Diet of St. Lawrence Estuary Beluga (*Delphinapterus leucas*) in a changing ecosystem

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**Abstract**

Ecosystems and community structure fluctuate over time as a result of natural and anthropogenic factors that may affect prey availability and population dynamics. Most of what we know about St. Lawrence Estuary (SLE) Beluga (*Delphinapterus leucas*) diet comes from stomach contents collected 80 years ago mainly from a hunting site that Beluga no longer use. How reflective these data are of Beluga diet at other sites and at the current time is unknown. In the context of the recent population decline, general information of prey species alone may help identify useful conservation actions for potentially important prey or habitats. Here, we examined the diet of SLE Beluga using digestive tracts collected from carcasses recovered over the past 30 years, in the context of historical diet data and recent changes in the St. Lawrence ecosystem. We showed they have a varied diet composed of fish and invertebrates generally <30 cm in length, and that adult males and females differ in their summer diet in a way that is consistent with the sex segregation observed in this population. Our results also indicate that polychaete worms, squid, and cod are still among the most prevalent prey, and that species such as redfish (*Sebastes* spp.) might be important prey items. This study shows that Beluga diet has changed since the 1930s, and that prey from digestive tracts identified to species are valuable for making comparisons to the past, and for improving applications of molecular analyses, such as stable isotopes and fatty acids.

**Key words:** *Delphinapterus leucas*; foraging ecology; diet; Beluga; ecosystem change

**Introduction**

Ecosystems and community structure fluctuate over time as a result of a variety of natural and anthropogenic factors. These environmental changes may modify prey availability and affect predator population dynamics. Without contemporary information on diet composition and foraging ecology, predicting a population’s response to human stressors and climate variability remains a challenge (Bowen 1997).

A small population of Beluga whale (*Delphinapterus leucas*) persists in the St. Lawrence Estuary (SLE), Canada (Figure 1), since the last glaciation (Harington 1977). Full protection from hunting since the late 1970s should have allowed this population to grow. Instead, the population has remained stable or may have increased slightly until the early 2000s but is in a steady decline at a rate of about 1% per year since then (Mosnier et al. 2015). This led to a change in conservation status from Threatened to Endangered Wildlife in Canada (COSEWIC 2014), and under the Canadian *Species at Risk Act* (Canada Gazette 2016). Reasons for the lack of recovery and current decline may include contamination, disruption of critical activities by vessel traffic, and reduced access or availability of prey as a result of ecosystem change (DFO 2014). Understanding Beluga diet and foraging ecology may help identify dietary sources of toxic substances, and prey species and habitats most valuable to Beluga recovery.

Most of what we know about SLE Beluga diet comes from stomach contents collected 80 years ago mainly from a hunting site no longer used by SLE Beluga (Vladykov 1946). How reflective these data are of the current Beluga diet and at other sites is uncertain. Since the 1930s, the St. Lawrence marine ecosystem has seen an increase in abundance of potential competitors such as Gray Seal (*Halichoerus grypus*) and Harp Seal (*Pagophilus groenlandicus*; Hammill et al. 2015, 2017), and the collapse of several com-
commercially exploited demersal fish species, with a concurrent expansion of some crustacean and small pelagic fish stocks (Worm and Myers 2003; Savenkoff et al. 2007). Species such as Northern Shortfin Squid (*Illex illecebrosus*) and Atlantic (*Gadus morhua*) or Greenland (*Gadus ogac*) Cod, which were consumed regularly during the 1930s, are scarce in recent SLE scientific fisheries, raising questions about their availability to Beluga. American Eels (*Anguilla rostrata*), which were suspected to be an important source of PCBs and other persistent organic pollutants including Mirex in Beluga, collapsed in the SLE in the 1990s (Hickie *et al.* 2000; Cairns *et al.* 2014). Meanwhile, severely depleted fish populations such as redfish (*Sebastes* spp.) and Striped Bass (*Morone saxatilis*) are currently rebounding from low levels (COSEWIC 2012; Brassard *et al.* 2017; DFO 2017; Vanalderweireldt 2019).

Insights into SLE Beluga contemporary diet might be obtained from quantitative dietary mixing mod-

![Study area, in the St. Lawrence Estuary, Canada. Upper estuary and lower estuary refer to sectors located west and east of the Saguenay River, respectively. The main hunting site in the Vladykov (1946) study was located on Manicouagan bank, right off Manicouagan River. In our study, Beluga (*Delphinapterus leucas*) were collected for stomach contents throughout the St. Lawrence Estuary.](image)
els that exploit molecular tracers such as stable isotopes or fatty acids (e.g., Iverson et al. 2004; Moore and Semmens 2008; Parnell et al. 2010). However, an important assumption of these models is that all potentially important prey are included in model inputs. Analysis of digestive tracts allows prey to be identified from hard structures such as fish otoliths or bones, cephalopod beaks, and polychaete jaws (Pierce and Boyle 1991). For SLE Beluga, opportunities to sample digestive tracts are limited to animals found dead, the majority of which have empty guts or contain only traces of food as they generally die after a period of anorexia (Lair et al. 2016). While these samples are unsuitable for quantitative diet assessment, they are valuable for identifying current prey species for comparison to the past and for other diet analyses. In the context of the recent population decline, identifying prey species may guide conservation actions important for SLE Beluga. Here, we examine the contemporary diet of SLE Beluga using digestive tracts collected from carcasses recovered over the past 30 years, in the context of historical diet data and recent changes in trophic structure of the St. Lawrence ecosystem.

**Methods**

Starting in 2007, digestive tracts were collected from well-preserved or moderately decomposed (freshness codes ≤3; Geracy and Lounsbury 1993) Beluga reported dead in the SLE and examined systematically for prey remains using standard protocols (Hammill et al. 2005). Sex and age were available for each individual; only individuals one year or older (i.e., likely to have ingested solid food; Brodie 1971; Matthews and Ferguson 2015) were included in the analysis. Age was determined from tooth dentinal layers, using a longitudinal midline section or half tooth, and high-resolution (4800 dpi optical resolution, 24-bit colour) digital imagery (Epson scanner Perfection V500 photo, Epson Canada Limited, Markham, Ontario, Canada) to allow for magnification, light, and contrast adjustments. One growth layer group (GLG) was assumed to be deposited each year (Stewart et al. 2006; Hohn et al. 2016; Waugh et al. 2018).

Digestive tracts were first examined for potential lesions. They were then extracted and frozen at −20°C until shipping and analysis for contents. They were confined to clean trays during the exam to avoid content loss. However, volume and mass of prey remains are likely to be imprecise due to digestion and are not reported here. Stomach and intestinal contents were examined separately but are presented in combination for this study. Each of the four stomach compartments were rinsed three times to ensure full recovery of contents. Stomach contents were then sorted using a fine mesh sieve (125 µm). Prey remains were identified to the lowest taxon possible using hard parts (i.e., otoliths and bones for fish, and beaks for cephalopods; Clarke 1986; Murie and Lavigne 1986).

Otoliths were assigned to one of three classes depending on degradation state. Class 1 included well preserved otoliths, Class 2 those eroded along margins but with few degradation marks, and Class 3 otoliths with erosion on both dorsal and ventral margins and internal and external areas. Prey size was estimated using otolith length/fish length relationships developed from samples collected during research cruises from Fisheries and Oceans Canada or using values from the literature (Bowen and Harrison 1996; Proust 1996; Hammill et al. 2007). A random subsample of 30 otoliths per species was measured when a large number of otoliths was present in a sample. Few Class 1 and 2 otoliths were obtained from the decaying Beluga carcasses; Class 3 otolith were also measured and reported separately to provide fish length minima. Given the small number of digestive tracts with some content (see Results), no attempt was made to quantify diet composition in terms of energy or mass contributions. Prey items were analyzed for frequency of occurrence only (Bowen and Harrison 1996). Empty stomachs were excluded from calculations.

**Results**

Between 2007 and 2019, 79 Beluga were examined systematically for prey remains. An additional 10 Beluga with prey remains sampled in the late 1980s (n = 2), mid-1990s (n = 2), and early 2000s (n = 6) were also included in this study. The sample (n = 89) was skewed toward females (61 females versus 28 males), mature individuals (87% were eight years or older), and ice-free months (only four carcasses collected during winter, i.e., December through March). Fifty-seven percent (45/79) of the systematically examined digestive tracts (i.e., 2007 onward) contained identifiable prey remains, with 13% (10/79) of the tracts having more than trace amounts, i.e., more than 15 otoliths or invertebrate parts.

Twenty-eight taxa, 18 fish and 10 invertebrate species, were represented in digestive tracts (Table 1; detailed diet data in Table S1). On average, 2.4 (SD = 2.2) prey species were detected per Beluga, although 11 different species were detected in one Beluga (nine fish, two invertebrates). Our limited data on fullness indices show no evidence for a fast and feast pattern over seasons in this population (Figure 2). Prey diversity in digestive tracts that contained food in amounts greater than trace, varied among months, but without following a clear seasonal pattern (Table 2). Both invertebrate and fish prey were detected in
Table 1. Species frequency of occurrence (% of digestive tracts with prey remains) in the diet of Beluga (*Delphinapterus leucas*) hunted mainly at the Banc de Manicouagan in 1938–1939 (Vladykov 1946: 60), or collected in various regions of the St. Lawrence Estuary via Beluga carcass recovery between 1989 and 2019 (our study).

| Taxon                        | Vladykov 1938–1939 | Our study 1989–2019 |
|------------------------------|--------------------|---------------------|
|                              | \( n \)  | \( \% \) (\( n = 107 \)) | \( n \) | \( \% \) (\( n = 59 \)) |
| **Fishes**                   |          |                      |          |                      |
| Ammodytidae                  |          |                      |          |                      |
| Sand lance (*Ammodytes sp.*) | 58       | 54                   | 4        | 7                    |
| Clupeidae                    |          |                      |          |                      |
| Atlantic Herring (*Clupea harengus*) | 2 | 2 | 2 | 3 |
| Osmeridae                    |          |                      |          |                      |
| Capelin (*Mallotus villosus*) | 54       | 51                   | 7        | 12                   |
| Rainbow Smelt (*Osmerus mordax*) | 1 | 1 | 4 | 7 |
| Scombridae                   |          |                      |          |                      |
| Atlantic Mackerel (*Scomber scombrus*) | — | 1 | 2 |
| Gadidae                      |          |                      |          |                      |
| Atlantic Cod/Greenland Cod (*Gadus morhua/Gadus ogac*) | 45 | 42 | 10 | 17 |
| Atlantic Cod (*Gadus morhua*) | — | 3 | 5 |
| Atlantic Tomcod (*Microgadus tomcod*) | 18 | 17 | 1 | 2 |
| Haddock (*Melanogrammus aeglefinus*) | 2 | 2 | — |
| White Hake (*Urophycis tensis*) | — | 5 | 8 |
| Silver Hake (*Merluccius bilinearis*) | — | 1 | 2 |
| Red Hake (*Urophycis chuss*) | 1       | 1                   | —        |          |
| Fourbeard Rockling (*Enchelyopus cimbrias*) | — | 3 | 5 |
| Ocean Pout (*Zoarces americanus*)/Lycodes sp. | 2 | 2 | 2 | 3 |
| Gadidae (unspecified)        | —       | 5                   | 8        |          |
| Macrouridae                  |          |                      |          |                      |
| Marlin-spike (*Nezumia bairdii*) | — | 2 | 3 |
| Scorpaenidae                 |          |                      |          |                      |
| Redfish (*Sebastes sp.*)     | —       | 9                   | 15       |          |
| Cyclopteridae                |          |                      |          |                      |
| Snailfish (*Liparis sp.*)†   | 4        | 4                   | 1        | 2                    |
| Lumpfish (*Cyclopterus lumpus*) | 1 | 1 | 1 | 2 |
| Cottidae                     |          |                      |          |                      |
| Sculpins (*Myxoceplus m. sp.*) | 35 | 33 | 1 | 2 |
| Daubed Shanny (*Leptoctenus maculatus*) | — | 1 | 2 |
| Cottidae (unspecified)       | —       | 3                   | 5        |          |
| Anguillidae                  |          |                      |          |                      |
| American Eel (*Anguilla rostrata*)† | — | 1 | 2 |
| Pleuronectidae               |          |                      |          |                      |
| Witch Flounder (*Glyptoceplus cynoglossus*) | 1 | 1 | — |
| Winter Flounder (*Pseudopleuronectes americanus*) | 9 | 9 | 1 | 2 |
| Smooth Flounder (*Pleuronectes putnami*) | 5 | 5 | 1 | 2 |
| Rajidae                      |          |                      |          |                      |
| Smooth and Thorny Skate (*Malacoraja senta, Amblyraja radiata, and skate sp.*) | 6 | 6 | — |
| Petromyzontidae              |          |                      |          |                      |
| Sea Lamprey (*Petromyzon marinus*) | 2 | 2 | — |
| Acipenserida                 |          |                      |          |                      |
| Atlantic Sturgeon (*Acipenser oxyrinchus*) | 3 | 3 | — |
digestive tracts (Table 1). Fish with the highest occurrences were demersal species, i.e., cod (either or both *G. morhua* and *G. ogac*), redfish (*Sebastes* sp.) and hake (*Urophycis tenuis* and *Merluccius bilinearis* Hake), with occurrences varying from 10 to 22%. Small pelagic or bottom-dwelling species such as Capelin (*Mallotus villosus*), sand lance (*Ammodytes* sp.), and Rainbow Smelt (*Osmerus mordax*) were present in 12, 7, and 7% of the tracts, respectively. Among invertebrates, polychaete worms were the most common prey with a 39% occurrence, followed by decapod shrimp (15%) and Northern Shortfin Squid (8%).

There was no clear seasonal trend in different prey occurrences in SLE Beluga in general or by sex (not shown). However, some patterns emerged when examining prey assemblages in individual Beluga per sector/month. Except for one adult male sampled at Rivière-Ouelle (upper estuary) in early May, which contained 1933 Capelin otoliths, all other Beluga sampled in the upper estuary between June and September (*n* = 8) were adult females. The females fed on small pelagic or bottom-dwelling fish such as Capelin, sand lance, Atlantic Herring (*Clupea harengus*) or Rainbow Smelt, on Northern Shortfin Squid and polychaete worms, and on prey not reported elsewhere in the SLE, which included Atlantic Tomcod (*Microgadus tomcod*), Smooth Flounder (*Pleuronectes putnami*), and Winter Flounder (*Pseudopleuronectes americanus*). Although some Beluga found dead in the lower estuary might have drifted there from the upper estuary, lower estuary Beluga differed from upper estuary Beluga by including both females and males that contained multiple demersal fish species, including cod (Atlantic or Greenland Cod), redfish, and White and Silver Hake. Note that while Atlantic Cod were specifically identified among prey remains, cod otoliths in seven other samples were too eroded to be identified to species as Atlantic or Greenland Cod.

Polychaete worms, Capelin, hakes, and cephalopods (Northern Shortfin Squid or Northern Atlantic Octopus [*Bathypolypus bairdii*]) followed no clear gender-based, seasonal, or spatial trends in our sample. However, some species showed a seasonal pattern in Beluga digestive tracts: American Eels were detected only in October (one Beluga); sand lance and Atlantic Herring only in April or September samples; and Rainbow Smelt only in April, and then from late August through October (Figure 3). Demersal fish species from the families Zoarcidae, Macrouridae, Liparidae, Cyphootheridae, and Cottidae, were found in trace amounts in samples, and only outside of summer months, i.e., in April, May, and from September

| Taxon | Vladykov 1938–1939 | Our study 1989–2019 |
|-------|---------------------|---------------------|
|       | *n* | % (*n* = 107) | *n* | % (*n* = 59) |
| **Salmonidae** | | | | |
| Atlantic Salmon (*Salmo salar*) | 1 | 1 | — |
| **Invertebrates** | | | | |
| Polychaeta | 91 | 28 | | |
| polychaete worm (*Nereis virens*) | 64 | 60 | 23 | 39 |
| *Cistenides gouldii* | 22 | 21 | — |
| **Crustacea** | | | | |
| Decapod shrimp | 69 | 65 | 9 | 15 |
| Amphipod gammarid | 37 | 35 | 1 | 2 |
| Other | 4 | 4 | — | |
| **Mollusca** | | | | |
| Gastropods Waved Whelk (*Buccinum undatum*) and periwinkle (*Littorina* sp.) | 19 | 18 | 4 | 7 |
| Bivalvia lamellibranch (*Cyttodaria/Mesodesma*) | 37 | 35 | 1 | 2 |
| Cephalopod Northern Shortfin Squid (*Illex illecebrosus*) | 35 | 33 | 5 | 8 |
| Cephalopod Northern Atlantic Octopus (*Bathypolypus bairdii*) | 21 | 20 | 3 | 5 |
| Cephalopod (unspecified) | — | 2 | 3 | |
| Other | 68 | 64 | — | |

*Named *Neoliparis atlanticus* in Vladykov (1946).
†Most likely identification from eroded otolith.
‡*Bathypolypus obesus* in Vladykov (1946).
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through November. Males consumed redfish in all sampled seasons, while females only in April, or September and October (Figure 4).

The estimated overall mean length of prey found in SLE Beluga digestive tracts using unworn or moderately worn otoliths was 19.8 cm (SE = 1.2 cm, \( n = 97 \), range 5.9–54.8 cm), and when including worn otoliths was 20.3 cm (SE = 0.4 cm, \( n = 533 \), range 4.6–54.8 cm). This mean value changed little (by 0.4–0.5 cm) depending on whether cod otoliths were assumed to be Atlantic or Greenland Cod. The smallest fish consumed were Capelin with a mean length of 11.4 cm (SE = 0.15 cm; \( n = 49 \)), while the largest were White Hake with a mean length of 45.9 cm (SE = 2.97 cm; \( n = 4 \)). With the exception of Atlantic/Greenland Cod and hake, most Beluga preys were on average 30 cm or less in length (Table 3, Figure 5).

**Discussion**

A variety of physiological and ecological factors can influence prey selection, energy intake, and feeding strategies of marine predators like Beluga (Stephens and Krebs 1986). These include prey availability and energy content, the predator’s energy requirements, behavioural and physiological constraints such as those that body size or the presence of a dependent calf impose on prey type and size, and on dive duration and depth (Salton et al. 2019). Seasonal and spatial patterns that are observed in diet composition among populations or among individuals of different reproductive, age, or sex classes likely reflect some of these constraints.

The Estuary and Gulf of St. Lawrence like other ecosystems worldwide have undergone profound ecosystemic changes as a result of overfishing and ocean warming (Worm and Myers 2003; Stenseth et al. 2004). An analysis incorporating 94 physical and biological variables over a 40-year period for the Gulf of St. Lawrence underscored the massive drop in demersal fish biomass in the early 1990s, the increase in atmospheric and water temperatures, and decrease in sea ice extent and thickness since 2000, with extremes recorded since 2010 (Plourde et al. 2014). While we know little about prey abundance in the 1930s, environmental changes since the 1990s likely affected Beluga prey availability in recent times. The abundance of potential competitors to SLE Beluga also changed since the 1930s. They include Harp Seals, Grey Seals, juvenile Harbour Seals (*Phoca vitulina*), and female Hooded Seals (*Cystophora cristata*),

| Month | Our study \((n = 16)\) | Vladykov (1946) |
|-------|----------------------|-----------------|
| Jan   | —                    | —               |
| Feb   | —                    | —               |
| Mar   | 2 (1)                | —               |
| Apr   | 6 (1)                | —               |
| May   | 2 (3)                | —               |
| June  | —                    | 2.8 (13)        |
| July  | 5 (1)                | 3.9 (24)        |
| Aug   | 3.5 (2)              | 7.3 (31)        |
| Sep   | 5.8 (5)              | 5.2 (21)        |
| Oct   | 7 (2)                | —               |
| Nov   | 4 (1)                | —               |
| Dec   | —                    | —               |

**Figure 2.** Seasonal distribution of Beluga (*Delphinapterus leucas*) digestive tract sampling in a. our study (2007 and onward) and b. that of Vladykov (1946), and relative index of contents volume. A ‘Trace’ content had fewer than 15 otoliths or invertebrate identifiable parts.

**Table 2.** Monthly diet diversity expressed as the mean number of taxa detected in digestive tracts containing prey remains in more than trace amounts (≥15 hard parts) for St. Lawrence Estuary Beluga (*Delphinapterus leucas*) hunted at three different sites in the late 1930s (Vladykov 1946; see Figure 1), or found dead between 1983 and 2019 (our study). Sample size is indicated in parentheses.

| Month | Our study \((n = 16)\) | Vladykov (1946) |
|-------|----------------------|-----------------|
| Jan   | —                    | —               |
| Feb   | —                    | —               |
| Mar   | 2 (1)                | —               |
| Apr   | 6 (1)                | —               |
| May   | 2 (3)                | —               |
| June  | —                    | 2.8 (13)        |
| July  | 5 (1)                | 3.9 (24)        |
| Aug   | 3.5 (2)              | 7.3 (31)        |
| Sep   | 5.8 (5)              | 5.2 (21)        |
| Oct   | 7 (2)                | —               |
| Nov   | 4 (1)                | —               |
| Dec   | —                    | —               |
which occupy trophic positions similar to adult female and male Beluga (Lesage et al. 2001). Baleen whales occupy lower trophic positions but share prey items with Beluga (Gavrilchuk et al. 2014). Several of these populations are increasing in size (Stevick et al. 2003; Hammill and Stenson 2006; Hammill et al. 2010, 2015, 2017), but competition extent has not been documented.

Similarities but also differences were observed when comparing present and past diet of SLE Beluga. Sand lance and Capelin were prey with the highest occurrences in SLE Beluga stomachs in the 1930s (Vladykov 1946), while large demersal fish such as cod, hake, and redfish were the most frequent fish prey in our study. Redfish, American Eel, and two species of hake were present in Beluga contemporary diet but were undetected in Vladykov’s study. The reverse was noted for Atlantic Salmon (Salmo salar), Atlantic Sturgeon (Acipenser oxyrinchos), Sea Lamprey (Petromyzon marinus), Haddock (Melanogrammus aeglefinus), and skates. Polychaete worms and cephalopods were frequently ingested invertebrates in both studies. There was no obvious bias or difference in age- or sex-class sampling in Vladykov’s nor our study; adults from both sexes were well represented in both studies, along with lower occurrences of calves and juveniles. However, sampling timing and location might explain some of the observed differences among studies; for instance, American Eel is more likely to be abundant in the fall in the SLE, particularly in the upper estuary (e.g., Vladykov 1946) or in the Saguenay River—times and places that were not sampled by Vladykov. Whether the absence of hake and redfish in Vladykov’s study results from the strong sampling bias toward a sandy habitat no longer used by Beluga (the Manicouagan River mouth) or to a change in their availability over time is unknown. Temporal trend data for redfish are relatively recent; two summer studies from the 1930s and 1950s suggest that redfish were scarce in the SLE in the 1930s (Vladykov and Tremblay 1935 as cited in Steele 1957).
Otoliths are calcium carbonate structures that progressively deteriorate when exposed to gastric fluid, and at a different rate depending on size and robustness (Tollit et al. 1997). Our reliance on decomposing carcasses reduced the chances of detecting small otoliths that are typical of smaller species (e.g., sand lance and Capelin), possibly biasing prey relative occurrences. In contrast, cephalopod beaks and hard parts of polychaete worms can accumulate over a few meals, possibly overestimating their importance (Jobling and Breiby 1986; Tollit et al. 1997). While the presence of some benthic invertebrates in digestive tracts might have resulted from secondary ingestion or suction feeding on other prey, others such as Northern Atlantic Octopus, Northern Shortfin Squid, polychaete worms, and shrimp were in volumes compatible with direct ingestion (Vladykov 1946; Seaman et al. 1982; Lowry et al. 1985; Quakenbush et al. 2015).

Our study confirmed SLE Beluga past (Vladykov 1946) and present have a varied diet as they do elsewhere (Kleinenberg et al. 1964; Seaman et al. 1982; Heide-Jorgensen and Tellmann 1994; Hobbs et al. 2008; Quakenbush et al. 2015). Capelin was the most important prey for Beluga during early summer, with sand lance and demersal fish such as cod progressively replacing Capelin in late summer and early fall as water warmed, suggesting some seasonality in prey selection or availability (Vladykov 1946). There was no seasonal pattern detected in Capelin occurrence in our study. Spawning for Capelin begins around mid-April in the upper estuary and lasts until the end of June in the lower estuary (Jacquaz et al. 1977). The dominance of Capelin in our March and May samples supports their importance for Beluga at that period, but whether their ingestion is supplemented with other species at these times is unknown. There was evidence of seasonality for sand lance but also other species in our study. Sand lance along with American Eel, Rainbow Smelt, and Atlantic Herring were detected in Beluga diets exclusively in late summer and fall, whereas other species from the families Zoarididae, Macrouridae, Liparidae, Cyplopteridae, and Cottidae were detected in spring and/or fall. The coincidence of SLE Beluga aggregation areas with

### Table 3. Average (± SE) fork length for Beluga (*Delphinapterus leucas*) prey, based on otolith length that were well preserved and moderately eroded (Class 1 and 2, respectively), and including eroded otoliths (all classes).

| Species                        | Class 1 and 2 | All classes |
|-------------------------------|---------------|-------------|
|                               | Mean length (cm) | n | Mean length (cm) | n |
| Sand lance (*Ammodytes sp.*)   | 13.2 (0.15)    | 49 | 12.1 (0.46)       | 8 |
| Atlantic Herring (*Clupea harengus* ) | 28.5 (0.85) | 10 | 23.6 (1.64)       | 20|
| Fourbeard Rockling (*Enchelyopus cimbrius*) | — | — | 22.4 (3.05)       | 5 |
| Atlantic Cod (*Gadus morhua*)  | —             | — | 33.7 (4.75)       | 7 |
| Atlantic Cod/Greenland Cod (*Gadus morhua/Gadus ogac*) | 40.8 (0.91) | 10 | 30.0 (0.71)       | 137|
| Daubed Shanny (*Leptoclinus maculatus*) | — | — | —                | — |
| Lycodes (*Lycodes sp.*)       | —             | — | 28.2 (1.16)       | 5 |
| Capelin (*Mallotus villosus*)  | 11.4 (0.15)    | 49 | 12.7 (0.22)       | 90|
| Silver Hake (*Merluccius bilinearis*) | — | — | 29.6 (0.57)       | 26|
| Marlin-pike (*Nezumia hairdi*) | —             | — | 23.4 (0.62)       | 10|
| Rainbow Smelt (*Osmerus mordax*) | — | — | 10.7 (0.26)       | 101|
| Redfish (*Sebastes sp.*)      | —             | — | 20.2 (0.40)       | 92|
| Deepwater Redfish (*Sebastes mentella*) | 18.5 (0.63) | 14 | —                | — |
| White Hake (*Urophycis tenuis*) | —             | — | 45.9 (2.97)       | 4 |

![Figure 5](image-url) **Figure 5.** Frequency distribution of fish size estimated from the length of 533 otoliths recovered from digestive tracts of St. Lawrence Estuary Beluga (*Delphinapterus leucas*) that were found dead between 1988 and 2019. All otoliths that allowed identification of species (i.e., regardless of degree of degradation) were included in this analysis.
sand lance habitat is also evidence for potential use of this species in recent years (Mosnier et al. 2016).

The St. Lawrence Estuary is a highly heterogeneous and dynamic environment, with expected effects on prey community structure and availability. The upper estuary is an area of shallow, warm water of relatively low salinity (<26 ppm), whereas the lower estuary consists of the deep, cold, and saline water of the Laurentian Channel, and the shallower water of intermediate salinity and temperature of the south shore (El-Sabh et al. 1979; Figure 1). While some prey, such as Capelin, Atlantic Herring, and sand lance, are relatively abundant in both sectors, others are more abundant in, or are exclusive to, one or the other. This is the case for Atlantic Tomcod, American Eel, Smooth Flounder, American Shad (Alosa sapidissima), and Rainbow Smelt, that occur mainly, or are more abundant, in the upper estuary (Bourget 2011). Conversely, redfish, cod, hake, poachers, Greenland Halibut (Reinhardtius hippoglossoides), Northern Shortfin Squid, Sea Lamprey, lycodes, American Plaice (Hippoglossoides platessoides), and most skate species are more abundant or found exclusively in the lower estuary (Scallon-Chouinard et al. 2007).

The upper and lower estuary are used differentially by adult male and female Beluga during summer, consistent with the sex- and age-class spatial segregation documented for the species (Michaud 1993; Smith and Martin 1994; Smith et al. 1994; Richard et al. 1997; Heide-Jorgensen and Lockyer 2001; Loseto et al. 2006, 2008). In the SLE, adult females and juveniles use primarily the upper estuary and south shore of the lower estuary during summer, while large individuals (presumed to be adult males) concentrate mainly in the lower estuary (Michaud 1993; Figure 1). Adult males overlap with females and juveniles in the shallower waters of the lower estuary, and in the Saguenay River and river mouth. Our upper estuary sample was dominated by females (7/8 carcasses) that had fed on a mix of small pelagic or bottom-dwelling fish and less on demersal fish. Our lower estuary sample was composed of individuals from both sexes, that had fed on multiple species of demersal fish. Isotopic mass balance models using a preliminary set of prey items and a wider range of species (Wilson 1975), and reach deeper depths than females (Schreer and Kovacs 1997), predictions that were verified in other Beluga populations (Seaman et al. 1982; Lowry et al. 1985; Szpak et al. 2019). In the SLE, differential prey access by sexes due to diving capacity is unlikely given that maximum bottom depth (350 m) is shallower than the species diving capacity (in excess of 1100 m; Richard et al. 1997). While our sample was too small to document sex differences in ingested prey size, Vladykov (1946) reported adult males ingested larger fish such as cod and sculpins, and females ate smaller prey such as squid, polychaete worms, and sand lance more frequently. Beluga swallow prey whole (Quakenbush et al. 2015), and feed using suction (Brodie 1969), a strategy particularly efficient for capturing squid or capelin (Werth 2000) or when feeding on benthic or concealed prey such as sand lance and polychaete worms (Kane and Marshall 2009), where substrate enhances effective suction distances (Nauwelaerts et al. 2008). While suction feeding may theoretically limit prey size, as suggested by Vladykov (1946), reports of Alaskan Beluga ingesting whole Coho (Oncorhynchus kisutch) or Chum Salmon (Oncorhynchus keta) 60 cm or more in size (Quakenbush et al. 2015), suggest that SLE Beluga preference for prey <30 cm and on average 20 cm in length is unrelated to anatomical or feeding mode limitations.

Local prey availability likely explained the fall ingestion of American Eel, Rainbow Smelt, and Atlantic Tomcod as these catadromous or anadromous species are present or particularly abundant in the SLE at that time of year, especially in the upper
Atlantic Herring spawns in multiple localities in the SLE in both spring and fall (Munro et al. 1998) and are particularly lipid-rich just before spawning. The scarcity of Atlantic Herring in SLE Beluga diet in this study and that of Vladykov (1946) may reflect our inability to capture this short event in our sample, the mismatch between Vladykov sampling sites and Atlantic Herring spawning sites, or the preference of Beluga for laid eggs instead of Atlantic Herring themselves (i.e., absence of hard parts; Vladykov 1946). Observations of persistently large numbers of SLE Beluga (hourly average of 70 to 80 Beluga) in a known Atlantic Herring spawning area during spring spawning (late May; Lesage and Kingsley 1995), and hunter reports of Beluga eating substantial amounts of Atlantic Herring in the spring at Rivière-Ouelle and near Ile Verte (north of Rivière-du-Loup, Quebec, Canada; Vladykov 1946) highlight their likely importance for SLE Beluga at least at that time of year.

Beluga are considered opportunistic feeders, but there might be prey or feeding times that are key to their fitness and survival, even though there was no evidence of a cycle of fast and feast in either Vladykov’s (1946) or our study (Figure 2). Peak calving is in July for SLE Beluga (Sergeant 1986), and captivity studies indicate that energy intake increases 1.5- to 2-fold during the last two months of pregnancy. It peaks at four times normal during the first month after birth and remains at 1.5 to 2 times normal for the following three months of lactation (Kastelein et al. 1994). Accordingly, energy demands on pregnant SLE Beluga females start rising in May and remain high through at least early fall. Casgrain (1873) reported that SLE Beluga at Rivière-Ouelle in the spring are thin and voracious, feeding on Capelin and Rainbow Smelt in such a way that they put on 13 to 15 cm, sometimes 20 cm of fat in 8–10 days. Although the reported gain in blubber thickness appears extreme, these observations suggest that spring feeding might be critical in SLE Beluga for replenishing fat stores just before entering the last months of the gestation and calving period. Vladykov (1946), based on condition and stomach fullness indices, suggest that Beluga are fat in June, less in July and August, and fatter again in September. If this is the case, then spring and fall spawning species such as Capelin and Atlantic Herring, and catadromous or diadromous prey such as Rainbow Smelt, and possibly the large demersal fish that gain in importance in female diet in the fall, might be important for Beluga. Capelin and sand lance are still present in the SLE (e.g., Dutil et al. 2009), but their abundance is unknown. In Newfoundland, Capelin stocks have collapsed in recent decades (Buren et al. 2019); whether similar patterns prevail in the SLE and Gulf of St. Lawrence is unknown (DFO 2015). Stock abundance of other species such as spring Atlantic Herring, Rainbow Smelt, American Eel, and Atlantic Cod, are known to be considerably reduced compared to historical levels (Mingelbier et al. 2001; DFO 2010, 2019; Swain 2016; Équipe de Rénestabilissement de l’Épervier arc-en-ciel, population du sud de l’estuaire du Saint-Laurent 2019). Whether the SLE Beluga recent high female and calf mortality rates (Lair et al. 2016; Gosselin et al. 2017) and failure to recover since the 1980s might at least be partially related to inadequate access to lipid-rich food at crucial times cannot be dismissed, and warrants further investigation. In eastern Beaufort Sea Beluga, there are concerns that the low body condition index (based on blubber thickness) reported in recent years might be caused by a lower availability of Arctic Cod (Boreogadus saida) (Choy et al. 2017), and ingestion of prey of a lower lipid quality requiring higher energy output for their capture (Loseto et al. 2018).

At a time when several Beluga populations worldwide are threatened by previous overhunting and habitat degradation (i.e., COSEWIC 2004; National Marine Fisheries Service 2016), access to information on current and past diet and seasonal feeding cycles is critical for predicting and mitigating potential impacts of anthropogenic activity and climate at times and places where they matter the most. While our sample size was too small to quantitatively evaluate the contemporary diet of SLE Beluga, our results indicate that fish from stocks believed to be depleted (Atlantic Cod, American Eel) or that are now recovering (Striped Bass, redfish) should be considered as possible prey and not dismissed from diet estimations using quantitative models based on molecular tracers, or when trying to understand current contamination sources affecting this population. Approaches for investigating diet should also consider seasonality in prey availability and quality, and inter-individual diet variability as mechanisms for reducing potential competition (Tinker et al. 2008).

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Writing – Original Draft: V.L.; Writing – Review & Editing: S.L., S.T., and P.B.; Conceptualization: V.L.; Investigation: V.L., S.L., S.T., and P.B.; Methodology: V.L. and S.T.; Formal Analysis: V.L. and S.T.; Funding Acquisition: V.L.

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Supplementary Material:

Table S1. Numerical abundance of fish and invertebrate species in the digestive tracts of Beluga (Delphinapterus leucas) collected in various regions of the St. Lawrence Estuary through Beluga carcass recovery, 1989–2019.