Check for updates

Received: 12 June 2023 | Accepted: 16 April 2024

DOI: 10.1111/mms.13162

ARTICLE

Marine Mammal Science

Estimating spatial mixing within the St. Lawrence Estuary beluga population by comparing local individual diversity and abundance

Tyler R. Bonnell[1] | Robert Michaud[2] | Angélique Dupuch[3,4] | Véronique Lesage[5] | Clément Chion[3,4]

[1]Department of Computer Science, University of Calgary, Calgary, Alberta, Canada

[2]Groupe de Recherche et d'Éducation sur les Mammifères Marins (GREMM), Québec, QC, Canada

[3]Department of Natural Sciences, Université du Québec en Outaouais, Québec, Canada

[4]Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, Québec, Canada

[5]Maurice Lamontagne Institute, Fisheries and Oceans Canada, Québec, Canada

Correspondence
Tyler Bonnell, Department of Computer Science, 602 ICT Building, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada.
Email: tyler.bonnell@ucalgary.ca

Abstract

Interindividual variability in habitat preferences affect local abundance and residency times. Within a population range, this can lead to sectors having a continuous flow of unique individuals, with others being used by the same set of resident individuals. These patterns of habitat use by individuals, referred to here as individual spatial mixing, can have important implications for ecological and evolutionary processes. This study proposes a novel approach for estimating the degree of individual spatial mixing in an endangered beluga population, based on the comparison of local individual diversity obtained from photo-identification data against abundance indices derived from systematic aerial surveys. Divergences between long-term indices of abundance and diversity were observed across many sectors within the population's summer habitat. This was the case notably for the Saguenay Fjord, where on average only 1.8% of the total population count was detected during summer aerial surveys, but where 41% of all individuals identified in the photo-identification data were found at least once. The comparative approach proposed in this study to estimate individual spatial mixing can help quantify site fidelity patterns in wildlife populations and estimate its vulnerability to local stressors such as anthropogenic noise.

KEYWORDS
abundance, aerial survey, beluga, capture-recapture, *Delphinapterus leucas*, habitat use, individual diversity, photo-identification

1 | INTRODUCTION

Estimating the abundance of a population is a common task that can provide insights into ecological and evolutionary processes and inform conservation efforts (Evans & Hammond, 2004). In field ecology, abundance estimates are generally obtained by cue counting (individuals, scats, calls, etc.) in quadrats or along transects using a variety of survey platforms (Buckland et al., 2015; Evans & Hammond, 2004; Guirado et al., 2019; Kingsley & Reeves, 1998; Maire et al., 2015). These estimates can provide information on the proportion of a population using a given sector at any one time (Williams et al., 2006), or how consistently certain sectors are used (Heath et al., 2012), and generally provide insights into the links between environmental variables and habitat use patterns of populations (Brown et al., 1995). Abundance estimates, however, are generally ineffective at assessing local individual diversity. For example, sectors of high abundance could result from a large resident population or the continuous flow of an even larger number of transient individuals. In other words, abundance measures alone cannot provide information about spatial mixing of individuals within a population.

Spatial mixing of individuals within populations has been suggested as an important feature for understanding population dynamics (Morales et al., 2010), and can be particularly valuable for estimating the cumulative impacts of localized anthropogenic stressors at the individual level. Impacts of local stressors such as toxic substances, anthropogenic noise, vessel interactions (e.g., whale watching), are likely to accumulate faster over time for individuals that are largely resident to these exposed sectors (i.e., low individual spatial mixing) than if the latter are characterized by a high turnover of individuals (high spatial mixing). A better understanding of spatial mixing of individuals within specific sectors, can therefore lead to a better assessment of cumulative impacts of local stressors on marine mammals.

Capture-recapture methods of sampling, which rely on recognizable cues (a tag or a natural marking) for identifying unique individuals, explicitly collect information about where specific individuals have been seen (Hammond, 1990) and can work as a natural complement to abundance estimates. While capture-recapture methods are largely applied to assess population size and obtain demographic or life history parameters (Pace et al., 2017), these methods also offer the ability to estimate the number of unique individuals at a given location (Gormley et al., 2005) and thus, local individual diversity.

While abundance and individual diversity indices are likely correlated to some extent, there are notable conditions under which this might not be the case. In a population with low spatial mixing and high site fidelity of individuals to relatively restricted home ranges, we would expect a high correlation between abundance and individual diversity measures across multiple sectors of a population's spatial range; sectors of high or low abundance would simply have a large or low number of unique individuals. If individuals, however, are using multiple but not necessarily common habitats, and are traveling between these habitats using common corridors, the latter would show low abundance but high diversity from their brief use by many individuals, indicative of high spatial mixing of individuals. More generally, we propose that a mismatch between individual diversity and abundance might provide insights into individual spatial mixing within sectors.

Under ideal conditions a more direct route to estimating individual spatial mixing within a population would be to rely on individual movement data collected from a large sample of the population. Where technically and ethically feasible, this method would allow for estimates of overlap between individual home ranges (Frere et al., 2010), and provide a direct estimate of individual spatial mixing, i.e., identifying sectors that are used by many unique individuals, for how long, and whether that use is concurrent. For many marine mammal populations, however, collecting individual movement data, for example using satellite tagging, can pose a significant financial barrier and it is often difficult to tag a representative sample of the population. The proposed approach, which relies on two common data sources for marine mammals, photo-identification and aerial survey data, may offer an interesting alternative for estimating spatial mixing of individuals within populations.

Similar work in estimating the proportion of the population that are residents or transients has been carried out using capture-recapture data alone (Pradel et al., 1997). These approaches have focused on relaxing the assumption in capture-recapture models that populations are closed, and attempts to provide an unbiased estimate of the resident population (Conn et al., 2011; Haughey et al., 2020). These approaches, however, differ from our goal to identify spatial locations of high and low spatial mixing, rather than to directly classify animals as resident or transient or to estimate the size of the population.

In this paper, we tested a combined approach to estimate spatial mixing in our population by using an 18-year photo-identification data set of beluga whales, (*Delphinapterus leucas*) to estimate sector-specific individual diversity (Michaud, 1993) and compare those diversity estimates to existing abundance estimates from 35 systematic aerial surveys conducted over the entire population summer range in the St. Lawrence Estuary, Canada (Mosnier et al., 2016).

2 | MATERIAL AND METHODS

2.1 | Study population

Belugas in the St. Lawrence Estuary (SLE) are considered endangered in Canada (Bill C-5, An act respecting the protection of wildlife species at risk in Canada, 2002; COSEWIC, 2014). The summer range of this population is among the smallest for the species (Mosnier et al., 2010; Figure 1), and is exposed to concerning levels of local stressors such as anthropogenic noise, disturbance by directed recreational or commercial activities (e.g., whale watching), and high burdens of toxic substances (Lesage, 2021). Some of these stressors are unevenly distributed in the SLE beluga habitat. For instance, some contaminants such as HAP are known to be at higher levels in the Saguenay Fjord and downstream portion of the SLE than in other sectors; shipping traffic is much heavier along the SLE north shore; directed whale-watching activities even if prohibited, can be high in some sectors such as the Saguenay Fjord and Fjord mouth, or islands in the Upper Estuary (Higham et al., 2014; Ménard et al., 2014); smaller vessel and ferry traffic reach their maximum at the Saguenay Fjord mouth (Chion et al., 2018; Turgeon, 2019). Site fidelity exists in belugas (Colbeck et al., 2013; O'Corry-Crowe et al., 2018). In SLE belugas, individual belugas were shown to vary in their habitat preference within their summer range (Bonnell et al., 2022), but spatial mixing has not been characterized.

2.2 | Study area

The distribution of SLE belugas during summer range extends from Battures-aux-Loups-Marins and Rivière-Portneuf/Rimouski, including the Saguenay Fjord up to St-Fulgence (Mosnier et al., 2010). While aerial surveys have covered the entirety of this sector each time (e.g., Gosselin et al., 2017), photo-identification efforts have been restricted to a sector generally comprised of the area between Baie-Saint-Paul/Kamouraska in the Upper Estuary, Les Escoumins/Trois-Pistoles in the Lower Estuary, and downstream of Baie Ste-Marguerite in the Saguenay Fjord (Figure 1).

2.3 | Data

2.3.1 | Aerial survey data and population abundance estimates by sector

Aerial surveys to estimate SLE beluga population size are conducted using the same line-transect survey design since 1988 (Gosselin et al., 2014, 2017). A kernel density approach (Worton, 1989) applied to 35 visual and photographic

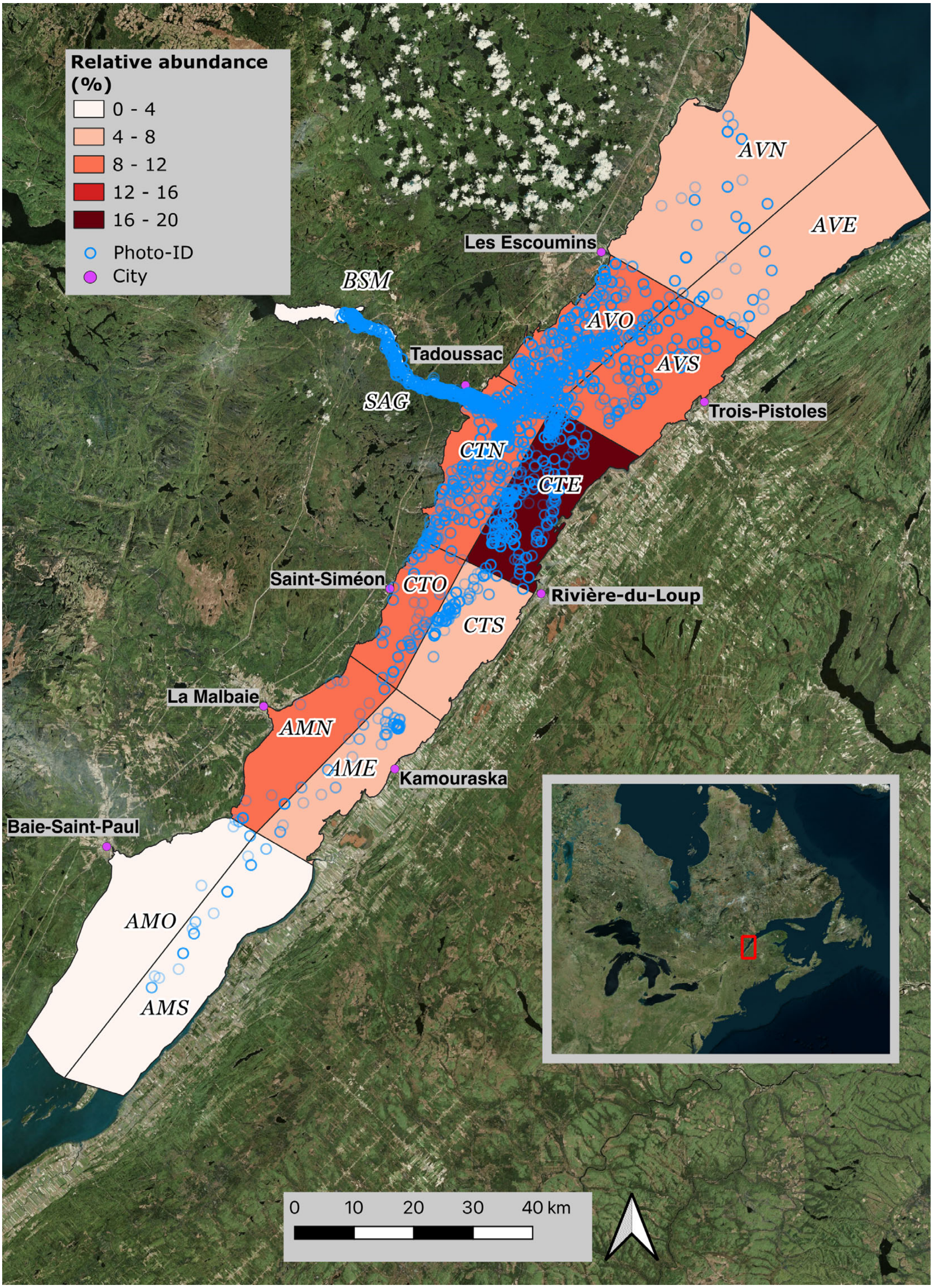

FIGURE 1 Relative abundance of the St. Lawrence Estuary beluga population in each sector during summer, derived from 35 systematic aerial surveys conducted between 1989 and 2009 (Mosnier et al., 2016). The 14 sectors and aerial surveys covered the entirety of the summer range of the population. Individual photo-IDs are represented by blue circles.

surveys conducted at the same period each year (mid-August to early September), and spread over 12 years between 1990 and 2009, produced a continuous distribution of beluga density within their summer range (Mosnier et al., 2016). From this continuous distribution, we used the proportion of total density found within each of the 14 sectors to estimate a relative index of spatial abundance (Figure 1).

For our analysis, we needed to describe the relative abundance of belugas in two subregions in the Saguenay Fjord, neither of which was included in the systematic surveys (Gosselin et al., 2017). In a recent study, the average proportion of the population found in the Fjord during aerial surveys was estimated to be 1.8% (Mosnier et al., 2016; Ouellet et al., 2021). We then used the spatial distribution of photo-ID sightings, using GPS points taken for each photo-ID, to weight that 1.8% and attribute individuals to the Saguenay Fjord per se (SAG; 87.4%) and the Baie Sainte-Marguerite (BSM; 13.6%), a small bay within the Saguenay Fjord which is regularly used by tens of individuals at a time (Conversano et al., 2017; Ménard et al., 2022; Mosnier et al., 2010). Finally, we spatially joined the two maps, and multiplied the proportion estimates of the SLE by 0.982 so that the sum of proportion values from all sectors was equal to 1. This provided an estimate of the relative abundance of beluga sightings in each sector (Figure 1).

2.3.2 | Capture-recapture data

Boat surveys were conducted from June to October between 1989 and 2007 as part of an ongoing long-term study on beluga social organization. These surveys followed a defined photo-identification procedure (Michaud, 2014). The choice of survey area on a given day was selected based on weather conditions as well as to avoid resampling areas covered the previous days. When belugas were encountered, the GPS position of the research vessel was noted, and a herd follow was undertaken to photograph as many individuals as possible within the herd using a handheld camera. A herd follow was limited to 3 hr, with GPS location noted at least every 30 min. Surveys were neither systematic nor random in design, but covered various sectors of a large portion of the population's summer distribution and a broad range of habitats. Sampling effort was distributed across the summer range divided into three strata, each subdivided into four zones, resulting in 12 sectors (Figure 1; Appendix S1). These sectors were delineated with the marine and middle estuary limits and islands dividing the estuary into south and north channels with respect to prior knowledge of beluga age–sex segregation at the start of the data collection (i.e., 1989). We excluded photo-IDs in which the individuals could not be assigned to a known individual. As photo-identification process is ongoing, we included only years where photographs have been fully processed, i.e., 1989–2007, which also closely match the 1990–2009 aerial survey data set. The final photo-ID data consisted of 8,052 photo-IDs, 858 unique individuals, and a mean of nine photo-IDs per individual (Figure 1). There are two biases in the resulting photo-ID data set that impact the use of methods and the interpretation of the results. The first is that the data are unevenly distributed across the population summer range, the second is that by taking only recognizable individuals we are capturing patterns in the adults more than the young (Figure 1). In the next section we show how our methods account for the uneven sampling, whereas the bias towards adults must be considered when interpreting the final results.

2.4 | Statistical analysis

2.4.1 | Individual diversity

The spatial extent of the summer range of this population, and the difficulty of reaching the extremes given the research vessel homeport in Tadoussac, resulted in our sampling effort being unevenly distributed within the study area (Figure 1). To account for this sampling bias, we used a diversity curve approach that uses the cumulative number of unique individuals observed as a function of increasing sampling effort to estimate individual diversity in each sector (Chao, Gotelli, et al., 2014; Colwell et al., 2004; Williams et al., 1993). These curves are generally characterized by a number of unique individuals increasing rapidly at the beginning of the study, then leveling off as the identification of new individuals becomes progressively more difficult. It is possible to use the shape of a diversity curves to estimate total diversity, i.e., the number of unique individuals that would have been identified if an area had been exhaustively sampled.

However, obtaining a reliable estimate of total diversity generally requires a high level of sampling, which was lacking in many sectors of the SLE beluga summer range. A coverage-based rarefaction approach was thus also applied to the data to enable the comparisons of individual diversity estimates among a greater number of sectors (Chao & Jost, 2012). This approach uses the number of individuals captured only once or twice to estimate sample coverage, and effectively compare diversity measures across sites at a common level of sample coverage (Appendix S1). The method was deemed more effective at estimating diversity across sectors (hereafter referred to as relative diversity) than using raw sampling effort (e.g., number of photographs taken) (Chao & Jost, 2012).

Both total and relative diversity estimates were obtained using the “iNEXT” package in R (Hsieh et al., 2016). As relative diversity estimates were going to be used to compare across sectors, all estimates of relative density were compared at 0.5 coverage. Given total diversity estimates were used to estimate the asymptote of the diversity line within sectors sampling effort and not coverage was used. Additionally, diversity was measured in multiple ways expressed in terms of (1) individual richness, which represents a simple count of unique individuals in a sector; (2) Shannon diversity; and (3) Simpson's diversity index (Chao, Chiu, et al., 2014; Hill, 1973). In the case of Shannon and Simpson's diversity these can be viewed as extensions of richness that also considers how many times each individual has been seen in addition to the number of unique individuals. From this point of view Shannon diversity can be interpreted as the diversity of common individuals, while Simpson's diversity captures diversity of only the most common individuals (Chao, Gotelli, et al., 2014; Colwell, 2009). It is important to note that the methods proposed to estimate individual diversity in our photo-IDs are more generally used to estimate species diversities. While diversity curves have been used to estimate individual diversity (Gormley et al., 2005), it is important to highlight that we are using individuals and not species numbers with these methods. As such, some baseline assumptions are altered, for example, the number of recaptures of an individual will be treated similarly as the number of recaptures of a certain species when calculating diversity.

We used the diversity curve approach to estimate: total diversity of recognizable individuals (1) in the population over the period 1989–2007 and (2) within each sector, (3) relative diversity of recognizable individuals among sectors, and (4) the mismatch in estimates of relative diversity and abundance for each sector. To estimate the mismatch between relative diversity and abundance, we calculated the deviation from the expectation that sectors with higher abundances should have proportionally higher individual diversity estimates (Figure 2). For example, using an individual richness measure, if a sector contains 11% of the relative abundance of belugas according to aerial survey estimates, this sector would be expected to have 11% of the relative individual richness. If the sector presents a relative richness lower/greater than the expected 11%, then we estimate the size of this deviation as the number of individuals above/below the expected level. A sector that shows relatively fewer individuals than expected from abundance estimates is one that is likely to be used repeatedly by the same individuals. Conversely, a sector that shows a larger number of individuals than expected from abundance estimates is one likely used by more transient individuals, where a more diverse set of individuals are observed during surveys (Figure 2). By taking this relativistic approach we can identify areas of high or low turnover of individuals.

It is important to note that our estimate of effort when calculating diversity is the number of successfully identified individuals. An implicit assumption when making this choice is that when taking a picture, we assume that each sector has the same chance of a recapture, and it is only the distribution/movement of belugas that alter this rate of successful recapture. Another option, not taken in this manuscript due to data limitations, would be to record the time spent actively searching for individuals to photograph. Our results must therefore be interpreted as the diversity of individuals found given how many successful photo-identifications were achieved, and not how much time was spent searching for individuals to photograph.

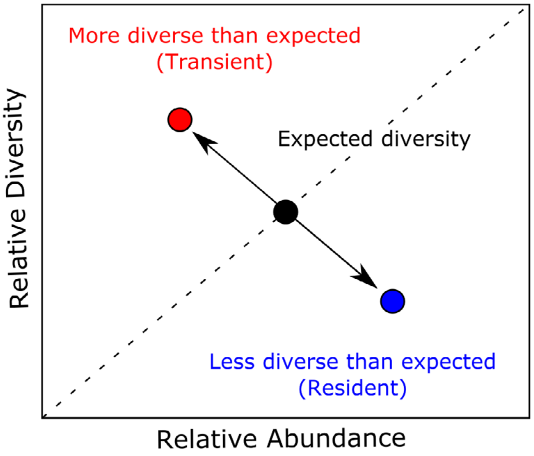

FIGURE 2 Conceptual diagram comparing relative abundance and diversity indices, as well as our interpretations of deviations from expected values. Sectors where relative diversity is higher (in red) and lower (in blue) than expected from relative abundance estimates are associated with high (transient) and low (resident) turnover of individuals, respectively. Sectors where expected individual diversity is proportional to abundance estimates (dashed line) captures the case where sectors with higher/lower abundance estimates are also those of higher/lower diversity of unique individuals, with no trend toward higher or lower residency.

2.4.2 | Testing performance using simulated data

We generated test data sets with known individual diversity to test the ability of the diversity curve approach to estimate total and relative diversity. Specifically, we determined the minimum number of photo-IDs and sampling coverage needed to obtain reliable individual diversity estimates. We generated two data sets using the observed photo-ID data. The first data set was generated to mimic a well-mixed population, i.e., where individuals show no site fidelity, by permuting all individual identifications in the photo-ID data set. This approach retained differences in the number of times each individual was observed, and any possible bias as a result of some individuals being photographed more often than others, while creating a data set where it was possible to see any particular beluga ID in any of the sectors. The second data set was generated to mimic a spatially structured population, i.e., where individuals had some preference for certain sectors, by dividing individuals into one of four equally-sized communities. Each community was attributed a fixed number of sectors where they were more likely to be found (i.e., individuals were given site fidelity behavior). In defining which sectors each community used, we explicitly chose sectors to allow for spatial mixing of two communities in one sector. This setup produced a known number of users in each sector. A total of 1,000 randomized and 1,000 spatially structured test data sets were generated.

3 | RESULTS

3.1 | Simulated data on spatial mixing

Diversity curves run over 1,000 completely randomized and 1,000 spatially structured data sets indicated that a minimum of 50 photo-IDs within a sector, and more than 80% sample coverage (i.e., capture of >80% of the recognizable individuals) were needed to produce reliable estimates of total diversity within sectors (Appendix S2). A minimum of 50 photo-IDs were also required to estimate relative diversity. These thresholds were used throughout our analyses below.

3.2 | Total diversity and relative diversity of recognizable individuals

Results from individual richness, Shannon diversity, and Simpson's diversity indices were qualitatively very similar (i.e., the conclusions drawn from the results are the same). As such, only results from individual richness analyses are presented below; those derived from the Shannon diversity and Simpson's diversity indices are provided in Appendix S3.

3.2.1 | Population level

The diversity curve asymptote indicated a total of 1,046, 95% CI [987, 1,133] recognizable individuals in the population for the period 1989–2007 (Figure 3). The estimated sample coverage was 98%, i.e., well above the 80% threshold for estimate reliability.

3.2.2 | Sector level (total diversity)

When the diversity curves approach was applied to each sector individually, only four sectors met the 80% sample coverage threshold (Figure 4a). The CTN sector was where the highest estimated number of recognizable individuals

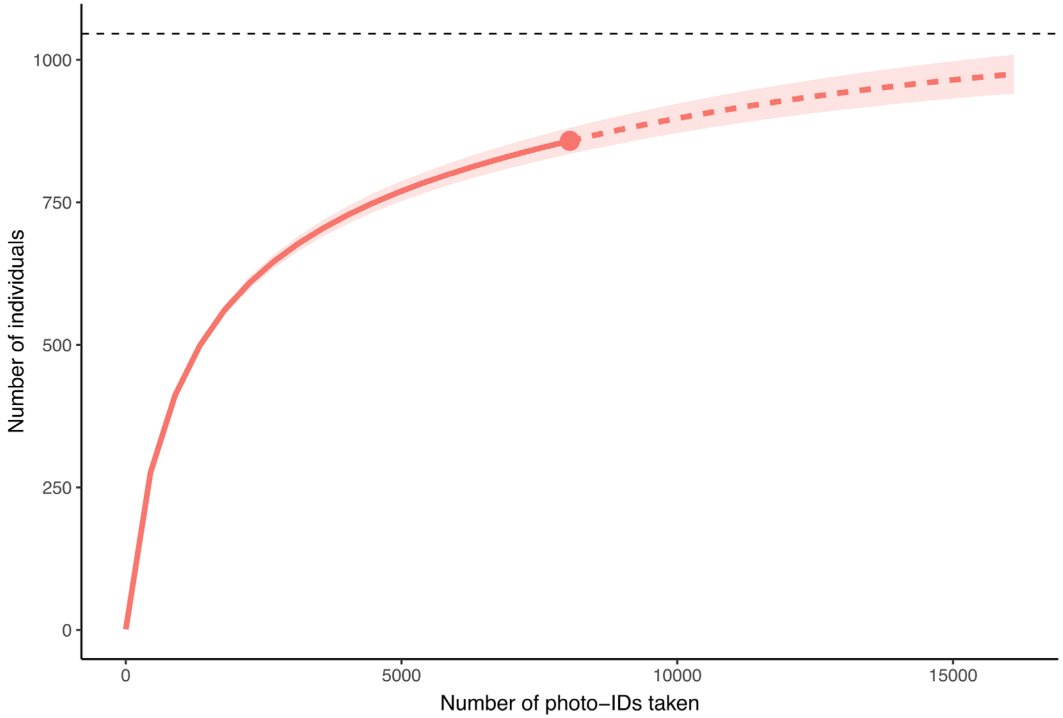

FIGURE 3 Individual richness as a function of sampling effort (i.e., number of photographs taken) for the full photo-ID data set. The red dot indicates the observed individual richness estimate, whereas the red line represents the interpolated (solid) and extrapolated (dashed) estimates of individual richness. The black dashed line indicates the point where the extrapolated line reaches asymptote, and provides the estimated richness of recognizable individuals in the population for the period 1989–2007 (i.e., 1,046 unique individuals).

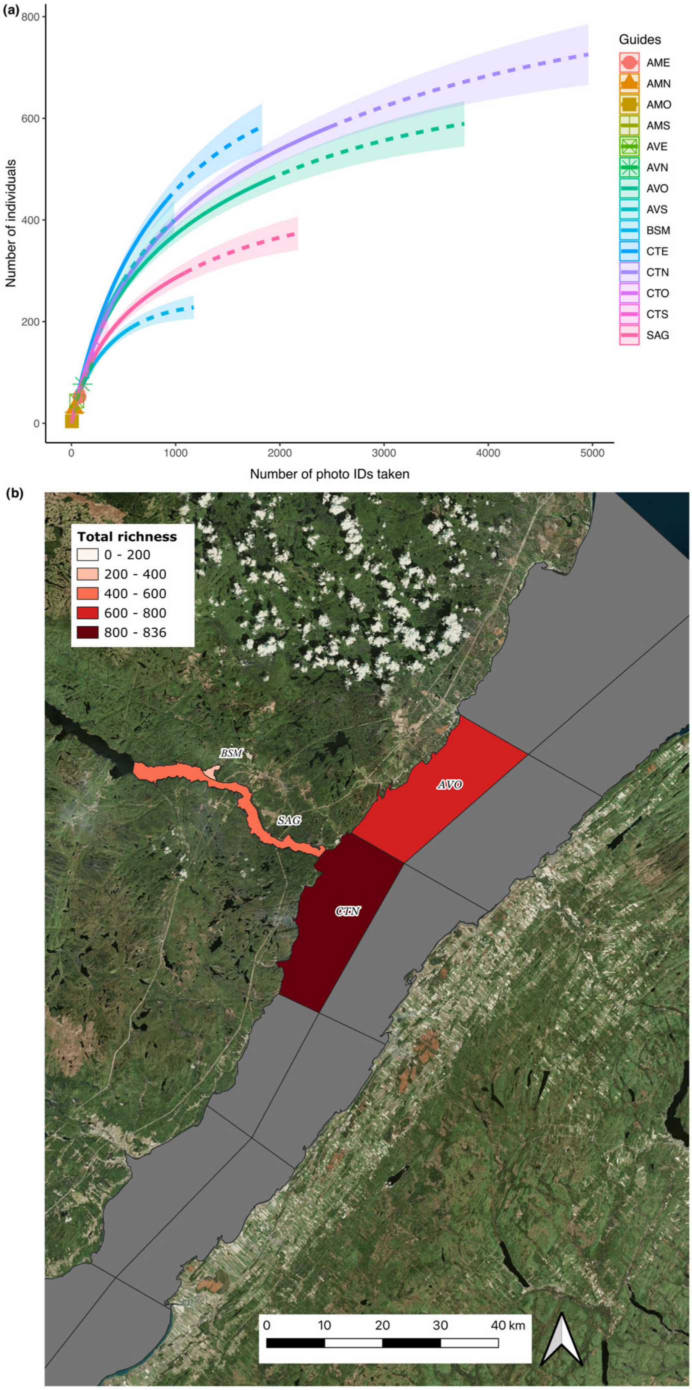

FIGURE 4 Total individual richness by sector, as expressed as (a) a function of sampling effort (i.e., number of photo-IDs taken) for each of the sectors (color coded), and (b) mapped over the study area. The line in (a) represents the interpolated (solid) and extrapolated (dashed) richness estimates. Sectors that did not meet the threshold for reliable estimates of total richness were shaded in (b) as gray.

were observed (836, 95% CI [740, 990]), followed by AVO (657, 95% CI [585, 777]), SAG (427, 95% CI [366, 541]), and BSM (240, 95% CI [213, 298]) (Figure 4b). Other sectors that did not meet the threshold for reliability of diversity indices (in gray in Figure 4b) likely yielded low quality estimates of total diversity. When compared to the total number of recognizable individuals using all sectors, estimated at 1,046, 95% CI [987, 1,133], the four sectors with reliable total richness estimates suggest a large variation in the proportion of unique individuals: e.g., the CTN sector contained 80%, AVO contained 63%, SAG contained 41%, and the BSM sector contained 23% of the total number of individuals.

3.2.3 | Sector level (relative diversity)

Individual richness per sector was also examined at a fixed 0.5 sample coverage allowing relative individual richness to be estimated for 11 of the 14 sectors. The CTE and AVS sectors surpassed CTN in individual richness (Figure 5), although, CTN was predicted to increase in richness faster than CTE and AVS with additional sampling.

3.3 | Comparing individual richness and survey abundance estimates

Several sectors with low survey abundance estimates were found to be used by a relatively high number of individuals, suggesting a high degree of mixing or turnover of individuals (Figure 6a, Table S2). This is the case notably for the sectors CTS, BSM, and SAG (Figure 6b). Conversely, other sectors such as CTE, CTO, and to a lesser extent AVN, were used by fewer individuals than expected from survey abundance estimates, suggesting lower mixing or individual turnover (i.e., higher site fidelity in these sectors; Figure 6b). Given the higher uncertainty in the estimate of spatial abundance in the Saguenay Fjord, i.e., 1.8%, we also present results in Appendix S4 for a range of spatial abundance values 0.5%–5.0%. Changing the spatial abundance estimate in the Saguenay Fjord, however, did not meaningfully alter the main findings (Appendix S4).

4 | DISCUSSION

The combination of photo-ID and aerial survey data in this study altered the view on summer distribution patterns of SLE belugas compared to when interpreting the two indices on their own. It did so by adding the perspective of local mixing or degree of turnover of individuals in a given sector. Individual richness in this study was estimated at ∼1,000 individuals over an 18-year period using distinguishable individuals only. Given the mortalities and births occurring over this period and exclusion of individuals without markings, this index cannot be interpreted as an estimate of population size. However, this index when taken on its own and when compared among sectors, was instructive on the areas where the highest abundance of animals was likely to be observed.

The substantial mismatch between the (low) survey abundance estimates and (high) diversity indices in the Saguenay Fjord, including BSM, and in the CTS sector suggests a high degree of mixing or turnover of individuals in these sectors. As a result, a local stressor in these areas, which are all part of the Critical Habitat of SLE belugas, would be likely to expose a large proportion of the population for short durations. Conversely, several other sectors in the Upper Estuary, again part of the Critical Habitat of the population, had low diversity indices relative to abundance estimates, suggesting low mixing. A stressor in these sectors would likely expose repeatedly the same segment of the population. The Upper Estuary and Saguenay Fjord are both heavily used by females accompanied by calves and juveniles during summer (Michaud, 1993; Michaud et al., 1993; Ouellet et al., 2021). For a stressor such as noise, which can significantly affect communication between females and calves in SLE belugas (Vergara et al., 2021), accounting for the persistent use of the same areas by this vulnerable segment of the population can modify the assessment of cumulative impacts of such stressors on individual and population.

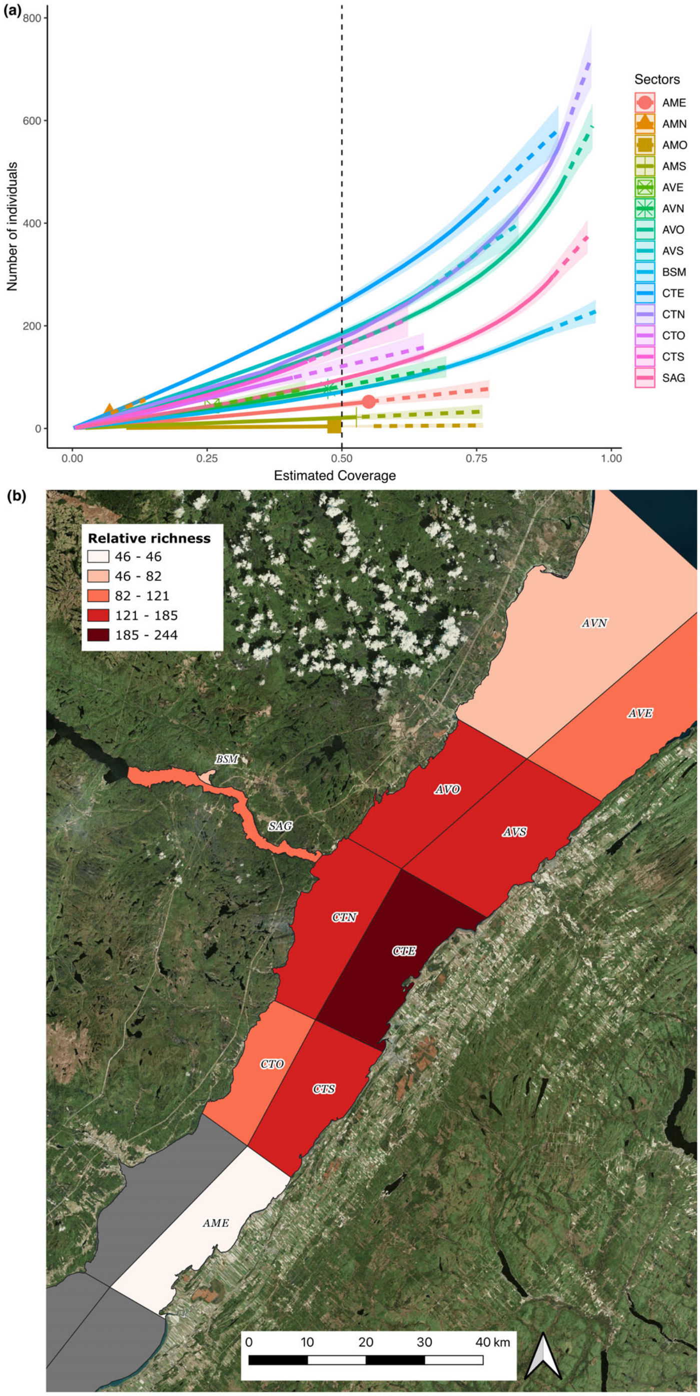

FIGURE 5 Relative individual richness by sector, as expressed as (a) a function of sample coverage (i.e., how completely have we sampled the population) for each of the sectors (color coded), and (b) mapped over the study area. The line in (a) represents the interpolated (solid) and extrapolated (dashed) richness estimates. Sectors that did not meet the threshold for reliable estimates of relative richness were shaded in (b) as gray.

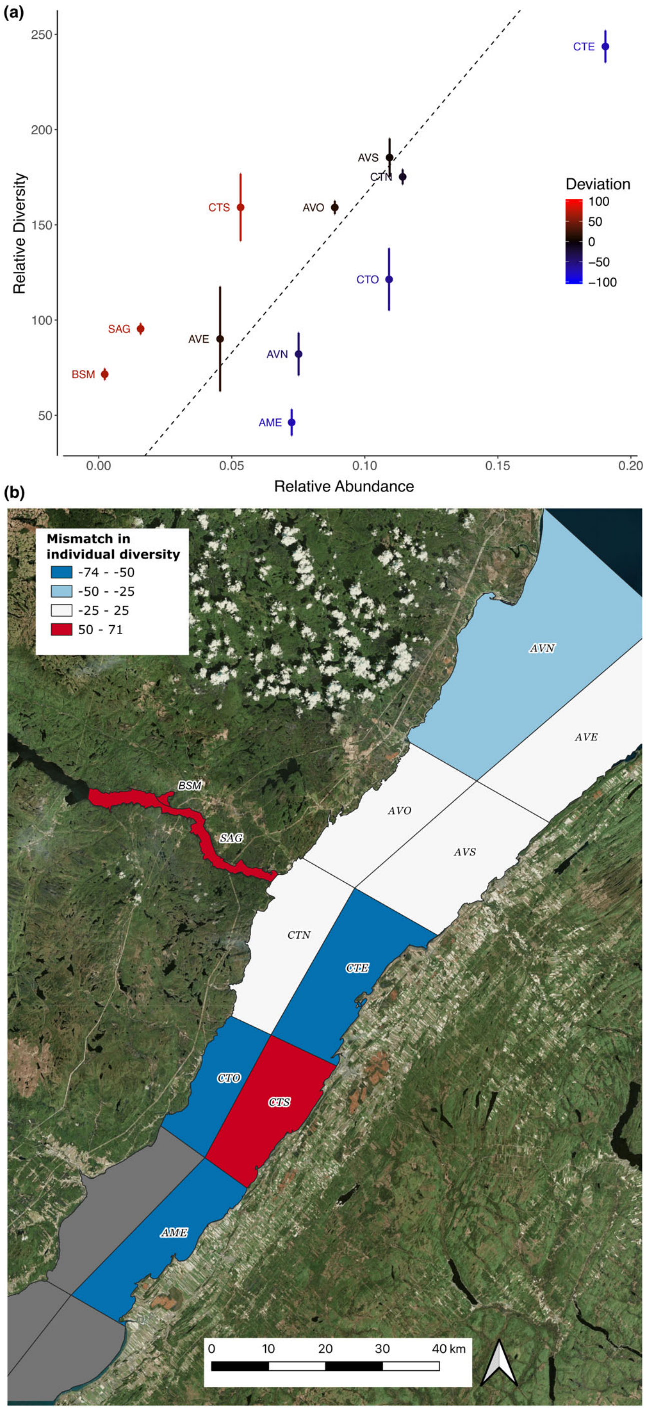

FIGURE 6 Comparison between relative diversity (i.e., individual richness) and relative survey abundance per sector, expressed as (a) deviations from the expected pattern if a sector had equal proportions based on both indices (dashed line), and (b) mapped over the study area. Only sectors with a minimum sample coverage of 0.5 were consider. Deviations from expected values are color-coded according to strength and direction of the deviation of relative diversity as red: higher-than-expected (i.e., higher mixing); blue: lower-than-expected (i.e., lower mixing); white: as-expected.

Beyond providing a means of estimating exposure risk, spatial mixing can add to our understanding of site fidelity patterns, especially when combined with other indices of habitat use patterns. For example, it is possible to combine the spatial mixing results with previously found spatial community results to identify site fidelity patterns of a subset of the population that uses the Saguenay fjord. In Bonnell et al. (2022) photo-ID data was used to estimate spatial communities within the same study population. These spatial communities provided an understanding of which sectors contained similar individual user profiles: e.g., if two sectors share similar patterns of common and uncommon users they were said to belong to the same spatial community. One prominent spatial community identified used the Saguenay Fjord and mouth (i.e., SAG, BSM, and CTN), which encompassed two sectors (BSM and SAG) where our diversity measures were much higher than expected given survey abundance estimates (Figure 6, Table S2). The combination of these spatial community and individual mixing results suggests that within the Saguenay Fjord/CTN spatial community, a subset of individuals may be traveling regularly up the Saguenay Fjord in greater numbers than is apparent from the survey abundance estimates. It is important to note that this does not imply that only common users found in the Saguenay Fjord/CTN spatial community use the Saguenay Fjord, rather the results suggest that this subset of the population makes more use of it than others. Additionally, given that the mouth of the Saguenay Fjord was found to have a high total individual richness (Figure 4), and low variation in the probability of seeing individual beluga (Bonnell et al., 2022), it suggests the mouth is a high mixing zone, i.e., it is a sector shared by many belugas. This interpretation is also supported from an analysis of focal follows of beluga groups, which found that the region around the mouth of the Saguenay Fjord interconnects strongly with other sectors (Ouellet et al., 2021).

There is also some evidence for site fidelity patterns in the Upper Estuary. From our previous spatial community analysis, it was found that sectors in the Upper Estuary generally shared similar individual user profiles. Diversity estimates in the current study, however, suggest a high individual mixing in one sector of the Upper Estuary (i.e., CTS), and low mixing in surrounding sectors (i.e., CTE, CTO, AME). One potential interpretation of these diversity patterns is that individuals are traveling through CTS to/from specific sectors upstream. This would explain why the same individuals are seen more often than expected in the upstream sectors of the Upper Estuary (i.e., low turnover/spatial mixing), and why diversity is higher than expected in CTS. Yet, caution needs to be taken with the results from the Upper Estuary as the number of photo-ID samples is low for this region, especially when compared to the sectors around the Saguenay Fjord.

The interpretations of our results highlight the existence of site fidelity patterns in this beluga population, a feature described in other beluga populations (Hauser et al., 2014; O'Corry-Crowe et al., 2018), but not yet fully demonstrated for the SLE population. Using large scale genetic sampling of belugas in the North Pacific, O'Corry-Crowe et al. (2018) found evidence to suggest that belugas often mix in certain sectors of their habitat (e.g., in wintering areas), but return reliably to specific locations during the summer. This high level of site fidelity is thought to be learned individually and is likely passed through cultural means during juvenile development. More work could be done at a smaller scale to identify if subsets of the SLE beluga population follow similar site fidelity patterns (e.g., individuals in the CTN, SAG, BSM subset), and to identify: where those high fidelity sites are, what functions they serve, and how best to mediate impacts to these sites (e.g., Chion et al., 2021; Ménard et al., 2022). By refining our view of individual-level site fidelity, it would be possible to identify management units from a movement ecology perspective and develop better estimates of how localized anthropogenic disturbances will impact subsets of the SLE beluga population.

Finally, from a methodological point of view, we have used an individual diversity curve approach to estimate both the total and relative individual richness, and aerial surveys to estimate relative abundance across sectors. These are common approaches to estimating diversity and abundance indices, though by no means the only way. We suggest that methodological advancements in either case would be welcome, and ultimately provide better estimates of individual diversity and abundance that can be compared to estimate spatial mixing in populations: e.g., using alternative methods to estimate diversity, or using mark-recapture models to achieve abundance estimates (Citta et al. 2018; Roswell et al. 2021). Similarly, more direct means of estimating spatial mixing using for instance long term tracking of many individuals could provide a more precise method for estimating spatial mixing within populations. Here, we showed that when long-term telemetry (i.e., months, years) is not methodically/ethically feasible or available, using two common data sources for marine mammal populations, photo-IDs and aerial surveys, can be used to estimate spatial mixing in marine mammals, and other wildlife populations. It is important to note, however, that by using an aggregate of aerial surveys to define population density in the summer months, our results must be treated as an aggregate pattern over the entire time scale of the study. Increased temporal resolution of data collection could allow for similar investigations at finer temporal scales.

4.1 | Conclusions

Overall, our results provide strong evidence that the beluga population in the St. Lawrence Estuary cannot be assumed to be randomly mixing within their summer habitat. We have shown that it is possible to use the mismatch between patterns of abundance and individual diversity to quantify individual spatial mixing. We suggest that insights into spatial mixing within a population can provide critical information for estimating the distribution of impacts from localized anthropogenic stressors.

ACKNOWLEDGMENTS

We would like to thank Jean-François Gosselin and Arnaud Mosnier for the beluga survey abundance estimates they provided, as well as all the field workers who contributed to the collection/management of the photo-ID database.

AUTHOR CONTRIBUTIONS

Tyler Bonnell: Conceptualization; formal analysis; methodology; writing – original draft; writing – review and editing. **Robert Michaud:** Conceptualization; data curation; funding acquisition; project administration; writing – original draft; writing – review and editing. **Angelique Dupuch:** Conceptualization; writing – original draft; writing – review and editing. **Veronique Lesage:** Conceptualization; data curation; writing – original draft; writing – review and editing. **Clément Chion:** Conceptualization; funding acquisition; project administration; writing – original draft; writing – review and editing.

CONFLICTS OF INTEREST

All authors declare no conflicts of interest.

FUNDING

The funding to support this research project was provided by the Ministère des Forêts, de la Faune et des Parcs du Québec.

ORCID

Tyler R. Bonnell https://orcid.org/0000-0001-6041-5177

REFERENCES

Bill C-5. An act respecting the protection of wildlife species at risk in Canada (2002). https://www.parl.ca/Content/Bills/372/Government/C-5/c-5_3/90106bE.html

Bonnell, T. R., Michaud, R., Dupuch, A., Lesage, V., & Chion, C. (2022). Extracting spatial networks from capture–recapture data reveals individual site fidelity patterns within a marine mammal's spatial range. *Ecology and Evolution*, *12*(2), e8616.

Brown, J. H., Mehlman, D. W., & Stevens, G. C. (1995). Spatial variation in abundance. *Ecology*, *76*(7), 2028–2043. https://doi.org/10.2307/1941678

Buckland, S. T., Rexstad, E. A., Marques, T. A., & Oedekoven, C. S. (2015). *Distance sampling: Methods and applications*. Springer.

Chao, A., Chiu, C.-H., & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, *93*(12), Article 12. https://doi.org/10.1890/11-1952.1

Chion, C., Bonnell, T. R., Lagrois, D., Michaud, R., Lesage, V., Dupuch, A., McQuinn, I. H., & Turgeon, S. (2021). Agent-based modelling reveals a disproportionate exposure of females and calves to a local increase in shipping and associated noise in an endangered beluga population. *Marine Pollution Bulletin*, *173*, Article 112977. https://doi.org/10.1016/j.marpolbul.2021.112977

Chion, C., Turgeon, S., Cantin, G., Michaud, R., Ménard, N., Lesage, V., Parrott, L., Beaufils, P., Clermont, Y., & Gravel, C. (2018). A voluntary conservation agreement reduces the risks of lethal collisions between ships and whales in the St. Lawrence Estuary (Québec, Canada): From co-construction to monitoring compliance and assessing effectiveness. *PLoS ONE*, *13*(9), e0202560. https://doi.org/10.1371/journal.pone.0202560

Citta, J. J., O'Corry-Crowe, G., Quakenbush, L. T., Bryan, A. L., Ferrer, T., Olson, M. J., Hobbs, R. C., & Potgieter, B. (2018). Assessing the abundance of Bristol Bay belugas with genetic mark-recapture methods. *Marine Mammal Science*, *34*(3), 666–686. https://doi.org/10.1111/mms.12472

Colbeck, G. J., Duchesne, P., Postma, L. D., Lesage, V., Hammill, M. O., & Turgeon, J. (2013). Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1752), Article 20122552. https://doi.org/10.1098/rspb.2012.2552

Colwell, R. K. (2009). III.1 Biodiversity: Concepts, patterns, and measurement. In S. A. Levin, S. R. Carpenter, H. C. J. Godfray, A. P. Kinzig, M. Loreau, J. B. Losos, B. Walker, & D. S. Wilcove (Eds.), *The Princeton guide to ecology* (pp. 257–263). Princeton University Press. https://doi.org/10.1515/9781400833023.257

Colwell, R. K., Mao, C. X., & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, *85*(10), 2717–2727. https://doi.org/10.1890/03-0557

Conn, P. B., Gorgone, A. M., Jugovich, A. R., Byrd, B. L., & Hansen, L. J. (2011). Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. *Journal of Wildlife Management*, *75*(3), 569–579. https://doi.org/10.1002/jwmg.94

Conversano, M., Turgeon, S., & Ménard, N. (2017). Caractérisation de l'utilisation de l'embouchure du Saguenay et de la baie Sainte-Marguerite par le béluga du Saint-Laurent et par le trafic maritime entre 2003 et 2016 (Characterization of the use of the Saguenay Mouth and Sainte-Marguerite Bay by St. Lawrence beluga and maritime traffic between 2003 and 2016). *Analyse Des Données d'observation Terrestre et Recommandations Sur Les Mesures de Gestion Visant à Réduire Le Dérangement Dans Les Aires de Haute Résidence Du Béluga Dans Le Parc Marin Du Saguenay–Saint-Laurent* (Beluga [*Delphinapterus leucas*]: Report on progress in the implementation of the St. Lawrence estuary recovery programme for the period 2012–2019). Fisheries and Oceans Canada.

COSEWIC. (2014). *COSEWIC assessment and status report on the Beluga whale* Delphinapterus leucas, *St. Lawrence Estuary population, in Canada*. Committee on the Status of Endangered Wildlife in Canada.

Evans, P. G., & Hammond, P. S. (2004). Monitoring cetaceans in European waters. *Mammal Review*, *34*(1–2), 131–156. https://doi.org/10.1046/j.0305-1838.2003.00027.x

Frere, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Animal Behaviour*, *80*(3), 481–486. https://doi.org/10.1016/j.anbehav.2010.06.007

Gormley, A. M., Dawson, S. M., Dawson, S. M., Slooten, E., & Bräger, S. (2005). Capture-recapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science*, *21*(2), 204–216. https://doi.org/10.1111/j.1748-7692.2005.tb01224.x

Gosselin, J.-F., Hammill, M. O., & Mosnier, A. (2014). *Summer abundance indices of St. Lawrence Estuary beluga* (Delphinapterus leucas) *from a photographic survey in 2009 and 28 line transect surveys from 2001 to 2009* (Research Document 2014/021). Canadian Science Advisory Secretariat, Fisheries and Oceans Canada.

Gosselin, J.-F., Hammill, M. O., Mosnier, A., & Lesage, V. (2017). *Abundance index of St. Lawrence Estuary beluga,* Delphinapterus leucas, *from aerial visual surveys flown in August 2014 and an update on reported deaths* (Research Document 2017/019). Canadian Science Advisory Secretariat, Fisheries and Oceans Canada.

Guirado, E., Tabik, S., Rivas, M. L., Alcaraz-Segura, D., & Herrera, F. (2019). Whale counting in satellite and aerial images with deep learning. *Scientific Reports*, *9*(1), Article 14259. https://doi.org/10.1038/s41598-019-50795-9

Hammond, P. S. (1990). Capturing whales on film–estimating cetacean population parameters from individual recognition data. *Mammal Review*, *20*(1), 17–22. https://doi.org/10.1111/j.1365-2907.1990.tb00099.x

Haughey, R., Hunt, T., Hanf, D., Rankin, R. W., & Parra, G. J. (2020). Photographic capture-recapture analysis reveals a large population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) with low site fidelity off the North West Cape, Western Australia. *Frontiers in Marine Science*, *6*, Article 781. https://doi.org/10.3389/fmars.2019.00781

Hauser, D. D., Laidre, K. L., Suydam, R. S., & Richard, P. R. (2014). Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biology*, *37*(8), 1171–1183. https://doi.org/10.1007/s00300-014-1510-1

Heath, J. P., Montevecchi, W. A., & Esler, D. (2012). A method for quantifying consistency in animal distributions using survey data. *PLoS ONE*, *7*(9), e44353. https://doi.org/10.1371/journal.pone.0044353

Higham, J., Bejder, L., & Williams, R. (2014). *Whale-watching: Sustainable tourism and ecological management*. Cambridge University Press.

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, *54*(2), 427–432. https://doi.org/10.2307/1934352

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Kingsley, M., & Reeves, R. R. (1998). Aerial surveys of cetaceans in the Gulf of St. Lawrence in 1995 and 1996. *Canadian Journal of Zoology*, *76*(8), 1529–1550. https://doi.org/10.1139/z98-054

Lesage, V. (2021). The challenges of a small population exposed to multiple anthropogenic stressors and a changing climate: The St. Lawrence Estuary beluga. *Polar Research*, *40*(S1). https://doi.org/10.33265/polar.v40.5523

Maire, F., Alvarez, L. M., & Hodgson, A. (2015). Automating marine mammal detection in aerial images captured during wildlife surveys: A deep learning approach. In B. Pfahringer & J. Renz (Eds.), *AI 2015: Advances in artificial intelligence* (Vol. 9457, pp. 379–385). Springer. https://doi.org/10.1007/978-3-319-26350-2_33

Ménard, N., Michaud, R., Chion, C., & Turgeon, S. (2014). *Documentation of maritime traffic and navigational interactions with St. Lawrence Estuary beluga* (Delphinapterus leucas) *in calving areas between 2003 and 2012* (Research Document 2014/003). Canadian Science Advisory Secretariat, Fisheries and Oceans Canada.

Ménard, N., Turgeon, S., Conversano, M., & Martins, C. C. A. (2022). Sharing the waters: Application of a marine spatial planning approach to conserve and restore the acoustic habitat of endangered beluga whales (*Delphinapterus leucas*) in and around the Saguenay–St. Lawrence Marine Park. *Marine Pollution Bulletin*, *175*, Article 113325. https://doi.org/10.1016/j.marpolbul.2022.113325

Michaud, R. (1993). *Distribution estivale du béluga du Saint-Laurent: Synthèse 1986 à 1992* (Summer distribution of the St. Lawrence beluga: Summary 1986 to 1992). Ministère des pêches et des océans. Direction de la gestion de l'habitat du poisson.

Michaud, R. (2014). *St. Lawrence Estuary beluga* (Delphinapterus leucas) *population parameters based on photo-identification surveys, 1989–2012* (Research Document 2013/130). Canadian Science Advisory Secretariat, Fisheries and Oceans Canada.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H., & Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2289–2301. https://doi.org/10.1098/rstb.2010.0082

Mosnier, A., Larocque, R., Lebeuf, M., Gosselin, J. F., Dubé, S., Lapointe, V., Lesage, V., Lefaivre, D., Senneville, S., & Chion, C. (2016). *Définition et caractérisation de l'habitat du béluga* (Delphinapterus leucas) *de l'estuaire du Saint-Laurent selon une approche écosystémique* (Definition and characterisation of the St. Lawrence Estuary beluga [*Delphinapterus leucas*] habitat following an ecosystemic approach) (Research Document 2016/052). Canadian Science Advisory Secretariat, Fisheries and Oceans Canada.

Mosnier, A., Lesage, V., Gosselin, J.-F., Lemieux Lefebvre, S., Hammill, M. O., & Doniol-Valcroze, T. (2010). *Information relevant to the documentation of habitat use by St. Lawrence beluga* (Delphinapterus leucas), *and quantification of habitat quality* (Research Document 2009/098). Canadian Science Advisory Secretariat, Fisheries and Oceans Canada.

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K., & Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLoS ONE*, *13*(3), e0194201. https://doi.org/10.1371/journal.pone.0194201

Ouellet, J.-F., Michaud, R., Moisan, M., & Lesage, V. (2021). Estimating the proportion of a beluga population using specific areas from connectivity patterns and abundance indices. *Ecosphere*, *12*(6), e03560. https://doi.org/10.1002/ecs2.3560

Pace, R. M., III, Corkeron, P. J., & Kraus, S. D. (2017). State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecology and Evolution*, *7*(21), 8730–8741. https://doi.org/10.1002/ece3.3406

Pradel, R., Hines, J. E., Lebreton, J.-D., & Nichols, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics*, *53*(1), 60–72. https://doi.org/10.2307/2533097

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*(3), 321–338. https://doi.org/10.1111/oik.07202

Turgeon, S. (2019). *Portrait de la navigation dans le parc marin du Saguenay-Saint-Laurent, 2017* (Portrait of navigation in the Saguenay-Saint-Laurent marine park, 2017). *Parc marin du* Saguenay-Saint-Laurent.

Vergara, V., Wood, J., Lesage, V., Ames, A., Mikus, M.-A., & Michaud, R. (2021). Can you hear me? Impacts of underwater noise on communication space of adult, sub-adult and calf contact calls of endangered St. Lawrence belugas (*Delphinapterus leucas*). *Polar Research*, *40*(S1). https://doi.org/10.33265/polar.v40.5521

Williams, J. A., Dawson, S. M., & Slooten, E. (1993). The abundance and distribution of bottlenosed dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Canadian Journal of Zoology*, *71*(10), 2080–2088. https://doi.org/10.1139/z93-293

Williams, R., Hedley, S. L., & Hammond, P. S. (2006). Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. *Ecology and Society*, *11*(1). https://doi.org/10.5751/ES-01534-110101

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*(1), 164–168. https://doi.org/10.2307/1938423

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Bonnell, T. R., Michaud, R., Dupuch, A., Lesage, V., & Chion, C. (2024). Estimating spatial mixing within the St. Lawrence Estuary beluga population by comparing local individual diversity and abundance. *Marine Mammal Science*, e13162. https://doi.org/10.1111/mms.13162