

# Conservation implications of white shark (*Carcharodon carcharias*) behaviour at the northern extent of their range in the Northwest Atlantic

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## Abstract

Assessing progress for the endangered white shark (*Carcharodon carcharias*) relative to Canadian conservation objectives requires understanding distribution patterns. From the largest tagging data set in the Northwest Atlantic (2010–2020; 272 deployments), we determined the proportion of the population detected in Canadian waters, characterized patterns in occupancy, and explored the behavioural characteristics of animals while in Canadian waters versus elsewhere in their range. The component of the population detected in Canadian waters annually was highly variable, yet proportionately small. Juveniles and subadults were 4.7 and 3.4 times more likely, respectively, to move northward than adults. From June to November, all pop-up satellite archival tagged white sharks remained primarily in coastal locations within the 200 m bathymetric contour and exhibited shallow diving behaviour within the top 100 m of the water column. However, individuals in Canadian waters experienced a more restricted temperature range and used proportionately less of the water column. Accounting for behavioural effects on distribution when predicting habitat use from environmental associations will become critical to evaluate the population-level impact of recovery actions implemented under Canadian legislation.

**Key words:** conservation, telemetry, white shark, distribution, dive behaviour, Northwest Atlantic

## Résumé

L'évaluation des progrès en ce qui concerne le grand requin blanc (*Carcharodon carcharias*), une espèce en voie de disparition, par rapport aux objectifs de conservation canadiens nécessite une compréhension de ses motifs de répartition. À la lumière du plus important ensemble de données de marquage pour l'Atlantique Nord-Ouest (2010–2020, 272 déploiements), nous avons déterminé la proportion de la population détectée dans les eaux canadiennes, caractérisé les motifs d'occupation et comparé les caractéristiques comportementales d'individus alors qu'ils étaient présents en eaux canadiennes et ailleurs dans leur aire de répartition. La composante de la population détectée en eaux canadiennes annuellement est très variable, bien que proportionnellement faible. Les juvéniles et subadultes sont, respectivement, 4,7 et 3,4 fois plus susceptibles de se déplacer vers le nord que les adultes. De juin à novembre, tous les requins blancs dotés d'étiquettes satellites autodétachables à archivage demeurent principalement dans des sites littoraux à l'intérieur de la courbe bathymétrique de 200 m et présentent un comportement de plongée peu profonde dans les 100 premiers mètres de la colonne d'eau. Les individus dans les eaux canadiennes sont cependant exposés à une fourchette de températures plus restreinte et utilisent une moins grande proportion de la colonne d'eau. La prise en compte d'effets comportementaux sur la répartition dans la prédiction de l'utilisation d'habitats à partir d'associations environnementales sera d'importance clé pour l'évaluation de l'incidence à l'échelle des populations de mesures de rétablissement mises en œuvre en vertu de la législation canadienne. [Traduit par la Rédaction]

**Mots-clés :** conservation, télémétrie, grand requin blanc, répartition, comportement de plongée, Atlantique Nord-Ouest

## Introduction

Abiotic conditions are considered to be the predominant factors shaping pelagic shark distributions, where modeling typically uses water temperature or related characteristics of the water column to describe or predict space use

(Andrzejczek et al. 2018; Bangle et al. 2018; Braun et al. 2018, 2019). While highly informative, this perspective presupposes that physiological tolerances determine distribution, and it averages over demographic processes (those linked to survival and reproduction; Thomson et al. 2009)

that could be equally important determinants of distribution at a population level (Thornton et al. 2011). The distribution and range of a species relative to suitable habitat results from individual movement, which is inherently linked to population dynamics through fitness. Because ocean productivity varies in space and time (Le Traon et al. 1990; Martin et al. 2002), the tendency to disperse as well as behaviour in specific areas becomes a trade-off between energy expenditure and resource procurement. In other words, the animal chooses where it remains, when to leave, and how far to go relative to the conditions it encounters in its immediate environment, tempered by previous experience, individual fitness, and physiological requirements (Bowler and Benton 2005; Kubisch et al. 2014). Thus, movement is a behavioural process that is closely associated with habitat selection, where the density of conspecifics and general community structure affect the relationship between habitat quality and expected fitness (Matthysen 2012). As a result, many species exhibit spatially distinct sex-based or size-based groupings (e.g., Coelho et al. 2017; Franks et al. 2021) and (or) substantial variation in movement behaviour among individuals (e.g., Vaudo et al. 2014; Francis et al. 2015) or over time (e.g., Wang et al. 2020). The physiological capacity of endothermic sharks to exploit habitats with a broad range of water temperatures (e.g., Campana et al. 2010; Vaudo et al. 2016; Skomal et al. 2021) makes it unlikely that such patterns result solely from environmental tolerances and suggests that behavioural processes have measurable influence on population structuring. Thus, characterizing distribution and habitat use from static environmental predictors (e.g., assuming a constant preferred temperature range) may be misleading (Hazen et al. 2013), particularly within the seasonally available habitats along the edge of a species' range.

The white shark (*Carcharodon carcharias*) presents an interesting opportunity to explore ideas related to behavioural variation in movement characteristics and how these may influence distribution patterns. In the Northwest Atlantic, the population is seasonally found throughout the continental shelf of North America (Skomal et al. 2017), and Canadian waters represent the northern extent of the species' range (COSEWIC 2006; DFO 2017). While historical sighting records are relatively sparse, the available data indicate that this northern edge of white shark distribution has not changed (Casey and Pratt 1985; Curtis et al. 2014) although it is possible that species presence in Canadian waters may be increasing (Bastien et al. 2020). Distinct differences in movement characteristics have been documented from satellite-tagged animals, with all individuals exhibiting time periods of coastal, shelf-oriented behaviour but some larger animals also shifting to pelagic habitat much farther offshore (Skomal et al. 2017). Early tagging efforts in Canadian waters confirmed seasonal, interannual presence of white sharks and suggested highest relative abundance along the southeastern coast of Nova Scotia (Bastien et al. 2020; Franks et al. 2021). A small number of tagged animals remained primarily off the southern coast of Newfoundland (Bastien et al. 2020), also suggesting that specific individuals have higher tendency to disperse. For many taxa, evolutionary research suggests that the tendency to disperse is positively correlated with popula-

tion density and negatively correlated with food availability (Bowler and Benton 2005; Kubisch et al. 2014), where wide-ranging movement behaviour helps to reduce inter- or intraspecies competition and to locate suitable resources. Inter-annual variation in species density tends to be greatest at the edge of a species' range, given the greater energetic costs associated with accessing distant habitats (Bonte et al. 2012) and with sustaining metabolic processes (e.g., growth) within edge habitats (Schlaff et al. 2014). From an evolutionary perspective, white sharks moving to Canadian waters would be expected to be those with greater behavioural tendency to disperse relative to the wider population. Specific ontogenetic stages or sexes may respond differently to abiotic conditions (Schlaff et al. 2014), leading to spatial population structure. Thus, a small and non-random component of the population may be expected to be found in Canadian waters, exhibiting seasonal behaviour and movement characteristics that differ from the wider population in the Northwest Atlantic.

Understanding habitat use and movement behaviour is critical to assess progress relative to Canadian conservation objectives for white shark. The population in the Northwest Atlantic was designated as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and was listed on Schedule 1 of the Species at Risk Act. Listed species require an action plan to promote recovery, where the identified recovery objectives are (1) to maintain or increase the population of white sharks that frequents Atlantic Canadian waters and (2) to maintain the distribution of white sharks in Atlantic Canadian waters (Fisheries and Oceans Canada 2021). Thus, being able to explain distribution patterns and predict future changes in distribution becomes critical to assess progress relative to Canadian conservation objectives. Recovery targets that specify what abundance should be in Canadian waters (number of individuals) will likely be developed once population size in the Northwest Atlantic is known. Other Canadian management priorities relate to understanding seasonal and yearly movement patterns, in addition to using long-term monitoring and pop-up satellite archival tag (PSAT) tagging to quantify distribution from environmental associations (Bastien et al. 2020; Fisheries and Oceans Canada 2021). Unfortunately, current information is considered inadequate to represent the population's actual range and seasonality in Canadian waters (Bastien et al. 2020).

We compiled extensive acoustic and satellite tag data from a decade of collaborative research on the Northwest Atlantic white shark population to address research priorities and Canadian conservation objectives for distribution, seasonality, and movement patterns. Specifically, we have (1) quantified the proportion of the tagged population making use of Canadian waters; (2) demonstrated Canadian distribution and seasonal patterns in occupancy relative to monitoring effort over a >10-year timespan; and (3) assessed whether the life history characteristics of animals moving to the northern edge of their range differed. Characterizing movement patterns and seasonality enabled us to provide guidance on the design of future monitoring efforts in Canadian waters, and to comment on the life stages that may benefit most from conservation actions implemented in Canada. White shark

**Table 1.** Summary of the tagging locations, attachment methods, and tag types used for 227 white sharks in the Northwest Atlantic.

Country	Study site	Type	Years	N	Internal	External	Acoustic	PSAT
US	Cape Cod, Massachusetts	Research trip	2009–2020	240 (195)	4	197	201	39
US	Jacksonville, Florida	Research trip	2013	1 (1)	All	0	All	All
US	New Jersey	Opportunistic tagging	2017	1 (1)	0	All	All	None
US	South Carolina	Opportunistic tagging	2016–2020	31 (28)	0	28	18	13
Canada	Port Mouton, Nova Scotia	Research trip	2018–2019	2 (2)	0	All	1	All

**Note:** Instances where all animals were tagged with a given transmitter type or attachment method are identified. The total number of tags deployed (N) is given, followed by the number of individuals tagged in brackets. Single animals could carry two types of transmitters (acoustic and pop-up satellite archival tags (PSAT)), which could be deployed internally (acoustic) or externally (acoustic and PSAT). Other animals carried one type of tag and several animals were tagged twice (i.e., after expiry of the original tag and (or) due to tag loss). Note that because of this variability, the numbers given in the Internal/External or Acoustic/PSAT columns do not necessarily sum to N.

sensitivity to threats may be greatest at the northern extent of their range (Fredston-Hermann et al. 2020; Yan et al. 2021), underscoring the need for such targeted research to support Canadian recovery objectives.

## Methods

We analyzed data from an ongoing, large-scale white shark research program initiated in 2009 by the Massachusetts Division of Marine Fisheries (MDMF), with later contributions from the Atlantic White Shark Conservancy (AWSC; 2013 onward) and Fisheries and Oceans Canada (DFO; 2016 onward). Among other objectives, this research program has collected the largest set of acoustic tagging and monitoring as well as PSAT data on this species in the Northwest Atlantic. Given our study objectives, we focused on the subset of data from animals that were detected or were tagged in Canadian waters.

### Tagging methodology

Activities in the US were conducted under Exempted Fishing Permits (SHK-EFP-11-04, SHK-EFP-12-08, SHK-EFP-13-01, SHK-EFP-14-03) issued by the NMFS Highly Migratory Species Management Division and permits issued by the MDMF. Activities in Canada were permitted under Section 73 of the Species at Risk Act (#DFO-MAR-2017-07) as well as under the general science research license of DFO (#323354). Field teams adhered to animal care protocols as determined by the Canadian Council for Animal Care (AUP #17-30, #19-33).

White sharks were tagged off the east coast of the US between September 2009 and March 2021 and off the southwest coast of Nova Scotia in September 2018 and 2019 (Table 1). The vast majority (97%) of transmitters (PSAT and (or) acoustic) were tethered to an intramuscular titanium dart with stainless-steel wire and embedded externally in the dorsal musculature using a modified harpoon technique (Chaprales et al. 1998; Skomal et al. 2017; Winton et al. 2021). Acoustic tags were implanted internally in five individuals in 2012 and 2013; these sharks were captured on handlines and tagged following the methods described by Domeier and Nasby-Lucas (2012). Externally tagged animals were free-swimming, except for the first-ever tagging event in Canadian waters (2018), which followed capture by handline. Unlike the 2012–2013 deployments (Domeier and Nasby-Lucas 2012),

total interaction time (initial capture to release) was <5 min and the shark remained in the water throughout. The non-capture methodology was preferred to minimize tagging effects and ensure that movement data were more likely to represent natural behaviour. Tagging onboard following capture is known to alter movement behaviour during a prolonged recovery period for lamnid sharks (Hoolihan et al. 2011; Bowlby et al. 2021) and carcharhinid species (Vaudo et al. 2014). Also, our non-capture tagging methodology was unaffected by gear selectivity, unlike capture-based sampling that is known to be size-selective (Maunder et al. 2006; Rotherham et al. 2007; Christiansen et al. 2020).

Shark total length (TL) was estimated relative to reference length markings on the gunnel of the vessel (Canadian tagging), from aerial photos, and (or) from expert opinion using the vessel pulpit length (320 cm) as a size reference (MDMF tagging; Skomal et al. 2017). Animals were assigned to juvenile (<3 m), subadult (males: 3–3.4 m; females: 3–4.7 m), and adult (males: ≥3.5 m; females: ≥4.8 m) life stages on the basis of sex-specific estimates of size at maturity (Francis 1996; Pratt 1996; Castro 2011). Slightly different cutoffs were used for recent work in the Northwest Atlantic, notably assigning females as mature at 4.2 m TL (Franks et al. 2021). However, for consistency with previous analyses of data from the MDMF and AWSC white shark research program (Skomal et al. 2017), we retained the original size classes. Given the relative uncertainty in size at age relationships for white shark (Natanson and Skomal 2015), we did not attempt to account for growth over the duration of the study. If the underside of the pelvic fins was not clearly visible in video footage collected at the time of tagging and sex could not be determined, animals <3 m were considered juveniles, ≥4.8 m were considered adults, and the remainder were not assigned a life stage.

### Acoustic tag deployments and acoustic monitoring

Acoustic tag deployments (Supplement A; Table S1) used individually coded transmitters (models V16 or V16TP, Innovasea, Bedford, Nova Scotia). All acoustic tags were programmed to transmit at high power (69 kHz), but nominal transmission intervals varied among tag batches. The majority of transmitters deployed (N = 185) had random transmission intervals between 60 and 100 s and an estimated battery life of 1741–3217 days (~4.7–8.8 years). A subset of transmit-

ters deployed near the beginning ( $N = 32$ ; 2010–2014) and end ( $N = 10$ ; 2019) of the tagging period had random transmission intervals of 30–90 and 80–160 s and a battery life of 1365–1642 (~3.7–4.5) and 2435 days (~6.7 years), respectively. The minimum timeframe that a tag was at large occurred between its deployment date and its most recent detection anywhere along eastern North America. Summing the number of tags at large in any given year gave the minimum size of the tagged population with the potential to be detected. Six tags deployed in South Carolina did not have the possibility of being detected given the download date from the Ocean Tracking Network (OTN) data center and were removed from further analyses.

In Canadian waters, tag transmissions were detected by multiple acoustic receiver arrays deployed by DFO Science and (or) archived via the OTN data center ([https://members.oceantrack.org/OTN/projects?sorts\[ocean\]=1andsorts\[collectioncode\]=1](https://members.oceantrack.org/OTN/projects?sorts[ocean]=1andsorts[collectioncode]=1); accessed December 2020; citations and metadata provided in Supplement A; Table S2). Any array that was active at any time from 2009 onwards and had receivers deployed in coastal or estuarine locations (as opposed to being exclusively in fresh water) was incorporated to characterize acoustic listening effort in Canadian waters ( $N = 6911$  receivers). We considered two or more acoustic detections within a 24 h period, either at a single receiver or multiple receivers within an array, to be valid (Friess et al. 2021). Because there were differences in study objectives for each array, deployment designs differed in receiver number, spatial orientation (e.g., lines and grids), detection range (VR2 vs. VR4 installations), distance from the coast (shallow vs. deep water), and duration (months to years). In conjunction with the white shark research program initiated by DFO Science, seven receiver arrays were specifically placed in locations where white sharks had been sighted in the past to increase the potential for species-specific data collection. We consider the acoustic data to be presence-only, rather than presence-absence, given variable detection efficiency among deployments.

## Data analyses: annual and seasonal patterns

To prevent overestimation of white shark occurrences, simultaneous detections on multiple closely positioned acoustic receivers needed to be counted as single, discrete detection events. The majority of acoustic projects undertaken by DFO and (or) archived with the OTN data center contained multiple, closely positioned receivers with overlapping detection ranges. As in Friess et al. (2021), we grouped these individual receivers into spatially distinct units for analyses, resulting in 120 arrays in Canadian waters (Supplement A; Table S2). A detection event was the amount of time between the first detection of a particular tag at any individual receiver within the array until the last detection of that tag at any individual receiver within the same array. We calculated the duration in seconds of each detection event using the GLATOS package in R (Holbrook et al. 2019). Given that white sharks are highly mobile, we assumed that detections within a receiver array separated by 1 h (3600 s) or more represented discrete events. This condensed 12 831 individual transmit-

ter detections into 893 valid detection events, where the time (seconds) between the first detection and the last within each array became the duration of the detection. Similarly, we approximated monitoring effort as the sum of the number of days between deployment and the archived retrieval date of each receiver, or the last download date when retrieval was unknown. We considered receivers without these dates to be deployed and not yet downloaded (2019 onward) or lost (prior to 2019). For the individual animals included in this study, there were also detections at acoustic receivers outside of Canadian waters reported through the OTN data center. It was outside of the scope of this manuscript to compile a complete list of acoustic monitoring installations along the eastern seaboard in addition to those available through the OTN (Bangley et al. 2020), so all US detections were grouped as a single category. These US detections were only used to indicate whether or not tagged white sharks spent the majority of their detected time in Canadian waters, recognizing that detections in the US were underestimated and (or) not available for certain individuals.

We evaluated whether the acoustically tagged individuals detected in Canadian waters represented a random sample of the tagged population using a simple randomization test (Manly 1991), where the relative probability of detecting a specific animal over the duration of Canadian monitoring (2009–2020) was determined by the number of years its acoustic tag was active. Tags that were active for longer durations had a higher probability of being selected multiple times under random sampling. This makes the assumption that each active tag has equivalent detection probability. While it is possible that animals tagged in Canada may have higher detection probability, this source of bias would have been negligible for this study. It would only apply for a single animal, which was tagged outside the range of nearby coastal acoustic monitoring installations (3 nmi offshore; 1 nmi = 1.852 km). The null distribution for the test statistic was generated by taking 10 000 random samples from the pool of potential dispersers (active tags), accounting for differences in selection probability among years. For example, if there were 9 unique tag numbers active in a specific year and 2 of them were detected in Canada, we took a random sample of size 2 from the 9 active tags for that year. The sampled tag numbers from all years were aggregated and summed to get a total number of unique tags. The null distribution represents the number of tagged individuals that we would expect to visit Canadian waters if a random sample of the tagged population moved northward. The test statistic was simply the actual number of tagged animals detected in Canadian waters from 2011 to 2020. The proportion of the null distribution to the left of the test statistic represents the  $P$  value of the test (Manly 1991). If the actual number of unique individuals was smaller than that expected by random sampling, it indicated that specific animals tended to return multiple times to Canadian waters.

## PSAT deployments

PSATs deployments included MK10-PAT, miniPAT, and MK10-AF tags manufactured by Wildlife Computers (Supplement A; Table S3). Tags were programmed to record depth

(MK10 models: range = 0–1000 m, resolution  $0.5 \text{ m} \pm 1.0\%$ ; miniPAT: range 0–1700 m, resolution  $0.5 \text{ m} \pm 1.0\%$ ), water temperature (range  $-40$  to  $60 \text{ }^\circ\text{C}$ , resolution  $0.5 \text{ m} \pm 1.0\%$ ), and light level (470 nm, logarithmic range =  $5 \times 10^{-12}$  to  $5 \times 10^{-2} \text{ W}\cdot\text{cm}^{-2}$ ) at regular intervals (MK10 models: 10 s, miniPAT: 15 s).

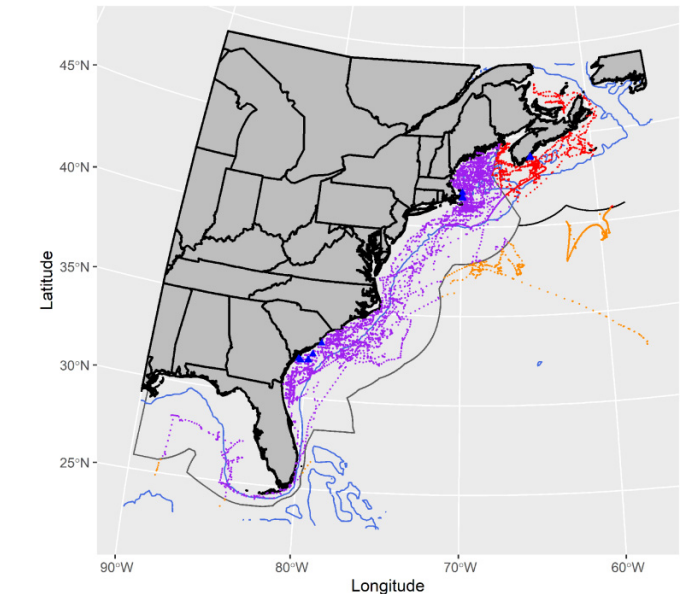
## Data analyses: temperature and depth associations

Archived depth and temperature information were aggregated into 12 bins to generate 12 h summaries (miniPAT) or 14 bins to generate 24 h summaries (MK10 models). The PSAT data were transmitted to the ARGOS satellite system and decoded using Wildlife Computer's proprietary software. Movement tracks were estimated using an integrated state-space hidden Markov model (HMM) called GPE3 (Wildlife Computers; Pedersen et al. 2011). This HMM combines a movement model conditional on swimming speed with an observation model conditioned by light, temperature, and depth data to generate the posterior probability distribution of the animal's position. Maximum swimming speed was set at  $2 \text{ m}\cdot\text{s}^{-1}$  following Skomal et al. (2017). If available, known locations of an animal from other sources (e.g., acoustic detections) were included to reduce uncertainty in position estimates. Incorporating known locations tended to shift the movement track closer to the coast. Time-at-depth (TAD) was assessed from data aggregated into 12 bins: 0–2, 3–10, 11–25, 26–50, 51–75, 76–100, 101–200, 201–400, 401–600, 601–800, 801–1000, >1000 m. Time-at-temperature (TAT) was assessed relative to 12 bins: 0–5, 6–7, 8–9, 10–11, 12–13, 14–15, 16–17, 18–19, 10–21, 22–23, 24–25, and >25  $^\circ\text{C}$ .

For PSAT data, we used the boundaries of the Canadian and US Exclusive Economic Zones (EEZ) relative to the most probable location estimate of each animal from GPE3 to separate tracks into Canadian, US, and international components. We recognize that the EEZ is a regulatory boundary rather than one that identifies sub-components of the population. The one animal that entered Canadian waters briefly (3 days) before remaining offshore in international waters was removed from further analyses (Fig. 1). We used the corresponding date that an animal moved into or out of each EEZ to similarly partition the temperature and depth information when calculating TAD and TAT using the "RchivalTag" package in R (Bauer 2020). Partitioning by EEZ reduced the amount of available binned temperature and depth data, resulting in usable information from 16 tags for TAD and 10 tags for TAT. We compared the range of temperatures and depths that white sharks used while in Canada versus the US using Levene's test for homogeneity of variances. This test is based on the differences between the absolute deviations of each depth or temperature observation from the median value for each group (Canada, US) and is appropriate for skewed distributions (Derrick et al. 2018). Variances are equal under the null hypothesis, indicating equivalent variability in the depths or temperatures frequented while in Canada versus the US.

Mean swimming speeds and daily horizontal displacements were calculated using the adehabitatLT package in R (Calenge 2006) from each movement track. This involved re-

projecting the most probable location estimates relative to UTM Zone 20 North, transforming the track into a raster layer, and partitioning it into daily segments. To characterize vertical movement in the water column, we correlated track location estimates with bathymetric data (1 arc min resolution; approximately 1 nmi) accessed from the NOAA ETOPO1 database via the "marmap" package in R (Pante and Simon-Bouhet 2013) and partitioned shark dive depths relative to quartiles of the water column (e.g., top 25%, 50%, 75%, or 100%). At coastal aggregation sites, white sharks tend to be bottom-oriented during periods of nearshore residency (Goldman and Anderson 1999; Bradford et al. 2012). Over larger spatial scales, carcharhinid species exhibit substantial variability in individual dive behaviour, with no functional relationship between dive depth and location (e.g., Vaudo et al. 2014). If sharks regularly dove to the bottom, they would use all quartiles of the water column (i.e. 100%) and dive depths would be dependent on water depth at the particular location of the shark. Conversely, no relationship between dive depth and location would suggest that animals are choosing to remain at specific positions in the water column.



Given the potentially large errors associated with daily light-based geolocation estimates (Braun et al. 2015), we eval-

uated the sensitivity of our categorization of PSAT tracks into Canadian and US components as well as inferences on diving behaviour to inaccuracies in position. In addition to point locations, we extracted the 50% likelihood profile ellipse for each daily position estimate in addition to using a 100 km buffer around each point estimate to re-extract bathymetry (Supplement B; Fig. S1). The 50th percentile ellipse around the maximum likelihood position estimates tended to encompass more than a 25 km radius, even though GPE3 incorporates ancillary information on bathymetry, real-time positions, and sea surface temperature (SST) relative to the depth and temperature information recorded by each PSAT tag to improve positional accuracy (Aarestrup et al. 2009; Braun et al. 2018). Thus, the sensitivity analyses evaluated two alternate scenarios with progressively lower positional accuracy, relative to the point estimates.

### Data analyses: population structure

We evaluated population structuring in the Northwest Atlantic using logistic regression, to assess whether animals with specific life history characteristics were preferentially found in Canadian waters. Sex and life stage were categorical predictors, and data from all tagged individuals (PSAT and acoustic) was combined. Only observations in which both biological characteristics were known were included in the regression and repeated detections of the same animal were removed. To prevent misclassifications of life stage due to growth, we identified animals that were close to the upper size of a particular life stage when tagged, but were not detected in Canada for >2 years following tagging, and removed these individuals from consideration ( $N = 4$ ; MA1301, MA1202, SC1702, and MA1617). We identified the preferred model using stepwise selection and  $AIC_c$  from nested models (Johnson and Omland 2004). A crucial metric of logistic model performance is how well it can predict the target variable from out-of-sample observations. We split the data into training (60%) and test sets (40%), and determined how accurately the model fit to the training set could predict the individuals that came to Canada in the test set (Giancristofaro and Salmaso 2003). An appropriate model will have high prediction accuracy.

To evaluate smaller-scale population structuring within Canadian waters, we initially separated animals that came to Canada by sex and life stage for analyses on movement rates, seasonal occupancy, locations visited, and diving behaviour. Recall that a low proportion of the tagged animals came to Canada, which meant that there was much less data available for these comparisons. Differences were not visually apparent, and the sparse data were highly unbalanced, which precluded statistical testing. While our results represent all animals combined, this does not preclude the possibility that finer-scale partitioning among components of the population while in Canadian waters would be evident from additional data.

## Results

The opportunistic tagging resulted in study animals ranging in size from 1.2 to 5.5 m (2.2–5.5 m for females and 1.2–

4.4 m for males), representing early juvenile to mature life stages of both sexes. The animals that came to Canadian waters spanned a similar size range at the time of tagging, 2.3–4.9 m for females and 2.1–4.0 m for males (Supplement A; Tables S2 and S3). Of the 53 animals tagged with PSATs by the wider research program, only 16 (30%) spent a portion of their time in Canadian waters. Similarly, of the 205 acoustically tagged animals, 51 (25%) had valid detection events in Canadian waters.

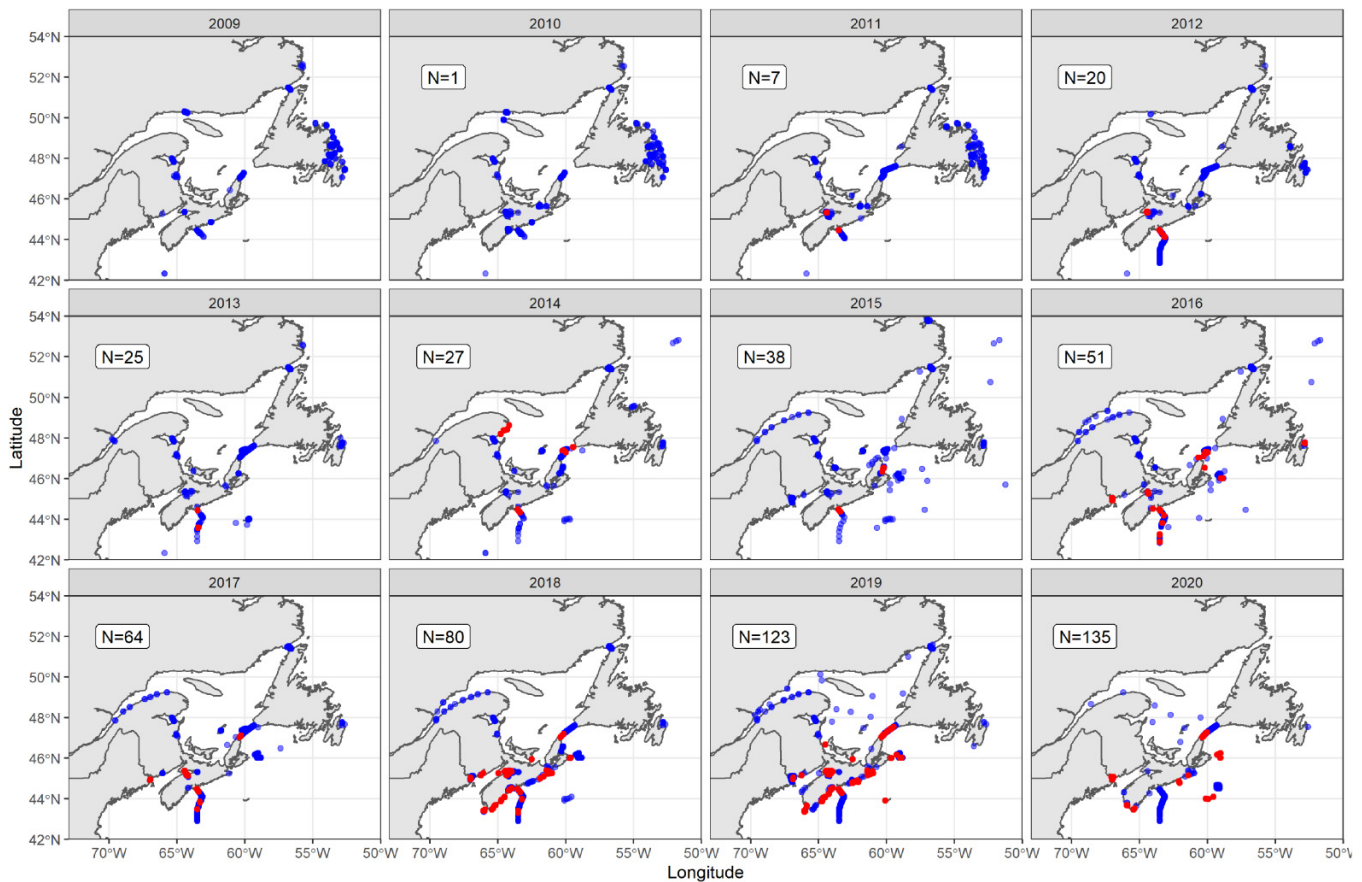
### Acoustic monitoring

Total acoustic monitoring effort was greatest along the Atlantic coast of Nova Scotia, with lesser amounts in the Bay of Fundy (primarily the Minas Basin) and Gulf of St. Lawrence, and the least off Newfoundland and Labrador (Fig. 2; Table 2). After 2016, the amount of listening effort and number of deployments increased substantially along the South Shore (Yarmouth to Halifax), in the Gulf of St. Lawrence, and in the Bay of Fundy (Table 2). However, it is difficult to determine if this pattern remained consistent for 2020, given that a large number of receivers had yet to be downloaded and (or) have their metadata archived on the publicly accessible OTN platform. In particular, listening effort off Newfoundland was substantially underestimated in 2019 and 2020, given that download dates for multiyear deployments contributing to a substantial Northern Atlantic cod project were not yet available. Also, restrictions and operational limitations for field work related to the COVID-19 pandemic likely reduced monitoring effort and caused delays in data archival throughout 2020. Annual detections of tagged white sharks on Canadian acoustic monitoring arrays were sporadic until 2016 and became more frequent thereafter. This increase was concurrent with increases in both the number of acoustically tagged animals (Fig. 2) as well as listening effort (Table 2). For example, increased detections in 2018 and 2019 coincide with the initiation of the white shark acoustic monitoring program by DFO Science, which deployed seven arrays at locations with historic sightings. However, COVID pandemic restrictions prevented deployment of these same arrays in 2020.

### Yearly and seasonal patterns

The total duration of all detection events within a region varied by orders of magnitude among years, with Yarmouth to Halifax having detection events in all years but all other regions having zero detections in at least 3 years from 2011 to 2020 (Supplement A; Table S4). Similarly, time spent in the vicinity of acoustic arrays (detection events) relative to the total number of monitoring days was extremely variable among regions and years. Considering data from 2016 to 2019, median values sequentially increased by an order of magnitude, from 0 s-monitored day<sup>-1</sup> off the coast of Newfoundland and Labrador, to 0.07 s-monitored day<sup>-1</sup> in the Gulf of St. Lawrence, 0.16 s-monitored day<sup>-1</sup> along the Eastern Shore of Nova Scotia (Halifax to Glace Bay), 0.44 s-monitored day<sup>-1</sup> along the South Shore (Yarmouth to Halifax), and 4.3 s-monitored day<sup>-1</sup> in the Bay of Fundy. However, it is important to note that the confined geography of the Bay of Fundy (Fig. 2; Fig. 3A) coupled with a very high density of

**Fig. 2.** Acoustic monitoring deployments in Canadian waters where white sharks were detected (red points) or not detected (blue points) by year. The total number of study animals with an active acoustic tag in each year ( $N$ ) is shown by the inset text. Note that receiver deployments and tag detections in 2020 are known to be incomplete. Refer to [Table 2](#) for the number of individuals represented by the detections each year. Coastal boundaries were freely available from Natural Earth. Coordinate reference system: WGS84. [Colour online.]



receivers within the Minas Basin increased the number and duration of detection events relative to more exposed coastlines. Therefore, we do not consider the estimate for the Bay of Fundy to be comparable with the other areas, and it should not be interpreted as being the geographic region where white sharks spent the majority of their time in Canadian waters. Conversely, total monitoring effort off Newfoundland was an order of magnitude lower than in other regions, and it is possible that white shark presence was underestimated from the acoustic monitoring data.

White sharks were detected most consistently along the South Shore of Nova Scotia (Yarmouth to Halifax), with a range of 1–17 individual animals detected each year ([Table 3](#)). At least one animal was detected in all other regions from 2016 to 2019 inclusive, with the exception of Newfoundland and Labrador. Between 2011 and 2020, a similar total number of acoustically tagged white sharks visited the Bay of Fundy, the South Shore (Yarmouth to Halifax), and the Eastern Shore (Halifax to Glace Bay), at 24, 31, and 32 animals, respectively ([Table 3](#)). Only 12 different white sharks were recorded within the Gulf of St. Lawrence (the majority in a single year), and only one was detected off the coast of Newfoundland and Labrador. Annual detection rates were quite variable, with

a median of 17% (range 5%–29%) of acoustically tagged white sharks transiting to Canada ([Table 4](#)). Of these animals, acoustic detections reported through the OTN data center were still more frequent in US waters than in Canadian ([Fig. 3](#)), suggesting that individuals predominantly use habitats outside of Canadian waters on an annual basis.

There were distinct seasonal patterns in the acoustic data, where the vast majority of animals were detected from July to early November in Canadian waters ([Table 4](#); [Fig. 3](#)). In any year from 2011 to 2020, there were sporadic detections of single animals in December, February and March, and no detections in any year during January, April, or May ([Table 4](#)). While there was generally lower listening effort over the winter months, regional coverage was still quite high (example given for 2018; Supplement B; [Fig. S2](#)) so we do not expect that seasonal patterns were solely a function of monitoring effort. The same animal was often detected in multiple months, and individuals tended to return habitually to the same region in subsequent years ([Fig. 3](#)). For example, MA1702 and MA1512 each returned to Canadian waters in 4 consecutive years and were detected mainly in one area, Halifax to Glace Bay and Yarmouth to Halifax, respectively. Similarly, MA1606 returned to the Bay of Fundy in 3 consecutive years ([Fig. 3](#)).

**Table 2.** Summarized acoustic monitoring data showing the total number of monitoring days and number of receivers, compared to the number of receivers that detected white sharks and the number of individuals detected for five geographic regions in Canadian waters (Fig. 3A).

Year	Total monitoring (days)	No. of receivers	No. of receivers detecting sharks	No. of unique sharks detected
<b>Bay of Fundy</b>				
2011	13 068	64	4	1
2012	11 243	37	17	3
2013	4 110	20	0	0
2014	3 556	17	0	0
2015	5 319	34	0	0
2016	10 254	70	43	3
2017	12 276	66	37	3
2018	25 803	113	35	5
2019	25 695	213	34	9
2020	1 108*	3*	16*	7*
<b>Yarmouth to Halifax</b>				
2011	48 408	50	2	1
2012	283 695	226	7	2
2013	88 665	84	7	2
2014	28 899	34	9	2
2015	9 723	14	4	2
2016	176 007	168	21	5
2017	187 193	201	16	4
2018	198 877	230	42	8
2019	201 032	353	88	17
2020	170 481*	196*	4*	3*
<b>Halifax to Glace Bay</b>				
2011	36 892	154	0	0
2012	76 996	164	0	0
2013	171 461	195	0	0
2014	70 559	155	5	1
2015	57 164	150	19	1
2016	41 668	109	11	4
2017	174 505	221	3	1
2018	166 029	219	17	4
2019	160 134	194	75	20
2020	114 229*	152*	33*	16*
<b>Gulf of St. Lawrence</b>				
2011	11 446	74	0	0
2012	6 972	69	0	0
2013	9 134	67	0	0
2014	11 425	96	6	1
2015	19 520	213	0	0
2016	13 137	112	0	0
2017	12 185	127	0	0
2018	10 508	121	1	1
2019	14 471	127	14	11
2020	1 495*	8*	0*	0*
<b>Newfoundland</b>				
2011	42 778	118	0	0
2012	6 294	30	0	0
2013	6 224	19	0	0
2014	6 828	20	0	0



**Table 2.** (concluded).

Year	Total monitoring (days)	No. of receivers	No. of receivers detecting sharks	No. of unique sharks detected
2015	6 156	28	0	0
2016	6 717	15	4	1
2017	2 172	8	0	0
2018	1 304	7	0	0
2019	0*	4*	0*	0*
2020	76*	1*	0*	0*

**Note:** Recent years in which deployments have yet to be downloaded and (or) publicly accessible deployment data are considered incomplete are identified with an asterisk (\*). The same shark may be detected in multiple regions within a single year. The total number of monitoring days was a sum of the deployment durations from each of the receivers deployed in a specific region.

Fidelity to Canadian waters was also suggested by the results of the randomization test, which indicated that the subset of animals detected in Canadian waters did not represent a random sample of the individuals with active tags ( $P$  value  $\ll 0.001$ ). The total number of tagged animals moving to Canada (the test statistic) was outside of the null distribution (Supplement B; Fig. S3), being much smaller than expected (51 individuals, compared to an expected median of 71). This means that specific animals were detected more frequently in Canadian habitats than would be predicted by chance, providing further evidence that a subset of the tagged population tended to return multiple times to northern habitats. This subset was composed primarily of juvenile and subadult animals. The preferred logistic regression model retained life stage as a predictor (Supplement A; Tables S5 and S6). Although the AICc from the next-best model incorporating sex and life stage was only 1.6 units greater, the coefficient estimate for sex was not significant ( $P$  value = 0.155) and the difference in residual deviance was marginal. Model validation by assessing the classification rate indicated high predictive accuracy, with 81% of observations in the test data being accurately assigned. Estimated coefficients were 1.5449 (SE = 0.5452) for juveniles and 1.2233 (SE = 0.4889) for subadults, with an intercept of  $-2.0149$  (SE = 0.4346) for adults. After exponentiation, these coefficients suggested that the odds of a tagged juvenile or subadult white shark transiting to the area monitored by receiver arrays in Canadian waters were 4.7 and 3.4 times higher, respectively, than for a tagged adult. Converting to probabilities, a tagged adult had a 12% chance of being detected in Canadian waters, while a tagged subadult had a 31% chance and a tagged juvenile had a 38% chance.

### PSAT monitoring

The high-resolution information from PSAT-tagged animals was consistent with the seasonal patterns in the acoustic data. Collectively, these 16 animals were in Canadian waters between June and early November (Fig. 4, cf. panels A and D), yet also spent the majority of their time along the continental US (Fig. 1; Supplement A; Table S3). The PSAT-tagged animals that were also detected via acoustic monitoring tended to be those that spent longer durations in Canadian waters, and represented animals of all size classes (Supplement A; Table S3). Mean  $\pm$  SD deployment duration was  $211 \pm 97$  days

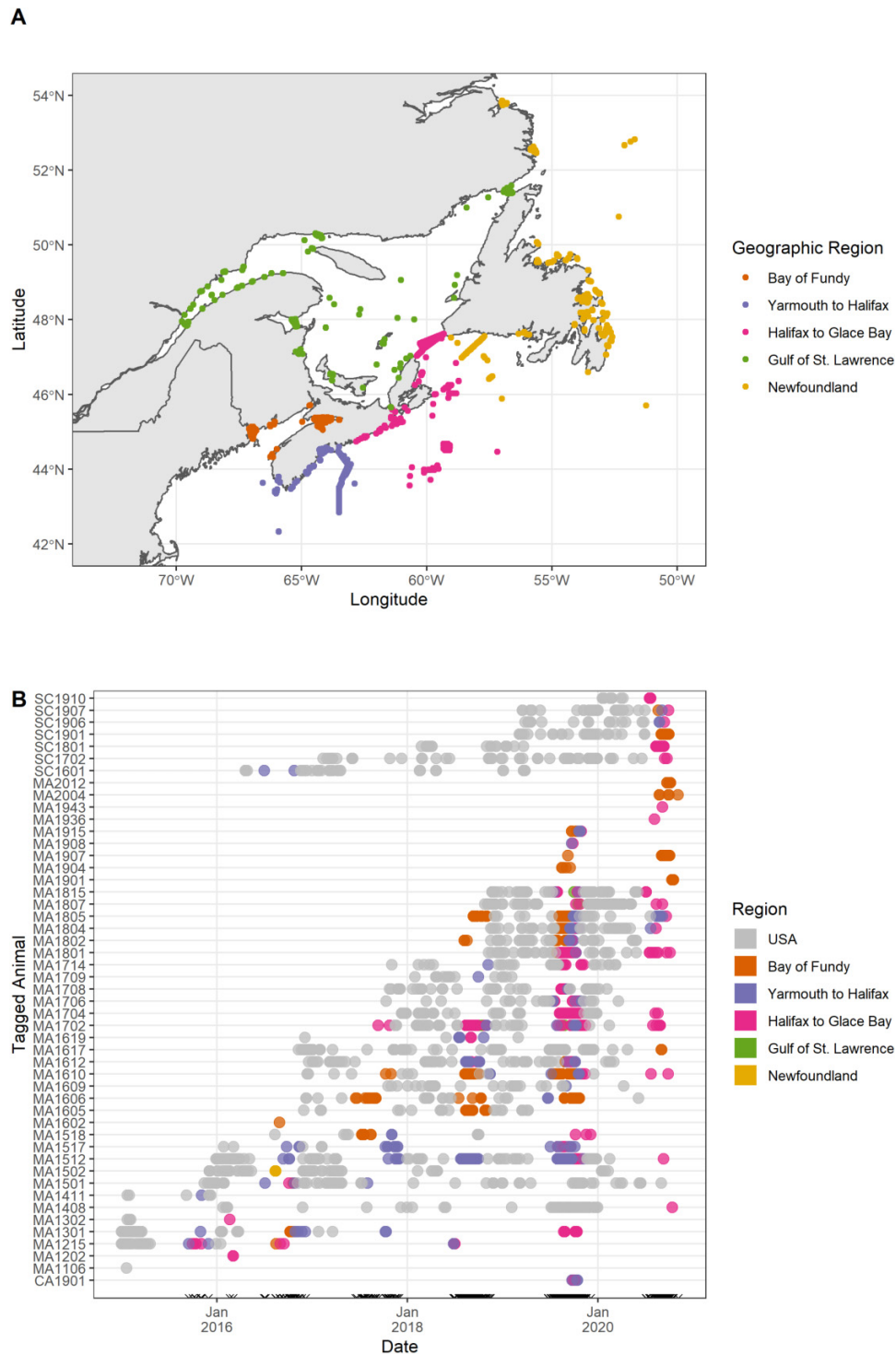
and mean recorded track length was  $7676 \pm 5098$  km (Supplement A; Table S3). The density distribution of estimated movement speeds for white sharks in the US or Canada were essentially overlapping, indicating that they traveled similar distances over similar durations in both regions (Supplement B; Fig. S4). This analysis was at a relatively coarse resolution because it aggregated information throughout the movement tracks. This means it would not detect fine-scale heterogeneity in movement speeds over short timeframes and relatively small horizontal displacements.

### Temperature and depth associations

While in Canadian waters, animals remained almost exclusively in depths  $<50$  m. These same animals tended to undertake deeper dives while in US waters, yet the deeper diving behaviour occurred almost exclusively during the months that white sharks were outside of Canadian waters (November to early June; Supplement B; Fig. S5, cf. panels A and B, D and E). Considering data from the same times of year, white sharks in US waters also remained predominantly in the top 50 m of the water column (Fig. 4, cf. panels A and D), indicating that the tagged population exhibited shallow diving behaviour even when in distinctly different locations along the continental shelf. Median dive depths were very similar (19.4 m in Canada, 20.8 m in the US) and Levene's test indicated that variance in depth was equivalent in both regions ( $F$  value = 0.007;  $P$  value = 0.934). The similarity in diving behaviour during the summer and fall suggests that white sharks are using similar habitats and exhibiting similar behaviour during these months in both US and Canadian waters. However, there were greater differences in the TAT histograms, where animals in Canadian waters experienced a narrower range of temperatures as compared to animals in the US (Fig. 4, cf. panels C and F). Even though the median temperature was similar (cf.  $10.4^\circ\text{C}$  in Canada with  $12.5^\circ\text{C}$  in the US), the variance in temperature was significantly smaller in Canadian waters ( $F$  value = 19.06;  $P$  value  $\ll 0.001$ ).

Qualitative evaluation of the movement tracks of PSAT-tagged animals indicated that tagged white sharks preferentially remained within the 200 m depth contour while in Canadian waters (Fig. 1). Splitting the movement track into components where each shark was in deep ( $>200$  m) versus shallow ( $<200$  m) depths demonstrated that animals in Canadian waters almost always remained in the top 25% of the

**Fig. 3.** Acoustic monitoring locations in Canadian waters (A) and detection timelines for acoustically tagged sharks that moved into Canadian waters (B), categorized by geographical region. Note that there were differences in deployment dates among receivers and not all monitoring locations in panel A were active at the same time. To better evaluate seasonality, any detection in Canadian waters is represented by a black "x" along the x-axis in panel B. Coastal boundaries were freely available from Natural Earth. Coordinate reference system: WGS84. [Colour online.]



water column when in deep water, and in the top 50% of the water column (i.e., <100 m deep) when in shallow water (Fig. 5A). Conversely, white sharks made greater use of the deeper quartiles of the water column when in US waters irre-

spective of whether they were at locations within or beyond the 200 m depth contour (Fig. 1; Fig. 5A). When white sharks were in Canadian waters, their dive depths appeared largely unrelated to bathymetry. This result was robust to positional

**Table 3.** The number of acoustically tagged white sharks detected in 5 regions within Canadian waters from 2011 to 2020.

Area	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	Total
Bay of Fundy	1	3	0	0	0	3	3	5	9	7	24
Yarmouth to Halifax	1	2	2	2	2	5	4	8	17	3	31
Halifax to Glace Bay	0	0	0	1	1	4	1	4	20	16	32
Gulf of St. Lawrence	0	0	0	1	0	0	0	1	11	0	12
Newfoundland	0	0	0	0	0	1	0	0	0	0	1

**Note:** The total represents the number of unique animals detected in each region throughout the entire monitoring period (2011–2020 inclusive). The same animal could be detected in multiple regions. Refer to Fig. 3A for the regional boundaries. Refer to Fig. 2 for information on the number of active tags and the spatial distribution of detections relative to monitoring effort each year.

**Table 4.** The number of acoustically tagged white sharks detected by month in Canadian waters from 2011 to 2020.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total	Rate (%)
2011	0	0	0	0	0	0	0	1	0	1	0	0	2	29
2012	0	0	0	0	0	0	1	2	1	2	1	0	4	19
2013	0	0	0	0	0	0	0	1	0	1	0	0	2	9
2014	0	0	0	0	0	0	0	1	2	1	1	0	2	7
2015	0	0	0	0	0	0	0	0	1	2	1	0	2	5
2016	0	1	1	0	0	0	2	3	3	4	2	1	10	19
2017	0	0	0	0	0	1	2	3	2	4	3	0	7	11
2018	0	0	0	0	0	1	4	6	8	8	3	0	12	15
2019	0	0	0	0	0	1	9	14	18	18	6	1	23	19
2020	0	0	0	0	0	0	5	12	15	4	1	0	22	19

**Note:** The total represents the number of unique animals detected each year, aggregating over all months. The same animal could be detected in multiple years. The rate represents the percentage of active acoustic tags detected in each year.

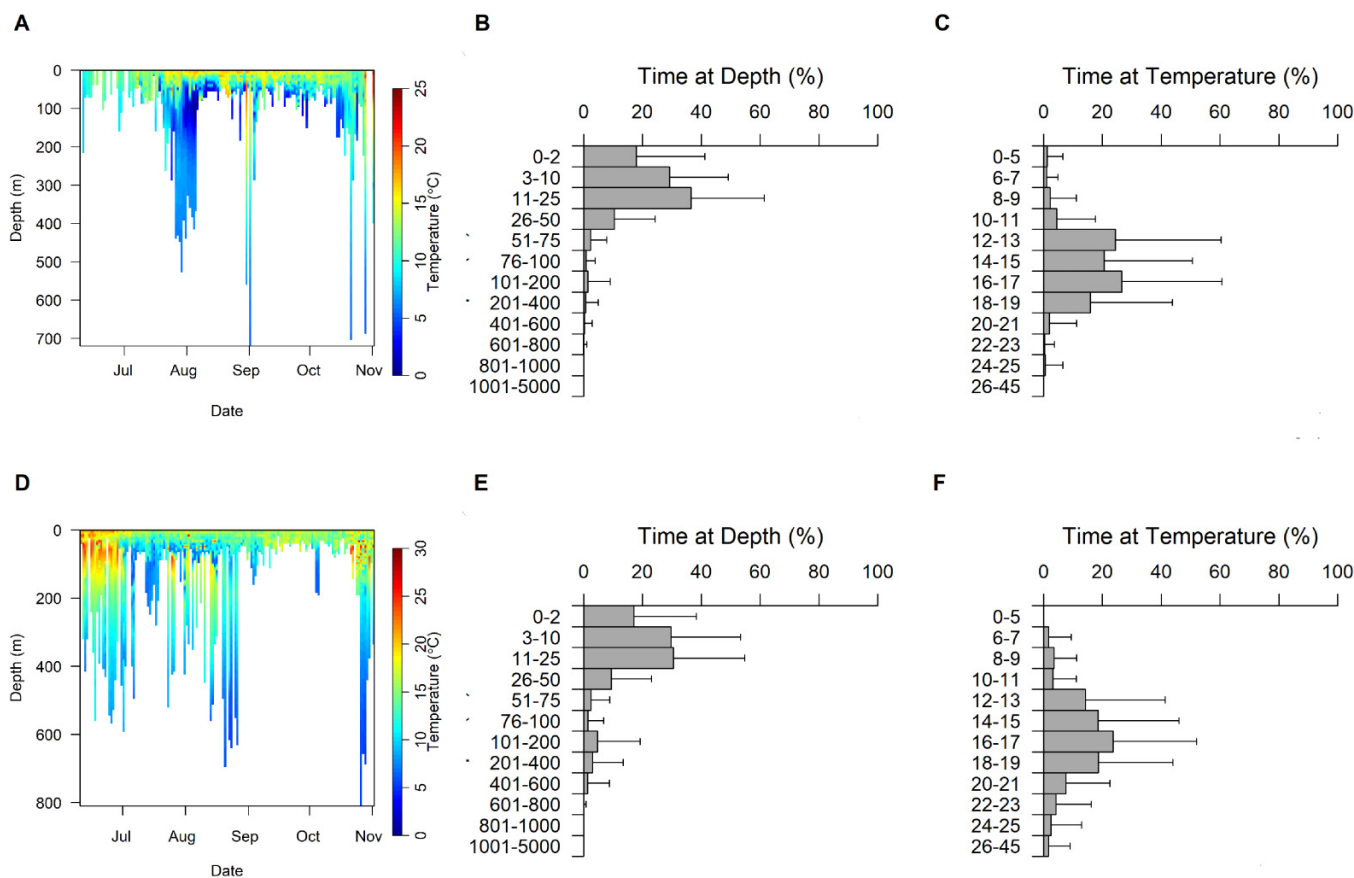
uncertainty given that all methods to extract bathymetry led to the same overall conclusions on white shark behaviour. While there were slight differences in the extracted bathymetric profile of the water column around each position (Supplement B; Fig. S1), these differences had minimal effect on the proportion of each track assigned to Canadian waters or on the quartile of the water column being used by each shark. In addition, positional uncertainty was not systematically greater in either US or Canadian waters, ensuring that comparisons between regions were informative.

## Discussion

Consistent with theoretical predictions on how behavioural processes can influence population structure, both short and long-term monitoring confirm that a small and non-random component of the tagged population entered Canadian waters on a seasonal and (or) yearly basis. More individual animals were detected for longer periods of time in the more southern portions of the Canadian EEZ (e.g., Bay of Fundy, Atlantic coast of Nova Scotia) with lesser numbers, shorter detection periods, and years with no detections in more northerly areas (e.g., Gulf of St. Lawrence and Newfoundland and Labrador). While the disparity in acoustic monitoring effort in Newfoundland as compared to other regions would have affected this comparison, the movement tracks from PSAT tagged animals were also concentrated in more southern areas. Higher relative abundance along coastal Nova Scotia and in the Bay of Fundy, with lesser con-

centration in the Gulf of St. Lawrence and Newfoundland is consistent with other movement tracking data from Canada (Bastien et al. 2020; Franks et al. 2021). In terms of population structure, animals demonstrated some fidelity (sensu Chapman et al. 2015) to Canadian waters, habitually returning during the summer months before spending the majority of time in US waters. The observed seasonality in our data in terms of when animals entered and exited Canadian waters was consistent with the migratory cycle described by Franks et al. (2021) for white sharks in the Northwest Atlantic. Suitable overwintering habitats tend to be located outside of Canadian waters in the southerly portions of the species' range. Juveniles were the most likely to move northward, followed by subadult animals, suggesting that ontogenetic stage is related to dispersal behaviour and population structuring in the Northwest Atlantic. For a tagged juvenile to be nearly 5 times more likely of being observed in Canadian waters than a tagged adult, it seems likely that younger animals are dispersing more widely through suitable coastal habitats than the older age classes (Franks et al. 2021), making them more likely to be detected on acoustic monitoring arrays. This behavioural pattern is unlikely to be an artifact of higher detection probability, given (1) acoustic detection of double-tagged animals seemed to be related to duration spent in Canadian waters as opposed to ontogenetic stage and (2) there was no indication of differences in detection duration or number of detection events among life stages (Supplement A; Table S1). Although there may be the expectation of lower detectability of adult females in particular on acoustic arrays due to off-

**Fig. 4.** Temperature–depth profiles, time-at-depth (TAD), and time-at-temperature (TAT) plots for PSAT-tagged animals, separated into Canadian (A–C) and US (D–F) components, for the time period covered by the Canadian data (6 June to 2 November). Supplement B Fig. S5 shows the entire time series of US data. Note the slight difference in the y-axes in panels A and D. [Colour online.]



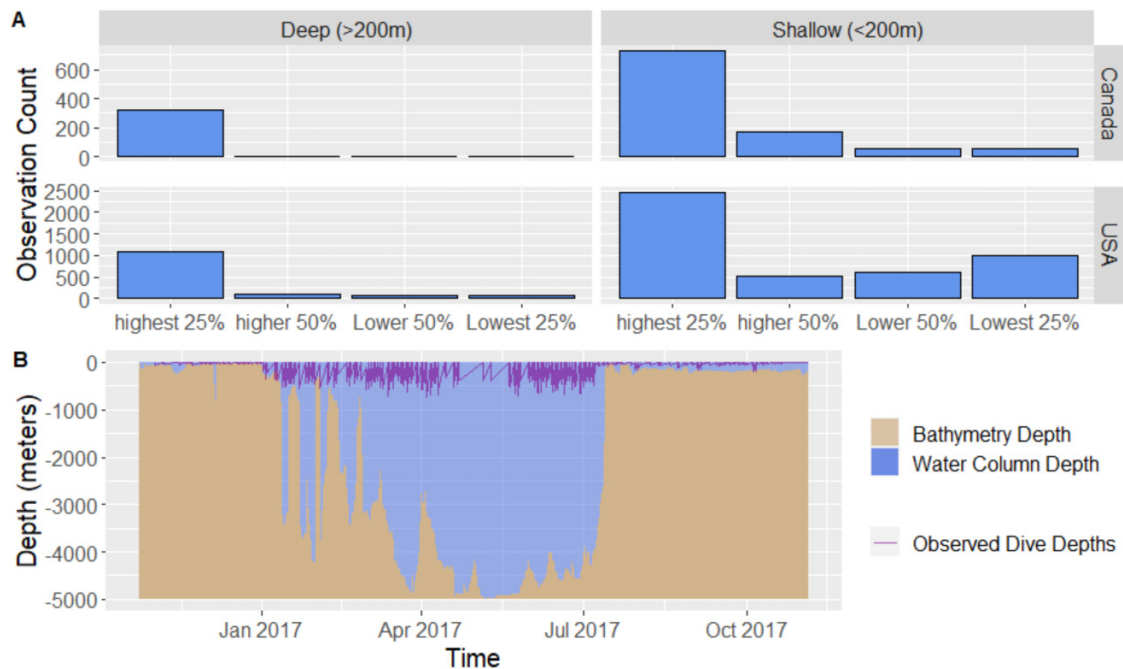
shore movement behaviour (Skomal et al. 2017; Franks et al. 2021), this would affect detectability throughout the species range rather than introducing systematic bias into the probability of detection within Canadian waters.

The degree to which these seasonal and yearly movement patterns characterize the broader population of white shark in the Northwest Atlantic depends on the representativeness of tagging and monitoring efforts. Most tags were deployed off Cape Cod, where white sharks seasonally aggregate to feed on the recovering pinniped population (Skomal et al. 2012; Winton et al. 2021). Individual white sharks exhibit differing degrees of residency and habitat use at seasonal aggregation sites, with larger individuals often occupying smaller home-range areas and returning to the same areas more frequently than smaller individuals (Jewell et al. 2013). These behaviours would also make them more available to tagging effort than “transient” sharks (Hewitt et al. 2018), increasing representation of individuals that exhibit a higher degree of fidelity to Cape Cod than is typical of the broader population. While it is often assumed that the majority of white sharks travel to aggregation sites on an annual or biennial basis, the extent of Cape Cod’s importance to the broader Northwest Atlantic population remains unclear. Of the individuals tagged off Cape Cod with more than 1 year of detection data (129), approximately 40% (48) did not return in at

least 1 subsequent year. This is consistent with the proportion of sharks tagged south of the region that have subsequently been detected off Cape Cod (61%), indicating that tagging location does not seem related to the proportion of the population using the waters along Cape Cod. Conversely, 13 of 25 (52%) white sharks tagged off South Carolina moved to Canadian waters, while only 35 of 119 (29%) animals tagged off Cape Cod did so. Thus, differences in movement strategy and habitat preference among distinct components in the population are likely, similar to those documented in the Pacific (Jorgensen et al. 2010, 2012). Additional acoustic tagging effort and monitoring capacity throughout the species’ range is needed to better refine patterns in residency over ontogeny and population structure in the Northwest Atlantic.

The possible existence of distinct movement strategies among different components of the population does not imply that animals moving to or tagged in Canada make up a distinct sub-population, nor does it necessarily suggest the possible existence of an aggregation site similar to that found in Cape Cod. In terms of reproduction, higher concentrations of juvenile animals might be associated with nursery areas. However, neither neonates nor young-of-the-year (YOY) have been previously observed in Canada, despite there being a geographically proximate white shark nursery area in the New York Bight (Curtis et al. 2018; Shaw et al. 2021) and substan-

**Fig. 5.** Histograms of the proportion of time spent in each quartile of the water column while in Canadian and US waters (A), separated by locations with a depth > 200 m (left side) and < 200 m (right side). Panel B gives an example of the data used to derive panel A, showing the depths recorded over time by the archival satellite tag (observed swim depths) relative to the depth of the water column at the estimated location of the white shark. Bathymetry data (1 arc min resolution) were accessed from the NOAA ETOPO1 database (Amante and Eakins 2009). Coordinate reference system: WGS84. [Colour online.]



tial Canadian fishing activity using gear types associated with YOY catches in the US (DFO 2017). In terms of aggregation, it is well established from historical records that white sharks can be widely distributed in Atlantic Canadian waters (Casey and Pratt 1985; Curtis et al. 2014; DFO 2017). However, the available acoustic monitoring data are not indicative of high degrees of residency in localized areas. The white shark aggregation at the Cape developed in association with the increasing grey seal (*Halichoerus grypus*) colony, which provides predictable access to abundant prey (Skomal et al. 2012). Canadian waters boast the two largest grey seal breeding colonies in the world, with the largest on Sable Island and the second largest in the Southern Gulf of St. Lawrence (Bowen et al. 2007; Hammill et al. 2017). Long-term acoustic monitoring in the vicinity of Sable Island has shown minimal evidence of white sharks, possibly because grey seals redistribute to numerous smaller summer feeding colonies throughout the Eastern seaboard in the summer months. However, juvenile white sharks have not reached sufficient size to effectively prey on grey seals and are known to be predominantly piscivorous, targeting pelagic or demersal fishes and squid (Casey and Pratt 1985; Estrada et al. 2006; French et al. 2017). The distribution of prey populations in addition to ontogenetic shifts in diet may be contributing to the more widespread and coastal distribution observed for white sharks in Canadian waters.

### Conservation implications

Canadian recovery goals and management priorities center around being able to describe white shark distribution

and changes in distribution, so the seasonal patterns and behavioural differences we documented have potentially important implications. Models to explain and predict distribution (species distribution models (SDMs); Robinson et al. 2011; Robinson et al. 2017) seek to model the correlation between environmental data and species presence, predicated on the assumption that environmental tolerances determine distribution. Water temperature becomes a key environmental variable because it is both recorded by PSAT tags and is one of the most readily available oceanographic covariates to evaluate (Fourcade et al. 2018). Typically, PSAT data collected throughout ocean basins are aggregated to increase sample size (e.g., Bowlby et al. 2021) and longer-term deployments are considered optimal (Sippel et al. 2015). However, our comparisons show that the distribution of temperatures experienced by white sharks during seasonal movements to Canadian waters is significantly narrower than those experienced at the same times of year in the US and differs markedly from other times of the year. This likely reflects the restricted temperature range within temperate Canadian waters as compared to tropical and sub-tropical components of US waters. Distinct shifts in diving behaviour have been primarily attributed to predation (i.e., shifts in target prey) and are hypothesized to maximize resource acquisition and (or) reduce inter- or intraspecific competition. Choosing to remain predominantly within the 200 m depth contour and within the top 100 m of the water column would ensure proximity to coastal pinniped haul out sites (e.g., Benoît et al. 2011) as well as high overlap with other large pelagic fishes (e.g., Lam et al. 2013) along the Canadian continental shelf. However,

when developing SDMs for white shark in Canadian waters, temperature associations should be based on TAT data collected exclusively in Canadian waters to better represent the species' environmental associations in northern habitats. In addition, the general decrease in white shark detections in more northerly regions as well as the tendency of tagged animals to remain at locations within the 200 m depth contour suggests that white sharks were not equally likely to be found in all locations with similar water temperatures. We recognize that our approximation of time spent in different geographic regions does not quantify density directly, but it does imply that 12–19 °C waters off Newfoundland might be expected to contain fewer white shark than 12–19 °C waters off Southwest Nova Scotia. Given the focus on distribution set out in Canadian recovery goals, our results suggest that the magnitude of bias arising from regional variation in white shark presence and behavioural processes leading to restricted dive depths and a more coastal distribution should be explicitly quantified when attempting to predict habitat use in Canada from environmental associations. If biases are found to be substantial, any predictive model would need to account for geographic differences in white shark presence owing to behavioural factors.

Beyond distribution and the question of where white sharks are found, our results have several implications for broader conservation objectives and recovery planning. Key management priorities relate to (1) increasing Canadian capacity to track abundance and changes in abundance, (2) evaluating the population-level impact of recovery actions implemented under Canadian legislation, and (3) limiting the vulnerability of specific life history stages to incidental captures in fisheries, the only identified threat in the Northwest Atlantic (COSEWIC 2006). In relation to (1), we are the first to demonstrate how acoustic monitoring effort has expanded in Canadian waters in conjunction with increases in the number of acoustically tagged white shark. Although substantial abundance increase has been hypothesized on the basis of sightings data collected during 2011–2016 (Bastien et al. 2020), we found limited corroborating evidence. There was no systematic increase in the proportion of the tagged population visiting Canadian waters, which has remained relatively constant during the years where an appreciable number of animals had been tagged (2016 onwards). Different metrics of catch-per-unit effort from the acoustic data were extremely variable, yet years with higher monitoring effort were consistently associated with more frequent white shark detections as well as more individual sharks detected (Table 2). In relation to (2), evaluating outcomes from future mitigation actions will require information on the proportion of the population affected when calculating overall changes in productivity or survival for Northwest Atlantic white sharks. Assuming the tagged population is representative of the broader population, the detection rates of tagged animals suggest that recovery actions implemented in Canada will benefit less than a quarter of the wider population in any given year. In relation to (3), we found that juvenile and subadult animals were much more likely to move to Canadian waters. These may be the life stages that would be expected to benefit most from recovery actions

implemented in Canada. However, we found no associated evidence of spatial partitioning among life stages while in Canada, given that movement rates, seasonal occupancy, locations visited, and diving behaviour were similar on the basis of preliminary analyses. While partitioning may become evident with greater sample sizes and longer-term monitoring, commonly proposed mitigation measures, such as delineating and protecting nursery areas (Kinney and Simpfendorfer 2009; Heupel et al. 2018), are unlikely to be tractable objectives in the near-term.

To maximize progress towards Canada's conservation goals for the white shark, data collection and research projects should be designed to target specific questions. Continuation of large-scale acoustic monitoring, in which all receiver deployments and downloads are registered with the OTN (Cooke et al. 2011; Iverson et al. 2019) or a similar publicly accessible platform, will be critical to quantify habitat connectivity for white shark in addition to monitoring long-term changes in habitat use, density, and (or) distribution within Canada (Bangley et al. 2020). To improve our understanding of environmental associations and behaviour while in Canada, the location and timing of tagging becomes a critical question. Even though PSATs can be deployed for a year, tagging in September may increase the likelihood of premature tag release because animals leaving Canadian waters transitioned to deeper diving behaviour in the winter and spring. As seen from one of two Canadian PSAT deployments, the white shark exceeded the crush depth of the tag ~5 months into its 12-month deployment, resulting in only 44 days of Canadian data. Although Canadian tagging in September has been shown to be successful (our research; Bastien et al. 2020; Franks et al. 2021), shifting field work to earlier in the summer (e.g., July) as well as continuing tag deployments outside of Canadian waters (e.g., South Carolina) would optimize data collection.

While recent tagging and monitoring demonstrates that white sharks are more abundant in Canadian waters than previously assumed from historical sightings and capture data (DFO 2017; Bastien et al. 2020), their population dynamics leave them highly vulnerable to mortality, even low levels of mortality (Bowlby and Gibson 2020). This vulnerability may be greatest while in Canada, given that species sensitivity to fishing interactions and climate change can be higher at range boundaries (Yan et al. 2021), particularly northern range boundaries (Fredston-Hermann et al. 2020). Even though interactions leading to mortality from Canadian fisheries are extremely rare (maximum of 3 per decade since the 1950s; DFO 2017), this sensitivity underscores the need for targeted research to support Canadian recovery objectives, so that every effort can be taken to mitigate harm and limit the potential for mortality under the Canadian Species at Risk Act.

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### Data availability

Acoustic data and tagging metadata associated with this manuscript are provided in the Supplementary information. Geospatial data will be archived on the Open Data Information System of DFO.

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### Author notes

The authors have no competing interests to declare.

### Author contributions

HDB conceived research and analyses, developed and led Canadian field program, and wrote the manuscript. WNJ and PJC contributed to Canadian data collection, undertook quality control and analyses, and contributed to writing and review. MVW and GBS conceived and led US research program (research methodology, data collection, quality control, archival), undertook and reviewed analyses, and contributed to writing and review.

## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2021-0313>.

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