03	-0.04	
SST7			0.94	0.93	0.94	0.95	0.79	0.73	0.47	-0.22	0.02	-0.04	
SST5			0.98	0.90	0.96	0.96	0.93	0.73	0.68	0.41	-0.21	0.02	-0.04
SST3		0.98	0.95	0.85	0.97	0.96	0.89	0.68	0.63	0.33	-0.20	-0.01	-0.05
SST1	0.96	0.93	0.90	0.80	0.96	0.94	0.83	0.64	0.61	0.29	-0.15	-0.02	-0.06
	SST3	SST5	SST7	SST15	SSTc3	SSTc5	SSTlag3	SSTlag5	SSTlag7	SSTlag15	SSS1	Depth	Slope

Table 3. Pearson's correlation coefficients (r) of environmental variables in the initial dataset. SST1, SST3, SST5, SST7 and SST15 stand for mean sea surface temperature over the 1, 3, 5, 7 and 15 days previous to the sighting including survey date. SSTc3 and SSTc5 stand for mean sea surface temperature averaged and centered on 3 and 5 d periods. SSTlag3, SSTlag5, SSTlag7 and SSTlag15 stand for mean sea surface temperature averaged and centered on a 3 d period with 3, 5, 7 and 15 d lags. SSS1 stands for mean sea surface salinity on survey date.

Table 4. Characteristics of the environmental variables selected for the analysis.

Variable	Name used	Unit	Type	Spatial resolution	Temporal resolution
Depth	Depth	m	Static	50 m	-
Slope	Slope	°	Static	50 m	-
Sea surface temperature	SST	°C	Dynamic	1 km	15 days
Sea surface salinity	SSS	psu	Dynamic	≈ 6 km	1 day

A hierarchical clustering of the 4,012 marine mammal sightings (no missing data), using the variables presented in Table 3, identified four different assemblages which varied significantly in environmental characteristics (Kruskal-Wallis: $H = 1185 - 2051$, $df = 3$, all $P < 0.01$). The only exceptions were assemblages 2 and 4, which were statistically similar in SST15 (pairwise comparisons, Wilcoxon test, Bonferroni-adjusted $P = 1.0$) (Figure 8). The ANOSIM analysis confirmed that the assemblages were highly distinct in their environmental characteristics ($R = 0.67$, $P < 0.01$), indicating that sightings most similar in characteristics were indeed classified in the same assemblages. Assemblage 1 was observed in colder and deeper waters than the other assemblages, in relatively saline waters and over relatively flat bottoms. Assemblage 2 was also found in relatively saline waters, over flat bottoms, but in the shallowest sectors of the study area where water was generally slightly warmer. Assemblage 3 generally occupied the warmest and freshest waters of the study area, where bottoms were flat and waters deep. Assemblage 4 was observed in relatively saline waters of intermediate surface temperatures but along steep slopes where water depths were intermediate.

Plotting the distribution of the assemblages highlighted some spatial segregation among them within the study area (Figure 9). Sightings from assemblage 1 (black) were mainly located in the deep-water environment of the LC, whereas those from assemblage 2 (red) came mostly from waters closer to shore and near the head of the LC. Sightings classified in assemblage 3 (green) were scattered over the study area, with what appeared to be no distinct geographical patterns. In contrast, the majority of sightings associated with assemblage 4 (yellow) were concentrated in the small region over the slope of the LC.

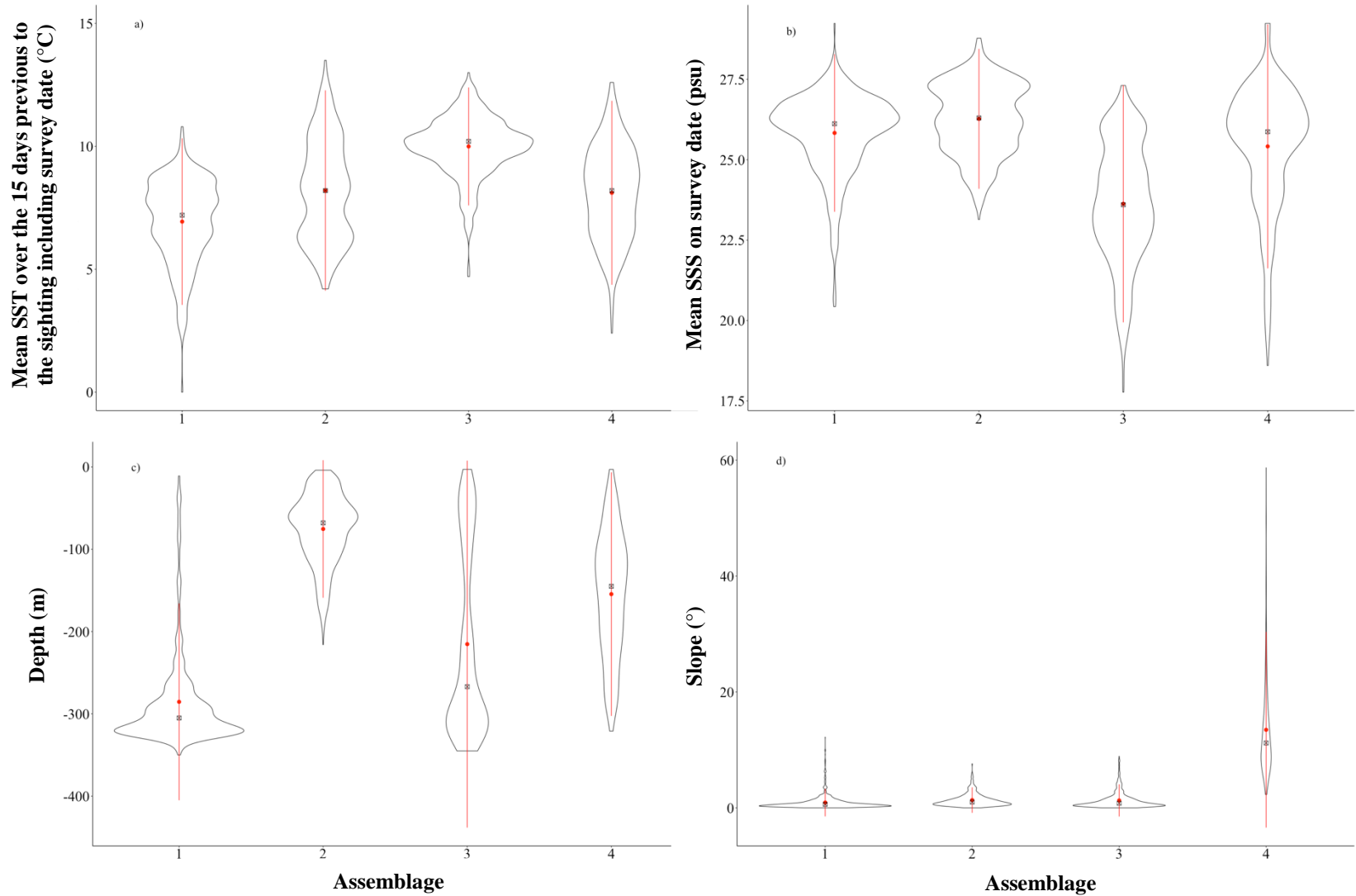
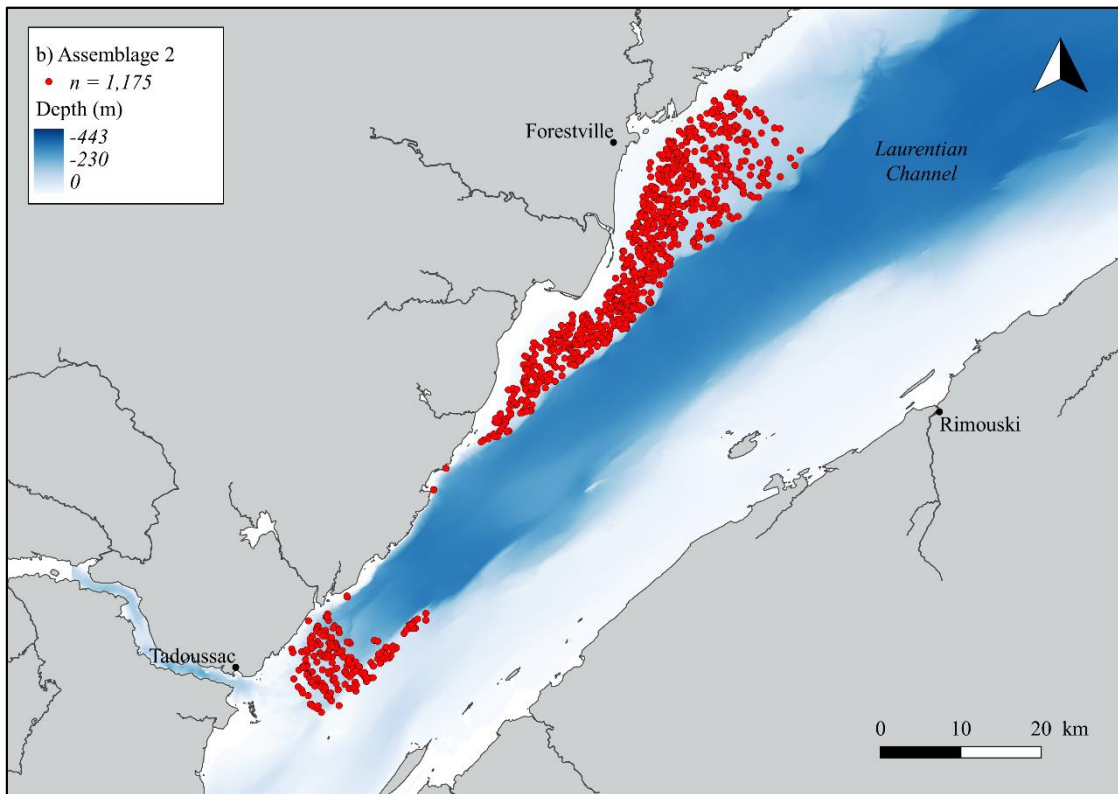
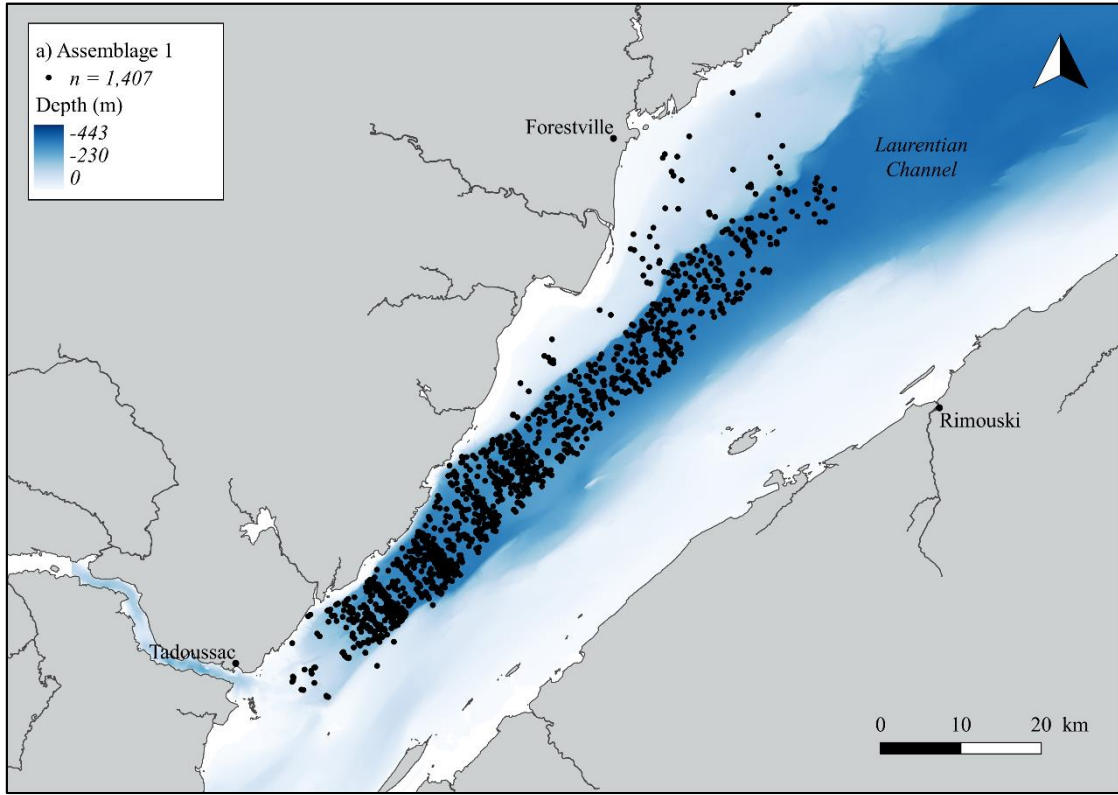


Figure 8. Data distribution of a) mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15), b) mean sea surface salinity on survey date (SSS1), c) depth and d) slope for each assemblage. Red dots and lines indicate the mean and standard deviation respectively; black crossed squares indicate the median.



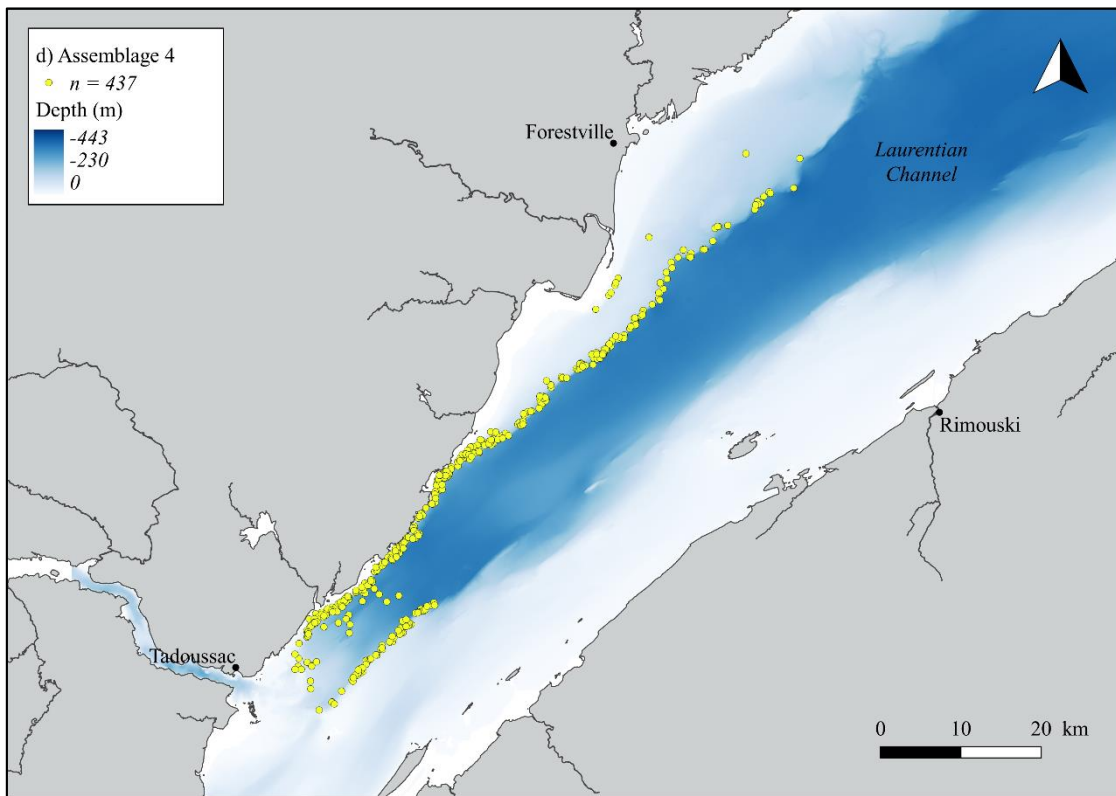
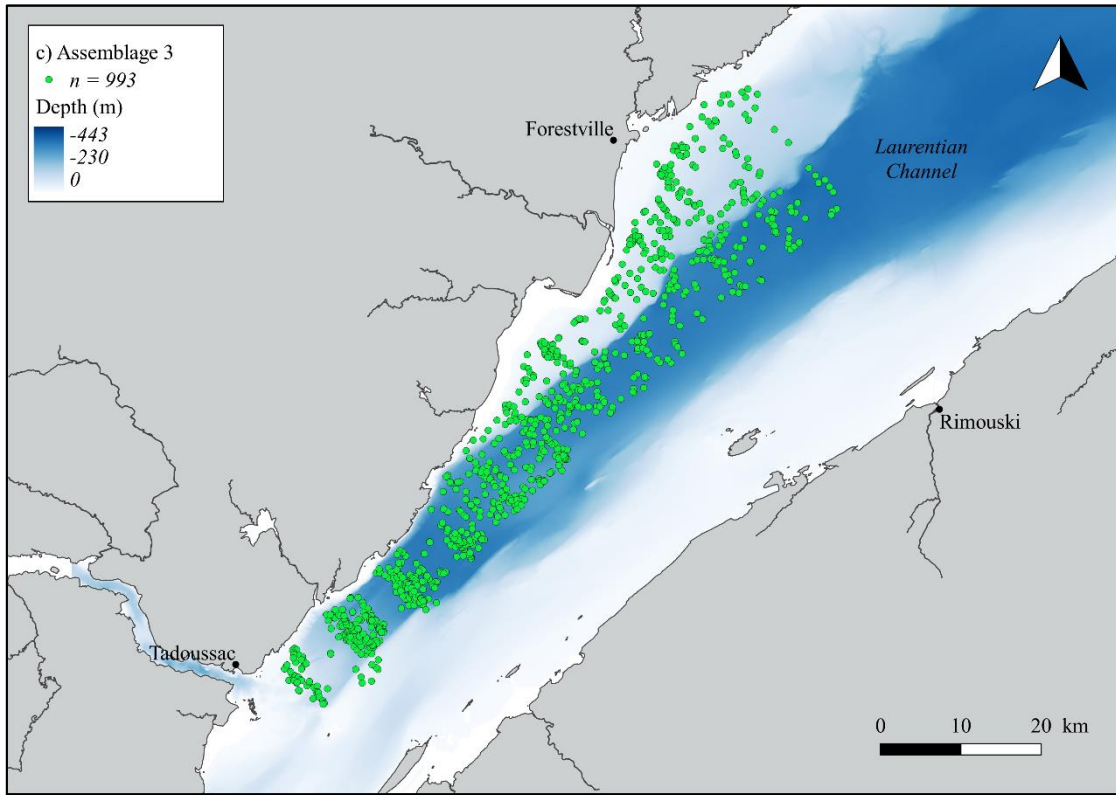


Figure 9. Distribution of the four marine mammal assemblages ($k = 4$) in the Lower St. Lawrence Estuary (LSLE). Assemblage 1 ($n = 1,407$) is shown in black, assemblage 2 ($n = 1,175$) in red, assemblage 3 ($n = 993$) in green and assemblage 4 ($n = 437$) in yellow.

1.3.3 Species composition and biodiversity of marine mammal assemblages

The nine marine mammal species occurred in each of the four assemblages, but the relative abundances of sightings varied among assemblages for each species (Figure 11). All four assemblages were dominated by harbour porpoises. Belugas, grey seals and minke whales were three other abundant species in all assemblages except assemblage 1, where blue whales replaced minke whales in the top four most abundant species (Figures 10 and 11). Belugas and porpoises were most often seen in assemblage 1, whereas grey seals were most often associated with assemblage 2. Belugas were particularly few in assemblage 2 compared to other assemblages. Blue whales were most frequently observed in assemblages 1 and 3, whereas harp seals, humpback whales and minke whales most often occurred as part of assemblage 4. In general, two to three species made up over 70 to 80% of an assemblage (Figure 11).

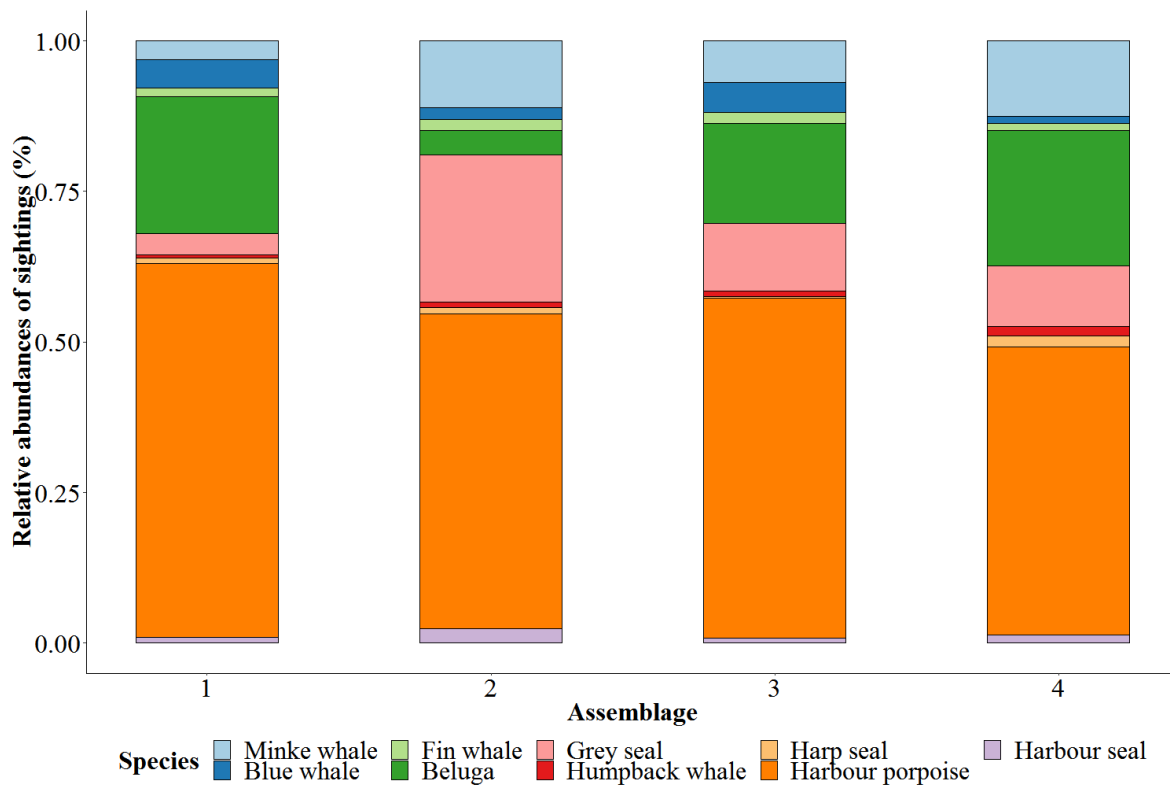


Figure 10. Relative abundances of sightings (%) for assemblages 1 ($n = 1,407$), 2 ($n = 1,175$), 3 ($n = 993$) and 4 ($n = 437$).

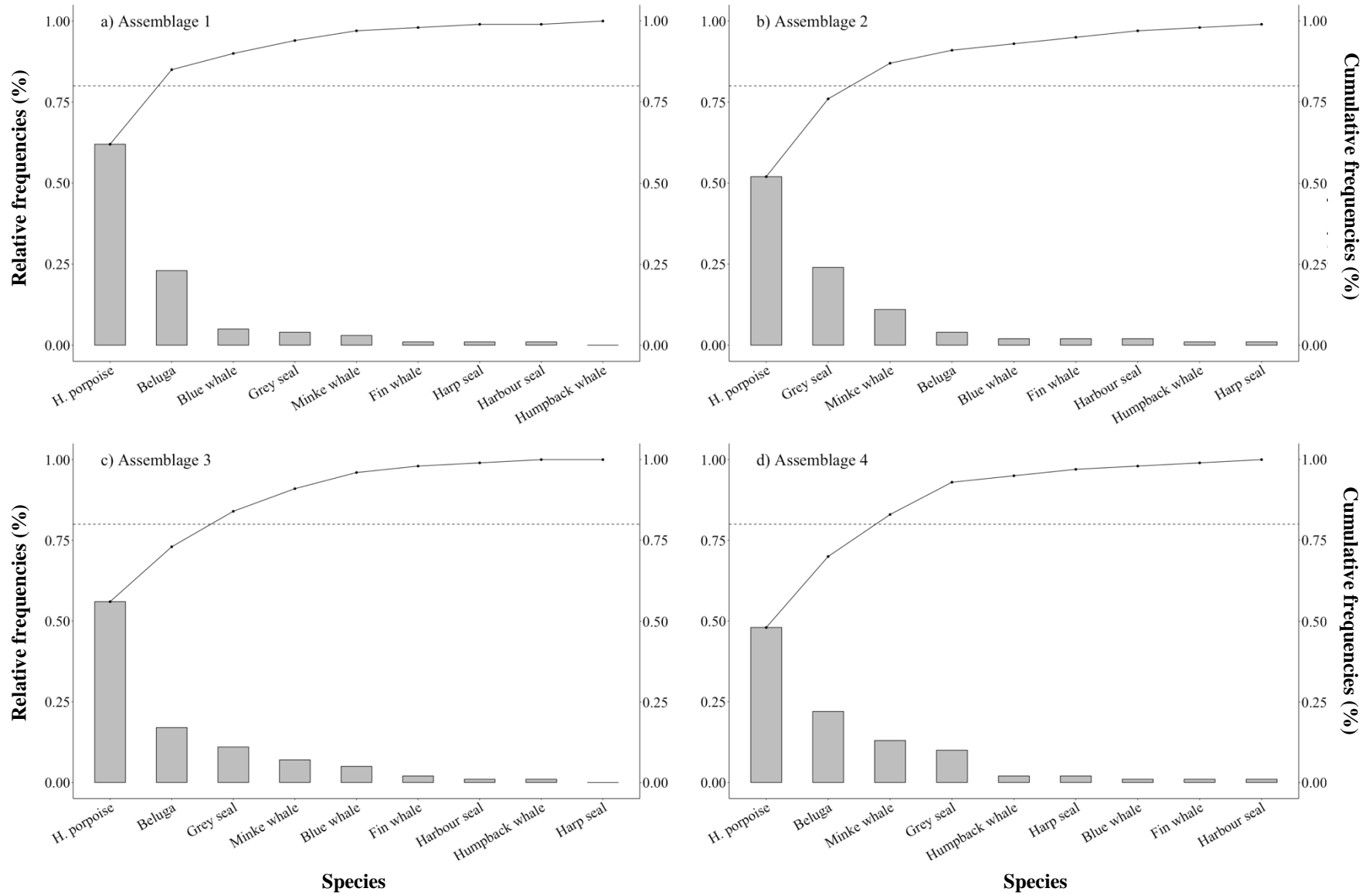


Figure 11. Relative (grey bars) and cumulative (black curve) frequency (in %) of sightings for each species and assemblage. The dashed horizontal line indicates the number of species contributing to 80% of assemblages.

Significant variations existed in the proportions of sightings of species among the four assemblages (Chi-squared: $\chi^2 = 8.11 - 396.28$, $df = 3$, all $P < 0.05$), except for humpback whales (Chi-squared: $\chi^2 = 1.30$, $df = 3$, $P = 0.73$), which were equally partitioned into the four assemblages. Three species had the highest proportions of sightings assigned to assemblage 1: belugas (50%), blue whales (46%) and harbour porpoises (39%). Four species had the highest proportions of sightings assigned to assemblage 2: grey (58%) and harbour seals (49%), minke whales (44%) and fin whales (33%). Only 8% of harp seal sightings were assigned to assemblage 3 (Figure 12).

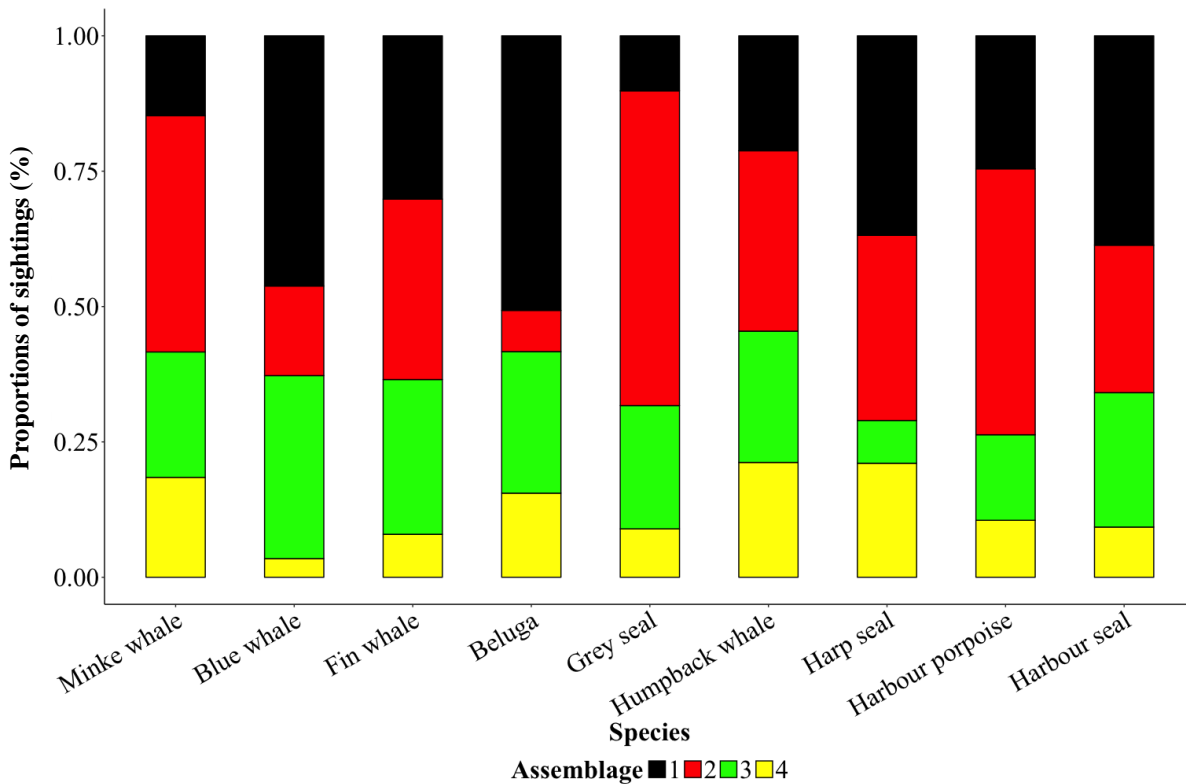


Figure 12. Proportions of sightings (%) of minke whales ($n = 298$), blue whales ($n = 145$), fin whales ($n = 63$), belugas ($n = 631$), grey seals ($n = 492$), humpback whales ($n = 33$), harp seals ($n = 38$), harbour porpoises ($n = 2,255$) and harbour seals ($n = 57$) in assemblages 1 (black), 2 (red), 3 (green) and 4 (yellow).

Species richness was the same for all assemblages. However, when accounting for the relative abundances of sightings or the distribution of individuals across species, biodiversity indices revealed that diversity and species evenness were the lowest in assemblage 1 and the highest in assemblage 4, with assemblages 2 and 3 being similar in values but intermediate between assemblages 1 and 4 (Table 5). Spatially transposing this information revealed that the deep-water environment of the study area, the LC, was associated with the lowest biodiversity, whereas the slope region of the LC was where biodiversity was the highest. Coastal areas, which were occupied by both assemblages 2 and some species of assemblage 3, supported intermediate levels of biodiversity.

Table 5. Species richness, diversity and evenness for the four marine mammal assemblages within the Lower St. Lawrence Estuary (LSLE).

Assemblage	Species richness (R)	Diversity index (H')	Species evenness (J)
1	9	1.18	0.54
2	9	1.39	0.63
3	9	1.37	0.62
4	9	1.48	0.67

1.3.4 Predictive modeling of marine mammal assemblage distribution

The model best fitting the data included all four environmental characteristics (AIC = 1.4×10^3 ; Table 6). Misclassification rate associated with model predictions was 6.3%. Misclassification errors were the highest for assemblage 4 (13.6%) and were most common among assemblages with more similar environmental characteristics (Table 7; Figure 8).

Table 6. Set of models explaining the occurrence of marine mammal assemblages. Variables included were mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15), mean sea surface salinity on survey date (SSS1), depth and slope. Residual deviance is a measure of goodness of fit and AIC indicates the quality of models. For both measures, the highest number reflects the worst fit.

Model	Residual deviance (x 10³)	AIC (x 10³)
SST15 + SSS1 + Depth + Slope	1.3	1.4
SSS1 + Depth + Slope	3.1	3.1
SST15 + Depth + Slope	3.5	3.5
SST15 + SSS1 + Depth	3.8	3.9
SST15 + SSS1 + Slope	5.2	5.2
SST15 + Depth	5.3	5.3
Depth + Slope	5.6	5.6
SSS1 + Depth	5.8	5.8
SST15 + Slope	6.5	6.5
SSS1 + Slope	6.6	6.6
Depth	7.6	7.6
SST15 + SSS1	7.9	7.9
Slope	8.1	8.2
SST15	9.0	9.0
SSS1	9.1	9.1
(null)	10.5	10.6

Table 7. Misclassification matrix. Columns represent the actual assemblage membership of marine mammal sightings. Lines represent the predictions of the model. Numbers on the diagonal represent the correct classification.

	1	2	3	4	Misclassification %
1	247	4	2	1	2.8
2	7	227	10	3	8.1
3	4	5	206	3	5.5
4	1	5	5	70	13.6

Using assemblage 1 as the pivot category, it was possible to examine the increase or decrease in odds of observing a given assemblage based on values of different variables (Table 8; Figure 13). A one-unit increase in slope decreased the log odds of observing assemblage 2 vs. assemblage 1 by 0.39, but greatly increased (by 9.01) the log odds of seeing assemblage 4. The model also predicted that a one-unit increase in SST15 increased the log odds of seeing assemblage 3 vs. assemblage 1 by 6.26. In contrast, a one-unit increase in SSS1 decreased the probability of seeing assemblage 3 but increased that of seeing assemblage 2. Effect of an increase in depth would be negative for the probability of seeing assemblage 1, but positive for the chances of seeing assemblage 2.

The estimated regression parameters (Table 8) indicated that all parameters (except slope for assemblage 2 vs. assemblage 1) were significant ($P < 0.05$) for discriminating assemblages. However, some variables were likely more important than others in predicting the likelihood of seeing some assemblages. For example, an increase in SST15, depth and SS1 made the occurrence of assemblage 2 more likely, but the influence of depth on this probability was greater than for the other two variables. In the four-parameter model, depth had the highest overall significance for predicting the occurrence of the four assemblages, as indicated by the relatively large change (3.0×10^3) in residual deviance of the model when leaving this parameter out compared to the optimal model (Table 6). Leaving out slope, SSS1 or SST15 resulted in smaller (1.8×10^3 to 2.5×10^3) changes in residual deviance.

Table 8. Output of the multinomial logistic regression pertaining to the significance of environmental variables with the a) estimated coefficients, b) standard errors and c) Wald statistics. Assemblage 1 was used as the pivot category. Coefficients are relative to the pivot category and estimate the rate at which the log of the odd ratios of two assemblages changes as predictor variables change in ratio per unit. The generic equation of the MLR model is $\ln\left(\frac{Prob. Y}{Prob. 1}\right) = \beta_0 + \beta_1(SST15) + \beta_2(SSS1) + \beta_3(Depth) + \beta_4(Slope)$, where the response variable Y , i.e., the probability of sightings falling into a given assemblage in terms of the four environmental variables (X), are the log odds for all other assemblages (2, 3 or 4) relative to the pivot assemblage (1). Asterisks next to coefficients indicate significant estimated regression coefficients at $P < 0.05$.

a) Coefficients					
Assemblage	Intercept	SST15	SSS1	Depth	Slope
2	0.41	5.11*	3.43*	9.25*	-0.39
3	1.19	6.26*	-2.29*	3.83*	1.43*
4	-1.06	5.32*	0.80*	5.54*	9.01*
b) Standard errors					
Assemblage	Intercept	SST15	SSS1	Depth	Slope
2	0.26	0.27	0.26	0.39	0.48
3	0.25	0.29	0.15	0.30	0.45
4	0.37	0.32	0.35	0.39	0.59
c) Wald statistics					
Assemblage	Intercept	SST15	SSS1	Depth	Slope
2	1.56	18.82	13.28	23.54	-0.80
3	4.80	21.62	-14.75	12.97	3.20
4	-2.84	16.63	3.23	14.16	15.35

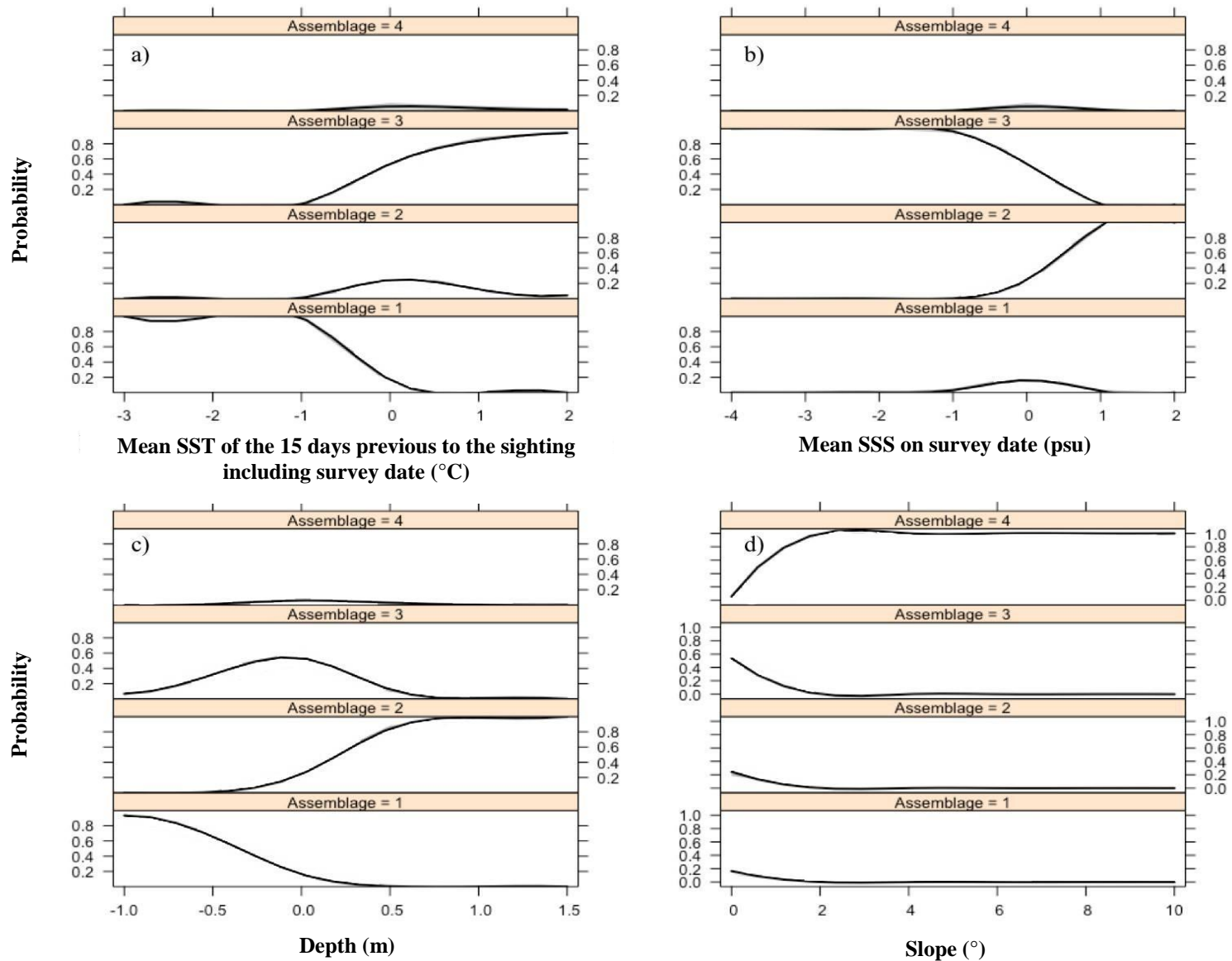


Figure 13. Predicted probabilities of assemblage membership of sightings estimated by multinomial logistic regression (MLR) for a) mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15), b) mean sea surface salinity on survey date (SSS1), c) depth and d) slope. The x-axis of each plot represents the standardized values of variables (mean = 0, variance = 1).

A spatial representation of combined probabilities for the five scenarios (April, June, July, August and September), essentially representing combined changes in SST15 and SSS1, indicated little variability in the predicted distribution of assemblages among scenarios, with the exception of a few key areas (Figures 14, 15, 16, 17 and 18). Generally, assemblage 1 (black), associated with a deeper environment, was mostly found in the deeper regions of the study area, i.e., the LC. Assemblage 2, linked to shallow waters, was predicted to occur mostly on both sides of the LC and west of the Saguenay Fjord. Assemblage 3 (green) was consistently predicted to occur in the southwestern part of the grid, starting offshore of La Malbaie. Assemblage 4 (yellow), associated with higher values of slope, was consistently restricted to the steep slope of the LC.

Drawing a parallel between scenarios and their respective SST15 and SSS1 maps helped highlighting areas that showed higher variability. SSS1 varied little between months in the LSLE and was not very useful for this exercise. In contrast, SST15 varied greatly between months and influenced the probability of encountering the various assemblages. For example, only in scenario 1 (April), when SST15 was higher near the head of the LC, did the model predict a higher probability of seeing assemblage 3 (green) in this area (see Box 1; Figure 14). The model also predicted a higher probability of seeing assemblage 1 (black) in the northeast part of the area in April compared with other months (see Box 2; Figure 14). Assemblage 3 appeared in scenario 2 (June) on both sides of the LC area (see Box 3; Figure 15). This assemblage was consistently predicted to appear in the southwest part of the study area regardless of SST15 variations.

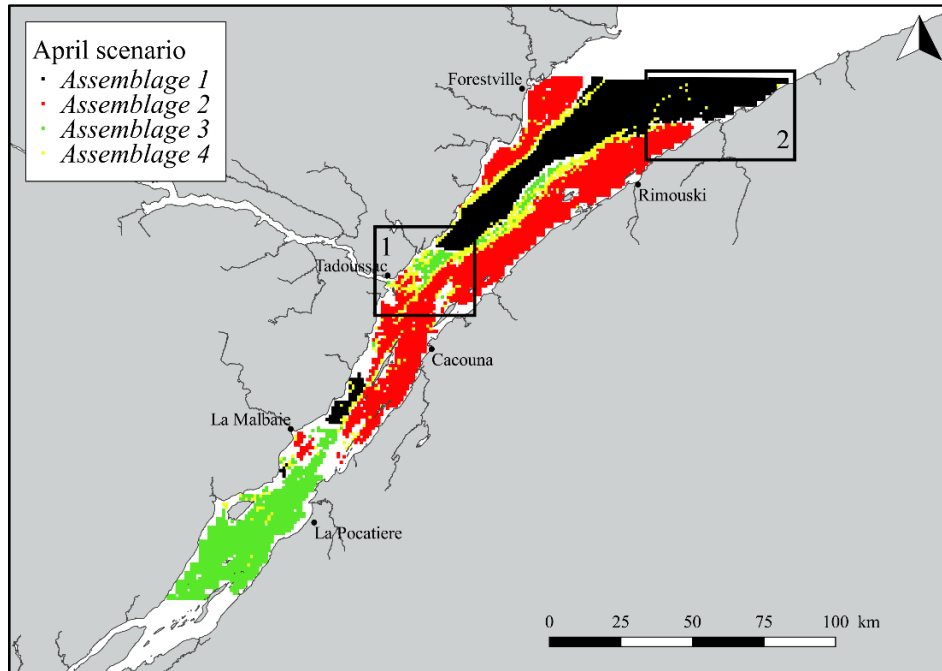
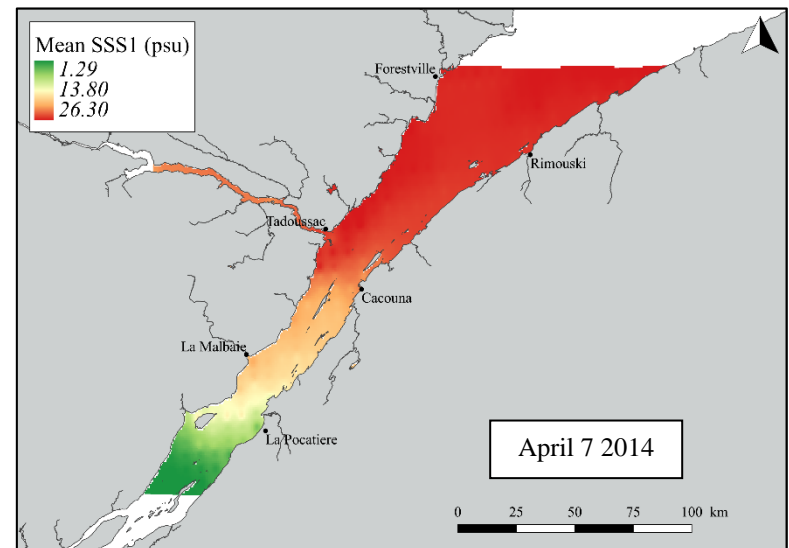
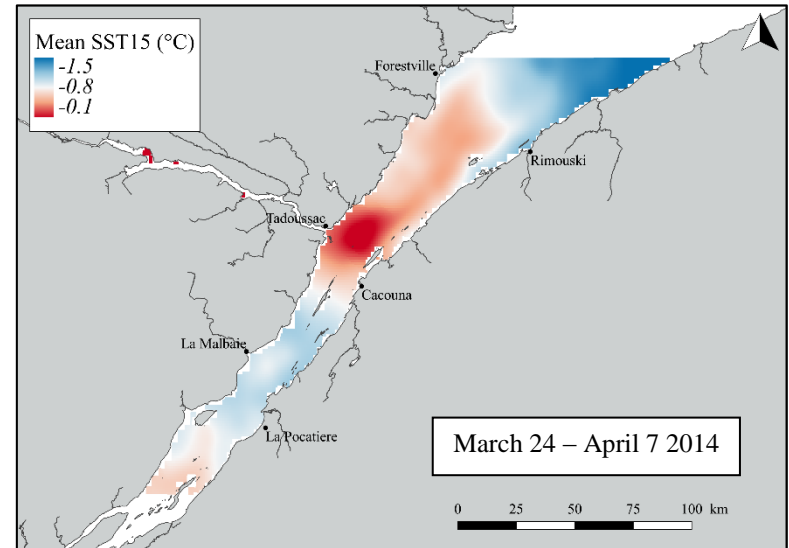


Figure 14. Probable distribution of marine mammal assemblages based on the first (April) scenario of combined changes in mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15) and mean sea surface salinity on survey date (SSS1).



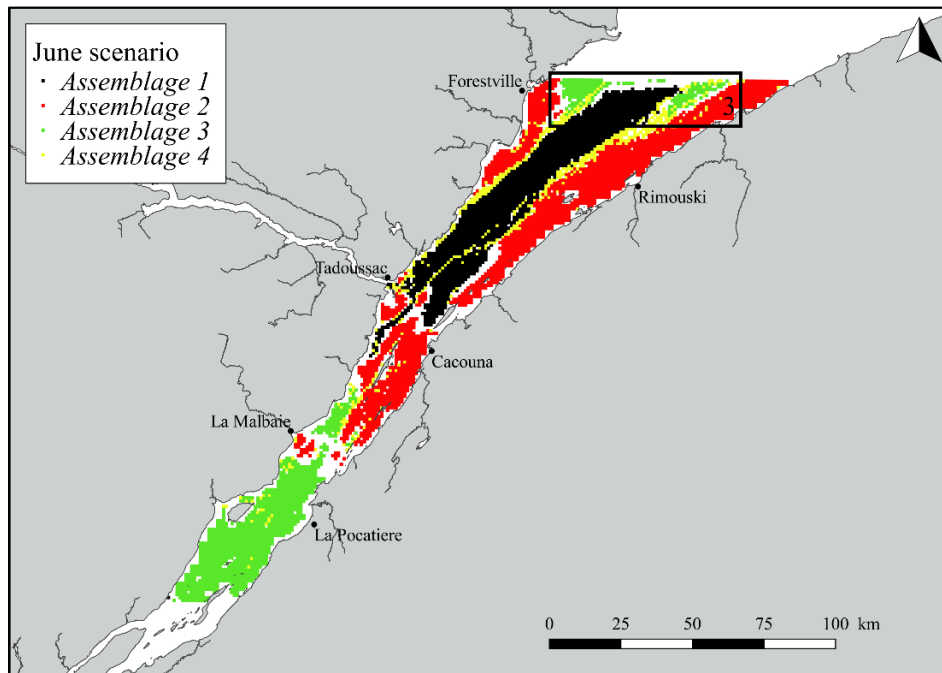
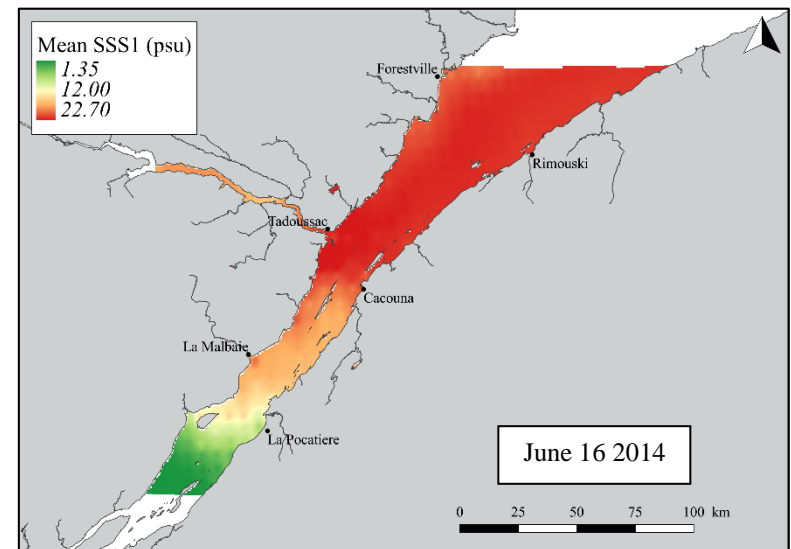
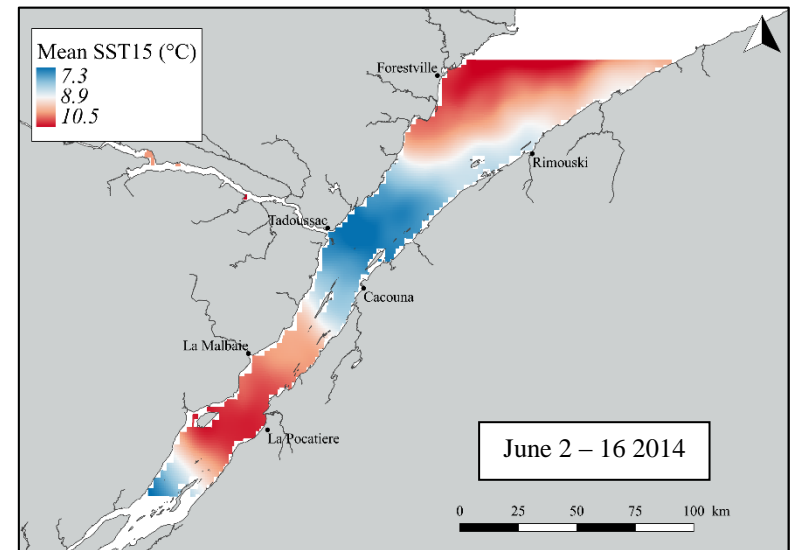


Figure 15. Probable distribution of marine mammal assemblages based on the second (June) scenario of combined changes in mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15) and mean sea surface salinity on survey date (SSS1).



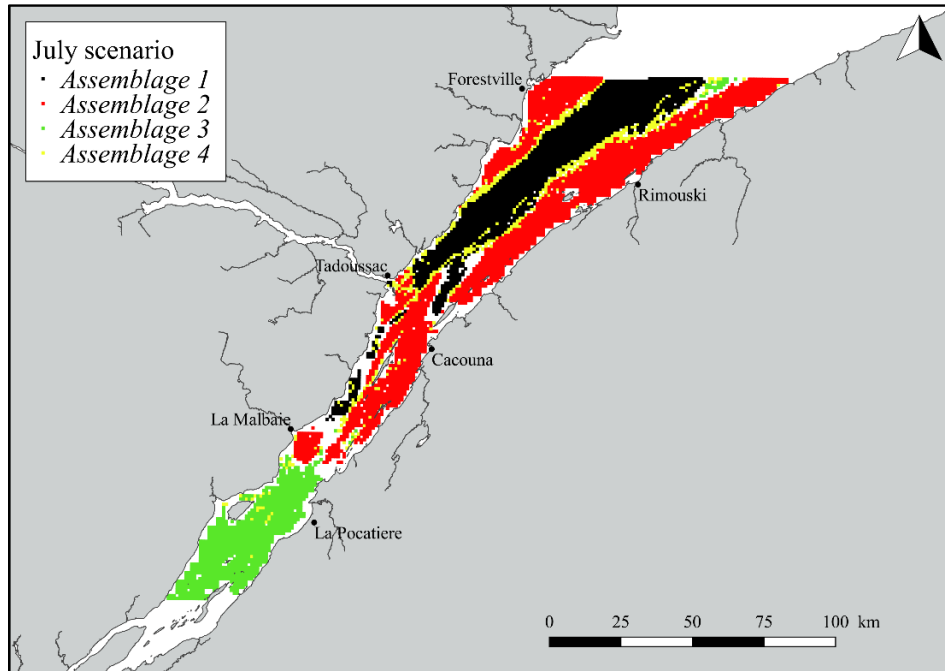
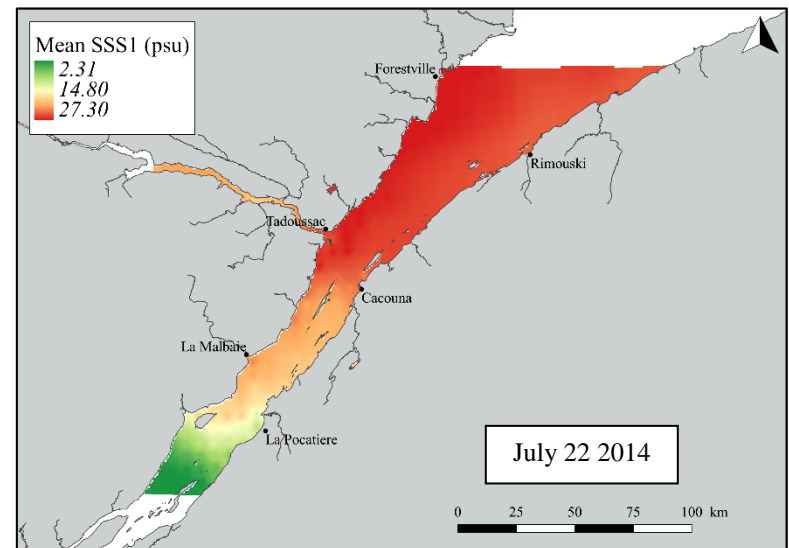
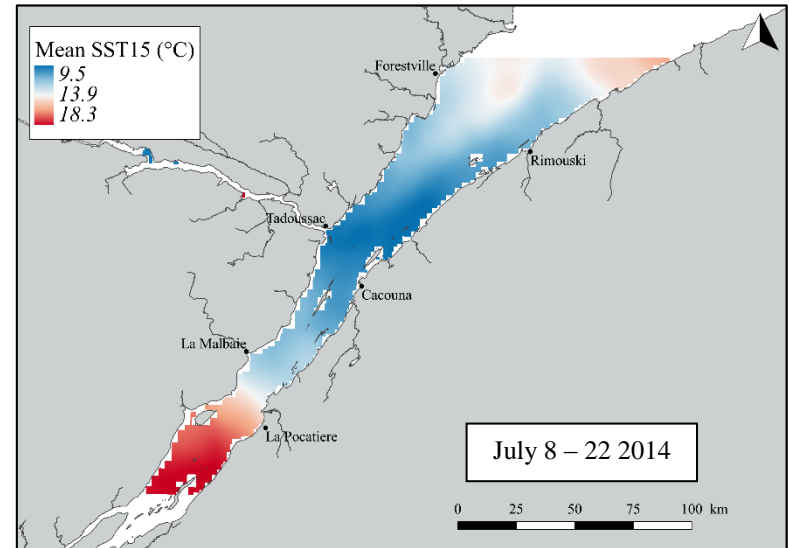


Figure 16. Probable distribution of marine mammal assemblages based on the third (July) scenario of combined changes in mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15) and mean sea surface salinity on survey date (SSS1).



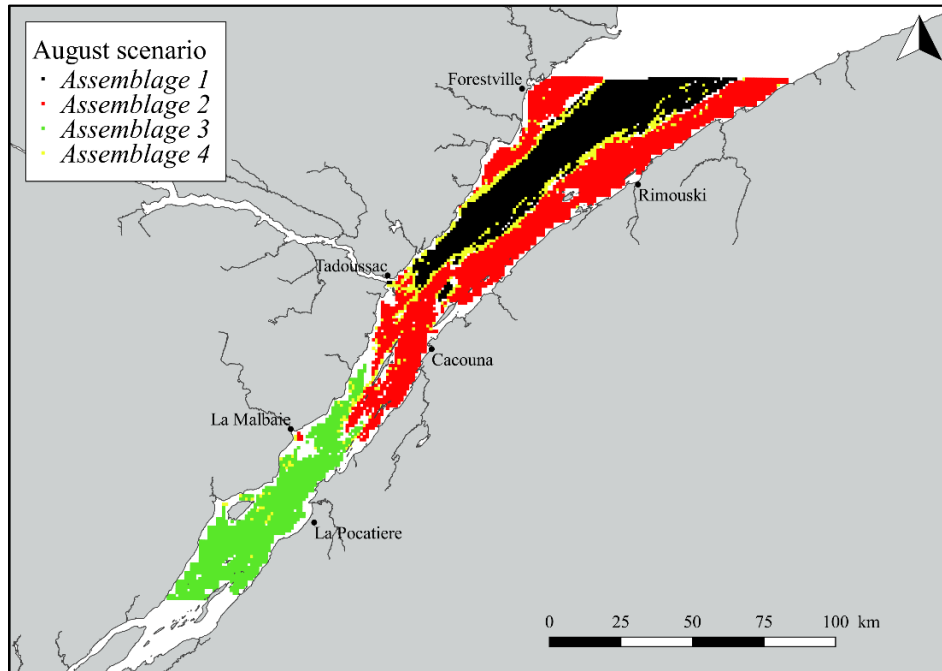
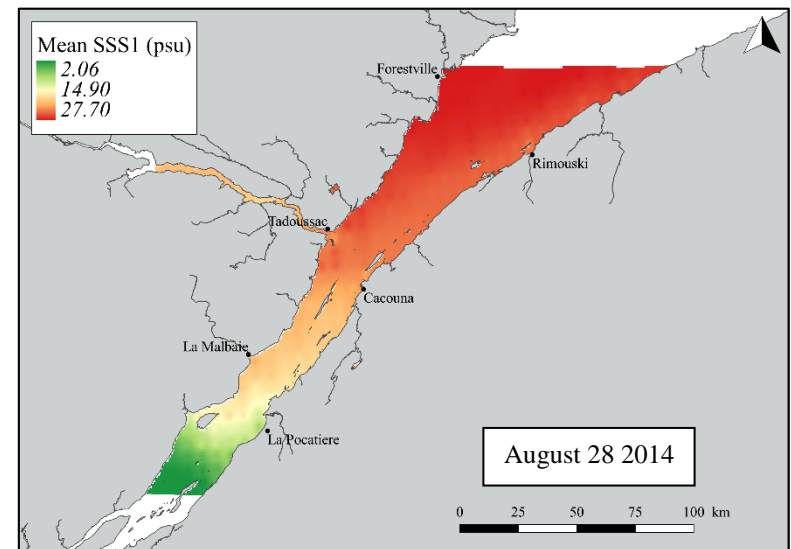
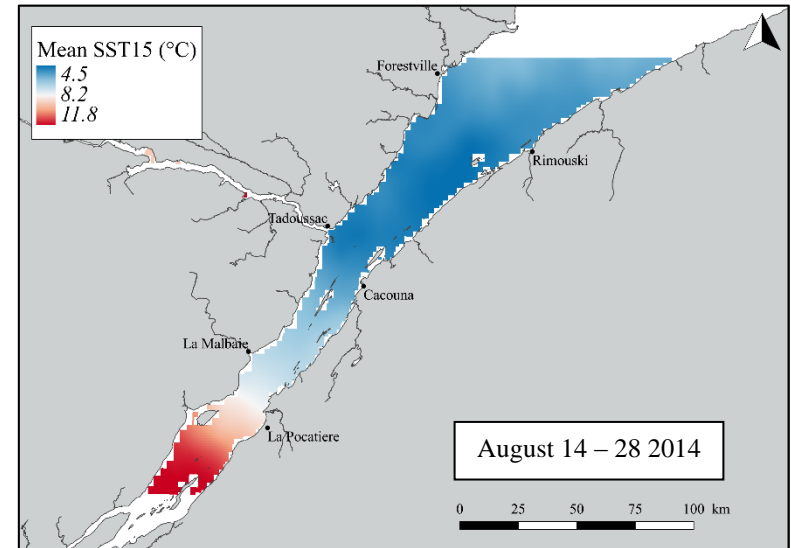


Figure 17. Probable distribution of marine mammal assemblages based on the fourth (August) scenario of combined changes in mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15) and mean sea surface salinity on survey date (SSS1).



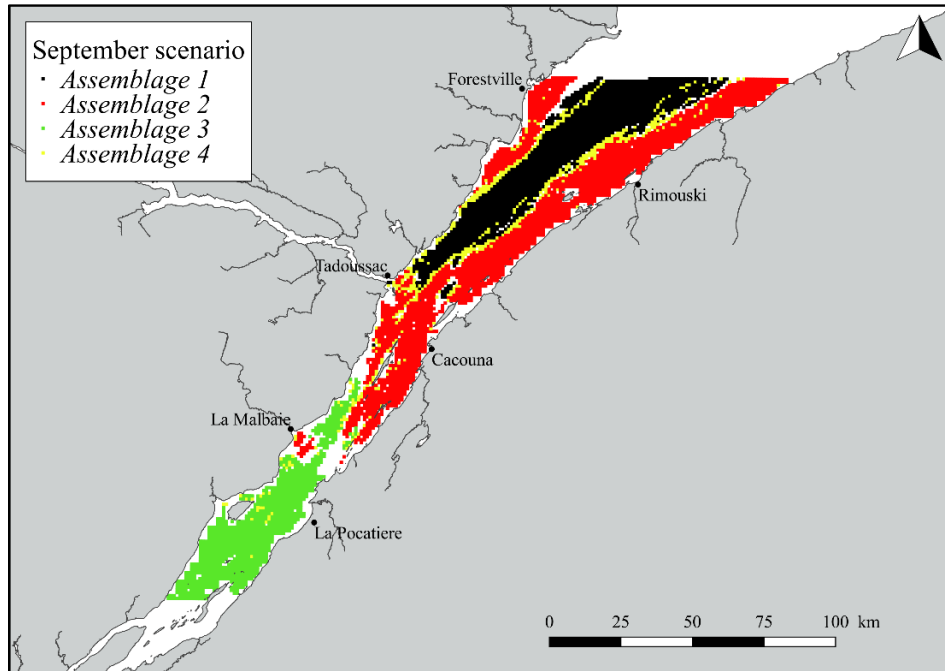
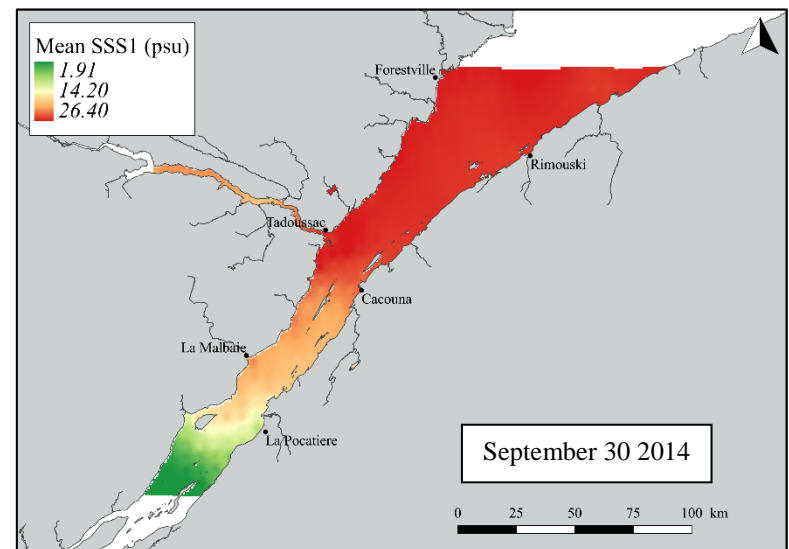
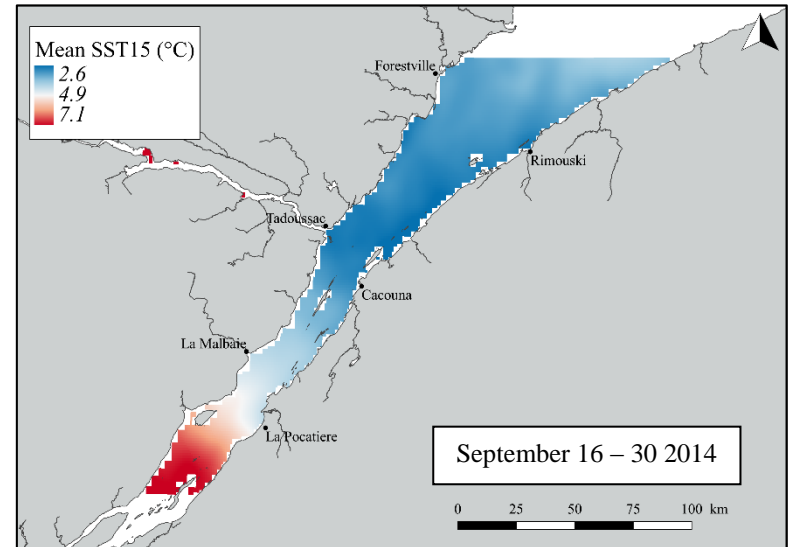


Figure 18. Probable distribution of marine mammal assemblages based on the fifth (September) scenario of combined changes in mean sea surface temperature over the 15 days previous to the sighting including survey date (SST15) and mean sea surface salinity on survey date (SSS1).



1.4 DISCUSSION

1.4.1 Marine mammal assemblages and the role of environmental variables

This study examined marine mammal diversity in the SLE and identified the environmental factors that shape species assemblages using an approach combining multivariate and geostatistical techniques. Predictive models applied to the data allowed the identification of suitable habitats, as well as changes that might be expected in assemblage and species occurrences with changing environmental conditions.

TOPOGRAPHIC VARIABLES

Both topographic and dynamic variables were retained as factors defining marine mammal assemblages. As expected, depth and slope were important factors influencing assemblage distribution in the SLE, given their importance in shaping the distribution of marine mammal prey, from low-motility species (e.g., zooplankton), to small forage fish, and benthic or demersal prey. Topography acts indirectly on prey species by inducing nutrient upwellings and other water mass movements that enhance productivity and aggregation of prey into specific areas (Cañadas, 2002). These processes occur in the SLE, especially at the head of the LC, which ends abruptly at the mouth of the Saguenay Fjord (Simard, 2009). The highly variable bottom topography of the SLE also regulates benthic and demersal prey species communities (Archambault & Bourget, 1999) by directly limiting their distribution and abundance (Cañadas, 2002). The interactive effects of local topography and encounter of different water masses at the head of the LC contribute to the aggregation of large quantities of krill and small pelagic fishes (Simard & Lavoie, 1999), which in turn, attract dozens of species including fishes, marine mammals and seabirds (Cotté & Simard, 2005; Lesage et al., 2007).

Some assemblages were confined to areas of homogeneous slope, over the shelf or the deeper waters of the LC, while others were confined to the abrupt margin and steep slope of the LC. These areas are likely characterized by different prey communities, whose composition may

provide insights into prey preferences and foraging habits of marine mammal species forming the different assemblages. For example, the shallow plateau habitat where assemblage 2 occurred was more optimal for benthic organisms preferring shallower waters closer to the coast with coarse sediments (e.g., shrimps). Conversely, the deeper waters associated with weaker current and fine sediments (e.g., echinoderms), located in the LC where assemblage 1 was found, were more likely to be used by species such as echinoderms (Moritz et al., 2013), or by low-motility zooplankton species, such as krill, which sometimes form patches several kilometers wide over these areas (McQuinn et al., 2016). However, a study examining the distribution of feeding blue whales in the SLE indicated that krill can form high density patches in various habitats including shallow plateaus and deep channels, as well as along the abrupt topography formed by the LC (Doniol-Valcroze et al., 2012). These observations are supported by studies on krill distribution and densities in this area (Maps et al., 2015; McQuinn et al., 2016; Simard et al., 1986), and may explain the occurrence of blue whales in various assemblages. Fish communities in the SLE are also spatially structured. Some communities, mostly dominated by flatfish and redfish, are found in the deeper channels, whereas others, with a larger representation of species from the cod family, occupy plateaus and slope waters (Chouinard & Dutil, 2011).

DYNAMIC VARIABLES

Surface temperature and salinity also influenced marine mammal assemblages. These variables potentially have direct and indirect impacts on marine mammal distribution through effects on homeostasis and prey distribution (Learmonth et al., 2006; Ortiz, 2001). However, in the SLE, effects were more likely to be on prey distribution. Indeed, several marine mammal species occurring in the SLE regularly undertake seasonal migrations between high latitude feeding grounds and low latitude breeding grounds. These species have good thermoregulatory abilities and are able to withstand temperature variations that are much wider than the temperature gradients observed within our study area (Hokkanen, 1990). Similarly, salinity gradients in the SLE, which result from freshwater inputs from the Great Lakes and large spring river runoffs (Bourgault, 2001), were well under what marine mammals are known to experience and are unlikely to have directly acted on their homeostasis (Ortiz, 2001).

Indirect effects of dynamic variables on marine mammal distribution stem from the fact that their prey vary in terms of their tolerance to temperature and salinity, and therefore may be limited to specific water masses and areas (Learmonth et al., 2006; Robinson et al., 2005). Since marine mammals vary in diet and prey preferences, their distribution may be indirectly linked to that of their preferred prey. Krill species, for instance, vary in temperature preferences, resulting in vertical stratification (e.g., McQuinn et al., 2017) and horizontal segregation among species (e.g., Plourde et al., 2016). Variations in temperature and salinity at the surface indicate below-surface oceanographic processes that translate into a change in water masses. Zooplankton and forage fish communities in estuaries such as the SLE are driven by spatial gradients of parameters, like temperature and salinity, that generate environmental variability, shifting their distribution to avoid potential osmotic and thermic stress (Laprise & Dodson, 1994; Ollier et al., 2018). Temperature is also a determinant factor of benthic and demersal species distribution in the SLE (Chouinard & Dutil, 2011; Moritz et al., 2013).

In this study, differences between assemblages due to surface temperature and salinity were most likely the result of seasonal effects of these variables, more than that of a spatial gradient and effect on the distribution and composition of assemblages. For instance, harp seals are Arctic animals migrating from Greenland to our latitudes in winter to breed on ice (Sergeant, 1991). These species enter the SLE during winter to feed, mainly occupying the more saline waters of the Lower SLE. They thus occur in assemblages characterized by cold and saline waters given they are essentially gone from our latitudes during summer when water gets warmer.

1.4.2 Species composition of marine mammal assemblages

All nine marine mammal species were present in the four assemblages. This was somewhat expected considering the relatively small size of the study area compared to other larger-scale studies where a variety of habitats (e.g., coastal, oceanic) and a much wider range of environmental variables were sampled (Schick et al., 2011). In addition, all except one species

(i.e., the blue whale) sampled in our study are generalist predators that feed on a variety of invertebrate and fish species, which in turn vary in habitat preferences (Pauly et al., 1998). Moreover, marine mammal prey preferences can change over time due to fluctuation in prey abundance and distribution (Gavrilchuk et al., 2014; Vladykov, 1946). Therefore, the occurrence of species in more than one assemblage was thought to reflect potential diversity in consumed prey punctually or seasonally, or spatial heterogeneity in habitat use and distribution of these prey. Temporal heterogeneity in habitat use and distribution of prey could also explain some patterns shown in the results; however, the lack of information on seasonal distribution and use of the SLE by potential marine mammal prey (Mosnier et al., 2016) precluded us from further exploring this hypothesis.

While species richness, i.e., the number of species, was the same for the four assemblages, measures of diversity and evenness varied due to differences in species composition among assemblages. These differences, seen both in proportions and in relative abundances of sightings, could reflect differences in preferred environmental variables among species in the assemblages, which are thought to be driven largely by those of their prey. This is assuming that selection of areas by marine mammals is based on a particular set of conditions that lead to high density patches of their preferred prey (Brown & Winn, 1989). Studying the proportions and relative abundances of sightings allowed different but complementary information to be gathered on habitat selection by the species forming the assemblages.

RELATIVE ABUNDANCES OF SIGHTINGS

Harbour porpoises, belugas, grey seals and minke whales were the most common species in every assemblage and habitat type of the study area. These four species also happen to be amongst the most abundant species in the Estuary and Gulf of St. Lawrence (EGSL) (Gosselin et al., 2014; Kingsley & Reeves, 1998; Robillard et al., 2005). They are also all known to live primarily over continental shelves and in coastal waters, and are common in the SLE, year-round for belugas and harbour seals, and seasonally for the other species (Lesage et al., 2007). They also share the feature of being relatively small in size. Body size is a key trait defining ecological niche and habitat use. Smaller species have lower absolute energy requirements than larger

species. They generally tend to consume a broader range of food resources, in smaller quantities (Galetti et al., 2016), making potentially a wider range of habitats suitable for their needs. Similarly, belugas occur over a wide range of habitats within the SLE, and studies that have used static and dynamic physical variables to explain their distribution and habitat preferences have failed to detect patterns in their distribution (Mosnier et al., 2016). It was therefore not surprising to see them in every assemblage.

SPECIES DISTRIBUTION AMONG ASSEMBLAGES

Species generally showed a stronger association with particular assemblages, which was interpreted as a selection for particular environmental characteristics (and habitats). The only species that was homogeneously distributed among assemblages, and thus that showed no clear association with any particular assemblage, was the humpback whale. This could be due to the low number of humpback whale sightings (33 sightings on a total of 4,012) detected during surveys in the SLE, which likely reflects their relative low abundance in what has been described as a potentially marginal habitat for this species (Comtois et al., 2010; Edds & Macfarlane, 1987; Ramp, 2008). Species associations with each assemblage and their environmental characteristics are described in the following paragraphs.

Assemblage 1

Belugas occupy a variety of habitats in the SLE, including the LC, the habitat associated with the assemblage with the most beluga sightings (assemblage 1). Belugas are known to segregate spatially by sex and age class during summer, with adult females (mostly) and younger individuals occupying mainly the Upper SLE and the shallower south shore area of the Lower SLE, and adult males (mostly) and groups of older juveniles occupying the latter area, but also the deeper and colder waters of the LC (Michaud, 1993; Mosnier et al., 2010). All age and sex classes also use the Saguenay River during summer. Surveys in our study were conducted almost exclusively over the LC and thus, unlikely reflect habitat selection for the species as a whole, but

instead the characteristics of the summer and early fall habitat of some of the adult males and older juveniles. The LC is a relatively deep area (around 300 m), but still shallow compared to beluga diving capacities; thus, belugas can reach the bottom of the LC and prey on pelagic, as well as on demersal or benthic species (Citta et al., 2013; Martin & Smith, 1992; Suydam, 2009). Belugas in the SLE have a varied diet that include pelagic prey (capelin, herring), nectobenthic prey (sand lance), neritic prey (squid), as well as demersal species (cod, redbfish, flatfish, hake) (Lesage, 2014; Vladykov, 1946), several of which are known to be abundant in the LC. Demersal species appear to be particularly important in the diet of adult males compared to females or individuals of younger age classes, which might at least partly explain the presence of belugas (possibly males) over the LC and in assemblage 1. The higher proportion of beluga sightings in assemblage 1 could indicate an association with the distribution and higher abundance of their preferential prey near or at the bottom of the LC.

Greater use of the LC by blue whales could be related to their feeding ecology in the SLE during summer. The habitat type in which assemblage 1 occurred, characterized by deep waters and low slopes, corresponded to one of the habitat types described by Doniol-Valcroze et al., (2012), where feeding blue whales were regularly observed. Similarly to belugas, blue whale aerobic dive limit well exceeds that dictated by bottom depth in the LC (Schreer & Kovacs, 1997). A recent study suggests that blue whales in the EGSL may prefer Arctic krill over northern krill (McQuinn et al., 2017), feeding closer to the surface when they can and at depths that rarely exceed 100 m (Doniol-Valcroze et al., 2011). It has been shown that krill patches can aggregate and drift downward along the LC slope into the channel, where they accumulate due to a counter-downwelling depth retention mechanism (Cotté & Simard, 2005; Genin, 2004). The stronger association of blue whales with assemblage 1 could also reflect the stronger association of their preferred prey with the colder and more saline surface waters found in the LC (McQuinn et al., 2016; Plourde et al., 2014).

Harbour porpoises are the most abundant cetacean species to reach the SLE. Their main prey in the SLE is capelin, although herring and redbfish, and possibly other species such as flatfish, squid and crustaceans, also constitute important prey for this small species (COSEWIC, 2006; Fontaine et al., 1994). A stock assessment in the EGSL indicated that capelin has a higher probability (60 to 100%) of being found in the LC area (DFO, 2011). It is therefore plausible that

higher use of the LC by harbour porpoises, through a stronger association with assemblage 1, reflects their preference for capelin and the distribution of this prey. However, given their opportunistic feeding ecology, small size and energy requirements, harbour porpoises are likely to exploit other habitats, which could explain their high relative abundances of sightings in other assemblages and habitat types of the LSLE.

Assemblage 2

Grey seals, harbour seals, minke whales and fin whales were generally more associated with assemblage 2 than with the other assemblages. Grey and harbour seals are generalist predators that feed on a variety of fish and invertebrates (Hammill & Stenson, 2000). Some studies that have examined the harbour and grey seal diving behaviour revealed that, for both species, a large proportion of foraging dives are made at or near the sea-bed (Bjorge et al., 1995; Thompson et al., 1991; Tollit et al., 1998). Foraging strategy depends on many factors, including costs and benefits of feeding at different depths and on different species (Tollit et al., 1998). Even though several seal species can dive well over the maximum depth of our study area (around 300 m) (Schreer et al., 2001), the shallowest areas of the SLE might offer more attractive foraging areas for harbour and grey seals, especially given the fact that they both need to return regularly to haul-out sites to rest, molt or breed (in the case of harbour seals). The north shore of the LSLE comprises several haul-out sites for these species (Lesage et al., 1995; Robillard et al., 2005), so it is logical to see seals closer to shore and near haul-out sites in this area.

Minke whales were also more strongly associated with assemblage 2, with almost half of the sightings being attributed to this group. This cetacean uses particular hunting techniques to feed pelagically on krill and small forage fish, but also directly on the bottom and on a variety of benthic and nectobenthic prey, such as sand lance and herring (Naud et al., 2003). The distribution of these types of prey is highly determined by geomorphology and sediment type (Nordoy & Blix, 1992). Assemblage 2 used preferentially shallow areas, which correspond to the typical feeding habitats described for minke whales in the northern GSL, where they use

shallower waters on average than other rorqual species, possibly as a way to reduce competition for pelagic fishes with other species (Doniol-Valcroze et al., 2007). A study on the influence of topography and geomorphology on minke whale distribution in the northern GSL also shows that most sightings occurred near shore in shallow waters at depths between 20 and 40 m, and where sand dunes were present (Naud et al., 2003).

A third of fin whale sightings were located in the shallowest environment of the study area as well. Fin whales have an omnivorous diet and feed on both zooplankton and fishes. In the EGSL, the diet of fin whales is likely composed of krill and sand lance (Gavrilchuk et al., 2014). These animals are generally associated with regions of high topographic variation and well mixed waters (Sergeant, 1977; Woodley & Gaskin, 1996), and they are often observed along steep contours where biological productivity is high (Doniol-Valcroze, 2008), such as at the convergence of water masses at the head of the LC. In the northern GSL, fin whales tend to occupy nearshore waters less than other species like minke whales (Doniol-Valcroze et al., 2007). The fact that there were more sightings of fin whales in the most nearshore assemblage of this study could reflect their ability to switch prey types and hunting techniques depending on prey availability and habitat. It could also indicate their ability to change their targeted prey when confronted to inter-specific competition (Gavrilchuk et al., 2014).

Assemblage 3

None of the species were particularly strongly associated with assemblage 3; in fact, the only pattern of association was for harp seals, which were particularly weakly associated with this assemblage. Habitat characteristics suggest that assemblage 3 might represent a subset of the other assemblages, but at periods when sea surface temperatures are particularly warm during summer. Harp seals were the only “true” winter species documented in this study and therefore, were unlikely to be observed in warm conditions. This highly pagophilic species spends the summer in the Canadian Arctic and usually moves into the EGSL during the fall and winter to feed and breed before heading north following the moult, around the time of ice break up (Hammill et al., 2014). In comparison to the other seal species of this study, harp seals are more pelagic, and haul-out exclusively on ice, making them less dependent on the coastline and

shallow waters than grey and harbour seals. The spatial distribution of sightings pertaining to this group did not show clear associations with bathymetric variables, suggesting a greater influence of dynamic variables on sightings of this assemblage. Unfortunately, the resolution of dynamic variables used in our analyses was coarse. Marine mammals are likely to select their habitat using dynamic variables over fine scales (Redfern et al., 2006). Alternatively, assemblage 3 could reflect a temporal dimension to environmental parameters that was not explored in this study. Temporal dynamics are an important factor in the marine realm since species, and obviously species assemblages, are bound to shift distribution over time (Schick et al., 2011).

Assemblage 4

No species in assemblage 4 were particularly strongly associated with its characteristics; they were instead generally more strongly associated with the environmental characteristics typical of the other assemblages. Assemblage 4 was the smallest of the assemblages, both in terms of sample size and spatial distribution, being strictly restricted to the narrow northern slope of the LC. While the other three assemblages were characterized by extreme values for some of the environmental characteristics (e.g., the lowest SST and greatest depth for assemblage 1, the lowest depth for assemblage 2, and the highest SST and lowest SSS for assemblage 3), assemblage 4 was extreme by its steep slope and intermediate in all other characteristics. This might explain the large diversity of species in that specific assemblage.

1.4.3 Biodiversity of marine mammal assemblages

Habitat heterogeneity influences biodiversity. In our study, assemblage 1 occurred in the deeper parts of the study area and was characterized by a low biodiversity value. This area corresponds to a more homogeneous habitat and might have provided a suitable environment for a smaller number of species. For example, this deep-water environment might be less optimal for species that feed on prey found mainly on or near the seabed, such as grey and harbour seals. The

relative abundance of sightings of these two species were indeed the lowest in assemblage 1. Even though grey and harbour seals are not physically or physiologically limited by depth in the study area, they are, in theory, more likely to select more accessible prey when given the choice, with the additional benefit of being closer to haul-out sites when in coastal, shallower waters. At the opposite of the spectrum, biodiversity value of assemblage 4 was the highest. Reasons could be that this assemblage occurs in the most variable habitat of the study area, i.e., the LC slope, where upwelling and tidal mixing meet the steep topography of the SLE, allowing for a more complex community of species to co-exist.

It is important to note that biodiversity values were calculated from diversity and evenness indices, which are numerically inferred from species composition of assemblages. Therefore, biodiversity values were expected to be similar between assemblages, as they were composed of the same species, and because these values increased as the occurrence of harbour porpoises, which were dominant in all four assemblages, also increased. Moreover, because of the low number of species in this study, similarities between indices values were expected. For example, studies on benthic communities often consider hundreds of species in grid cells that are of much smaller sizes than the ones used in this study. This is expected to lead to a higher variability between biodiversity indices (P. Archambault, pers. comm.).

1.4.4 Interpretation of model predictions in the context of climate change

A community ecology approach was applied to the marine mammal and environmental data to predict habitat suitability over a wider spatial scale, and to quantitatively forecast the likely effects of different environmental scenarios on the probability of occurrence of assemblages. Modeling of marine mammal assemblages was done using environmental drivers to build predictive occurrence maps on a larger scale. Individual species can respond to environmental change in many ways, for instance by variations in their phenology, physiology, or shifts in their distribution and range. Because species within assemblages are likely interconnected through their trophic interactions with prey species and other components driving

these assemblages, it is important to consider the consequences of environmental and climate change on ecological networks and multi-species assemblages (Walther, 2010).

Because of the close similarity of assemblages in terms of species composition, and therefore biodiversity, the interpretation of the effects of varying sea surface temperature and salinity on the probability of occurrence of assemblages was challenging. The model did suggest one clear trend: under warming conditions, the assemblage representing species that are more likely to be observed in the SLE during warmer conditions of the summer months had a higher probability of occurrence. This assemblage had the lowest proportion of harp seal sightings, which are an apex predator and important consumer given the large population size and abundance in the EGSL (Hammill & Stenson, 2000; Lesage et al., 2001), making them likely to have major impacts on their ecosystem. Generally, such abundant predators with highly varied diets have negative effects on their dominant prey, but also have indirect and positive effects on the prey of their preferred prey (Morissette et al., 2006). Because of the potentially great impact of harp seals on all other species of their ecosystem, the consequences of a reduction in the number of harp seals due to warming water temperatures might be felt throughout the SLE food web.

The model also predicted a decrease in the probability of occurrence of assemblage 1 with warming conditions. This assemblage was mainly found over deep and cold waters of the LC and comprised a high proportion of sightings (around 50%) of two endangered species, namely belugas and blue whales. Currently, Arctic krill forms the bulk of blue whale diet in the EGSL (Gavrilchuk et al., 2014). Climate change may affect prey availability and is a concern in the case of blue whales given their almost exclusive diet on krill. Although the diet of krill is varied (Cabrol et al., 2018), their abundance strongly depends on the availability and abundance of marine algae and phytoplankton (Schmidt et al., 2011), which bloom in the ocean during summer. Ice diminishes as a consequence of global warming, and feeding opportunities for blooming krill become increasingly rare, which affects population growth of this primary producer, and thereby the stability of entire ecosystems (Learmonth et al., 2006). Also in the context of warming oceans, a study conducted on the two main krill species of the LSLE, *Meganyctiphanes norvegica* and *Thysanoessa raschii*, showed that the increasing probability of

encountering increasingly warmer waters could change their migration behaviour and spatial distribution (Ollier et al., 2018), with potential consequences for foraging blue whales. Blue whales are usually associated with areas of cool upwelling waters, which are a feature of the habitat in which assemblage 1 was observed. A rise in sea surface temperature could reduce the extent and distribution of these preferred areas in the SLE, which could force blue whales to shift their distribution (Harwood, 2001).

In the case of belugas, an Arctic species, the importance of the SLE lies with the cold and productive environment combined with estuarine characteristics that resemble those sought by other beluga populations during summer (Mosnier et al., 2010; Würsig et al., 2017). If changes in environmental features are such that conditions in the SLE reduce productivity or are no longer similar to arctic conditions, it is unlikely that belugas will adapt rapidly. This species shows a strong degree of site fidelity (Caron & Smith, 1990; Turgeon et al., 2012) and appears to learn about migration routes by travelling with relatives. This cultural conservatism may limit exchanges with other populations as well as the capacity of belugas to adapt to climate change by modifying their distribution (Colbeck et al., 2012). Because of the restricted distribution of this endangered species, any degradation of its habitat is likely to have consequences on its fitness given the already precarious status of the population (DFO, 2014; Mosnier et al., 2016).

A decrease in biodiversity as a result of climate change (e.g., higher temperature, higher salinity) has been revealed in many studies and for many marine species and assemblages in global studies (Cheung et al., 2009). Sea surface temperature has emerged as a powerful determinant and predictor of large-scale patterns of biodiversity and has been proven to be by far the best determinant of diversity for many pelagic species (Rutherford et al., 1999; Worm et al., 2005). A decline of cetacean diversity with increasing temperatures has been documented in the North Atlantic Ocean (Whitehead et al., 2008), and changes in the cetacean community of northwest Scotland have been related to recent ocean warming (Macleod et al., 2007). Marine mammals can be seen as arctic, temperate or tropical species and in this perspective, can be affected directly by changing water temperature. However, effects of changing water temperature on marine mammals are likely to be generally indirect, affecting the distribution and abundance of their ectotherm prey, which are likely to be less tolerant to temperature variations

and may be more prone to shift in distribution or abundance with changing conditions (Learmonth et al., 2006).

The consequences of warming conditions on marine mammal distribution and every marine species are increasingly complex and remain largely unclear. Knowing that the relationship between marine mammals and their habitat is scale-dependent, the addition of dynamic variables, such as prey distribution and abundance, in our dataset would have undoubtedly refined the output of our model. However, this type of information is currently not available in our study area, and when it is, layers of dynamic data lack sufficient temporal or spatial resolution. Our model did provide a coherent picture of the probable distribution of marine mammal assemblages in the SLE. The boundaries of assemblages fitted closely to the bottom physiography despite variations in dynamic variables. This suggests that bathymetry and slope were the strongest environmental parameters driving marine mammal assemblages. Further research on the effects of dynamic variables in a highly topographically heterogeneous environment, in addition to using the distribution and abundance of prey, would greatly increase our knowledge on marine mammal assemblages in the SLE.

1.4.5 Acknowledgments

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CONCLUSION GÉNÉRALE

Les assemblages de mammifères marins créés dans le cadre de ce projet témoignent de l'incidence de l'hétérogénéité spatiale de l'estuaire du Saint-Laurent sur leur distribution et leur composition. Les caractéristiques d'habitat utilisées pour constituer ces assemblages ont été choisies notamment en fonction de leur influence sur l'agrégation et la distribution des proies des espèces de mammifères marins. Par exemple, la température et la salinité moyennes de surface peuvent être indicatrices de remontées d'eaux froides riches en nutriments qui attirent des quantités considérables de proies. La profondeur et la pente du fond ont également des effets, directs et indirects, sur l'abondance et la distribution des proies des mammifères marins. Les assemblages obtenus donnent à croire que la topographie de l'estuaire du Saint-Laurent a une grande influence sur la distribution spatiale des mammifères marins. De plus, en soumettant notre modèle prédictif à cinq scénarios présentant des conditions environnementales différentes en termes de température et salinité moyennes de surface, il a été possible de produire des cartes de la distribution probable des assemblages de mammifères marins, ce qui a permis d'évaluer l'effet potentiel des variations saisonnières sur leur distribution et leur composition. Cet exercice a également permis d'obtenir un aperçu de la tendance de la distribution des assemblages de mammifères marins dans des conditions de température et de salinité qui rappellent celles des changements globaux à prévoir. Cette approche multi-spécifique a aussi permis de mieux comprendre quelles conditions environnementales favorisent une plus grande biodiversité de mammifères marins dans l'estuaire du Saint-Laurent.

Limites de l'étude et suggestions pour de futures recherches

Tout projet de recherche ne peut se conclure sans avoir posé un regard critique sur les démarches effectuées. Dans le cas d'un projet comme celui-ci, au cours duquel plusieurs obstacles ont été rencontrés, il est essentiel de prendre du recul pour comprendre comment ceux-ci ont forcé la recherche de solutions respectant le plus possible les objectifs de recherche établis au départ. Les prochaines sections se veulent donc une revue des limites imposées par la présente étude, accompagnée de certaines suggestions destinées à quiconque souhaiterait entreprendre un projet semblable.

DONNÉES D'OBSERVATIONS DE MAMMIFÈRES MARINS

Le jeu de données utilisé pour ce projet est de taille importante (plus de 4000 observations), mais il ne représente en réalité qu'une fraction des données potentiellement utilisables. En effet, des données d'observations supplémentaires recueillies à l'occasion de relevés dirigés par Pêches et Océans Canada sont disponibles. Ces relevés ont été effectués dans l'estuaire (incluant l'estuaire moyen) et dans le golfe du Saint-Laurent à partir de différents types de plateformes, à savoir des avions ou des navires, et en suivant différents plans d'échantillonnage, systématiques ou opportunistes. Les données recueillies lors de ces relevés auraient le potentiel de venir compléter notre étude. Par exemple, l'on pourrait considérer toutes les données d'observations couvrant l'estuaire et le golfe du Saint-Laurent. Une plus grande échelle spatiale aurait peut-être permis de détecter des signaux plus clairs dans la séparation des assemblages, notamment en raison de la distinction entre les espèces qui fréquentent l'estuaire et celles qui ne se retrouvent que dans le golfe. En effet, bien qu'ils soient reliés et interdépendants, l'estuaire et le golfe du Saint-Laurent sont souvent considérés comme deux écosystèmes caractérisés par des phénomènes océanographiques distincts. Cette différence se traduit de plusieurs façons, notamment par les communautés biologiques qui s'y retrouvent. L'inclusion de relevés couvrant le golfe aurait probablement introduit davantage d'observations de globicéphales

et autres espèces océaniques (p. ex., dauphins à nez blanc, dauphins à flancs blancs, cachalots, etc.), ce qui aurait peut-être donné lieu à une séparation plus claire des assemblages d'espèces. L'on aurait peut-être obtenu, par exemple, des assemblages caractérisés par des espèces plus côtières et d'autres par des espèces plus océaniques, entraînant ainsi une moins grande ressemblance entre les assemblages, autant au niveau de leur distribution que de leur composition.

Si tous les relevés n'ont pas été pris en compte, c'est que le temps nécessaire à la validation de l'ensemble de ces données était incompatible avec les échéanciers du programme de maîtrise. Les couvertures spatiales et temporelles variaient également entre les inventaires, ce qui aurait demandé un tout autre niveau d'analyse et une homogénéisation exhaustive des données. Il a alors été convenu de ne retenir que les relevés systématiques effectués à bord de navires dans l'estuaire maritime, qui représentaient une quantité convenable de données. Ces relevés devaient donc couvrir la même aire d'échantillonnage, de manière hebdomadaire et durant plusieurs années consécutives. Ceci visait entre autres à assurer une constance au niveau de l'effort, de la qualité et de la fiabilité de l'échantillonnage malgré la réduction des dimensions de l'aire d'étude et la diminution du nombre d'observations.

DONNÉES ENVIRONNEMENTALES

Trois sources de données environnementales ont été utilisées pour regrouper les espèces de mammifères marins en assemblages : des données provenant d'images satellitaires pour la température de surface, des données provenant d'un modèle océanographique pour la salinité de surface, et des données dérivées de la bathymétrie pour la profondeur et la pente du fond. Le choix des variables environnementales s'est d'abord fait en fonction de leur pertinence supposée par rapport à la distribution des mammifères marins, et ensuite de leur disponibilité ainsi que de leur couverture et de leur résolution spatiale. Étant donné que nous ne possédions pas de connaissances *a priori* sur les

assemblages de mammifères marins de l'estuaire du Saint-Laurent, il était prévu d'intégrer le plus grand nombre possible de variables dans nos analyses. Une analyse exhaustive des variables environnementales et biologiques caractérisant l'estuaire du Saint-Laurent avait justement été entreprise dans le cadre d'un projet mené par Pêches et Océans Canada sur l'habitat du béluga (Mosnier et al., 2016), et certaines de ces variables (p. ex., classification des sédiments de surface, vitesse du courant, probabilité d'occurrence du lançon, etc.) auraient pu apporter une information intéressante dans notre modèle. Cependant, la couverture spatiale de la plupart des variables environnementales et celle de nos relevés d'observations ne coïncidaient pas. Couvrant une région moindre que celle des relevés, l'inclusion des couches de variables environnementales aurait entraîné l'exclusion d'un trop grand nombre de données d'observations, ce qui rendait ces variables inutilisables. D'autres variables, comme la hauteur de la surface de l'eau, qui avait été utilisée lors d'un projet parallèle afin de décrire l'habitat de la mégafaune marine dans le golfe du Saint-Laurent (Mosnier et al., 2018), avaient aussi été envisagées. Bien que la résolution des images satellitaires de cette variable soit suffisante pour le golfe du Saint-Laurent, elle s'est avérée trop grossière pour l'estuaire du Saint-Laurent, qui est considérablement plus petit. Il serait intéressant de faire suite à ce projet en tenant compte d'un plus grand nombre de variables ayant une incidence directe sur la distribution des mammifères marins, en particulier les données de proies, au lieu de n'inclure que des variables d'approximation. Mosnier et al. (2016) avaient également exploré l'option d'ajouter davantage de variables biologiques ayant un lien avec les proies du béluga et ont dénoté la quantité insuffisante de données à cause du faible effort de pêche commerciale et de relevés scientifiques dans l'estuaire du Saint-Laurent. La distribution des mammifères marins étant intimement liée à la distribution, à l'abondance et à la composition de leurs proies préférentielles, l'intégration de données de proies dans notre modèle prédictif aurait probablement augmenté sa performance en matière de prédiction et mené à des résultats semblables, mais plus affinés.

Un échantillonnage de données environnementales *in situ* effectué en simultané avec les relevés d'observations aurait permis d'avoir accès à un plus grand nombre de variables et de construire un modèle à plus fine résolution spatiale. De telles données fournissent

d'avantage d'informations sur les caractéristiques de la colonne d'eau (p. ex., profondeur de la thermocline, de la couche de mélange et de la zone euphotique), caractéristiques qui ont certainement une influence sur la distribution des mammifères marins (Redfern et al., 2006). L'ajout de ces caractéristiques aurait entre autres permis de tenir compte davantage de composantes spatiales tridimensionnelles (Duffy & Chown, 2017). En effet, la tridimensionnalité du milieu marin est souvent négligée en modélisation écologique. Or elle ajoute d'énormes variations environnementales et possède une importance écologique significative (Bentlage et al., 2013; Pawar et al., 2012).

Perspectives de recherche

À notre connaissance, aucune recherche n'a considéré les mammifères marins du Saint-Laurent en tant qu'assemblages d'espèces auparavant. D'ailleurs, même en ne considérant que les espèces individuellement, les connaissances sur l'abondance et la distribution d'un grand nombre d'entre elles demeurent incomplète et ce, malgré l'importance écologique et biologique du Saint-Laurent pour elles. Quelques espèces de baleines et de phoques ont fait l'objet d'un plus grand nombre d'études, notamment les espèces en voie d'extinction [p. ex., béluga (DFO, 2012), rorqual bleu (DFO, 2016)] et celles ayant un impact sur les activités de pêche commerciale [p. ex., phoque gris (Hammill et al., 2014), phoque du Groenland (Hammill & Stenson, 2000)], mais l'information demeure tout de même fragmentaire. En raison de leur rôle écologique, la protection des mammifères marins est nécessaire si l'on veut préserver la biodiversité de cet écosystème.

L'utilisation d'une nouvelle méthode, qui combine des analyses fréquemment utilisées en écologie des communautés benthiques et l'étude de la distribution des mammifères marins, a mené à une vision nouvelle et différente de la diversité des mammifères marins du Saint-Laurent. Cette méthode s'ajoute à la liste grandissante de travaux de recherche qui visent à contribuer au renforcement de la préservation des écosystèmes marins dans une région d'intérêt économique majeur, qui sera sans nul doute

touchée par les changements globaux. Dans ce contexte, il serait intéressant de faire suite à ce projet en tenant compte de variables indicatrices des changements climatiques. La température et la salinité de surface utilisées dans le cadre de ce projet sont certes des facteurs importants pour ce qui est des mammifères marins, mais d'autres variables pourraient également être considérées. Les changements climatiques affecteront les caractéristiques physiques, biologiques et biogéochimiques des océans; les impacts prédits, en plus d'une hausse de la température et de la salinité, incluent des changements du niveau de la mer, de la circulation océanique du couvert de glace, des concentrations en CO₂, du pH, de la fréquence des tempêtes, de la vitesse du vent, etc. (Learmonth et al., 2006). Ces conséquences sur l'environnement marin seront complexes et méritent d'être investiguées afin de mieux protéger la faune marine.

L'intégration de variables anthropiques entraînerait également des résultats intéressants. Par exemple, Mosnier et al. (2016) ont caractérisé l'habitat du béluga du Saint-Laurent du point de vue des menaces susceptibles d'affecter l'utilisation de certains secteurs par le béluga, en l'occurrence, les contaminants et le trafic maritime. Les menaces introduites dans l'environnement par les activités d'origine anthropique sont effectivement si constantes qu'elles peuvent maintenant être considérées comme des caractéristiques clés des habitats pouvant influencer la distribution des espèces. Il serait aussi pertinent de considérer les effets des impacts cumulés de ces menaces croissantes, qui, imposées simultanément, peuvent agir en synergie et entraîner des effets indésirables de façon exponentielle sur les mammifères marins du Saint-Laurent et les communautés biologiques du Saint-Laurent (Beauchesne et al., 2016).

Comme l'ont démontré Ferrier & Guisan (2006), et, plus récemment, Ovaskainen et al. (2017), la modélisation des communautés écologiques offre de nombreux avantages par rapport à la modélisation ne visant qu'une seule espèce. Elle permet entre autres un traitement plus rapide des données et une capacité de synthétiser des données complexes rapidement dans une forme facilement interprétable et utilisable par les scientifiques. Elle permet aussi de conserver les données sur les espèces rares, et de mieux comprendre les

réponses environnementales que celles-ci partagent avec les espèces plus communes. Les perspectives de recherche reliées à l'écologie des communautés sont nombreuses parce que cette méthode offre un cadre de travail cohérent et complet pouvant répondre à une foule de questions.

Nous croyons donc que les résultats de ce projet sont pertinents et ouvrent la porte à d'autres études visant à comprendre et à protéger, non seulement les mammifères marins, mais toutes les communautés biologiques du Saint-Laurent. Les assemblages d'espèces sont d'importants éléments de leur écosystème et contribuent à sa stabilité. L'étude des assemblages d'espèces et des communautés écologiques génère de plus en plus d'intérêt dans la communauté scientifique grâce à son potentiel d'informer sur la biodiversité d'un milieu, sur les interactions entre les espèces et sur les interactions entre les espèces et leur environnement. Si l'on vise à comprendre l'écologie d'un écosystème dans son ensemble, il est important de connaître les facteurs qui déterminent la distribution et l'abondance des espèces, et ceci ne peut être fait sans considérer les interactions possibles entre celles-ci. L'écologie des communautés représente donc une avenue prometteuse pour le futur et constitue une approche intégrative qui s'applique bien à n'importe quel projet utilisant une approche écosystémique.

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