Spatial distribution and count of harbour seals (Phoca vitulina) and grey seals (Halichoerus grypus) in the Estuary and Gulf of St. Lawrence from an aerial survey conducted in June 2019

Arnaud Mosnier, Antoine Dispas, and Mike O. Hammill

Fisheries and Oceans Canada Maurice Lamontagne Institute P.O. Box 1000 850 Route de la mer Mont-Joli, QC G5H 3Z4

2023

Canadian Technical Report of Fisheries and Aquatic Sciences 3541



Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques*.

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian technical report of fisheries and aquatic sciences 3541

2023

Spatial distribution and count of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the Estuary and Gulf of St. Lawrence from an aerial survey conducted in June 2019

Arnaud Mosnier, Antoine Dispas and Mike O. Hammill

Regional sciences branch Quebec region Pelagic and ecosystemic sciences division Fisheries and Oceans Canada Maurice Lamontagne Institute 850, Route de la Mer Mont-Joli, QC G5H 3Z4 © His Majesty the King in Right of Canada, as represented by the Minister of the Department of Fisheries and Oceans, 2023 Cat. No. Fs 97-6/3541E-PDF ISBN 978-0-660-48521-8 ISSN 1488-5379

Correct citation for this publication:

Mosnier, A., Dispas, A., and Hammill, M.O. 2023. Spatial distribution and count of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the Estuary and Gulf of St. Lawrence from an aerial survey conducted in June 2019. Can. Tech. Rep. Fish. Aquat. Sci. 3541 : v + 60 p.

TABLE OF CONTENTS

1.	INT	RODUCTION 1
2.	ME	THODS
2	.1	Study area 3
	2.1.	1 The Saint Lawrence Estuary and the Saguenay fjord:
	2.1.	2 The Gulf of Saint Lawrence: 4
2	.2	Aerial survey4
2	.3	Analyses 6
3.	RES	SULTS
3	.1	General spatial distribution of Harbour seals and Grey seals during the survey
3	.2	Harbour seal in the St. Lawrence Estuary 8
3	.3	Harbour seal in the gulf of St. Lawrence
3	.4	Grey seal in the St. Lawrence Estuary
3	.5	Grey seal in the gulf of St. Lawrence10
4.	DIS	CUSSION11
4	.1	Harbour seals11
4	.2	Grey seals13
4	.3	Survey observations and perspective15
AC	KNO	WLEDGMENTS16
RE	FERE	ENCES17
TAE	BLES	S24
FIG	URE	S28
APF	PEND	DICES

ABSTRACT

Mosnier, A., Dispas, A., and Hammill, M.O. 2023. Spatial distribution and count of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the Estuary and Gulf of St. Lawrence from an aerial survey conducted in June 2019. Can. Tech. Rep. Fish. Aquat. Sci. 3541 : v + 60 p.

In June 2019, a helicopter survey was conducted to determine harbour and grey seals distribution and abundance in the Estuary and Gulf of St. Lawrence. A total of 5,714 harbour seals and 14,691 grey seals were counted at haul-out sites. In the estuary, 2,140 harbour seals and 839 grey seals were counted, representing a significant increase from surveys conducted in 1995-96 and 2000, particularly in the upper estuary for grey seals and in the lower estuary for harbour seals. In the Gulf, grey seals were dominant (13,852 grey seals versus 3,574 harbour seals). Counts were higher than in previous surveys, due to both a larger survey area being covered in 2019, and a greater number of animals present in areas covered during previous surveys. The 2019 survey provides the first comprehensive count and spatial distribution data for harbor seals and grey seals over the entire Estuary and Gulf of St. Lawrence. Combined with information from similar surveys conducted in other regions in eastern Canada, these data will serve to improve knowledge of the population size and distribution of both species in this area.

RÉSUMÉ

Mosnier, A., Dispas, A., and Hammill, M.O. 2023. Spatial distribution and count of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the Estuary and Gulf of St. Lawrence from an aerial survey conducted in June 2019. Can. Tech. Rep. Fish. Aquat. Sci. 3541 : v + 60 p.

En juin 2019, un relevé héliporté a été réalisé afin de déterminer la distribution et l'abondance du phoque commun et du phoque gris dans l'estuaire et le golfe Saint-Laurent. Au total, 5714 phoques communs et 14691 phoques gris ont été dénombrés sur les sites d'échouerie. Dans l'estuaire, 2140 phoques communs et 839 phoques gris ont été dénombrés, représentant une augmentation significative par rapport aux relevés de 1995-96 et 2000, surtout dans l'estuaire moyen pour le phoque gris et dans l'estuaire maritime pour le phoque commun. Dans le golfe, le phoque gris était dominant (13852 phoques gris contre 3574 phoques communs). Les dénombrements étaient plus élevés que lors des relevés précédents en raison d'une plus grande superficie couverte en 2019, et d'un plus grand nombre d'animaux présents dans les zones couvertes lors des relevés précédents. Le relevé de 2019 est le premier à fournir des données de l'estuaire et du golfe Saint-Laurent. Combiné aux informations de relevés similaires effectués dans d'autres régions de l'est du Canada, ces données permettront d'améliorer les connaissances sur la taille et la distribution des populations de ces deux espèces dans cette région.

1. INTRODUCTION

Seals are top predators and can alter the dynamics and structure of communities in the marine ecosystem (Bowen, 1997). They are present in various habitats ranging from the Arctic to Antarctica. Information about their spatial distribution and abundance is crucial to inform management decisions, understanding effects of management strategies, to estimate their impacts on commercial fisheries and other marine species, and to evaluate the repercussions of anthropogenic activities (maritime transport, industrial developments etc.) on seals populations (Lesage et al. 1995; Olesiuk et al. 2010). However, the availability of this information generally depends on their status, with greater interest in threatened or commercially harvested species.

The harbour seal, *Phoca vitulina*, is globally the most widely distributed pinniped occupying a wide variety of habitats and climatic zones across the Northern Hemisphere (Boulva and McLaren, 1979; Härkönen and Heide-Jørgensen, 1990; Stanley et al. 1996; Liu et al. 2022). Three subspecies are recognized (Berta and Churchill, 2012): the Pacific harbour seal (*P. v. richardii*, Gray, 1864), the Atlantic harbour seal (*P. v. vitulina*, Linnaeus, 1758), and the Lacs des loup marins harbour seal (*P. v. mellonae*, Doutt, 1942; Figure 1). Only the last two are present in eastern Canada: *P. v. vitulina* (previously referred to as *P. v. concolor*), is found along the Atlantic and Arctic coasts and *P. v. mellonae*, is a small population endemic to a chain of a freshwater lakes in Nunavik (northern Quebec). The latter is listed as "Endangered" by both the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; COSEWIC 2007) and the International Union for the Conservation of Nature (IUCN; Lowry, 2016), however, other harbour seals populations are globally listed as "Least Concern" by the IUCN, or "Not at risk" in Canada (COSEWIC, 2007).

The extensive range of this species, its coastal habits, and its relatively small size (adult 1.5-1.85 m and ~100kg), contributed to that fact that it is one of the most well-studied pinniped in the world (Teilmann and Galatius, 2018). Several studies, conducted in particular in the northeast Atlantic and Pacific, have examined the role of harbour seals as predators (Aarts et al. 2019), or prey (Shields et al. 2018), the changes in their demographic parameters (Harkonen et al. 2002), their response to disease (Harkonen et al. 2006) and inter-specific competition with other seal species (Svensson, 2012). However, the availability of information on abundance and population trends across their range shows considerable variation between subspecies, regions, or populations, with detailed long term information available for some regions, while in other areas estimates of abundance, trends and demography are lacking (Blanchet et al. 2021).

In the early 20th century, harbour seals were abundant in Canada, but conflicts with fisheries led to the implementation of bounty programs between 1927 and 1976, that probably resulted in declines in abundance (Stobo and Fowler, 1994; Hammill et al. 2010). Based on questionnaires, distributions of bounty kills and interviews, Boulva and McLaren (1979) estimated that the harbour seal population in eastern Canada was 12,700 individuals in 1973. This included 5,140 in the Estuary and the Gulf of St Lawrence, 5,250 in Nova Scotia (1,250 on Sable Island), 2,010 in Newfoundland, and 300 in St. Pierre and Miquelon. Since 1979, hunting has been prohibited, but the assessment of harbour seal spatial distribution and abundance has been limited to specific areas including Sable Island, the Bay of Fundy, and portions of the St. Lawrence Estuary (Estuary) and the Gulf of St Lawrence (Gulf) (Lucas and Strobo, 2000; Bowen et al. 2003a; Stobo and Fowler; Lavigueur et al. 1993; Lesage et al. 1995, Robillard et al. 2005). Harbour seal abundance appeared to have increased in all these areas, but had

declined on Sable Island, partly due to interactions with the larger and more abundant grey seal (Robillard et al. 2005; Bowen et al. 2003a) and shark predation (Stobo, 2000). Since the early 2000's, data are lacking in eastern Canada due to limited survey efforts (Teilmann and Galatius, 2018; Blanchet et al. 2021), in part because of the low economic importance of this species (Baird, 2001), and the fact that it likely has less impact on commercial fish populations than other more abundant seal species (Dubé et al. 2000, Swain et al. 2019).

Aerial surveys to estimate seal abundance in eastern Canada (e.g. grey and harp seals) are generally flown during the breeding season, when animals aggregate on island colonies or the ice. At these sites, only reproductively mature adults and pups are present and surveys focus on counting only the number of pups that have been born. Estimates of pup abundance are then incorporated into a population model along with information on age specific reproductive rates, and anthropogenic removals to provide an estimate of total abundance (e.g. Hammill et al. 2015). Harp seals, grey seals and hooded seals all pup during winter-early spring, thus most seal surveys have been conducted at this time. In the case of harbour seals, pupping occurs during late spring-early summer (Dubé et al. 2003). Unlike the other species, the formation of large aggregations or colonies of breeding animals does not occur. Instead, there are some local groups of breeding animals, but animals from all age-classes can be hauled out in varying proportions near females with pups. Also, unlike many other species, harbour seal pups enter the water soon after they are born and can follow the female to sea and to alternative haul-out sites. Therefore, for this species, the aerial surveys are total counts of hauled out animals, rather than just counts of pups. Estimates of total abundance can be obtained by adjusting the counts of hauled out animals to account for the proportion of the population that is in the water when the aircraft passes overhead (Olesiuk et al. 1990). An additional complication is that grey seals also haul-out on land during the spring and summer. either as separate herds or in some cases animals may be interspersed among hauled out harbour seals, complicating efforts to estimate harbour seal abundance. However, recording their occurrence during harbour seal surveys was also a great opportunity to improve the information on their late spring- early summer spatial distribution.

Northwest Atlantic grey seals (*Halichoerus grypus*) were abundant throughout the region during the 16th and the 17th centuries, and were reported to have declined significantly during the 18th centuries due to intensive exploitation (Chantraine, 1980; Stobo and Fowler, 1994; Härkönen et al. 2007; Hammill et al. 2017a). Until 1950, they were considered rare throughout eastern Canada (Lavigueur and Hammill, 1993). However, since the first surveys in the 60's, the size of the northwest Atlantic grey seal population has grown considerably, reestablishing breeding colonies in Canadian and U.S. waters, supported by a large growth of the colony of Sable Island (Mohn and Bowen 1996; Hammill et al. 1998; Bowen et al. 2003a; Härkönen et al. 2007; den Heyer et al. 2020). Grey seal abundance has thus increased from a few thousand animals in the early 1960s to a current estimate of 366,400 individuals in 2021 (DFO, 2022).

In this study, an aerial survey was flown to obtain information on the spatial distribution and abundance of harbour seals and grey seals in the Estuary and the Gulf of St. Lawrence during June 2019. The survey was completed within a relatively short window of one month and is the first survey to provide complete coverage of the study area. Previous surveys flown during the 1990s had a more limited spatial coverage but provided an opportunity to examine local changes in abundance (Robillard et al. 2005). In addition to addressing regional management needs, the data acquired from this survey will also contribute to Canada's international commitment to support fishery exports into United States markets by establishing systems for monitoring marine mammals and sustainable harvesting comparable to those that are currently implemented in that country. (U.S. Marine Mammal Protection Act; 81 FR 54390; August 15, 2016; NOAA-NMFS-2020-0127). This study was the first of three regional survey initiatives that subsequently covered the coasts of Nova Scotia/New Brunswick in the summer of 2020 and Newfoundland and Labrador in summer 2021. The combination of these three surveys will provide the first comprehensive representation of the late spring-early summer spatial distribution of harbour seal and grey seal in eastern Canada and the first estimate of the harbour seal population size in this area. The grey seal abundance estimate will remain based on winter pup production surveys (DFO 2022).

2. METHODS

2.1 STUDY AREA

The study area included the entire coastline and islands of the St. Lawrence Estuary ("Estuary"), the lower portion of the Saguenay River ("Saguenay") and the Gulf of St. Lawrence ("Gulf") (Figure 1). Particular attention was paid to areas where high numbers had been reported or observed in previous surveys (Boulva and McLaren 1971; Robillard et al. 2005)

2.1.1 <u>The Saint Lawrence Estuary and the Saguenay fjord:</u>

The St. Lawrence River, originating from the Great Lakes, becomes an estuary starting from Îsle d'Orleans and extends about 400 km seaward to Pointe des Monts / Sainte-Anne-des-Monts (Figure 1; Savenkoff et al. 1997). It is naturally divided into two parts on either side of the mouth of the river Saguenay (Tadoussac / Cacouna) due to differences in salinity, bathymetry and hydrographic characteristics. The Upper Estuary extends over a distance of 150 km between Quebec City and Tadoussac. It is characterized by high tides, low salinity and depth (up to 100 m). The Lower Estuary occurs downstream, from Tadoussac to a north-south line between Pointe des Monts on the north shore and Sainte-Anne-des-Monts on the south shore. This area is characterized by higher salinity and depths to 350 m (El-Sabh and Silverberg 1990; Savenkoff et al. 1997). The North shore of the Estuary is generally characterized by a steep coastline with deeper waters and limited littoral zones, while the South shore has a gentler slope, shallower waters and the presence of several islands (Lesage et al. 1995; Robillard et al. 2005). Similar to Robillard et al. 2005, this study considers the following islands: Ile aux Grues, Iles aux Loups Marins, Ile aux Fraises, Ile aux Lièvres, Ile blanche and Ile Rouge as part of the South shore of the Upper Estuary.

The Saguenay River, flows in the St. Lawrence river at Tadoussac. Its fjord has steep cliffs with few rocks on the shore, a few bays and deep water (up to 275 m; Drainville, 1968). It is also characterized by high tides and low salinity. In the Upper Estuary and the fjord, the tides are semi-diurnal with fairly large tidal ranges (mean range = 3.9 and 3.6 m; max range = 5.2 and 5.4 respectively) while they are greatly smaller in the Lower Estuary (mean range = 2.6 m; max range = 4.1 m; Canadian Hydrographic Service 2019 - tide tables for Saint-Jean Port Joli, Pointe au Père and Port Alfred in June 2019).

2.1.2 The Gulf of Saint Lawrence:

The Gulf of St. Lawrence is considered to be a semi-enclosed sea because its internal current circulation restricts interaction with the Atlantic Ocean (Therriault, 1990). It covers an area of over approximately 240,000 km² that extends from Pointe des Monts/Sainte-Anne-des-Monts to the west to the Atlantic Ocean through the Cabot Strait and the Strait of Belle Isle to the east (Figure 2; Saucier et al. 2003). Salinity is high (>28 ‰) and organic production is particularly important. Based on geophysical characteristics, the Gulf can be divided from north to south into several zones: The North shore, which has an average depth of 50 to 70 m, is characterized by an abrupt shelf with a rocky bottom that favours upwelling of deep cold water from the current of Labrador (Saucier et al. 2009). The Lower North shore area is characterized by shallower waters and the presence of numerous islands and reefs close to the coast (Figure 2). The Laurentian and Esquiman channels present deep waters up to 400 m deep). The southwestern part of the Gulf, is characterized by the Magdalen shelf with warmer, shallower waters (about 50 m) and sandy bottoms with a limited coastline (Figure 2). Finally, the Gaspé Peninsula and the western coasts of Cape Breton Island and Newfoundland are characterized by sharp coastlines with few islands, reefs or bays (Figure 2; Therriault 1990, Robillard et al. 2005). The tidal range in the Gulf is very small compared to the Estuary.. Depending on the area, the mean tidal range varies between 0.5 to 1.6 m (Max 1.1 to 2.6 m; Canadian Hydrographic Service 2019).

2.2 AERIAL SURVEY

The coastal aerial survey was conducted from June 4 to 30, 2019 using a Bell 429 helicopter flying at a ground speed of 70 knots, an altitude of 152.4 m (500 feet) and within 300m of the coastline. The survey dates were chosen to coincide with the birth and lactation period for harbour seals during which they are known to spend more time hauled out and thus more likely to be detected (Ashwell-Erickson et al. 1986; Olesiuk, 1999, Dubé et al. 2003).

Survey was flown on days with good weather conditions defined as days with no rain, no fog and low winds (Beaufort 3 max; see ECCC 2017), ensuring good visibility and maximizing again the chances of seals being hauled-out (Pauli and Terhune, 1987). In areas where the tidal range was considered minimal (<1 m; e.g. Southern from the Gulf), flights were conducted within a 4-hour period centered on noon. In the Estuary and the northern Gulf where the tidal range was higher, overflights were carried out in the range of -2 h to +2 hours around the low tide (Olesiuk et al. 1990; Robillard et al. 2005).

The aircraft flew keeping the shore on the left side of the platform at a distance of 300 m from the shore edge. The goal was to be able to observe seals while minimizing noise disturbance that would cause them to rush into the water (Robillard et al. 2005, Hammill et al. 2010). The helicopter's track was recorded by two GPS (Garmin GPS 73 and a Bad Elf GPS Pro+). The Bad Elf GPS was connected via Bluetooth to a Microsoft Surface tablet running

QGIS, to track the helicopter position in real-time. Observations from previous surveys (Robillard et al. 2005) were overlaid on the map to avoid missing areas with known colonies.

Two observers were located on the left side of the helicopter, one in the co-pilot seat and the second, in the forward facing seat located behind the co-pilot. Each observer was equipped with a digital voice recorder (SONY UX560F), a camera (Canon EOS Rebel T6 EF-S 55-250 mm f/4-5.6 IS STM or NIKON D850 55-300 mm 4.5-5.6G ED) and a watch synchronized with the GPS time. Sightings on and near the haulout sites were recorded on the voice recorder mentioning at a minimum the time stamp (allowing merging with the GPS positioning), the species and their numbers. Most of the seals observed were also photographed for confirmation of species identification and count.

On two occasions, the observations had to be conducted using different methodologies. (i) Along the Lower North shore (Figure 2), in areas characterized by numerous little islands, it was not possible to cover the whole coastline, so the helicopter followed a line transect design (i.e. series of parallel lines) during which there were one observer on each side of the helicopter. An additional camera (NIKON D850: 24.0 mm f/1.4), installed into a "pod" located under the nose of the helicopter and pointing downward, allowed to take images directly under the helicopter. Controlled via a CamRanger device and an Ipad interface with WiFi connection, the camera automatically took one photo every three seconds. Observer sightings were recorded as indicated before and the "pod" photos were later checked for seals. (ii) On Brion Island, where very high densities of grey seals were encountered, the helicopter overflew the beaches at an altitude varying between 500 and 650 feet, with the pod camera taking one photo every three seconds. The three seconds interval allowed for a slight overlap between the photos, ensuring a total coverage of the area. Reference points on the successive images were used to avoid double counts. The total seal count was obtained directly from these photos.

All photo observations were double checked for species identification and count. GPS positioning allowed for the detection of potential duplicated observations. In cases where the animals were not visible on the images, but were mentioned on the voice recorder, the voice record was considered valid, as the animals may already have been under the water when the photo was taken. When the number of seals visible on the images was higher than the number recorded on the voice recorder, the highest count was kept. The seal count based on images was carried out by the two observers/photo readers for the first half of the survey. Preliminary comparison between observers counts showed negligible differences. Therefore, only one of the two readers completed the rest of the counts for the remaining images. The observer examined both sets of images to ensure that no seals were missing. When doubts arose, the other reader double checked the observations and a final decision was taken.

From June 4 to 30, the survey included 18 flying days and 9 days with no flights ("down days") due to weather conditions or logistic constraints. The Southern Gulf was flown in 7 days, from June 4 to 11 with one down day. Day 1) Magdalen Islands, Brion Island, Corps-Mort and Rocher-aux-Oiseaux; Day 2 and 3) Prince Edward Island; Day 4) West Coast of Cape Breton; Day 5) Port Hawkesbury to Moncton; Day 6) Moncton to Bathurst; Day 7) Bathurst to Gaspé. The areas of Kouchibouguac National Park (New Brunswick - Parks Canada) and Île-Bonaventure-et-du-Rocher-Percé Park (Gaspésie -SEPAQ) were not overflown, as low altitude flights were prohibited in these areas owing to the presence of nesting birds. Since these two regions are known to have concentrations of seals during summer, especially in Kouchibouguac (Lavigne 1978; Boulva and McLaren 1979; Robillard et al. 2005), a count was obtained from

photos and videos taken from a drone flight conducted by Parks Canada on June 7 in Kouchibouquac National Park (Karyne Bellehumeur, Daniel Gallant, personal communication). After one down day on June 12, the survey of the South shore of the Estuary was completed in 2 days (June 13 and 16), interspaced with two days with no flights because of weather. Day 8) Gaspé to Rimouski. The bay of Gaspé was surveyed a second time as we thought we missed individuals on our first pass on day 7 due to windy conditions at the end of the day. Day 9) Rimouski to Québec City. Bad weather precluded flying on June 17 and June 18 and instead the aircraft transited from Quebec to Sept-Iles. The North shore of the Estuary was covered in 2 days: June 19 and June 21. The survey was conducted from east to west to follow the tide and maximize the survey period (Robillard et al. 2005). Day 10) Sept Iles to Forestville; Day 11) Forestville to Baie-St-Paul. We were not authorized to fly over the fjord of the Saguenay, however, Parks Canada (Sarah Duguette, Felix Ledoux, Samuel Turgeon, personal communications) and SÉPAQ staff were able to conduct boat surveys at low tide covering 85 km of the downstream portion of the Saguenay river from Cap à l'Est to Tadoussac. After a repositioning to Sept-Iles at the end of Day 11, the Northern Gulf including Anticosti Island was surveyed in 5 days interspersed with 2 days off (from June 22 to June 28). Day 12) Sept-Îles to Havre St. Pierre; Day 13) Mingan Archipelago National Park Reserve. The sector of "Îles aux Perroquets", located at the extreme west of the park, where large groups of grey seals are known to occur in summer (Parks Canada, 2017) was not overflown due to the presence of a bird sanctuary. Parks Canada (Marie-Claude Roy, personal communication) provided opportunistic observations coming from this area on July 12. Unfortunately, these observations were obtained outside the -2h, +2h window around the low tide. In addition, it was mentioned that co-occurring anthropogenic activities probably drove the seals away before those observations were taken, suggesting an underestimation of the number of animals. Day 14) Anticosti Island. The survey extended slightly outside the 4h window centered on the low tide (survey ended 02h51 after the low tide), because we found the carcass of a right whale stranded on the island and stopped to collect some samples; Day 15) Havre St. Pierre to Harrington Harbor; Day 16) Harrington Harbor to Blanc Sablon. Finally, the west coast of Newfoundland was covered in 2 days: Day 17) Blanc Sablon to Norris Point; Day 18) Norris Point to Red Rock.

For areas where flying was not permitted, including the Saguenay fjord, Île-Bonaventureet-du-Rocher-Percé, Kouchibouguac National Park and Îles aux Perroquets (Mingan Archipelago National Park Reserve), a basic research protocol was sent to the local Parks Canada teams to obtain surface counts from a boat, or using a drone, during the survey period. The protocol ensured that the observation conditions were consistent with those of the aerial survey, in particular the delay (± 2 hours) relative to the low tide to be respected to ensure a greater probability of detection.

2.3 ANALYSES

Recordings of counts and their respective date and time information were transcribed in Excel and saved as a text file. A script written in R programming software (R core Team, 2020) was used to georeference each observation by merging the corresponding GPS positioning with the observation time. A second R script applied a spatial clustering function to group individual

observations based on a defined distance threshold between observations to create readable maps of the sightings. This function uses a hierarchical clustering approach (function "hclust" from the "stats" package) considering the distance between observations. A distance threshold value cut the clustering "tree" obtained from the complete linkage method (Everitt et al. 2001), The resulting clusters identified by the function corresponded to neighboring observations occurring in a circular area with radius equal to the selected distance threshold. Groups were obtained using distance thresholds of 500 m, 1, 2.5, 5, 10 and 20 km respectively. The number of animals belonging to the same group was added together and these counts were associated with a geographical position calculated as the weighted average position of the sightings considering the number of individuals recorded in each of these sightings. However, in doing so, the final location of each group was biased toward the location of the sightings with the highest number of individuals (see example in Appendix 1). Both the raw sighting locations and the spatially clustered sightings were converted into shapefiles. Maps showing the location and number of animals sighted were produced using the geographic information system QGIS (QGIS.org, 2022). Depending on the scale of the map, the version of the spatially clustered sightings offering the best readability was used, i.e. generally considering sighting grouped using the 20 km distance threshold for the global overview of the survey and a smaller threshold for maps showing smaller specific areas.

Trends in the number of harbour and grey seals present in June in different sectors of the Estuary, as well as at the scale of the entire Estuary, were estimated using an exponential growth rate model (Caughley 1977). This model assumes no density-dependence on the growth rates of these populations. This is considered appropriate under the assumption that historical population sizes of both species were much larger than at present. This model was fitted to the survey time series which included count data from surveys flown in 1995, 1996 and 2000 (Robillard et al. 2005) and from the 2019 survey.

3. RESULTS

A total of 12,151 km was flown during the survey, including 9,985 km of active searching. From this, 1,560 km were flown in the Estuary and 8,425 km in the Gulf. Almost all the coasts and islands of the Estuary and the Gulf were overflown (Figure 3). In areas that could not be flown, counts were obtained from drone or boat surveys conducted simultaneously with our aerial survey. No effort data was recorded during these complementary surveys, however, both shores of approximately 85 km of the downstream portion of the Saguenay river was covered, adding at least another 170 km of coast surveyed.

Flight plan and survey conditions considered as optimal for harbour seal observation were respected throughout the survey (except the day in Anticosti). Nearly all observations were conducted in the range of -2 h to +2 h around low tide in the Estuary and northern Gulf (Hydrographic Service of Canada, 2019) where the tide range was considered large enough to have an impact on harbour seal haul-out patterns (Olesiuk, 2010). In the other areas, the survey period was centered around noon. Moreover, due to favorable weather conditions, the number of "down-days" was very low (9 down-days / 18 survey days) and flying conditions were good (no rain, fog or strong winds).

3.1 GENERAL SPATIAL DISTRIBUTION OF HARBOUR SEALS AND GREY SEALS DURING THE SURVEY

Only two species of seals were observed in the study area including 5,714 harbour seals and 14,691 grey seals. Both species were present in the Estuary and the Gulf, but showed large differences in their spatial distribution (Figure 4). Overall, harbour seals were observed more frequently (380 vs 65 groups of observations for harbour and grey seals, respectively, when spatially clustered using a distance threshold of 500 m; 162 vs 7 in the Estuary; 218 vs 58 in the Gulf), but grey seals were more abundant. Grey seals dominated overall and in the Gulf, where they accounted for 79% of observations (13,852 grey seals and 3,574 harbour seals; Figure 6). However, harbour seals were more abundant in the Estuary, where they represented 70% of observations (2150 harbour seals and 839 grey seals; Figure 5). Harbour seals were generally seen in small groups, unlike grey seals. The largest groups of harbour and grey seals were found in the Gulf and included 725 versus 10,739 individuals, respectively (Figure 4, 5 and 6). Grey and harbour seals rarely shared the same haul-out site, but were regularly observed in the same areas.

3.2 HARBOUR SEAL IN THE ST. LAWRENCE ESTUARY

A total of 2,140 individuals were counted in the Estuary, between Isle-aux-Grues to the west and Méchins and Baie Comeau to the east (Figure 7). The counts were much higher than reported from surveys flown during the 1990s (Table 1; Table 2). The trend analysis using estimates from all surveys showed a significant positive growth of 7% per year. This annual rate of increase was not different when comparing North to South shore, but numbers of harbour seal in the Lower Estuary has increased significantly (p < 0.01) and at a slightly more rapid rate than in the Upper Estuary (7.3% versus 6.2%, respectively; Table 3; Figure 8).

Previous aerial surveys had shown that while harbour seals occurred in all parts of the Estuary, a larger number were present on the South shore and in the lower part of the Estuary. In 1995, for example, 75% of harbour seal sightings occurred along the South shore and nearing islands. In 2019, this proportion was down to 65%. The Upper / Lower Estuary percent observation ratio also changed from 40/60 in 1995 to 30/70 in 2019 (Figure 9, Figure 10, Figure 11). Only 21 animals were observed in the Saguenay, representing less than 1% of the total number of harbour seals counted in the Estuary (Table 2, Figure 9 - Figure 12).

Areas of highest counts (> 100 individuals) included, in decreasing order: Bic National Park (N = 372; Figure 13), Battures aux Outardes (N= 266; Figure 14), Métis-sur-Mer (N= 233, including both Pointe Mitis and Baie Mitis; Figure 15), Ile aux Basques (N= 200), Battures aux Loups Marins (N= 145), Battures aux Alouettes (N= 129), Hauts-fonds des Mille-Vaches (N= 112; Figure 16) and Ile aux Lièvres (N= 102) (Table 4; Figure 7, Figure 13-Figure 16;). Harbour seals were seen in all of these areas in previous surveys, but some of them have undergone major changes with counts increasing from a few individuals before 2000, to hundreds of them in 2019 (Ile aux Lièvres, 0-1 vs 102, Battures aux Loups Marins 2-8 vs 145, Battures aux

Outardes 12-49 vs 266, see Table 4 for details). For sites showing co-occurrence with grey seals across the different surveys, including Bic Archipelago, Ile Blanche, Ile aux Lièvres, Ile aux Fraises and Battures aux Outardes, large numbers of harbour seals were only observed when grey seals were in low number or absent (Table 4). For Île aux Lièvres, the increase in the number of grey seals is concomitant with a decrease in the number of harbour seals (correlation = -0.90), however, the time series is not long enough to obtain a significant relationship (p = 0.1).

3.3 HARBOUR SEAL IN THE GULF OF ST. LAWRENCE

A total of 3,574 harbour seals were observed in the Gulf (Table 5; Figure 17). They were sighted much less frequently than in the Estuary (1.4 harbour seals / km of observation effort versus only 0.4 harbour seals per km in the Gulf). Harbour seal counts in the Gulf were much higher than in the previous surveys (467 and 423 in 1996 and 2001 respectively; Table 5). Harbour seals were mostly found in the northwestern part of the Gulf (Figure 6), including large numbers of animals observed in Forillon (N=852; Figure 18), Anticosti Island (N=639; Figure 19), and Mingan Islands (N = 264; Figure 20). However, they were almost absent on the coasts west of Longue-Pointe de Mingan (north shore; Figure 17), and west of Grande-Vallée (north of the Gaspé Peninsula). Large numbers of animals were also found in the southern Gulf, along the southern coast of Prince Edward Island (N=696; Figure 21), and on the south coast of the Northumberland Strait (N=164; Figure 22). In addition, two large harbour seal groups were seen along the Newfoundland west coast, located respectively next to Gros Morne National Park (N = 228; Figure 23) and along the south west coast of George's Bay (N=525; Figure 24). In the Magdalen Island area fewer harbour seals were observed compared to previous surveys (23 in 2019 vs 32 in 2016). However, overall, as observed in the Estuary, the 2019 counts were generally 1.6 to 25 times higher than those obtained from previous surveys (Table 6).

3.4 GREY SEAL IN THE ST. LAWRENCE ESTUARY

A total of 839 grey seals were observed in the Estuary, which is more than double the number of individuals observed in the 2000 survey. Trend analysis based on the exponential model suggested an annual growth rate of ~5% for the entire Estuary (Table 3; Figure 8). However, when the Upper Estuary and Lower Estuary were considered separately, it showed no trend in the number of grey seals observed in the Lower Estuary with a mean of 238 (95% CI = 183-312) individuals (annual growth rate = ~ 0%) but a large increase in the Upper Estuary going from a few dozen animals prior to 2000 to more than six hundred in 2019 (annual growth rate = 12.5%; Table 2; Table 3, Figure 8).

The spatial distribution of grey seals in the Estuary was less extensive than that of harbour seals (Figure 5). They were concentrated in large groups in four areas (Figure 25; Note: 1 and 2 individuals were observed outside of these main areas off Baie Comeau and south of Chafaud aux Basques, respectively). In 2019, the largest groups were observed in the Upper Estuary on Ile aux Fraises (N=278) and Ile Rouge (N=341; Figure 25). The two other large

groups were located in the Lower Estuary, on a small island called La Razade d'en Bas (N=50) off the south shore and at the Betsiamite River mouth (N= 167; Figure 23, Figure 25). Important changes in grey seal spatial distribution seem to have occurred in the Estuary since the first surveys conducted in 1995. Prior to 2000, the majority of grey seals were observed in the Lower Estuary (> 70% of observations in 1995, 1996, 2000), but in 2019 survey, 74% of the individuals were observed in the Upper Estuary and only 26% of the animals were observed in the Lower Estuary (Table 1; Figure 26). To be consistent with Robillard et al. 2005, counts obtained from the islands located in the Upper Estuary were associated to the South shore (see methods; Table 2). However, the largest grey seal counts obtained in this area were from Ile Rouge and Ile aux Fraises which are located approximately at the center of the Estuary. At a finer scale, more than a hundred grey seals were seen on Battures aux Outardes in June 1995 and 1996, but none were observed in this area in 2000 and 2019 (Table 4). No grey seals were observed at the Betsiamite River mouth in 1995 and 1996, but 275 and 167 individuals were counted in this area in 2000 and 2019 respectively. Similarly, no grey seals were observed on Ile Rouge in 1995, 1996 and 2000 but 341 animals were present in 2019. No grey seals were seen in the Saguenay in previous surveys (1995-2000; Table 2), and none were detected by Parks Canada and SÉPAQ in June 2019.

3.5 GREY SEAL IN THE GULF OF ST. LAWRENCE

A total 13,852 grey seals were observed in the Gulf in June 2019 (Figure 27). This represented 94.3% of the total number of grey seals counted during this survey. Overall, the 2019 survey covered a larger area than previous surveys, but the sectors comprising the largest groups were also covered in 1996 (Table 5). The greater number of animals observed per unit effort in 2019 (1.57 individuals/km) compared to 1996 (0.45 grey seals/km) indicates that the increase in area covered in 2019 is not the primary factor explaining the increase in animals counted. As in Robillard et al. 2005, grey seals were absent from the North shore west of Rivière-au-Tonnerre (~80 km west of Mingan Islands; Figure 28) and west of the Forillon National Park along the Gaspé peninsula (Figure 27 and Figure 18). In the eastern portions of the Gulf, grey seals were seen both in the Cabot strait (on St. Paul Island) and in the Strait of Belle Isle (along the Newfoundland coast; Figure 27, Figure 29). The largest group was observed on Brion Island (20 km North East of the Magdalen Islands), and represented 77.5% (N= 10,739 individuals) of the animals counted in the Gulf of St Lawrence (Figure 27, Figure 30). Other groups were seen on Anticosti Island (N=1763; Figure 19), in Kouchibouguac National Park (N=649; Figure 31), and along the North shore (N=325; Figure 28). Only a few groups were observed along the southern coast of the Northumberland Strait and along the western coast of Newfoundland (Figure 22; Figure 29).

Several areas covered by previous surveys had shown a considerable increase in the number of animals present (Table 6). Brion Island has undergone a major increase in its local grey seal population from 100 individuals in 1996, to nearly 11,000 in 2019 (N = 10,739; Figure 30; Table 6). The Kouchibouguac area has also experienced a more than 10-fold increase in the number of grey seals during the same period (Figure 31). On the North shore the population was similar to 1996 but tripled when the Lower North shore is also considered (Figure 28). On Anticosti Island, the numbers decreased slightly from 2,110 individuals in 1996 to 1,763 in 2019

(Figure 19). Prince Edward Island is the only place where grey seals were seen in 2001 but not in 2019 (but see note under Table 6; Figure 21). The west coast of Newfoundland has not been surveyed before this inventory. In 2019, several groups of grey seals were detected (Figure 29) with the two largest groups located in St. Margaret Bay (N=64) and on Red Island (N=77; north of Cape St. George).

4. DISCUSSION

Monitoring trends in species abundance and spatial distribution is important to evaluate conservation status and inform management decisions. However, collecting this kind of information over a large area is inherently expensive and resource limitations in the past have generally restricted survey effort to economically important or threatened populations. The extensive coverage of this study has provided the first comprehensive overview of harbour seal spatial distribution and abundance in the Estuary and the Gulf of St. Lawrence, as well as detailed information on the late spring-early summer distribution and abundance of grey seals at or near haul-out sites.

Surveying harbour seals is particularly challenging. Unlike grey seals that generally form large aggregations, harbour seals can be found hauled out individually or in small groups dispersed in low density (Baird 2001, Lesage et al. 1995). While they are considered to be typically non-migratory and faithful to their haul-out locations (Thompson 1993; Härkönen and Harding 2001; Westlake and O'Corry-Crowe, 2002), the time they spend at these sites can vary depending on time of the year, weather conditions, tides and disturbance from human activities (Terhune and Almon, 1983; Thompson and Harwood, 1990; Watts, 1992; Frost et al. 1999; Henry and Hammill, 2001). Our survey methodology aimed to reduce availability and detectability bias by flying during a period in which harbour seals spend more time hauled out (pupping and lactating period; Ashwell-Erickson et al. 1986; Olesiuk, 1999, Dubé et al. 2003). All flights were conducted around low tide in high tidal amplitude areas (>1 m) or around noon elsewhere (Robillard et al. 2005), and only when weather conditions were optimal (no wind, rain or fog). Nonetheless, an unknown part of the population was at sea and missed by the aerial survey (Thompson et al. 1997; Huber et al. 2001; Simpkins et al. 2003, Olesiuk 2010; Hammill et al. 2010). Therefore, this study provides an index of seal abundance that must be corrected by the proportion of individuals in the water to obtain an estimate of total abundance.

Surveying all the coasts and islands of the Estuary and the Gulf also provided an opportunity to obtain information on the number of grey seals hauled out and their spatial distribution in this area. Most information on this population comes from winter surveys that focus on counts of pups (den Heyer et al. 2021, *in press*). Our survey provides a snapshot of grey seal abundance and spatial distribution outside of the breeding season. However, as in harbour seals, counts must be adjusted to account for the proportion of the population in the water at the time the survey was flown to obtain an estimate of total abundance in the study area.

4.1 HARBOUR SEALS

Since the 1970s, when harbour seals were afforded protection from harvesting by the passing of the Marine Mammal Protection Act (1972; U.S.A.) and revisions to the Fisheries Act (1979; Canada), harbour seal abundance has increased considerably in several areas. Along the Maine coast (northeast U.S.), harbour seal abundance increased from approximately 10,500 individuals in 1981 to 38,000 in 2001 for an annual rate of increase of 6.6% (Gilbert et al. 2005). Their numbers appear to have levelled off since then, partly due to competition from grey seals (Bowen et al. 2003b), mortality associated with increasing predation by white sharks in the Gulf of Maine (Curtis et al. 2014; Sigourney et al. 2021; see also Lucas and Stobo, 2000 for cases at Sable Island, Canada) and several mass mortalities linked to infectious disease epidemics such as influenza (Webster et al. 1981; Johnston et al. 2015; Runstadler et al. 2013).

In eastern Canada, there has been no range wide survey to obtain information on harbour seal spatial distribution and abundance. In the Estuary and the Gulf of St. Lawrence, differences in methodologies and spatial coverage between previous studies (Lavigne 1978; Boulva and McLaren, 1979) and the aerial surveys conducted after 1994 (i.e. 1994 -2001), prevented Robillard et al. (2005) from examining abundance trends in these areas before the 1990s. Moreover, the short time series of aerial surveys available at that time was insufficient to detect a clear trend. However, by using a similar protocol, the combination of our results with those from surveys conducted since 1995, was possible. This made it possible to demonstrate a considerable increase in the number of harbour seals over the last two decades in both the Estuary and the Gulf. The number of harbour seals counted in the Estuary has more than quadrupled since 1995-2000 (mean \pm sd = 469 \pm 60 in 1995-2000 versus 2,140 individuals in 2019). Their spatial distribution in the Estuary changed little, with individuals found in the same areas as observed in previous surveys. However, their numbers have increased faster in the Lower Estuary than in the Upper Estuary (7.3% vs 6.2% annually, respectively). Overall, these annual growth rates are similar to the range of values observed elsewhere, with growth rates of 6.6% between 1981 and 2001 in eastern USA (Gilbert et al. 2005) and rates of 6.8% between 1973-2014 in the Canadian Pacific (Majewski and Ellis 2021). In the Saguenay River, only a small number of harbour seals (N=21; Figure 14) were detected during the boat survey conducted on the same day the survey helicopter flew passed the mouth of the river. However, another boat survey conducted in the Saguenay River on June 10 (10 days before our survey) using the same protocol, counted 67 animals (Parc Canada, pers. Communication), thus suggesting potential movement in and out of this area. In the Gulf, 3574 harbour seals were counted, greatly exceeding the numbers obtained in 1996 and 2001.

The 2019 survey covered a larger area than the previous surveys, with the addition of the Lower North shore, the southern coast of the Gulf (Northumberland Strait to the north west coast of Cape Breton) and the western Newfoundland coast. This corresponded to an additional ~1,800 km of flight effort, and a 27% increase relative to the 1996 and 2001 surveys combined. In areas covered by both surveys, the number of harbour seal observed increased significantly (multiplied by 1.6, 2.1, 25.3, for Prince Edward Island, Anticosti Island, North shore respectively). The more extensive coverage of the 2019 survey provided new information on the spatial distribution of harbour seals with a few groups of animals observed along the Lower North shore and on the southern Gulf and several large groups on the western Newfounland coast. Counts from western Newfoundland represented 28.4 % of the total number of harbour seals observed in the Gulf.

Region-specific correction factors allowing to correct haul-out counts for the proportion of the population in the water at the time the survey were not available. Robillard et al. (2005) conducted a literature review of the correction factors available and used those from Huber et al. (2001; i.e. correction factors ranging from 1.36 to 1.62), corresponding to behaviour observed specifically during the harbour seal pupping season (period targeted for the 2019 survey). Although an updated review of these methods is needed, the large range of correction factor values considered in Huber et al. (2001) may provide a reasonable way to account for uncertainty in estimates of population size. Robillard et al. (2005) obtained population size estimates of 721-858 for the Estuary and 1,210-1,442 for the Gulf when combining the 1996 and 2001 counts. Applied to the 2019 survey counts, correction factors in the range 1.36-1.62 would result in an estimated harbour seal population of 2,910 - 3,467 individuals in the Estuary. Similarly, in the Gulf, an estimated population of 3480 - 4156 individuals would be obtained considering only the area covered by the 1996 and 2001 surveys or 4861 – 5790 harbour seals when considering the entire Gulf as covered by the 2019 survey. Unfortunately, the large temporal gap between the last two aerial surveys, prevents us from determining if the increase has been continuous, or represents a rapid increase, followed by a levelling off in abundance as observed further south along the Maine coast (Sigourney et al. 2021). A more regular and shorter survey interval is needed to detect such trends. Finally, while interesting, these numbers are preliminary and have to be considered with caution. A further review of the correction factor approaches will be conducted when counts obtained from Nova Scotia and Newfoundland and Labrador will be integrated to estimate the total population size in eastern Canada.

4.2 GREY SEALS

Population dynamic models based on pup production estimates obtained from aerial surveys conducted from the early 1960s to 2021 (33, 26 and 16 estimates for Sable Island, the Gulf of St. Lawrence and the coast of the Scotian shelf, respectively), estimated that the number of grey seals in Canadian waters has increased at a mean rate of 4.0 - 4.4% per year but has shown signs of slowing since 2007 (Hammill et al. 2017, Rossi et al. 2021). The total number of grey seals in Canadian waters was estimated to have increased from a few thousand in the 1960s to approximately 370,000 individuals in 2021, including 56,000 in the Gulf of St. Lawrence (Hammill et al. in Press). During the 2019 June survey, 14,691 grey seals were observed in the Estuary and Gulf of St. Lawrence. This count is considerably larger than the numbers obtained from previous late spring-early summer aerial surveys (e.g. Robillard et al. 2005). The differences result in part from the substantially increased spatial coverage by the 2019 survey, however, large increases in numbers were also observed in areas covered in the previous surveys such as Brion Island.

Overall, the 2019 count is much lower than model estimates from the winter assessments (14,691 animals counted during the 2019 aerial survey vs the 2019 model estimate of ~ 54,000 (95% CI = 45,000-65,000)). However, the 2019 June aerial survey counts were not corrected for the proportion of the grey seal population that was in the water when the survey was flown. As with harbour seals, a literature review of the various correction factors available is necessary but was beyond the scope of this study. Currently, there are no correction factors developed for our study area, but preliminary estimates based on a limited number of published studies suggested

interesting results. In the Baltic sea, the proportion of a grey seal population hauled out varied from 3-5 % during the day to a maximum of 28% at night (Sjöberg et al. 1999). In the United Kingdom, grey seals are also counted during harbour seals surveys conducted in August (harbour seals moulting period). The proportion of the grey seal population hauled out was estimated to be 23.9% (95% CI = 19.2-28.2%; Special Committee on Seals (SCOS, 2020)). No seasonal change in this proportion was observed for grey seals equipped with satellite tags from April (i.e. just after grey seal moulting period in this area) to November (Russell et al, 2015). In correcting the 2019 count with the SCOS correction factor, an estimate of ~61,500 animals (95%CI = 52,100-76,600) was obtained, which is consistent with model estimates from the winter assessment (Hammill et al., in press). This might suggest limited exchange with areas located outside of the Gulf (but see movements shown in Goulet et al., 2001 or Nowak et al. 2020) or balanced rates of movement from and to the Gulf. However, the 2019 survey was conducted during the month of June, which is part of the moulting period for grey seals in the western Atlantic (Stobo et al. 1990; Stobo and Fowler, 1994). The correction factor applied here was obtained outside of this period and the preliminary estimated population size should thus be considered with caution. Hauled-out behavior data are obtained primarily from satellite tags glued to the fur of seals and are therefore lost during the moult period, preventing any data collection. If the real proportion of animals hauled-out during the moulting season was to be higher, it would result in a lower population size estimate.

As observed in our study, previous surveys conducted during grey seal moulting period (e.g. Robillard et al. 2005), also found large groups concentrated in a small number of locations in both the Estuary and Gulf. While their number has more than doubled in the Estuary since 2000, with an estimated annual growth rate of ~5%, this increase has occurred mainly in the Upper Estuary. There, the local annual growth rate was estimated to be 12.5%, with two sites experiencing a large increase in the number of grey seals since the last surveys. The formation of such large groups at the boundary of their range may serve as sources for further expansion in the Estuary, as observed along the east coast of the USA with the colonization of new areas (Wood et al. 2020, den Heyer et al. 2021).

It should also be noted that on some islands, for which a time series of counts was present and showing a co-occurrence of harbour and grey seals, the variation in the number of harbour seals seemed to be inversely correlated with the number of grey seals in the same area. For example, on Ile aux Fraises, the number of harbour seals decreased from 26 in 1995 to 15 in 2000 and only 2 in 2019, while grey seal presence increased successively from 29, to 35 and 278 for the same years. In the same period, harbour seals appeared on the neighboring island (Ile aux lièvres) in 2019, while they were generally absent from this area before. Similar patterns have been reported on Sable Island (Bowen et al. 2003a) and at U.S. haul-out sites that have been recolonized by grey seals (Pace et al. 2019) suggesting potential competitive exclusion or physical displacement of smaller harbour seals. Grey seal predation on harbour seals has also been documented (van Neer et al. 2015, see also Appendix 2) and may contribute to spatial displacement, but the extent to which this kind of interaction take place remains unknown.

The largest proportion of the greys seals counted in 2019 was found in the Gulf, particularly on Brion Island comprising more than 70% of the animals sighted. The number of grey seal on this island has been multiplied by more than 100 times since 1996. This area is now considered the second largest breeding colony of grey seals in the Northwest Atlantic after

Sable Island (den Heyer et al., in Press). Although much smaller than the one on Brion Island, other large groups of grey seals (range = 325 - 1763 individuals) were also seen on Anticosti Island, in the Kouchibouguac National Park and along the North shore. The first ever seal aerial survey of Newfoundland's west coast detected several groups of grey seals with the two largest (N = 63 and 77 individuals, respectively) located in St. Margaret Bay and on Red Island (north of Cape St. George).

4.3 SURVEY OBSERVATIONS AND PERSPECTIVE

The 2019 aerial survey used a standardized protocol based on previous harbour seal surveys conducted in the study area and along the Pacific coast, by defining flying conditions and the use of a handheld camera (Olesiuk, 2010, Robillard et al. 2005). To complement the handheld camera system, a camera pod attached under the nose of the helicopter and pointing downward was used. This system was very useful when large groups of grey seals were encountered, e.g. Brion Island, where it would not have been possible to obtain reliable counts visually or using only the handheld camera system. The system was also valuable when large number of small islands precluded the use of the general protocol of following the coast with the two observers on the same side of the aircraft. In these cases, linear transects were flown with an observer seated and searching on each side of the helicopter, while the "pod" camera ensured that nothing was missed underneath.

As mentioned in previous surveys, seals sometimes responded to the presence of the helicopter by entering the water (Robillard et al. 2005). Fortunately, the use of hand-held zoom cameras allowed us to take several pictures before they reacted. Moreover, relying only on visual observations, Robillard et al. (2005) used approximated counts for large groups, resulting in lower accuracy and potential underestimation. In the 2019 survey, reliable counts were obtained from images, however, the impact of this improvement over visual counts cannot be estimated. Using the most accurate counts will facilitate population trends detection in the future assessments.

In some areas, including bird sanctuaries, or simply areas where flying was not permitted (e.g. Saguenay River), seal counts were provided by local conservation authorities such as Parks Canada or SÉPAQ. In such cases, a basic protocol was provided and applied to ensure consistency in the timing and detection capacity across survey initiatives i.e. low tide (+/- 2 hours). The latter was respected, except in Mingan Islands where there may have been an underestimation of the local grey seal population (Îles aux Perroquets area, see methods).

In other areas not accessible with the helicopter, seal counts were obtained from images and videos acquired with a small drone. Such an approach has been shown to be as efficient as the use of oblique photos taken from an helicopter with the advantage of not disturbing the seals hauled out (Hammill et al. 2017b) and the birds nesting in the neighborhood. However, current limitations in flight capabilities of the commercial drones and aviation regulations preclude their use over large areas such as the region considered in this study. For future surveys, the use of an infrared camera system installed on the aircraft seems to be a promising alternative offering a high seal detection rate while flying higher and thus significantly reducing potential disturbances (Christman et al. 2022). The 2019 survey is the first in a series of three regional survey initiatives that, when combined, will have covered the vast majority of eastern Canada's coasts. This will provide an opportunity to estimate the size of the harbour seal population occurring throughout eastern Canada and to obtain the first comprehensive representation of the spatial distribution of both harbour and grey seals in eastern Canadian waters in spring/early summer. Finally, this survey could also be the starting point of a more regular survey of the harbour seals population that would provide insights into how harbour seals respond to a rapidly changing environment.

ACKNOWLEDGMENTS

We would like to thank the teams from Park Canada (Karyne Bellehumeur, Daniel Gallant, Sarah Duquette, Felix Ledoux and Samuel Turgeon) and the SEPAQ for providing seal count and spatial distribution data in areas that we were not allowed to fly over. A big thanks to the Canadian Coast Guard who allowed us to conduct this aerial survey, in particular our two pilots: Alain Roy and Sebastien Tremblay for their professionalism. Finally, we thank Nell den Heyer and Xavier Bordeleau for their review and suggestions on this manuscript and Marie-Julie Roux as editor of this technical document.

The project was supported by the Department of Fisheries and Oceans Marine Mammal Survey Fund.

REFERENCES

- Aarts, G., Brasseuer, S., Poos, J.J., Schop, J., Kirkwood, R., Van Kooten, T., Mul, E., reijnders, P., Rinjsdrop, A., Tulp, I. 2019. Top-down pressure on a coastal ecosystem by harbor seals. Ecosphere 10(1):e02538. 10.1002/ecs2.2538.
- Ashwell-Erickson, S., Fay, F.H., Elsner, R., Wartzok, D. 1986. Metabolic and hormonal correlates of molting and regeneration of pelage in Alaskan harbor and spotted seals (*Phoca vitulina* and *Phoca largha*). Canadian Journal of Zoology, 64: 1086-1094.
- Baird, R.W. 2001. Status of Harbour Seals, *Phoca vitulina*, in Canada. Canadian Field-Naruralist 115: 663-675.
- Berta, A., and Churchill, M. 2012. Pinniped taxonomy: review of currently recognized species and subspecies, and evidence used for their description. Mamm. Rev. 42: 207-234.
- Blanchet, M.A., Vincent, C., Womble, J.N., Steingass, S.M., Desportes, G. 2021. Harbour Seals: Population Structure, Status, and Threats in a Rapidly Changing Environment. Oceans 2: 41-63.
- Boulva, J., and McLaren, I.A. 1979. Biology of the harbour seal, *Phoca vitulina*, in eastern Canada. J. Fish. Res. Board Can., Bull. No. 200: 24p.
- Bowen, W.D. 1997. Role of marine mammals in aquatic ecosystems. Mar. Ecol. Prog ser. 158:267-274.
- Bowen, W.D., McMillan, J., Mohn, R. 2003a. Sustained exponential population growth of grey seals at Sable Island, Nova Scotia. ICES J. Mar. Sci. 60: 1265-1274.
- Bowen, W.D., Ellis, S.L., Iverson, S.J., Boness, D.J. 2003b. Maternal and newborn life-history traits during periods of contrasting population trends: Implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. J. Zool. 2000, 252, 405–414.
- Caughley, G. 1977. Analysis of vertebrate populations. Wiley & Sons, New York, New York, USA. 234 p.
- Chantraine, P. 1980. The living ice: the story of the seals and the men who hunt them in the Gulf of St. Lawrence. McClelland and Stewart, Toronto. 238p .
- Christman, C.L., London, J.M., Conn, P.B., Hardy, S.K., Brady, G.M., Dahle, S.P., Hou, B.X., Ziel, H.L. 2022. Evaluating the use of thermal imagery to count harbor seals in aerial surveys. Mammalian Biology, 10.1007/s42991-021-00191-6.
- COSEWIC. 2007. COSEWIC assessment and update status report on the harbour seal Atlantic and Eastern Arctic subspecies *Phoca vitulina* concolor and Lacs des Loups Marins subspecies *Phoca vitulina mellonae* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii: 40p.
- Curtis, T.H., McCandless, C.T., Carlson, J.K., Skomal, G.B., Kohler, N.E., Natanson, L.J., Burgess, G.H., Hoey, J.H., Pratt, H.L. 2014. Seasonal distribution and historic trends in

abundance of white sharks, Carcharodon carcharias, in the western North Atlantic Ocean. PLoS ONE 9(6): e99240.

- den Heyer, C.E., Mosnier, A., Stenson, G.B., Lidgard, D., Bowen, W.D., Hammill, M.O. Pup production of Northwest Atlantic grey seals in Canadian waters. DFO Can. Sci. Advis. Sec. Res Doc. *In press*.
- den Heyer, N., Bowen, W., Dale, J., Gosselin, J. F., Hammill, M., Johnston, D., Lang, S., Murray, K., Stenson, G., Wood, S. 2021. Contrasting trends in gray seal (*Halichoerus grypus*) pup production throughout the increasing northwest Atlantic metapopulation. Marine Mammal Science. 37: 611–630. https://doi.org/10.1111/mms.12773.
- DFO. 2022. Stock assessment of Northwest Atlantic grey seals (*Halichoerus grypus*) in Canada in 2021. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2022/018.
- Drainville, G. 1968. Le Fjord du Saguenay I. Contribution à l'océanographie. Le Naturaliste can. 95: 809-855.
- Dubé, Y., Hammill M.O., Huot J. 2000. Description de la saison des naissances du Phoque commun, *Phoca vitulina*, de Bic et de Métis, dans l'estuaire du Saint- Laurent. Rapp. manus. can. sci. halieut. aquat : vi 22p.
- Dubé, Y., Hammill, M.O., Barrette, C. 2003. Pup development and timing of pupping in harbour seals (*Phoca vitulina*) in the St. Lawrence River estuary, Canada. Can. J. Zool. 81: 188-194.
- ECCC Environment and Climate Change Canada. 2017. Beaufort wind scale table. https://www.canada.ca/en/environment-climate-change/services/general-marine-weatherinformation/understanding-forecasts/beaufort-wind-scale-table.html [accessed 18 April 2023].
- El-Sabh, M.I. and Silverberg, N. 1990. Oceanography of a large-scale estuarine system, the St. Lawrence. Coastal and Estuarine Studies. Springer-New York, NY.: Vol. 39 : 434p.

Everitt, B.S., Landau, S., Leese, M. 2001. Cluster Analysis. 4th Edition, Arnold, London.

- Frost K.J., Lowry, L.F., Ver, Hoef, J.M. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Vuldez oil spill. Marine Mammal Science 15: 494-506.
- Gilbert, J.R., Waring, G.T., Wynne, K.M., Guldager, N. 2005. Changes in abundance and distribution of harbor seals in Maine, 1981–2001. Marine Mammal Science, 21: 519-535.
- Goulet, A.M., Hammill, M.O., Barrette, C. 2011. Movements and diving of grey seal females (Halichoerus grypus) in the Gulf of St. Lawrence, Canada. Polar Biol 24, 432–439.
- Hammill, M.O., Bowen, D.W., Sjare, B. 2010. Status of harbour seals (*Phoca vitulina*) in Atlantic Canada. NAMMCO Sci. Publ. 8: 175-189.
- Hammill, M.O., Gosselin, J-F., Stenson, G.B. 2017a. Pup production of Northwest Atlantic grey seals in the Gulf of St. Lawrence. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/043. iv + 14

- Hammill, M.O., Dale, J., Stenson, G.B., den Heyer, C., Gosselin, J-F., Leblanc, P., and Johnston, D.W. 2017b. Comparison of methods to estimate grey seal pup production at different colonies. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/041. iv + 19 p.
- Hammill, M.O., Stenson, G.B., Doniol-Valcroze, T., Mosnier, A. 2015. Conservation of northwest Atlantic harp seals: Past success, future uncertainty? Biological Conservation 192:181-191. http://dx.doi.org/10.1016/j.biocon.2015.09.016.
- Hammill, M.O., Stenson, G.B., Myers, R.A., W. Stobo. 1998. Population trends of the grey seal (*Halichoerus grypus*) in the Gulf of St Lawrence. Can. J. Fish. Aquat. Sci. 55: 423-430.
- Hammill, M.O., Rossi, S.P., Mosnier, A., den Heyer, C.E., Bowen, W.D. Stenson, G.B. Grey Seal Abundance and Harvest Advice in Canadian Waters. DFO Can. Sci. Advis. Sec. Res. Doc. *In press*.
- Härkönen, T., and Heide-Jørgensen, M-P. 1990. Comparative life histories of East Atlantic and other harbour seal populations. Ophelia, 32: 211-235.
- Härkönen, T., and Harding, K.C. 2001. Spatial structure of harbour seal populations and the implications thereof. Can. J. Zool. 79: 2115-2127.
- Härkönen, T., Harding, K.C., Heide-Jørgensen, M-P. 2002. Rates of increase in age-structured populations: a lesson from the European harbour seals. Canadian Journal of Zoology, 80(9), 1498–1510.
- Harkonen, T., Dietz, R., Reijnders, P., Teilman, J., Hrding, K., Hall, A., Brasseur, S., Siebert, U., Goodman, S.J., Jepson, P.D., Rasmussen, T.D., Thompson, P. 2006. The 1988 and 2002 phocine distemper virus epidemics in European harbour seals. Diseases of Aquatic Organisms 68:115-130.
- Härkönen, T., Brasseur, S., Teilmann, T., Vincent, C., Dietz, R., Abt, K Reijnders, P. 2007. Status of grey seals along mainland Europe from the Southwestern Baltic to France. NAMMCO Sci. Publ. 6: 57-68.
- Henry, E., and Hammill, M.O. 2001. Impact of small boats on the haulout activity of harbour seals (*Phoca vitulina*) in Mitis Bay, Saint Lawrence Estuary, Quebec, Canada. Aquat. Mamm. 27: 140-148.
- Huber, H.R., Jeffries, S.J., Brown, R.F., DeLong, R.L., G. VanBlaricon. 2001. Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. Mar. Mamm. Sci. 17: 276-293.
- Hydrographic Service of Canada. 2020. Canadian tide and current tables. Available from Fisheries and Oceans Canada, 615 Booth St., Ottawa, Ontario, Canada. K1A 0E6. Vol. 2 and 3.
- Johnston D.W., Frungillo J., Smith A., Moore K., Sharp B., Schuh J., et al. (2015). Trends in Stranding and By-Catch Rates of Gray and Harbor Seals along the Northeastern Coast of the United States: Evidence of Divergence in the Abundance of Two Sympatric Phocid Species? PLoS ONE 10(7): e0131660. https://doi.org/10.1371/journal.pone.0131660.

- Lavigne, P.-J. 1978. La chasse estivale du phoque dans le Saint Laurent. Rapport Préliminaire non-publi. 54p. + tables.
- Lavigueur, L. and Hammill, M.O. 1993. Distribution and seasonal movements of grey seals, *Halichoerus grypus*, born in the Gulf of St. Lawrence and eastern Nova Scotia shore. Can. Field-Nat. 107: 329-340.
- Lesage, V., Hammill, M.O. and Kovacs, K.M. 1995. Harbour seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) abundance in the St Lawrence Estuary. Fisheries and Aquatic Sciences 2307: 1-19.
- Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata [10th revised edition], vol. 1: 824p.
- Liu, X., Rønhøj Schjøtt, S., Granquist, S.M., Rosing-Asvid, A., Dietz, R., Teilmann, J., Galatius, A., Cammen, K., O'Corry-Crowe, G., Harding, K., Härkönen, T., Hall, A., Carroll, E.L., Kobayashi, Y., Hammill, M., Stenson, G., Kirstine Frie, A., Lydersen, C., Kovacs, K.M., Andersen, L.W., Hoffman, J.I., Goodman, S.J., Vieira, F.G., Heller, R., Moltke, I., Tange Olsen, M. 2022. Origin and expansion of the world's most widespread pinniped: Range-wide population genomics of the harbour seal (*Phoca vitulina*). Mol. Ecol.: mec.16365. doi:10.1111/mec.16365.
- Lowry, L. 2016. *Phoca vitulina*. The IUCN Red List of Threatened Species 2016. :e.T17013A45229114. https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T17013A45229114.en.
- Lucas, Z., and Stobo, W.T. 2000. Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. J. Zool. 252: 405-414.
- Majewski, S.P., and Ellis, G.M. 2021. Abundance and distribution of Harbour Seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia; synthesis of the 2014 aerial survey and long-term trends. DFO Can. Sci. Advis. Sec. Res. Doc. 2021/nnn. vi + xx p.
- Mohn, R. and Bowen, W.D. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. Can. J. Fish. Aquat. Sci. 53: 2722-2738.
- Nowak, B.V.R., Bowen, W.D., Whoriskey, K., Lidgard, D.C., Mills Flemming, J.E., Iverson, S.J. 2020. Foraging behaviour of a continental shelf marine predator, the grey seal (*Halichoerus grypus*), is associated with in situ, subsurface oceanographic conditions. In: Movement Ecology, 8, pp. 1–14.
- Olesiuk, P.F., Bigg, M.A., Ellis, G.M. 1990. Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. Can J Fish Aquat Sci 47(5): 992–1003.
- Olesiuk, P.F. 1999. An assessment of the status of harbour seals (*Phoca vitulina*) in British Columbia. DFO. Can. Sci. Advis. Sec. Res. Doc. 1999/33: 71p.
- Olesiuk, P.F. 2010. An assessment of population trends and abundance of harbour seals (*Phoca vitulina*) in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/105. vi: 157 p.

- Pace, R.M., Josephson, E., Wood, S.A., Murray, K., Waring, G. 2019. Trends and Patterns of Seal Abundance at Haul-out Sites in a Gray Seal Recolonization Zone. NOAA technical memorandum NMFS-NE; 251. https://doi.org/10.25923/qd3s-we77.
- Parks Canada. 2017. Réserve de parc national de l'Archipel-de-Mingan https://www.pc.gc.ca/fr/pn-np/qc/mingan/decouvrir-discover/Naturel/1-Faune_Wildlife#a02.
- Pauli, B.D., and Terhune, J.M. 1987. Meteorological influences on harbour seal haul-out. Aquatic Mammals 13: 114-118.
- QGIS.org. 2022. QGIS Geographic Information System. QGIS Association. http://www.qgis.org.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robillard, A., Lesage, V. Hammill, M.O. 2005. Distribution and abundance of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the estuary and Gulf of St Lawrence, 1994-2001. Can. Tech. Rep. Fish. Aquat. Sci 2613: 152p.
- Rossi, S.P., Cox, S.P., Hammill, M.O., den Heyer, C.E., Swain, D.P., Mosnier, A., Benoît, H.P. 2021. Forecasting the response of a recovered pinniped population to sustainable harvest strategies that reduce their impact as predators. ICES Journal of Marine Science, doi:10.1093/icesjms/fsab088.
- Runstadler J., Hill N., Hussein I.T.M., Puryear W., Keogh M. 2013. Connecting the study of wild influenza with the potential for pandemic disease. Infect Genet Evol. 17:162–87. pmid:23541413.
- Saucier, F.J., Roy, F., Gilbert, D., Pellerin, P. Ritchie, H. 2003. The formation and circulation processes of water masses in the Gulf of St. Lawrence. J. Geophys. Res 108: 3269-3289.
- Saucier, F.J., Roy, F., Senneville, S., Smith, G., Lefaivre, D., Zakardjian, B. Dumais, J.-F. 2009. Modelling of the circulation in the Estuary and Gulf of St. Lawrence in response to variations in fresh water runoff and winds. Journal of Water Science, 22: 159-176.
- Savenkoff, C., Vezina A.F. and Gratton Y. 1997. Effect of a freshwater pulse on mesoscale circulation and phytoplankton distribution in the lower St. Lawrence Estuary. J. Mar. Res. 55: 353-381.
- Shero, M.R., Dale, J., Seymour, A.C., Hammill, M.O., Mosnier, A., Mongrain, S., Johnston, D.W. 2021. Tracking wildlife energy dynamics with unoccupied aircraft systems and threedimensional photogrammetry. Methods in Ecology and Evolution. 12: 2458-2472.
- Shields, M.W., Hysong-shimazu, S., Shields, J.C., woodruff, J. 2018. Increased presence of mammal-eating killer whales in the Salish Sea with implications for predator-prey dynamics. PeerJ. DOI 10.7717/peerj.6062.
- Sigourney, D.B., Murray, K.T. Gilbert, J.R., Ver Hoef, J.M., Josephson, E., DiGiovanni, R.A. 2021. Application of a Bayesian hierarchical model to estimate trends in Atlantic harbor seal (*Phoca vitulina vitulina*) abundance in Maine, U.S.A., 1993–2018. Marine Mammal Science. DOI: 10.1111/mms.12873.

- Simpkins, M.A., Withrow, D.E., Cesarone, J.C., Boveng, P.L. 2003. Stability in the proportion of harbor seals hauled out under locally ideal conditions. Marine Mammal Science 19: 791-805.
- Sjöberg, M., McConnell, B., Fedak, M.A. 1999. Haulout patterns of grey seals *Halichoerus grypus* in the Baltic Sea. Wildl.Biol. 5: 37-48.
- Special Committee on Seals (SCOS). 2020. Scientific Advice on Matters Related to the Management of Seal Populations: 2020. Available at http://www.smru.standrews.ac.uk/files/2021/06/SCOS-2020.pdf.
- Stanley, H.F., Casey, S., Carnahan, J.M., Goodman, S., Harwood, J. Wayne, R.K. 1996. Worldwide patterns of mitochondrial DNA differentiation in the harbour seal. Mol. Biol. Evol 13: 368-382.
- Stobo, W.T., Beck, B., Home, J.K. 1990. Seasonal movements of grey seals (*Halichoerus grypus*) in the Northwest Atlantic. Pages 199-213 dans W.D. Bowen (édit.). Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Cm. Bull. Fish. Aquat. Sci. 222.
- Stobo, W.T., and Fowler, G.M. 1994. Aerial surveys of seals in the Bay of Fundy and off southwest Nova Scotia. Can. Tech. Rep. Fish. Aquat. Sci. 1943: 57p.
- Svensson, C.J. 2012. Seal dynamics on the Swedish west coast: Scenarios of competition as Baltic grey seal intrude on harbour seal territory. J of Sea Research doi:10.1016/j.seares.2012.03.005
- Swain, D.P., Benoît, H.P., Hammill, M.O., Sulikowski, J.A. 2019. Risk of extinction of a unique skate population due to predation by a recovering marine mammal. Ecological Applications, 18p.
- Teilmann, J., and Galatius, A. 2018. Harbor Seal. In Encyclopedia of Marine Mammals. 3rd ed.; Würsig, B., Thewissen, J.G.M., Kovacs, K.M., Eds.; Academic Press: Cambridge, MA, USA 451-455.
- Terhune, J.M., and Almon, M. 1983. Variability of harbor seal numbers on haul-out sites. Aquatic Mammals 10: 71-78.
- Therriault, J-C. 1990. The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113: 359p.
- Thompson, P.M., Tollit, D.J., Wood, D., Corpe, H.M., Hammond, P.S., and A. Mackay. 1997. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. J. Appl. Ecol. 34: 43-52.
- Thompson, P.M., and Harwood, J. 1990. Methods for estimating the population size of common seals, *Phoca vitulina*. Journal of Applied Ecology 27: 924-938.
- Thompson, P.M. 1993. Harbour seal movement patterns. Symp Zool Soc (Lond) 66:225-239.
- van Neer, A., Jensen, L.F., Siebert, U. 2015. Grey seal (*Halichoerus grypus*) predation on harbour seals (*Phoca vitulina*) on the island of Helgoland, Germany. Journal of Sea Research, 97, 1– 4. https://doi.org/10.1016/j.seares.2014.11.006

- Watts, P. 1992. Thermal constraints in hauling out by harbour seals (*Phoca vitulina*). Canadian Journal of Zoology 70: 553-560.
- Webster R.G., Hinshaw, V.S., Bean W.J., Van Wyke K.L., Geraci J.R., St Aubin D.J., et al. 1981. Characterization of an influenza A virus from seals. Virology. Sep;113(2):712–24. pmid:6267805.
- Westlake, R.L., and O'Corry-Crowe, G.M. 2002. Macrogeographic structure and patterns of genetic diversity in harbor seals (*Phoca vitulina*) from Alaska to Japan. J. Mammal. 83: 1111-112.
- Wood, S.A., Murray, K.T., Josephson, E., Gilbert, J. 2020. Rates of increase in gray seal (*Halichoerus grypus atlantica*) pupping at recolonized sites in the United States, 1988-2019. J Mammal. 101(1):121-128.

TABLES

Table 1: Total number of harbour seals and grey seals observed in the St. Lawrence Estuary and Saguenay River during aerial surveys in 1995–1997, 2000 and 2019.

Survey						
period	Dates	Harbour Grey Seal seal		Unidentified	Effort (km)	
June 1995	15-18	410	268	5	1898*	
June 1996	18-20	467	244	1	1908*	
June 2000	19-21	530	354	0	1908*	
June 2019	13, 16,19-20	2140***	839***	0	1560**	

* Effort calculated from a digital 1:250,000 scale map using Mercator projection following the length of the coastline

** Effort estimated from the GPS tracks of the helicopter when observers actively searching for seals

*** These numbers includes counts obtained from boat surveys conducted by Parks Canada and SÉPAQ in the Saguenay River (21 harbour seals and 0 grey seals)

Table 2: Number of harbour seals and grey seals observed in the Saguenay River and the two portions of the St. Lawrence Estuary (Upper and Lower) during aerial surveys in 1995–1997, 2000 and 2019.

	I	Harbour seals					Grey Seals			
	1995	1996	2000	2019		1995	1996	2000	2019	
South shore	309	287	318	1380		142	94	79	669*	
North shore	100	179	199	739		126	150	275	170*	
Saguenay River	1	1	13	21**		0	0	0	0**	
Upper Estuary	158	133	168	597		33	63	35	621	
Lower Estuary	251	333	349	1522		235	181	319	218	
Entire Estuary	410	467	530	2140		268	244	354	839	

* Large counts obtained on Ile aux Fraises and Ile Rouge (see Table 4), located in the center of the Estuary, were associated to South shore counts as in Robillard et al. (2005)

** We were not allowed to fly over the Saguenay River. Counts were obtained from boat surveys conducted by Parks Canada and SÉPAQ

Table 3: Estimated rate of increase (\pm SE) in the number of harbour seals and grey seals occurring in June in the St. Lawrence Estuary between 1995 and 2019, calculated using non-linear regression analyses and assuming an exponential annual growth rate. Statistically significant (p < 0.01) rate of increase are indicated with an asterisk.

Species	Sector	Estimated rate of increase (± SE)	Range
Harbour Seal			
	St. Lawrence Estuary	0.070 (0.002)*	
	South shore	0.069 (0.005)*	
	North shore	0.070 (0.006)*	- 0.062-0.073
	Upper Estuary	0.062 (0,004)*	
	Lower Estuary	0.073 (0.004)*	
		_	-
Grey Seal			
·	St. Lawrence Estuary	0.049 (0.003)*	
	South shore	0.086 (0.015)*	
	North shore	0.003 (0.022)	0.001 - 0.125
	Upper Estuary	0.125 (0.017)*	
	Lower Estuary	-0.001 (0.016)	
		_	

	Harbour seal				Grey seal				
Estuary zones	1995	1996	2000	2019	199)5	1996	2000	2019
Pointe Mtis	59	63	71	210		0	0	0	0
Baie Mitis	0	6	4	21		0	0	0	0
Bic archipelago	109	105	128	372*	4	1	24	42	0*
Razades	0	0	0	0	6	8	0	2	50
lle Rouge	1	0	0	0		0	0	0	341
lle Blanche	49	37	45	48		4	10	0	0
lle aux Lièvres	1	1	0	102		0	52	0	0
lle aux Fraises	26	20	15	2	2	9	0	35	278
lles Les Pélerins	7		4	82		0	1	0	0
Battures aux Loups Marins	6	8	2	145		0	0	0	0
Ile aux Coudres	0	0	0	3		0	0	0	0
Battures aux Alouettes Hauts fonds de Mille-	67	66	102	129		0	0	0	0
Vaches	13	31	43	51		0	0	0	0
Baie des Îlets Jérémie	0	28	38	81		0	0	0	0
Betsiamites River mouth	0	0	0	0		0	0	275	167
Battures aux Outardes	17	49	12	266	11	5	150	0	0

Table 4: Number of harbour seals observed in different important haul out zones of the St. Lawrence Estuary during aerial surveys in June 1995–2019.

* The survey covered the Bic sector at the end of the day while a scientific capture program aimed at harbour seals had taken place the morning of the same day. This may have resulted in an underestimate of the number of animals of both species present in the area.

Table 5 : Total number of harbour seals and grey seals observed in the Gulf of St. Lawrence during aerial surveys in 1996, 2001 and 2019. Observations reported in Kouchibouguac Park where aerial surveys were not possible due to restrictions over bird sanctuaries, are also provided in parenthesis.

Survey	Dates		Effort (km)		
period	Dales	Harbour seal	Grey Seal	Unidentified	Effort (km)
June 1996	15-17, 21-23	467	2394 (55)	36	5355*
June 2001	12-13	423	80	0	1275*
June 2019	4-5,7-11,21,25-30	3574	13203 (649)	109	8425**

* Effort estimated from a digital 1:250,000 scale map (Lambert conformal conic NAD 83 projection) by calculating the total distance of coastline and islands perimeter in the areas overflown.

** Effort estimated from the GPS tracks of the helicopter as the distance travelled when observers were actively searching for seals

Table 6 : Number of harbour and grey seals observed during the month of June in the different regions of the Gulf when present in at least two different aerial surveys between 1996 to 2019. Kouchibouguac area was also covered twice but with boat and drone surveys respectively.

	Harbour Seal			Grey seal				
	1996	96 2001 2019		1996	2001	2019		
Kouchibouguac	-	-	-	55 (boat)	-	649 (drone)		
Îles-de-la-Madeleine*	32	-	23	151	-	10779		
Anticosti Island	308	-	639	2110	-	1763		
North shore	12	-	304 (+ 53)**	111	-	122 (+ 203)**		
Prince Edward Island	-	423	696	-	80	0***		

*Îles-de-la-Madeleine also included: Brion Island, Rocher aux Oiseaux and Le Corps-Mort ** The 2019 survey included the Lower North Shore east of Natashquan (not covered in previous

surveys). The number of animals observed in this area is indicated in parenthesis

*** In the harbour seal groups observed on Governor Island, a few animals whose species identification was uncertain could be considered juvenile grey seals

FIGURES

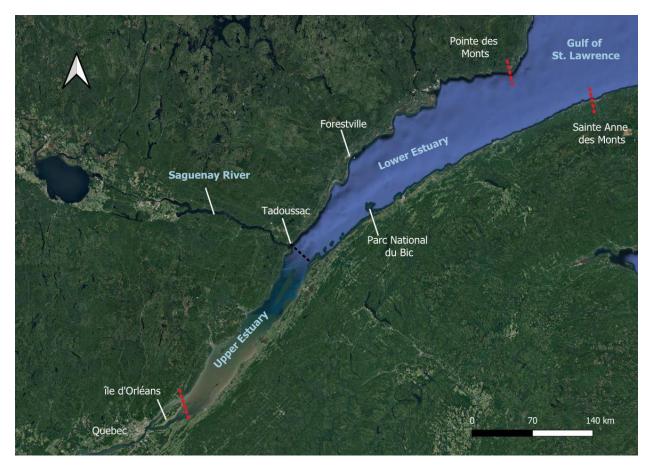


Figure 1 : Survey area in the St. Lawrence Estuary (delimited by red dotted lines) showing the Lower and Upper parts of the Estuary separated at Tadoussac (black dotted line).

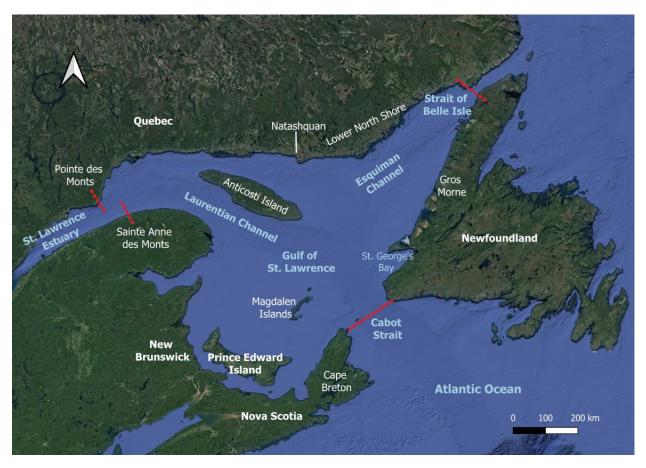


Figure 2 : Survey area in the Gulf of St. Lawrence (delimited by red dotted lines) showing the different provinces, channels and straits



Figure 3 : GPS track showing the entire area covered by the helicopter during the 2019 June survey. Overflights carried out in the range of -2 h to +2 hours around the low tide are shown in red (tidal range >1m), and those carried out in the range of -2h to +2 hours around noon (tidal range <1m) are shown in green

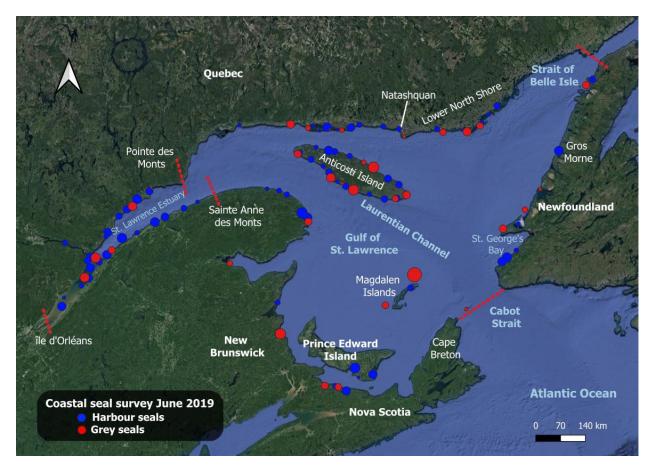


Figure 4 : Spatial distribution of harbour and grey seals in the Estuary and Gulf of St. Lawrence. Blue and red dots represent harbour and grey seals observations respectively, spatially clustered using a threshold of 20 km (see "Analysis" section).

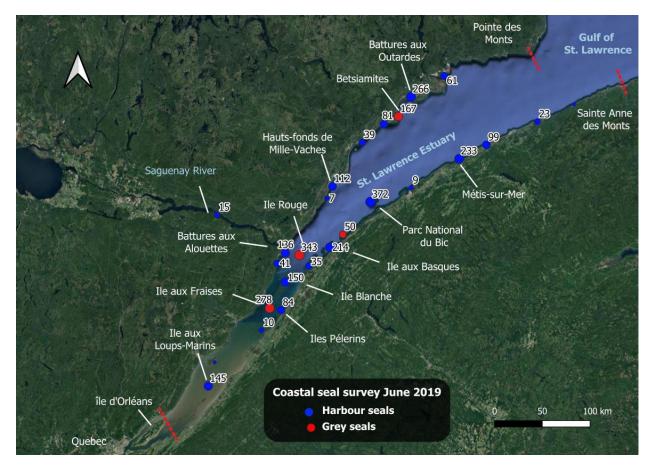


Figure 5 : Distribution and abundance of harbour and grey seals in the St. Lawrence Estuary. The limits of the survey area in the Estuary are indicated by the red dotted lines. Count data are presented as spatially clustered points based on a threshold of 20 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

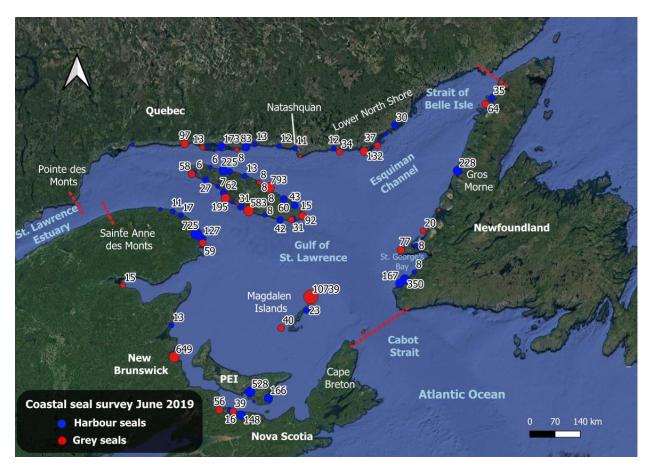


Figure 6 : Distribution and abundance of harbour and grey seals in the Gulf of St. Lawrence. The limits of the survey area in the Gulf of St Lawrence are indicated by the red dotted lines. Count data are presented as spatially clustered points based on a threshold of 20 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

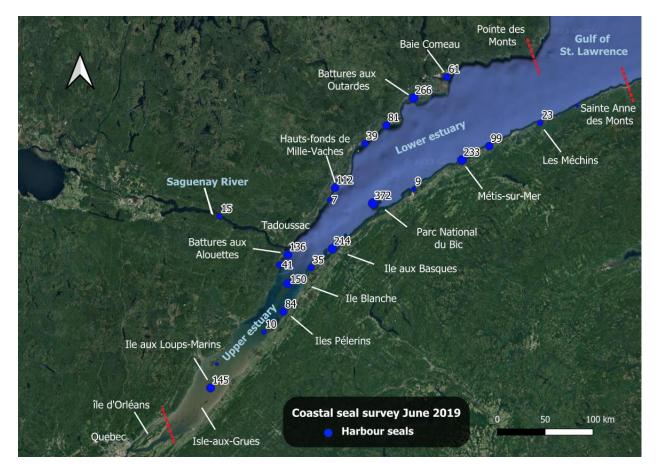


Figure 7: Distribution and abundance of harbour seals in the Estuary of St. Lawrence. Count data are presented as spatially clustered points based on a threshold of 20 km (see "Analysis" section). Dots without associated number represent count lower than five individuals. HARBOUR SEAL

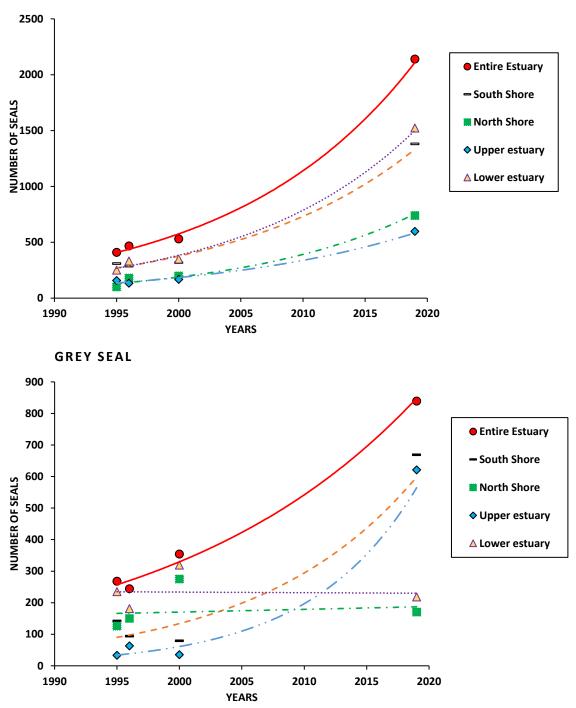


Figure 8 : Exponential rate of increase of harbour seals and grey seals in the different portions of the St. Lawrence Estuary and the Entire Estuary for the month of June from aerial surveys in 1995-2019.

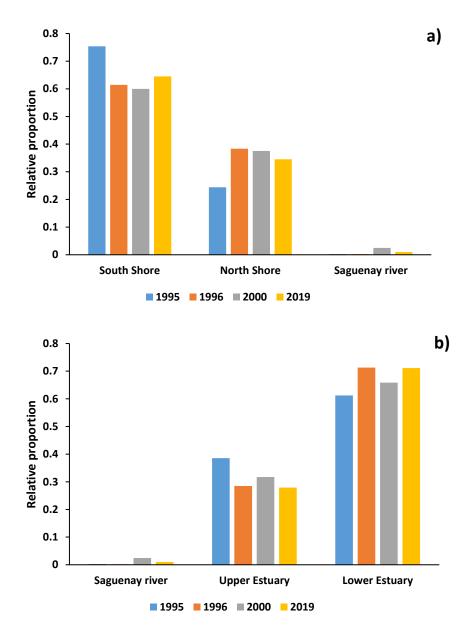


Figure 9 : a) Relative distribution of harbour seals observations along the south vs north shore and the Saguenay river and b) in the upstream vs downstream portions of the Estuary and the Saguenay river during June for aerial surveys conducted between 1995 and 2019.

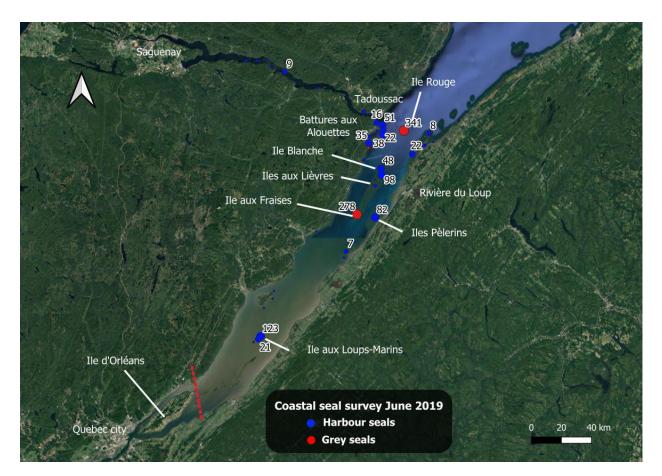


Figure 10: Distribution and abundance of harbour and grey seals in the Upper Estuary. Count data are presented as spatially clustered points based on a threshold of 2.5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

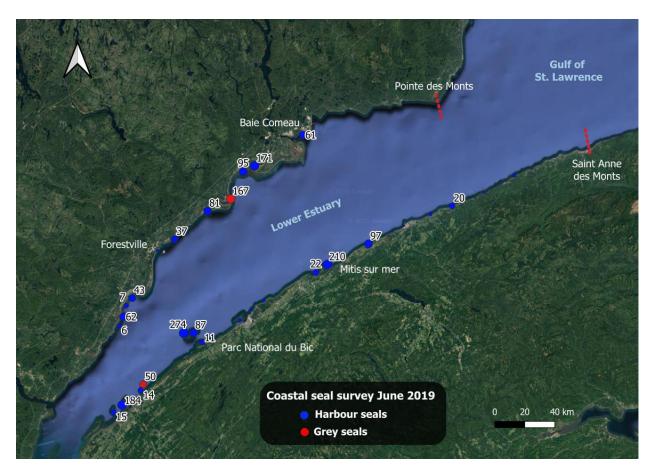


Figure 11 : Distribution and abundance of harbour and grey seals in the lower Estuary. Count data are presented as spatially clustered points based on a threshold of 5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

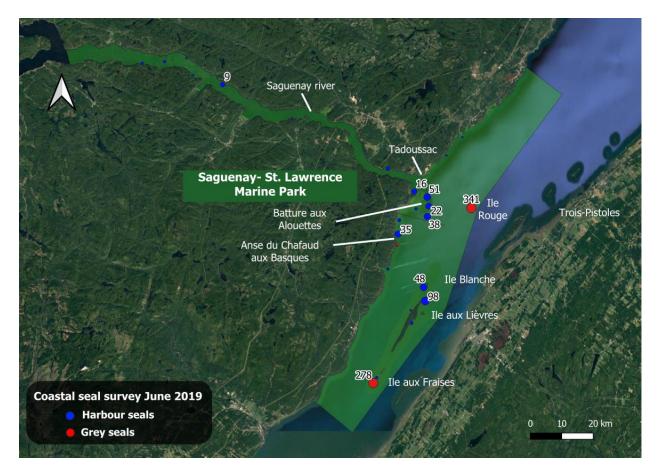


Figure 12 : Distribution and abundance of harbour and grey seals in Saguenay St. Lawrence Marine Park. Count data are presented as spatially clustered points based on a threshold of 2.5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 13: Distribution and abundance of harbour seals in the Parc national du Bic. Count data are presented as spatially clustered points based on a threshold of 500 m (see "Analysis" section). Dots without associated number represent count lower than five individuals.

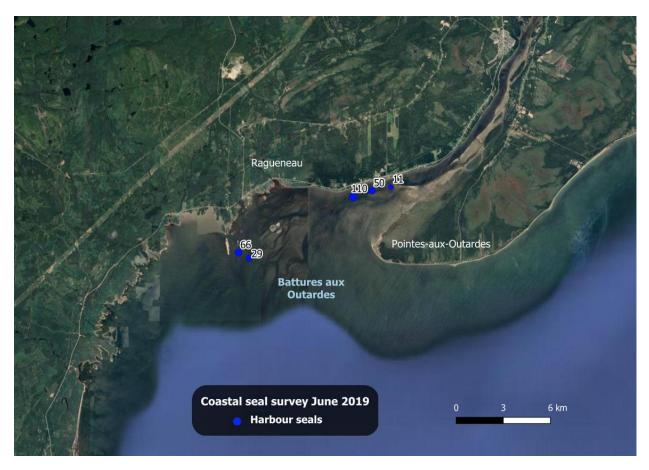


Figure 14 : Distribution and abundance of harbour seals in the Battures aux Outardes. Count data are presented as spatially clustered points based on a threshold of 500 m (see "Analysis" section).



Figure 15: Distribution and abundance of harbour seals in Métis-sur-Mer. Count data are presented as spatially clustered points based on a threshold of 500 m (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 16 : Distribution and abundance of harbour seals in the Hauts-fond de Mille-Vaches. Count data are presented as spatially clustered points based on a threshold of 500 m (see "Analysis" section). Dots without associated number represent count lower than five individuals.

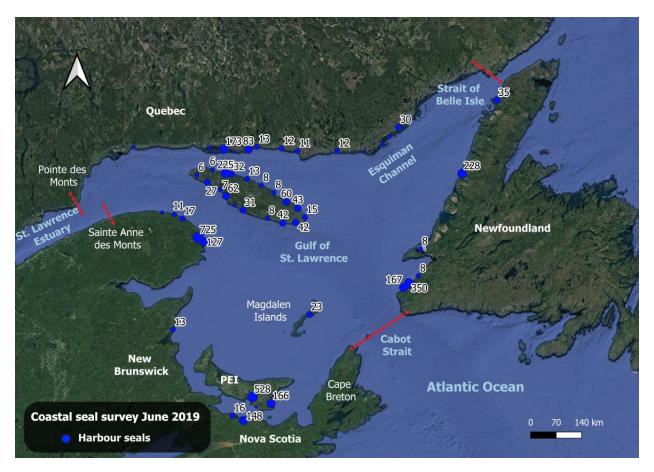


Figure 17 : Distribution and abundance of harbour seals in the Gulf of St. Lawrence. Count data are presented as spatially clustered points based on a threshold of 20 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 18 : Distribution and abundance of harbour and grey seals in the Bay of Gaspé and around the Forillon National Park of Canada. Count data are presented as spatially clustered points based on a threshold of 1 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 19 : Distribution and abundance of harbour and grey seals in Anticosti. Count data are presented as spatially clustered points based on a threshold of 2.5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 20 : Distribution and abundance of harbour and grey seals in Mingan Islands National Park. Count data are presented as spatially clustered points based on a threshold of 5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 21 : Distribution and abundance of harbour seals Prince Edward Island. Count data are presented as spatially clustered points based on a threshold of 500 m (see "Analysis" section). Dots without associated number represent count lower than five individuals.

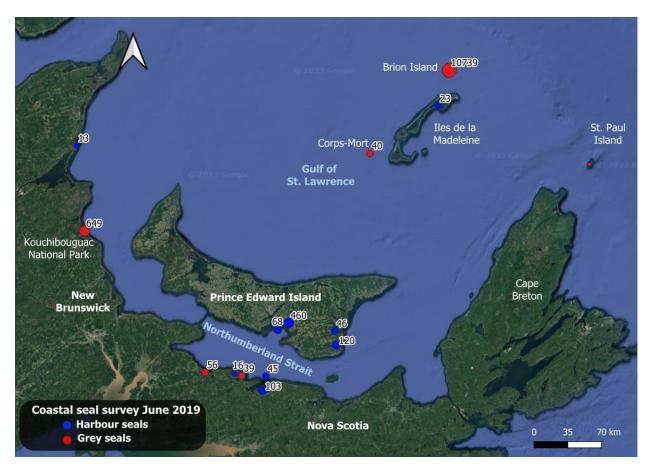


Figure 22 : Distribution and abundance of harbour and grey seals in the South of St-Lawrence Gulf. Count data are presented as spatially clustered points based on a threshold of 10 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 23 : Distribution and abundance of harbour seals In Gros Morne National Park in Newfoundland. Count data are presented as spatially clustered points based on a threshold of 2.5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.



Figure 24 : Distribution and abundance of harbour seals in St. George's Bay. Count data are presented as spatially clustered points based on a threshold of 5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

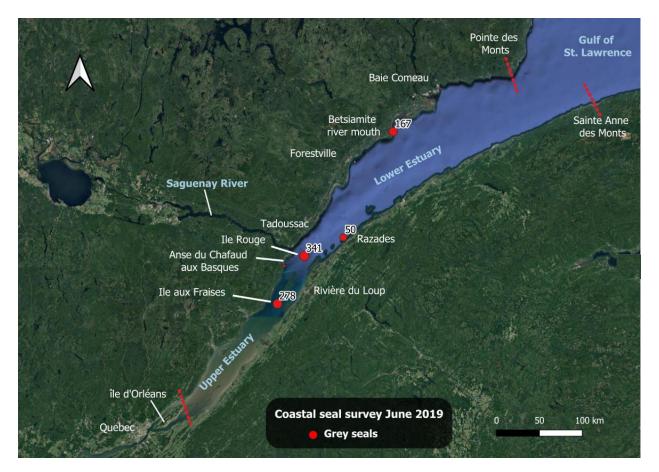


Figure 25: Distribution and abundance of grey seals in the Estuary of St. Lawrence. Count data are presented as spatially clustered points based on a threshold of 2.5 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

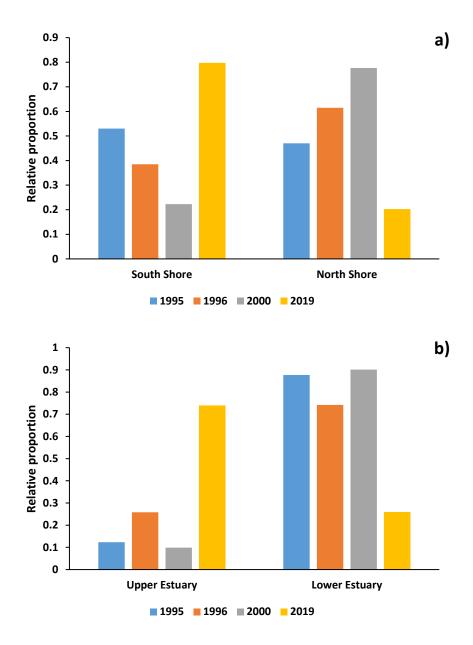


Figure 26 : a) Relative distribution of grey seals observations along the south vs north shore and the Saguenay river and b) in the upstream vs downstream portions of the Estuary and the Saguenay river during June for aerial surveys conducted between 1995 and 2019.

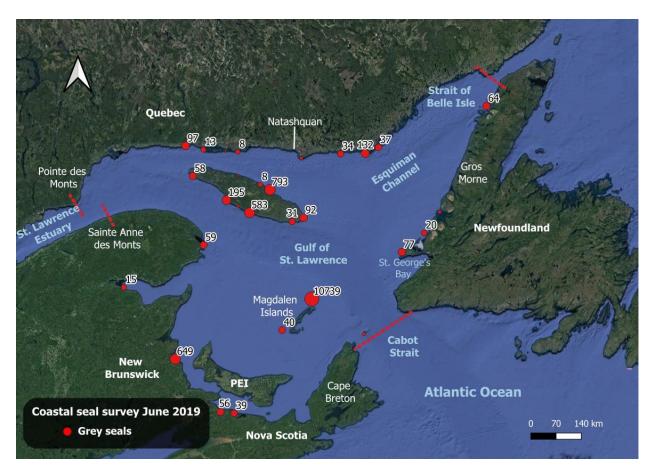


Figure 27: Distribution and abundance of grey seals in the Gulf of St. Lawrence. Count data are presented as spatially clustered points based on a threshold of 20 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

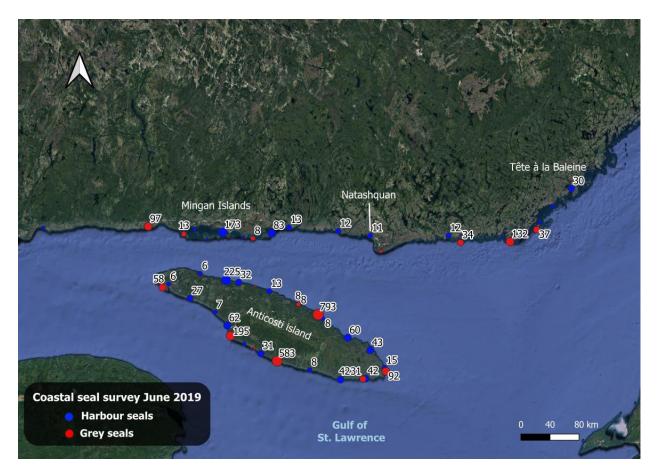


Figure 28 : Distribution and abundance of harbour and grey seals in Anticosti and the North Shore of the Gulf. Count data are presented as spatially clustered points based on a threshold of 20 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

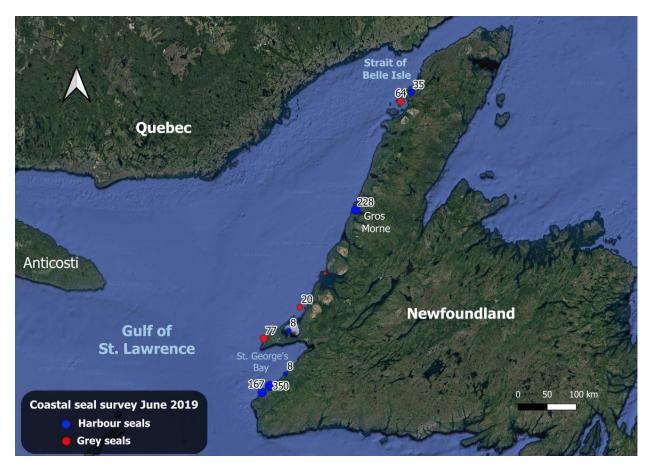


Figure 29 : Distribution and abundance of harbour and grey seals only in West coast of Newfoundland. Count data are presented as spatially clustered points based on a threshold of 20 km (see "Analysis" section). Dots without associated number represent count lower than five individuals.

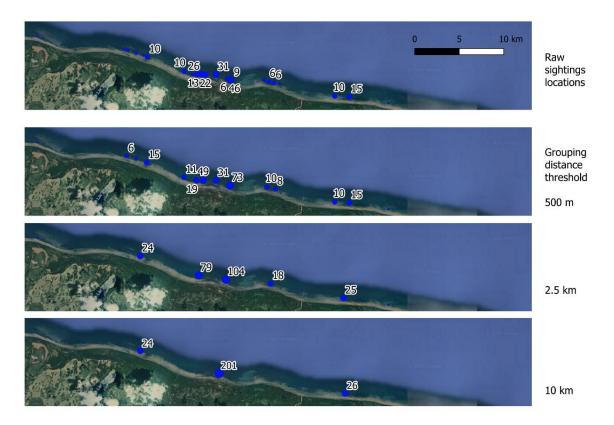


Figure 30: Distribution and abundance of harbour seals the Corps-Mort, Iles de la Madeleine and Brion Island. Count data are presented as spatially clustered points based on a threshold of 10 km (see "Analysis" section).



Figure 31: Distribution and abundance of grey seals in the Kouchibouguac National Park. Count data are presented as spatially clustered points based on a threshold of 500 m (see "Analysis" section).

APPENDICES



Appendix 1. Effect of the spatial clustering algorithm on the grouping of sightings. Dots without associated number represent count lower than five individuals.



Appendix 2. Photo showing predation of a harbour seal by a grey seal in the St. Lawrence Estuary near Île rouge (off the Saguenay river mouth). August 26 2022. Photo credit: Catherine Dubé.