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Thirty years of herd focal follows reveal the functions of important habitats identified for the endangered St. Lawrence Estuary beluga

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ABSTRACT: Identifying habitat functions is crucial for understanding how endangered populations such as the St. Lawrence Estuary (SLE) beluga *Delphinapterus leucas* use their environment, and for guiding effective conservation measures. Often, the only way to infer the behavior of cetacean herds is by observing their surface activity and configuration. A previous study developed a classification connecting SLE beluga herd surface characteristics to their underwater diving behavior, enabling the inference of behavior from surface cues alone. Using this method, we analyzed surface activity descriptors collected every 30 min during multi-hour focal follows of 1496 beluga herds tracked in 1991–2020 to classify their behavior into 6 categories: (1) benthic feeding/resting/caring for young, (2) pelagic feeding, (3) pelagic exploration, (4) socialization/benthic feeding, (5) transit, and (6) mixed activities. The relative frequency of these behaviors within each of 27 previously identified key beluga areas formed the basis for statistically grouping areas by their dominant function. Two groups characterized by high directional movement closely matched (≥90%) previously hypothesized transit corridors. The other 2 groups predominantly exhibited foraging and social behaviors, and matched mainly (≥70%) areas with high beluga residency whose specific function was previously unclear. Although habitat groups varied in environmental characteristics, no clear separation was observed, suggesting other factors may shape habitat use at multiple scales. This study highlighted that beluga have limited alternative habitats to support vital functions should local stressors compromise habitat quality or accessibility. These findings are critical because segments of the population show strong fidelity to specific summer sites.

KEY WORDS: Beluga · *Delphinapterus leucas* · St. Lawrence Estuary · Behavioral classification · Habitat use · Habitat functions · Herd focal follow · Spatial management

1. INTRODUCTION

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

Habitat degradation, through contamination or chronic high noise levels or human activity, may pose a significant threat to the survival of wildlife

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species (Williams et al. 2022), including cetaceans (Reeves 2018). Small populations showing high site fidelity and small home ranges may be especially vulnerable to habitat degradation, as they may have few alternative habitats to support their biological needs (Forney et al. 2017, Merkle et al. 2022). For mitigation measures to be effective, there is a need to understand habitat use patterns and habitat functions (Redfern et al. 2006, Ross et al. 2011, Brakes & Dall 2016). Boat-based surveys, aerial surveys, and short-term visual tracking (hereafter 'focal follows') of herds or groups often constitute the most comprehensive long-term data sets for cetaceans; when analyzed alongside environmental characteristics and herd behaviors, they can reveal the life functions supported by specific habitats (Redfern et al. 2006, Ross et al. 2011, Brakes & Dall 2016).

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

This population is among the most extensively studied within the species, and has the longest time series of observation data from aerial surveys and herd follows (Norman et al. 2022, Lesage et al. 2024, St-Pierre et al. 2024). The use of these data sets formed the basis for the designation of the critical habitat of this population (Mosnier et al. 2010, Lesage et al. 2024), and has allowed the detection of site fidelity (Bonnell et al. 2024) and differential exposure of the various segments of this population to local stressors (Chion et al. 2021, Bonnell et al. 2022). Specifically, herd focal follows were analyzed with a focus on movement directionality relative to environmental characteristics to identify corridor routes (those with high travel speeds and strong directional movements) and highlight summer habitat connectivity (Ouellet et al. 2021). Herd movements and displacement speeds were further analyzed to identify areas where beluga showed area-restricted search and a higher degree of residency (areas of high residency, AHRs; Lemieux Lefebvre et al. 2012). Similarly, aerial survey data were analyzed using a kernel approach to identify areas of high beluga densities (Mosnier et al. 2016, Harvey et al. 2025. While these 3 studies spatially located key areas for beluga, their functions were either presumed as based on indirect evidence (corridor routes) or unknown (high-use area).

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

Beluga are highly gregarious and exhibit a fission–fusion grouping pattern (Michaud 2005, O'Corry-Crowe et al. 2020), and they are spatially segregated by sex and age in the SLE and other ecosystems (Michaud 1993, Ouellet et al. 2021). Furthermore, recent studies indicated that specific segments of the population exhibit site fidelity to different sectors within their summer habitat (Bonnell et al. 2022, 2024). On top of these social factors, a number of environmental features can affect beluga distribution and habitat use over time and space. Bathymetric features and oceanographic processes (e.g. water mass movement, up- and downwelling zones) may promote pelagic prey concentration and enhance foraging opportunities (Michaud 1990, Mosnier et al. 2016, Scharffenberg et al. 2019, Ouellet et al. 2021). Areas near large river mouths (resulting in larger catchment and greater discharge, i.e. of higher Strahler stream order) can generate environmental gradients (e.g. salinity, temperature) and increase prey availability (Goetz et al. 2012, Hauser et al. 2017, McGuire et al. 2020, Ausen et al. 2023). Beluga may profit from tidal and surface currents when traveling (Ouellet et al. 2021) to minimize energetic costs (Goetz et al. 2012, McGuire et al. 2020).

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

2. MATERIALS AND METHODS

Fig. 1 summarizes the data sources, along with both the analyses from prior work utilized in this study and the analyses newly conducted as part of our research. Briefly, the foundation for the current study is a previously developed classification method, which connected SLE beluga herd surface activity and configuration to their underwater diving behavior, and which enabled herd behavior to be inferred from surface cues alone (Lemieux Lefebvre et al. 2018). Using this method, the current study analyzed surface activity descriptors collected every 30 min during multi-hour focal follows of 1496 beluga herds tracked in 1991–2020 to classify herd behaviors into 1 of the 6 potential categories defined by Lemieux Lefebvre et al. (2018). For each of the 26 previously identified high-use areas or presumed corridor routes, the relative frequency of these 6 behavioral categories was then used to statistically group areas based on similarity in main functions. Groups of habitats were then examined for potential differences in environmental characteristics and usage according to beluga herd composition.

2.1. Data collection

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

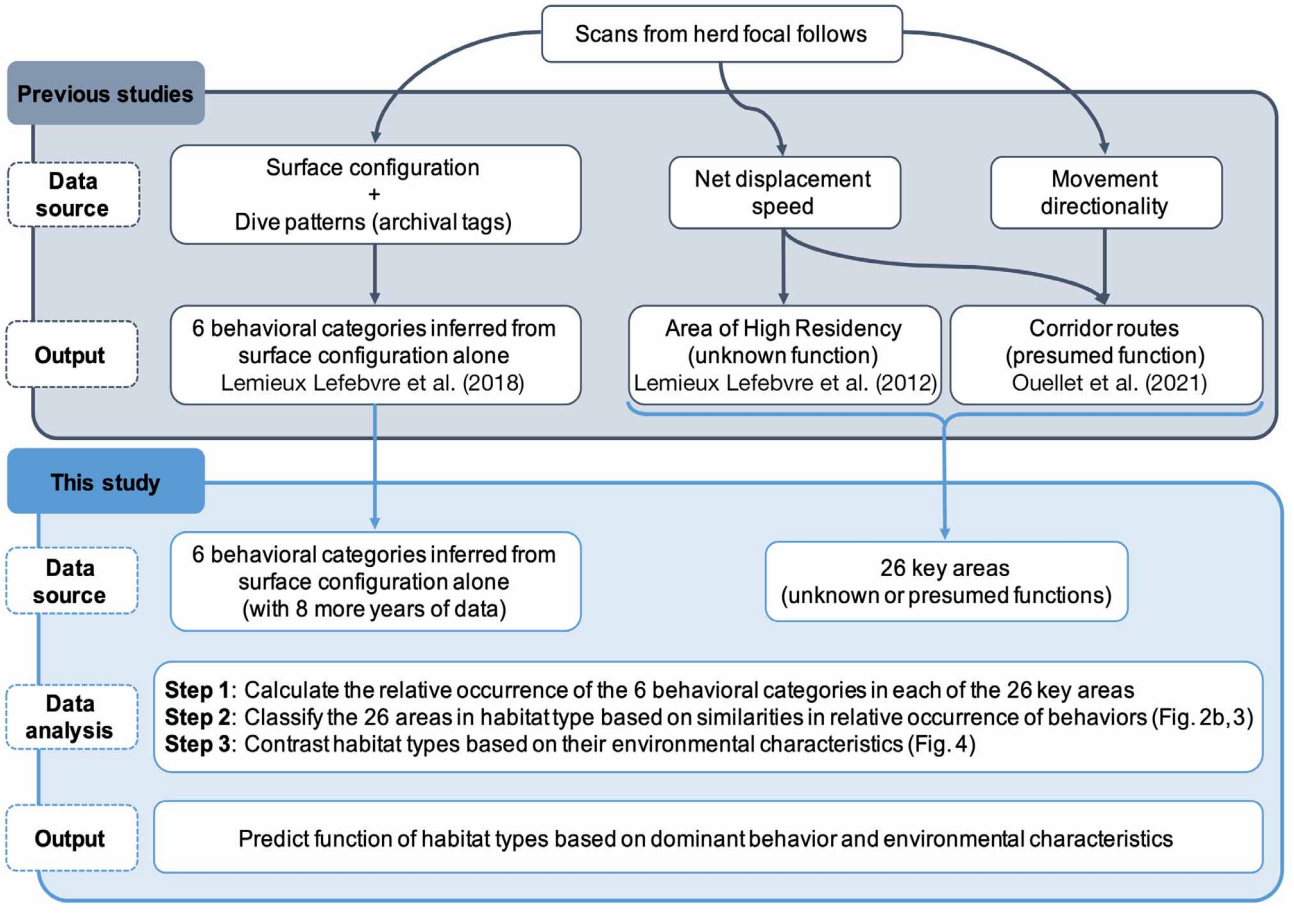

Fig. 1. Summary of specific data sources, analytical procedures, and outputs from studies that have used scans of beluga herd focal follows, with previous studies indicated by grey arrows and boxes, and the current study by blue arrows and boxes. Scans refer to the collection of herd surface configuration and activity characteristics ('surface configuration') that were recorded at 30 min intervals during focal follows

~300 m away from the herd for approximately 15 min. A herd was defined as an assemblage of groups, each composed of animals swimming within 1 body length of each other, generally in a relatively coordinated fashion. Following this 15 min observation period, the research vessel proceeded into the herd at a slow cruising speed (<5 knots) to approach groups in turn for photo-identification or other research protocols. A detailed description (hereafter called scan) of the herd surface configuration and activity was made every 30 min, using 10 specific herd metrics: (1) herd size, (2) herd type based on age composition, (3) radius, (4) geometrical structure, (5) form, (6) dispersion, (7) predominant movement patterns, (8) swimming dynamism, and presence or absence of (9) acrobatic surface events and (10) surface vocalizations. Categories for each of these descriptors are presented in Table S1 in the Supplement at www.int-res.com/articles/suppl/n058p435_supp.pdf. Age composition was based on skin color for juveniles (shades of grey) and adults (white). Young of the year (calves) were identified by a combination of length (half the body length of adults), color (dark grey or brown), and for neonates, also by fetal folds, consistent chin ups when breaking the surface, close proximity to an adult, and dark circles around the eyes (Michaud 2014). Herd composition was derived from these age classes (see Table S1). A herd follow was usually limited to 3 h, and produced up to 5–6 scans per herd, though occasionally fewer due to factors like changing weather. Location of the research vessel was used as a proxy for the centroid of the herd; previous work has indicated that there was no systematic bias in the research vessel positioning relative to the herd center (Lemieux Lefebvre 2009).

2.2. Herd surface activities and inference of behavior

In a previous study, Lemieux Lefebvre et al. (2018) developed a methodology to infer the behavior of SLE beluga herds based on surface cues alone. Specifically, using the 10 descriptors of herd configuration and surface activity (see Section 2.1) in a cluster analysis, the authors assigned beluga surface activities to 1 of 6 potential categories. By using dive characteristics from 45 belugas equipped with archival tags while conducting focal follows and scan surveys of their respective herds, Lemieux Lefebvre et al. (2018) were able to infer, from 16 descriptors of dive characteristics, the most likely behaviors associated with each of these 6 surface activity categories. The inferred behavior for each of these categories were: (1) benthic foraging/resting/caring for young, (2) socialization/benthic foraging, (3) pelagic foraging, (4) pelagic exploration, (5) traveling, and (6) mixed activity (definitions in Table 1). Note that some categories may include multiple potential behaviors; limits on the type of sensors for archival tags and the availability of other contextual information precluded further refinements of these classes (see Lemieux Lefebvre et al. 2018).

Lemieux Lefebvre et al. (2018) developed their classification scheme using SLE beluga focal follows conducted from 1991 to 2012. In our study, their classification was applied to an additional 497 herds followed between 2013 and 2020; each scan during these focal follows was assigned to 1 of the 6 predefined behavioral categories. Combining assignments from the most recent period with the assignments made by Lemieux Lefebvre et al. (2018) for the previous years provided 30 yr of focal follows

Table 1. Definitions of the 6 inferred behavioral categories that were identified by Lemieux Lefebvre et al. (2018) from the combined analysis of herd surface activity and configuration ('surface activity'), and corresponding dive characteristics ('dive type') from beluga equipped with archival tags and tracked within herds with these surface activity characteristics

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

(1991–2020) and herd-inferred behaviors to assess the spatial occurrence of these behavioral categories and habitat functions and characteristics. As in Lemieux Lefebvre et al. (2018), only scans with a complete set of surface configuration variables (Table S1) were retained for this classification. The cluster analysis was carried out in SAS® (PROC 'fastclust' function, version 9.2, SAS).

2.3. Spatial occurrence of behavioral categories

The assessment of the spatial occurrence of the 6 behavioral categories required that corridor routes identified by Ouellet et al. (2021) and AHRs defined by Lemieux Lefebvre et al. (2012) be merged (Fig. 2a). ARHs were defined on a per-cell basis (1 km^2) using displacement speeds of beluga herds, resulting in polygons with irregular boundaries (see Fig. 2a). While corridors were also identified using quantitative movement metrics (i.e. correlated movement directions in adjacent cells), and same cell size as in Lemieux Lefebvre et al. (2012), polygon boundaries were guided by, but not fully based on, geomatic methods. To ensure connectivity of AHRs with the transit corridors, scans classified as foraging behavior or other non-transit activities, and falling outside AHR zones but within corridor routes, were used to adjust AHR zone boundaries (see Fig. 2a). No expansions were done beyond the predicted contours of corridors identified by Ouellet et al. (2021).

Polygons with fewer than 15 scans available to characterize the occurrence of the 6 categories of behavior were discarded. The minimum number of scans per polygon was determined through a sensitivity analysis examining the stability of the clustering results for minimum sample sizes per polygon of 10, 15, 20, and 30 scans (not shown). AHR polygons with at least 15 scans that were located within 2 km (i.e. 2 cells) from another AHR polygon with 15 or more scans were merged, leading to 27 habitat polygons composing the spatially explicit mosaic of beluga habitat (Fig. 2a).

2.4. Identification of habitat types

The relative occurrence of the 6 previously defined behavior categories was calculated for each of the 27 habitat polygons. As an initial step to evaluate whether

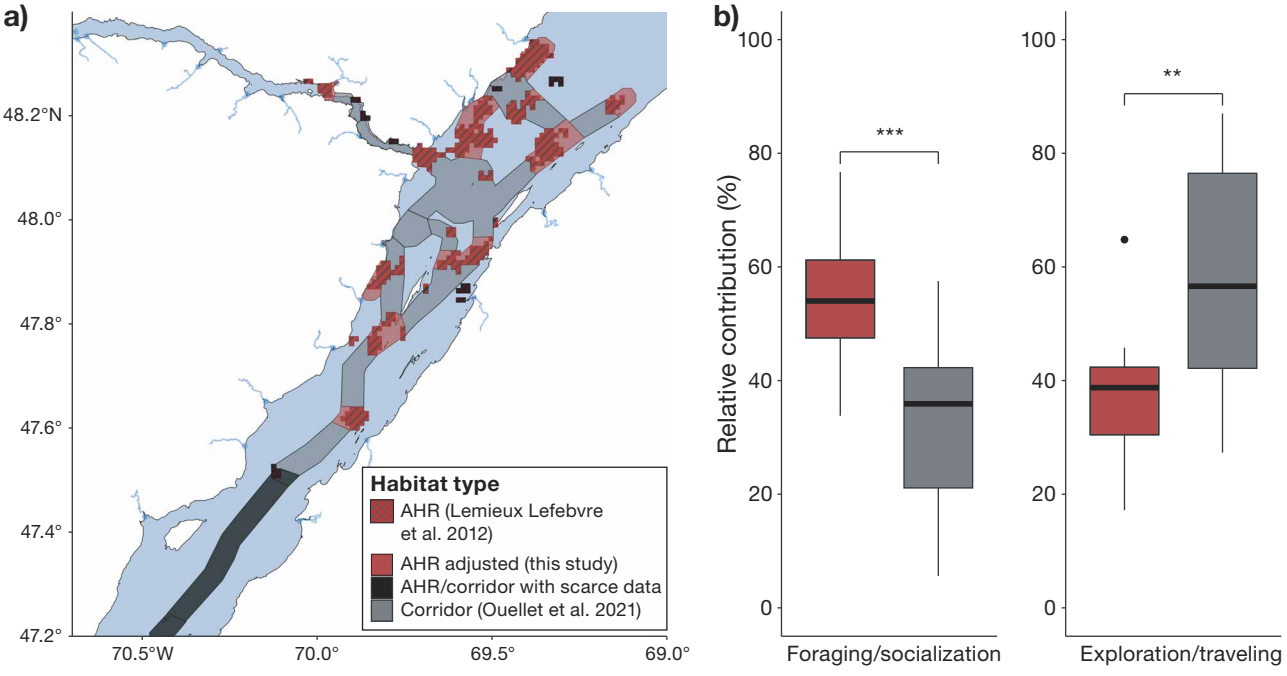

Fig. 2. (a) Existing information on the location of areas of high residency (AHR, in red) and corridor routes (in grey) for St. Lawrence Estuary beluga, based on Lemieux Lefebvre et al. (2012) and Ouellet et al. (2021). Original limits for AHR (red with black stripes) and those adjusted to fit corridor routes (limits in red solid) are both presented. AHR/corridor with scarce data (in black) corresponds to polygons with less than 15 scans. The blue lines correspond to locations of river mouths with a Strahler stream of order 4. (b) Our own analysis of descriptors for surface activity of beluga herds that were collected every 30 min from herds followed between 1991 and 2020, and which contrasts the relative occurrence of predicted categories of behavior between AHR and corridor routes. Each box represents the interquartile range, with the median indicated by a horizontal line inside the box. Asterisks mark significant differences between groups: $^{**}p < 0.01$, $^{***}p < 0.001$

AHRs truly represented behaviors involving greater residency and corridor routes being used for transit behavior, the 6 categories were consolidated into 3 categories. Foraging (both benthic and pelagic) and socializing activities (Categories 1 to 3 in Table 1) were combined, as these behaviors likely involved frequent changes in movement direction. Pelagic exploration and traveling categories were also combined (Categories 4 and 5 in Table 1), as they likely implied more directional movements. Mixed behavior (Category 6 in Table 1) was not considered in this first analysis. The frequency of these 2 behavioral classes was compared across the 27 corridor and AHR polygons using Welch's 2 sample *t*-tests (with independent observations), hypothesizing that foraging/socializing behavior should prevail in AHR polygons, and pelagic exploration/traveling should dominate in corridor polygons. Frequency distributions were checked for normality and heteroscedasticity (Levene's test). Bonferroni-adjusted p-values were applied to 2-sample *t*-tests to reduce Type I error from multiple comparisons.

In a second step, habitat polygons were grouped according to similarities in the relative frequency of occurrence of the 6 behavior categories using an agglomerative hierarchical cluster analysis based on Euclidean distance among groups and the Ward D2 minimum variance method (Murtagh & Legendre 2014) (R packages 'FactoMineR' version 2.7 and 'Factoextra' version 1.0.7). The optimal number of habitat types was determined using the most popular solution provided by 30 different indices (R package 'NBclust' version 3.0). Following this analysis, each scan during a focal follow was assigned a behavior among the 6 potential categories, and a habitat type.

2.5. Environmental characteristics of habitat types

To improve the characterization of the identified habitat types and underlying functions, each scan was assigned 8 environmental characteristics likely relevant to SLE beluga ecology (Table 2), based on the closest matching location and time. Bathymetry data (10 m horizontal and <1 m vertical resolutions) were obtained from the Canadian Hydrographic Service (https://open.canada.ca/data/en/dataset/d3881c4c-650d-4070-bf9b-1e00aabf0a1d). Following Mosnier et al. (2016), the slope was determined using a reference grid of 50 × 50 m, and by comparing slope and seafloor depth at the center of each grid cell with the bathymetric variation observed within a 15 km radius around that cell (Fig. S1; Jenness 2006). Slopes close to the coast could not be a ridge and were classified as mid-slopes. Distance to the nearest coastline and to river mouths were calculated as the shortest distance between these features; interfering islands were accounted for by calculating the shortest distance that bypassed the obstacle. Location of river mouths with a Strahler stream of order 4 (i.e. mid-sized tributaries

Table 2. Environmental characteristics used to discriminate among habitat types

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

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

Environmental characteristics were used as explanatory variables in multinomial logistic regressions (MLRs) to assess their capacity to discriminate among the 4 habitat types (the response variable), and determine if environmental characteristics selected to explain habitat use were the same for all types of herds. Conceptually, MLR generalizes a model with a response variable following a binomial distribution, by allowing multiple (i.e. more than 2) categorical response variables. Covariates having a significant influence on the response variable are determined by comparing each categorical response variable (here, each habitat type, coded 1) with a predefined habitat type baseline (coded 0) (Agresti 2012). For instance, in the case where 4 habitat types were identified, 3 logistic regressions would be estimated simultaneously, with each of 3 habitat types being compared to the fourth habitat type serving as a baseline. The habitat type with the most uniform behavior composition (i.e. at least 50% in one behavioral category) was chosen as the baseline.

MLRs were implemented using the 'mclogit' R package (version 0.9.6), while first considering all herd types together, then each of the 3 herd types separately (i.e. adults only, adult−grey, adult−grey−calf), for a total of 4 models. Environmental variables were first examined for their distribution and presence of outliers (continuous variables) or balance among categories (categorical variables). Due to convergence issues, it was not possible to use mixed-effects models; thus, only fixed-effects MLRs were implemented, with several scans contributed by each herd. The potential for residual temporal autocorrelation was assessed graphically ('acf' function in the R package 'car' version 3.1-2); residual spatial autocorrelation was assessed using Moran's test (R package 'SPDEP' version 1.3-11). All possible combinations of the 8 environmental variables were considered (R package 'Mumin' version 1.47.1). For categorical variables, the intercepts were set to 'Low' (tidal phase), 'Mid-slope' (slope) and 'Mix' (sediment size). Generalized variance inflation factors (GVIFs) corrected for degrees of freedom were used to quantify multicollinearity among explanatory variables. Model selection for the MLRs on adults only was constrained to a maximum of 3 explanatory variables due to the smaller sample size for this herd type (see Table S3; Agresti 2012). Model selection was based on the lowest value of Akaike's information criterion corrected for small sample size (AICc) (see Table S4; Anderson & Burnham 2002). Model fit and potential within-herd correlation were assessed from the distribution of median Pearson residuals per herd and behavioral class.

The efficiency of MLR models in classifying habitat types from environmental variables was assessed using misclassification rates (R package 'caret' v6.03.95). Model accuracy represented the proportion of correctly classified scans, whereas sensitivity and specificity measured true positives and true negatives per habitat type, respectively. Sensitivity and specificity were averaged over habitat types to assess the overall performance of models. Balanced accuracy, i.e. the mean of sensitivity and specificity, accounted for potential imbalanced sample size between habitat types, and was used as an additional measure of model performance. These 4 metrics assessed model robustness to the chosen baseline. Nagelkerke pseudo-R^2 evaluated model fit and predictive strength of environmental variables (Nagelkerke 1991). Predictive margins plots illustrated how the probability of falling into each habitat type (including the baseline) changed with each environmental variable (R package 'mpred' version 0.2.4.1), revealing the direction and strength of associations. All statistical analyses were conducted in R (version 4.2.2, R Core Team 2022).

3. RESULTS

3.1. Data collection

Of the 3500 herds followed between June and October of 1989–2020, approximately half (n = 1496 herds) had 1 or more scans with complete information on herd surface configuration and activity. Overall, 3098 scans (all from 1991–2020) from these 1496 herds were assigned a behavioral category following the methodology developed by Lemieux Lefebvre et al. (2018). Nineteen of them were excluded from the MLR analysis due to missing values for sediment type.

3.2. Spatial occurrence of behavioral categories

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

3.3. Identification of habitat types

The hierarchical cluster analysis grouped the 27 high-use areas and corridors into 4 habitat types, which differed in the relative occurrence of the various behaviors (Fig. 3). Two habitat types, travel dominant (TD) and travel and pelagic foraging (TPF), included exclusively (100%) or almost exclusively (88%) polygons identified as corridor routes (Fig. 3). Behaviors involving directional movements or exploratory dives dominated these 2 habitat types (80 and 60% for TD and TPF, respectively), with infrequent occurrence of foraging behaviors (Fig. 3). In contrast, pelagic foraging dominant (PFD) and benthic foraging dominant (BFD) habitat types were respectively composed of 73 and 100% of habitat polygons identified as AHRs. These habitat types showed a high prevalence (>60%) of foraging or mixed behaviors, mainly pelagic foraging in PFD, and benthic foraging in BFD (Fig. 3). Socialization and some rarely observed behaviors such as resting or caring for young (behavioral Category 1 in Table 1) occurred at low frequencies in all habitat types, but were overall more frequent in habitats classified as BFD.

3.4. Environmental characteristics of habitat types

The TD habitat type was selected as the baseline, as it was the only type with a behavior (traveling) accounting for at least 50% of all observed behaviors (Fig. 3b). Despite imbalanced sample sizes among polygons (Table S2), MLR performance indicators suggested a moderately good accuracy of the global and herd type-specific models in defining habitat types based

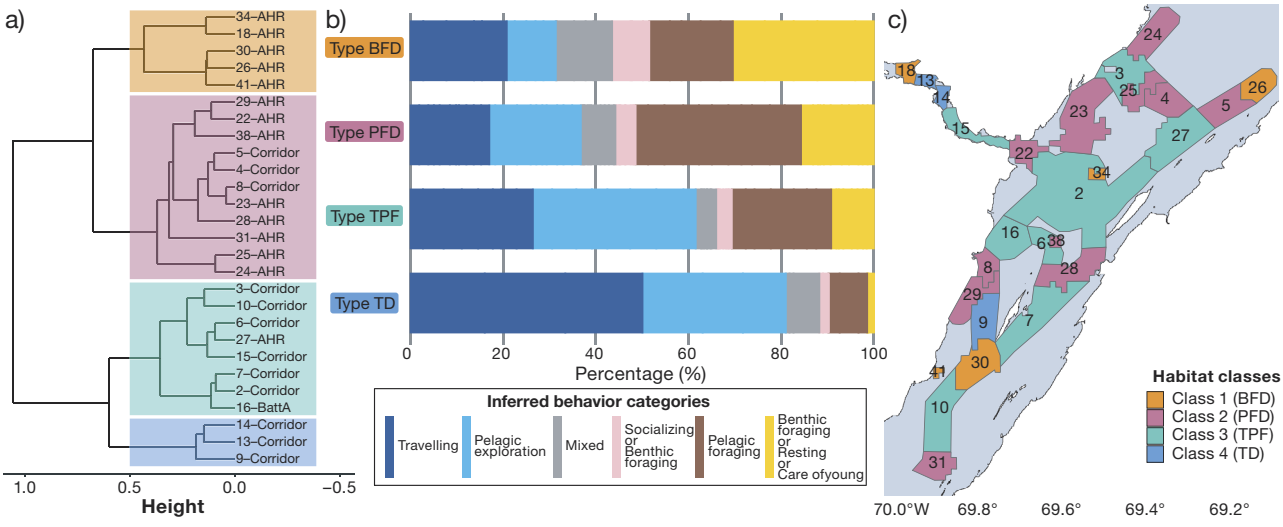

Fig. 3. (a) Habitat types identified by hierarchical cluster analysis of habitat polygons (see panels b and c), using the relative occurrence of various inferred behaviors as input variables. The 4 habitat types identified (different colors in panels a and b) are described as: benthic foraging dominant (BFD), pelagic foraging dominant (PFD), travel and pelagic foraging (TPF), and travel dominant (TD). (b) Relative contribution of the 6 behavioral categories to each habitat type, and (c) distribution of habitat polygons and associated types within the St. Lawrence Estuary beluga summer habitat. Behavior categories are as defined by Lemieux Lefebvre et al. (2018)

on environmental characteristics (Table 3). Overall accuracy varied from 61 to 70% depending on models (i.e. equivalent to misclassification rates of 30 to 39%), and had generally slightly higher balanced accuracy indicators compared to overall accuracy indicators, suggesting model robustness to imbalanced sample sizes. In all cases, specificity surpassed sensitivity, indicating a higher efficiency at accurately recognizing scans as belonging to particular habitat types than at identifying scans that did not fit those habitat types. Model goodness of fit (Nagelkerke R^2) was 0.70 or more for all models (Table 3). Performance metrics were similar regardless of the habitat type chosen as the baseline. Generally, temporal autocorrelation did not exceed 2 consecutive scans (i.e. beyond 1 h) (Figs. S2–S5). Median residuals were centered around zero for habitat types TD and BFD but were more dispersed or skewed for TPF and PFD (Figs. S6–S9). However, spatial autocorrelation in residuals was detected for all models (Moran's I values ranging from 0.26 to 0.57, all with $p < 0.05$), indicating that some spatial patterns in habitat use were not fully accounted for by the environmental predictors. Together, these results suggest that models may have limited predictive power for identifying habitat functions based on environmental characteristics alone (see black areas in Fig. 2a).

The top-ranked model for the various herd types included the same 7 environmental variables (i.e. all but tidal phase), except adult-only herds, which were allowed only 3 variables (i.e. bathymetry, distances to coast and river mouth; Tables S4 & S6). GVIF indicated no significant correlation among environmental variables (Table S5). Predicted probabilities for all models showed that habitats dominated by travel behaviors (TD) were most likely near the coastline, in deeper waters with mid-slope, medium sediments, low current, and fewer sand lance, although the effects were weak (probabilities <0.20). Predicted probabilities for habitats associated with travel and pelagic foraging (TPF) remained stable across environmental gradients, and increased only slightly with depth, suggesting that environmental characteristics were not as specific for this habitat type. Habitats where pelagic foraging dominated (PFD) were more likely farther from the coast and closer to river mouths, predominantly in shallower waters with mid-slope or valley-shaped seafloor, higher currents, and smaller and mixed sediments. Habitats suitable for benthic foraging (BFD) were generally the opposite, i.e. in shallow areas close to shore and away from river mouths, where current speed is low and probability of sand lance occurrence is high.

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

4. DISCUSSION

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

Table 3. Comparison of accuracy metrics for multiple logistic regressions (MLRs) predicting habitat types from environmental variables using all types of herds ('all types') or each herd type separately. Grey corresponds to juveniles identified based on their skin grey color

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

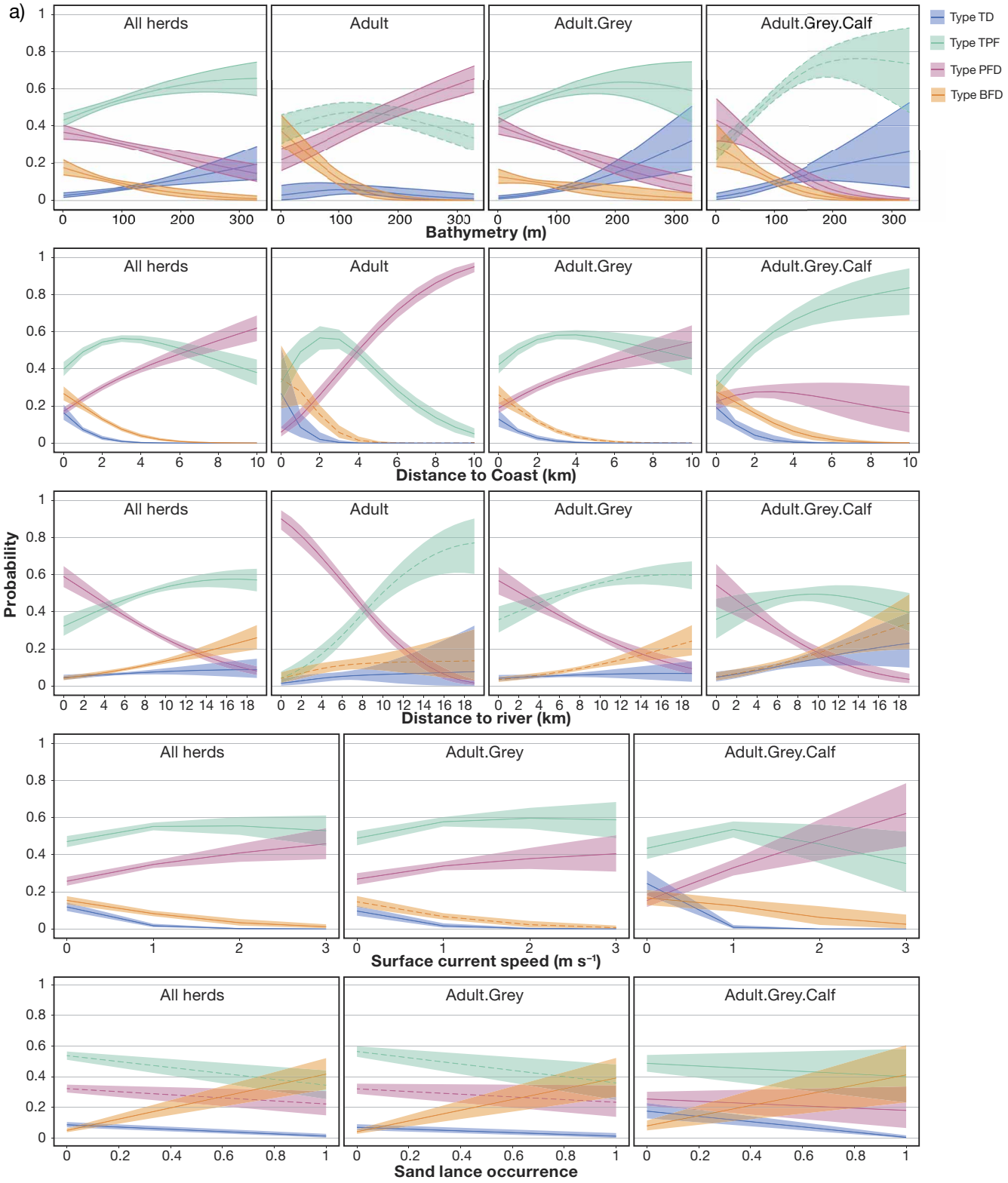

Fig. 4. Predictive margins plot assessing, from the fitted multiple logistic regressions (MLRs) for different herd compositions, the probability of falling into each habitat type (response) according to (a) continuous and (b) categorial environmental variables. The 4 habitat types are described as benthic foraging dominant (BFD), pelagic foraging dominant (PFD), travel and pelagic foraging (TPF), and travel dominant (TD). Note that only the first 3 continuous variables were included in the model for adult-only herds given the small sample size for this herd type. Effect sizes are shown by 95% confidence intervals. Dashed lines in (a) and empty points in (b) indicate non-significant associations with environmental variables (see Table S5)

Figure continues on next page

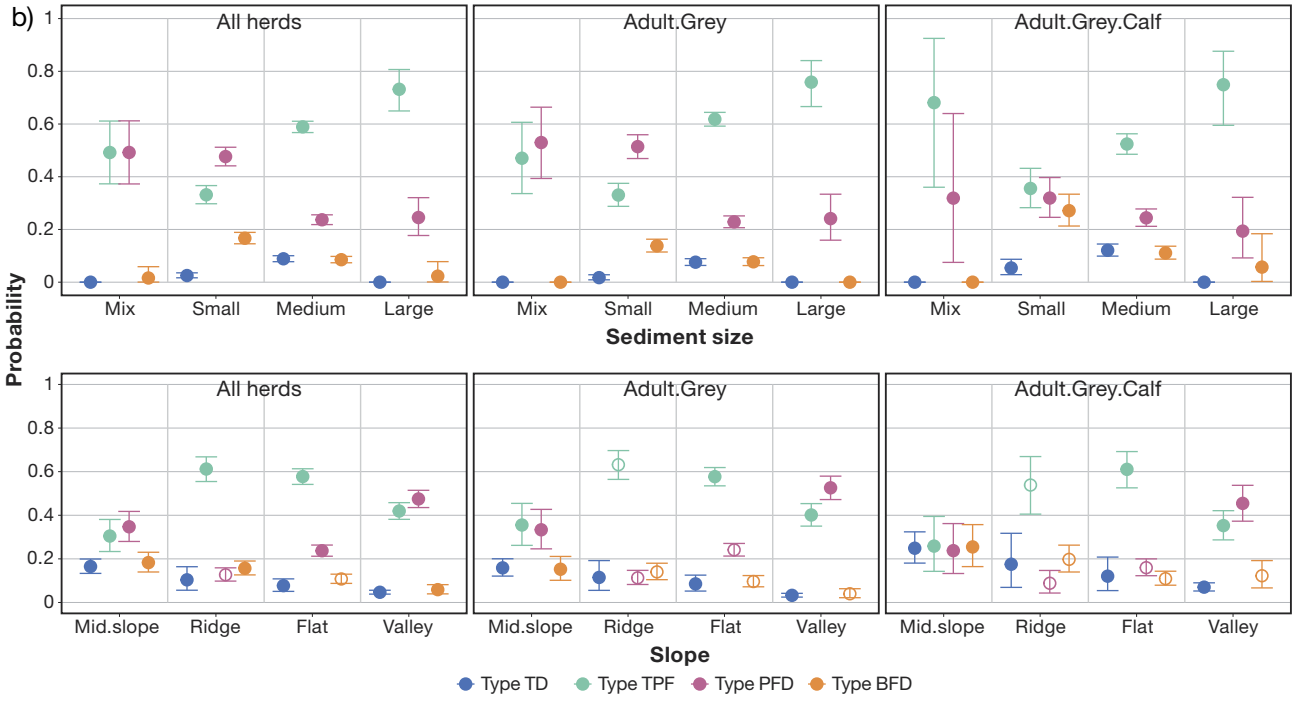

Fig. 4 (continued)

4.1. Habitat functions

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

Habitats categorized as PFD and BFD in which belugas were mostly engaged in foraging were mainly composed of AHRs, supporting predictions of their role as foraging areas (Michaud 1993, Lemieux Lefebvre et al. 2012). The spatial variation in benthic and pelagic foraging behaviors across habitat types indicated that SLE beluga use distinct areas to target different prey type, reflecting both habitat-specific prey availability and the species' generalist diet (Vladykov 1946, Lemieux Lefebvre et al. 2018, Lesage et al. 2020, Cabrol et al. 2025). Benthic foraging was included in both BFD and PFD habitat types, but differed in associated movement and dive characteristics. In the BFD type, benthic foraging was generally linked to slower swim speeds and v-shaped dives (Lemieux Lefebvre et al. 2018), suggesting sit-and-wait or slow-patrolling strategies (Bowen et al. 2002). Conversely, benthic foraging observed in the PFD type involved higher swim speeds and more dynamic dives, suggesting a more active search or pursuit strategy. Furthermore, the presence of sand lance, a benthic prey for beluga strongly associated with fine sediment (Mosnier et al. 2016), had a larger influence on the probability of habitat being assigned to BFD, where benthic foraging may involve stationary tactics (i.e. slow patrol or sit-and-wait) to a larger extent. However, due to the non-exclusive nature of behavioral categories (e.g. 'benthic foraging or resting or caring for young'), and the limitations of

movement data alone, some ambiguity remained. Future work incorporating information on pitch, roll, and yaw and on acoustic environment (click emission, or sounds associated with prey capture) could improve the discrimination of these behaviors and confirm prey capture events (e.g. Wright et al. 2021).

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

AHRs were also used for socializing and possibly for other behaviors that are suspected, though rarely observed, such as resting, nursing, or giving birth (see Béland et al. 1990, Lemieux Lefebvre et al. 2018, Lesage et al. 2024). While socializing activities were detected in all habitat types, they occurred with the highest frequency in BFD habitats. These habitats were generally located in the shallow and warm waters of the Saguenay Fjord and Upper Estuary, and along the south shore in the Lower Estuary, possibly providing shelter from wind and waves (Loseto et al. 2006, Anderson et al. 2017, Scharffenberg et al. 2019).

4.2. Methodological considerations and future directions

While the long-term data set exploited in our work is extensive, this study was limited by the amount of data available and the broad and non-exclusive behavioral categories that could be derived from the match between herd surface configuration and activity and diving data (see Lemieux Lefebvre et al. 2018). Some important behaviors like nursing and parturition were not quantified, as these cryptic behaviors were not observed during herd follows (Béland et al. 1990, Lesage et al. 2024). Moreover, the identified habitat functions represent averages over the summer period, and do not extend to other seasons due to temporal limitations in data collection. The purpose and importance of these habitats, including prey availability, are likely to change seasonally and possibly over the long term (Rioux et al. 2023, Cabrol et al. 2025). Whether the observation of multiple behaviors in a given habitat was related to uncaptured seasonal changes in habitat functions or to their true overlap in space due to the small summer range and residency of this population cannot be determined. The small sample size of the focal follow data set, once divided by cell and habitat polygon, precluded the examination of change in habitat functions over time, even at a decadal scale. However, the analysis of 3 decades of aerial survey data does not support a change in the location of key areas over time, though a greater use of key areas of the eastern portion of the summer habitat was noted in recent years (Lesage et al. 2024, Harvey et al. 2025).

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

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

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

4.3. Implications of habitat use patterns for conservation

This study estimated the relative frequency of various behaviors in previously identified key summer areas in the SLE, and identified habitat types and their main functions by combining observed behaviors with environmental characteristics. Since the impact of anthropogenic threats varies with context, this information provides a basis for guiding planning and prioritization of mitigation measures (Redfern et al. 2006, Ross et al. 2011, Brakes & Dall 2016).

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

5. CONCLUSIONS

Identifying areas of aggregation or regular use is often the initial step for understanding habitat use by wildlife species. This study built on a previous study which identified key areas for SLE beluga. Using an existing method developed to identify herd behavior from surface activity alone, we were able to determine the relative occurrence of various behaviors in each of these areas and identify their primary functions. This exercise has emphasized the limited number of alternative habitats available to SLE beluga in the event that local stressors would degrade habitat quality or accessibility. This is of paramount importance for this endangered population, given that its summer range is among the smallest for the species (COSEWIC 2014) and is fragmented by the site fidelity of the species and small home ranges within this habitat.

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