



Relationship between nutritional condition and causes of death in beluga whales *Delphinapterus leucas* from the St. Lawrence estuary, Quebec, Canada

Sylvain Larrat¹, Véronique Lesage², Robert Michaud³, Stéphane Lair^{4,*}

¹Consultant in Wildlife Health Veterinarian, 920 Guernic, 56330 Pluvigner, France

²Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, 850 Rte de la Mer, Mont-Joli, QC G5H 3Z4, Canada

³Groupe de recherche et d'éducation sur les mammifères marins, 108, de la Cale-Sèche, Tadoussac, QC G0T 2A0, Canada

⁴Centre québécois sur la santé des animaux sauvages / Canadian Wildlife Health Cooperative, Faculté de médecine vétérinaire, Université de Montréal, St. Hyacinthe, QC J2S 7C6, Canada

ABSTRACT: Carcasses of endangered beluga whales *Delphinapterus leucas* from the St. Lawrence Estuary, Canada, have been examined consistently since 1983 to determine causes of death. The objective of this study is to compare the nutritional condition of belugas that died of different causes. Previously published categories of death were refined to discriminate acute from chronic pathological processes. Bayesian linear models were used to predict cause of death from the scaled mass index (SMI). Causes of death were as follows: 'bacterial diseases', 'verminous pneumonia', 'toxoplasmosis', 'other parasitic diseases', 'other infectious diseases', 'trauma — entrapment', 'other noninfectious diseases', 'dystocia — postpartum complications', 'neonatal mortality', 'cancer', 'primary starvation' and 'undetermined'. The models predicted a lower nutritional condition for the 'neonatal mortality' in belugas <290 cm in length and for 'primary starvation' and 'verminous pneumonia' categories for belugas ≥290 cm. Belugas that died from 'dystocia — postpartum complications' or from 'undetermined causes' had a higher-than-average SMI. Animals in the 'trauma — entrapment' category did not exhibit the highest nutritional condition, which was unexpected since individuals that died from trauma or entrapment are often used as references for optimal nutritional condition in other cetacean populations. Females that died from dystocia and postpartum complications were in similar nutritional condition as females dead from other causes during, or shortly after, pregnancy. This suggests that these females are not obese, ruling out a possible cause of dystocia. Although studying dead animals biases results toward low nutritional condition, our findings support the link between chronic pathological processes and poorer nutritional condition in belugas.

KEY WORDS: Beluga whale · Nutritional condition · Dystocia · Neonatal mortality · Verminous pneumonia · Neoplasia · Starvation

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1. INTRODUCTION

The beluga whale *Delphinapterus leucas* is a cetacean primarily inhabiting the Arctic regions, with a small, isolated population residing in the St. Law-

rence Estuary, Quebec, Canada. This population experienced a marked decline of approximately 80% due to overhunting (Pippard 1985), which prompted the designation of St. Lawrence beluga as endangered by the Committee on the Status of Endangered

*Corresponding author: stephane.lair@umontreal.ca

Wildlife in Canada in 1983. This status was re-affirmed in 1995 (Lesage & Kingsley 1995) but re-assessed as threatened in 2004 following harmonization of assessment criteria with those of the International Union for the Conservation of Nature (Smith 2004). The status of this population was again modified as endangered in 2014, following the observation of a 1% annual decrease in population size since the early 2000, an increased neonate mortality and a decline in the proportion of young individuals in the population (COSEWIC 2014, Lair et al. 2014). Efforts toward recovery have been ongoing since 1983 (Fisheries and Oceans Canada 2022), but despite its protected status, this population has failed to recover (Mosnier et al. 2015, Fisheries and Oceans Canada 2023).

Since 1983, an ongoing necropsy program has been conducted on beluga whales found dead in the St. Lawrence Estuary. This program, which aims to investigate the causes of mortality in this population (Lair et al. 2016), has raised several concerns about the health of the beluga in this profoundly anthropized ecosystem. Notably, this beluga population has been found to be highly contaminated by organic pollutants (e.g. Lebeuf 2009, Lebeuf et al. 2014, Simond et al. 2017, 2023, Barrett et al. 2021, Blouin et al. 2022) and exhibits the highest rate of cancer among free-ranging cetaceans (Lair et al. 2016). This population also faces other threats, such as noise and anthropogenic disturbance, which can impede communication (Lesage et al. 1999, Gervaise et al. 2012, Vergara et al. 2021) and possibly interfere with foraging as demonstrated in other species (Lussseau et al. 2009, Williams et al. 2021). Furthermore, changes in beluga diet (Lesage et al. 2020) and blubber lipid composition (Bernier-Graveline et al. 2021) over the last decades might have had an impact on the nutritional condition of belugas and general health.

Over the years, numerous causes of mortality have been documented. To facilitate the characterization of the threats faced by this population and to evaluate temporal changes in the occurrence of these threats, each diagnosis was reviewed in 2016 and assigned to one of the following categories: 'infectious diseases,' 'cancer,' 'dystocia — postpartum complications,' 'mortality of dependent calves,' 'ship/boat strikes,' 'entrapment in fishing gear,' 'primary starvation,' 'intoxication,' 'other noninfectious causes' and 'undetermined' (Lair et al. 2016). This classification was determined based on the type and the intensity of the pathological processes present, the circumstances of the stranding, and the subjective evaluation of the nutritional condition of the animal. Cetaceans that died following acute events are expected to be in opti-

mal nutritional condition, whereas chronic pathological processes are generally expected to be associated with a decrease in nutritional condition, due to increased metabolic demand and/or a lesser food intake (Kershaw et al. 2017). In addition, a poor nutritional condition in cetaceans can be the consequence of low prey availability and secondarily result in poor health and increased risk of disease (Lair et al. 2016, Raverty et al. 2020). An objective nutritional condition index has been developed for St. Lawrence Estuary beluga using morphometric data collected during necropsies (Larrat & Lair 2022).

In this study, the nutritional condition of St. Lawrence Estuary beluga is compared among individuals that died of different causes. Our hypothesis was that deaths following chronic processes would be associated with a lower nutritional condition than deaths following acute events. The categories reviewed in 2016 were first refined to discriminate between chronic and acute processes and provide a better portrait of the chronicity of the conditions.

2. MATERIALS AND METHODS

2.1. Necropsy, scaled mass index and categorization of mortality

All beluga carcasses that were in an acceptable preservation state and that were accessible and found either on the beach or drifting in the St. Lawrence Estuary (Quebec, Canada) from 1983 to 2022 were transported to an indoor necropsy facility for a full postmortem examination. Necropsies were performed on each carcass in a laboratory setting under the supervision of veterinary pathologists using an evolving but relatively uniform standard protocol (Lair et al. 2015, 2016). The carcasses included in this study were whole animals, with a preservation state graded 2 or 3, occasionally 4, on a 1 to 5 scale (1 = live animal, 5 = bones/mummified remains; Geraci & Lounsbury 2005). The weight (M) and total length (L) of carcasses were recorded and used to calculate a nutritional condition index, called the scaled mass index (SMI), using the following formula: $SMI = M \times (L_0/L)^b$, where L_0 and b are constants adequate for individuals under 290 cm ($L_0 = 186.8$ and $b = 3.3$) and those over or at 290 cm ($L_0 = 382.6$ and $b = 3.5$) (Larrat & Lair 2022). The primary cause of death was determined for each beluga by the supervising veterinary pathologist based on the circumstances of the death and results of the postmortem examination (Lair et al. 2016). These diagnoses were reviewed by an experi-

enced pathologist to increase the consistency of the diagnosis over time (S. Lair). During that review, causes of death were classified into one of the following categories: 'infectious diseases,' 'cancer,' 'dystocia — postpartum complications,' 'neonatal mortality,' 'ship/boat strikes,' 'entrapment in fishing gear,' 'primary starvation,' 'intoxication,' 'other non-infectious causes,' 'undetermined' (Lair et al. 2016). For the purpose of the present study, the 'infectious diseases' category was subdivided into the following 5 subcategories based on the etiopathogenesis of the conditions: 'bacterial diseases' (such as abscesses, mastitis, peritonitis, bacterial pneumonia, or septicemia), 'verminous pneumonia' (severe pulmonary infections with *Stenurus* sp. or *Halocercus* sp. nematodes), 'toxoplasmosis' (fatal systemic infections by *Toxoplasma gondii*), 'other parasitic diseases' (diseases caused by parasites that do not seem to be directly transmissible per se, such as protozoal pneumonia, or digestive perforation and peritonitis caused by nematodes) and 'other infectious diseases' (diseases potentially transmissible between belugas, such as herpesvirus infections, infectious hepatitis, or infectious encephalitis). Two new categories were formed by combining previous categories to achieve a sample size of over 10 beluga per category, to ensure robustness of statistical analyses. Belugas that died following vessel strikes, fishing gear entrapment and conspecific interactions were grouped under 'trauma — entrapment'. This category did not include any animals chronically entangled in fishing gear such as described in other cetacean species (Knowlton et al. 2022). Cases previously categorized as non-infectious diseases and saxitoxin intoxication were grouped under 'other noninfectious diseases.' The categories 'primary starvation,' 'verminous pneumonia' and 'cancer' were speculated to be associated with chronic pathological processes, whereas 'dystocia — postpartum complications' and 'trauma — entrapment' were seen as acute events (Table 1).

2.2. Comparison of the SMI between categories of causes of mortality

Analyses were conducted separately for belugas measuring <290 and ≥ 290 cm in total length, given the differences previously documented in allometric relationship between mass and length, and thus SMI calculations, for these 2 groups (Larrat & Lair 2022). Statistical analyses were performed with R 4.3.0 and STAN, and the R packages {rstanarm} and {bayestestR} (Carpenter et al. 2017, Muth et al. 2018, Makowski et

al. 2019, R Core Team 2023). Preliminary univariate regression suggested an absence of effect of the year of stranding on SMI. Consequently, this time variable was not included in the present analysis. The effect of cause of death on nutritional condition was tested using Bayesian linear models exploiting 4 Markov chains with 6000 iterations each, and 2000 iterations as burn-in, for a total of 16 000 posterior samples. The prior distribution of the intercept was specified as a normal distribution with the mean and standard deviation of the SMI, SD(SMI), serving as the location and scale parameters, respectively. The prior distributions for the different causes of death were also normally distributed, with locations for very poor, poor, good and very good nutritional condition corresponding to $-0.2 \times \text{SD}(\text{SMI})$, $-0.1 \times \text{SD}(\text{SMI})$, 0, or $0.2 \times \text{SD}(\text{SMI})$, respectively. The scale was set at $0.5 \times \text{SD}(\text{SMI})$ for all causes of death. The region of practical equivalence (ROPE) was defined as $\pm 0.1 \times \text{SD}(\text{SMI})$ (Kruschke 2018) and compared to the 95% credible interval (95%CI). The model was evaluated graphically (traceplots and auto-correlation plots) with the package {shinystan} and using a leave-one-out cross-validation method. We also verified that the Rhat was <1.05, that the Monte Carlo standard error was below 0.05 times the SD of the posterior distribution and that the effective sample size was >10% of the total sample size (Vehtari et al. 2017, Gabry et al. 2019). The medians reported in the results are for

Table 1. Number of belugas *Delphinapterus leucas* classified in each cause of death category among the individuals found dead in the St. Lawrence Estuary between 1983 and 2022 and examined. Data for beluga under and over 290 cm. Numbers marked with an asterisk (n = 2) are outliers. Categories in bold were hypothesized to be associated with acute deaths; underlined categories were regarded as chronic death processes

Cause of death	— Length (cm) —		
	<290	≥ 290	Total
Bacterial diseases	1	30	31
<u>Verminous pneumonia</u>	13	13	26
Toxoplasmosis	1	6	7
Other parasitic diseases	1	13	14
Other infectious diseases	3	5	8
Dystocia — postpartum complications	0	30*	30*
Neonatal mortality	35	0	35
<u>Cancer</u>	0	31	31
<u>Primary starvation</u>	0	7	7
Trauma — entrapment	2	12*	14*
Other noninfectious diseases	2	13	15
Undetermined	4	73	77
Total	62	233*	295*

posterior distributions of each parameter. The effect size was calculated using standardized coefficients and the following thresholds: 0.01 = very small effect, 0.2 = small effect, 0.5 = medium effect, 0.8 = large effect, 1.2 = very large effect, and 2.0 = huge effect (Sawilowsky 2009). The package {modelbased} was used to evaluate the contrasts. The evidence that a category had an effect on the SMI was quantified statistically with the probability of direction (pd), i.e. probability of a negative or positive effect of the factor, and clinically with the percentage of the posterior distribution in the ROPE (% in ROPE). A $pd > 80\%$ or a % in ROPE $< 10\%$ were suggestive of an effect; the higher the pd or the lower the % in ROPE within this category, the stronger the statistical significance. Cases where pd was $> 80\%$ but % in ROPE was $> 10\%$ were interpreted as effects that, although statistically significant, were clinically unimportant.

Cause of death categories were attributed the following priors: very poor nutritional condition for 'primary starvation'; poor nutritional condition for 'verminous pneumonia' and 'cancer'; very good nutritional condition for 'dystocia — postpartum complications'; and good nutritional condition for all other categories. The subset of females which were pregnant or had signs of recent parturition (lactation and enlarged uterus) were further examined with a similar method. Due to small sample size, categories for cause of death were simplified as 'acute', 'chronic' and 'dystocia — postpartum complications', based on the results of the previous model.

3. RESULTS

3.1. Comparison of the SMI between categories of causes of mortality

Out of the 638 dead belugas found dead ashore or drifting in the St. Lawrence Estuary between 1983 and 2022, 297 underwent partial or full necropsies. A final diagnosis was available for 295 belugas, including 62 individuals < 290 cm and 233 individuals ≥ 290 cm in length. Final diagnoses were assigned to one of 14 potential categories (Table S1 in the Supplement at www.int-res.com/articles/suppl/d159p159_supp.pdf).

3.1.1. Belugas < 290 cm in length

Of the 62 individuals with a body length < 290 cm with a diagnosis, 56 had information available on their

SMI (Table S1). Cause of death fell under 8 of the 14 possible categories for this length class: 'verminous pneumonia' ($n = 12$), 'neonatal mortality' ($n = 31$), and 6 other categories with fewer than 5 cases each ('bacterial diseases' $n = 1$, 'toxoplasmosis' $n = 1$, 'other infectious diseases' $n = 3$, 'trauma — entrapment' $n = 2$, 'other noninfectious diseases' $n = 4$, and 'undetermined' $n = 2$). The latter 6 categories were combined into a single one ('other causes' $n = 13$) for the statistical analyses (Fig. 1). The model intercept (i.e. median SMI) of the posterior distribution for this length class was 103.1 kg (95%CI = [94.8, 111.3]). The ROPE was [-1.4, 1.4]. The model provided evidence ($pd = 89.7\%$, % in ROPE = 11.7%) for a lower nutritional condition in belugas from the category 'neonatal mortality' (median = -5.6 kg, 95%CI = [-14.2, 3.0]). The effect size was qualified as small (standardized median = -0.4). In contrast, the model did not provide any evidence of an effect of cause of death on SMI for animals dead of 'verminous pneumonia' (median = 1.1 kg, 95%CI = [-8.2, 10.3], $pd = 59\%$, % in ROPE = 22.7%) and 'other causes' (median = 2.5 kg, 95%CI = [-6.8, 11.5], $pd = 69.6\%$, % in ROPE = 20.9%).

3.1.2. Belugas ≥ 290 cm in length

Of the 230 belugas with total length ≥ 290 cm, 199 were assigned a SMI and diagnosed with cause of death (Table S1). Two individuals with SMI > 1450 kg exerted a significant influence on the estimates derived from the model. They were removed from the analysis, which resulted in more conservative estimates. One was a pregnant female dead from dystocia. The other was an intersex individual dead from trauma. Eleven categories of cause of death were represented in belugas ≥ 290 cm: 'bacterial diseases' ($n = 27$), 'verminous pneumonia' ($n = 16$), 'toxoplasmosis' ($n = 6$), 'other parasitic diseases' ($n = 9$), 'other infectious diseases' ($n = 5$), 'dystocia — postpartum complications' ($n = 25$), 'cancer' ($n = 27$), 'primary starvation' ($n = 7$), 'trauma — entrapment' ($n = 11$), 'other noninfectious diseases' ($n = 10$), and 'undetermined' ($n = 6$) (Fig. 2). The median of the posterior distribution of SMI was 764.13 kg for animals > 290 cm (95%CI = [714.6, 814.1]). The ROPE was [-14.54, 14.54]. The model provided strong evidence ($pd = 99.6\%$, % in ROPE = 0%) that belugas dead from 'primary starvation' had a lower SMI (median = -120.9 kg, 95%CI = [-211.7, -28.9]) compared to the overall median for animals in this length category. This effect was considered large (standardized median = -0.82). Similarly, the model provided evidence ($pd = 85.9\%$,

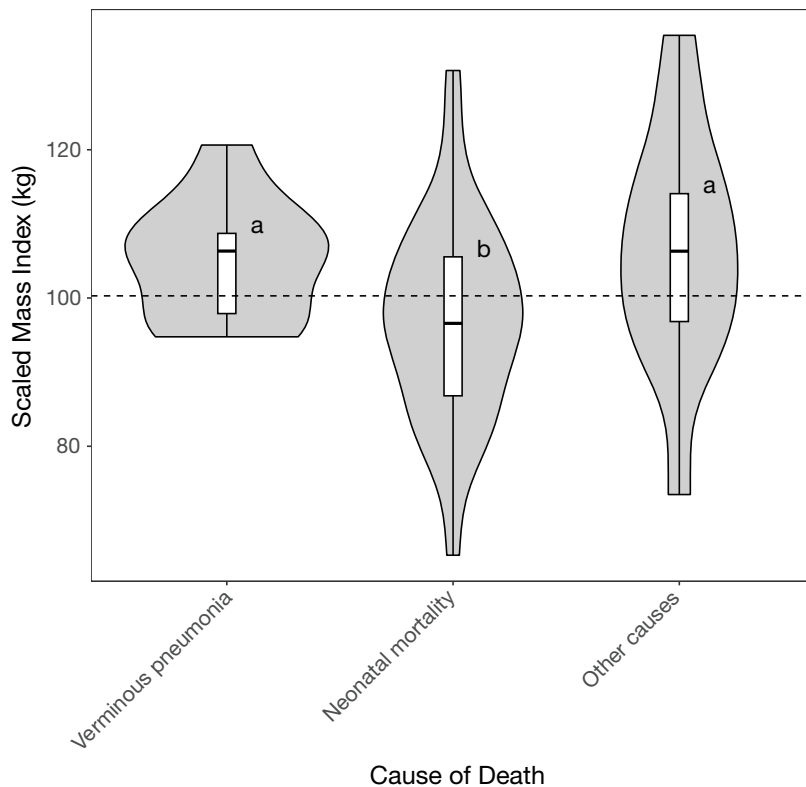


Fig. 1. Violin plot and box plot of the scaled mass index (SMI, kg) of belugas *Delphinapterus leucas* <290 cm in length found dead in the St. Lawrence Estuary between 1983 and 2022 based on their cause of death ($n = 56$). Gray shapes: density of distribution of the SMI. White boxes: 25 to 75% quantiles. Dashed horizontal line: overall median of the SMI. Bold horizontal lines: median of each group. Vertical whiskers (black lines) extend to the minimum and the maximum. Causes of death with $n < 5$ were grouped in the 'other causes' category. Different letters are printed for categories with a probability of direction (i.e. a probability of having different median SMI) >80%

% in ROPE = 16.2%) that SMI for belugas that died from 'verminous pneumonia' (median = -43.8 kg, 95%CI = [$-122.4, 35.8$]) was lower compared to the median for individuals in this length category. This effect was qualified as small (standardized median = -0.3). In contrast, the model provided strong evidence (pd = 98.7%, % in ROPE = 0.8%) that the SMI of belugas dead from 'dystocia — postpartum complications' (median = 77.8 kg, 95%CI = [$9.6, 145.7$]) was higher than for individuals in that length category. This effect was qualified as medium-sized (standardized median = 0.53). The model also provided evidence that belugas from the 'undetermined' category had a higher SMI than the overall median for that length category (pd = 84.2%, % in ROPE = 24.9%, median = 29.9 kg, 95%CI = [$-27.95, 88.29$]), but effect size was small (standardized median = 0.20). The detailed results of the Bayesian model are presented in Table 2.

Comparing median SMI among the various cause of death categories, belugas dead from 'primary starvation' were in poorer nutritional condition than belugas in any other categories (all pd >90%, all % in ROPE <10%; Table 3, Fig. 2). While belugas dead from 'verminous pneumonia' had a larger SMI than animals dead from 'primary starvation', their SMI remained lower than for belugas in the 'bacterial diseases,' 'toxoplasmosis,' 'other infectious diseases,' 'dystocia — postpartum complications,' 'cancer,' and 'undetermined' categories (all pd >80%). The lower SMI associated with 'verminous pneumonia' was clinically relevant (% in ROPE <10%) when compared with the categories 'other infectious diseases,' 'dystocia — postpartum complications,' and 'undetermined' but not 'bacterial diseases,' 'cancer, and 'toxoplasmosis.' The SMI of belugas dead from the 'dystocia — postpartum complications' category spanned a wide range (Fig. 2); however, the model still provided evidence that this category was associated with a higher SMI than all the other categories with the exception of 'other infectious diseases' (all pd >80%; Table 3, Fig. 2). Clinically, this difference was relevant (% in ROPE <10%) for all categories except 'other

noninfectious diseases' and 'undetermined'. Animals dead from 'trauma — entrapment' had a lower SMI than individuals dead from 'dystocia — postpartum complications' and from 'undetermined' causes but were no different from individuals dead from any other causes (Fig. 2). Overall, animals in the 'other infectious diseases,' 'other noninfectious diseases' and 'undetermined' categories had a relatively high posterior median SMI (i.e. ranging from 789 to 794 kg), especially in comparison with belugas that died from 'bacterial diseases,' 'verminous pneumonia' or 'cancer' (all median SMI <763 kg) (Table 3).

3.1.3. Female beluga dead during pregnancy or shortly after parturition

Among the females dead during pregnancy or shortly after parturition, with complete information

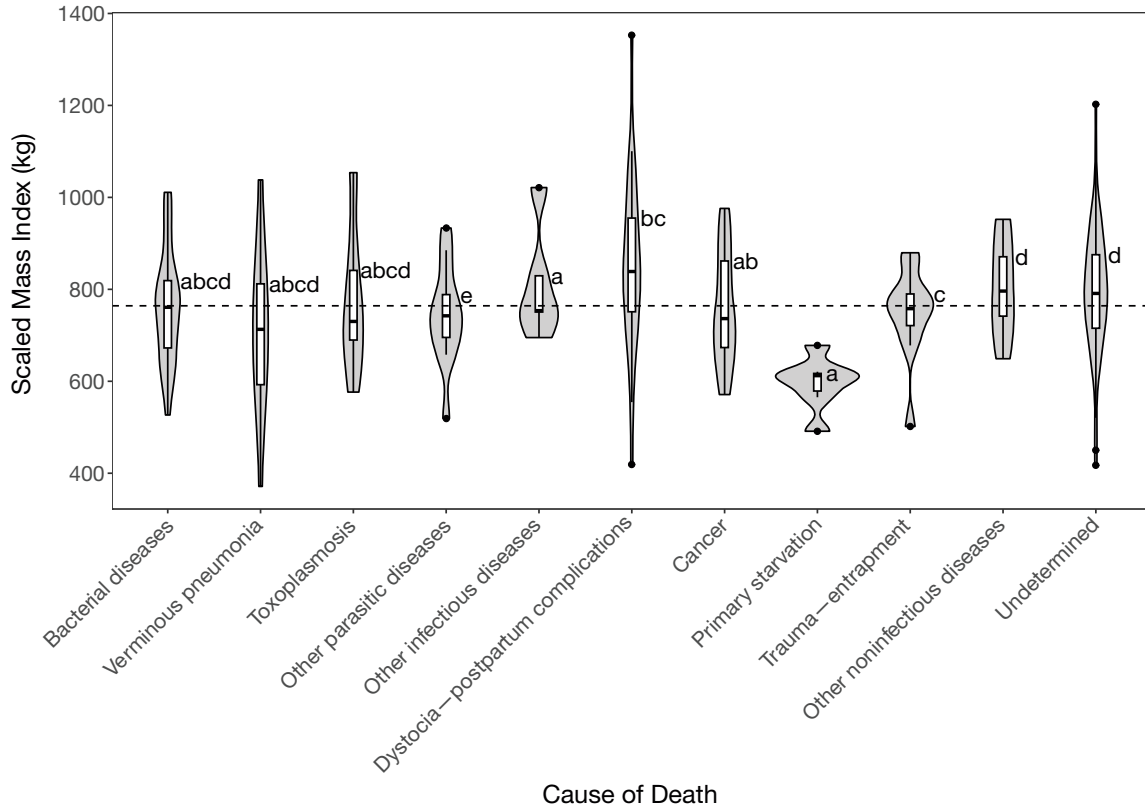


Fig. 2. Violin plot and box plot of the scaled mass index (SMI, kg) of belugas *Delphinapterus leucas* ≥ 290 cm stranded in the St. Lawrence Estuary between 1983 and 2022, depending on their cause of death ($n = 196$). Letters are different for groups having a probability of being different (probability of direction) $> 80\%$. Gray shapes: density of distribution of the SMI. White boxes: 25 to 75% quantiles. Dashed horizontal line: overall median of the SMI. Bold horizontal lines: median of each group. Vertical whiskers (black lines) extend to the minimum and the maximum within 1.5 times the interquartile (25 to 75%) range. Different letters are printed for categories with a probability of direction (i.e. a probability of having different median SMI) $> 80\%$. Two outliers with SMI > 1450 kg were removed

($n = 43$), 9 died because of other infectious diseases, other noninfectious diseases or undetermined causes (Fig. 3). Based on the high posterior median SMI

reported above, they were considered to have died from an acute cause. Twenty-five were in the category 'dystocia — postpartum complications', and the

Table 2. Results of a Bayesian regression of the scaled mass index (SMI) of belugas *Delphinapterus leucas* ≥ 290 cm in length in relation with their cause of death ($n = 196$, 2 outliers removed). Median of the posterior distribution, 95% credible interval (95%CI), probability of direction and the percentage of the distribution in the region of practical equivalence (ROPE) are presented. The ROPE was $[-14.54, 14.54]$

Parameter	Median SMI (standardized median)	[95%CI]	Probability of direction (%)	ROPE (%)
Intercept	764.1 (—)	[714.6, 814.1]	—	—
Bacterial diseases	-0.7 (-0.01)	[-67.2, 66.7]	50.9	35.04
Verminous pneumonia	-43.8 (-0.3)	[-122.4, 35.8]	85.9	16.2
Toxoplasmosis	6.3 (0.04)	[-86.3, 100.6]	55.3	24.4
Other parasitic diseases	-15.5 (-0.11)	[-94.0, 65.1]	65.0	27.2
Other infectious diseases	25.7 (0.18)	[-73.0, 126.8]	69.6	21.5
Dystocia — postpartum complications	77.8 (0.53)	[9.6, 145.7]	98.7	0.8
Cancer	-7.4 (-0.05)	[-73.0, 59.9]	58.0	33.5
Primary starvation	-120.9 (-0.82)	[-211.7, -28.9]	99.6	0
Trauma — entrapment	-11.5 (-0.09)	[92.4, 68.9]	61.2	28.3
Other noninfectious diseases	27.4 (0.18)	[-55.7, 111.3]	74.2	23.5
Undetermined	29.9 (0.20)	[-27.95, 88.29]	84.2	24.9

Table 3. Contrast analysis of the Bayesian regression of the scaled mass index (SMI) of belugas *Delphinapterus leucas* ≥ 290 cm in relation to the categories of cause of death. **Bold** numbers in the diagonal are medians of the posterior distribution (in kg). Percentages in the upper right triangle are the probabilities of direction, which corresponds to the probability of a cause of death to effectively be associated with a higher or a lower SMI than another category. Percentages $>80\%$, which are suggestive of a statistically significant difference are underlined. Lower left triangle corresponds to the proportion of the posterior distribution of the SMI in the ROPE (region of practical equivalence [$-14.54, 14.54$]). Percentages $<10\%$, indicative of a clinically significant difference, are underlined

	Bacterial diseases	Verminous pneumonia	Toxoplasmosis	Other parasitic diseases	Other infectious diseases	Dystocia — postpartum complications	Cancer	Primary starvation	Trauma — entrapment	Other noninfectious diseases	Undetermined
Bacterial diseases	763.4	83.9%	55.5%	62.8%	68.5%	98.2%	56.5%	99.2%	60.2%	73.3%	83.4%
Verminous pneumonia	177.0%	720.3	81.1%	72.1%	87.8%	99.7%	80.3%	91.3%	73.7%	91.5%	96.8%
Toxoplasmosis	22.6%	15%	770.4	64.7%	61.6%	91.2%	60.2%	97.7%	62.0%	64.1%	68.2%
Other parasitic diseases	25.0%	20.5%	19.4%	748.7	75.5%	98.1%	57.4%	96.8%	52.7%	79.5%	86.8%
Other infectious diseases	19.5%	10.1%	16.9%	15.4%	789.8	82.1%	72.8%	98.7%	73.2%	51.3%	52.6%
Dystocia — postpartum complications	1.8%	0%	9.4%	1.4%	14.2%	842.0	99.0%	100%	97.6%	86.1%	93.4%
Cancer	31.7%	19.6%	21.9%	26.6%	18.3%	0%	756.8	98.6%	55.0%	78.0%	87.7%
Primary starvation	0%	8.7%	1.2%	3.4%	0%	0%	0.2%	643.2	97.2%	99.5%	99.9%
Trauma — entrapment	26.2%	20.1%	19.8%	23.7%	16.2%	2.3%	27.1%	2.5%	752.6	77.0%	84.1%
Other noninfectious diseases	21.7%	9.2%	19.7%	16.4%	19.5%	14.8%	20.1%	0%	17.0%	791.6	51.9%
Undetermined	24.1%	4.6%	21.9%	16.4%	23.0%	12.8%	19.8%	0%	17.5%	27.6%	794

remaining 9 beluga were considered in a chronic group of causes of death. The posterior median SMI of the subset of gestating or recently gestating females was 834.2 kg (95%CI = [741.3, 927.2]). The ROPE was [$-16.09, 16.09$]. Although a trend towards higher SMI seemed present for the 'acute' group (median = 23.9 kg, 95%CI = [$-80.7, 127.6$]) and the category 'dystocia — postpartum complications' (median = 17.1, 95%CI = [$-80.0, 115.1$]), the model did not provide convincing evidence that the SMI of gestating females or recently gestating females was different according to the cause of death (all $pd < 80\%$, all % in ROPE $> 10\%$, see also Table 4).

4. DISCUSSION

This study exploited an exceptional dataset of full necropsies conducted rigorously over a period of 40 yr to examine the relationship between nutritional condition and cause of death. Our findings on St. Lawrence Estuary beluga are consistent with previous studies on cetaceans indicating that nutritional condition can be predicted from cause of death. Additionally, whether death resulted from an acute or chronic stressor impacts the expected SMI. In St. Lawrence Estuary beluga, SMI differed statistically among the following 4 causes of death: 'dystocia — postpartum complications', which represents females in late gestation or that have died shortly after giving birth or in the first days of lactation (highest median SMI at 842 kg); 'undetermined' (second highest median SMI at 800 kg); 'primary starvation' (lowest median SMI at 643 kg), and 'verminous pneumonia' (second lowest median SMI at 720 kg). Beluga dead from all other causes, including 'trauma — entrapment', had similar and intermediate SMI with values ranging from 749 to 796 kg (Table 3). The SMI for beluga dead from 'trauma — entrapment' had a median SMI of 752 kg, one of the lowest predicted for St. Lawrence Estuary beluga (Table 3, Fig. 2).

This result is unusual since cetaceans that die from trauma or bycatch typically exhibit good nutritional condition, which in turn is considered a hallmark of an acute cause of death (Arbelo et al. 2013). However, a study using harbor porpoises by-caught in fishing gear challenged this notion, revealing that several of the by-caught individuals did not display favorable health or nutritional condition (IJseldijk et al. 2021). The value for St. Lawrence Estuary beluga dead from 'trauma — entrapment' and 'cancer' were similar (SMI of 752.4 and 757.1 kg, respectively), suggesting that the situation of St. Lawrence Estuary belugas may be

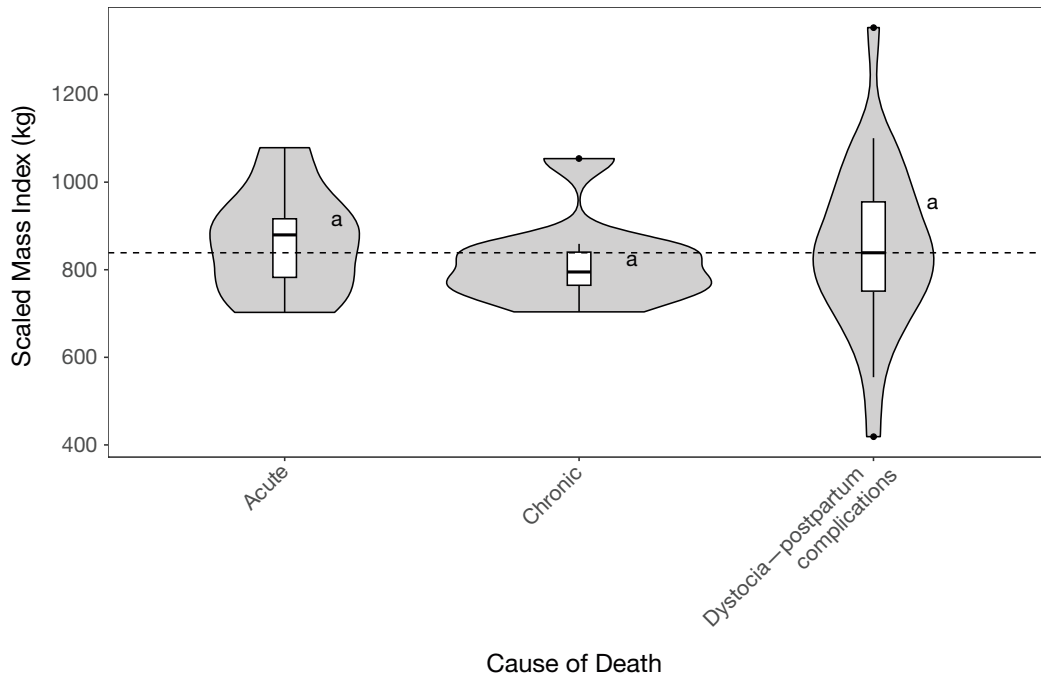


Fig. 3. Violin plot and box plot of the scaled mass index (SMI, kg) of gestating or recently gestating female beluga *Delphinapterus leucas* found dead in the St. Lawrence Estuary between 1983 and 2022, according to primary cause of death ($n = 42$). Gray shapes: density distribution of the SMI. White boxes: 25 to 75% quantiles. Dashed horizontal line: overall median SMI. Bold horizontal lines: median of each group. Vertical whiskers (black lines) extend to the minimum and the maximum values. Different letters are printed for categories with a probability of direction (i.e. a probability of having different median SMI) $> 80\%$

analogous to what has been reported in harbor porpoises by IJsseldijk et al. (2021). In contrast with what is observed in most other cetacean populations, St. Lawrence belugas dead from 'trauma — entrapment' could be individuals with compromised health status, which may exhibit modified risk behaviors. They do not seem to accurately reflect the optimal nutritional condition of healthy belugas in this population.

Our results otherwise match the expectation of a better nutritional status in animals dead from acute causes compared with those dead from chronic causes. This is consistent with findings from studies on Pacific killer whales *Orcinus orca* (Raverty et al. 2020) and harbor porpoises (Kershaw et al. 2017).

Beluga that died of 'undetermined causes' exhibited relatively good nutritional condition (second highest SMI after females dying from 'dystocia — postpartum complications'). This suggests that a portion of these belugas may have died acutely, keeping their nutritional condition closer to that of the healthiest belugas in the population.

Nutritional condition is a recognized predictor of fitness, reproductive success, and behavior in several cetacean species (Castrillon & Bengtson Nash 2020). In southern resident killer whales, a low food availability has been proposed as an important driver of

Table 4. Scaled mass index (SMI) of female belugas dead during or shortly after gestation in relation to other causes of death. **Bold** numbers in the diagonal are medians of the posterior distribution (in kg) from a Bayesian regression. Percentages in the upper right triangle are the probabilities (in %) of direction, which corresponds to the probability of a cause of death being effectively associated with a higher or a lower SMI than another category. Lower left triangle corresponds to the proportion (in %) of the posterior distribution of the SMI in the ROPE (region of practical equivalence [$-16.09, 16.09$])

	Acute	Chronic	Dystocia — postpartum complications
Acute	858.2	74.1%	55.0%
Chronic	18%	818.6	73.3%
Dystocia — postpartum complications	24.7%	21.2%	851.3

the failure of reproduction, including late abortion (Wasser et al. 2017). Although our results only apply to dead belugas, the overall good nutritional condition seen in females that died of dystocia or postpartum complications does not support an identical mechanism in St. Lawrence belugas. Although the SMI can be biased by the mass of the fetus and over-

estimate the true nutritional condition of a pregnant female, the subjective evaluations of the carcasses during necropsy were consistent with a good nutritional condition in most individuals examined. This observation leads us to conclude that the decline in the abundance of essential fatty acids in the blubber from St. Lawrence Estuary belugas since the late 1990s, which was interpreted as a decrease in body condition (Bernier-Graveline et al. 2021), does not appear to have reached levels sufficient to be reflected in the SMI or to cause visible nutritional stress in gestating females. In some domestic artiodactyl species, obesity has also been identified as a risk factor for dystocia (Jacobson et al. 2020). In the population studied here, females which died from 'dystocia — postpartum complications' had a median SMI similar to that of females which died of other causes while being pregnant or having recently given birth to calves. While the largest variance in SMI was observed among females in the 'dystocia — postpartum complications' class, this suggests that belugas in the category 'dystocia — postpartum complications' are not obese, and that body condition did not play a clinically significant role in the death of these animals.

The occurrence of dystocia and postpartum complications has increased in St. Lawrence belugas since 2010 (Lair et al. 2016). The St. Lawrence Estuary is undergoing changes in terms of physical parameters, biotic communities, prey availability, and presence of pollutants (Savenkoff et al. 2007, Plourde et al. 2014, Lesage et al. 2020, Lesage 2021). Identifying the causes or risk factors of dystocia in belugas is complex; nutritional stresses, disturbance of parturient females and exposure to endocrine-disrupting chemicals have been proposed as potential causes of dystocia in this population (Lair et al. 2016).

Polychlorinated biphenyls (PCB), although clearly involved in reproductive disorders in several animal species, have not been reliably identified as causes of dystocia or post-partum complications (He et al. 2021). Polybrominated diphenyl ethers (PBDEs) and perfluoroalkyl substances (PFAS) may have an impact on pregnancy and birth by interfering with the thyroid function (Ballesteros et al. 2017). Exposure to PFAS also dysregulates lipid metabolism in humans, increasing the risk of maternal obesity, metabolic disorders, preeclampsia, reduced fetal weight, and other complications in pregnant women (Szilagyi et al. 2020). PCB, PBDE and PFAS have been detected in St. Lawrence belugas (Wilson et al. 2005, Raach et al. 2011, Barrett et al. 2021). Barrett et al. (2021) reported a decrease in the presence of legacy PFAS and an increase in short-chain PFAS. Despite the lower

potential for bioaccumulation in short-chain PFAS, they appear to have a higher propensity to cross the placental barrier, retaining significant reproductive effects (McAdam & Bell 2023). Further studies would be warranted to better understand the role of the different risk factors of dystocia in beluga.

In belugas <290 cm, the lowest nutritional condition was observed in the category 'neonatal mortality', which essentially consists of newborn calves only a few days or weeks old. These results are consistent with the progressive increase in nutritional condition with age observed in other species, such as harbor porpoises (Kershaw et al. 2017). Neonatal death may be caused by starvation following separation from the mother (Lair et al. 2016). Endocrine disrupting chemicals might also play a role, potentially impairing neurological development of fetuses or reducing birth weight (Herbstman et al. 2010, Ballesteros et al. 2017).

Verminous pneumonia is common in cetaceans, including belugas (Guimarães et al. 2015, Lair et al. 2016). Severe parasitic infections of the respiratory system, frequently associated with secondary bacterial pneumonia, can lead to death in cetaceans (Guimarães et al. 2015). The lower nutritional condition observed in belugas that died from verminous pneumonia is consistent with findings in other cetacean species (Arbelo et al. 2013, Giorda et al. 2017), indicating that this cause of death is indeed a chronic process. However, it remains unclear whether belugas in poor nutritional condition had an impaired immune system favoring nematode infection or whether heavy loads of respiratory parasites were responsible for progressive weight loss due to reduced feeding that could be secondary to a decrease in pulmonary, and therefore diving, capacity.

In humans and domesticated animals, cancer is reported to be associated with decreased nutritional condition (Tisdale 1997, Baez et al. 2007). Although our results did not demonstrate lower-than-average nutritional condition in belugas affected by cancer, beluga in this category exhibited a SMI at the low end of the intermediate group, which encompassed most causes of deaths.

Our study population consisted of dead individuals, which, in general, for population dying from chronic illness, are expected to be inherently biased toward lower nutritional condition. Therefore, animals in categories with a median SMI close to the average of our sample may be in poorer body condition than healthy, living belugas. Nevertheless, the data presented here is consistent with the hypothesis that chronic causes of death, such as primary starvation or verminous pneumonia, are associated with poorer nutritional

condition than more acute processes like herpesviral diseases (included in 'other infectious diseases'). In order to increase our ability to interpret the nutritional condition of beluga during necropsy, it is essential to document the nutritional condition of healthy animals. Comparative photogrammetry of dead and live belugas in relation with SMI calculations in carcasses could provide the necessary information to achieve the objective of assessing nutritional condition of free-ranging St. Lawrence Estuary belugas.

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