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In plane sight: a mark–recapture analysis of North Atlantic right whales in the Gulf of St. Lawrence

Leah M. Crowe[1,*], Moira W. Brown[2,3], Peter J. Corkeron[3,4], Philip K. Hamilton[3], Christian Ramp[5,6], Stephanie Ratelle[7], Angelia S. M. Vanderlaan[8], Tim V. N. Cole[9]

[1]Integrated Statistics Under Contract to the Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, MA 02543, USA
[2]Canadian Whale Institute, Welshpool, New Brunswick, Canada, E5E 1B6
[3]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA 02110, USA
[4]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[5]Mingan Island Cetacean Study, St. Lambert, Québec, Canada, J4P 1T3
[6]Sea Mammal Research Unit, University of St. Andrews, St. Andrews, Fife KY16 8LB, UK
[7]Gulf Fisheries Center, Department of Fisheries and Oceans, Moncton, New Brunswick, Canada, E1C 9B6
[8]Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada, B2Y 4A2
[9]Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, MA 02543, USA

ABSTRACT: North Atlantic right whales *Eubalaena glacialis* are most commonly observed along the eastern seaboard of North America; however, their distribution and occupancy patterns have become less predictable in the last decade. This study explored the individual right whales captured photographically from both dedicated and opportunistic sources from 2015 to 2019 in the Gulf of St. Lawrence (GSL), an area previously understudied for right whale presence. A total of 187 individuals, including reproductive females, were identified from all sources over this period. In years when more substantial survey effort occurred (2017–2019), similar numbers of individuals were sighted (mean = 133, SD = 1.5), and dedicated mark–recapture aerial surveys were highly effective at capturing almost all of the whales estimated in the region (2019: $N = 137$, 95% CI = 135–147). A high rate of inter-annual return was observed between all 5 study years, with 95% of the animals seen in 2019 sighted previously. Capture rates indicated potential residencies as long as 5 mo, and observed behaviors included feeding and socializing. Individuals were observed in the northern and southern GSL, regions divided by a major shipping corridor. Analyses suggest that individuals mostly moved less than 9.1 km d^{-1}, although rates of up to 79.8 km d^{-1} were also calculated. The GSL is currently an important habitat for 40% of this Critically Endangered species, which underscores how crucial protection measures are in this area.

KEY WORDS: Aerial survey · Abundance estimate · Age–sex structure · Movement · Residency

1. INTRODUCTION

While the habitat range for the Critically Endangered North Atlantic right whale *Eubalaena glacialis* (hereafter referred to as 'right whale') spans across the entire North Atlantic (IUCN 2012, Cooke 2020), they are predominately sighted and studied along the eastern seaboard of North America (Kraus & Rolland 2007). Whaling records highlight right whale use of the northern and eastern Atlantic Ocean from Greenland to northwest Africa, but in the last 40 yr, sightings outside of the habitat offshore from Florida, USA, to Nova Scotia, Canada, have been considered remarkable (Knowlton et al. 1992, Jacobsen et al.

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*Corresponding author: leah.crowe@noaa.gov

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2004, Silva et al. 2012). Critical habitats for this species have been established in the western Atlantic (Fig. 1A) in the USA (NMFS 2016) and Canada (Brown et al. 2009), and include the Southeastern US Calving Area, the Northeastern US Foraging Area, Grand Manan Basin in the Bay of Fundy, and Roseway Basin, south of Nova Scotia.

Critical habitat designations differ slightly between the USA and Canada, but in both countries, these areas are habitats that have been identified as important to the survival and recovery of a species (Brown et al. 2009, DFO 2014, NMFS 2016). In the USA, right whale critical habitat designation under the Endangered Species Act primarily delineates areas of importance for right whales, including for feeding and calving (NMFS 2016). The right whale critical habitats in Canada, designated under the Species at Risk Act, were established to protect foraging areas (Brown et al. 2009). However, designation alone does not directly provide protection from the 2 leading causes of right whale mortality in either country: entanglement in commercial fishing gear and vessel strikes (Vanderlaan & Taggart 2009, Vanderlaan et al. 2011, Sharp et al. 2019). These pressures have been shown to inhibit population growth of this species (Robbins et al. 2015, Corkeron et al. 2018), and they occur throughout their range (Sharp et al. 2019).

In both the USA and Canada, the management of fisheries and shipping activity to protect right whales is done through a series of static and dynamic strategies. Right whale protection strategies in the USA are implemented through seasonal area fishing closures (NMFS 2019) and vessel speed management zones for large ships (NMFS 2013). Only shipping activity is dynamically managed federally in the USA, and voluntary dynamic management zones are declared when a threshold density of right whales is sighted (NMFS 2008) or their presence is detected acoustically (NOAA Fisheries 2020a) outside of seasonally established protection areas (NMFS 2008). Unlike in the seasonal management zones, vessels 19.8 m (65 ft) or greater are not required — but are instead encouraged — to avoid these dynamically designated areas or to limit their speed to 10 knots while transiting through (NMFS 2008); voluntary compliance has not seen overwhelming cooperation (NMFS 2020). In Canada, fishing and shipping activities are currently both managed dynamically in response to right whale sightings and acoustic detections outside of static fishing closures (DFO 2021) and seasonal slowdown areas for vessels 13 m or greater (Transport Canada 2021). Strategies in Canada are predominately compulsory, are currently triggered by a sighting of at least one whale or the detection of one acoustic call, and require monitoring efforts to extend or end the period of slowdown or closure (DFO 2021, Transport Canada 2021). Beginning in 2020, Transport Canada initiated seasonal, voluntary slowdown periods for the Cabot Strait in the late spring/early summer and the late autumn to coincide with when the majority of right whales are thought to migrate in and out of the Gulf of St. Lawrence (GSL), as well as when the weather is less favorable for navigation and whale monitoring aerial surveys (Transport Canada 2021). Additionally, the boundaries of the Roseway Basin critical habitat are recommended as an ‘area to be avoided’ during the summer and autumn as sanctioned by the International Maritime Organization (DFO 2014). In both countries, there have also been successful stewardship projects that have moved shipping traffic separation schemes based on years of right whale sightings (Merrick 2005, Vanderlaan et al. 2008).

Changes in habitat use can impact the effectiveness of wildlife conservation measures and threat mitigation strategies (Davies & Brillant 2019). Beginning in 2010, a shift was observed in how right whales were using habitats, which made the timing and location of management schemes and monitoring studies more challenging (Davis et al. 2017, Mayo et al. 2018, Davies et al. 2019). At the same time, right whale abundance estimates indicated a downward population trend (Pace et al. 2017), and at the end of 2019, the species was estimated to consist of less than 400 individuals (Pace 2021, Pettis et al. 2021). The warming of the Gulf of Maine (Pershing et al. 2015) and the impact this has had on the abundance and distribution of *Calanus finmarchicus*, the primary food source of right whales in the North Atlantic (Record et al. 2019), explains, in part, the decrease in right whale detections throughout most of the Northeastern US Foraging Area critical habitat (Davis et al. 2017, Mayo et al. 2018, Davies et al. 2019, Record et al. 2019). Meanwhile, increased detections in other regions in the past decade (Leiter et al. 2017, Davies & Brillant 2019) have relied on the ability to anticipate right whale presence in a changing environment (Pendleton et al. 2012), and have led to dynamic management strategies, including voluntary ones, to provide some measure of protection to right whale aggregations outside of existing conservation zones (Johnson et al. 2020).

Although right whales face risks of entanglement and vessel strike throughout their range, an increase in right whale use of the GSL in recent years has coincided with these activities with catastrophic results (Davies & Brillant 2019). Prior to 2015, opportunistic sightings had been reported in this region since right

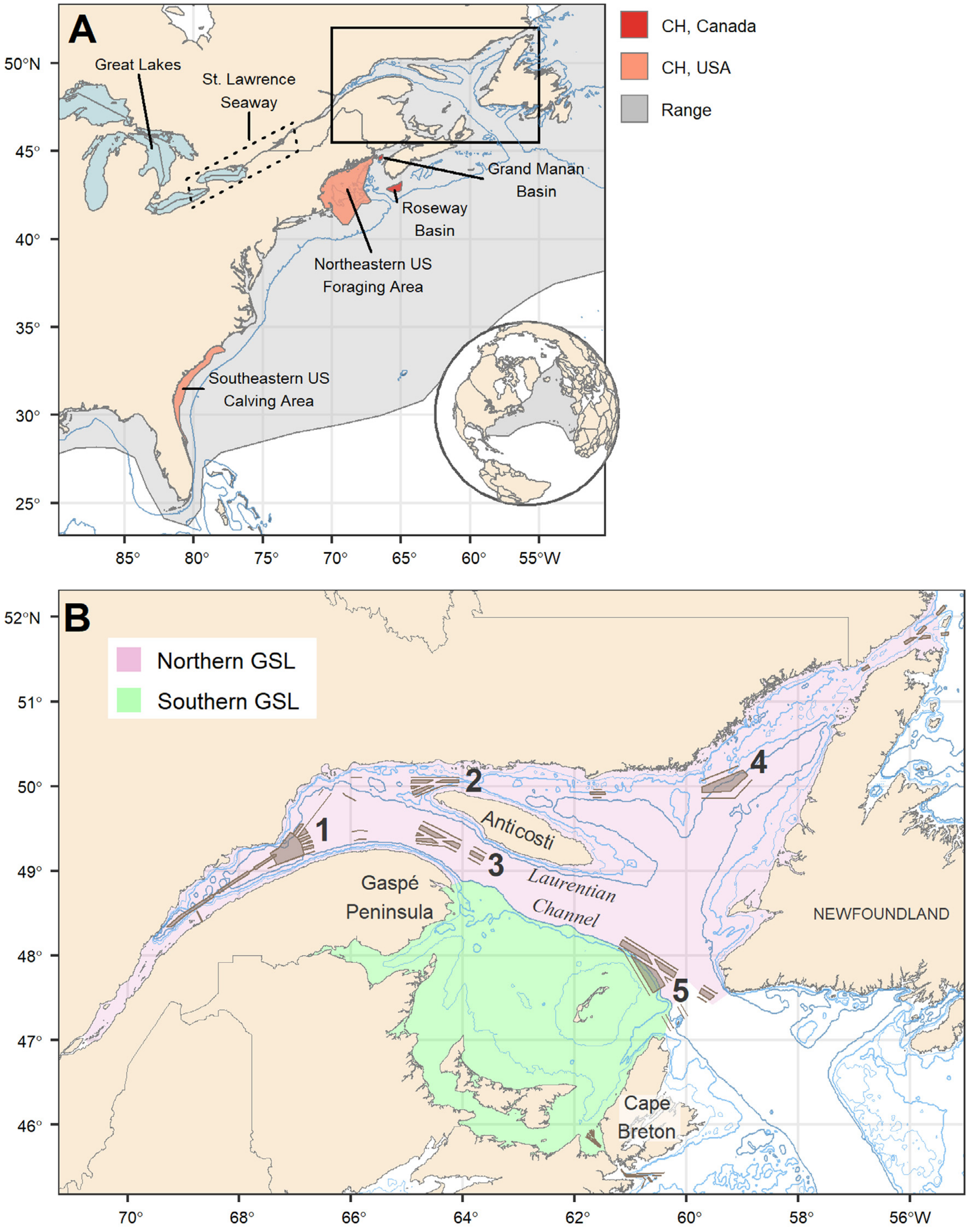

Fig. 1. (A) The range of the North Atlantic right whale (IUCN 2012), and the only designated critical habitats (CHs) for this species. These CHs are along the eastern seaboard of Canada and the USA, the portion of their range where they are most commonly sighted. The dark blue line indicates the 200 m isobath, and the black box encompasses the Gulf of St. Lawrence (GSL). (B) A detailed map of the GSL in eastern Canada, where the northern and southern regions are divided along the southern 200 m isobath (dark blue line). The shipping traffic separation schemes are displayed including those in the: (1) St. Lawrence Estuary, (2) Jacques Cartier Passage, (3) Honguedo Strait, (4) Strait of Belle Isle and (5) Cabot Strait. The section of the Laurentian Channel between the Honguedo and Cabot Straits is a major shipping corridor that connects commercial shipping traffic from the Atlantic Ocean to the St. Lawrence Seaway and the Great Lakes. The light blue line indicates the 100 m isobath, and the thin light blue line indicates the 50 m isobath

whale research programs began in the late 1970s (Lien et al. 1989, Brown et al. 2009), but dedicated visual effort was limited to a few isolated surveys (Kingsley & Reeves 1998, Lawson & Gosselin 2009, M. Brown unpubl. data). Sightings accompanied by photographs captured some individuals (including cows with calves) not frequently seen in other habitats (Hamilton et al. 2007). Modeling studies have suggested that right whales were present in the GSL in the summer season (Brillant et al. 2015). An increase in acoustic detections of right whales in some areas of the GSL was recorded beginning in 2015 (Simard et al. 2019), and in that same year, dedicated visual survey efforts in the GSL began expanding (Davies & Brillant 2019). Additionally, habitat studies have shown that the GSL appears to provide suitable foraging habitat for right whales during the summer and autumn seasons (Plourde et al. 2019, Sorochan et al. 2021); however, to what extent is still undetermined (Gavrilchuk et al. 2021).

An unusual mortality event (UME) was triggered in the USA in 2017 when an unprecedented number of dead right whales was observed across their range (n = 17; NOAA Fisheries 2020b), of which, 12 were in the GSL (Daoust et al. 2018). A UME is declared under the Marine Mammal Protection Act when there is a significant increase and/or change in observed morbidity, mortality or strandings of a marine mammal population, and its establishment requires the implementation of a working group to focus on the cause of these events to develop strategies to minimize further impacts (NMFS 2006). The cause of death for these 12 whales sighted in the GSL included entanglement in fishing gear and blunt force trauma likely caused by vessel strike (Daoust et al. 2018). These events, along with observations of live entangled animals in the GSL, sparked several iterations of management schemes in the GSL and throughout Atlantic Canada, as well as increased monitoring efforts in subsequent years (DFO 2021). While no dead right whales were detected in the GSL in 2018 or 2020, 7 dead and 4 live entangled animals were sighted there in 2019 (Bourque et al. 2020).

In this study, we analyzed the individual right whales sighted in the GSL from 2015 to 2019 to characterize how this region was being used by this species during a time when their distribution and occupancy patterns had shifted throughout their range, including outside of previously established protection zones and the designated critical habitat areas. We used individual identifications to explore the age–sex structure, sighting timing, and movement patterns of right whales within the GSL to inform conservation strategies in this region.

2. MATERIALS AND METHODS

2.1. Sightings and individual identification

The GSL was defined and divided into a northern and southern region in accordance with previous studies that separate this semi-enclosed sea based on bathymetry and oceanographic processes (Fig. 1B) (e.g. Nozères et al. 2015). These 2 regions are also separated by a major shipping corridor running through the Laurentian Channel that connects commercial shipping traffic from the Atlantic Ocean to the St. Lawrence Seaway and the Great Lakes.

Sightings data of right whales captured in photographs or video (hereafter collectively referred to as ‘photographed’) from 2015 to 2019 in the GSL were used in this study. Additionally, high confidence, unphotographed right whale sightings in the GSL (i.e. the observer was certain they saw a right whale) reported to Fisheries and Oceans Canada for management purposes were gathered to determine the earliest and latest sightings in 2017–2019, the years with higher levels of dedicated survey effort. Effort and sightings were summarized and analyzed using R v3.6.3 (R Core Team 2020).

2.1.1. Mark–recapture aerial surveys

The mark–recapture aerial surveys (MRASs) focused on areas of recent and previous right whale sightings and acoustic detections to maximize the number of individuals captured photographically during each survey (approximately 6 h duration). This method has been employed since 2015 both in the GSL, primarily in the southern region (Fig. S1A in Supplement 1 at www.int-res.com/articles/suppl/n046p227_supp1.pdf), and throughout the Greater Atlantic region in the USA (from Virginia to the Canadian border, including offshore waters; see Khan et al. 2018 for more information on the general regions that are targeted). These surveys were flown in a De Havilland DHC-6 Twin Otter high-wing aircraft at an altitude of 305 m and at a speed of 185 km h^{-1}. Primary observers scanned the water on both sides of the aircraft through bubble windows to maximize the search area. Track-lines were generated based on best available information of right whale sightings, and varied between systematic efforts (i.e. evenly spaced track-lines or a sawtooth pattern) and directed efforts (i.e. an expanding box search pattern around a specific location). When a right whale was sighted perpendicular to the platform, the plane would break from the track to circle the animal until there was relative confidence amongst observers that all individuals noted in the area were photographed.

In the GSL, MRASs were conducted during different time periods each year: there was no effort in 2016, and efforts in 2015, 2017 and 2018 were continuous, whereas efforts in 2019 included roughly 2-wk survey periods during the months of June, July, August and October (Fig. S1B). Notably, the survey effort in 2017 was often repurposed for carcass relocation and disentanglement support, and was generally more exploratory than in other years. Specific to the surveys in the GSL, a secondary observer was seated at an aft window during most flights, and, with few exceptions, only animals larger than minke whales *Balaenoptera acutorostrata* were recorded. For more details on the survey methodology in the GSL, see Cole et al. (2020).

2.1.2. 'All data'

The best available photo-identification data were gathered and referred to in this study as 'All data'; these data are inclusive of sightings collected from the MRAS efforts, and are used for analyses of population structure, abundance estimates, residency and movement. The primary repository for these data is the North Atlantic Right Whale Consortium (NARWC) Identification Database, which began in 1986, and contains sightings of photographed right whales from dedicated photo-identification surveys and opportunistic sources as far back as 1935 (Zani & Hamilton 2017, Pettis et al. 2021). This database was queried to obtain the most complete data available for individual right whales sighted and identified in the GSL from 2015 to 2018 (Right Whale Consortium 2019, 2020). Altogether, over 37 organizations and individuals contributed photographed sightings (see 'Acknowledgements' for details on these key partners). At the time of analysis, 2019 data were not available from the NARWC Identification Database; however, the 2019 'All data' includes the first sighting of dead individuals (Bourque et al. 2020), as well as photo-identification data from MRASs, single-day shipboard surveys in the northern GSL (conducted by the Mingan Islands Cetacean Study; see Schleimer et al. 2019 for survey methodology) and multi-week shipboard surveys (conducted by the Canadian Whale Institute/New England Aquarium; Knowlton et al. 2020). Additionally, available opportunistic sightings (from the public and the Canadian Coast Guard), as well as sightings from dedicated aerial survey efforts (conducted by Transport Canada and the Department of Fisheries and Oceans; DFO 2020) that occurred before the first and after the last MRAS, as well as in September when MRASs did not occur, were integrated into this data set.

Dedicated photo-identification efforts contributing to the sightings within 'All data', aside from the MRASs (detailed in section 2.1.1), included several shipboard and aerial efforts. Multi-week shipboard surveys occurred in the southern GSL in July and August (2015–2019), and single-day vessel surveys in the northern GSL on the northwest side of Anticosti Island (Fig. 1B) occurred from June through September (2015–2019). Broad-scale systematic aerial surveys for marine mammals (September–November 2017, May–November 2018 and May–December 2019) prioritized both collecting data on right whale sightings and photo-identification efforts. Dedicated right whale aerial surveillance efforts throughout the GSL (August–December 2017, April–November 2018 and May–November 2019) and the shipping lanes and corridors (April–November 2018 and May–November 2019) primarily focused on surveying the dynamic management zones to trigger protection measures (see DFO 2021 and Transport Canada 2021 for more details on these zones), and while many sightings were photographed, photo-identification was not the primary objective of these efforts. See Supplement 1 for a map detailing the distribution of most of these efforts in each month across all study years (Fig. S1A), and a timeline of these efforts across this study period (Fig. S1B).

2.1.3. Photo-identification

Images of photographed right whales within 'All data' were compared to the North Atlantic Right Whale Catalog (hereafter referred to as 'the Catalog') to access life-history information including age, sex and calving history (Brown et al. 1994, Hamilton et al. 1998, Malik et al. 1999, Frasier et al. 2007). Individual right whales are identified by the callosity pattern — cornified skin colonized by cyamids — on the top and sides of their heads (Payne et al. 1983, Kraus et al. 1986), as well as scars and markings on their bodies (Hamilton et al. 2007). 'All data' from 2015 to 2018 were fully integrated into the NARWC Identification Database and Catalog, while all identifications in the 2019 data were confirmed by at least 2 experienced analysts. Age class was determined by actual age, if known, or sighting history as follows: adults were known-age whales at least 9 yr old, or unknown-age whales that had at least an 8-yr sighting history or were known to be reproductive; calves were animals seen in their birth year; and juveniles were known-age whales between 1 and 9 yr old that had never calved (Hamilton et al. 1998).

2.2. Number of individuals observed and the estimated number undetected

2.2.1. Number observed and population structure

The total number of identified right whales sighted in the GSL was compiled across all years for both data sets. The number of individuals currently known to be dead was subtracted from the total sighted in 'All data' to obtain the best estimate of the number of right whales presumably still alive by the end of 2019. Discovery curves, both by cumulative survey day effort for each data set and by year for 'All data', were created using data summarized by the Rcapture (Rivest & Baillargeon 2019) R package to examine the patterns of identifying new animals.

Available age and sex data were used to characterize population structure within years. Age and sex proportions were additionally compiled for the animals presumed alive in the Catalog at the end of 2019 for comparison to the whole population. The number of individuals sighted in each month was summarized, and months when the MRASs occurred were compared to the other months. The sex ratio of known sexed animals was assessed within each month and year combination within 'All data'. The percentage of cows with calves, subsequently known pregnant cows and resting cows (life stage between having a dependent calf and being pregnant) sighted in the GSL each year in 'All data' were used to assess the reproductive females that were sighted in this region.

2.2.2. Estimates of undetected animals and abundance

The POPAN formulation of Jolly-Seber (JS) open population models (Schwarz & Arnason 1996) was used to estimate the super-population (*N*: the estimated number of undetected individuals + the number of individuals observed) across all years (2015–2019) and within years (2017–2019). It is assumed that (1) animals do not lose their identifiable markings; (2) animals are identified correctly; (3) the study area is constant; (4) sampling is instantaneous; (5) survival probability is the same for all animals whether they are captured or not; and (6) there is no capture heterogeneity, i.e. there is equal capture probability between marked and unmarked animals (Schwarz & Arnason 1996).

Estimations within years were restricted to periods when dedicated MRASs occurred, as the effort outside of these periods did not collect photo-identification data on a comparable scale. *N* was derived from the MRAS data set as well as from the subsampled 'All data' data set ('All data_S') in each year (2017–2019). These 2 estimations within years provided a metric to assess how effective the MRAS methods were in capturing the individuals estimated to be present from the best available data ('All data').

Surveys did not occur at regular intervals due to weather and scheduling; therefore, capture histories were pooled into sampling blocks based on when they occurred. In 2017 (21 June–30 July) and 2018 (1 June–9 August), each data set was divided into sampling blocks spanning 10 d, which ensured each block contained at least 2 MRAS sampling days (the final MRAS survey in 2018 was not included). In 2019, capture histories were pooled into two 8-d blocks within each sampling month so that the pooled blocks spanned the MRAS survey effort (1–16 June, 9–24 July, 13–28 August and 14–29 October). To estimate the total number of right whales that used the GSL within the 5-yr period (2015–2019), capture histories were pooled by year within 'All data'. The data used in these analyses included dependent calves and the first sighting of a dead animal. A formal test for capture heterogeneity does not exist, but the fit of each pooled data set was approximated using a fully parameterized Cormack-JS model in the R2ucare R package (Gimenez et al. 2018) to test for trap-dependence (Pradel 1993), the presence of transients (Pradel et al. 1997) and potential overdispersion of the data (Pradel et al. 2005). The goodness-of-fit results at significance of <0.01 did not indicate consideration of any of these factors for the data sets used here (see 'Results' in Supplement 1).

To derive *N*, tested models included combinations of constant (.) and time-varying (*t*) probability of survival (ϕ), capture (*p*) and entry (*pent*) applied to the pooled capture histories using the marked R package with Hessian to estimate uncertainty (Laake et al. 2013). *A priori*, only time-varying *pent* was included in tested models because a constant rate of emigration or births was not considered biologically realistic for these data sets (e.g. Carroll et al. 2011). JS models are parameterized over *K* capture occasions where one parameter is included for *N*, ϕ on the final occasion and *pent* on the first occasion are not estimable, and, although capture probability is estimated at all occasions, in the fully parameterized model, it is confounded at the initial occasion with the initial *pent* and on the final occasion with the terminal estimation of ϕ (Schwarz & Arnason 1996). For maximum likelihood estimation, a logit link function was used to estimate p and ϕ, a multinomial logit link function was used to estimate *pent*, and a log link function was used to estimate N (Laake et al. 2013). The best-supported models were determined by Akaike information criteria corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002). Associated ΔAIC_c, corrected weight (w_i) and relative model likelihood were calculated using the qpcR R package (Spiess 2018), and results were model averaged according to w_i (Burnham & Anderson 2004).

The MRAS sampling effort in 2019 was the longest temporally of the 3 yr investigated, and the estimated number undetected within the 'All $data_s$' data set was used to provide the best and most currently available estimate for seasonal right whale abundance in the GSL.

2.3. Inter-annual return, capture rates, recapture lag and residency

'All data' were used to evaluate inter-annual return, capture rates, recapture lag and residency.

To assess inter-annual return, individuals captured (excluding dependent calves born in 2019) between years were analyzed using the nVennR R package (Quesada 2020). Life-history characteristics, including known death year, were used to investigate individuals not sighted in subsequent years.

To estimate patterns of residency within the GSL, capture rates, recapture lags and the time between initial and final sightings in the region were calculated. Capture rates were determined by the number of unique days on which an individual was photographed within each year. The recapture lag was calculated as the number of days between subsequent sightings of an individual within each year, and one recapture lag per individual per year was randomly chosen to avoid autocorrelation. Only the first sighting was retained for animals with multiple sightings on one day, and the first sighting as a carcass was included if the animal was sighted dead in the GSL. Residency duration was calculated as the number of days between the initial and final sighting in the GSL for each individual per year. The NARWC Identification Database was consulted for sightings outside of the GSL between these sighting dates; if an individual was not sighted elsewhere during these periods, it was assumed that the whale was resident within the GSL for the entire time between its first and last sighting there. The timelines of the residency periods were aggregated by year to understand when right whales were sighted in the GSL throughout the year as well as likely periods of highest whale concentrations. First and last sightings were normalized to ordinal day within a calendar year for comparison across years. The date of the first sighting of all carcasses in the GSL (both those that could be identified to individual and those that could not) was included along the timeline as these sightings still represented use of the habitat and can inform when deaths occurred and/or were detected.

2.4. Behavior and movement within the GSL

Sightings of live whales within 'All data', excluding sightings of dependent calves, were used to analyze behavior and movement. Dependent calves were not included in these analyses as their feeding and social behaviors are mostly reflective of their life stage (Cusano et al. 2018), and the location of their sightings are often the same as their mother's.

The proportions of sightings where feeding or socializing was observed were compiled by month and year to generalize the behaviors throughout the season. Individuals may have had multiple sightings per day if they were observed by several platforms, or were observed by one platform in a different association state or at a different location (Right Whale Consortium 2020). Feeding behaviors included visible feeding (i.e. surface or visibly subsurface swimming with the mouth open), and an observation of the mouth closing as the animal surfaced to breathe was considered an indication of probable feeding at depth. Social behaviors reflected observations of surface-active groups, which are defined as at least 2 whales interacting physically at the surface — this behavior is considered to have a social function for all age classes (Parks et al. 2007).

The straight-line distances between consecutive sightings of an individual were examined to gain an improved understanding of movement patterns within the GSL. These distances were calculated as 'great-circle distance' using the Vincenty (ellipsoid) method in the geosphere R package (Hijmans 2019). The time between consecutive sightings was calculated, and the distances traveled were normalized to a daily rate. These data were filtered to include only the recaptures that occurred within the median recapture lag (d) of the distribution assessed in section 2.3. This restriction was applied given that the recapture lag distribution was skewed toward shorter time periods, and, therefore, this filter ensured that the distances analyzed were between sightings that occurred within more appropriate intervals to derive a meaningful daily rate. One daily rate per individual was randomly chosen (both by year and by month) to avoid autocorrelation, and boxplots were generated scaled to sample size (Wickham et al. 2019). Speed was calculated to generalize behavior based on previous studies (Baumgartner & Mate 2005). The distances and speeds calculated here represent a proxy for movement rates as actual right whale behavior is more dynamic than the coarse view available in these data.

2.4.1. Minimum convex polygon analysis

Minimum convex polygon (MCP) analyses were conducted for the years with more dedicated effort (2017–2019) to examine the distribution of all photographed sightings as well as the movement of individuals using the adehabitatHR R package (Calenge 2006). The MCP polygon represents the minimum range that encompasses a specified percentage of observation points (Mohr 1947). A 90% MCP analysis was applied to all photographed sightings as the static closure area in 2019 had been determined by the geographic area occupied by 90% of right whale sightings during the snow-crab *Chionoecetes opilio* fishing season to regulate the fishery (DFO 2019). To gain a coarse perspective of movements by individuals, a 90% MCP analysis was conducted for each whale that was identified on 5 or more days within each year (Calenge 2006). The spatial extent and the number of overlapping polygons from the 90% MCP analysis per individual were analyzed to identify movement patterns and high-use areas. All area calculations were done using the geosphere R package (Hijmans 2019), and the count of overlapping polygons was calculated within a 0.5-min resolution raster using the raster R package (Hijmans 2020).

2.4.2. Seasonal distribution and travel between the northern and southern GSL

Photographed sightings from all 5 yr were compiled by month to assess seasonal patterns of right whale distribution within the GSL. Sightings were then summarized by counts within a 10 × 10 min grid, the resolution of the grid used to manage fisheries when right whales are detected (DFO 2019). Straight-line minimum paths were identified for animals that were sighted multiple times within the same month and year. The number of sampling days contributing to the monthly sightings across all years was tallied to evaluate effort.

Individuals sighted in both the northern and southern regions within a year were identified, life-history data were compiled, and the sightings were analyzed to narrow in on timing and general directionality of travel (i.e. from the northern region to the southern, or vice versa) intersecting with shipping traffic separation schemes and corridors. Sighting dates for observations of individuals were normalized to ordinal day per calendar year for comparison across years.

2.5. Code availability and additional R packages used

The R code used in these analyses is available on Github at https://github.com/NEFSC/READ-PSB-LWT-Crowe_et_al_GSL_right_whales. In addition to packages referenced above, data were wrangled, and tables and figures were created using the tidyverse (Wickham et al. 2019), cowplot (Wilke 2019), ggpubr (Kassambara 2020), ggridges (Wilke 2020), marmap (Pante & Simon-Bouhet 2013), maptools (Bivand & Lewin-Koh 2019), mapview (Appelhans et al. 2020), knitr (Xie 2020), kableExtra (Zhu 2020), rgdal (Bivand et al. 2019), rnaturalearth (South 2017), sf (Pebesma 2018), viridis (Garnier 2018) and wesanderson (Ram & Wickham 2018) R packages.

3. RESULTS

3.1. Sightings and individual identification

Photographic effort, in terms of sampling days, seasonal temporal coverage and number of sightings, was greater in 2017–2019 than in the earlier years (2015 and 2016; Table 1). Seasonally, the earliest photographed sightings occurred in mid-May (2017–2019), and the latest was in early December in 2017. In 2018 and 2019, the MRASs captured almost all of the animals in 'All data'. The yearly proportion of cows with calves sighted in the GSL out of the total known for the entire species varied between years. All cows sighted with calves in the GSL in 2019 (n = 4) had also been captured there in 2018 while pregnant, whereas the other 3 known cows that had calved in

Table 1. Details on the right whale sighting period and overall number of photographed sightings and individuals observed in the Gulf of St. Lawrence (GSL) each year from 2015 to 2019. The numbers of cows sighted in the GSL in each year are also provided, including those with calves (out of the total known for the species each year), those subsequently known to have been pregnant, and those resting (life stage between having a dependent calf and being pregnant). MRAS: mark–recapture aerial survey (see Section 2.1.1 for details). See Section 2.1.2 for details on 'All data'

Dataset	Sighting days	First	Last	Sightings	Ind.	Cows		
						With calves	Pregnant	Resting
2015								
MRAS	4	07 Aug	20 Aug	58	35			
All data	27	12 Jun	01 Sep	94	48	3/17 (18 %)	6	4
2016								
All data	26	07 Jul	08 Oct	136	50	6/14 (43 %)	0	9
2017								
MRAS	16	22 Jun	29 Jul	345	108			
All data	69	12 May	05 Dec[a]	769	133	0/5	0	37
2018								
MRAS	26	04 Jun	12 Aug	809	131			
All data	56	19 May	31 Oct[b]	1379	132	0/0	4	35
2019								
MRAS	26	04 Jun	29 Oct	882	132			
All data	69	13 May	29 Oct	1470	135	4/7 (57 %)	6	30

Unphotographed sightings outside of 'All data' time frame listed above:
[a] 2017: 3 right whales sighted on 12 December.
[b] 2018: 3 and 2 right whales sighted on 01 and 05 November, respectively

2019 did not have a sighting history in the GSL within this study period. However, in 2015 and 2016, 47 % (8 of 17) and 71 % (10 of 14), respectively, of the total cows with calves in the entire species population in those years had been captured in at least one other year in the GSL within this study period.

No unphotographed sightings were reported earlier in the year than those within 'All data' in 2017–2019, but a few were reported later (2017: 3 whales on 12 December; 2018: 3 and 2 whales on 1 and 5 November, respectively; 2019: none; DFO, unpubl. data).

3.2. Number of individuals observed and the estimated number undetected

3.2.1. Number observed and population structure

Across all 5 yr, the discovery curve began to plateau by the middle of 2018 (Fig. 2A), and seasonally, in 2017–2019, similar total numbers of individuals were observed each year by mid-July–mid-August (Fig. 2B). Overall, 187 individuals were captured during this period (Supplement 2 at www.int-res.com/articles/suppl/n046p227_supp2.xlsx), including 169 individuals that were captured

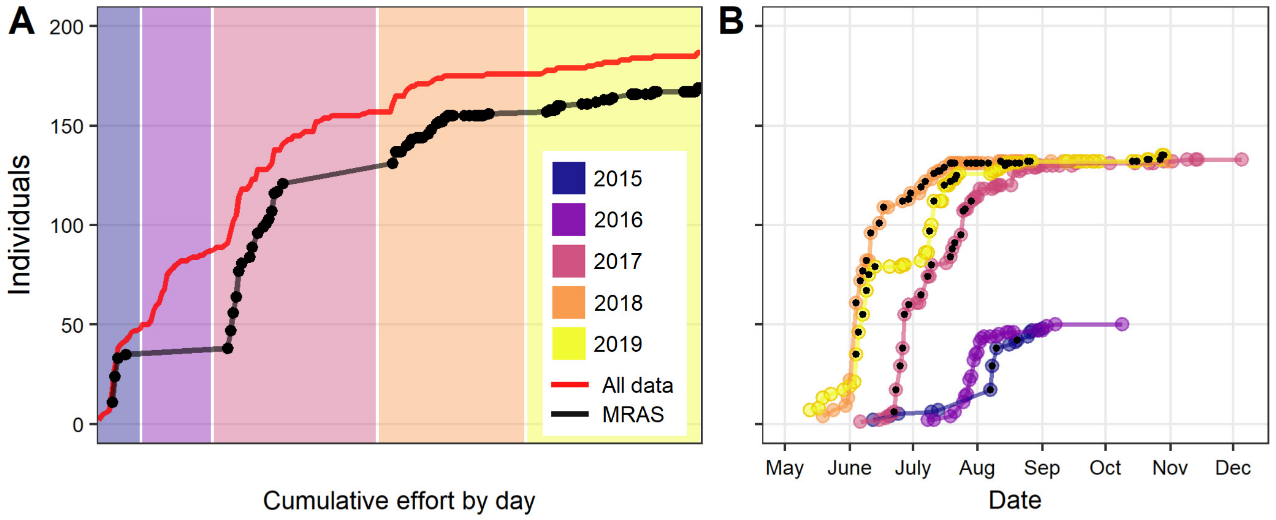

Fig. 2. (A) Cumulative discovery curve by day for individual right whales, including dead animals, sighted in the GSL on mark–recapture aerial surveys (MRASs) and from all sources ('All data') between 2015 and 2019. MRASs captured 169 individuals, and 187 individuals were captured within 'All data'. Photographed sightings occurred at every point along the *x*-axis for 'All data', whereas the black circles on the MRAS line represent survey days along the timeline. (B) The yearly discovery curves by date of individuals photographed from 'All data'. The days when MRASs occurred are represented by the black circles

by MRAS efforts. The difference between the total individuals captured in the 2 data sets (n = 18) can largely be attributed to dead whales that were only sighted within 'All data' (n = 7), animals only sighted in the northern GSL (n = 3) and one that was only sighted in the region as a calf; the remaining 7 had each been captured once (2015: n = 3; 2016: n = 2; 2017: n = 1; 2018: n = 1). Altogether, 25 individuals sighted in the GSL during this period are known to have died, either detected in Canadian or US waters, leaving 162 individuals as the maximum total number alive from these data. During the study period, 7 unidentifiable right whale carcasses were detected, both in the GSL (n = 5) and in the USA (n = 2; NOAA Fisheries 2020b); therefore, it is currently unknown whether these dead animals are included in this total.

Despite differences in total animals captured in 2015 and 2016 (range: 48–50) compared to the latter 3 yr (range: 132–135), similar proportions of known age and sex classes were present each year, which was also similar to the proportions in the Catalog (Table 2). In months when the MRAS efforts occurred, between 42 and 120 individuals were captured each month (mean = 91, SD = 25), whereas between 1 and 36 individuals were captured photographically in the other months (mean = 10, SD = 10). The most common sex ratio within each month and year combination was 2:3 (females:males), and of the months when dedicated mark–recapture effort occurred, the

Table 2. The age–sex structure of the right whales sighted within 'All data' each year, including the number and proportions of sex and age classes presumed alive within the North Atlantic Right Whale Catalog at the end of 2019. Age classes are defined as adult (A), juvenile (J), unknown (U) and calf (C), and sex includes male (M), female (F) and unknown (X)

Age class	M	F	X
2015: n = 48			
A	23 (48 %)	13 (27 %)	0
J	4 (8 %)	3 (6 %)	0
U	0	1 (2 %)	1 (2 %)
C	1 (2 %)	2 (4 %)	0
2016: n = 50			
A	23 (46 %)	15 (30 %)	0
J	1 (2 %)	5 (10 %)	0
U	0	1 (2 %)	0
C	2 (4 %)	3 (6 %)	0
2017: n = 133			
A	66 (50 %)	37 (28 %)	0
J	16 (12 %)	11 (8 %)	0
U	0	3 (2 %)	0
2018: n = 132			
A	66 (50 %)	39 (30 %)	2 (2 %)
J	15 (11 %)	8 (6 %)	0
U	0	1 (1 %)	1 (1 %)
2019: n = 135			
A	68 (50 %)	40 (30 %)	1 (1 %)
J	12 (9 %)	8 (6 %)	0
U	0	1 (1 %)	1 (1 %)
C	1 (1 %)	3 (2 %)	0
Catalog 2019: n = 458			
A	230 (50 %)	144 (31 %)	14 (3 %)
J	29 (6 %)	30 (7 %)	3 (1 %)
U	0	1 (<1 %)	7 (2 %)

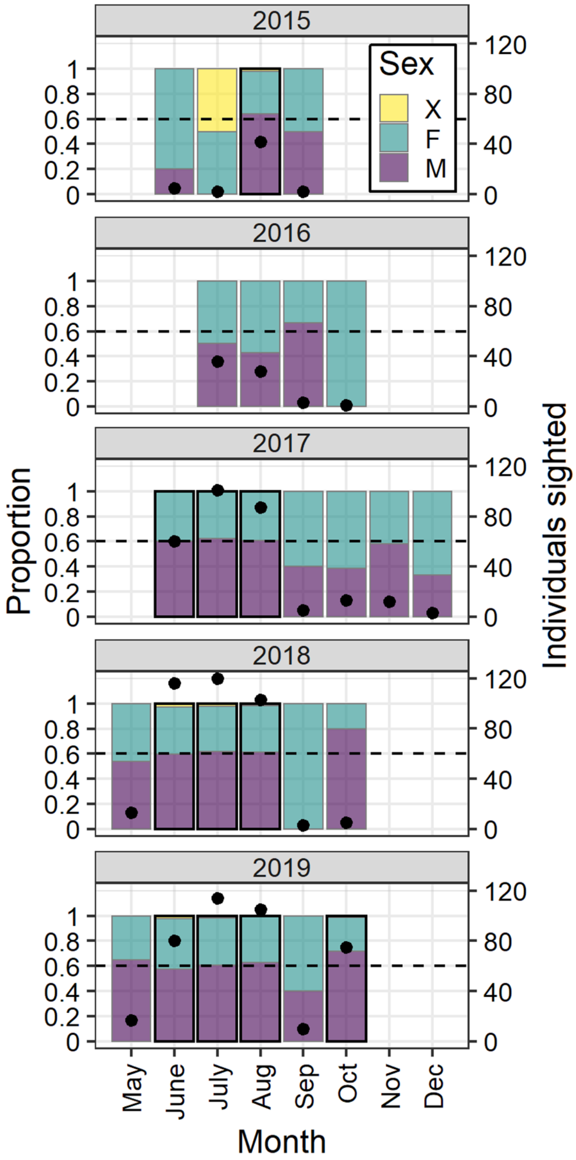

Fig. 3. Proportion of right whale males (M), females (F) and individuals of unknown sex (X) captured in the GSL by all sources ('All data') within each month by year. The dashed black line represents the most common sex ratio (2:3, females: males) based on observed individuals of known sex. The total number of individuals sighted each month is indicated by the black circles, and the months when dedicated MRAS efforts occurred are indicated by the black outline of the bar

October 2019 ratio differed the most (3:7, n = 73; Fig. 3).

3.2.2. Estimates of undetected animals and abundance

For each combination of year and data set, the best-supported model was constant survival and time-varying capture and entry, and the fully parameterized model ranked second; only these 2 models carried weight (Table 3). The estimated number of undetected animals was similar between the 2 data sets in each year, including the same estimates in 2017 and 2019 (Table 4). The resulting abundance estimates differed by a few animals in each year (range of the difference: 1–4). The estimated number undetected from 'All data_s' in 2019 indicated the best estimate of seasonal abundance (N) of right whales in the GSL to be 137 animals (95% CI = 135–147). The estimated abundance (N) across all years within this period was 198 (95% CI = 192–212; Table 4). Model-averaged estimates of survival across all years are included in Supplement 1 (Fig. S2).

Table 3. Model performance for each year/data set combination in years with more dedicated survey effort (2017–2019) as well as across all years of this study (2015–2019). 'All data_s' refers to the sample of 'All data' capture histories that occurred during the MRAS sampling periods. Within each year/data set combination, the number of parameters (n_{par}), the corrected Akaike information criteria (AIC_c), the difference between the AIC_c value and that of the model with the lowest AIC_c value (ΔAIC_c), the model weight (w_i) and the relative model likelihood are provided. Models are ordered by ΔAIC_c. ϕ: survival probability; p: capture probability; *pent*: entry probability; (t): time-varying; (.): time constant

Data set	Model	n_{par}	AIC_c	ΔAIC_c	w_i	Relative likelihood
2017						
MRAS	$\phi(.)\ p(t)\ pent(t)$	8	320.06	0.00	0.80	1.00
	$\phi(t)\ p(t)\ pent(t)$	9	322.87	2.81	0.20	0.25
	$\phi(t)\ p(.)\ pent(t)$	8	333.35	13.29	0.00	0.00
	$\phi(.)\ p(.)\ pent(t)$	6	333.94	13.87	0.00	0.00
All data_s	$\phi(.)\ p(t)\ pent(t)$	8	330.83	0.00	0.77	1.00
	$\phi(t)\ p(t)\ pent(t)$	9	333.26	2.43	0.23	0.30
	$\phi(t)\ p(.)\ pent(t)$	8	345.61	14.77	0.00	0.00
	$\phi(.)\ p(.)\ pent(t)$	6	345.69	14.85	0.00	0.00
2018						
MRAS	$\phi(.)\ p(t)\ pent(t)$	14	937.59	0.00	0.99	1.00
	$\phi(t)\ p(t)\ pent(t)$	18	946.26	8.67	0.01	0.01
	$\phi(.)\ p(.)\ pent(t)$	9	979.47	41.89	0.00	0.00
	$\phi(t)\ p(.)\ pent(t)$	14	984.60	47.01	0.00	0.00
All data_s	$\phi(.)\ p(t)\ pent(t)$	14	928.28	0.00	0.92	1.00
	$\phi(t)\ p(t)\ pent(t)$	18	933.05	4.77	0.08	0.09
	$\phi(.)\ p(.)\ pent(t)$	9	977.14	48.86	0.00	0.00
	$\phi(t)\ p(.)\ pent(t)$	14	982.55	54.27	0.00	0.00
2019						
MRAS	$\phi(.)\ p(t)\ pent(t)$	16	981.21	0.00	1.00	1.00
	$\phi(t)\ p(t)\ pent(t)$	21	994.81	13.60	0.00	0.00
	$\phi(.)\ p(.)\ pent(t)$	10	1013.64	32.43	0.00	0.00
	$\phi(t)\ p(.)\ pent(t)$	16	1022.53	41.32	0.00	0.00
All data_s	$\phi(.)\ p(t)\ pent(t)$	16	957.00	0.00	0.98	1.00
	$\phi(t)\ p(t)\ pent(t)$	21	965.31	8.31	0.02	0.02
	$\phi(t)\ p(.)\ pent(t)$	16	1000.29	43.29	0.00	0.00
	$\phi(.)\ p(.)\ pent(t)$	10	1001.52	44.52	0.00	0.00
Across years 2015–2019						
All data	$\phi(.)\ p(t)\ pent(t)$	10	453.09	0.00	0.84	1.00
	$\phi(t)\ p(t)\ pent(t)$	12	456.38	3.29	0.16	0.19
	$\phi(t)\ p(.)\ pent(t)$	10	516.40	63.31	0.00	0.00
	$\phi(.)\ p(.)\ pent(t)$	7	532.01	78.92	0.00	0.00

3.3. Inter-annual return, capture rates and residency

Overall, 79% of the individuals sighted in the GSL over this study period had been captured there in multiple years (n = 144; Fig. 4A). Approximately 60% of individuals were sighted in at least 3 different years (n = 109), 4% (n = 7) were seen in all 5 yr, and excluding 4 dependent calves, 95% of the animals sighted in 2019 had been sighted in prior years (n = 124). Of the 52 animals not seen in the GSL in 2019, 17 were known to have died, and 13 had last been sighted in the GSL (2015: n = 2; 2016: n = 1; 2017: n = 6; 2018: n = 4), of which 3 were entangled in fishing gear. Eight animals sighted dead in 2019 (7 in the GSL, and one in the USA) had been sighted in the GSL previously, each in 3–4 different years of this study period.

Residency patterns varied by year, and reflected the periods of photo-identification efforts. In the years with more dedicated right whale survey effort (2017–2019), higher capture rates and longer residency periods were observed. Overall, individuals were captured on 1–18 d in a season, and were captured more times in years with more effort (Fig. 4B). Almost all individuals photographed in 2018 and 2019 were captured more than once, including calves and dead individuals (2015: 25%; 2016: 50%; 2017: 79%; 2018: 98%; 2019: 94%),

Table 4. The number of individual right whales observed and the estimated number undetected both within years when more dedicated photo-identification effort occurred (2017–2019), as well as across all years of this study (2015–2019). Within years, estimates were made within 2 data sets: the MRAS data set and the sample of 'All data' capture histories that occurred during the MRAS sampling period ('All data$_s$'). The numbers of animals observed within 'All data$_s$' from all efforts excluding the MRAS are in parentheses to give context to the number of individuals captured from these other efforts

Date range	Data set	Sampling days	Observed	Number undetected			Abundance	
				Estimate	SE	95% CI	Estimate (*N*)	95% CI
2017[a]								
21 Jun–30 Jul	MRAS	16	108	7	4	2–23	115	110–131
	All data$_s$	29	112 (27)	7	4	2–23	119	114–135
2018[b]								
01 Jun–10 Aug	MRAS	25	130	1	2	0–13	131	130–143
	All data$_s$	48	131 (89)	1	1	0–17	132	131–148
2019[c]								
01 Jun–29 Oct	MRAS	26	132	3	2	1–13	135	133–145
	All data$_s$	55	134 (113)	3	2	1–13	137	135–147
Across years								
2015 – 2019	All data	220	187	11	4	5–25	198	192–212

Blocks:
[a] 2017: 21–30 Jun, 01–10 Jul, 11–20 Jul, 21–30 Jul.
[b] 2018: 01–10 Jun, 11–20 Jun, 21–30 Jun, 01–10 Jul, 11–20 Jul, 21–30 Jul, 31 Jul–09 Aug.
[c] 2019: 01–16 Jun, 09–24 Jul, 13–28 Aug, 14–29 Oct

and across all years, the distribution of recapture lags skewed toward shorter periods, where most recaptures within a year occurred within approximately 1 wk of a previous sighting (days: median = 8, mean = 14, SD = 18, range = 1–125; Fig. 4C). Mean residency per year varied (days: mean = 50, SD = 33, range = 15–96), and more animals were resident for longer periods in 2019 (days: mean = 96, SD = 49, range = 1–169) than in previous years (Fig. 4D). Among all years, right whales were present between May and December in the GSL, and the highest numbers of animals presumed present in the GSL occurred between the beginning of June and the end of August of each year (maximum count = 120 individuals on 11 July 2018; Fig. 4E). Almost all observed dead whales were sighted before the start of August, including many sighted before periods of presumed peak abundances in July.

3.4. Behavior and movement within the GSL

Generally, observations of visible feeding and social behaviors increased throughout the season (Fig. 5A). Of the 3707 total sightings across all years, there were more sightings in each month when the MRASs occurred (range = 67–603, mean = 331, SD = 177) compared to the other months (range = 1–95, mean = 22, SD = 27). In most years, aside from October 2019, there were few sightings in the months from September to December (range = 1–37, mean = 11, SD = 12), but in many of these months, larger proportions of surface feeding and social behaviors were observed. There was also an increase in these observed behaviors in October 2019, when MRAS effort occurred and more sightings were observed compared to October sightings in the other years.

The distribution of the calculated distances traveled per day between sightings occurring 8 or fewer days apart varied by year and by month. Across all years, 75% of daily distances traveled were less than 9.1 km d^{-1}, but longer movements (up to 36.5–79.8 km d^{-1}) were inferred in each year (Fig. 5B). In the years with more effort (2017–2019), there were more samples of calculated rates (2015: n = 6; 2016: n = 14; 2017: n = 81; 2018: n = 123; 2019: n = 118). When pooling the daily rates by the month of the second sighting, the longest inferred movements occurred in June, July and August (up to 46.3–79.8 km d^{-1}), months that included more samples (May: n = 5; June: n = 98; July: n = 134; August: n = 125; September: n = 5; October: n = 38; November: n = 1) and when more effort occurred (Fig. 5C).

The individuals that traveled the maximum distance in each year across all calculated daily movements represented a range of age and sex classes between and within several areas, including an entangled juvenile male that moved from west to east in the southern GSL in 2015 (254 km in 4 d), 2 adult

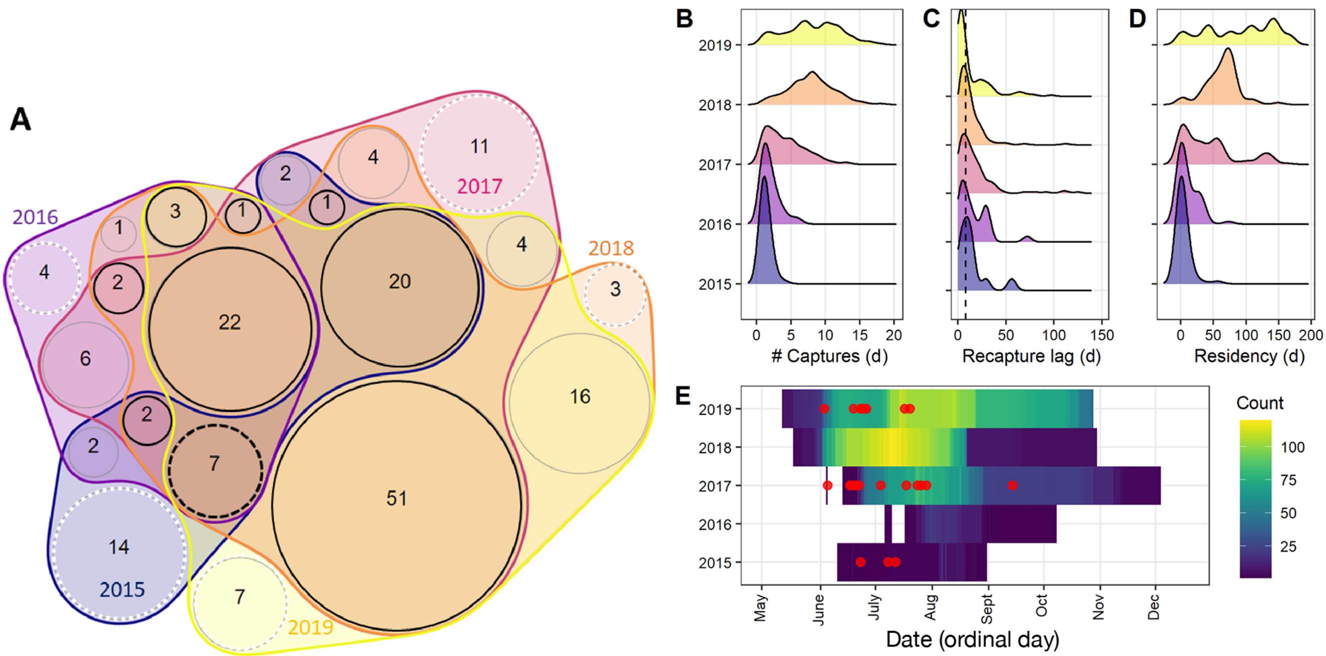

Fig. 4. (A) Inter-annual return: right whales sighted within each year (excluding calves born in 2019) are indicated by the different colors, and overlapping colors indicate the number of individuals sighted in multiple years. Circles outlined by white dotted lines indicate the number of individuals sighted in only one year, the grey outline indicates those sighted in 2 yr, and the black outline indicates those sighted in at least 3 different years with the dashed black line indicating those sighted in all 5 yr. Twenty-five of the animals included here are currently known to be dead. (B) Capture days: distribution of the number of days on which individuals were captured within a year (range: 1–18). In years when efforts spanned less of the season (2015 and 2016), individuals were captured on fewer days. The positively skewed distribution in 2017 is likely due to sightings of dead whales and less extensive photo-identification efforts compared to 2018 and 2019. (C) Recapture lag: distribution of the number of days between recaptures of an individual in each year. Across all years, the lag between recaptures most commonly occurred within about 1 wk (8 d) of a previous sighting within each year (days: median = 8, mean = 14, SD = 18, range = 1–125); the vertical dashed line indicates the median lag time. The lags were shortest during periods when continuous, directed photo-identification efforts occurred, and the peaks of longer recapture lags in each year reflect the periods of photo-identification effort. (D) Residency: distribution of the number of days between an individual's first and last sighting in the GSL. More animals were presumed resident for longer periods in 2019 when dedicated photography efforts occurred over more of the season compared to other years, and the pattern of the distribution for each year reflects the periods of photo-identification effort. (E) Temporal residency: timelines of residency for each individual are overlaid within each year, where the colors indicate how many animals were presumed to be in the GSL throughout each season. Dead whales (red circles) were observed most often at the beginning of the season. The month labels are placed along the *x*-axis at the first day of the month according to ordinal day within a calendar year on non-leap years (2016 is the only leap year in this study)

females seen together on the western side of Anticosti Island and then in the St. Lawrence Estuary in 2016 (399 km in 5 d), 2 adult males that moved north to south in the southern GSL (2017: 162 km in 4 d; 2019: 60 km in 1 d) and an adult female that moved south to north in the southern GSL (50 km in 1 d).

3.4.1. MCP analysis

Most photographed sightings within each year (2017–2019) occurred in the southern GSL, but individuals also moved between the northern and southern regions (Fig. 6A). The area encompassing 90% of all photographed sightings was smallest in 2018, when sightings and effort were more concentrated (2017: 15 927 km^2; 2018: 3321 km^2; 2019: 18 743 km^2). Within the individual movement MCP analysis, the overall area calculated was largest in 2019, when there were more sightings to the south and east (2017: 17 409 km^2; 2018: 12 073 km^2; 2019: 21 622 km^2). Between the 3 yr, the number of individuals sighted on 5 or more days was lowest in 2017 (2017: n = 55; 2018: n = 112; 2019: n = 104), and in all years investigated here, there were sightings of right whales outside of the individual movement MCP (these included animals that could not be identified to individual, or individuals photographed on fewer than 5 survey days). The highest number of overlapping individual polygons occurred in the southern GSL in all 3 years

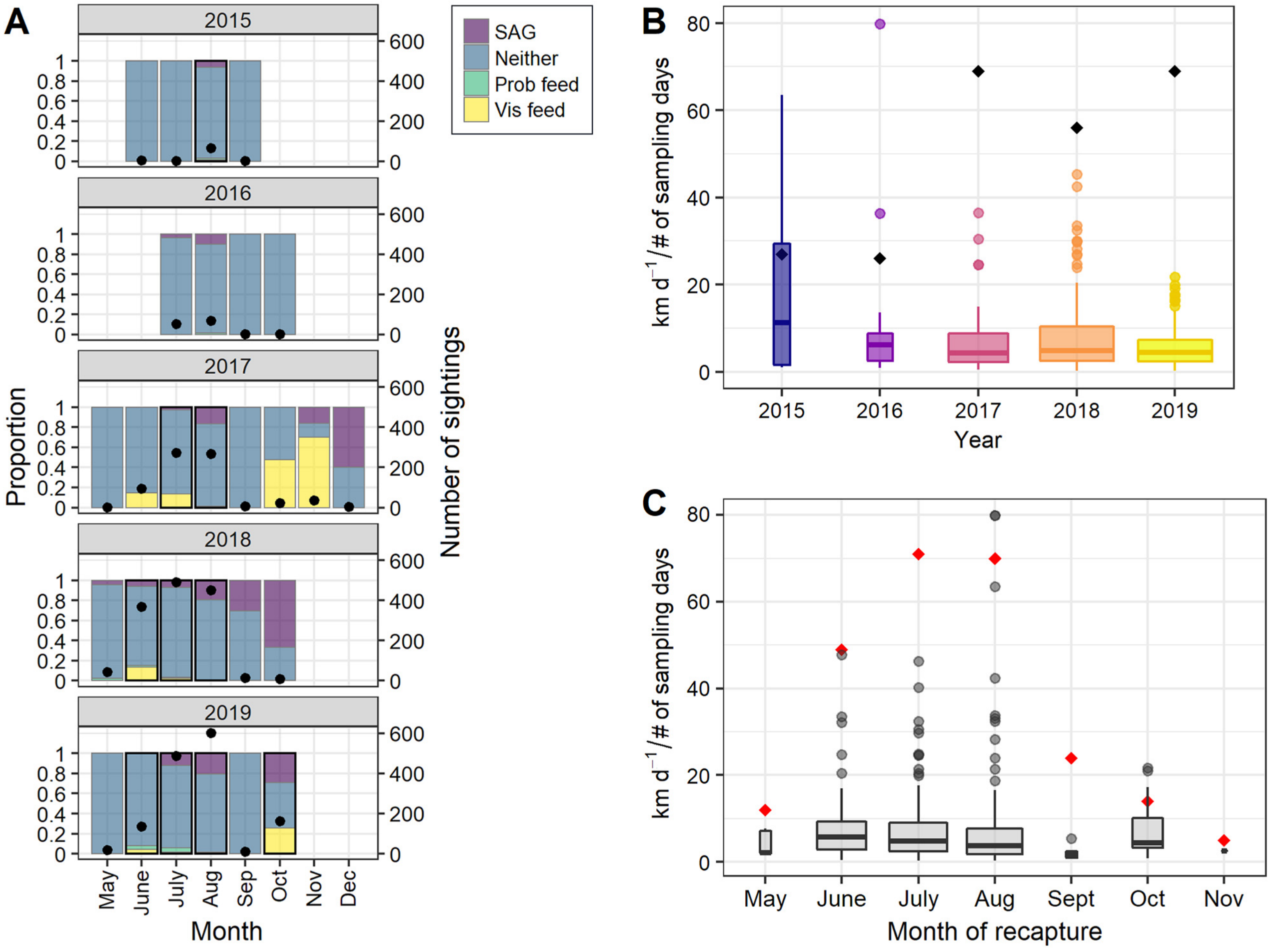

Fig. 5. (A) The proportions of monthly right whale sightings where surface active groups (SAGs), visible feeding (Vis feed), probable feeding (Prob feed) or neither social or feeding behaviors (Neither) were observed. The total number of sighting events each month is indicated by the black circles. The yearly (B) and monthly (C) distribution of straight-line distances traveled between 2 sightings of an individual occurring within the median re-sight lag (8 d) or less normalized to a daily rate. One rate per individual was randomly sampled per year and also per month. The colored box represents the interquartile range (25th to 75th percentiles), the horizontal line within each box represents the median value, the upper and lower whiskers represent values that fall within 1.5 times the interquartile range, the circles represent the outlying points, and the width of the box is proportional to the square-root of the number of individuals included in each year (Wickham et al. 2019). The number of sampling days per year (B) and by month (C) are indicated by the black and red diamonds, respectively

(Fig. 6B), where the maximum ranged from 31 overlapping polygons in 2017 to 85 in 2019, and 81 in 2018. Across the 3 yr, individual MCPs ranged between 13 and 10 633 km^2, and there were examples of animals photographed in both the northern and southern GSL in all years.

3.4.2. Seasonal distribution and travel between the northern and southern GSL

Right whales were photographed in all months between May and December, indicating a general shift from the western side of the southern GSL in May and June to a broader dispersal between the northern and southern regions (including down the St. Lawrence Estuary and across to western Cape Breton in July–September), and then a shift to the southeastern GSL in October (Fig. 7A). The lack of dedicated photography efforts in the southern GSL in November and December led to a temporal gap in photographed sightings toward the end of the season, but even so, sightings occurred in the northern GSL and the eastern side of the southern GSL in both months. Across all months, the range of the number of sightings per occupied grid cell was 1–317 (mean = 13, SD = 35), where the cells with the highest sighting counts (>100) occurred in July and August.

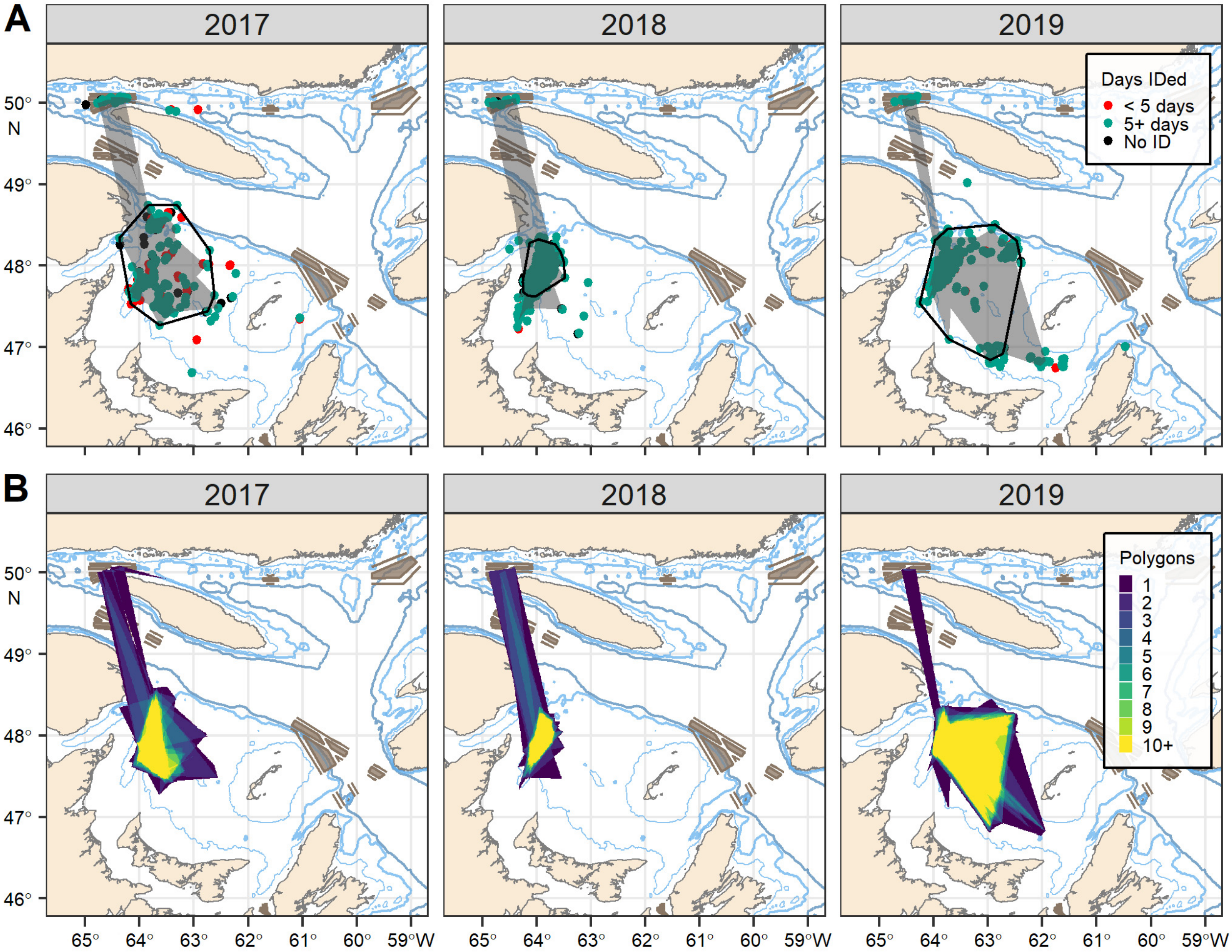

Fig. 6. Minimum convex polygon (MCP) analyses were conducted to examine the distribution of all photographed right whale sightings, the movement patterns by individuals and the overlap of these patterns. The shipping traffic separation schemes and 50, 100 and 200 m isobaths are displayed (see Fig. 1B). (A) The MCP (black outline) that encompasses 90% of all photographed sightings in each year, as well as the collective area covered by the MCPs (grey) encompassing 90% of photographed sightings for each individual captured on at least 5 different days in a year (teal circles). The sightings of animals photographed on less than 5 d within each year are indicated by the red circles, and photographed sightings where individual identification could not be determined are indicated by the black circles. (B) All MCPs for each individual are overlaid and the number of overlapping polygons is displayed where 10 or more are grouped together in yellow. The maximum number of overlapping polygons ranged from 31 in 2017 to 85 in 2019, with 81 in 2018

Across all years, right whales were sighted in both the northern and southern GSL as well as in shipping traffic separation schemes. Of the animals sighted alive in this 5-yr period, 37 individuals were sighted in the northern GSL, 182 in the southern GSL, 33 in both regions, 4 only in the northern region and 149 only in the southern region — 1 animal was only seen dead during this period, and was found on a western Newfoundland beach. From 2015 to 2019, individuals were photographed in the Jacques Cartier Passage shipping traffic separation scheme between July and November (n = 29), down the St. Lawrence estuary in July and August (n = 3) and in the shipping corridor between the Honguedo and Cabot Straits in May (n = 1).

There were 14 examples of 10 individuals sighted in both the northern and southern GSL within the same season (Fig. 7B). Altogether, most transits between regions from these data would have occurred between 30 June and 15 October. These included 3 adult males, 1 juvenile male, 1 individual of unknown age and sex, and 5 adult females, including 2 that were known to be pregnant in 2018 (nos. 2503 and 2791). Assumed crossings of the shipping corridor occurred in both directions among this overall group, and also for some individuals within the same year

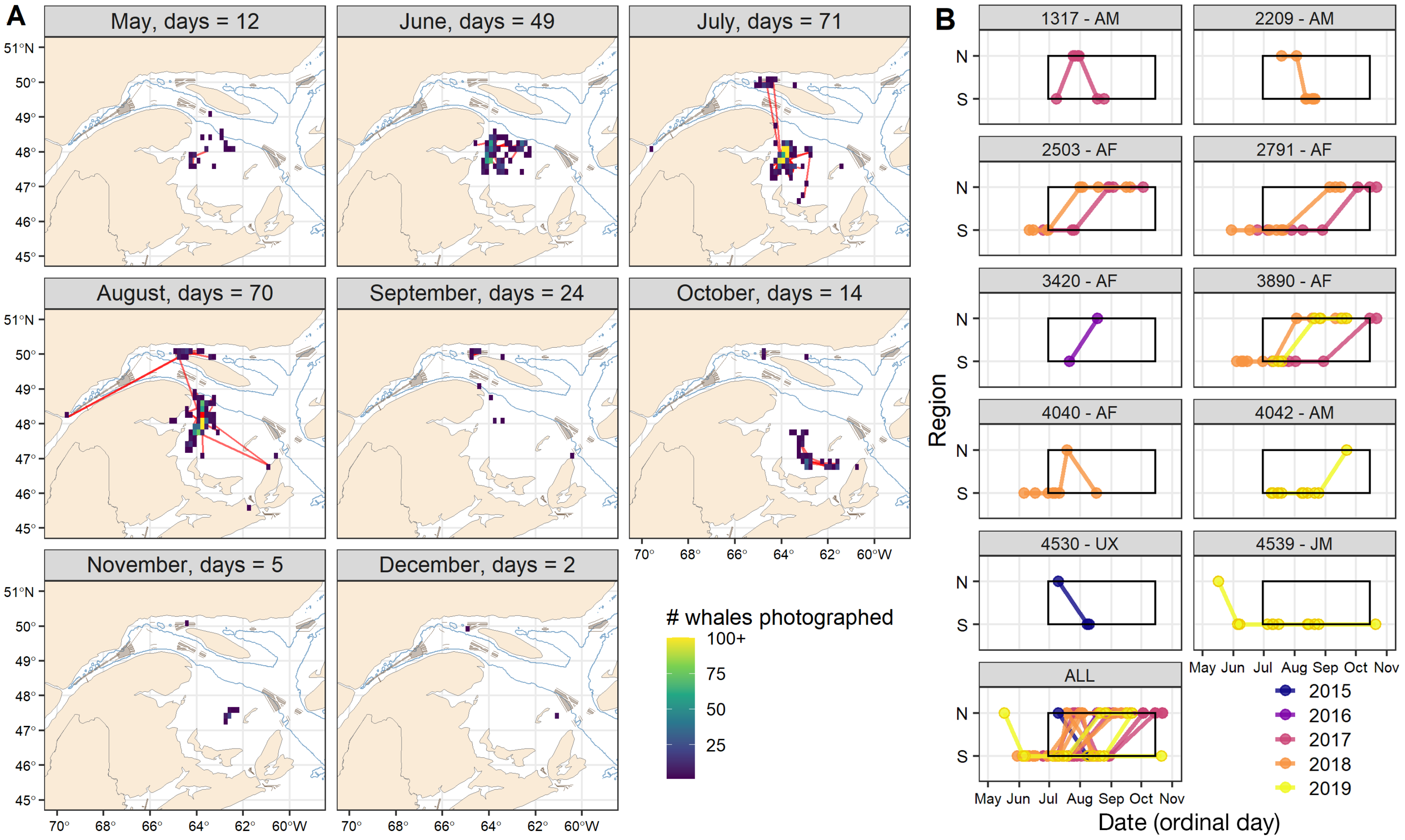

Fig. 7. (A) The locations of photographed sightings from all sources by month from 2015 to 2019 are summarized by the number of photographed sightings within a 10 × 10 min grid. Grid cells containing more than 100 sightings are combined into '100+', and the red lines connect subsequent sightings of an individual within a year in the month specified. The number of sampling days collectively across all years is detailed in the grey header bar for each month. The shipping traffic separation schemes (grey areas) and the 200 m isobath (dark blue line) are also displayed. (B) The dates of sightings for individuals observed in both the northern (N) and southern (S) GSL within a year are displayed to gain a perspective on timing and direction of movement between the 2 regions both overall and by individual. Right whale identification number, age class (A: adult; J: juvenile; U: unknown) and sex (F: female; M: male; X: unknown) are detailed along the horizontal header bars. Of note, both individuals 2503 and 2791 were pregnant in 2018. The black boxes indicate the period when all but one intersection with the shipping corridor presumably occurred (between 30 June and 15 October). The month labels are placed along the *x*-axis at the first day of the month according to ordinal day within a calendar year on non-leap years (2016 is the only leap year in this study)

(n = 2). For the animals that were captured moving between these regions in multiple seasons, all were adult females and the crossings occurred earlier in the season in 2018 and 2019 compared to 2017.

4. DISCUSSION

The shift in right whale distribution and occupancy, coupled with the current downward trajectory of the population estimate (Pace et al. 2017, Pettis et al. 2021), highlights how important it is to understand where these animals are in order to implement effective protection measures. This study clearly demonstrates that the GSL is currently an important habitat for approximately 40 % of this species from the beginning of May to December, with the highest numbers observed from June through October. The individuals sighted in the GSL currently consist of a particular group of individuals from this species exhibiting a high rate of inter-annual return that is not typical in other regions. Individual identifications of right whales indicate that the movements of at least some individuals, including reproductive females, span the northern and southern GSL within a season.

4.1. Effort and assumptions

Capture rates, recapture lags and residency times reflected differences in survey effort each year. The photo-identification efforts in 2015–2017 were concentrated over shorter time periods that did not afford the opportunity for the multiple captures observed in later seasons. Efforts in July and August 2018 yielded more daily captures, but the longer residency signals seen in other years were not observed as surveys did not occur later in the season. Finally, the multi-modal signal in the recapture lags between sightings in 2019 likely reflected, in part, the time between the MRAS sampling periods, including the lack of effort in September.

In estimating abundance, JS assumptions of equal capture and survival for marked and unmarked animals may have been violated in this analysis. Other works that have estimated right whale abundance for the entire species have cautioned that capture and survival can vary by habitat, sex and/or age class (Fujiwara & Caswell 2001, Pace et al. 2017); however, in this study, we did not delineate between these factors for several reasons. First, we treated the entire GSL as the study area. Right whales in the GSL are primarily attracted to the region to feed, and all individuals are subject to spatial prey availability, both horizontally and vertically, and this is likely the prominent driver of capture probability. For example, the regional and behavioral shift observed in October 2019 was likely a response to prey availability caused by seasonal oceanographic changes (Plourde et al. 2019), but this shift would have altered the motivation of spatial use patterns for all right whales in the GSL. Second, the age and/or sex class proportions of captured animals did not indicate large differences from those in the entire population. Additionally, by the time of year that cow–calf pairs are in the GSL, the calf is already quite large and independent (Cusano et al. 2018); therefore, cow–calf behavior and availability are different from what is observed on the calving grounds, for example. However, this study does not include extensive dedicated photo-identification effort in the autumn and winter periods, and future studies including data from these periods should consider age and sex as factors as there may be staggered exit times from the region for the different age–sex classes. Third, based on the high rate of inter-annual return, there are not likely to be many transients in these data sets, suggesting that, in 2019, the few new animals captured at the end of the season in October were probably a reflection of seasonal differences in habitat use; more effort is needed in the later periods of the season to better understand these trends. And fourth, the survival pressures are present for all whales in the GSL; however, future studies should consider the region of the GSL in which animals are sighted (northern and/or southern) as it does appear that movement patterns of at least some animals may expose them to more risks.

The abundance estimates suggest that the MRASs photographed virtually all right whales that were in the GSL during the survey periods in 2017–2019, and the yearly abundance is not likely to estimate many more animals present than the number of individuals captured using these methods. The MRAS sampling in 2019 struck a balance between fine-scale monitoring to the extent seen in previous years and surveying more comprehensively throughout the entire season. While consecutive photo-identification aerial surveys during periods of high whale numbers is excessive for what is needed to estimate abundance using mark-recapture methods, in addition to the other analyses presented in this study, it provides valuable population monitoring for health assessments, injuries, deaths and entanglements (Pettis et al. 2004, Henry et al. 2020).

Over the 5 yr investigated here, dedicated right whale survey effort varied for several reasons (i.e. reacting to whale deaths, funding, platform availability, discovery period for whale distribution, etc.). While few unphotographed sightings were observed outside the periods of photo-identification efforts in 2017–2019, there has not been a standard photo-identification sampling method across all months in one right whale season. The October 2019 effort gave insight into not only how many whales were in the GSL in the autumn season, but also into the behavioral differences (increased observations of surface feeding and surface-active groups) and distribution shift to the southeast GSL. Continued efforts using the 2 wk per month MRAS sampling method, but in at least all ice-free months of the year, would allow for more robust mark–recapture methods exploring more variables to be applied in the future, as well as a more complete understanding of the distribution over a year. This would also help establish the pattern of arrival and departure of right whales to and from the GSL, especially considering that acoustic detections of right whales have occurred as early as April and as late as January of the following calendar year (Simard et al. 2019).

4.2. Implied mortality

The plateau of the discovery curve after the middle of 2018, and the markedly high rate of inter-annual return, demonstrates that dedicated photo-identification efforts were essential to characterizing the individuals in this habitat. These trends suggest not only that few individuals come to the GSL that have not already been documented there, but also that there may have been more mortalities of right whales that use the GSL than were observed. A comparison of the number of right whales in the GSL across all years to the number there in the 2019 season suggests that many individuals that were expected to be seen there were not, and some were not seen anywhere else since a last sighting in the GSL.

Between 1990 and 2017, the highest mortality estimates were in 2015 and 2016, and, overall, only 36% of right whale mortalities were estimated to have been detected throughout their range (Pace et al. 2021). At this rate of detection, the 25 detected mortalities of animals sighted in the GSL between 2015 and 2019 implies 69 total mortalities, a number similar to the 61 animal difference between the overall number estimated in the GSL over the study period ($N = 198$) and the best seasonal estimate in 2019 ($N = 137$). Pace et al. (2021) described a lower mortality detection rate in the period from 2010 to 2017 (29%), reflecting the challenge of initially finding and documenting right whales during a range-wide distribution shift; however, a strikingly similar number of detected and estimated mortalities in 2017 was attributed to increased survey effort in Canada (Pace et al. 2021). This suggests that the increased levels of effort in the GSL since 2017 have been effective in detecting mortalities that occurred there. The previous years, 2015 and 2016, may have also been catastrophic years for right whale mortalities in the GSL but survey effort was not extensive enough in those years to detect it.

The individuals sighted in the GSL are regularly seen in other habitats (Quintana-Rizzo et al. 2021, Northeast Fisheries Science Center unpubl. data), and encounter survival threats throughout their range (Sharp et al. 2019); however, injuries sustained in a region may not always be first detected in that area. For example, an adult male (no. 3530) was disentangled from rope attached to a Canadian crab pot off the coast of the southeast USA in 2017 (Henry et al. 2020), and continued to be sighted in the GSL in subsequent years (Right Whale Consortium 2020). There are also examples of whales leaving the GSL after experiencing trauma, suggesting that some injured whales may actually die elsewhere. Within the data set used in the present study, an adult male (no. 3312) was sighted entangled in 2018 after being sighted gear-free 2 h earlier in the day, and has not been sighted since (Right Whale Consortium 2020). In another example, a severely entangled adult male (no. 3125) was equipped with a satellite tag in the GSL in 2019, and was last sighted in waters east of Cape Cod, MA, USA, where a disentanglement attempt was made (Center for Coastal Studies 2019). Also in 2019, an adult male (no. 1226) that was first seen entangled in the GSL was found dead off Long Island, NY, USA, 6 wk later (Anderson Cabot Center 2019). These examples serve as reminders for how mobile even whales with debilitating entanglements and injuries can be, and that some whales go undetected, not from lack of trying to find them, but because they have left the region where survey effort is focused.

4.3. Distribution and movement relative to anthropogenic pressures

This study offers an improved understanding of right whale distribution in the GSL, and these findings have implications for effective management. While sightings data alone can provide important information on right whale presence, we have demonstrated the insight gained from connecting even a few sightings of an individual. Determining the drivers behind where and when right whales aggregate is beyond the scope of this study, but we have demonstrated the variability in the area they use over the course of a season and between years.

Fishing regulations implemented to reduce the threat of entanglement were previously focused on the western side of the southern GSL based on the number of right whales sighted there (DFO 2019), but have since shifted to include a strategy reactive to sighting locations throughout Atlantic Canadian waters (DFO 2021). We have shown that within a year, right whales primarily aggregate in the southern GSL (on the western side, but also throughout), and in the Jacques Cartier Passage in the northern GSL. Most individuals were sighted once they were in these aggregation areas, and the tendency for individuals to move less than 9.1 km d^{-1} could reflect that they stay in an area for some time once they arrive or that they are most often sighted in the aggregation areas where much of the photo-identification effort is concentrated. As demonstrated here, inferring spatial use based on sighting positions alone leads to an incomplete understanding of how right whales use the region, and can mask the intersection of whales and conservation threats.

The shipping traffic separation schemes and corridors in the GSL are important economic highways, and since 2017, an unprecedented number of right whale deaths observed in the GSL have been attributed to injuries consistent with vessel strike (Daoust et al. 2018, Bourque et al. 2020). There are 2 narrow entrances from the North Atlantic Ocean into the GSL — the Strait of Belle Isle and the Cabot Strait — and a previous study of vessel traffic from July to mid-September 2017 estimated an average of 7 vessels (>300 gross tons or >20 m) transited through the main shipping lanes in the Honguedo Strait each day (range: 2–16; M. Carr, unpubl. data). However, many vessels travel outside of the main shipping lane, including those that hug the coastline of the Gaspé Peninsula when traveling between ports in the southern GSL and the St. Lawrence Seaway (Daoust et al. 2018). In addition, the shipping corridor and other sections of the GSL are heavily trafficked by smaller vessels (Daoust et al. 2018), and modeling studies have suggested that vessels of all sizes can exert forces capable of inflicting lethal injuries to right whales (Kelley et al. 2021).

Through the analysis of re-sightings of individuals, we have demonstrated that right whales intersect with shipping traffic separation schemes and corridors in the GSL. Of the animals sighted in the northern and southern regions, the animals that have made repeated trips were adult females, including females that were later known to have been pregnant at the time. The precise timing and actual routes traveled by these animals cannot be known from these data, but, for whales seen in both the northern and southern regions, there are no possible routes between these areas that do not intersect the shipping corridors. For a species where less than 100 breeding females remain, and calving, survival and population growth is inhibited by human activities (Fujiwara & Caswell 2001, Corkeron et al. 2018), these movement patterns reveal a risk to right whale recovery.

Migrating right whales are more challenging to detect both visually (Firestone et al. 2008, Whitt et al. 2013) and acoustically (Parks et al. 2011), and at a minimum, these whales travel through the narrow entrances, predominantly undetected, at least twice in a season. In our analysis, individuals were not sighted outside of the GSL between their initial and final sightings within the GSL, but most concurrent right whale survey efforts during the summer (June–October) were limited to studies occurring in the Bay of Fundy and in southern New England (Johnson 2018, Canadian Whale Institute unpubl. data, New England Aquarium unpubl. data, Northeast Fisheries Science Center unpubl. data). There were only a few instances during the study period where live right whales were sighted near the Cabot Strait entrance and none were sighted on the eastern side of the northern GSL, though there was little survey effort in these regions (Johnson 2018). Feeding and socializing bowhead whales *Balaena mysticetus* (a species closely related to the right whale) are more likely to be visually detected from an aerial survey than traveling animals (Thomas et al. 2002). These previous studies, along with the sighting history of right whales in and around the GSL, indicate that transiting right whales are also difficult to detect. Due to the apparent lower probability of detecting transiting right whales as they immigrate and emigrate from the GSL, they will likely not be protected by compulsory dynamic management measures.

Previous tagging studies have demonstrated that assuming residency between an initial and final sighting can be misleading as right whales are very mobile (e.g. Mate et al. 1997). While the maximum calculated time lag between re-sightings was approximately 5 mo, most re-sightings occurred over a period (8 d or less) that suggested residency. Each season, few new animals were captured after the end of August, suggesting that most animals visiting the GSL each season had at least already entered by that time. However, we currently cannot rule out the possibility that the whales are emigrating and re-immigrating into the GSL within a year, as has been estimated in other habitats (Vanderlaan 2010, Quintana-Rizzo et al. 2021). If these animals are not remaining resident inside of the GSL over the entire season, there is potentially increased co-occurrence with shipping traffic in the Cabot Strait and/or Strait of Belle Isle than is currently recognized.

From these data, it does appear that many individuals do not go very far within a day, but there are also examples of the opposite; this study includes examples of right whales traveling up to approximately 80 km d^{-1} (0.92 m s^{-1}). While the motivation of these movements cannot be determined in this study, both the western side of the southern GSL and the area west and north of Anticosti Island are regions where suitable prey densities for right whales have seasonally occurred (Plourde et al. 2019). Previous studies considered speeds of up to 1.5 m s^{-1} as reasonable swimming speeds for foraging right whales (e.g. Baumgartner & Mate 2003); therefore, it is possible that even the whales traveling the furthest distances within the GSL were foraging along the way.

4.4. Implications for management

In the GSL, right whales appear to stay close to the same location for days at a time, and based on our knowledge of the behavior of foraging animals, this is likely when the food supply is sufficient. However, they can also move tens of kilometers in a few days or less, often undetected, and intersect with shipping corridors and active fishing zones. In this study, we were able to calculate a minimum amount of movement within the GSL, both in terms of the number of events as well as the distance traveled. The ability to detect longer movements and animals outside of aggregation areas is more challenging, and visual and acoustic survey effort has been patchy and imperfect. However, it is clear that aspects of whale behavior make them difficult to detect visually and/or acoustically, and the reliance on detections to trigger protection zones does not eliminate the risks from encounters with fishing gear and shipping activity. Scenarios of whales staying localized, as well as moving into, out of and around the entire GSL, should be considered as possibilities throughout most of the year. For conservation planning, less reliance on detections to trigger management actions would minimize the risk of missing whale presence.

4.5. Implications for the North Atlantic right whales not sighted in the GSL

Although the high rate of inter-annual return and the low estimates of undetected individuals suggest a particular group of right whales use the GSL, it is possible that more animals will go there in the future. Preliminary observations from the 2020 season are consistent with the patterns described here (DFO, unpubl. data), but as right whale foraging habitats continue to be altered due to climate change (Record et al. 2019), right whale use of the GSL may also change. The prey resources in this region may attract more individuals, or they may degrade leading to an abandonment of this region as has been observed elsewhere (Davis et al. 2017, Davies et al. 2019). However, our findings relative to the high rate of inter-annual return may further support that the species is composed of subpopulations or feeding groups that divide along some social and/or biological lines that we do not currently understand (Schaeff et al. 1993), but that have been observed in other large whale species (e.g. Stevick et al. 2006).

In the summer season (June–August), the only other known aggregations of right whales observed in 2017–2019 were detected in southern New England waters (Quintana Rizzo et al. 2021) and in the Bay of Fundy (USA and Canada; Canadian Whale Institute unpubl. data, New England Aquarium unpubl. data), but too few individuals were sighted to explain where most of the remaining population was during this time (Johnson 2018). There was one animal (no. 4605) whose alternate whereabouts in the summer were known — this animal had only been sighted in the GSL as a calf with its mother in 2016 and has been sighted in southern New England waters (south of the islands of Martha's Vineyard and Nantucket, MA, USA) every summer since (Northeast Fisheries Science Center unpubl. data). Other calves that were sighted in the GSL with their mothers have subsequently returned to the region in years post-weaning.

This study not only improves the understanding of right whale use in the GSL, but also raises the question of where the other individuals of the species are in the summer. In recent years, right whales have largely abandoned the summer foraging grounds where they were reliably sighted for decades (Davis et al. 2017, Davies et al. 2019), and this current lack of knowledge of the distribution of the entire North Atlantic right whale species population in the summertime illuminates the likelihood that many right whales are using habitats that currently lack protection measures. The downward trajectory of the

North Atlantic right whale continues to call for broad, urgent and effective management (Davies & Brillant 2019, Record et al. 2019, Pettis et al. 2021). Considering the human impacts that have been observed in the GSL, a substantial, international effort to identify right whale habitats in other parts of the North Atlantic Ocean is necessary to avert future catastrophic impacts on this species.

4.6. Conclusions

North Atlantic Right whales have increased their use of the GSL in recent years, and there were unprecedented numbers of whales found dead in 2017 and 2019. Our analyses also indicate that substantial, undetected mortality of these right whales probably occurred in the GSL in 2015 and 2016. The increase in observed mortalities in 2017 prompted implementation of protection measures to prevent further lethal and sub-lethal impacts from commercial fishing gear entanglements and vessel strikes, and these management measures have evolved since then. While the GSL is certainly not the only habitat where right whales co-occur with these threats, this study has shown that there is a unique opportunity in this region to protect a large portion of the population, including reproductive females and calves, that reliably returns to the GSL each year.

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Editorial responsibility: Nicola J. Quick,
Beaufort, North Carolina, USA
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