

From calls to communities: acoustic monitoring of contact calls indicates spatial structure in endangered belugas

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Animal populations often exhibit complex patterns of spatial or social structure, with various levels of organization below the population level. Acoustic monitoring can reveal such structure, particularly when animals produce calls that contain individual or group-level signatures. In this study, we monitored the complex contact calls of belugas, *Delphinapterus leucas*, in the St Lawrence Estuary, Canada, across six sites during five field seasons. Using a mark–recapture-based movement network, we examined the movement of belugas by tracking the occurrence of distinctive contact calls across sites. Our movement network revealed a high degree of population structure and the presence of two distinct communities: one within the Saguenay Fjord, recorded at two locations (i.e. the ‘Saguenay community’), and another along the southern shore of the estuary, recorded at four locations (i.e. the ‘South Shore community’). These results align with findings of a previous photo-identification-based study that suggested the presence of clusters of individuals inhabiting the Saguenay Fjord and southern shore of the estuary. Our study provides the first acoustic evidence of fine-scale population structure in the endangered St Lawrence Estuary beluga population. These findings, together with the population’s exposure to significant anthropogenic disturbances across its range, reinforce the need to expand the Saguenay–St Lawrence Marine Park to protect the core habitats and home ranges of both communities. More broadly, our results demonstrate that passive acoustic monitoring can reveal population spatial structure and inform behaviour-driven conservation action.

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Effective conservation practices require an in-depth understanding of the spatial structure of wild animal populations. Animal populations are often mistakenly considered to be panmictic, despite comprising discrete units with behavioural and ecological differences. For example, the mid-Atlantic winter flounder, *Pseudopleuronectes americanus*, stock has been managed as a uniform population, but a recent study revealed distinct subpopulations of bay-dwelling fish, ocean-dwelling fish and migratory fish (Siskey et al., 2020). The failure to recognize these differences within this near-depleted population may explain why past management decisions have not resulted in population recovery (Dolan et al., 2024). Similarly, Indo-Pacific humpback dolphins, *Sousa chinensis*, in the Pearl River Estuary

were once considered to represent a single unit, but a study of association patterns revealed a Northern and a Western social community with no overlap in their core use areas (Dungan et al., 2012). Habitat destruction may disproportionately affect the Northern community, potentially contributing to an observed range shift (Dungan et al., 2012). When population structure is misunderstood, conservation decisions are compromised and biodiversity is likely to suffer.

Acoustic analyses of vocal behaviour promise to strengthen our understanding of spatial structure in wild animal populations (Oestreich et al., 2024; Ross et al., 2023; Sugai et al., 2019). Passive acoustic monitoring offers several advantages. First, it allows researchers to study animals that are difficult to observe directly, such as nocturnal species, animals living in visually occluded habitats and marine species (Blumstein et al., 2011; Gayk et al., 2021; Mellinger et al., 2007). In marine environments, passive acoustic monitoring may be particularly advantageous due to the

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efficiency of sound propagation underwater (Duarte et al., 2021). Second, passive acoustic monitoring is noninvasive compared to other methods requiring direct observation, resulting in smaller impacts on animal behaviour (Mennill, 2024; Sugai et al., 2019). Third, passive acoustic monitoring allows for continuous, long-term monitoring of spatial behaviour, which is typically unachievable or impractical through direct observation methods (Mellinger et al., 2007; Sugai et al., 2019). Passive acoustic monitoring is particularly powerful for studying populations with individual or group-level vocal signatures (Knight et al., 2024; Mennill, 2011; Oestreich et al., 2024).

Belugas, *Delphinapterus leucas*, produce complex contact calls that may function as vocal signatures (i.e. vocalizations that encode individual identity or group membership; Vergara & Mikus, 2019), offering opportunities for fine-scale passive acoustic monitoring of behaviour. Beluga contact calls can be simple, consisting of a pulse train of rapid broadband pulses, or complex, including both a pulse train and an overlapping tonal or pulsed component that may function as a signature element (Vergara & Mikus, 2019; Fig. 1). Complex contact calls with different signature element contours are considered to represent distinct contact call types. Within groups of wild belugas, there is a positive linear relationship between the number of contact call types recorded and the number of individuals present (Panova & Agafonov, 2023; Vergara & Mikus, 2019), and beluga contact call diversity may provide an accurate measure of population abundance (Panova & Agafonov, 2024). These findings suggest that signature elements vary between individuals and that these calls serve as signals of individual identity or group membership (Fig. 1). Contact calls comprise a modest proportion of beluga vocalizations in free-ranging herds

(~6–12%; Vergara & Mikus, 2019; Vergara et al., 2021), but belugas vocalize at high rates overall. As a result, even a small proportion of contact calls can yield substantial sample sizes over extended recordings. Passive acoustic monitoring of beluga contact calls may yield valuable insights into the spatial structure of wild beluga populations, but this idea has not received careful attention to date.

In this study, we used passive acoustic monitoring of beluga complex contact calls across a wide geographical range to quantify the spatial structure of the endangered St Lawrence Estuary population on their summering grounds. St Lawrence belugas display seasonal movements, travelling upstream into the Upper Estuary during the summer calving season and returning downstream to the Lower Estuary and the Gulf of St Lawrence in the winter months (DFO, 2014, p. 17). Based on previous evidence of social structure in St Lawrence belugas during the summer period (Bonnell et al., 2022), we predicted that the distribution of contact calls would reveal strong spatial structure and distinct communities within the population (in social network analysis, a community refers to an assemblage of conspecific animals within a population, rather than an assemblage of species within an ecosystem; Arnberg et al., 2015; Grueter et al., 2020; Pinter-Wollman et al., 2014). Using a nonacoustic photo-identification approach, Bonnell et al. (2022) identified three clusters in different areas of the St Lawrence beluga population range: the Saguenay Fjord, Upper Estuary and Lower Estuary. Using a passive acoustic monitoring approach, we investigated whether the first two clusters represent distinct communities in the Saguenay Fjord and the Upper Estuary (Fig. 2). By confirming such spatial structure, we aim to enhance our understanding of the social structure of St

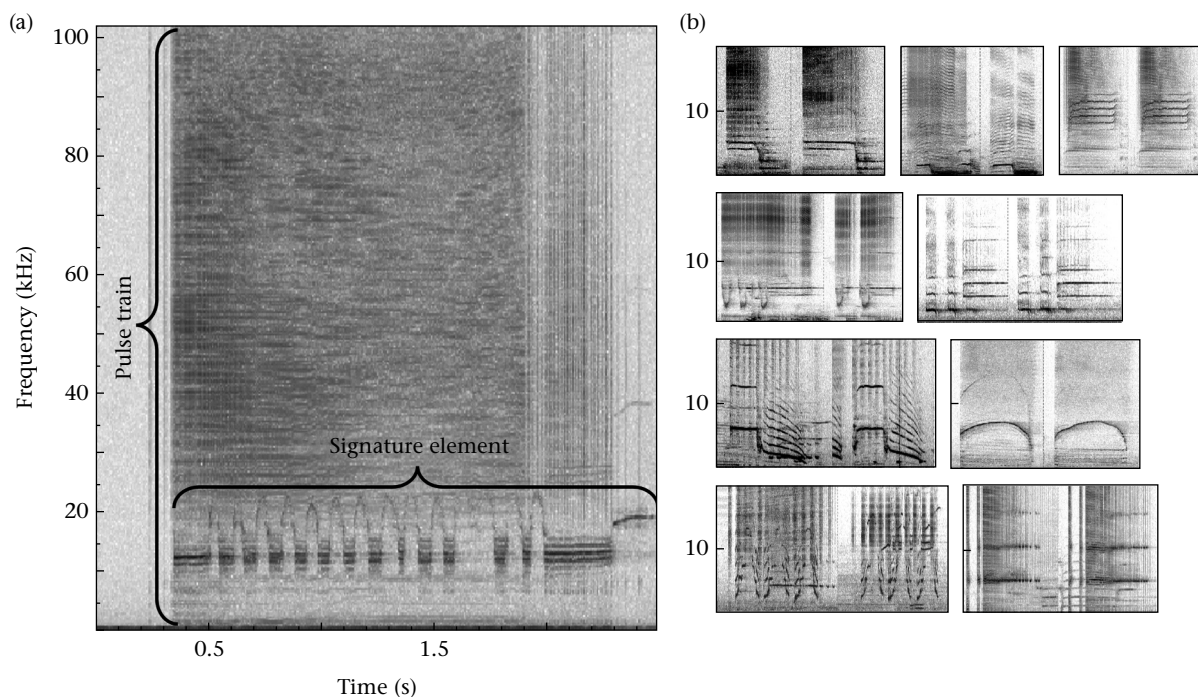


Figure 1. (a) Example of a beluga contact call with a signature element from the St Lawrence Estuary. This call consists of a broadband pulse train, a rapid series of pulses (2–100 kHz; reminiscent of an air raid siren) and a highly modulated signature element (10 and 20 kHz; similar to a telegraph key). (b) Examples of the diversity of signature elements present in contact calls recorded in the St Lawrence Estuary. We present nine contact call types, each represented by two examples to display the degree of stereotypy present.

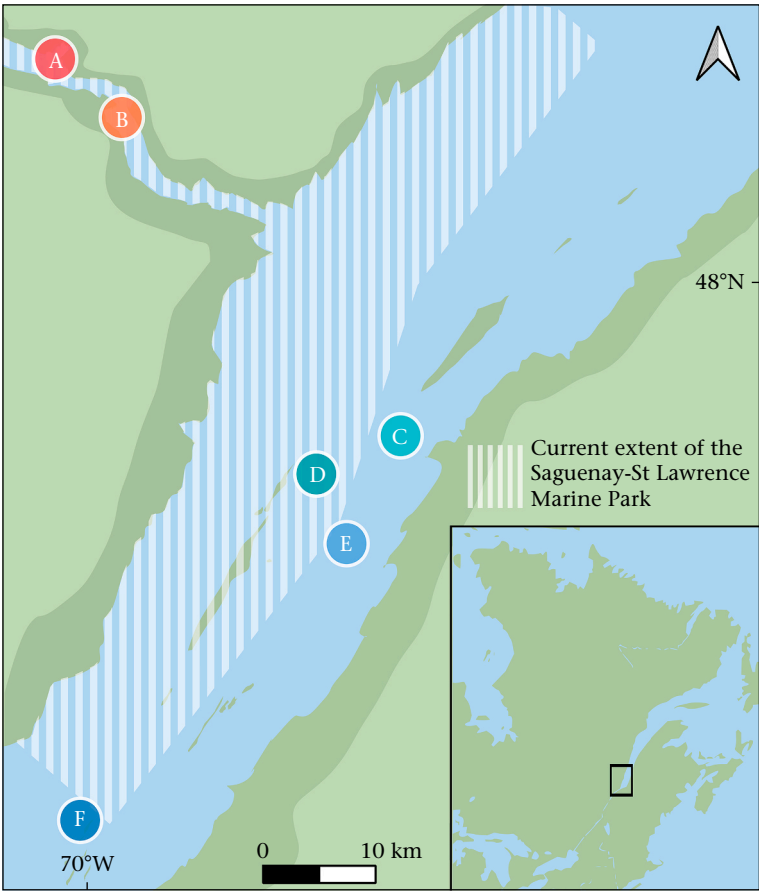


Figure 2. Passive acoustic monitoring sites in the St Lawrence Estuary, Québec, Canada. The two northern-most sites, sites A and B, are located within the Saguenay Fjord, while four sites, C, D, E and F, are located in the Upper Estuary. Recording sites C, E and F are located outside of the current boundaries of the Saguenay–St Lawrence Marine Park.

Lawrence belugas and highlight the need to critically evaluate conservation strategies for this endangered population.

METHODS

Field Methods

We collected acoustic recordings of belugas using moored SoundTrap hydrophones (Ocean Instruments models ST300HF,

ST500HF, ST600HF; Ocean Instruments, Warkworth, New Zealand) at six sites in the St Lawrence Estuary and Saguenay Fjord over five summers (Fig. 2, Table 1). Hydrophone deployments lasted 25–83 days. We deployed hydrophones at site A (Baie-Sainte-Marguerite) in 2017, 2018 and 2022, at sites B (Anse-Sainte-Étienne), C (Port of Gros-Cacouna) and F (La Grande-Île, Kamouraska) in 2021 and 2022, at site D (Île-Blanche) in 2022 and at site E (Rivière-du-Loup ferry terminal) in 2020 (Fig. 2). These sites were specifically chosen to examine population structure in two of the three clusters

Table 1
Hydrophone deployments across six sites and five summers

Site	Location	Year	Sampling period	Depth (m)	Hydrophone model	Sampling rate (kHz)	Duty cycle
A	Baie-Sainte-Marguerite	2017	24 Jul – 18 Aug	~20	ST300HF	288	24 h
		2018	7 Jul – 17 Aug	~20	ST600HF	288	24 h
		2022	15 Jul – 4 Oct	~20	ST300HF	384	24 h
B	Anse-Sainte-Étienne	2021	6 Jul – 17 Sep	~25	ST500HF	192	12 h
		2022	15 Jul – 8 Sep	~25	ST600HF	192	12 h
C	Port of Gros-Cacouna	2021	14 Jul – 21 Sep	~30	ST300HF	192	12 h
		2022	28 Jul – 6 Sep	~30	ST600HF	384	24 h
D	Île-Blanche	2022	28 Jul – 6 Sep	~10	ST300HF	192	12 h
E	Rivière-du-Loup	2020	21 Jul – 5 Oct	~40	ST300HF	288	12 h
F	Grande-Île de Kamouraska	2021	14 Jul – 20 Sep	~30	ST300HF	192	24 h
		2022	7 Jul – 6 Sep	~30	ST300HF	384	24 h

The SoundTrap hydrophones (Ocean Instruments, New Zealand) had a 20 Hz to 150 kHz (± 3 dB) flat frequency response and a 16-bit depth resolution. Recording sites A and B were located in the Saguenay Fjord, while recording sites C, D, E and F were located in the Upper Estuary.

identified by [Bonnell et al. \(2022\)](#): the Saguenay Fjord and the Upper Estuary. Sites A and B were 8.6 km apart; sites B and C were approximately 35 km apart; sites C, D and E were all within 10 km of each other; site F was the most isolated site, located 32.8 km from its nearest neighbour, site E ([Fig. 2](#)). Our acoustic monitoring was restricted to the summer period when belugas occupy these sites.

The hydrophones used (ST300HF, ST500HF, ST600HF) differ primarily in their size and battery capacity but have the same flat frequency response (20 Hz–150 kHz, ± 3 dB) and resolution (16-bit depth; [Table 1](#)). We were constrained to using different sampling rates (192, 288 or 384 kHz) across years and sites to optimize sampling duration depending on internal memory capacity.

Ethical Note

Our fieldwork methods were reviewed and approved by the University of Windsor Animal Care Committee (Animal Use Protocol: 20-09). All fieldwork was carried out under the following permits: SAGMP-2016-21958, SAGMP-2018-28703, SAGMP-2019-32682, SAGMP-2021-39518, SAGMP-2022-42881, issued by Parks Canada, and QUE-LEP-003-2017, QUE-LEP-001-2018, QUE-LEP-005-2020, QUE-LEP-002B-2021, QUE-LEP-012B-2022, issued by Fisheries and Oceans Canada. The data presented in this study were obtained via passive acoustic monitoring, with no direct handling of animals, such that the potential for disturbance and stress to study subjects was extremely low.

Acoustic Analyses

We reviewed recordings, annotating and extracting all high-quality complex contact calls. Recordings were first scanned with a machine-learning call detector that identified files likely to contain contact calls ([Cotillard et al., 2024](#)). The detector had a relatively low false negative rate (0.11), such that the vast majority of contact calls in each recording were likely to be detected ([Cotillard et al., 2024](#)). We manually reviewed all files likely to contain contact calls using Raven Pro 1.6.5 (Cornell Lab of Ornithology). The machine learning model detected both simple and complex contact calls. However, we did not select any simple contact calls due to their lack of a signature element. Complex contact calls were distinguished from other call types based on their broadband structure, long duration (typically exceeding 0.7 s) and the presence of a signature element, usually a tonal sound between 5 and 20 kHz ([Fig. 1](#)). Complex contact calls with highly degraded or ambiguous signature elements were also omitted from the analysis; we only selected contact calls with a subjective quality rating of 3/5 or greater. Contact calls were often produced in bouts of highly stereotyped calls. Each contact call was labelled with its site of

origin and a date–time–stamp. Given the distances between sites ([Fig. 2](#)) and the estimated communication range of beluga contact calls (median of 6.7 km in quiet environments, reduced to 2.9 km in noisy environments; [Vergara et al., 2021](#)), it is unlikely that we recorded clear, unambiguous contact calls at multiple sites simultaneously. In total, we analysed 5934.8 h of recordings and obtained a total of 2155 high-quality contact calls ([Table 2](#)).

Contact Call Classification

We categorized complex contact calls into types following methods used in previous studies (e.g. [Panova & Agafonov, 2023, 2024](#); [Vergara & Mikus, 2019](#)). All contact calls with the same signature contour were considered to belong to the same type ([Fig. 1](#)). Based on previous studies, we assumed that each call type represented the vocal signature of a single individual or small group of affiliated individuals ([Panova & Agafonov, 2023](#); [Vergara & Mikus, 2019](#)). To facilitate contact call classification, we developed a contact call catalogue that contained high-quality examples of each type. Each newly detected contact call was cross-referenced against the catalogue and assigned to either a pre-existing or new type. In total, we classified our 2155 complex contact calls into 235 contact call types (representing 235 individuals or small groups of individuals).

Classification Validation

We measured several acoustic features of each call's signature element and pulse train using Raven Pro, following the approach used by [Vergara and Mikus \(2019\)](#) (see Supplementary Material). Because our hydrophones operated at different sampling rates, we first downsampled all calls to 192 kHz (the minimum rate used; [Table 1](#)). We also normalized the amplitude of all calls to -1 dB. We performed both operations using the warbler package in the R environment ([Araya-Salas & Smith-Vidaurre, 2017](#); [R Core Team, 2024](#)). We measured most acoustic features using Raven Pro's automated selection measurement tools (maximum, peak, centre, 5% and 95% frequency, bandwidth, duration and aggregate, minimum and maximum entropy). We manually counted other features, such as the number of segments and inflection points, from the sound spectrograms.

We performed a stepwise linear discriminant analysis (step-class function, klaR package; [Roever et al., 2023](#)) to assess differences between call types. This method iteratively adds and removes measurements from the model to determine which predictors best discriminate between contact call types. We constructed a model with 'contact call type' as a response variable and the previously described acoustic features as predictors. Many acoustic features were intercorrelated. To reduce collinearity, we arbitrarily removed one feature from each pair of highly correlated features (correlation coefficients exceeding 0.80). We considered that an acoustic feature was a good predictor if it improved model accuracy by at least 1%. We retained eight features as good predictors (Supplementary Material). Our initial data set contained 2155 contact calls belonging to 235 types. Because discriminant analyses are sensitive to classes with low sample sizes, we removed contact call types with fewer than 10 occurrences in our data set. Our remaining data set contained 1505 contact calls belonging to 50 types.

We randomly split the data set into a training set (95% of calls, $N = 1430$) and a test set (5% of calls, $N = 75$) by random number

Table 2
Summary of the sampling effort, the number of calls retained from each site and the call rate associated with each site

Site	Hours analysed	Number of contact calls	Calls/h
A	1676.7	855	0.51
B	1108.3	236	0.22
C	1411.6	274	0.20
D	483.0	109	0.23
E	563.0	84	0.15
F	692.2	597	0.87
Total	5934.8	2155	0.36

assignment. Using the training data set, we constructed a linear discriminant analysis model that included the eight retained features as predictor variables (lda function, MASS package; Venables & Ripley, 2002). We assessed classification accuracy by applying the model to the test data set and calculating the proportion of correctly classified calls. We repeated this process 100 times, each time using a different randomly selected subset of the data for the training and test sets. The linear discriminant analysis achieved a mean accuracy of $82.3 \pm 3.9\%$, confirming that our subjective call classification aligned with an objective classification. Our results are consistent with previous studies showing that human judges can effectively categorize individually distinctive cetacean vocalizations (Sayigh et al., 1995, 2007; Watwood et al., 2005), including those of belugas (Vergara & Mikus, 2019).

Repertoire Accumulation Curves

To assess how exhaustively each site was sampled, we constructed randomized repertoire accumulation curves for each site. Because contact calls were often repeated over minutes to hours, we excluded repeated calls of the same type within 24 h periods. To account for sampling order effects, we randomized the order of observations 100 times for each site and generated repertoire accumulation curves. Each curve represents the mean number of call types identified after encountering x calls, averaged across all 100 permutations. The shaded areas around the curves represent ± 1 SD from the mean. None of the curves reached an asymptote (Fig. 3), confirming incomplete sampling and suggesting that we should avoid methods that assume exhaustive sampling. This was expected given the estimated population size (~ 1850 individuals; DFO, 2023) relative to our 235 identified call types. Results were similar when the redetection interval was reduced to 12 h.

Generating Movement Networks

We inferred beluga movements across the six sites by applying a mark–recapture movement network analysis to our contact call data set. We constructed a movement network using the

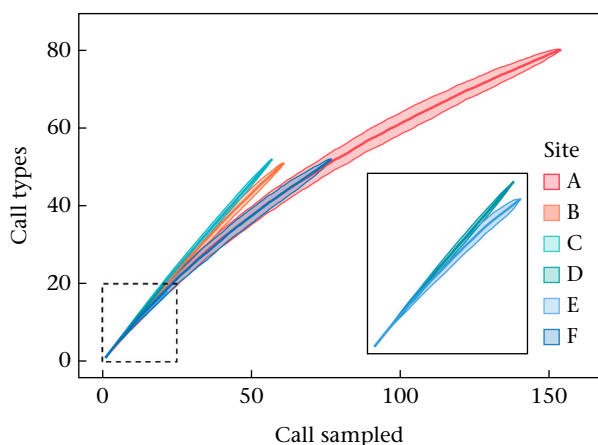


Figure 3. Mean $\pm$ SD repertoire accumulation curves, generated from 100 randomized iterations of the sampling data for each site. Site A was the most extensively sampled site, followed by site F. Sites D and E were both suboptimally sampled (inset shows zoomed-in portion delineated by the dashed rectangle with data for site D and E only). None of the curves reached an asymptote, suggesting that none of the sites were exhaustively sampled.

MoveNetCreate function from the CMRnet R package (Silk et al., 2021). In movement networks, nodes represent sampling sites, and edges (i.e. connections between nodes) represent the movement of individuals between sites. Because belugas are long-lived and reproduce slowly, we constructed a single global network spanning the years 2017–2022. We calculated the edge density of the network (the proportion of realized edges between nodes relative to the total number of possible edges). We also calculated the modularity of the network (degree of division into distinct communities) using the cluster_infomap function, as appropriate for directed networks (igraph package; Csárdi et al., 2025). To determine whether the modularity observed in the network could have arisen by chance, we generated 1000 randomized permutations and calculated mean network metrics for the random networks (DatastreamPermSpat function, CMRnet package; Silk et al., 2021). We used Wilcoxon signed-rank tests to compare the edge density and modularity of the true network to the random networks. Similar movement network analyses have been applied to giant sea bass, *Stereolepis gigas* (Spector et al., 2022), piping plovers, *Charadrius melodus* (Swift et al., 2023), and tigers, *Panthera tigris* (Carter et al., 2023).

RESULTS

Over 5 years of recording free-living belugas in the St Lawrence Estuary across six sites, we collected a total of 2155 high-quality complex contact calls. We reliably classified these calls into 235 types likely representing vocal signatures of individuals or small groups of related belugas (Panova & Agafonov, 2024; Vergara & Mikus, 2019). Of the 235 types, 70 were redetected beyond a 24 h interval: 40 at the same site only, 24 at two sites, 5 at three sites and 1 at five sites (Fig. 4). On average, these call types were redetected 3.27 ± 2.33 times (range 2–17), with an interredetection interval of 273.5 ± 460.1 days (range 1 day–5 years; see Supplementary Material for a more detailed breakdown).

Movement Networks

Our movement network analysis revealed clear spatial structure across the six sites, characterized by two distinct communities and high modularity. The true network showed strong community structure, with a modularity score of 0.40 (values above 0.3 indicate strong community structure). We identified two distinct communities: hereafter the ‘Saguenay community’ (sites A and B) and the ‘South Shore community’ (sites C, D, E and F; Table 3, Fig. 5). Randomized networks did not show strong community structure (mean modularity $< 0.001 \pm < 0.001$). We found very strong evidence that the true network had greater modularity than the randomized networks ($W = 0$, $P < 0.0001$; Table 3), indicating that the observed structure is unlikely to have arisen by chance. We also found very strong evidence that the true network had a lower edge density than the random networks ($W = 500500$, $P < 0.0001$; Table 3), suggesting that belugas moved less between sites than expected by chance, consistent with spatial population structuring.

DISCUSSION

Through passive acoustic monitoring of complex contact calls and a mark–recapture-informed movement network, we detected spatial structure within the St Lawrence Estuary beluga population

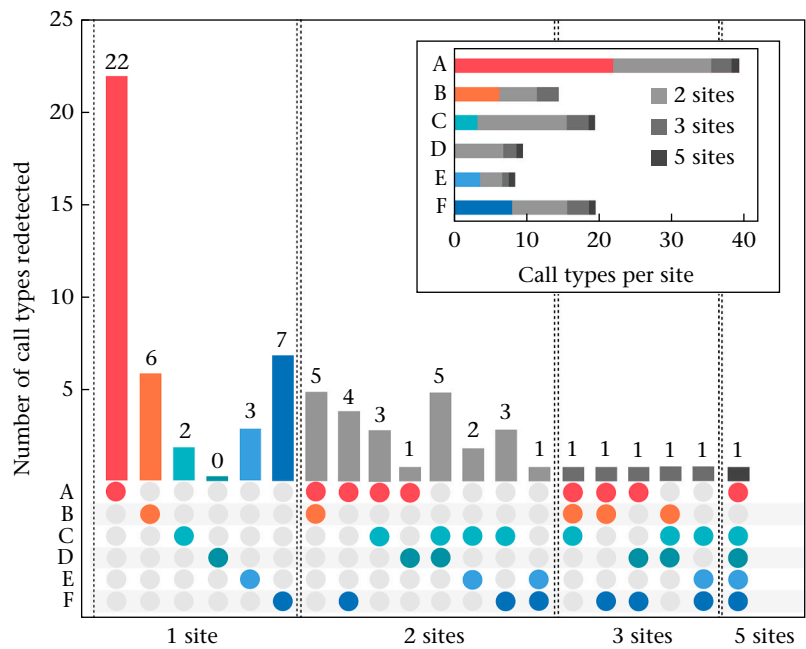


Figure 4. UpSet plot illustrating redetections of beluga contact call types at the six recording sites. In total, 70 call types were redetected beyond a 24 h interval. Of the 70 call types redetected, 40 were only redetected at a single site (22 at site A, 6 at site B, 2 at site C, 3 at site E and 7 at site F). No calls were redetected only at site D. A total of 30 calls were redetected at multiple sites (24 were redetected at two sites, 5 were redetected at three sites and 1 was redetected at five sites).

during the summer calving season. We confirmed that our subjective classification of contact call types aligned with an objective linear discriminant analysis based on measured acoustic features. Although our repertoire accumulation curves showed that no recording site was exhaustively sampled, a network describing beluga movements across sites revealed the presence of two communities. These findings align with prior research (Bonnell et al., 2022), involving spatial modelling of photo-identified belugas to identify three clusters occupying different regions of the estuary, two of which overlap with our study area. We conclude that the endangered St Lawrence Estuary beluga population is composed of at least two distinct communities.

Many animal populations exhibit social or spatial structure, a phenomenon that can arise through social learning and cultural transmission (Allen, 2019; Cantor & Whitehead, 2013). Examples include resident killer whales, *Orcinus orca* (Ford, 1991), East African chimpanzees, *Pan troglodytes* (Wakefield, 2013), and Californian golden-crowned sparrows, *Zonotrichia atricapilla* (Shizuka et al., 2014). Among belugas, mothers culturally transmit migratory routes to their calves, resulting in strong natal philopatry to

specific summering areas (Colbeck et al., 2013; O’Corry-Crowe et al., 2018). St Lawrence Estuary belugas, although considered resident, show seasonal movements within the estuary (Lesage et al., 2024), and the spatial structure we observed may reflect migratory culture. Belugas born into the Saguenay community may primarily migrate to the Saguenay Fjord and surrounding areas during the summer, while belugas from the South Shore community concentrate along the south shore.

Table 3
Network metrics for the true movement network and 1000 random networks

Network metrics	True network	Random networks	W	P
Modularity	0.40	<0.001 ± <0.001	0	<0.0001
Edge density	0.37	0.80 ± 0.01	500 500	<0.0001

Metrics for the random networks are reported as means with standard deviations. Modularity (range -1 to 1) represents the likelihood of community structure, with values above 0.3 representing strong community structure. Edge density (range 0–1) represents the number of connections between nodes compared to all possible connections and quantifies network connectivity. We found very strong evidence that the true network had greater modularity and lower edge density than the random networks.

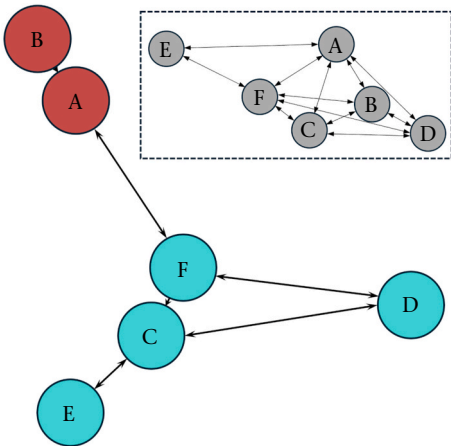


Figure 5. Movement network representing the movement of St Lawrence Estuary belugas between sites, based on redetection of their distinctive contact calls. The true network clustered into two communities, one (red, the Saguenay community) that included sites A and B, and another (teal, the South Shore community) that included sites C, D, E and F. Dashed inset: one example of a random movement network. The random network clustered into a single community (grey) and was much better connected than the true network.

Spatial and Social Structure

Our acoustic analyses reveal the spatial structure, and possibly the social structure, of St Lawrence Estuary belugas during the summer period. Spatial and social behaviour are often linked because social interactions usually require proximity (Webber et al., 2023). Among cetaceans, association patterns are often defined by spatial proximity (i.e. the gambit of the group; Whitehead & Dufault, 1999), and it is not always clear what constitutes 'spatial proximity' for animals that can communicate across long distances (Aubin et al., 2026). Although we could not directly assess fine-scale association patterns from our acoustic data, the communities we identified represent networks of potential associates. Belugas exhibit multilevel social structure (Aubin et al., 2026), and these spatially defined communities may represent an important social level within this hierarchy.

Sexual Segregation and Social Structure in Belugas

Like many sexually dimorphic animals, belugas are sexually segregated throughout most of the year (Michaud, 2005; Ouellet et al., 2021). Our passive acoustic monitoring could not differentiate between sexes, but sexual segregation may influence the observed spatial structure. Prior research demonstrates that the Saguenay Fjord is primarily occupied by mixed herds, while the South Shore is mainly used by females with young (Lemieux Lefebvre et al., 2012; Michaud, 1993, p. 23). Bonnell et al. (2022) identified a third cluster in the Lower Estuary used by both mixed herds and herds of presumed males (Lemieux Lefebvre et al., 2012; Michaud, 1993, p. 23) in an area we have not yet acoustically sampled. The limited number of contact call types recorded across multiple sites may represent the calls of roving males, consistent with observations from the White Sea, where males range widely rather than remaining in fixed summering areas (Alekseeva et al., 2013). Future investigations should examine the influence of sexual segregation on beluga spatial structure.

Historical Perspectives on the Two Communities

The South Shore community seems to span a much greater spatial extent than the Saguenay community (Fig. 2). The Saguenay community includes only two sites separated by less than 10 km, whereas the South Shore community includes four sites spanning over 40 km. It is possible that this difference arose as an artefact of the spatial extent of the chosen recording sites; further sampling throughout the St Lawrence Estuary would help to address this possibility. However, this difference could also reflect historical patterns of exploitation of St Lawrence belugas. Historically, the St Lawrence Estuary beluga population numbered over 12 000 individuals and ranged from Québec City to the Gaspé Coast (Lesage et al., 2024; Vladykov, 1944). Beluga hunting increased dramatically in the 1800s; one account describes a harvest of 500 belugas during a single tide at a fishery in Rivière-Ouelle (Casgrain, 1896), and another productive fishery operated at l'Île aux Coudres (Vladykov, 1944). Both sites are located in the Upper Estuary, with Rivière-Ouelle located only 25 km from site F. If overhunting influenced the spatial structure of this population, the South Shore community may represent the remnants of multiple depleted communities within this area. Alternately, the entire preharvest population may have been contiguous, and the structure we

detected could reflect harvesting impacts. These hypotheses are speculative and difficult to test.

Conservation Implications

Our results have important implications for beluga conservation, particularly because areas occupied by the South Shore community have been overlooked by conservation legislation. The St Lawrence Estuary beluga population's habitat is intersected by the St Lawrence Seaway, an economically important shipping corridor that connects the Atlantic Ocean to the Great Lakes. This population is listed as endangered under Canada's Species at Risk Act and anthropogenic disturbance has been identified as a major threat to this population (DFO, 2023). It was once thought that the Saguenay Fjord (site A in particular) represents an important calving and resting area for St Lawrence belugas generally (Pippard & Malcolm, 1978). However, our findings suggest that this is not the case. These sites are favoured by a subset of the population, and other areas along the southern shore are likely just as important to a different subset of the population. The Saguenay–St Lawrence Marine Park protects approximately 60% of beluga critical habitat, encompassing the Saguenay Fjord and portions of the northern shore (Fig. 2). A proposed expansion of the park, aiming to encompass all critical beluga habitats, has been approved but has yet to be implemented. This expansion will more than triple the park's size and extend north, south and east beyond the shaded region in Fig. 2. Our findings strongly support the park's expansion, given that the South Shore community is largely unprotected under current park boundaries (Fig. 2). Existing protections, such as speed limits for vessels, special permits for commercial operators and restrictions relating to whale watching (Maltais & Pelletier, 2018), currently mainly benefit the Saguenay community. Such protections are particularly important for mothers and calves during the summer calving season, when anthropogenic disturbance can cause fatal birthing complications and dangerous separations (Lair et al., 2014; Lesage et al., 2014; Vergara et al., 2021).

Limitations

Several aspects of our study design and findings warrant further investigation. Although our data collection spanned a 5-year timescale, our acoustic sampling was opportunistic, depending on belugas travelling within hydrophone range, which resulted in uneven site representation (Fig. 3). Sites D and E recorded fewer belugas than the other four sites, despite nearly 6000 h of total recording effort. Managing and analysing the large data sets generated by passive acoustic monitoring remains a methodological challenge, although advances in machine learning show promise for addressing this issue.

Our analysis assumed that each contact call type represented a single individual or small group, but our limited understanding of beluga vocal behaviour introduces some uncertainty. In captive settings, some belugas produce more than one contact call type ('variants of the Type A call'; Vergara et al., 2010), and belugas may imitate the calls of close associates, similar to other cetaceans (Tyack, 1986). Pairing acoustic monitoring with photo-identification and visual observations could clarify whether individual belugas consistently produce a single contact call type in the wild.

Future research should investigate potential cultural differences between the Saguenay and South Shore communities,

including differences in foraging strategies, prey preferences, vocal dialects and seasonal movements. These investigations would deepen our understanding of beluga culture and behavioural ecology. Additionally, because the two communities experience different levels of anthropogenic disturbance (Chion et al., 2017; McQuinn et al., 2011), examining whether their vocal behaviour reflects adaptation to noise would be valuable.

Conclusion

Our acoustic analyses of 5 years of field recordings confirm that the St Lawrence Estuary beluga population consists of at least two distinct communities, a result that is consistent with a previous photo-identification study (Bonnell et al., 2022). Our findings demonstrate that passive acoustic monitoring can effectively characterize cetacean spatial structure, offering an alternative to more invasive and resource-intensive methods. Our results have direct conservation implications: the South Shore community occupies areas largely unprotected by current legislation, highlighting the need for expanded habitat protections. More broadly, this research advances our understanding of social complexity in this endangered population and illustrates how vocal behaviour can illuminate population-level patterns critical for management.

Author Contributions

Jaclyn A. Aubin: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Daniel J. Mennill:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Marie-Ana Mikus:** Writing – review & editing, Investigation. **Robert Michaud:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Valeria Vergara:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Data Availability

The data and code used for all analyses are available at the following link: https://github.com/JAAubin/Calls_to_Communities.

Declaration of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Material

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The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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