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Distribution, movements, and habitat use of northern bottlenose whales (*Hyperoodon ampullatus*) on the Scotian Shelf

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Foreword

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

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ABSTRACT

The Scotian Shelf population of northern bottlenose whales (*Hyperoodon ampullatus*) is listed as Endangered under Canada's *Species at Risk Act*. Partial critical habitat was identified for this population in the Recovery Strategy first published in 2010, and three critical habitat areas located along the eastern Scotian Shelf, encompassing the Gully, Shortland Canyon, and Haldimand Canyon, have been designated. In this report, we used several sources of data to examine the distribution, movements and habitat use of northern bottlenose whales within and between designated critical habitat areas. Year-round passive acoustic monitoring conducted with bottom-mounted recorders at two inter-canyon sites revealed the presence and foraging activity of northern bottlenose whales in these areas throughout much of the year, with a seasonal peak in acoustic detections during the spring. Visual sighting records and acoustic recordings collected during vessel-based surveys provided a broader spatial view of species occurrence; these surveys were limited to summer months with effort focused in the canyons. Photo-identification data collected in the Gully, Shortland, and Haldimand canyons in six years of surveys between 2001 and 2017 were used to model the residency and movement patterns of northern bottlenose whales within and between the canyons. Model results suggested that individuals move between canyons over periods of days to months, with an average residency time in the Gully of approximately 20 days. Residency and movement patterns in the other canyons appear to differ from the Gully, but more photo-identification data from these areas are needed to improve the precision of model estimates. We did not find evidence that individuals prefer certain areas, and a low but consistent rate of movement into and out of the Gully suggests that the population may be fully mixing over approximately 6 months. Together, these results indicate a strong degree of connectivity between the Gully, Shortland, and Haldimand canyons and suggest that these areas are open to immigration from and emigration to other outside areas. Inter-canyon areas along the continental slope between the designated critical habitat areas likely represent important foraging habitat for northern bottlenose whales as well as a corridor for frequent movements between the canyons.

INTRODUCTION

Northern bottlenose whales (*Hyperoodon ampullatus*) inhabit offshore waters in northern regions of the North Atlantic Ocean. Off eastern Canada, centres of population abundance are documented in two geographic areas: along the edge of the eastern Scotian Shelf and in the Davis Strait and Baffin Bay off northern Labrador (Reeves et al. 1993). These are recognized as distinct populations, and have been assessed separately by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) since 1996, however, population structure and connectivity with populations outside of Canada is currently poorly understood (Feyrer et al. 2019). The Scotian Shelf population was given the designation of "Endangered" by COSEWIC in 2002, due to an extremely small population size, estimated at less than 150 individuals. Additional evidence including size differences (Whitehead et al. 1997), genetic analyses (Dalebout et al. 2006) and photo-identification mark-recapture studies (Whitehead and Wimmer 2005) suggest that the Scotian Shelf population of northern bottlenose whales is largely isolated from the more northern populations in the North Atlantic. In April 2006, the Scotian Shelf population was listed as Endangered under the *Species at Risk Act* (*SARA*), mandating legal protections and the explicit identification of critical habitat for the population, defined as important habitat areas deemed necessary for the survival or recovery of a listed species.

Northern bottlenose whales are typically found in waters greater than 500 m depth, and most commonly along the continental slope in waters between 800 m and 1500 m deep (Hooker et al. 2002b, Wimmer and Whitehead 2004). Like other beaked whales, northern bottlenose whales are deep divers, regularly diving to depths exceeding 800 m to forage on deepwater squid and fish (Hooker and Baird 1999, Miller et al. 2015). Stomach content analyses conducted by Hooker et al. (2001) suggested that squid from the genus *Gonatus* likely constitute their primary prey in the Scotian Shelf region, and that they may occupy a relatively narrow dietary niche. Little is known about the abundance or distribution of *Gonatus* species off eastern Canada. Oceanographic and bathymetric features are often used as proxies to identify habitat and predict species distributions when data on prey distributions are not available. Habitat suitability modeling performed by Gomez et al. (2017) identified depth and summer sea-surface temperature as significant indicators for northern bottlenose whale habitat, and predicted that much of the continental slope off the Scotian Shelf, Newfoundland, and Labrador could be potentially suitable habitat for the species.

The distribution of the Scotian Shelf population of northern bottlenose whales appears to be highly concentrated around three submarine canyons along the eastern Scotian Shelf: the Gully, Shortland Canyon, and Haldimand Canyon (Wimmer and Whitehead 2004).The Gully has long been recognized as a habitat center for this population, with high densities of whales present during the summer (Hooker et al. 2002a, Hooker et al. 2002b), repeated sightings of the same individuals at different times of year (Whitehead et al. 1997), and consistent year-round acoustic detections of northern bottlenose whale echolocation clicks (Moors 2012, Stanistreet et al. 2017). Gowans et al. (2000) estimated that approximately one-third of the Scotian Shelf population may be found in the Gully at any given time. More recently, northern bottlenose whales were found to be regularly present in Shortland and Haldimand canyons as well, and the same individuals have been sighted in all three canyon areas (Wimmer and Whitehead 2004, O'Brien and Whitehead 2013).

Based on the year-round use of the Gully, Shortland, and Haldimand Canyons for foraging, socializing, mating, and rearing young, these areas have been identified as critical habitat in the Recovery Strategy for the Scotian Shelf population of northern bottlenose whales (Fisheries and Oceans Canada 2016). Designated critical habitat currently includes Zone 1 of the Gully Marine

Protected Area and waters greater than 500 m depth in Shortland and Haldimand canyons, encompassing three non-contiguous areas separated by 20–30 km.

Individual northern bottlenose whales are known to move between canyons on the Scotian Shelf (Wimmer and Whitehead 2004, O'Brien and Whitehead 2013), but little is known about their use of inter-canyon areas other than as a presumed corridor to move between the canyons. Far less visual survey effort has occurred outside of the Gully, Shortland, and Haldimand canyons compared to within these areas, and few beaked whale studies have been conducted anywhere on the Scotian Shelf outside of the summer months. However, acoustic recordings collected from 2006–2009 during both summer and winter months at recording sites within and outside the canyons provided initial evidence that northern bottlenose whales may be present year-round in inter-canyon areas (Moors 2012). The detection of potential echolocation clicks from northern bottlenose whales in these recordings suggested that they may utilize slope areas for foraging, and Moors (2012) recommended additional acoustic monitoring to confirm this finding. At present, the full geographic range and seasonal habitat use of this population is not known, and additional important habitat areas may include the continental slope areas and other canyons along the Scotian Shelf, as well as slope areas extending east and north into Newfoundland.

As habitat requirements for northern bottlenose whales on the Scotian Shelf are not fully understood, the Recovery Strategy outlines a schedule of studies aimed at identifying additional critical habitat and providing further information necessary to support recovery objectives (Fisheries and Oceans Canada 2016). Among the studies outlined, a primary research goal is to conduct year-round passive acoustic monitoring of northern bottlenose whales in areas outside currently designated critical habitat, to address the following questions:

- How does species presence in the inter-canyon areas compare to that within canyons?
- What are the biophysical functions, features, and attributes of the inter-canyon habitat for northern bottlenose whales?
- What are the spatial extents of the areas that support the above habitat properties?
- What are the activities likely to destroy the functions, features, and attributes of inter-canyon habitats?

In this paper we primarily aim to address the first question listed above, presenting data from year-round autonomous passive acoustic monitoring conducted within the Gully and between the Gully, Shortland, and Haldimand canyons to provide information on species presence throughout the year, as well as visual sightings and acoustic detections from survey effort occurring within and between canyons during the summer. Additionally, we present the results of analyses conducted using photo-identification data to model the movement and residency patterns of northern bottlenose whales in and around the Scotian Shelf canyons, expanding on the results of an earlier study of movement and habitat use by Wimmer and Whitehead (2004). The remaining questions regarding the characteristics, spatial extent, and risks to inter-canyon habitat for northern bottlenose whales are discussed in the context of these results.

METHODS

AUTONOMOUS BOTTOM-MOUNTED PASSIVE ACOUSTIC MONITORING

Data Collection

Stationary passive acoustic monitoring was conducted along the edge of the Scotian Shelf to assess the year-round presence of northern bottlenose whales. Bottom-mounted recorders were deployed in the Gully (MidGul) and at two inter-canyon sites along the eastern Scotian Shelf: GulSho, located between the Gully and Shortland Canyon, and ShoHald, located between Shortland and Haldimand Canyons (Figure 1). At each site, an Autonomous Multichannel Acoustic Recorder (AMAR) (JASCO Applied Sciences, Dartmouth, NS) was moored at a depth between 1400 and 1700 m, with the recorder suspended approximately 55 m above the seafloor. Data were collected concurrently at all three sites over four consecutive deployments: October 2012 to April 2013, May to September 2013, November 2013 to April 2014, and May to September 2014. AMARs were programmed to collect high-frequency (HF) and low-frequency (LF) recordings on an alternating duty cycle throughout each deployment. During the first two deployments, each AMAR was equipped with an omnidirectional Geospectrum M8E-51 hydrophone, and HF recordings were made at a sampling rate of 128 kHz for 2 min (120 s), followed by LF recordings at a sampling rate of 16 kHz for 13 min (780 s), resulting in four HF recording files per hour. During the last two deployments, each AMAR was equipped with an omnidirectional Geospectrum M8Q-51 hydrophone and HF and LF recordings were made at sampling rates of 375 kHz for 2.2 min (130 s) and 16 kHz for 17.8 min (1070 s), respectively, resulting in three HF recording files per hour. Acoustic data were stored on internal hard drives and downloaded to *.wav* format audio files after instrument recovery.

Data Analysis

High-frequency acoustic recordings were analyzed for the presence of northern bottlenose whale echolocation clicks using a multi-step detection and classification process based on methods developed by Baumann-Pickering et al. (2013). The methods are described in detail in Stanistreet et al. (2017). Briefly, an automated detection algorithm was applied to detect and extract echolocation signals from the recordings. Each detected signal was band-pass filtered between 5 kHz and 95 kHz, and spectra were calculated using a 512-point fast-Fourier transform (FFT) and Hann-windowed data centered on the click. Peak and center frequencies, bandwidth, duration, signal-to-noise ratio, and inter-click-intervals (ICIs) were measured. A set of criteria based on spectral and temporal characteristics were applied to each detected signal to distinguish potential beaked whale clicks from signals produced by other odontocetes. Potential beaked whale clicks were initially identified as those having peak and center frequencies above 23 kHz, durations of at least 0.355 ms, and waveform energy remaining above a 50% energy threshold for at least 0.1 ms.

Potential beaked whale click detections in each file (120 or 130 s duration) were manually reviewed using summary figures displaying histograms of peak frequency and ICI, a plot of mean click spectra overlaid on mean noise, and a concatenated spectrogram of all detected clicks. Waveforms and spectrograms of individual clicks were also inspected, and species classifications were assigned to confirmed beaked whale clicks. Echolocation clicks produced by northern bottlenose whales were identified by their peak frequency of approximately 26 kHz, ICIs of approximately 0.4 s, and distinctive frequency-modulated upsweep shape (Clarke et al. 2019; Figure 2). Clicks from other beaked whales were identified to the species level when possible. Detected signals that did not exhibit clear, unambiguous characteristics of beaked whale clicks were marked as false detections and excluded from the analysis.

To evaluate detector performance, approximately 1% of files without detections at each recording site were randomly selected for manual review (1135 files in total). No more than 1 file was selected per day from each site to ensure temporal coverage throughout the year. Each selected file was reviewed using PAMLab Lite software (JASCO Applied Sciences, Dartmouth, Nova Scotia) to view a spectrogram and waveform using a 15–30 s window length, and the presence or absence of visible, clearly identifiable northern bottlenose whale clicks was noted.

To assess the spatiotemporal presence of northern bottlenose whales at each recording site, detections were binned into hourly and daily presence or absence, and compared across months and years.

VISUAL SURVEYS

Northern bottlenose whale sightings data were collected by the Whitehead Lab of Dalhousie University during cetacean research trips aboard the auxiliary sailing vessel *Balaena*. Surveys for northern bottlenose whales in the Gully have been part of an ongoing research program led by the Whitehead Lab, with data collected during the summer months in 24 years between 1988 and 2017. Beginning in 2001, survey effort was expanded to include surveys for northern bottlenose whales in Shortland and Haldimand canyons, and this effort continued in five subsequent years (2002, 2011, 2015, 2016, and 2017). However, to maximize survey effort in core habitat within the canyons, transits between the Gully and other canyons often occurred at night or in poor weather conditions, reducing visual survey effort outside and between critical habitat areas.

Visual surveys were conducted only during the daytime, and only in reasonably good weather conditions (Beaufort sea state < 5). Vessel speed varied between 1 and 6 kn. During encounters with northern bottlenose whales, photographs, videos, and acoustic recordings were regularly collected as well as information on other species that were incidentally sighted. Metadata collected included the GPS location and time of the initial sighting, species, group size, behaviour, distance and bearing from vessel and environmental conditions. Visual encounters began when northern bottlenose whales were first sighted and ended ten minutes after they were last seen. Additional location, visibility and environmental data were collected every hour, 24 hours a day while the research vessel was surveying or transiting.

Sightings of northern bottlenose whales from surveys in 2001, 2002, 2011, and 2015–2017 were summarised by encounter and mapped in ArcGIS; each sighting represents one or more northern bottlenose whales. The density of sightings across the study area during this period was assessed using a kernel density estimator (KDE) in ArcGIS 10.5 with a 1 km bandwidth. This bandwidth was selected because it is the maximum distance at which a sighting of a northern bottlenose whale might be recorded.

To estimate the amount of visual survey effort that occurred outside the Gully and between the other canyons, all coordinates from ship locations (> 200 m depth) were classified as on or off visual effort. On-effort locations, classified as being in daylight hours with Beaufort sea state < 5, no fog, and visibility > 1 nautical mile, were selected for further analysis. A KDE was used to generalize the density of hourly effort over the region using a 10 km bandwidth. This bandwidth was chosen to smooth the hourly log of effort from a single point location to the maximum distance the vessel could travel in one hour.

TOWED ARRAY ACOUSTIC RECORDINGS

Data Collection

During cetacean research trips in the summers of 2015–2017, the Whitehead Lab of Dalhousie University collected acoustic data using a two-element hydrophone array (Benthos AQ4 elements: -204 dBV re 1μPa, Magrec HP-02 preamplifier: 29 dB gain) recording at a sampling rate of 192 kHz, and towed approximately 100 m behind the ship. The array was typically recording continuously while surveying under sail or motor as well as during visual encounters with northern bottlenose whales. Unlike visual survey effort, acoustic surveys were not restricted by daylight and visibility, and were also conducted at night and under a range of weather conditions. Acoustic surveys were classified as being "shelf edge", if recordings were collected while surveying outside the Scotian Shelf canyons along a predetermined trackline that roughly followed the 1000 m isobath, or "opportunistic", if recordings were collected within the canyons, during transits between canyons, or offshore beyond the 1000 m isobath.

Acoustic Analysis

All 1500 hours of acoustic recordings collected during 2015–2017 were binned into ~10 min segments and processed using an automated beaked whale classifier detector (JASCO Applied Sciences, Dartmouth, Nova Scotia) to screen recordings for presence of northern bottlenose whale clicks. For data from the shelf edge surveys and a selection of the opportunistic surveys, recording segments with > 1 northern bottlenose whale detection were visually validated using PAMLab software. This validation involved visual inspection of spectrograms to find beaked whale clicks using a window length of 8 s, frequency scale of 0–96 kHz, and FFT settings of 94 Hz frequency step, 0.001 s frame length, 50% overlap and a Hamming window. When potential beaked whale clicks with a frequency-modulated upsweep occurred in a click train (three or more clicks in a row, spaced approximately equidistantly), they were then viewed individually at an enhanced spectrogram resolution allowing for more detailed examination of the click structure, using a window length of 0.0025 s, frequency scale of 0–96 kHz, and FFT settings of 375 Hz frequency step, 0.000266 s frame length, 6% overlap and a Hamming window. Recordings were confirmed to contain northern bottlenose whales if clicks occurred within a click train and had a peak frequency of approximately 26 kHz, an ICI of approximately 0.4 s, and a distinctive frequency-modulated upsweep (Clarke et al. 2019).

The locations of all recordings and validated detections were mapped based on the GPS coordinate associated with the start of each 10-minute recording. Density of recording effort was estimated using a kernel density estimator (KDE) weighted on the length of each file, and generalized using a 2 km bandwidth based on the estimated maximum distance at which northern bottlenose whales may be detected while the boat was traveling in a 10-minute period.

PHOTO-IDENTIFICATION

Field Data Collection

When northern bottlenose whales were encountered during surveys, effort was made to photograph both sides of the dorsal fin and the melon of all individuals without bias for how well-marked they were. Digital photographs were taken with Canon 50d and 7d cameras, fitted with a fixed 300 mm lens. These photo-identification field protocols have been used by researchers since 1988 and are described in detail by Gowans et al. (2000) and O'Brien and Whitehead (2013).

Photo-Identification Analyses

All photographs of northern bottlenose whales taken in the 24 years of surveys occurring between 1988 and 2017 were digitized and imported into the photo management software program Adobe Lightroom along with associated metadata, including the date and time the photo was taken and the GPS location. Photographs were given a quality rating (Q) based on the angle, focus, exposure, and proportion of dorsal fin visible, using criteria based on O'Brien and Whitehead (2013). Poorest quality photographs were given a rating of Q1, while highest quality photographs were rated Q4. Any unique marking, such as dorsal fin notches, large scars, and patches occurring within one dorsal fin width on either side of the fin were associated with each photo as a keyword. Any mark type could be used for initial identification, except for diatom patches or slough skin, which can change shape rapidly within a sampling year (Gowans and Whitehead 2001). Only fin notches or back indents are considered markings reliable enough to persist over the 29-year study period. All photographs rated Q3 and above were iteratively scanned for matches using unique markings and each individual whale received a unique identification number (ID). The highest quality right or left side photograph of each individual identified in each year was used to match individuals across sampling years.

Movement and Population Analyses

All photographs rated ≥ Q3 were considered for population and movement analyses within one field season. Only reliably marked individuals were considered in analyses that spanned multiple years. Estimates of population size for reliably marked individuals (N_m) were scaled to account for the proportion of the population without reliable marks, by multiplying N_m by the proportion of reliably marked individuals within the entire population, estimated to be 51% (Whitehead and Wimmer 2005, O'Brien and Whitehead 2013). For all movement analyses Shortland and Haldimand canyons were grouped together as the "Other Canyons" (OC) to increase the sample size for modelling movement into and out of these areas. All models were run using 1000 bootstrap replicates.

(1) Modelling Lagged Identification Rate

The lagged identification rate (LIR) is the probability that an individual identified in an area at one time is identified in the area at a later time lag (Whitehead 2001). Emigration or mortality will cause LIRs to decrease with time, and models fitted to LIR can estimate the length of residency in an area. Overall lagged identification rates can also be calculated among more than one area indicating the probabilities that individuals are found again in the same area or in a different one after a particular time lag. Models of LIR are calculated using maximum likelihood methods and can be used to estimate individual residency, population size at a specified time period, and mortality parameters. The form of these models is specific to whether one or two areas are being considered and is further described by Whitehead (2001). For one area, we looked at models of: (a) Emigration + Mortality, where individuals leave a study area but never return, (b) Emigration - Reimmigration, where individuals leave a study area and then return, and (c) Emigration - Reimmigration + Mortality, where individuals leave a study area and then some return while others don't. For two areas we considered models of either (d) Migration - Full Interchange, where individual movement is random and on average the same amount of time is spent in each area before moving on, or (e) Full Mixing, where movement within one time unit is sufficient to fully mix the population. We modelled all LIRs using 1000 bootstrap replicates in the social analysis software program SOCPROG, implemented in MATLAB (Wimmer and Whitehead 2004, Whitehead 2009). Minimum QAIC was used as an indicator of best fit for model comparisons of each dataset.

Residency within the Gully

Using the full 24 years of photo-identifications acquired only in the Gully, we estimated the residency period for two datasets, one including all identifications and one for only reliably-marked identifications. All LIR model forms for residency in one area were considered.

Residency across the Scotian Shelf area

Using only reliably-marked identifications from the six years of data where photo-identification work was conducted in the Gully and the OC, we estimated the LIR probability that an individual found in one of the Scotian Shelf areas (Gully or OC) stayed in the same area or moved to a different one. LIR models for one area and two areas were considered to compare residency within and rate of movement out of both areas (Wimmer and Whitehead 2004).

Differences in residency between the Gully and other canyon areas

Using only reliably-marked identifications from the six years of data where photo-identification work was conducted in the Gully and the OC, we estimated the LIR for an individual found in the OC to stay or leave and considered the results in light of LIR model estimates for the Gully during this time period. LIR probabilities were also calculated between Gully-OC and OC-Gully data using movement models for two areas as per Wimmer and Whitehead (2004).

(2) Markov Movement Models

The probabilities of movement between the Gully, OC and another “Outside Area” (OA), defined as all areas not surveyed, were calculated using a parameterized Markov model in SOCPROG. The model estimates the probability at each time period of an individual moving from the area it is in to another area, as well as the population size and a mortality rate (including permanent emigration). Data for these models came from the six years of surveys where photo-identification work was conducted in the Gully and the OC, and results were compared between models using the full dataset containing all identifications and the dataset based on only reliably-marked identifications. Seven-day periods were used to increase sample sizes within time units. We used a fixed population size of 127 (65 reliably-marked individuals) based on the best fit results of open-population mark-recapture models for the dataset.

RESULTS

AUTONOMOUS BOTTOM-MOUNTED PASSIVE ACOUSTIC MONITORING

Passive acoustic recordings from bottom-mounted recorders were analyzed across a total of 605 days (14,520 h) at the MidGul and GulSho recording sites, and 606 days (14,544 h) at the ShoHald site. Acoustic detections were identified from northern bottlenose whales and three other beaked whale species: Cuvier’s beaked whale (*Ziphius cavirostris*), Sowerby’s beaked whale (*Mesoplodon bidens*), and a third click type likely produced by True’s beaked whale (*M. mirus*) and/or Gervais’ beaked whale (*M. europaeus*).

Northern bottlenose whale clicks were detected on 605 (100%), 150 (25%), and 259 (43%) of the recording days at the MidGul, GulSho, and ShoHald recording sites, respectively. Detections occurred continuously throughout the year in the Gully. At the ShoHald site, northern bottlenose whale clicks were detected during all months with recording effort, while at the GulSho site no detections occurred in September, November, or December 2013, or in August or September 2014. At both inter-canyon recording sites, detection of northern bottlenose whales appeared to be more seasonal than in the Gully, with higher detection rates occurring from February to June of each year (Figure 3 & Figure 4).

The detection sensitivity (recall) for northern bottlenose whale clicks (per acoustic recording file) was estimated to be 0.75-0.90 across sites, indicating that at each site, 75% to 90% of files containing northern bottlenose whale clicks were detected. Results are presented here on the basis of hourly and daily presence of click detections; it is important to note that recall will be higher at both of these temporal scales than on the per file basis at which it was estimated, since there were 3–4 acoustic files recorded per hour and 72–96 files recorded per day. Since all detections were manually validated and false detections were removed from the analysis, the specificity (precision) of the results is considered to be 100%.

VISUAL SURVEYS

Sighting locations of northern bottlenose whales and hourly visual survey effort in six years between 2001 and 2017 are shown in Figure 5. Sightings are based on the first location recorded during visual surveys and longer behavioral encounters with northern bottlenose whales. These coordinates reflect the location of the vessel which was typically within 10–1000 m of sighted animals. Although survey effort extended beyond the Gully in these years, the density of visual effort outside the Gully and between canyons was very low, less than 30 minutes per km^2, compared to within canyons, where effort density was more than six hours per km^2 in some areas (Figure 5). During 2001, 2002, 2011 and 2015–2017, all visual encounters with northern bottlenose whales on the Scotian Shelf occurred within the canyon areas. There were 265 visual encounters in the Gully, 83 in Shortland Canyon and 53 in Haldimand Canyon across 82 survey days (Table 1). Peak density of sightings (14 per km^2) occurred within the deeper areas of each canyon. Within the Gully, the density of sightings appeared to be highest on the northeast side of the canyon at the edge of the critical habitat boundary, close to the bathymetric feature known as the Southwest Prong (Figure 5). During encounters when behavioral observations were recorded for longer periods of time, individuals have been observed moving outside the critical habitat boundary to cross over the Southwest Prong (L. Feyrer, personal observation).

TOWED ARRAY ACOUSTIC RECORDINGS

Acoustic recording effort and validated detections of northern bottlenose whales from shelf edge and opportunistic surveys in 2015–2017 are shown in Figure 6. Although shelf edge and opportunistic surveys went beyond the current Scotian Shelf population designated unit boundary, for this report summary statistics were calculated based on the extent of surveys within this region. During this period, there were 770 hours of recordings collected in the Scotian Shelf region, with approximately 398 hours occurring within critical habitat areas and 60% of these hours within the Gully. Similar to visual surveys, the recording effort was higher within critical habitat areas, with a maximum effort of 402 minutes per km^2, compared to far lower survey effort outside critical habitat where maximum recording effort was 42 minutes per km^2. Manual validation of northern bottlenose whale click detections included 115 hours (15%) of all the Scotian Shelf recordings (45 hours inside critical habitat and 70 hours outside). Within critical habitat areas there were 126 confirmed detections of northern bottlenose whales on 14 different days, in the Gully (N = 74), Haldimand (N = 40) and Shortland canyons (N = 12). Outside critical habitat areas, there were 35 confirmed detections across all three years; 29 of these occurred within 50 km of the canyon areas, mainly between canyons and to the northeast of the region along the shelf edge. Detections occurred between and just outside the canyons on 4 consecutive survey days in 2015, 1 day in 2016, and 1 day in 2017, and were generally clustered along the 1000 m depth contour. Although limited survey effort extended into waters > 2000 m depth, there were no confirmed detections of northern bottlenose whales in deeper water regions.

These results are part of an ongoing project for which analyses are not yet completed, and represent an initial minimum estimate of the extent and distribution of northern bottlenose whale detections during acoustic surveys of the area. As these detections were manually validated and false detections were removed, the precision of these results is considered to be 100%.

PHOTO-IDENTIFICATION ANALYSES

Effort in the Gully

Between 1988 and 2017 there were 24 years with photo-identification data and 21 years with effort on more than one day, comprising a total of 238 survey days in the Gully. Using only high-quality photographs (≥ Q3, N = 22,835), there were a total of 572 (188 reliably-marked) left side identifications and 557 (183 reliably-marked) right side identifications of northern bottlenose whales. A discovery curve of new identifications by year is shown for all IDs and for only reliably-marked identifications in Figure 7.

Effort outside the Gully

In the six years of surveys between 2001 and 2017 that included the other canyons on the Scotian Shelf, there were 16,874 high-quality photographs (≥ Q3) of northern bottlenose whales. All unique photo-identifications found in each location during this period are detailed in Table 2.

Re-identifications between the Gully, Shortland and Haldimand canyons

Across the six years of surveys occurring in all canyons, multiple individuals (66 left side IDs, 68 right side IDs) who were identified in the Gully were also observed in one or more of the other canyons (Table 2 & Table 3). While survey effort in the other canyons was considerably less than effort in the Gully during this period, the daily identification rate was similar overall with an average of 8.1 whales/day identified in both the Gully and the other canyons.

MOVEMENT AND POPULATION ANALYSES

(1) Modelling Lagged Identification Rate

Residency within the Gully

Residence time in the Gully-only dataset was calculated over two time scales. The first used all identifications and calculated the LIR over a 100-day period, given the assumption that more subtle marks would not change over this period (Figure 8a). The second used only reliably-marked individuals and calculated the LIR over a 1000-day period to understand movement patterns of animals in the Gully over longer time periods (Figure 8b). Based on minimum QAIC, (c) the Emigration - Reimmigration + Mortality model performed the best on both datasets, although with high standard errors (SE) for parameter estimates when including non-reliably-marked IDs (Table 4).

The models for the reliably-marked dataset suggest that average residency in the Gully lasted between 10-25 days, with about 20 reliably-marked individuals (or approximately 40 individuals total) in the Gully at any given time. For reliably-marked whales that return, estimates of residency outside the Gully have less precision, but appear to range from a few days to months, within the 95% confidence interval. Other estimated parameters from all ID models have high SE and are insufficiently precise to have much utility.

Residency across the Scotian Shelf area

For the six years where survey effort occurred outside the Gully, we assessed residency and movement based on whales resighted across the entire area. Best fit models of movement within and between areas are described in Figure 9 and Table 5. For residency in the same area, Emigration - Reimmigration models had the best fit, while for movement to different areas, Migration Full-Interchange models fit the movement data best. The models for movement between areas suggest the probability of an individual moving to a different area over 1-10 days was less than half the probability of staying in the same area. Probability of movement increased after approximately 22 days, and after 40 days, the probabilities of movement or residency in any area (the Gully or OC) were nearly equivalent.

Differences in residency patterns between the Gully and other canyon areas

For the expanded dataset we also considered whether there was a difference in residency and movement specific to the Gully or the other canyons. Using LIR models we estimated the residency of an individual in the Gully separately from the residency of individuals found in the OC. We then assessed differences in movement out of the OC into the Gully, and movement out of the Gully into the OC. Residency and movement estimates among each of the areas and their best fit models are shown in Figure 10. Average residency estimates in the Gully-Gully and Gully-OC models suggest that whales are found in the Gully for 20-40 days before moving to other canyons (Figure10d, Figure10c). For the OC, where there were fewer data points, residency appeared lower over shorter periods with values peaking somewhere around 10 days, however high SE values make these model estimates uncertain (Figure10a). The probability of movement from the OC to the Gully was consistently low over all time lags, averaging less than 0.01 (Figure 10b). However, trends in movement from the Gully to other canyons indicate that the probability of movement was lower over shorter periods (< 10 days) and then increased. Overall the trends were consistent with residency in the Gully being around 20 days, and similar probabilities of movement among all canyons after a few months. Although there is some uncertainty, the results suggest that residency patterns may differ between the Gully and the OC.

(2) Markov Movement Models Between Canyons

Movement models of all identifications and reliably-marked identifications over a seven-day time period generated similar results (Table 6). For the models based on all identifications, results suggest a probability of 0.89 that any individual found in the Gully will stay in the Gully during a one-week time period, which means there is an inverse probability of ~0.11 that an individual found in the Gully will move to another canyon or an outside area (OA). This amounts to approximately 1 individual moving out of the Gully per day, based on an estimated equilibrium population size of 63 (SE ± 9.8) individuals in the Gully at one time. The probability of movement from the OC is similar to the Gully, but movement from an OA is higher. The probability of movement out of the OC into the Gully over a 7-day period (0.11, SE ± 0.03) is slightly higher than movement out of the Gully into the OC (0.082, SE ± 0.03). Probability of movement from an OA into (0.001, SE ± 0.21) or out of (0.025, SE ± 15.1) the Gully is also different, although there is high uncertainty for OA estimates. At this scale it appears that there is a low rate of movement into and out of the Gully, with individuals coming from the OC as well as an OA.

For the models that considered only reliably-marked identifications, probabilities of movement appeared similar to estimates based on all identifications (Table 7). Differences between movement from an OA to the Gully and to the OC include higher SE in some cases, and marginal increases in movement probabilities between areas. Based on equilibrium population estimates, approximately 6 whales move from the Gully to the OC per week, and approximately 1.5 whales move from the Gully to an OA (Table 7). From the OC, approximately 8 individuals move to the Gully within a week and movement to an OA is highly uncertain. Estimates of the equilibrium population size of the OA have high SEs and it would not be appropriate to specify movement by number of individuals. Despite uncertainty regarding the degree of movement to and from an OA, results suggest there is movement outside the Gully, Shortland and Haldimand canyons over relatively short temporal periods, supporting other lines of evidence that indicate that the population is not completely closed at this spatial scale.

DISCUSSION

SPECIES PRESENCE IN INTER-CANYON AREAS

Passive acoustic monitoring is an effective method of assessing the spatial and temporal distributions of cetaceans, and can be particularly useful for understanding patterns in habitat use of deep-diving species such as beaked whales (e.g. Baumann-Pickering et al. 2014, Stanistreet et al. 2017). In this study, year-round passive acoustic monitoring at recording sites located between the Gully, Shortland, and Haldimand canyons provided evidence that northern bottlenose whales are present in these inter-canyon areas throughout most of the year. Among the inter-canyon areas monitored, we found higher overall presence at the ShoHald recording site, located between Shortland and Haldimand canyons. This may be partly due to the fact that this site was located closer to the mouth of Haldimand Canyon, while the GulSho site was located approximately equidistantly between the Gully and Shortland Canyon. We did not collect recordings from within Shortland or Haldimand canyons in this study, but the results of an earlier passive acoustic monitoring study on the Scotian Shelf by Moors (2012) revealed that clicks likely produced by northern bottlenose whales were detected at similar rates both within these two canyons and in the inter-canyon areas along the slope. While the recording systems used by Moors (2012) did not have sufficient bandwidth to conclusively identify northern bottlenose whale echolocation clicks, our results support the initial findings of that study, which suggested that northern bottlenose whales may be found in inter-canyon areas in all seasons of the year. Additionally, we were able to better assess seasonal variation in detection rates with recordings collected nearly continuously over two years. Detections of northern bottlenose whales at both inter-canyon sites exhibited a similar seasonal pattern, with higher detection rates occurring during the spring followed by a decrease in detections during the summer and fall. It is not clear whether this seasonal variation in detection rates reflects a change in the density or distribution of whales over the course of the year, or a change in foraging activity occurring in the vicinity of the recorders.

The detection of echolocation clicks from northern bottlenose whales on bottom-mounted recorders indicates that they are foraging or at least performing exploratory dives near the recording sites. Northern bottlenose whales may produce clicks at or near the surface in social contexts (Hooker and Whitehead 2002), however, these clicks are less likely to propagate to recorders moored on the seafloor. The clicks we detected on the bottom-mounted recorders in this study exhibited typical characteristics of echolocation clicks produced during deep foraging dives (Wahlberg et al. 2011, Clarke et al. 2019). Detection ranges for beaked whale clicks on bottom-mounted recorders are generally estimated to be no more than a few kilometers (e.g. Hildebrand et al. 2015). It is possible that whales just inside the southwest corner of the Haldimand Canyon critical habitat area may have been detected at the ShoHald recording site, but whales foraging within any of the core canyon areas, where the highest density of sightings occurred (Figure 5), would not have been detected at either of the inter-canyon recording sites due to the attenuation of high-frequency acoustic signals over these ranges.

Passive acoustic monitoring is an effective method for detecting northern bottlenose whales engaged in foraging activity, but does not allow the detection of whales that are passing through an area without vocalizing. A series of shallow, silent dives performed in between deep foraging dives is a common feature of the diving behaviour of several beaked whale species (e.g. Tyack et al. 2006), and northern bottlenose whales exhibit similar diving patterns, typically producing echolocation clicks only at depths greater than 200 m (Hooker and Baird 1999, Miller et al. 2015). The opportunity to detect northern bottlenose whales on bottom-mounted recorders is limited to the vocally-active period of these deep foraging dives. Here, recordings were collected using duty-cycled recording schedules in order to extend the deployment duration for each instrument, and the high-frequency recordings represent < 15% of the total time during which each instrument was deployed. Duty-cycled recordings are likely to lead to the underestimation of beaked whale presence, particularly at sites where whales are present infrequently or in low numbers (Stanistreet et al. 2016). Additionally, a small percentage of northern bottlenose whale clicks in the recordings were missed in the detection process, further contributing to the possible underestimation of species presence. Consequently, the results presented here provide a conservative estimate of the minimum occurrence of northern bottlenose whales at each recording site, and whales may be present in these areas more often than indicated by the acoustic records.

Visual sighting records provide a useful complement to acoustic data for assessing species presence, as they occur when whales are at the surface rather than at depth, and vessel-based surveys typically encompass a wider spatial area than the detection range of stationary, bottom-mounted recorders. Historically, visual survey effort along the Scotian Shelf has been extremely low in the inter-canyon areas compared to within the canyons, with a clear focus on the Gully, and we caution that the distribution of sighting records must be carefully interpreted in the context of the relative density of survey effort. The majority of visual survey effort reported in this paper occurred within and near the Gully, and to a lesser extent within Shortland and Haldimand Canyons, and there were no sightings of northern bottlenose whales during the more limited visual survey effort that occurred outside the canyons. However, the concentration of visual survey effort over the Gully does provide some insight into habitat use within and around this critical habitat area at a finer spatial scale. Notably the records of northern bottlenose whales sighted in the Gully across six years of survey effort indicate that the density of sightings is highest just inside the northeast critical habitat boundary, close to the shallower bathymetric feature known as the Southwest Prong. It is important to note that these points indicate the first location recorded when northern bottlenose whales were encountered, with a spatial accuracy of 10–1000 m, and should not be interpreted as whales strictly staying within the critical habitat boundary. Visual and behavioural surveys for northern bottlenose whales typically begin inside the core area of critical habitat, so most sightings are recorded as starting in this area by default. The maps presented here do not account for the movement of whales some distance from the original sighting location and even outside the critical habitat boundary, which has been observed to occur during longer encounters. In particular, individuals have been observed crossing over the Southwest Prong (L. Feyrer, personal observation). This feature is excluded from the designated critical habitat due to its shallower depth profile, but does not represent a barrier to movement of northern bottlenose whales accessing the deeper waters on either side or moving between the Gully and inter-canyon areas.

Acoustic recording effort during vessel-based surveys only occurred in three recent years, but resulted in more extensive coverage than visual survey effort, since it is possible to collect acoustic recordings at night and across a wider range of weather conditions. Acoustic recording effort and detections were still biased toward the canyon and slope edge areas, and while there were a number of detections of northern bottlenose whales outside the critical habitat areas, none were found on surveys extending beyond the slope to waters deeper than approximately 2000 m. Most detections outside designated critical habitat occurred in areas between the canyons or within 50 km of critical habitat, and were generally clustered along the 1000 m isobath. Although these results represent a preliminary analysis with a focus on detections collected during the shelf edge survey, they confirm that this area is used by northern bottlenose whales moving and foraging between canyons. Further analysis of recordings in this dataset will help to confirm the extent and distribution of northern bottlenose whales in waters deeper than 1000 m and areas outside the canyons.

RESIDENCY AND MOVEMENT PATTERNS WITHIN, BETWEEN, AND OUTSIDE THE CANYONS

Six years of photo-identification survey effort in the Gully, Shortland, and Haldimand canyons resulted in the identification of a number of individual northern bottlenose whales that moved between the Gully and Shortland and Haldimand canyons across multiple time scales, from periods of weeks to months to years. This effort also provided an expanded dataset to analyze the residency and movement patterns of northern bottlenose whales first reported in Wimmer & Whitehead (2004). The results of the residency and movement models presented here indicate a strong degree of connectivity between the three canyons and suggest that the population is open to immigration and emigration to other outside areas.

Results of the lagged identification rate (LIR) models using photo-identification data from the Gully suggest that the probability of residency within the Gully is initially high and remains steady over a period of 10-20 days, consistent with previous studies (Wimmer and Whitehead 2004). Although the estimates are less precise for residency outside the Gully, it appears that individual whales spend anywhere from a few days up to two months outside the Gully before returning. These patterns remain largely the same when photo-identifications from the other canyons are added to the models. LIR models for residency in the other canyons have larger confidence intervals, due to fewer data points at these sites, and do not appear to fit the data as well as models for the Gully. However, LIR models for the other canyons indicate that the probability of residency is initially lower and then increases around 10 days, suggesting that movement and residency patterns in these areas may be different from the Gully. If movement and residency patterns in the Gully are different from the other canyons, given the assumptions of the LIR models it would not be appropriate to model the entire region as one sample area. Ultimately more photo-identification data in the other canyons is required to understand the significance of potential differences between the Gully and other canyons, as well as to investigate differences between Shortland and Haldimand canyons. Additional research is also required to understand the motivations and constraints on movement and residency for northern bottlenose whales in these areas.

The results of the Markov movement models largely confirm the LIR model results, suggesting that there is a difference in movement patterns into and out of the Gully as compared to the other canyons. Using the Markov models, we estimated a consistent but low rate of movement into and out of the Gully, on the rate of one individual per day. Given this rate of movement, over the course of six months most of the population (currently estimated at 127 individuals) will have moved between the Gully and other canyons on the Scotian Shelf. Again, these results highlight the strong degree of connectivity between the canyons, suggesting that while the Gully is the most highly-utilized habitat area, all three canyons may be visited by all individuals in the population.

In an earlier study using photo-identification data collected in all three canyons in 2001 and 2002, Wimmer and Whitehead (2004) found that the population was not fully mixing over this 2-year time scale, and that some individuals seemed to have a preference for a particular canyon. Here, we have expanded on the original analysis done by Wimmer and Whitehead (2004), by adding four additional years of photo-identification data across a 16-year time span. With this expanded dataset, we did not find evidence of a preference for particular sites among individuals. There are some individuals that have only been conclusively identified in the Gully to date, which could suggest the possibility of a resident population; however, photo-identification survey effort has only occurred consistently in the summer months and we cannot account for movement of individuals that might occur in other seasons or in non-survey years. While movement modeling is subject to uncertainty outside the survey season, the results of year-round passive acoustic monitoring between canyons show that whales are present in inter-canyon areas throughout most of the year. Acoustic detections in the inter-canyon areas were highest during the spring, and detections decreased during summer at all recording sites including within the Gully, suggesting that if movement is estimated using datasets collected only in the summer, the model results may in fact underestimate the degree of movement between sites occurring at other times of year.

Further research is necessary to understand the ecological and/or social factors driving the observed movement patterns. Hooker et al. (2002b) suggested that northern bottlenose whale distributions within the Gully are largely driven by prey distribution and foraging opportunities, and therefore there may be a density-dependent driver of movements into and out of the canyon as the abundance and availability of prey fluctuates. Social factors may also play a role in the residency and movement patterns of northern bottlenose whales. Wimmer and Whitehead (2004) suggested that males move between canyons more frequently than females, on average, suggesting that female distributions are primarily driven by prey availability, while male movements may also reflect access to females and mating opportunities. We did not assess any potential sex bias in the movement models presented here, but further analyses may be conducted using the existing photo-identification dataset to better address these questions.

Both the LIR and Markov movement models indicate that northern bottlenose whales move not only between canyons, but also to and from outside areas, suggesting that the population is not closed to immigration from regions beyond currently designated critical habitat. No clear photo-identification matches have been made between the Scotian Shelf population and the limited datasets available for northern bottlenose whales found off Newfoundland, Labrador or the Davis Strait (L. Feyrer, unpublished data). However, our current understanding of the genetic structure of these populations suggests that there is a low level of migration between regions which is particularly important for maintaining the genetic diversity of the small Scotian Shelf population (Feyrer et al. 2019). The geographic extent of habitat used by the Scotian Shelf population likely extends beyond the Gully and other canyons where this population has been most extensively studied. Opportunistic sightings of northern bottlenose whales have occurred more broadly throughout the Scotian Shelf region (See Appendix, Figure A1). Furthermore, records of northern bottlenose whales sighted along the shelf edge off Newfoundland (e.g. Gomez et al. 2017) and recent observations over multiple years of surveys along the Sackville Spur, located east of Newfoundland near the Flemish Cap (L. Feyrer, personal observation) imply that the current description of the population structure of northern bottlenose whales off eastern Canada is incomplete. Ongoing genetic and acoustic studies will help address broader questions of population structure and connectivity (Feyrer et al. 2019).

CHARACTERISTICS OF INTER-CANYON HABITAT AND RISKS TO THIS HABITAT

The biophysical functions of habitat important to northern bottlenose whales include supporting life processes such as foraging, socializing, mating, giving birth, and rearing young. The Gully, Shortland, and Haldimand canyons are presumed to support all necessary life-history functions for northern bottlenose whales on the Scotian Shelf, but it is not known whether all three canyons serve all of these functions (Fisheries and Oceans 2016). Here, acoustic detections of northern bottlenose whales at inter-canyon monitoring sites provide evidence that individuals are present and foraging in areas between the canyons throughout most of the year. Results of the residency and movement models suggest that individuals in the Scotian Shelf population frequently move between all three canyons, and the inter-canyon areas likely function as important movement corridors as well as foraging habitat. It is unknown if these inter-canyon areas are also important areas for socializing, mating, giving birth and rearing young, as is the presumed function of all three canyon habitats.

The biophysical features and attributes of this inter-canyon habitat are presumed to be similar to those of the canyons, featuring deep water, steep topography, access to sufficient quantity and quality of prey, an adequate acoustic environment to support foraging and movement, and adequate space to allow for unimpeded movement of individuals (Fisheries and Oceans 2016). The canyons are a unique feature of the Scotian Shelf, particularly the Gully, which has a large influence on local oceanography likely resulting in enhanced productivity and the aggregation of prey (Hooker et al. 2002a, Moors-Murphy 2014). However, northern bottlenose whales are not strongly associated with submarine canyons in other regions of the North Atlantic, including the Davis Strait (Benjaminsen and Christensen 1979). Depth, topographic slope, and sea-surface temperature have been identified as more broadly important habitat features (Hooker et al. 2002b, Gomez et al. 2017). In addition to the Scotian Shelf, Gomez et al. (2017) identified potential habitat for northern bottlenose whales along the outer margins of the continental shelves off Newfoundland and Labrador as well as offshore areas near the Flemish Cap, and recommended further monitoring of these areas to better characterize important habitat for the species.

The Recovery Strategy for the Scotian Shelf population of northern bottlenose whales outlines several examples of activities likely to destroy critical habitat, including acoustic disturbance, changes to food supply, contaminants, and alteration of biological or physical oceanographic conditions (Fisheries and Oceans 2016). Inter-canyon areas are likely to face the same habitat risks as those described for currently designated critical habitat areas. In addition, due to the importance of these areas as movement corridors, physical obstructions (e.g. high densities of fishing gear or vessels) that could prevent movement may pose a risk to habitat function. Other threats to the species include the potential for ship strikes, ingestion of debris such as plastics, and entanglement in fishing gear, which have been documented for northern bottlenose whales and other beaked whale species on the Scotian Shelf and elsewhere (Narazaki 2013, Fernández et al. 2014, Fisheries and Oceans 2017, Lusher et al. 2018).

CONCLUDING REMARKS & RECOMMENDATIONS

The results presented and discussed in this paper highlight the high degree of connectivity between the Gully, Shortland, and Haldimand canyons for northern bottlenose whales on the Scotian Shelf. Inter-canyon areas located between the existing critical habitat areas are used throughout the year as foraging habitat, and likely function as important corridors necessary for movement to occur between the core habitats within the canyons. We suggest that these areas comprise important habitat, functionally connecting the three canyons (Figure 11). We delineate the area identified as important habitat using the 500 m depth contour as an upper boundary, and straight lines connecting the lower corners of the existing critical habitat areas as a lower boundary. The lower boundary is represented by a dotted line in Figure 11 to emphasize the paucity of data upon which to base this deeper water habitat delineation. In addition, we identify the area encompassing the Southwest Prong bathymetric feature located on the eastern side of the Gully as important for the movement of northern bottlenose whales between existing critical habitat areas on either side of this feature and from the Gully to the inter-canyon area. While our understanding of the full extent of important habitat for this population is still incomplete, available data indicate that individuals found on the Scotian Shelf are genetically related as a distinct population (Feyrer et al. 2019), frequently move among all three canyons, and regularly forage in the inter-canyon areas, suggesting that the important habitat for this population is best represented by a contiguous area.

Additional research effort should focus on improving our understanding of the full extent of habitat along the Scotian Shelf utilized by northern bottlenose whales. This includes consideration for areas to the east and west of current critical habitat areas, the functions of different habitat areas, and the ecological and social factors driving the distribution and movements of northern bottlenose whales. Passive acoustic monitoring with bottom-mounted recorders has been conducted in Logan and Dawson canyons (located along the Scotian Shelf southwest of the Gully) and these efforts are being expanded to include additional sites in slope waters along the western Scotian Shelf, near the mouth of the Laurentian Channel. When available, these datasets will provide new insight into the seasonal presence and foraging activity of northern bottlenose whales in other canyons and shelf edge areas which have not been extensively surveyed. Northern bottlenose whales have been opportunistically sighted along most of the Scotian Shelf (See Appendix, Figure A1), and expanded visual surveys, acoustic towed array surveys and photo-identification efforts in other areas along the Scotian Shelf, particularly the area extending from Haldimand Canyon to the Laurentian Channel as well as east into Newfoundland, could provide further information on the extent and frequency of the ranging behaviour of individuals in this population. As outlined in the Recovery Strategy (Fisheries and Oceans 2016), studies on the distribution and abundance of prey would lead to a better understanding of the attributes of critical habitat and help inform the identification of additional important habitat areas.

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TABLES

Table 1: Number of northern bottlenose whale sighting records and number of days with sightings by location over six years of Scotian Shelf surveys between 2001 and 2017.

Year	Gully	Shortland	Haldimand	Total	Days
2001	6	3	3	12	6
2002	28	31	5	67	16
2011	64	9	1	74	20
2015	76	4	15	95	17
2016	83	36	22	141	21
2017	8	0	7	15	2
Total	265	83	53	401	82

Table 2: Number of unique photo-identifications of northern bottlenose whales by location, including number of individuals observed at more than one location, over six years of Scotian Shelf surveys between 2001 and 2017.

Location(s) Observed	Unique IDs		Sample Days
	Left	Right	
Gully	149	136	53
Shortland	64	63	13
Haldimand	15	23	9
Gully + Shortland	34	32	-
Gully + Haldimand	20	25	-
Shortland + Haldimand	7	7	-
Gully + Shortland + Haldimand	12	11	-

Table 3: Number of unique left side photo-identifications of northern bottlenose whales by year and location with annual survey effort (N days), number of these photo-identifications that were shared across both locations, and total number of survey days.

Year	Gully	Other Canyons	Shared IDs: Gully & Other Canyons	Total Days
2001	26 (2)	18 (4)	1	6
2002	43 (9)	50 (6)	6	16
2011	76 (15)	42 (2)	4	18
2015	78 (14)	12 (3)	4	17
2016	65 (12)	45 (6)	17	18
2017	15 (1)	3 (1)	0	2

Table 4: Lagged identification rate models of residency for northern bottlenose whales in the Gully. Population estimates are per day and are shown as scaled estimates (unscaled in brackets) when only reliably-marked identifications were used. Best-fit models are indicated in bold.

Model Description	Maximum Likelihood Parameter Values	Bootstrapped SEs	Summed Log-Likelihood	QAIC
All IDs (100 days, see Fig. 8a)				
Emigration + Mortality	N = 48.2 Mean residence time = 44.8	2.66 4.55	-10544.7	21091
Emigration - Reimmigration	N = 43.9 Mean residence time in = 26.1 Mean time out = 66.9	3.5 9.09 *Very large*	-10539.0	21082
Emigration - Reimmigration + Mortality	**N = 38.9** **Mean residence time = 14.2** **Mean time out = 9.1** **Mortality = 0.014**	**3.82** **367,924** **108,988** **0.010**	**-10534.6**	**21075**
Reliably-marked IDs (1000 days, see Fig. 8b)				
Emigration + Mortality	N = 65.8 (33.6) Mean residence time = 1059.9	2.48 231.68	-119122.5	20403
Emigration - Reimmigration	N = 40.8 (20.8) Mean residence time in = 20.5 Mean time out = 34.4	2.05 6.46 9.83	-11851.9	20303
Emigration - Reimmigration + Mortality	**N = 39.3 (20.05)** **Mean residence time = 16.5** **Mean time out = 24.2** **Mortality = 0.00024121**	**2.15** **6.2** **9.8** **0.000242**	**-11851.2**	**20302**

Table 5: Probability of northern bottlenose whale movement within the same area and between different areas in one day based on reliably-marked identifications over a 100-day period.

Model Description	**Maximum Likelihood Parameter Values**	**Bootstrapped SEs**	**Summed Log-Likelihood**	**QAIC**
Same Area				
Emigration - Reimmigration	N = 28.8 Mean residence time = 73.6 Mean residence time out = *n.s.*	3.6 31.3 *Very large*	-1789.2	3582.3
Different Area				
Migration - full interchange	N = 6.2 Mean residence time in = 14,481	23.9 *Very large*	-257.1	297.6
Full mixing	N = 162.6	39.1	-273.9	315.0

Table 6: Probabilities and standard errors (SE) of individual northern bottlenose whales moving between the Gully, other canyons (Shortland and Haldimand) and an outside area using all left side IDs (fixed population size 127). Movement was modeled over 7 days, with a maximum time lag of 14 weeks and no mortality. Summed log-likelihood for model = 214.83.

Area *Scaled pop. size (SE)*	**To Gully**	**To Other Canyons**	**To Outside Area**
From Gully *N = 63.8 (12.2)*	0.8929	0.0817 (0.03209)	0.0254(0.15158)
From Other Canyons *N = 63.2 (9.2)*	0.1100 (0.0307)	0.8900	0.000 (0.15158)
From Outside Area *N = 0.0 (14.6)*	0.0013 (0.2109)	0.4335 (0.26207)	0.5653

Table 7: Probabilities and standard errors (SE) of individual northern bottlenose whales moving between the Gully, other canyons (Shortland and Haldimand) and an outside area using reliably-marked left side IDs (fixed population size 65). Movement was modeled over 7 days, with a maximum time lag of 14 weeks and no mortality. Summed log-likelihood for model = 39.95.

Area *Scaled pop. size (SE)*	**To Gully**	**To Other Canyons**	**To Outside Area**
From Gully *N = 63.5 (9.8)*	0.8833	0.0918 (0.0530)	0.0249 (0.0956)
From Other Canyons *N = 63.9 (15.49)*	0.1238 (0.0434)	0.8752	0.0010 (0.1544)
From Outside Area *N = 0.0 (15.88)*	0.0000 (0.1990)	0.2574 (0.2542)	0.7426

FIGURES

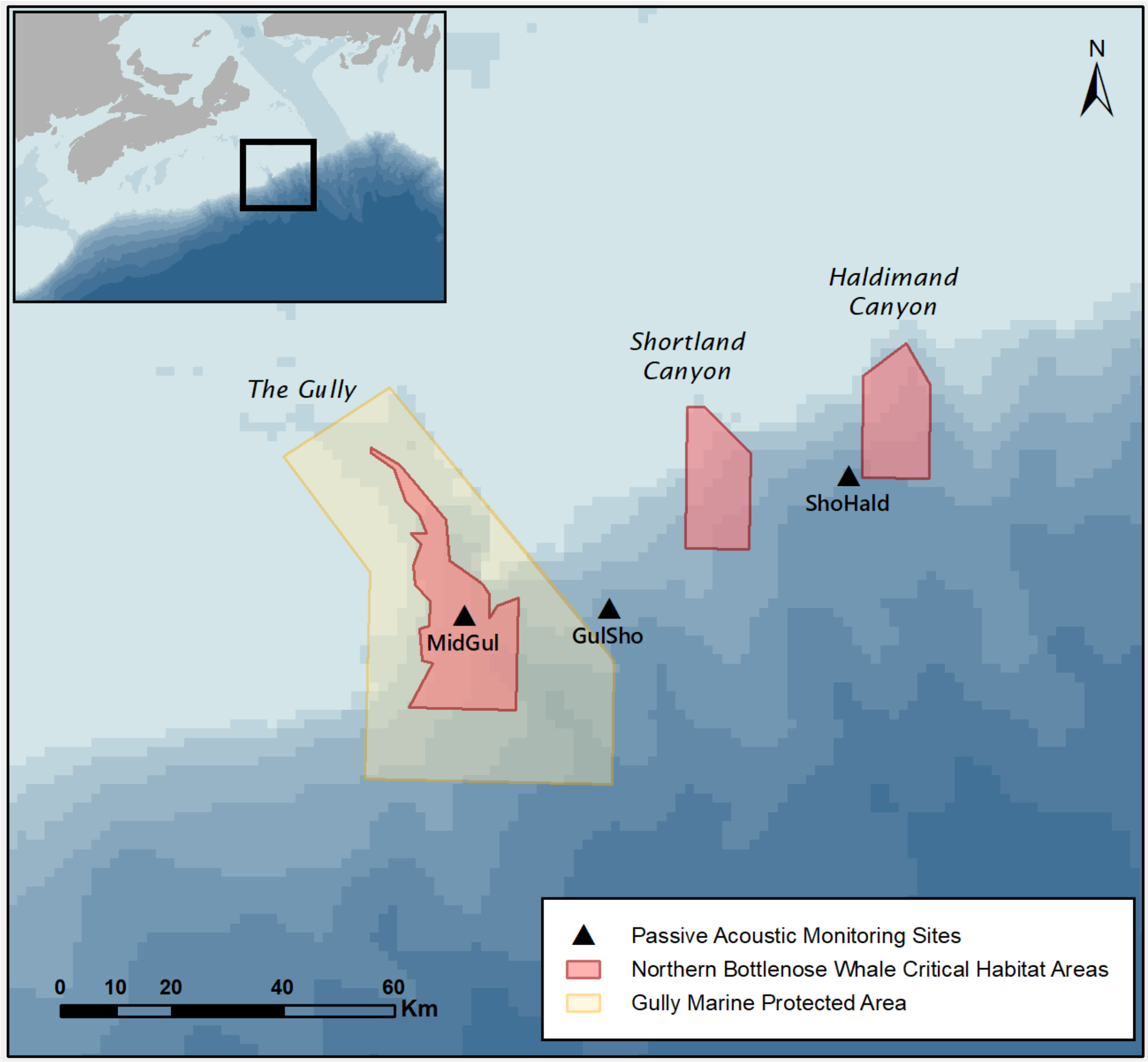

Figure 1: Map of stationary passive acoustic monitoring sites on the Scotian Shelf where Autonomous Multichannel Acoustic Recorders (AMARs) were deployed from 2012-2014. Areas designated as critical habitat for northern bottlenose whales are shown in red, and the Gully Marine Protected Area is shown in yellow.

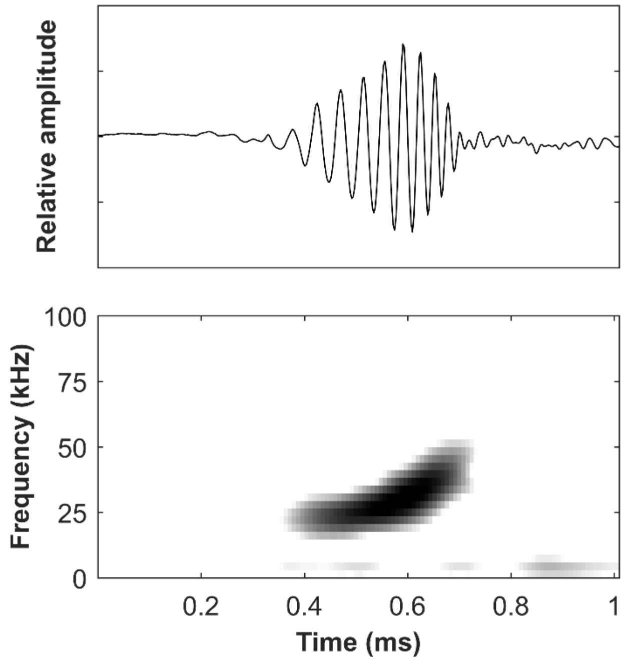

Figure 2: Example northern bottlenose whale echolocation click, shown as a waveform (above) and spectrogram (below) using a 1 ms window. Spectrogram calculated using a 60-point window, 95% overlap, and 128-point fast-Fourier transform, with data collected at a sampling rate of 375 kHz.

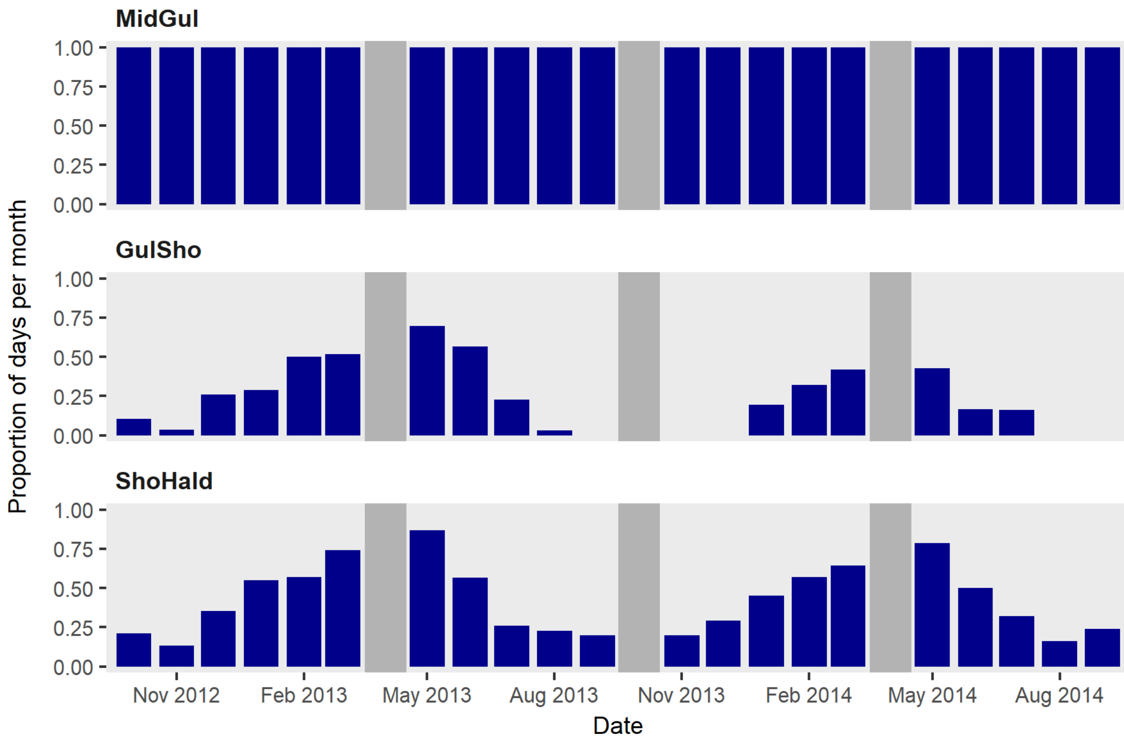

Figure 3: Proportion of days per month with northern bottlenose whale acoustic detections at each stationary (AMAR) recording site from October 2012 to September 2014; months with fewer than 10 recording days are omitted from plot (grey shading).

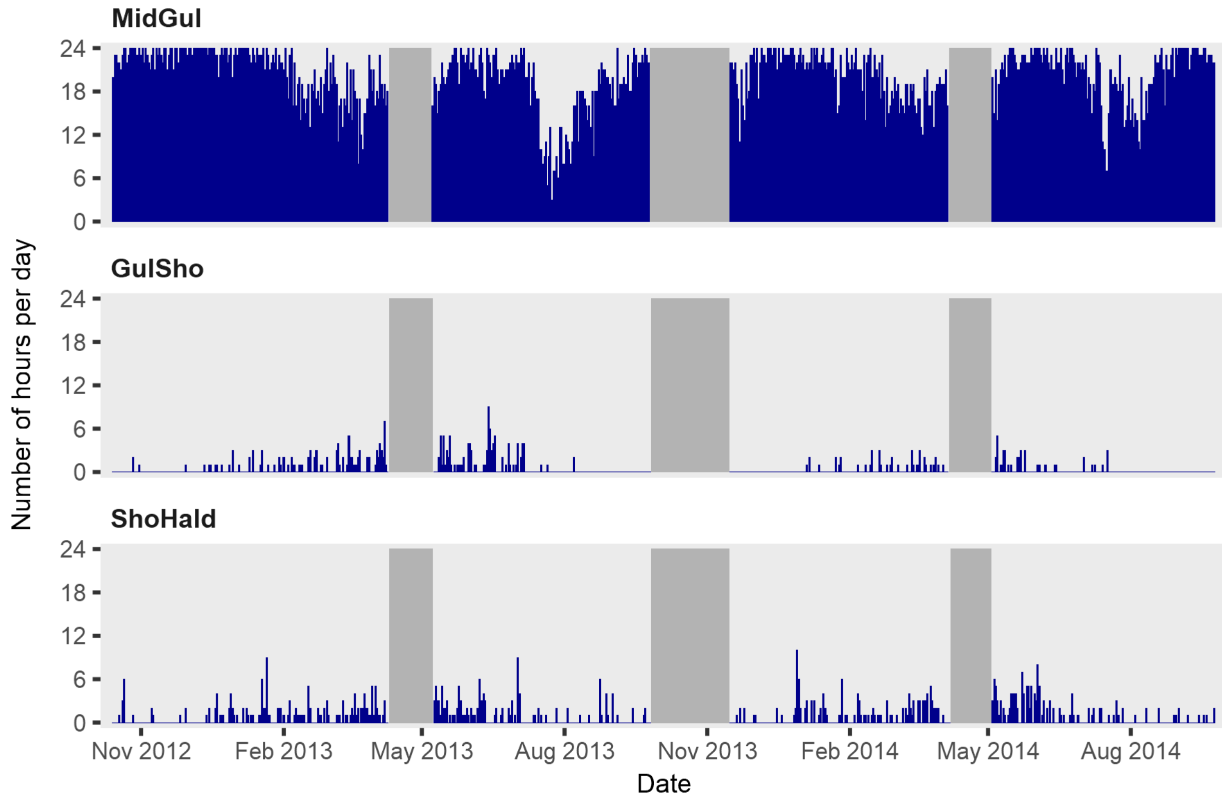

Figure 4: Number of hours per day with northern bottlenose whale acoustic detections at each stationary (AMAR) recording site from October 2012 to September 2014; days with no recordings or less than 24 hours of recording time are omitted from plot (grey shading).

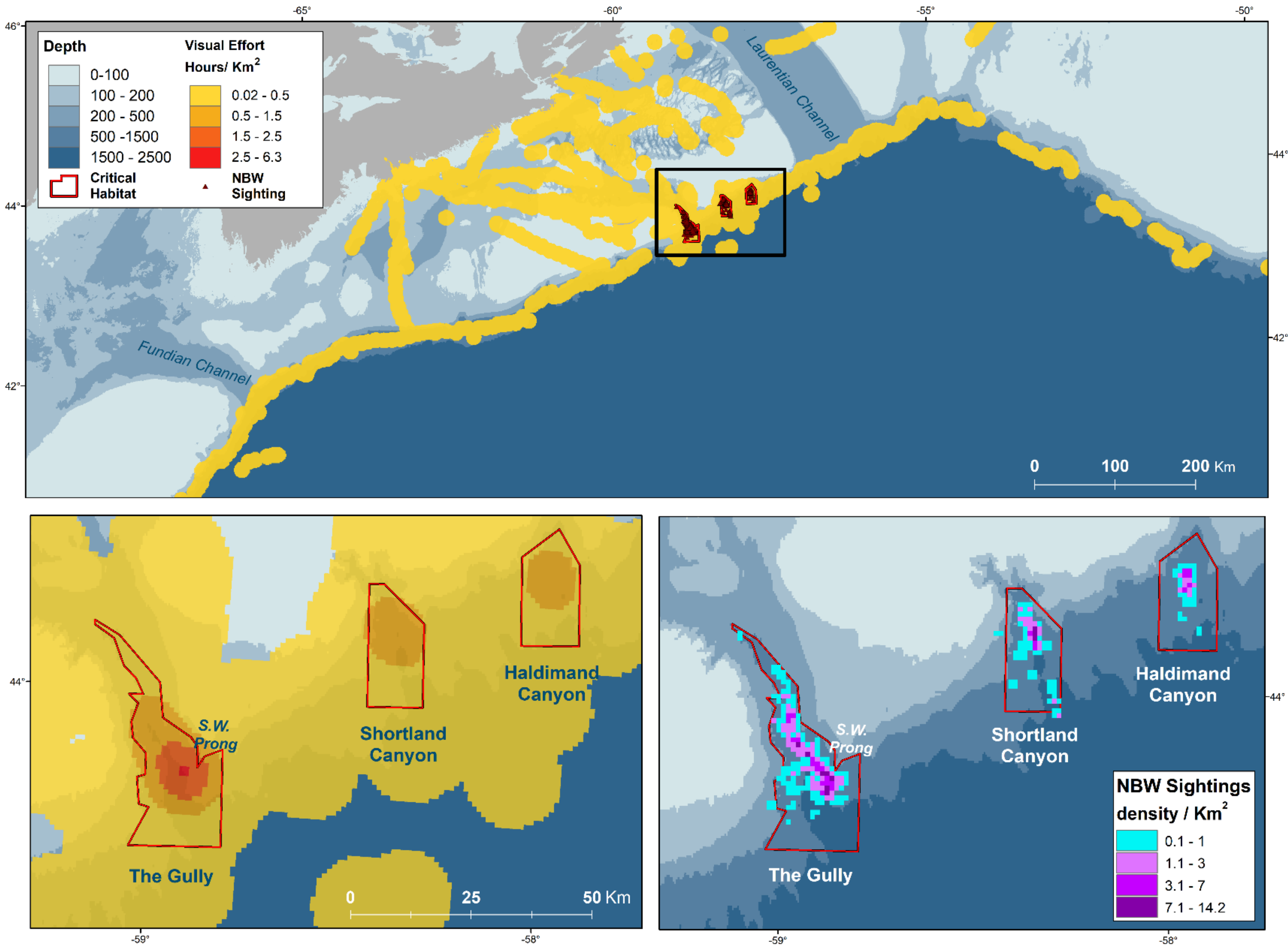

Figure 5: Map of visual survey effort per km² in 2001, 2002, 2011 and 2015–2017. Red indicates higher effort and yellow indicates lower effort, based on observation time during daylight hours with visibility greater than 1 km and Beaufort sea state of 4 or less. Locations of northern bottlenose whale (NBW) sightings and hourly survey effort are shown on the upper map; the density of survey effort (left) and NBW sightings (right) in and around the canyons are shown on the lower maps. Red outlines delineate the boundaries of designated critical habitat areas.

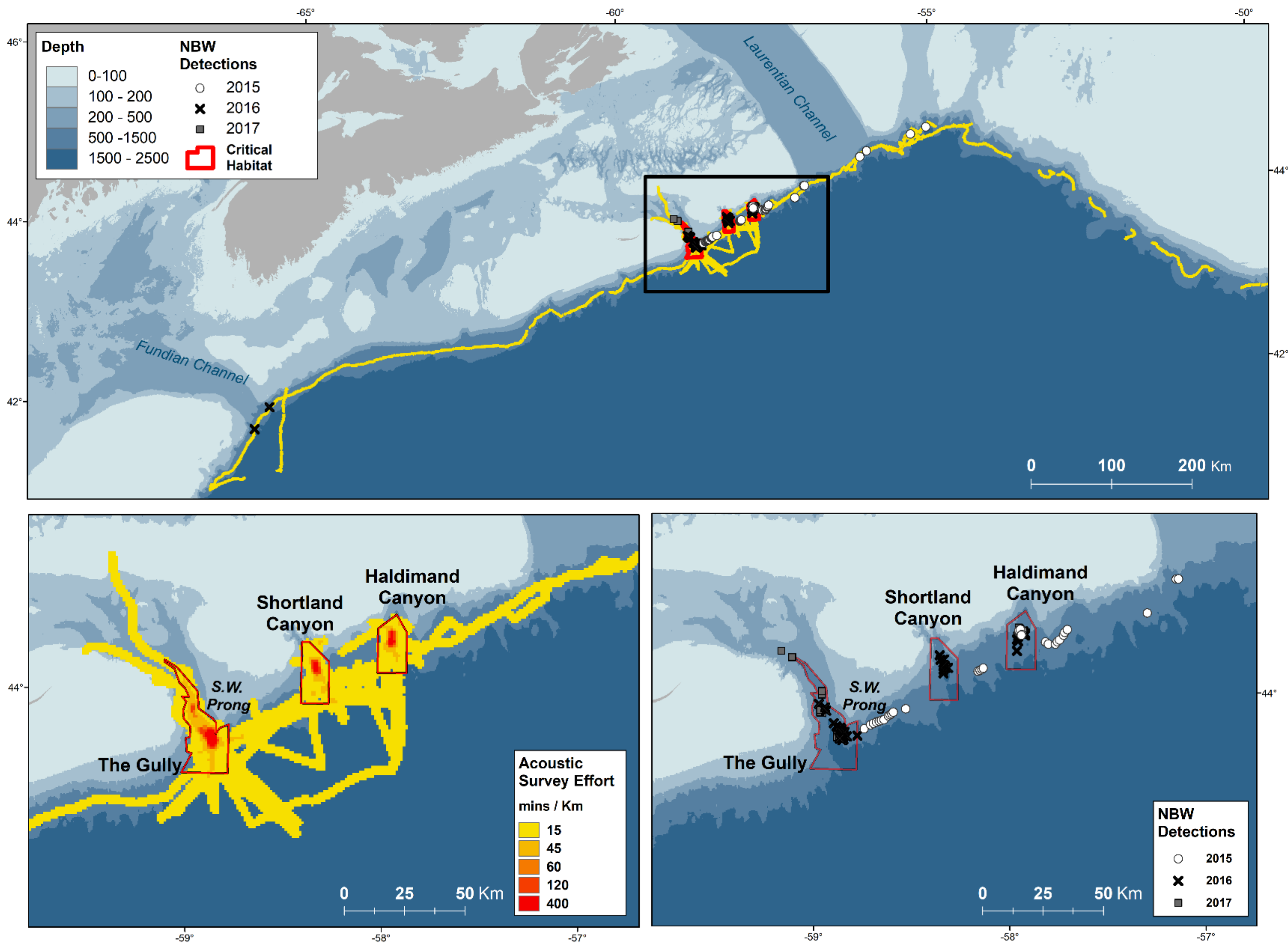

Figure 6: Map of acoustic survey effort per km² in the study area from 2015–2017. Confirmed northern bottlenose whale (NBW) detections are represented by symbols based on survey year, and shown with total acoustic survey effort on the upper map; the density of acoustic survey effort (left) and locations of NBW detections (right) in and around the canyons are shown on the lower maps. Red outlines delineate the boundaries of the currently designated critical habitat areas.

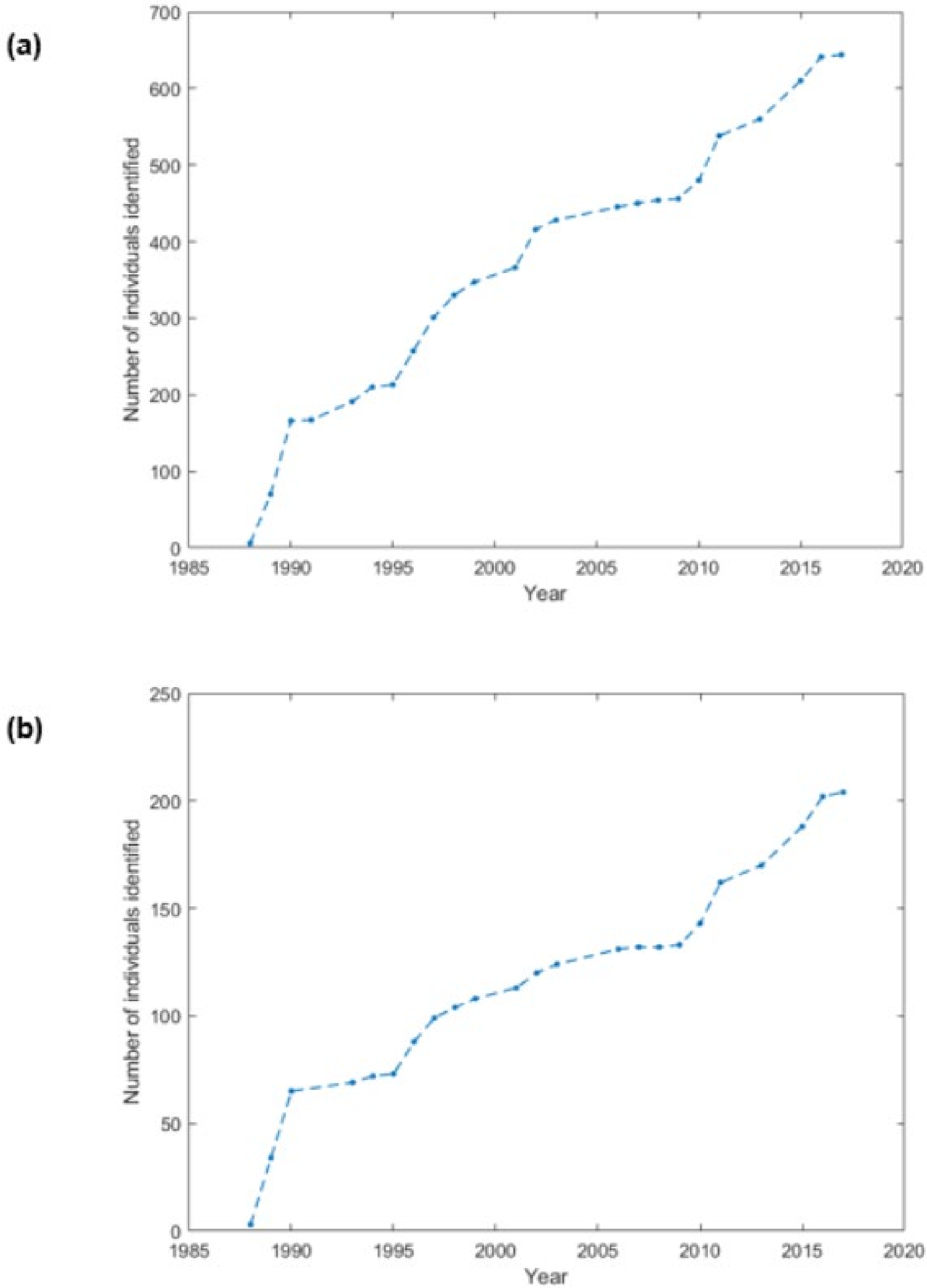

Figure 7: Discovery curve for uniquely-identified individual northern bottlenose whales in the Gully, based on analysis of left side photographs by sample year for (a) all identifications and (b) reliably-marked identifications only.

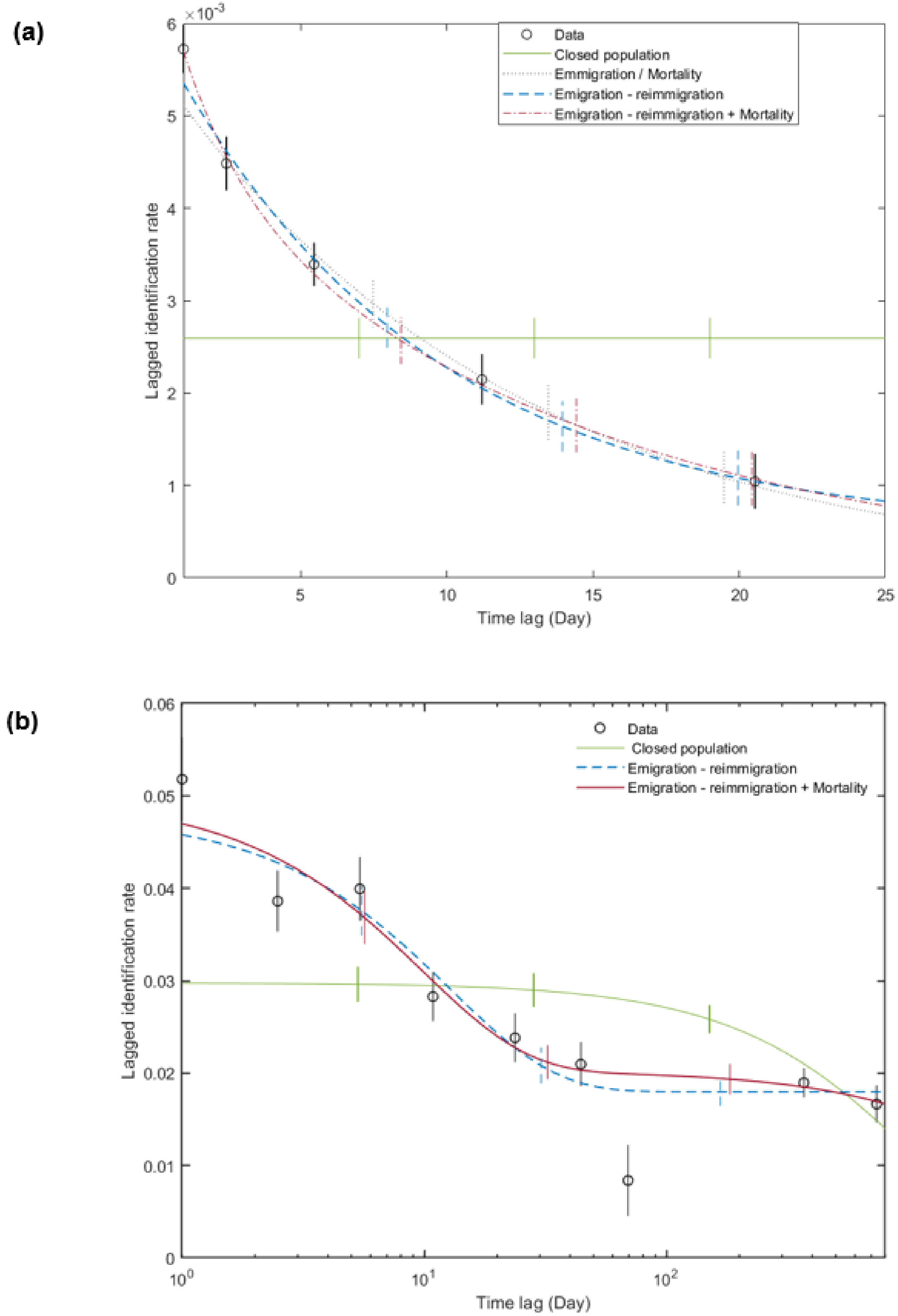

Figure 8: Lagged identification rate model results for northern bottlenose whales in the Gully based on (a) all left side IDs, 100-day maximum, and (b) reliably-marked left side IDs, 1000-day maximum.

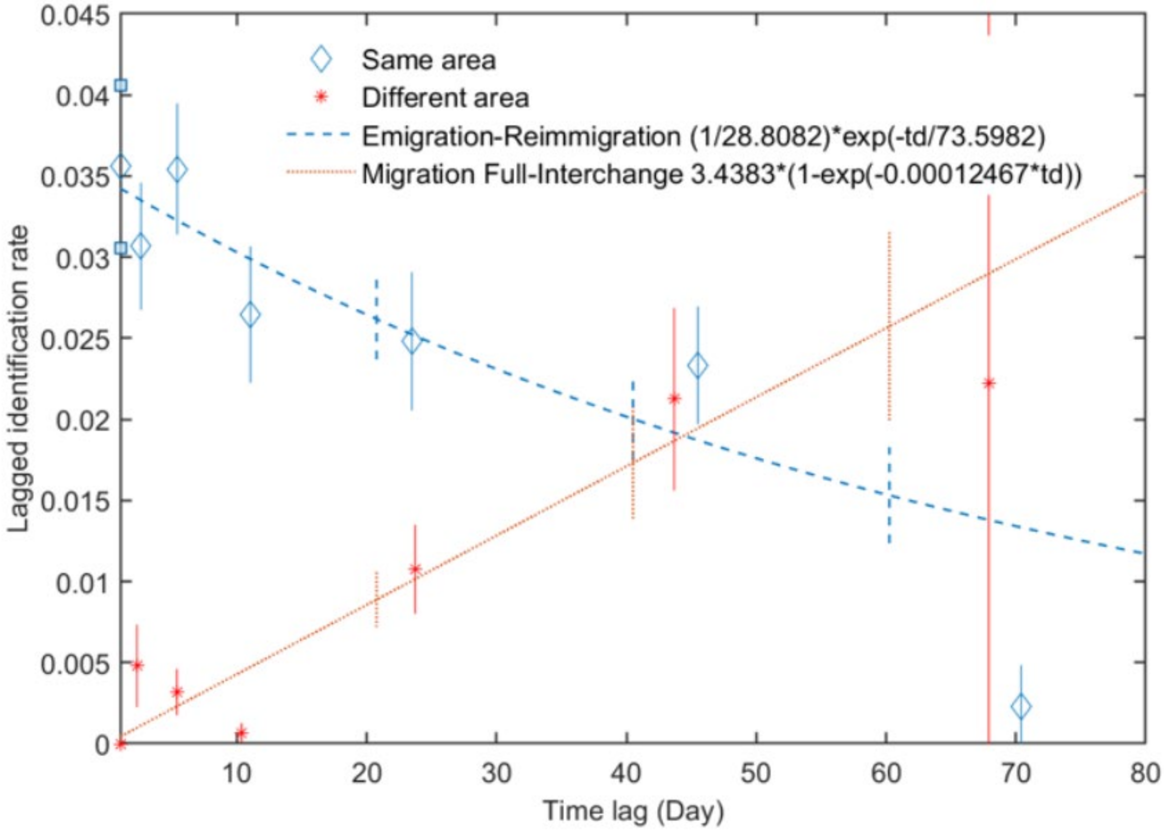

Figure 9: Probability of northern bottlenose whale movement within and between same or different areas in one day based on reliably-marked identifications, modeled over a 100-day period. Movement models are shown with vertical lines indicating bootstrap estimates of standard error.

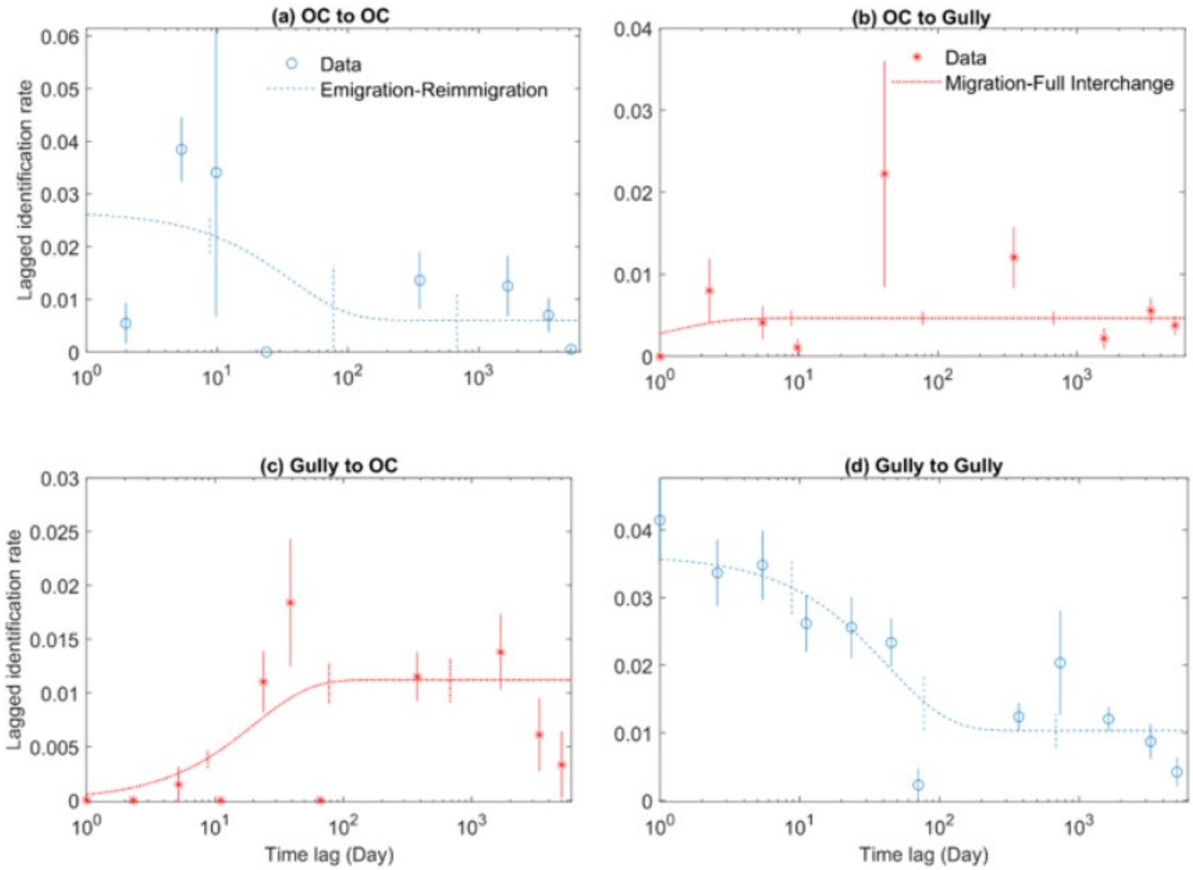

Figure 10: Lagged identification rate models among the Gully and Shortland/Haldimand canyons (OC) for reliably-marked left side IDs, with no maximum time lag over the study period.

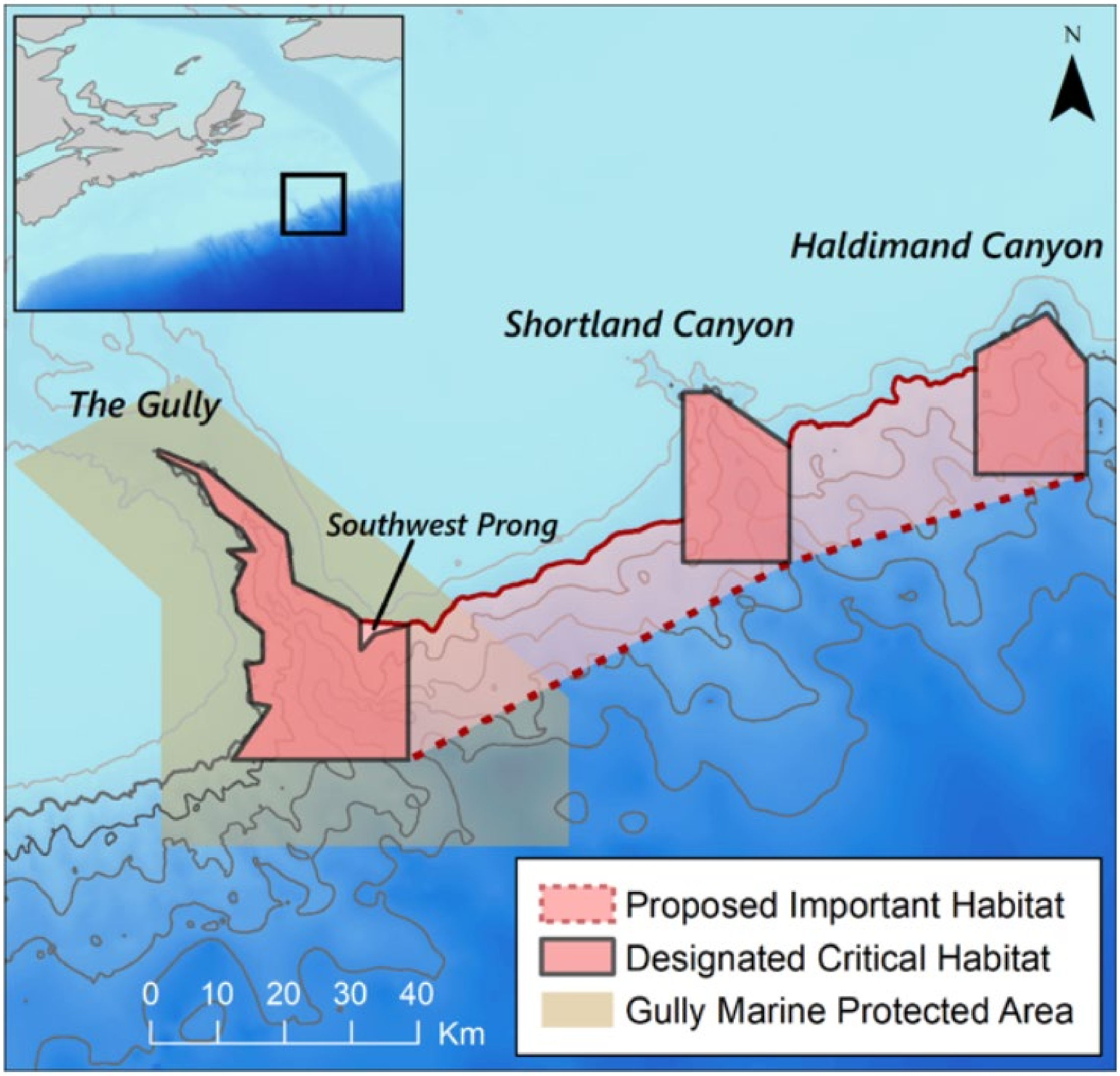

Figure 11: Map of currently designated Critical Habitat for northern bottlenose whales and proposed important habitat in inter-canyon areas on the eastern Scotian Shelf.

APPENDIX

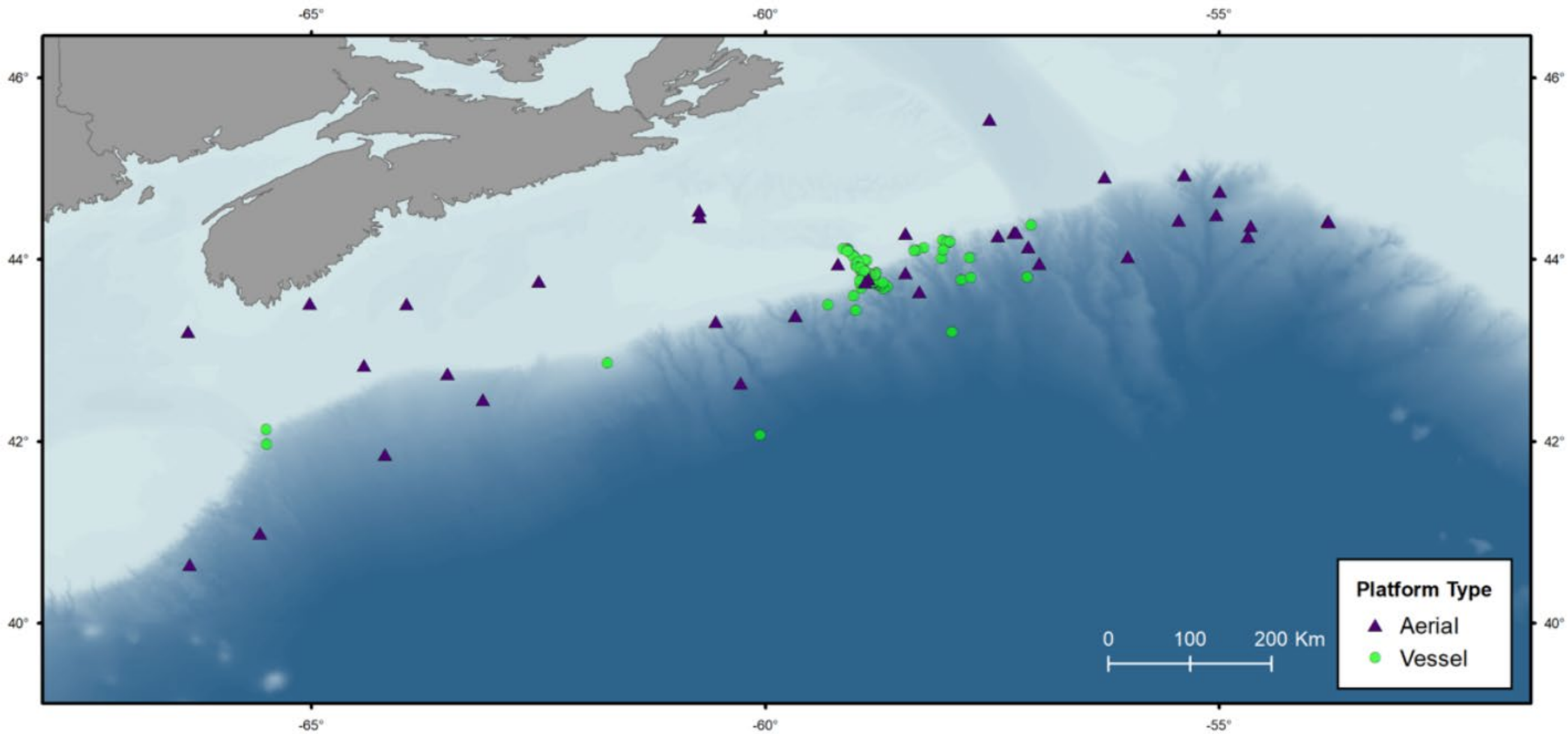

Figure A1: Locations of visual sightings of northern bottlenose whales in the Scotian Shelf region, occurring from 2001–2018. Sighting records from aerial platforms (purple triangles) were obtained from Department of Fisheries and Oceans (DFO) aerial cetacean surveys including the 2007 Trans-North Atlantic Sightings Survey (TNASS), 2016 Northwest Atlantic International Sightings Survey (NAISS), and other DFO surveys, and from the National Oceanic and Atmospheric Administration. Sighting records from vessel platforms (green circles) were obtained from opportunistic DFO vessel surveys, the Eastern Canadian Seabirds at Sea Program, and various other platforms of opportunity, excluding effort-based Whitehead Lab survey data shown in Figure 5. All points shown on this map represent locations where groups of one or more northern bottlenose whales were identified by trained observers. Full survey effort associated with these observations is not available, and they should be interpreted only as opportunistic sightings.