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Harbour Seal (*Phoca vitulina vitulina*) Haulout Behaviour and Correction Factors for Aerial Surveys Conducted in Atlantic Canada from 2019 to 2021

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Foreword

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

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TABLE OF CONTENTS

ABSTRACT

Aerial surveys were conducted between 2019-2021 to estimate the abundance and distribution of harbour seals (*Phoca vitulina vitulina*) throughout Atlantic Canada: coastlines of the St. Lawrence Estuary and Gulf of St. Lawrence, the Bay of Fundy, southwest Nova Scotia, Eastern Shore and Cape Breton, as well as the Newfoundland and Labrador Shelves. These surveys were conducted in favourable conditions, during the pupping period of harbour seals, except in some areas of Newfoundland and Labrador Shelves where the survey was conducted during the moulting period. To account for animals not available to be counted during aerial surveys (i.e., at sea), haulout correction factors were calculated from: 1) data collected via satellite telemetry deployments on harbour seals in the St. Lawrence Estuary; and 2) published literature values. Twelve harbour seals (combination of adults or juveniles, and pups) were instrumented with satellite transmitters in the St. Lawrence Estuary, providing data on their haulout behaviour during the survey period (May 15-June 30, 2022). Haulout periods were identified from the transmitted hourly percent dry timelines. The proportion of the population hauled out at any given time during the survey window was estimated using a bootstrap approach, which corrected for the unbalanced sex-age sample of tagged animals. This method estimated that a proportion of 0.33 (95% CI: 0.09-0.60) of the harbour seal population was hauled out on average at any given time during survey-like conditions, corresponding to a mean correction factor of 3.0 (CV: 41.7%). When combined with published pupping correction factors in the Northwest Atlantic (range: 2.30-2.58), the weighted mean of the proportion hauled out was 0.39 (95% CI: 0.27-0.52) for a correction factor of 2.55 (CV: 16.02%). For parts of Newfoundland and Labrador Shelves surveyed during the moulting period, we calculated a weighted proportion hauled out of 0.61 (95% CI: 0.50-0.71) from published literature estimates, corresponding to a correction factor of 1.64 (CV: 8.67%). The bootstrap framework developed for this analysis of haulout behaviour from satellite telemetry data provides an important way forward in capturing behavioural variability and generating correction factors for aerial surveys. Additional tagging effort in different regions and across multiple years would be required to provide correction factors for harbour seals that reflect local conditions and thereby improve estimates of abundance and the associated uncertainty.

INTRODUCTION

Harbour seals (*Phoca vitulina*) are the most widely distributed pinniped in coastal areas, found in temperate and sub-Arctic waters throughout the northern hemisphere (Burns 2009; Teilmann and Galatius 2018). Three subspecies of harbour seals exist in Canada: Eastern Pacific harbour seals (*P. v. richardsi)*, Western Atlantic harbour seals (*P. v. vitulina),* and Ungava harbour seals (*P. v. mellonae*), which are found along the Pacific coastlines, along the Atlantic and Arctic coastlines, and in the freshwater lakes of the Ungava Peninsula in northern Quebec, respectively (Mansfield 1967; Smith et al. 2006; Hammill et al. 2010; Berta and Churchill 2012).

Harbour seals haul out on a diversity of strata including sandy beaches, small islets, rocks, reefs, sea ice, or glacier ice pieces throughout their range. Harbour seals have a seasonal pattern in the proportion of time spent hauled out, with seals hauling out for greater proportions of the time in the late spring and summer during the pupping and moulting periods (Watts 1996; Dubé et al. 2003; Harris et al. 2003; Cunningham et al. 2009; Granquist and Hauksson 2016; Rosing-Asvid et al. 2020). The proportion of time hauled out throughout the pupping and moulting periods varies between different life history stages and sexes. Females spend time on land nursing pups while males spend more time at sea performing underwater displays and vocalizations as part of their mating behaviour (Thompson et al. 1997; Van Parijs et al. 1997; Rosing-Asvid et al. 2020). Females and pups spend more time in the water later in the nursing period (Boness et al. 1994; Thompson et al. 1994; Jørgensen et al. 2001). Variation in the proportion of time hauled out during the moulting period occurs due to moulting phenology, with immature seals moulting before mature seals (Härkönen et al. 1999; Daniel et al. 2003). The exact time of breeding and moulting may also vary spatially, with pupping occurring later in the year at more northern latitudes (Temte et al. 1991). Harbour seals in most locations also have a higher probability of hauling out in the hours around low tide, during daytime, and in weather conditions characterized by low wind speeds, warm temperatures, no fog and no precipitation (Pauli and Terhune 1987; Watts 1996; Simpkins et al. 2003; Hamilton et al. 2014; Granquist and Hauksson 2016). Accordingly, most harbour seal surveys are conducted during the pupping and moulting seasons, in the hours around low tide, and when environmental variables are considered favourable.

Despite efforts to conduct surveys when maximum numbers of animals are expected to be hauled out, a proportion of animals remain in the water and consequently are not available for counting. Multiple methods exist for creating correction factors (CF) to account for seals that are not available to be counted during aerial surveys. Most CFs are calculated using data collected by biotelemetry devices such as VHF transmitters or animal-borne loggers (bio-loggers) attached to seals (Jeffries et al. 2003; Simpkins et al. 2003; Olesiuk 2010; Lonergan et al. 2013; Womble et al. 2020), ideally including all age classes and sexes in proportion to what is present in the population. VHF radio transmitters continuously send out pulsed signals which are detected by a receiver and antenna installed at fixed or mobile stations. Although small and cost effective, detection of tagged individuals is limited by the detection range of the receiver/antenna. In contrast, bio-loggers record data from various sensors that can be used to study animal behaviour and physiology. Data are either archived within the unit and/or transmitted via satellite (e.g., ARGOS) to the user. Due to a limited satellite bandwidth, only a fraction of the collected data is transmitted. Thus, it is always preferable to physically recover bio-loggers to access the full record, although not always possible for many study sites and species (Read 2018; Nowak et al. 2020). Geographical locations recorded by bio-loggers are either derived from Fastloc-GPS or ARGOS data (Rutz and Hays 2009; CLS 2016). Given their capability, biologgers are often preferred over VHF transmitters for studying haulout behaviour. Haulout data can be analysed to examine seasonal and daily variability, and can be modelled with environmental and meteorological data to estimate the proportion of the tagged population hauled out under different conditions. Given this is not always feasible, CFs from other time periods and locations have been used, while acknowledging that haulout behaviour can vary in time and space (Boveng et al. 2003; Hayward et al. 2005; Harvey and Goley 2011; London et al. 2012).

Current information on population abundance is limited for harbour seals in Atlantic Canada. In the past, a bounty for harbour seals was introduced in Atlantic Canada (except Newfoundland and Labrador, NL) in 1927, and in NL in 1952 over concerns about their impacts on fish stocks. The bounty ended in 1976 after Boulva and McLaren (1979) noted that harbour seals had disappeared from areas where they were previously abundant and over concerns that population declines were occurring in many regions. Boulva and McLaren (1979) used bounty returns, interviews and questionnaires to estimate an abundance of 12,700 harbour seals south of Labrador in 1973. Since that time, surveys to assess harbour seal abundance have occurred in some regions of Atlantic Canada, including in the St. Lawrence Estuary (SLE), Gulf of St. Lawrence (GSL), Bay of Fundy, and southwest Nova Scotia (SS) (Stobo and Fowler 1994; Lesage et al. 1995; Robillard et al. 2005). In other regions of Atlantic Canada, such as the Newfoundland and Labrador Shelves (NLS), aerial surveys to assess abundance have not taken place, although limited areas have been covered by land- and boat-based surveys (Sjare et al. 2005). Notably, only one of these surveys (Robillard et al. 2005) was corrected for the proportion of harbour seals hauled out at the time of the survey, using a CF developed for Northeast (NE) Pacific harbour seals.

Aerial surveys were flown during the summers of 2019-2021 to address the need for a comprehensive portrait of harbour seal abundance and distribution across Atlantic Canada (Hamilton et al. 2023; Lidgard et al. 2023; Mosnier et al. 2023). In this study, we used data on haulout patterns collected from satellite telemetry deployments on harbour seals in the SLE, and values from the published literature to estimate CF to be applied to these aerial survey estimates. These CF values are used by Lang et al. (2024) to estimate the current abundance of harbour seals in Atlantic Canada.

METHODS

AERIAL SURVEYS

Aerial surveys to estimate the abundance and distribution of harbour seals in Atlantic Canada were conducted along the coastline of the GSL and SLE (2019), the SS (2020-2021) and the NLS (2021; Table 1; Figure 1; Hamilton et al. 2023; Lidgard et al. 2023; Mosnier et al. 2023). These surveys were conducted during the harbour seal pupping (SLE, GSL, SS, NLS) or moulting (NLS) season (Harris et al. 2003; Granquist and Hauksson 2016), on days with favourable conditions for hauling out and observing seals (i.e., within two hours of low tide with no rain or fog and wind speeds below 10 knots; Pauli and Terhune 1987; Simpkins et al. 2003; Robillard et al. 2005; Hamilton et al. 2014). In areas with minimal tidal range (<1 m, southern GSL) flights occurred in a four-hour period centred at noon. Harbour seals hauled out on land and those that had flushed into the water from their haulout locations due to disturbance from the helicopter were counted (Hamilton et al. 2023; Lidgard et al. 2023; Mosnier et al. 2023).

SATELLITE TELEMETRY DEPLOYMENTS AND DATA PROCESSING

In fall 2021, we deployed satellite transmitters to collect haulout information (SPLASH10-F-296A and SPLASH10-BF-296C, Wildlife Computers, Redmond, WA, USA) on eight harbour seals (two at Bic Island and six at Metis-sur-Mer, QC: Table 2), following the annual moult (see

Lesage et al. 2004 for capture and handling procedures). While this group likely comprised both adults and juveniles, information on sexual maturity was not available to distinguish these two age classes (except for two harbour seals whose age was estimated using growth layer groups from extracted teeth; Lockyer et al. 2010). In addition, we also lack information on population age structure, therefore the two life-stages were not differentiated in subsequent analyses. This sample comprised a single female (122.0 cm length, 6.5 years-old) and seven males (116.0 – 137.0 cm length; Table 2). In spring 2022, we also equipped five weaned harbour seal pups (4 at Bic Island and 1 at Metis-sur-Mer, QC) with smaller satellite transmitters (SPOT-S395C, Wildlife Computers) between 9 – 16 June 2022 (see Dubé et al. 2003 for capture and handling procedures). This sample comprised two females (91.5 – 92.0 cm length) and three males (93.0 – 96.0 cm length: Table 2). All transmitters were placed on the back of the head of the seals.

Haulout behavioural information was derived from Percent Dry Timelines (PDT) – a data product of Wildlife Computers – provided by the conductivity sensor of the transmitter. This sensor samples every three seconds to provide the percentage of an hour during which the tag was dry (dry readings), for all 24 hours of a UTC day for which data were transmitted (see example in Figure 2.A). These hourly summaries were collected at high resolution (i.e., to the nearest one percent) for adults and juveniles, and at low resolution (i.e., rounded to the nearest ten percent) for pups. As PDT are available for all hours of the day, they are amenable to estimation of proportion of time hauled out. In addition, PDT are not sensitive to the programming options of the tag model or to how users define haulout events, which makes comparisons of haulout duration across studies easier. PDT are also available for smaller tag models (e.g. SPOT), which allows for information on haulout behaviour to be derived for pups. A seal was considered to have been hauled out for the reported percentage of time spent dry of each hour, if the hourly percent dry value was:

1. **≥50% dry**
   This threshold allowed us to eliminate hours where the majority of dry readings resulted from time spent at the surface in between dives (mode: 20%; range: 0 - 48%; Figure 2.B). In Lesage et al. (1999), surface time accounted for 21.1% – 44.9% of each dive cycle for SLE harbour seals. Consequently, hours with percent dry values of <50% were assigned a haulout probability of zero (Tucker et al. In press), with the exception of the following condition:

2. **<50% dry, but adjacent to an hourly bin value with ≥95% dry**
   Given that an hour or multi-hour haulout event likely began and/or ended with adjacent haulout hours, the percentage dry contribution of these “tail” bins were included in the haulout event.

Applying the above conditions (represented in Figure 2.A) provided hourly percentages of time spent hauled out for each individual, which we used as the probability that a seal was hauled out and available to be surveyed at any time during the survey. We restricted data to the harbour seal pupping period (May 15 – June 30 for the SLE; Bordeleau, unpublished data), corresponding to the survey window (Mosnier et al. 2023). This was also the period with adequate overlap of data between pups and older age-groups (seven of the eight adult or juvenile seals and all five pups; Figure 3) due to differences in deployment timing. After confirming that the harbour seals tagged in our study hauled out preferentially around low tide during daylight hours (Figure 4), we further restricted our haulout data to the time and tide conditions corresponding to the SLE survey period (i.e., five hourly bins centred on peak low tide during daylight hours; Mosnier et al. 2023). As tagged animals remained within the SLE throughout the survey period and the deployment sites were nearby (~65 km; Figure 5), tidal period (Canadian Hydrographic Service Tide Tables) and daylight times (*suncalc* R package; Thieurmel and Elmarhraoui 2022; R Core Teams 2023) were estimated for a location between the two deployment sites (i.e., Rimouski, QC; Figure 5). To test for relationships between weather conditions and haulout behaviour, we estimated Pearson's correlation coefficients between the hourly time spent hauled out and available climatic variables (i.e., precipitation, wind speed, air temperature, dew point temperature and atmospheric pressure) extracted from a meteorological station located between our two deployment sites (i.e., Mont-Joli; Canadian Centre for Climate Service; Figure 5). No strong environmental correlations (-0.12 to 0.31) were identified between the hourly percent dry values and any of the extracted weather variables, consistent with an earlier study conducted at these two haulout sites (Lesage 1999). Hence, hourly bins were filtered only for tide and time of day, with no further filtering based on environmental conditions.

DATA ANALYSIS

2022 SLE correction factor

Twelve instrumented harbour seals (six adult or juvenile males, one adult or juvenile female, five pups) transmitted 1,172 hours of data during the period of interest (Figure 6). For each hour where haulout data for at least two individuals (range: 2-7 seals) were available (total of 282 hours), we first calculated the proportion of animals hauled out. The resulting distribution was non-gaussian (Figure 7), which could cause an underestimation of variance when using parametric statistics. Furthermore, due to inconsistent transmission of data among seals, large variability existed in the number of hours contributed by each seal (range: 11-176 hours).

To overcome this limitation, we used a bootstrap framework to generate a non-parametric variance estimate of the proportion of the population hauled out (P_p; Figure 8), while also reducing the disparity in the hours contributed by individuals within each sex-age group, under a theoretical population structure. To do so, we simulated a theoretical population comprised of 80% adults and juveniles (1:1 sex ratio) and 20% pups (no differentiation based on sex; Olesiuk 2010). Each iteration included 10 individuals (i.e., four adult or juvenile males, four adult or juvenile females and two pups) randomly selected with replacement from our tagged animals. We used a sampling size of 10, despite having data for 12 individuals, to maintain realistic subsample sizes within each sex-age group. Sampling with replacement allowed us to account for inter-individual but also intra-individual variability. Multiple iterations ensured similar weighting for individuals within each sex-age group. A one-hour period and corresponding proportion of time spent hauled-out (P_i) was then randomly selected from the tracking data of each individual included in the iteration. Given that we only had data from a single adult or juvenile female, each bootstrap iteration randomly sampled (with replacement) 4 hours within the 176 hours available for this individual, to simulate the haulout behaviour of the four individuals needed to represent this sex-age group. The overall estimated proportion of the population hauled out for the i^{th} iteration was calculated as the sum of hourly P_i for the n individuals', divided by the number of individuals in the simulated population (i.e., n = 10):

$$P_i = (P_1 + P_2 + \dots + P_n) / n; \text{ where } n = 10 \ \& \ i \in [1,10\,000]$$

This process was iterated 10,000 times to create a distribution of the proportion of the population hauled out. The resulting distribution appropriately represented each sex-age group and was normally distributed, which allowed the estimation of the overall mean (P_p), 95% confidence interval (CI_{95}), and coefficient of variation (CV):

$$P_P = \frac{\sum_{i=1}^{10000} P_i}{10000}$$

$$CI_{95} = P_P \pm 1.96 * \sigma$$

$$CV = \sigma / P_P$$

where σ is the standard deviation. The correction factor (CF) is the inverse of the mean proportion of the population hauled out (P_P):

$$CF = 1 / P_P$$

Literature review

A scientific literature search was conducted to source studies that estimated CFs for the pupping and moulting period from telemetry data to derive abundance estimates of harbour seals from aerial surveys. Studies presented in peer-reviewed journals, theses, and grey literature were reviewed. Only studies conducted on harbour seals during the pupping and/or moulting season, that used telemetry devices (i.e., VHF transmitters or bio-loggers) to collect data on haulout behaviour were evaluated (Table 3). CF estimates were then grouped by study region (i.e., Northwest Atlantic (NWA), Northeast Atlantic (NEA), and Northeast Pacific (NEP)) to assess potential system-specific differences (Table 4).

Combination of correction factors

Many of the published studies did not report a confidence interval around the reported proportion of the population hauled out or around the CF. Hence, to combine estimates from these studies, we estimated the variance using the Agresti-Coull method and calculated 95% binomial confidence intervals for the proportion hauled out, using the estimated mean haulout proportion and the number of seals tagged (*binom* R package, Agresti and Caffo 2000; Dorai-Raj 2022). For consistency in variance estimation, we used the same method to recalculate the variance for our telemetry data. A CV for each study was then calculated, using the reported mean proportion of the population hauled out and the newly estimated standard deviation.

We used a weighted average approach to combine CFs, wherein the contribution of the proportion hauled out from each study to the overall mean was weighted by its associated variance (Mood et al. 1974). This method was used to calculate two mean CFs, one for the pupping period and one for the moulting period. Due to observed system-specific differences in published CF estimates (Table 4), the four CFs available for the pupping period in the NWA, including our own, were combined (Gilbert et al. 2005, Lambert 2012, Waring et al. 2015, study herein). Similarly, for the moulting period, the four literature CFs for the moulting season only (Lambert 2012, Lonergan et al. 2013) or for both the moulting and pupping periods (Ries et al. 1998, Merkel et al. 2013), from the NWA and NEA were combined. Estimates from the NEA were included in the calculation of the combined CF for the moulting period due to insufficient number of estimates from the NWA alone for this period (n=1).

RESULTS

2022 SLE CORRECTION FACTOR

The resulting distribution of the bootstrap framework (10,000 iterations of 10 individuals, assuming a theoretical population structure) was normally distributed. Using this distribution, we estimated a mean proportion of the population hauled out of 0.33 (95% CI: 0.09-0.60; Figure 8). This mean value was not sensitive to changes in threshold values (20% - 70%) used to distinguish haul-out events from PDT due to the bimodal distribution of PDT (Figure 2.B). Using the inverse of the mean, we estimated a CF of 3.0 (CV: 41.7%). This large variability is representative of the large intra- and inter-individual variation in haulout behaviour (Figure 6).

LITERATURE REVIEW

Fourteen published studies met the criteria for providing a CF to account for the proportion of harbour seals that were hauled out during aerial surveys (Tables 3 and 4, Figure 9). Study areas include the NWA (n=4), the NEA (n=4), and the NEP (n=7; Tables 3 and 4, Figure 9). Nine studies calculated a CF for the pupping season, two studies covered the pupping and moulting seasons, and four studies covered the moulting period only. These CFs ranged from 1.20 to 2.58. CFs from the NWA were larger than those from the NEA and NEP (Tables 3 and 4, Figure 9).

COMBINATION OF CORRECTION FACTORS

A large portion of the survey was conducted during the harbour seal pupping period. Three CF estimates were available from published literature for NWA during the pupping period (two from VHF deployments on harbour seals in Maine and one from the SLE, between 1995 and 2012; Table 3). We combined these estimates with the CF herein to calculate a weighted mean of the proportion of the population hauled out of 0.39 (95% CI: 0.27-0.52), corresponding to a CF of 2.55 (CV: 16.02%).

A small portion of the survey in the NLS took place during the harbour seal moulting period (Table 1). One CF was available from published literature for NWA during the moulting period (VHF deployments on harbour seals in the SLE, between 1995-96) and three for NEA during the moulting and combined pupping/moulting period (between 1994 and 2009; Table 3). We combined these estimates to calculate a weighted mean of the proportion of the population hauled out of 0.61 (95% CI: 0.50-0.71), corresponding to a CF of 1.64 (CV: 8.67%).

DISCUSSION

Using our bootstrap framework, we estimated a mean proportion of the population hauled out of 0.33 (95% CI: 0.09-0.60; Figure 8), corresponding to a CF of 3.0 (CV: 41.7%). Our estimated CF is among the highest values reported in the literature for harbour seals (Table 3; Figure 9). It is, however, similar to previous harbour seal studies in the NWA during the pupping period (CF range: 2.33 – 2.58; Table 3 and 4), including a study conducted on harbour seals from the same SLE colonies as the present study (Lambert 2012). Moreover, using the same analytical framework as the present study, we found a similar estimate of the proportion of the population hauled out of 0.40 (95% CI: 0.12-0.68) and a CF of 2.48 for 10 adult or juvenile harbour seals (7 males and 3 females) equipped with satellite transmitters in the Gulf of Maine between 2021 and 2022 (DeAngelis, DiGiovanni Jr., Doughty, Reese, Bort, Murray; unpublished data).

We developed this approach of CF calculation primarily to adequately capture variation given our small sample size and unbalanced representation of sex-age groups. By resampling with replacement, our bootstrap framework accounted for the high level of inter- and intra-individual variability in haulout behaviour of harbour seals. This translated into the large confidence intervals for the estimated proportion of the population hauled out at any given time during survey conditions (mean = 0.33; 95% CI: 0.09-0.60). Additionally, individuals were selected randomly irrespective of the amount of transmitted data, to ensure similar weighting for individuals within each sex-age group. The theoretical population structure was then applied to ensure that each sex-age group was represented appropriately. Notably, the theoretical population structure offers a common ground for comparison of haulout behaviour among studies, which is important given the ontogenetic and sex differences in haulout behaviour. During the pupping season mature male harbour seals spend most of their time in the water exhibiting courtship behaviour (Lesage 1999; Robillard et al. 2005), while mature females spend their time on land nursing the pup (Coltman et al. 1997; Van Parijs et al. 1997). As a result, mature males are less available to be counted during the survey. While the information on sexual maturity of tagged animals was not available, we likely had a contribution of both mature and immature males based on variability in size (116-137 cm: Table 2). Nevertheless, inter-individual differences in haulout behaviour among the males that might indicate maturity status were not apparent (Figure 6). Furthermore, as pups likely have different haulout behaviour than older age classes, decreasing their time on land as nursing progresses (Jørgensen et al. 2001), their lack of representation could impact the proportion of the population hauled out (and consequently the CF; e.g., Hamilton et al. 2014). While our approach accounts for the dominance of males in our tagged sample and better represents pup haulout behaviour, our data were limited to the presence of a single adult or juvenile female, restricting the representability and variability of female haulout behaviour. If the female was lactating, it would tend to overestimate the time spent hauled out for females and vice versa, leading to biased estimates for this age-sex group. Furthermore, as a single individual represents the age-sex group, it could potentially cause an underestimation of variance for this subgroup, if intra-individual variation is smaller than the inter-individual variation.

We combined CF from previously published literature, to overcome the limitations of small sample size from a limited geographical area inherent to our telemetry data. However, there are numerous challenges involved with properly combining CFs, while appropriately representing the variability in haulout behaviour. The most fundamental challenge is the selection of studies that adequately represent the area of interest. We observed that the proportion of time spent hauled out differed depending on the ocean-system in which the study was conducted (Table 4). Notably it appears that harbour seals in the NWA spend less time hauled out during May and June compared with those in the NEA or NEP. Differences in haulout correction factors may reflect small sample sizes, differences in phenology of pupping and moulting, differences in response to terrestrial and marine predators such as killer whales or sharks (Nordstrom 2002; Bowlby et al. 2022), disturbance (London et al. 2012), or competition for haulout space with conspecifics or other species such as grey seals (Bowen et al. 2003a, 2003b; den Heyer et al. 2021; Rossi et al. 2021). In light of these system-specific conditions and/or community structure that change over time, it is important to document haulout behaviour in the system and time period of interest. We hence combined our estimate with those conducted only in the NWA (4 studies), to obtain a resultant proportion of the population hauled out of 0.39 (95% CI: 0.27-0.52) and a CF of 2.55 (CV: 16.02%). Telemetry data during the moulting period were limited to a single study in the SLE, we hence included literature values from the NEA (nearest ocean-system) to create a combined CF for the aerial survey in NLS. The combined CF for the moulting period from the four literature values was 1.64 (CV: 8.67%). A limitation of this combined approach is that combined CVs mostly reflect the uncertainty between studies and underestimate the uncertainty (both inter- and intra-individual) of the haulout behavior displayed by harbour seals. Another limitation is that as CF are often estimated around low tide, combining CF does not address the uncertainty in haulout behaviour for the GSL where haul-out sites were surveyed around midday due to minimal tidal range (<1 m).

A majority of published estimates used VHF deployments to provide information on haulout behaviour, which have their own limitations. Several of the reviewed studies used VHF transmitters that were small enough to be combined with a flipper tag that was attached to the webbing of the hind flippers (e.g., Huber et al. 2001). These tags have the advantage of continuing to transmit during the moulting period, but have a restricted geographical range of detection and are vulnerable to tag damage or loss due to increased drag (Gilbert et al. 2005). More importantly, haulouts occurring outside of the VHF range are not detectable and would underestimate overall haulout time. However, detection of tagged individuals can be increased through searching for signals from the survey aircraft (e.g., Gilbert et al. 2005). While satellite telemetry has its own limitations (e.g., loss during moult, tag damage, incomplete temporal coverage and high costs), data collected via this technology can reduce these biases, as it is not spatially restricted.

Basic demographic information on harbour seals, such as the timing of pupping and moulting, is currently lacking for some regions of Atlantic Canada. Recent pupping estimates are only available for the SLE (first births starting May 12, a median date of pupping of May 25–28 and a median date of weaning of June 25 to July 1; Dubé et al. 2003; Van de Walle 2013; Renaud et al. 2023). Studies conducted in the 1980-90s suggest that pupping on Sable Island is similar to the SLE and Maine (May 19 to June 15 in the late 1990s on Sable Island; Bowen et al. 2003a; Dubé et al. 2003; Gilbert et al. 2005). As the abundance of harbour seal severely declined on Sable Island, the dates of first and last birth were delayed by about a week in the late 1990s compared to the late 1980s (Bowen et al. 2003a). It is unknown whether a similar change in pupping dates also occurred in Maine or elsewhere in Atlantic Canada, although the date of first and last birth in the SLE does not appear to have changed from 1998 to 2023 (Bordeleau, unpublished data). A latitudinal cline in timing of pupping had been observed in Atlantic Canada (Temte et al. 1991). However it is uncertain whether this cline still exists and extends to NLS. The limited data on the timing of pupping for harbour seals that exists for southern Newfoundland suggests that pupping might occur a bit later than in the SLE, Sable Island or Maine. Harbour seal pups were observed in survey test flights over St. Pierre and Miquelon in mid-June 2021. Also, nursing harbour seal pups were seen in Fortune Bay in mid-July 2022, a few weeks after the median date of weaning in the SLE (Lang and Sheppard, unpublished data). A large number of harbour seals also occur in northern Newfoundland (Hamilton et al. 2023) for which no demographic data are available. Due to this, the survey counts in NLS were split into two periods. Surveys from July 6 to 14 likely occurred during the pupping period and use the combined CF calculated from the harbour seal tagging data in the SLE (presented herein) and the three published values from the NW Atlantic. Surveys from July 24 to August 19 likely occurred during the moulting period and use the weighted CF calculated from the four literature values from the pupping/moulting and moulting periods.

We provide pupping and moulting CFs to account for the proportion of seals in water, not available to be counted during aerial surveys conducted in Atlantic Canada from 2019-2021. Due to our low sample size, limited representativity, and limited spatial coverage in deployments, we combined our calculated estimate with those from literature. Improving these estimates require increasing sample size and ensuring each life history stage is well represented, as well as tagging seals across Atlantic Canada for better spatial representativity. Due to unfavourable weather conditions during the pupping period, future surveys might also be conducted during the moulting period in some regions. Therefore, data from the moulting period are also needed to determine the amount of regional and seasonal variability in haulout behavior. On a finer scale, increased sample size could eventually allow us to formally include temporal autocorrelation and the non-independence of haulout data obtained from the same individual, while also characterising the effect of climatic variables on haulout behaviour (see Cronin et al. 2009). In addition to increasing sample size, future work, using PDT, could also benefit from higher certainty in behavioural states by using a combination of PDT thresholds (described herein) and positional information (distance from coast or bathymetry) to assign states.

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TABLES

Table 1. Details of the aerial surveys flown between 2019 and 2021 to assess counts and distribution of hauled out harbour seals in Atlantic Canada.

Region	Year	Sub-region	Survey dates	Timing
Gulf of St. Lawrence	2019	St. Lawrence Estuary	Jun 13-21	Pupping
		Southern Gulf	Jun 4-11	Pupping
		Northern Gulf	Jun 22-28	Pupping
		West Coast NL	Jun 29-30	Pupping
Scotian Shelf	2020	Bay of Fundy	Jun 14-28	Pupping
		SWNS	Jun 18-25; Jul 5-7	Pupping
		Eastern Shore	Jun 19, Jul 2-17	Pupping
		Cape Breton	Jun 26; Jul 4-16	Pupping
	2021	Sable Island	Jun 2	Pupping
Newfoundland and Labrador Shelves	2021	South Coast	Jul 6-8	Pupping
		South Coast	Jul 24-Aug 19	Moulting
		Northeast Coast	Jul 9-14	Pupping
		Sandwich Bay, Labrador	Jul 14	Pupping

Table 2. Metadata of harbour seals instrumented with satellite transmitters. Age group: pup (P), juvenile (J) or adult (A).

Unique identifier	Capture site	Date tagged	Date of last transmission	Age group	Sex	Weight (kg)	Length (cm)	Age (years)
213560	Bic	2021-09-04	2022-07-14	J/A	M	77.0	132.0	5.5
212408	Bic	2021-09-23	2022-07-24	J/A	F	73.0	122.0	6.5
213561	Metis	2021-09-24	2022-03-18	J/A	M	41.0	117.0	–
213562	Metis	2021-09-24	2022-06-10	J/A	M	57.0	137.0	–
213563	Metis	2021-09-24	2022-06-04	J/A	M	48.0	116.0	–
212410	Metis	2021-10-01	2022-05-18	J/A	M	72.0	129.0	–
212409	Metis	2021-10-01	2022-06-05	J/A	M	71.0	136.0	–
212411	Metis	2021-10-01	2022-06-09	J/A	M	69.0	130.0	–
228949	Bic	2022-06-11	2022-07-30	P	F	21.0	92.0	0.1
228952	Bic	2022-06-11	2022-07-10	P	M	22.5	95.0	0.1
228953	Bic	2022-06-11	2022-08-31	P	F	21.0	91.5	0.1
228950	Bic	2022-06-17	2022-08-03	P	M	25.0	93.0	0.1
228951	Métis	2022-06-18	2022-07-25	P	M	25.0	96.0	0.1

Table 3. Correction factors to account for the harbour seals not hauled out during aerial surveys from the published literature including the timing of the survey, region (NWA stands for Northwest Atlantic, NEA for Northeast Atlantic and NEP for Northeast Pacific), location (SLE stands for St. Lawrence Estuary and BC for British Columbia), study year, instruments used (VHF, SatLog (biologgers, recovered and unrecovered satellite-linked transmitters)), number of seals tagged (n), sex and age group (pup (P), juvenile (J) or adult (A)) of tagged seals, proportion hauled out (P ± 95% CI), correction factor (CF), CV (%) and reference. The confidence intervals for the proportion hauled out are estimated using the Agresti-Coull interval method and estimated binomial error based on the proportion hauled out and the sample size.

Timing	System	Location	Study year	Tag	n	Sex	Age group	P	CF	CV	Reference
Pup	NWA	SLE, CAN	2022	Sat Log	12	M/F	P/J/A	0.33 (0.09-0.60)	**3.00**	41.7	Current study
Pup	NWA	Maine, USA	2012	VHF	18	M/F	J/A	0.43 (0.23-0.65)	**2.33**	27.2	Waring et al. 2015
Pup	NWA	SLE, CAN	1995-96	VHF	11	M/F	J/A	0.42 (0.19-0.69)	**2.40**	35.7	Lambert 2012
Pup	NWA	Maine, USA	2001	VHF	19	M/F	J/A	0.39 (0.21-0.61)	**2.58**	28.8	Gilbert et al. 2005
Pup	NEA	Scotland	1993	VHF	26	M/F	P/J/A	0.61 (0.42-0.77)	**1.64**	15.7	Thompson et al. 1997
Pup	NEP	BC, CAN	2019-21	Sat Log	32	M/F	P/J/A	0.79 (0.62-0.90)	**1.27**	9.2	Tucker et al. In press
Pup	NEP	California, USA	2004 & 2007	VHF	180	M/F	P/J/A	0.64 (0.57-0.71)	**1.56**	5.6	Harvey and Goley 2011
Pup	NEP	BC, CAN	1990-94	Sat Log	34	M/F	P/J/A	0.63 (0.46-0.77)	**1.60**	13.3	Olesiuk 2010
Pup	NEP	Washington, USA	1999-2000	VHF	72	M/F	P/J/A	0.67 (0.55-0.77)	**1.50**	8.3	Jeffries et al. 2003
Pup	NEP	Washington & Oregon, USA	1991-93	VHF	156	M/F	P/J/A	0.65 (0.58-0.72)	**1.53**	5.8	Huber et al. 2001
Pup-Moult	NEA	Svalbard, Norway	2000	VHF	31	M/F	P/J/A	0.53 (0.36-0.69)	**1.90**	17.0	Merkel et al. 2013
Pup-Moult	NEA	Wadden Sea, Netherlands	1994	VHF	15	M/F	J/A	0.68 (0.43-0.86)	**1.47**	17.7	Ries et al. 1998
Moult	NWA	SLE, CAN	1995-96	VHF	11	M/F	J/A	0.40 (0.17-0.68)	**2.50**	36.9	Lambert 2012
Moult	NEA	Scotland	2009	Sat Log	25	M/F	A	0.72 (0.52-0.86	**1.39**	5.6	Lonergan et al. 2013
Moult	NEP	Alaska, USA	2006-09	Sat Log	25	M/F	J/A	0.53 (0.34-0.71)	**1.90**	19.0	Womble et al. 2020
Moult	NEP	Alaska, USA	1994 & 2000	VHF	63	M/F	P/J/A	0.83 (0.72-0.91)	**1.20**	5.6	Simpkins et al. 2003

Table 4. Published correction factors grouped by time periods and systems (NWA stands for Northwest Atlantic, NEA for Northeast Atlantic and NEP for Northeast Pacific). Moulting refers to correction factors obtained from studies conducted in moulting alone, as well as pupping and moulting periods.

Time period/system	Mean	SD	Range	n
Pupping/NWA	2.44	0.13	2.33 – 2.58	3
Pupping/NEA	1.64	–	–	1
Pupping/NEP	1.49	0.13	1.27 – 1.60	5
Moulting/NWA	2.50	–	–	1
Moulting/NEA	1.59	0.27	1.39 – 1.90	3
Moulting/NEP	1.55	0.50	1.20 – 1.90	2

FIGURES

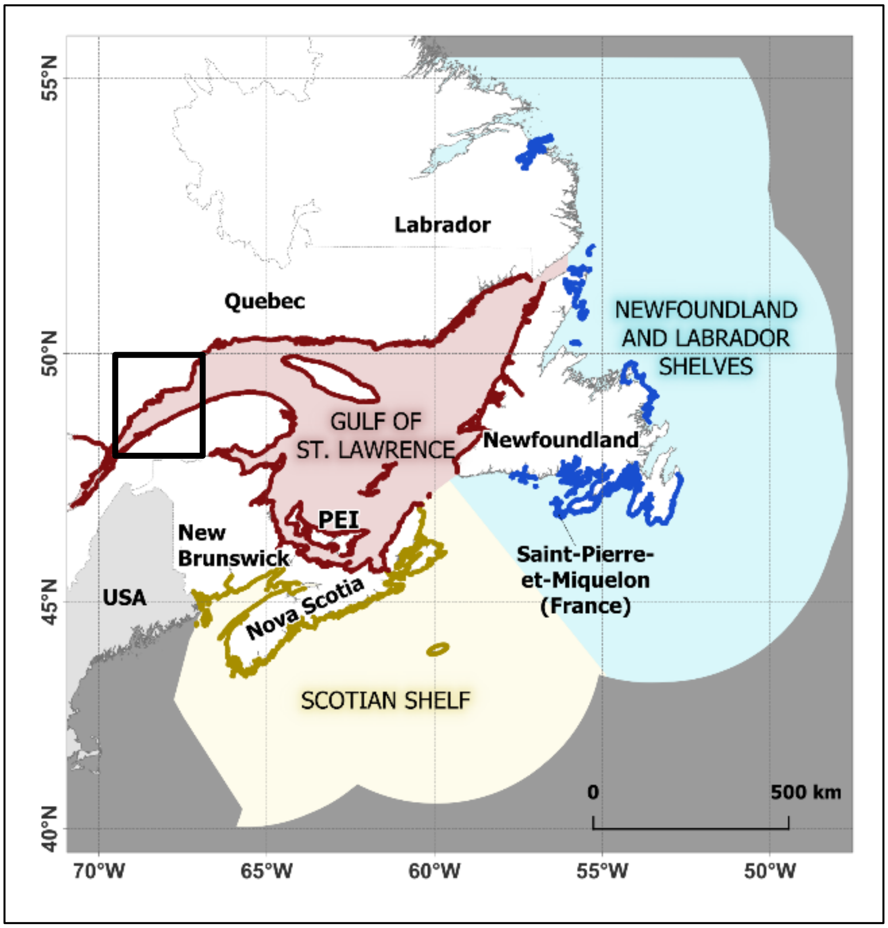

Figure 1. Map of Atlantic Canada showing the three survey regions and the aerial survey effort (darker colored lines) within each region. The black box indicates the area of the St. Lawrence Estuary (SLE) where seals tagged with satellite transmitters were located during the pupping period (Figure 5).

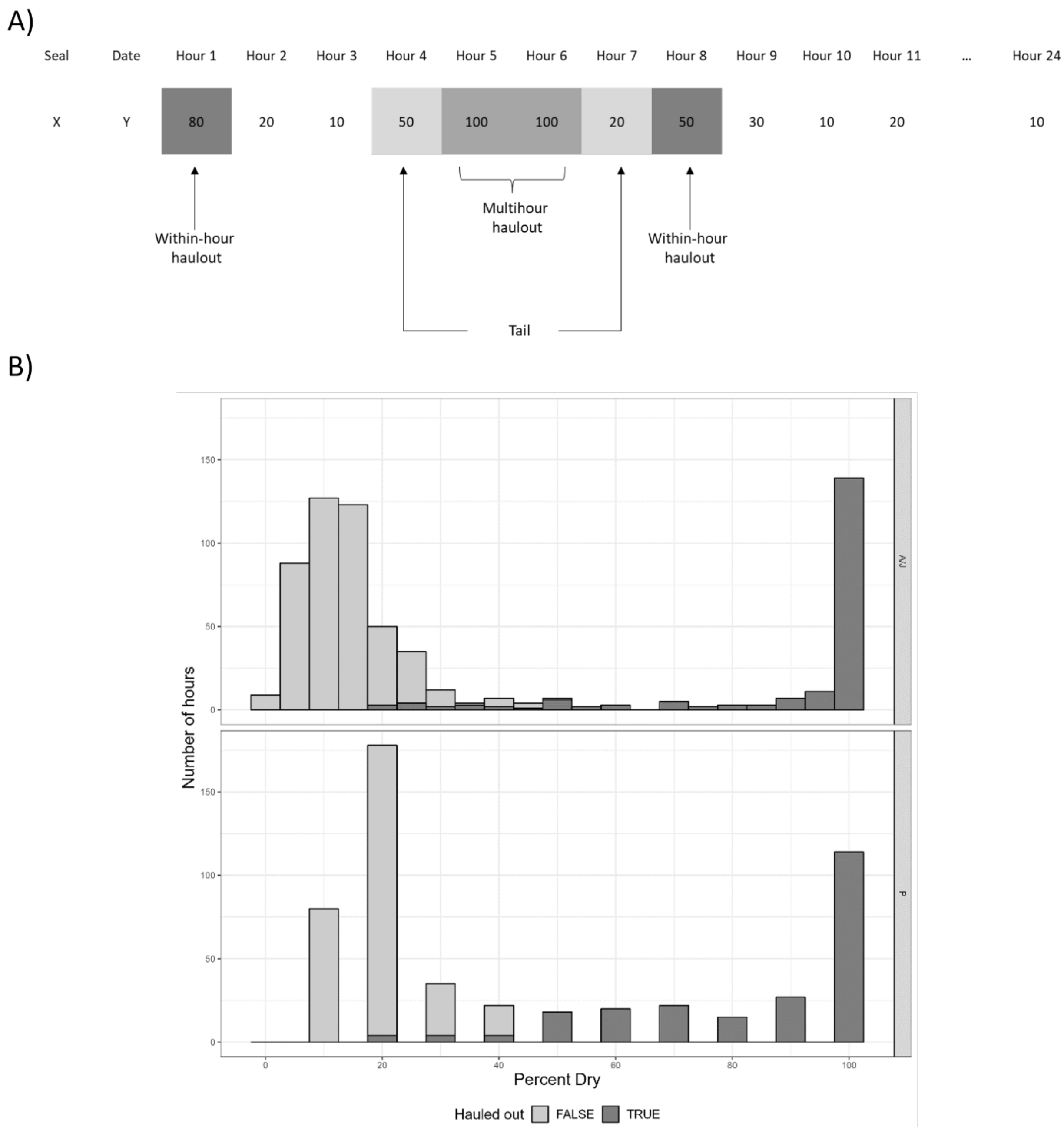

Figure 2. (A) Scheme representing the identification of haulout events from low-resolution (10% bins) hourly Percentage Dry Timelines data. (B) Distribution and classification of hourly Percentage Dry Timelines based on applied haulout event definition for all hourly bins occurring during survey-like conditions between May 15 – Jun 30, 2022, for both high- (1% bins; top) and low-resolution (10%; bottom) settings.

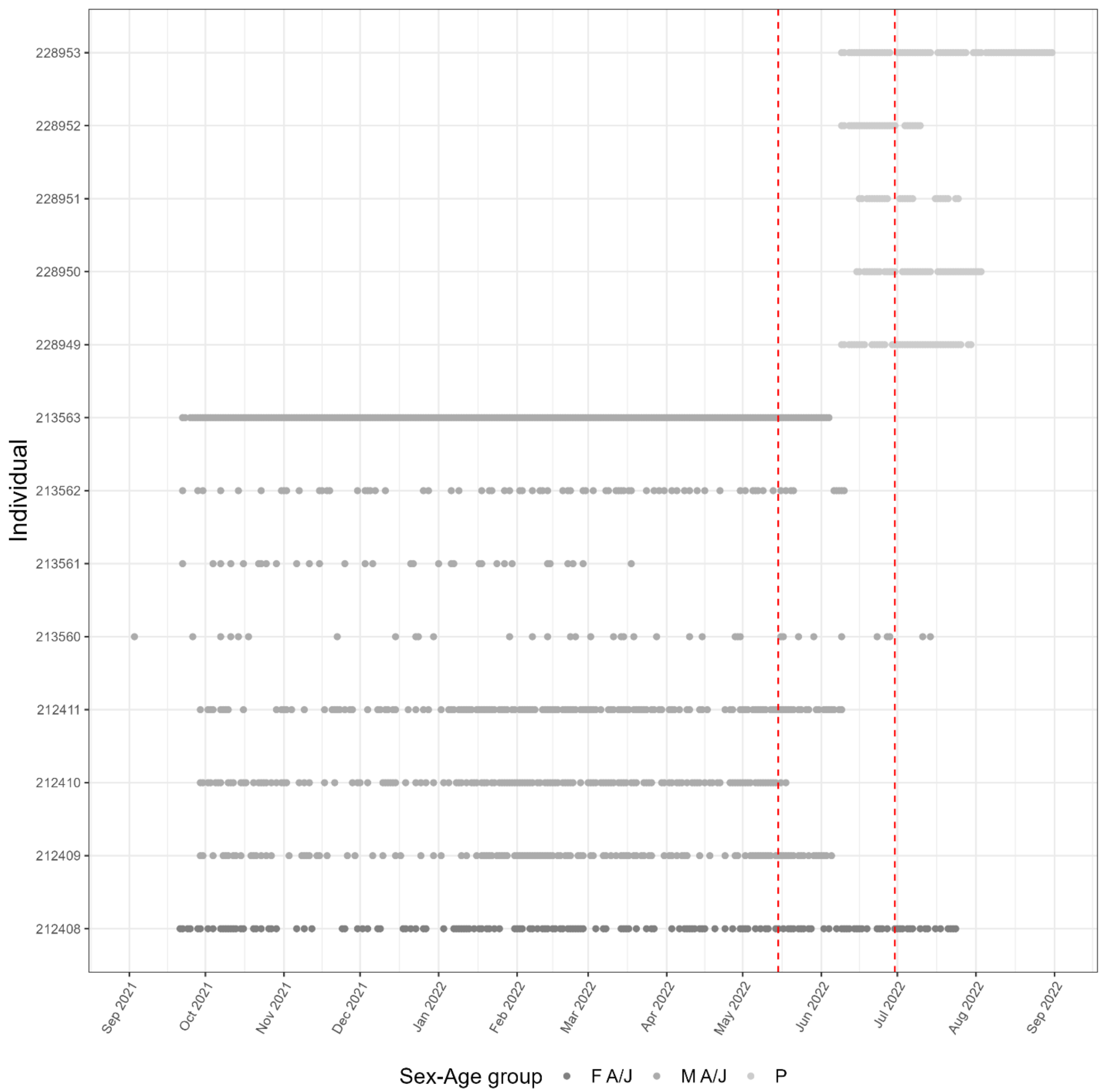

Figure 3. Abacus plot of the successful transmission of hourly Percentage Dry Timelines data since tagging for each seal. The red dashed lines represent the study period of interest (May 15 – Jun 30, 2022). F, M, and P stand for female, male, and pup, respectively, and A/J stands for adult or juvenile.

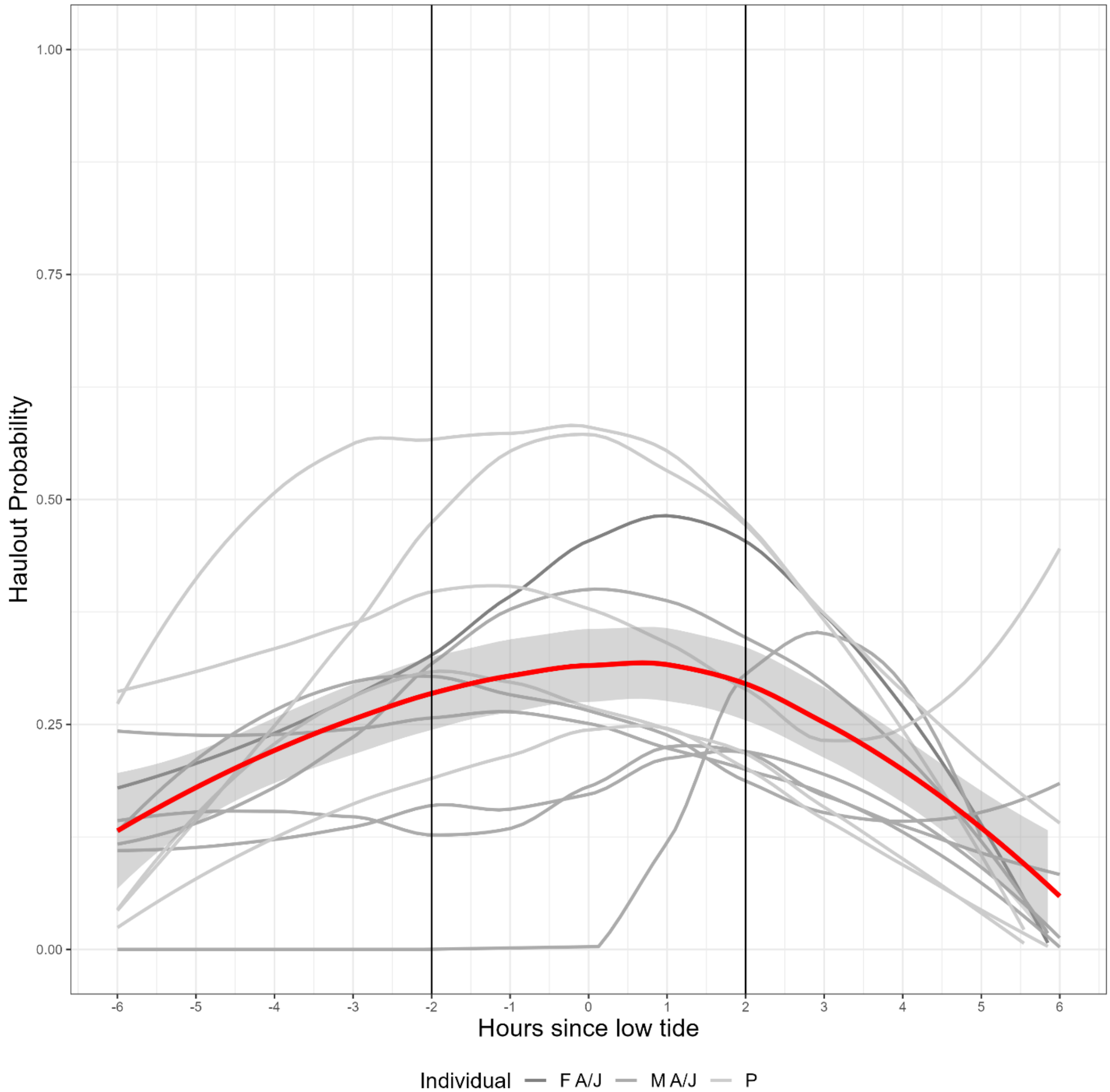

Figure 4. Average individual haulout probability as a function of hours since low tide during daylight between May 15 - June 30, 2022. The horizontal black lines indicate the survey window where 0 represents the hour during which low tide occurred along with two hours on either side for a total of 5 hourly bins. We used a loess smooth to represent the average for each individual. The overall average probability and 95% confidence intervals are represented by the red line and its corresponding shaded area. F, M, and P stand for female, male, and pup, respectively, and A/J stands for adult or juvenile.

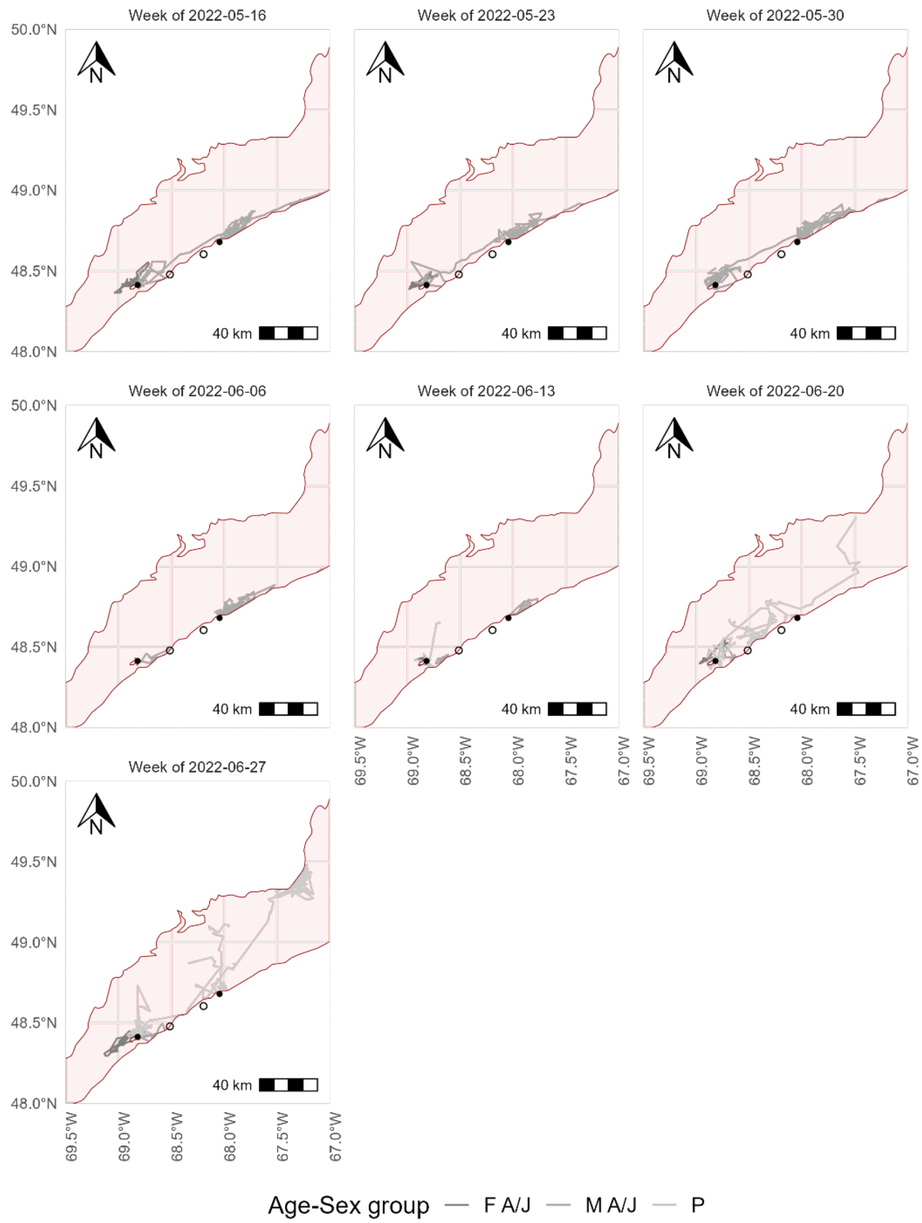

Figure 5. Weekly spatial distribution of harbour seals instrumented with satellite transmitters. Solid circles represent the two tagging sites : Bic (south-west) and Metis (north-east). Hollow circles represent Rimouski Tidal station (south-west) and Mont-Joli Meteorological Station (north-east). F, M, and P stand for female, male, and pup, respectively, and A/J stands for adult or juvenile.

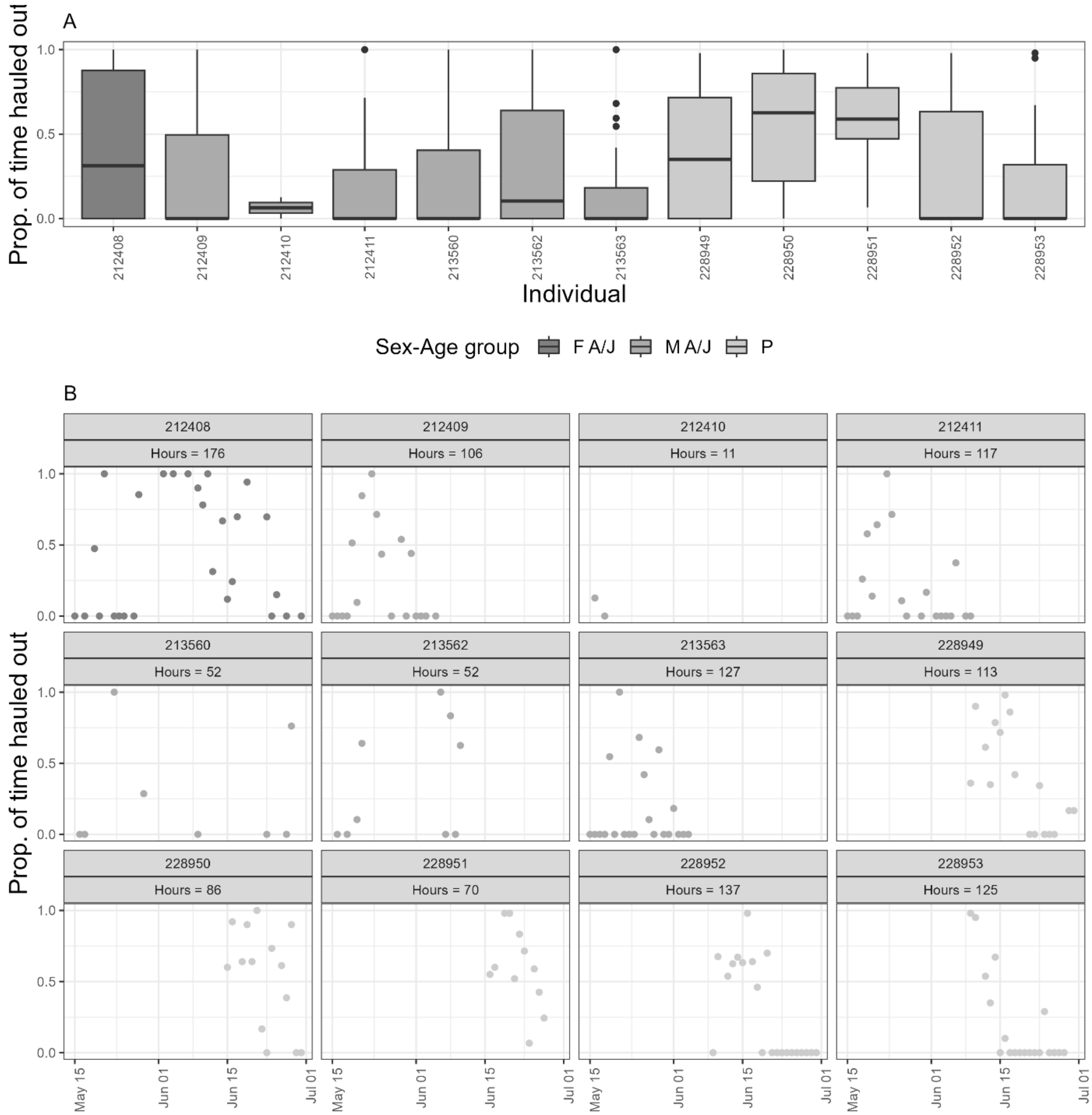

Figure 6. Inter- (A) and Intra- (B) individual variability in daily haulout proportion during survey conditions (five-hour window around low tide, daylight hours) between May 15 - June 30, 2022. Daily haulout proportion is the proportion of the total time spent hauled out over all hours that meet the survey conditions for every day for which data were available. F, M, and P stand for female, male, and pup, respectively, and A/J stands for adult or juvenile.

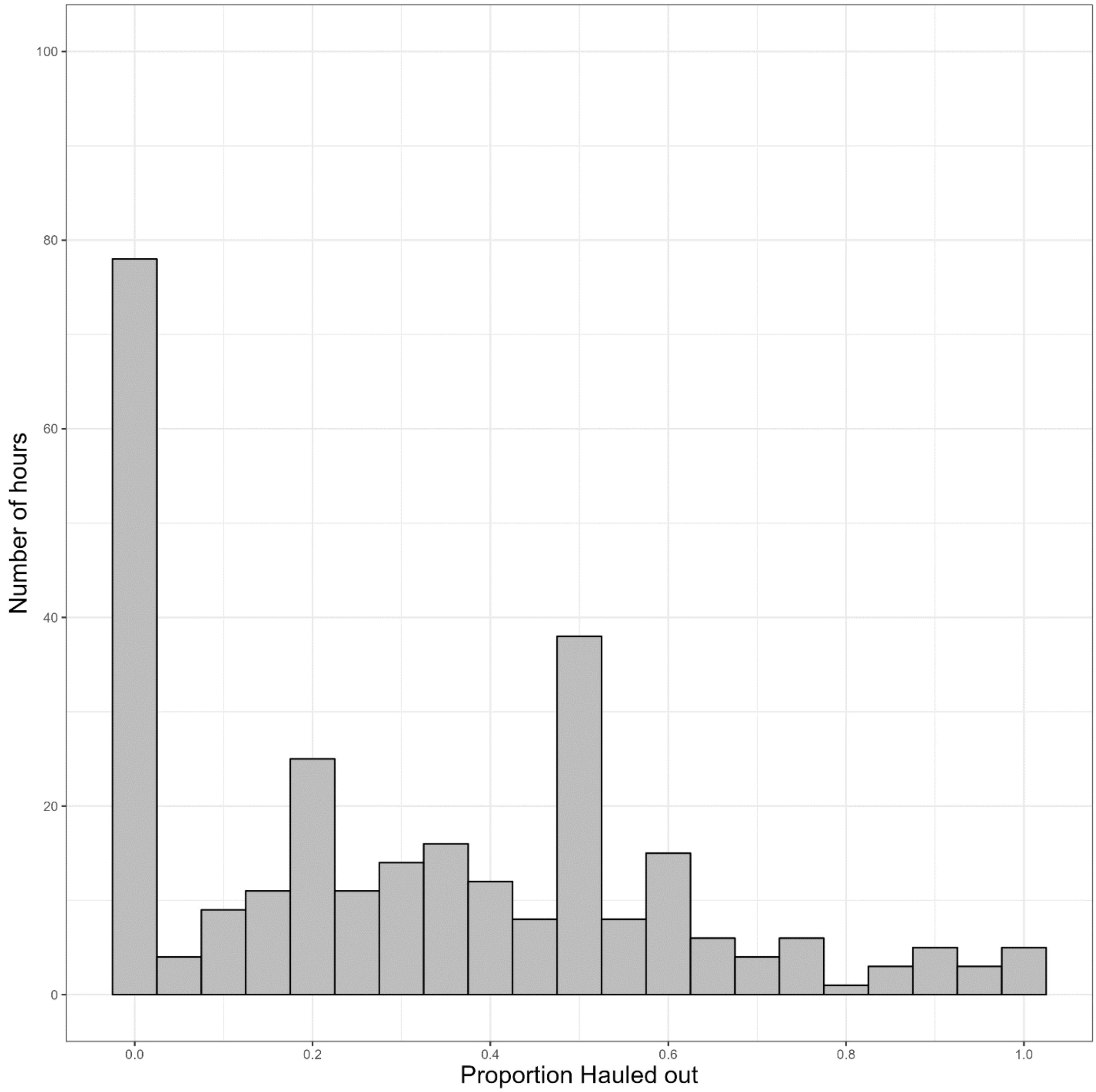

Figure 7. Raw distribution of all hours (n = 282) where haulout data for at least two of the 12 tagged seals (range: 2-7) were available.

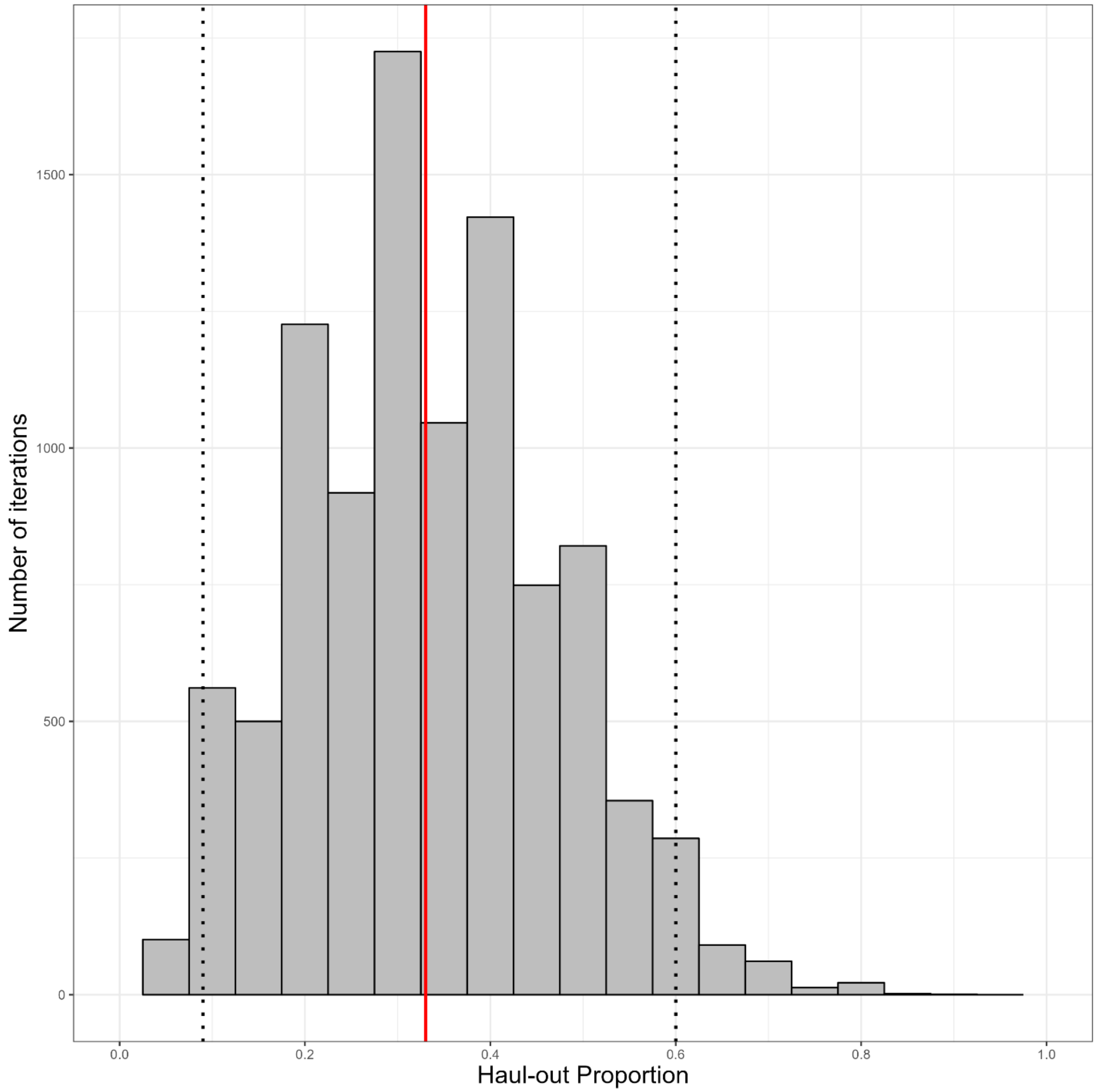

Figure 8. Bootstrap distribution of hourly proportion of the population hauled out with 10 000 iterations. The red line represents the mean value of 0.33. The dotted lines represent the 95% confidence interval of [0.09; 0.60] calculated around the mean.

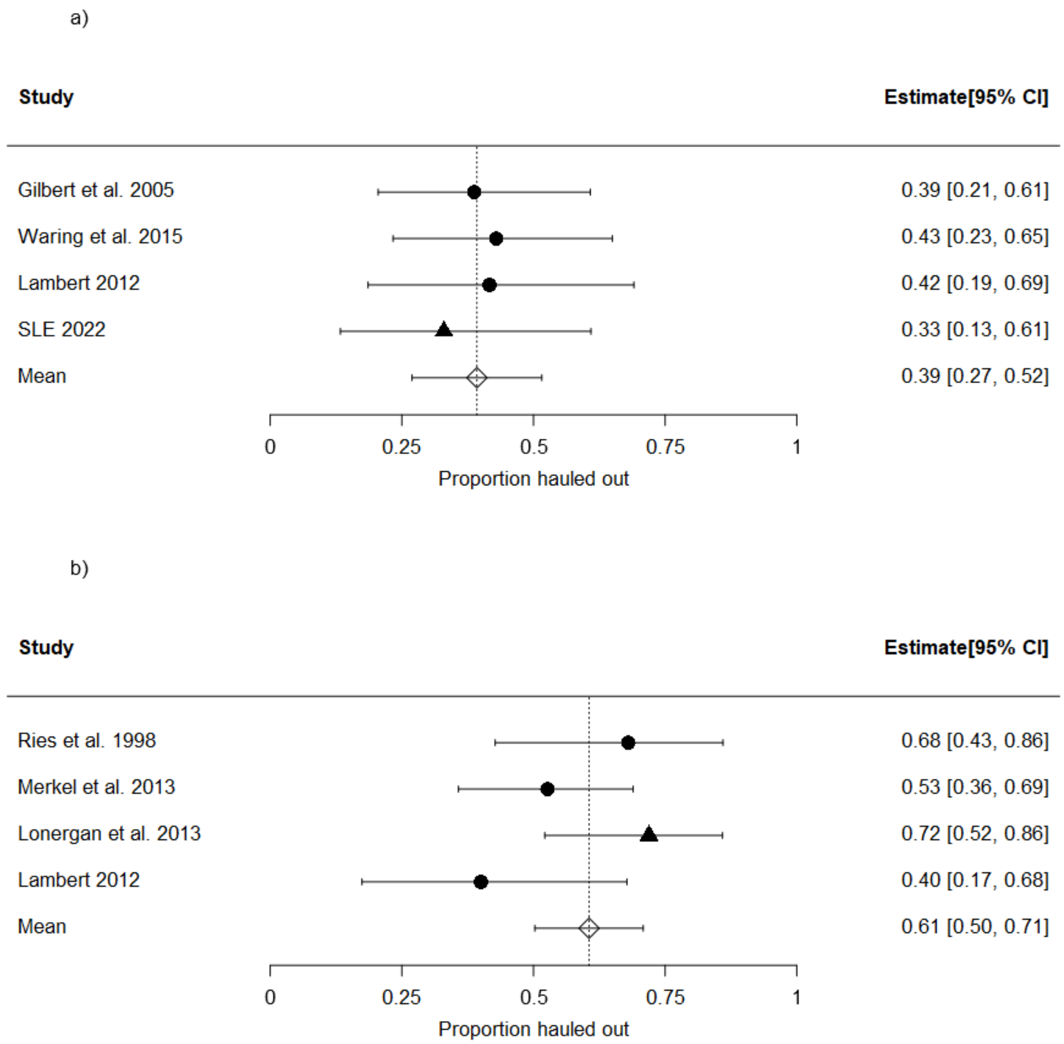

Figure 9. Forest plot of the proportion of harbour seals hauled out to estimate survey correction factors (see Table 3). The confidence intervals for the proportion hauled out are estimated using the Agresti-Coull interval method and estimated binomial error based on the proportion hauled out and the sample size. The upper panel (a) is pupping in Northwest Atlantic and lower panel (b) Pupping/Moulting and Moulting. In Northeast and Northwest Atlantic. The symbols indicate the instruments used (circles = VHF transmitters, triangles = recovered and unrecovered satellite transmitting biologgers).