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Wintering areas, fall movements and foraging sites of blue whales satellite-tracked in the Western North Atlantic

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Foreword

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

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TABLE OF CONTENT

ABSTRACT

The blue whale (*Balaenopterus musculus*) is a wide-ranging cetacean that can be found in all oceans, inhabiting coastal and oceanic habitats. In the North Atlantic, little is known about blue whale distribution and genetic structure, and if whether animals found in Icelandic waters, the Azores, or Northwest Africa are part of the same population as those from the Northwest Atlantic. In the Northwest Atlantic, seasonal movements of blue whales and habitat use, including the location of breeding and wintering areas, are poorly understood. In this study, we used satellite telemetry to track the seasonal movements of 24 blue whales from eastern Canada.

We provide the first record of the full migration of a blue whale from the western North Atlantic. We locate transiting corridors in eastern Canada, and what represents part of the western North Atlantic blue whale wintering, and possibly breeding or calving, area in and off the mid-Atlantic Bight. Our results confirm the extension of some key summer feeding areas into the fall, identify new ones, and provide evidence for sporadic foraging outside of the feeding season in this population. Finally, our study highlights underwater seamounts and other deep ocean structures as potentially important habitat for blue whales, and emphasizes the large scale (i.e., many thousands of square kilometers) one needs to consider for addressing conservation issues for this population.

Aires d’hivernage, mouvements automnaux et sites d’alimentation de rorquals bleus suivis par satellite dans le nord-ouest Atlantique

RÉSUMÉ

Le rorqual bleu (*Balaenopterus musculus*) est un cétacé qui se déplace sur de grandes distances et qui se retrouve dans tous les océans du monde, occupant des habitats côtiers autant que hauturiers. Dans l’Atlantique Nord, nous en savons peu sur la distribution et la structure génétique du rorqual bleu, et l’appartenance des animaux trouvés dans les eaux de l’Islande, des Açores, du nord-ouest de l’Afrique et du Nord-Ouest Atlantique à une seule et même population demeure incertaine. Dans le nord-ouest Atlantique, les mouvements saisonniers des rorquals bleus et leur utilisation de l’habitat, incluant l’emplacement des aires d’hivernage et de reproduction sont peu connus. Dans le cadre de la présente étude, nous avons utilisé la télémétrie satellitaire pour suivre les mouvements saisonniers de 24 rorquals bleus de l’est du Canada.

Nous présentons les premières données sur la migration saisonnière complète d’un rorqual bleu du nord-ouest Atlantique. Nous localisons les corridors de transit, et ce qui représente une partie de l’aire d’hivernage et possiblement de reproduction et d’élevage des rorquals bleus, dans et au large du mid-Atlantic Bight. Nos résultats confirment l’extension de certains habitats d’été clés dans la période automnale, en identifient de nouveaux, et procure des évidences d’une alimentation sporadique en dehors de la saison d’alimentation chez cette population. Finalement, notre étude met en lumière les chaines de montagnes sous-marines et autres structures géologiques des océans profonds comme des habitats potentiellement importants pour les rorquals bleus, et souligne la vaste échelle (c.-à-d., plusieurs milliers de kilomètres carrés) qui doit être considérée pour adresser les problématiques de conservation de cette population.

INTRODUCTION

The blue whale (*Balaenopterus musculus*) is a wide-ranging cetacean that can be found in all oceans, inhabiting coastal and oceanic habitats (Schoenherr 1991; Fiedler et al. 1998; Rice 1998; Sears and Calambokidis 2002). In the North Atlantic, blue whales belong to the subspecies *B. m. musculus*, but little is known about their distribution and genetic structure. Stranding and sighting data indicate a distribution ranging from Iceland, Spitzbergen and Davis Strait, south to New England, the Caribbean, and West Africa (Senegal, Mauritanious, Canary Island and Cape Verde) (reviewed in Sears and Larsen 2002; Sears and Calambokidis 2002). However, the interconnection between these areas of potential aggregations remains largely unresolved. Early whalers believed that there were two populations in the North Atlantic (Ingebrigtsen 1929). The IWC never adopted this view and recognizes a single North Atlantic population (Donovan 1991).

Photo-identification studies have confirmed that blue whales seen during the ice-free period in eastern Canada and eastern US belong to the same population (Sears and Calambokidis 2002), and the re-sighting of a blue whale from eastern Canada in West Greenland (Sears and Larsen 2002) supports the view that this stock could also include individuals from Davis Strait (Jonsgård 1955; Ingebrigtsen 1929). However, whether blue whales found in Icelandic waters, the Azores, or East Africa and those from the Northwest Atlantic are part of the same populations is unknown. The photo-identification data suggest a low degree of mixing between western and eastern North Atlantic blue whales (Ramp and Sears 2013; Sears and Calambokidis 2002). Recent satellite telemetry data from a few blue whales tagged in the Azores also have failed to support movements across the North Atlantic (Silva et al. 2013). Currently, Northwest Atlantic blue whales are considered as a separate population under the Canadian legislation, and are listed as *Endangered* under the Species at Risk Act since 2005.

Like other baleen whales, blue whales are considered capital breeders, provisioning their offspring using energy stores accumulated earlier (Houston et al. 2007). This characteristic allows for the theoretical separation of feeding and breeding areas, with seasonal movements in baleen whales occurring typically between productive feeding areas at high-latitude in summer, and oligotrophic calving and mating areas of tropical or sub-tropical regions in the winter (Kellogg 1929; Norris 1967). In the Northwest Atlantic, seasonal movements of blue whales and habitat use, including the location of breeding and wintering areas, are poorly understood (Lesage et al. 2007; Ramp and Sears 2013). Based largely on photo-identification studies, the summer distribution of blue whales in the Northwest Atlantic likely extends from the Gulf of Maine, USA to the Davis Strait off western Greenland (Wenzel et al. 1988; Sears et al. 1990; Sears and Larsen 2002). Although data are extremely sparse, stranding and whaling reports suggest that winter range may extend as far south as the Caribbean and the Gulf of Mexico in the western Atlantic. Occasional winter sightings and early spring ice entrapment reports suggest that some individuals may remain in eastern Canadian waters throughout the winter (Sears and Williamson 1982; Dickinson and Sanger 1990; Clark 1995; Sears and Calambokidis 2002; Stenson et al. 2003; Reeves et al. 2004; Gagné et al. 2013). Blue whale vocalizations have been detected near the Mid-Atlantic Ridge during this period, suggesting some individuals migrate to the central Atlantic although it is unknown if these whales originated from the east, west or both (Nieukirk et al. 2004).

Data available to understand the distribution, movement patterns and habitat use of blue whales in the Northwest Atlantic have been acquired through photo-identification of individuals in coastal waters that can be reached by small boats. The vast majority of efforts were concentrated in the St. Lawrence Estuary and northwestern Gulf of St. Lawrence during the summer and early fall. As a result, summer feeding areas have been generally well described

for this sector of their summer range (Ramp and Sears 2013; Doniol-Valcroze et al. 2007; 2011). However, information is generally lacking for other parts of their summer range, and in other seasons (but see Whitehead 2013; Stenson et al. 2003).

In this study, we use satellite telemetry to track the seasonal movements of blue whales from eastern Canada, identify key foraging areas, transiting corridors, and what may constitute part of their winter breeding and calving areas.

MATERIALS AND METHODS

DATA COLLECTION

Platform terminal transmitters (PTTs or tags) were attached to 24 blue whales between 30 August and 18 November in 2002, and 2010-2015 (except 2011). Deployment locations were off the Gaspé Peninsula in the Gulf of St. Lawrence (GSL), and at various sites in the St. Lawrence Estuary (SLE) (Figure 1). All recent deployments involved SPOT5 location-only Argos PTTs in the LIMPET configuration (Wildlife Computers, Redmond, WA); the single deployment made in 2002 was made using a custom-designed implantable PTT (Sirtrack, Havelock North, NZ) inserted into a 16-18 cm long casing made of surgical cement and surgical steel. Tags were fastened onto the tip of a carbon-fibre arrow using a quick-release mechanism, and discharged from a distance of 4 to 7 m using either a crossbow (in 2002), or a CO2-injection rifle with adjustable pressure (JM Special 25 model, DAN-INJECT, Børkop, Denmark) (in 2010-2015). Recent tags were designed to be inserted into the dorsal fin, whereas the 2002 model was made to anchor into the blubber. Accordingly, the implantation system for the SPOT5 PTTs consisted of two titanium prongs, each with 6 backwards-facing petals, which penetrated a maximum of 7 cm into the skin and blubber to avoid anchoring into the muscle tissue if the dorsal fin was missed. The implantation system for the 2002 PTT also included a quick release system on impact, but consisted of two actively sprung plates and a circle of passively deployed petals to implant into the skin and blubber, often resulting in a third of the tag remaining outside the whale. These tags were attached near the shoulders of whales to increase exposure to passing satellites. All tagged whales were photo-identified using their pigmentation patterns (Sears et al. 1990) and compared to a catalogue of known individuals from the northwest Atlantic that was built over a 37 year period (R. Sears, Mingan Island Cetacean Study, MICS). Sex was available for some of the whales as a result of an ongoing tissue sampling program (R. Sears, MICS).

In 2002, tags were duty cycled to transmit every other day; all other tags were programmed to transmit on a daily basis, every hour of the day, and up to a maximum of 300 messages per da. All other tags were programmed to transmit on a daily basis, every hour of the day, and up to a maximum of 300 messages per day at a repetition rate of 15 s. Raw location data were processed using the Argos service positioning algorithm based on a multiple model Kalman filter (least-square algorithm for the 2002 tag), which enhances the number and accuracy of positions retrieved, especially when the number of messages per satellite pass is low (Lopez et al. 2014; Silva et al. 2014).

SWITCHING STATE-SPACE MODEL

The behaviour of remotely-monitored animals can be inferred from a time series of location data. This is because animals tend to demonstrate stochasticity in their movement paths as a result of spatial variation in environmental characteristics, such as topography or prey density (Curio 1976; Gardner et al. 1989; Turchin 1991; Wiens et al. 1993), Predators are expected to decrease travel speed and/or increase turning frequency and turning angle when a suitable

resource, e.g., food patch, is encountered (Turchin 1991), otherwise known as area-restricted search (ARS). In contrast, animals in transit or travelling tend to move at faster and more regular speeds, with infrequent and smaller turning angles (Kareiva and Odell 1987; Turchin 1998).

To assess movement and behaviour of blue whales, we applied a Bayesian switching state-space model (SSSM) to Argos-derived telemetry data (Jonsen et al. 2005; Jonsen et al. 2013). A SSSM essentially estimates animal locations at fixed time intervals, movement parameters, and behavioural modes. A first-difference correlated random walk (DCRW) is used to model movement dynamics by assigning a distinct DCRW equation to two discrete behavioural modes, and allowing movement parameters to switch between each mode (in this case, transiting and ARS). Each DCRW mode differs in its values of mean turning angle (theta θ) and move persistence (gamma γ; autocorrelation in speed and direction). A Markovian process model then describes the evolution of behaviour (b) through time by estimating the probability of switching states from transiting at time *t* to ARS and time *t + 1* (Jonsen et al. 2013). By using Bayesian inference, two important sources of uncertainty can be measured separately: the estimation error resulting from inaccurate observations (Argos location error), and the process variability related to stochasticity in the movement process (behavioural mode estimation) (Jonsen et al. 2003; Patterson et al. 2008).

SSSMs can also be implemented under a hierarchical framework (hSSSM), by assuming individuals are 'samples' from a population, or that their movement and behaviour parameters come from a common distribution (Jonsen et al. 2003; Jonsen et al. 2006; Mills Flemming et al. 2010). The advantage of this approach is to reduce uncertainty of parameter estimates at the individual level by simultaneously evaluating location information from multiple individuals of a population (Morales et al. 2004; Jonsen et al. 2006). The process model of the hSSSM (Jonsen et al. 2007) can be formulated as follows:

$$d_{t,k} \sim N_2\,(\gamma_{bt,k} T(\theta_{bt,k}) d_{t-1,k}, \Sigma)$$

Where *k* represents each individual whale, $d_{t,k}$ is the displacement of whale *k* from unobserved location x_t to x_{t-1}, and $d_{t-1,k}$ is the displacement of whale *k* between unobserved locations x_{t-1} and x_{t-2}. The transition matrix T(θ) specifies the rotation required to move from d_{t-1} to d_t, where θ is the mean turning angle. *γ* is the move persistence coefficient (combined autocorrelation in direction and speed). N_2 is a bivariate Gaussian distribution with covariance matrix Σ, representing the variability in animal movement. The behavioural mode b_t is a continuous variable ranging from 1 to 2, and is indexed by combining parameters θ and γ (Morales et al. 2004). Behavioural mode estimates closer to 1 are indicative of transiting, while values close to 2 represent ARS. Values at b = 1.5 are considered uncertain, or without sufficient information to clearly distinguish behaviours (Jonsen et al. 2005). Some studies have adopted conservative cut-off values to readily bin behaviour, where mean estimates of $b \geq 1.25$ represent transiting, $b \geq 1.75$ ARS, and values between are unclassified.

For the hSSSM analysis, only individuals with a minimum of three PTT days were retained for the hSSSM analysis. Tracks with PTT days under this threshold, and with temporal gaps in positional data in excess of 4 days resulted in poor model fit. In order to keep a maximum of information, and reduce uncertainty for the days without position data, tracks with data gaps > 4 days were split into two or more sub-tracks.

Priors used on movement parameters are similar to previous studies (Bailey et al. 2009; Jonsen et al. 2013; Kennedy et al. 2014; Silva et al. 2013; Prieto et al. 2014), and assume that during transiting, turn angles should be closer to 0° and autocorrelation in speed and direction should be higher than during ARS. Blue whale locations and movement parameters were interpolated at a regular time step adapted to the temporal resolution of the data. The hSSSM ran two

parallel MCMC chains each comprised of 180,000 iterations. The first 100,000 samples were discarded as a burn-in, and the remaining samples were thinned by retaining every 15th sample to reduce sample autocorrelation. Thus model parameters were estimated using a total of 4000 samples from the joint posterior distribution. Convergence and sample autocorrelation were assessed by visually inspecting trace and autocorrelation plots. The effect of changing the time step for estimating location and movement patterns on the performance of the hSSSM, including the location and number of ARS areas, percent positions assigned as uncertain, in ARS or in transit, was examined.

The R package *bsam* was used to fit the hSSSM (code available from Jonsen et al. 2013) via an MCMC sampler executed in JAGS 3.1.0 (Just Another Gibbs Sampler, created and maintained by Martyn Plummer; http://mcmc-jags.sourceforge.net).

Potential foraging areas were identified using the locations for which the hSSSM predicted ARS behaviour. The beginning of an ARS behaviour was defined as three or more successive locations assigned a mean behavioural mode $b \geq 1.75$, and ending with three consecutive locations of $b < 1.75$ (Bailey et al. 2009). An ARS area was defined by the estimated locations in ARS mode, including a buffer around the line connecting these estimated locations. Buffer size was set using a radius of 8.35 km, equivalent to the average error associated with Class B positions, which constituted the majority (83%) of our dataset. The location, number and duration of use of ARS areas were determined for each individual track and for all tracks combined to give an estimate of population-level ARS dynamics in the study area. Relationships between these variables were examined using linear models and in case where non-linear patterns were detected, using generalized additive mixed models using individual whale as a random effect. Mean swimming speed associated with the two behavioural modes was calculated as the distance (km) between successive hSSSM-estimated locations at the chose time step (4 h or 6 h) divided by the time step.

We defined departure of whales (n = 21) from the SLE and GSL as a consecutive period ≥ 48h of hSSSM-predicted travelling (or transiting) behaviour (i.e. b-values ≤ 1.25). This was validated by visual inspection of track lines. Our definition of departure differed slightly from Silva et al. (2013) due to the nature of our study area. For example, Silva et al. (2013) defined departure as the “first of ≥ 48 consecutive hours with the whale travelling at speeds higher than the median ARS speed estimated from all whale tracks”. Taking the *first* of ≥ 48 h of consistent travelling behaviour in our case did not always represent departure as some whales travelled for 48h to reach a distant ARS (foraging) patch within the ESGL. Secondly, we chose to use hSSSM-predicted b-values instead of speed to define travelling behaviour since b-values represent the combination of turning angle and autocorrelation in direction and speed.

RESULTS

SUMMARY OF DEPLOYMENTS AND MODEL PERFORMANCE

Twenty-three of the 24 blue whales equipped with Argos satellite transmitters successfully provided location data (Table 1; Figure 2). Of the tagged whales, 16 were individuals of known sex, including an equal number (i.e., 8) of males and females. The delay period from tagging to first position received ranged from 0 to 34 days. Twelve tags began transmitting positions on the day of deployment. Except for one individual that provided positions for 6 mo (177 d), tag longevity (from tagging day until day of last position received) was of 70 d or less for the other PTTs, with a median longevity of 23 d (Table 1).

Despite some irregularity, location data were received on average (± SD) every 3.2 ± 7.1 h (median = 1.5 h) when considering only tracks retained for the hSSSM analysis (Table 1).

Occasional time gaps of 1 to 21 d were documented. The mean (± SD) number of positions received per day was 7.3 ± 3.5. A total of 4,782 valid Argos locations were received from the 23 tags; the majority was classified as low quality (83% B, 8% A; S1). Class B locations were estimated using an average (± SD) of 1.2 ± 0.4 satellite messages, while class A locations were estimated based on 3.0 ± 0.1 messages on average. No qualitative relationship was found between tag placement on body and tag longevity, fixes per day or location quality (not shown).

The hSSSM was run on a total of 24 tracks from 21 individual blue whales. Since 7.3 locations were received on average each day, and given the variance (SD = ± 3.5), the hSSSM was run using a 4 h and 6 h time step to compare classification of behaviour modes. Overall, the state-space model included a few Argos locations on land. However, given the local topography, where waters deeper than 100 m can be found relatively close to shore, the narrowness of the SLE (ca. 25-45 km wide), and generally low quality of Argos locations, some locations remained on land even post-analysis. We presented hSSSM-estimated locations as is, to illustrate how the model processed locations (Figure 3). The absence of overlap in the marginal posterior distributions of the movement parameters between ARS and transiting modes indicates the hSSSM was successful in distinguishing among movement classes. There was a clear contrast for turning angles (θ) and autocorrelation in speed and direction (γ) between blue whales presumed to be transiting and performing ARS movements (Figure 4). Swimming speeds were significantly lower during ARS behaviour (1.4 ± 1.3 km/h) than during transiting (5.9 ± 2.6 km/h) (Mann-Whitney Wilcoxon test, W = 80592, $p < 0.001$). Based on hSSSM-derived positions, the mean travel distance of tagged whales was 1832 ± 2932 km (range 99 to 13630 km).

RESIDENCE, MOVEMENTS AND MODEL PERFORMANCE

The short retention time of PTTs (i.e., < 3 mo for all but one PTT) and concentration of tagging sites in the Estuary and northwestern Gulf of St. Lawrence resulted in a large portion of the behavioural estimations and local movements being documented for the fall period, and in this portion of the study area (Figure 3). However, two PTTs that transmitted positions for more than 2 and 6 mo allowed us to document behavioural parameters and migratory movements through the winter and early spring (Figure 3). Movement behaviour for each whale is presented in detail as part of the supplementary material (S2 and S3).

Of the 21 whales used for the hSSSM analysis, departure date from the SLE and GSL was successfully determined for 10 whales. For the remaining 11 whales, tag transmission ceased prior to departure. Of the 10 whales where departure time was established (observed event), all had left the GSL by 18 December.

Generally, once blue whales departed from the SLE and northwestern GSL, their fall movements were southward, with all migrating individuals exiting via Cabot Strait. Of the 23 transmitting whales, only 5 continued to transmit positions outside of the SLE and GSL. Movements extended to areas south of Newfoundland, including the Grand Banks, the Scotian Shelf and the continental shelf edge, where ARS behaviour was documented (Figure 5). Two additional individuals stopped transmitting within the Laurentian Channel, about 200-300 km before reaching the shelf edge (Figure 2, S3).

During the fall migration, two adult females (B244 and B197) tagged in different years transited south through the continental shelf off Nova Scotia, to offshore areas north-east of the underwater New England Seamount chain in waters over 5,000 m deep. The two females proceeded west towards the eastern U.S. continental waters, although one of the females (B244) turned around and moved back within 20 km of the southeast coast of Nova Scotia in mid-December, before reappearing in the continental waters of the eastern U.S. in late December, after a 12-d gap in transmissions (Figure 5).

Between late December and mid-February, movements of these two females extended in and off the mid-Atlantic Bight from Delaware to North Carolina (B197) and South Carolina (B244) (Figure 6). B197 generally remained in waters hundreds of kilometers from the U.S. continental shelf and mid-Atlantic Bight until its last transmission on 30 January 2016 (Figure 6). However, this was not the case for B244, which, after spending 11 days in late December approximately 360 km east of Delaware in the mid-Atlantic Bight, moved southeast along the edge of the Hudson Canyon (a submarine canyon that originates from the Hudson River estuary and extends 640 km seaward across the continental shelf), and then back northwest along a parallel canyon, all the way to within 40 km of Delaware Bay. The whale then spent some time off Pamlico Sound in North Carolina, the largest lagoon on the east coast of the USA. Pamlico Sound is separated from the Atlantic Ocean by the Outer Banks, a long, thin barrier of low-lying sandy islands, including Cape Hatteras. B244 continued moving south along the coast until Jan 16 before heading more offshore to the continental shelf edge, to then followed the continental shelf back north to within approx. 45 km east of Cape Hatteras on Jan 23. Following 21 days of silence, the tag re-transmitted locations on Feb 12 from the continental shelf, approximately 400 km east of Charleston, South Carolina, the southernmost location reached by this female. The return journey was made northeasterly, roughly staying parallel to the south-bound route, but farther offshore, between 60 and 200 km from the continental shelf break. After remaining in U.S. waters for approximately 2 mo, i.e., to approximately mid-February, the animal moved back to the Canadian continental waters and headed to the entrance of the SLE and GSL, which it reached by mid-March. B244 then turned around almost immediately, likely as a result of heavy ice coverage in Cabot Strait, and returned to the areas north of the New England Seamounts where the whale remained until the tag stopped transmitting on May 1 2015 (Figure 6). B244 was photographed again in the SLE and GSL the following summer, i.e., in September 2015 (R. Roy, contributor to MICS database, Unpublished data).

AREAS OF RESTRICTED SEARCH

Whale (n = 21) behaviour interpolation at 4h and 6h time steps resulted in similar proportions of estimated hSSSM locations being attributed to ARS (57 vs 58%) and transit (23 vs 22%) modes, or as being uncertain (21 vs 20%) (3773 and 2406 locations in total, respectively; Table 2). However, the 4-h time step resulted in a slightly larger number of ARS zones being identified compared to the 6-h time step (75 vs 70) and so the shorter time step was used in subsequent analyses. When considering only tracks within the SLE and GSL, the proportion of estimated hSSSM locations allocated to ARS mode was 70%, with 13% of locations being allocated to transiting mode, and 17% of locations being considered as uncertain behaviour (n locations = 2554; see S3 for individual hSSSM tracks). Outside of the SLE and GSL, there were more hSSSM locations considered in transit than in ARS mode (43% vs 28%, for n = 5 individuals).

Interpreting inter-annual differences in the proportion of time spent in each behavioural mode would not have been appropriate given low annual sample sizes (i.e. n=1 in 2002, and n = 2 in 2010 and 2014). When pooling data from all individual whales per month, the percentage of hSSSM locations in ARS behaviour remained relatively stable and above 50 to 60% on average between September and November. However, the percentage of ARS behaviour declined drastically to less than 30% between December and February, with a reversed trend observed for transiting mode (Figure 7). ARS behaviour persisted throughout the winter to reach a minimum in February, and increased again to 27 and 38% in March and April, respectively. This type of behaviour was associated with the New England seamounts, as well as underwater canyons and the U.S. shelf edge (Figures 3 and 5). Transiting was the predominant behaviour in February with 71% of the estimated hSSSM locations, and represented generally above 40% of the locations between December and April. Within the SLE and GSL, i.e., prior to migration,

females (n = 7) spent a greater proportion of their time in ARS than males (n = 8; F: 0.81 ± 0.19 vs M: 0.55 ± 0.23; Kruskal-Wallis χ^2 =3.88, p = 0.04).

A total of 75 ARS patches were identified from the 21 individuals using the 4h time step, including 31 within the Lower SLE (comprising n = 14 individuals), 8 patches within the northwest GSL (NWG; n = 4), 16 within the mid-GSL (n = 10), and 20 outside of the SLE and GSL system (n = 4) (S3 and S4, Figure 5). Within the SLE and GSL, time spent within ARS patches and patch area (km^2) did not vary significantly with year (Kruskal-Wallis rank sum tests comparing mean time spent within ARS patch between years: chi-squared = 2.115, df = 5, p-value = 0.83; means of ARS patch area between years: chi-squared = 2.033, df = 5, p-value = 0.845). Years were thus combined for subsequent analyses. There was a significant positive relationship between time spent in an ARS patch (delta_d) and patch area (Generalized linear mixed model with random intercepts for 'individual' and a log-linked Gaussian probability distribution; delta_d: β = 0.01, SE = 0.01, p < 0.001). The largest ARS patches were located in the Lower SLE (1534 ± 1084 km^2, median 1371 km^2) and in the NWG (1743 ± 1248 km^2, median 1729 km^2). In these regions, whales spent on average 6.7 ± 8.9 d (LSLE, median 3.3 d) and 4.5 ± 3.4 d (NWG, median 4.3 d) per ARS patch. In general, ARS areas in the SLE and GSL overlapped between years, included tagging locations, and except for ARS areas outside of the SLE and GSL, were defined based on ARS behaviour from more than one individual whale (Figure 5).

Within the SLE and GSL, ARS areas were mainly located in the Lower SLE, extending from the confluence of the Saguenay River east to Baie-Comeau along the north shore, and to Matane/Les Méchins/Cap Chat area along the south shore, and including the Anticosti Gyre. Additional ARS areas were located along the coast of the Gaspé Peninsula east of Rivière-au-Renard, off, and south of, the tip of the peninsula (e.g., the American Bank, and the area north of Bonaventure Island), in the offshore area east of Baie-des-Chaleurs (Orphan Bank area and Shediak Valley), as well as approximately 70 km northwest of the Magdalen Islands. Outside of the SLE and GSL, ARS areas used during the autumn came from three whales and three different locations, i.e., the continental shelf edge of the Grand Banks, 400-500 km southeast of Newfoundland, the shelf edge of the Scotian Shelf, and an area located 400-850 km southeast off Nova Scotia, north and northeast of the New England Seamount chain (Figure 5). Patches of ARS behaviour outside of the fall period came from two whales, which performed ARS behaviour in January on or off the shelf break in the Cape Hatteras region in North Carolina or off Delaware, and either south or north and northeast of the New England Seamount chain (Figure 3). ARS in the latter region occurred both in late fall – early winter, as well as in April and early May when the tag stopped transmitting.

Within the SLE and GSL, there was no trend in the time spent within ARS patches over the course of a season, either when considering all years separately (all Adjusted R^2 < 0.386, all p > 0.157) or in combination (R^2: 0.004, p: 0.279). There was also no significant trend in the size (km^2) of ARS areas over the course of a season either when considering all years separately (all R^2 < 0.356, all p > 0.171) or in combination (R^2: 0.001, p: 0.823).

DISCUSSION

Tagging blue whales late in the summer allowed for examining their movement patterns and habitat use during the fall season. The short duration of most deployments resulted in most areas being confined to the SLE and GSL. Areas with extended periods of ARS behaviour (7 days and over) were considered to have foraging value for blue whales (Figure 5). Several of these areas have been previously identified as summer feeding areas using 30+ years of observational effort and radio-telemetry data (Doniol-Valcroze et al. 2011; Ramp and Sears

2013). However, other zones such as those located several tens of kilometers off the Gaspé Peninsula and Baie des Chaleurs (Orphan Bank, Shediak Valley or the sector located north of the Magdalen Islands) are newly identified potential foraging locations for blue whales in the SLE and GSL. ARS behaviour also occurred in various other locations distributed along the continental shelf edge off Nova Scotia and the Grand Banks, suggesting they may also represent potential foraging locations for blue whale. These areas have in common abrupt changes in topography (steep slopes). This type of habitat is known to be favorable to krill aggregations (Simard et al. 1986; Genin 2004; McQuinn et al. 2015).

In the SLE and GSL, the large-scale physical and biological processes contributing to the formation of dense krill aggregations are relatively well understood and involve a combination of topographic forcing of surface circulation, temperature and salinity gradients, and vertical migratory behaviour of krill (Simard et al. 1986; Maps et al. 2014; Plourde et al. 2014; McQuinn et al. 2015; Maps et al. 2015). Areas where blue whales spent several days in ARS coincided with the occurrence of large and recurrent krill aggregations (Simard and Lavoie 1999; Lavoie et al. 2000; Sourisseau et al. 2006; McQuinn et al. 2015). These areas included the SLE, a sector north of Pointe-des-Monts, the north coast of the Gaspé Peninsula (Gaspé Current), and the area off Gaspé and Baie-des-Chaleurs. Krill aggregations were found mainly along the slope waters of the Laurentian Channel for all regions surveyed in the SLE and GSL, but also within shelf habitats (depth < 100 m) where biomasses were dominated by *T. raschii.* Satellite-tagged blue whales were often associated with slope habitats along the Laurentian Channel in the SLE and GSL, and their use as foraging areas is corroborated by a study in the SLE where blue whale feeding attempts were monitored using archival tags and documented in these slope habitats (Doniol-Valcroze et al. 2012).

Substantial krill concentrations have also been reported off the west coast of Newfoundland (McQuinn et al. 2015), although none of the tagged blue whales spent time in this part of the GSL. This may be due to temporal offset between the period of krill surveys (June and August) and when blue whales were tagged (Sept to Nov). Likewise, large biomasses of krill have been identified in the Jacques Cartier Strait (between Anticosti Island and the Quebec north shore; McQuinn et al. 2015), but no blue whales in this study engaged in ARS behaviour there. This area was formerly visited by blue whales on an annual basis (1979 to ~1992), although few sightings have been reported since the early 1990s (Ramp and Sears 2013). This may be partly explained by the physical environment of the region; areas in the GSL with limited topographic discontinuities and strong surface circulation like the Jacques Cartier Strait and the wide shelf area along its north shore, show greater variation in terms of number, size and location of krill patches (Maps et al. 2015). Other regions such as the SLE or Gaspé area, may provide better foraging conditions with predictably high krill densities and biomasses.

The limited satellite tagging data provided no support for movements across the North Atlantic although samples sizes were very small. Tracking of only two individuals to their wintering areas was insufficient for inferring winter distribution of the population, or for concluding unequivocally the existence of a northwest Atlantic population. Two individuals undertook a north-south migration in northwest Atlantic waters; deployment duration for the other five whales tracked outside the SLE and GSL was too short to determine where they were heading for the winter. Winter reports from different areas of the Estuary and northern GSL, the southern and southwestern Newfoundland (St. Georges Bay), and acoustic recordings of blue whales on the Grand Banks, Newfoundland, indicate that a portion of the population remains in Canadian waters throughout the year (Lawson and Gosselin 2009; Lavigueur et al. 1993; Clark 1995; Mitchell 1975; Sears and Calambokidis 2002; Sears and Williamson 1982; Sergeant 1982; Stenson et al. 2003). However, termination of satellite transmissions before the winter period in

all but two individuals prevented us from substantiating these anecdotal observations, and determining the proportion of the population these individuals represent.

However, the tagging data provided the first insights into what may constitute a wintering area, and possibly a breeding area, for at least some blue whales in the northwest Atlantic. The two individuals tracked over their full migration south, two females, spent nearly two months in and off the mid-Atlantic Bight, in waters 40 to 400 km off the U.S. coast, between Delaware and South Carolina. The influence of the Gulf Stream is strong in this area, providing warm water habitats throughout the year. During this period, the behaviour of the two females was considered mostly either as in transit or uncertain, with occasional ARS behaviour in canyons or off shelf edge areas (Figure 3, S3). Data to document the winter distribution of blue whales in the northwest Atlantic are fragmentary, and come from two strandings of blue whales reported from the Gulf of Mexico (Baughman 1946; Lowery 1974), one blue whale killed near the eastern entrance to the Panama Canal (Harmer 1923), and one blue whale individual acoustically tracked south of Bermuda (Clark 1995). Based on sightings, catch and attempted catch data extracted from the 18th and 19th century whaling logbooks, Reeves et al. (2004) provided what constitutes the most exhaustive review of the potential wintering areas for blue whales in the North Atlantic. While 75 blue whale 'encounters' were used in their study, only a handful were made in the northwest Atlantic during the winter months, a period where whaling effort was spent mainly south of the Tropic of Cancer. Of the encounters reported by whalers between January and April, all were made off South Carolina down to southern Florida, and at distances that varied from a few tens to a few hundreds of kilometers from the continent (Reeves et al. 2004). These latitudes are comparable or south of the southernmost latitude reached by B244. The wide-ranging movements of the two adult females while in their wintering area, i.e., mostly transit or uncertain behaviour with only sporadic episodes of ARS, suggests a possibly diffuse and relatively large wintering habitat for this population.

The return journey of B244 was undertaken in early-March, when the whale travelled northeast within the Gulf Stream, to waters off Nova Scotia. The whale then attempted to enter the GSL via Cabot Strait but turned around, heading southeast to the New England Seamount chain area where it remained until transmissions stopped in early May. The extensive ice coverage (9/10) present in mid-March likely blocked the entrance to the GSL or acted as a deterrent (Canadian Ice Service of Environment Canada: www.ec.gc.ca/glaces-ice/). In fact, the winter of 2014-2015 broke a 30-year record for thickness of sea-ice in the GSL. The timing of entry attempt corroborates previous observations reporting blue whales in the GSL soon after the ice break up in late-Mach, early April (Lien et al. 1987; Sears et al. 1990). Early entry into the GSL may also account for the numerous records of blue whale entrapments in sea ice along the south and west coasts of Newfoundland at this time of year (reviewed in Stenson et al. 2003). As an example, at least nine blue whales were reported dead in this area at the end of March 2014 (J. Lawson, DFO Newfoundland-Labrador, Unpublished data).

ARS behaviour was documented in the two adult females during winter months while they were in or off the mid-Atlantic Bight (Figure 3 and 5, S3). While ARS behaviour can result from behaviours other than foraging, their association with structures that may result in upwelling such as canyons and the U.S. shelf edge suggests they reflect foraging activity. The case of the New England Seamounts is not as clear; the whales performed ARS behaviour in proximity, but still at several tens of kilometers from this deep-ocean structure. Whether the ARS behaviour reflected foraging or another behaviour that involved slow displacement and high turning angles cannot be ascertain with the current data. Regardless, these results indicate that the classical depiction of a yearly cycle in these capital breeders, where feast and famine alternate as the animals move from their feeding to breeding areas, may be in need of revision. Our limited data indicate a migration out of the feeding area (the SLE and GSL) by late November to mid-

December. If the sustained ARS behaviour observed near the New England seamounts in mid-March is indeed foraging, this would indicate a period of famine shorter than previously assumed, of the order of 3-4 months, and characterized by what looks like episodic foraging. There is mounting evidence that baleen whales take advantage of locally abundant food resources outside their typical foraging grounds (Mate et al. 1999; Reilly et al. 1990; Silva et al. 2013 and references therein). For instance, recent studies in the northeastern Pacific have documented ARS behaviours in blue whales throughout their migratory cycle (Bailey et al. 2009). A study in the northeast Atlantic has documented extensive ARS behaviour in two of three blues whales during their spring migration (May-June) as they passed near the Azores on their way North towards their summer feeding areas (Silva et al. 2013).

Biological needs during different periods of the blue whale lifecycle may influence the need to migrate seasonally, with some individuals perhaps not migrating at all. The selective benefits of travelling great distances to warmer waters during the winter (around 2,600 km one-way in B244's case) may be to breed, to favor survival of newborn calves, or to optimize energy budgets by expending less energy to stay warm, while profiting from areas with some food resources (Corkeron and Connor 1999). Minimizing risks of ice entrapments may also be a driver of baleen whale migrations. In low ice years, it is plausible that resting or immature individuals may stay longer in the SLE and GSL, although more data are needed to examine this question. B244 did not take a direct, shortest-distance migratory route to the south. She meandered to areas with particular topographic features, such as the continental shelf break off Georges Bank, Massachusetts, the Hudson Canyon (part of the Hudson River drainage system) off New Jersey, other submarine canyons in the area off Chesapeake Bay, as well as coastal, shelf and pelagic/offshore areas around Cape Hatteras, North Carolina. These areas may have food available at this time of year.

The Cape Hatteras region, where B244 spent a month's time, represents a distinct biogeographic boundary, where the two great basins of the western Atlantic converge, and where mixing of water masses favors primary production (Lohrenz et al. 2002) and supports a diverse biological assemblage (Colvocoresses and Musick 1984; Sherman et al. 1998; Cook and Auster 2007; Gartner Jr. et al. 2008). Numerous cetacean species are found within the Cape Hatteras region during the summer (Hamazaki 2002), peaking in abundance around springtime (Hain *et al.* 1985). Minke whales have been acoustically detected in the southeastern US shelf break offshore region during the winter months, and may use this area for calving (Risch et al. 2014). Historically, North Carolina had a well-established shore whaling industry which took mainly right whales, although larger and faster whales such as blue whales were targeted in the second half of the 19th century (Reeves et al. 1999; 2004). Peak catches occurred between February and May, when whalers believed they were seizing whales migrating north (Reeves and Mitchell 1988). Some food availability, albeit likely in lower concentrations than on northern feeding grounds, together with warmer water temperatures, may offer an attractive combination for some blue whales during the winter months. The return migration within the Gulf Stream, which can have a maximum velocity of around 9 km/h flowing north-easterly (average 6.4 km/h) (NOAA 2014), may reduce energy expenditure before summer feeding grounds are reached (Risch et al. 2014).

The New England Seamount chain - the longest chain of submarine volcanos in the North Atlantic, harbours a rich deep sea biodiversity (Hogg 1992). The two adult females spent time in this area, possibly feeding given the detection of ARS behaviour, with B244 visiting this region twice within the same migratory cycle. These observations suggest that these seamounts may be important for blue whales, as suggested for other species. Reports of cetaceans spending time near similar deep-sea structures in the Pacific exist for humpback whales (Mate et al. 2007; Garrigue et al. 2015). In the Atlantic, a humpback whale on its migration south to its wintering

area performed ARS behaviour near the New England Seamounts (Kennedy et al. 2014). The purpose of ARS in these areas, and degree of habitat use by marine mammals warrant further investigation.

CONCLUDING REMARKS

This study summarizes a five-year satellite tagging effort to better assess the late summer-early fall foraging habitat for the endangered blue whale population in eastern Canada and to determine their winter distribution. The results presented in this study are of significance for several reasons. They provide the first record of the full winter migration of a blue whale from the Northwest Atlantic which, so far, does not support cross-Atlantic movements. They allow for the identification of transiting corridors, and what might represent part of their wintering and possibly breeding or calving area in and off the mid-Atlantic Bight. Our results also confirm the extension of some key summer feeding areas into the fall, identify new ones, and provide evidence for sporadic foraging episodes outside of the feeding season in this population. In addition, our study highlights underwater seamounts, canyons, and other deep ocean structures as potentially important habitats for blue whales from this population. Finally, it emphasizes the scale one needs to consider for addressing conservation issues, and need for dedicated survey efforts during winter time off the coast and continental shelf of the mid-Atlantic Bight to establish the importance of this habitat for blue whales.

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TABLES AND FIGURES

Table 1. Summary deployments for 24 blue whales equipped with ARGOS platform terminal transmitters (PTT) in the Estuary or Gulf of St. Lawrence, Canada. Horizontal lines separate tagging years. First and last loc: date of first and last Argos location received; Delay: no. of days between tagging and first position received; PTT lifetime: no. of days between tagging date and last location received; Total PTT d: no. of days positions were acquired; Valid loc: no. of non-Z location class positions; Loc/d: no. of locations received per day; Time step: median number of hours elapsed between received locations (for consecutive PTT days only).

PTT ID	Whale ID	Sex	Tagging date	First loc	Last loc	Delay	PTT lifetime	Total PTT d	Valid loc	Loc/d	Time step (h)
2002_36037	B276	M	2002-09-04	2002-09-04	2002-09-29	0	26	19	128	6.8	1.7
2010_100383	B391		2010-09-07	2010-09-11	2010-09-21	4	15	11	85	7.2	1.6
2010_100384	B434		2010-09-07	2010-09-07	2010-10-07	0	31	31	292	9.5	1.1
2012_106738	B320		2012-09-02	2012-09-02	2012-09-14	0	13	13	94	7.3	1.8
2012_106739	B161	M	2012-09-03	2012-09-03	2012-09-07	0	5	5	68	13.8	1.0
2012_100386	B324	F	2012-09-21	2012-09-24	2012-10-22	3	32	7	21	2.9	2.7
2012_100387	B311	M	2012-09-26	2012-09-26	2012-12-04	0	70	70	518	7.5	1.8
2012_100388	B122	F	2012-09-28	2012-09-28	2012-10-15	0	18	18	216	12.1	1.3
2013_106741	B378	M	2013-09-05	2013-09-05	2013-09-25	0	21	18	168	9.4	0.8
2013_106740			2013-09-05	NA	NA	NA	0	0	0	0.0	NA
2013_100386	B458		2013-09-26	2013-09-27	2013-10-11	1	16	15	127	8.0	1.3
2013_100389			2013-09-27	2013-10-01	2013-12-02	4	67	16	103	6.2	0.9
2013_106743	B166	F	2013-09-28	2013-10-15	2013-11-02	17	36	3	15	4.0	0.9
2013_106742	B347	M	2013-09-28	2013-09-29	2013-10-03	1	6	3	17	4.5	1.1
2013_106734			2013-09-28	2013-10-01	2013-10-07	3	10	3	24	6.3	0.8
2013_106737	B181	M	2013-10-01	2013-10-01	2013-10-25	0	25	16	87	5.5	1.7
2013_100388	B405		2013-10-15	2013-11-18	2013-11-22	34	39	2	2	1.0	457.2
2014_100383	B057	F	2014-10-21	2014-10-21	2014-11-12	0	23	23	181	7.9	0.9
2014_141343	B244	F	2014-11-04	2014-11-06	2015-05-01	2	177	131	759	5.8	2.1
2015_141346	B186	F	2015-08-30	2015-08-30	2015-09-17	0	19	19	151	8.1	1.7
2015_106741	B335	M	2015-10-06	2015-10-06	2015-10-28	0	23	22	279	12.8	1.2
2015_141344	B082	F	2015-11-03	2015-11-04	2015-12-01	1	29	28	244	8.7	1.6
2015_141349	B197	F	2015-11-03	2015-11-05	2016-01-29	2	88	86	1086	13.5	1.1
2015_141350	B120	M	2015-11-18	2015-11-18	2015-12-05	0	18	18	119	6.7	1.8

Table 2. Location and behavioural mode estimation using a hierarchical Bayesian switching state-space model with a 4h time step for 21 satellite tracked blue whales; n = number of tagged whales per year (note that 2 individuals each transmitted over two different years).

Year	n	Total locations	ARS locations	Transit locations	Uncertain locations	ARS %	Transit %	Uncertain %
2002	1	151	82	18	51	54.3	11.9	33.8
2010	2	261	199	27	35	76.2	10.3	13.4
2012	5	686	498	76	112	72.6	11.1	16.3
2013	6	603	361	68	174	59.9	11.3	28.9
2014	2	413	182	133	98	44.1	32.2	23.7
2015	6	1477	747	456	274	50.6	30.9	18.6
2016	1	182	65	79	38	35.7	43.4	20.9
Total		3597	2018	779	800	56.1	21.7	22.2

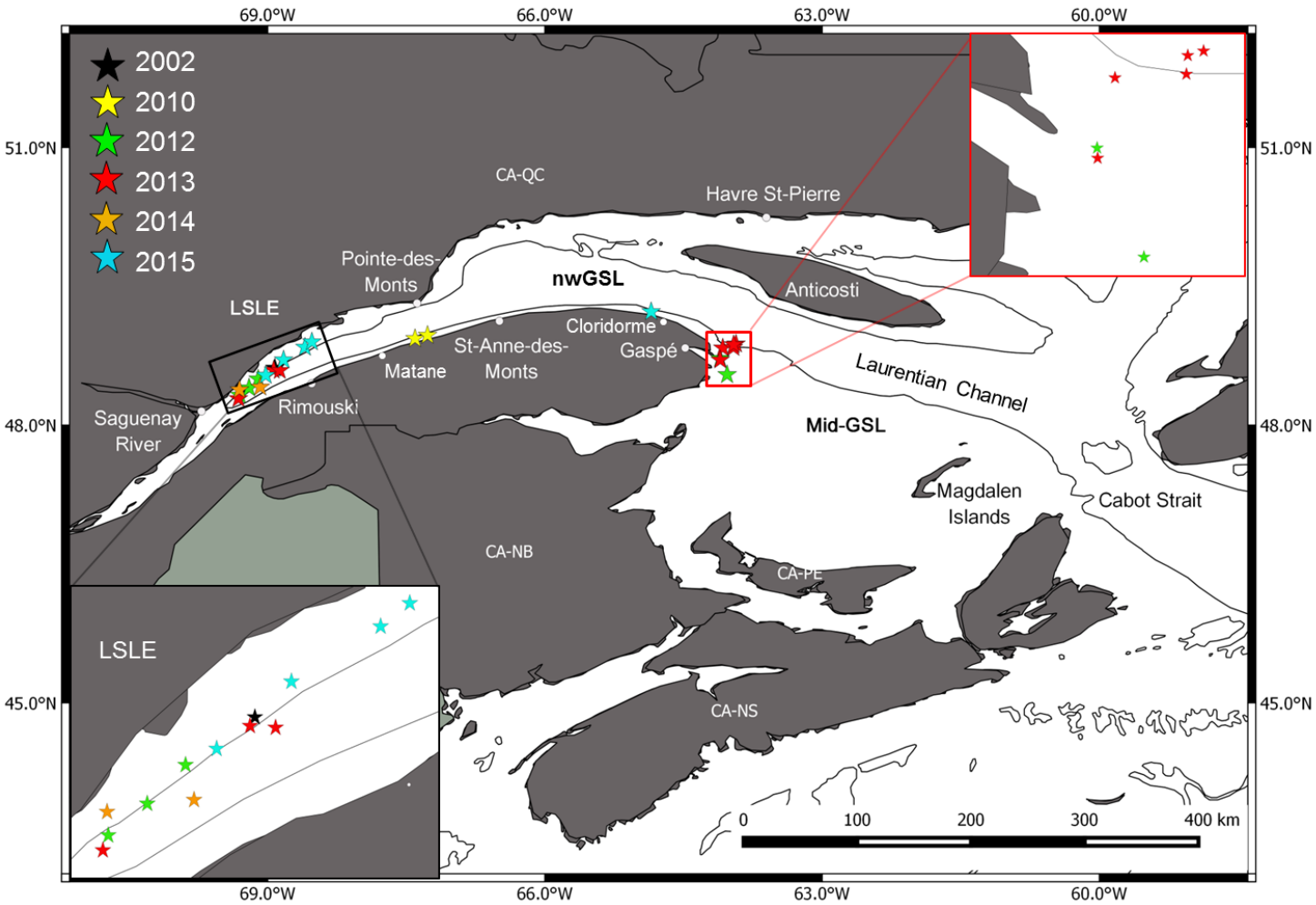


Figure 1. Tagging locations of 24 blue whales in the Estuary and Gulf of St. Lawrence in 2002, and from 2010 to 2015.

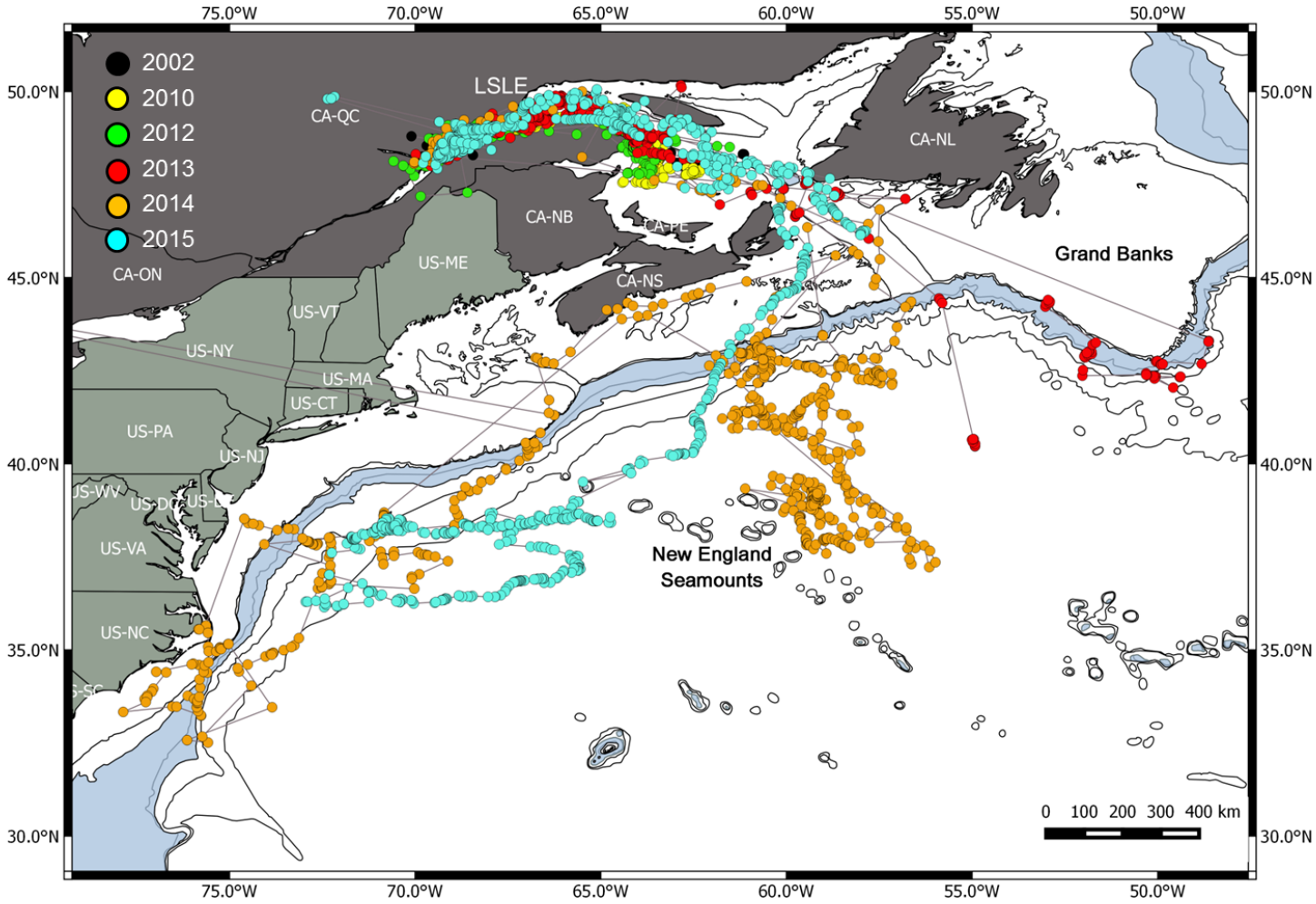


Figure 2. Argos raw satellite tracks from 23 blue whales tagged in the Estuary and Gulf of St. Lawrence, Quebec in 2002 (n = 1), 2010 (n = 2), 2012 (n = 5), 2013 (n = 8), 2014 (n = 2), and 2015 (n = 5). Shaded blue polygon depicts the continental shelf slope (depth 500–2500).

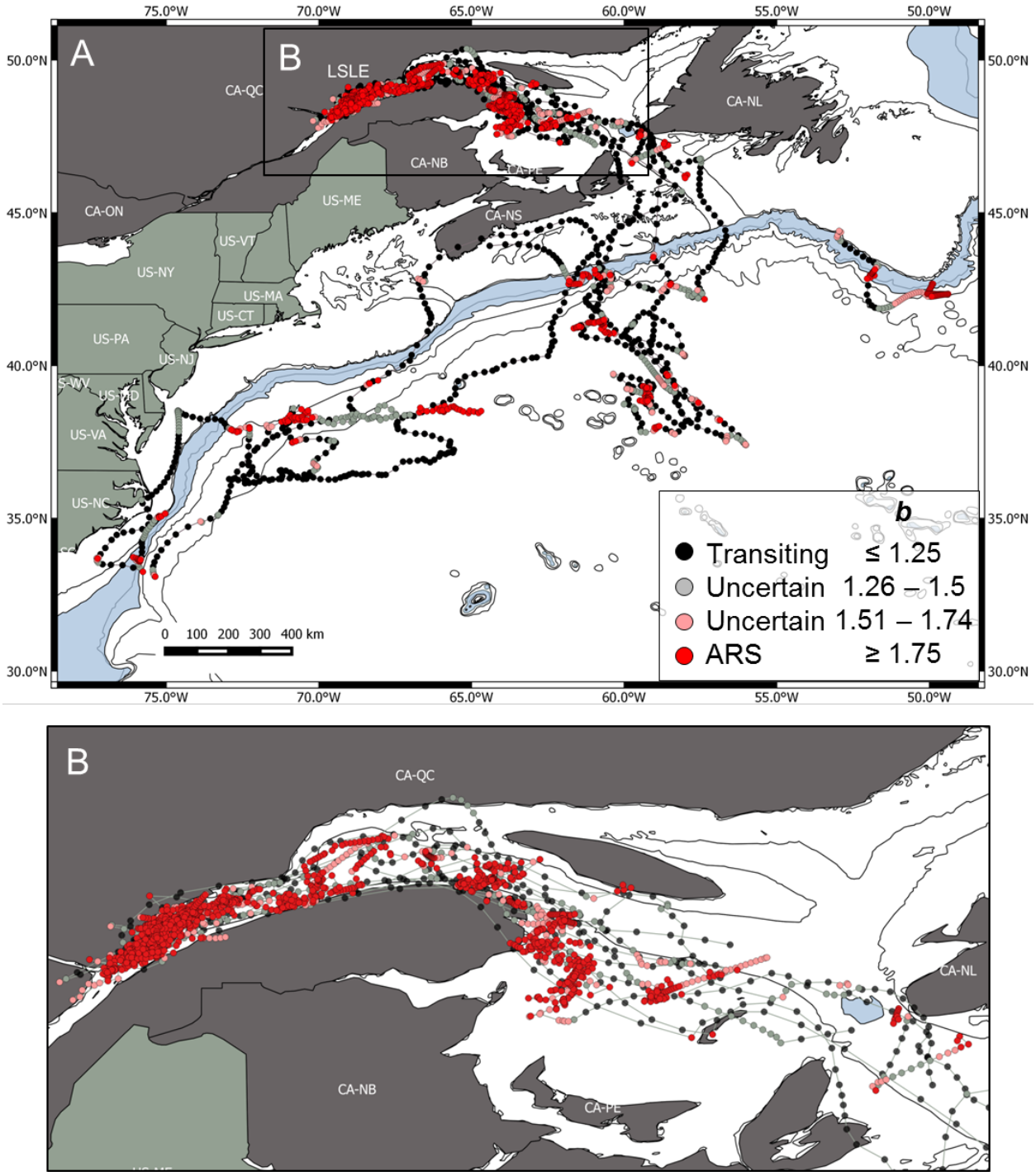


Figure 3. Switching state-space model location and behaviour estimates for blue whales (n = 21) satellite tagged in the Estuary and the Gulf of St. Lawrence, Canada in 2002, 2010 and from 2012 to 2015. Black circles: transiting behaviour (b ≤ 1.25); red circles: ARS behaviour (b ≥ 1.75); uncertain behaviour was divided into two categories: values closer to transiting (grey circles: b = 1.26 – 1.50) and values closer to ARS (pink: b = 1.51 – 1.74). A: entire map of tracks and B: inset showing the Gulf of St. Lawrence.

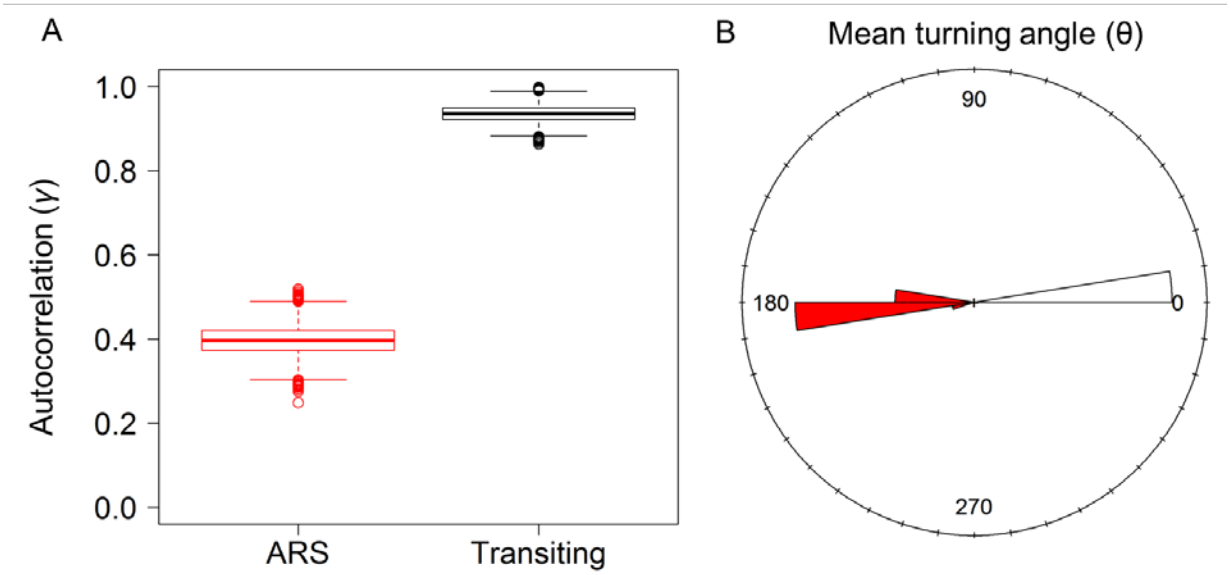


Figure 4. Distribution of movement parameters used to infer behaviour of blue whales tagged in 2002, 2010 and from 2012 to 2015 (n = 21). Area-restricted search (ARS) in red and transiting in black. (A) Combined autocorrelation (γ) of speed and direction (i.e. move persistence), depicting medians (dark horizontal bars), 25th and 75th percentiles (box), 5th and 95th percentiles (whiskers) and outliers (points). (B) Mean turning angle (θ), where the radii of the binned sectors are equal to the square root of the relative frequencies of observations in each sector (function rose.diag in circular package for R).

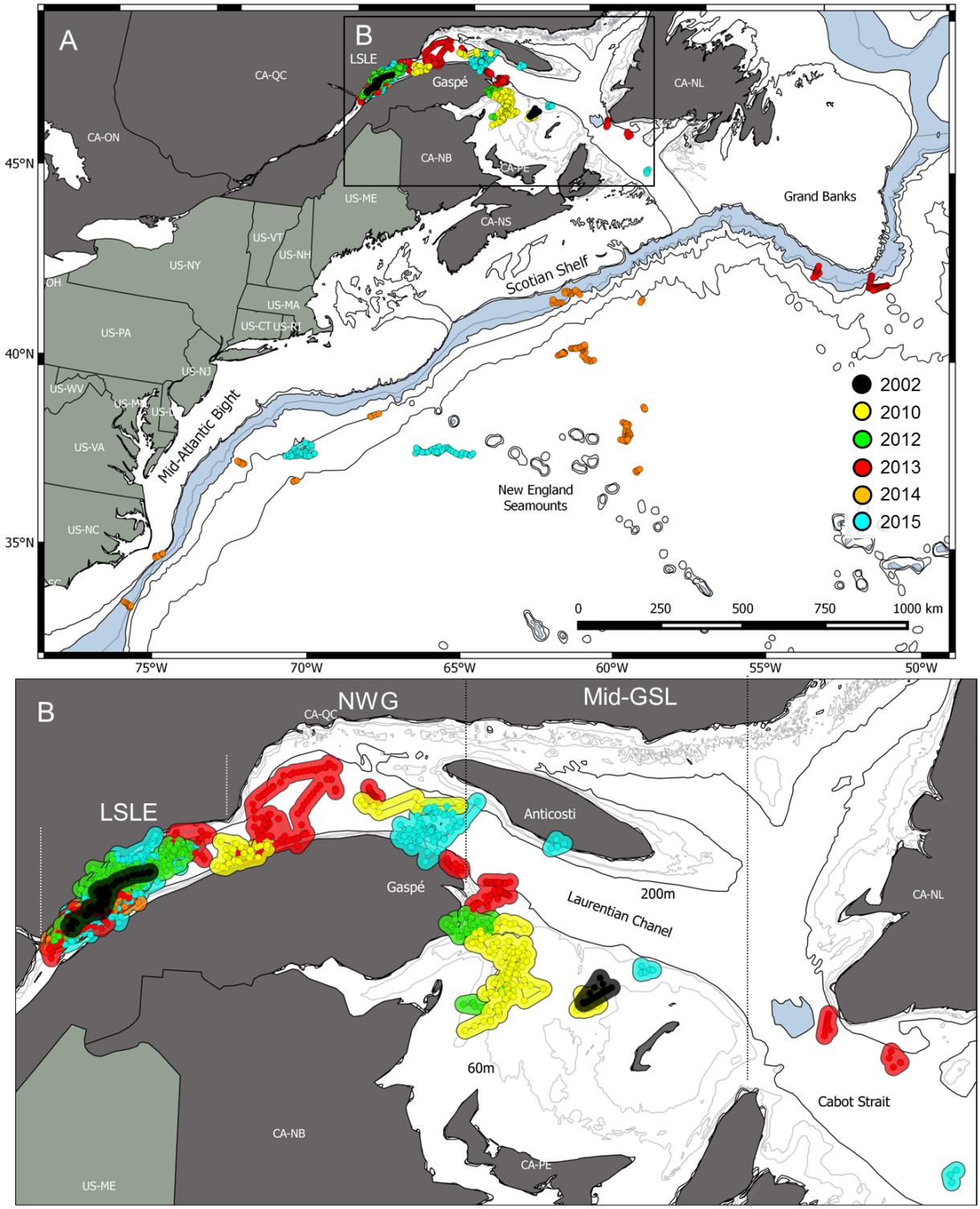


Figure 5. Area-restricted search (ARS) patches identifed for blue whales (n = 21) tagged in the Estuary and Gulf of St. Lawrence, Quebec in 2002, and from 2010 to 2015. Each ARS patch is a unique individual, and several different patches may correspond to the same individual. Points represent hSSSM-estimated locations in which ARS behaviour was inferred at a 4 h time interval. Refer to Table S2 for details. ARS ptaches within the LSLE comprise 14 individuals; NWG (n = 4); mid-GSL (n =10); and outside of the SLE and GSL (n=3).

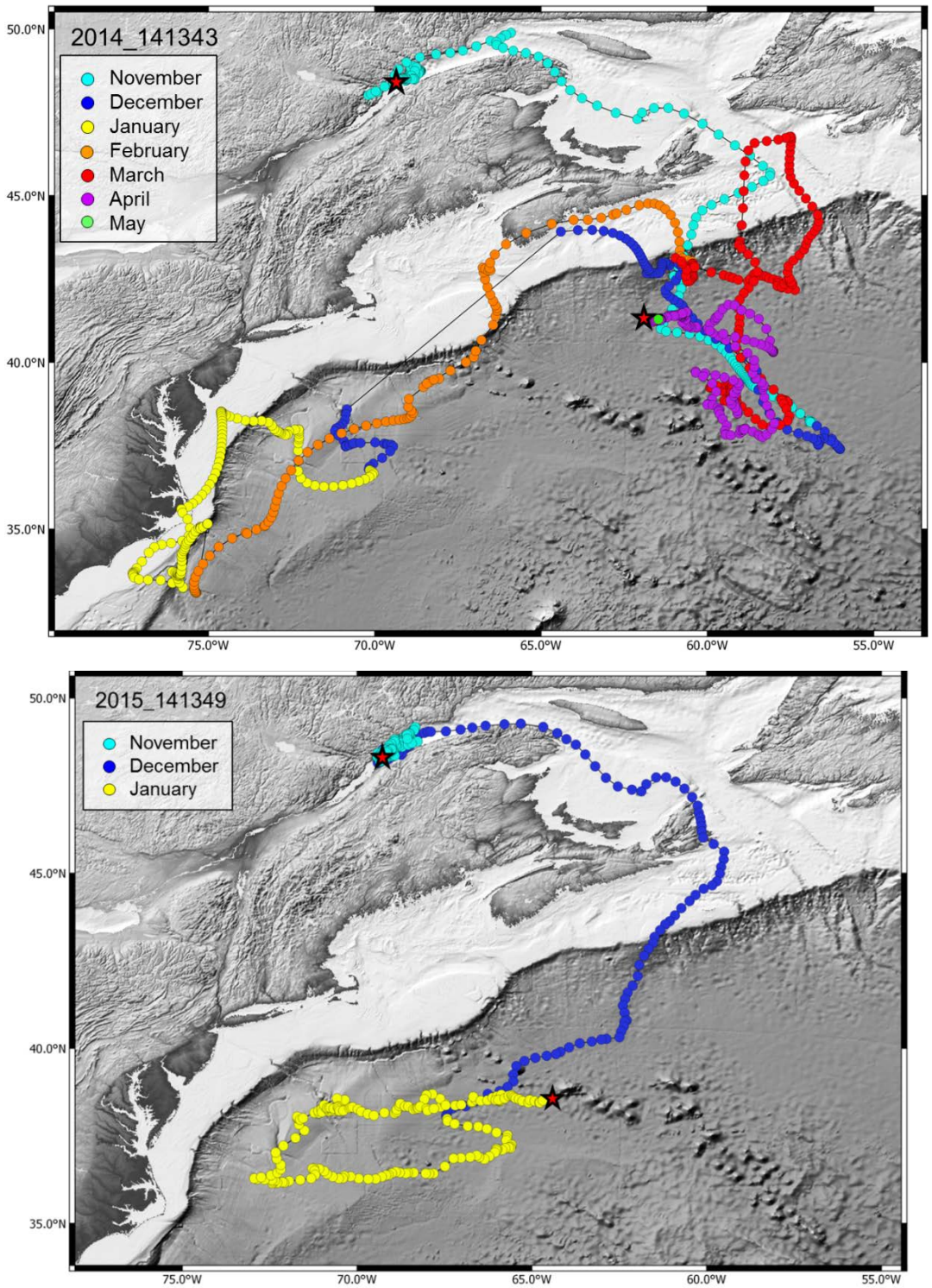


Figure 6. Switching state-space model-estimated positions for two female blue whales tagged on November 4, 2014 (B244 Upper panel) and November 3, 2015 (B197 Lower panel) in the St. Lawrence Estuary, Quebec. Stars indicate where tag was deployed in the St. Lawrence Estuary, and where transmissions ceased (1 May 2015 and 30 January 2016, respectively) off the mid-Atlantic Bight.

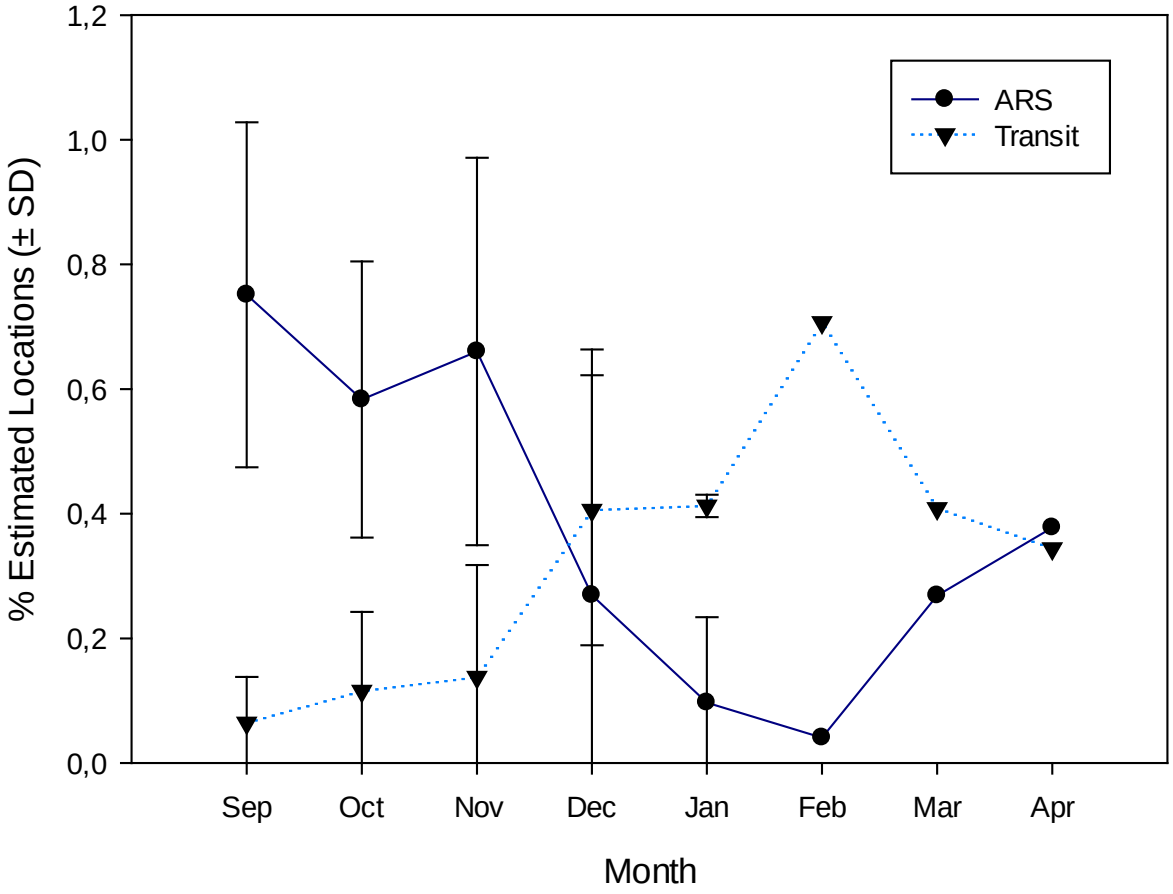


Figure 7. Seasonal change in the proportion (in %) of estimated locations considered as area-restricted search (ARS; circle) and transit (triangle) behaviour.

APPENDIX / SUPPLEMENTARY MATERIAL

S1. Argos Track Summary

Visual inspection of blue whale Argos tracks clearly showed areas of persistent occurrence within the SLE and GSL, as well as transiting corridors. Notably, from Tadoussac to Pointe-des-Monts in the SLE; from Pointe-des-Monts to Gaspé Bay, especially along the north shore of the Gaspé Peninsula; in the Anticosti Gyre (northwestern part of the GSL); and the region east and south of the tip of the Gaspé Peninsula, American Bank in particular (Fig. 1).

In 2002, one blue whale was tagged in the LSLE-W on Sept 4 and spent at least 12 days in the same sector. The tag stopped transmitting for five days and re-appeared on Sept 20 in the Gaspé offshore region. The whale travelled south and east towards the mi-GSL, and gave its final position on Sept 29 from within the Laurentian Channel, likely on its way out of the GSL via Cabot Strait.

In 2010, two blue whales were tagged on Sept 7 off Matane (SLE) and stayed in the same general area until Sept 12 before both heading east along the Gaspé Peninsula. One whale stopped transmitting on Sept 21, about 45 km east of Miscou Island (located at the southern entrance to Chaleur Bay, a large bay south of the Gaspé Peninsula). The second whale stopped transmitting on Oct 7, 65 km northwest of the Magdalen Islands.

In 2012, two blue whales were tagged in Gaspé on Sept 2 (106738) and Sept 3 (106739). The first whale stayed in the same general area off Gaspé for 10 days before heading south and ceasing communication on Sept 14, 45 km southeast from Miscou Island. The second whale stopped transmitting on Sept 7, around 10 km east of its tagging location, after spending five or so days in the waters north and east of Bonaventure Island. Another blue whale (100386) was tagged Sept 21 off Portneuf (SLE), and stayed in the SLE for 10 days before heading northeast towards the GSL. This whale stopped transmitting on Oct 13 for 10 days, until giving its final position within the Laurentian Channel, around 80 km north of the Magdalen Islands. Whale 100387 was tagged Sept 26 off Escoumins (SLE) and stayed in the SLE for over two months (68 d) until heading east along the Gaspé Peninsula on Dec 2. Once reaching the northern end of the Gaspé Peninsula on Dec 3, this whale headed easterly in a relatively straight line towards the middle of the Gulf, staying within the Laurentian Channel, before a last position was sent on Dec 4, about 85 km north of the Magdalen Islands. Whale 100388 was tagged on Sept 28 at Îlets Boisés (SLE) and stayed within the SLE during the entire lifetime of the tag (18 d), although moved gradually northeast along the north shore of the SLE.

In 2013, two blue whales were tagged on Sept 5 in Gaspé (106740 and 106741), although one tag failed to transmit entirely (106740). Whale 106741 stayed in the vicinity of its tagging site for five days before venturing out ~135 km east-southeast towards the middle of the GSL in the Laurentian Channel. Two days later it returned to the tagging location. From there, whale 106741 headed west along the Gaspé coast towards the SLE, where it stayed until its final position on Sept 25 just south of Baie-Comeau. Three blue whales were tagged on Sept 28, also in Gaspé: Whale 106734 stayed in the Gaspé region until Oct 3, stopped transmitting for three days, and showed up south of the Magdalen Islands on Oct 7. It moved east and reached Cabot Strait in the evening of Oct 7, where the signal was lost. Whale 106742 only gave four days of positions, during which it stayed in the same general zone it was tagged. Whale 106743 only gave its first position 17 days after it was tagged, by which time it was outside the GSL, 145 km east of Nova Scotia, within the Laurentian Channel. Signal was then lost until Oct 19, when the whale was where the Laurentian Channel meets the continental shelf. Signal was again lost until Nov 2, by which time the whale was 510 km south of where the Laurentian Channel meets the shelf edge. Thus, whale 106743 travelled a total of approx. 1220 km in 36 days. Whale

106737 was the last animal tagged in Gaspé in 2013, on Oct 1. After being tagged, it headed west into the northwest part of the GSL, and then looped back towards Gaspé before ending communication on Oct 25, 6 km north of Gaspé Bay.

Still in 2013, two whales were tagged off Portneuf (SLE) on Sept 26 (100386) and 27 (100389). Whale 100386 remained in the SLE, near where it was tagged for the entire tag lifetime, until Oct. 11. Whale 100389 stayed in the area it was tagged for five days until signal was lost until seven days later, when it was heading east along the Gaspé Peninsula, giving positions regularly for two days, until signal was lost again. Positions were received five days later off the southwest coast of Newfoundland in the Cabot Strait, heading out of the GSL. The tag was silent until Nov 4, when animal was on the continental shelf heading west along the shelf edge, until its last transmission on Dec 2, around 245 km south of Newfoundland. The last whale of 2013 was tagged on Oct 15 off Escoumins (100388). This whale transmitted only two locations - one on Nov 18 in the Cabot Strait, middle of the Laurentian Channel, and one on Nov 22, 40 km west of Saint Pierre and Miquelon, French Islands near the south coast of Newfoundland.

In 2014, two blue whales were tagged in the SLE - one whale (100383) on Oct 21 off Escoumins, and one whale (141343) on Nov 4 off Sault-aux-Moutons. Whale 100383 stayed in the SLE, close to its tagging location, until its final position on Nov 12, 65 km northeast of the tagging site.

Whale 141343 (B244; female) holds the record for tag longevity (177 days), and provides the first long-term record of blue whale fall and winter migratory behaviour in the northwest Atlantic. B244 remained in the area she was tagged for nearly two weeks before moving northwest into the GSL. By Nov 18, she had made it south to the Magdalen Islands, and continued heading southeast along the edge of the Laurentian Channel, exiting the GSL via Cabot Strait by Nov 20. She then headed ~1000 km southeast from Nova Scotia to 37˚N and then moved back along her track over the course of 26 days, returning to within 20 km of the southeast coast of Nova Scotia on Dec 16. The signal was then lost for 10 days, by which time she had travelled around 780 km southwest, about 360 km east of Delaware, USA. Here, she spent the next 11 or so days moving southeast along the edge of the Hudson Canyon (a submarine canyon that originates from the estuary of the Hudson River and extends 640 km seaward across the continental shelf), and then back northwest along a parallel canyon, all the way to within 40 km of Delaware Bay. The tag then stopped transmitting for five days, when she showed up off Pamlico Sound in North Carolina, the largest lagoon on the east coast of the USA. Pamlico Sound is separated from the Atlantic Ocean by the Outer Banks, a long, thin barrier of low-lying sandy islands, including Cape Hatteras. B244 continued moving south along the coast until Jan 16 before heading more offshore to the continental shelf. From there, she followed the continental shelf back north to within approx. 45 km east of Cape Hatteras on Jan 23. Following 21 days of silence, the tag re-transmitted locations on Feb 12 from the continental shelf, approximately 400 km east of Charleston, South Carolina, at her southernmost position. From there, she headed back northeast, roughly staying parallel to her south-bound route, although staying farther offshore, between 60 and 200 km from the continental shelf break. On Feb 22, she crossed the shelf at the Gulf of Maine and headed towards the southwestern end of Nova Scotia, following the edge of the coast towards Cabot Strait. By mid-March, she was within the Cabot Strait, but did not enter the GSL. Instead, she turned south and headed to the same offshore region she had visited in Nov and Dec of the previous year (north-east of the New England Seamount chain - a series of underwater volcanoes extending over 1000 km from the edge of the Georges Bank off the coast of Massachusetts, USA). B244 spent until at least early May in this area, which measures approximately 670 km in length and 440 km wide.

In 2015, a total of 5 blue whales were tagged - four in the LSLE and one in the Gaspé region. The first whale (2015_141346, a female) was tagged at the end of August and stayed within the

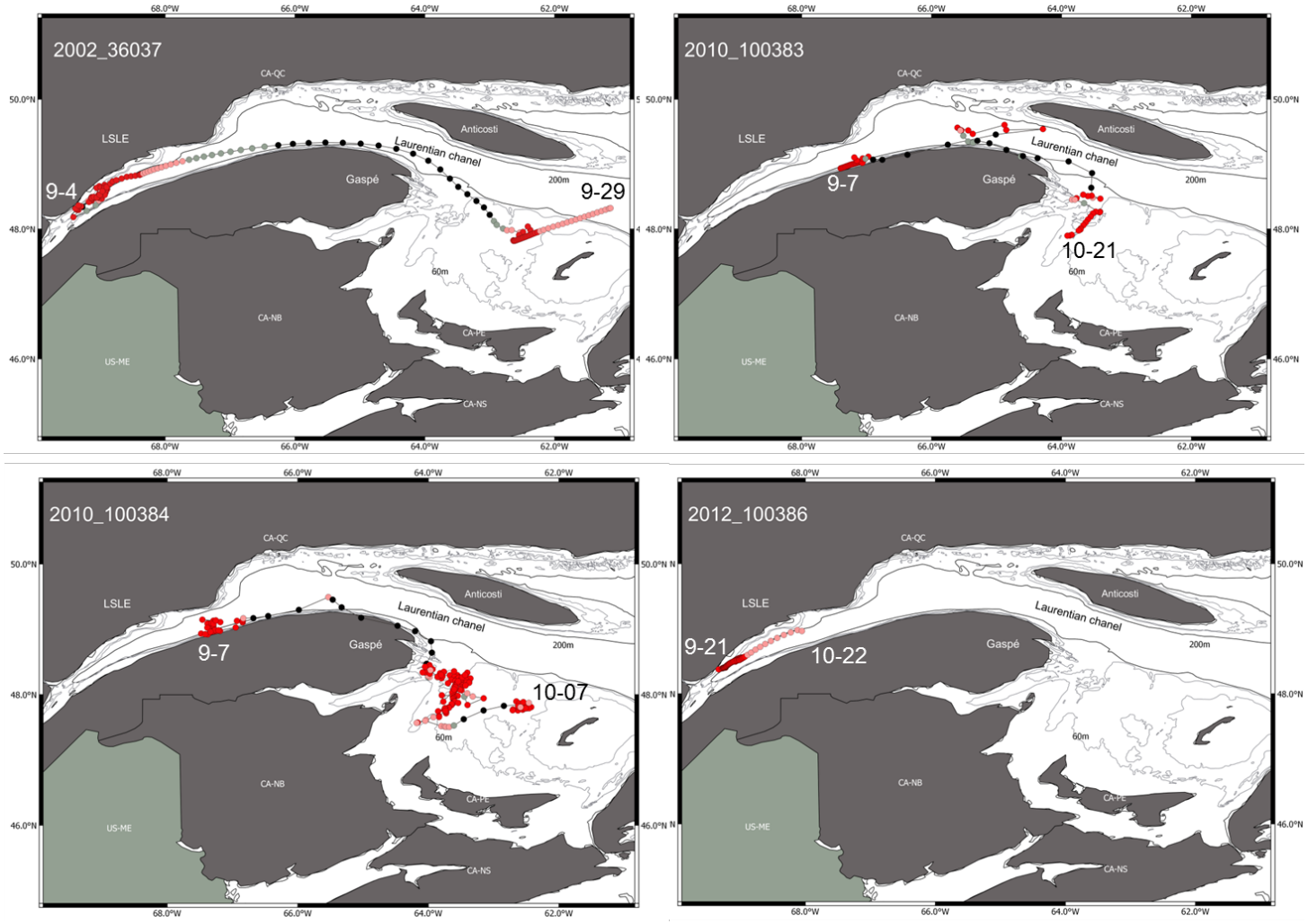
same general area north of the Gaspé Peninsula until transmission ceased, nearly 20 days later. The second whale (2015_106741, a male) was tagged in early October off Portneuf-sur-Mer on the north shore of the LSLE. This individual stayed within the LSLE for about 8 days after being tagged, moving gradually north-easterly. On Oct 16, this whale showed directional movement, heading towards the northwestern GSL and the south coast of Anticosti, then moving southward towards the Magdalen Islands. On Oct 21, just north of the Islands, the whale changed course to head easterly towards Newfoundland and entered the Cabot Strait by Oct 25. Contact was lost 2 days later (Oct 27) when the whale was in the Laurentian Channel outside of the GSL, heading towards the shelf edge.

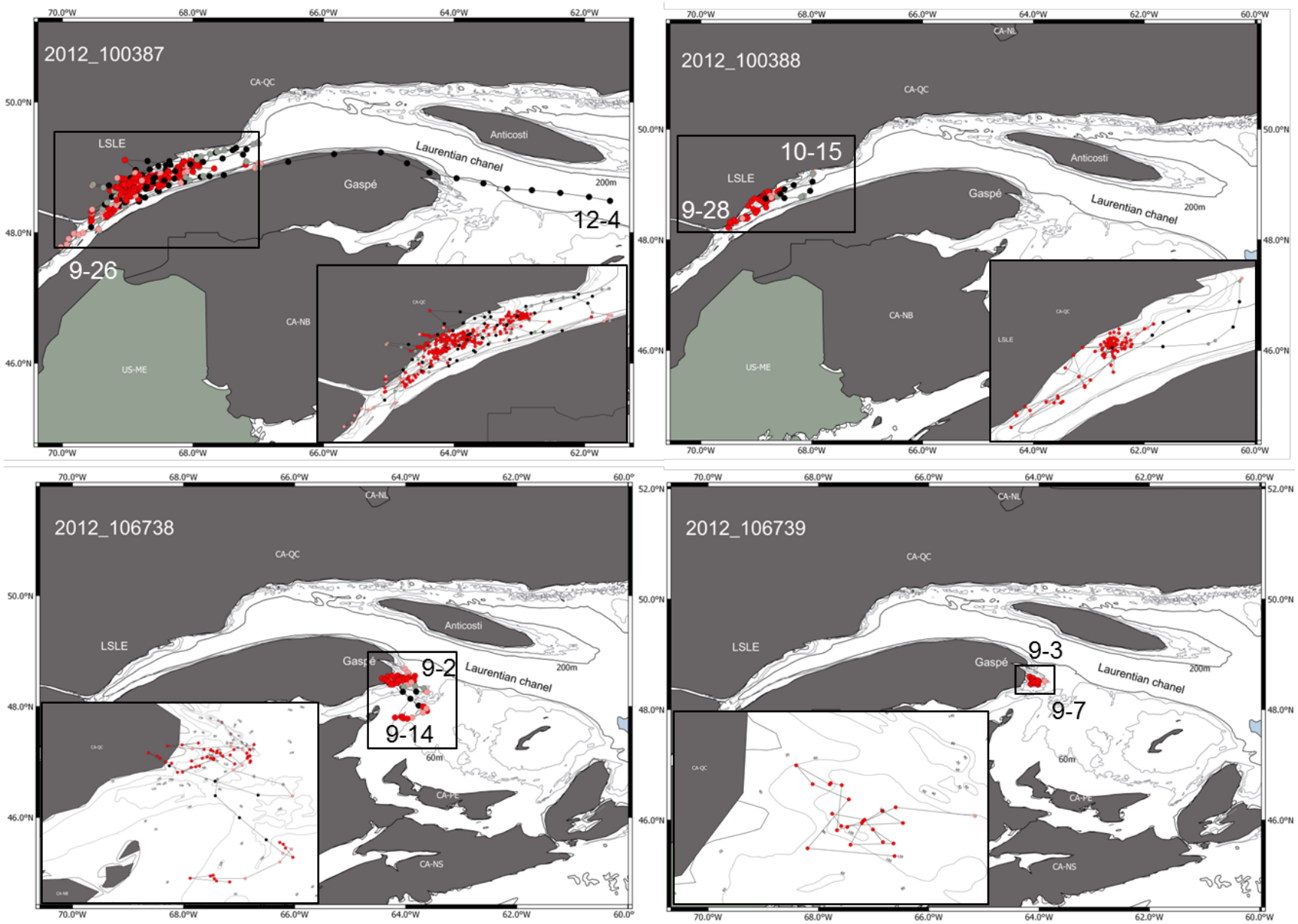
Two females were tagged on Nov 3 off Betsiamites on the north shore of the LSLE. Before transmission ceased, the first whale (2015_141344) spent nearly one month in the same area (between Portneuf-sur-Mer and Pointe-aux-Outardes), staying between the coast and the northern 200m isobath of the Laurentian Channel. The second female, 2014_141349, provided the second longest track record of all satellite-tagged blue whales in this study. After remaining the LSLE for 1.5 months (46d) following tagging, this whale initiated directional travelling behaviour towards the GSL. In 1 d, the whale moved from the waters off Baie Comeau to the eastern tip of the Gaspé Peninsula, following the Peninsula's northern coastline. She took again only 1d to reach the Magdalen Islands, and by Dec 22 the whale had entered Cabot Strait heading south, hugging the coast of Cape Breton Island, NS. She continued travelling south-west, passing north of Sable Island and the Gully Marine Protected Area. At the end of Dec, the whale was at the north-western portion of the New England Seamount chain (near the Kelvin and Balanus seamounts, approximately 200km (shortest distance) offshore from continental shelf edge/George's Bank, or 500km south of NS). The whale's movement pattern changed in this area; over the course of the next month until contact was lost on Jan 29, the whale made a large clockwise loop (covering nearly 2000km), and eventually returned back to the initial position on Dec 30. The southern-most position recorded was on Jan 10, approx. 390km east of Pamlico Sound, NC (36°9'N, 72°5'W). The last blue whale of 2015 (2015_141350) was tagged on Nov 18 off Forestville in the LSLE. Around 1 week later, the whale began heading towards the northwest GSL, passing north of the Anticosti Gyre on Nov 26. The whale continued its course south east, passing north of the Magdalen Islands, reaching the Cabot Strait on Dec 4. The tag stopped transmitting just outside of the Cabot Strait, within the Laurentian Channel on Dec 5.

S2. Argos-defined location classes for blue whales (n = 21) satellite tagged in the Estuary and Gulf of St. Lawrence, Quebec, in 2002, and from 2010 to 2015.

	Location class						
PTT ID	**B**	**A**	**0**	**1**	**2**	**3**	**Z**
2002_36037	88	25	9	4	1	1	2
2010_100383	63	11	3	3	3	2	0
2010_100384	142	60	29	38	10	13	0
2012_106738	92	2	0	0	0	0	0
2012_106739	63	5	0	0	0	0	0
2012_100386	19	2	0	0	0	0	1
2012_100387	503	10	1	1	3	0	4
2012_100388	196	7	3	6	4	0	1
2013_106741	109	29	20	7	2	1	0
2013_100386	123	3	1	0	0	0	0
2013_100389	97	5	0	0	1	0	1
2013_106743	10	3	0	1	1	0	0
2013_106742	15	2	0	0	0	0	0
2013_106734	17	2	5	0	0	0	0
2013_106737	81	5	0	1	0	0	0
2013_100388	1	1	0	0	0	0	0
2014_100383	108	33	8	22	7	3	0
2014_141343	715	32	10	1	1	0	11
2015_141346	144	5	2	0	0	0	0
2015_106741	236	22	14	7	0	0	2
2015_141344	224	15	3	2	0	0	0
2015_141349	669	124	59	45	19	16	4
2015_141350	115	2	0	0	0	0	2

S3 (over next 6 pages). State-space switching model location and behaviour estimates for blue whales (n = 21) satellite tagged in the Estuary and Gulf of St. Lawrence, Quebec in 2002, and from 2010 to 2015. Each figure corresponds to a single individual. Black circles: transiting behaviour (b ≤ 1.25); grey: b = 1.26 – 1.50; pink: 1.51 – 1.74; red: ARS behaviour (b ≥ 1.75). Tagging date and date of last position received are indicated on each track (month-day).

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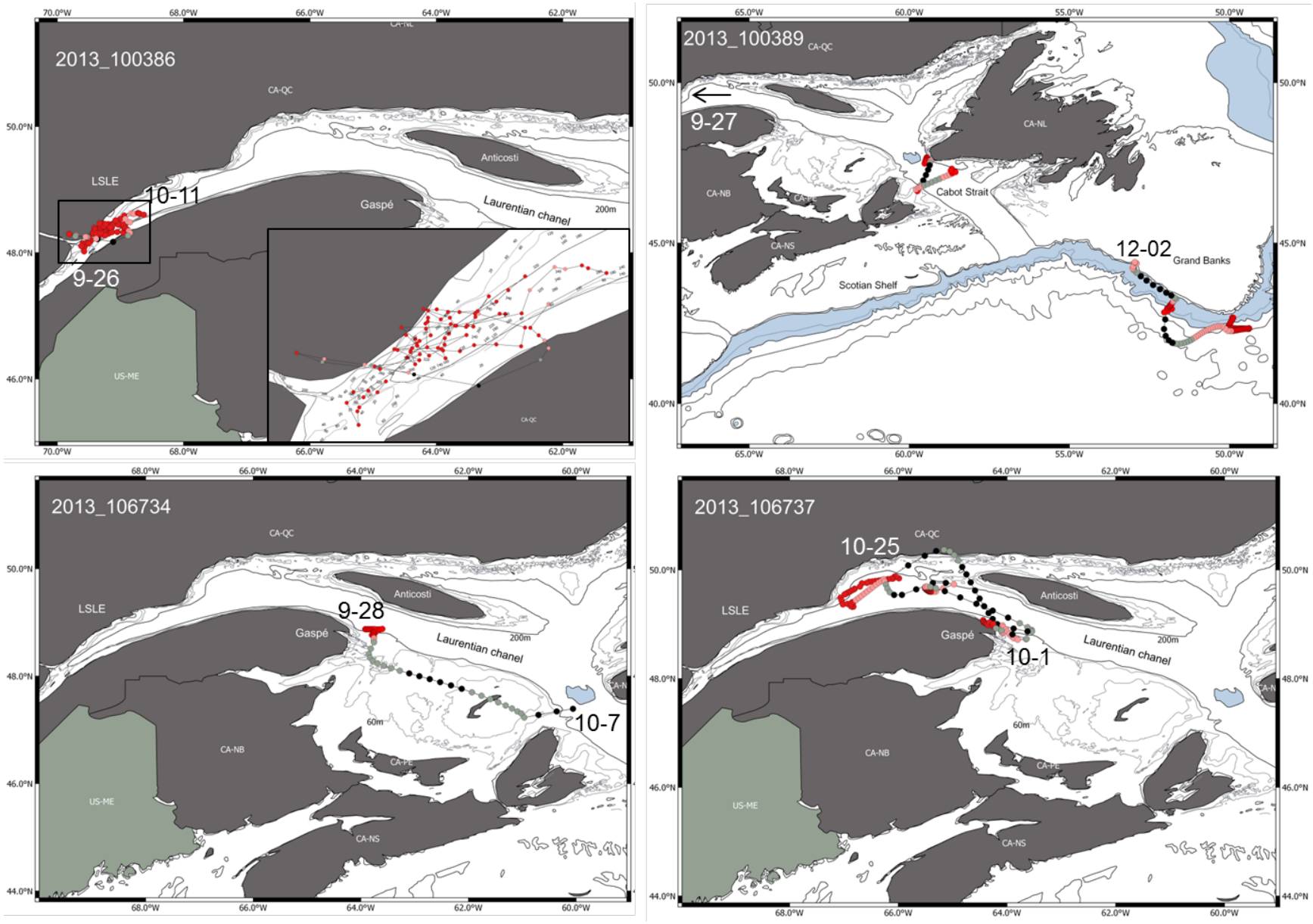
Anticosti
Laurentian chanel
Gaspé
200m
12-4
9-26
CA-NB
US-ME
2012_100388
CA-NL
10-15
9-28
2012_106738
9-2
9-14
60m
CA-PE
CA-NS
2012_106739
9-3
9-7
70.0°W
68.0°W
66.0°W
64.0°W
62.0°W
60.0°W
50.0°N
48.0°N
46.0°N
52.0°N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9-26
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Gaspé
Laurentian chanel
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US-ME
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CA-QC
9-27
CA-NL
CA-NB
Cabot Strait
CA-NS
12-02
Grand Banks
Scotian Shelf
2013_106734
CA-QC
LSLE
9-28
Anticosti
Gaspé
Laurentian chanel
200m
60m
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CA-QC
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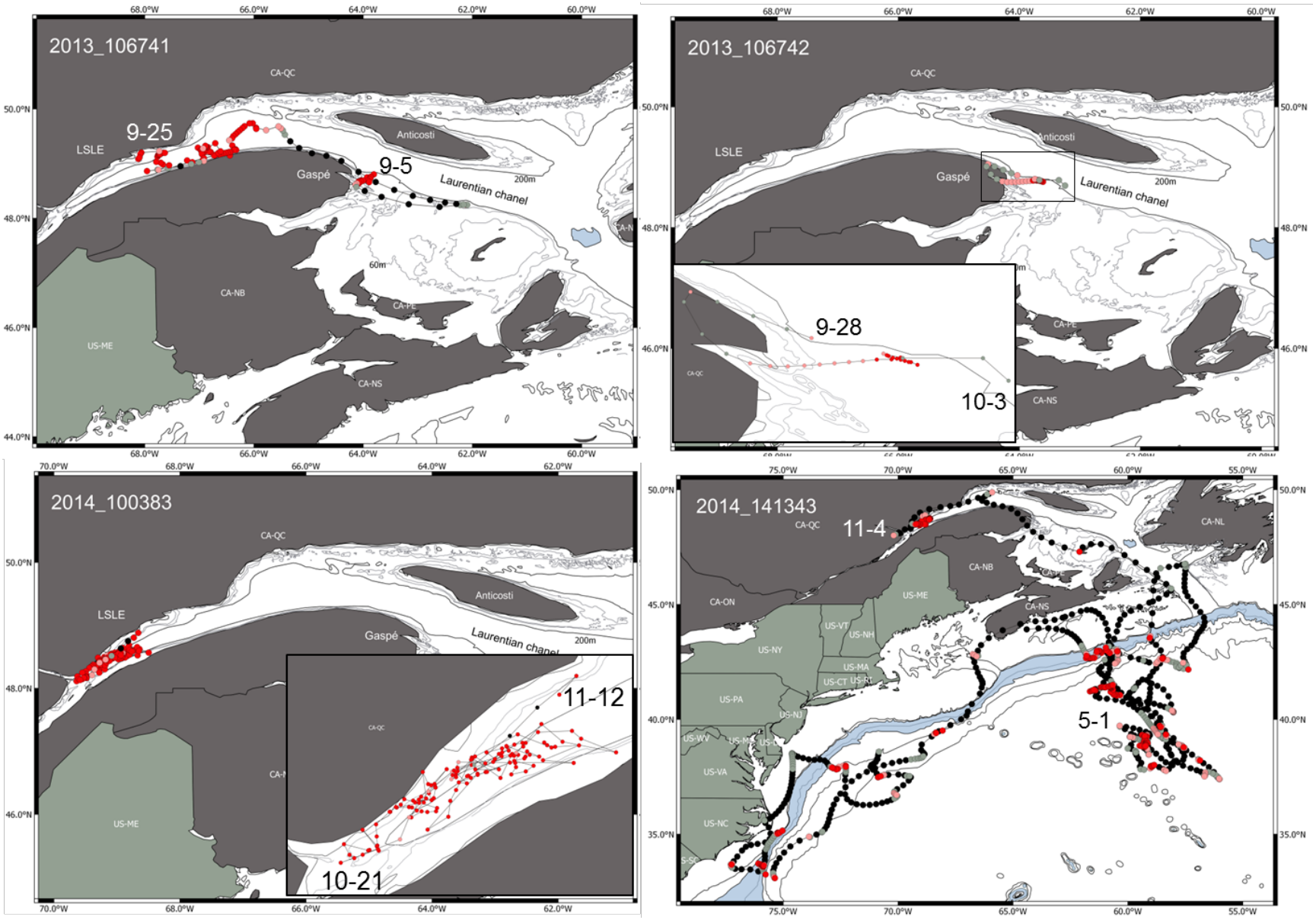
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9-25
9-5
LSLE
Gaspé
Anticosti
Laurentian chanel
200m
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CA-QC
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2013_106742
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US-CT
US-RI
US-NJ
US-WV
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66.0°W
64.0°W
62.0°W
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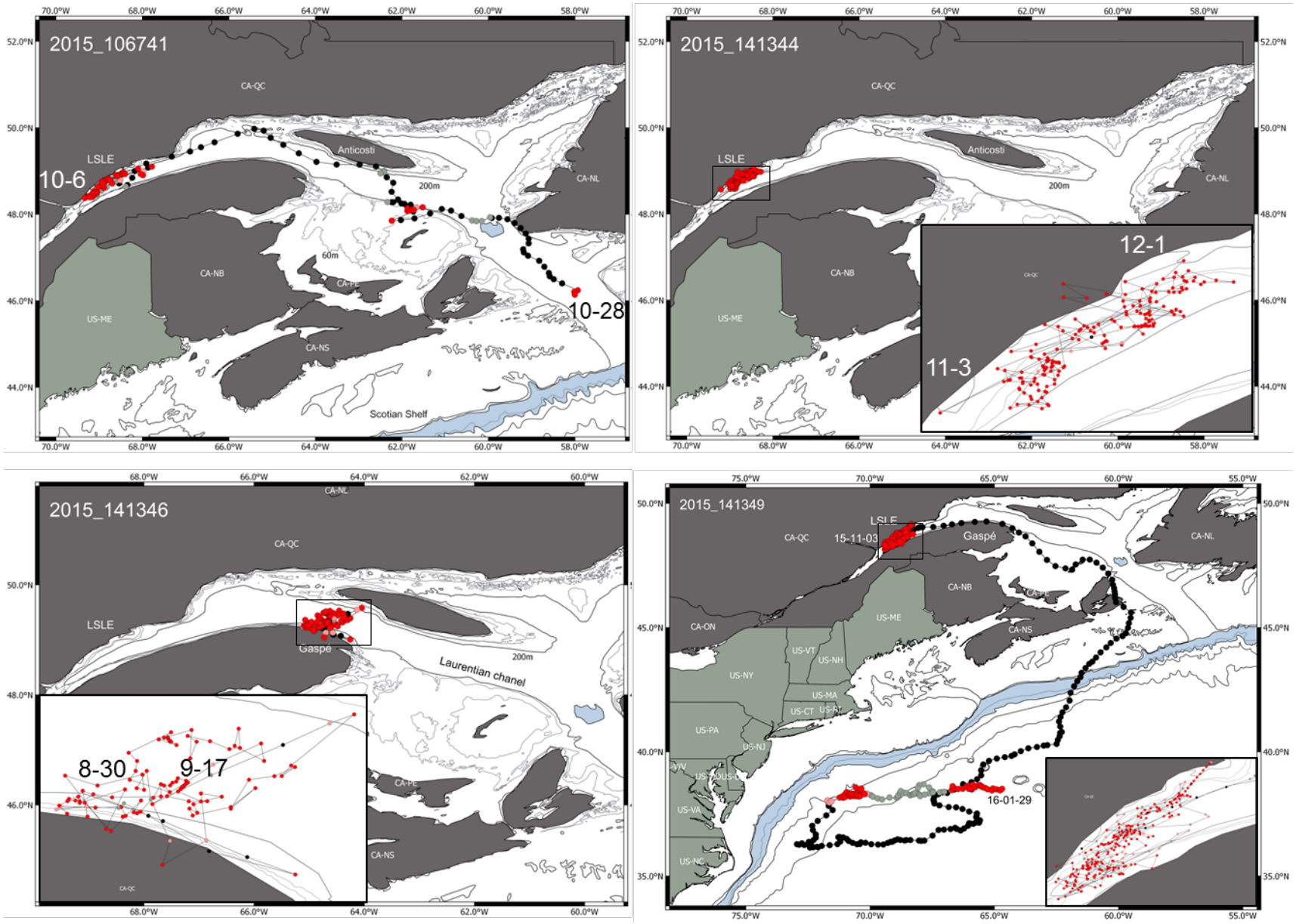
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Anticosti
200m
12-1
11-3
2015_141346
LSLE
Gaspé
Laurentian chanel
200m
8-30
9-17
2015_141349
LSLE
15-11-03
Gaspé
16-01-29
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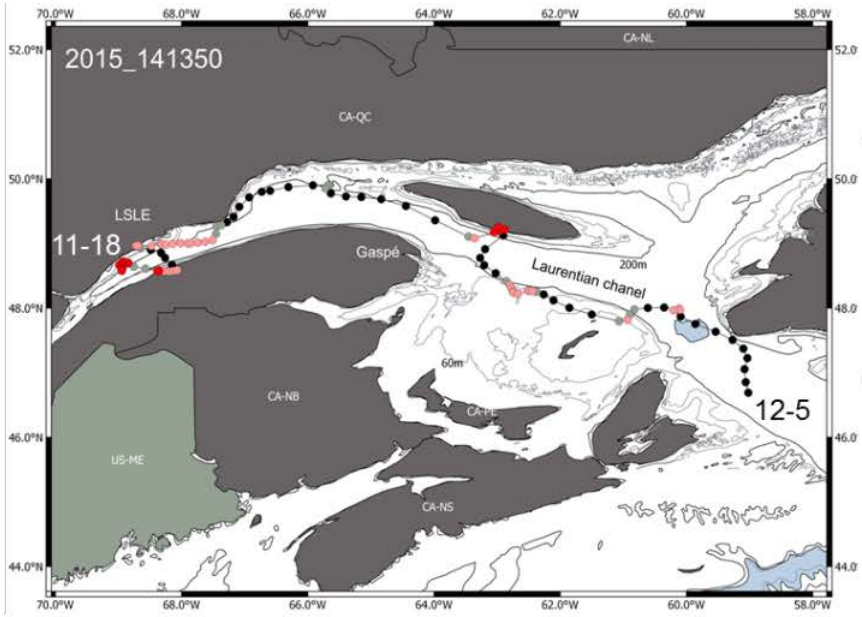
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Gaspé
Laurentian chanel
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12-5
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US-ME
CA-NS
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68.0°W
66.0°W
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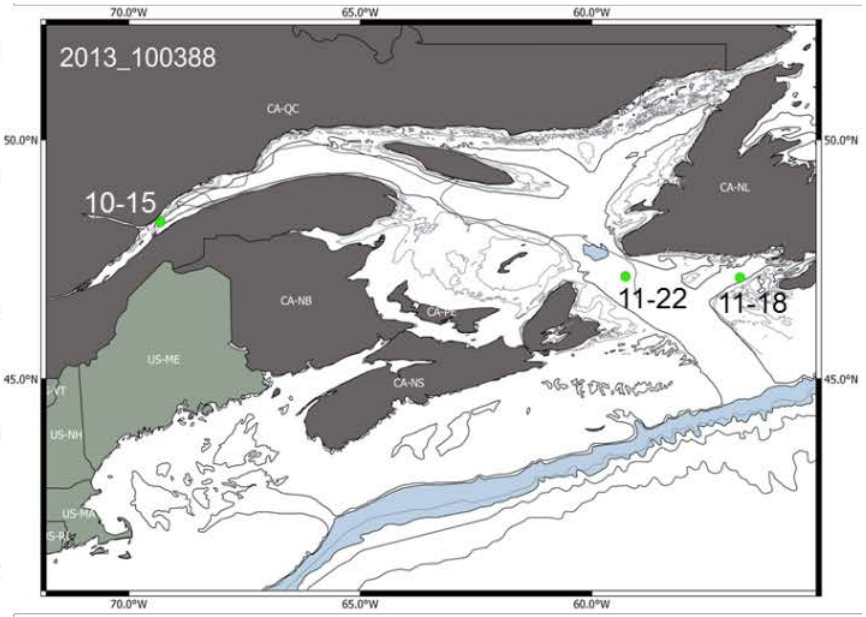
44.0°N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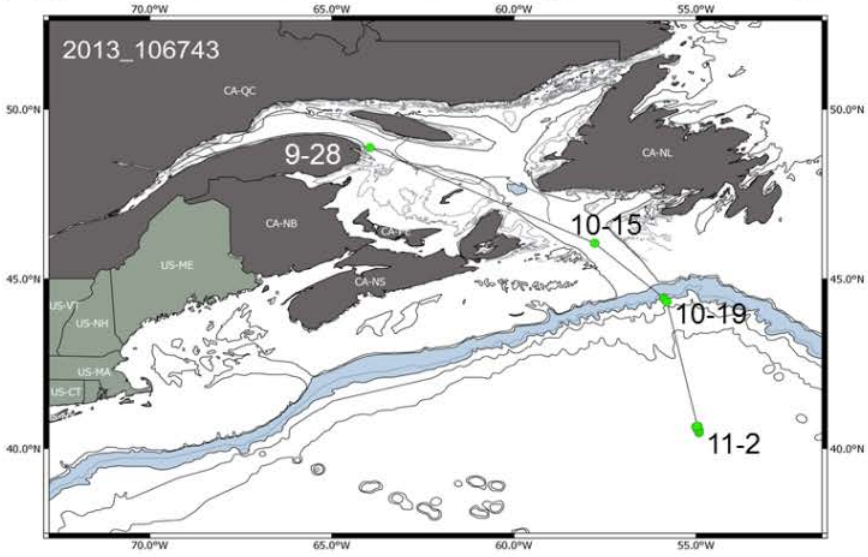
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65.0°W
60.0°W
55.0°W
50.0°N
45.0°N
40.0°N

S4. Areas of area-restricted search (ARS) identified for blue whales (n = 21) satellite tagged in the Estuary and Gulf of St. Lawrence, Quebec in 2002, and from 2010 to 2015. Grey shaded rows correspond to ARS patches outside of the SLE and GSL.

Patch	PTT ID	Start date	End date	Delta (d)	Area (km^2)	Region*
1	2002_36037	2002-09-04	2002-09-07	2.7	605.9	LSLE
2	2002_36037	2002-09-09	2002-09-15	6.7	2135.7	LSLE
3	2002_36037	2002-09-23	2002-09-26	3.8	1059.4	Mid-GSL
4	2010_100383	2010-09-07	2010-09-12	4.5	994.2	LSLE
5	2010_100383	2010-09-13	2010-09-14	1.2	1950.8	NWG
6	2010_100383	2010-09-17	2010-09-17	0.7	709.3	Mid-GSL
7	2010_100383	2010-09-18	2010-09-21	2.7	1215.0	M-GSL
8	2010_100384	2010-09-07	2010-09-12	4.7	1816.0	LSLE
9	2010_100384	2010-09-15	2010-10-01	16.2	4877.0	Mid-GSL
10	2010_100384	2010-10-03	2010-10-07	3.8	912.6	Mid-GSL
11	2012_100386	2012-09-21	2012-10-01	10.0	884.0	LSLE
12	2012_100387	2012-09-26	2012-09-27	1.0	669.6	LSLE
13	2012_100387	2012-09-28	2012-09-29	1.3	1012.6	LSLE
14	2012_100387	2012-10-02	2012-10-04	1.8	977.7	LSLE
15	2012_100387	2012-10-07	2012-10-15	7.5	1479.6	LSLE
16	2012_100387	2012-10-17	2012-10-18	1.8	1523.3	LSLE
17	2012_100387	2012-10-19	2012-10-26	6.8	1079.8	LSLE
18	2012_100387	2012-10-27	2012-10-28	0.5	628.9	LSLE
19	2012_100387	2012-10-30	2012-10-31	1.7	1370.8	LSLE
20	2012_100387	2012-11-01	2012-11-02	0.7	541.2	LSLE
21	2012_100387	2012-11-02	2012-11-12	9.2	1847.8	LSLE
22	2012_100387	2012-11-14	2012-11-16	1.8	533.2	LSLE
23	2012_100387	2012-11-19	2012-11-29	10.3	1821.7	LSLE
24	2012_100388	2012-09-28	2012-10-13	15.0	3059.4	LSLE
25	2012_106738	2012-09-02	2012-09-03	0.5	362.6	Mid-GSL
26	2012_106738	2012-09-03	2012-09-08	4.2	1283.2	Mid-GSL
27	2012_106738	2012-09-09	2012-09-10	1.3	913.2	Mid-GSL
28	2012_106738	2012-09-11	2012-09-12	0.5	403.1	Mid-GSL
29	2012_106738	2012-09-13	2012-09-13	0.8	516.3	Mid-GSL
30	2012_106739	2012-09-03	2012-09-07	3.7	822.6	Mid-GSL
31	2013_100386	2013-09-26	2013-10-09	13.0	3194.1	LSLE
32	2013_100389	2013-10-15	2013-10-17	1.7	628.1	CS
33	2013_100389	2013-10-21	2013-10-21	0.5	619.2	CS
34	2013_106734	2013-09-28	2013-10-02	4.0	863.2	M-GSL

Patch	PTT ID	Start date	End date	Delta (d)	Area (km^2)	Region*
35	2013_106737	2013-10-04	2013-10-11	6.8	2379.1	NWG
36	2013_106737	2013-10-15	2013-10-18	2.5	434.5	NWG
37	2013_106737	2013-10-21	2013-10-23	2.0	592.1	NWG
38	2013_106741	2013-09-05	2013-09-08	2.5	840.2	Mid-GSL
39	2013_106741	2013-09-12	2013-09-21	8.5	3764.8	NWG
40	2013_106741	2013-09-23	2013-09-25	2.7	1456.5	LSLE
41	2013_106742	2013-10-01	2013-10-03	1.8	433.6	Mid-GSL
42	2013_100389	2013-11-12	2013-11-21	9.2	2015.8	GB
43	2013_100389	2013-11-26	2013-11-29	3.3	1083.1	GB
44	2014_100383	2014-10-21	2014-10-29	7.5	1519.2	LSLE
45	2014_100383	2014-10-30	2014-11-11	12.3	2214.5	LSLE
46	2014_141343	2014-11-04	2014-11-07	3.3	1091.8	LSLE
47	2014_141343	2014-11-10	2014-11-10	0.5	446.1	LSLE
48	2014_141343	2014-11-12	2014-11-13	1.3	742.6	LSLE
49	2014_141343	2014-12-05	2014-12-05	0.3	363.5	NES
50	2014_141343	2014-12-10	2014-12-11	1.5	1270.2	SS
51	2014_141343	2014-12-12	2014-12-13	1.2	850.1	SS
52	2014_141343	2014-12-28	2014-12-29	0.5	411.4	US-CS
53	2014_141343	2015-01-05	2015-01-06	0.8	653.8	US-CS
54	2014_141343	2015-01-17	2015-01-19	1.5	732.4	US-CS
55	2014_141343	2015-01-22	2015-02-12	21.5	678.1	US-CS
56	2014_141343	2015-02-20	2015-02-20	0.3	669.9	US-CS
57	2014_141343	2015-03-05	2015-03-05	0.3	391.0	SS
58	2014_141343	2015-03-24	2015-03-31	7.0	2114.1	NES
59	2014_141343	2015-04-08	2015-04-08	0.7	516.2	NES
60	2014_141343	2015-04-19	2015-04-25	5.7	2259.8	NES
61	2014_141343	2015-04-26	2015-05-01	4.5	658.6	NES
62	2015_106741	2015-10-06	2015-10-09	2.5	808.2	LSLE
63	2015_106741	2015-10-09	2015-10-13	3.3	1847.4	LSLE
64	2015_106741	2015-10-14	2015-10-16	1.5	2096.2	LSLE
65	2015_106741	2015-10-20	2015-10-21	0.7	488.2	Mid-GSL
66	2015_106741	2015-10-27	2015-10-27	0.3	464.1	CS
67	2015_141344	2015-11-03	2015-12-01	28.3	2789.1	LSLE
68	2015_141346	2015-08-30	2015-08-30	0.5	381.1	NWG
69	2015_141346	2015-09-01	2015-09-10	8.7	2936.4	NWG
70	2015_141346	2015-09-11	2015-09-17	6.2	1506.2	NWG
71	2015_141349	2015-11-03	2015-12-16	42.9	5753.6	LSLE

Patch	PTT ID	Start date	End date	Delta (d)	Area (km^2)	Region*
72	2015_141349	2016-01-14	2015-01-20	5.6	3741.4	US-CS
73	2015_141349	2016-01-25	2016-01-30	4.5	4090.3	NES
74	2015_141350	2015-11-18	2015-11-20	1.7	623.6	LSLE
75	2015_141350	2015-11-28	2015-11-29	0.5	525.0	Mid-GSL

* Region description:
LSLE: Lower St. Lawrence Estuary, from Tadoussac to Pointe-des-Monts (north shore) or Ste-Anne-des Monts (south shore).
NWG: Northwest Gulf of St. Lawrence, from Pointe-des-Monts/Ste-Anne-des-Monts to approximately western tip of Anticosti/eastern coast of Gaspé Peninsula (includes Anticosti Gyre and north coast of Gaspé Peninsula).
Mid-GSL: middle of the Gulf of St. Lawrence; includes southern slope of Laurentian Channel, up until Cabot Strait.
CS: Cabot Strait.
GB: Grand Banks, on the continental shelf southeast of Newfoundland.
SS: Scotian Shelf; on the continental shelf south of Nova Scotia.
NES: New England Seamount chain area, Northwest Atlantic.