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St. Lawrence Estuary beluga (*Delphinapterus leucas*) population parameters based on photo-identification surveys, 1989-2012

Robert Michaud

Groupe de recherche et d'éducation sur les mammifères marins (GREMM)
108, de la Cale-Sèche
Tadoussac, Québec G0T 2A0

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Between June and October of 1989-2012, small-boat photo-identification surveys (PID) were conducted throughout the St. Lawrence Estuary beluga's summer range. A total of 1 476 PID surveys were completed for a total of 2 754 encounters, an average of 62 (± 17 SD) surveys and 115 (± 32 SD) encounters per year. Of these encounters, 1 702 and 1 285 where retained to estimate the proportion of grey individuals (in %), so called "greys" (as an index of younger individuals), and calves. Calf production indices varied between 1.2% and 4.2% (coefficients of variation: 16.6% - 35.0%) with marked year-to-year variations following 2 to 3-year cycles, with a pause of 5 years, between 1999 and 2004, when calf production remained low. The proportion of greys varied between 22.6% and 39.6% (coefficients of variation: 10.3% - 18.1%) with a slight but significant increase over the study period ($R^2 = 0.20$, $p < .05$) and a recent transition to a negative trend in the mid- to late 2000s. This transition followed the 1999-2004 period of low calf production, suggesting the low calf production in the early 2000's resulted in low juvenile recruitment in the following years. Both time series presented here provide useful independent data set to test predictions from an aged-structured Bayesian population model and explore both short-term and long-term population level reactions to environmental changes.

Paramètres de la population de béluga du Saint-Laurent (*Delphinapterus leucas*) basés sur les relevés de photo-identification, 1989-2012

RÉSUMÉ

Entre juin et octobre 1989 à 2012, des recensements par photo-identification ont été effectués à bord de petites embarcations sur l'ensemble de l'aire de répartition estivale des bélugas de l'estuaire du Saint-Laurent. Au total, 1 476 recensements ont été complétés pour un ensemble de 2 754 contacts, soit en moyenne 62 (écart-type de ± 17) recensements et 115 (écart-type de ± 32) contacts par année. Parmi ceux-ci, respectivement 1 702 et 1 285 contacts ont été utilisés pour estimer la proportion d'individus gris (qui sert d'indice des jeunes individus) et de nouveaux-nés. La proportion de nouveaux-nés (en %) variait d'une année à l'autre entre 1,2 % et 4,2 % avec des coefficients de variation entre 16,6 % et 35,0 %. Les variations interannuelles marquées révèlent une succession de cycles d'une durée de 2 à 3 ans et une période prolongée de faible production entre 1999 et 2004. La proportion de gris a varié annuellement entre 22,6 % et 39,6 % avec des coefficients de variation de 10,3 % à 18,1 %. La série temporelle recueillie suggère une augmentation progressive de la proportion de gris dans la population au cours de la période d'étude ($R^2 = .20$, $p < .05$) suivie d'une transition vers une tendance négative entre le milieu et la fin des années 2000. Cette transition qui survient quelques années après la réduction marquée dans la production de nouveaux-nés (1999-2004) suggère que celle-ci a entrainé une baisse du recrutement des juvéniles dans la population. Les deux séries temporelles présentées ici offrent des données indépendantes précieuses pour valider les prédictions d'un modèle Bayesien de la structure de la population, et permet d'explorer des relations à différentes échelles temporelles entre la population des bélugas et son environnement.

INTRODUCTION

St. Lawrence Estuary (SLE) belugas live at the southernmost limit of the species' range. The SLE population is considered isolated from the nearest northern populations (Reeves and Katona 1980, Michaud et al. 1990, de March et al. 2002). Listed as an *Endangered* population under COSEWIC in 1983 and 1997 (Pippard 1983, Lesage and Kingsley 1997), the status of the SLE population has been re-examined and was downlisted to *Threatened* in 2004 (COSEWIC 2004). The SLE population, estimated to around 1100 individuals, has not shown any sign of increase since it was protected in 1979 (Gosselin et al. 2001, Michaud and Béland 2001, Hammill et al. 2007). Recent apparent increases in newborn and near-term female mortality raised concerns regarding current and future population trajectories.

In the fall of 2012, DFO (V. Lesage, Mont-Joli) convened a working group to discuss various hypotheses to explain the recent changes in the mortality pattern and invited participants to review existing long-term datasets. The objective was to look for trends or abnormalities that could help explain recent observations.

In this paper we explore a long-term dataset from a series of photo-identification (PID) surveys (1989-2012) to detect changes in the population structure, namely: 1) the proportion of grey individuals, also referred to as "greys", (as an index of younger individuals) and 2) calf production. These two parameters were intended to provide information or external validation for the modelling of population trends and dynamics of the SLE belugas (Mosnier et al. 2014).

The PID surveys were not designed to produce these population structure parameters but to study social structure of SLE beluga. However, a series of systematic boat-transect and visual aerial surveys conducted between 1986 and 1992 and designed to assess distribution and population structure provided a framework for analysing the PID long-term dataset and a baseline against which the population structure estimates derived from the PID dataset could be compared. Methods used in the combined systematic boat-transect and visual aerial surveys were published as a technical report in the Canadian fisheries and aquatic sciences series in French only (Michaud 1993). The methods used in the 1986-1992 surveys are briefly reviewed here before presenting the methods used in the 1989-2012 PID surveys, methods used to analyse the data, and results.

METHODS

COMBINED SYSTEMATIC BOAT-TRANSECT AND VISUAL AERIAL SURVEYS (1986-1992)

Summer distribution pattern and survey design

Belugas are highly gregarious and exhibit a fission-fussion grouping pattern with aggregation size varying from two to a few hundred individuals. In the summer they are distributed over a 200-km long portion of the SLE and display a clear segregation between herds of adults found downstream and herds of adults and young found upstream (Michaud 1993; Figure 1). Due to this heterogeneous spatial distribution, a stratified sampling strategy was adopted to estimate the proportion of grey individuals in the population. The study area was divided into three strata corresponding to segments of comparable length along the main axis of the Estuary (Figure 2). Despite the recurrent presence of belugas in the Saguenay River, reaching almost 50% of the days during the summer (Michaud et al. 1990), the average number of whales observed in the Saguenay River represents only 5% of the total population (Michaud 1993). This portion of the summer range was not included in the systematic surveys conducted between 1986 and 1992 (Figures 3 and 4).

Two separate sampling methods were used to estimate the proportion of grey individuals. Visual aerial (VA) surveys were chosen to estimate the proportion of the population found in each stratum of the study area. These surveys can cover the entire summer range in less than four hours and provide very detailed counts for each observation. However, the ability of observers to distinguish white from grey individuals during aerial observations varies considerably depending on the detection angle and turbidity (Hay and McClung 1976, Burns and Seaman 1985, Sergeant 1986). Aerial surveys are therefore of little use to evaluate the composition of the population based on the colour phases. For the evaluation of herd composition, we conducted systematic boat-transect (SBT) surveys. The details of the protocols used for these two survey designs are presented in the following sections.

Visual aerial (VA) surveys

The study area was divided into 23 parallel transverse lines separated by a distance of 7.4 km (Figure 3). Two equivalent portions of the study area were covered simultaneously by two planes (Islander type) at an altitude of 925 meters and a speed of 130 km/h. Surveys were made when weather conditions and forecasts were considered to be ideal (visibility of 11 km and more, cloud ceiling over 1000 m and surface winds of less than 30 km/h). Navigation during aerial survey was performed using a Loran-C or GPS. Two experienced observers were stationed in each plane, one in the front, to the right of the pilot and the other in the back seat on the left side. Each observer was in charge of recording observations on one side of the plane.

Each herd spotted was surveyed in closing mode to allow observers obtain more detailed accounts. After circling the spotted herd once or twice, the aircraft returned to the location where the transect had been interrupted. Group size, swimming direction, time and location of the observations were recorded by each observer.

Systematic boat-transect (SBT) surveys

The boat-transect sampling grid covered the entire summer range divided into three strata (Figure 4). Each stratum was divided into four zones, in which two or three parallel lines were drawn parallel to the main axis of the Estuary. These lines were 27.8 km long and spaced 3.2 to 4.6 km apart, with a smaller distance between the lines in the downstream data. The increased effort in the downstream strata aimed at maximizing the accuracy of the estimation in this area where greater variability in herd composition and size had previously been documented (Michaud et al. 1990). The allocation of the sampling effort between the three strata thus followed a 2 : 2 : 3 distribution for the upstream, central and downstream strata, respectively. The sampling effort within each stratum was evenly distributed between the zones. Each zone was further divided into two or three lines (figure 4). The choice of line within a given zone was determined by a random draw.

Surveys were conducted from two Boston Whalers (7 and 8 m), each equipped with an observation platform, one 1 m and the other 2 m above sea level. A Loran-C (Micrologic Commander) or GPS (Magellan NAV 1000) were used to aid in navigation. One observer located at the bow of each vessel searched for belugas with and without the aid of binoculars (8X35 and 10X50) over a 180 ° field of view. Vessel speed was 25 km/h and was reduced to 15 km/h when belugas were seen within 1000 m from the vessel and to 10 to 15 km/h when observed within 500 m from it. When belugas were spotted 500 m beyond the transect line, the boat could depart up to 2000 m from the original transect line, with an angle of 60 °. The boat followed a line parallel to the original transect line to encounter the spotted whales. One such deviation was allowed for each observation of individual whales or herd. In this study, herds are defined as a spatio-temporally distinct assemblage of groups, and groups are defined as a set of animals swimming side by side in a coordinated fashion with at a maximum of one body length between each animal. The course was maintained until the end of the count. Once the boat was 1000 m away from the herd, the course was corrected to return to the original transect line and the initial speed was restored. For each observation, the detection angle, distance, the swimming direction and the size and composition of each group were recorded.

Partly following Caron and Smith (1990), size, colouration and behavioural cues were used to classify individuals into six categories. *Neonates*, also referred to as calves, were recognized as such when at least three of the following characteristics could be observed: small size (between 1/3 and 1/2 of the length of accompanying adult), swimming very close to the presumed mother, presence of fetal folds, wrinkled fluke, chin up at each surface and dark circle around the eye. Yearlings, or *bleuvets* as they are called in the St. Lawrence River (Vladykov 1944), stay very close to their presumed mother, are often chin-up when breaking the surface, and measure between 1/2 and 2/3 the length of the accompanying adult. *Bleuvets* are much bulkier than calves, of darker colour, and often marbled. *Juveniles*, also referred to as “greys”, measure from 2/3 up to almost the length of adult females (Heide-Jørgensen and Teilmann 1994; Sergeant 1973) and associate loosely with adults. They gradually turn from grey to white with increasing age and size (Brodie 1971; Burns and Seaman 1985; Heide-Jørgensen and Lockyer 2001; Kleinenberg *et al.* 1964; Ognetev 1981; Sergeant 1973). The juveniles were divided into two categories of greys: *small greys* if they were clearly smaller and darker than nearby white animals (> 2/3 to < ¾ the length) or *large greys* if they were larger and paler. The remaining individuals of adult size were categorized as *pure white* or *off-white* if they had remaining shades of grey. This classification is however only possible during close approaches for photo-identification. Along transects, only three age classes were used: white (including off-white), grey (juveniles and bleuvets) and calf.

In a first series of surveys conducted by boat in 1986, Michaud (1990) showed that the ability of observers to distinguish white from grey animals decreased significantly beyond 400 m. To ensure consistency in the detection of whites and greys, only observations within bands of 400 m on either side of the transect line were retained.

In order to retain observations made on a transect line, weather had to be acceptable during the whole time a transect was surveyed. Acceptable conditions were: wind < 15 kn (30 km/h) or wave height < 30 cm, and > 2 km visibility. The direction of a transect was chosen as to minimize the effect of glare. In the absence of cloud cover, transects were generally surveyed upstream in the morning and downstream in the afternoon. The presence of glare on one side or the other of the transect line did not affect the selection of transects.

In 1992, two vessels were used simulateously to complete the survey. A series of transects was carried out with the two observers on the same boat to compare their counts and their ability to distinguish white from grey belugas. Over these 10 transects, the two observers counted 329 and 337 individuals respectively with 31.0 and 27.9% of grey. No significant difference was detected between observers in the total number of individuals (paired t-test, df = 9, t = 0.82, p > 0.40) or number of grey individuals (df = 9, t = 0, 82, p > 0.40). Consistency in the classification of colour suggests that despite the inherent subjectivity of such judgements, the simple categories used in the survey ensure the reliability of these assessments. The data sets collected by the two vessels were grouped into a single database for analysis.

Estimating the proportions of greys and calves

The proportions of greys (G_{pop}) and calves (C_{pop}) in the population (*pop*) estimated from aerial surveys were calculated by weighting each stratum estimate (G_s *or* C_s) by the proportion of the population found in that stratum (W_s), where a stratum (*s*) can be the upstream (*up*), Center (*ct*) or downstream (*dn*) portion of the Estuary:

$$G_{pop} = G_{up}W_{up} + G_{ct}W_{ct} + G_{dn}W_{dn}$$

$$C_{pop} = C_{up}W_{up} + C_{ct}W_{ct} + C_{dn}W_{dn}$$

Where G_s *and* C_s represent the proportions of greys and calves in a given stratum, which were estimated as the ratio of the average number of greys (g_s) or calves counted in that stratum (c_s) over the average number of whales (whites, greys and calves) counted in the same stratum (x_s).

$$G_s = \frac{\overline{g_s}}{\overline{x_s}} \quad \text{and} \quad C_s = \frac{\overline{c_s}}{\overline{x_s}}$$

The proportion of whales found in each stratum (W_s) was in turn estimated by the ratio of the average number of whales in a given stratum ($\bar{x}_s$) over the average number of whales counted in the entire survey area ($\bar{x}$).

$$W_s = \frac{\overline{x_s}}{\bar{x}}$$

The variances of G_{pop} and C_{pop} were estimated using the following formula:

$$VarG_{pop} = Var\left(G_{up}W_{up}\right) + Var(G_{ct}W_{ct}) + Var(G_{dn}W_{dn})$$

and

$$VarC_{pop} = Var\left(C_{up}W_{up}\right) + Var(C_{ct}W_{ct}) + Var(C_{dn}W_{dn})$$

where

$$Var(G_sW_s) = G_s^2 VarW_s + VarG_s W_s^2 + VarG_s VarW_s$$

and

$$Var(C_sW_s) = C_s^2 VarW_s + VarC_s W_s^2 + VarC_s VarW_s$$

and

$$VarG_s = \frac{\sum g^2 - 2\left(\frac{\bar{g}}{\bar{x}}\right)\sum xg + \left(\frac{\bar{g}}{\bar{x}}\right)^2 \sum x^2}{(\sum x)^2(n-1)(n)}$$

$$VarC_s = \frac{\sum c^2 - 2\left(\frac{\bar{c}}{\bar{x}}\right)\sum xc + \left(\frac{\bar{c}}{\bar{x}}\right)^2 \sum x^2}{(\sum x)^2(n-1)(n)}$$

$$VarW_s = \frac{\sum w^2 - 2\left(\frac{\bar{w}}{\bar{x}}\right)\sum xw + \left(\frac{\bar{w}}{\bar{x}}\right)^2 \sum x^2}{(\sum x)^2(n-1)(n)}$$

PHOTO-IDENTIFICATION (PID) SURVEYS (1989-2012)

Between June and October of 1989-2012, small-boat surveys were conducted throughout the beluga summer range (Figure 1). Surveys were neither random nor systematic but covered various sectors of a large portion of the population's summer distribution and a broad range of habitats The PID surveys included the lower stretches of the Saguenay River (which were not included in the previous surveys). Prior to 1995, the study area encompassed the full extent of the summer distribution (ca. 2790 km^2). From 1995 to 2012, the study area was limited to the central and downstream portions of the summer distribution, as required by a concurrent study (carried out from the same boat) investigating social networking of specific sex- and age-classes.

One or two observers conducted surveys aboard a 8 m vessel, from a platform located 2 m above sea level. When a herd was encountered, the survey was interrupted and the boat remained at a distance of 300-500 m for 15 minutes before initiating a herd-follow (*sensu* group-follow in Mann 1999) by approaching the herd, hereafter called *encounter*. An encounter, which is treated as the sampling unit of a herd, ended when the observers were confident that every group within the herd had been approached and photographed, after an arbitrary limit of 3 hours, or for weather, light or fuel considerations.

During the first 15 min, preliminary information was collected on herd composition and size while maintaining a distance of 300-500 m from the herd. Herd characteristics were then described every 30 min. These summary descriptions (SD) included the herd position, geometry and spatial extent, an estimation of the herd size and composition, the predominant movement pattern and direction of movement, presence / absence of specific behaviours and a detailed description of the composition of as many groups as possible within in the herd. Of the 6 age classes described above, only 4 were used in the SD: white, grey (juvenile), *bleuvet* and calf. (Note that in this survey *bleuvets* and juveniles were not grouped together). The position of the research vessel and prevailing weather conditions were also recorded.

A total of four observers including the first author conducted the PID surveys and performed the SD over the 24 years of study. In order to maximize consistency in data collection, all observers worked at least one season with the first author prior to being responsible for the collection of data.

Estimating the proportions of grey and calves

Detailed descriptions (DD) of groups recorded during SDs were used to calculate the proportion of greys and calves in a herd. Only one DD, including at least 30% of the estimated total number of individuals in a herd, was retained per encounter. Whenever more than one DD matched that criteria, the DD including the highest number of individuals relative to the estimated herd size was retained.

The proportions of greys (G_{pop}) and calves (C_{pop}) in the population were calculated for each year (1989-2012) following the approach described above for the boat-transect survey. For strata where less than 5 encounters were completed during a given sampling year, the overall average (1989-2012) for the specific strata was used to calculate the annual G_{pop} and C_{pop}. The proportion of the population found in each stratum W_s was calculated with annual density estimates obtained from the 1990-2009 photographic and VA surveys conducted by the Mont-Joli DFO team (Gosselin et al. 2014). The density estimates did not include the Saguenay River. The weight of each stratum was therefore adjusted using the proportion of whales found in the Saguenay River calculated from the 1988-1992 VA surveys. For the estimation of calf production, only encounters after the median date of the first annual sighting of a live calf (July 12th) were retained.

The trend in the proportion of calves and greys over the study period was analysed in two ways. First, a linear regression model was applied to the percentage of calves and greys observed during PID surveys. Second, to investigate the possibility that there have been recent changes in the age structure of SLE beluga, a piecewise regression model with one breakpoint (which could vary from 1990 to 2011) was fitted to the data. The breakpoint was estimated following Hinkley (1969), using the method implemented in NLIN proc in SAS (SAS 2011). Model selection based on Akaike Information Criterion (AIC) was used to determine whether piecewise regression models had more statistical support than the linear model (Burnham and Anderson 2002).

RESULTS

PHOTO-IDENTIFICATION SURVEYS

A total of 1 476 PID surveys were conducted between 1989 and 2012 for a total of 2 754 encounters, an average of 61.5 (± 16.8 SD) surveys per year (Table 1). Of these encounters, 1 702 and 1 285 were retained to estimate the proportion of greys and calves. An example of the spatial coverage of the surveys and encounters for year 2010 is presented in Figure 5.

PROPORTIONS OF THE POPULATION FOUND IN EACH STRATUM

The proportion of the population found in each stratum for the five years in which multiple visual aerial surveys (VAS) were conducted, in 1989 and 1992 (Michaud 1993) and in 2003, 2005 and 2009 (Gosselin et al. 2014) are presented in Figure 6. Values calculated from these independent series of surveys showed little variation, suggesting whale distribution among the different strata were relatively stable over the study period. Weighted proportions calculated on the complete 1990 – 2009 series of photographic and visual surveys were therefore used to estimate W_s (Table 2).

PROPORTIONS OF CALVES

No estimates of the proportion of calves could be derived from the 1992 PID survey and compared to the 1992 SBT survey estimates. The proportion of calves estimated from the 1992 SBT surveys is inserted as a distinct data point in the 1989-2012 PID survey series in Figure 7. Overall proportions of calves estimated form the PID surveys varied between 1.2% and 4.2% with coefficients of variation ranging between 16.6% and 35.0%. Means and standard errors for each individual stratum are presented in Table A1a and b of Annex 1.

Calf production indices showed marked year-to-year variations with 2 to 3-year cycles and a pause of 5 years, between 1999 and 2004, when calf production stayed low. Regression models were not applied to this time series.

PROPORTIONS OF GREYS

Proportions of greys and coefficients of variation estimated from the 1992 PID surveys closely follow the 1992 SBT survey estimates. Overall proportions of greys (in %) estimated from the PID surveys varied between 22.6% and 39.6% with coefficients of variation ranging between 10.3% and 18.1% (Figure 8). Means and standard errors for each individual stratum from both the 1989-2012 PID surveys and the 1992 SBT surveys are presented in Table A2a and b of Annex 1.

Linear regression of the entire time series suggested an increasing trend in the proportion of greys ($p < 0.05$). However, this trend explained little of the overall variance ($R^2 = 0.20$), due to high inter-annual variability.

The piecewise regression model identified a transition point in 2010 ($p = 0.05$), with an increase in the proportion of greys before that date, followed by a steeper decline. However, the model explained only 32% of the variance (Pseudo-R), and the 95% coefficient interval for this breakpoint extended from 2006 to 2014 (i.e., included dates beyond the end of the time series). Moreover, model selection based on AIC showed that six other models, including the unbroken linear model, received substantial support (delta-$AIC_c < 2$, Table 3). All these models had a breakpoint after 2005.

Because of the wide uncertainty surrounding the estimate of the breakpoint, as well as the difficulty to distinguish between piecewise models with breakpoints from 2006 to 2011 and the linear model, we decided to use model-averaging (Mazerolle 2006). To represent the trajectory of the proportion of greys, we weighted the proportions predicted by each model and their 95% confidence interval by their Akaike weights (Figure 8).

DISCUSSION

Several features of the beluga distribution patterns, mainly their gregariousness and fission-fusion dynamics as well as their tendency to segregate by age and sex classes, are challenges to surveying populations of this species. The stratified sampling strategy adopted for the 1992 SBT surveys was designed to control at least part of the variability introduced by these characteristics of the beluga's behaviour. Results presented here strongly support the initial observations of the presence of a clear segregation pattern (Michaud 1993) on which the survey design was developed.

The similarity of the estimates of proportions of greys obtained from the SBT and PID surveys in 1992 suggests that applying the same strategy to explore the long-term PID survey dataset provides useful indices for the beluga population parameters. Coefficients of variation calculated on these estimates (range: 10.3% – 18.1%) are comparable to those reported for photographic and visual surveys of the same population (Gosselin et al. 2007). Unfortunately most of the 1992 PID surveys were conducted before the onset of the calving season and were therefore not available for a comparison with the same year SBT calf production index. Values obtained from 1992 SBT however fall into the range of those derived from the PID surveys.

Variance estimates calculated for both indices did not include perception errors. Prior tests on the effect of distance on the detection of grey and white individuals as well as between observers showed a high consistency in the classification of colour, suggesting that despite the inherent subjectivity of such judgements, simple categories used here ensured the reliability of these assessments. No test were however done on the detection of calf, which, because of their smaller size and tendency to swim next to their mothers, could be more variable. This is possibly partly reflected in the larger coefficients of variation associated to the calf production indices (range 16.5% – 35.0%).

Small sample size in some strata and exclusion of the upstream stratum beyond 1994 constitute an important limitation of the PID survey dataset to estimate overall population parameters. Estimates for the upstream stratum were available for only 6 of the 24-year data series. 67% and 79% of annual surveys yielded 10 or more encounters suitable for the estimation of the proportions of greys in the downstream and Saguenay strata. The coverage for the central stratum was much better, with a minimum of 15 encounters completed each year and an average of 37 encounters ± 13. For the estimation of the proportions of calves, surveys selected had to be conducted after the median date of the first annual sighting of a live calf (July 12th), which further reduced the number of surveys available for the estimations. Only 63% of the annual surveys yielded 10 or more encounters suitable for the estimation of the proportions of calves in the downstream and Saguenay strata. The coverage for the central stratum was also much better with only one year missing: 1992. For all other years, the minimum number of encounters completed was 14 and the average was 26 encounters ± 10.

We examined the level of correlation between strata estimates for those years with extended coverage to investigate the possibility of using a data imputation approach to fill in missing data in order to compute overall estimates. These levels were too low to adopt such an approach. The choice to replace missing values and very small samples (< 5) by stratum means artificially reduced variance estimates and the value of these estimates as actual population parameters. It however allowed to calculate overall means to look for trends in the selected parameters.

The time series of calf production indices revealed important year-to-year variations with marked cycles. Prior to 1993, it is difficult to comment on cycles because of the missing 1992 value. After 1993, calf production followed 2 to 3-year cycles, with a pause of 5 years, between 1999 and 2004, when calf production stayed low. The beluga reproductive cycle is considered to extend on a 3-year schedule with a 14-month gestation followed by a 12 to 18-month lactation period (Brodie 1971, Sergeant 1973, Burns and Seaman 1985). The presence of cycles in calf production indices could result from a convergence in females reproductive cycles in reaction to adverse environmental conditions. Any large scale reproductive failure in the population for a given year would result in a larger proportion of females becoming available for reproduction the following year, producing a larger number of calves two years later. The examination of these cycles and their amplitude could therefore be an indication of population level effects of environmental changes. In the 1989-2012 time series, the lows of 1999-2004 followed by a step increase in 2005 may be indicative of an important change in the beluga whale environment.

Despite high variances associated with annual indices of the proportions of greys, the analysis indicated a progressive change in the population age structure with a significant increase in the proportions of greys over the study period. The application of piecewise regression models however suggested a transition to a negative trend near the end of the study period. The model selection approach could not clearly choose between the broken and unbroken models applied to explore the changes in the population structure. Because the apparent transition in the proportions of greys occurred near the end of the study period (95% CI 2006-2014), the model-averaging seems to best capture the recent evolution of the population structure. Continued monitoring using the photo-identification surveys to derive population parameter indices will however be needed to confirm this downward trend.

The possible transition between increasing proportions of greys in the population to a negative trend follows the 1999-2004 period of low calf production measured from the same data set. This suggests the low calf production in the early 2000's resulted in low juvenile recruitment in the following years.

In order to use the proportions of grey as a formal index in population modelling, a reliable estimate of age associated with the color change in belugas will be needed. Whereas the change in the colouration from grey to white is not associated with physical or sexual maturity in either males or females, it can be associated to a class of juveniles and young adults, a useful index to track long term changes. Colour changes have been documented from whaling data in several populations (Brodie 1971, Sergeant 1973, Ognetev 1981, Burns and Seaman 1985). These studies showed that color change occurs between 10 and 20 GLG's, between 10 and 20 years old assuming 1 GLG/year (Stewart et al. 2006, Luque et al. 2007). In this photo-identification ongoing survey programme, individual long-term tracking also supports these conclusion with transition from grey to white occuring between 12 and 24 year old (Michaud *unpublished data*).

Both time series presented here provide useful independent data set to test predictions from the aged-structured Bayesian population model built with aerial survey and stranding records (Mosnier et al. 2014) and explore both short term and long term population level reactions to environmental changes (Lebeuf et al. 2014, Ménard et al. 2014, Plourde et al. 2014) and other intrinsic characteristics of the population (Lair et al. 2014. Lesage 2014, Lesage et al. 2014).

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Table 1. Number of encounters completed per stratum during the photo-identification surveys conducted between 1989 and 2012. The number of encounters selected to estimate the proportion of greys and calves is presented in brakets.

	N encounters (selected for % greys ; % calves)				
Year	Upstream	Central	Downstream	Saguenay	Total
1989	20 *(15 ; 15)*	38 *(32 ; 14)*	18 *(12 ; 12)*	22 *(19 ; 11)*	98 *(78 ; 52)*
1990	21 *(19 ; 19)*	60 *(44 ; 33)*	43 *(25 ; 21)*	8 *(3 ; 2)*	132 *(91 ; 75)*
1991	11 *(11 ; 2)*	63 *(51 ; 38)*	54 *(36 ; 27)*	5 *(1 ; 1)*	133 *(99 ; 68)*
1992	16 *(10 ; 6)*	34 *(17 ;)*	30 *(8 ; 4)*	21 *(5 ; 3)*	101 *(40 ; 13)*
1993	19 *(16 ; 16)*	76 *(64 ; 42)*	48 *(36 ; 28)*	23 *(15 ; 9)*	166 *(131 ; 95)*
1994	15 *(13 ; 9)*	78 *(56 ; 49)*	58 *(36 ; 28)*	15 *(14 ; 13)*	166 *(119 ; 99)*
1995	0 *(;)*	69 *(29 ; 18)*	63 *(29 ; 20)*	28 *(12 ; 11)*	160 *(70 ; 49)*
1996	1 *(;)*	87 *(54 ; 30)*	30 *(15 ; 11)*	20 *(8 ; 5)*	138 *(77 ; 46)*
1997	2 *(2 ; 2)*	53 *(38 ; 34)*	29 *(24 ; 23)*	14 *(14 ; 12)*	98 *(78 ; 71)*
1998	3 *(2 ; 2)*	70 *(49 ; 29)*	18 *(11 ; 7)*	10 *(8 ; 7)*	101 *(70 ; 45)*
1999	12 *(8 ; 2)*	74 *(54 ; 46)*	10 *(8 ; 4)*	25 *(24 ; 22)*	121 *(94 ; 74)*
2000	6 *(6 ; 6)*	52 *(40 ; 26)*	7 *(4 ; 4)*	19 *(14 ; 12)*	84 *(64 ; 48)*
2001	0 *(;)*	47 *(23 ; 18)*	14 *(11 ; 10)*	16 *(10 ; 8)*	77 *(44 ; 36)*
2002	0 *(;)*	45 *(31 ; 20)*	21 *(15 ; 11)*	28 *(13 ; 12)*	94 *(59 ; 43)*
2003	0 *(;)*	47 *(34 ; 21)*	19 *(14 ; 13)*	14 *(12 ; 9)*	80 *(60 ; 43)*
2004	0 *(;)*	69 *(49 ; 37)*	16 *(6 ; 4)*	22 *(17 ; 16)*	107 *(72 ; 57)*
2005	0 *(;)*	48 *(36 ; 27)*	14 *(7 ; 6)*	31 *(26 ; 24)*	93 *(69 ; 57)*

	N encounters (selected for % greys ; % calves)				
Year	Upstream	Central	Downstream	Saguenay	Total
2006	0 *(;)*	32 *(25 ; 19)*	15 *(12 ; 10)*	18 *(18 ; 17)*	65 *(55 ; 46)*
2007	0 *(;)*	55 *(36 ; 23)*	31 *(18 ; 10)*	22 *(18 ; 17)*	108 *(72 ; 50)*
2008	3 *(2 ; 2)*	39 *(24 ; 22)*	11 *(9 ; 9)*	27 *(22 ; 20)*	80 *(57 ; 53)*
2009	0 *(;)*	35 *(26 ; 23)*	14 *(11 ; 10)*	17 *(17 ; 16)*	66 *(54 ; 49)*
2010	0 *(;)*	40 *(28 ; 23)*	10 *(6 ; 4)*	18 *(16 ; 14)*	68 *(50 ; 41)*
2011	3 *(3 ;)*	40 *(32 ; 21)*	24 *(21 ; 17)*	17 *(16 ; 6)*	84 *(72 ; 44)*
2012	0 *(;)*	21 *(15 ; 14)*	7 *(4 ; 4)*	17 *(14 ; 13)*	45 *(33 ; 31)*
Total	*132* *(107 ; 81)*	*1272* *(887 ; 627)*	*604* *(378 ; 297)*	*457* *(336 ; 280)*	*2465* *(1708;1285)*

Table 2. Proportion (in % ± SE) of the population found in each stratum W_s estimated by the weighted density estimates of observations from a series of photographic aerial surveys (N=8) and visual aerial surveys (N=28) conducted between 1990 and 2009 (Gosselin et al. 2014). An adjustment was made to account for 4.9% of the population found in the Saguenay as estimated from an independent survey series (Michaud 1993).

	Upstream	Central	Downstream	Saguenay
	% of density estimates ± SE			
1990-2012 *excluding Saguenay*	22.5 ± 2.0	39.2 ± 5.9	38.3 ± 4.6	—
1990-2012 *adjusted for Saguenay*	21.4 ± 2.0	37.3 ± 5.9	36.4 ± 4.4	4.9 ± 1.0

Table 3. Set of models with substantial support among piecewise regression models with various breakpoints (e.g., "Break=2010") and the linear regression model ("Linear"). K: number of parameters. AICc: second-order information criteria. Delta-AICc: difference with best model. W: Akaike weights.

Model	K	AIC_c	Delta-AIC_c	W
Break=2010	4	143.07	0	0.21
Break=2009	4	143.72	0.65	0.15
Break=2008	4	143.85	0.78	0.14
Break=2011	4	143.86	0.79	0.14
Linear	3	143.96	0.89	0.14
Break=2007	4	144.09	1.02	0.13
Break=2006	4	144.93	1.86	0.08

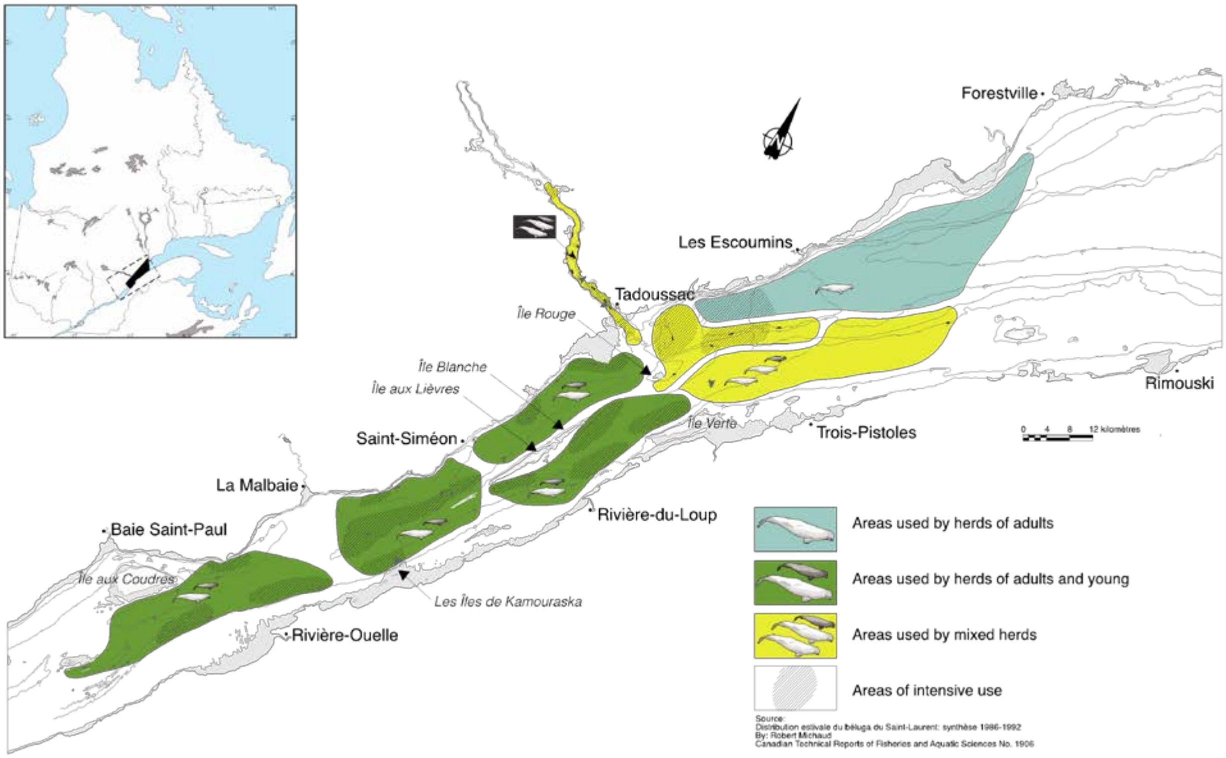

Figure 1. Summer distribution of the St. Lawrence Estuary belugas.

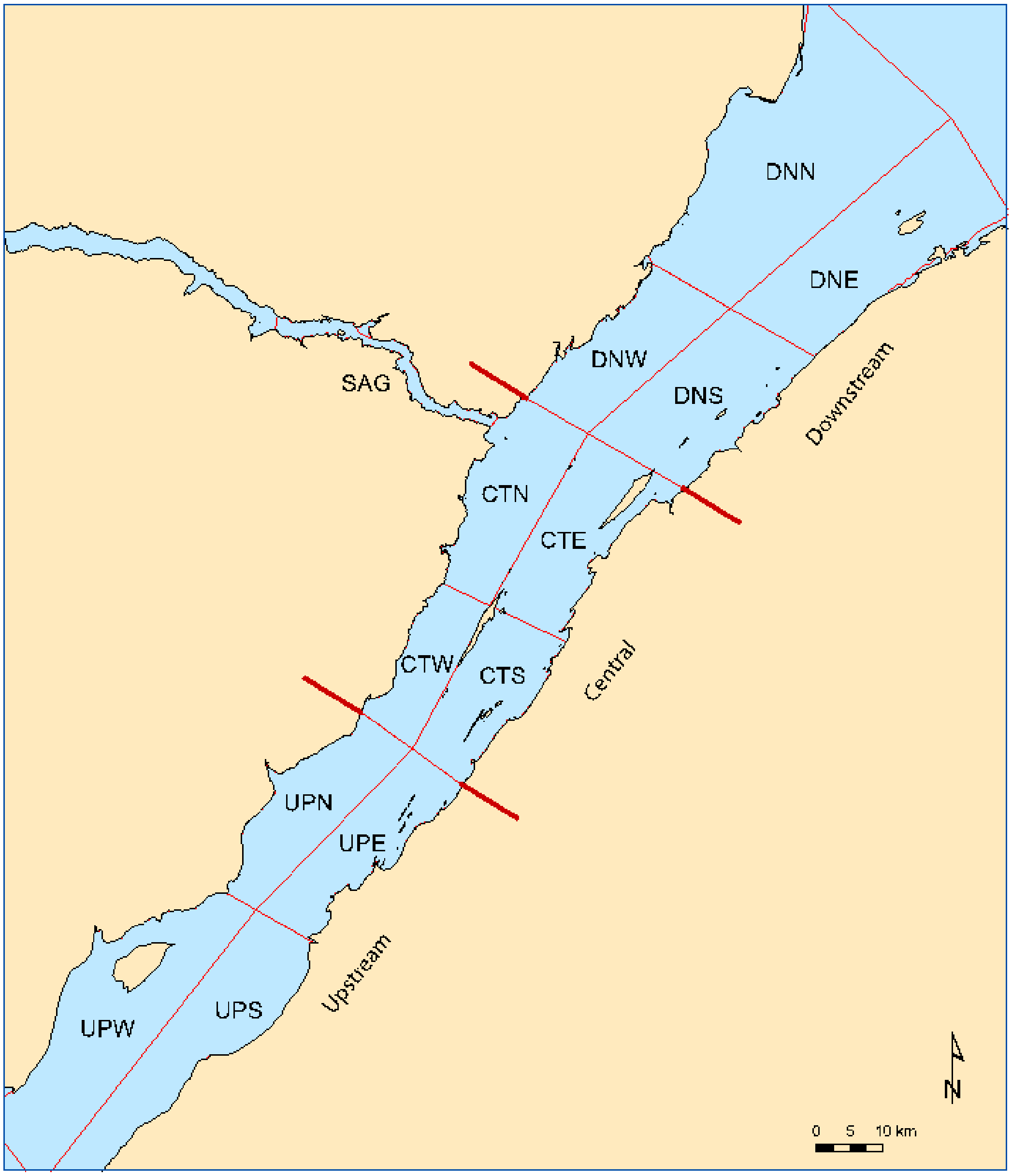

Figure 2. The study area was divided into three strata, upstream, central and downsteam, each further divided into four zones.

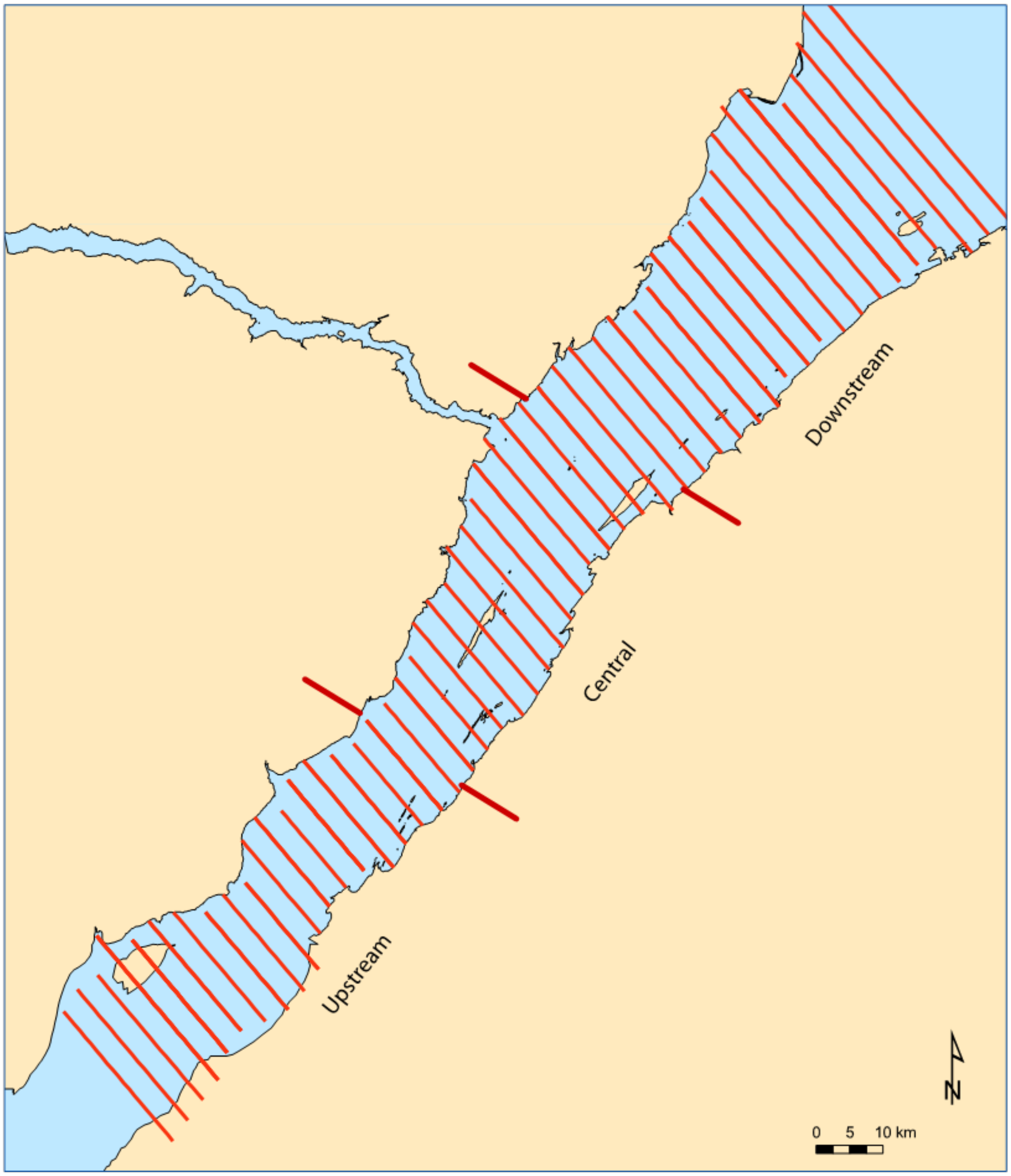

Figure 3. Visual aerial survey design.

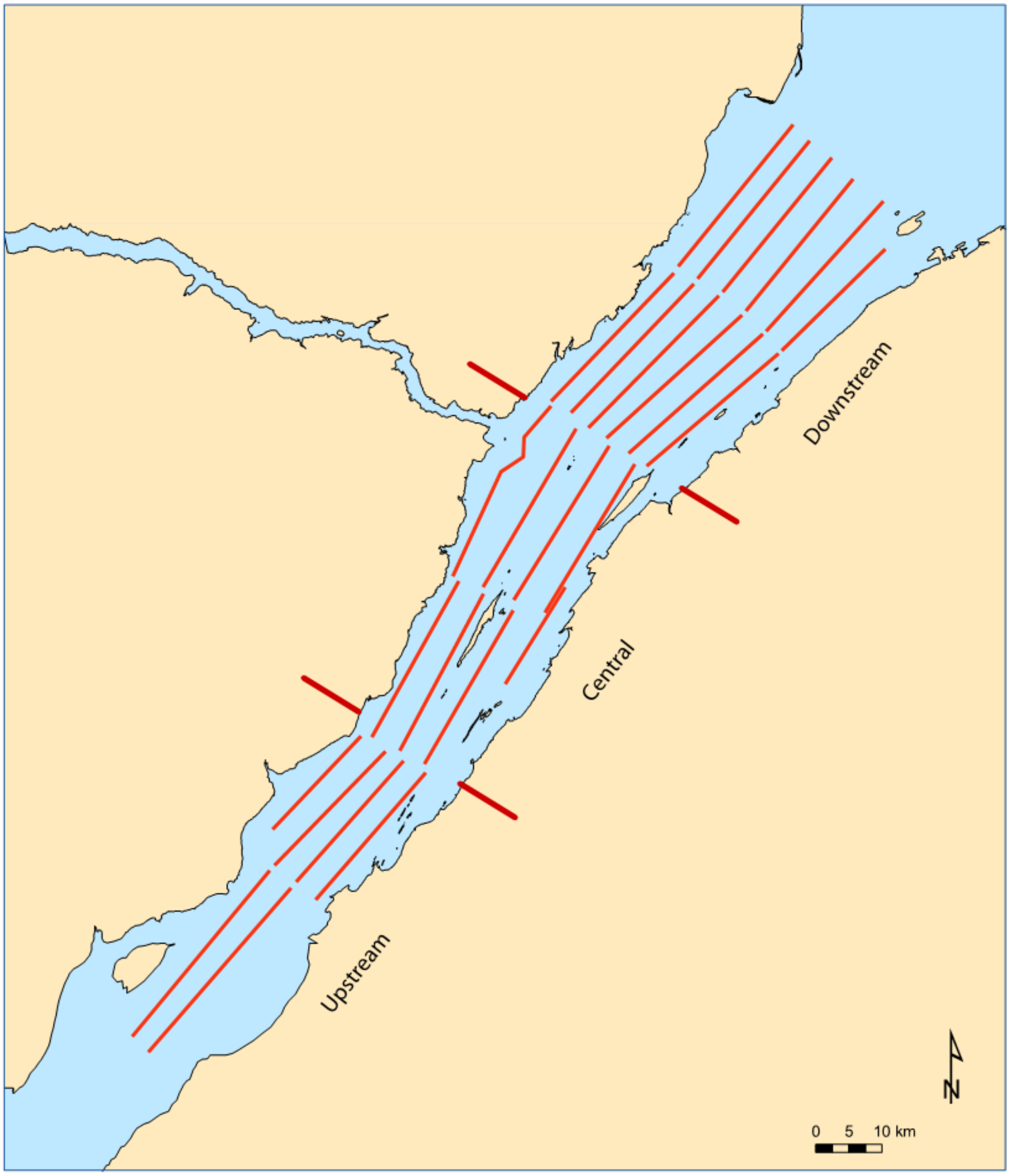

Figure 4. Systematic boat-transect survey design.

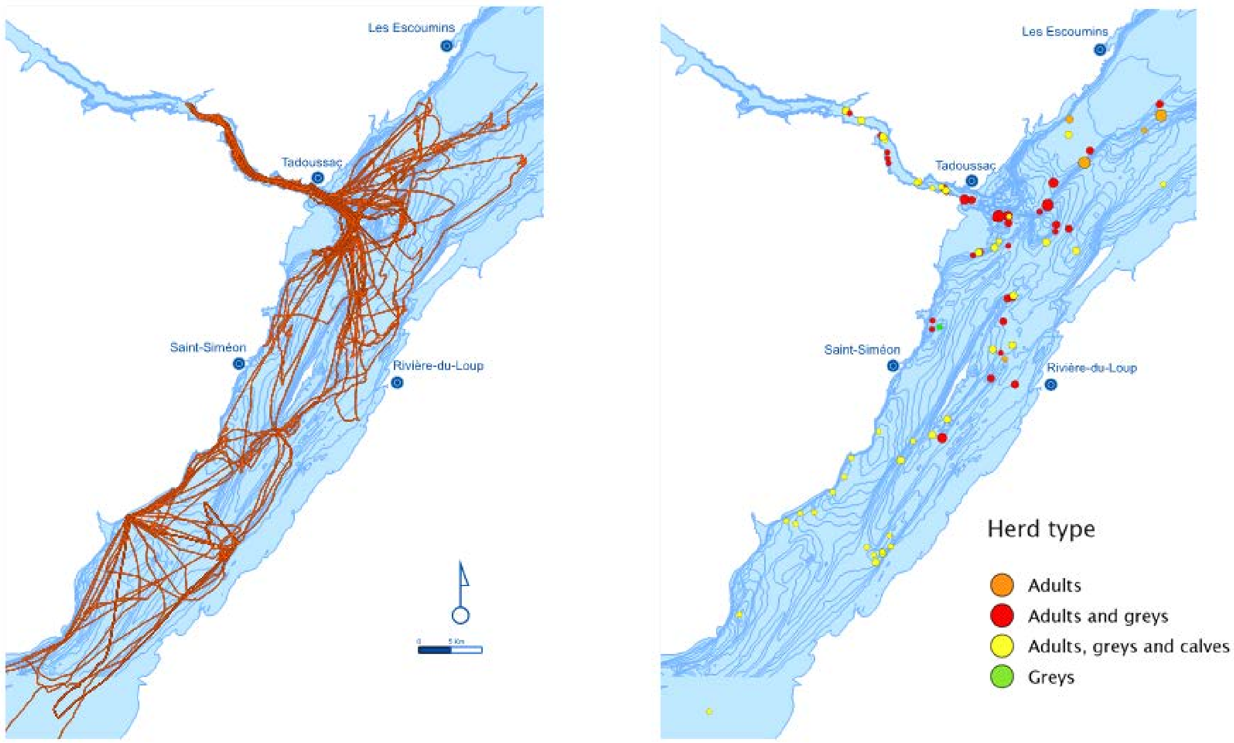

Figure 5. Total coverage of the 2010 photo-identification surveys (left) and locations of encounters (right).

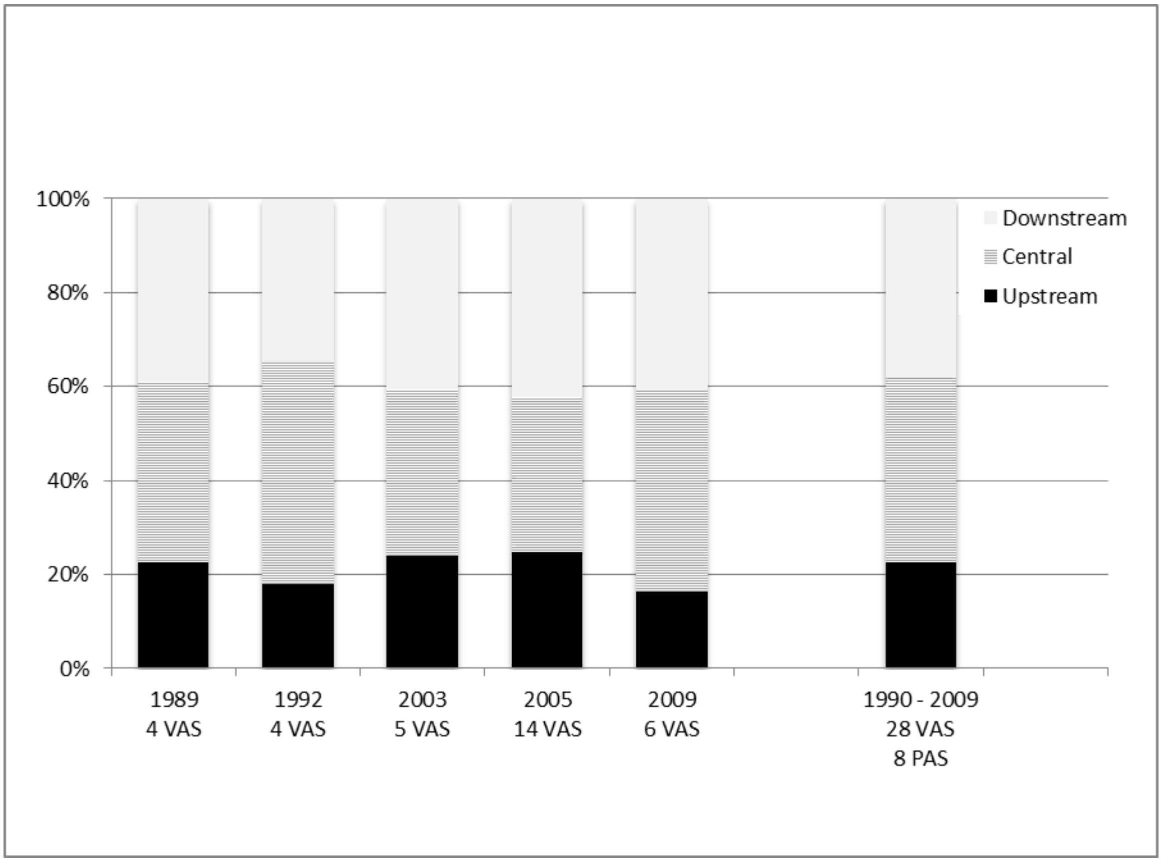

Figure 6. The percentage of the population found in each stratum W_s calculated for the 5 years for which multiple visual aerial surveys (VAS) were conducted (1989 and 1992; Michaud 1993, and 2003, 2005 and 2009; Gosselin et al. 2014), and averaged (weighted) over the complete 1990 -2009 series of VAS and photographic aerial surveys (PAS) (Gosselin et al. 2014).

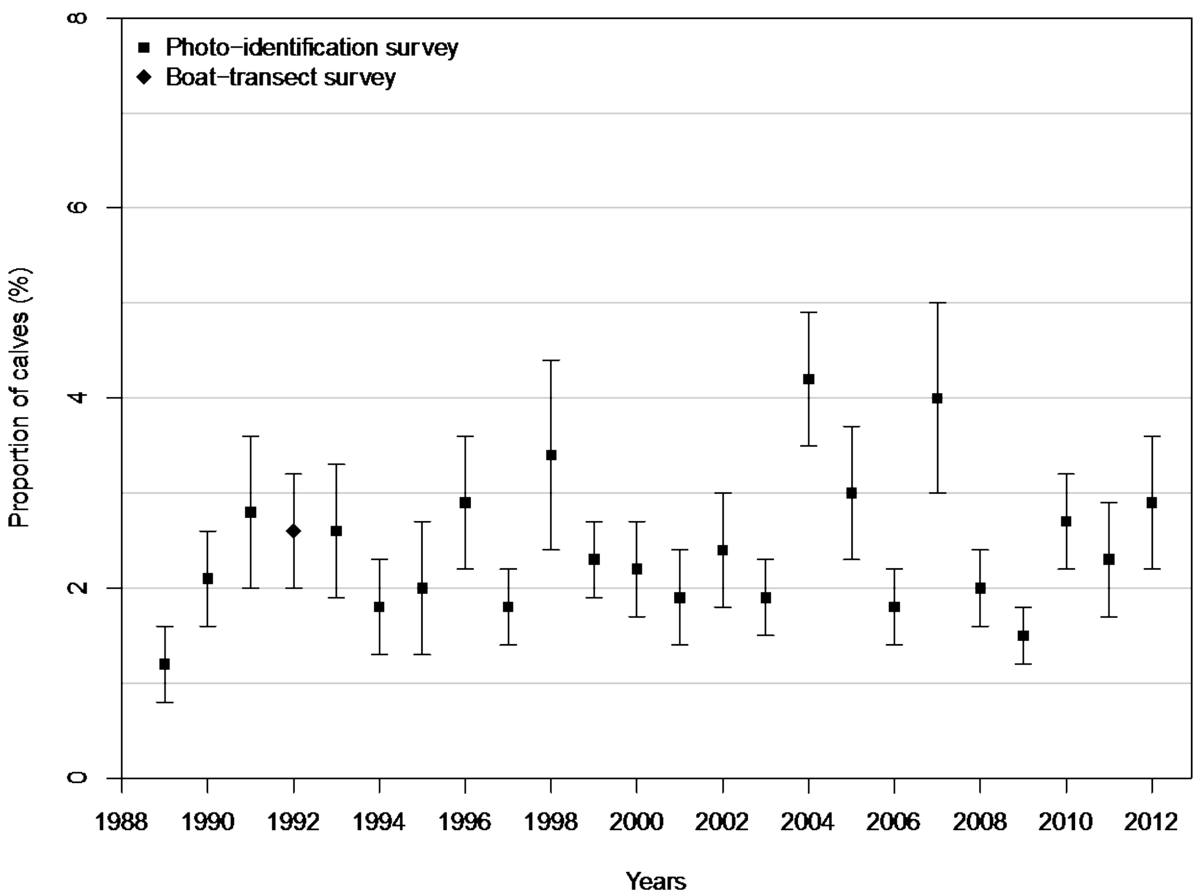

Figure 7. Annual overall proportion of calves estimated from the photo-identification surveys between 1989 and 2012. An independent data point was estimated for 1992 from the combined systematic boat-transect and visual aerial survey.

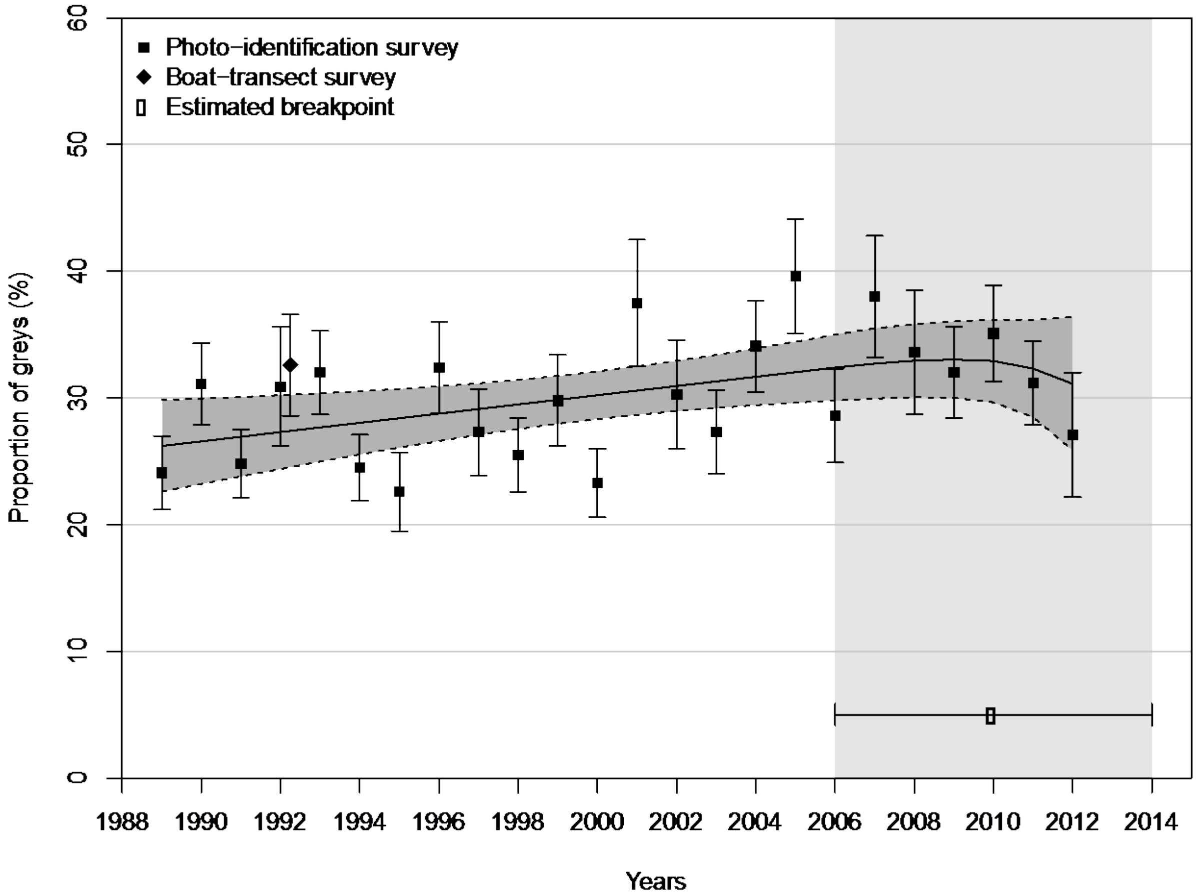

Figure 8. Annual overall proportion (in %) of greys and standard errors estimated from the photo-identification surveys between 1989 and 2012. An independent data point was estimated for 1992 from the combined systematic boat-transect and visual aerial survey. Solid line represents the model-average of the linear model and six piecewise regression models (with breakpoints between 2006 and 2011). Dashed lines represent the corresponding model-averaged 95% CI. Light grey area represents the 95% CI around the 2010 breakpoint identified by the Hinkley method.

APPENDIX

Table A1. Individual stratum and overall proportion of calves (in %) estimated from a) the photo-identification surveys between 1989 and 2012 and b) the 1992 systematic boat-transect surveys.

A1a % of calves ± SE (*N encounters; N individuals counted*)

Year	Upstream	Central	Downstream	Saguenay	Total
1989	4.3 ± 1.6 *(15 ; 232)*	0.4 ± 0.4 *(14 ; 228)*	0.3 ± 0.3 *(12 ; 304)*	0.5 ± 0.5 *(11 ; 198)*	1.2 ± 0.4 *(52 ; 962)*
1990	2.5 ± 0.9 *(19 ; 237)*	3.6 ± 1.1 *(33 ; 521)*	0.0 ± 0.0 *(21 ; 302)*	*na*	2.1 ± 0.5 *(75 ; 1109)*
1991	*na*	3.9 ± 0.9 *(38 ; 545)*	0.9 ± 0.5 *(27 ; 465)*	*na*	2.8 ± 0.8 *(69 ; 1050)*
1992	4.4 ± 2.2 *(6 ; 68)*	*na*	*na*	*na*	*na*
1993	3.2 ± 1.9 *(16 ; 158)*	3.6 ± 1.0 *(42 ; 555)*	1.1 ± 0.7 *(28 ; 370)*	4.6 ± 1.9 *(9 ; 153)*	2.6 ± 0.7 *(95 ; 1236)*
1994	3.0 ± 1.5 *(9 ; 100)*	1.2 ± 0.5 *(49 ; 806)*	1.2 ± 0.6 *(28 ; 411)*	4.7 ± 1.5 *(13 ; 190)*	1.8 ± 0.5 *(99 ; 1507)*
1995	*na*	2.9 ± 1.6 *(17 ; 279)*	0.6 ± 0.7 *(20 ; 308)*	0.0 ± 0.0 *(11 ; 123)*	2.0 ± 0.7 *(48 ; 710)*
1996	*na*	4.9 ± 1.3 *(30 ; 365)*	0.6 ± 0.6 *(11 ; 168)*	3.0 ± 3.0 *(5 ; 066)*	2.9 ± 0.7 *(46 ; 599)*
1997	*na*	2.8 ± 0.8 *(34 ; 388)*	0.0 ± 0.0 *(23 ; 201)*	0.7 ± 0.7 *(12 ; 135)*	1.8 ± 0.4 *(69 ;724)*
1998	*na*	4.4 ± 1.4 *(29 ; 294)*	2.6 ± 2.2 *(7 ; 116)*	2.1 ± 2.0 *(7 ; 095)*	3.4 ± 1.0 *(43 ; 505)*
1999	*na*	3.1 ± 0.7 *(46 ; 541)*	*na*	0.4 ± 0.4 *(22 ; 255)*	2.3 ± 0.4 *(72 ;835)*
2000	*na*	2.8 ± 1.2 *(26 ; 361)*	*na*	2.7 ± 1.4 *(12 ; 146)*	2.2 ± 0.5 *(42 ; 585)*
2001	*na*	3.2 ± 1.2 *(18 ; 189)*	0.0 ± 0.0 *(10 ; 069)*	0.0 ± 0.0 *(8 ; 082)*	1.9 ± 0.5 *(77 ; 745)*
2002	*na*	3.4 ± 1.1 *(20 ; 298)*	0.7 ± 0.7 *(11 ; 139)*	2.8 ± 1.3 *(12 ; 145)*	2.4 ± 0.6 *(43 ; 592)*
2003	*na*	1.9 ± 0.8 *(21 ; 310)*	0.6 ± 0.6 *(13 ; 163)*	4.5 ± 1.5 *(9 ; 111)*	1.9 ± 0.4 *(43 ; 584)*
2004	*na*	7.7 ± 1.5 *(37 ; 417)*	*na*	5.7 ± 1.6 *(16 ; 210)*	4.2 ± 0.7 *(57 ; 664)*
2005	*na*	3.5 ± 1.0 *(27 ; 287)*	1.7 ± 1.4 *(6 ; 060)*	6.3 ± 1.6 *(24 ; 318)*	3.0 ± 0.7 *(57 ; 665)*

A1a	% of calves ± SE (*N encounters; N individuals counted*)				
Year	Upstream	Central	Downstream	Saguenay	Total
2006	*na*	2.4 ± 0.9 *(19 ; 248)*	0.0 ± 0.0 *(10 ; 141)*	2.3 ± 1.0 *(17 ; 266)*	1.8 ± 0.4 *(46 ; 655)*
2007	*na*	7.3 ± 2.3 *(23 ; 248)*	1.2 ± 0.9 *(10 ; 167)*	3.2 ± 1.8 *(17 ; 219)*	4.0 ± 1.0 *(50 ; 634)*
2008	*na*	3.0 ± 0.8 *(22 ; 335)*	0.0 ± 0.0 *(9 ; 106)*	3.2 ± 1.2 *(20 ; 308)*	2.0 ± 0.4 *(51 ; 749)*
2009	*na*	1.5 ± 0.7 *(23 ; 396)*	0.0 ± 0.0 *(10 ; 242)*	3.4 ± 1.1 *(16 ; 297)*	1.5 ± 0.3 *(49 ; 935)*
2010	*na*	3.9 ± 1.1 *(23 ; 380)*	*na*	4.0 ± 1.5 *(14 ; 198)*	2.7 ± 0.5 *(41 ; 640)*
2011	*na*	2.7 ± 1.2 *(21 ; 258)*	0.6 ± 0.6 *(17 ; 342)*	4.3 ± 2.0 *(6 ; 093)*	2.3 ± 0.6 *(44 ; 683)*
2012	*na*	4.2 ± 1.5 *(14 ; 191)*	*na*	6.4 ± 1.4 *(13 ; 218)*	2.9 ± 0.7 *(31 ; 479)*

A1b	% of calves ± SE (*N encounters; N individuals counted*)				
Year	Upstream	Central	Downstream	Saguenay	Total
1992	5.0 ± 1.3 *(25 ; 383)*	2.9 ± 0.9 *(41 ; 763)*	0.5 ± 0.2 *(41 ; 1083)*		2.4 ± 0.6 *(107 ; 2229)*

Table A2. Individual stratum and overall proportion of greys estimated from a) the photo-identification surveys between 1989 and 2012 and b) the 1992 systematic boat-transect surveys.

A2a	% of greys ± SE (*N encounters; N individuals counted*)				
Year	Upstream	Central	Downstream	Saguenay	Total
1989	25.2 ± 1.9 *(15 ; 735)*	29.4 ± 4.4 *(32 ; 1813)*	17.9 ± 3.8 *(12 ; 658)*	25.2 ± 5.1 *(22 ; 1107)*	24.9 ± 2.9 *(81 ; 4313)*
1990	39.7 ± 2.8 *(19 ; 237)*	35.8 ± 3.2 *(44 ; 688)*	21.9 ± 5.9 *(25 ; 379)*	*na*	31.9 ± 3.2 *(91 ; 1367)*
1991	30.3 ± 5.5 *(11 ; 155)*	36.9 ± 3.0 *(51 ; 715)*	12.4 ± 2.9 *(36 ; 579)*	*na*	24.8 ± 2.7 *(100 ; 1456)*
1992	39.1 ± 5.6 *(10 ; 115)*	36.9 ± 3.7 *(17 ; 279)*	22.0 ± 11. *8(8 ; 82)*	16.1 ± 7.8 *(5 ; 87)*	30.9 ± 4.7 *(40 ; 563)*
1993	34.8 ± 3.2 *(16 ; 158)*	35.1 ± 3.3 *(64 ; 873)*	27.5 ± 6.0 *(36 ; 429)*	29.9 ± 6.7 *(15 ; 234)*	32.0 ± 3.3 *(131 ; 1694)*
1994	36.7 ± 4.3 *(13 ; 128)*	28.7 ± 3.5 *(56 ; 883)*	11.9 ± 3.4 *(36 ; 488)*	33.2 ± 4.9 *(14 ; 202)*	24.5 ± 2.6 *(119 ; 1701)*
1995	*na*	29.2 ± 5.4 *(29 ; 390)*	8.6 ± 3.3 *(29 ; 405)*	21.7 ± 6.6 *(12 ; 138)*	22.6 ± 3.1 *(111 ; 1425)*
1996	*na*	39.5 ± 3.6 *(54 ; 703)*	24.2 ± 7.4 *(15 ; 207)*	27.8 ± 8.2 *(8 ; 097)*	32.4 ± 3.6 *(118 ; 1499)*
1997	*na*	40.4 ± 4.6 *(38 ; 485)*	11.3 ± 5.2 *(24 ; 212)*	11.4 ± 4.6 *(14 ; 176)*	27.3 ± 3.4 *(117 ; 1365)*
1998	*na*	38.5 ± 3.9 *(49 ; 587)*	7.1 ± 3.2 *(11 ; 169)*	20.8 ± 9.7 *(8 ; 096)*	25.5 ± 2.9 *(109 ; 1344)*
1999	45.2 ± 4.5 *(9 ; 084)*	34.6 ± 3.8 *(54 ; 645)*	16.7 ± 7.4 *(8 ; 084)*	23.7 ± 4.0 *(24 ; 278)*	29.8 ± 3.6 *(95 ; 1091)*
2000	21.4 ± 4.4 *(6 ; 028)*	46.0 ± 3.3 *(40 ; 494)*	*na*	22.9 ± 4.0 *(14 ; 166)*	23.3 ± 2.7 *(64 ; 766)*
2001	*na*	36.2 ± 4.1 *(23 ; 268)*	40.5 ± 12.2 *(11 ; 079)*	35.0 ± 9.9 *(10 ; 117)*	37.5 ± 5.0 *(85 ; 956)*
2002	*na*	50.2 ± 7.2 *(31 ; 428)*	6.6 ± 3.9 *(15 ; 166)*	32.9 ± 5.9 *(13 ; 158)*	30.3 ± 4.3 *(100 ; 1244)*
2003	*na*	35.6 ± 3.9 *(34 ; 472)*	13.9 ± 6.5 *(14 ; 180)*	34.5 ± 6.7 *(12 ; 116)*	27.3 ± 3.3 *(101 ; 1260)*
2004	*na*	42.2 ± 2.8 *(49 ; 554)*	25.7 ± 7.5 *(6 ; 070)*	29.6 ± 5.3 *(17 ; 223)*	34.1 ± 3.6 *(113 ; 1339)*
2005	*na*	43.6 ± 5.1 *(34 ; 401)*	42.3 ± 8.1 *(7 ; 071)*	40.5 ± 3.1 *(26 ; 343)*	39.6 ± 4.5 *(108 ; 1307)*
2006	*na*	43.8 ± 5.8 *(25 ; 322)*	07.9 ± 3.9 *(12 ; 152)*	39.0 ± 5.0 *(18 ; 277)*	28.6 ± 3.7 *(96 ; 1243)*

A2a	% of greys ± SE (*N encounters; N individuals counted*)				
Year	Upstream	Central	Downstream	Saguenay	Total
2007	*na*	48.2 ± 4.5 *(36 ; 409)*	28.2 ± 10.7 *(18 ; 238)*	46.6 ± 4.7 *(18 ; 232)*	38.0 ± 4.8 *(113 ; 1371)*
2008	*na*	50.0 ± 3.2 *(24 ; 380)*	14.2 ± 12.5 *(9 ; 106)*	47.1 ± 4.2 *(22 ; 323)*	33.6 ± 4.9 *(96 ; 1301)*
2009	*na*	46.6 ± 3.2 *(26 ; 442)*	13.9 ± 7.2 *(11 ; 244)*	40.9 ± 2.3 *(17 ; 313)*	32.0 ± 3.6 *(95 ; 1491)*
2010	*na*	50.3 ± 4.0 *(28 ; 445)*	18.6 ± 7.0 *(6 ; 118)*	42.1 ± 3.7 *(16 ; 228)*	35.1 ± 3.8 *(91 ; 1283)*
2011	*na*	42.1 ± 3.3 *(32 ; 387)*	16.0 ± 5.9 *(21 ; 394)*	45.2 ± 3.7 *(16 ; 217)*	31.2 ± 3.3 *(110 ; 1490)*
2012	*na*	33.7 ± 7.0 *(15 ; 199)*	*na*	26.8 ± 4.1 *(14 ; 228)*	27.1 ± 4.9 *(74 ; 989)*

A2b	% of greys ± SE (*N encounters; N individuals counted*)				
Year	Upstream	Central	Downstream	Saguenay	Total
1992	35.5 ± 2.5 *(25 ; 383)*	39.8 ± 2.1 *(41 ; 763)*	22.0 ± 2.4 *(41 ; 1083)*	*na*	32.6 ± 4.0 *(107 ; 2229)*