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COASTAL AND MARINE ECOLOGY

Estimating the proportion of a beluga population using specific areas from connectivity patterns and abundance indices

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Abstract. An understanding of habitat use and connectivity is key to preserving wildlife habitat integrity. In this study, we present an innovative approach to habitat connectivity and quantitative assessment of their use that is applicable to any terrestrial or aquatic species. Specifically, we aimed at estimating the proportion of the St. Lawrence Estuary beluga population (Canada) likely to use specific habitats within their summer range from habitat connectivity. To achieve this goal, we used a long-term (~30 yr) observational database of beluga herd movements to derive transit corridor and an index of connectivity among habitats. These were then coupled with relative abundance estimates from aerial surveys for each of these habitats. Specifically, our objectives were to (1) verify the existence and location of transit corridors, (2) examine the effect of environmental factors on movement patterns and corridor routes, (3) describe their use by different age classes, and (4) based on connectivity patterns, determine the proportion of the population likely to transit along these corridors and to be present in each habitat. Our results highlighted the existence of a network of transit corridors among habitats that are connected to a central confluence zone, and expanding with three main branches into the three main regions of their summer range (Upper and Lower Estuary, and Saguenay River). They also highlighted the existence of a spatial segregation of sex and age classes in the population. Previously published aerial survey data indicate that on average, <6% of the population can be found within the limits of each habitat at any given time. Using this information within the framework of habitat connectivity provided a minimum estimate of the proportion of the population likely to visit each habitat, with minimum proportions reaching 45% in habitats of the central confluence zone (Île Rouge area). While we detected no evidence of an influence of bottom depth on corridor routes, we identified a tendency of beluga for moving with surface and ebb tide currents. The application of this approach to beluga and other wildlife populations will contribute to better assessing their potential exposure to natural or human-related stressors.

Key words: abundance; animal movement; circular statistics; corridors; focal follows; habitat connectivity; St. Lawrence Estuary beluga.

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INTRODUCTION

Preserving habitat integrity is an essential component to strategic conservation planning for wildlife species. High habitat integrity refers to a state of the environment where animals benefit from the best possible fitness while performing vital activities. In many wildlife species, habitats are composed of concentration areas connected by transit corridors (Roever et al. 2013, Pendoley et al. 2014, Sawyer et al. 2019). Concentration areas are habitat patches where the animals spend most of their time and engage in activities such as foraging, breeding, resting, or socializing. Transit corridors are used for commuting between concentration areas on a periodic basis. Corridors are typically characterized by consistent directional patterns in animal movements. In a context of high habitat integrity, corridors are beneficial by providing access to resources and mates, and allowing migration, dispersal, and recruitment. Their location may be associated with a gain in fitness resulting from protection against predators and disturbance, and an advantageous energetic cost of utilization (Monteith et al. 2018). In contrast, the location of corridors in low-quality habitats may result in adverse effects on individual health and increased risk of injury or mortality if stressors are located on the trajectory (Henein and Merriam 1990, Hobbs 1992, Sawyer et al. 2019). In species showing some level of fidelity to a home range, individuals concentrate their activities and movements within a subset of their population's distribution range. A corollary of this behavior is that not every individual or population segment would be equally exposed to potential stressors. Understanding habitat connectivity is thus an essential step for qualifying habitat integrity.

Habitat connectivity is generally investigated with a spatial matrix representing the landscape features and habitat patches (Kindlmann and Burel 2008, Cushman et al. 2013). The corridors connecting habitat patches across the matrix are ideally determined from observational data, but these data are often lacking or insufficient given that animal movement studies are resource-intensive. In such cases, the corridors connecting habitat patches across the matrix are delineated using a modeling approach where the resistance of the matrix is tested against the movements of the target species. Matrix resistance is estimated according to proxies like the species' habitat preferences or avoidance of landscape features that hinder movements (Fall et al. 2007, McRae et al. 2008, Cushman et al. 2013). This framework offers a wide variety of applications in terrestrial anthropized landscape settings, and the literature is flourishing in the field of habitat fragmentation for terrestrial species. In marine environments, the biotope is often far less spatially structured, and habitat preferences or hindrance associated with the landscape features are not as well defined. Most marine connectivity studies to date have dealt with larval dispersion, and comparatively, little effort has been devoted to delineating corridors or assessing habitat connectivity in marine megafauna (Bryan-Brown et al. 2017).

The beluga (*Delphinapterus leucas*) population from the St. Lawrence Estuary (SLE), Canada, has been depleted by commercial and bounty hunting, and is currently small (<900 individuals), endangered, and declining (Mosnier et al. 2015). It is exposed to multiple anthropogenic stressors, notably contamination from toxic substances, noise pollution from vessel traffic and marine infrastructure development, and small vessel collision risk (COSEWIC 2014). The population's summer range is downstream of a heavily industrialized watershed and overlaps a busy seaway. Areas within their summer range where a large proportion of the population gather (50% kernel densities) or where beluga movements are less directional have been documented by multiple investigators using different datasets and are highly consistent among studies (Michaud 1993, Lefebvre et al. 2012, Mosnier et al. 2016, Fig. 1). Current knowledge indicates ample movement among these areas. For instance, residency time of individual beluga within these areas is notably short, lasting a few hours only, with considerable time spent moving between them (Chadenet 1997, Lefebvre et al. 2012). This information suggests a high turnover of individual beluga within each area. The beluga is also well known for its spatial segregation between sexes and age classes at least during summer (Smith et al. 1994, Loseto et al. 2006), a characteristic also documented in the SLE (Michaud 1993). Genetic and behavioral evidences indicate high site fidelity to general summering areas in beluga, as well as to specific habitats within them (Caron and Smith 1990, Turgeon et al. 2012, Colbeck et al. 2013, O'Corry-Crowe et al. 2018, 2020). A better understanding of connectivity patterns among SLE beluga of different age and sex classes has important implications as it can reveal the proportion of a population occurring in specific areas and that is potentially exposed to stressors impacting any one of these areas or connecting corridors.

Fig 1

Using a long-term database of SLE beluga herd summer movements coupled with spatially

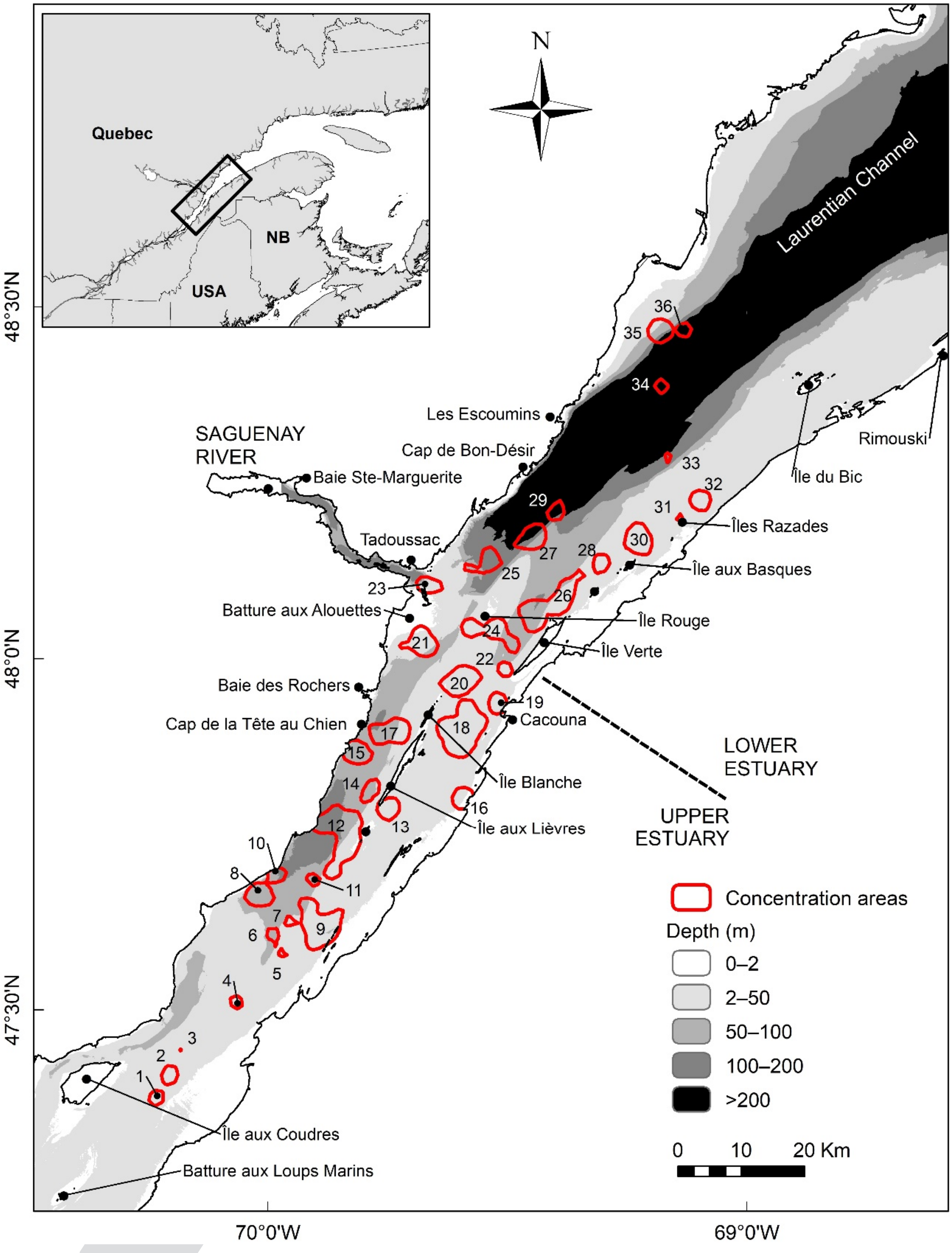

Fig. 1. Portions of the St. Lawrence Estuary and Saguenay River (Quebec, Canada) included in this study. Concentration areas are 50% kernel contours taken in Mosnier et al. (2016). Depth data are from Canadian Hydrographic Service.

explicit aerial survey results on population distribution among concentration areas, we aimed at investigating how these areas are interconnected. More precisely, our objectives were (1) to verify the existence and location of transit corridors, (2) to describe their use by different age- and sex classes, (3) estimate the proportion of the population likely to use each area from connectivity patterns, and (4) test the effect of environmental factors on herd movements and corridor routes. The originality of our study stems in the combination we made of observational data of herd movements and aerial survey results on distributional data.

METHODS

Study area and data collection

Connectivity studies require information on three spatial components: a landscape matrix, concentration areas (high-use areas or habitat patches), and corridors. The landscape matrix used in this study was a grid with 1-km^2 cells. This cell dimension is consistent with Lefebvre et al. (2012) who analyzed a subset of the same data for a different purpose. Concentration areas (CA; hereafter referred to as such) corresponded to the 36 areas published in Mosnier et al. (2016) for the SLE beluga population (Fig. 1). These CAs were based on 35 systematic line transect aerial surveys of their entire summer range. They were delineated with the kernel method and represent areas where 50% of the observations were cumulated during these surveys (K_{50}). They are each conveniently associated with a proportion of the population (summing to 50% not 100% given they are K_{50}), which was assumed to be 1100 individuals at the time of their study (Appendix S1: Table S1). The Saguenay River represents an important component of the SLE beluga summer range, but was not included in Mosnier's study given that counts were obtained using a different method, that is, they were assumed to be total counts (Gosselin et al. 2017). The proportion of the population using the Saguenay River was obtained using visual (n = 36) and photographic (n = 8) counts for the Saguenay River extracted from Gosselin et al. (2017) and assuming a population size of 1100 individuals as in (Mosnier et al. 2016). On average, an estimated 1.9% and 1.6% (mean 1.8%) of the population was present in the Saguenay River according to visual and photographic surveys, respectively.

The existence of transit corridors and their routes were examined using observational data of herd movements obtained from vessel-borne focal follows of beluga herds. Data collection spanned 28 yr (1989–2016) and was conducted on average 2.4 times a week between June and October, inclusively, in most years. Most of the data were collected by the Group for Research and Education on Marine Mammals (GREMM) and a second team (DFO, Mont-Joli, Quebec, Canada) contributed to sampling in 2003, 2005, 2010, and 2011. Details of data collection are described in Lefebvre et al. (2012). Briefly, selection of daily survey area was not random nor systematic, but rather made according to weather conditions prevailing in different parts of the summering area. Caution was taken to maximize spatial coverage within the summer distribution range and to prevent resampling the same area on consecutive days. However, most of the search effort was allocated to the central portion of the SLE beluga summer distribution (Mosnier et al. 2010, Gosselin et al. 2014, 2017), within a 35 km radius from the Saguenay River Mouth and main port in Tadoussac, and decreased from there on with increasing distance (Fig. 2). In the Saguenay River, effort remained high up to Baie Sainte-Marguerite, but was low past this point where beluga occurrence is much lower (Gosselin et al. 2014, 2017). All segments of the population occur on a regular basis in the sampled portion of the summer range (Michaud 1993); thus, no systematic bias was anticipated from the sampling scheme. Search effort was not systematically recorded in the early years of this program and thus could not be used here to distinguish areas with an absence of effort from those with effort but absence of beluga (see also Lefebvre et al. 2012).

Fig 2

A herd was defined as an assemblage of groups of individuals where inter-group distance was small relative to herd extent. Groups were defined as assemblages of beluga less than one body length apart from one another. During focal follows, point sampling sessions recorded herd location and surface configuration including herd size, radius, and age composition, and were made at 30-min intervals (see Lefebvre et al.

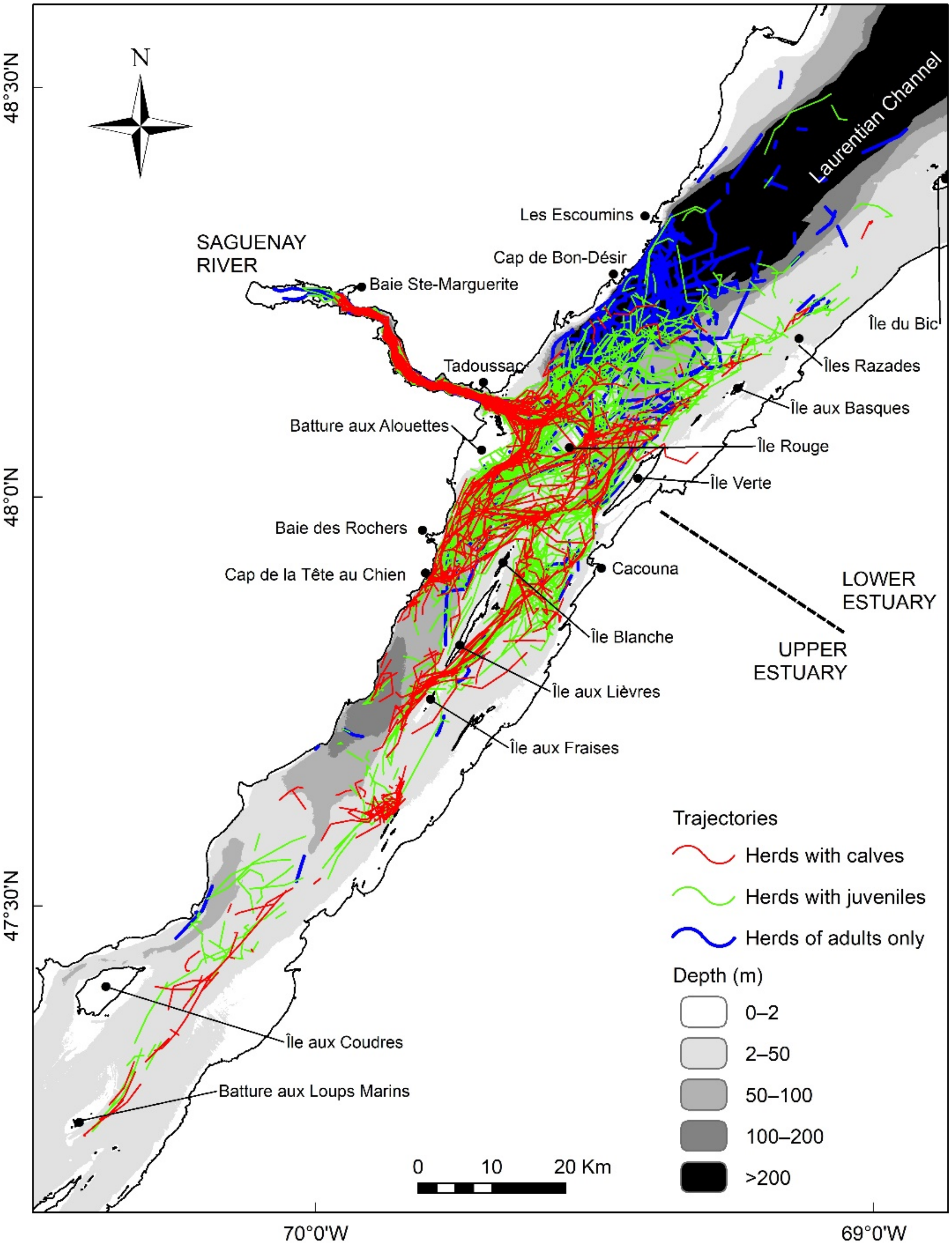

Fig. 2. Beluga herd trajectories from vessel-borne visual follows with a segregation by age classes. Depth data are from Canadian Hydrographic Service.

2018, for the full set of sampled herd characteristics). Upon detection of a herd, a 15-min period of observation from outside the herd was undertaken, after which the vessel approached at slow speed, took position within the herd, and observers proceeded with the first point sampling session. Keeping pace with the animals, the vessel remained within the herd for an average of 93 min (SD = 59; range 548) or until the contact was lost. The location recorded during the point sampling sessions was that of the vessel. Age composition consisted in the estimation of numbers of individuals in age classes with the following bins: calf (small-sized, beige, or dark-colored individuals, jerky surfacing and fetal fold if apparent), juveniles (medium-sized, gray-colored individuals), and adults (white-colored individuals). Male and female beluga cannot be reliably differentiated in the field, and thus, sex composition was not recorded.

Data analysis

Given the large amount of observational movement data available for SLE beluga, and the challenges we would have faced estimating resistance matrix in this spatially unstructured biotope where cost-associated habitats (other than very shallow waters and islands) are undefined, application of methods typically used in data-poor connectivity assessments was unnecessary. Instead, we proceeded directly with the delineation of the corridors by a spatially explicit statistical analysis of aggregated herd movement data. Spatial data treatment and analysis was conducted in ArcGIS (ver. 10.4; ESRI, Redlands, California, USA). Only locations obtained from a GPS (2005 and onward) or Loran-C receiver (1989–2007) or those recovered from marine charts according to accurate field notes (1989 and onward) were considered valid. Herd locations recorded in decimal degrees were converted into UTM coordinate system to facilitate subsequent computations. The 30-min interval rule between point sampling sessions was not always strictly followed in the field. Any gap between two point sampling sessions longer than 60 min terminated a follow. Throughout this paper, step refers to an interval, in time and space, between two point sampling sessions. The data collected during a point sampling session were associated with the step it terminated. Step length corresponds to the Euclidean distance between two point sampling sessions and was calculated according to the Pythagorean theorem. Step direction of movement was calculated relative to true north with trigonometric functions. When two successive point sampling sessions were on either side of a headland, the resulting step crossed over land. In those cases, the step was manually forced to detour the headland with the shortest route by adding a location splitting the step in two parts. The time associated with this artificial location was calculated based on its relative distance between the adjoining locations, and assuming a constant travel speed. Most such occurrences were found in the Saguenay River. Spatial buffers were generated around the steps (using the herd radius recorded in the field), to account for herd spread. Data associated with each step (direction of movement and configuration) were assigned to the cells intersecting their respective buffers.

The verification of the existence of corridors and their delineation were achieved with two methods: vectors of movement and probability of orientation. Vectors of movement were produced in each matrix cell with mean step direction as an index of vector direction and resulting vector length (rho) as an index of vector amplitude. Rho is a measure of dispersion for circular data. This parameter conveniently scales from 0 to 1 where the latter indicates absence of dispersion (Mardia and Jupp 2009). The distribution of the direction data in each cell was compared to a uniform distribution with Rao's test for homogeneity, Kuiper's one-sample test of uniformity, and Watson's goodness of fit test (circular package in R). Only cells with a minimum number of 10 steps, that is, with a minimum sample size of 10 beluga herds, were tested (n = 1153). A uniform distribution would indicate that, in a particular cell, herds were likely to move in any direction. In contrast, a heterogeneous distribution would indicate a directional pattern. A visual examination of the circular diagrams produced for those cells revealed anything between a unimodal distribution to a sharp multimodal distribution (herds likely to move in more than one direction, sometimes in strict opposite direction). In the latter cases, direction data could obviously not be aggregated in a single mean value. Therefore, the cells with heterogeneous distribution were included in a modal analysis for circular data (circular package in R). Because of the circular nature of direction data, there was a risk that a mode that overlapped the point 0° was split in two, artificially inflating the rho parameter. One way to prevent this possibility was to rotate the data so that the point 0° fell outside the modes. The direction data were therefore rotated eight times by one-eighth of a circle (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°) each time. After each rotation, a modal analysis for circular data was conducted, the data points were divided into the resulting modes, and rho was calculated for each mode. For each cell, the modes kept for further analysis were the ones produced by the rotation that issued the smallest number of modes and the highest cumulative rho value. In cells with heterogeneous data distribution, vector direction and amplitude (rho) were calculated for each mode in each cell with the un-rotated data. In cells where data distribution was uniform or not tested, vector direction and amplitude were calculated using data aggregated in a single vector. In order to compare our results with what can be expected by chance alone, this procedure was repeated with simulated data where random direction values were generated in each matrix cell in equal number to its number of observed steps. In order to allow contiguous vectors to graphically form parallel patterns, vector directions were subsequently assigned an octant number according to its direction of movement rounded to the nearest multiple of 45°. In this case, each octant pointed toward the centroid of one of the eight neighboring cells, with octant 1 being centered at 90°, and numbers proceeding clockwise from octant 1 to octant 8, which was centered at 45°.

In order to ensure some robustness in corridor delineation, we used a second approach where we conducted a hierarchical cluster analysis using Euclidean distance and complete linkage as the agglomeration method, where the matrix cells were grouped according to their probability of movement along each one of four axes. This probability was calculated with the following procedure: Step directions were rounded to the nearest multiple of 45° and assigned the corresponding octant value. Octants were binned in four axes of movement as follows: N-S, NE-SW, E-W, SE-NW. An axis of movement differs from a true direction in that it assumes complete bi-directionality. For example, two steps going at 45° and 180° were assigned to the NE-SW and N-S axes, respectively. Then for each cell, we calculated the proportion of steps moving along each axis relative to the total number of steps in the cell. Only matrix cells with 5 steps or more were included. The optimal number of clusters was assessed with the following methods and using packages factoextra and NbClust in R: average silhouette width (Kaufman and Rousseeuw 1990), gap statistics (Tibshirani et al. 2001), Calinski and Harabasz index (Calinski and Harabasz 1974), and total within sum of square.

Patterns in connectivity using the vector method were examined from maps where the degree of directionality for each cell (rho) was assessed using a varying level of severity. Vectors were considered strong in a cell when direction data distribution was heterogeneous and based on at least five steps, when amplitude (rho) was 0.70 or higher, and when the cell was contiguous to at least one neighboring vector with the same characteristics. Vectors were considered weak otherwise. The amplitude condition of 0.70 corresponds to a range equal to 45° (which is the width of an octant and our rounding uncertainty) with a sample size of 2. Under a high level of severity, a corridor had to be based on strong vectors showing a parallel pattern. A low level of severity allowed gaps in contiguity and vector amplitude lower than 0.70. The connective value of each corridor was determined by summing the averaged proportion of the population associated with every CA it connected and where each CA was assigned to only one corridor.

The existence of a match between herd movement direction and surface current direction was examined by assigning to each point sampling session the tidal phase and surface current conditions (direction and speed) that prevailed at the time of the observation. Tidal phases were extracted from water level data referenced at Tadoussac and provided by the *Canadian Hydrographic Service* (http://www.tides.gc.ca/eng/find/zone/2). Data were aggregated in 3-h bins (low, rising, high and ebb tides) where high tide occurs from 5 to 7 h after low tide. Surface current data were obtained from a model (Saucier et al. 1999, Saucier and Chassé 2000) predicting planar vectors (u, v) of surface current speed with a time 4

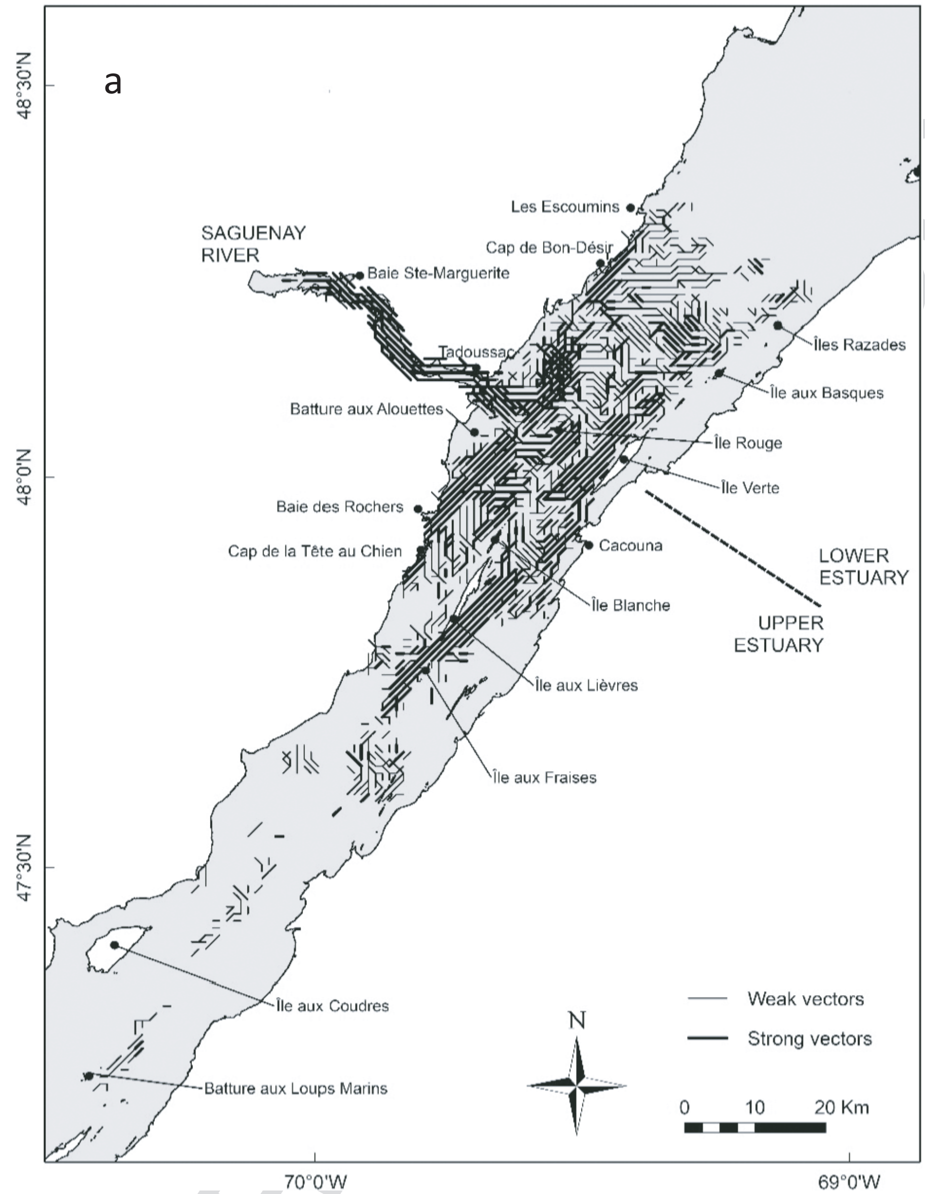

Fig. 3. Direction and amplitude of vectors of movements based on (a) beluga herd trajectories and (b) random directions from simulated movement data as if movements were driven by chance alone.

and spatial resolution of one hour and 400 × 400 m pixels, respectively. A spatial buffer was generated around each point sampling session using herd radius recorded in the field. Each point sampling session was assigned the mean planar vector values averaged over every pixel contained in its buffer. Resulting current speed was calculated with those mean planar vectors according to the Pythagorean theorem. Resulting current direction was calculated relative to grid north using trigonometric functions.

The influence of current direction on directionality of movements was assessed at two time and spatial scales. The concordance between step direction and current direction was first verified globally using any steps associated with strong and contiguous vectors ($\rho > 0.70$). This was done separately for rising and ebb tides (when currents

(Fig. 3. *Continued*)

are expected to be the strongest), and separately for the SLE and Saguenay River. To account for potential local differences in the influence of currents on movement directionality, the absolute difference between step direction and current direction was calculated (range = 0°–180°) and averaged over each strong vector. Data from all tidal phases were examined, but only strong and contiguous vectors were included.

The water depth data (resolution 20 m) were obtained directly from the Canadian Hydrographic Service. Each cell centroid was assigned its corresponding depth value through a spatial joint. Water depth was compared with a *t*-test between cells belonging to a corridor and cells not belonging to a corridor. Cells belonging to a corridor were those that contained at least one strong vector, in accordance with our highest

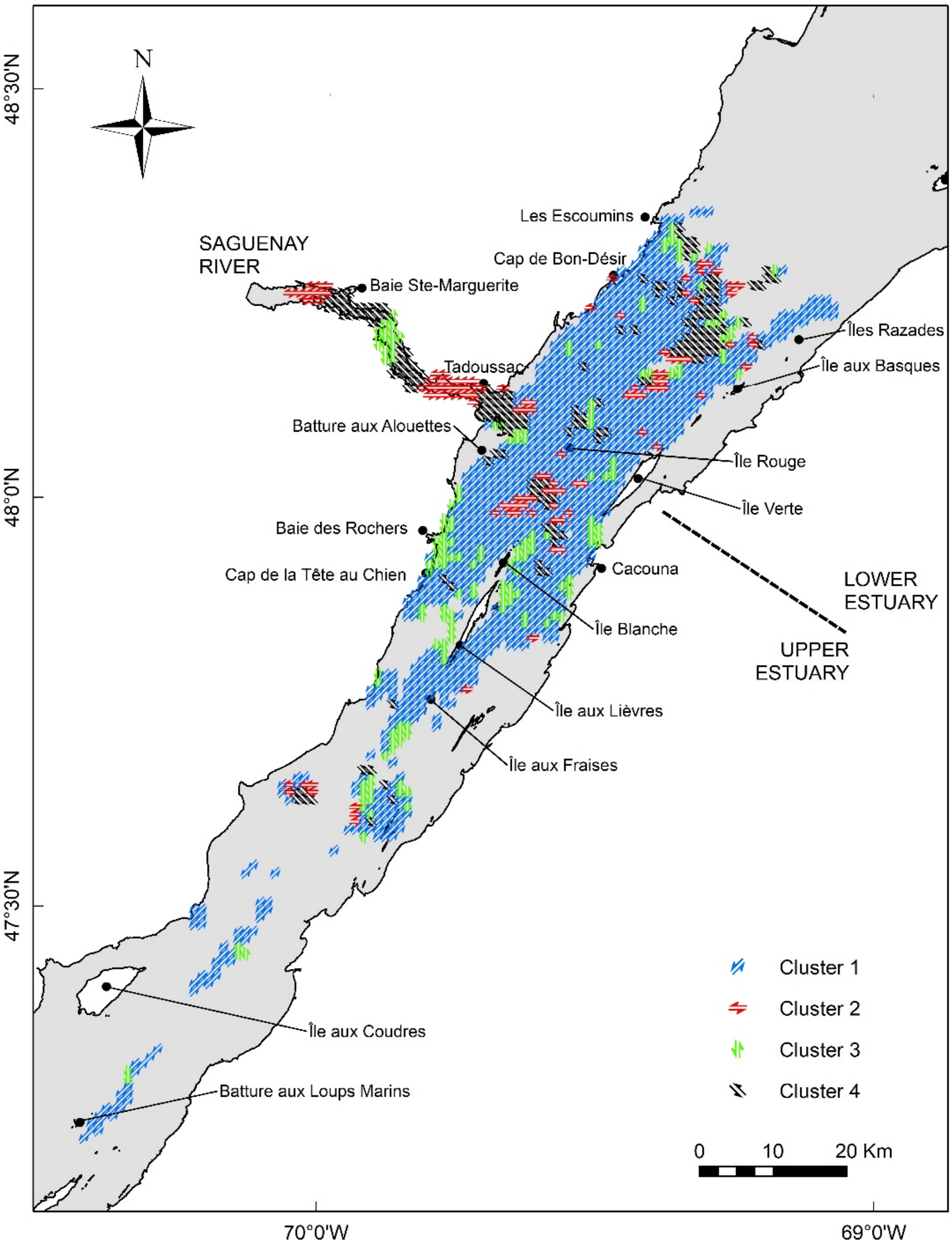

Fig. 4. Spatial distribution of clusters based on probability of orientation of herd movements.

level of severity and ignoring the parallelism aspect. This analysis included only the cells containing a minimum of 5 steps, to allow the possibility of a strong vector. Water depths <2 m were excluded due to possible navigational constraints for beluga. The Saguenay River was excluded from this analysis because its narrowness (<2 km) caused it to be almost completely covered with strong vectors, leaving no possibility for the comparison.

RESULTS

Of the 2897 herd follows conducted between 1989 and 2016, 2224 provided two or more point sampling sessions with valid location data, for a total of 9127 point sampling sessions, and an average of 4 valid point sampling sessions per follow. The spatial distribution of herd follows (Fig. 2) reflects in general terms the distribution of search effort, with a concentration within approximately 35 km from the Saguenay River mouth (see *Methods*). Blank areas in the extreme ends of the study area, in the Estuary and the Saguenay River, need to be interpreted with caution as they may not reflect a true absence of beluga but a lack of effort.

The steps that compose herd trajectories are Euclidean lines joining pairs of locations, and the locations are those of the vessel moving within the herd. As a result, successive steps of a herd trajectory may comprise some artificial variability. Nevertheless, the distribution of herd trajectories highlights some notable spatial patterns (Fig. 2). First, the trajectories showed a fluctuating level of parallelism across the study area. Notable examples of a sharp parallel pattern among trajectories were observed in the Saguenay River, along the south shore of Île aux Lièvres, north shore of Île Verte and Batture aux Alouettes. Examples of a contrasting lack of parallelism among trajectories can be found off Cacouna and near the Saguenay River mouth. Second, a gyre-like pattern taking the shape of a roundabout, with many trajectories branching off to multiple directions, circled around Île Rouge bank. This feature appeared as a major confluence zone in the summer range of the SLE beluga population. Finally, herd compositional data associated with each trajectory highlighted an age-specific spatial distribution in beluga movements in the Estuary, but not in the Saguenay River (Fig. 2).

Combining steps into vectors of movement resulted in a total of 2016 vectors comprised of 5 steps or more, half of which (947) were considered strong vectors (Fig. 3a). Examining parallelism among vectors reinforced patterns observed at the level of individual trajectories and steps in Fig. 2. Parallel patterns among strong vectors could be found in multiple places in the study area, notably in the four areas indicated above, that is, in the Saguenay River, along the south shore of Île aux Lièvres, the north shore of Île Verte and along the Batture aux Alouettes. In most instances, these sets of strong vectors were oriented parallel to the coastlines. The randomly generated data showed multiple strong vectors but no parallel pattern (Fig. 3b), indicating that chance alone was unlikely to explain patterns observed in beluga movement orientations.

Fig 3

The average silhouette width method, the gap statistic method, and the Calinski and Harabasz's index applied to the probability of orientation in different directions indicated optimal numbers of clusters of 2, 4, and 6, respectively. The total within sum of square method was inconclusive. We chose a number of four clusters as an average point. This cluster-based approach showed less spatial structure in beluga movement orientation than the one using vectors and was therefore less informative (Fig. 4). Nevertheless, the most notable result was the dominance of cluster 1 with 70% of the cells (n = 1077). This cluster grouped cells characterized by a northeast-southwest axis of movement, that is, within the main flowing axis of the Estuary, and was distributed exclusively in the Estuary (i.e., none in the Saguenay River). The other three clusters were found in the Estuary and the Saguenay River. Cluster 2 was the smallest one with 117 cells. It was dominated by an east-west axis of movement. Aggregations of cells belonging to cluster 2 were found in Saguenay River and near the eastern end of Île Blanche in the Estuary. Cluster 3 and 4 showed a nearly similar number of cells (173 and 191) and were characterized by a north-south and a northwest-southeast axes of movement, respectively. Notable aggregations of cells from cluster 3 were found in Saguenay River, along Île Blanche, along a stretch of coastline between

Fig 4

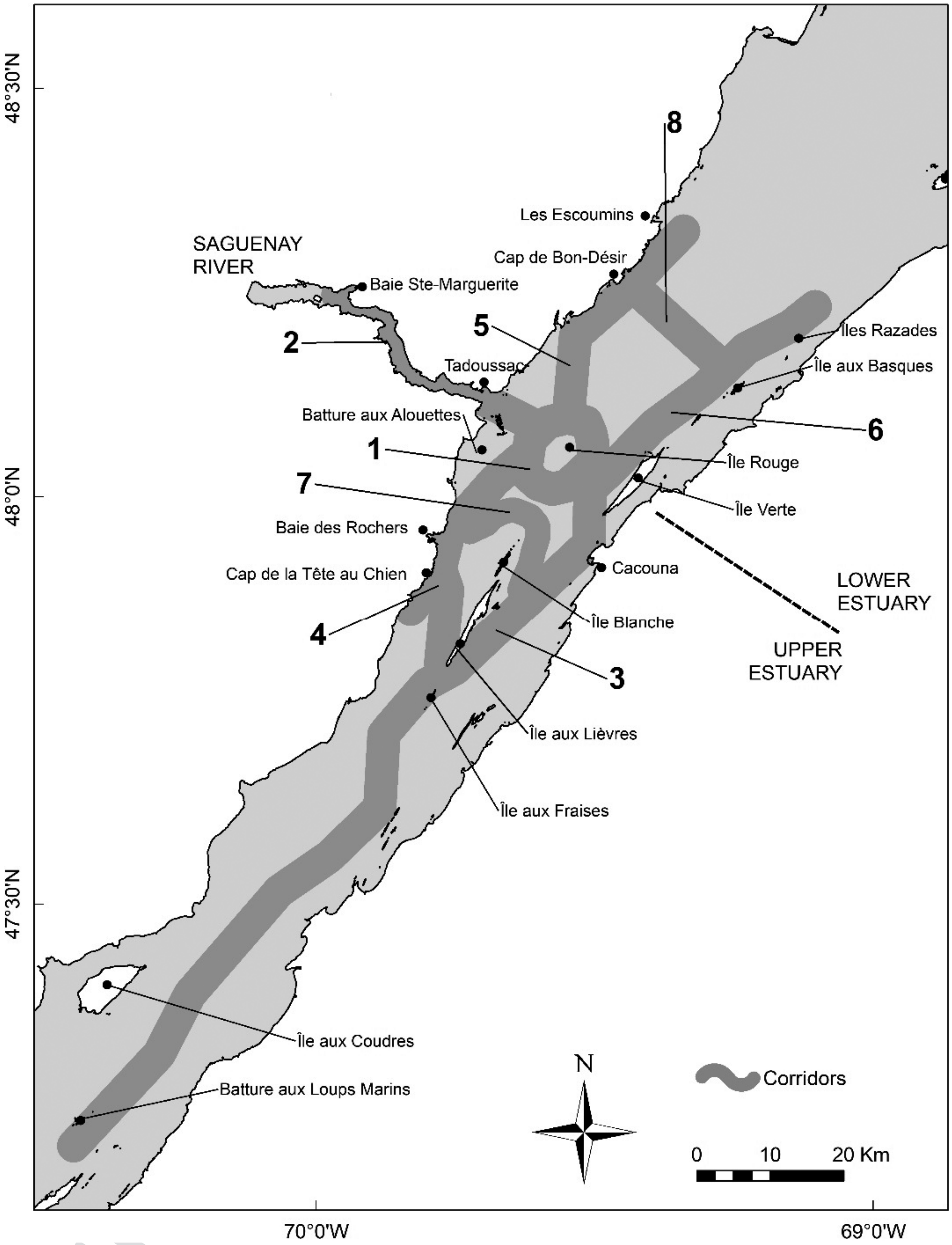

Fig. 5. Network of corridor routes based on observational data of beluga herd movements. Gray lines indicate the shape and location of the corridors, but the actual width and endpoints of the corridors are unknown.

Table 1. Connective value for each transit corridor delineated in the study area.

Corridor	Connected CAs	Connective value	Connected corridors
1	20, 24	5.6	2, 3, 4, 5, 6
2	23, Saguenay River	3.0	1
3	12, 13, 18, 19, 22 (1, 2, 3, 4, 5, 6, 7, 9, 11)	12.1 (18.3)	1, 7 (4)
4	15, 17, 21 (14)	5.7 (6.3)	1, 7 (3)
5	25, 27, 29	3.4	1, 8
6	26, 28, 30 (31, 32)	7.5 (8.5)	1, 8
7			3, 4
8			5, 6

Notes: Values represent the sum of the percentage of the population associated with each concentration area (CA) connected by each corridor. Parentheses show the connective value and connected CAs and corridors when accepting a lower level of severity in corridor delineation. Corridors 7 and 8 do not directly connect any CA. Summary of corridors location: (1) Île Rouge bank, (2) Saguenay River, (3) Upper Estuary, south shore, (4) Upper Estuary, north shore, (5) Lower Estuary, north shore, (6) Lower Estuary, south shore.

Batture aux Alouettes and Cap de la Tête au Chien. Aggregations of cells belonging to cluster 4 were found in Saguenay River, between Île aux Basques and Cap de Bon-Désir and between Île Verte and Batture aux Alouettes, reflecting movements across the Estuary.

The level of connectivity among the CAs was high with eight corridors emerging from the spatial patterns of vectors or cluster aggregations (Fig. 5). A detailed description of these corridors, including vector strength, clusters that support them, CAs that these corridors connect, and type of herds using them is presented in Appendix S2. In summary, corridor 1 circled around Île Rouge and appeared to be a central confluence zone. It was connected to five other corridors (2, 3, 4, 5, 6) extending into the Upper and Lower Estuary and into the Saguenay River. These five corridors were roughly parallel to the coasts. Two other corridors (7, 8) were stretched across the Upper and Lower Estuary (Fig. 5). Generally, corridors extending in the Upper Estuary were seldom used by herds of adults only, while those extending over the Laurentian Channel in the Lower Estuary were mainly used by herds of adults only, and to a lesser extent herds including juveniles (Fig. 2). Based on survey data about the relative distribution of beluga, the results on connectivity among concentration areas indicate that a CA could be visited by anywhere between 3.0 and 12.1% of the population, depending on CAs when considering each of the six delineated corridors separately (Table 1). The maximum value rose to 18.3% when accepting a lower level of severity. The highest connective values were associated with corridor 3 and 6 running near the southern shore in the Upper and Lower Estuary, respectively. The lowest connective value was in corridor 2 in the Saguenay River. Corridors 7 and 8, running across the Estuary, had no associated connective value because there were no CA on their route. CAs near Île Blanche and Île aux Fraises are those likely to be used by the largest proportions of the population. Due to its central place and to the multiple corridors it connected, the connective value of corridor 1 around Ile Rouge can be increased to 37.3% if we add the connective values of each corridor it connected. Accepting a lower level of severity, this value is further increased to 45.1% and these estimates are probably minimum values since they were based on 50% kernel densities.

Fig 5

Table 1

Step direction data belonging to strong vectors and recorded during rising and ebb tides showed a bimodal distribution in both the Estuary and the Saguenay River (Rao', Kuiper's, Watson's tests, $P < 0.01$; Fig. 6). Surface current direction data were multimodal at rising tide and unimodal at ebb tide (Rao', Kuiper's, Watson's tests, $P < 0.01$). In the Estuary, mean modal step directions matched the direction of surface current and the orientation of the Estuary in the study area, that is, 226 ± 62° ($n = 819$) and 48 ± 24° ($n = 195$) at rising tide, and 65 ± 52° ($n = 634$) and 245 ± 38° ($n = 272$) at ebb tide (Fig. 6). In the Saguenay River, mean modal step directions generally also followed the direction of surface current and the orientation of the River (see Fig. 2), and were 305 ± 30° ($n = 318$) and 129 ± 30° ($n = 164$) at rising tide, and 311 ± 33° ($n = 166$) and 128 ± 34° ($n = 151$) at ebb tide.

Fig 6

Our analysis examining the data at fine scale to identify local peculiarities of movement-current associations revealed ample consistency between herd and surface current directions (Fig. 7). The average difference between movement and current directions for the 968 strong vectors included in the analysis was mostly comprised between 45° and 90° and, to a lesser extent, within less than 45° of each other.

Fig 7

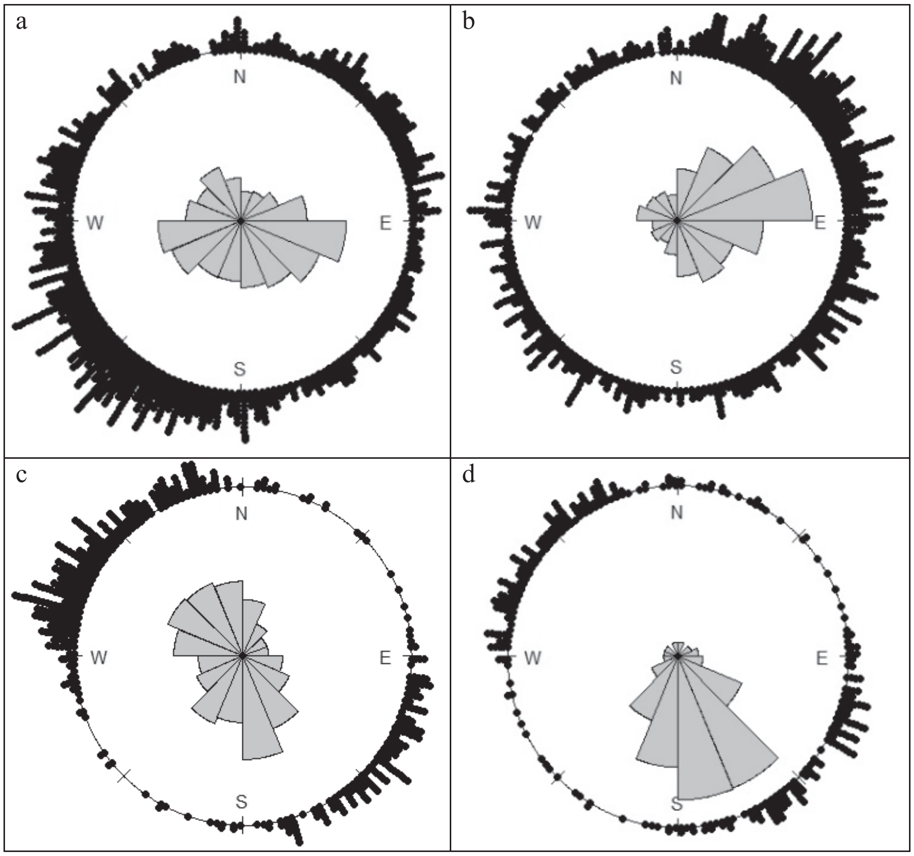

Fig. 6. Step directions associated with strong and contiguous vectors (dots) and surface current directions simultaneous with either one of the steps (petals). (a) Estuary, rising tide, (b) Estuary, ebb tide, (c) Saguenay River, rising tide, (d) Saguenay River, ebb tide. Petal length indicates relative frequency.

Counter current movements were rare. The areas showing the highest level of consistency were corridor 3 along the southern shore of Île aux Lièvres, corridor 4 and 7 off the Batture aux Alouettes, and corridor 8 off Île aux Basques.

Mean water depths (± SD) were 59 ± 63 m (n = 450 cells) and 92 ± 102 m (n = 927 cells) for corridors and non-corridors, respectively (Fig. 8). The kernel density curves and mean (± 95% CI) depth distributions differed significantly between corridors and non-corridors (Fig. 8; t-test on log-transformed data: t = 4.11, df = 1053, P < 0.001). Distributions for corridors and non-corridors were similar for the most part, with a mode near 25 m and a long right tail. However, non-corridors showed a second mode near 320 m. The greatest depth value associated with a point sampling session was 328 m.

DISCUSSION

Our study presented an innovative approach to habitat connectivity and the quantitative assessment of habitat use that is applicable to any terrestrial or aquatic species. Our framework where we analyzed direct observational data with two independent approaches confirmed the existence of an elaborate network of transit corridors in the core of the summer range of SLE beluga. Combining these connectivity results with survey data allowed to estimate the minimum proportion of the population likely to transit along the corridors (i.e., the corridor connective value), to use each of the delineated concentration areas, and to be exposed to local stressors.

The corridor network within the SLE beluga summer range consisted in a central confluence

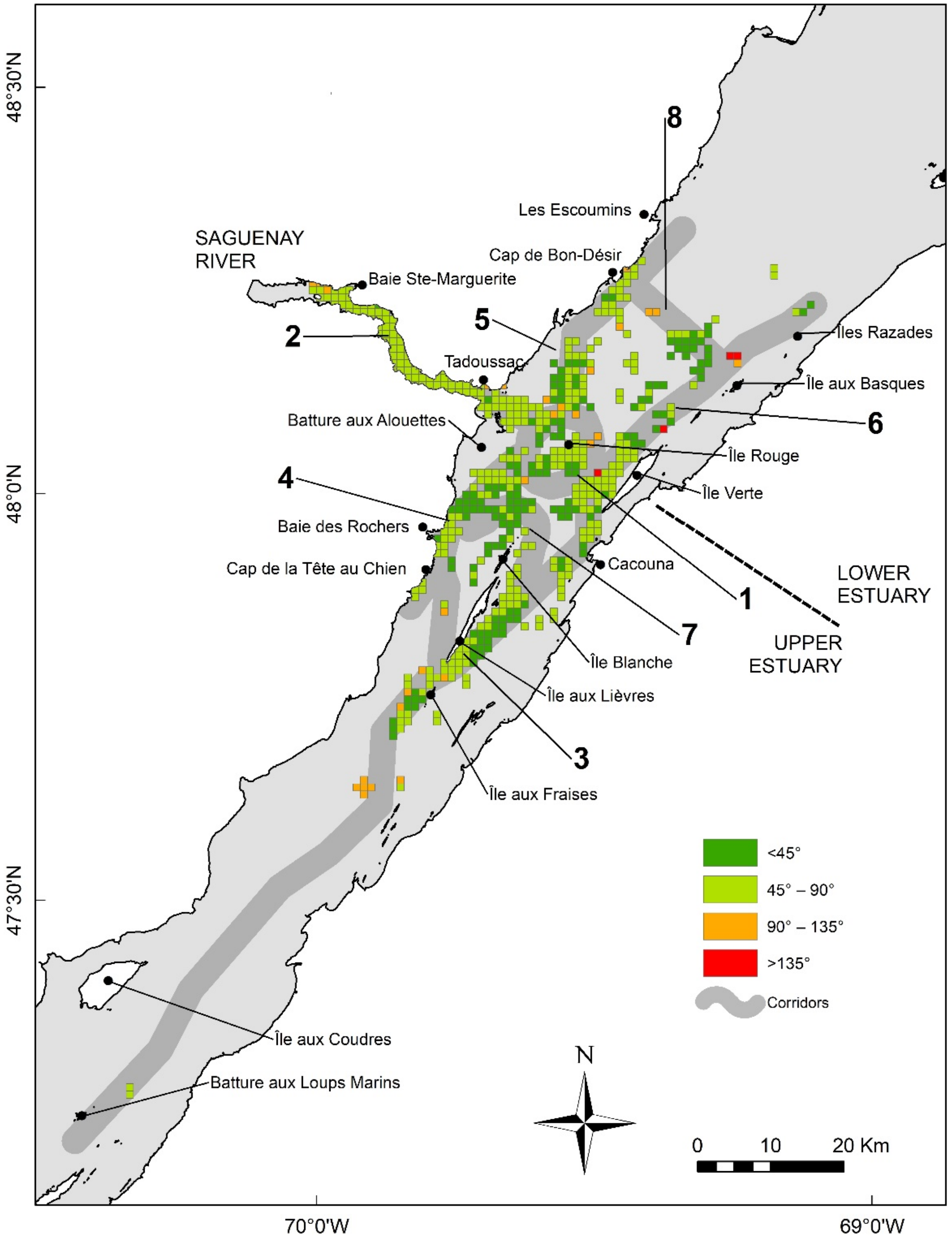

Fig. 7. Absolute difference (from 0° to 180°) between step direction and simultaneous surface current direction averaged over every strong and contiguous vectors. In cells with multiple strong vectors, the results from the vector with the smallest average difference were shown. Also shown are the corridors labeled from 1 to 8.

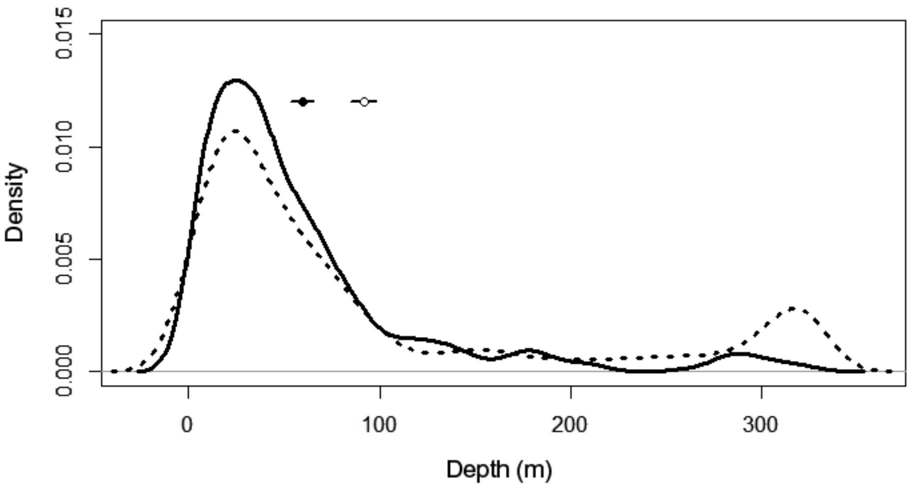

Fig. 8. Kernel density curves and mean (± 95% CI) of depth in cells belonging to a corridor (solid line, filled symbol) and cells not belonging to a corridor (dashed line, open symbol). Whether cells belong to corridors or not is in accordance with the highest level of severity. The Saguenay River and depths <2 m were not included.

zone connected with three main branches to the Upper and Lower Estuary, and to the Saguenay River. Although an increased coverage of the summer range extremes is needed, the network appears to reach almost every end of the summer range, which is consensually recognized as Batture aux Loups Marins, Rimouski, and Baie Sainte-Marguerite (Mosnier et al. 2010, Gosselin et al. 2017). The majority of herd movements were performed along the main axis of either the Estuary or the Saguenay River, leading to most corridors being oriented roughly parallel to the nearest coast. Notable exceptions were corridors 1, 7, 8 (Fig. 5) which provided some connectivity among concentration areas across the Estuary. These results confirm the existence of a high level of connectivity among the SLE beluga concentration areas. The existence of transit corridors in the SLE beluga summer range was proposed by Lefebvre et al. (2012) based on travel speed profiles of beluga herds, although the authors did not speculate on their location.

Using a multi-level severity approach to corridor delineation provided the flexibility but also the robustness to acknowledge the possibility that a corridor route crossed a concentration area or data-poor areas. In the first case, vector amplitude would be typically low, and the steps associated with transiting herds would be masked by the lack of directionality in movement by resident herds. In the second case, a lack of strong vector in that specific area would be explained by a low sampling effort.

The spatial segregation pattern we found is consistent with previous observations for this population (Michaud 1993) and with reports from multiple investigators where females with calves used shallower waters and ventured further upstream in estuaries (Smith et al. 1994, Loseto et al. 2006). Hypotheses for sex- and age-based spatial segregation in odontocetes in general and in beluga in particular were reviewed by Michaud (2005) and Loseto et al. (2006). They include avoidance of predation and intraspecific competition, age-specific or sex-specific forage selection and energy budget, and social preference. While sex cannot be determined accurately from field observations, biopsy samples collected over the years from SLE beluga confirmed that groups of white adults are predominantly composed of males only, and that white adults in groups where juveniles and calves are present are females (Michaud and Lesage, *personal observation*). Based on this assumption, herds of females with calves and/or juveniles would use the shallower, warmer, and brackish Upper Estuary, typical of a nearshore environment or an estuary proper. In the Lower Estuary, these segments of the population would also use waters near the south shore and on the southern slope of the LC, but rarely the deeper and colder marine waters of the Laurentian Channel which were used mostly by herds of adult males only. Corridor 8, which ran across the Lower Estuary, was particularly interesting given the heterogeneity in herd compositions described for this general sector. All types of herds likely transited via corridor 8 (Figs. 2, 5), although movements of white adults across the Estuary axis were clearly more extensive than those of herds with juveniles or calves as they reached the deeper waters of the LC.

The configuration of the corridor network suggests that a large proportion of the population is susceptible to visit the Île Rouge area. Also, all population segments are likely to visit this latter area along with the Saguenay River, and, to a lesser extent, the south shore of the Lower Estuary. In a conservation perspective, this also indicates that a large portion of the population could be exposed to any habitat degradation or stressor located in those areas, even stationary ones with a spatially restricted reach. A consequence of sex- and age-based spatial segregation is that all segments of the population are not equally vulnerable to a stressor, assuming it is localized with a spatial extent of effects less than the full summer range of the population. A stressor located in the Upper Estuary would mostly impact females, calves, and juveniles, whereas a stressor in the Laurentian Channel would impact mainly adult males.

The corridor network overlaps the St. Lawrence Seaway, a busy seaway with an average 5000-6000 transits annually (McQuinn et al. 2011), and which crosses the entire beluga summer range, mostly along the north shore of the Estuary, thereby exposing all age and sex classes. A secondary seaway branches off at the Saguenay River mouth and reaches the upper Saguenay River. Also, the Saguenay River mouth is considered the noisiest and busiest concentration area for SLE beluga (McQuinn et al. 2011, Gervaise et al. 2012), as a consequence of whale-watching activities, recreational boating, and the simultaneous operation of two or three ferries depending on season and time of day. The location of the corridors, and degree of connectivity among concentration areas, indicate that a large proportion of the individuals in the population might be exposed to noise pollution and risks of collision. Collision risk with merchant ships is not considered problematic for beluga, but collisions with small crafts have been reported in the past (Lair et al. 2016). Both merchant ships and small craft can interfere with the normal behavior of beluga and reduce their acoustic space, with potential consequences on foraging efficiency, health, and social bonds (Lesage et al. 1999, Gervaise et al. 2012, Williams et al. 2017). Previous studies examining beluga exposure to noise in several of their habitat, and the potential benefits of mitigation measures reducing noise exposure emphasized the existence of noise refuge in the beluga summer range (McQuinn et al. 2011, Lesage et al. 2014, Chion et al. 2017, DFO 2018). These areas of lesser exposure to noise were located in the Saguenay River, and in the southern portion of the Estuary where islands in the center of the Estuary acted as a barrier to the noise issued from traffic along the north shore. While we cannot exclude that some spatial structure in site fidelity exists within regions used by a specific type of herd, the NW-SE connectivity documented both in the Upper and Lower Estuary suggests that no segment of the population is likely to be fully protected from noise exposure by constraining their domain to these noise refuges.

Herds transiting in corridors showed a strong propensity to move upstream during rising tide and downstream during ebb tide in the Estuary. The pattern was not as evident in the Saguenay River. Also, herd movement directions were highly consistent with local surface current directions. This is consistent with the energy landscape principle which should lead animals to move at the best possible cost:benefit trade-off (Shepard et al. 2013). This includes reducing costs of locomotion between habitat patches by taking advantage of the current, which constitutes in the marine environment the equivalent of the well-documented avian behavior of migrating with tailwinds. Situations where beluga synchronized their movements with current schedule were reported in Alaska and Canadian Arctic populations (Smith et al. 1994, EzEr et al. 2008). In both studies, the beluga took advantage of flooding tidal currents when transiting to shallow waters at the mouth of tributaries. The study area exhibits a highly complex hydrology. The St. Lawrence Estuary belongs to the salt-wedge type, and the lower Saguenay River included in our study area is a fiord (El-Sabh and Silverberg 1990). This means that both waterways are strongly stratified marine environments. Consequently, the tidal current during rising tide, composed of marine water, flows upstream underneath the fresh water layer. This typical estuarine circulation results in weaker current at the surface during rising tide than during ebb tide (Saucier and Chassé 2000). This tidal phenomenon may explain the contrast we found in distribution of current data between tidal phases.

The cells belonging to a corridor were located on average in shallower waters than cells not belonging to a corridor. This result may indicate that a selection process is occurring on the part of transiting beluga herds. The difference in water depth is mainly due to the larger representation of the non-corridors in the deepest waters (>200 m) of the Laurentian Channel. But we question the meaning of this result because, despite its great depths exerting a strong influence on the bathymetric profile, the actual relative importance of the Laurentian Channel (depths > 200 m) in the study area was small with only 13% of relative surface and 8% of the sampling effort. This leaves perhaps little possibility to detect the existence of a corridor in that area and allows us to conclude that, for the most part, there is no difference in water depth between cells belonging to a corridor and cells not belonging to a corridor. Excluding the Laurentian Channel from the dataset, the difference in water depth between corridors and non-corridors vanishes completely (49 ± 4 m, $n = 429$ and 48 ± 3 m, $n = 762$ for corridors and non-corridors, respectively).

Our study indicates that beluga use currents when transiting but depth does not seem to be a driver in shaping habitat selection process and routes of the transit corridors. The amount of connectivity we found is probably an underestimation of total connectivity since the sampling effort was low near the ends of the study area, and therefore, focal follows were limited. Additional observations through photo-identification work or radio or satellite tracking of individual whales might reveal more transit corridors connecting the CAs in those areas, as well as a substructure in site fidelity and spatial segregation within the summer distribution range.

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